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N° D.U.: 2532 ANNEE: 2011-2014

ECOLE DOCTORALE SCIENCES DE LA VIE, SANTE, AGRONOMIE, ENVIRONNEMENT
N° ordre : 655

Thèse:

Présentée à l'INRA de Crouel
pour l'obtention du grade de

DOCTEUR D'UNIVERSITE

(Spécialité : Physiologie et génétique moléculaires)

Soutenue le 16 Décembre 2014

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Thèse préparée au sein des laboratoires:
Limagrain Europe, Native Trait, Genetic Resources and Pre-breeding Team, Chappes, France
CIMMYT, Bread Wheat Physiology Group, El Batan, Texcoco, Mexico
UMR UBP/INRA Génétique, Diversité et Ecophysiologie des Céréales, Clermont-Ferrand, France
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Acknowledgement

During my PhD, there were many people who helped me, gave me support, and made that this work became a reality. I would like to thank all of them and decided to address my thanks into the appropriate language for each of them.

Firstly, I wish to acknowledge all my supervisors. Alain and Matthew, thank you for organizing the PhD project and building the collaboration between your two laboratories where my thesis was done. Jacques, thank you very much for having accepted to be my supervisor. Alain, Matthew, and Jacques, thank you very much for having given me the opportunity to realize one of my professional objectives. I've really appreciated that you've made everything that was required to allow the thesis to be done in such good conditions. Thanks for having made me comfortable within each one of your laboratory, for always having had time to discuss, for having guide and encourage me along these years, for having given me the opportunity to share my work during international conferences, and for having given me the possibility to train myself during these years. A special thanks to Jeremy Derory, my "roommate" in the C175 office at Chappes. I would like to thank you very much for always having had time to discuss with me, answer my questions, and share your knowledge and experience with me. I strongly beneficiate from your experience at each step of my PhD, not only in Genetics, but also in Agronomy, data analysis, organization, *etc*. Your input strongly improved the quality of my work. Jeremy, Jacques, Alain, and Matthew, thank you for all the time you spent to correct and improve my scientific productions, but also, for having helped me to have hindsight in the data analysis with so many results.

I would like to thank the members of the jury, especially François Tardieu and Patrice This who accepted to review this manuscript.

Me gustaría dar las gracias a todo el personal del CIMMYT por su bienvenida, su ayuda, disponibilidad y consejos durante todas mis estancias en México.

En primer lugar, quiero dar las gracias a Rodrigo Rascón quien me dió la bienvenida en la estación del CENEB a Ciudad Obregón.

Me gustaría dirigir todos mis sinceros agradecimientos al grupo de fisiología de trigo, especialmente a los ingenieros y el personal técnico (Araceli, Eugenio, Syhara,

Mayra, Pimi, Nayeli, Abisai, Edgar, Chema, Jazmin, Israel, Arturo, Raymundo, Jessy, Vania, Manuel, Gilberto, Gera, Martha, Joaquín, Román, Don Bicho, etc.) y también a todos los estudiantes de doctorado y los post-docs (Julián, Mariano, Gemma, Alistair, Maria, Perla, Arnauld, Carolina, Eliseo, Francisco, Suzuky, Alejandro, Oscar, Máximo, Sean, Ruth, etc.). Me ha encantado pasar cada ciclo con ustedes y ser parte de su equipo. Fué un placer trabajar con personas tan capacitadas y calificadas, pero sobre todo con gente a quien le gusta tanto enriquecerse de conocimientos.

Sería injusto que mis agradecimientos conciernan solamente al trabajo. Plebes, muchas gracias por todas nuestras salidas, de las famosas carne-asadas de Julián y Mariano, las fiestas de Maria y Gemma, las noches de pizza y sushi… ¡qué rico!, todas las noches de puras risas con el Take, el JP y mi Syhara; también a Malena y su familia a quienes agradezco por recibirme en su casa.

L'administratif a occupé une part non-négligeable de ma thèse, surtout avec mes voyages transcontinentaux. Je voudrais donc pour cela adresser mes sincères remerciements à Sylvie Guillaume du côté Limagrain Europe pour sa disponibilité et son aide avec tous mes petits tracas administratifs, mais aussi pour nos fous rires dans le bureau avec Jeremy.

Del lado del CIMMYT, agradezco muchísimo a Norma Hernández y Eloisa Carillo por toda la ayuda y por haber hecho que todo fuera siempre muy sencillo con las visas y los viajes. Fué un grato placer conocerlas.

Une thèse c'est avant tout savoir ce que les autres ont déjà fait et publié dans la littérature. Christine, Pierre, qu'est-ce que j'ai pu vous embêter avec toutes mes demandes d'article... mais vous avez toujours réussi à me dégoter rapidement ce que je recherchais. Je tiens à vous remercier pour votre gentillesse et votre disponibilité à chacune de nos rencontres. Nos échanges ont toujours été un véritable bonheur pour moi.

Aurélien, Aurélien, Aurélien…, s'il y en a un que j'ai pu « e…… », je crois que c'est bien toi. Tu as toujours été disponible pour m'aider et m'expliquer ces petits concepts statistiques sur lesquels je butais mais aussi pour identifier du premier coup d'œil dans mon code la petite erreur qui m'ennuyait. J'aime à croire que tu as également de ton côté pu apprécier et profiter du travail et des réflexions que nous avons menés et

solutionnés ensemble. Ce fut toujours très stimulant d'être en contact avec quelqu'un d'aussi talentueux que toi en statistique et codage.

Je tiens également à remercier Zivan Karaman, Chloé Boyard, Stéphanie Chauvet et Sébastien Ducrocq pour nos discussions statisticiennes autour de mes données et de mes expériences

Mes plus sincères remerciements s'adressent également aux autres membres de l'équipe Native Trait de Limagrain Europe de Chappes, Morgan Renault, Philippe Dufour, Fabienne Henriot, et Manuel Personne. J'ai toujours pris beaucoup de plaisir dans nos discussions scientifiques ou non, lesquelles furent toujours fructueuses et passionnantes. Ce fut très enrichissant pour moi de travailler au côté de personnes aussi compétentes et passionnantes que vous. J'espère de mon côté avoir également pu au travers de mes travaux vous apporter quelques éléments de réponses dans l'approche de l'étude des stress abiotiques.

I would like to thank Suzanne Dreisigacker from the CIMMYT genotyping laboratory, and also Jean-Pierre Martinant, Sébastien Specel, Valérie Gauthier, and Jordi Comadran from the Limagrain Europe Genotyping Laboratory for their great work concerning the genotyping of my three populations, the construction of the genetic maps, their advices in QTL detection with GenStat, but also the time spent for my numerous questions. I have been so blessed to work with so skilled people.

Merci au gens du couloir du Bâtiment 1 de la Garenne, Benoit, Luc, Samantha, Delphine, Perrine, Noémie, Romain, Anne-Marie, Elena, et Eliette, pour vos encouragements, et m'avoir soutenu tout au long de cette aventure.

Je tiens également à remercier Pierre Dubreuil de Biogemma que j'ai eu la chance de côtoyer et qui a toujours accepté de partager ses incroyables connaissances sur les modèles mixtes et l'interaction génotype x environnement avec moi. J'ai toujours beaucoup apprécié nos échanges scientifiques, ce fut toujours un régal !

Merci également à Bruno Poupard, François Torney, et Fabien Lecouviour de Limagrain Europe pour leurs conseils et l'ouverture à d'autres sujets plus éloignés du mien.

Je tiens enfin à remercier infiniment toute ma famille, en particulier Syhara, mes parents, mes frères et sœur, papi, mais aussi Ouragan, Chifouille et Dingo. Je n'ai jamais vraiment eu l'occasion de vous remercier durant toutes ces années d'avoir toujours cru en moi, d'avoir toujours été à mes côtés, d'avoir absolument tout fait pour que se concrétisent toutes mes études, mais également pour votre soutien indéfectible et vos continuels encouragements...et Dieu sait que parfois je ne le méritai pas.

Finalmente, pero ciertamente lo más importante, a mi prometida Syhara, quien siempre me ha sostenido y alentado durante todo mi doctorado. Syhara mi amor, te agradezco infinitamente por siempre estar a mi lado y también por haber creído en mí aun cuando yo dudaba. Lamento haberme ausentado por tanto tiempo pero te aseguro, mi amor, que jamás me alejare de ti, que siempre estaré a tu lado y que siempre podrás contar conmigo. Te amo mi hermosita, por siempre.

Abstract

B. Bouffier (2014) - Genetic and ecophysiological dissection of tolerance to drought and heat stress in bread wheat: from environmental characterization to QTL detection

A stagnation of wheat yield was reported in France and other countries worldwide since the 1990's, which incriminated mainly drought and heat stress. Improving the European wheat tolerance to them is of first importance. This study aimed to investigate the genetic determinism of the tolerance to such stresses. Three CIMMYT bread wheat populations combining complementary heat and drought adaptive habits were grown in Northern Mexico under irrigated, drought and heat-irrigated treatments from 2011 to 2013. The trial network comprised 15 trials and both physiological and agronomic traits were scored.

First, an environmental characterization methodology was developed and resulted in the identification of six main environmental scenarios in the network. A representative environmental covariate was extracted from each of them. Then, a factorial regression model leaded to the dissection of the genotype-by-environment interaction and highlighted differential stress sensitivity of the germplasm. Finally, a multi-environmental QTL detection resulted in the discovery of genomic regions involved in the control of both physiological and agronomic traits and the study of their sensitivity to the environment.

From the environmental characterization to the QTL detection, this study resulted in the development of a tool for breeders which may enable the evaluation of the potential of any genotypes in front of a range of environment, but also the identification of genomic regions involved in the control of the tolerance to drought and heat stress in bread wheat. This may help in improving the tolerance of the European bread wheat germplasm to drought and heat stress.

Résumé

B. Bouffier (2014) – Dissection génétique et écophysiologique de la tolérance au stress hydrique et thermique chez le blé tender: de la caractérisation de l'environnement à la detection de QTL

L'étude des rendements en blé a mis en évidence une stagnation apparue dans les années 1990, notamment en France, et principalement lié aux stress hydrique et thermique. Dans ce contexte, améliorer la tolérance du blé européen à ces stress est de première importance. Cette étude avait pour but d'étudier le déterminisme génétique de la tolérance à ces stress chez le blé. Pour ce faire, trois populations de blé tendre du CIMMYT combinant des caractères d'adaptation à ces stresse ont été cultivées en conditions irriguée, sèche et stress thermique irriguée plusieurs années. Des caractères physiologiques et agronomiques ont été mesurés sur un réseau de 15 essais.

Une méthodologie de caractérisation environnementale a été développée et a permis l'identification de six scenarii de stress au sein du réseau. Une covariable environnementale représentative de chacun a été extraite. L'utilisation des modèles de régression factorielles a permis la décomposition de l'interaction génotype x environnement ainsi que la mise en évidence d'une sensibilité différentielle au stress dans le germplasm. Une recherche de QTL multi-environnementale a conduit à la détection de régions génomiques contrôlant les caractères physiologiques et agronomiques ainsi que leurs interactions avec l'environnement.

De la caractérisation environnementale à la détection de QTL, cette étude a abouti au développement d'un outil pour les sélectionneurs permettant l'évaluation du potentiel des génotypes face à une gamme d'environnement, mais aussi à l'identification de régions génomiques impliquées dans le contrôle de la tolérance aux stress hydrique et thermique chez le blé tendre. Ceci pourrait améliorer la tolérance à ces stress au sein du germplasm européen.

Key-words

Drought; Heat stress; Abiotic stress; Wheat; Stress tolerance; Agronomic traits; Physiological traits; Environmental characterization; Environmental covariates; Factorial regression; Genotype-by-environment interaction; Quantitative trait loci; Quantitative trait loci-by-environment interaction.

Mots-Clés

Sécheresse; Stress thermique; Stress abiotique; Blé ; Tolerance au stress; Caractères agronomiques; Caractères physiologiques; Caractérization environnementale; Covariables environnementales; Régression factorielle; Interaction génotype-environnement; Locus de caractère quantitatif (QTL); Interaction QTL-environnement.

Summary

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- **CHAPTER I: Literature review**

Formulas presented in Chapters III, IV, and V (papers) are not listed here.

General introduction

The birth of the Agriculture in the Fertile Crescent around 10,000 years ago was concomitant with the agricultural birth of the hexaploid wheat. Several centuries after the wheat domestication, rice (*Oriza sativa* L.) and corn (*Zea mays* L.) were domesticated in south-east Asia and in Central America, respectively. Because grains of these three species are used as food both for humans and domestic animals, they are called cereals[1] (Bonjean and Picard, 1990). Cereals share diverse features continuously improved by humankind (1) grain starch and proteins content which make cereals suitable for basal ration of human diet, (2) ease of harvesting and conservation and (3) suitability for transportation (Bonjean and Picard, 1990).

From the birth and the beginning of selection of hexaploid wheat by the first men to the XVIIIe, wheat-related species were spread worldwide leading to their diversification and resulting in the constitution of many locally adapted groups of genotypes: the landraces. Indeed, a plant has to adapt (germinates, grows, reproduces and matures) to its environment as fundamentally immobile. Until the XVIIIe, landraces were the only form of cultivated wheat, corn, and rice. During the XVIIIe century, plant breeding started with the first phenotypical selection of varieties. Through decades of breeding efforts, wheat yield have tremendously increased in many countries worldwide, and especially in France. Calderini and Slafer (1998) reported a constant growth trend due to the progress of both genetics and agronomical practices. In France, from the 1950's to 1996, an increase of wheat yield of 0.12 t ha^{-1} $year^{-1}$ was reported (Brisson et al., 2010).

However, over the last 25 years, several studies have reported a stagnation in grain yield of several crops such as wheat (Brisson et al., 2010) and rice (Ladha et al., 2003) in many countries in Europe, like in France, but also worldwide, in Mexico, China, and India. In France, the inflexion of bread wheat yield continuous increase occurred around 1996 (Figure Int-1) (Brisson et al., 2010). Brisson et al. (2010) explored different putative causes for this yield plateau, such as genetics, agronomy (nitrogen fertilization, disease protection, effect of the preceding crop, soil organic matter) and climate. They concluded (i) that there was a constant genetic gain even during the last 20 years, which ranged between 0.10 and 0.12 t ha^{-1} $year^{-1}$ and (ii) that drought during stem elongation and heat stress during grain filling were responsible for

[1] from Ceres, the Roman goddess of agriculture, harvest, and fertility

most of the stagnation of wheat yield observed in France. For France (4th wheat world producer), but also, China (1st) and India (2nd), such stagnation is very worrying, particularly in the context of increasing human population and increasing worldwide food demand.

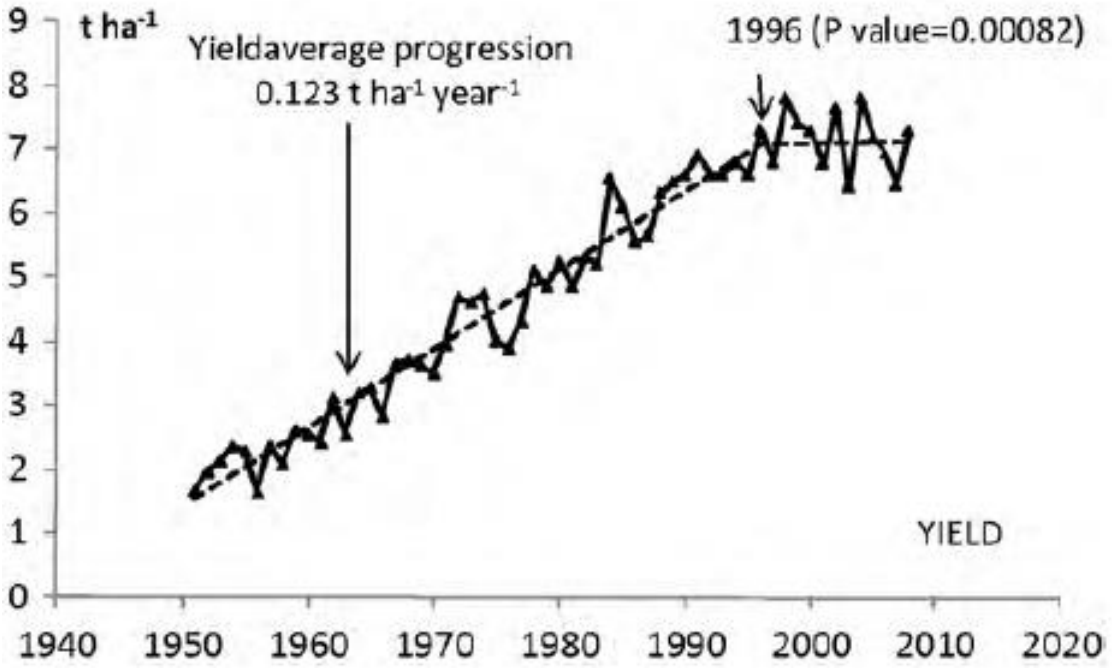

Figure Int-I-1: Annual evolution of bread wheat yield in France since the 1950's to the time of the study (Source: Brisson et al., 2010)

CO_2 and other gazes emission released by human activity were reported as the direct cause of the current global warming which leads to such drier conditions for farming (IPCC, 2007, 2014; Smith and De Smet, 2012). The IPCC (2007, 2014) expected an increase in frequency and intensity of drought and heat stress around the world. The recent simulation works of Dai (2012) strongly supported such an assumption by concluding to a severe drought widespread in the incoming decades in several countries worldwide, as resulting from either an increased evaporation, or a decrease of the or rain fall.

Worldwide, water deficit and high temperature stress are referred as ones of the most common abiotic stresses occurring in crop production nowadays. In 2012, the European Environment Agency (EEA) reported simulation works on the impact of water limitation in Europe on wheat production by 2030 (Figure Int-2). Whatever the climate change scenario tested, the coolest (ECHAM5) or the warmest (HadCM3), most of the European bread wheat production area might be strongly impacted leading to a decrease of the production.

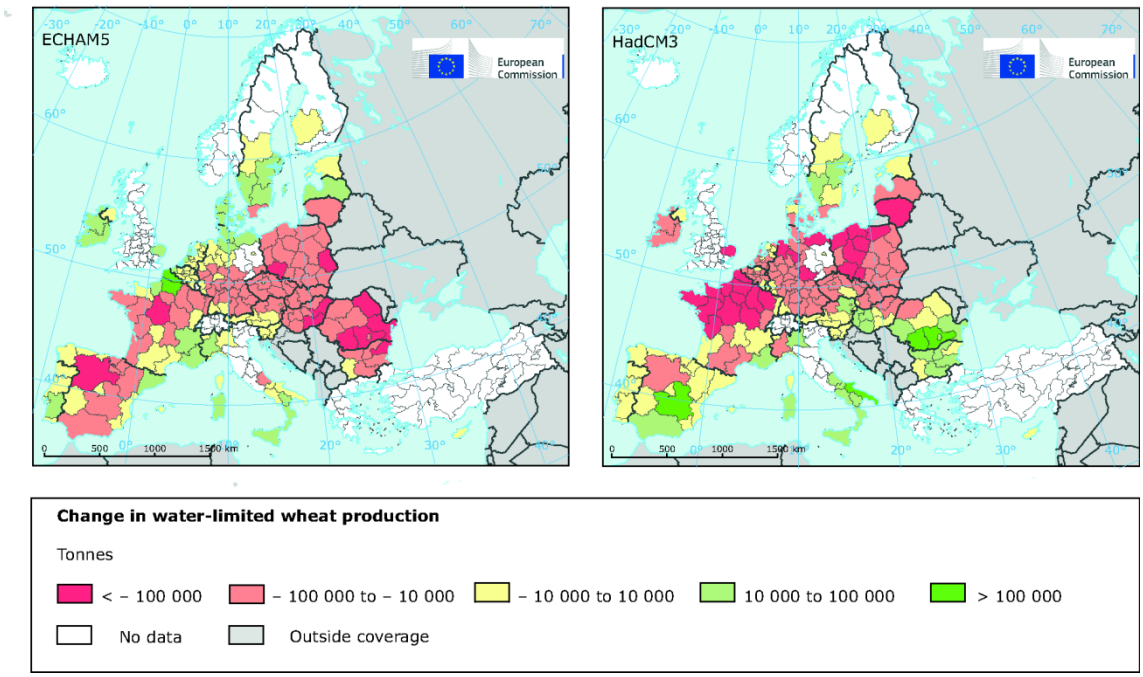

Figure Int-I-2: Simulated change in water-limited wheat production for 2030 compared with 2000 with the model A1B for two meteorological scenarios of CO2 emission: (i) low-emission scenario, i.e., cold climate change projection (ECHAM5) (left) and (ii) high-emission scenario, i.e., a warm climate change projection (HADCM3) (right). Simulation performed on a 25x25 km grid (assuming current area of wheat cropping) (Source: European Environment Agency, 2012)

Although no model is perfect in terms of predictions, even if climate predictions are only the results of simulation and are subjected to a large uncertainty, they can be useful in giving a glimpse on what the weather may look like in the incoming decades. Such information is highly valuable for a plant breeder as it is of great help to design the varietal ideotype for the future decades.

In such a drying context, the big challenge of the whole European wheat breeding community is the improvement of the tolerance to both drought and heat stress. Limagrain Europe, the fourth worldwide seed company and the current leader of the European seed wheat market, has to tackle this challenge. However, the study of drought in open field in Europe is difficult and uncertain due to the high inter-annual climate variations. The International Maize and Wheat Improvement Center, better known by its Spanish acronym, CIMMYT, already studies the impact of these stresses on wheat and breed for increased tolerant genotypes since several decades at its experimental station based at Ciudad Obregon, in the northwestern Mexican Sonora desert (CENEB). In such a place, inter-annual variations are reduced, enabling the experimentation of targeted stresses in good conditions every year. Over there, the CIMMYT beneficiates from well-established facilities, well-trained people, and adapted germplasm. The bread wheat physiology group led by Matthew Reynolds, is in charge

of CIMMYT research on wheat physiology under abiotic stress conditions. The objective is to identify and dissect mechanisms involved in tolerance, but also, to look for native novel drought and heat stress tolerance sources to improve worldwide-spread wheat varieties. Collaboration had therefore been established between the CIMMYT and Limagrain Europe.

Several ways exist to improve the tolerance of European wheat to drought and heat stress. The CIMMYT and Limagrain Europe agreed on a collaborative project, which was my Phd research, on the dissection of the genetic determinism of drought and heat stress tolerance using populations of crosses whose parents were chosen to combine complementary and relevant traits to tolerate such stresses. The uncertainty of drought and heat stress in open-field experiments in Europe, combined with the experience of the CIMMYT facilities, made the Sonora platform the most relevant choice as a first step towards the improvement of European bread wheat through possible CIMMYT germplasm introgression.

The present study has been put in place to meet this objective by studying of the genetic determinism of the tolerance to drought and heat stress in various bread wheat genetic backgrounds. Firstly, a review of the literature is presented in the first chapter. Secondly, the research questions and the strategy are defined. Then, the results of the study are presented as scientific articles, either accepted or submitted or other that will be submitted in the near future. These articles deal with the characterization of the environment, the quantification of the genotype-by-environment interaction, and finally, the dissection of the genetic determinism through the identification of QTL for drought and heat stress tolerance and QTL-by-environment interaction. The manuscript ends with a general discussion and a general conclusion.

CHAPTER I: Literature review

I. Bread wheat features

Wheat is a vascular (*Tracheobionta*), flowering (*Magnoliophyta*), and monocotyledon (*Liliopsida*) plants (*Plantae*) related to the grass family (*Poaceae*). The precise classification of wheat is not such an easy task. There are many taxonomic classifications which diverge on some controversial points such as the genus classification; considering one unique *Triticum* genus, or two different genera: *Triticum* and *Aegilops* (National Germplasm Resources Laboratory, Beltsville, Maryland, 2004).

Conventionally, a species is defined as a set of inter-fertile organisms, i.e., able to cross and give fertile progeny. However a set of individuals displaying various degrees of interbreeding is referred as a 'complex of species'. Wheat is a vernacular name associated with different species within the *Triticum* genus (Auriau et al., 1992). They form a complex of annual herbaceous species. *Triticum aestivum* (L.) Thell., the bread wheat, represents 95% of all wheat species cultivated worldwide (Shewry, 2009).

a. Economic importance

Bread wheat is cultivated from Scandinavia (67°N) to Argentina (45°S), Chile and New-Zealand (Trethowan et al., 2005). In 2012, it was grown in at least 124 different countries, on the five continents. In 2012, 57 % of the 671 million tons of the world wheat production was achieved by only six countries among which, by order, (1) China (18.0 %), (2) India (14.1 %), (3) United States of America (9.2 %), (4) France (6.0 %), (5) Russia (5.6 %) and (6) Australia (4.0 %) (Figure I-1).

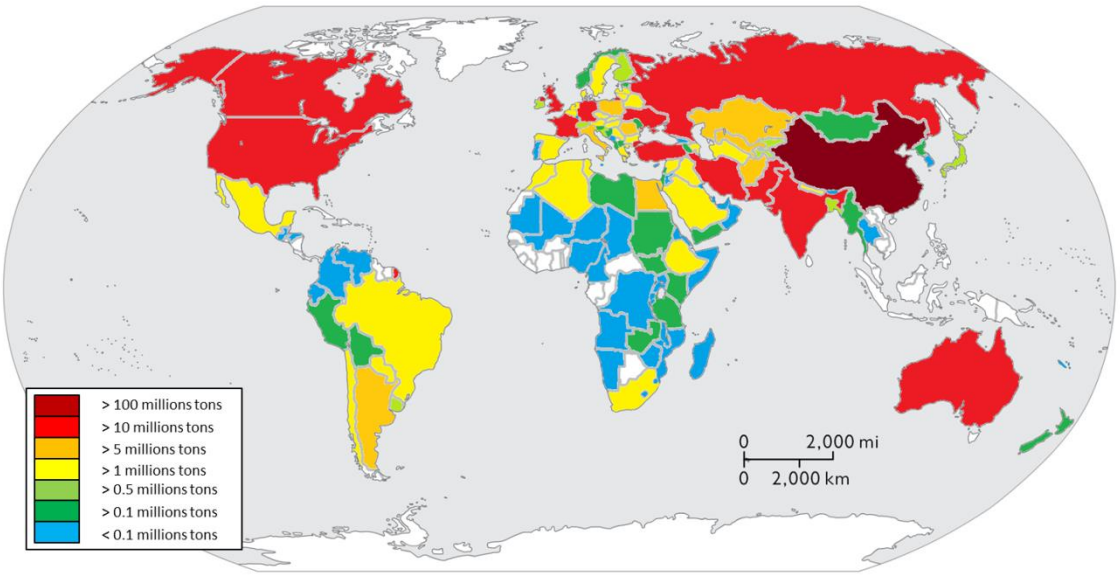

Figure I-1:Country map of bread wheat cultivation in 2012, in millions tons (based on FAO (2014a))

Five of the biggest bread wheat producers reached such production thanks to their high wheat acreage. Indeed, with Kazakhstan, these five countries represented more than 56 % of the 215 million hectares of wheat grown worldwide, with by order, (1) India (13.9 %), (2) China (11.2 %), (3) Russia (9.9 %), United States of America (9.2 %), (5) Australia (6.5 %) and (6) Kazakhstan (5.8 %) (Figure I-2).

In 2012, bread wheat yield ranged from 0.3 t ha^{-1} in Venezuela to 8.9 t ha^{-1} in New-Zealand. France reached 7.6 t ha^{-1}. Indeed, it belongs to the list of the top six highest wheat productive countries. These countries displayed at least twice more than the 3.1 t ha^{-1} average wheat yield. It was leaded by (1) New Zealand (8.9 t ha^{-1}) followed by (2) Netherlands (8.6 t ha^{-1}), (3) Belgium (8.5 t ha^{-1}), (4) France (7.6 t ha^{-1}), (5) Denmark (7.4 t ha^{-1}) and (6) Germany (7.3 t ha^{-1}). In 2012, UK reached 6.7 t ha^{-1} and was at the 11 position on the list of the biggest world wheat yield (FAO, 2014a).

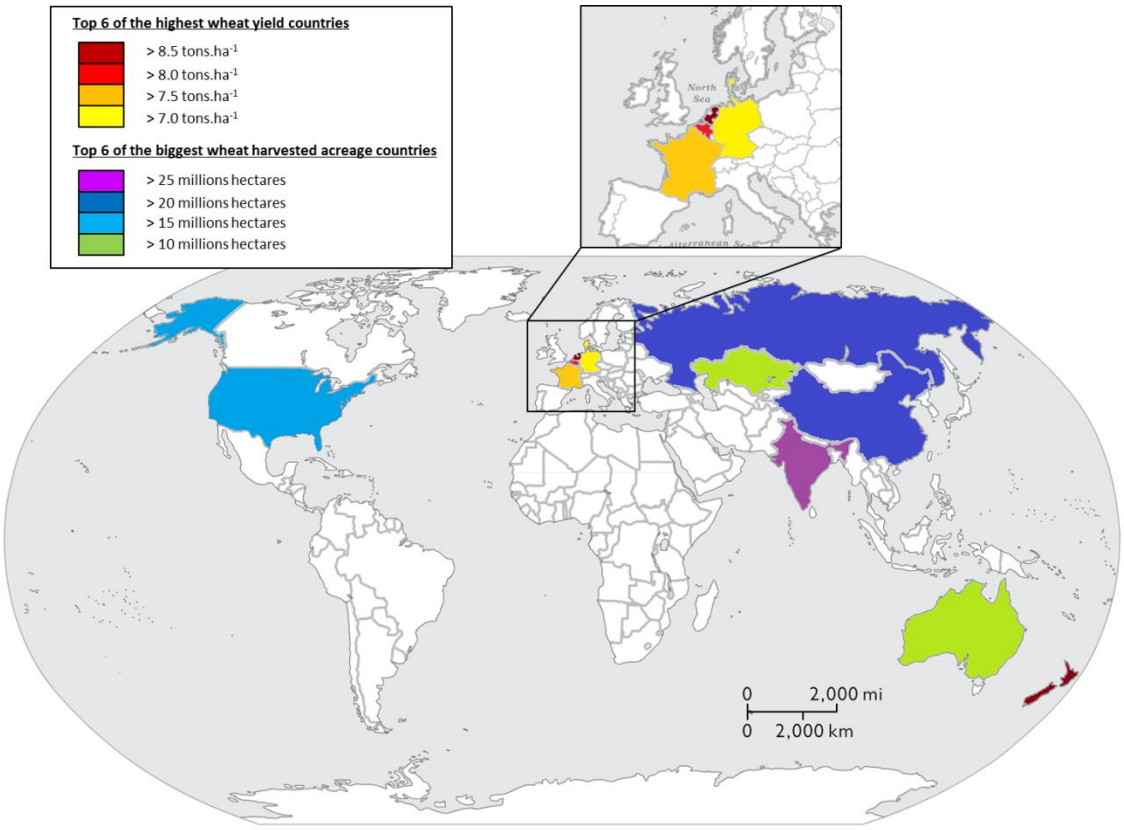

Figure I-2: Map of (a) the six biggest wheat harvested acreage countries (cold colours) and (b) the six highest wheat yield countries (hot colours), worldwide in 2012 (based on FAO (2014a))

For the trade season 2012/2013, the world wheat disponibilities (WWD) represented 841 million tons (world wheat 2012 productions + stock from the 2011/2012 season). The trade concerned 16.7 % of WWD (140.9 million tons). Stocks represented 18.7 % of WWD (187 million tons). The three biggest wheat exporters were (1) the United Stated of America, (2) France and (3) Australia (FAO, 2014b). In 2012,

the value of the total world production was estimated to 79 billion $US, with a price per ton around 118 $US (FAO, 2014a). The world wheat price has become particularly volatile since the beginning of 21st century. Price volatility is intrinsic to agricultural markets coming from agriculture specificity (seasonality, climate influence, *etc.*). Such volatility has strongly increased with the financialisation of the agricultural sector which strongly accelerated since the beginning of the 1990's.

b. Nutritional importance and industrial uses

Wheat, corn (*Zea mays* L.) and rice (*Oriza sativa* L.) are the three main staple foods worldwide. Altogether, 44 % of calories and 37 % of proteins are covered by these three crops. Alone, wheat provides more calories and proteins for humans than any other single food crop in the world. Indeed, wheat represented 19 % of calories and 20 % of proteins of the human diet (Braun et al., 2010; Braun and Payne, 2012).

Bread wheat has multiple end-uses. The industrial sector is structured into five main trades: (1) flour, (2) starch, (3) ethanol, (4) animal feed, and (5) seed trades. These trades regroup diverse activities such as industrial and artisanal bread making, biscuit and cake making, extraction of starch and gluten[2], biofuel production, *etc*. The development and diversification of bread wheat processes need to look for constant and specific bread wheat qualities.

French bread wheat is still mainly used for bread making on the national or international markets. Due to the main target of the French bread wheat production, wheat varieties are classified depending on their behavior in bread making. Many countries have their own bread wheat quality scale such in the United Kingdom, the United States of America, Mexico, *etc*. In France, a distinction must be done between the classification of wheat varieties quality on the official registration list (potential of the registered varieties) and the classification of wheat quality at harvest. In the former classification, four main classes are distinguished: BAF ("blé améliorant ou de force", cover wheat or strength wheat), BPS ("blé panifiable supérieur", superior bread making wheat), BP ("Blé panifiable", standard bread making wheat), and BAU ("blé pour autres usages", wheat for other uses). In 2013, 69 % of the French wheat acreage was sowed with BPS and BAF, 23 % with BP, and 9 % with BAU (FranceAgriMer, 2013). In the

[2] Gluten is the main bread wheat grain protein. It is responsible of the bread making feature of bread wheat flour.

latter classification, i.e., at harvest, four main classes exist (E, 1, 2, and 3, by decreasing quality order), mainly based on the protein content and the bread making strength. In 2014, 2% of the French production belonged to class E, 20 % to class 1, 33 % to class 2, and 45 % to class 3 (FranceAgriMer et al., 2014).

Bread wheat is one of the most important agricultural resources for economy and human diet worldwide. Our interest is focused on wheat grown under drought and high temperature stress conditions. Therefore, the origin and the developmental process of wheat are essential regarding our work. The deciphering of tolerance to drought and heat stress requires the perfect understanding of the plant behavior under stressful conditions.

c. Origin, domestication and geographical distribution of wheat

Polyploidization has played a major role in the evolution within the grass family, *Poaceae* (Salse et al., 2008), and was one of the key of the success of the wheat evolution (Dubcovsky and Dvorak, 2007). Wheat evolution faced two independent events of allopolyploidization. First, between 300,000 to 500,000 years before present, in the Fertile Crescent area, wild diploid wheat (*Triticum urartu*, 2n=2x=14, genome AA) hybridized with the BB genome ancestor, nowadays disappeared. Its closest relative species is a goat grass (*Aegilops speltoides*, 2n=2x=14, genome SS). They produced the wild emmer (*Triticum dicoccoides*, 2n=4x=28, genome AABB) (Dvorak and Akhunov, 2005). About 10,000 years ago, the wild emmer was cultivated by the hunter-gatherers. Gradually, a cultivated emmer was selected subconsciously (*Triticum turgidum*, 2n=4x=28, genome AABB), the durum wheat. Secondly, about 9,000 years ago, a spontaneous hybridization occurred with another grass (*Triticum tauschii*, 2n=2x=14, genome DD) and leaded to the production of the hexaploid wheats such as bread wheat (*Triticum aestivum*, 2n=6x=42, genome AABBDD) and spelt (*Triticum spelta*, 2n=6x=42, genome AABBDD) (Figure II-1) (Feldman, 2001). Wheat domestication resulted in the loss of two main features in bread wheat, the brittle rachis and the hulled grains (except for spelt), resulting in non-dehiscent spikes and naked grains (Peng et al., 2011).

Although bread wheat emerged as a crop only around 10,000 years ago (8,000 BC), it has been greatly diversified since then in terms of adaptation, partly due to its worldwide spread (Figure II-2). Diversification occurred along this long period through

mutations or hybridization and leads to the accumulation of a pool of genetic variability (Feldman, 2001).

Nowadays, worldwide wheat cultivation (Figure I-1) encompasses a wide range of environmental conditions, on the five continents. It is cultivated in locations ranging from sea level to more than 3000m above sea level, as in Tibet, Percival (1921) cited by Curtis (2002) and Nepal, and in locations with rainfall ranging from 250 to more than 1700mm per year (Braun et al., 2010).

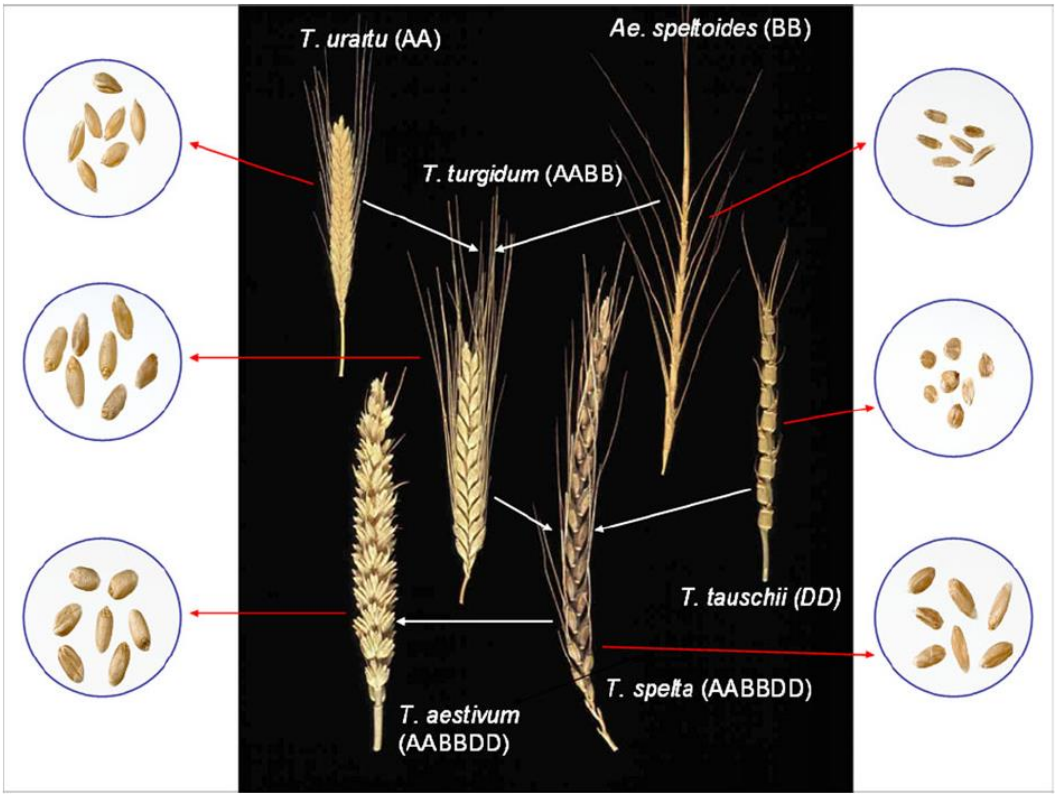

Figure I-3: The evolutionary and genome relationships between cultivated bread and durum wheats and related wild diploid grasses, showing examples of spikes and grains (Source: Shewry, 2009)

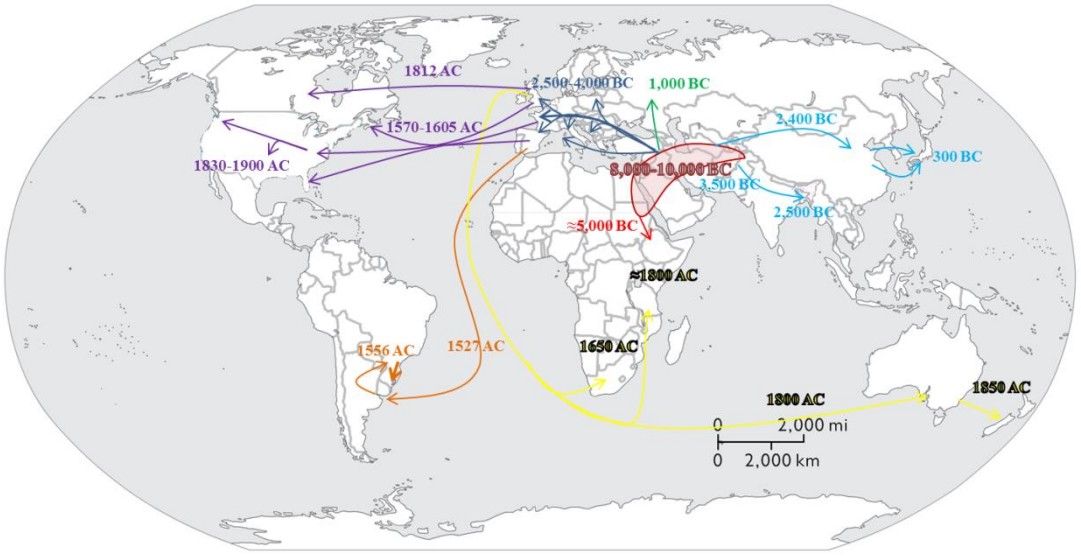

Figure I-4 : Worldwide spread of Wheat from the expected origin of the species (red area) according to Bonjean and Angus (2001). BC: Before Christ; AC: After Christ

d. Wheat genetic resources

During its history, wheat experienced two events of polyploidization resulting in a very large genome. Bread wheat, *Triticum aestivum* L. is constituted of 21 pairs of chromosomes grouped into seven groups of homoeologous chromosomes (Figure II-3). Within each group of homoeologous chromosomes, the three chromosomes come from three genome ancestors: Genome A from *Triticum urartu*, Genome B from a close species of *Aegilops speltoides* today disappeared, and Genome D from *Aegilops tauschii* (Figure II-1). A gene located in each homoeologous chromosome is also referred as homoeologous. The bread wheat genomes contained around 17 billion base pairs, approximately five times larger than maize (*Zea mays* L.) and 40 times larger than rice (*Oryza sativa* L.) genomes, with more than 80 % of repeated sequences (Paux et al., 2008). Further details will be presented in part VI. Bread wheat polyploid genome is stable despite the three homoeologous genomes thanks to the Ph1 locus (Griffiths et al., 2006). Indeed, this locus avoids pairing between related chromosomes resulting in diploids behavior at meiosis.

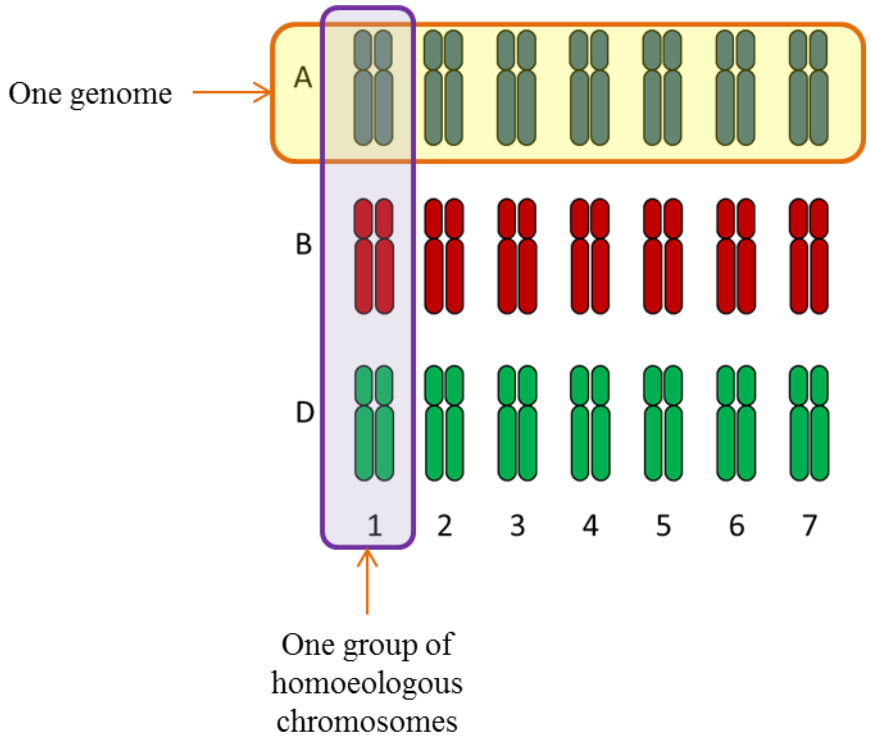

Figure I-5 : Organization of the hexaploid genome of bread wheat (*Triticum aestivum* L.) into three different genomes (A, B, and D) and seven homoeologous groups (Adapted from Laperche, 2005).

Before the advent of plant breeding during the XVIIIe, farmers only grew landraces and mixtures of landraces (Skovmand et al., 2002). Figure II-2 illustrates the fact that since the Neolithic age, wheat and its relatives were spread in different environments among which several were drought-prone and heat stress-prone areas. Such spread and diversification of wheat along its evolutionary history is particularly important as we will see later on. Jones et al. (2008) and FAO (2013) defined a landrace as a local ecotype of a domesticated animal or plant breed that has been largely improved by traditional agricultural methods and adaptation to its natural and cultural environment. Nowadays, wheat landraces are not the only material which is considered as genetic resources. Indeed, as mentioned by Becker (1993) and reported by Haussmann et al. (2004), genetics resources can be defined as 'all materials that are available for improvement of a cultivated plant species'. They can be classified according to the 'gene pool concept' into primary, secondary, and tertiary gene pools, and isolated genes representing the fourth class (Harlan and de Wet, 1971; Haussmann et al., 2004). The four classes correspond to (Haussmann et al., 2004):

- Pool I: the crop species itself and other species that can be easily crossed with it

- Pool II: related species for which crosses with targeted crop species lead to a low percentage of viable kernels and a progeny partially sterile
- Pool III: species for which crosses with targeted crop species are almost impossible and require the use of biotechnological techniques like embryo rescue or protoplast fusion.
- Isolated genes: all organisms containing DNA

For wheat, pool I consists of the cultivated, wild and weedy forms of the crop species (Skovmand et al., 2002), i.e., hexaploid landraces, cultivated tetraploids (AABB), wild *Triticum dicoccoides*, and the diploid donors of the A and B genomes of durum/bread wheat. Pool II contains *Triticum tauschii* (2n=2x=14, DD), other *Aegilops* and *Triticum* species sharing one genome with wheat, and diploid species of the Sitopsis section (putative donors of their B/G genomes; Salina et al. 2006) (Mujeeb-Kazi and Rajaram, 2002; Mujeeb-Kazi, 2003). Within pool III are present all diploid and polyploid wheat species with non-homologous genome to those of wheat (Mujeeb-Kazi and Rajaram, 2002).

Börner et al. (2002) reported that wheat represented the largest collection of accessions with around 900,000 accessions preserved worldwide, with 858,000 of the *Triticum* genus and 48,000 of the wild ancestor *Aegilops*. CIMMYT preserved the largest collection of wheat accessions worldwide with more than 110,000 accessions, followed by the National Center for Genetic Resources Preservation (NCGRP) in the USA with more than 57,000 accessions. The ten biggest wheat genebank worldwide represent more than half of the 900,000 preserved accessions (Börner et al., 2011). Such variability and its characterization are of paramount importance for the future of breeding, especially in drought and heat stress prone environments.

e. Wheat developmental stages and yield achievement

i. Aerial development and yield achievement

Wheat development is constituted by successive and partially overlapping developmental phases. Wheat development is the result of exogenous factors such as temperature, vernalization, and photoperiod needs. Bread wheat development is mainly dependent on temperature due to its insensitivity to vernalization (Prasad et al., 2008). Therefore, the plant development is usually expressed in terms of thermal time unit, or growing degree days. It corresponds to a measure of the heat accumulation by plants

along its development (McMaster and Wilhelm, 1997; Acevedo et al., 2002). Organ differentiation occurs during the various stages of wheat development. In 1974, Zadoks et al. published a scale for cereal development. Such scale is used to 'quantify' the wheat development. The Zadoks scale starts with the germination and then the emergence with the leaf production, the tillering with the tiller production, the stem elongation with the "node" production, the booting, the heading, the anthesis, and the physiological maturity (Figure II-4 and II-5).

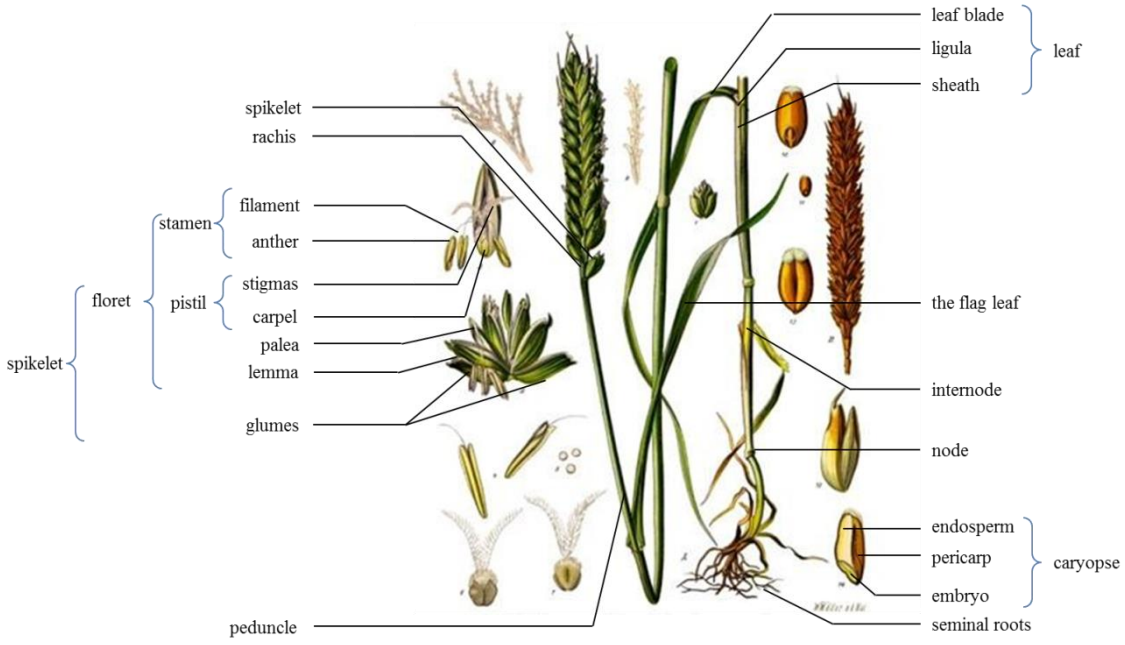

Figure I-6: Wheat, *Triticum aestivum* L., anatomy adapted from an image processed by Thomas Schoepke (www.plant-pictures.de)

The wheat crop cycle is divided into three periods: (i) the vegetative period, from sowing to floral initiation, occurring during tillering stage, (ii) the reproductive period, from floral initiation to anthesis, and (ii) the grain filling period, from anthesis to physiological maturity (Slafer, 2012). Leaf appearance starts at emergence and ends before booting with emergence of the last leaf, named the flag leaf. Plant height is set from emergence to some days after anthesis. Most of plant height is achieved within the stem growth phase starting some days before terminal spikelet stage (i.e., stem elongation) and ending some days after anthesis with the end of the peduncle growth (Figure II-5) (Acevedo et al., 2002).

Wheat grain yield can be dissected into various components. Each one is established at a more or less specific given period of the crop cycle. We are going to detail it now.

Wheat grain yield is established during the whole crop cycle. It is the combination of two main components set during the growth cycle overlapping at anthesis; from emergence to a week after anthesis: the number of grains per square meter, and during the grain development and filling, from grain set stage to physiological maturity: the kernel weight (Figure II-5). At a constant sowing density, the number of grains per square meter can then be dissected into: (i) the number of spikes per square meter and (ii) the number of grains per spike. All tillers produced by a wheat plant will not lead into spikes. Some will abort before anthesis (Gallagher and Biscoe, 1978a; Gaudillère and Barcelo, 1990). Compensation mechanisms exist between the different yield components in wheat. If one is impacted, the other ones might compensate loss (Slafer et al., 1996). In wheat, meiosis coincides with the booting stage (Z4.0). It starts in the middle of the spike and is spread toward both the base and the tip of the spike (Zadoks et al., 1974). In corn (*Zea mays* L.), Jones et al. (1985) reported at anthesis, after fecundation, a rapid cell division period leading to the appearance of endosperm cells and amyloplast of the future grains. Then, these cells grow, are differentiated and the starch deposition starts. This is the beginning of the grain filling phase (Figure II-5).

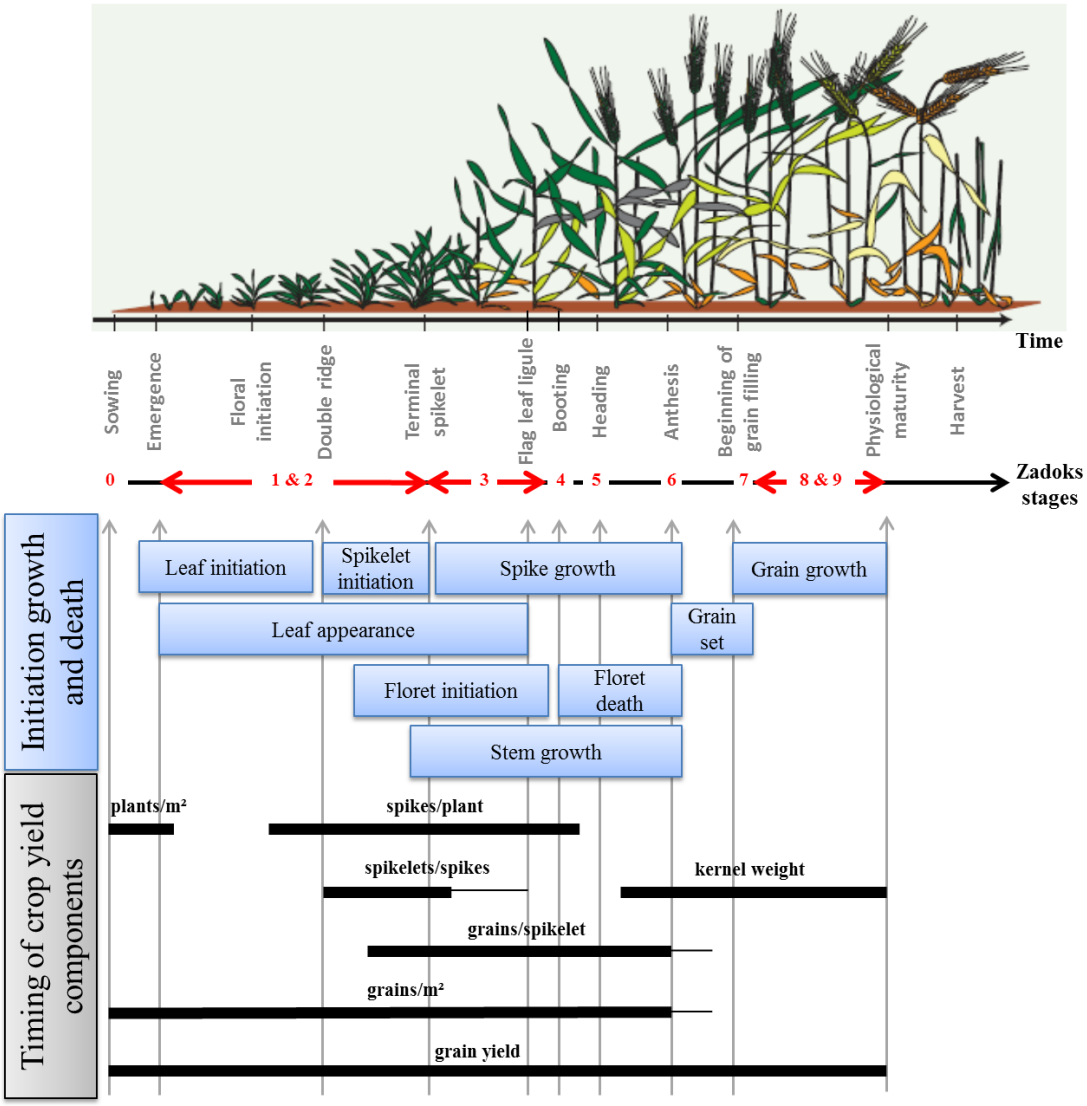

Figure I-7:Schematic diagram of wheat growth and development adapted from Slafer and Rawson (1994), Rawson and Gómez Macpherson (2000), and Slafer (2012), showing the main developmental stages of wheat growth, their correspondences within the Zadoks' scale (Zadoks et al., 1974; Tottman, 1987) and the timing of initiation of crop yield components. Periods of initiation of growth (or death) of specific organs and those of when different components of grain yield are produced are represented in bottom boxes.

There are two main flowering types in wheat due to their response to vernalization[3] (Flood and Halloran, 1986): (i) winter wheat and (ii) spring wheat. The former one shows a strong response to vernalization and requires a period of cold wheather to initiate flower development. In its early stages, winter wheat is highly resistant to frost (-20°C). The latter one has a very mild response or no response to vernalization. It is sensitive to frost (Acevedo et al., 2002). To acquire the ability to flower, some wheat genotypes may require specific day-length: they are sensitive to

[3] (from Latin: vernus, of the spring) is the acquisition of a plant's ability to flower or germinate in the spring by exposure to the prolonged cold of winter.

photoperiod. Most of cultivated wheat genotypes are long-day plants, i.e., flowering is accelerated with day-length increase, but they do not really need specific length of day to initiate flowering (Major and Kiniry, 1991). The major vernalization and photoperiod genes have been identified, molecular studies have identified their interactions, and gene networks showing their inter-relationship have been proposed (Trevaskis et al., 2007; Distelfeld et al., 2009; Shimada et al., 2009; Trevaskis, 2010). Major genes will be presented on part V.

ii. Roots establishment and growth in cereals

Cereal roots can reach 2m depth in field conditions by the end of anthesis (Lucas et al., 2000; King, 2003). Basic morphology of cereal root systems is well known. It grows following a consistent pattern and, as a consequence, has a relatively predictable architecture in uniform soils (Robinson, 1994). King (2003) reported that dynamic morphology of cereal root systems can be summarized with only a few variables without reducing significantly the resolution of the model.

The whole root system of a plant can be organized in three main schemes: (i) the taproot system found in most of Dicotyledonous and Gymnosperm, (ii) the fascicular root system characteristic of most of Monocotyledonous, and (iii) adventitious roots system (Prat and Rubinstein, 2005). Root system of many cereals like wheat, barley, and oats is classified as fascicular root system. However, it consists in two different root systems occurring successively. First, seminal roots grow from the seeds and then, starting at tillering (Z2.0, Zadoks et al., 1974; Tottman, 1987), nodal roots, also known as adventitious roots, appear at the base of the main stem and tillers, and develops abundant root hair. Each tiller develops its own roots allowing it to be independent of the plant (Lucas et al., 2000). Authors reported a root extension rate, sensitive to temperature and environment, ranging from around 5 mm d^{-1} for cereals sown in autumn to 15-25 mm d^{-1} in spring. At full emergence and maximum canopy size, with a root depth reaching 1.5 to 2.0 m depth, maximum root weight is around 1 t ha^{-1} and total root length range between 16 and 32 km m^{-2}.

f. Grain yield progress from the XVIIIe to the 1990's

A recurrent purpose in agronomic science is the improvement of crop yield. Many studies focused on bread wheat yield evolution due to its importance in both economy and in human food supply: for the UK winter wheat (Austin et al., 1980, 1989),

for the Canadian Prairies spring wheat (Stewart and Dwyer, 1990), for the north western mexican bread wheat (Bell et al., 1995), for the French winter wheat (Brancourt-Hulmel et al., 2003; Brisson et al., 2010; Oury et al., 2012) and for many other countries (Calderini and Slafer, 1998).

In France, first bread wheat varieties cultivated were landraces. One of the first traces of bread wheat variety recorded is 'Rouge d'Alsace' and 'Noé' around 1826 (Doré et al., 2006). At the beginning of 19th century, yield was around 0.9 t ha^{-1}. In 1950, 150 years later yield had just doubled to reach 2.0 t ha^{-1}. The global grain yield increase was really slow with around +0.01 t ha^{-1} year^{-1} (Bonjean et al., 2001; Brancourt-Hulmel et al., 2003). A the end of 19th century, the first variety bred by Henry De Vilmorin, so called 'Dattel', from a cross between two English wheats, was the result of a kind of pedigree breeding. At this time, English varieties were late, displayed good resistance to yellow rust (*Puccinia striiformis*) and to lodging, but had a really poor bread quality. Such quality was brought by "Aquitaine wheat", originating from Russia. The 'Bordier' variety, released in 1889, sign the start of variety combining both habits from Aquitaine and English wheats (Doré et al., 2006). With 1920s came the development of public and private breeding stations that represent an important change in plant breeding. Just before the Second World War, in 1938, with the progresses achieved, France became temporarily self-sufficient in wheat (Bonjean et al., 2001). From 1950 to 1990, yield more than tripled to reach 7.3 t ha^{-1}, corresponding to a progress of +0.13 t ha^{-1} year^{-1} (Bonjean et al., 2001). This progress came from the improvement both of agronomic crop management (higher level of input such as nitrogen and pesticide, use of certified seeds, *etc.*) and of genetic of cultivated varieties. Genetic progress can be dissociated from yield progress due to crop management modernization. In 2003, Brancourt-Hulmel et al. estimated the genetic progress between 1950 and 1990 at +0.063 t ha^{-1} year^{-1}. Genetic progress was mainly due to the introgression of dwarfing genes, known as the Green Revolution[4], which strongly improved harvest index and enabled higher imput levels with reduced lodging risks. It is also the consequence of a better disease resistance (Bonjean et al., 2001).

[4] Initiated by Norman Borlaug, the Green Revolution is the result of a series of investigations and technology transfer initiated in the 1940's and lasted until 1960's. It leaded to an dramatic increased of the worldwide agricultural production by the development of high yielded cereal varieties, irrigation, modernization of agronomic practices, and the wider use of improved seeds and chemical products (Wikipedia, 2014b).

Most of the breeding efforts to improve wheat grain yield resulted in an increase in the number of grains per square meter, by through the number of grains per spike. In 1989, Austin *et al.* compared older and 'modern' US winter wheat varieties, with higher grain yield. He showed that the grain per square meter increased by more than 59 %, with 14 % more spikes per square meter and 30 % more grains per spike, and with a relatively constant grain weight. Similar conclusions were also reached by other studies (Perry and D'Antuono, 1989). A well-known hierarchy of yield components in yield achievement is that the number of grains per square meter is much more important than the grain size, i.e., the number of grains per square meter is the coarse-regulation mechanism and the grain size, only a fine-tuning mechanism (Slafer et al., 2014). As a consequence, modern wheat cultivars are able to sustain grain filling of much more grains per square meter.

After the Green Revolution, the Mexican wheat programme was led by the INIFAP[5] and the CIMMYT[6]. It mainly focused on the creation of varieties adapted to the northwestern Mexican irrigated conditions. Since 1969, three different environments were targeted in Mexico: the northwestern irrigated areas, the Bajio and central Mexico irrigated areas, and the central highlands rainfed areas (Rajaram and Van Ginkel, 2001). Between 1966 and 2001, in northern Mexican and in the Bajio and Central Mexico irrigated areas, a yield increase of +0.07 t ha^{-1} $year^{-1}$ and +0.058 t ha^{-1} $year^{-1}$ was reached, respectively. However, in the central highlands rainfed areas, the grain yield progress was lower than in irrigated conditions and reached only +0.024 t ha^{-1} $year^{-1}$. Historical genetic gain in absolute values is almost always lower under stressed environments than in unstressed conditions (Rajaram and Van Ginkel, 2001). However, Blum (2006) shown that when the genetic gain is regarded as a percentage of average yield, whatever the environment considered, genetic gains are quite close. Austin et al. (1989) observed a gain from 0.6 to 0.7 % in unstressed conditions and from 0.4 to 0.6 % under stressed environments.

It was necessary to present the origin, genetic structure, and growth and development of bread wheat. However, the main interest of this PhD is about the adaptation of plants under abiotic stress conditions; drought and heat stress. But what is

[5] National institute of forestry, agriculture and animal research
[6] International center for maize and wheat improvement

a stress, how can it be defined? What is drought stress? Heat stress? How can it be determined during the crop cycle, when plants are suffering from drought and/or heat stress? The following part aimed to answer these questions with the introduction of the concept of stress and a review of the methods to characterize the environment.

II. From the concept of stress to the characterization of the environment

The environment is composed of many biotic (insects, pathogens, *etc.*) and abiotic factors (soil water availability, soil nutrients, light intensity, *etc.*) varying constantly, in time and intensity. During its growth, a plant interacts and is used to live in a changing environment. Although every environmental change impacts its growth and development, a plant displays a certain metabolism flexibility enabling constant adaptation (Gaspar et al., 2002). Therefore, a deviation of a factor from its optimum does not always lead to a stress (Figure III-1) (Gaspar et al., 2002; Taiz and Zeiger, 2010a). Plants are also able to acclimate to their environment.

The term stress is properly defined in Physics[7] as a force exerted per unit area of an object (see p46; Chen, 2007). However, in biology, defining a 'stress' is not such an easy task. In 1980, Levitt proposed to define a stress as 'any environmental factors unfavorable for a considered living organism'. More recently, Nilsen et al. (1996) proposed a definition of a stress in a physiological sense, as "the condition caused by factors that tend to alter an equilibrium" (Gaspar et al., 2002). In the whole manuscript, the term stress always refers to abiotic stress except otherwise mentioned.

[7] Stress is defined as the average force per unit area that some particle of a body exerts on an adjacent particle, across an imaginary surface that separates them (Chen, 2007)

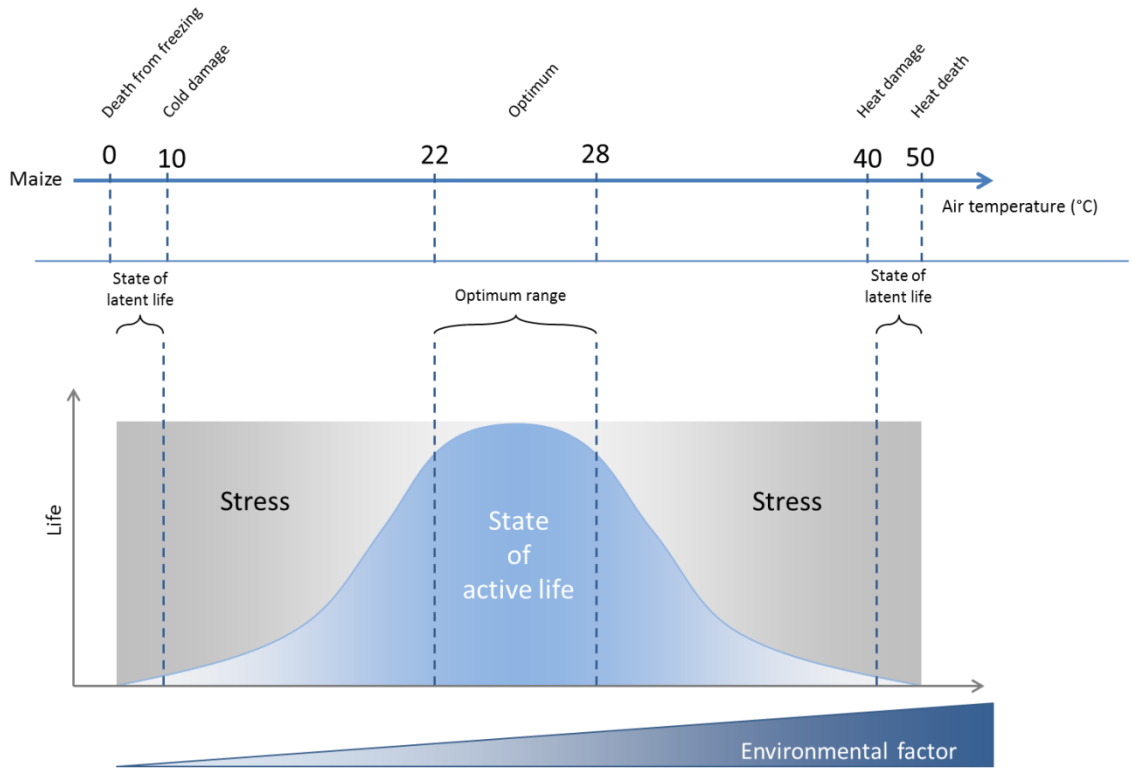

Figure II-1 : Life processes of maize (*Zea mays* L.) described as a function of an abiotic environmental factor (ex.: air temperature). Adapted from Schulze (2005)

a. Definition and description of water deficit and high temperature stresses

High temperature and water deficit stresses are classified as abiotic stress (Reddy et al., 2004). As for every factor mentioned in (III-a) and leading to a stress for the plant, a thermal stress is considered when temperatures evolve outside of plant optimum temperature for growth during a period of time long enough to cause injury or irreversible damages (Figure III-1). Temperatures above the plant optimum for growth are classified as high temperature stress, i.e., heat stress (Wahid et al., 2007; Farooq et al., 2011).

Concerning water deficit stress, we should clarify some terms before going into more details. The term of 'aridity' is used to characterize a type of climate or an area, characterized by a low average rainfall. Several general definitions of the 'drought' term exist depending on the scientific area considered. However, all of these definitions agree with the following basic definition: a climatic event characterized by a period of abnormally dry weather, i.e., abnormally low rainfall, sufficiently prolonged to cause a serious hydrologic imbalance in the affected area (Huschke and American Meteorological Society, 1959; Yevjevich et al., 1977; Seguin, 2006; U.S. Geological

Survey, 2012). In agriculture, this climatic event is defined as a shortage of precipitation sufficient to adversely affect crop production or range production (Rosenberg, 1979; U.S. Geological Survey, 2012).

In plants, water absorption is done by roots exploring a volume of soil. The lack of rainfall has a direct impact on the amount of water stored in the soil and available for plant (Seguin, 2006; Jaleel et al., 2009; Farooq et al., 2009), but also on the relative air moisture. As a living organism at the interface between soil and atmosphere, water deficit may impact plants from the soil, i.e., osmotic stress, and from the air, i.e., evaporative stress (Monneveux and This, 1997). In maize, the kinetic of the leaf elongation rate had been reported to be sensitive to the two components of drought, i.e., the air component through the evaporative demand and the soil component, with the soil water deficit (Equation III-1) (Salah and Tardieu, 1997; Reymond et al., 2003; Tardieu et al., 2008).

Equation II-1 : Equation of the leaf elongation rate in corn as a function of the temperature, the inherent elongation rate (a), the sensitivity to the evaporative demand (b), and the sensitivity to the soil water deficit (c) (Source: Salah and Tardieu (1997), Reymond et al. (2003), and Tardieu et al. (2008))

$$\frac{dl}{dt} = (T - T_0)(a - b \times VPD_{la} - c \times \Psi)$$

However, in the vast majority of the open-field experiments on drought, the water deficit stress refers almost exclusively to soil water deficit. A plant suffered from water deficit stress when the water uptake is less than the amount of water that should be lost by transpiration (Bray, 1997; Reddy et al., 2004) according to the climate conditions, the development stage and the genotype. It is usual to encounter the use of all the previously mentioned terms within the scientific literature indistinctly. In the whole present manuscript, ‘drought’, ‘soil water deficit’, or simply ‘water deficit’ terms always refer to the same meaning except otherwise mentioned.

b. Distribution of water deficit and heat stresses worldwide on wheat cultivated areas

Worldwide agricultural production is mainly limited by environmental stresses. Indeed, with productivity limitation, such stresses also reduce the possible acreage for crop on Earth (Gaspar et al., 2002). From 1980 to 2012, drought and heat stress combined within the USA was estimated responsible of 200 billion USD agricultural losses although only 50 billion was estimated due to the only effect of drought over the same period (Suzuki et al., 2014).

Nowadays, wheat is widely cultivated worldwide and exhibit very large geographical adaptation. Wheat growing areas worldwide displayed strong variations in term of rainfall patterns, evaporative demand, type of soil, water availability, temperature, crop management, and many other abiotic and biotic stresses (Braun et al., 2010). Compilation and analyses of worldwide wheat growing areas features lead CIMMYT scientists to identify twelve wheat-growing mega-environments on Earth.

A mega-environment is a concept developed by Rajaram et al. (1995). It corresponds to "a broad, not necessarily contiguous area, occurring in more than one country and frequently transcontinental defined by similar biotic and abiotic stresses, cropping system requirements, consumer preferences, and for convenience, by a volume of production" (Braun and Payne, 2012). Such mega-environments help to determine the type of adapted wheat germplasm to a given area. Among these twelve mega-environments (ME), five are drought or heat stress-related. Indeed, ME4 (low rainfall, i.e., <500mm.year^{-1}; area of 21.6 Mha), ME5 (high temperature; 7.2 Mha), and ME6, ME9, and ME12 (drought stress and high temperature during the crop cycle; 25.7 Mha) represent more than 25 % (54.5 Mha) of 2012 world wheat-growing areas (Figure III-2). Gupta et al. (2012) displayed specifically these growing areas which are found on the five continents: America (South Canada, US central plains, northern Mexico, Brasil, Argentina, Chile, and Bolivia), Africa (Morocco, Algeria, Tunisia, Mauritania, Niger, Sudan, Ethiopia, Somalia, and South Africa), Europe (Spain, Portugal, and Romania), Asia (Russia, Turkey, the whole Middle-East, Pakistan, India, and China), Oceania (Australia).

However, the five ME where drought and/or heat stress occurred referred to the date of the study (1995). With the climate change, it is more than likely that the picture of the current drought and heat stress ME will evolve in the coming decades.

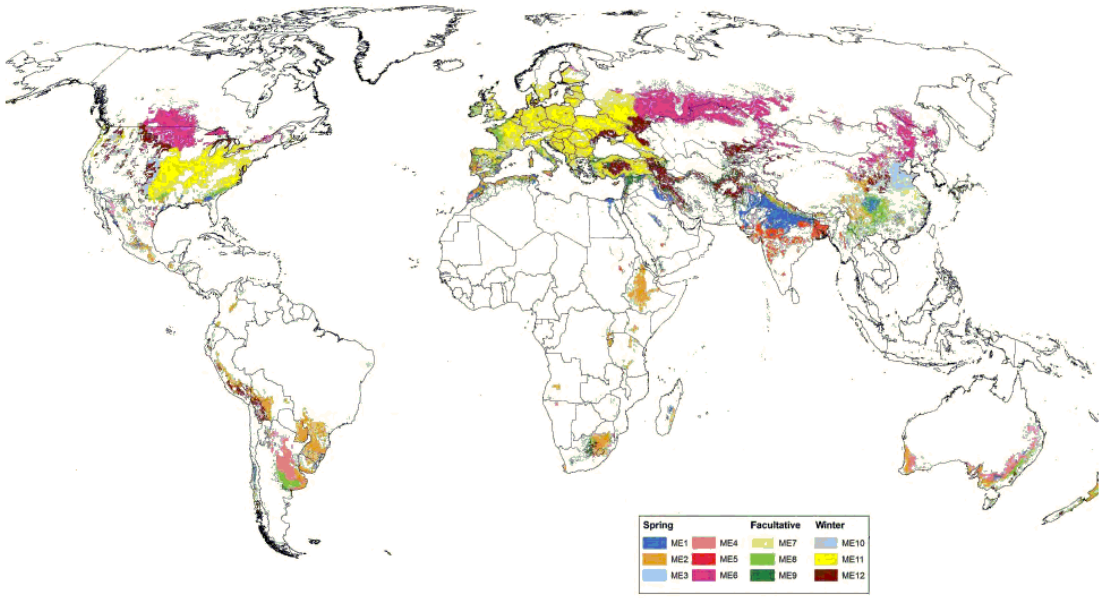

Figure II-2 : Distribution of the twelve wheat growing mega-environments identified by the CIMMYT (Source: Braun and Payne, 2012)

c. Water movements from the soil to the atmosphere through the plant

As fundamentally immobile, a plant has to adapt (germinates, grows, reproduces and matures) to its environment, or dies. Plants, as any other living organisms, could be conceptualized as a thermodynamic system which requires a constant input of free energy[8] to maintain and repair its highly organized structure (Taiz and Zeiger, 2010b). Land living plants are highly organized organism living at the interface between soil and atmosphere. As such, they extract water and nutrients from the soil with their roots, i.e., soil-plant interface, and evaporate and exchange gazes at the leave level, i.e., plant-atmosphere interface.

i. Theory and concepts of water potential (Taiz and Zeiger, 2010b)

The chemical potential of water corresponds to the quantitative expression of the free energy associated with water. It is expressed in energy per mole of water (J mol^{-1}) and represents the difference of the potential of the water between a given state and the reference state, i.e., pure water stored at ambient temperature and at standard atmospheric pressure.

[8] Thermodynamic free energy, the energy in a physical system that can be converted to do work (source: Wikipedia (2014a))

In physiology, the term 'water potential' refers to the measure of free energy per unit of volume (J m^{-3}). It is directly related with its chemical potential (ratio of the water chemical potential and the volume of a mole of water). It is constituted by three components (Equation III-1) and can be expressed as a pressure. It is influenced by three factors: (i) the concentration of solutes within the water, (ii) the pressure, and (iii) the gravity.

Equation II-2: Water potential formula (Ψ_w) decomposition into osmotic potential (Ψ_s), pressure potential (Ψ_p), and gravity potential (Ψ_g) (Source: Taiz and Zeiger, 2010b)

$$\Psi_w = \Psi_s + \Psi_p + \Psi_g$$

The osmotic potential (Ψ_s) represents the effects of the concentration of solutes within water. Dissolved solutes decrease the water potential of a solution compared to its reference. The pressure potential represents the effects of the pressure and is measured as a deviation from the atmospheric pressure. Finally, the gravitational pressure refers to effects of gravity. This theory can be applied to any compartments, i.e., soil, cell, atmosphere, *etc*.

ii. Water in the soil

The soil is a mix of (i) solid particles (different in size, shape and constitution), called the matrix. The matrix is constituted by mineral particles (originating from the degradation of rocks), and by organic particles (originating from residues of plants or animals). The size of those particles defines the soil texture. A porosity network is created within the matrix and can be filled with (i) air and (ii) water. The water content of a soil depends of its permeability and the size of its pores (Beauchamp, 2006).

From an agronomic point of view, if the soil is assimilated to a tank within which water is available for plants, several parameters must be considered to describe the relationships to water between plants and soil.

The field capacity (Θ_{FC}) is defined as the soil moisture value under which, capillarity forces are dominating and the water is retained in the soil (no gravity flux). The field capacity depends on the soil composition. At field capacity, the soil content is at its maximum moisture capacity. The permanent wilting point (Θ_{PWP}) is the soil moisture value to which capillarity and adsorption forces are so high that the plant cannot extract water from the soil anymore. The plant is definitively wilted and dies. The total available water (TAW) is the potential total amount of water in the soil

available for the plant (Figure III-3). This definition could be more precise considering the volume of soil explored by roots at a given stage (Brouwer et al., 1985; Seguin, 2006). Between both edges, an intermediate water level is estimated as the temporary wilting point (Allen et al., 1998a). It separates the readily available water (RAW) that plants can extract without "effort" from the hardly available water (HAW), that plants can still extract but with increased efforts. When plants start extracting the hardly available water, they are experiencing water stress (Allen et al., 1998a).

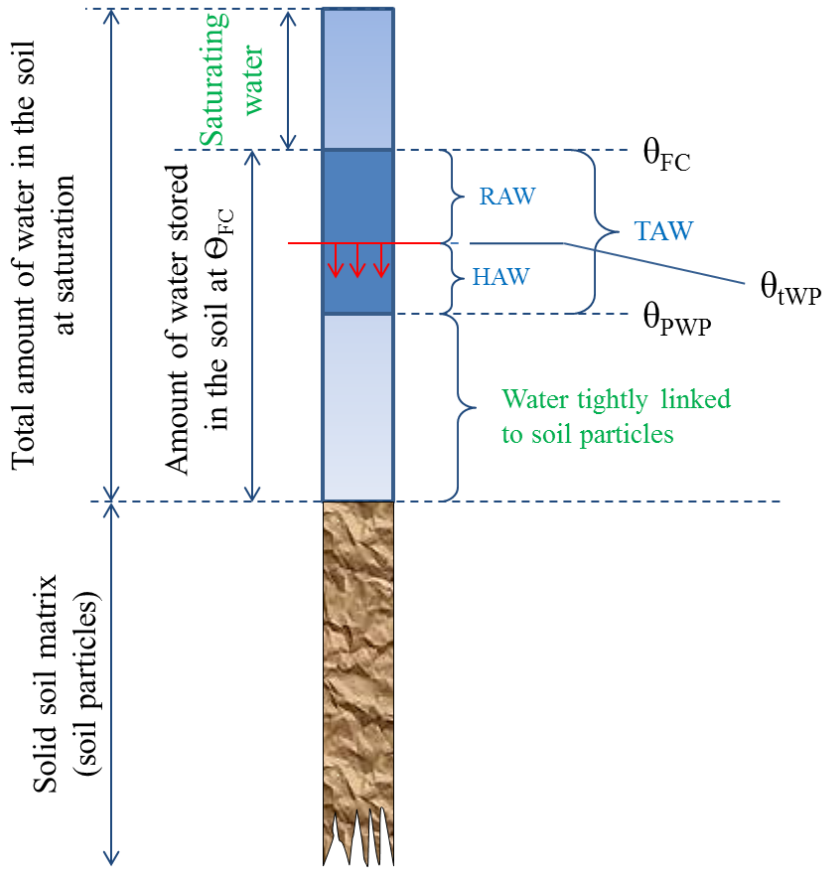

Figure II-3 : Diagram of the different water compartments in a soil in terms of availability for plant. RAW: Readily available water; HAW: Hardly available water; TAW: Total available water; Θ_{FC}: Field capacity; Θ_{PWP}: Permanent wilting point; Θ_{tWP}: temporary wilting point. In green are displayed water compartments unavailable for plants

iii. The gradient of water potential drives the water through the soil-plant-atmosphere continuum

Water potential is the driving force of water movement through the soil-plant-atmosphere system. The water flux through the system is controlled by the rate of evaporation during the day. The concept of soil-plant-air continuum (SPAC) was first edicted by van den Honert (1948) to represent the water flow through the system. A gradient of decreasing negative water potential exist from water in the soil, to water

within roots, to water within leaves to finally water in the atmosphere (Figure III-4) (Taiz and Zeiger, 2010c).

In the soil, the water potential is mainly influenced by gravitational and pressure potential. Except in saline soil, the osmotic component can be considered as negligible. The soil exerts suction on water molecules. Thinner is the soil porosity, larger is the specific surface of the soil water/particle interface, higher the suction force, the stronger the water is retained by the soil (Beauchamp, 2006; Vauthier, 2011). In other words, in a wet soil, the pressure potential is closed to zero and become lower and lower in drying soil (Taiz and Zeiger, 2010c). So, within drying soil, if the water potential gradient changes between soil and roots, i.e., $\Psi_{w,soil} > \Psi_{w,roots}$, the water uptake by plant is stopped. A constant competition occurs between plants and soil particles for water. However, as a living organism, plants have a limit in the strength they can exert to extract water from the soil particles.

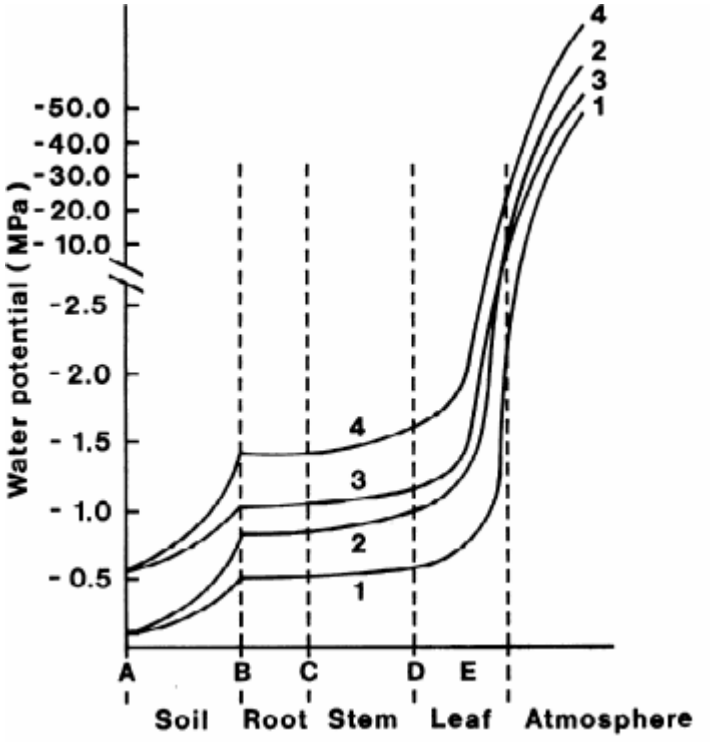

Figure II-4: Idealized water potential gradients through the soil plant water atmosphere continuum (SPAC). Curves 1 and 2 represent plant water removal from relatively wet soil at low and high transpiration rates, respectively; curves 3 and 4 represent plant water removal at low and high transpiration rates, respectively, after soil water potential has been reduced to -0.6 MPa (Source: Hillel, 1980).

The tight contact between hair roots and soil particles enables plants to extract water. Water can enter within roots by three pathways: (i) the apoplast, (ii) the symplast, and (iii) the transmembrane pathway (Figure III-5). The apoplast is a continuous system

of cell walls and intercellular spaces. In this pathway water moves without crossing any membranes as it travels across the root cortex. The symplast pathway corresponds to the entire network of interconnected cytoplasm of each cell within the cortex via plasmodesmata. Finally, the transmembrane pathway refers to water molecules travelling across cells through membranes (Taiz and Zeiger, 2010c). Then, after crossing the whole cortex, water molecules have to pass to the plasma membranes as the Casparian strip breaks continuity of the apoplast pathway.

Water molecules are then transported within the xylem vessels, i.e., the tracheids, to the leaves where photosynthesis takes place. Tracheids provide a low-resistance pathway for the transport of water. In leaves, water is pulled from the xylem vessels to the mesophyll cell walls before diffusing to the leaf's air space as vapour (Figure III-5). The transpiration depends on two major factors: (i) the difference in vapor concentration between the leaf's air space and the atmosphere and (ii) the diffusional resistance of the pathway. The stomata control couples leaf transpiration with leaf photosynthesis. The stomata are constituted by two subsidiary cells and two guard cells. An increase in turgor of the guard cells opens the stomata (Taiz and Zeiger, 2010c).

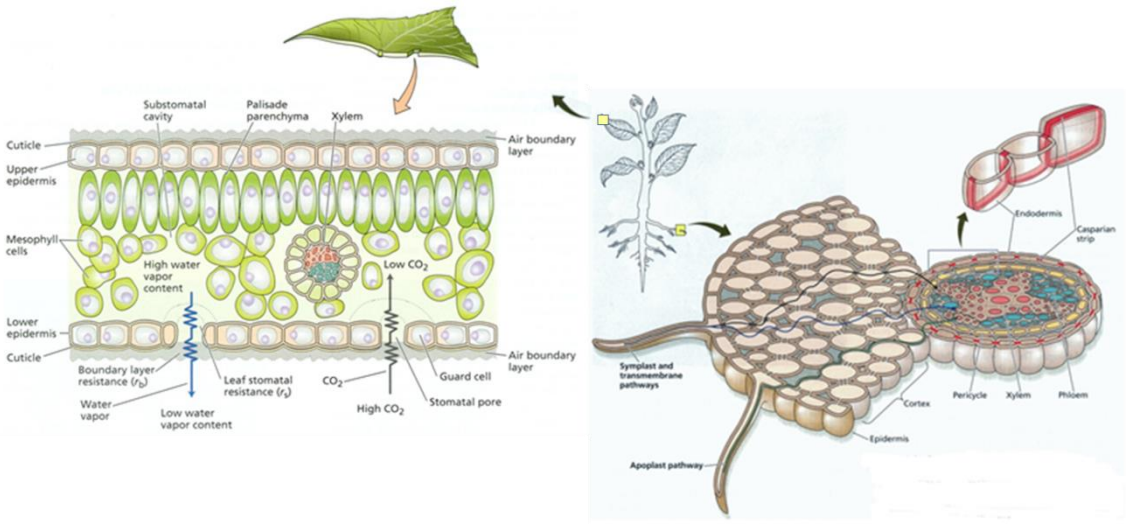

Figure II-5: Water moves from the soils to the roots (on the right), showing the three pathways (symplast, transmembrane and apoplast) for water uptake by the root, and water and gazes exchanges from the leaf to the atmosphere (on the left) (Adapted from Taiz and Zeiger, 2010c)

d. Characterization of the environment

Drought and heat stress can be characterized by their intensity (importance of the difference between optimum needs for plants and the experienced values of water deficiency or high temperature), their extent (duration of the stress period), their predictability (e.g., cyclic rainfall, i.e. Mediterranean areas, or areas with more

variability, i.e., Northern Europe), and their temporal distribution within the crop cycle (Seguin, 2006).

i. An agronomic diagnostic using probe genotypes

The description of environmental constraints can be performed either by using a set of environmental parameters (Voltas et al., 2005) or by establishing synthetic variables defined on probe genotypes (Cooper and Fox, 1996; Brancourt-Hulmel, 1999; Laperche et al., 2008; Zheng et al., 2010) and based on an agronomic method of diagnosis (Sebillotte, 1980). At a given location, crop yield is dissected into yield components (e.g., kernel per square meter until anthesis and thousand kernel weight from anthesis to maturity). These values are then compared with unstressed values for reference. It allows pinpointing the yield components impacted by (i) the timing of the stress (e.g. if the number of grains per square meter is less than the reference value, it implies pre-anthesis stress) during the crop cycle (Slafer, 2012), and (ii) the intensity of the stress estimated as the difference between measured values under stress and the reference values. The growth constraint is then associated with environmental parameters measured during the crop cycle. For example, reduction of the number of kernels per square meter -compared to a reference value- may be concomitant with high temperature observed during the pre-anthesis growth phase (Lecomte, 2005).

ii. Characterizing the water deficit along the crop cycle

Several studies provided an environmental characterization of their trial network. In 2004, Campbell et al. built environmental covariates based on meteorological data *per se*, i.e., without using stress thresholds applied to meteorological data. These authors divided the crop cycle into three consecutive and non-overlapping development phases, to consider the differential sensitivity of wheat along the crop cycle, similarly to Brancourt-Hulmel (1999) and Brancourt-Hulmel et al. (2000).

Recently, a model-based approach was used by Chenu et al. (2011) to characterize the different drought pattern scenarios occurring in southern Australia. This technic enables the reconstruction of the plant development cycle, and determining whether a stress occurred or not at any given developmental stage using historial environmental records. The strength of such an approach is also one of its limitation: the collection of meteorological data over many years and information on soil type, and their integration into a crop simulation model (Lacaze and Roumet, 2004).

Drought is probably one of the most complex stresses to characterize. Allen et al. (1998b) proposed a complete guideline to characterize it considering all the parameters of influence: a water balance is performed. The methodology proposed by Allen et al. (1998b) consisted in estimating the real evapotranspiration of the plant along its development with as a known starting point the available amount of water in the soil at the beginning of the crop. The evolution of water available in the soil is modelized and can be followed during crop growth. The first step consists in determining the reference evapotranspiration (ET_0) using environmental factors such as radiation, temperature, wind, *etc*. Usually, this value is given by a meteorological station on a daily basis at least. It corresponds to the amount of water evapotranspirate by a grass reference crop under optimum conditions. Secondly, the evapotranspiration of a wheat crop under optimum-conditions (ET_c) is estimated through the use of a crop coefficient (kc) representing the evolution of the transpirating biomass along the crop cycle for a given crop species. Finally, the real evapotranspiration of a wheat crop under real conditions ($ET_{c,adj}$) is determined (Figure III-6). The drought stress coefficient (ks) indicates the water stress status of a plant. If plants can totally satisfy their water needs, they are not in a water deficit situation, $ET_{c,adj}=ET_c$ and ks=1, (ii) if plants cannot satisfy their water needs and the soil reached the permanent wilting point, the water deficit is total, $ET_{c,adj}=0$ and ks=0, and (iii) if plants are in water deficit, they evapotranspirate $ET_{c,adj}<ET_c$ and ks ϵ]0;1[. The intensity of the stress increases with lower values of ks.

As we will see later in the document, one of the first limitations to understand the genotype-by-environment interaction (GEI) is the lack of informative environmental covariates. The environmental characterization aimed to produced covariates which can be used into GEI analyses and also on QEI (QTLxE) analysis, and as a consequence, try to identify the environmental factors which can have an impact on the quantitative traits of interest.

Building on the knowledge of the wheat plant and of what are drought and heat stress, but also the way of characterizing them, the next logical step concerns the confrontation of both. In other words, it is now time to investigate the impact of drought and heat stress on wheat.

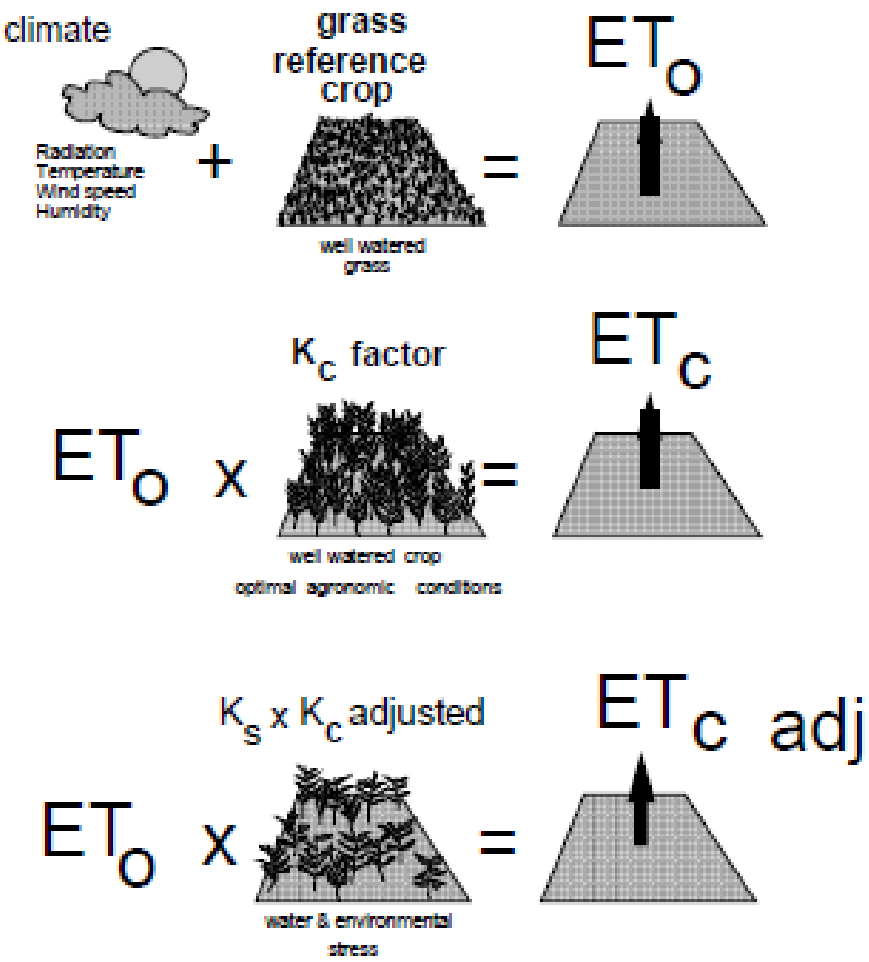

Figure II-6: Diagram representing the three equation steps structuring the whole process to characterize the water stress status of the plant. Reference (ET_0), crop evapotranspiration under standard (ET_c) and non-standard conditions ($ET_{c\ adj}$). kc corresponds to the crop coefficient; ks correspond to the drought stress coefficient (Source: Allen et al., 1998b)

III. Impact of drought and heat stress on wheat

Plants are able to recognize and respond to specific stress and stress combinations (Suzuki et al., 2014). Drought due to its complex determinism cannot be predicted precisely at the field scale, so does heat stress. These two types of stresses are likely to be the major environmental factors which impact and limit crop growth and yield around the world. Combination of these two stresses is responsible of many physiological changes affecting crop yield and quality (Mittler, 2006; Prasad et al., 2011; Suzuki et al., 2014).

Evaluating the impact of both drought and heat stress conditions in wheat is usually done by comparison to irrigated potential conditions. Concerning drought, a similar date of sowing, in winter is usually used, enabling plants to experience drought

conditions without suffering from another independent stress (heat stress) (e.g., Olivares-Villegas et al., 2007). Concerning the study of heat stress on wheat in open fields, a late sowing complemented with several irrigations along plant growth cycle is used.. The later sowing enable plant to experience hotter temperatures of summer without suffering any drought stress (Figure IV-1) (e.g., Pinto et al., 2010).

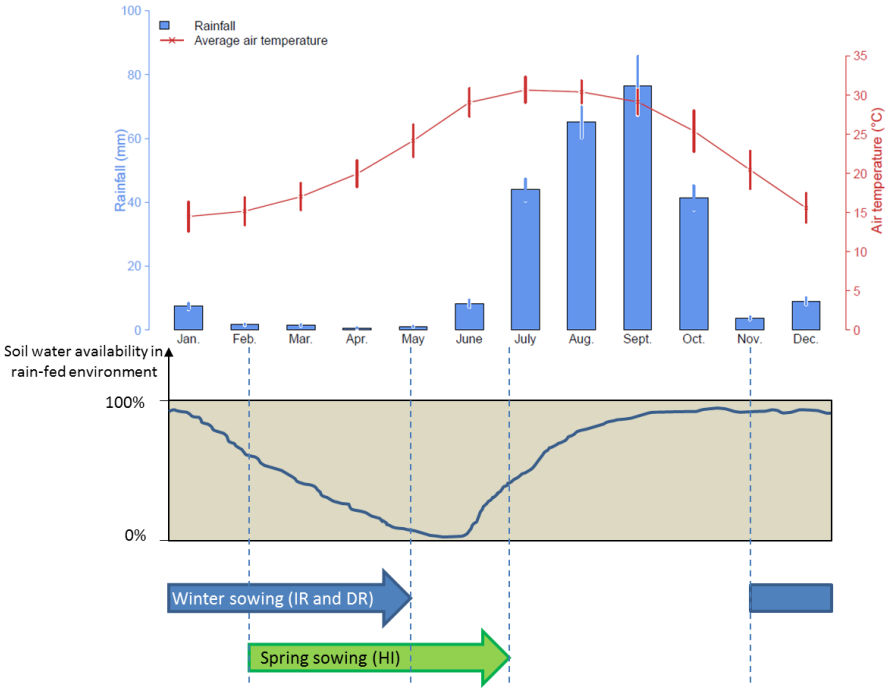

Figure III-1 : Evolution of the average temperature (red) and the precipitations at Ciudad Obregon, Sonora, Mexico, during the year (top part) and the estimated evolution of the soil water availability in that location under rainfed conditions. Are indicated the period of winter sowing trials (irrigated and drought conditions) and spring sowing trials (heat-irrigated conditions)

The basis for growth is the net assimilation of carbon dioxide (CO_2) at the tissue level. Many factors were reported to affect such assimilation, as drought and heat stress.

a. Differential sensitivity to drought and heat stress along the crop cycle

Many papers report the effects of drought, heat, or even the combined stresses (Saini and Aspinall, 1981; Saini et al., 1983; Robertson and Giunta, 1994; Sheoran and Saini, 1996; Wang et al., 2003, 2011a, 2012; Kumar et al., 2007; Pinto et al., 2010). All of them concluded to a negative impact on many traits (Suzuki et al., 2014). However, comparing them remains quite difficult as the severity, the duration and also the plant developmental phases at which the stress occurs are rarely all described (Prasad et al., 2008; Slafer, 2012). Yet, such information is of first importance, especially for annual crop plant species such as wheat.

Abiotic stresses impacting wheat at a given growth phase are likely to impact most of physiological processes, i.e., organs development for example, and so yield components set at that phase, leading to a reduction in yield potential. The reproductive phase is usually referred to be the most sensitive stage of wheat (Prasad et al., 2008; Slafer, 2012). In rice, such assumption was confirmed, as drought around flowering caused the largest damages to grain yield compared to other developmental phases (O'Toole, 1982). In wheat, yield components importance was ranked: grains/m^2 > grain size (Slafer et al., 2014). Prasad et al. (2008) reported that the greater sensitivity of reproductive processes might be due to their inability to acclimate to stress whereas vegetative development and photosynthesis can be regulated to adapt with productions of osmolyte and heat shock protein for example.

Under field conditions, heat and drought are likely to occur simultaneously. Some studies reported that combined, they cause worse damages on crop yield and quality than separately (Savin and Nicolas, 1996; Rizhsky et al., 2002, 2004; Prasad et al., 2011; Vile et al., 2012). Rizhsky et al. (2002, 2004), who worked on two plant models, Arabidopsis and Tobacco, revealed that molecular responses of the combination of drought and heat stress was unique and cannot be extrapolated from neither drought nor heat only. Suzuki et al. (2014) hypothesized a kind of additive impact, revealing certain independence between regulatory mechanisms of the plant responses to drought or heat.

The impact of drought and heat stress, combined or taken one by one, on physiological processes, plant growth and development, grain yield achievement is described in the following sections.

b. Grain yield achievement

Several studies have studied the effects of drought, heat or combination of both stresses on wheat and other cereals. In wheat, comparatively to irrigated conditions, drought was reported to cause grain yield reduction ranging from 23 % to 77 % (Olivares-Villegas et al., 2007; Pinto et al., 2010; Prasad et al., 2011; Xue et al., 2014) and heat stress around 59 % (Pinto et al., 2010). Blum reported that under moderate stressed conditions, yield is highly dependent on the yield potential of the variety. As a consequence, for wheat and barley, in conditions where grain yield reductions is less than 60 to 70 %, breeders should better focus on improving wheat potential than

drought stress resistance (Blum, 2006). Depending on the stage when the stress occurred, papers revealed a decrease in the corresponding yield components. With a severe drought occurring during the whole crop cycle, Xue et al. (2014) reported a significant decrease in the number of spikes per square meter and also on thousand kernel weight compared to irrigated conditions (number of grains per spikes was not available). On barley, with a stress starting at heading date, drought decreased the number of spikes per square meter whereas, heat stress was reported to decrease the kernel weight (Rollins et al., 2013). Such results may reveal that the reduction of the tillers/m² compared to irrigated conditions was due to tiller regression, i.e., abortion of tillers due to water limited resources (Gaudillère and Barcelo, 1990).

When heat and/or drought impact the crop cycle during the grain filling stage, they both lead to smaller seed size and as a consequence less heavy seeds. Heat impaired grain filling by reducing its duration which tends to decrease the size of the grain. Drought influenced grain filling indirectly, by limiting the amount of assimilate available for remobilization (Prasad et al., 2008).

c. Physiological effects of drought and heat stress on plant development and growth

i. Aerial development and growth

1. Impact on aerial vegetative tissues

Aerial biomass is established during the vegetative stage enabling plant development. During grain filling, it also participates to fill the grains. The impact at both stages must be considered.

A common feature resulting from the impact of drought stress during biomass establishment is a reduction of plant growth. Studies reported the expansion of plant organs is inhibited when experiencing drought (Westgate and Boyer, 1985; Tardieu, 2006) leading to shorter plants with smaller organs due to less numerous and smaller cells (Tardieu et al., 2000). More specifically, corn leaf growth was reported as one of the most sensitive processes affected by water deficit (Boyer, 1970; Westgate and Boyer, 1985; Alves and Setter, 2004). Indeed, under drought, the leaf elongation rate depends on the meristem temperature, the soil water status, and the evaporative demand (Salah and Tardieu, 1997; Reymond et al., 2003; Welcker et al., 2007).

Yield is strongly influenced by the duration of the biomass accumulation during the crop cycle; longer the crop cycle, higher the maximum potential yield (Tardieu, 2013). So, intuitively higher temperature or heat stress should lead to shorter crop cycle and as a consequence to a reduction in grain yield potential. On drought conditions, a decrease of the vegetative growth phase was also reported (Robertson and Giunta, 1994; Prasad et al., 2008). In soybean (*Glycine max* (L.) Merr.), De Souza et al. (1997) showed that a continued drought can also lead to an increase of leaf senescence rate, reducing the grain filling period. Grain filling duration under drought and heat stress may be reduced but might be partly compensated by a higher grain filling rate if abundant carbohydrates are available, from the leaf photosynthesis or from stems or leaves reserve (Yang and Zhang, 2006; Prasad et al., 2008). The grain filling rate may be slightly increased and the duration strongly decrease with heat stress (Tashiro and Wardlaw, 1989).

2. Impacts on reproductive organs

The reproductive phase of wheat can be divided into early reproductive phase, from floral initiation to the end of tillering, and late reproductive phase, from the beginning of stem elongation to a couple of days after anthesis (Figure II-5) (Slafer, 2012). Prasad et al. reported that all reproductive processes are highly sensitive to drought and/or heat stress including microsporogenesis [9] and macrosporogenesis, anthesis, pollination, fertilization, and early embryo development (Prasad et al., 2008).

During the meiosis of wheat, i.e., around the boot stage, drought stress significantly impacted gametophyte development (Sheoran and Saini, 1996). Important florets abortion was observed in wheat due to a stress just before anthesis, with 40% of abortion (Saini and Aspinall, 1981), but also in rice (O'Toole, 1982) and corn (Moss and Downey, 1971). However, divergent results appeared in the literature. Some studies showed a higher impact of drought on male fertility, i.e., pollen, than female fertility, i.e., embryo sac in various species (Moss and Downey, 1971; Saini and Aspinall, 1981). Others ones indicated that drought had greater impacts on embryo sac development in corn and wheat than on pollen, but the opposite was observed with heat stress (Westgate and Boyer, 1985; Prasad et al., 2011).

[9] Annex 1 : scheme of microsporogenesis and macrosporogenesis in Angiosperms

In 1983, Saini et al. reported that heat stress during reproductive development phase strongly impaired both pollen and embryo sac fertility in wheat. Similar results were shown in rice (Jagadish et al., 2007) and flax (*Linum usitatissimum* L.) (Cross et al., 2003) which revealed high sensitivity of both pollen and embryo sac developments to heat stress.

Although all physiological mechanisms are not yet known, such divergences could be the result of different periods of application of the stress, the different 'intensity' of drought and/or heat stress, but also the genetic background tested in each study. Just after fertilization, drought events are expected to lead to a reduction of seed size instead of their number (Prasad et al., 2008).

ii. Impact on the rooting system

All plants physiological processes depend on an adapted functioning of the plant engine, i.e., ability to deal with the differential of water pressure between water in the soil and the atmosphere. As nutrient and water are absorbed by roots, water deficit may cause highly deleterious damages to plant growth and life.

Extreme climatic scenarios such as a shortage of water resources for example, but also some soil features as compaction and type of soils for example, limit root growth (Lucas et al., 2000). In a soil, drought leads to a change of the soil physical properties by increasing strength (Martino and Shaykewich, 1994) and the formation of air gaps between roots and soil reducing the water uptake ability (Nye, 1992) as water movement are driven by water potential gradient (Lucas et al., 2000).

When facing to drought stress, different results were reported by the literature. On an open-field rape seed (*Brassica napus* L.) experiment under irrigated and drought stress but with water at depth, plants produced a reduced amount of roots, but found 20 cm deeper in drought than in irrigated conditions (Barraclough, 1989). In Nebraska, Weaver (1926) reported an open-field wheat experiment with irrigated and drought conditions with no water available in the subsoil. Author observed a strong reduction of deeper root growth but a great increased of lateral root spread under drought compared with irrigated treatment. Although species were different between these studies, the reason explaining the differential response of the root system facing to drought stress might be the results of the different soil water profile in each study. Prasad et al. (2008)

mentioned that under moderate water deficit conditions, root growth can be increased due to the increased partitioning of water soluble carbohydrates to roots.

The heat stress has also an impact on root. As other developmental process, root growth depends on temperature. In 1991, Sharratt reported that higher barley root temperature leaded to an increase in root length density. However, under heat stress conditions, growth, number, length of roots was reported to decrease, even during reproductive stage due to high competition for assimilates between the different organs (Porter and Gawith, 1999; Prasad et al., 2008).

iii. Drought and heat stress impact the photosynthesis process

Studies revealed the impact of drought and heat stress on plant photosynthesis. In order to better understand and explain damages reported, a brief reminder is presented on what is photosynthesis.

1. Reminder on the photosynthesis

Photosynthesis is the process leading to the production of organic carbon molecules (carbohydrates) from mineral carbon molecules (CO_2) using light energy. It takes place within the chloroplast (Figure IV-2). It is constituted by two phases: the light phase and the dark phase.

The light phase is located in the membranes of the thylakoids within the chloroplast and corresponds to the photochemical phase. Light energy is transformed into chemical energy through electron transport chains. It is constituted of two photosystems, photosystem I and photosystem II. Many pigments constitute a photosystem. Most of them, the antennas, absorb in the visible light, but only one of them is able to convert the light energy into chemical energy, the reactional center. When a pigment absorbs a photon, one of its electrons moves from a stable to an excited state. At that stage three things can happen accordingly to the bipartite model for photosystem presented by Butler (1978). The photon's energy can be (i) either dissipated as heat, this is referred as the non-photochemical quenching, or (ii) released

as fluorescence [10], or (iii) channeled through photosynthesis which is called the photochemical quenching (Maxwell and Johnson, 2000; Taiz and Zeiger, 2010d).

Through the photosynthesis channel of photon's energy dissipation, the pigment transmits its 'excitation', i.e., the energy, by resonance between antennas until reaching the reactional center which transmit its electron to other molecules of the photosystems in the sense of increasing the redox potential. Photosystem II is involved firstly and leads to an accumulation of protons within the thylakoid space coming from partly the hydrolyze of water molecules (H_2O). Dioxygen molecules are released. An ATP synthase uses the gradient of protons to synthetize ATP molecules released within the stroma. Electron transferred through the photosystem I is finally caught by the $NADP^+$ molecules, becoming NADPH (Figure IV-2) (Freeman, 2005; Taiz and Zeiger, 2010d).

The dark phase corresponds to the Calvin cycle, occurring in the stroma of the chloroplast. This is an enzyme-dependent and light-independent process. It aims to convert mineral carbon molecule into organic carbon molecule using chemical energy. The dark phase is shared into four steps. Within the Calvin cycle, first, a molecule of CO_2 is combined with a RuBP molecule (ribulose-biphosphate; five-carbon-sugar molecule) by the Rubisco enzyme (Ribulose Biphosphate Carboxylase Oxygenase) leading to an instable six-carbon-sugar molecule. The latter molecule is broken into two three-carbon-sugar molecules (3-phosphoglycerate). Then, with energy and redox potential brought respectively by ATP and NADPH (chemical energy), these two molecules are reduced into two G3P molecules (phosphoglyceraldehyde). Two molecules of G3P can lead to the formation of a six-carbon-sugar phosphate. Finally, the RuBP is regenerated from G3P using ATP (Figure IV-2) (Freeman, 2005; Taiz and Zeiger, 2010e).

[10] Fluorescence: re-emission of a photon light by an excited molecule usually excited by photon.

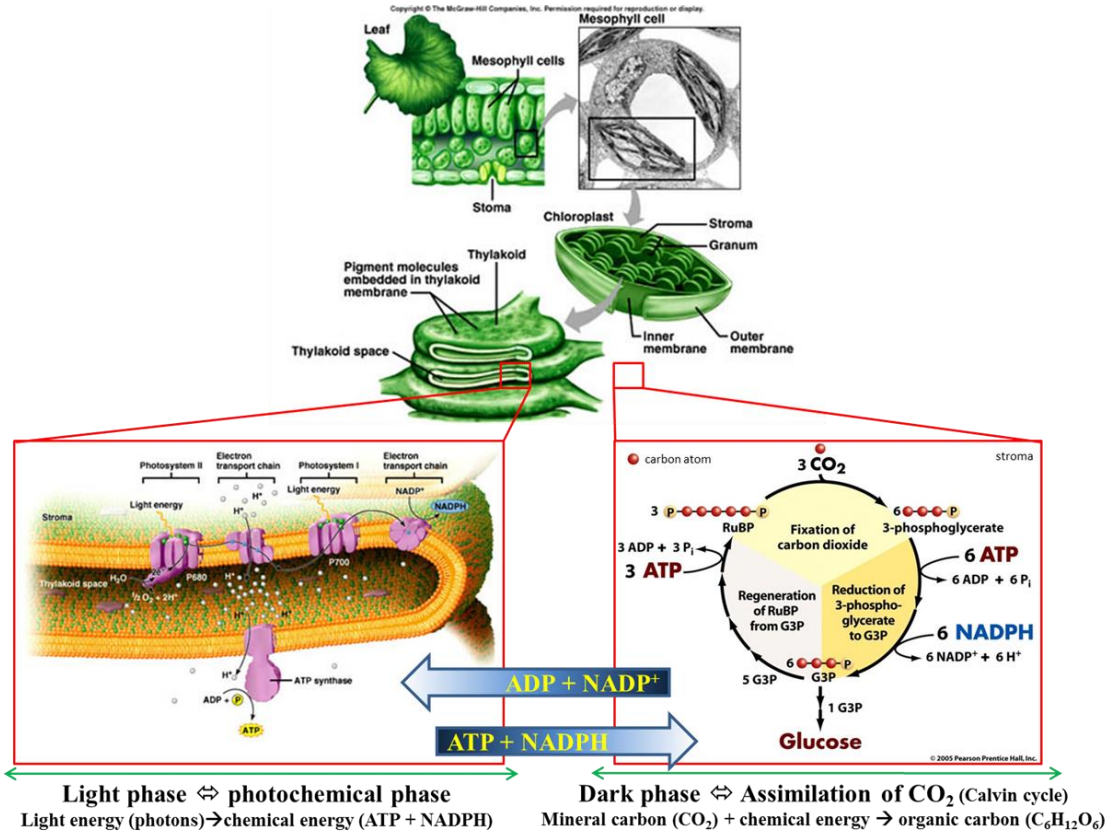

Figure III-2: Diagram of the photosynthesis process of C3 plants (Adapted from Freeman (2005) and http://www.citruscollege.edu/lc/archive/biology/Pages/Chapter06-Rabitoy.aspx); ATP: Adenosine Tri-Phosphate; ADP: Adenosine Di-Phosphate; P: Phosphate; $NADP^+$/NADPH: Nicotinamide Adenine Dinucleotide Phosphate; G3P: Phosphoglyceraldehyde; H^+: proton

2. Impact of drought and heat stress on photosynthesis

Prasad et al. (2008) reported two main consequences of drought on photosynthesis. Photosynthesis can be impacted through either stomatal closure leading to a decrease of CO_2 into the stomatic chamber or by disturbed metabolic activities.

In plants, photosynthesis and transpiration are tightly associated. All gases involved in both phenomena, i.e., CO_2, O_2, and H_2O, take the same stomatal pathway as exchange gate between atmosphere and plant environments following a decreasing gradient between stomatic plant tissues and atmosphere. One of the fastest responses of plant to water deficit stress is the stomata closure to limit water losses. Such closure hampers gases exchange between plants and atmosphere. As a consequence, with decreasing CO_2 into the stomatic chamber, photosynthesis is progressively reduced. It is a collateral victim of the plant preventing-water-loss strategy (Chaves et al., 2003). Under strong drought conditions, Lawlor and Cornic (2002) reported that the synthesis

of RuBP may be limited due to ATP deficiency, as a consequence of the limited CO_2 assimilation.

Heat stress impacts diversely photosynthesis. Heat impacts membrane fluidity, substrates solubility, and protein features (integrity and substrate affinity). By modifying affinity of Rubisco for its substrates, i.e., CO_2 (photosynthesis) and O_2 (photorespiration), heat stress may favor photorespiration at the cost of photosynthesis (Prasad et al., 2008). Indeed, O_2 solubility is less decreased than CO_2's at high temperature leading to increased competition between the two processes. Photorespiration has negative consequences on plants. It results into a net loss of organic matter created by photosynthesis (Sharkey, 1988), and leads to the production of active oxygen species, which can strongly damage membranes (Levitt, 1980; Liu and Huang, 2000). Crafts-Brandner and Salvucci (2000) reported a deactivation of the Rubisco under heat stress due to the inhibition of the Rubisco activase in cotton and tobacco. Havaux, (1992), on various species of the *Solanaceae* family, reported the resistance of photosystem II to drought but its sensitivity to heat leading to its inhibition. As previously mentioned, three different metabolic pathways enable plants to evacuate light energy accumulated (photosynthesis, fluorescence, and heat). Under heat stress, a deactivation of the photosynthesis resulted in higher chlorophyll fluorescence (Prasad et al., 2008). Chlorophyll fluorescence measurement can be a good indicator of heat stress for plants. Ristic et al. (2007) demonstrated its usefulness on wheat to quantify heat stress. At the plant level, Zhao et al. (2007) reported that post-anthesis heat stress significantly reduced the concentration of soluble proteins and the chlorophyll content (SPAD estimate) of flag leaves of two wheat cultivars compared to optimum treatment.

We presented the different impacts of drought and heat stress on wheat, from the morphological, anatomical, and chemical damages to their agronomic consequences. Henceforth, the plant responses to these unfavorable conditions will be detailed.

IV. Adaptive responses of cereals to water deficit and heat stresses

a. Concepts of tolerance and resistance to drought and heat stress

Several studies referred to the terms of tolerance, resistance, avoidance, escape, *etc*. In 1980, Levitt proposed that when a plant is experiencing stress, all mechanisms enabling its survival should be considered as 'resistance'. We proposed to review these different terms first.

Escape usually refers to the ability of plant to flower and performed the majority of the whole crop cycle before stress arrival. According to Levitt (1980) definition, escape cannot be considered as a "resistance mechanism" as plant does not really experience stress. However, it constituted a valuable plant strategy widely used worldwide under frequent- and consistent-stress-period areas. However, if favorable conditions occur, plants with a reduced short cycle are penalized.

Within resistance mechanisms, Gaspar et al. (2002) suggested two main physiological responses: tolerance and avoidance. A tolerant plant maintains a high metabolic activity under mild stress and reduced it under severe stress. Stress avoidance responses takes place through a reduction of the metabolic activity under stress (Figure IV-1). On the same physiological responses, Levitt (1980)'s definitions of avoidance differed from Gaspar's one. Indeed, from Levitt (1980)'s point of view, avoidance corresponds to the ability of a plant to reduce its exposure to low water potential conditions through modification of its environments (e.g., high transpiration rate under heat stress leading to a cooler direct environment of plant), or through the modification of its crop cycle (e.g., escape). It seems that there is no worldwide recognized definition of these terms by the scientific community. In the whole manuscript, the term tolerance is used in reference to a greater grain yield performance under heat and/or drought stress conditions except otherwise mentioned.

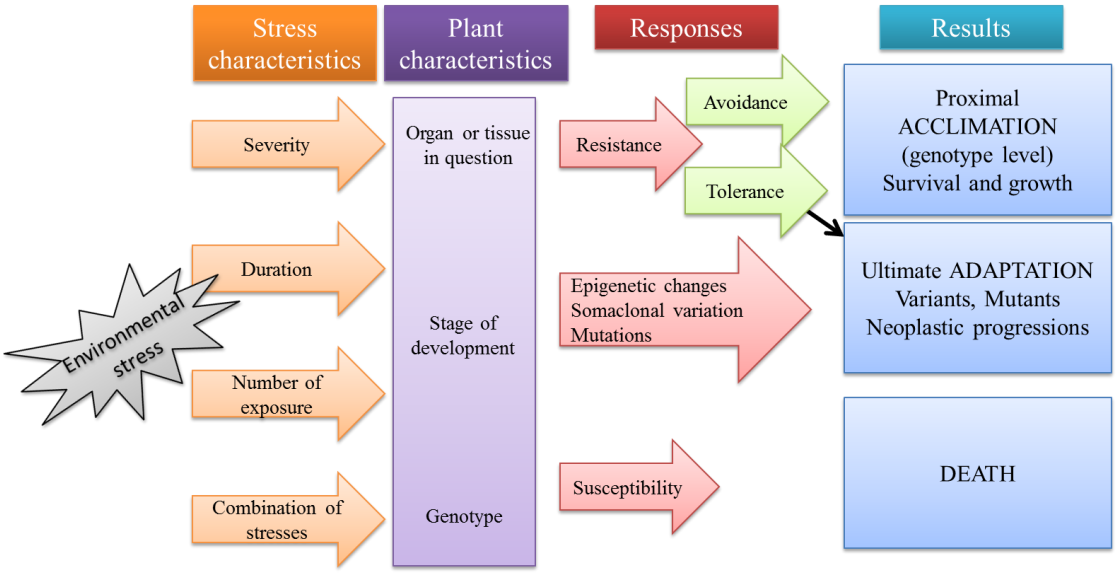

Figure IV-1: Plant responses to environmental stress in correspondence with stress and plant characteristics (Adapted from Gaspar et al., 2002); The neoplastic progression refers to the development of tumors

b. Conceptual models for traits associated with adaptation to drought and heat stress prone environments

In 1977, Passioura provided a theoretical framework that enabled trait-based breeding and genetic dissection of drought-adaptive mechanisms (Reynolds and Trethowan, 2007; Reynolds and Tuberosa, 2008). The yield of cereals is dissected into three components (Equation IV-1), the water uptake (WU), the water use efficiency (WUE), and the harvest index (HI). Each component constitutes a pillar where traits can be classified. Each one of these traits is associated with the main yield drivers and can be exploited by breeders to improve tolerance of cereals to water deficit conditions (Figure IV-2 (A)).

Equation IV-1: Dissection of the cereals grain yield under drought-prone environments as proposed by Passioura (1977)

$$YLD = WU \times WUE \times HI$$

A similar model was developed for wheat under non-limiting water conditions. It includes yield decomposition under heat stress conditions. The grain yield (YLD) is dissected into light interception (LI), radiation use efficiency (RUE), and harvest index (HI) (Figure IV-2 (B); Equation IV-2) (Reynolds et al., 2007b).

Equation IV-2: Dissection of the cereals grain yield under heat stress conditions proposed by Reynolds et al. (2007b)

$$YLD = LI \times RUE \times HI$$

In both equations (Equations IV-1 and IV-2), the first term refers to the plant ability to capture a given element (water or light), the second one refers to the efficiency of the plant to convert the absorbed element into biomass, and finally, the harvest index expresses the plant ability to convert the plant biomass into grain yield.

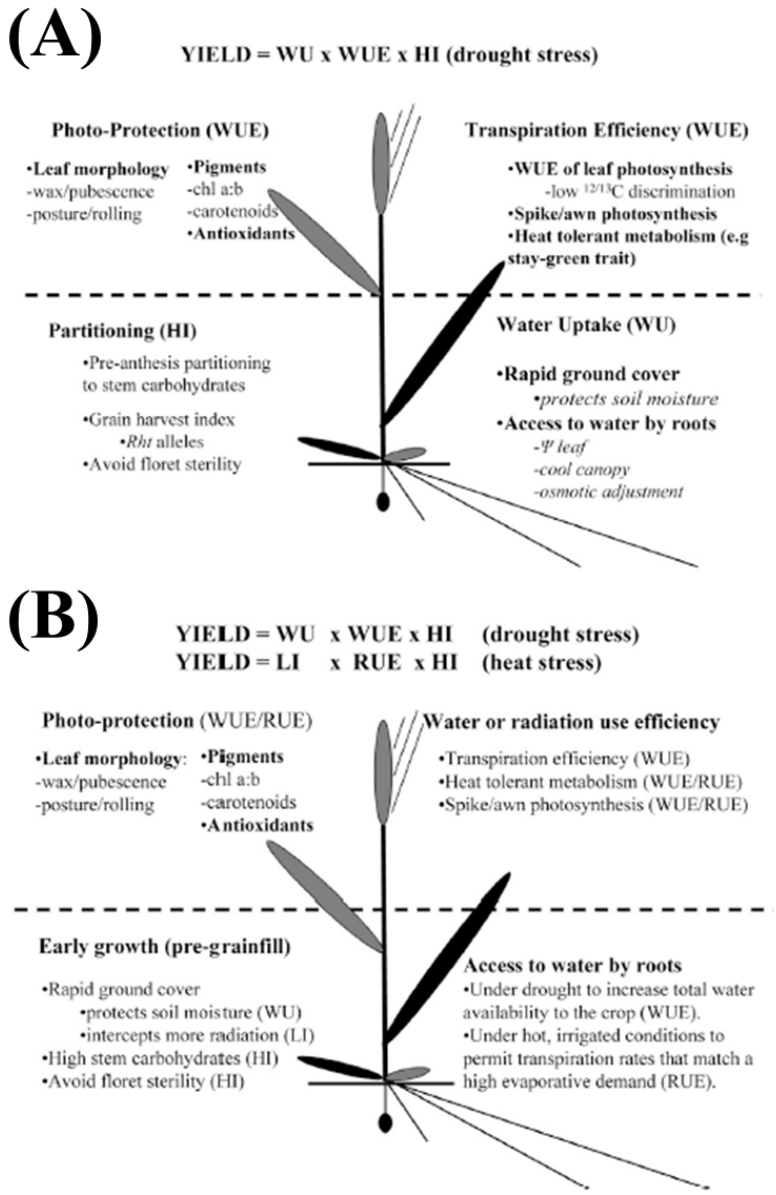

Figure IV-2: Conceptual models representing: (A) traits associated with adaptation to drought-prone environments. They are gathered according to the main grain yield determinants under drought (yield = water uptake [WU] × water use efficiency [WUE] × harvest index [HI] according to Passioura (1977)), (B) traits associated with adaptation to water deficit stressed and/or high temperature with irrigation environments (adaption from Reynolds and Trethowan (2007)). These traits are grouped by main grain yield determinants under non-drought prone environment (yield = light interception [LI] × radiation use efficiency [RUE] × harvest index [HI]) (Source: Reynolds et al., 2007b)

c. Traits to improve tolerance to drought and heat stress

To achieve its yield, a plant involves numerous physiological processes along the whole crop cycle. Most of them are sensitive to environmental stress. These physiological processes can be evidenced by traits (Figure IV-2). Determining which of them are of interest in a given environmental scenario is important (e.g., deep root system in drought environment with water at depth). Indeed, it is of first importance to be conscious that any of these traits may have positive, negative, or no effects

depending on the environmental conditions (Tardieu et al., 2008). The most frequent and important traits described in the literature are described below.

i. Water uptake, WU

Many different drought stress environment exists. However, two classes may be established. Drought stress environment where water is available at depth (Northern Mexico) and drought stress where there is no available water at depth (Southern Australia). In the former case, i.e., drought prone-environment resulting in drying top-soil profile but with available water at depth, proliferation of roots downwards is important; it allows plants having access to deeper available water. In the latter case, i.e., rainfed drought prone-environment, where water is not available in the subsoil, proliferation of roots in the topsoil should be supported as most of water comes from rains. It enables a quick capture of most of the resources (Lucas et al., 2000). Ability to extract more water from the soil, i.e., decreasing the permanent wilting point of the plant is also of interest in such an environment.

1. Access to water by roots: the osmotic adjustment

The osmotic adjustment is one of the most important components of drought tolerance. It corresponds to the maintenance of the cell osmotic potential through the accumulation of solutes to counter balance the declining water potentials of the cellular environment (Hellebusi, 1976). The larger decreased in cell water potential enables the water diffusion within the cell, which contributes to the turgor pressure to be maintained, for both roots and shoot. Turgor dependent processes such as stomatal activity, are able to work under lower water potential (Blum et al., 1999; Francia et al., 2005). Blum et al. (1999) showed a positive correlation between osmotic adjustment and biomass and yield under pre-flowering drought stress. Authors mentioned that it also avoids premature senescence and as a consequence enables a greater translocation of assimilates during grain filling. Similar results were reported by Ludlow and Muchow (1990). Munns and Weir (1981) reported that sugar accounted for 70 to 100 % of the osmotic adjustment in the leaves elongation and expansion zones. Osmotic adjustment within roots and root tips in maize was reported to maintain a well-watered root extension rate under severe water stress, allowing a deeper root penetration to access to more water (Sharp et al., 2004).

2. Access to water by roots: the canopy temperature proxy

Under drought condition, the trait of interest is root depth. As previously mentioned, this trait is of interest under drought-prone environment with water available at depth. This relationship was established in that conditions by Reynolds et al. (2007a) where genotypes with increased rooting depth had a cooler canopy. Under heat stress with non-limiting water, the water uptake capacity of the root system is the relevant trait which enables plant to prevent heat damages to its canopy by transpiration.

In these conditions canopy temperature is a proxy of the root-system desired feature. The potential of infrared thermometry to screen for drought tolerant genotypes was first established by Blum et al. (1982). Since the end of the 90's, advances in the infrared thermography technology enable a cost-effective screening of plants (Amani et al., 1996). Under drought or heat stress, authors reported a better behavior of genotypes with a cooler canopy temperature (Olivares-Villegas et al., 2007; Pinto et al., 2010). Indeed, cooler canopy are related with increased evaporative cooling and transpiration rates in wheat crops under drought (Reynolds et al., 2007a) and heat stress (Reynolds et al., 1998) conditions.

Canopy temperature is one of the most important physiological traits scored by the CIMMYT. An early generation canopy temperature screening in CIMMYT breeding programs is done (Reynolds et al., 2009). However the methodology followed, i.e., hand-held, suffers from its high sensitivity to the environment as reported by Olivares-Villegas et al. (2007), Cossani et al. (2012) and Pietragalla (2012). The use of unmanned aerial vehicle, UAVs, should be of great help for physiologist and breeders to solve this issue.

ii. Water and radiation use efficiency, WUE/RUE

1. Carbon isotope discrimination (CID)

In environment where soil water resource is limited as in Southern Australia, the improvement of the water use efficiency is of great interest. It enables the increase of the dry matter produced by unit of water available. The carbon isotope discrimination is the proxy of the transpiration and photosynthesis efficiency (Richards et al., 2001).

Around 1 % of the carbon in the atmospheric CO_2 exists under the isotope form ^{13}C, heavier than the dominant form, ^{12}C. Plants affinity for ^{12}C is higher resulting in

relatively less ^{13}C incorporated into plant tissues (Condon et al., 1987). Principle of the measurement is based on the relative $^{13}C/^{12}C$ ratio in plant tissues and in the air that plants used for photosynthesis. Overall stomatal aperture leads to an increase of the gaze exchanges, to favor the ^{12}C but leads to an increase of water loss (Richards et al., 2001).

Under drought conditions, as previously mentioned, plants close their stomata. By closing their stomata, gaze exchanges and water loss are limited. The internal ^{12}C concentration falls. Plant with a low ability to discriminate against ^{13}C tends to accumulate more ^{13}C in its tissue. This reduced discrimination, i.e., low CID, enables plant to increase its transpiration efficiency and as a consequence its water use efficiency (Araus et al., 2003; Cossani et al., 2012).

This proxy combined great advantages. It is easier and faster to score than the transpiration efficiency, it has a high heritability, and it can be scored on any kind of plant tissues (Richards et al., 2001). It constitutes almost a perfect breeding tool for environment where WUE is of interest. Until today, it has only been successively used once in a commercial breeding program in Australia to improve the variety Australian elite variety Hartog which was released in 2001 (Richards et al., 2001). Indeed, it remains a costly trait to score and improved WUE is not desired in all drought-prone environments worldwide. Moreover, Blum (2009) cautioned on not targeting exclusively variety with higher water use efficiency as it will likely lead to a reduced their yield.

2. Leaf morphology

In this part, leaf morphology refers to change in leaf characteristics under drought and heat stress: leaf rolling, glaucousness, pubescence, erect posture, *etc*. Glaucousness corresponds to the production of epicuticular waxes on leaf surfaces. The accumulation of wax is dynamic and starts from seedling emergence to reach a peak around anthesis (Richards et al., 1986; Bennett et al., 2011). Glaucousness was reported to increase radiation reflectance and reduce leaf temperatures, water loss and epidermal conductance which as a consequence was leading to a reduction of the rates of transpiration and photosynthesis (Richards et al., 1986; Ludlow and Muchow, 1990; Francia et al., 2005). The importance and interest of glaucousness differ in between the different studies.

Under drought and/or heat stress conditions, where plants are submitted to strong constraints, constant radiations received at the leaf surfaces usually lead to further damages. All these leaf morphology traits can help in reducing the amount of radiation absorbed at the leaf surface (Reynolds et al., 2006). The same authors also reported that erected leaves allow a better penetration of radiations within plants canopy. As a consequence, it helps in maintaining plant photosynthetic capacity without overloading individual leaves.

3. Stay green

Senescence is a genetically programmed but environmentally influenced physiological process leading to the destruction of the chlorophyll and the remobilization of nutrients to younger or reproductive parts of plants (Vijayalakshmi et al., 2010). A decreased rate of senescence in plants results into their stay-green ability. The stay-green refers to the delay of the plant senescence compared to a standard reference.

It has been considered as an important ability for tolerance to drought (Borrell et al., 2000; Francia et al., 2005) and heat stress (Fokar et al., 1998). Górny and Garczyński (2002) reported a positive correlation between the water use efficiency and both, the duration of the flag leaf stay-green and the harvest index under drought conditions. Under drought conditions, studies mentioned that genotypes able to maintain flag-leaf photosynthesis resulted in higher yield and biomass produced (Borrell et al., 2000; Farooq et al., 2014). Under heat conditions, loss of chlorophyll is linked with a reduced assimilation of carbon within grains. Therefore, stay-green genotypes may be able to maintain grain filling even under high temperature stress conditions (Farooq et al., 2011). Studying sorghum genotypes under drought stress conditions, Harris et al. (2007) highlighted the importance of the rate of senescence for the stay-green.

In 2012, Lopes and Reynolds showed that stay-green in spring wheat can be determined by high throughput phenotyping spectral reflectance measurements (Normalized Difference Vegetation Index) independently from phenology. Authors found significant correlation between stay-green and grain yield under drought and heat stress conditions.

iii. Harvest index, HI

1. Water soluble stem carbohydrate

Also known as total non-structural-sugar, water soluble carbohydrates (WSC) corresponds to the basic molecules for stem storage. Most plants store starch or sucrose as carbohydrate reserves. However, in cereals, fructans, linear and branched polymers of fructose, the end product of photosynthesis, are also stored at the bases of leaves (Vijn and Smeekens, 1999). In Artichoke, Darwen and John (1989) reported that fructans are synthetized and stored in the vacuole of cells. In grasses, fructans and starch represent a significant part of stored carbohydrate in the grains under drought and heat stress conditions, particularly for post-anthesis drought (Blum et al., 1999; Goggin and Setter, 2004; Saint Pierre et al., 2010; Farooq et al., 2011). WSC accumulates in the stem during pre-anthesis growth and is highly dependent of growing conditions at that development phase (Wardlaw and Willenbrink, 1994, 2000).

Several authors reported the usefulness of WSC especially under stress conditions (Blum, 1998; Tahir and Nakata, 2005; Dreccer et al., 2009; McIntyre et al., 2012). Grain filling in wheat depends on two carbon sources: (i) the current assimilation and (ii) the remobilization of stored WSC (Pheloung and Siddique, 1991). Under irrigated conditions, stem water carbohydrate can contribute to around 40 % of the final grain yield dry matter. When grain filling photosynthesis is inhibited under drought or heat stress conditions, reserve remobilization can represent until 80 % of total grain yield dry matter (Borrell, 1993; Zhang et al., 2013).

Enzymes in charge of WSC remobilization to the grain are sensitive to temperature. Higher temperature accelerates metabolic processes and so, results in a reduction of the duration of the process of biosynthesis and grain starch deposition leading to a reduced dry matter (Farooq et al., 2011). The remobilization process depends on the sink size (size of the grains), environment and genetic background (Blum, 1998).

2. Abscissic acid

The abscissic acid, or ABA, is the universal hormone of plant stress. It is a phytohormone critical for growth and development and it plays an important role in integrating various stress signals and controlling downstream stress responses (Tuteja, 2007). It is synthetized in the root tips as a response to various external stresses.

Under drought stress conditions, it is rapidly accumulated in the leaves to optimize the balance between survival and productivity. It results in stomatal closure, reduction of leaf expansion, increased water use efficiency and decreased photosynthetic rate (Ludlow and Muchow, 1990; Gupta, 2005; Liu et al., 2005; Farooq et al., 2014). In the case of continuous drought stress period, ABA can be seen as a help in plant adaptation to enable plant to complete its cycle. However, under short-time stress period during the crop cycle, precautionary measures settled by ABA can have very deleterious effect because it may handicap plant recovery. For example, some authors reported a negative effect of ABA on pollen viability (Ji et al., 2011) which lead Loss and Siddique (1994) to conclude that high abscissic lines can result into a negative impact on yield.

d. Bread wheat breeding: improvement of tolerance to drought and heat stress

Conceptual models presented in Figure V-2 are parts of the CIMMYT strategy to improve wheat tolerance to drought and heat stress. They consist in the accumulation of physiological traits in selected progenies and to the distribution of advanced lines worldwide. It consists first of all in the careful choice of the parents combining interesting physiological traits to tolerate drought and heat stress in a given target area. Secondly, crosses are reasoned to encompass as many of the targeted features as possible for the considered regions. Thirdly, F2 plants are screened for disease resistance, height, and phenology. Finally, a screening step is conducted on early generation bulks for canopy temperature in water-stressed environment (Reynolds et al., 2009). It was showed that compared to conventional crosses, physiological crosses resulted in the release of consistently more advanced lines above the controls under drought conditions (Figure IV-3).

A high water use efficiency (WUE) wheat genotypes has been the target of long-term breeding efforts (Rizza et al., 2012). A genetic variability exists in durum wheat (Araus et al., 2003) but also in bread wheat (Rebetzke et al., 2002). Rizza et al. (2012) reported the release of the two first varieties of bread wheat in Australia bred for high transpiration efficiency, i.e., high WUE, based on the selection of low CID genotypes by Rebetzke et al. (2002). Under drought conditions, an increased biomass (+2.7 %), grain yield (+5.8 %), harvest index (+3.3 %), and grain size (+4.8 %) were reported between low-CID and high-CID variety under drought conditions.

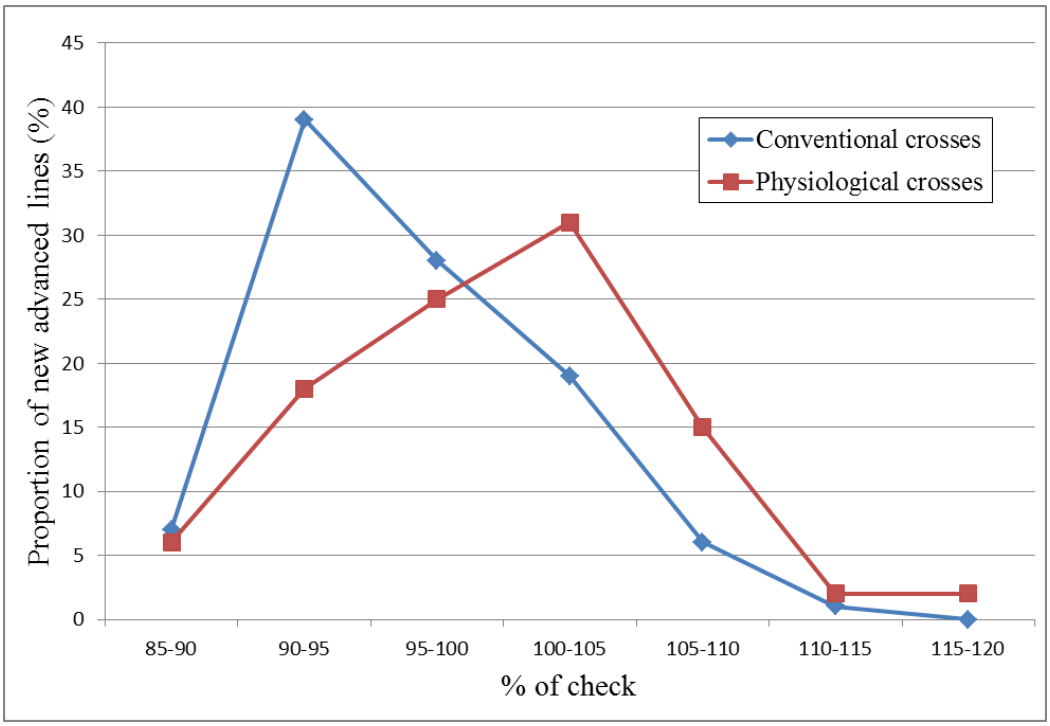

Figure IV-3: Percentage of new advanced lines deriving from both conventional and physiological trait based CIMMYT breeding per yield categories expressed in percent of the drought adapted check varieties used between 2006 and 2008. CIMMYT (Source: Reynolds et al., 2009)

An exhaustive review of the efforts to improve wheat yield under drought and heat stress condition using native trait approaches were presented. Efforts on genetically modified (GM) traits to better tolerate abiotic stress are also on going today. Concerning drought tolerant GM, until today, the Genuity® DroughtGard™ corn hybrids of Monsanto had been released (2013) (Monsanto, 2012). In Indonesia, a sugarcane variety was also released. However, efforts must continue on wheat. For now, no GM drought tolerant variety was released in Wheat.

V. Highlighting and assessing the huge available natural genetic diversity of bread wheat for drought and heat stress tolerance

a. Genetic variability for yield driving traits under drought and heat stress conditions

Genetic variability is at the base of the breeding. Without variability, breeding is impossible. Many studies reported wide genetic variability in wheat and other species for several traits related to improvement of drought and heat stress tolerance. Some examples are detailed below.

Under water limited conditions, root architecture appears to represent a key target trait to increase wheat productivity (Motzo et al., 1992; Manschadi et al., 2006,

2008; Kashiwagi et al., 2006; Narayanan et al., 2014). By comparing drought sensitive and tolerant wheat and barley genotypes, Manschadi et al. (2006) highlighted important genotypic variation in root features. However, as reported previously, the type of drought stress has its importance in the choice of the most relevant architecture. Narayanan et al. (2014) reported a structuration of the spring wheat germplasm studied for root depth by the origin of the material.

Genetic variability of bread wheat cultivars was also observed for photosynthesis related traits under irrigated and heat stress conditions (Reynolds et al., 2000). Authors revealed clear differences among cultivars on the net photosynthetic rate which was associated with genotypes' performance. Such differences were consistent across time of measurement, phenological stage and environment. Stay-green was reported as highly variable and was associated (Vijayalakshmi et al., 2010) to wheat performance under heat and drought-heat conditions (Lopes and Reynolds, 2012). Moreover, highly significant genotype-by-environment interaction was also highlighted by authors.

Canopy temperature had been reported many times to display large genetic variability under many environments such as irrigated, drought, heat-irrigated, heat-drought, *etc*. (Amani et al., 1996; Ayeneh et al., 2002; González-Dugo et al., 2005; Balota et al., 2007; Olivares-Villegas et al., 2007; Pinto et al., 2010).

Bread wheat stem water soluble carbohydrate revealed an important genetic variability, ranging from 10 to 50 % as reported by Cossani et al. (2012) under irrigated, drought, and heat-irrigated conditions (Reynolds et al., 2007b; Rebetzke et al., 2008b; Saint Pierre et al., 2010). Genetic variability was also reported on other traits such as seedling vigor under heat condition (Richards and Lukacs, 2002), wax and ear emergence (Bennett et al., 2011). However, important genetic elements (genes and translocation) have been shown to influence this variability and to be highly involved in plant response to drought and heat stress.

b. Genetic elements influencing the genetic variability: *Ppd*, *Rht*, 1BL-1RS

The precocity is probably the most important of the adaptive traits. At the world scale, earliness is the most used adaptation mechanisms to drought. According to Tardieu (2013), the maximum potential grain yield of a crop is correlated with the duration of the crop cycle; long-cycle varieties for none to low drought environment such as England, and short-cycle varieties for stress areas. According to Garner and

Allard (1923), precocity is split into three components: (i) photoperiod sensitivity (*Ppd* genes; Ppd-1 on Chr. Group 2), (ii) need of vernalization (*Vrn* genes; Vrn-1 on Chr. Group 5), and (iii) the intrinsic precocity. Variation in precocity is more than likely involved in the variation of most of the agronomic, physiological, biochemical, *etc*. traits. Variable precocity of individuals within a population make difficult the use of such population for drought/heat related traits and scientist look Indeed, the development of the SeriM82 x Babax population with a strongly reduced range of phenology aimed to be free from the effect of precocity, but also to propose a reduced range of height (see: Olivares-Villegas et al. 2007; Pinto et al. 2010; Lopes et al. 2012).

The introduction of dwarfing genes (*Rht* genes: mainly *Rht-B1b* and *Rht-D1b and in some instance Rht8;*) was at the basis of the development of dwarf and semi-dwarf varieties, with a decreased internode length Worland et al. 1998, Wojciechowski et al., 2009) or not. Literature concerning the impact of such genes on wheat root architecture features is not consistent. Wojciechowski et al. (2009), pointing out the different genetic background to explain these inconsistent results, developed Near Isogenic Lines (NIL) for several *Rht* genes. Non-significant differences in root architecture were found between semi-dwarf and tall NILs, but differences were significant between dwarf and tall NILs on the root length. However, global root architecture was not modified, i.e., no significant differences for root diameter and lateral/total root ratio (Wojciechowski et al., 2009).

The 1B /1R translocation is made of the 1B wheat chromosome substitution by the rye chromosome 1R). This introgression is the result of the works of two German scientists at the beginning of the XXe. This alien translocation is nowadays present in many top yielding varieties worldwide, among others several CIMMYT elite varieties (Worland and Snape, 2001). Originally introduced because carrying many resistance genes (Lr26 for leaf rust resistance, Yr9 for yellow rust resistance, *etc*.), this rye chromosome fragment strongly reduced the bread making quality. However, this translocation was reported to enhance grain yield in optimum and drought-stressed environments (Villareal et al., 1998), but also yield components and biomass (Worland and Snape, 2001).

c. Study of the GEI, or how better benefit can be taken from the understanding of how the genetic variability interacts with the environment

The main aim of a plant breeder is to develop varieties with better and stable phenotypes under a considered range of environmental conditions. The ability of an organism to modify its physiology and morphology when facing changes in environmental condition is known as phenotypic plasticity (Schlichting, 1986; El-Soda et al., 2014). In breeding, two types of genotypes may be distinguished: widely and specifically adapted genotypes. The first type of genotypes performs well under a wide range of conditions, whereas the latter one displays higher skills in a restricted set of environments (Malosetti et al., 2013). The genetic variation for plasticity among genotypes is usually known as genotype by environment interaction (GEI) (Via and Lande, 1985). In 1972, Bowman defined GEI as "a change in the relative performance of a character of two or more genotypes measured in two or more environments". Changes between environments may be of two types: (i) genotypes rank order, but also (ii) absolute magnitude of the genetic, environmental and phenotypic variances. Environments may differ in type, intensity and quality of inputs and stimuli to which plant will react (Malosetti et al., 2013). Biologically, plant abilities to efficiently perform within a range of environments are driven by specific group of genes within its genome. More specifically, the level of expression of the genes controlling a given trait differ among environments (Basford and Cooper, 1998).

The GEI may be studied in terms of both, the relative differences between genotypic means, or the heterogeneity of genetic variance and covariance or correlation (Sial et al., 2000; Malosetti et al., 2013).

i. Importance of the GEI

GEI is a common phenomenon in multi-environment trials (MET) (van Eeuwijk, 1995; Yan and Hunt, 1998; Zheng et al., 2010). Understanding the environmental and genotypic causes of GEI is of first importance in plant breeding (Jackson et al., 1996; Yan and Hunt, 1998, 2001). Indeed, analyses of this phenomenon provide very helpful knowledge for genetic improvement of stable crop productivity, allowing identification of superior and stable alleles and genotypes within a range of environment (Zhang et al., 2010a; Campbell et al., 2012; El-Soda et al., 2014). Study of GEI also helps in the selection of parents, the design of ideotypes (Yan and Hunt, 2001) and selection criteria

(Campbell et al., 2012). Understand GEI enable identification of (i) traits contributing to better cultivar performance and (ii) the environments in which evaluation of cultivars is easier (Yan and Hunt, 2001).

ii. Presentation of the GEI

Studies relating GEI analysis were performed in many species as in wheat (Brancourt-Hulmel et al., 2000; Yan and Hunt, 2001; Campbell et al., 2004; Laperche et al., 2007; Zhang et al., 2010a), maize (van Eeuwijk et al., 1995; Vargas et al., 2006; Malosetti et al., 2007), chickpea (ALwawi et al., 2010), cotton (Campbell et al., 2012), sorghum (Chapman et al., 2000a; b), barley (Voltas et al., 1999), potato (Baril et al., 1995) or sunflower (Foucteau et al., 2001). Moreover, even if many different traits are addressed for GEI, the most popular is undoubtedly the yield, whatever the species condidered (e.g., Voltas et al. (1999), Brancourt-Hulmel and Lecomte (2003), and Campbell et al. (2012). The part of the total genetic variation varies between studies for a same species and trait. In wheat, Cormier et al. (2013) reported that 41 % of the total genetic variance of grain yield was GEI, Mohammadi and Amri (2009) 92 %, and Brancourt-Hulmel and Lecomte (2003) 81 %.

In the first situation, for a given genotype, the 'norm of reaction' refers to the phenotypic performance depending on the environment (Griffiths et al., 1996). When considering performances of two genotypes grown into two different environments, two cases may occur: in one hand, reactions norms of both genotypes are parallels, there is additivity but no GEI, or, in the other hand, reaction norms are not parallels, and GEI is occurring. Three types are then distinguished: (b) divergence, (c) convergence, and the most problematic for a breeder, (d) cross-over, where a significant change in rank order happen from an environment to another (Figure VI-1) (Blum, 1983; Baker, 1988; Matus et al., 1997; Sial et al., 2000; Malosetti et al., 2013).

Understanding the basis of the phenotypic response across changing environments is very complex. To this end, dedicated analytical tools were created to help the breeding community to model GEI. There are many statistical procedures to analyze GEI and they were reviewed several times (van Eeuwijk, 1995; Cooper and Hammer, 1996; Kang and Gauch, 1996; Malosetti et al., 2013). There are also many ways of classifying them. The later one, proposed by Malosetti *et al.* (2013), was chosen. GEI can be analyzed as mentioned before by modeling the means or modeling the heterogeneity of the genetic variance and covariance or correlation.

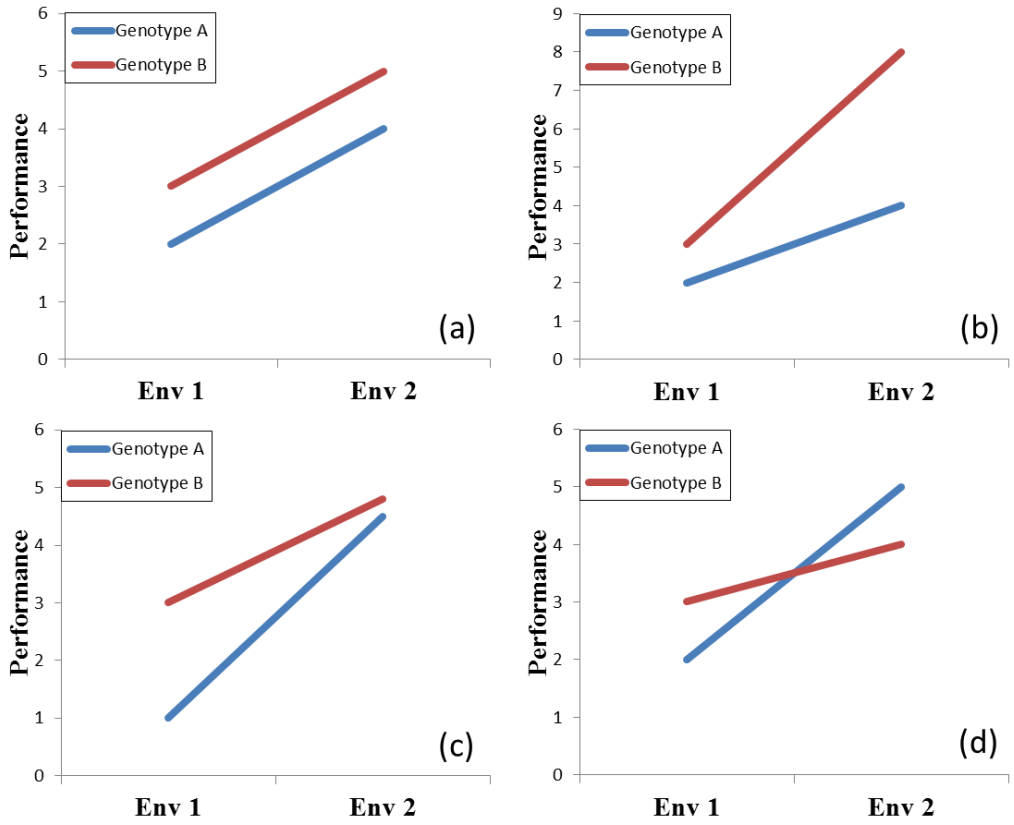

Figure V-1: Descriptive diagrams of the different cases of genotype-by-environment interaction between two genotypes (A and B) in terms of mean performance across environments (Env 1 and Env 2); (a) additive model, (b) divergence, (c) convergence, and (d) cross-over interaction (Adapted from Malosetti et al., 2013)

iii. Analytical tools to study the GEI

Based on either managed stress trial or MET data, evolution of the way to model the means for GEI analyzes followed a need of clarity and preciseness. A distinction can be done in the way of formulating GEI. Indeed, the first generation of models developed a linear formulation of GEI as in the additive model, i.e., ANOVA, which preceded the joint regression. The second generation of models led to a multiplicative formulation of GEI. This allowed interpretation of the interaction as a differential sensitivity to environmental variables. The additive main effect and multiplicative interaction models, the factorial regression models and the reduced rank factorial regression models belonged to that generation (Crossa, 1990; van Eeuwijk, 1995; Vargas et al., 1999; Malosetti et al., 2013). All these models are fixed models which allow interpretations by comparing variance of genotypic and environmental effects against the variance of error.

a. Simple additive models

The statistical formulation of the decomposition of the phenotype P as P=G+E (Falconer and Mackay, 1996; Lynch and Walsh, 1998), with G, the genotype and E, the environment, allowed estimating that P is determined by both genotypic and environmental effects. However, predicted and observed means for performance in a

given environment were not usually correlated. Malosetti *et al.* (2013) proposed that such discrepancy may come from either specific effect related to the particular combination of G and E and/or from experimental error. So, to identify the putative cause, the GEI term was included within the model. Such models allowed giving an estimate of GEI, but not its understanding.

To better explain GEI, Finlay and Wilkinson (1963) proposed analyzing GEI as a regression line on the environment fertility (van Eeuwijk et al., 1995; Malosetti et al., 2013), so called joint regression. Indeed, without available environmental information within the trial network, environments were classified according to the mean performance of the genotypes in each one. As a consequence, the best environment displayed the highest average genotypic performance. This kind of model is characterized by four main features: GEI is explained in terms of differential sensitivities from an environment to another, estimated parameters may permit some biological interpretations and predictions of genotypic performance can be done for untested environments whose fertility ranged within the range of environments tested. However, an important part of GEI may remain unexplained as environmental characterization is unidimensional.

Partial least square regression was used by Aastveit and Martens (1986) to understand differences in barley straw length under different conditions, through a direct and parsimonious modeling of GEI. Explicit environmental data were used to understand differences. In 1998, Vargas *et al.* performed the same type of analyses on two CIMMYT bread wheat datasets to interpret GEI.

b. Multiplicative models

As genotype responses are very complex, multidimensional model approaches were developed for more flexibility and efficiency than univariate model approaches (Gauch and Zobel, 1988; Nachit et al., 1992; van Oosterom et al., 1993) with the additive main effect and multiplicative interaction models. Two models are very popular in that category: AMMI, additive main effect and multiplicative interaction model (Gollob, 1968; Mandel, 1969; Gabriel, 1978; Gauch, 1988; Zobel et al., 1988) and GGE, genotype main effect and GEI, models (Malosetti et al., 2013). These types of models combine two powerful features, a multidimensional way of decomposing GEI and a graphical output through the use of biplots as a help for interpretation of GEI (Gabriel, 1971). Such graphics allowed the exploration of the relationship between genotypes and/or environments (Gabriel, 1978; Yan et al., 2000; Yang et al., 2009). AMMI models

are a subset of bilinear models, also called biadditive models (Denis, 1991 and Denis et Gower, 1992, 1994, cited by van Eeuwijk, 1995) and use K multiplicative terms based on the genotypic sensitivity, so called genotypic score, with a completely hypothetic characterization of the environment, so called environmental score. The simultaneous assessment of genotype and environment greatly facilitate interpretation and identification of specific interaction (Zobel et al., 1988; Gauch, 1992; Mohammadi and Amri, 2009; Malosetti et al., 2013). AMMI models dissect GEI in two parts, additive from ANOVA and multiplicative from a PCA (Gauch, 1988) which make them more efficient for complex genotypic patterns under different environments (Voltas et al., 1999). The first example of AMMI was presented by Zobel et al. (1988) who dissected soybean MET GEI and showed that maturity of genotypes and day length of the locations were associated. GGE models were developed because of the interest of breeders to get G and GEI together. Among all previously models described, any of them considered explicit environmental information which strongly limits the biological interpretation of results, although they can provide a good estimation and explanation of GEI.

The factorial regression model approaches were then developed (Denis 1988; van Eeuwijk *et al.*, 1996). With this type of model, explicit environmental data, such as temperature, precipitations *etc*., can be included directly in the model as explanatory variables and allow splitting GEI when they are significant (Zheng et al., 2010). With such models, GEI can be described as differential sensitivity to environmental components. As a consequence, GEI interpretation is brought into a more biological context, combining both statistical criteria for model selection with physiological knowledge on the trait involved (Malosetti et al., 2013). For example, the slopes from a factorial regression including significant environmental covariate of drought represent the sensitivities of genotypes to drought. Are retained only covariates explaining the largest amount of GEI without consuming too many degrees of freedom (Brancourt-Hulmel et al., 1997). Factorial regression remains easy with few covariates, allows testing effects of each ones, but leads to generation of too many parameters with more covariates introduced, impacting the parsimonious principle and makes GEI harder to interpret (Leflon et al., 2005; Zheng et al., 2010).

Reduced rank regressions belong to the bilinear regression model. This category of model generalized both AMMI and factorial regression models on environmental variables (Denis, 1991). Indeed, environmental covariables remain hypothetical and

maximize differences in genotypic sensitivity as in AMMI models but must be linear combinations of explicit environmental variables (Davies and Tso, 1982; van Eeuwijk, 1992, 1995).

Some studies compared different methods to analyze GEI, as Baril *et al.* (1995) on potato who dissect GEI using both factorial regression and biadditive (i.e., AMMI) model or Vargas et al. (1999) who compared partial least square regression and factorial regression on wheat, reaching similar results, i.e., similar genotypes and environmental covariates were identified as explaining an important GEI part, with both methods. Baril et al. (1995) reported that biadditive and factorial regression models used explained similar amount of GEI. However, authors reported that factorial regression permitted much more biological explanations than the biadditive model. For Yan and Hunt (2001), the most limiting remains the quality of datasets dedicated to GEI analyses than the method used to understand it.

c. Use of the mixed models to study the GEI

Analyzing GEI through the heterogeneity of the genetic variance and covariance or correlation requires the use of mixed models, usually fitted using the restricted maximum likelihood, REML (Patterson and Thompson, 1971). A model is considered as mixed when it contains at least two fixed and two random terms (Searle, 1971; Malosetti et al., 2013). If data are scored on all the level of a factor, such term must be considered as fixed, and random when many possible levels of the factor exist and data were only scored on a sample of them, i.e., levels coming from a normal distribution (van Eeuwijk, 1995). However, a term with less than ten degree of freedom should not be considered as random (Searle, 1971; van Eeuwijk, 1995).

The process of estimation with REML is performed in two consecutive steps: (i) estimating the components of the variance by maximizing the likelihood and then (ii) estimating fixed and random terms based on previously estimates of components of variance. Parameters of fixed terms are estimated by generalized least square, whereas random factor realization of an unobserved variables are predicted (van Eeuwijk, 1995). Mixed models were reviewed in a general context (Verbeke and Molenberghs, 2000; Galwey, 2006) and also in a more specific one as plant breeding (Smith et al., 2001, 2005; Mathews et al., 2008).

Mixed models are relevant when datasets are complicated as in case of MET, where all genotypes are not tested each year at each location, and present some interesting features for the study of GEI (Cooper et al., 2006). By taking appropriates

terms as random, estimating both parameters of fixed and random terms and corresponding components of the variance by the method of the REML (Patterson and Thompson, 1971), mixed models allow considering, efficiently combining all the available information and recovering information on the genotypic differences. These characteristics correspond to the optimal procedure described by Robinson (1987). Mathews et al. (2008) showed that mixed model best captured the variance and covariance structure, including the genetic correlation between environments (Zheng et al., 2010). Moreover, in case of MET data, assumption of a constant genetic variance and genetic correlation across environments is not realist. If enough genotypes are involved, mixed models may provide more realistic estimates than with fixed-term models, considering genotype-related terms as random within the model. On this way, a genetic variance-covariance matrix is imposed on the data (Malosetti et al., 2013). Several authors (Malosetti et al., 2004, 2013; Boer et al., 2007) proposed various mixed models to analyze GEI between environments in terms of heterogeneity of variance and covariance. As highlighted by Malosetti et al. (2013), as an iterative process, data analysis must lead to test several models in order to choose the best one on the basis of the Akaike criteria (AIC) (Akaike, 1974).

d. Methods to assess the stability of the genotypes across environments

An extensive set of methods exists to help breeder in analyses of MET data but also interpreting GEI. Several paralleled statistical methods have also been proposed with the objective of analyzing stability in performance of genotypes with specific and wide environmental adaptations, i.e., at the opposite, the discrimination ability of an environment, to explain information contained in the GEI. Stability performance depends on the magnitude of GEI (Ahmad et al., 1996). In 2009, Mohammadi and Amri reviewed several different stability parameters.

Stability can be considered for a genotype or a trait. If the focus is put on a genotype i, authors mentioned the ecovalence W^2_i (Wricke, 1962), the regression coefficient b_i (Eberhart and Russell, 1966) and two AMMI based parameters, the AMMI statistic coefficient D_i (Zhang et al., 1998) and the AMMI stability value, AVS_i (Purchase et al., 2000). Eberhart and Russell (1966) also proposed the deviance from regression, S^2_d, as parameter of stability. If the environment j is of interest, both the type-B ecovalence, W^2_j (Burdon, 1977; Isik and Kleinschmit, 2005) and the regression

coefficient b_j to describe reaction of a test environment to an increase in genotypic quality (Isik and Kleinschmit, 2005; Mohammadi and Amri, 2009) were proposed.

Stability analyses were performed on many species, as in bread wheat (Sial et al., 2000; Mohammadi and Amri, 2009), durum wheat (Mohammadi and Amri, 2009), in chick pea (Khan et al., 1988; Atta et al., 2009), in barley (Voltas et al., 1999), in bermudagrass (*Cynodon dactylon* (L.) Pers.) (Chakroun et al., 1990), in oat (Helms, 1993), in oil seed rape (Brandle and Mcvetty, 1988) and in cotton (Abou-El-Fittouh et al., 1969; Campbell et al., 2012). In their study on durum wheat (*Triticum turgidum* L.), Mohammadi and Amri (2009) compared W^2_j, D_j, ASV_j and b_j. Except for b_j, they reached both similar ranking and similar conclusions with all other methods. Moreover, they indicated that more stable genotypes, i.e., less interacting with the environment, were the ones closer to the center of the biplot.

Through the use of all the previously presented GEI models, breeders are now able to estimate GEI. With the environmental covariates presented in (Chapter I, III.e), they are also able to give to GEI a more or less biological sense to try to beneficiate of the potential brought by such a wide existing genetic variability for drought and heat stress tolerance. At that stage, genotypes can be grouped and targeted to environment where they display both performance and stability. Determining the genetic basis of the performance of these genotypes is of great help for a breeder with the identification of genomic regions involved in the control of the trait.

VI. Assessing the genetic determinism of tolerance to drought and heat stress

a. From genetic and physical maps to whole wheat genome sequencing

Two types of maps are currently used in plant genetics. The first one, the physical map corresponds to the representation of the genome with ‘real’ distance, in base pair (kbp or Mbp), which are the molecules constituting the DNA molecules. They are the results of a total or partial DNA sequencing. According to Pagani et al. (2012), in september 2011, 2907 genomes were completely sequenced. Most of them concerned bacteria and viruses. The genome of twelve plant species have already been sequenced such as *Arabidopsis thaliana* L. (The Arabidopsis Genome Initiative, 2000), *Oryza sativa* L. (Goff, 2002), *Oryza brachyantha* L.(Chen et al., 2013), *Zea mays* L. line B73 (Schnable et al., 2009). Due to the size and complexity of wheat genome, it has not yet

been fully sequenced. However, since 2005, the International Wheat Genome Sequencing Consortium (IWGSC), involving more than 1,000 members from 57 countries, is in charge of its sequencing. The physical map of the chromosome 3B was released by Paux et al. (2008). Recently, the sequence of the same chromosome were released by Choulet et al. (2014).

The other useful map is the genetic map. In most of the case, such a map involves a segregating population of homozygous individual from the cross between two homozygous parents. The segregating feature within the offspring comes from the occurrence of crossing-overs between homologous chromosomes at meiosis. The offspring is genotyped for marker chosen to be polymorphic between parents. Recombined (parental) genotype corresponds to genotype for which allele at two consecutive markers are inherited from not the same parent. The rate of recombination corresponds to the proportion of recombined genotypes within the population (Laperche, 2005). The centiMorgan (cM) is the unit of distance in genetic maps, i.e., 1 cM corresponds to a crossing-over occurring on a given haplotype for 100-meiosis; the closer the markers, the lower is their rate of recombination. Estimation of genetic distance between two markers is based on the assumption of a Mendelian segregation of marker within the offspring. When such assumption is not respected, both, order and distances between two markers are affected (Zhu et al., 2007).

First wheat molecular maps were based on RFLP[11] markers (Devos et al., 1993). Table VI-1 presents a summary of the some of the main and most recent physical and genetic wheat maps. The International *Triticea* Mapping Initiative (ITMI) population is one of the most polymorphic wheat mapping populations and has been extensively mapped with RFLP, AFLP, and SSR markers (Somers et al., 2004). The first microsatellite wheat map was reported by Röder et al. (1998), with 279 loci. In 2004, Somers et al. build a consensus high-density microsatellite wheat genetic map using four others maps. More recently, the diversity arrays technology (DArT) enables the development of hundreds high-quality genomic markers efficiently (http://www.diversityarrays.com/). DArT markers were used for wheat genetic mapping (Mathews et al., 2008; Wang et al., 2011b; Cui et al., 2014). Nowadays, single nucleotide polymorphism (SNP) is the reference marker. It corresponds at the variation

[11] RFLP: Restriction Fragment Length Polymorphism

at a single position in the DNA sequence among different genotypes of the same species. These markers are quite frequent in the genome with around 1 SNP every 1000bp in the human genome.

Genetic mapping is of great interest for (i) positional cloning with dense map, (ii) studying the syntheny and compare genomes, (iii) help in constructions of physical map with dense maps, (iv) studying meiosis, but also and mainly for (vi) identifying genomic regions associated with variation of a trait of interest (grain yield, yield components, drought tolerance, diseases, *etc*.).

Table VI-1 Synthesis of the main wheat physical and genetic map studies displaying the species involved, the date of release, the type of map, authors of the study, the cross, the structure of the mapping population, the number and type of markers used, the chromosome mapped and the size in centiMorgan (cM) when available in total and for each one of the genome A, B, and D. p+ Physical map; G=Genetic map

Species	Release	Map	References	Cross	Population structure	Markers		Chromosome mapped	Size (cM)			
						Number	Type		Total	A	B	D
T. aestivum	2003	P	http://wheat.pw.usda.gov/cgi-bin/graingenes/report.cgi?class=mapdata&name=Wheat%2C%20Physical%2C%20EST	Chinese Spring Deletion Lines		6963	EST	1A-7D	-	-	-	-
T. aestivum	2004	P	(Sourdille et al. 2004)	Chinese Spring Deletion Lines		774	SSR	1A - 7D	-	-	-	-
T. aestivum	2008	P	(Paux et al. 2008)	-		1396	ISBP, EST, SSR	3B	-	-	-	-
A. tauschii	1995	G	(Boyko et al. 1999)	Meyeri (TA1691) x Typica (TA1704)	F2	547	AFLP, RFLP	1D - 7D	-	-	-	-
T. aestivum	1998	G	(Röder et al. 1998)	W-7984 x Opata M85 (ITMI population)	RIL	581	RFLP, SSR	1A-7D	-	-	-	-
T. aestivum	2003	G	(Paillard et al. 2003)	Forno x Arina	RIL	401	SSR, RFLP	1A - 7D	3086	1131	920	1036
T. aestivum	2003	G	(Song et al. 2005)	Altar84/Aegilops squarrosa x Opata M85 (ITMI population)	RIL	1410	SSR, RFLP	1A - 7D	-	-	-	-
T. aestivum	2004	G	(Somers et al. 2004)	Consensus map (4 mapping studies)	RIL, DH	1249	SSR, Genes	1A - 7D	2569	944	847	778
T. aestivum	2005	G	(Quarrie et al. 2005)	Chinese Spring x SQ1	DH	640	SSR, RFLP, AFLP	1A - 7D	3522	-	-	-
T. aestivum	2008	G	(Xue et al. 2008)	Nanda2419 x Wangshuibai	RIL	887	SSR, STS	1A - 7D	4223.1	-	-	-

Table VI-1 (continued)

Species	Release Map		References	Cross	Population structure	Markers		Chromosome mapped	Size (cM)			
						Number	Type		Total	A	B	D
T. aestivum	2013	G	(Saintenac et al. 2013)	Altar84/Aegilops squarrosa x Opata M85 (ITMI population)	DH	>400K	SNP, DArT, SSR	1A - 7D	-	-	-	-
T. aestivum	2014	G	(Cui et al. 2014)	Consensus map	RIL	1,127	PCR-based (G-SSR, EST-SSR, ISSR, STS, SRAP, RAPD), biochemical markers (high molecular weight glutenin subunits	1A-7D	2976.75	985.93	922.16	1068.65

b. Quantitative trait loci analyses

In genetics traits are classified as qualitative or quantitative. In qualitative traits, phenotypes fall into discrete categories. Such trait is considered as discontinuous. Traits for which individuals cannot be grouped obviously into distinct and specific classes of individuals are considered as quantitative. In agronomy, most of the traits of interest follow such a distribution. Genetic variation underlying quantitative phenotypes is the results of the segregation of numerous genes or loci called quantitative trait loci (QTL). QTL are genomic regions involved in the control of the variation of a continuous trait, controlled by many genes, each segregating according to Mendel's law, and which expression can be modified by interaction with other genes and by environment (Mackay, 2001).

QTL mapping is used to localize and to study the genetic basis of quantitative traits. The principle is based on the identification of genomic regions where occurs statistical association between the phenotype of an individual and its genome. QTL mapping analysis involves the cross of parents usually contrasted for the trait of interest leading to the production of a segregating population (e.g.: F2, backcross lines, recombinant inbred lines, double-haploids, *etc*.). The genotyping of the segregating population enables the construction of a genetic map on which will be located QTLs. In plant, homozygous lines from recombinant inbred lines and double-haploids lines are highly interesting despite the cost and time necessary to produce them. Such material can be multiplied easily and therefore, the same genetic structure can be tested in many different environments and during many years if necessary. They also enable the study of the only additive effects of alleles. Other methods exists to detect QTL (see Crépieux, 2004). QTL principles were reviewed by Laperche (2005). Loci involved in the variation of a quantitative trait can also be influenced by the environment to various degrees (Mackay, 2001). In this case we talk about the quantitative trait loci-by-environment interaction term, or QEI.

c. Impact of the segregation distortion on QTL analysis

The segregation distortion is a common phenomenon observed in many genetic experiments. It corresponds to the deviation of the segregation ratio of a locus from the expected Mendelian ratio (Xu, 2008). SD comes from genes subjected to gametic or zygotic selection, sterile gene and chromosome translocation (Hedrick and Muona, 1990;

Lorieux et al., 1995; Zhu et al., 2007). They are referred as segregation loci distorters (SDL).

As previously presented, genetic mapping distances are estimated on the hypothesis of a Mendelian segregation of markers. SD results in a bad establishment of the linkage group and also in the estimate of the recombinant fractions between marker loci. It can be then easily understood how this kind of markers can be deleterious in the construction of a genetic map and disturb the order of the marker loci. Due to their deleterious effects, geneticists usually remove them. However, Wang et al. (2005) reported that genomic regions under SD are equally if not more than likely to contain QTL, resulting in likely some true QTL removal. As a consequence, the use of adjusted marker map after inclusion of the distorted markers was proposed (Wang et al., 2005; Xu, 2008). In this process as a first step, the architecture of the map is established using exclusively non-distorted markers. Then, recombinant fractions between marker loci are estimated *de novo* after adjusting for SD (for more details, see Wang et al., 2005). It results in higher marker coverage of the genome.

Through *in silico* simulations, Xu (2008) investigated how SD among markers arises and impacts QTL mapping studies. Contrary to the belief that the SDL is always harmful to QTL mapping, it can potentially but not necessarily benefit from SDL. Indeed, if SD is always detrimental to the power of detecting QTL with dominant effects, for QTL mapping with additive effects, authors reported that SD was not always deleterious (Xu, 2008). More generally, the impact of segregation distortion depends of the degree of dominance of the QTL, the frequencies of the three marker types (AA, Aa, aa), the linkage distance between the distorted markers and the QTL, and finally the size of the mapping population (Zhang et al., 2010b)

They discussed also the fact that with a dense map, SD effects on QTL detection are minimal. Nevertheless, they concluded to a minimal power loss if SDL is ignored in QTL mapping studies.

d. QEI: dissection of the genetic component of the GEI

The most frequent protocol of plant breeders, especially field crop ones, is based on a multi-environmental trialing. When an interesting QTL has been located within a cross, the underlying objective of the breeder is to introgress it to improve the targeted trait. Marker assisted selection (MAS) is of great help to follow and guide breeder for

the introgression into its elite breeding material. However, the expression of this QTL may be environment- and/or genetic background- dependent.

Sensitivity of the QTL expression to environmental conditions is known as QTL-by-environment interaction, QEI. Such a feature can be interesting to overperform in a given environment. Studying the QEI of a given trait leads to the dissection of the genetic part of GEI, represented by the QTL, i.e., the closest marker of the QTL peak, and the rest of the genetic effect (Malosetti et al., 2004; Boer et al., 2007; Tardieu, 2013; El-Soda et al., 2014). QEI can be further investigated using environmental covariates. As for GEI, it enables QEI (i) to be interpreted with a more biological sense, but also (ii) to identify specific environmental variable, or stress influencing the interaction.

A procedure was proposed to study the QEI. It has been well summarized by Malosetti et al. (2004), Boer et al. (2007), and Malosetti et al. (2013), and applied on rapeseed (El-Soda et al., 2014), wheat (Kuchel et al., 2007a; Mathews et al., 2008), and corn (Malosetti et al., 2013). It consisted in first (i) identifying the best variance-covariance model for the multi-environmental phenotypic dataset, (ii) a genome wide scan simple interval mapping (SIM) to detect significant QTL (QTL effects are fitted as fixed environment-specific effects), (iii) one or two run of composite interval mapping, and finally (iv) establish a final QTL model with all positions that were found significant in the restricted CIM scans. During that last step, effects of QTL by environment are estimated.

On bread wheat in Australia, Kuchel et al. (2007) found that the number of days during the growing season with maximum temperature exceeded 30°C was the variable with the largest effect on site mean grain yield.

e. Synthesis of the previously reported QTL for traits associated with drought and heat stress tolerance in wheat

Bread and hard wheat QTL from 37 studies representing a wide range of environmental conditions encompassing irrigated, drought, and heat stress conditions were summarized. Results are presented in Table VI-2 and Table VI-3. The QTL associated with the expression of 46 traits, which most of them referred to drought and heat tolerance traits reported in the previous section of the manuscript, were grouped into three classes: (i) traits associated with ‘sink’ organs, (ii) traits associated with ‘source’ organs, and (iii) traits influencing the sink-source balance.

Table VI-2: Table summarizing the studies reported for the synthesis of QTL found for many traits under irrigated, drought, and heat conditions. Here is represented, the number of the species studied, the cross involve, the genetic structure of the material studied, and the reference of the studied

Number	Species	Cross(es)[†]	Genetic structure[‡]	References
1	*T. aestivum* L.	CS x CS (Kanto107 4A)	RICL	Araki et al. (1999)
2	*T. aestivum* L.	Halberd x Cutter	RIL	Beecher et al. (2012)
3	*T. aestivum* L.	Kukri x Rac875	DH	Bennett et al. (2011)
4	*T. aestivum* L.	Kukri x Rac875	DH	Bennett et al. (2012a)
5	*T. aestivum* L.	Kukri x Rac875	DH	Bennett et al. (2012b)
6	*T. aestivum* L.	Courtot (Rht-B1b; Rht-D1b) x CS	DH	Cadalen et al. (1998)
7	*T. aestivum* L.	-	-	Ciuca and Petcu (2009)
8	*T. aestivum* L.	CS x SQ1	DH	Czyczyło-Mysza et al. (2011)
9	*T. turgidum*	Jennah Khetifa x Cham1	RIL	Diab et al. (2008)
10	*T. aestivum* L.	7C (heat tolerant) x Seri M82 (heat susceptibility)	RIL	Do (2007)
11	*T. aestivum* L.	AMP WAMII	-	Edae et al. (2014)
12	*T. aestivum* L.	Renan x Récital	RIL	Hanocq et al. (2004)
13	*T. aestivum* L.	Flair x XX86	BC2F3	Huang et al. (2004)
14	*T. aestivum* L.	Dharwar Dry x Sitta	RIL	Kirigwi et al. (2007)
15	*T. aestivum* L.	Trident x Molineux	DH	Kuchel et al. (2007)
16	*T. aestivum* L.	WL711 x PH132; ITMI population	RIL	Kumari et al. (2007)
17	*T. aestivum* L.	-	-	Kumar et al. (2010)
18	*T. aestivum* L.	Hanxuan 10 x Lumai 14	DH	Liu et al. (2013)
19	*T. aestivum* L.	-	-	Mason et al. (2013)
20	*T. aestivum* L.	Seri M82 x Babax	RIL	Mathews et al. (2008)
21	*T. aestivum* L.	AMP WAMII	-	Molero et al. (2014)
22	*T. aestivum* L.	Red Egyptian x ...	F2	Morgan (1991)
23	*T. aestivum* L.	-	-	Morgan and Tan (1996)
24	*T. aestivum* L.	Seri M82 x Babax	RIL	Olivares-Villegas et al. (2008)
25	*T. turgidum*	Langdon x Emmer (acc# G18-16)	RIL	Peleg et al. (2009)
26	*T. aestivum* L.	Seri M82 x Babax	-	Pinto et al. (2010)
27	*T. aestivum* L.	Ciano 67 (high-ABA) x CS (low-ABA)	RICL	Quarrie et al. (1994)
28	*T. aestivum* L.	CS x SQ1 (high abscisic acid-expressing line)	DH	Quarrie et al. (2005)
29	*T. aestivum* L.	Cranbrook x Halberd	DH	Rebetzke et al. (2001)
30	*T. aestivum* L.	Cranbrook x Halberd; Sunco x Tasman; CD87 x Katepwa; Kukri x Janz	DH	Rebetzke et al. (2007)
31	*T. aestivum* L.	CD87 x Katepwa	-	Rebetzke et al. (2008a)
32	*T. aestivum* L.	-	-	Rebetzke et al. (2008b)
33	*T. aestivum* L.	Sunco x Tasman; CD87 x Katepwa; Cranbrook x Halberd	DH	Rebetzke et al. (2013)
34	*T. aestivum* L.	-	-	Snape et al. (2001)
35	*T. aestivum* L.	Beaver x Soisson	DH	Verma et al. (2004)
36	*T. aestivum* L.	-	-	Vijayalakshmi et al. (2010)
37	*T. aestivum* L.	Hanxuan 10 x Lumai 17	DH	Yang et al. (2007)

[†] CS: Chinese spring

[‡] RICL: Chromosome substitution lines; RIL: Recombinant inbred lines; DH: Double-haploid; BC: backcross;

Table VI-3 : Table summarizing QTL found in the literature in wheat under different environmental conditions encompassing irrigated, drought and heat conditions. References refers to Table VII-2

Class of trait	Trait[†]	Environment[‡]	Chromosome																				References
			1A	1B	1D	2A	2B	2D	3A	3B	3D	4A	4B	4D	5A	5B	5D	6A	6B	6D	7A	7B	7D	
Sink	GFr	DR	-	-	-	-	-	-	-	-	-	4A	-	-	-	-	-	-	-	-	-	-	-	14
		IR, DR	-	1B	-	2A	-	-	-	-	-	-	4B	-	5A	-	-	6A	6B	-	-	7B	-	37
	HI	DR	-	1B	-	2A	-	-	-	3B	3D	-	-	4D	-	-	-	-	-	-	7A	-	-	4
		HI	-	-	-	-	-	-	-	-	-	-	-	-	-	5B	-	-	-	-	-	-	7D	19
		IR, DR	1A	1B	-	-	-	-	-	-	-	4A	-	-	5A	5B	-	-	-	-	-	-	-	11
		IR, DR	-	1B	-	2A	2B	-	-	3B	-	4A	-	-	5A	5B	-	6A	6B	-	-	7B	-	25
		IR, HI	-	-	-	-	2B	-	3A	3B	-	4A	4B	-	-	-	-	6A	-	-	-	-	-	16
	KN	AMC	-	-	-	-	-	-	-	-	-	-	-	-	-	5B	-	-	-	-	-	-	7D	15
		DR	1A	1B	-	-	2B	-	3A	3B	-	-	4B	4D	-	-	-	6A	-	6D	7A	7B	-	4
		DR	-	-	-	-	2B	-	-	-	-	-	-	-	-	-	5D	-	-	6D	-	-	-	8
		DR	-	-	-	-	-	-	-	-	-	4A	-	-	-	-	-	-	-	-	-	-	-	14
		DR	-	1B	-	-	2B	-	-	-	-	-	-	-	5A	-	-	-	6B	-	-	7B	7D	24
		HI	1A	-	1D	2A	2B	-	-	3B	3D	4A	4B	4D	5A	5B	5D	6A	6B	6D	-	7B	-	10
		HI	-	-	-	-	-	-	-	-	-	-	4B	-	-	-	-	-	-	-	7A	-	7D	19
		IR, DR	1A	1B	1D	-	-	-	-	3B	3D	-	4B	-	-	5B	-	-	-	-	7A	7B	-	11
		IR, DR, HI	-	-	-	-	-	-	-	3B	3D	-	-	-	5A	5B	-	-	-	-	7A	-	-	5
		IR, DR, HI	-	1B	-	-	-	-	-	3B	-	4A	-	-	-	5B	-	-	6B	-	-	-	-	26
		IR, HI	1A	1B	-	2A	2B	-	-	3B	3D	-	4B	-	-	-	-	-	-	-	7A	-	-	16
		NEC, GH	-	-	1D	2A	-	-	-	-	3D	-	-	-	-	-	-	6A	-	-	7A	-	7D	13
	KS	HI	-	-	-	-	-	-	-	-	-	-	-	-	5A	-	-	-	-	-	-	-	-	19
		IR, DR	-	1B	-	-	-	-	3A	3B	3D	4A	-	-	-	-	-	-	6B	-	-	7B	7D	11
	KW	AMC	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6A	-	-	-	-	7D	15
		DR	-	-	1D	-	2B	-	-	-	3D	4A	-	-	-	5B	-	6A	6B	-	7A	-	7D	4
		DR	-	1B	-	-	2B	-	3A	3B	-	4A	4B	-	-	-	-	-	-	-	-	-	-	24
		HI	-	-	1D	-	-	-	3A	-	-	-	-	4D	-	5B	5D	6A	-	6D	7A	7B	7D	10
		HI	-	-	-	-	-	-	-	-	-	-	-	-	5A	-	-	-	-	-	-	-	-	19
		IR	-	-	-	-	-	-	-	-	-	4A	-	-	-	-	-	-	-	-	-	-	-	1
		IR, DR	-	1B	1D	2A	-	-	-	3B	-	4A	4B	-	-	5B	-	6A	-	-	7A	-	7D	11

Table VI-3 (continued)

Class of trait	Trait[†]	Environment[‡]	Chromosome																				References
			1A	1B	1D	2A	2B	2D	3A	3B	3D	4A	4B	4D	5A	5B	5D	6A	6B	6D	7A	7B	7D	
	KW	IR, DR	-	-	-	2A	-	-	3A	3B	-	4A	-	-	-	5B	-	6A	-	-	7A	-	-	37
		IR, DR, HI	-	-	1D	-	2B	-	3A	3B	-	-	-	-	-	5B	-	6A	-	-	7A	7B	-	5
		IR, DR, HI	-	-	-	-	-	-	-	3B	-	4A	4B	-	-	-	-	-	-	-	-	-	-	26
		NEC, GH	-	1B	1D	2A	-	-	3A	3B	3D	-	4B	-	-	-	-	6A	-	6D	7A	-	7D	13
		NT, DR, ST	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6B	-	-	-	-	28
	QLTY	DR	-	1B	1D	2A	-	-	3A	-	-	4A	-	4D	-	-	-	6A	-	-	-	-	-	4
		HI	-	1B	1D	-	-	-	-	-	-	4A	-	-	-	-	-	-	-	-	7A	-	-	2
		HI	-	-	-	-	-	-	-	-	-	-	4B	-	-	5B	5D	-	-	-	-	-	7D	19
		IR, DR	1A	1B	1D	-	2B	-	3A	3B	3D	4A	4B	-	-	5B	-	-	6B	-	7A	7B	7D	11
	SN	AMC	-	-	-	-	-	-	-	-	-	-	-	-	-	5B	-	-	-	-	-	-	-	15
		DR	-	-	1D	-	2B	-	-	-	-	4A	4B	-	-	-	-	6A	-	-	-	-	-	4
		DR	-	-	-	-	-	-	-	-	-	4A	-	-	-	-	-	-	-	-	-	-	-	14
		HI	1A	-	-	-	2B	-	-	3B	-	-	-	-	5A	5B	5D	6A	-	6D	-	-	-	10
		HI	-	-	-	-	-	-	-	3B	-	-	-	-	-	5B	-	-	-	-	-	-	7D	19
		IR, DR	-	-	-	-	-	-	-	-	-	-	4B	-	-	5B	-	-	6B	-	7A	7B	-	11
		IR, HI	1A	1B	-	-	-	-	3A	3B	3D	4A	-	-	-	-	-	-	-	6D	7A	7B	-	16
		NEC, GH	-	1B	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7A	-	-	13
	SPL	IR, DR	-	1B	-	-	-	-	-	-	-	-	4B	-	-	5B	-	-	-	-	-	-	-	11
		IR, HI	1A	1B	1D	-	2B	-	-	-	-	4A	-	-	5A	-	5D	-	-	-	-	-	-	16
	SPN	IR	-	-	-	-	-	-	-	-	-	4A	-	-	-	-	-	-	-	-	-	-	-	1
		IR, DR	-	-	-	-	2B	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7B	-	11
		IR, HI	-	-	-	-	2B	-	-	-	-	4A	-	4D	5A	-	-	6A	-	-	-	-	-	16
	YLD	AMC	-	-	-	-	-	-	-	-	3D	4A	-	4D	-	5B	-	6A	-	6D	-	7B	-	15
		DR	1A	1B	-	2A	2B	-	-	-	-	-	-	4D	-	-	-	-	-	6D	7A	-	-	4
		DR	-	-	-	-	-	-	-	-	-	-	-	-	5A	-	-	-	6B	-	-	-	-	8
		DR	-	-	-	-	-	-	-	-	-	4A	-	-	-	-	-	-	-	-	-	-	-	14
		DR	-	1B	1D	-	-	-	-	-	-	-	4B	-	5A	5B	-	6A	6B	6D	7A	7B	-	20
		DR	-	-	1D	-	2B	-	3A	3B	-	4A	4B	-	-	5B	-	6A	-	-	-	7B	-	24
		HI	1A	1B	1D	2A	2B	-	3A	3B	-	4A	4B	4D	5A	5B	5D	6A	6B	6D	7A	7B	7D	10
		HI	-	-	-	-	-	-	-	3B	-	-	-	-	-	-	5D	-	-	-	-	-	7D	19

Table VI-3 (continued)

Class of trait	Trait[†]	Environment[‡]	Chromosome																				References
			1A	1B	1D	2A	2B	2D	3A	3B	3D	4A	4B	4D	5A	5B	5D	6A	6B	6D	7A	7B	7D	
	YLD	IR	-	-	-	-	-	-	-	-	-	4A	-	-	-	-	-	-	-	-	-	-	-	1
		IR, DR	-	1B	1D	2A	2B	-	-	-	-	-	4B	-	-	5B	-	-	-	-	7A	7B	-	11
		IR, DR	1A	1B	-	2A	-	-	-	-	-	-	-	-	5A	-	-	6A	-	-	-	-	-	18
		IR, DR	-	-	-	-	2B	-	-	-	-	4A	4B	-	5A	-	-	-	-	-	-	7B	-	25
		IR, DR, HI	-	-	-	-	-	-	3A	3B	3D	4A	-	4D	-	5B	-	-	-	-	7A	-	-	5
		IR, DR, HI	-	1B	-	-	-	-	-	3B	-	4A	-	-	-	-	-	-	-	-	-	-	-	26
		IR, HI	1A	-	1D	2A	2B	-	-	3B	-	4A	4B	4D	-	-	-	-	-	6D	7A	-	-	16
		NEC, GH	1A	-	-	-	-	-	-	-	3D	-	-	4D	5A	5B	-	-	6B	6D	-	-	-	13
		NT, DR, ST	-	-	1D	-	-	-	-	-	-	4A	4B	-	5A	5B	-	-	-	6D	7A	-	-	28
Source	BM	DR	-	-	-	-	-	-	-	-	3D	-	-	-	-	-	-	-	-	-	-	-	-	4
		DR	-	-	-	-	-	-	-	-	-	4A	-	-	-	-	-	-	-	-	-	-	-	14
		HI	-	-	-	-	-	-	-	3B	-	-	-	-	-	-	-	-	-	-	-	-	-	19
		IR, DR	1A	-	-	-	-	-	-	-	-	-	-	-	-	5B	-	-	-	-	-	7B	7D	11
		IR, DR	-	1B	-	2A	2B	-	-	-	-	4A	4B	-	5A	-	-	-	-	-	7A	7B	-	25
	CHL	DR	-	1B	1D	2A	-	-	3A	3B	-	-	4B	-	5A	-	-	6A	6B	-	7A	-	-	24
		HI	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7B	-	36
		IR, DR	1A	1B	-	-	2B	-	-	-	-	4A	-	-	5A	5B	-	6A	-	-	7A	-	-	25
		IR, DR, HI	1A	-	-	-	2B	-	-	3B	-	-	4B	4D	-	5B	-	6A	6B	6D	-	7B	-	5
		IR, DR, HI	-	-	-	2A	-	-	-	-	-	-	4B	-	5A	-	-	6A	6B	-	-	-	-	9
		IR, DR, HI	-	1B	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	26
	CID	DR	-	1B	-	-	2B	-	-	3B	-	4A	4B	4D	5A	-	-	-	6B	-	7A	-	-	31
		DR	-	1B	-	2A	-	-	-	3B	-	4A	4B	-	5A	5B	-	-	-	6D	7A	7B	-	31
		DR	-	1B	1D	2A	2B	-	-	3B	-	4A	4B	4D	-	-	-	-	-	6D	7A	7B	-	31
		IR, DR	1A	-	-	2A	-	-	-	-	-	4A	-	-	5A	5B	-	6A	6B	-	-	7B	-	25
		IR, DR, HI	-	-	-	-	-	-	-	-	-	-	4B	-	-	-	-	-	-	-	-	-	-	9
	CL	CST	-	-	-	-	2B	-	-	-	-	4A	-	-	-	-	5D	-	6B	-	-	-	-	30
	CT	DR	1A	1B	-	2A	2B	-	3A	3B	-	4A	4B	4D	5A	5B	5D	6A	6B	-	7A	-	-	24
		HI	-	-	-	-	-	-	-	3B	-	-	-	-	-	-	5D	-	-	-	7A	-	-	19
		IR, DR	1A	1B	1D	2A	2B	-	3A	3B	3D	4A	4B	4D	5A	5B	-	-	6B	6D	7A	7B	7D	33
		IR, DR, HI	-	1B	-	2A	-	-	3A	3B	-	-	4B	-	-	5B	5D	6A	6B	-	7A	7B	-	5

Table VI-3 (continued)

Class of trait	Trait[†]	Environment[‡]	Chromosome																				References
			1A	1B	1D	2A	2B	2D	3A	3B	3D	4A	4B	4D	5A	5B	5D	6A	6B	6D	7A	7B	7D	
	CT	IR, DR, HI	-	-	-	2A	-	-	-	-	-	-	4B	-	-	5B	-	-	6B	-	-	7B	-	9
		IR, DR, HI	-	1B	-	-	2B	-	-	3B	-	4A	-	-	5A	-	-	-	-	-	7A	-	-	26
	EV	AMC	-	-	-	-	-	-	-	-	-	-	4B	-	-	-	-	-	-	-	-	-	-	29
		DR	-	-	-	-	2B	-	-	3B	3D	-	-	-	-	5B	-	6A	-	-	7A	7B	-	4
		IR, DR, HI	-	-	-	-	2B	-	-	3B	3D	4A	-	-	-	5B	-	-	6B	-	-	-	-	5
	FLG	AMC	-	-	1D	-	2B	-	3A	3B	3D	-	-	4D	-	5B	-	6A	-	-	-	-	7D	3
		IR, DR, HI	-	-	-	2A	-	-	3A	-	-	-	-	-	-	-	-	-	-	-	7A	-	-	5
	FLL	DR	-	-	-	-	2B	-	-	3B	-	4A	-	-	-	5B	-	-	-	-	-	7B	7D	4
		IR, DR	-	1B	-	-	2B	-	3A	3B	-	-	-	-	-	5B	-	-	-	-	-	-	-	11
	FLR	DR	-	1B	1D	-	-	-	3A	-	-	-	4B	4D	-	5B	-	-	-	-	7A	7B	7D	24
		IR, DR	1A	-	-	2A	2B	-	-	-	-	-	4B	-	5A	5B	-	6A	6B	-	7A	7B	-	25
	FLW	DR	-	-	-	-	2B	-	-	-	-	-	-	-	5A	-	-	6A	-	-	-	-	-	4
		IR, DR	-	-	-	-	-	-	-	3B	-	-	-	-	-	5B	-	6A	6B	-	7A	-	-	11
		IR, DR, HI	1A	-	-	-	2B	-	-	-	-	-	-	-	-	5B	-	6A	-	-	-	7B	-	5
	LA	IR, DR	1A	1B	-	-	2B	-	-	3B	3D	-	-	-	5A	5B	-	6A	6B	-	-	-	-	11
		IR, HI	1A	-	-	-	-	-	-	3B	-	-	-	-	-	-	-	-	-	-	-	-	7D	17
	MS	DR	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7A	-	-	7
	NC	IR, DR	1A	1B	1D	2A	2B	-	-	-	3D	4A	4B	4D	-	-	-	-	6B	-	7A	7B	7D	32
	NDVI	DR	-	-	-	2A	2B	-	-	-	-	4A	-	-	-	-	-	-	-	-	-	-	-	24
		IR, DR	1A	1B	-	2A	-	-	-	-	-	-	-	-	-	-	-	-	6B	-	-	-	-	11
		IR, DR, HI	-	1B	-	2A	2B	-	-	3B	3D	4A	4B	-	-	5B	-	-	-	-	7A	-	-	5
		IR, DR, HI	-	1B	-	-	2B	-	-	-	-	4A	-	-	-	-	-	-	-	-	-	7B	-	26
	POR	IR, DR	-	1B	1D	2A	2B	-	3A	3B	3D	4A	4B	4D	5A	5B	5D	-	6B	6D	7A	7B	7D	33
	PTS	DR	-	1B	-	2A	-	-	-	-	-	4A	4B	-	-	-	-	-	6B	-	-	-	-	8
		HI	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7A	-	-	36
		IR	-	-	-	-	-	-	3A	3B	-	-	-	-	-	-	-	-	-	-	7A	-	-	21
		IR, DR, HI	-	1B	-	2A	-	-	-	3B	-	-	4B	-	-	5B	-	6A	-	-	-	7B	-	9
	RA	IR, DR	1A	-	-	-	2B	-	3A	-	-	-	-	-	-	-	-	-	-	-	-	-	7D	18
	RL	IR, DR	-	-	-	-	2B	-	-	3B	3D	-	-	-	5A	-	-	-	-	-	7A	-	-	18

Table VI-3 (continued)

Class of trait	Trait[†]	Environment[‡]	Chromosome																				References
			1A	1B	1D	2A	2B	2D	3A	3B	3D	4A	4B	4D	5A	5B	5D	6A	6B	6D	7A	7B	7D	
	RML	IR, DR	-	1B	-	-	-	-	3A	-	-	-	-	-	-	5B	5D	-	-	-	-	7B	-	18
	RPA	IR, DR	-	-	-	-	2B	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	18
		IR, DR	-	-	-	-	2B	-	-	3B	-	4A	4B	-	-	5B	-	-	-	-	-	-	7D	18
	RSA	IR, DR	-	-	-	-	2B	-	-	3B	-	4A	4B	-	-	5B	-	-	-	-	-	-	7D	18
	RTL	IR, DR	1A	1B	-	-	-	-	-	3B	-	-	4B	-	-	5B	5D	-	-	-	-	-	7D	18
	SEN	DR	-	-	-	-	2B	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	35
		HI	-	-	-	2A	-	-	3A	3B	-	4A	4B	-	5A	-	5D	6A	6B	-	7A	7B	7D	36
		IR, DR	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6B	-	-	-	-	11
Source-Sink balance	ABA	NT, DR, ST	-	-	-	-	-	-	-	-	-	-	-	-	5A	-	-	-	-	-	-	-	-	27
	ANT	DR	-	1B	1D	-	2B	-	-	-	-	4A	-	4D	5A	-	-	-	-	-	7A	7B	-	20
		IR, DR, HI	-	-	1D	-	-	-	-	-	-	-	-	4D	5A	-	-	-	-	-	-	-	-	26
	DSI	DR	-	-	-	-	-	-	-	-	-	4A	-	-	-	-	-	-	-	-	-	-	-	14
		IR, DR	-	-	-	-	-	-	-	-	-	4A	-	-	-	-	-	-	-	-	7A	7B	-	11
		IR, DR, HI	-	-	-	2A	-	-	-	-	-	-	4B	-	-	5B	-	6A	-	-	-	-	-	9
	GFl	HI	-	-	1D	-	2B	-	3A	3B	-	4A	4B	4D	-	5B	5D	6A	-	6D	-	-	7D	10
		HI	-	-	-	-	-	-	-	-	-	-	-	-	5A	-	-	-	-	-	7A	-	-	19
		IR, DR	1A	1B	-	-	-	-	-	3B	3D	-	-	-	-	5B	-	-	-	-	7A	-	-	11
		IR, DR	-	1B	-	-	2B	-	-	-	-	4A	4B	-	5A	5B	-	-	-	-	7A	7B	-	25
	HD	AMC	1A	-	-	-	2B	-	-	-	-	-	4B	-	5A	5B	-	-	-	-	7A	7B	-	3
		HI	-	-	-	-	-	-	-	-	-	-	-	-	-	5B	-	-	-	-	7A	-	7D	19
		IR	-	-	-	-	-	-	-	-	-	4A	-	-	-	-	-	-	-	-	-	-	-	1
		IR, DR	-	-	1D	2A	2B	-	3A	3B	-	-	4B	-	-	-	-	-	-	-	-	-	7D	11
		IR, DR	-	1B	-	-	2B	-	3A	-	-	-	4B	-	5A	-	-	-	-	-	-	7B	-	25
		IR, DR, HI	-	-	-	-	2B	-	-	-	-	-	-	-	5A	5B	-	-	-	-	7A	7B	-	5
		NEC, GH	-	-	-	-	-	-	3A	-	-	4A	-	-	-	-	-	-	-	-	7A	-	7D	13
	HSI	HI	-	-	-	-	-	-	-	3B	3D	-	-	-	-	-	5D	-	-	-	7A	-	-	19
	OA	AMC	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7A	-	-	23
		DR	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7A	-	-	22
		IR, DR	-	-	-	2A	2B	-	3A	3B	-	-	4B	-	5A	5B	-	6A	6B	-	-	-	-	25

Table VI-3 (continued)

Class of trait	Trait[†]	Environment[‡]	Chromosome																				References
			1A	1B	1D	2A	2B	2D	3A	3B	3D	4A	4B	4D	5A	5B	5D	6A	6B	6D	7A	7B	7D	
	OA	IR, DR, HI	-	-	-	2A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9
	PH	DR	-	-	1D	-	-	-	3A	-	-	-	-	-	5A	-	-	-	-	-	-	-	-	4
		DR	-	1B	1D	-	2B	-	3A	-	-	4A	4B	-	5A	5B	-	-	6B	-	-	-	-	20
		DR	1A	-	1D	-	2B	-	-	-	-	4A	4B	-	-	-	5D	-	-	-	-	-	7D	24
		HI	-	-	-	-	-	-	-	-	-	-	4B	-	-	-	-	-	-	-	-	-	-	19
		IR	-	-	-	-	-	-	-	-	-	4A	-	-	-	-	-	-	-	-	-	-	-	1
		IR, DR	-	-	-	-	-	-	-	3B	-	-	-	-	-	5B	-	6A	-	-	7A	7B	-	11
		IR, DR, HI	-	-	-	-	-	-	-	-	-	-	4B	-	-	-	-	-	-	-	-	-	-	26
		NEC, GH	-	-	-	-	-	-	-	-	3D	-	-	-	5A	5B	-	-	6B	6D	7A	7B	-	6
		NEC, GH	1A	-	1D	-	-	-	3A	3B	-	4A	4B	-	5A	5B	-	6A	-	6D	7A	-	7D	13
	Phenology	AMC	1A	-	-	-	2B	-	-	-	-	4A	-	-	5A	5B	-	-	-	-	7A	7B	-	3
		DR	-	-	-	2A	2B	-	3A	3B	-	-	-	-	5A	5B	5D	6A	6B	-	7A	7B	-	34
		NEC, GH	-	-	-	-	2B	-	-	-	-	-	-	-	5A	5B	5D	-	-	6D	7A	-	7D	12
	PL	DR	-	-	-	-	-	-	3A	3B	-	-	-	-	5A	-	-	-	-	-	-	-	-	4
		IR, DR, HI	-	-	-	-	-	-	3A	3B	-	-	4B	-	5A	-	-	-	-	-	-	-	-	5
	PM	HI	-	-	-	-	-	-	-	-	-	-	-	-	-	5B	-	-	-	-	7A	-	7D	19
		IR, DR	-	-	-	2A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7A	-	-	11
		IR, DR, HI	-	1B	-	2A	-	-	3A	-	-	-	4B	-	5A	-	-	6A	6B	6D	-	7B	-	5
		IR, DR, HI	1A	-	1D	-	-	-	-	-	-	-	-	4D	5A	-	-	-	-	-	-	7B	-	26
	STL	IR, DR	-	-	-	-	2B	-	-	3B	-	4A	4B	-	-	-	-	-	6B	-	7A	7B	-	25
	WSC	DR	-	-	-	-	-	-	3A	-	-	-	-	-	-	-	-	6A	-	-	-	-	-	4
		IR, DR	1A	1B	1D	2A	2B	-	3A	3B	3D	4A	4B	4D	5A	5B	5D	-	6B	6D	7A	7B	7D	32
		IR, DR	1A	-	1D	2A	-	-	-	3B	-	4A	4B	-	5A	-	-	-	6B	-	7A	7B	7D	37
		IR, DR, HI	-	1B	-	-	-	-	3A	3B	-	-	-	-	-	5B	-	-	-	-	-	7B	-	5

[†]Traits related: ABA: abscissic acid; ANT: Anthesis; BM: Biomass; CHL: Chlorophyll; CID: Carbon isotopic discrimination; CL: Coleoptile length; CT: canopy temperature; DSI: Drought stress index; EV: early vigor; FLG: Flag leaf glaucousness; FLL: Flag leaf length; FLR: Flag leaf rolling; FLW: Flag leaf width; GFl: Grain filling length; GFr: grain filling rate; HD: Heading; HI: Harvest index; HSI: Heat stress index; KN: kernel number (per m², plants, or spike); KS: kernel size; KW: kernel weight (for 50 or 1000 grains); LA: Leaf area; MS: Membrane stability; NC: Nitrogen content; NDVI: Normalized difference vegetative index; OA: osmotic adjustment; PH: Plant height; PL: Peduncle length; PM: Physiological maturity; POR: leaf porosity; PTS: photosynthesis; QLTY: grain quality traits; RT: Root architectural traits; SEN: senescence; SN: Spike number (per m² or plants); SPL: Spike length; SPN: Spikelet number (per plants or spike); STL: Stem length; WSC: Water soluble carbohydrate; YLD: grain yield

[‡] IR: Irrigated/potential conditions; DR: drought; HI: Heat stress; AMC: Australian Mediterraneean conditions; NEC: North European conditions; GH: Green house; NT: Nutrient stress; ST: salt stress

QTL of main agronomic components such as yield and its components phenology traits, and plant height are reported. Other traits referring to the plant morphology (size of leaves, biomass, and architecture of the root system) and to plant physiology under irrigated, drought, and heat stress (CT, NDVI, osmotic adjustment, abscissic acid, chlorophyll, photosynthesis, water soluble carbohydrate, *etc*.) are also presented.

Among the 37 studies reported so far, whatever the environment, the highest numbers QTL were identified on some chromosomes; 5B, 7A, 4A, 3B, 2B, and 4B by decreasing order of importance. The lowest numbers of QTL were listed on several chromosomes of the D genome: 5D, 6D, 4D, and 3D by increasing order. Absolutely no QTL were found on the chromosome 2D. The low number of QTL found on the genome D could be explained by its really low polymorphism on *Triticum aestivum* L., as previously reported by Akhunov et al. (2010) compared with genome A and B. This feature of the genome D has motivated among others reasons, the creation of synthetic wheat. Whatever the traits and the environment tested, QTL were found on almost the whole genome.

The major genes *Rht*, *Ppd*, and *Vrn* when segregating in a mapping population can have strong effect on yield under abiotic stress conditions in particular (Richards et al., 2010; Eagles et al., 2014). On chromosome of the group 2 are present major genes involved in the sensitivity to the photoperiod (*Ppd* genes): *Ppd-B1* (2B) and *Ppd-D1* (2D) genes (Seki et al., 2011). On 2D is also present the dwarfing *Rht8* gene (Worland et al., 1998 p. 8). Major vernalization genes (*Vrn*) are located on chromosomes of the group 5. On chromosomes 4B and 4D are located the two major wheat height reducing genes, so called *Rht-B1* and *Rht-D1*, respectively (Ellis et al., 2002).

QTL for grain yield (YLD) and yield components (KN, KW, and SN) were reported on the whole genome. The chromosome 4A was the most frequently reported for yield QTL (papers 1, 5, 10, 14, 15, 16, 24, 25, 26, and 28; Table VI-2). The review of the literature reveals that some chromosomes are more or less specialized for a given trait (e.g.: 3A, 6A, and 6D for KW, 4D and 5A for YLD), and other, with a more wide influence where QTL for several traits were reported (the whole Genome B, 4A, and 5D). Pinto et al. (2010) reported a major QTL on 4A for yield which was co-located with a canopy temperature QTL under high temperature stress conditions. Many studies

also reported frequent grain yield QTL on 4B and 4D. Kumar et al. (2007) reported a QTL on the long arm of the 4D. Concerning yield components, KN, KW, and SN QTL were frequently detected on 4A and 4B, and very few on 4D (Table VI-3). Kuchel et al (2007) reported a yield QTL on chromosome 1B which interacted with high temperature stress. However, these results should be considered with care as most of QTL found in regions where are located some of the major reducing genes.

QTL of physiological traits were reported on many studies (3, 4, 5, 7, 8, 9, 11, 19, 21, 22, 23, 24, 25, 26, 27, 29, 30, 31, 32, 33, 35, 36, and 37; Table VI-2). Most of them were found on chromosomes of the group 3 where was localized QTL for chlorophyll content, carbon isotope discrimination, canopy temperature, early vigor, flag leaf glaucousness, NDVI, osmotic adjustment, flag leaf porosity, photosynthesis, senescence, and stem water soluble carbohydrate (WSC). The presence of the photoperiod-sensitivity genes on these chromosomes let expect a strong impact of the phenology on all of these traits scored under abiotic stress. Some studies reported QTL of water soluble carbohydrate, canopy temperature, osmotic potential, and grain yield on chromosome 5B (Yang et al., 2007; Kuchel et al., 2007b; Rebetzke et al., 2008b; Peleg et al., 2009). WSC is frequently reported in the literature for its importance under abiotic stress conditions. Rebetzke et al. (2008b) and Yang et al. (2007), working on Doubled Haploid lines from different crosses, reported similar chromosomes involved in the control of the WSC under irrigated and drought conditions.

Under northern Mexican and southern Australian drought and heat stress conditions, Olivares-Villegas et al. (2008) and Rebetzke et al. (2013) highlighted some common chromosomes involved in the control of canopy temperature in different genetic background (Table VI-3). Common QTL for canopy temperature identified by both studies may suggest common genetic basis in the transpiration cooling system between these two environments. Indeed, types of drought differ between these locations which impact the plant drought adaptation mechanisms too[12].

A deeper analysis of QTL found in the literature could be performed by realizing a Meta-QTL analysis (Sosnowski et al., 2012).

[12] The ability to extract water from increasing drought soil conditions constituted the main mechanism of drought adaptation in northern Mexican drought conditions (Olivares-Villegas et al., 2008). The improvement of the water use efficiency constituted one of the main drought adaptation mechanism under Australian drought conditions (Richards et al., 2001; Rebetzke et al., 2002).

CHAPTER II: Objectives and strategy developed during the thesis

I. Frame and objective of the thesis

The PhD had been established in a context of awareness of the needs to improve the tolerance to drought and heat stress of the European winter wheat germplasm. Several options are possible in order to move in this direction including the dissection of drought tolerant traits in stress adapted germplasm followed by a transfer of the relevant variability into the targeted diversity. The objective of the PhD consisted therefore in the study of the genetic determinism of the tolerance to drought and heat stress in various spring bread wheat genetic backgrounds. The results obtained should contribute to the improvement of CIMMYT and Limagrain Europe germplasms.

The CIMMYT bread wheat physiology group headed by Matthew Reynolds focuses its efforts on the dissection and understanding of the physiological traits relevant to improve bread wheat tolerance to drought and heat stress. The germplasm studied during the thesis was evaluated under different water and heat stress conditions. Agronomic and physiological traits were scored in each trial to understand how plants were able to tolerate abiotic stress conditions. The strategy to decipher grain yield consisted in dissecting it into yield components and then identifying physiological traits associated with the variation of yield components of interest. Irrigated conditions enable getting reference values for the different traits of interest (grain yield, yield components, *etc.*). Material was then studied under drought and heat stress with irrigation conditions. Further details are given below.

Several questions are raised at this stage and will be tentatively answered in the manuscript:

- Is there a differential tolerance of the studied germplasm to drought and heat stress?
- What do physiological traits bring for comprehensive analysis of this observed tolerance?
- Do the results found in Mexican germplasm under northern Mexican conditions help in a European context with European germplasm?
- Does the protocol followed is the best one to tackle such a long-term issue like the improvement of European winter wheat for the tolerance to drought and heat stress?

II. Research questions and strategy developed

The tolerance to drought and heat stress of various spring bread wheat genetic backgrounds was studied through the agronomic and physiological evaluation of this material within a multi-annual and multi-environmental trial network where irrigated, drought and heat-irrigated treatment were applied to plants. Then, a detection of QTL involved in the control of the traits associated with the tolerance to targeted abiotic stress was conducted.

In a multi-environment trial network, the observed phenotype can be dissected into an effect of the genotype, the environment, and the interaction between the genotype and the environment according to the formula presented in Equation II-1.

Equation II-1: Dissection of the phenotype (P) into an effect of the genotype (G), the environment (E), and an effect of the interaction between the genotype and the environment (GxE). ε_{ij}, the residual term and μ, the general mean.

$$P_{ij} = \mu + G_i + E_j + G_i \times E_j + \varepsilon_{ij}$$

The study of the literature emphasized the importance of the environmental characterization. Indeed, it is of paramount importance when studying abiotic stress such as drought and heat stress, to determine the type of stress experienced by plants, its period of impact, and also its intensity. It corresponds to the study of the first term of the Equation II-1, the environment (E): the first pillar of this study. As described in Chapter I paragraph II-d, environmental characterization are classicaly performed on MET but using probe-genotypes. In our situation, neither probe-genotypes nor reference values were available in northern Mexican conditions. Accordingly, the environmental characterization was then adapted to tackle the particularity of our experiment. As mentioned in the literature, characterizing drought requires the establishment of a water balance model. Dynamical water model was then established for each trial of the network. Moreover, the study of the literature revealed an important component poorly considered in previous studies, i.e., the differential sensitivity of bread wheat during its crop cycle. The wheat development was then considered for the overall characterization. Such characterization should enable us to identify exactly what plants experienced in the field and establish relevant and informative environmental covariates.

The plant performances within the trial network can then be studied in light of what they have really experienced in the field. Indeed, experimenting genotypes in various conditions leads naturally to differential performances. To understand the

behavior of its performance under different environments, the genotype-by-environment interaction must be explored. The study of the GEI is the second pillar of this work. The GEI was performed using factorial regression. It was performed using the informative environmental covariates previsously developed. Interestingly, the present study overcomes a recurrent issue of the GEI analysis highlighted by the review of the literature, i.e., the lack of biological sense given to the interaction.

Finally, after the characterization of the environment in which plants have evolved, and the study of the GEI of the traits associated with the tolerance to drought and heat stress, this work investigated the genomic regions involved in the tolerance , i.e. the genotype effect, G. At this stage, with the help of the environmental characterization, the interaction of the QTL with the environment were also studied and complete the second pillar of the PhD. Multi-environmental QTL analysis procedure proposed in the GenStat software were used. It enabled the identification of QEI which can then be compared to environmental covariates in order to determine how the effects of QTL behave with specific environmental covariates.

III. Plant material and experimental design of the study

a. The plant material

Three bread wheat populations were used in this study: (i) Population 1 consisted of a set of 196 F7:8 recombinant inbred lines (RIL) from the Pastor//hxl7573/2*Bagula/3/Weebill1 cross (PW), (ii) Population 2 consisted of a set of 228 F7:8 RILs from the Sokoll/Weebill1 cross (SW), and (iii) Population 3 consisted of a set of 266 F5:8 RILs from the Vorobey//Parus/Pastor cross (VP); all of them have been created at the CIMMYT (International Maize and Wheat Improvement Center) nurseries. These populations are bi-parental crosses between CIMMYT elite lines combining interesting physiological traits for drought and heat stress tolerance. Parents were chosen because the crosses had produced outstanding elite lines distributed worldwide to national programs. The pedigree of the population is presented in Figure III-1.

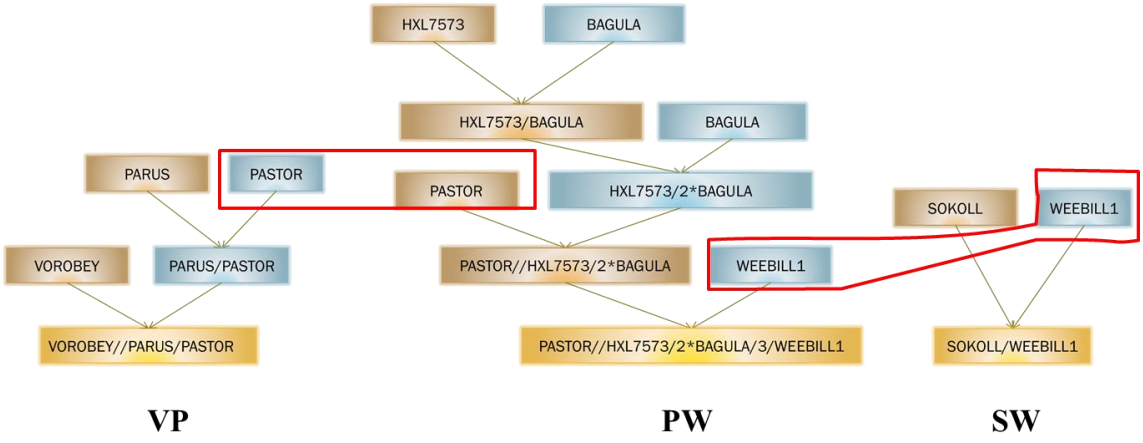

Figure III-1 : Pedigree of each one of the bread wheat recombinant inbred lines populations worked during the PhD. PW: Pastor//hxl7573/2*Bagula/3/Weebill1; SW: Sokoll/Weebill1; VP: Vorobey//Parus/Pastor. In red are indicated common ancestors between populations leading to connected population system.

b. Experimental trial network design

All trials were sown between 2011 and 2013 at one location, in the north-western Mexican desert of Sonora, in the Yaqui Valley at CIMMYT's Experimental Station, Norman E. Borlaug (CENEB) near Ciudad Obregon (Block '810'). Three treatments were applied: winter sowing Irrigated (IR) and Drought (DR), and spring sowing Heat-Irrigated (HI). The whole trial network is constituted of 15 trials and seven environments (year x treatment: 11IR, 11DR, 11HI, 12IR, 12DR, 12 HI, and 13DR). In this paper, we will refer to the seven experimental environments as the Environment. Population PW was sown six times (11IR, 11HI, 12IR, 12DR, 12 HI, and 13DR), SW five times (11HI, 12IR, 12DR, 12 HI, and 13DR) and VP four times (11DR, 11HI, 12DR, and 12 HI) (Figure III-2).

		Population		
		PW	**SW**	**VP**
Environment	**IR**	2011 2012 -	- 2012 -	- - -
	DR	- 2012 2013	- 2012 2013	2011 2012 -
	HI	2011 2012 -	2011 2012 -	2011 2012 -

Figure III-2: Table representing the trial network tested during the study in terms of population sowed (PW: Pastor//hxl7573/2*Bagula/3/Weebill1; SW: Sokoll/Weebill1; VP: Vorobey//Parus/Pastor) under three different treatments (IR: winter sowing irrigated; DR: winter sowing drought; HI: spring sowing heat irrigated)

Different traits were scored and estimated within the whole trial network: agronomic (grain yield, number of spikes per square meter, number of grains per spike, number of grains per square meter, and thousand kernel weight), phenological (heading, anthesis, physiological maturity, and other minor development stages), architectural (plant height and peduncle length), biochemical (stem water soluble carbohydrate), visual (flag leaf glaucousness), physiological (normalized difference vegetative index -NDVI- and canopy temperature -CT-). All these traits were presented and described along the manuscript within the incoming chapters of the study.

The chapter III deals with the environmental characterization of the whole trial network. It was written as a paper submitted to Agronomy Journal. The manuscrit was accepted. It summarized the methodology developed to characterize the whole environmental network. The aim of this paper was to identify the type of abiotic stress factors experienced (type, occurrence, and relative intensity) and determine how they affected agronomic traits

Tables and Figures are included in the text. Supplementary Data were added after the conclusion.

CHAPTER III: E, environmental characterization of the trial network

Clustering of Environmental Parameters Discriminates Drought and Heat Stress Bread Wheat Trials

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ABSTRACT

Wheat (*Triticum aestivum* L.) is the most widely cultivated crop worldwide and faces a wide range of stresses. To make effective crop improvement decisions, environmental characterization is of paramount importance. This study presents a new methodology for characterizing the environment that statistically incorporates the nature, timing and relative intensity of stresses, with reference to previously established stress thresholds.

Three CIMMYT bread wheat populations -combining complementary heat and drought adaptive traits- were grown over three years in NW Mexico under limited irrigation, heat stress, and optimal conditions. The network comprised 15 trials including three populations sown in seven 'treatment x year' combinations as experimental environments, referred to here as the 'Environment'.

Environmental characterization was performed at the trial scale. Twelve abiotic stress thresholds related to eight environmental factors were combined to obtain eleven potential growth limiting factors. Thirty-three environmental covariates were obtained by calculating when these limiting factors occurred for each of three key-developmental-phases across all trials of the network. Cluster analysis allowed grouping environmental covariates into six distinct clusters corresponding to six 'environmental scenarios'. One representative environmental covariate was extracted from each cluster and, taken together, they explained over 90 % of the variance for yield in the overall Environment. Principal component analysis discriminated the seven experimental

environments of the Environment and identified its stress characteristics. We conclude that the analytical method developed characterized the main stresses and their impact on average population performance. The environmental covariates established will facilitate the dissection of genotype–by-environment interaction for performance related traits.

Abbreviations

DR: Drought treatment; ET_c: Crop evapotranspiration; $ET_{c,adj}$: Adjusted crop evapotranspiration; GDD: Growing degree days; GEI: Genotype-by-environment interaction; HI: Heat-irrigated treatment; IR: Irrigated treatment; ks: Drought stress coefficient; PCA: Principal component analysis; PW: Population 1, Pastor//hxl7573/2*Bagula/3/Weebill1; QTL: Quantitative trait loci; RIL: Recombinant inbred lines; SW: Population 2, Sokoll//Weebill1; VP: Population 3, Vorobey//Parus/Pastor

INTRODUCTION

Wheat is the most widely planted cereal worldwide with more than 216 million hectares sown in 2012 (FAO, 2014a). It is grown from 15 ° to 60 °N and 15 ° to 45 °S in latitude and over a wide range of environmental conditions, encompassing variations in temperature, altitude, and rainfall (Braun et al., 2010).

Wheat faces many biotic and abiotic stresses in its environmental range (Lobell et al., 2011; Semenov and Shewry, 2011). Sensitivity to abiotic stress varies throughout the crop cycle (Slafer, 2012). Many studies confirm highly significant genotype x environment interaction (e.g. Chapman et al., 2000; Sial et al., 2000; van Eeuwijk et al., 2005; Chapman, 2007) because of the differential response of genotypes to the range of biotic or abiotic factors occurring during crop development. Clearly, well-characterized environments can improve the value of experimental data. Description of environmental constraints can be performed using either a set of environmental parameters (Voltas et al., 2005) or by establishing synthetic variables defined on probe genotypes (Cooper and Fox, 1996; Brancourt-Hulmel, 1999) based on an agronomic method of diagnosis (Sebillotte, 1980). At a given location, the crop yield is dissected into yield components (e.g., kernel per square meter until anthesis and thousand kernel weight from anthesis to maturity). These values are then compared with unstressed values for reference. It allows pinpointing which yield components are impacted by (i) the timing of the stress (e.g. if the number of grains per square meter is less than the reference value, it implies pre-anthesis stress) during the crop cycle (Slafer, 2012), and (ii) the intensity of the stress estimated as the difference between measured values under stress and the reference values. The growth constraint is then associated with environmental parameters measured during the crop cycle. For example, reduction of the number of kernels per square meter -compared to a reference value- may be concomitant with high temperature observed during the pre-anthesis growth phase (Lecomte, 2005).

Simple (Woodruff and Tonks, 1983) or multiple linear regression (Lacaze and Roumet, 2004) can help find association between agronomic variables and limiting factors. Whereas simple linear regression allows identification of direct links between these two types of variables, multiple linear regression allows the selection of a subset of environmental parameters that better explain variations of the agronomic variable of interest. However, overfitting the model is a common pitfall that should be avoided (Babyak, 2004).

Variety trials usually involve large experimental networks with different locations and years providing variation in meteorological conditions, soil types, trial management, and abiotic components (e.g. Brancourt-Hulmel et al., 2000; Lecomte, 2005). Large genotype panels have been evaluated over a range of environmental conditions to detect quantitative trait loci (QTL). In wheat, photoperiod, temperature, nitrogen stress, and the severity of stripe rust infection were the major environmental variables causing QTL for grain yield and its components to interact with environments (Campbell et al., 2004; Laperche et al., 2007, 2008; Zheng et al., 2010). In recent years, tolerance to heat and drought became major issues for wheat breeding. Brisson et al. (2010) showed that water deficit and high temperature stresses were the main factors explaining wheat yield stagnation observed in France and many other countries despite constant genetic gains since 1990's. In its 2007 report, the Intergovernmental Panel on Climate Change forecasts an increase in intensity and frequency of drought and heat stress in most regions worldwide (IPCC, 2007). It is therefore very important to develop experimental trials where the effect of drought and heat can be characterized. As genotyping is getting less and less expensive, high throughput phenotyping is now the bottleneck for genetic dissection of traits (Yang et al., 2013). The response of genotypes to drought in the field can be tested by comparing irrigated and non-irrigated plots grown in close proximity. Additionally the response to heat is often obtained by comparing different sowing dates that place growth and development in different thermal environments.

The broad aim of this paper is to describe a methodology which identifies environmental covariates associated with specific types of stress that can be used to study genotype-by-environment interaction of traits and their association with yield. The specific objectives of this study were to identify (i) the type of abiotic stress factors experienced (physical limitation to growth, duration, and relative intensity) and (ii) how they affected agronomic traits.

MATERIALS AND METHODS

Plant material

Three bread wheat populations were used in this study: (i) Population 1 consisted of a set of 196 F7:8 recombinant inbred lines (RIL) from the Pastor//hxl7573/2*Bagula/3/Weebill1 cross (PW), (ii) Population 2 consisted of a set of

228 F7:8 RILs from the Sokoll/Weebill1 cross (SW), and (iii) Population 3 consisted of a set of 266 F5:8 RILs from the Vorobey//Parus/Pastor cross (VP); all of them created at the CIMMYT (International Maize and Wheat Improvement Center) nurseries. These populations are bi-parental crosses between CIMMYT elite lines combining interesting physiological traits for drought and heat stress tolerance. Parents were chosen because the crosses had produced outstanding elite lines distributed worldwide to national programs. In this study, the term stress always refers to abiotic stress except otherwise mentioned.

Experimental design

All trials were sown between 2011 and 2013 at one location, in the north-western Mexican desert of Sonora, in the Yaqui Valley at CIMMYT's Experimental Station, Norman E. Borlaug (CENEB) near Ciudad Obregon (Block '810'). Three treatments were applied: winter sowing Irrigated (IR) and Drought (DR), and spring sowing Heat-Irrigated (HI). The whole trial network is constituted of 15 trials and seven environments (year x treatment: 11IR, 11DR, 11HI, 12IR, 12DR, 12 HI, and 13DR). In this paper, we will refer to the seven experimental environments as the Environment. Population PW was sown six times (11IR, 11HI, 12IR, 12DR, 12 HI, and 13DR), SW five times (11HI, 12IR, 12DR, 12 HI, and 13DR) and VP four times (11DR, 11HI, 12DR, and 12 HI) (Table 1).

All trials were sown using a two-replicate alpha-plan design, a partially balanced incomplete blocks design (Patterson and Williams, 1976; Dagnelie, 2012), with the parents sown in each replicate. Two types of plots were used: (i) raised bed (2.0 x 0.8 m; two rows with 0.24 m row spacing) and (ii) flat bed (3.0 x 1.6 m; eight rows with 0.2 m row spacing). Only VP11DR and VP12DR trials were sown in flat bed plots, and with a slightly modified α-plan design. VP RILs were divided in five subsets of 60 genotypes, with: (i) four subsets of 55 RILs, two parents, and three varieties as controls and (ii) one subset of 46 RILs, two parents, and three controls repeated four times. Each subset was sown in two replicates (Table 1).

Table 1: Description of the crop management system of the whole trial network grown at Ciudad Obregon (Sonora, Mexico) between 2011 and 2013. Are included the average date of sowing, the average sowing density (g m^{-2}), the irrigation pattern, the fertilization pattern and both average date of flowering and physiological maturity for all trials.

Trial code	Year	Populations[†]	Treatment[‡]	Date of sowing	Sowing density g m^{-2}	Type of bed	Irrigation pattern[§]	Fertilization pattern[¶]	Flowering	Physiological maturity
PW11IR	2011	PW	IR	19 Nov. 2010	6.3	raised	$S_{f,80} + E_{f,80} + 4 \times I_{f,80}$	$FI1_{GM} + FI2_{50N+50P} + FI3_{150N}$	24 Feb. 2011[††]	5 Apr. 2011
PW12IR	2012	PW	IR	24 Nov. 2011	6.3	raised	$Rain + E_{f,80} + 4 \times I_{f,80}$	$FI1_{GM} + FI2_{50N+50P} + FI3_{150N}$	4 Mar. 2012[#]	14 Apr. 2012
SW12IR	2012	SW	IR	24 Nov. 2011	6.3	raised	$Rain + E_{f,80} + 4 \times I_{f,80}$	$FI1_{GM} + FI2_{50N+50P} + FI3_{150N}$	1 Mar. 2012[#]	15 Apr. 2012
VP11DR	2011	VP	DR	24 Nov. 2010	10.3	flat	$S_{d,84} + E_{d,36} + I_{d,64}$	$FI1_{GM} + FI2_{50N+50P} + FI3_{150N}$	4 Mar. 2011[#]	11 Apr. 2011
PW12DR	2012	PW	DR	9 Dec. 2011	9.4	raised	$S_{f,80} + E_{f,80} + I_{d,40}$	$FI1_{GM} + FI2_{50N+50P} + FI3_{150N}$	2 Mar. 2012[#] ; 4 Mar. 2012[††]	6 Apr. 2012
SW12DR	2012	SW	DR	9 Dec. 2011	9.4	raised	$S_{f,80} + E_{f,80} + I_{d,40}$	$FI1_{GM} + FI2_{50N+50P} + FI3_{150N}$	2 Mar. 2012[#] ; 4 Mar. 2012[††]	7 Apr. 2012
VP12DR	2012	VP	DR	9 Dec. 2011	10.3	flat	$S_{d,84} + E_{d,36} + I_{d,36}$	$FI1_{GM} + FI2_{50N+50P} + FI3_{150N}$	1 Mar. 2012[#]	3 Apr. 2012
PW13DR	2013	PW	DR	29 Nov. 2012	9.4	raised	$S_{f,80}$	$FI1_{GM} + FI2_{50N+50P}$	26 Feb. 2013[#]	31 Mar. 2013
SW13DR	2013	SW	DR	29 Nov. 2012	9.4	raised	$S_{f,80}$	$FI1_{GM} + FI2_{50N+50P}$	26 Feb. 2013[#]	31 Mar. 2013
PW11HI	2011	PW	HI	24 Feb. 2011	9.4	raised	$S_{f,80} + E_{f,80} + 5 \times I_{f,80}$	$FI1_{GM} + FI2_{50N+50P} + FI3_{150N}$	27 Apr. 2011[††]	24 May 2011
SW11HI	2011	SW	HI	24 Feb. 2011	9.4	raised	$S_{f,80} + E_{f,80} + 5 \times I_{f,80}$	$FI1_{GM} + FI2_{50N+50P} + FI3_{150N}$	26 Apr. 2011[††]	23 May 2011
VP11HI	2011	VP	HI	24 Feb. 2011	9.4	raised	$S_{f,80} + E_{f,80} + 5 \times I_{f,80}$	$FI1_{GM} + FI2_{50N+50P} + FI3_{150N}$	26 Apr. 2011[††]	23 May 2011
PW12HI	2012	PW	HI	24 Feb. 2012	9.4	raised	$S_{f,80} + E_{f,80} + 5 \times I_{f,80}$	$FI1_{GM} + FI2_{50N+50P} + FI3_{150N}$	28 Apr. 2012[#] ; 29 Apr. 2012[††]	25 May 2012
SW12HI	2012	SW	HI	24 Feb. 2012	9.4	raised	$S_{f,80} + E_{f,80} + 5 \times I_{f,80}$	$FI1_{GM} + FI2_{50N+50P} + FI3_{150N}$	30 Apr. 2012[#]	27 May 2012
VP12HI	2012	VP	HI	24 Feb. 2012	9.4	raised	$S_{f,80} + E_{f,80} + 5 \times I_{f,80}$	$FI1_{GM} + FI2_{50N+50P} + FI3_{150N}$	28 Apr. 2012[#]	26 May 2012

[†] PW: Pastor//hxl7573/2*Bagula/3/Weebill1; SW: Sokoll/Weebill1; VP: Vorobey//Parus/Pastor

[‡] IR: Irrigated; DR: Drought; HI: Heat-irrigated

[§] $Y_{f/d,x}$, with Y, the irrigation applied after sowing (S), after emergence (E) or during the rest of the crop cycle (I), by flooding (f) or drip (d), and X the number of millimeter applied at the given period

[¶] Fertilization applied three times, (1) FI1, (2) FI2 and (3) FI3 along the crop cycle; N: nitrogen, P: Phosphorus; GM=green manure ~50 kg N ha^{-1}

[#] Heading date at Zadoks 5.5 (Zadoks et al., 1974; Tottman, 1987)

[††] Flowering date at Zadoks 6.1 (Zadoks et al., 1974; Tottman, 1987)

Table 2: Description of the main items used to characterize the environments at Ciudad Obregon (Sonora, Mexico): (i) the constraint characterized in our trial network, (ii) the environmental factors considered and combined with (iii) the stress thresholds to build (iv) the limiting factors. References for the stress threshold extracted from the literature and a description of the limiting factors per development phase were also included.

Constraint	Environmental factor[†]	Threshold	Name of limiting factor	Reference	Description per developmental phase
Impact of frost on plants	Tmin	<0 °C	TminLow	Based on Gate (1995) at GS stage	Number of GDD[‡] with Tmin<0 °C
High temperature stress	Tmax ks	30<x≤33 °C <1	HtSt	Based on Acevedo et al. (2002)	Number of GDD[‡] with (a) 30 °C<Tmax≤33 °C & ks<1 and (b) Tmax>33 °C
	Tmax	>33 °C			
Deficit of solar radiation	SolRad	<8.4 MJ m^{-2}	SolRadLow	Demotes-Mainard et al. (1996)	Number of GDD[‡] with SolRad<8.4 MJ m^{-2}
Evolution of the solar radiation received by crop	SolRad	-	SumSolRad	Monteith (1972), Gallagher and Biscoe (1978), and Gosse et al., (1986)	Sum of solar radiation received by the crop
Very strong wind	WdSp	>8 m s^{-1}	WdSpHigh	Allen et al. (1998)	Number of GDD[‡] with WdSp>8 m.s^{-1}
None to light drought stress	ks	>0.67	ksLightSt	-	Number of GDD[‡] with ks<0.67
Moderate drought stress	ks	0.33<x<0.67	ksModerSt	-	Number of GDD[‡] with ks ϵ]0.33; 0.67]
Strong drought stress	ks	≤0.33	ksStrongSt	-	Number of GDD[‡] with ksmber
Highly evapotranspirating atmosphere	ET0	>5 mm d^{-1}	ET0High	Allen et al. (1998)	Number of GDD[‡] with ET0>5 mm.d^{-1}
Highly drying out atmosphere	VPD	>0.95 kPa	VPDHigh	Allen et al. (1998)	Number of GDD[‡] with VPD>0.95 kPa
	HRavg	<55 %	HRavgLow	Allen et al. (1998)	Number of GDD[‡] with HRavg<55 %

[†] Tmin: minimum air temperature; Tmax: maximum air temperature; ks: drought stress coefficient; SolRad: Incident solar radiation; WdSp: wind speed; ET0: reference evpotranspiration; VPD: Vapour pressure deficit; HRavg: average relative humidity

Phenological scoring

Key developmental stages were scored according to Zadoks et al. (1974) and Tottman (1987). A stage was reached when 50% of the plants in the plot fulfilled the expected conditions. The scored stages were: emergence (Z1.2), tillering (Z2.1), stem elongation (Z3.1), booting (Z4.1), heading (Z5.5), anthesis (Z6.1), and physiological maturity (Z9.2). Eleven trials were scored for heading date and seven for anthesis (Table 1). Three of the fifteen trials were scored for both and displayed a high coefficients of determination ($r^2>0.9$ and p-value<0.05; data not shown). It allowed prediction for unscored plots to retrieve both heading and anthesis traits for the overall trial network. Phenological traits were expressed in thermal time units since sowing, i.e. growing degree days (GDD), according to the canonical form presented in McMaster and Wilhelm (1997) with a base temperature of 4.5 °C (Dhillon and Ortiz-Monasterio, 1993).

Trial management

After sowing, irrigation by flooding (~80 mm) or by drip (4 mm h^{-1}) was applied on all trials and the soil was kept wet to get a uniform emergence of plants. Under drought conditions, before emergence, around 62mm was available in the soil for plants (0-30 cm: 33 mm; 30-60 cm: 20 mm; 60-90 cm: 7 mm; 90-120 cm: 3mm). With following watering applied, total available water range from 139 mm (VP12DR) to 183 mm in PW12DR and SW12DR) (Table 1).In non-limiting water trials, i.e., IR and HI trials, several irrigations were applied regularly during the rest of the crop cycle, by flooding (Table 1). In DR trials, except for PW13DR and SW13DR, irrigation was also applied after emergence to get a full crop establishment (Table 1). For some DR trials, an extra third irrigation was applied; before booting stage (PW12DR, SW12DR and VP12DR) or between booting and heading stages (VP11DR).

Fertilizer was applied in three steps. Chronologically, it consisted of (FI1) green manure of Sesbania buried crop (*Fabaceae*) during the off-season (Jul. to Nov.) which represented the equivalent of ~50 Kg ha^{-1} of nitrogen. Then, (FI2) 50 Kg ha^{-1} of both urea and phosphorus, were applied during soil preparation before sowing. Finally, (FI3) 150 Kg ha^{-1} of urea, were applied with the first post-emergence irrigation, excepted for PW13DR and SW13DR (Table 1). Soil analyses performed at the CENEB did not revealed any mineral deficiencies, toxicities, or salinity issues at various depths

(Olivares-Villegas et al., 2007). Weeds, diseases, or pests were controlled following an appropriate and identical protocol within the trial network.

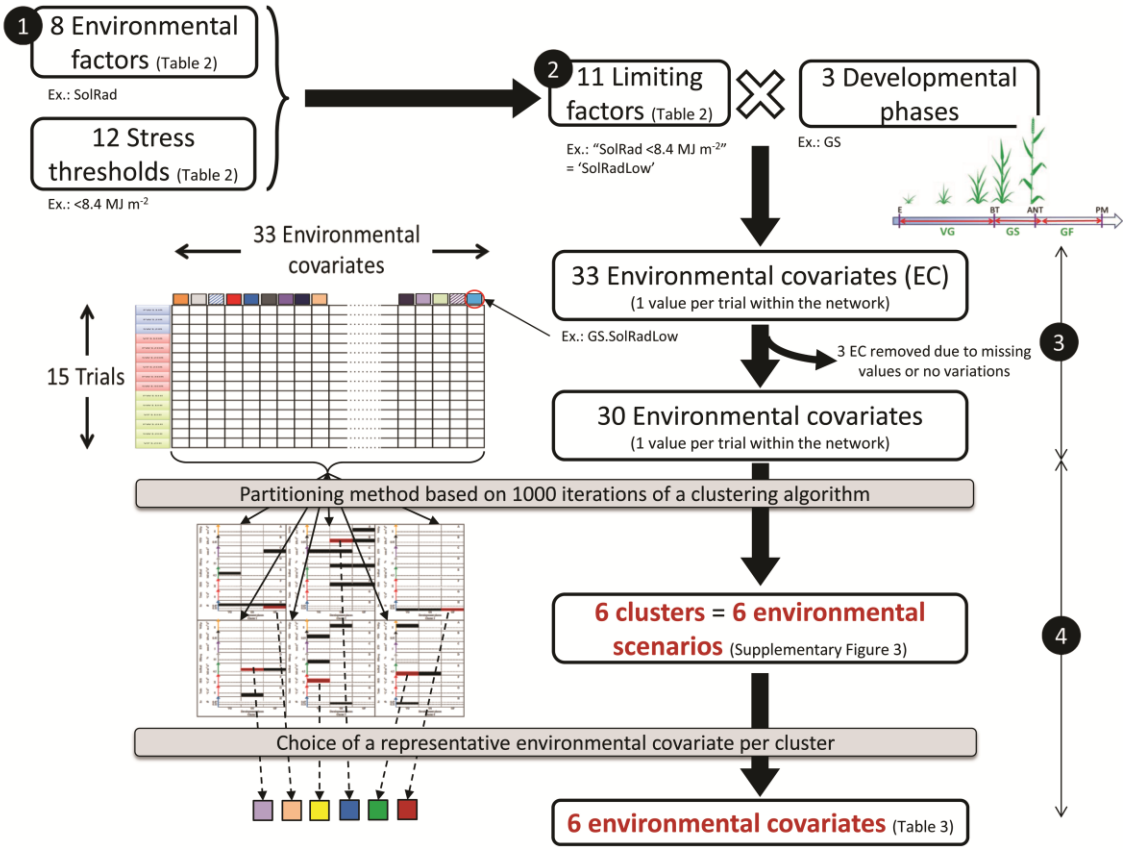


Figure 1: Diagram of the environmental characterization methodology developed. Numbers from 1 to 4 referred to the structure of the materials and methods, results and discussion parts. Examples displayed in the figure referred to Table 2. E: emergence stage; BT: booting stage; ANT: anthesis; PM: physiological maturity; VG: vegetative phase; GS: grain set phase; GF: grain filling phase.

Environmental characterization

Strategy

The environmental characterization of the trial network followed a four-step strategy. It consisted of (1) identifying the relevant environmental factors which potentially impact plants within the trial network, (2) establishing limiting factors based on thresholds of putative stresses which may have occurred within the trial network, (3) building environmental covariates by computing the frequency of each limiting factor during each developmental phase of the crop cycle, and (4) determining the best set of environmental covariates representing the Environment. At the end, the robustness of the overall characterization was tested. A detailed diagram of the strategy is presented in Figure 1, and an example referring to Table 2 was added at each step.

(1) Identification of relevant environmental factors within the whole trial network

Meteorological data

All meteorological data were taken from weather stations belonging to the CIMMYT (http://www.wunderground.com/weatherstation/WXDailyHistory.asp?ID=ISONORAC3), the PIEAES, **Patronato para la Investigación y Experimentación Agrícola del Estado de Sonora** (http://pieaes.dyndns.org/), the INIFAP, Instituto Nacional de Investigaciones Forestales, Agricolas y Pecuarias (http://clima.inifap.gob.mx/redinifap/), and the CONAGUA, Comisión Nacional del Agua (http://smn.cna.gob.mx/emas/). They were all situated at a distance of 2 to 15 km from the experimental field and a uniform and complete database was computed.

Available water for plants and daily stress coefficient

A computed water balance model was developed for bread wheat cultivated in Sonora's conditions, mainly based on the work done by Allen et al. (1998). Initial amount of water available in the soil was estimated by core soil samples of 1.2 m depth (four horizons of 30 cm) taken before the sowing of each DR trial. The water balance model was calibrated using parameters (macrorelief slope, texture of the soil, ground water level, effective soil depth, and bulk density of each horizon) determined by Verhulst et al. (2009) for "block 810". Field capacity and permanent wilting point were estimated by the CIMMYT for each considered horizon of the soil (data not shown). The main output of the model is the daily water stress coefficient (ks) that varies between 0 and 1. It is related to the adjusted crop evapotranspiration ($ET_{c,adj}$) – crop evapotranspiration (ET_c) ratio. At a given development stage, with a given estimate of available water in the soil, a wheat 'plot' (soil, evaporation; plant, transpiration) is expected to evapotranspirate ET_c, relative to a non-water-deficit-stressed wheat plot at the same development stage.(i) If plants can totally satisfy their water needs, they are not in a water deficit situation, $ET_{c,adj}=ET_c$ and ks=1, (ii) if plants cannot satisfy their water needs and the soil reached the permanent wilting point, the water deficit is total, $ET_{c,adj}=0$ and ks=0, and (iii) if plants are in water deficit, they evapotranspirate $ET_{c,adj}<ET_c$ and ks ϵ]0;1[. The intensity of the stress increases with lower values of ks. Supplementary Figure 1 shows a synthetic output of the model. Relative to transpiration

rate, ks=1 corresponds to a maximal transpiration rate. Then, with ks ϵ[0;1[, the transpiration rate decreases linearly (Allen et al., 1998b).

(2) Establishment of all relevant limiting factors

The combination of a stress threshold and an environmental factor was named limiting factors (Figure 1). For bread wheat, several abiotic stress thresholds were proposed in the literature as for example a daily solar radiation lower than 8.4 MJ m^{-2} d^{-1} (Deswarte, 2013). Indeed, during the reproductive stage (Fischer, 1985; Triboï and Ntonga, 1993; Demotes-Mainard et al., 1996; Deswarte, 2013) and especially around meiosis, i.e., from booting to booting+7 d (Demotes-Mainard et al., 1996), such a radiation level was shown to cause spike fertility issues. The full list of abiotic stress thresholds found in the literature is available in Table 2. Three thresholds were arbitrarily established for water deficit stress corresponding to a continuous increase of drought intensity: ks>0.67, none to light water deficit stress; 0.33<ks≤0.67, moderate water deficit stress; and ks≤0.33 strong water deficit stress. High temperature stress thresholds were designed by the experiment as described in the results section.

Canopy temperature was scored using a calibrated infrared thermometer 'Hand-Held Infrared Thermometer Sixth Sense LT300' (http://www.instrumart.com/assets/lt300.pdf). It was scored regularly during plant development, for all the genotypes in all trials. It was scored around noon (10 am-2 pm), when air temperature was relatively stable and around its daily maximum (Pietragalla, 2012). The air temperature was measured at the beginning and end of every canopy temperature scoring on a trial at a given date.

(3) Establishment of relevant environmental covariates

An environmental covariate corresponds to a limiting factor whose frequency had been computed for a given developmental phase (Figure 1). The observed crop cycles were divided into three consecutive and non-overlapping developmental phases: (i) the vegetative phase, from emergence to booting (Z4.1), (ii); the grain set phase, from booting to anthesis+7 d; and (iii) the grain filling phase, from anthesis+7 d to physiological maturity (Zadoks et al., 1974; Tottman, 1987; Slafer, 2012). A time scale in number of GDD was computed to take into account differences in developmental phase lengths between trials. To build the set of environmental covariates, the frequency of occurrence of every limiting factor was computed on a daily basis for every trial at every given developmental phase. If the threshold was reached, the day was taken into

account for the calculation of the environmental covariates, either as a number of days or a number of thermal units. For example, "GS.SolRadLow" is an environmental covariate which recorded for each trial of the network the "number of GDD during the grain set phase where SolRad<8.4 MJ m^{-2} (=SolRadLow), i.e., deficit of solar radiation during the grain set phase" (Figure 1; Table 2)

(4) Determining the best set of environmental covariates representing the Environment

In order to determine the most appropriate number of k-cluster among the environmental covariate dataset, i.e., the number k of cluster which structure the environmental dataset, we combined a partitioning-based method (1000 iterations of a clustering algorithm) with the estimation of the sum of variance within groups for all values of k-groups, with k ϵ [1; n-1] and n, the number of trials (n=15) (Supplementary Figure 2; Supplementary Figure 3).

Within each cluster, environmental covariates exhibited a high level of correlation (data not shown). Because of that, the most representative variable was extracted from each cluster, by using the partitioning around medoid (pam) procedure of the R package 'cluster'. This representative variable was called a medoid and corresponded to the 'barycentric variable' of the cluster (Maechler et al., 2013), i.e. displaying the minimal average dissimilarity to all other variables. A set of k-representative environmental covariates was identified and used in analysis. They were named EC1 for the representative environmental covariate of the cluster 1, EC2 for cluster 2, *etc.* (Table3; Supplementary Table 1).

Testing of the environmental characterization methodology

Before applying the environmental characterization methodology (i.e., choice of the environmental factors, choice of the stress thresholds, and the identification of the six environmental covariates representing the whole trial network) to the entire set of trials, we tested the robustness of the methodology. To this end, we focused on two points: (i) Do these six environmental covariates provide us with a better way of discriminating each experimental environment constituting the Environment than agronomic data does? (ii) How do they explain the Environment term in an analysis of variance?

Agronomic traits dataset

Plant height, grain yield at 0 % moisture and thousand kernel weight were scored in the field on the whole trial network. The number of spikes per square meter was scored in the whole trial network excepted for PW11IR, VP11DR, and VP12DR. The average number of kernels per spike and the number of kernels per square meter were computed per plot using previously scored variables. Protocols of the CIMMYT (Pask et al., 2012) were applied for the scoring of all agronomic traits, excepted for the number of spikes per square meter. Tillers with spikes were counted using a 25 cm-width U-gauge mark within each one of the two rows of a plot. We only considered averaged values for all genotypes within a trial. Missing values for spikes per square meter, and as a consequence, for grains per spike and kernel per square meter, were handled using a principal component analysis (PCA) model with the 'missMDA' procedure in the R missMDA package (Husson and Josse, 2013).

Raw phenotypic data were adjusted for field effects. For each trial, row-column design mixed models were computed to get best linear unbiased predictions, with replication as fixed effect and genotypes, row and column coordinates, sorted by replication, as random effects. Finally, a matrix was created containing mean trait values of the eight agronomic traits scored for the fifteen trials constituting the network (Table 3).

Environmental covariates dataset

A principal component analysis was performed per type of dataset, i.e., agronomic and reduced environmental covariates datasets (Table 3), using the PCA procedure of the R 'FactoMineR' package (Husson et al., 2013). In both PCA, the fifteen trials were considered as the individuals and variables were either the eight agronomic traits or the representative environmental covariates.

For a given agronomic trait, two ANOVA models were performed using Table 3 values. First models enabled to estimate the experimental environments, i.e. the Environment, sum of square compared to the total sum of square. The following fixed model was built:

$$Y_{ij} = \mu + G_i + E_j + \varepsilon_{ij}$$

where Y_{ij}, the average phenotypic value (for example the grain yield) of the population G_i in the Environment E_j (year x treatment) and ε_{ij} the residual. Second models enabled

to estimate the part of the Environment sum of square explained by each representative environmental covariate with the following fixed model:

$$Y_{ik} = \mu + G_i + \sum_{k=1}^{6} ECk + \varepsilon'_{ik}$$

where ECk the representative environmental covariate of the cluster k (k=1…6) replaced the Environment term (year x treatment) and ε'_{ik} the residual variance.

Joint analysis between agronomic and environmental data

Simple and multiple linear regression analyses were performed to explain the agronomic traits using the six representative environmental covariates. The final multiple linear regression retained to explain a given agronomic variable was obtained by testing successively each one of the six environmental covariates and keeping at each stage the better correlated one (stepwise forward regressions). The procedure was stopped at the last significant environmental covariate ($p<0.05$).

Software

All statistical analyses were performed using R.2.13.2 (R Development Core Team, 2011). Data adjustment analyses were performed using also the ASReml-R package v3.0.1 (Butler et al., 2009).

Table 3: Description of the two datasets characterizing the trial network (i) average of the main agronomic traits scored and (ii) the six clusters representative environmental covariates, ECx with xϵ[1;6], representing the whole environment for three different bread wheat populations grown at Ciudad Obregon (Sonora, Mexico) from 2011 to 2013

Trial code[#]	Agronomic traits[†]								Environmental covariates[§]					
	YLD	SM2	GSP	KM2	TKW	PH	HD	PM	EC1	EC2	EC3	EC4	EC5	EC6
									GF.ksModerSt[¶]	GS.VPDHigh[#]	GF.ksStrongSt[††]	GS.SumSolRad[‡‡]	VG.HtSt[§§]	VG.SolRadLow[¶¶]
	g m^{-2}	spikes m^{-2}	grains spike^{-1}	grains m^{-2}	g	cm	GDD[##]	GDD[##]	GDD[##]	GDD[##]	GDD[##]	MJ m^{-2}	GDD[##]	GDD[##]
PW11IR	596	324[‡]	42.8[‡]	13,707	43.8	98	1089	1702	236	15.6	179.8	656.7	0	0
PW12IR	943	362	55	19,721	48	107	1115	1755	281.6	0	93.9	641.2	0	33.4
SW12IR	849	358	50	17,661	48.4	112	1142	1768	255	0	107.2	672	0	33.4
VP11DR	215	223[‡]	26.3[‡]	6990	31.3	69	1147	1712	0	59.8	426.2	924.8	0	0
PW12DR	392	328	36	11,569	34	80	974	1442	0	0	358.9	541.6	0	23.2
SW12DR	380	300	34	10,220	37.3	82	979	1462	0	0	348.2	572.9	0	23.2
VP12DR	258	293[‡]	25.7[‡]	8034	32.2	75	959	1403	0	0	329	537	0	23.2
PW13DR	245	269	25.7	6825	36	75	1028	1502	0	0	341.8	549.9	0	80.4
SW13DR	236	260	24.7	6344	37.5	72	1031	1501	0	0	341.8	496.9	0	80.4
PW11HI	349	336	29.7	9888	35.7	84	900	1444	165.5	307.5	35.3	466.1	68.3	0
SW11HI	387	311	33	10,142	38.4	85	900	1432	185.1	287.9	35.3	441	100.8	0
VP11HI	417	358	31	10,790	39	93	882	1433	187.4	287.9	52.1	441	68.3	0
PW12HI	227	266	25.7	6796	33.9	69	943	1512	196.6	308.3	130.5	470.2	16.8	0
SW12HI	276	305	27.2	8179	33.6	71	981	1558	195.5	351.6	68.2	524.8	16.8	0
VP12HI	325	314	29.4	9043	36.2	82	938	1533	217.8	308.3	89.3	470.2	16.8	0

[†] YLD: Grain yield; SM2: Number of spikes per square meter; GSP: Number of grains per spikes; KM2: Number of kernel per square meter; TKW: Thousand kernel weight; PH: Plant height; HD: Heading date at Zadoks 5.5 (Zadoks et al., 1974; Tottman, 1987); PM: Physiological maturity

[‡] Estimated data using missMDA procedure (Husson and Josse, 2013)

[§] ECx: Representative Environmental Covariate of the cluster 'x', xϵ[1;6]

[¶] GF.ksModerSt: Number of growing degree days during the grain filling phase where 0.33<ks<0.67, i.e., moderate drought stress during GF phase

[#] A trial is defined as a combination of population x year x treatment (e.g. PW12IR).

[#] GS.VPDHigh: Number of growing degree days during the grain set phase where VPD>0.95 kPa, i.e., highly drying out atmosphere on vapour pressure deficit coefficient during GS phase

[††] GF.ksStrongSt: Number of growing degree days during the grain filling phase where ks≤0.33, i.e., strong drought stress during GF phase

[‡‡] GS.SumSolRad: Sum of solar radiation received by crop during the grain set (GS) phase

[§§] VG.SolRadLow: Number of growing degree days during the vegetative phase where SolRad<8.4 MJ m-2, i.e., lack of solar radiation during VG phase

[##] Growing degree days

RESULTS

In this paper, we will refer to the seven experimental environments as the Environment.

The trial network

Average trial grain yield ranged from 215 g m^{-2} for the population VP under drought in 2011 (i.e. VPDR11) to 943 g m^{-2} for the population PW under irrigated treatment in 2012 (PW12IR) (see Table 3). On average, higher yield was observed under IR (796 g m^{-2}) than under DR (288 g m^{-2}) or HI (330 g m^{-2}) treatments. In stressed treatments, lower values for yield components, plant height and phenology were observed compared with the irrigated treatment. For example, when comparing IR with DR treatments for the population PW in 2012, decreases were observed in the number of spikes per square meter (9%), number of grains per spike (36%), plant height (25%), and heading date (13%). On the other hand, despite different treatments, some trials show similar mean values for traits (Table 3), despite significant GxE (as will be shown in subsequent publications). For a given experimental environment, the phenology of the three populations was similar and the range was 7-10 days.

Environmental characterization

(1) Identification of relevant environmental factors within the whole trial network

Within this trial network, eight environmental factors were considered relevant (Supplementary Figure 4): (1) the minimum, and (2) maximum air temperatures, (3) incident solar radiation, (4) average wind speed, (5) the reference evapotranspiration, (6) vapour pressure deficit, (7) relative humidity, and (8) the drought stress coefficient (Table 2). IR and HI trials were similar in the drought stress coefficient (ks) pattern at each development stage. In comparison with IR and HI, the ks for DR trials decreases progressively during the crop cycle (data not shown).

(2) Establishment of all relevant limiting factors

Based on the eight environmental factors identified, we established a list of 10 stresses that can be quantified, such as the ‘impact of frost’ on plants (Table 2). The combinations of a stress threshold and an environmental factor were named limiting factors (Figure 1). Most of the thresholds we used were extracted from the literature.

Canopy temperature as an aid to establish high temperature stress thresholds

Canopy temperature and air temperature were compared in limiting (DR) and non-limiting (IR and HI) water treatments (Figure 2). A strong linear relationship existed between canopy and air temperatures: in DR, $r^2=0.72$ ($p<0.01$) and in IR/HI, $r^2=0.67$ ($p\leq0.01$). In both cases, air temperature was always higher than canopy temperature. As proposed by Acevedo et al. (2002) based on physiological data, a canopy temperature above 26 °C was considered harmful for plant and grain development. Based on our regression lines, this corresponded to 30 °C (DR) and 33 °C (IR/HI) air temperatures. The two thresholds were then used to define heat stress occurrence as: Tmax≥33°C if ks=1 and Tmax≥30 °C if ks<1 (Table 2). A list of 12 stress thresholds was established. When combining the eight environmental factors to the twelve stress thresholds, eleven limiting factors were created Table 2.

(3) Establishment of all relevant environmental covariates

Sensitivity of wheat to stress was established during the crop cycle. The frequency of 11 limiting factors was computed during the three development phases in the 15 trials that constituted the network. A matrix was created with 33 environmental covariates (11x3) in columns and the 15 trials in rows. Three environmental covariates were removed because of missing values and/or without variations between trials (Figure 1).

(4) Determining the best set of environmental covariates representing the Environment

Despite a unique meaning of each of the 30 environmental covariates, first analyses on the environmental covariate matrix revealed a high level of redundancy within the trial network (data not shown). A clustering analysis was then performed to organize all environmental information.

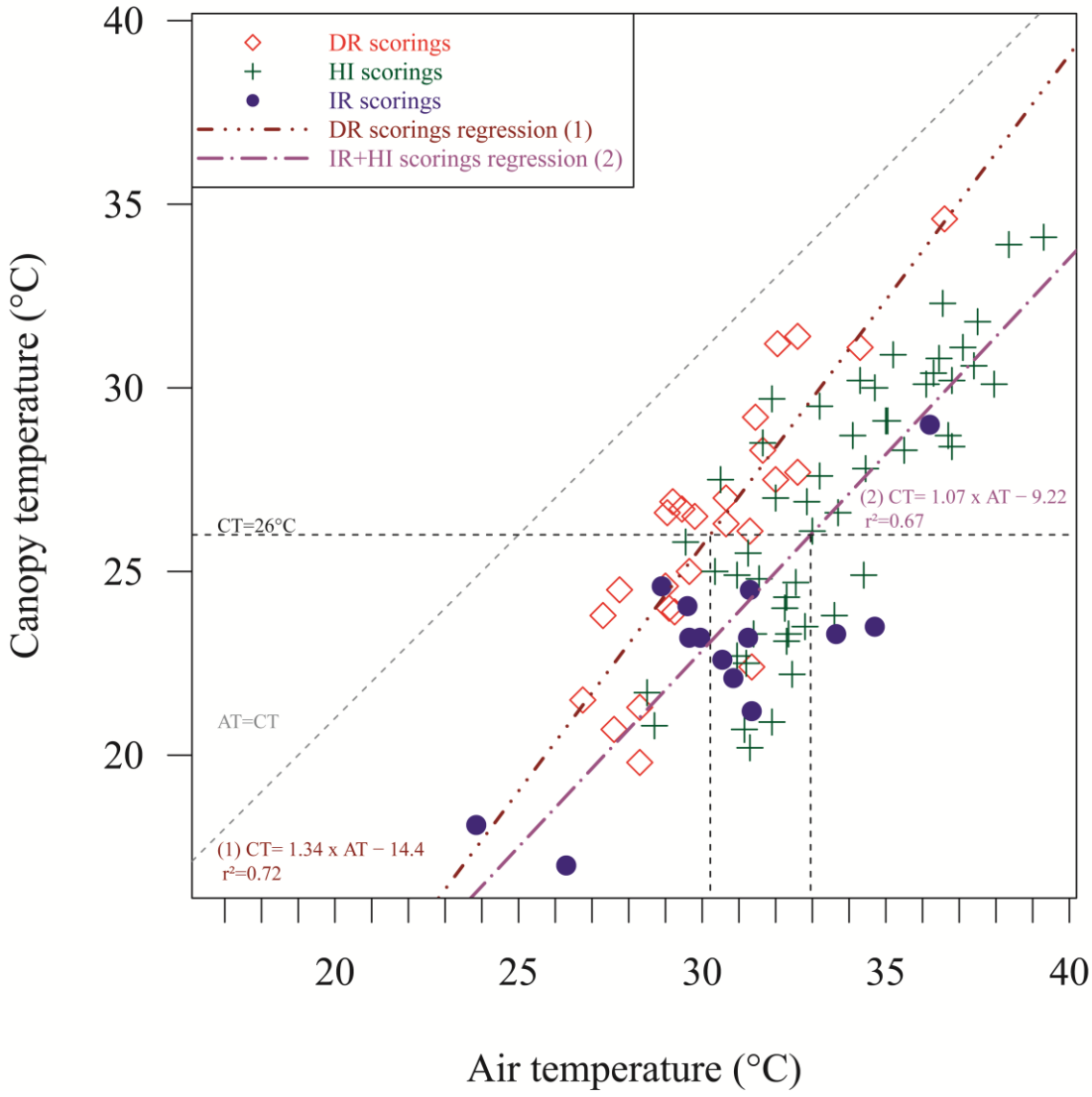


Figure 2: Plot of the relation between canopy temperature (CT) and air temperature (AT) measured on irrigated (IR), drought (DR) and heat-irrigated (HI) environments. Canopy temperatures were averaged over all adjusted canopy temperatures measured on a given day on a trial. For a given canopy temperature scoring on a trial at a given date, a mean air temperature was computing with air temperatures scorings taken when starting and ending the whole trial. Empty diamonds represents canopy temperatures scored in DR treatment, Greek crosses, canopy temperatures scored in HI treatment and bullet points, canopy temperatures scored in IR treatment. Two linear regressions were performed and drawn respectively for (1) water limiting (i.e., DR) and (2) water non-limiting (i.e., IR and HI) treatments.

Clustering the whole environmental covariate dataset

The best number of k-clusters identified was k=6. This value was based on the minimum sum of variance within groups (Supplementary Figure 2), but respecting the parsimony principle. Indeed, as the Environment is constituted by seven experimental environments (combination year x treatment: 11IR, 11DR, 11HI, 12IR, 12DR, 12HI, and 13DR), the number of environmental covariates determined cannot exceeded 7-1=6 variables. Six clusters of environmental covariates represented the main environmental

scenarios experienced by plants during their growing cycle (Supplementary Figure 3). For example, cluster 1 constituted six environmental covariates. It was described as: "Zero to light drought stress from vegetative to grain filling phases (ks>0.67), associated with a high level of incident solar radiation during the vegetative phase, a highly evaporating atmosphere (ET0>5 mm d^{-1}) and moderate drought stress (0.33<ks≤0.67) during the grain filling phase". It was simplified as "Zero to light drought stress from vegetative to grain filling phase". Cluster 2 was described as "heat stress during grain set and grain filling phases", cluster 3 as "strong drought stress from vegetative to grain filling phases", cluster 4 as "frost in grain set phase and the solar radiation in grain set and grain filling phases", cluster 5 as "heat stress in vegetative phase associated with moderate drought stress in grain set phase" and cluster 6 as "deficit of solar radiation in vegetative and grain set phase and moderate drought stress in vegetative phase" (Supplementary Table 1; Supplementary Figure 3).

Identifying the best environmental covariates dataset

Within each cluster, environmental covariates were highly correlated (data not shown). A representative environmental covariate was identified within each cluster (Supplementary Table 1; Table 3). The environmental covariate 'GF.ksModerSt', so called EC1, represented cluster 1 (Table 3; Supplementary Table 1; Supplementary Figure 3). It corresponds to the "number of GDD during the grain filling phase where 0.33<ks<0.67", i.e., moderate drought stress during the grain filling phase.

Testing of the environmental characterization methodology

These six representative environmental covariates aim at representing the Environment in analysis (Figure 1). To test this, first a PCA on agronomic data was performed (Table 3; Figure 3). The first two axes of the PCA explained more than 95 % of the overall variation with 75.4 % attributed to the first axis and 20.1 % to the second axis. All agronomic variables were in the same quadrant on the PCA plot. All yield components and plant height were strongly associated with grain yield, ranging from r=0.75 (p≤0.01) for the number of spikes per square meter to r=0.99 (p≤.001) for the kernel per square meter (Figure 3; Table 4). This PCA also enabled discrimination of five experimental environments: 11IR, 12IR, and 11DR and to a lesser extent, 13DR and 11HI. However it did not discriminate 12HI and 12DR.

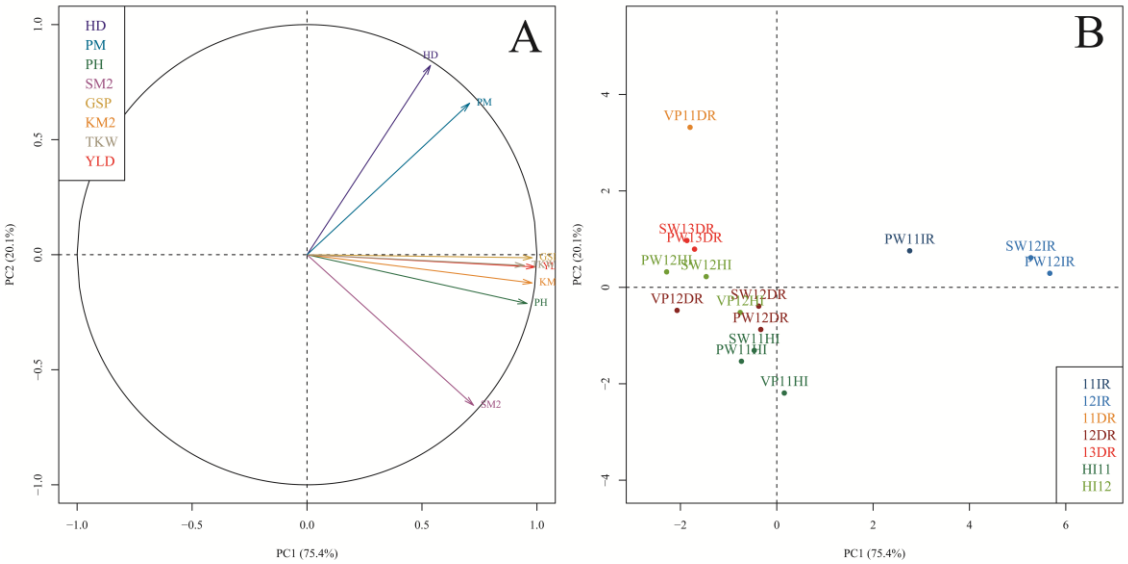


Figure 3: Plots of variables (A) and individuals (B) of the principal component analysis (PCA) performed with the agronomic data. Agronomic traits dataset presented in Table 3 was used to perform the PCA. Grain yield (YLD), heading date (HD), physiological maturity (PM), plant height (PH), thousand kernel weight (TKW), number of kernel per square meter (KM2), number of grains per spike (GSP) and number of spikes per square meter (SM2). Only principal component 1-principal component 2 plan is drawn. The percentage of variation accounted by each principal component is indicated between brackets on each axis.

Then, a PCA was performed on the six representative environmental covariates (Table 3; Figure 4). The first two axes of the PCA explained more than 78.4 % of the overall variation with 59.6 % attributed to the first axis and 18.8 % to the second axis. Environmental covariates explore each quadrant of the PCA plot. These six environmental covariates were not totally independent as several strong correlations existed (Figure 4). EC1, EC2 and EC5 in one direction, and EC3 and EC6 in the other, strongly contributed to the first axis. The second principal component was mainly defined by EC4. The first axis allowed discrimination of all HI environments in the direction of EC1, EC2 and EC5. In the opposite direction (toward EC3 and EC6) on first axis, 12DR and 13DR were plotted separately. The second axis enabled the discrimination of 11DR (EC4). EC4 and EC1 discriminated 11IR from 12IR (Figure 4; Supplementary Table 1). This PCA enabled the discrimination of all seven experimental environments constituting the Environment.

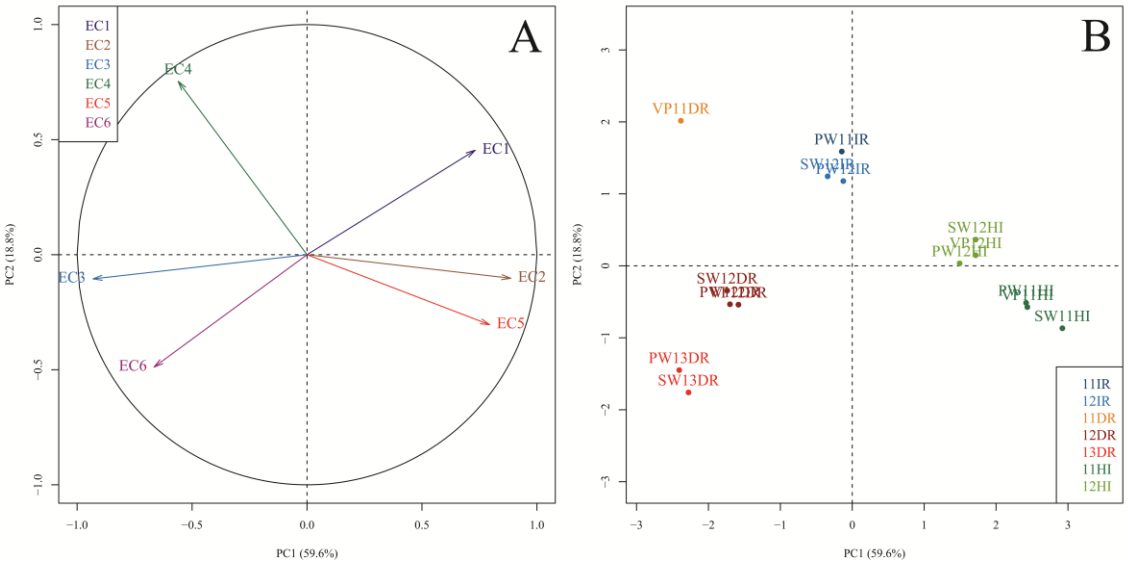


Figure 4: Plots of variables (A) and individuals (B) of the principal component analysis (PCA) performed with the six cluster representative environmental covariates (ECx, with xε[1;6]). Environmental covariates dataset presented in Table 3 was used to perform the PCA. Each environmental covariate is representative a cluster of environmental covariates displayed in Supplementary Figure 4. Only principal component 1-principal component 2 plan is drawn. The percentage of variation accounted by each principal component is indicated between brackets on each axis, i.e., the principal components.

Does the reduced environmental covariate dataset efficiently replace the Environment term in an analysis of variance?

Two ANOVA models were performed for yield (Table 5) and yield components. The total sum of square decomposition of grain yield was shared between the population effect (8.7 %, p≤0.05), the Environment effect (88.1 %, p≤0.001) and the residual (3.2 %) (Table 5-1). The environment was then replaced by a linear combination of the six representative environmental covariates. Only two were significant: 39.5 % (p≤0.01) for EC1 and 50.8 % (p≤0.001) for EC2 (Table 5-2). 90.3 % of the Environmental variance was explained using 67% less degrees of freedom, i.e., two covariates significant. These two significant environmental covariates explained from 82 % (number of spikes per square meter) to 99 % (thousand kernel weight) of the environmental variance (data not shown).

Do environmental covariates predict agronomic data?

EC1 and EC4 were the only two environmental covariates displaying positive correlations with agronomic traits. Within our trial network, EC1 was associated with higher yields (r=0.63; p≤0.05), taller plants (r=0.65; p≤0.01), and higher yield

components (Supplementary Table 1; Table 4). In EC4, phenological traits were delayed: heading (r=0.86; p≤0.001) and physiological maturity (r=0.74; p≤0.01) (Supplementary Table 1; Table 4). Plants headed early in EC2 (r=-0.67; p≤0.01) and EC5 (r=-0.68; p≤0.01). The number of spikes per square meter tended to decrease in EC3 (r=-0.65; p≤0.01) (Supplementary Table 1; Table 4).

Table 4: Matrix of correlation coefficients (r) among agronomic traits and between agronomic traits and the six clusters representative environmental covariates over populations and treatments.

		Agronomic traits†							
		YLD	SM2	GSP	KM2	TKW	PH	HD	PM
Agronomic traits†	SM2	0.75**							
	GSP	0.98***	0.71**						
	KM2	0.99***	0.79***	0.99***					
	TKW	0.94***	0.68**	0.9***	0.89***				
	PH	0.95***	0.83***	0.92***	0.94***	0.94***			
	HD	0.49ns	-0.14ns	0.52*	0.43ns	0.46ns	0.34ns		
	PM	0.66**	0.11ns	0.67**	0.6*	0.62*	0.54*	0.89***	
Environmental covariates‡	EC1	0.63*	0.64**	0.57*	0.61*	0.64*	0.65**	0.02ns	0.45ns
	EC2	-0.32ns	0.1ns	-0.37ns	-0.3ns	-0.3ns	-0.24ns	-0.67**	-0.33ns
	EC3	-0.38ns	-0.65**	-0.3ns	-0.38ns	-0.41ns	-0.46ns	0.37ns	-0.06ns
	EC4	0.23ns	-0.31ns	0.29ns	0.22ns	0.12ns	0.12ns	0.86***	0.74**
	EC5	-0.12ns	0.29ns	-0.16ns	-0.09ns	-0.06ns	0.05ns	-0.68**	-0.45ns
	EC6	0.02ns	-0.21ns	-0.01ns	-0.06ns	0.16ns	-0.05ns	0.32ns	0ns

*, **, *** Significant at the 0.05, 0.01, and 0.001 level of probability, respectively; ns: non-significant at 0.05 level of probability

† YLD: Grain yield; SM2: Number of spikes per square meter; GSP: Number of grains per spikes; KM2: Number of kernel per square meter; TKW: Thousand kernel weight; PH: Plant height; HD: Heading date at Zadoks 5.5 (Zadoks et al., 1974; Tottman, 1987); PM: Physiological maturity

‡ ECx: Representative Environmental Covariate of the cluster 'x', xϵ[1;6]

Multiple linear stepwise forward regressions were performed to estimate the best combination of environmental scenarios explaining each agronomic trait (Table 6). Coefficients of multiple determination (R^2) ranged from 0.66 (spikes per square meter) to 0.99 (physiological maturity date). All models were significant (at least at p≤0.05). Between two and four environmental covariates were involved in each model. Cluster 1 was the most often involved (EC1: 35 %), then cluster 2 (EC2: 26 %), cluster 3 and 5 (EC3=EC5=13 %), cluster 6 (EC6=9 %) and cluster 4 (EC4=4 %). EC1 and EC2 went back frequently within the models, i.e., 75 % of times. For grain yield, the multiple linear regression model included successively, a none to light drought stress cluster throughout the crop cycle (EC1), associated with a heat stress cluster from grain set to grain filling phases (EC2) and finally strong drought stress along the whole crop cycle (EC3) as: yield = $6.68x10^2$ + 1.04 EC1 – 1.51 EC2 – 1.03 EC3 (R^2=0.89, p≤0.05) (Table 6). In our trial network, grain yield was mainly positively determined by occurrence of cluster 1, i.e., zero to light drought stress from vegetative to grain filling phase with

moderate drought stress in grain filling phase. It was negatively impacted then first by heat stress occurring during grain set and grain filling phases, i.e., cluster 2, and by strong drought stress from vegetative to grain filling phases.

Table 5: Tables of analyses of variance for YLD with G, the effect of the population (PW, SW or VP), E, the effect of the environment (Year x Treatment; Ex.: 12IR, 13DR …), ECx with xϵ[1;6], the six clusters representative environmental covariates, and ε and ε', the residuals

(1) YLD=μ+G+E+ε

Tested effect	df	SS†	MS‡	Fvalue	Significance threshold
G	2	60,379	30,190	8.0418	*
E	6	611,011	101,835	27.1263	***
ε	6	22,525	3754		

(2) YLD=μ+G+EC1+EC2 ... +EC6+ε'

Tested effect	df	SS†	MS‡	Fvalue	Significance threshold
G	2	60,379	30,190	4.2140	ns
EC1	1	241,375	241,375	33.6921	**
EC2	1	310,340	310,340	43.3186	***
EC3	1	23,910	23,910	3.3374	ns
EC4	1	10,981	10,981	1.5328	ns
EC5	1	22	22	0.0031	ns
EC6	1	3923	3923	0.5476	ns
ε'	6	42,985	7164		

*, **, and *** Significant at the 0.05, 0.01, and 0.001 level of probability, respectively; ns: non-significant at 0.05 level of probability

† Sum square

‡ Mean square

Table 6: Best multiple linear stepwise forward regressions models of agronomic traits using combinations of some of the six clusters representative environmental covariates, ECx with xϵ[1;6]. R^2 corresponds to coefficient of multiple determination of the best model. For example: YLD = $6.68x10^2$ + 1.04 EC1 – 1.51 EC2 – 1.03 EC3, with R^2=0.89. All models were significant at p≤0.05.

Agronomic traits†	R^2	Multiple linear stepwise forward regression models
YLD	0.89	$6.68x10^2 + 1.04x10^0$ EC1 – $1.51x10^0$ EC2 – $1.03x10^0$ EC3
SM2	0.66	$3.99x10^2 – 3.38x10^{-1}$ EC3 – $2.02x10^{-1}$ EC2
GSP	0.83	$2.93x10^1 + 7.93x10^{-2}$ EC1 – $4.95x10^{-2}$ EC2
KM2	0.78	$8.54x10^3 + 3.37x10^1$ EC1 – 1.92 $x10^1$ EC2
TKW	0.90	$4.59x10^1 + 1.91x10^{-2}$ EC1 – $3.71x10^{-2}$ EC2 – $3.03x10^{-2}$ EC3
PH	0.86	$7.63x10^1 + 1.16x10^{-1}$ EC1 – $8.67x10^{-2}$ EC2 + $1.80x10^{-1}$ EC5
HD	0.98	$6.16x10^2 + 5.81x10^{-1}$ EC4 + $1.37x10^0$ EC6 + $3.21x10^{-1}$ EC1 – $4.86x10^{-1}$ EC5
PM	0.99	$9.80x10^2 + 7.85x10^{-1}$ EC4 + $8.54x10^{-1}$ EC1 + $1.30x10^0$ EC6 – $5.93x10^{-1}$ EC5

† YLD: Grain yield; SM2: Number of spikes per square meter; GSP: Number of grains per spikes; KM2: Number of kernel per square meter; TKW: Thousand kernel weight; PH: Plant height; HD: Heading date at Zadoks 5.5 (Zadoks et al., 1974; Tottman, 1987); PM: Physiological maturity

DISCUSSION

Three RIL populations were studied within a network of fifteen trials under three different treatments (winter sowing both irrigated and rain-fed, and spring sowing irrigated) between 2011 and 2013. A methodology to characterize the Environment was established and, then, tested. The environmental characterization methodology was structured into four consecutive steps (Figure 1). The testing step enabled the potential of such environmental covariates to be assessed.

Other studies performed similar levels of advanced characterization of the experimental environment (Brancourt-Hulmel, 1999; Brancourt-Hulmel et al., 2000; Campbell et al., 2004). These studies differed from ours, in the type of covariates, i.e., raw data or processed data considering stress thresholds and their nature, i.e., pure environmental covariates or agronomic and environmental covariates mixed, and also on the period of the cycle, i.e., a specific-period of stress known or no *a priori* consideration. Such methodologies were applied on winter wheat trial networks in France and Nebraska, USA. In 2004, Campbell et al. built environmental covariates based on meteorological data *per se*, i.e., without using thresholds, whereas Brancourt-Hulmel et al. (2000) used stress thresholds applied to meteorological data *per se*. Environmental covariates of Brancourt-Hulmel (1999) and Brancourt-Hulmel et al. (2000) were not only climate based covariates, but also agronomic (deviation from yield component reference values of probe genotypes) and biological (disease score). Crop cycle periods used to build the environmental covariates also differed. Campbell et al. (2004) divided the crop cycle into three consecutive and non-overlapping development phases, similar to those presented here. Brancourt-Hulmel (1999) and Brancourt-Hulmel et al. (2000) considered (i) two development stages for agronomic based environmental covariates (i.e., pre- and post-anthesis), and (ii) specific periods to which stress threshold were applied (e.g.: sum of solar radiation from ear 1 cm (Z3.0) to flowering). Our methodology tries to combine the best from both of these studies: (i) no assumptions were made that a given cofactor has an influence on a specific phase (Campbell et al., 2004), (ii) stress thresholds were based on proven yield limiting climatic factors (Brancourt-Hulmel et al., 2000), and (iii) not considering agronomic-derived environmental covariates from probe genotypes but using only environmental covariates to be free to apply this methodology to any genotypes. Both studies used

established covariates to dissect GEI. However, the part of the environment explained by their respective covariates was not described.

Establishment of environmental covariates to quantify the stress experienced by plants

We used twelve stress thresholds in this study. Several papers have considered a temperature threshold for wheat of around 25/26 °C (Brancourt-Hulmel et al., 2000; Acevedo et al., 2002; Wahid et al., 2007). The Acevedo et al. (2002) threshold is based on physiological data, namely when leaf temperature reaches 26 °C, photosynthesis is negatively affected, while the Brancourt-Hulmel et al., 2000 threshold referred to air temperature of 25 °C. Our analyses lead to the establishment of two air temperature thresholds, i.e., for water limiting and non-limiting conditions, respectively. This is because under water limited conditions air temperature and plant temperature are quite close, while under irrigated conditions plant temperature may be several degrees cooler due to transpiration, especially at high vapour pressure deficit (Amani et al., 1996). Nonetheless, in Sonora, transpiration is not sufficient to prevent heat stress effects at air temperatures above 33 °C, even under non-limiting water conditions (Figure 2). In summary, a single air temperature threshold cannot be reasonably defined considering the wide range of wheat water regimes worldwide. Thresholds might also depend on growing conditions, breeding history, genetic background and acclimation of the genotypes.

Two plants experiencing different stresses can display similar agronomic values based on both their timing of sensitive phenological stages and their differential sensitivity to abiotic stress (Slafer, 2012). The stronger the stress during a given development phase, the lower the yield component is expressed during this period. The number of spikes per square meter and plant height, both established during vegetative and grain set phases, were higher for PW11HI than for PW12HI. Yet, PW11HI and PW12HI experienced similar heat stress conditions during grain set and grain filling phases (EC2), but PW11HI experienced a higher occurrence of heat stress during vegetative stage (EC5), and PW12HI a higher occurrence of intense drought stress during the crop cycle (EC3) (Figure 4; Table 3). The intense water deficit occurring in PW12HI reduced plant tiller production (and/or increased tiller abortion) (Gaudillère and Barcelo, 1990). According to Zadoks et al. (1974), Tottman (1987) and Slafer (2012), wheat plant height is set between the terminal spikelet stage (Z3.0) and around a

week after anthesis, when the peduncle stops growing. A drought stress event occurring during this period reduces plant water uptake, leading to less turgor pressure within plant cells which reduces cell expansion, and consequently to shorter plants.

The six representative environmental covariates allowed a better discrimination of the Environment

An attempt to discriminate the seven experimental environments constituting the Environment was performed with agronomic traits (Figure 3) and with the six representative environmental covariates (Figure 4). PCA revealed the superiority of the reduced environmental dataset on the agronomic dataset. Indeed, it enabled discriminations of all seven environments, whereas PCA on agronomic data only discriminated five. Some trials experienced totally different types of stress during the crop cycle such as PW13DR (moderate (EC6), to strong drought stress in vegetative stage, and strong drought stress in grain set and grain filling phase, (EC3)) and PW12HI (heat stress, i.e., EC2 and EC5, associated with none to low drought stress, i.e., EC1, along the whole crop cycle) (Figure 4; Supplementary Table 1). Yet, both trials displayed highly similar agronomic values (Table 3). So, it is understandable that PCA on the agronomic dataset has difficulties discriminating trials with similar values, and the strength of the environmental covariates become apparent. Indeed, such variables enable the identification of what types of stress have been experienced by plants. This is of major importance, as it is likely that physiological mechanisms and genetic elements involved in tolerance to different types of stress are not all the same (Atkinson and Urwin, 2012; Suzuki et al., 2014).

The six environmental covariates represent an efficient substitution of the generic environmental term (e.g., year x treatment) for genetic studies

To assess the efficiency of replacing the Environment term by the six environmental covariates, it was necessary to estimate the proportion of the Environmental variance quantitatively explained by these covariates. For grain yield, most of grain yield environmental variance (90.3 %) was explained by only two environmental covariates using only 33% of total the Environment degrees of freedom (Table 5). In 2004, Lacaze and Roumet showed similar results with grain protein content: two environmental covariates explained 30.9 % of the Environmental sum of squares using less than 33% the degrees of freedom.

The use of informative environmental data is critical in dissection of genotype-by-environment interaction (GEI). The lack of explicit environmental information strongly limits the biological interpretation of results (Malosetti et al., 2013). GEI is common in multi-environment trials (van Eeuwijk, 1995; Yan and Hunt, 1998; Zheng et al., 2010). Understanding the environmental and genotypic causes of GEI is of first importance in plant breeding (Jackson et al., 1996; Yan and Hunt, 1998, 2001). The previous generation of GEI analytical tools considers the use of informative external environmental covariates such as air temperature *per se* (Denis, 1988; van Eeuwijk et al., 1996). More recent approaches used partial least squares analysis to partition variance associated with GEI from environmental factors -radiation and temperature- at different growth stages (Reynolds et al., 2004). The environmental covariates established here were based on 11 limiting factors which specifically aimed to consider all putative abiotic stress factors which might have impacted plants within the trial network (Figure 1; Table 2).

The establishment of a breeding program usually involves the choice of multi-location testing sites. To fit with breeding objectives within the considered target population of environments, an environment should be evaluated for main agronomic traits, i.e., the putative yield and phenology which can be achieved at the considered location. With the use of the current methodology, the main agronomic traits can be estimated in response to environmental stresses (Table 6).

The first step of the methodology is to characterize phenology of the whole trial network (date of sowing, date of emergence, relevant development stages desired, anthesis, and physiological maturity). However, neither disease, nor nutritional limiting factors were considered as they did not occur in our network. Drought stress can be estimated as proposed by Allen et al. (1998), or by approximation of P-ETP (e.g. Lacaze and Roumet, 2004). The frequency of each limiting factor at each development phase within each trial of the network enables the construction of environmental covariates. A clustering step helps to group environmental covariates if necessary. Then, such covariates can be directly used for the desired analyses.

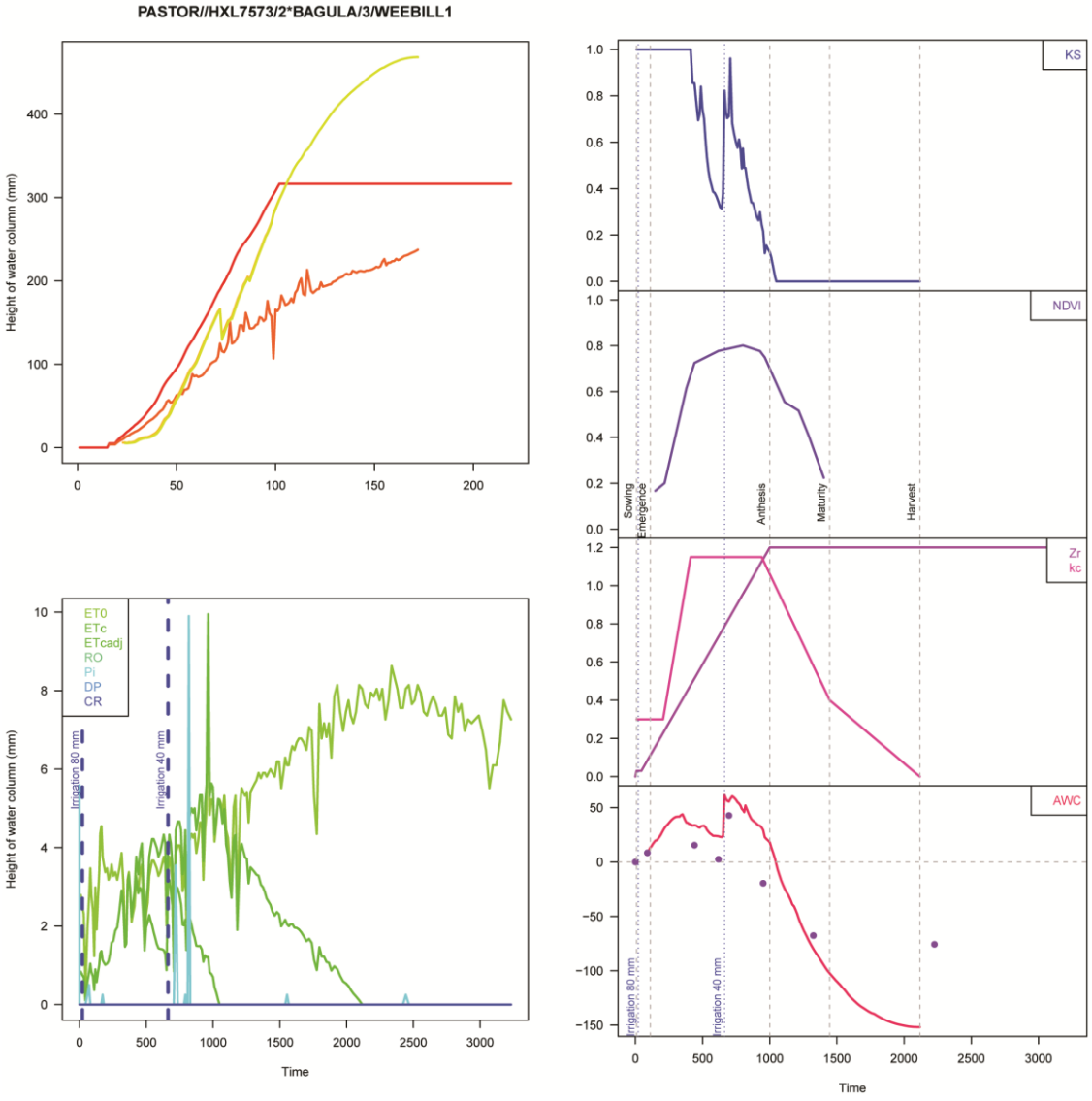
CONCLUSION

The analyses described here represent a paradigm where the Environment is not seen as ‘location x year’ or ‘treatment x year’ combinations, but rather as a series of

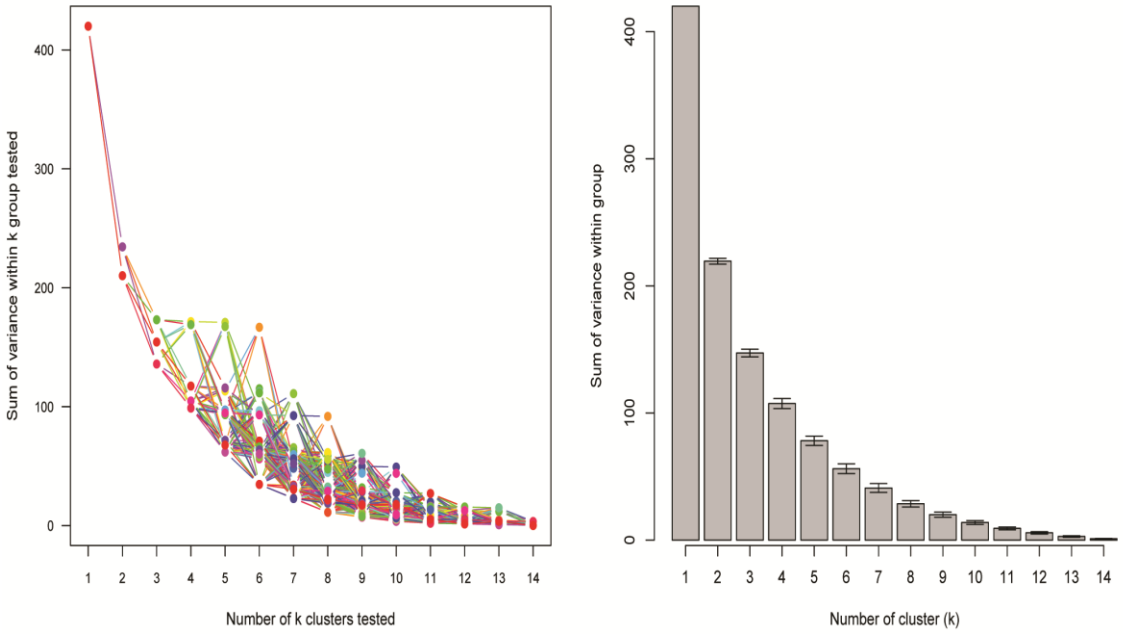
constraints, which, when combined, contribute to crop performance. The analytical methods developed in this study can be used to characterize the environments experienced by plants and help geneticists and breeders to interpret their results in a more quantitative framework. In particular, this will facilitate the analysis of GEI for grain yield and the dissection of interactions using the environmental covariates established. Such variables are more informative as they have a biological context related to specific types of stress.

Acknowledgments: Bruno Bouffier would like to thank all the staff of the CIMMYT for their welcoming, their help, availability and advices, especially in the bread wheat physiology group, with firstly all the engineer and technical staff (Araceli, Eugenio, Syhara, Mayra, Pimi, Nayeli, Abisai, Edgar, Chema, Jazmin, Israel, Arturo, Raymundo, Manuel, Gilberto, Geras, Martha, Joaquin, Roman, Don Bicho…) and the post-docs and PhD students (Julian, Mariano, Gemma, Alistair, Maria, Perla, Arnaud, Carolina, Eliseo, Francisco, Suzuky, Alejandro, Oscar, Sean, Ruth…). Moreover, Bruno Bouffier wants to thank Norma Hernandez and Eloisa Carillo. The authors are also grateful to Aurelien Audes and Zivan Karaman for their help, availability and advices in the analyses. Authors also thank the Native Trait team of Limagrain Europe and Pierre Roumet from INRA for their important and very useful comments and advices on the analyses and discussion. Authors are very grateful to François Torney from Limagrain for careful editing of the manuscript. This work was partly funded by the ANRT (Association Nationale de la Recherche et de la Technologie) through a CIFRE contract n° 2011/0550. Authors would also thanks the anonymous reviewers for their helpful comments on the manuscript.

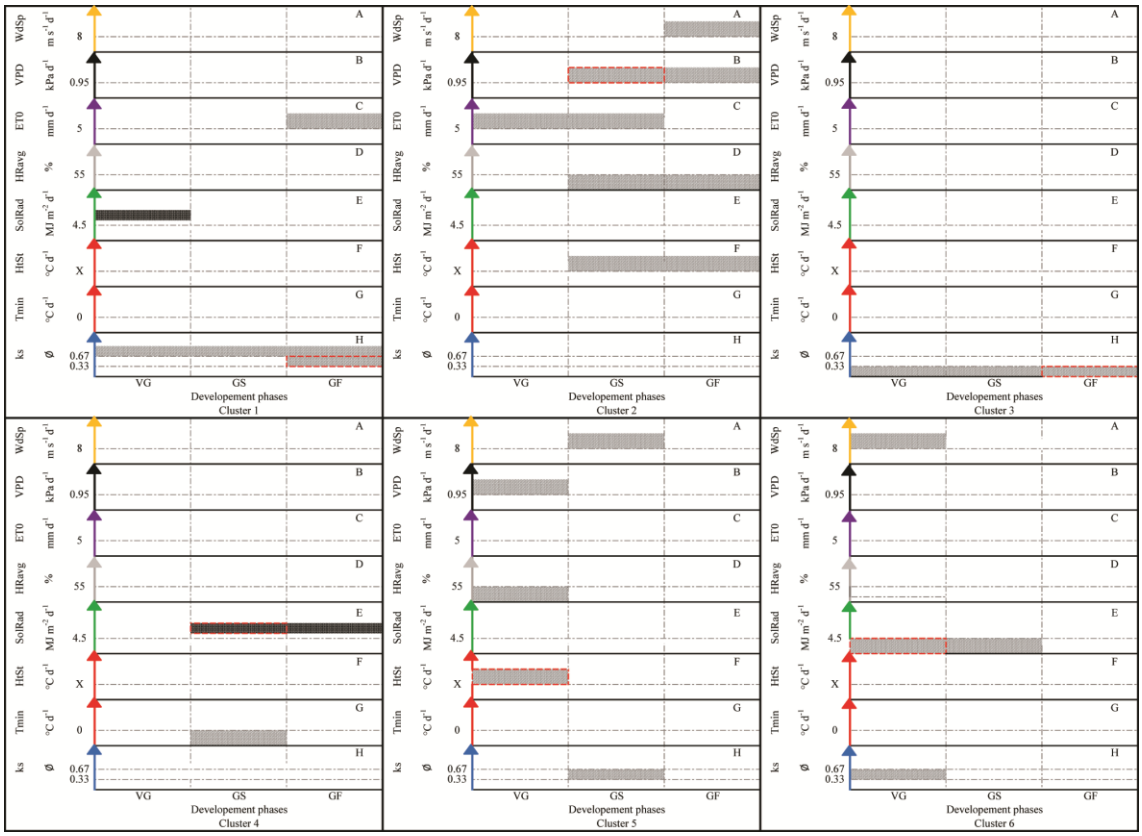
SUPPLEMENTARY DATA



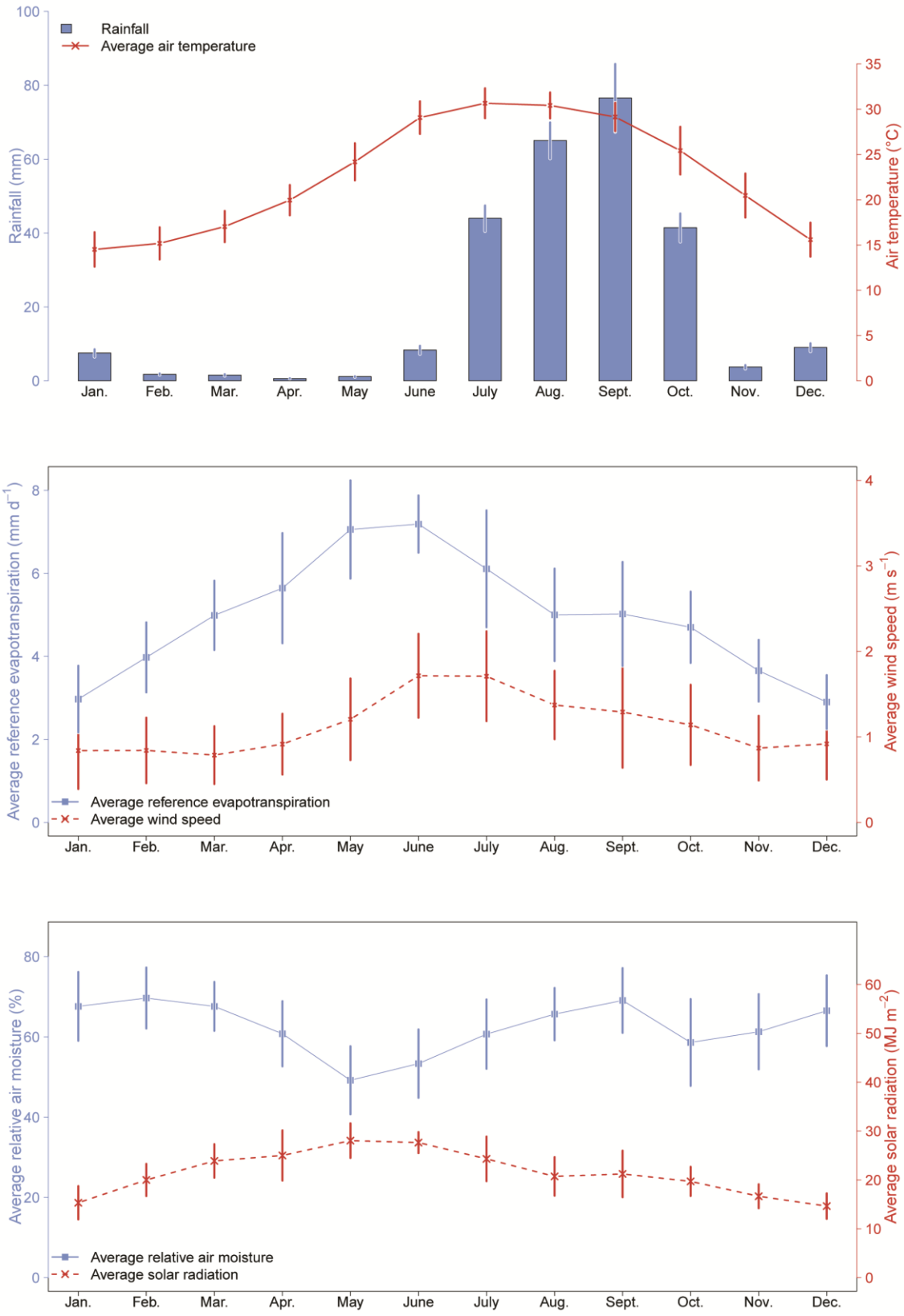
Supplementary Figure 1: Output of the water balance model built using Allen et al. (1998) in dynamics during the whole crop cycle for the trial PW12DR. The thermal time, in degree days since sowing, is on X-axis. In top left plot, in red, the evolution of the total theoretically available for plant (mm), in orange, the evolution of the readily available water in the soil for plant in millimeter (RAW) and in yellow, the estimated depletion of water in the soil (mm). In bottom left plot, ET0 corresponds to reference evapotranspiration (mm d-1), ETc, the maximum crop evapotranspiration (mm d-1), ETc,adj, the 'real' evapotranspiration (mm d-1), RO, the runoff of water (mm d-1), Pi, the precipitation (mm d-1) at the ith day, DP, the deep percolation (mm d-1) and CR the capillarity rise (mm d-1). The top right plot corresponds to the evolution of the drought stress coefficient, ks (ks=1, no water deficit stress; ks=0, total water deficit stress). On the right, from top to bottom, the second plot is the evolution of the NDVI during the crop cycle. On the right, from top to bottom, in the third plot, in pink, are displayed the modelized evolution of the crop coefficient kc, based on NDVI values and in purple, the Zr, (cm d-1) the absolute value of modelized roots length. Finally, in the bottom right plot, the curve plotted corresponds to the modelized evolution of the available water content (AWC) in the soil for plant (mm). Violet points correspond to the observed value of available water for plants during the crop cycle using soil coring. Vertical dotted blue lines in plot B to D correspond to the irrigations applied in the field. Other dotted lines correspond to, in order of increasing growing degree days to sowing, emergence, anthesis, maturity and harvest.



Supplementary Figure 2: Plots of the results of 1000-iteration algorithm to cluster the whole environmental covariates dataset with all 15 trials, i.e. irrigated, drought and heat-irrigated trials. On the left, plot of the sum of variance within groups (y axis) for each value of k group tested (x axis); on the right, bar plot of the average values of sum of square within group (y axis) per k-group tested (x axis) with the standard error associated.



Supplementary Figure 3: Diagram of the environmental covariates grouped into six different clusters. Per cluster, limiting factors are on the y-axis and development phases on x-axis. On x-axis are found the following developmental phases: vegetative (VG), grain set (GS) and grain filling (GF). On y-axis are found WdSp (A), the average wind speed, VPD (B), the average vapour pressure deficit, ET0 (C), the reference evapotranspiration, HRavg (D), the average relative air moisture, SolRad (E), the solar radiation received by crop, HtSt (F), the high temperature stress, Tmin (G), the minimum temperature, and ks (H), the drought stress coefficient. The darkest cells filled for the SolRad subplot correspond to the SumSolRad EP. For HtSt, threshold "X" represents "Tmax>33°C" + "30<Tmax≤33°C & ks<1". Red dotted outlined cell are the representative environmental covariate of each cluster.



Supplementary Figure 4: Evolution of various environmental factors during the year at Ciudad Obregon based on 5 years data: average rainfall and average temperature (A), relative air moisture and wind speed (B) and reference evapotranspiration and solar radiation (C)

Supplementary Table 1: Description of the six clusters representing the whole trial network environment, i.e., the Environment, and the six cluster representative environmental covariates.

Environmental clusters[†]			Representative environmental covariates[‡]			
Name	Description	Summary	Name	Code	Units	Meaning
Cluster 1	Zero to light drought stress from VG to GF, associated with the amount of incident solar radiation during the VG phase, and highly evaporating atmosphere and moderate drought stress during the GF phase	Zero to light drought stress from VG to GF with moderate drought stress in GF	GF.ksModerSt	EC1	GDD	Number of GDD during the GF phase where $0.33<ks\leq0.67$, i.e., moderate drought stress during the GF phase
Cluster 2	High temperature stress during GS and GF, associated with drying out atmosphere from VG to GF and strong wind during GF	Heat stress during GS and GF	GS.VPDHigh	EC2	GDD	Number of GDD during GS phase where VPD>0.95 kPa, i.e., highly drying out atmosphere during the GS phase
Cluster 3	Strong drought stress from VG to GF	Strong drought stress from VG to GF	GF.ksStrongSt	EC3	GDD	Number of GDD during the GF phase where $ks\leq0.33$, i.e., strong drought stress during the GF phase
Cluster 4	Frost stress during GS and incident solar radiation amount in GS and GF phases	Frost in GS and solar radiation amount during GS and GF	GS.SumSolRad	EC4	MJ m^{-2}	Sum of incident solar radiation received by crop during the GS phase
Cluster 5	High temperature stress associated with drying out atmosphere in VG phase, and strong wind and moderate drought stress during GS phase.	Heat stress in VG associated with moderate drought stress during GS	VG.HtSt	EC5	GDD	Number of GDD during the VG phase where (a) $30\ °C<Tmax\leq33\ °C$ & $ks<1$ and (b) $Tmax>33\ °C$, i.e., high temperature stress during the VG phase
Cluster 6	Deficit of incident solar radiation received by crop during VG and GS phase, associated with moderate drought stress and strong wind during VG phase	Deficit of solar radiation in VG and GS and moderate drought stress during VG	VG.SolRadLow	EC6	GDD	Number of GDD during the VG phase where SolRad<8.4 MJ m^{-2}, i.e., deficit of solar radiation during the VG phase

[†] VG: vegetative phase; GS: grain set phase; GF: grain filling phase

[‡] GDD: Growing degree days; ks: drought stress coefficient; VPD: vapour pressure deficit; Tmax: maximum air temperature; SolRad: Incident solar radiation

Chapter III resulted in the development of a new methodology to characterize the environment and in the establishment of a set of informative environmental covariates characterizing the whole trial network. Chapter IV was written as a paper. It will be submitted soon to the Journal Experimental Botany. It focused on the study and the dissection of the genotype-by-environment interaction of grain yield and the main grain yield determinants under environmental conditions experienced by plants using environmental covariates established on paper 1. It aimed first of all to identify the main yield determinants under irrigated, drought and heat-irrigated conditions within a multi-environment trial network. Then, it goaled to determine if these traits interacted with the environment and to what environmental conditions they were sensitive. Finally, we determined stability parameters to identify specific genotype behaviors regarding specific abiotic stresses.

As for paper 1, tables and figures were included in the text. Supplementary Data were added after the conclusion.

CHAPTER IV: GEI, study of the genotype-by-environment interaction

Environmental covariates enable to dissect the genotype-by-environment interaction of bread wheat agronomic and physiological traits within a drought and heat stress trial network

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ABSTRACT

Drought and high temperature are the most important abiotic stresses impacting bread wheat worldwide. Nowadays, breeding is usually done through trialing in multi-environmental locations in which drought and heat stress may occur frequently. Tolerance improvement to such abiotic stresses can be achieved by understanding plant behavior under these stresses in a given environment. The objective of this study was (1) to identify the main agronomic and physiological component having the main influence on yield within our network, (2) dissect their genotype-by-environment interaction using explicit informative environmental covariates and (3) study their stability.

Three bread wheat recombinant inbred lines populations created by the CIMMYT with elite lines combining complementary traits to tolerate drought and high temperature stresses were grown across three years under three different treatments in the north-western Mexican desert of Sonora: winter sowings inducing no specific heat stress, irrigated or under limited irrigation, and spring sowing inducing heat stress and irrigated. The trial network was made of 15 trials in total. Six explicit informative

environmental covariates representing the whole environment of the studied network were used.

The number of grains per m² through the number of grains per spike was the main agronomic component explaining variation for grain yield (yield driver). Among physiological traits, canopy temperature and NDVI derived traits were the main grain yield drivers. Agronomic and physiological components contribute differently to the total genetic variance, with more genotype by environment interaction than additive genetic for physiological traits (68 *vs*. 32 %) and more additive genetic than GEI for agronomic traits (46 vs. 54 %). From 64 to 100 % of the GEI was explained by environmental covariates and enabled identifying different population stress sensitivity. Stability analysis allowed the identification of similar and different reaction of population between types of stress.

Keywords: Abiotic stresses; Agronomic traits; Genotype-by-environment interaction; Informative environmental covariates; Physiological traits; Yield drivers

INTRODUCTION

Drought and high temperature are the most important abiotic stresses impacting bread wheat (*Triticum aestivum* L.) (Lobell et al., 2011; Semenov and Shewry, 2011). In 1977, Passioura established a conceptual framework of the main physiological determinants of grain yield in drought-prone environments. Nowadays, it is being used by the CIMMYT in order to improve tolerance to drought in wheat (Reynolds et al., 2009). A general conceptual model has also been developed for other stressing environments, such as irrigated trials conducted under high temperature. The model in this case is mainly based on the interception and use of solar radiation (Reynolds and Trethowan, 2007; Cossani and Reynolds, 2012). These different models can be used as decision support tools within a breeding program (Reynolds and Trethowan, 2007).

These conceptual models grouped relevant traits into four categories (Reynolds et al., 2012): (i) photo-protection, including traits linked to leaf morphology (wax…) and pigments, (ii) water or radiation use efficiency, for drought or heat-irrigated prone environments respectively, (iii) traits related to the period before grain filling such as rapid ground cover and amount of stem carbohydrates, and finally (iv) access to water by roots. The measurement of these physiological traits has been accompanied by the development of medium to high throughput phenotyping tools based for most of them on plant reflectance indices.

The normalized difference vegetation index (NDVI; Rouse *et al.*, 1974) is probably the most well-known and used criteria nowadays. It is calculated from measurements of radiation reflectance in the red and near infra-red regions of the spectrum. NDVI measurements have been correlated to ground cover, early vigor, leaf area, green area, senescence, yield, biomass accumulation, *etc*. (e.g. Govaerts and Verhulst, 2010; Verhulst and Govaerts, 2010; Pask *et al.*, 2012; Lopes and Reynolds, 2012). Canopy temperature (CT) is also of great help in physiological breeding. As a semi-high-throughput phenotyping tool and despite its sensitivity to environmental conditions (air temperature, clouds, winds …), CT informs on the evaporative cooling from the canopy. Canopy temperature depression , i.e., $CT_{depression}$=Air temperature – CT, is sometimes computed to take into account the effect of the air temperature (Ayeneh et al., 2002; Balota et al., 2007). CT is related to many traits and environmental factors such as stomatal conductance, plant water status, and availability of water for plants in the soils. High positive correlations have been established in

various conditions between wheat yield and canopy temperature: under drought, $r^2 \epsilon [0.51; 0.61]$ (Olivares-Villegas et al., 2007), and under irrigated, $r^2 = 0.16$, drought, $r^2 \epsilon [0.29; 0.38]$, and heat-irrigated conditions, $r^2 \epsilon [0.15; 0.68]$ (Pinto et al., 2010). In the same way, high positive correlations have been established between wheat yield and canopy temperature depression: in heat stress condition, $r^2 = 0.67$ (Ayeneh et al., 2002) and in drought stress condition, $r^2 \epsilon [0.41;0.56]$ (Balota *et al.*, 2007).

When facing different environmental conditions, plants will modify their physiology and morphology. This is the phenotypic plasticity (Schlichting, 1986; El-Soda et al., 2014). The genetic variation for plasticity among genotypes is usually known as genotype by environment interaction (GEI) (Via and Lande, 1985). It is a common phenomenon that is identified in multi-environment trials (MET) (van Eeuwijk, 1995; Zheng *et al.*, 2010) and that will translates in differences in (i) genotypes rank order, but also in (ii) absolute magnitude of the genetic, environmental and phenotypic variances (Malosetti et al., 2013). Understanding the environmental and genotypic causes of GEI is of first importance in plant breeding (Jackson *et al.*, 1996; Yan and Hunt, 1998). Indeed, analyses of this phenomenon provide very helpful knowledge for genetic improvement of stable crop productivity, allowing identification of superior alleles contributing to better cultivar performance within a range of environment (Zhang et al., 2010a; Campbell et al., 2012; El-Soda et al., 2014). Moreover, GEI analyses enable the identification of environments (Yan and Hunt, 2001) and also traits, which can facilitate evaluation of cultivars (Malosetti et al., 2013).

GEI analyses were performed in many species as in wheat (Brancourt-Hulmel et al., 2000; Yan and Hunt, 2001; Campbell et al., 2004; Laperche et al., 2007; Zhang et al., 2010a), maize (van Eeuwijk et al., 1995; Vargas et al., 2006; Malosetti et al., 2007), sorghum (Chapman et al., 2000a; b), and barley (Voltas et al., 1999). Due to the complexity of such phenomenon, many statistical procedures have been developed to analyze GEI. They were reviewed several times (e.g. van Eeuwijk, 1995; Cooper and Hammer, 1996; Kang and Gauch, 1996; Malosetti *et al.*, 2013).

The first generation of genotypic-mean based models developed a linear formulation of GEI as in the additive model, i.e., ANOVA, which preceded the joint regression. For more flexibility, the second generation of models led to a multiplicative formulation of GEI. This allowed interpretation of the interaction as a differential sensitivity to environmental variables. The additive main effect and multiplicative interaction, the factorial regression and the reduced rank factorial regression models

belonged to that generation (Crossa, 1990; van Eeuwijk, 1995; Vargas et al., 1999; Malosetti et al., 2013). All previously described models, except factorial and reduced rank factorial regression, were not able to consider explicit environmental information. This lack strongly limited the biological interpretation of results, although they can provide a good estimation and explanation of GEI.

Several parallel statistical methods have also been proposed with the objective of analysing the genotypes performance stability. Although this is an interesting trait over a range of environments, the stability depends on the magnitude of GEI (Ahmad et al., 1996). In 2009, Mohammadi and Amri reviewed several different stability parameters. Numerous methods were developed to study the genotypic stability as the joint regression analysis described by Yates and Cochran (1938). Mohammadi and Amri (2009) also mentioned the ecovalence (Wricke, 1962), the regression coefficient (Eberhart and Russell, 1966) and two AMMI based parameters (Zhang et al., 1998; Purchase et al., 2000). Eberhart and Russell (1966) also proposed the deviance from regression. In their study on durum wheat (*Triticum turgidum* L. subsp. *durum* (Desf.) Husn.), Mohammadi and Amri (2009) compared various of them and concluded to their similarity due to the similar genotype ranking and similar conclusions with all other methods.

Nowadays, breeding for tolerance to drought and heat is performed by testing the genetic material in a wide range of trials. The characterization of the environments is the first step to make better use of an experimental network and to account for what the plant have experienced in the field (Brancourt-Hulmel, 1999; Voltas et al., 2005; Bouffier et al., 2014). Environmental characterization as performed in Brancourt-Hulmel (1999), Campbell *et al.* (2004), and Bouffier *et al.* (2014) provided explicit environmental covariates based on stresses experienced by plants. In a context of breeding for tolerance to drought and heat stress, such knowledge is very useful and covariates allow understanding plant reactions to specific stresses. For a given trial, the environment is not seen as ‘location x year’ or ‘treatment x year’ combination anymore, but as a serie of constraints, which combined, contribute to the achievement of the yield. No study had so far been carried out on the dissection with environmental covariates of the genotype-environment interaction of both agronomic and physiological traits.

The objectives of our study were first to identify the main traits linked to yield under irrigated, drought and heat-irrigated conditions within a multi-environment trial network conducted on three wheat recombinant inbred lines populations. Secondly, it

consisted in determining if such traits interacted with the environment and to what environmental conditions they were sensitive. Finally, we determined stability parameters to identify specific genotype behaviors regarding specific abiotic stresses.

MATERIALS AND METHODS

Plant material, experimental designs and trial managements

Three bread wheat recombinant inbred lines populations were studied: (i) Population 1 consisted of a set of 196 F7:8 RILs from the Pastor//hxl7573/2*Bagula x Weebill1 cross (PW), (ii) Population 2 consisted of a set of 228 F7:8 RILs from the Sokoll x Weebill1 cross (SW), and (iii) Population 3 consisted of a set of 266 F5:8 RILs from the Vorobey x Parus/Pastor cross (VP). Parents of the populations are CIMMYT elite lines combining physiological traits to tolerate both drought and heat stress. These populations were sown in the northwestern Mexican desert of Sonora, Mexico, in 2011, 2012 and 2013 and under three different environmental scenario: winter sowing under Irrigated (IR) or limited irrigation (Drought (DR)) conditions, and spring sowing inducing Heat stress Irrigated conditions (HI). A trial is defined as a combination of population x treatment x year (e.g. Pastor//… x Weebill1 population in 2012 winter sowing irrigated PW12IR). Altogether the trial network represented fifteen trials in seven different environments (year x treatment: 11IR, 11DR, 11HI, 12IR, 12DR, 12HI, and 13DR). For more details, refer to Bouffier *et al.* (2014).

Phenotypic data

Crop cycles were divided into three developmental phases: (1) vegetative (VG), from emergence (Z1.2) to booting (Z4.1), (2) grain set (GS), from booting (Z4.1) to anthesis+7days (Z6.1) and (3) grain filling (GF), from anthesis+7d to physiological maturity (Z9.2) (Zadoks et al., 1974; Tottman, 1987; Slafer, 2012). Phenological data were expressed in growing degree days (GDD) using the formula described in McMaster and Wilhelm (1997) with a base temperature of 4.5°C (Dhillon and Ortiz-Monasterio, 1993). Anthesis and physiological maturity data were available for all plots within the network.

All variables mentioned thereafter were scored on all genotypes in some trials but all variables were not scored on all trials (Supplementary Data 1). Measured agronomic traits were grain yield at 0% moisture, thousand kernel weight, number of

spikes per m², and plant height. The average number of grains per spike and number of kernels per m² were derived from above variables.

Measured physiological traits were canopy temperature that was scored with a calibrated infrared thermometer 'Hand-Held Infrared Thermometer Sixth Sense LT300' (Instrumart, USA). Scorings were performed during vegetative (CTvg), grain set (CTgs) and grain filling phase (CTgf), around noon (10am-2pm), when air temperature is relatively stable and around its daily maximum. An average canopy temperature along the whole crop cycle was also computed as CTcycle. Means included between two and eight series of data. The normalized difference vegetation index (NDVI) was also scored. It is a reflectance ratio of both red (R_{680}) and far red (R_{900}) wavelengths estimated as: NDVI = $(R_{900}-R_{680})/(R_{900}+R_{680})$, where R_X is the spectral reflectance of wavelength X (nm). It was scored with an 'N-Tech Industries manufactured Greenseeker Handheld sensor' (Trimble, USA). Scorings were performed along the whole crop cycle, from emergence up until after physiological maturity, roughly at a frequency of once a week (around 12 scorings per trial per cycle). For more details, see Bouffier *et al.* (2014). The effect of the phenological stage was removed for each serie of NDVI, using the difference between anthesis date (scorings taken before anthesis) or physiological maturity (for grain filling series) and the date of the NDVI scorings as a covariate. A dynamical NDVI curve drawn per genotype allowed the determination of several complementary traits using the 'loess' R function, implemented in the R 'Stats' package (R Development Core Team, 2011), that performs local polynomial regression fitting. The slope of the phase of exponential growth (NDVIpeg) during vegetative phase, the second inflexion point indicating the end of the exponential growth (NDVIinf2), the NDVI value at anthesis (NDVIant), the slope of senescence (NDVIsen) between anthesis and physiological maturity, and the NDVI value at physiological maturity (NDVIpm) were considered for the analyses (See Supplementary Data 2). Finally, flag leaf glaucousness (FLG) was visually scored.

Environmental covariates

The trial network was characterized in Bouffier *et al.* (2014). The environments were clustered into six different stress scenarios. A representative environmental covariate (called medoid) was extracted and named ECx, with x ϵ[1;6] (see Bouffier *et al.*, 2014 for more details). The subset of six representative environmental covariates

represented 90.3 % of the total environmental variance for grain yield. A description of the six environmental scenarios is presented in Supplementary Data 3.

Statistical analysis

Field data adjustment

In all trials except VP11DR and VP12DR, raw data were first adjusted by replicate for field effects using a row column design, with rows and columns as fixed effects. VP trials in DR conditions were adjusted to field effects using the control plots spread within each trial.

Identifying yield correlated traits

GEI analyses were only focused on a subset of traits displaying frequent and significant correlations with grain yield or yield components within each population. Adjusted means were calculated using a linear model with replication as fixed effect. Significant correlations were observed between anthesis and physiological maturity, and most other traits (data not shown). Therefore, partial correlations were calculated between all traits considering anthesis and physiological maturity as covariates with the 'ppcor' R package (Seongho, 2011). Twenty relevant traits were finally considered to perform GEI analyses.

GEI models and variance decomposition

An anthesis genotypic covariate was built, for which value displayed by each genotype corresponds to the average of all its anthesis adjusted values within the network. On the same principle, a physiological maturity genotypic covariate was built. Both were used as covariates for GEI analyses and their effects removed at a previous step on all traits. GEI analyses were computed by population, following the three following steps:

(i) to decompose the total variance and estimate the total GEI sum of square using an ANOVA:

$$P_{ijk} = \mu + R_k + G_i + E_j + G_i \times E_j + \varepsilon_{ijk}$$

where P_{ijk} is the phenotype of the genotype G_i (i=1:198 for population PW, i=1:230 for SW or i=1:268 for VP) in environment E_j (11IR, 12IR, 12DR, 13DR, 11HI and 12HI for population PW, 12IR, 12DR, 13DR, 11HI and 12HI for SW, and 11DR, 12DR, 11HI and 12HI for VP) and replication R_k (k=1:2), μ the general mean, and $\varepsilon_{ijk} \sim N(0,\sigma^2)$ the residual error terms.

(ii) to decompose the total GEI variance using the environmental covariates established in Bouffier *et al.* (2014), using a multiple linear stepwise forward regression:

$$P_{ijk} = \mu + R_k + G_i + E_j + \sum_{z=1}^{6} G_i \times ECz + \varepsilon'_{ijk}$$

where ECz is the representative environmental covariate of the zth environmental cluster, zϵ[1;6], and ε'$_{ijk}$ ~ N(0,σ'²) the residual error terms. GEI dissection continued until the last significant (p<0.05) ECz.

(iii) to extract the interaction estimate (slope of interaction) of each genotype with each representative environmental covariate:

$$P_i = \mu + G_i + G_i \times ECz + \varepsilon''_i$$

where ε''$_i$ ~N(0,σ''²) are residuals error terms.

Broad sense heritability

Within each trial, broad sense heritability (H²) was computed using the following mixed model: $P_{ij} = \mu + R_j + G_i + \varepsilon_{ij}$ for all traits using:

$H^2 = \sigma^2 g / (\sigma^2 g + (\sigma^2 r / n_{rep}))$ where σ²g is the genetic variance, σ²r, the residual variance and n_{rep}, the number of replications (here, n_{rep}=2).

Software

All statistical analyses were performed on R2.13.2 (R Development Core Team, 2011) and the ASReml-R package v3.0.1 (Butler et al., 2009) (http://www.vsni.co.uk/)

RESULTS

Phenotyping the RIL populations within the trial network

Broad sense heritabilities (H²) in irrigated conditions did not tend to be higher than in stressed environments

The 15 experiments consisted of three populations sown under irrigated, drought and heat-irrigated conditions between 2011 and 2013. Agronomic traits tended to display higher mean values in IR condition, whereas most of physiological traits, except NDVI at anthesis and NDVI inflexion point, tended to display higher values in stressed environments (Table 1). Anthesis was later in IR (1130 to 1203 GDD) than DR (995 to 1188 GDD) and HI (911 to 1041 GDD). Averaged population grain yield ranged from

596 to 942 g.m^{-2} in IR, from 214 to 392 g.m^{-2} in DR, and from 227 to 418 g.m^{-2} in HI. All scored traits displayed a Gaussian-type distribution (Supplementary Data 4).

Table 1: Ranges (lower and upper limits) of trial adjusted means (red) and broad sense heritability (H^2; green) estimated per trait and treatment (IR: Irrigated, DR: Drought, HI: Heat irrigated); Colour scale rules per trait: (1) darker is the colour, higher is the value and (2) red for Mean, green for H^2. Dash symbol means the data were not available. This table is a sub-table extracted from the complete Table presented in Supplementary Data 3. Distribution of all adjusted means per trial with a common abscissa scale per trait is displayed in Supplementary Figure 4.

ANT, anthesis; PM, physiological maturity; CT, canopy temperature in vegetative phase (CTvg), grain set phase (CTgs), grain filling phase (CTgf) and along the whole crop cycle (CTcycle); FLG, flag leaf glaucousness; NDVIpeg, slope of the NDVI curve during the phase of exponential growth in vegetative phase; NDVIinf2, date of the inflection point of the NDVI curve at the end of the phase of exponential growth (see Supplementary Figure 1); NDVIant, NDVI value at anthesis; NDVIpm, NDVI value at physiological maturity; NDVIsen, slope of the NDVI curve during the senescence, i.e., during grain filling phase; PH, plant height; SM2, number of spikes per m²; GSP, number of grains per spike; KM2, number of kernels per m²; TKW, thousand kernel weight; YLD, the grain yield; GDD, growing degree days since sowing

Traits	Units		Treatment					
			IR		DR		HI	
			Min	Max	Min	Max	Min	Max
ANT	GDD	Mean	1130	1203	995	1188	911	1041
		H^2	0.85	0.89	0.79	0.91	0.70	0.84
PM	GDD	Mean	1701	1768	1402	1715	1432	1558
		H^2	0.78	0.84	0.79	0.85	0.60	0.85
CTvg	°C	Mean	21.3	21.6	21.5	26	20.9	23.5
		H^2	0.54	0.54	0.00	0.36	0.17	0.63
CTgs	°C	Mean	-	-	20.7	27.8	23.1	28.4
		H^2	-	-	0.11	0.36	0.12	0.67
CTgf	°C	Mean	22.6	24.7	24.8	32	27.4	30.9
		H^2	0.24	0.58	0.00	0.54	0.16	0.61
CTcycle	°C	Mean	21.9	22.7	23.1	25.4	24.5	27.4
		H^2	0.39	0.41	0.00	0.39	0.44	0.71
FLG	-	Mean	1.8	2.7	2.5	6.7	4.1	4.9
		H^2	0.38	0.71	0.33	0.62	0.29	0.56
NDVIpeg	GDD^{-1}	Mean	$1.01x10^{-3}$	$1.31x10^{-3}$	$1.68x10^{-3}$	$2.16x10^{-3}$	$1.31x10^{-3}$	$1.84x10^{-3}$
		H^2	0.44	0.45	0.20	0.58	0.58	0.70
NDVIinf2	GDD	Mean	767	941	554	641	575	686
		H^2	0.41	0.46	0.27	0.57	0.31	0.71
NDVIant	-	Mean	0.684	0.76	0.563	0.705	0.647	0.726
		H^2	0.50	0.67	0.54	0.77	0.67	0.79
NDVIpm	-	Mean	-	-	0.18	0.225	0.229	0.286
		H^2	-	-	0.35	0.80	0.24	0.62
NDVIsen	GDD^{-1}	Mean	-	-	$-1.18x10^{-3}$	$-8.60x10^{-4}$	$-8.60x10^{-4}$	$-7.60x10^{-4}$
		H^2	-	-	0.55	0.67	0.50	0.79
PH	cm	Mean	98	112	69	82	69	93
		H^2	0.73	0.86	0.35	0.71	0.70	0.77
SM2	spikes m^{-2}	Mean	358	362	260	328	266	358
		H^2	0.11	0.29	0.36	0.48	0.23	0.54
GSP	grains spike^{-1}	Mean	50	55	25	36	26	33
		H^2	0.44	0.45	0.38	0.60	0.43	0.76
KM2	grains m^{-2}	Mean	13.709	19.718	6.335	11.562	6.791	10.788
		H^2	0.67	0.72	0.53	0.76	0.69	0.85
TKW	g	Mean	44	48	32	38	34	39
		H^2	0.68	0.90	0.78	0.89	0.82	0.87
YLD	g m^{-2}	Mean	596	942	214	392	227	418
		H^2	0.59	0.67	0.43	0.64	0.63	0.83

Broad sense heritabilities ranged from 0.20 (CT in DR) to 0.91 (anthesis in DR) (Table 1). For most traits, H^2 were not different between irrigated and stressed conditions, i.e., DR and HI (Table 1, Supplementary Data 5). For CT traits, H^2 was generally higher in HI (mean H^2=0.48) than in DR (H^2=0.23) and IR (H^2=0.42) treatments (Figure 1). For CT traits, the environmental variance was higher in HI and DR than in IR as shown for CTcycle. In this case, the genotypic variance was higher in HI than DR and IR ($p<0.05$) (Figure 2).

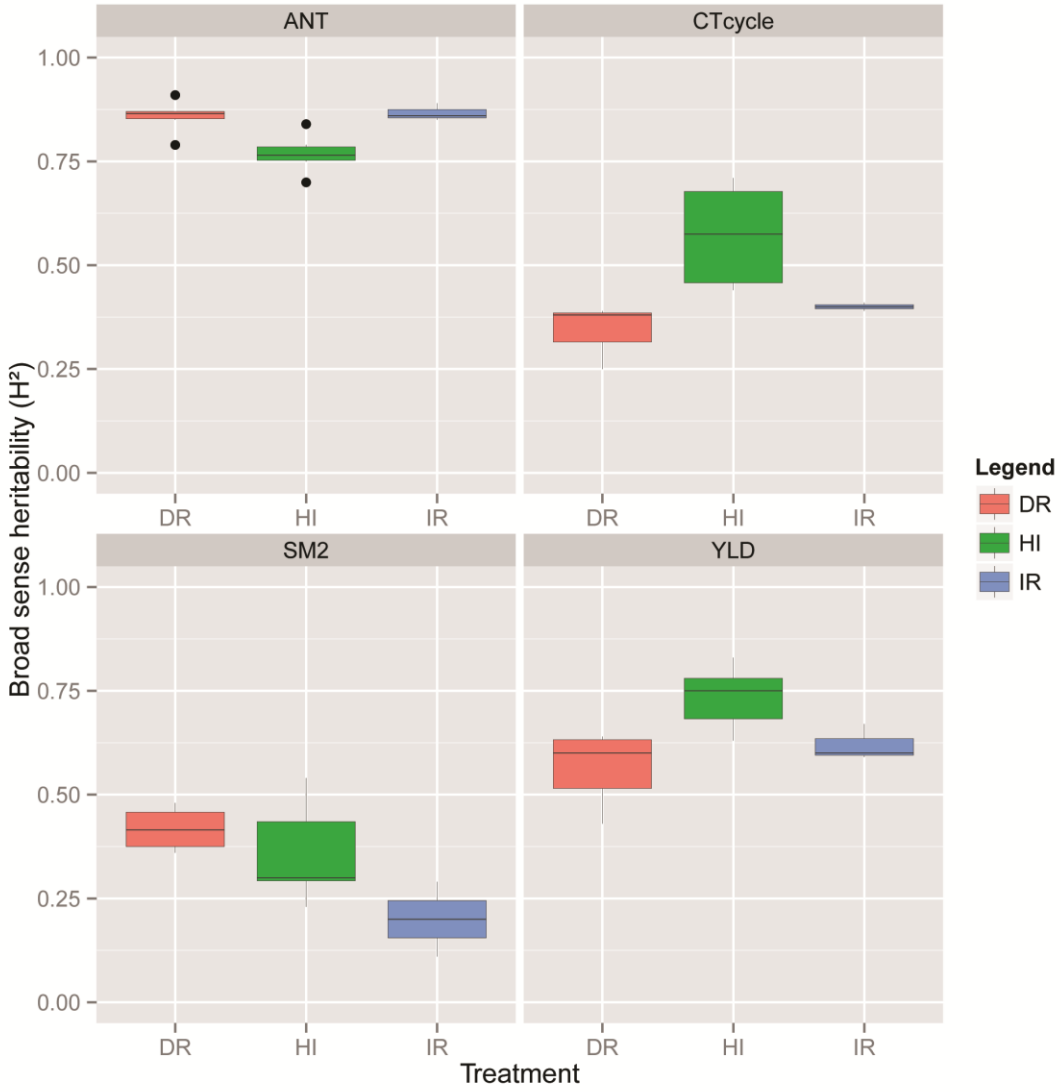


Figure 1: Boxplots of the broad sense heritability (H^2) estimated for all years and populations scored. Treatments were distinguished as irrigated (IR, blue), drought (DR, red), and heat-irrigated (HI, green). Trait abbreviations are given with Table 1

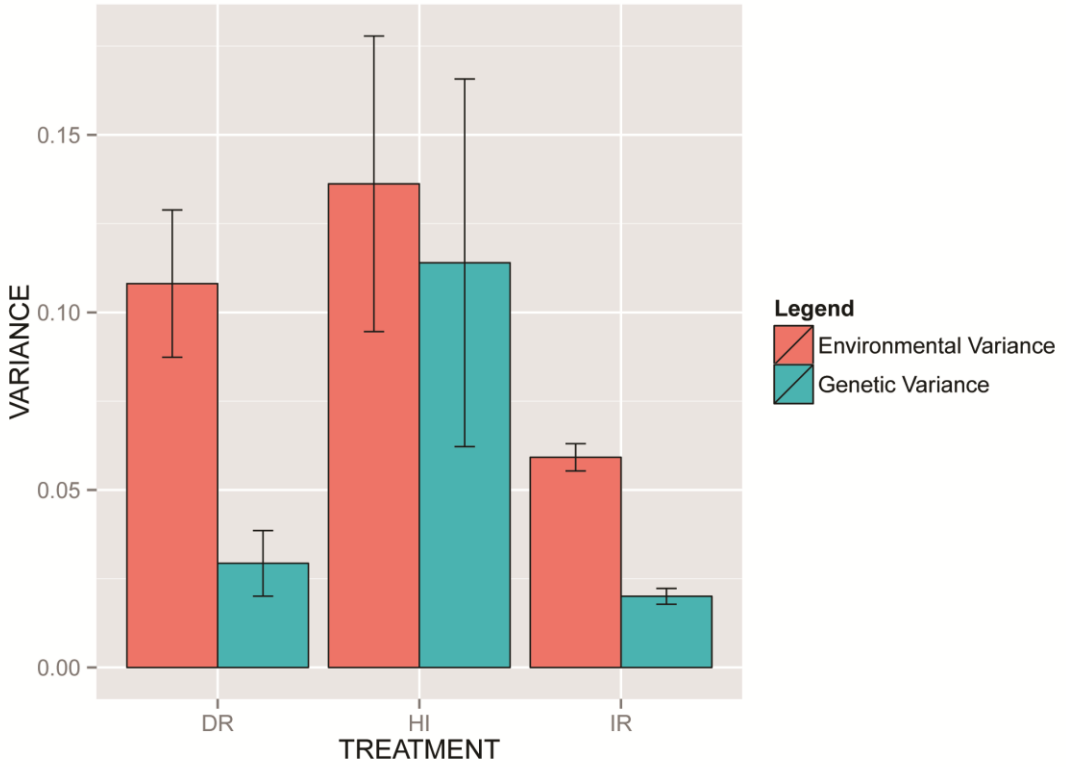


Figure 2: Barplot of the terms of variance, VG (genetic variance; blue) and VE (environmental variance; red), for CTcycle scored on all populations, per treatment: IR (irrigated), DR (drought) and HI (heat-irrigated). Errors bars were given at 95%.

The number of grain per spike is the main yield component associated with yield

In 2014, using the same dataset, Bouffier *et al.* showed that the genotypes experienced different types of stresses which had differently impacted their yield. The aim of scoring various agronomic and physiological traits within the network was to identify the main drivers of grain yield in order to be able to better understand how each genetic material reacted to a range of stresses. Coefficients of correlation were computed per trial between grain yield, its components, and all remaining traits. Anthesis and physiological maturity were considered as covariates in order to remove the possible confounding effect of different precocity.

Yield was dissected into three components: the number of spikes per m², the number of grains per spike, and the TKW. The number of grains per m² was highly correlated to yield (Table 2) with r=0.76 ($p<0.001$) in average, ranging from 0.38 (SW12IR) to 0.95 (PW12HI). The effect of TKW was not consistent across all the experiments, being either positively (r=0.50, SW12IR) or negatively (r=-0.39, PW11HI) correlated to yield. Among the two components of grains per m², the number of grains

per spike showed the strongest correlations with yield and was clearly the most important yield component in this network.

The pattern of correlations between yield and its components was dependent to the genetic background. Indeed, in population SW, all components were always strongly, significantly and positively correlated to YLD (Table 2), except for the number of spikes per m² that appeared significant only in HI treatments. Similar observations were made in 2011 and 2012 for population PW and even for population VP for which less measurements were conducted. A significant but low correlation (r=0.30) was observed for population VP in 2013 between YLD and the number of spikes per m² in DR.

Plant height displayed more significant, more frequent and stronger positive correlations with TKW ($r \in [0.13; 0.56]$; $p<0.05$;$p<0.001$) in many trials than with the other yield components (Table 2). Interestingly, it also showed significant, negative correlations with the number of spikes, the number of grains per m², and the number of grains per spike. These correlations were specific to population SW, with high average values in IR, r=-0.39, in DR r=-0.22 and then in HI r=-0.14.

Table 2: Partial correlation (r) with the grain yield and its components, considering ANT (anthesis) and PM (physiological maturity) as covariates for 15 wheat trials as a combination of 3 years (2011, 2012 and 2013), three populations (PW, SW and VP) and three treatments (IR: Irrigated, DR: Drought, HI: Heat irrigated). Colour scale rules: (1) darker is the colour, stronger is the correlation, (2) green/red for positive/negative significant correlation, and (4) white for non-significant correlation or non-scored data (-).*, **, and ***: significant at the 0.05, 0.01, and 0.001 level of probability; ns: non-significant at the 0.05 level of probability; Trait abbreviations are given with Table 1

Trait	YLD and comp.	Trial code														
		IR				DR					HI					
		PW11IR	PW12IR	SW12IR	VP11DR	PW12DR	SW12DR	VP12DR	PW13DR	SW13DR	PW11HI	SW11HI	VP11HI	PW12HI	SW12HI	VP12HI
CTcycle	SM2	-	-0.18 *	ns	-	ns	ns	-	ns	ns	-0.33 ***	-0.21 ***	-0.14 *	-0.55 ***	-0.22 ***	-0.31 ***
	GSP	-	-0.14 *	ns	-	-0.15 *	-0.14 *	-	ns	ns	-0.29 ***	-0.20 **	ns	-0.44 ***	-0.16 *	-0.21 ***
	KM2	-	-0.38 ***	ns	-	-0.21 **	ns	-	-0.18 **	ns	-0.49 ***	-0.41 ***	-0.20 ***	-0.64 ***	-0.26 ***	-0.49 ***
	TKW	-	ns	-0.25 ***	-	ns	-0.3 ***	-	ns	-0.15 *	ns	-0.24 ***	ns	ns	ns	ns
	YLD	-	-0.40 ***	-0.28 ***	-	-0.41 ***	-0.43 ***	-	-0.31 ***	-0.15 *	-0.58 ***	-0.57 ***	-0.30 ***	-0.69 ***	-0.28 ***	-0.62 ***
NDVIpeg	SM2	-	ns	ns	-	0.19 **	0.13 *	-	ns	ns	0.20 **	0.05 ns	-	0.49 ***	0.25 ***	-
	GSP	-	ns	ns	-	0.14 *	ns	-	ns	ns	0.16 *	0.18 **	-	0.36 ***	ns	-
	KM2	-	ns	ns	ns	0.39 ***	0.17 *	-	0.16 *	ns	0.28 ***	0.24 ***	-	0.55 ***	0.19 **	-
	TKW	-	ns	0.18 **	-0.19 **	-0.23 ***	ns	-	-0.14 *	-0.15 *	ns	ns	-	ns	0.32 ***	-
	YLD	-	ns	0.13 *	ns	0.31 ***	0.22 ***	-	ns	ns	0.30 ***	0.24 ***	-	0.61 ***	0.31 ***	-
NDVIinf2	SM2	-	ns	ns	-	-0.2 **	ns	-	ns	0.19 **	ns	ns	ns	-0.16 *	ns	ns
	GSP	-	ns	ns	-	ns	ns	-	ns	-0.18 **	ns	-0.24 ***	ns	ns	0.14 *	ns
	KM2	-	0.14 *	0.15 *	ns	-0.35 ***	ns	-	-0.2 **	ns	ns	-0.25 ***	ns	ns	ns	ns
	TKW	-	-0.22 **	-0.24 ***	ns	0.24 ***	-0.15 *	-	ns	-0.15 *	ns	0.13 *	ns	ns	-0.21 ***	ns
	YLD	-	ns	-0.13 *	ns	-0.25 ***	-0.19 **	-	-0.22 **	-0.20 **	-0.17 *	-0.14 *	ns	ns	ns	ns
NDVIant	SM2	-	0.15 *	ns	-	0.3 ***	ns	-	ns	ns	0.38 ***	0.27 ***	ns	0.51 ***	0.45 ***	0.19 **
	GSP	-	ns	ns	-	ns	ns	-	0.17 *	ns	ns	ns	0.14 *	0.48 ***	0.28 ***	0.16 **
	KM2	0.38 ***	0.27 ***	ns	0.22 ***	0.36 ***	ns	-	0.21 **	ns	0.29 ***	ns	0.23 ***	0.65 ***	0.5 ***	0.34 ***
	TKW	-0.20 **	-0.23 ***	ns	ns	ns	ns	-	ns	ns	ns	ns	ns	ns	0.37 ***	ns
	YLD	0.33 ***	0.14 *	ns	0.32 ***	0.41 ***	ns	-	0.27 ***	ns	0.35 ***	0.18 **	0.30 ***	0.70 ***	0.61 ***	0.43 ***
NDVIsen	SM2	-	-	-	-	-0.17 *	ns	-	ns	ns	-0.15 *	ns	ns	-0.34 ***	ns	ns
	GSP	-	-	-	-	ns	ns	-	-0.2 **	ns	ns	ns	-0.12 *	-0.62 ***	-0.20 **	-0.20 ***
	KM2	-	-	-	-0.44 ***	-0.32 ***	ns	-0.35 ***	-0.24 ***	-0.14 *	-0.23 ***	-0.18 **	ns	-0.71 ***	-0.24 ***	-0.19 ***
	TKW	-	-	-	ns	0.29 ***	ns	-0.15 *	ns	ns	ns	0.14 *	ns	0.26 ***	ns	ns
	YLD	-	-	-	-0.53 ***	-0.18 **	ns	-0.54 ***	-0.23 ***	-0.18 **	-0.25 ***	ns	ns	-0.73 ***	-0.17 **	-0.18 **
PH	SM2	-	0.16 *	ns	-	ns	ns	-	-0.22 **	ns	0.30 ***	ns	ns	0.49 ***	0.16 *	ns
	GSP	-	ns	-0.33 ***	-	0.15 *	-0.17 *	-	0.16 *	-0.17 **	ns	-0.13 *	ns	0.18 *	ns	ns
	KM2	ns	ns	-0.44 ***	0.37 ***	0.18 *	-0.29 ***	ns	ns	-0.23 ***	ns	-0.15 *	ns	0.38 ***	ns	ns
	TKW	ns	ns	0.4 ***	ns	ns	0.54 ***	0.33 ***	0.28 ***	0.32 ***	ns	0.56 ***	0.21 ***	ns	0.42 ***	0.13 *
	YLD	0.21 **	ns	ns	0.49 ***	0.37 ***	0.27 ***	0.40 ***	ns	ns	0.27 ***	0.29 ***	0.21 ***	0.39 ***	0.23 ***	ns
YLD	SM2	-	ns	ns	-	ns	ns	-	0.30 ***	ns	0.35 ***	0.23 ***	0.15 *	0.41 ***	0.30 ***	0.19 ***
	GSP	-	0.56 ***	0.31 ***	-	0.48 ***	0.40 ***	-	0.57 ***	0.56 ***	0.72 ***	0.44 ***	0.64 ***	0.85 ***	0.73 ***	0.57 ***
	KM2	0.89 ***	0.80 ***	0.38 ***	0.84 ***	0.69 ***	0.45 ***	0.73 ***	0.87 ***	0.69 ***	0.90 ***	0.70 ***	0.82 ***	0.95 ***	0.90 ***	0.80 ***
	TKW	ns	0.21 **	0.50 ***	-0.17 **	ns	0.39 ***	ns	ns	0.19 **	-0.39 ***	0.42 ***	-0.12 *	-0.34 ***	0.38 ***	ns

Physiological traits displayed strong and frequent correlations with yield

Among all considered canopy temperature traits, CTcycle displayed (i) strong correlations with all other CT traits, i.e., CTvg (r=0.73), CTgs (r=0.78) and CTgf (r=0.75) (Supplementary Data 6), and (ii) similar correlation patterns with yield and with its components (Table 2, Supplementary Data 7). Negative correlations between CT traits and yield (and its components) were usually stronger in HI (r ϵ[-0.69; -0.28], p<0.001) than in DR (r ϵ[-0.43; -0.15]; (p<0.001;p<0.05) and IR (r ϵ[-0.40; -0.28]; p<0.001).

Most NDVI derived traits showed (i) high and frequent associations to yield and to its components and (ii) different patterns of correlation (Table 2). The highest correlations were observed for treatment HI and NDVI at anthesis. NDVIinf2 and NDVIsen were usually negatively associated with yield and its components while NDVIpeg and NDVIant were positively correlated. Interestingly most correlations between NDVI traits were non-significant (Supplementary Data 6) meaning that they represent different plant characteristics. However, in average among the trials, three combinations displayed strong correlations: NDVIinf2 and NDVIpeg (r=-0.60; sd=0.25), NDVIant and NDVIpm (r=0.45; sd=0.17), and NDVIant and NDVIsen (r=-0.50; sd=0.16). However, among these three combinations we observed a large variation within the coefficients of correlation depending on the trials, i.e., important standard error of the coefficients of correlations by combination (in average on the three combinations 37 %). Among NDVI derived traits, NDVIpm displayed the lowest correlations with yield and its components, ranging from r=-0.23 (p<0.001) to r=0.41 (p<0.001). Moreover, NDVIpm was in average well correlated with NDVIsen (r=0.76, sd=0.11).

Flag leaf glaucousness was poorly correlated to yield and its components whatever the treatment considered, with only 9/45 significant correlations ranging from r=-0.25 (p<0.001) to r=0.32 (p<0.001).

In conclusion, CTcycle, NDVIpeg, NDVIinf2, NDVIant and NDVIsen were the main physiological drivers of yield within the network (Table 2).

Agronomic and physiological traits displayed different partitions of the total genetic variance

An ANOVA and then a multiple linear stepwise forward regression were performed for each yield driver per population. The effects of both anthesis and

physiological maturity were removed before running the ANOVA. The first models allowed decomposition of the genetic variance into additive genetic variance and GEI. Except for the number of spikes per m² for population SW, genetic additive and GEI terms were highly significant for all traits (data not shown).

In populations PW and SW, physiological traits displayed higher proportion of GEI variance ($p<0.001$; Student test), i.e., lower proportion of additive genetic variance, than agronomic traits (Table 3). In average, physiological traits had 68% of GEI and 32% of G, whereas agronomic traits had 46 % of GEI and 54 % of G. In population VP, for both types of traits the proportions of genetic and GEI variances were similar (50% vs 50%).

GEI variance of physiological traits ranged from 56 % (CTgf) to 75 % (NDVIant) with 65 % in average for population PW, from 58 % (CTgs) to 79 % (NDVIsen) with 70 % in average for SW, and from 42 % (NDVIant) to 67 % (NDVIsen) with 52 % in average for VP. In terms of agronomic traits, GEI variance of TKW was always the lowest whatever the population, with 37 % in PW, 17 % in SW and 40 % in VP. The traits with the highest GEI variance were dependent on the population: the number of spikes per m² in PW (57 %) and the number of grains per spike in SW (56 %) and plant height in VP (50 %).

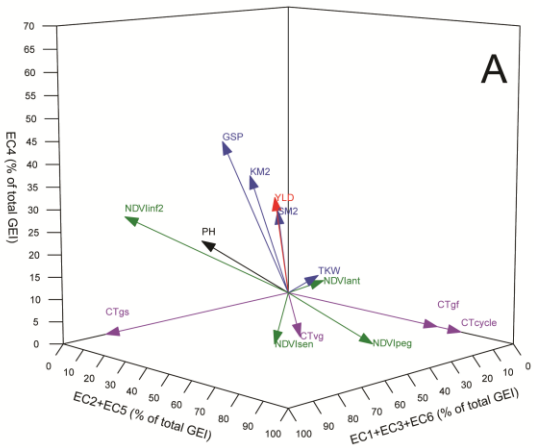
Dissecting GEI of main yield drivers with six explicit informative environmental covariates

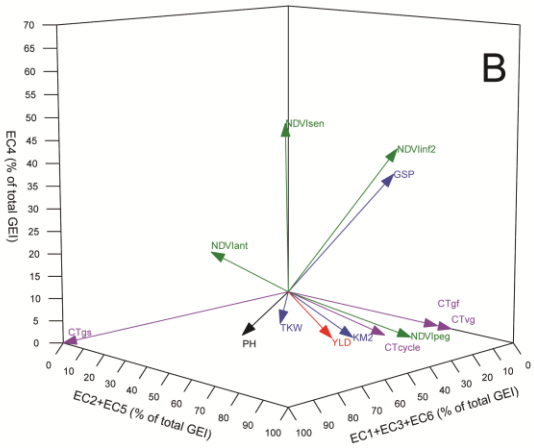
To dissect the GEI of the main yield drivers, multiple linear stepwise forward regressions were performed. This step permitted decomposing GEI variance using the six environmental covariates, established in Bouffier *et al.* (2014). Whatever the trait and the population, all complete models of GEI dissection were significant (Table 3); e.g.: in population PW, three environment covariates explained 85% of total GEI for yield with contributions of 31 % from EC1, 26 % from EC2 and 28 % from EC4 (Figure 3; Table 3). Coefficients of multiple determinations (R^2) ranged from 0.63 to 0.98 across traits and populations. Within each population, decomposition of GEI involved at least once each of the six environmental covariates (see Bouffier *et al.,* 2014). These covariates can be grouped into three classes: (i) EC1+EC3+EC6 representing mainly drought conditions, (ii) EC2+EC5, representing mainly heat stress conditions and (iii) EC4 related to large radiation levels and frost (Supplementary data

3). The part of GEI explained by the environmental covariates ranged from 64 % to 100 %, involving from one to five of them.

Table 3: Genetic variance (G) and Genotype-by-Environment Interaction variance (GEI) decompositions ($p \leq 0.001$) for traits scored on three wheat populations sowed within a network of 15 trials. GEI variance was decomposed using six environmental covariates (EC), (See Bouffier et al., 2014; Supplementary Figure 3). % cml, the cumulative percentage of the total GEI significantly ($p \leq 0.05$) explained by each environmental covariate. ns: non-significant at the 0.05 probability level; Dash symbol means data not available. R^2adj is the multiple adjusted coefficient of determination of the most complete model displayed for each trait: e.g. for CTvg, CTvg~G+E+GxEC6+GxEC2+GxEC5+ε, R^2=0.86 with E, the environment term and ε, the residual of the model. Trait abbreviations are given with Table 1

Population	Trait	Genetic variance decomposition		GxE variance decomposition										
		G	GEI	Rank 1		Rank 2		Rank 3		Rank 4		Rank 5		R^2adj
		%	%	EC	% cml	EC	% cml	EC	% cml	EC	% cml	EC	% cml	
PW	CTvg	37	63	EC6	41	EC2	59^{ns}	EC5	87					0.86
	CTgs	32	68	EC1	49	EC3	83							0.96
	CTgf	25	75	EC2	34	EC5	69							0.97
	CTcycle	35	65	EC2	43	EC5	79							0.97
	NDVIpeg	37	63	EC2	30	EC5	69	EC6	81^{ns}	EC1	100			0.92
	NDVIinf2	33	67	EC1	31	EC6	53	EC4	79	EC3	100			0.98
	NDVIant	44	56	EC6	31	EC2	57	EC5	79	EC4	91			0.81
	NDVIsen	41	59	EC5	47	EC3	73	EC6	100					0.87
	PH	56	44	EC1	38	EC4	58	EC3	73	EC5	87			0.96
	SM2	43	57	EC3	30	EC5	55	EC4	80					0.63
	GSP	44	56	EC4	40	EC1	71							0.87
	KM2	56	44	EC4	34	EC1	60	EC2	81	EC3	92			0.95
	TKW	63	37	EC2	32	EC3	56	EC5	74	EC4	87	EC1	100	0.93
	YLD	45	55	EC1	31	EC2	57	EC4	85					0.98
SW	CTvg	35	65	EC2	43	EC5	75							0.94
	CTgs	42	58	EC3	57	EC6	100							0.98
	CTgf	23	77	EC2	40	EC5	69							0.94
	CTcycle	32	68	EC2	39	EC5	65	EC6	86					0.96
	NDVIpeg	33	67	EC2	31	EC5	72	EC1	90					0.82
	NDVIinf2	31	69	EC4	39	EC2	65	EC5	90					0.88
	NDVIant	22	78	EC3	33	EC6	58	EC5	82	EC4	100			0.88
	NDVIsen	21	79	EC4	46	EC2	72	EC3	100					0.83
	PH	66	34	EC2	33	EC6	63	EC3	86					0.95
	SM2	40	60^{ns}	-										-
	GSP	44	56	EC4	33	EC2	57	EC5	82					0.82
	KM2	53	47	EC2	38	EC1	69	EC5	90					0.95
	TKW	83	17	EC1	34	EC2	64							0.91
	YLD	55	45	EC1	36	EC2	73	EC5	91					0.98
VP	CTgs	53	47	EC1	62	EC2	100							0.9
	CTgf	47	53	EC1	80									0.91
	NDVIant	58	42	EC3	71									0.95
	NDVIsen	33	67	EC6	50	EC3	85							0.84
	PH	50	50	EC6	57	EC3	87							0.87
	KM2	51	49	EC4	49	EC3	87							0.79
	TKW	60	40	EC4	64	EC3	94							0.83
	YLD	50	50	EC4	45	EC5	80	EC2	100					0.89





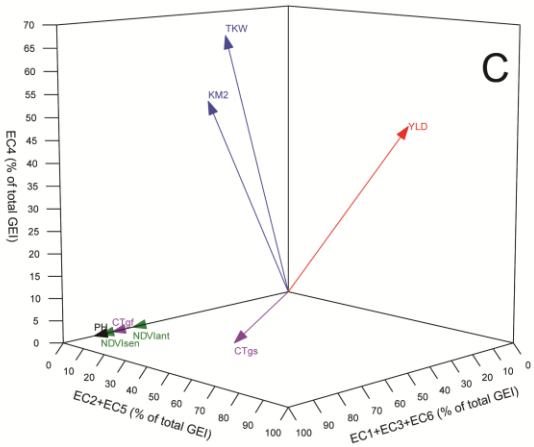


Figure 3: Tri dimensional plots of the trait GEI dissection for three wheat populations PW (A), SW (B) and VP (C); Colour scale: red, grain yield; blue, yield components; green, NDVI traits; purple, canopy temperature traits; black, plant height. The referential is defined by three axes representing three classes of environment covariates: (1) EC1+EC3+EC6 representing drought, (2) EC2+EC5 representing heat stress and (3) EC4 representing high radiation and frost. Coordinates of a vector corresponds to the significant part of the total GEI variance explained by each environmental covariate grouped into these three classes. Trait abbreviations are given with Table 1.

Among all environmental covariates used in GEI dissection, 43% were related to drought scenarios (EC1, EC3, and EC6) and 42% were heat related (EC2 and EC5). Overall, the GEI dissection of physiological traits emphasized the importance of heat related covariates (46% of the ECs involved in GEI are heat stress related), then drought related covariates (44% of the ECs), and for a few importance of EC4 (10% of the ECs); for agronomic traits, 41 % of the ECs involved are related to drought, 36 % to heat and 23 % to EC4 covariates. Population PW GEI traits dissection involved 47 % of all environmental covariates used, SW, 38 % and VP, 15 %.

However, differences appeared between populations. For PW, GEI dissection pattern of physiological traits involved 46 % of drought and heat related covariates and only 8 % for radiation. For SW, most of GEI dissection implicated heat related covariates (55 %), then drought (32 %) and finally radiation (14 %). For VP the pattern involved 83 % of drought and 17 % of heat covariates. Concerning GEI dissection of agronomic traits, most of covariates were drought related for population PW (43 %) and VP (44 %). For SW, the dominant class was heat related covariates (57 %) (Table 3).

Populations PW and SW were tested in almost the same conditions but GEI of yield was decomposed by different covariates. For population PW, GEI of yield was similarly explained (around 33 %) between each type of environmental covariates, whereas for population SW, GEI of yield was only influenced by heat stress (60 % of total GEI explained for yield) and then drought (40 %) (Figure 3A, B). More precisely, population PW genotypes interacted mainly with (i) EC1 that represents “none to light drought during the whole crop cycle, with moderate drought during grain filling” (31 %), with (ii) EC4 “important level of radiations received between grain set and grain filling phases associated with frost in grain set” (28 %), (iii) and EC2 “heat stress between grain set and grain filling phases” (26 %). For population SW genotypes, similar environmental covariates were involved, however with different intensities: EC1 (36 %), EC2 (37 %), and EC5 (18 %; “heat stress conditions during vegetative stage with moderate drought in grain set”) (Table 3; Supplementary Data 3).

Decomposing yield into yield components and then looking at their GEI allowed identification of the environmental covariates which interacted with yield along its achievement. For population PW, (i) the number of spikes per m² interacted with drought (38 % of total GEI explained), heat stress (31 %), and radiation (31 %), then (ii) the number of grains per spike interacted mainly with radiations (56 %), and drought (44 %), and finally (iii) grain size interacted with heat (50 %), drought (37 %) and

radiations (13 %) (Figure 3A). For population SW, interactions emphasized the predominance of heat stress (60 % for number of grains per spikes and 66 % for number of grains per m²) and then radiations (40 % for number of grains per spikes) or drought (34 % for number of grains per m²) and finally mainly with drought (53 %) and then heat (47 %), for TKW (Figure 3B). For population VP, yield was mainly influenced by radiation (56 % for number of grains per m² and 68 % for TKW) and then drought (44 % for number of grains per m² and 32 % for TKW). However, VP was only experimented in stressed environments and not in IR conditions (Figure 3C; Table 3).

CT traits were never influenced by radiation levels (EC4) whatever the population, but exclusively by drought and heat stress. However, CTgs only interacted with heat covariates in PW and SW, and slightly with drought covariates in VP. NDVI traits differently interacted with environmental covariates depending on the population but were sensitive to all three types of covariates, i.e., drought, heat stress and radiation related covariates. NDVIpeg interacted similarly in PW and SW, i.e., strong heat influence and then drought.

Stability feature of genotypes across environments

YLD and all its drivers displayed complex GEI patterns. Nevertheless, it appeared that certain populations were more susceptible to specific type of environmental covariates. Moreover, such specificity was also observed for certain traits at a given development stage whatever the population. However, the question is whether there are genotypes with performances depending on the environmental covariate considered. To this end, the slope of the linear regression of yield against a given environmental covariate was studied. A significant regression was considered as the presence of linear interaction with that given environmental covariate. We focused on populations PW and SW as these were tested in similar conditions within the network.

The grain yield of all genotypes significantly interacted with at least one of the environmental covariates. The largest proportion of interacting genotypes was observed for EC4 (100 % for populations PW and SW), then EC1 (97 % for PW and 76 % for SW) and the smallest with EC2, EC3, EC5 and EC6 (no significant linear interaction for SW; for PW, it concerned only EC3, EC5 and EC6) (Data not shown).

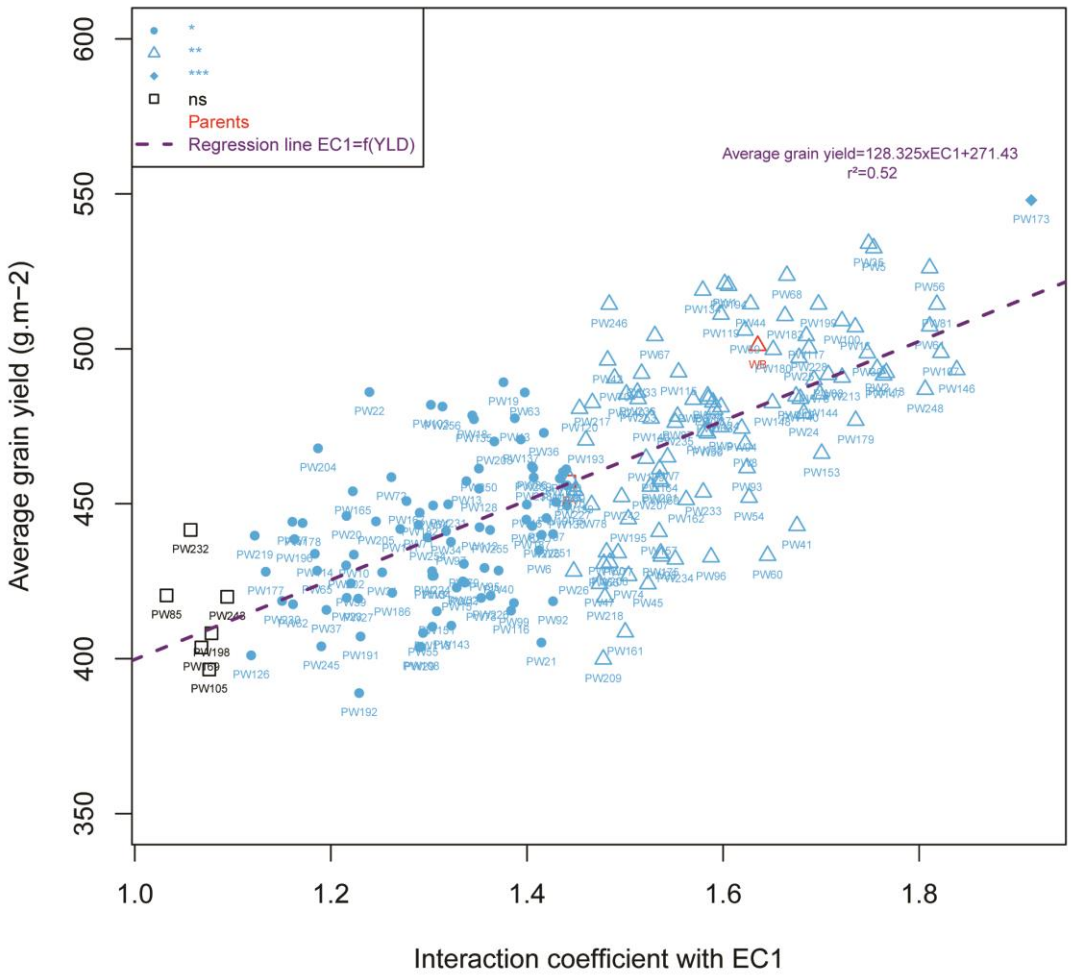


Figure 4: Plot of the average grain yield on all trials as a function of the interaction coefficients between PW grain yield and the environmental covariate EC4 (Supplementary Data 3). Bullet points, empty triangles, and filled diamonds represent significant linear slope at the 0.05, 0.01, and 0.001 level of probability. Parents of the population: WB: Weebill1; PA: Pastor//hxl7573/2*Bagula

EC1 corresponds to the occurrence of "none to light drought stress during the crop cycle with moderate drought stress during grain filling stage" (Supplementary data 3). The relationship between the slope of the regression to EC1 and average grain yield is presented on Figure 4. Significant linear interactions (Ic) with EC1 ranged from Ic=1.12 (PW126) to Ic=1.91 (PW173). The male parent, Weebill1, had higher average grain yield (501 $g.m^{-2}$) than the female parent, Pastor//hxl7573/2*Bagula (457 $g.m^{-2}$). A higher interaction to EC1 was also observed with Weebill1 (Ic=1.64) than with Pastor//hxl7573/2*Bagula (Ic=1.44). Many recombinant lines showed a clear transgressive expression, i.e., genotypes interacting more or less than the parents.

High yielding genotypes tended to react more to environmental covariates. EC1, EC2, and EC4 are the three most important environmental covariates. The genotype PW173, the highest yielding ones, had highly significant interaction with EC1 and EC4, but did not significantly interact with EC2. The individual PW232 (population PW) was the highest yielding genotype displaying a stable behavior, i.e., the slopes of interaction with EC1 and EC2 were not significant (but with EC4).

The slope between yield and each environmental covariate was compared within population (Supplementary Data 8). PW and SW displayed similar pattern of correlation. For example, higher was the interaction with EC1 (i.e., low drought stress along the crop cycle) for yield, lower was the interaction with EC3 (i.e., strong drought stress during the crop cycle) for yield (r^2=0.90; $p \leq 0.001$), or higher was the interaction of genotypes with EC2 (i.e., heat stress in grain set and grain filling phase) for yield, higher was their interaction for yield with EC5 (i.e., heat stress during vegetative phase). The only difference appeared when comparing interaction with EC1 and EC2, and EC4 and EC6. In PW, correlations were not significant ($p \leq 0.05$) but they were in SW (Supplementary Data 3; Supplementary Data 8).

DISCUSSION

Our trial network was made of fifteen trials as a combination of three populations, PW, SW and VP, sown in three treatments, IR, DR and HI, between 2011 and 2013. In 2014, Bouffier *et al.* characterized this entire network using six environmental covariates This paper is first dealing with the identification of the main agronomic and physiological grain yield drivers. Then, it focuses on the study of the genotype-by-environment interaction in order to identify environmental constraints to which these traits were sensitive to. Finally, the stability of the populations and genotypes is studied.

The grain set period, where grain number per m² is established, may be the most sensitive stage of wheat

Whatever the trial, the stress experienced within each trial, and the phase of development impacted, the number of grains per m² (more specifically the number of grains per spike) was the most correlated to yield with an average r=0.76 ($p \leq 0.001$) within the 15 trials of the network (Table 2). Despite compensation mechanisms which

may have occurred within each trial (negative correlations between number of grains per m² and TKW for example; data not shown), the number of grains per square meter may be considered as the limiting yield components for yield at the network scale.

The way we estimated the number of grains per spike and the number of grains per m² may influence the conclusions. Indeed, grain yield was used with thousand kernel weight to calculate the number of grains per m². Both these former variables were well scored and displayed a high heritability, so do the calculated one. The number of grains per spike was then estimated using the number of grains per m² and the number of spikes per m². This latter one was not well estimates in the field, i.e., low heritability. This resulted in an estimated trait, i.e., the number of grains per spike, with an intermediate heritability between the number of spikes per square meter and the number of grains per square meter. So, unfortunately, this medium heritability tends to restrict the following conclusion draw concerning this trait. However, although results need to be confirmed, the number of grains per spike is strongly suspected to have been the most sensitive stage of wheat in our network. Historically, most of breeding efforts on grain yield resulted in the improvement of the number of grains per spike (Austin et al., 1989). Authors compared very old, old, intermediate, and 'modern' variety in 1989. Between very old and modern cultivars, they reported 59% more yield, 14% more spikes per m², 30 % more grains per spike, and no change in the grain weight. Then, a more recent study of Slafer *et al.* (2014) reported a hierarchy in the yield components with the number of grains per m² more sensitive than the grain size. Moreover, the grain set stage encompasses for most of the reproductive development process in wheat. Prasad *et al.* (2008) reported that the inability of reproductive organs to produce protective molecules (e.g., heat shock protein) unabled them to adapt to stress conditions which make them particularly sensitive.

Canopy temperature and NDVI are highly interesting traits targeting specific mechanisms highly involved in the improvement of bread wheat tolerance to abiotic stress

Strong negative correlations were found for canopy traits with grain yield and yield components (Table 2). Stronger correlations were observed in HI than DR or IR conditions. Lopes and Reynolds (2012) observed similar correlations with grain yield (r=-0.4) in their trial network constituted of drought and heat-irrigated treatments. However, Olivares-Villegas *et al.* (2007) observed higher correlations with canopy

temperature in vegetative, grain set, grain filling or over the whole crop cycle in DR conditions using the the Seri x Babax population, although similar values to ours were observed in IR conditions. This might be due to the restricted range of phenology featuring the Seri x Babax cross they used.

In our experiment, CT traits were estimated with at least two series of CT per phase. Olivares-Villegas *et al.,* (2007) reported that they considered at least 5 measurements per phase. Indeed, CT is strongly influenced by environmental conditions. More repetitions at a given stage ensure drawing the general trend of plant CT at a given stage by getting more robust data.

Concerning NDVI derived traits, significant correlations were found with yield: positive correlation for the slope of NDVI during the phase of exponential growth and NDVI at anthesis, negative for the inflexion point after the phase of exponential growth and the senescence rate (Table 2). Only senescence rate coincided to traits presented in Lopes and Reynolds (2012), so called RS. In average, a similar level of correlations was observed in drought and heat conditions between the two studies. Concerning other traits developed from NDVI curves, no studies so far at the best of authors' knowledge was reported. The slope of NDVI during the phase of exponential growth informs on a composite trait consisting of early vigor and speed of ground cover establishment. The inflexion point after the phase of exponential growth complements the information obtained through the slope of NDVI during the phase of exponential growth, informing on the time when plants almost reach their maximum amount of biomass. Senescence rate, established in the same way as Lopes and Reynolds (2012) gives information on the speed of senescence, allowing among other the identification of the fastest genotypes to fill their grains. Although genetically programmed, senescence is also influenced by the environment (Vijayalakshmi et al., 2010). The higher performance of genotypes displaying stay-green phenotypes has been demonstrated under abiotic stress conditions in wheat (Verma et al., 2004; Vijayalakshmi et al., 2010; Lopes and Reynolds, 2012) and also in sorghum (Harris et al., 2007).

Different patterns of correlation were highlighted between NDVI derivative traits and grain yield and its components. We hypothesized that from the same data, i.e., NDVI, we were able to extract different traits related to the NDVI response function corresponding to early vigor and plant development, the maximum amount of biomass, and finally the chlorophyll loss with estimation of senescence. However, further

investigation on the genetic basis of both NDVI traits and grain yield need to be performed to confirm their relationship.

Broad sense heritabilities were higher in stressed treatments than in the potential treatment

In our study, for yield but also for some traits such as canopy temperature along the crop cycle, we found higher heritability in heat-irrigated condition than in drought and irrigated conditions (Table 1; Figure 1). The lower heritability in drought conditions is explained by the high environmental variance and the low genetic variance (Figure 2). The lower heritability in irrigated condition is explained by a very low genetic variance. With irrigations applied, environmental conditions were more controlled in IR than in DR conditions, explaining the lower environmental variance. Although irrigated, the HI condition resulted in high environmental variance. One hypothesis is that the spring sowing conditions may have exacerbated field heterogeneity. Indeed, HI crop cycles were shorter due to higher average temperature. With an increased developmental rate, plants were not able to compensate all field heterogeneity. Some processes such as biomass accumulation need time to reach their maximum values (Tardieu, 2013). Another putative hypothesis is that in HI conditions, stress enhanced the genetic variance because of very different genotypes reaction, i.e., there is a little or a strong effect of that treatment on plants.

The genetic variance was lower in DR and IR than HI. In water limited conditions, i.e., DR, water deficit has strongly prevented plants to evaporate and it seems that in these populations and conditions, genetic differences for resource capture was low. In IR, where water is abundant and other constraints limited, plants were able to transpirate at the maximum rate, and no difference could be seen between genotypes (Figure 2). Differences between genotypes were more important when both, water was available and plants were experiencing stressful conditions. In these conditions some genotypes were able to fully express their cooling metabolism. The conclusion which can be drawn from these results is that in these populations, there is more variability to cope with heat stress than with drought stress.

Similar maximum heritability values for CT traits were observed between Olivares-Villegas et al. (2007) and our study, with broad sense heritability around 0.6. However, the heritability estimated in Olivares-Villegas et al. (2007) was estimated for a given trait on many environments, so the total variance included some GEI variance.

We estimated the heritability for a given trait on each trial. This enabled to show that for some traits such as the canopy temperature, heritability was higher in stressed conditions than in potential conditions. Several papers compared results of heritability between non-stressed and stressed conditions with constrasted results. For example, Pfeiffer (1988) reported higher yield heritability in non-stressed environments and Olivares-Villegas *et al.* (2007) found the opposite. Under low nitrogen conditions (nitrogen stress), heritability for agronomic traits such as YLD, number of grains and TKW, was lower than in high nitrogen conditions (Laperche et al., 2006; Zheng et al., 2010). Bowman (1972) and Malosetti et al. (2013) expected heritability to be higher in optimum environments (i.e., irrigated) than in stress prone environments (i.e., drought and heat-irrigated) because of reduced environmental variance. Such expectation should be modulated in particular in the case of stress-adaptive physiological traits which can display higher genetic variance in environment as thei evolution of the genetic variance.

Physiological traits interacted more with the environment then agronomic traits?

In our study, we reported highly significant genetic and GEI variances for many agronomic and physiological traits. Physiological traits tended to display in average stronger GEI (63%) than genetic (37%) variances whereas agronomic traits had in average similar genetic (54%) and GEI (46%) variances (Table 3). For physiological traits, similar results were reported by Lopes and Reynolds (2012). However, surprisingly, for CTgf in their second population, GEI was not significant at all. This maybe could be due to a constitutive QTL controlling the CTgf trait in the second population

Linear relations are probably not the best way of explaining relationship between agronomic habit and environmental covariates

In our study, we used multiple linear forward regressions to dissect the GEI of all main yield determinants (Table 3). Moreover interaction coefficients between environmental covariates and grain yield were estimated on the base of linear models. It appeared that when considering average grain yield, for many environmental covariates (EC2, EC3, EC5, and EC6), only few or none genotypes significantly linearly interacted; a linear approach may not be the best way of doing. A reasonable hypothesis can be made on the non-trivial (i.e., linear) reaction of plant faced to complex environment with many impacting stress, (e.g., threshold effects, polynomial curve fitting, *etc.*). The

structure of the environment of the trial network may also be part of the explanation on the few significant linear interaction coefficients between yield and environmental covariates. Indeed, our environments were highly contrasted, i.e., IR, DR and HI. In 2014, Bouffier *et al.* discussed the point of different trials with similar agronomic values but having experienced different environmental stresses. A multi-dimensional approach may be a way of going beyond this limitation.

The population SW displayed particular but robust habit. Contrary to the other populations, i.e., PW and VP, and whatever the environment, grain size and grains per spike were similarly involved in yield achievement. Indeed, in average, TKW displayed consistent (100 % of the observations), positive and significant correlation with yield ($r=0.38$, $p<0.001$) (Table 2).

Looking at correlations between interaction coefficients with different environmental covariates may give indication on the breeding approach

For each genotype within a population we computed the regression between grain yield and each environmental covariate. We then calculated the correlations between the slopes (interaction coefficents) obtained with different covariates. A similar pattern of correlations was found in populations PW and SW. Most correlations between interaction coefficients were highly significant (Supplementary Data 8). Some were positives, and other negatives. In PW and SW, significant correlations were found between yield interaction coefficients with EC2 and with EC5, both heat stress environmental covariates, during the grain set and grain filling phase (EC2) and vegetative phase (EC5) (Supplementary Data 3). So, improving heat stress tolerance whatever the developmental phase is likely to involve the same genotypes, i.e., the tolerance to heat stress within the populations studied is not phase specific. However, in population PW and SW, the negative and highly significant correlation between EC1 and EC3 interaction coefficients indicates that it may be difficult to breed for genotypes adapted both to situations with none to light drought stress (EC1) and strong drought stress along the whole crop cycle (EC3).

CONCLUSION

The analyses presented in this study highlighted the use of the environmental covariates established in Bouffier et al. (2014) through the use of factorial regression models which enable to dissect most of the genotype-by-environment interaction variance. The analyses revealed a higher contribution of the genotype-by-environment interaction variance for physiological than for agronomic traits and also a differential sensitivity of the population studied to the environmental stresses experienced.

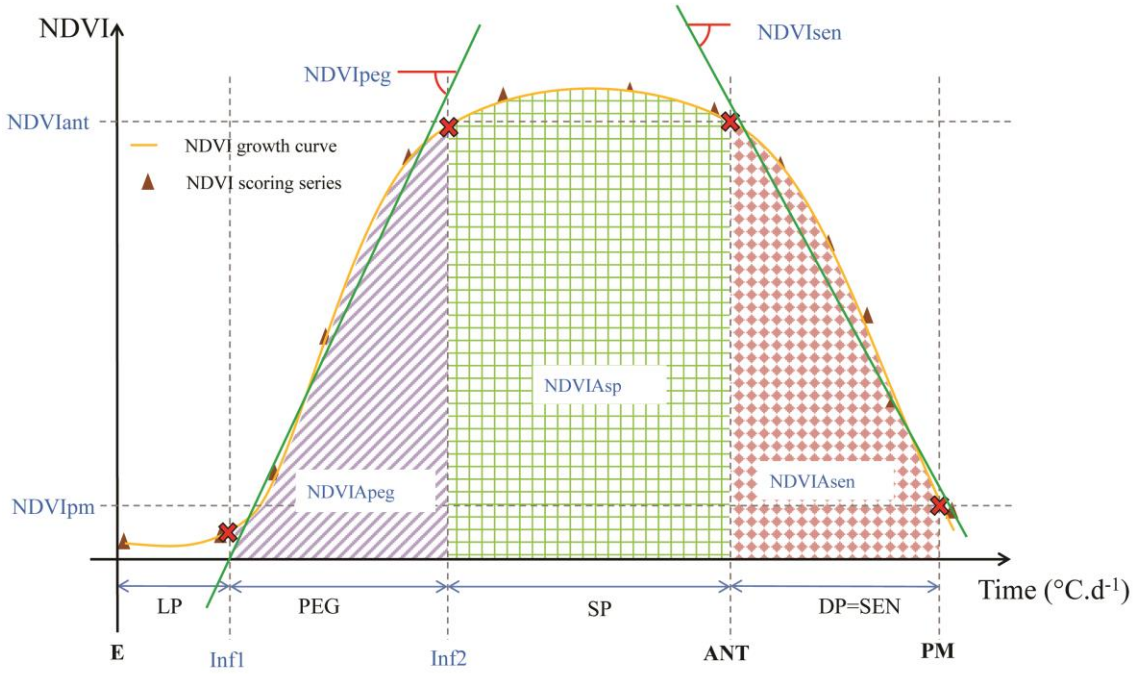
SUPPLEMENTAL DATA

Supplementary Data 1: Statistical summary and broad sense heritability (H^2) of the scored traits within the trial network per treatment. Trait abbreviations are given with Table 1. GDD: growing degree days since sowing. Dash symbols represent non-scored trait

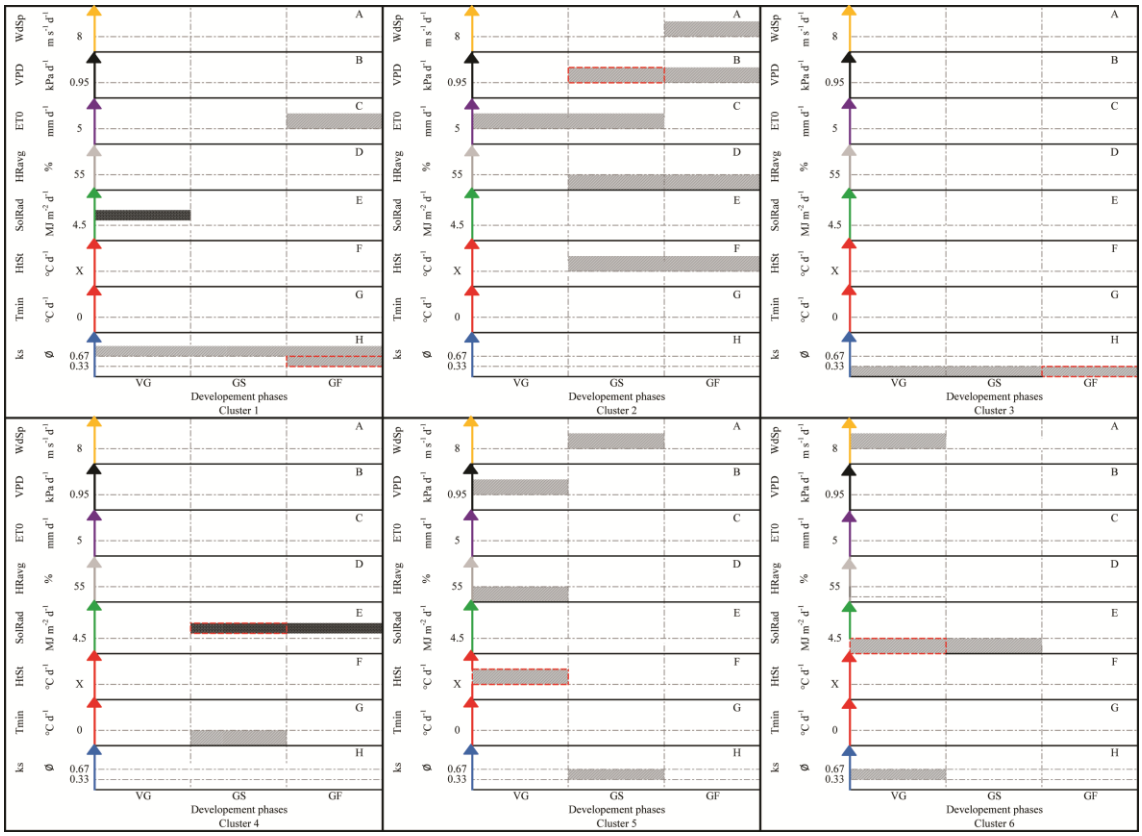
Traits	Units		TrialCode														
			PW11IR	PW12IR	SW12IR	VP11DR	PW12DR	SW12DR	VP12DR	PW13DR	SW13DR	PW11HI	SW11HI	VP11HI	PW12HI	SW12HI	VP12HI
ANT	GDD	Min	1048	1087	1103	1126	940	944	939	966	999	831	851	850	882	963	891
		Max	1210	1253	1299	1250	1047	1100	1067	1138	1175	1035	1005	982	1048	1124	1006
		Mean	1130	1177	1203	1188	1003	1028	995	1050	1078	931	921	911	963	1041	956
		SD	36	36	38	26	22	29	28	36	34	41	31	27	26	34	23
		H^2	0.89	0.86	0.85	0.79	0.86	0.87	0.85	0.91	0.87	0.84	0.75	0.7	0.79	0.77	0.76
PM	GDD	Min	1628	1685	1681	1625	1388	1373	1299	1424	1425	1363	1375	1370	1468	1496	1484
		Max	1790	1823	1854	1858	1528	1558	1468	1557	1574	1533	1531	1543	1598	1631	1627
		Mean	1701	1755	1768	1715	1442	1462	1402	1502	1501	1444	1432	1433	1512	1558	1533
		SD	34	32	34	45	21	36	23	27	26	34	31	34	20	25	17
		H^2	0.78	0.78	0.84	0.79	0.79	0.83	0.82	0.83	0.85	0.83	0.85	0.79	0.72	0.76	0.6
CTvg	°C	Min	-	20.5	21	-	24.1	25.3	-	21.2	20.7	22.5	22.2	21.3	21.7	21.9	19.7
		Max	-	21.9	22.3	-	26	26.5	-	23.7	22.7	24.2	24.1	22.9	25.2	25.7	22.2
		Mean	-	21.3	21.6	-	25	26	-	22.4	21.5	23.4	23.1	22.1	23.3	23.5	20.9
		SD	-	0.3	0.3	-	0.3	0.2	-	0.4	0.4	0.3	0.4	0.3	0.7	0.7	0.5
		H^2	-	0.54	0.54	-	0.17	0	-	0	0.36	0.63	0.61	0.17	0.59	0.5	0.46
CTgs	°C	Min	-	-	-	26.6	22.7	19.6	-	20	-	26	22.3	24.9	24.2	27.4	23.5
		Max	-	-	-	28.8	25.4	21.8	-	21.9	-	28.2	24.4	27.3	27.4	29.6	26.1
		Mean	-	-	-	27.8	23.9	20.7	-	20.9	-	27.3	23.1	25.8	25.8	28.4	24.9
		SD	-	-	-	0.4	0.4	0.4	-	0.3	-	0.4	0.4	0.3	0.7	0.4	0.5
		H^2	-	-	-	0.17	0.11	0.36	-	0.23	-	0.12	0.41	0.5	0.67	0.46	0.66
CTgf	°C	Min	23.9	21.9	22.9	-	26.4	27	30.4	24.9	23.4	28.9	26.7	28.8	29.1	28.2	28.1
		Max	25.4	23.6	24.7	-	28.2	29.4	33.5	26.8	26.1	30.3	28.3	30.1	33.3	32.8	30.7
		Mean	24.7	22.6	23.9	-	27.2	28	32	26	24.8	29.7	27.4	29.5	30.9	30.2	29.3
		SD	0.3	0.3	0.3	-	0.3	0.4	0.6	0.4	0.5	0.3	0.2	0.3	0.9	0.8	0.5
		H^2	0.58	0.26	0.24	-	0.32	0.39	0.54	0	0.21	0.29	0.57	0.28	0.61	0.16	0.49
CTcycle	°C	Min	-	21.4	22	-	24.7	24	-	22.4	22.2	26.2	23.7	25.3	25.2	26.5	24
		Max	-	22.4	23.3	-	26	25.6	-	24	24.3	27.4	25.6	26.4	28.4	29	26.2
		Mean	-	21.9	22.7	-	25.4	24.9	-	23.1	23.1	26.8	24.5	25.8	26.7	27.4	25
		SD	-	0.2	0.2	-	0.2	0.2	-	0.3	0.3	0.2	0.3	0.2	0.7	0.4	0.4
		H^2	-	0.39	0.41	-	0.25	0.38	-	0	0.39	0.48	0.67	0.45	0.71	0.44	0.68
FLG	-	Min	-	0.1	1.1	-	0.3	1.5	-	4.1	5.7	1.8	2.5	2.9	-	-	-
		Max	-	3.8	4.4	-	3.9	4.3	-	7.5	7.9	6.6	7.2	6.4	-	-	-
		Mean	-	1.8	2.7	-	2.5	3.2	-	5.9	6.7	4.1	4.9	4.6	-	-	-
		SD	-	0.7	0.7	-	0.7	0.6	-	0.6	0.5	0.9	0.8	0.6	-	-	-
		H^2	-	0.71	0.38	-	0.62	0.41	-	0.55	0.33	0.56	0.32	0.29	-	-	-
NDVIpeg	GDD^{-1}	Min	-	$9.20x10^{-4}$	$1.04x10^{-3}$	$1.81x10^{-3}$	$1.23x10^{-3}$	$1.41x10^{-3}$	-	$1.52x10^{-3}$	$1.61x10^{-3}$	$1.27x10^{-3}$	$1.20x10^{-3}$	-	$9.52x10^{-4}$	$9.69x10^{-4}$	-
		Max	-	$1.15x10^{-3}$	$1.60x10^{-3}$	$2.50x10^{-3}$	$1.97x10^{-3}$	$1.91x10^{-3}$	-	$1.80x10^{-3}$	$1.89x10^{-3}$	$2.07x10^{-3}$	$1.92x10^{-3}$	-	$1.67x10^{-3}$	$1.74x10^{-3}$	-
		Mean	-	$1.01x10^{-3}$	$1.31x10^{-3}$	$2.16x10^{-3}$	$1.73x10^{-3}$	$1.68x10^{-3}$	-	$1.70x10^{-3}$	$1.73x10^{-3}$	$1.84x10^{-3}$	$1.67x10^{-3}$	-	$1.37x10^{-3}$	$1.31x10^{-3}$	-
		SD	-	$2.94x10^{-5}$	$1.02x10^{-4}$	$1.40x10^{-4}$	$1.23x10^{-4}$	$8.23x10^{-5}$	-	$4.43x10^{-5}$	$4.53x10^{-5}$	$1.14x10^{-4}$	$1.09x10^{-4}$	-	$1.56x10^{-4}$	$1.44x10^{-4}$	-
		H^2	-	0.44	0.45	0.58	0.5	0.52	-	0.27	0.2	0.69	0.68	-	0.7	0.58	-
NDVIinf2	GDD	Min	-	877	657	617	509	498	-	615	612	553	588	603	554	585	479
		Max	-	1032	849	663	678	630	-	680	669	614	675	673	678	769	661
		Mean	-	941	767	638	554	556	-	641	640	575	622	635	595	686	579
		SD	-	13	40	9	27	21	-	12	11	7	13	12	23	34	27
		H^2	-	0.41	0.46	0.27	0.57	0.53	-	0.48	0.37	0.64	0.71	0.51	0.44	0.5	0.31
NDVIant	-	Min	0.591	0.709	0.714	0.493	0.657	0.591	-	0.584	0.524	0.586	0.594	0.597	0.553	0.512	0.672
		Max	0.782	0.803	0.783	0.633	0.756	0.722	-	0.682	0.649	0.74	0.711	0.745	0.744	0.719	0.76
		Mean	0.684	0.76	0.75	0.563	0.705	0.674	-	0.628	0.604	0.667	0.658	0.684	0.669	0.647	0.726
		SD	0.032	0.018	0.011	0.027	0.018	0.024	-	0.018	0.018	0.027	0.02	0.023	0.038	0.027	0.014
		H^2	0.5	0.62	0.67	0.57	0.54	0.75	-	0.77	0.77	0.74	0.67	0.75	0.79	0.78	0.71
NDVIpm	-	Min	-	-	-	-	0.164	-	0.155	0.191	0.18	0.154	0.159	0.216	0.224	-	0.224
		Max	-	-	-	-	0.28	-	0.221	0.259	0.255	0.301	0.316	0.352	0.338	-	0.309
		Mean	-	-	-	-	0.225	-	0.18	0.225	0.214	0.233	0.229	0.286	0.273	-	0.273
		SD	-	-	-	-	0.022	-	0.011	0.014	0.013	0.026	0.024	0.025	0.02	-	0.016
		H^2	-	-	-	-	0.8	-	0.57	0.35	0.63	0.62	0.6	0.53	0.59	-	0.24
NDVIsen	GDD^{-1}	Min	-	-	-	$-1.02x10^{-3}$	$-1.38x10^{-3}$	$-1.47x10^{-3}$	-4.351	$-1.01x10^{-3}$	$-1.03x10^{-3}$	$-1.02x10^{-3}$	$-1.05x10^{-3}$	$-9.23x10^{-4}$	$-9.18x10^{-4}$	$-1.14x10^{-3}$	$-9.94x10^{-4}$
		Max	-	-	-	$-7.06x10^{-4}$	$-1.01x10^{-3}$	$-8.59x10^{-4}$	$-8.56x10^{-4}$	$-7.81x10^{-4}$	$-7.32x10^{-4}$	$-6.29x10^{-4}$	$-6.62x10^{-4}$	$-5.31x10^{-4}$	$-5.68x10^{-4}$	$-6.41x10^{-4}$	$-7.13x10^{-4}$
		Mean	-	-	-	$-8.60x10^{-4}$	$-1.18x10^{-3}$	$-1.17x10^{-3}$	$-1.11x10^{-3}$	$-8.99x10^{-4}$	$-9.28x10^{-4}$	$-8.58x10^{-4}$	$-8.49x10^{-4}$	$-7.60x10^{-4}$	$-7.75x10^{-4}$	$-8.62x10^{-4}$	$-8.14x10^{-4}$
		SD	-	-	-	$6.82x10^{-5}$	$6.53x10^{-5}$	$1.10x10^{-4}$	$9.57x10^{-5}$	$4.19x10^{-5}$	$3.59x10^{-5}$	$7.81x10^{-5}$	$6.41x10^{-5}$	$6.57x10^{-5}$	$6.51x10^{-5}$	$6.24x10^{-5}$	$4.03x10^{-5}$
		H^2	-	-	-	0.56	0.63	0.67	0.66	0.61	0.55	0.5	0.65	0.67	0.79	0.72	0.61
PH	cm	Min	85	94	91	58	69	68	64	65	63	76	71	82	60	58	73
		Max	114	129	139	79	91	94	89	83	84	98	96	103	81	83	90
		Mean	98	107	112	69	80	82	75	75	72	84	85	93	69	71	82
		SD	4	4	4.8	3.6	3.5	4.5	4.3	3.7	3.6	3.3	4.4	3.4	3.5	4.3	3.2
		H^2	0.74	0.73	0.86	0.56	0.7	0.71	0.43	0.67	0.35	0.71	0.73	0.72	0.7	0.77	0.76
PL	cm	Min	32	36	35	-	22	23	-	19	17	27	27	32	20	18	22
		Max	45	50	48	-	30	35	-	26	27	35	37	41	28	29	34
		Mean	37	40	43	-	26	29	-	22	23	30	33	37	23	24	29
		SD	1.9	1.9	2.1	-	1.5	2	-	1.3	1.6	1.4	2	1.8	1.3	2	1.7
		H^2	0.68	0.65	0.79	-	0.72	0.71	-	0.42	0.6	0.76	0.7	0.73	0.64	0.7	0.56
WSC	%	Min	22.4	-	-	-	28.6	-	-	-	-	11.8	-	-	18.1	-	-
		Max	36.9	-	-	-	37.2	-	-	-	-	25.8	-	-	24.7	-	-
		Mean	30.3	-	-	-	33.3	-	-	-	-	18.2	-	-	21.7	-	-
		SD	2.5	-	-	-	1.3	-	-	-	-	2.7	-	-	1.1	-	-
		H^2	0.76	-	-	-	0.24	-	-	-	-	0.74	-	-	0	-	-
SM2	spikes m^{-2}	Min	-	295	295	-	248	236	-	207	203	244	245	267	203	182	222
		Max	-	475	477	-	429	379	-	355	325	449	394	462	372	405	391
		Mean	-	362	358	-	328	300	-	269	260	336	311	358	266	304	314
		SD	-	30	28	-	30	27	-	26	23	36	28	32	29	32	29
		H^2	-	0.29	0.11	-	0.36	0.38	-	0.45	0.48	0.54	0.3	0.3	0.48	0.29	0.23

Supplementary Data 1 (continued)

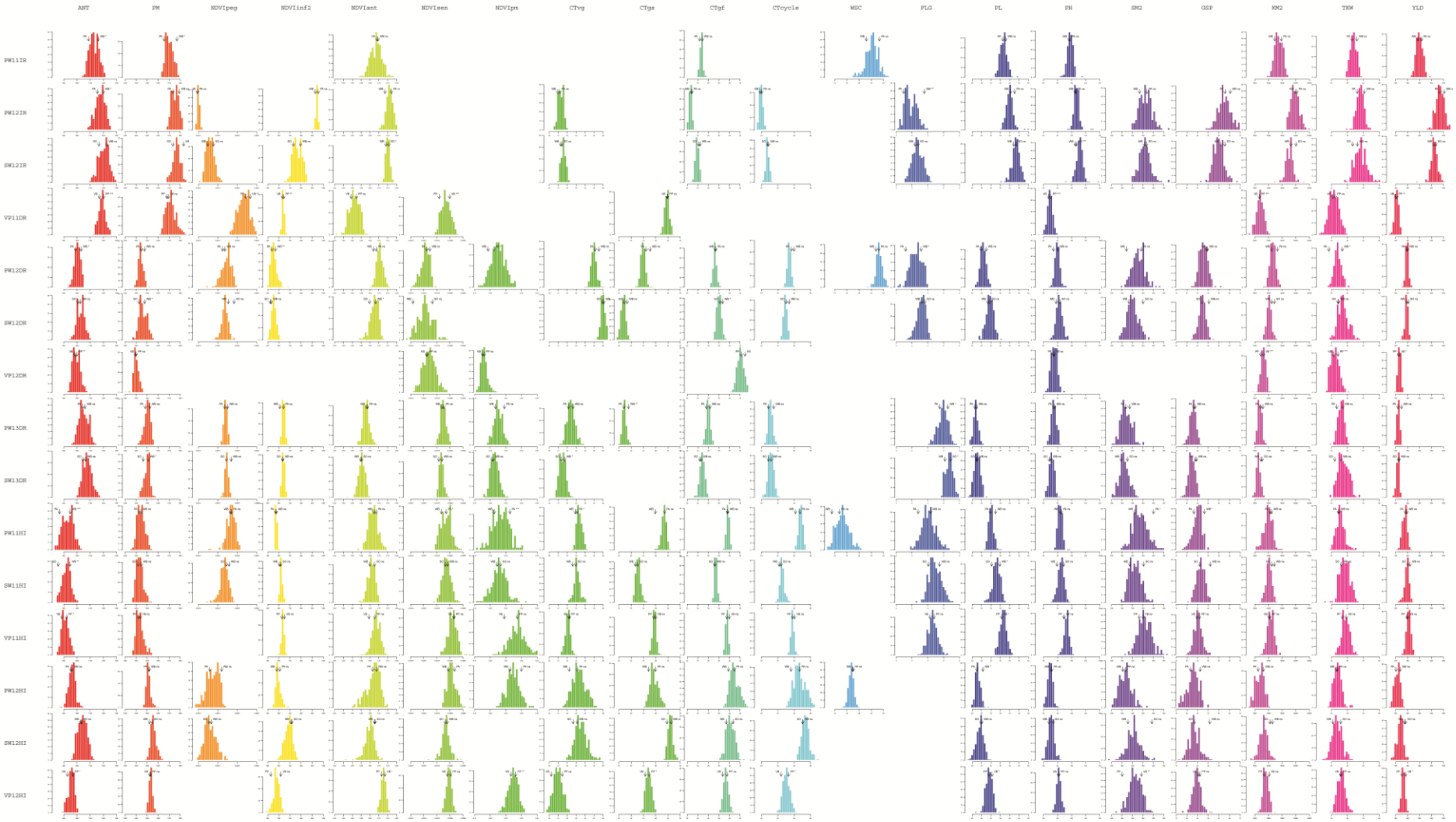
Traits	Units		TrialCode														
			PW11IR	PW12IR	SW12IR	VP11DR	PW12DR	SW12DR	VP12DR	PW13DR	SW13DR	PW11HI	SW11HI	VP11HI	PW12HI	SW12HI	VP12HI
GSP	grains spike^{-1}	Min	-	38.5	33.2	-	25.4	25.1	-	16.8	14.9	16.4	20.7	20.4	11.9	13.2	15.6
		Max	-	69.6	66.4	-	51.8	44.6	-	33.1	32.1	39.6	42.3	41.5	39.6	43.8	43.2
		Mean	-	55.2	49.8	-	35.6	34.4	-	25.7	24.6	29.7	32.9	30.5	25.7	27.1	29.3
		SD	-	5.9	4.8	-	4	3.4	-	2.9	3.1	4.3	3.9	3.8	5.5	4.9	3.7
		H²	-	0.44	0.45	-	0.51	0.38	-	0.38	0.6	0.65	0.49	0.47	0.76	0.54	0.43
KM2	grains m^{-2}	Min	9,922	16,610	12,254	3,179	8,467	7,230	4,424	5,066	4,207	5,592	6,650	6,765	2,652	3,734	6,181
		Max	16,808	25,225	22,915	10,426	14,402	13,053	10,619	8,969	8,414	14,755	12,760	14,107	10,231	12,134	12,233
		Mean	13,709	19,718	17,648	6,912	11,562	10,215	8,123	6,817	6,335	9,878	10,129	10,788	6,791	8,159	9,055
		SD	1,394	1,569	1,282	1,283	1,035	920	918	750	757	1,564	1,044	1,209	1,584	1,460	983
		H²	0.67	0.72	0.7	0.76	0.67	0.69	0.74	0.53	0.75	0.83	0.74	0.75	0.85	0.72	0.69
TKW	g	Min	40	39	39	22	29	29	27	30	29	30	26	33	29	25	29
		Max	48	54	61	40	41	47	41	40	47	45	46	46	43	42	43
		Mean	44	48	48	32	34	37	32	36	38	36	38	39	34	34	36
		SD	2	2	4	3	2	3	3	2	3	3	3	2	2	3	2
		H²	0.68	0.84	0.9	0.82	0.78	0.82	0.84	0.83	0.89	0.85	0.87	0.82	0.87	0.86	0.86
YLD	g m^{-2}	Min	463	751	554	108	315	286	140	193	157	230	239	316	108	128	244
		Max	755	1118	1008	294	470	449	326	302	285	460	493	529	335	416	421
		Mean	596	942	849	214	392	380	260	245	236	349	386	418	227	275	326
		SD	53	69	56	33	25	28	24	23	23	41	41	36	47	51	30
		H²	0.59	0.6	0.67	0.64	0.43	0.59	0.61	0.49	0.64	0.75	0.79	0.66	0.83	0.75	0.63



Supplementary Data 2: Scheme of a theoretical NDVI curve. Such curve can be assimilated to microorganism growth curve in which usually five phases can be chronologically identified: (1) the lag phase (LP), (2) the phase of exponential growth (PEG), (3) the slowdown phase (SdP), (4) the stationary phase (SP) and (5) the decline phase (DP). The biological significance of all phases described for microorganism growth curve is not adapted for plant. The SP better corresponds to the maximum greenness due to a continued accumulation and the lack of sensitivity of the tool used which reach saturation. DP may be better named senescence phase (SEN) for plants. In our situation, to simplify computation, neither LP nor SdP were considered. SdP was split between PEG and SP. The PEG started at the inflexion point abscissa between LP and PEG (Inf1, not shown). This is the starting point of each curve) and ended at the inflexion point abscissa between PEG and SP (Inf2), where SP started. It ended then at anthesis (ANT) of the considered plot, where SEN begun. Finally, SEN ended when PM was reached. Several traits were estimated based on NDVI growth curve. Estimating a trait during a whole phase as previously defined required using both boundaries of the considered phase and all scorings between them. First of all, specific points were established. For a given plot, the abscissa of the boundaries of the PEG, called Inf1 and Inf2 were computed to determine its own PEG phase. As usually Inf1 did not vary within a trial. It was not considered. Then, a prediction of NDVI value at ANT and physiological maturity (PM) was calculated. During the PEG, the slope (NDVIpeg) and the area under the curve (NDVIApeg) were estimated. Similar traits were computed during SEN called respectively NDVIsen and NDVIAsen. Finally, the area under the curve during the SP was estimated (NDVIAsp).



Supplementary Data 3: Diagram of the environmental covariates grouped into six different clusters. Per cluster, limiting factors are on the y-axis and development phases on x-axis. On x-axis are found the following developmental phases: vegetative (VG), grain set (GS) and grain filling (GF). On y-axis are found WdSpeed (A), the average wind speed, VPD (B), the average vapour pressure deficit, ET0 (C), the reference evapotranspiration, HRavg (D), the average relative air moisture, SolRad (E), the solar radiation received by crop, HtSt (F), the high temperature stress, Tmin (G), the minimum temperature, and ks (H), the drought stress coefficient. The darkest cells filled for the SolRad subplot correspond to the SumSolRad EP. For HtSt, threshold "X" represents "Tmax>33°C" + "30<Tmax≤33°C & ks<1". Red dotted outlined cell are the representative environmental covariates of each cluster.



Supplementary Data 4: Frequency distributions of non-normalized adjusted traits values organized by trial (rows) and by traits (columns). Each vertical axis indicates the number of lines per trait value class; each horizontal axis, the different trait value classes. Within a column, the abscissa is the same. Parents of each population are indicated: PW (PA: Pastor//hxl7573/2*Bagula; WB: Weebill1), SW (SO: Sokoll; WB: Weebill1), and VP (VB: Vorobey; PP: Parus/Pastor). Trait abbreviations are given with Table 1.

Supplementary Data 5: Table of average broad sense heritability (H^2) per trait per treatment, all populations considered. N.obs corresponds to the number of observations available, and sd, the standard error of mean. GDD: growing degree days. Trait abbreviations are given with Table 1. Dash symbols represent non-scored trait.

Traits	Treatment								
	DR			HI			IR		
	N.obs	H^2	sd	N.obs	H^2	sd	N.obs	H^2	sd
CTcycle	3	0.34	0.07	6	0.57	0.12	2	0.4	0.01
CTgf	4	0.37	0.13	6	0.4	0.17	3	0.36	0.17
CTgs	4	0.22	0.1	6	0.47	0.19	-	-	-
CTvg	2	0.27	0.11	6	0.49	0.16	2	0.54	0
FLG	4	0.48	0.12	3	0.39	0.13	2	0.55	0.19
Inf2	5	0.44	0.12	6	0.52	0.14	2	0.44	0.03
NDVIant	5	0.68	0.11	6	0.74	0.04	3	0.6	0.08
NDVIpm	3	0.52	0.13	5	0.52	0.15	-	-	-
NDVIpeg	5	0.41	0.16	4	0.66	0.05	2	0.45	0.01
NDVIsen	6	0.61	0.05	6	0.66	0.09	-	-	-
WSC	1	0.24	0	1	0.74	0	1	0.76	0
ANT	6	0.86	0.04	6	0.77	0.04	3	0.87	0.02
PM	6	0.82	0.02	6	0.76	0.09	3	0.8	0.03
PH	6	0.57	0.14	6	0.73	0.03	3	0.78	0.06
PL	4	0.61	0.13	6	0.68	0.07	3	0.71	0.07
GSP	4	0.47	0.1	6	0.56	0.12	2	0.45	0.01
KM2	6	0.69	0.08	6	0.76	0.06	3	0.7	0.02
SM2	4	0.42	0.05	6	0.36	0.12	2	0.2	0.1
TKW	6	0.83	0.03	6	0.86	0.02	3	0.81	0.1
YLD	6	0.57	0.08	6	0.74	0.07	3	0.62	0.04

Supplementary Data 6: Partial Pearson correlations considering anthesis and physiological maturity as covariates. GDD: growing degree days. Dash symbols represent non-scored trait. *, **, and *** Significant at the 0.05, 0.01, and 0.001 level of probability; ns: non-significant at 0.05 level of probability. Trait abbreviations are given with Table 1.

Trial code	Traits	PH	PL	CTvg	CTgs	CTgf	CTcycle	Inf2	NDVIant	NDVIpm	SlpSEN	SlpPEG	FLG	WSC	GSP	KM2	SM2	TKW	YLD
PW11IR	PH	1																	
	PL	0.53 ***	1																
	CTvg	-	-	1															
	CTgs	-	-	-	1														
	CTgf	-0.51 ***	-0.42 ***	-	-	1													
	CTcycle	-	-	-	-	-	1												
	NDVIinf2	-	-	-	-	-	-	1											
	NDVIant	0.25 ***	ns	-	-	ns	-	-	1										
	NDVIpm	-	-	-	-	-	-	-	-	1									
	NDVIsen	-	-	-	-	-	-	-	-	-	1								
	NDVIpeg	-	-	-	-	-	-	-	-	-	-	1							
	FLG	-	-	-	-	-	-	-	-	-	-	-	1						
	WSC	ns	-0.21 **	-	-	ns	-	-	-0.16 *	-	-	-	-	1					
	GSP	-	-	-	-	-	-	-	-	-	-	-	-	-	1				
	KM2	ns	ns	-	-	-0.23 ***	-	-	0.38 ***	-	-	-	-	-0.29 ***	-	1			
	SM2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1		
	TKW	ns	0.26 ***	-	-	ns	-	-	-0.20 **	-	-	-	-	ns	-	-0.50 ***	-	1	
	YLD	0.21 **	ns	-	-	-0.26 ***	-	-	0.33 ***	-	-	-	-	-0.27 ***	-	0.89 ***	-	ns	1
PW12IR	PH	1																	
	PL	0.56 ***	1																
	CTvg	-0.15 *	ns	1															
	CTgs	-	-	-	1														
	CTgf	ns	ns	ns	-	1													
	CTcycle	ns	ns	0.77 ***	-	0.69 ***	1												
	NDVIinf2	ns	ns	ns	-	ns	ns	1											
	NDVIant	0.35 ***	0.18 *	-0.37 ***	-	ns	-0.33 ***	0.37 ***	1										
	NDVIpm	-	-	-	-	-	-	-	-	1									
	NDVIsen	-	-	-	-	-	-	-	-	-	1								
	NDVIpeg	ns	ns	ns	-	-0.14 *	ns	-0.45 ***	ns	-	-	1							
	FLG	ns	-0.19 **	0.16 *	-	ns	ns	-0.27 ***	-0.48 ***	-	-	ns	1						
	WSC	-	-	-	-	-	-	-	-	-	-	-	-	1					
	GSP	ns	-0.14 *	-0.15 *	-	ns	-0.14 *	ns	ns	-	-	ns	ns	-	1				
	KM2	ns	-0.15 *	-0.38 ***	-	-0.17 *	-0.38 ***	0.14 *	0.27 ***	-	-	ns	-0.14 *	-	0.66 ***	1			
	SM2	0.16 *	ns	-0.17 *	-	ns	-0.18 *	ns	0.15 *	-	-	ns	ns	-	-0.68 ***	ns	1		
	TKW	ns	ns	0.17 *	-	-0.16 *	ns	-0.22 **	-0.23 ***	-	-	ns	0.32 ***	-	-0.21 **	-0.41 ***	-0.15 *	1	
	YLD	ns	ns	-0.3 ***	-	-0.28 ***	-0.40 ***	ns	0.14 *	-	-	ns	ns	-	0.56 ***	0.8 ***	ns	0.21 **	1

Supplementary Data 6 (continued)

Trial code	Traits	PH	PL	CTvg	CTgs	CTgf	CTcycle	Inf2	NDVIant	NDVIpm	SlpSEN	SlpPEG	FLG	WSC	GSP	KM2	SM2	TKW	YLD
PW12DR	PH	1																	
	PL	0.57 ***	1																
	CTvg	ns	ns	1															
	CTgs	-0.14 *	ns	0.26 ***	1														
	CTgf	-0.55 ***	-0.48 ***	ns	ns	1													
	CTcycle	-0.40 ***	-0.29 ***	0.66 ***	0.72 ***	0.57 ***	1												
	Inf2	ns	ns	ns	ns	ns	ns	1											
	NDVIant	0.46 ***	0.38 ***	-0.25 ***	ns	-0.39 ***	-0.38 ***	-0.25 ***	1										
	NDVIpm	-	-	-	-	-	-	-	-	1									
	SlpSEN	ns	ns	0.20 **	ns	ns	0.16 *	0.18 **	-0.57 ***	-	1								
	SlpPEG	0.19 **	ns	ns	ns	ns	ns	-0.94 ***	0.33 ***	-	-0.25 ***	1							
	FLG	-0.24 ***	-0.27 ***	ns	ns	0.17 *	ns	0.23 ***	-0.55 ***	-	0.34 ***	-0.20 **	1						
	WSC	ns	-0.19 **	0.16 *	ns	ns	ns	ns	ns	-	ns	ns	ns	1					
	GSP	0.15 *	0.17 *	ns	ns	-0.14 *	-0.15 *	ns	ns	-	ns	0.14 *	ns	ns	1				
	KM2	0.18 *	ns	-0.18 **	ns	-0.19 **	-0.21 **	-0.35 ***	0.36 ***	-	-0.32 ***	0.39 ***	-0.19 **	ns	0.64 ***	1			
	SM2	ns	ns	-0.19 **	ns	ns	ns	-0.20 **	0.30 ***	-	-0.17 *	0.19 **	ns	ns	-0.62 ***	0.18 **	1		
	TKW	ns	0.18 *	ns	ns	ns	ns	0.24 ***	ns	-	0.29 ***	-0.23 ***	0.18 *	ns	-0.40 ***	-0.71 ***	-0.22 **	1	
	YLD	0.37 ***	0.34 ***	-0.27 ***	-0.19 **	-0.37 ***	-0.41 ***	-0.25 ***	0.41 ***	-	-0.18 **	0.31 ***	ns	ns	0.48 ***	0.69 ***	ns	ns	1
PW13DR	PH	1																	
	PL	0.61 ***	1																
	CTvg	ns	ns	1															
	CTgs	-0.21 **	ns	0.43 ***	1														
	CTgf	-0.27 ***	-0.25 ***	ns	0.30 ***	1													
	CTcycle	-0.27 ***	ns	0.77 ***	0.76 ***	0.64 ***	1												
	Inf2	0.18 *	ns	ns	ns	ns	ns	1											
	NDVIant	0.33 ***	0.18 **	-0.17 *	-0.25 ***	-0.23 ***	-0.29 ***	ns	1										
	NDVIpm	0.43 ***	0.30 ***	ns	-0.22 **	-0.24 ***	-0.23 **	ns	0.65 ***	1									
	SlpSEN	ns	ns	ns	ns	ns	ns	0.18 *	-0.55 ***	0.24 ***	1								
	SlpPEG	ns	ns	ns	ns	ns	ns	-0.36 ***	ns	0.17 *	ns	1							
	FLG	ns	ns	ns	ns	ns	ns	ns	-0.30 ***	ns	0.30 ***	ns	1						
	WSC	-	-	-	-	-	-	-	-	-	-	-	-	1					
	GSP	0.16 *	ns	ns	ns	ns	ns	ns	0.17 *	ns	-0.20 **	ns	ns	-	1				
	KM2	ns	ns	-0.15 *	ns	-0.19 **	-0.18 **	-0.20 **	0.21 **	ns	-0.24 ***	0.16 *	ns	-	0.65 ***	1			
	SM2	-0.22 **	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	-	-0.46 ***	0.35 ***	1		
	TKW	0.28 ***	0.21 **	ns	-0.18 *	ns	ns	ns	ns	ns	ns	-0.14 *	ns	-	-0.35 ***	-0.54 ***	-0.20 **	1	
	YLD	ns	ns	-0.25 ***	-0.17 *	-0.23 ***	-0.31 ***	-0.22 **	0.27 ***	ns	-0.23 ***	ns	ns	-	0.57 ***	0.87 ***	0.3 ***	ns	1

Supplementary Data 6 (continued)

Trial code	Traits	PH	PL	CTvg	CTgs	CTgf	CTcycle	Inf2	NDVIant	NDVIpm	SlpSEN	SlpPEG	FLG	WSC	GSP	KM2	SM2	TKW	YLD
PW11HI	PH	1																	
	PL	0.47 ***	1																
	CTvg	-0.32 ***	-0.21 **	1															
	CTgs	-0.30 ***	-0.20 **	0.32 ***	1														
	CTgf	-0.27 ***	-0.23 **	0.43 ***	0.32 ***	1													
	CTcycle	-0.39 ***	-0.28 ***	0.75 ***	0.78 ***	0.72 ***	1												
	Inf2	ns	ns	0.14 *	ns	ns	ns	1											
	NDVIant	0.54 ***	0.28 ***	-0.36 ***	-0.25 ***	-0.35 ***	-0.42 ***	0.22 **	1										
	NDVIpm	0.30 ***	0.25 ***	ns	-0.15 *	ns	-0.16 *	ns	0.28 ***	1									
	SlpSEN	-0.22 **	ns	0.16 *	ns	ns	0.17 *	-0.15 *	-0.56 ***	0.55 ***	1								
	SlpPEG	0.21 **	0.16 *	-0.22 **	ns	ns	ns	-0.37 ***	0.18 *	ns	ns	1							
	FLG	-0.25 ***	ns	ns	0.25 ***	ns	0.22 **	-0.23 **	-0.47 ***	-0.24 ***	0.20 **	ns	1						
	WSC	-0.22 **	-0.25 ***	0.41 ***	0.21 **	0.20 **	0.36 ***	ns	ns	ns	ns	ns	0.15 *	1					
	GSP	ns	ns	-0.36 ***	ns	-0.20 **	-0.29 ***	ns	ns	-0.23 ***	ns	0.16 *	ns	-0.40 ***	1				
	KM2	ns	ns	-0.6 ***	-0.19 **	-0.36 ***	-0.49 ***	ns	0.29 ***	ns	-0.23 **	0.28 ***	-0.15 *	-0.56 ***	0.75 ***	1			
	SM2	0.30 ***	0.26 ***	-0.41 ***	ns	-0.24 ***	-0.33 ***	ns	0.38 ***	0.17 *	-0.15 *	0.20 **	-0.25 ***	-0.31 ***	-0.24 ***	0.45 ***	1		
	TKW	ns	ns	0.24 ***	ns	ns	ns	ns	ns	0.18 *	ns	ns	0.19 **	0.52 ***	-0.53 ***	-0.74 ***	-0.36 ***	1	
	YLD	0.27 ***	ns	-0.65 ***	-0.25 ***	-0.48 ***	-0.58 ***	-0.17 *	0.35 ***	ns	-0.25 ***	0.30 ***	ns	-0.44 ***	0.72 ***	0.9 ***	0.35 ***	-0.39 ***	1
PW12HI	PH	1																	
	PL	0.56 ***	1																
	CTvg	-0.47 ***	-0.24 ***	1															
	CTgs	-0.50 ***	-0.27 ***	0.77 ***	1														
	CTgf	-0.52 ***	-0.30 ***	0.7 ***	0.82 ***	1													
	CTcycle	-0.54 ***	-0.29 ***	0.89 ***	0.94 ***	0.93 ***	1												
	Inf2	-0.14 *	ns	0.20 **	0.23 ***	0.21 **	0.23 ***	1											
	NDVIant	0.63 ***	0.42 ***	-0.65 ***	-0.75 ***	-0.81 ***	-0.81 ***	ns	1										
	NDVIpm	0.65 ***	0.46 ***	-0.43 ***	-0.50 ***	-0.49 ***	-0.52 ***	ns	0.58 ***	1									
	SlpSEN	-0.27 ***	-0.14 *	0.46 ***	0.52 ***	0.59 ***	0.58 ***	ns	-0.76 ***	ns	1								
	SlpPEG	0.58 ***	0.39 ***	-0.63 ***	-0.73 ***	-0.76 ***	-0.77 ***	-0.51 ***	0.78 ***	0.52 ***	-0.53 ***	1							
	FLG	-	-	-	-	-	-	-	-	-	-	-	1						
	WSC	ns	ns	ns	ns	ns	ns	ns	ns	0.2 **	0.16 *	ns	-	1					
	GSP	0.18 *	0.14 *	-0.36 ***	-0.37 ***	-0.46 ***	-0.44 ***	ns	0.48 ***	ns	-0.62 ***	0.36 ***	-	-0.20 **	1				
	KM2	0.38 ***	0.28 ***	-0.55 ***	-0.56 ***	-0.63 ***	-0.64 ***	ns	0.65 ***	ns	-0.71 ***	0.55 ***	-	-0.18 *	0.88 ***	1			
	SM2	0.49 ***	0.33 ***	-0.50 ***	-0.52 ***	-0.49 ***	-0.55 ***	-0.16 *	0.51 ***	0.38 ***	-0.34 ***	0.49 ***	-	ns	ns	0.45 ***	1		
	TKW	ns	-0.19 **	ns	ns	ns	ns	ns	ns	0.17 *	0.26 ***	ns	-	0.34 ***	-0.55 ***	-0.58 ***	-0.21 **	1	
	YLD	0.39 ***	0.24 ***	-0.59 ***	-0.62 ***	-0.69 ***	-0.69 ***	ns	0.70 ***	0.14 *	-0.73 ***	0.61 ***	-	ns	0.85 ***	0.95 ***	0.41 ***	-0.34 ***	1

Supplementary Data 6 (continued)

Trial code	Traits	PH	PL	CTvg	CTgs	CTgf	CTcycle	Inf2	NDVIant	NDVIpm	SlpSEN	SlpPEG	FLG	WSC	GSP	KM2	SM2	TKW	YLD
SW12IR	PH	1																	
	PL	0.60 ***	1																
	CTvg	0.16 *	ns	1															
	CTgs	-	-	-	1														
	CTgf	-0.32 ***	-0.29 ***	ns	-	1													
	CTcycle	-0.15 *	-0.17 **	0.66 ***	-	0.81 ***	1												
	Inf2	-0.15 *	ns	ns	-	ns	ns	1											
	NDVIant	0.27 ***	0.16 *	ns	-	ns	-0.14 *	-0.22 ***	1										
	NDVIpm	-	-	-	-	-	-	-	-	1									
	SlpSEN	-	-	-	-	-	-	-	-	-	1								
	SlpPEG	ns	ns	ns	-	ns	ns	-0.93 ***	0.23 ***	-	-	1							
	FLG	ns	ns	ns	-	ns	ns	ns	-0.38 ***	-	-	ns	1						
	WSC	-	-	-	-	-	-	-	-	-	-	-	-	1					
	GSP	-0.33 ***	-0.20 **	ns	-	ns	ns	ns	ns	-	-	ns	ns	-	1				
	KM2	-0.44 ***	-0.25 ***	ns	-	0.13 *	ns	0.15 *	ns	-	-	ns	ns	-	0.61 ***	1			
	SM2	ns	ns	ns	-	ns	ns	ns	ns	-	-	ns	ns	-	-0.67 ***	0.17 **	1		
	TKW	0.40 ***	0.43 ***	ns	-	-0.28 ***	-0.25 ***	-0.24 ***	ns	-	-	0.18 **	ns	-	-0.31 ***	-0.6 ***	-0.18 **	1	
	YLD	ns	0.23 ***	-0.18 **	-	-0.23 ***	-0.28 ***	-0.13 *	ns	-	-	0.13 *	ns	-	0.31 ***	0.38 ***	ns	0.5 ***	1
SW12DR	PH	1																	
	PL	0.63 ***	1																
	CTvg	ns	ns	1															
	CTgs	-0.19 **	ns	0.16 *	1														
	CTgf	-0.59 ***	-0.51 ***	ns	ns	1													
	CTcycle	-0.47 ***	-0.36 ***	0.48 ***	0.68 ***	0.70 ***	1												
	Inf2	ns	ns	ns	ns	ns	ns	1											
	NDVIant	ns	ns	ns	ns	ns	ns	ns	1										
	NDVIpm	-	-	-	-	-	-	-	-	1									
	SlpSEN	ns	ns	ns	ns	ns	ns	ns	-0.18 **	-	1								
	SlpPEG	ns	ns	ns	ns	ns	ns	-0.90 ***	ns	-	ns	1							
	FLG	ns	ns	ns	ns	ns	ns	ns	ns	-	ns	ns	1						
	WSC	-	-	-	-	-	-	-	-	-	-	-	-	1					
	GSP	-0.17 *	ns	-0.16 *	-0.19 **	ns	-0.14 *	ns	ns	-	ns	ns	ns	-	1				
	KM2	-0.29 ***	-0.22 ***	-0.20 **	ns	ns	ns	ns	ns	-	ns	0.17 *	ns	-	0.53 ***	1			
	SM2	ns	-0.15 *	ns	0.19 **	ns	ns	ns	ns	-	ns	0.13 *	ns	-	-0.54 ***	0.42 ***	1		
	TKW	0.54 ***	0.54 ***	ns	-0.14 *	-0.31 ***	-0.30 ***	-0.15 *	ns	-	ns	ns	0.17 *	-	-0.22 ***	-0.64 ***	-0.38 ***	1	
	YLD	0.27 ***	0.36 ***	-0.30 ***	-0.17 **	-0.35 ***	-0.43 ***	-0.19 **	ns	-	ns	0.22 ***	0.16 *	-	0.4 ***	0.45 ***	ns	0.39 ***	1

Supplementary Data 6 (continued)

Trial code	Traits	PH	PL	CTvg	CTgs	CTgf	CTcycle	Inf2	NDVIant	NDVIpm	SlpSEN	SlpPEG	FLG	WSC	GSP	KM2	SM2	TKW	YLD
SW13DR	PH	1																	
	PL	0.53 ***	1																
	CTvg	-0.23 ***	-0.27 ***	1															
	CTgs	-	-	-	1														
	CTgf	-0.32 ***	-0.29 ***	0.38 ***	-	1													
	CTcycle	-0.34 ***	-0.34 ***	0.77 ***	-	0.88 ***	1												
	Inf2	ns	ns	ns	-	ns	ns	1											
	NDVIant	0.36 ***	0.45 ***	-0.20 **	-	-0.29 ***	-0.30 ***	0.24 ***	1										
	NDVIpm	0.37 ***	0.24 ***	-0.19 **	-	-0.28 ***	-0.29 ***	0.18 **	0.71 ***	1									
	SlpSEN	ns	-0.20 **	ns	-	ns	ns	ns	-0.54 ***	0.14 *	1								
	SlpPEG	-0.23 ***	-0.21 **	0.22 ***	-	0.18 **	0.23 ***	-0.25 ***	ns	ns	ns	1							
	FLG	ns	ns	ns	-	ns	ns	ns	-0.18 **	ns	0.19 **	ns	1						
	WSC	-	-	-	-	-	-	-	-	-	-	-	-	1					
	GSP	-0.17 **	ns	ns	-	ns	ns	-0.18 **	ns	-0.23 ***	ns	ns	ns	-	1				
	KM2	-0.23 ***	ns	ns	-	ns	ns	ns	ns	ns	-0.14 *	ns	ns	-	0.75 ***	1			
	SM2	ns	ns	ns	-	ns	ns	0.19 **	ns	0.16 *	ns	ns	ns	-	-0.43 ***	0.26 ***	1		
	TKW	0.32 ***	0.30 ***	ns	-	-0.15 *	-0.15 *	-0.15 *	ns	ns	ns	-0.15 *	ns	-	-0.38 ***	-0.57 ***	-0.24 ***	1	
	YLD	ns	0.22 ***	ns	-	-0.13 *	-0.15 *	-0.20 **	ns	ns	-0.18 **	ns	ns	-	0.56 ***	0.69 ***	ns	0.19 **	1
SW11HI	PH	1																	
	PL	0.59 ***	1																
	CTvg	ns	ns	1															
	CTgs	ns	ns	0.55 ***	1														
	CTgf	-0.16 *	-0.19 **	0.56 ***	0.72 ***	1													
	CTcycle	ns	-0.13 *	0.83 ***	0.89 ***	0.85 ***	1												
	Inf2	0.20 **	ns	ns	0.21 **	0.23 ***	0.22 ***	1											
	NDVIant	0.26 ***	0.19 **	ns	ns	ns	ns	0.34 ***	1										
	NDVIpm	0.44 ***	0.32 ***	ns	ns	ns	ns	ns	0.33 ***	1									
	SlpSEN	0.21 **	0.15 *	ns	ns	ns	ns	ns	-0.40 ***	0.67 ***	1								
	SlpPEG	ns	ns	-0.19 **	-0.21 **	-0.29 ***	-0.26 ***	-0.67 ***	ns	ns	ns	1							
	FLG	ns	ns	ns	ns	ns	ns	-0.18 **	-0.38 ***	-0.19 **	0.16 *	ns	1						
	WSC	-	-	-	-	-	-	-	-	-	-	-	-	1					
	GSP	-0.13 *	ns	-0.21 **	-0.15 *	-0.15 *	-0.20 **	-0.24 ***	ns	-0.21 **	ns	0.18 **	ns	-	1				
	KM2	-0.15 *	-0.14 *	-0.39 ***	-0.35 ***	-0.31 ***	-0.41 ***	-0.25 ***	ns	-0.18 **	-0.18 **	0.24 ***	ns	-	0.68 ***	1			
	SM2	ns	ns	-0.17 **	-0.21 **	-0.14 *	-0.21 **	ns	0.27 ***	ns	ns	ns	ns	-	-0.51 ***	0.27 ***	1		
	TKW	0.56 ***	0.47 ***	-0.22 ***	ns	-0.29 ***	-0.24 ***	0.13 *	ns	0.23 ***	0.14 *	ns	ns	-	-0.29 ***	-0.35 ***	ns	1	
	YLD	0.29 ***	0.25 ***	-0.54 ***	-0.44 ***	-0.51 ***	-0.57 ***	-0.14 *	0.18 **	ns	ns	0.24 ***	ns	-	0.44 ***	0.7 ***	0.23 ***	0.42 ***	1

Supplementary Data 6 (continued)

Trial code	Traits	PH	PL	CTvg	CTgs	CTgf	CTcycle	Inf2	NDVIant	NDVIpm	SlpSEN	SlpPEG	FLG	WSC	GSP	KM2	SM2	TKW	YLD
SW12HI	PH	1																	
	PL	0.53 ***	1																
	CTvg	-0.18 **	ns	1															
	CTgs	-0.36 ***	-0.25 ***	0.45 ***	1														
	CTgf	ns	-0.2 **	0.18 **	0.27 ***	1													
	CTcycle	-0.25 ***	-0.21 **	0.73 ***	0.67 ***	0.75 ***	1												
	Inf2	-0.31 ***	ns	ns	ns	ns	ns	1											
	NDVIant	0.35 ***	0.15 *	-0.55 ***	-0.39 ***	ns	-0.45 ***	-0.21 **	1										
	NDVIpm	-	-	-	-	-	-	-	-	1									
	SlpSEN	ns	ns	0.15 *	ns	ns	0.14 *	ns	-0.4 ***	-	1								
	SlpPEG	0.41 ***	0.15 *	-0.32 ***	-0.29 ***	ns	-0.25 ***	-0.81 ***	0.53 ***	-	-0.22 ***	1							
	FLG	-	-	-	-	-	-	-	-	-	-	-	1						
	WSC	-	-	-	-	-	-	-	-	-	-	-	-	1					
	GSP	ns	0.19 **	-0.14 *	-0.13 *	ns	-0.16 *	0.14 *	0.28 ***	-	-0.20 **	ns	-	-	1				
	KM2	ns	ns	-0.34 ***	-0.22 ***	ns	-0.26 ***	ns	0.50 ***	-	-0.24 ***	0.19 **	-	-	0.82 ***	1			
	SM2	0.16 *	ns	-0.36 ***	-0.20 **	ns	-0.22 ***	ns	0.45 ***	-	ns	0.25 ***	-	-	-0.24 ***	0.32 ***	1		
	TKW	0.42 ***	ns	ns	-0.24 ***	ns	ns	-0.21 **	0.37 ***	-	ns	0.32 ***	-	-	ns	ns	ns	1	
	YLD	0.23 ***	0.14 *	-0.36 ***	-0.30 ***	ns	-0.28 ***	ns	0.61 ***	-	-0.17 **	0.31 ***	-	-	0.73 ***	0.90 ***	0.30 ***	0.38 ***	1
VP11DR	PH	1																	
	PL	-	1																
	CTvg	-	-	1															
	CTgs	-0.44 ***	-	-	1														
	CTgf	-	-	-	-	1													
	CTcycle	-	-	-	-	-	1												
	Inf2	ns	-	-	-0.16 **	-	-	1											
	NDVIant	0.37 ***	-	-	-0.41 ***	-	-	0.20 ***	1										
	NDVIpm	-	-	-	-	-	-	-	-	1									
	SlpSEN	-0.35 ***	-	-	0.26 ***	-	-	-0.19 **	-0.73 ***	-	1								
	SlpPEG	-0.14 *	-	-	ns	-	-	-0.39 ***	-0.29 ***	-	0.22 ***	1							
	FLG	-	-	-	-	-	-	-	-	-	-	-	1						
	WSC	-	-	-	-	-	-	-	-	-	-	-	-	1					
	GSP	-	-	-	-	-	-	-	-	-	-	-	-	-	1				
	KM2	0.37 ***	-	-	-0.24 ***	-	-	ns	0.22 ***	-	-0.44 ***	ns	-	-	-	1			
	SM2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1		
	TKW	ns	-	-	ns	-	-	ns	ns	-	ns	-0.19 **	-	-	-	-0.64 ***	-	1	
	YLD	0.49 ***	-	-	-0.34 ***	-	-	ns	0.32 ***	-	-0.53 ***	ns	-	-	-	0.84 ***	-	-0.17 **	1

Supplementary Data 6 (continued)

Trial code	Traits	PH	PL	CTvg	CTgs	CTgf	CTcycle	Inf2	NDVIant	NDVIpm	SlpSEN	SlpPEG	FLG	WSC	GSP	KM2	SM2	TKW	YLD
VP12DR	PH	1																	
	PL	-	1																
	CTvg	-	-	1															
	CTgs	-	-	-	1														
	CTgf	-0.50 ***	-	-	-	1													
	CTcycle	-	-	-	-	-	1												
	Inf2	-	-	-	-	-	-	1											
	NDVIant	-	-	-	-	-	-	-	1										
	NDVIpm	0.27 ***	-	-	-	-0.21 ***	-	-	-	1									
	SlpSEN	-0.40 ***	-	-	-	0.34 ***	-	-	-	-0.24 ***	1								
	SlpPEG	-	-	-	-	-	-	-	-	-	-	1							
	FLG	-	-	-	-	-	-	-	-	-	-	-	1						
	WSC	-	-	-	-	-	-	-	-	-	-	-	-	1					
	GSP	-	-	-	-	-	-	-	-	-	-	-	-	-	1				
	KM2	ns	-	-	-	ns	-	-	-	-0.28 ***	-0.35 ***	-	-	-	-	1			
	SM2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1		
	TKW	0.33 ***	-	-	-	-0.35 ***	-	-	-	0.41 ***	-0.15 *	-	-	-	-	-0.59 ***	-	1	
	YLD	0.40 ***	-	-	-	-0.41 ***	-	-	-	ns	-0.54 ***	-	-	-	-	0.73 ***	-	ns	1
VP11HI	PH	1																	
	PL	0.6 ***	1																
	CTvg	-0.18 **	ns	1															
	CTgs	ns	ns	0.17 **	1														
	CTgf	-0.28 ***	-0.16 **	0.15 *	0.15 *	1													
	CTcycle	-0.25 ***	-0.15 *	0.65 ***	0.72 ***	0.61 ***	1												
	Inf2	0.15 *	0.18 **	ns	-0.12 *	ns	ns	1											
	NDVIant	0.38 ***	0.33 ***	-0.14 *	-0.13 *	ns	-0.16 **	0.67 ***	1										
	NDVIpm	0.49 ***	0.45 ***	ns	-0.13 *	-0.24 ***	-0.21 ***	0.14 *	0.33 ***	1									
	SlpSEN	0.14 *	0.15 *	ns	ns	-0.15 *	ns	-0.40 ***	-0.43 ***	0.63 ***	1								
	SlpPEG	-	-	-	-	-	-	-	-	-	-	1							
	FLG	ns	ns	ns	ns	ns	ns	-0.18 **	-0.20 **	-0.12 *	ns	-	1						
	WSC	-	-	-	-	-	-	-	-	-	-	-	-	1					
	GSP	ns	ns	ns	ns	ns	ns	ns	0.14 *	ns	-0.12 *	-	ns	-	1				
	KM2	ns	ns	-0.18 **	-0.18 **	ns	-0.20 ***	ns	0.23 ***	ns	ns	-	ns	-	0.71 ***	1			
	SM2	ns	ns	ns	ns	ns	-0.14 *	ns	ns	0.12 *	ns	-	ns	-	-0.47 ***	0.27 ***	1		
	TKW	0.21 ***	0.16 **	ns	ns	-0.17 **	ns	ns	ns	ns	ns	-	ns	-	-0.40 ***	-0.66 ***	-0.26 ***	1	
	YLD	0.21 ***	0.19 **	-0.21 ***	-0.20 ***	-0.19 **	-0.30 ***	ns	0.30 ***	0.12 *	ns	-	ns	-	0.64 ***	0.82 ***	0.15 *	-0.12 *	1

Supplementary Data 6 (continued)

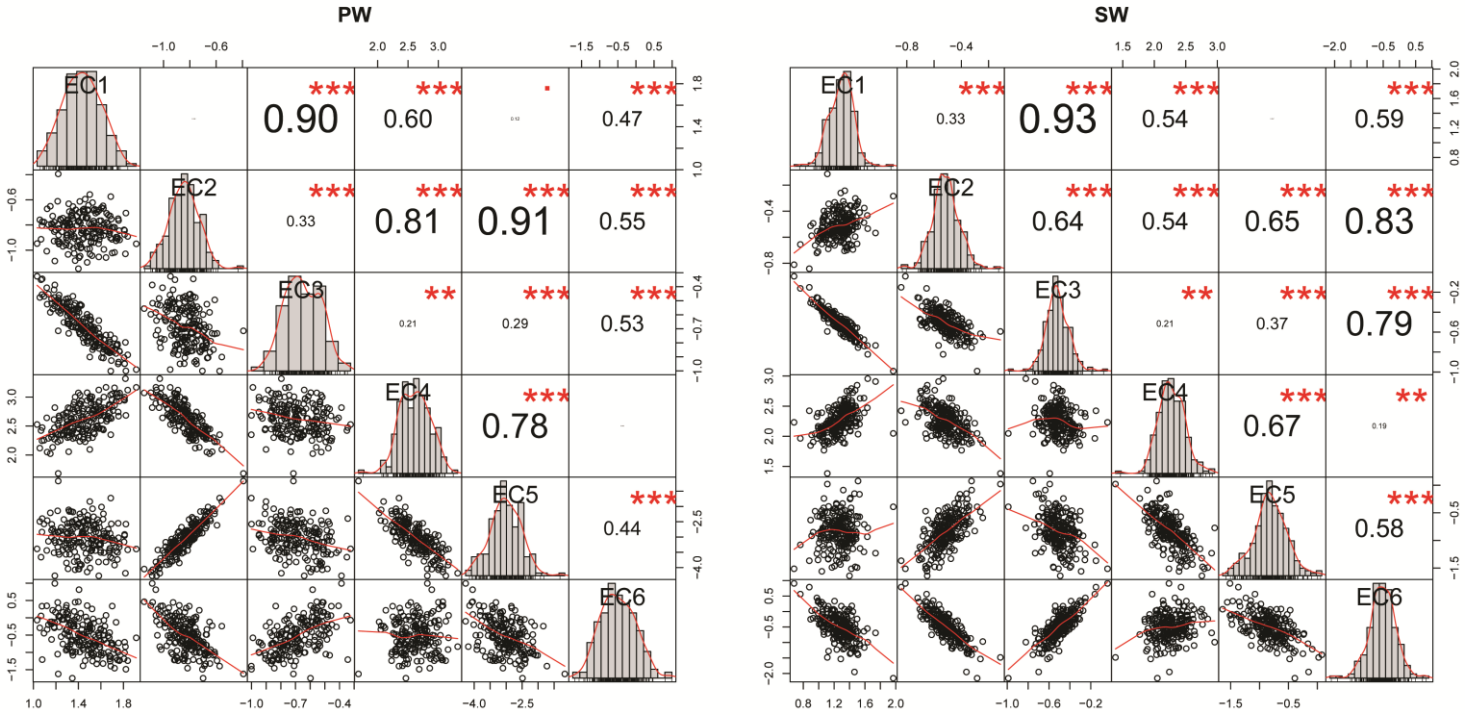
Trial code	Traits	PH	PL	CTvg	CTgs	CTgf	CTcycle	Inf2	NDVIant	NDVIpm	SlpSEN	SlpPEG	FLG	WSC	GSP	KM2	SM2	TKW	YLD
VP12HI	PH	1																	
	PL	0.63 ***	1																
	CTvg	ns	ns	1															
	CTgs	-0.20 **	-0.19 **	0.60 ***	1														
	CTgf	ns	-0.13 *	0.49 ***	0.72 ***	1													
	CTcycle	-0.13 *	-0.15 *	0.82 ***	0.90 ***	0.85 ***	1												
	Inf2	ns	ns	ns	ns	ns	ns	1											
	NDVIant	0.38 ***	0.37 ***	-0.22 ***	-0.48 ***	-0.43 ***	-0.43 ***	ns	1										
	NDVIpm	0.39 ***	0.34 ***	-0.21 ***	-0.29 ***	-0.33 ***	-0.32 ***	ns	0.32 ***	1									
	SlpSEN	0.14 *	0.13 *	ns	ns	ns	ns	ns	-0.39 ***	0.64 ***	1								
	SlpPEG	-	-	-	-	-	-	-	-	-	-	1							
	FLG	-	-	-	-	-	-	-	-	-	-	-	1						
	WSC	-	-	-	-	-	-	-	-	-	-	-	-	1					
	GSP	ns	ns	-0.19 **	-0.22 ***	-0.13 *	-0.21 ***	ns	0.16 **	-0.13 *	-0.20 **	-	-	-	1				
	KM2	ns	0.14 *	-0.40 ***	-0.46 ***	-0.40 ***	-0.49 ***	ns	0.34 ***	ns	-0.19 **	-	-	-	0.65 ***	1			
	SM2	ns	ns	-0.21 ***	-0.27 ***	-0.32 ***	-0.31 ***	ns	0.19 **	0.14 *	ns	-	-	-	-0.50 ***	0.30 ***	1		
	TKW	0.13 *	ns	ns	-0.13 *	ns	ns	ns	ns	0.18 **	ns	-	-	-	-0.26 ***	-0.54 ***	-0.22 ***	1	
	YLD	ns	0.18 **	-0.44 ***	-0.63 ***	-0.53 ***	-0.62 ***	ns	0.43 ***	ns	-0.18 **	-	-	-	0.57 ***	0.80 ***	0.19 **	ns	1

Supplementary Data 7: Partial correlation (r) of traits scored within the trial network with the yield and its components, considering ANT (anthesis) and PM (physiological maturity) as covariates. Trait abbreviations are given with Table 1. GDD: growing degree days. Dash symbols represent non-scored trait. Colour scale rules: (1) darker is the color, stronger is the correlation, (2) green/red for positive/negative significant correlation, and (4) white for non-significant correlation or non-scored data. *, **, and *** Significant at the 0.05, 0.01, and 0.001 level of probability; ns: non-significant at 0.05 level of probability. Trait abbreviations are given with Table 1.

Trait	YLD and comp.	Trial code															
		IR				DR					HI						
		PW11IR	PW12IR	SW12IR	VP11DR	PW12DR	SW12DR	VP12DR	PW13DR	SW13DR	PW11HI	SW11HI	VP11HI	PW12HI	SW12HI	VP12HI
CTvg	SM2	-	-0.17 *	ns	-	-0.19 **	ns	-	ns	ns	-0.41 ***	-0.17 **	ns	-0.5 ***	-0.36 ***	-0.21 ***
	GSP	-	-0.15 *	ns	-	ns	-0.16 *	-	ns	ns	-0.36 ***	-0.21 ***	ns	-0.36 ***	-0.14 *	-0.19 **
	KM2	-	-0.38 ***	ns	-	-0.18 **	-0.20 **	-	-0.15 *	ns	-0.6 ***	-0.39 ***	-0.18 **	-0.55 ***	-0.34 ***	-0.40 ***
	TKW	-	0.17 *	ns	-	ns	ns	-	ns	ns	0.24 ***	-0.22 ***	ns	ns	ns	ns
	YLD	-	-0.30 ***	-0.18 **	-	-0.27 ***	-0.30 ***	-	-0.25 ***	ns	-0.65 ***	-0.54 ***	-0.21 ***	-0.59 ***	-0.36 ***	-0.44 ***
CTgs	SM2	-	-	-	-	ns	0.19 **	-	ns	-	ns	-0.21 ***	ns	-0.52 ***	-0.20 **	-0.27 ***
	GSP	-	-	-	-	ns	-0.19 **	-	ns	-	ns	-0.15 *	ns	-0.37 ***	-0.13 *	-0.22 ***
	KM2	-	-	-	-0.24 ***	ns	ns	-	ns	-	-0.19 **	-0.35 ***	-0.18 **	-0.56 ***	-0.22 ***	-0.46 ***
	TKW	-	-	-	ns	ns	-0.14 *	-	-0.18 *	-	ns	ns	ns	ns	-0.24 ***	-0.13 *
	YLD	-	-	-	-0.34 ***	-0.19 **	-0.17 **	-	-0.17 *	-	-0.25 ***	-0.44 ***	-0.20 ***	-0.62 ***	-0.30 ***	-0.63 ***
CTgf	SM2	-	ns	ns	-	ns	ns	-	ns	ns	-0.24 ***	-0.14 *	ns	-0.49 ***	ns	-0.32 ***
	GSP	-	ns	ns	-	-0.14 *	ns	-	ns	ns	-0.2 **	-0.15 *	ns	-0.46 ***	ns	-0.13 *
	KM2	-0.23 ***	-0.17 *	0.13 *	-	-0.19 **	ns	ns	-0.19 **	ns	-0.36 ***	-0.31 ***	ns	-0.63 ***	ns	-0.40 ***
	TKW	ns	-0.16 *	-0.28 ***	-	ns	-0.31 ***	-0.35 ***	ns	-0.15 *	ns	-0.29 ***	-0.17 **	ns	ns	ns
	YLD	-0.26 ***	-0.28 ***	-0.23 ***	-	-0.37 ***	-0.35 ***	-0.41 ***	-0.23 ***	-0.13 *	-0.48 ***	-0.51 ***	-0.19 **	-0.69 ***	ns	-0.53 ***
CTcycle	SM2	-	-0.18 *	ns	-	ns	ns	-	ns	ns	-0.33 ***	-0.21 ***	-0.14 *	-0.55 ***	-0.22 ***	-0.31 ***
	GSP	-	-0.14 *	ns	-	-0.15 *	-0.14 *	-	ns	ns	-0.29 ***	-0.20 **	ns	-0.44 ***	-0.16 *	-0.21 ***
	KM2	-	-0.38 ***	ns	-	-0.21 **	ns	-	-0.18 **	ns	-0.49 ***	-0.41 ***	-0.20 ***	-0.64 ***	-0.26 ***	-0.49 ***
	TKW	-	ns	-0.25 ***	-	ns	-0.30 ***	-	ns	-0.15 *	ns	-0.24 ***	ns	ns	ns	ns
	YLD	-	-0.40 ***	-0.28 ***	-	-0.41 ***	-0.43 ***	-	-0.31 ***	-0.15 *	-0.58 ***	-0.57 ***	-0.30 ***	-0.69 ***	-0.28 ***	-0.62 ***
FLG	SM2	-	ns	ns	-	ns	ns	-	ns	ns	-0.25 ***	ns	ns	-	-	-
	GSP	-	ns	ns	-	ns	ns	-	ns	ns	ns	ns	ns	-	-	-
	KM2	-	-0.14 *	ns	-	-0.19 **	ns	-	ns	ns	-0.15 *	ns	ns	-	-	-
	TKW	-	0.32 ***	ns	-	0.18 *	0.17 *	-	ns	ns	0.19 **	ns	ns	-	-	-
	YLD	-	ns	ns	-	ns	0.16 *	-	ns	ns	ns	ns	ns	-	-	-
NDVIpeg	SM2	-	ns	ns	-	0.19 **	0.13 *	-	ns	ns	0.20 **	0.05 ns	-	0.49 ***	0.25 ***	-
	GSP	-	ns	ns	-	0.14 *	ns	-	ns	ns	0.16 *	0.18 **	-	0.36 ***	ns	-
	KM2	-	ns	ns	ns	0.39 ***	0.17 *	-	0.16 *	ns	0.28 ***	0.24 ***	-	0.55 ***	0.19 **	-
	TKW	-	ns	0.18 **	-0.19 **	-0.23 ***	ns	-	-0.14 *	-0.15 *	ns	ns	-	ns	0.32 ***	-
	YLD	-	ns	0.13 *	ns	0.31 ***	0.22 ***	-	ns	ns	0.30 ***	0.24 ***	-	0.61 ***	0.31 ***	-
NDVIinf2	SM2	-	ns	ns	-	-0.20 **	ns	-	ns	0.19 **	ns	ns	ns	-0.16 *	ns	ns
	GSP	-	ns	ns	-	ns	ns	-	ns	-0.18 **	ns	-0.24 ***	ns	ns	0.14 *	ns
	KM2	-	0.14 *	0.15 *	ns	-0.35 ***	ns	-	-0.20 **	ns	ns	-0.25 ***	ns	ns	ns	ns
	TKW	-	-0.22 **	-0.24 ***	ns	0.24 ***	-0.15 *	-	ns	-0.15 *	ns	0.13 *	ns	ns	-0.21 ***	ns
	YLD	-	ns	-0.13 *	ns	-0.25 ***	-0.19 **	-	-0.22 **	-0.20 **	-0.17 *	-0.14 *	ns	ns	ns	ns

Supplementary Data 7 (continued)

Trait	YLD and comp.	Trial code														
		IR			DR						HI					
		PW11IR	PW12IR	SW12IR	VP11DR	PW12DR	SW12DR	VP12DR	PW13DR	SW13DR	PW11HI	SW11HI	VP11HI	PW12HI	SW12HI	VP12HI
NDVIant	SM2	-	0.15 *	ns	-	0.3 ***	ns	-	ns	ns	0.38 ***	0.27 ***	ns	0.51 ***	0.45 ***	0.19 **
	GSP	-	ns	ns	-	ns	ns	-	0.17 *	ns	ns	ns	0.14 *	0.48 ***	0.28 ***	0.16 **
	KM2	0.38 ***	0.27 ***	ns	0.22 ***	0.36 ***	ns	-	0.21 **	ns	0.29 ***	ns	0.23 ***	0.65 ***	0.5 ***	0.34 ***
	TKW	-0.20 **	-0.23 ***	ns	ns	ns	ns	-	ns	ns	ns	ns	ns	ns	0.37 ***	ns
	YLD	0.33 ***	0.14 *	ns	0.32 ***	0.41 ***	ns	-	0.27 ***	ns	0.35 ***	0.18 **	0.30 ***	0.70 ***	0.61 ***	0.43 ***
NDVIpm	SM2	-	-	-	-	0.16 *	-	-	ns	0.16 *	0.17 *	ns	0.12 *	0.38 ***	-	0.14 *
	GSP	-	-	-	-	-0.17 *	-	-	ns	-0.23 ***	-0.23 ***	-0.21 ***	ns	ns	-	-0.13 *
	KM2	-	-	-	-	ns	-	-0.28 ***	ns	ns	ns	-0.18 **	ns	ns	-	ns
	TKW	-	-	-	-	0.24 ***	-	0.41 ***	ns	ns	0.18 *	0.23 ***	ns	0.17 *	-	0.18 **
	YLD	-	-	-	-	ns	-	ns	ns	ns	ns	ns	0.12 *	0.14 *	-	ns
NDVIsen	SM2	-	-	-	-	-0.17 *	ns	-	ns	ns	-0.15 *	ns	ns	-0.34 ***	ns	ns
	GSP	-	-	-	-	ns	ns	-	-0.20 **	ns	ns	ns	-0.12 *	-0.62 ***	-0.20 **	-0.20 ***
	KM2	-	-	-	-0.44 ***	-0.32 ***	ns	-0.35 ***	-0.24 ***	-0.14 *	-0.23 ***	-0.18 **	ns	-0.71 ***	-0.24 ***	-0.19 ***
	TKW	-	-	-	ns	0.29 ***	ns	-0.15 *	ns	ns	ns	0.14 *	ns	0.26 ***	ns	ns
	YLD	-	-	-	-0.53 ***	-0.18 **	ns	-0.54 ***	-0.23 ***	-0.18 **	-0.25 ***	ns	ns	-0.73 ***	-0.17 **	-0.18 **
PL	SM2	-	ns	0.01 ns	-	ns	-0.15 *	-	ns	ns	0.26 ***	ns	ns	0.33 ***	ns	ns
	GSP	-	-0.14 *	-0.20 **	-	0.17 *	ns	-	ns	ns	ns	ns	ns	0.14 *	0.19 **	ns
	KM2	ns	-0.15 *	-0.25 ***	-	ns	-0.22 ***	-	ns	ns	ns	-0.14 *	ns	0.28 ***	ns	0.14 *
	TKW	0.26 ***	ns	0.43 ***	-	0.18 *	0.54 ***	-	0.21 **	0.30 ***	ns	0.47 ***	0.16 **	-0.19 **	ns	ns
	YLD	ns	ns	0.23 ***	-	0.34 ***	0.36 ***	-	ns	0.22 ***	ns	0.25 ***	0.19 ***	0.24 ***	0.14 *	0.18 **
PH	SM2	-	0.16 *	ns	-	ns	ns	-	-0.22 **	ns	0.30 ***	ns	ns	0.49 ***	0.16 *	ns
	GSP	-	ns	-0.33 ***	-	0.15 *	-0.17 *	-	0.16 *	-0.17 **	ns	-0.13 *	ns	0.18 *	ns	ns
	KM2	ns	ns	-0.44 ***	0.37 ***	0.18 *	-0.29 ***	ns	ns	-0.23 ***	ns	-0.15 *	ns	0.38 ***	ns	ns
	TKW	ns	ns	0.40 ***	ns	ns	0.54 ***	0.33 ***	0.28 ***	0.32 ***	ns	0.56 ***	0.21 ***	ns	0.42 ***	0.13 *
	YLD	0.21 **	ns	ns	0.49 ***	0.37 ***	0.27 ***	0.40 ***	ns	ns	0.27 ***	0.29 ***	0.21 ***	0.39 ***	0.23 ***	ns
WSC	SM2	-	-	-	-	ns	-	-	-	-	-0.31 ***	-	-	ns	-	-
	GSP	-	-	-	-	ns	-	-	-	-	-0.4 ***	-	-	-0.20 **	-	-
	KM2	-0.29 ***	-	-	-	ns	-	-	-	-	-0.56 ***	-	-	-0.18 *	-	-
	TKW	ns	-	-	-	ns	-	-	-	-	0.52 ***	-	-	0.34 ***	-	-
	YLD	-0.27 ***	-	-	-	ns	-	-	-	-	-0.44 ***	-	-	ns	-	-
YLD	SM2	-	ns	ns	-	ns	ns	-	0.30 ***	ns	0.35 ***	0.23 ***	0.15 *	0.41 ***	0.30 ***	0.19 ***
	GSP	-	0.56 ***	0.31 ***	-	0.48 ***	0.4 ***	-	0.57 ***	0.56 ***	0.72 ***	0.44 ***	0.64 ***	0.85 ***	0.73 ***	0.57 ***
	KM2	0.89 ***	0.80 ***	0.38 ***	0.84 ***	0.69 ***	0.45 ***	0.73 ***	0.87 ***	0.69 ***	0.90 ***	0.70 ***	0.82 ***	0.95 ***	0.90 ***	0.80 ***
	TKW	ns	0.21 **	0.50 ***	-0.17 **	ns	0.39 ***	ns	ns	0.19 **	-0.39 ***	0.42 ***	-0.12 *	-0.34 ***	0.38 ***	ns



Supplementary Data 8: Scatterplots of the coefficients of interaction (between grain yield and the six environmental covariates (ECx, xϵ[1;6])) within population (PW, SW and VP); The upper diagonal part of the matrix display the coefficient of determination (r^2); *, **, and *** Significant at the 0.05, 0.01, and 0.001 level of probability; On the diagonal, distribution and density curves of each genotype 's coefficient of interaction with the indicated environmental covariates (see bouffier et al., 2014 for more precision)

With the use of environmental covariates established in Chapter III, in Chapter IV, we presented the dissection of the genotype-by-environment interaction of the main physiological and agronomic determinants of the grain yield of three mapping populations evaluated in a multi-environment drought and heat stress trial network. In Chapter VI, we reported the genetic dissection of the physiological and agronomic grain yield determinant under drought and heat stress conditions. This chapter wrote as a draft of a paper will be deepen further and split into two different papers.

It aimed to identify QTL associated with agronomic and physiological traits under a multi-environmental abiotic stress network, to dissect the NDVI response function under irrigated, drought, and heat-irrigated conditions into early vigor and development, maximum biomass and chlorophyll, and chlorophyll loss, and finally to analyze the sensitivity of the QTL identified to specific abiotic stresses. In chapter V, Bouffier et al. (in prep) refers to chapter IV, i.e., paper 2.

As for paper 1 and 2, tables and figures were included in the text. Supplementary Data were added after the conclusion.

CHAPTER V: G, study of the genetic component

Dissections of drought and heat stress adaptive strategies in wheat: QTL and QTL-by-environment interaction

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Abbreviations

ANT: Anthesis; CT: Canopy temperature; DR: Drought treatment; GDD: Growing degree days; GEI: Genotype-by-environment interaction; GSP: Number of grains per spike; HI: Heat-irrigated treatment; IR: Irrigated treatment; KM2: Number of grains per m²; NDVI: Normalized difference vegetative index; NDVIant: NDVI estimate at anthesis; NDVIApeg: Area under the NDVI curve during the PEG; NDVIAsen: Area under the NDVI curve during the SEN phase; NDVIAsp: Area under the NDVI curve during the SP; NDVIinf2: End of the PEG; NDVIpeg: Slope of the NDVI curve during the PEG; NDVIpm: NDVI estimate at physiological maturity; NDVIsen: Slope of the NDVI curve during the SEN phase; PA: Female population 1, Pastor//hxl7573/2*Bagula; PCA: Principal component analysis; PEG: Phase of exponential growth; PM: Physiological maturity; PP: Male population 3, Parus/Pastor; PW: Population 1, Pastor//hxl7573/2*Bagula/3/Weebill1; QEI: QTL-by-environment interaction; QTL: Quantitative trait loci; RIL: Recombinant inbred lines; RIL: Recombinant inbred lines; SEN: Senescence phase; SM2: Number of spikes per m²; SO: Female population 2, Sokoll; SP: Stationary phase; SW: Population 2, Sokoll//Weebill1; TKW: Thousand kernel weight; VB: Female population 3, Vorobey; VP: Population 3, Vorobey//Parus/Pastor; WB: Male population 1 & 2, Weebill1; WSC: Stem water soluble carbohydrate; YLD: Grain yield

INTRODUCTION

Drought and heat stress are widely recognized as two of the most impacting constraints on crop growth and productivity worldwide. Braun et al. (2010) reported that five out of the twelve worldwide wheat mega-environments identified by CIMMYT were mainly characterized by drought and/or heat stress events. The increasing human CO_2 emissions are estimated to lead to a global warming. Moreover, based on simulation, IPCC (2007) and Dai (2012) reported a positive association between the global warming and an increase in intensity and frequency of drought and heat stress worldwide in the incoming decades. Works of the European Environmental Agency on the impact of drought on European wheat productions in the incoming decades is worrying (European Environment Agency, 2012). According to the Agency, almost all bread wheat production basins in Europe might be confronted to a decrease in their production ranging from 10,000 to more than 100,000 tons depending on the region. Improvement of the European wheat tolerance to drought and heat stress is then of paramount importance.

Impact of drought and heat stress on wheat were largely described and reported (Ribaut, 2006; Farooq et al., 2011, 2014; Cossani et al., 2012; Gupta et al., 2012). Current breeding practices to improve tolerance to drought and/or heat stress require testing genotypes within a multi-environmental trials network with a wide range of the environmental conditions encompassing the target population of environment. Tolerance to drought on cereals had been conceptualized firstly by Passioura (1977), and widened to heat stress then by Reynolds and Trethowan (2007). These models aimed to emphasize physiological traits which may be of interest to improve the tolerance to drought and heat stress in a given area. However, it is of great importance to be aware of the fact that any of these traits can have positive, negative, or even no effect for a given drought or heat stress scenario (Tardieu, 2011). Nevertheless, this approach proved its efficiency comparatively to conventional breeding (Reynolds et al., 2009). A tangible success of this physiological approach under drought was the release of two Australian wheat cultivars with improved transpiration efficiency, i.e., more efficient use of the water uptake, breeding for low carbon isotope discrimination (CID) (Richards et al., 2001; Rebetzke et al., 2002).

Among physiological traits involved, either as a proxy or directly, only a few are recognized widely as being important within the breeding community (Araus et al., 2008). Among them, the canopy temperature (CT) and the normalized difference vegetative index (NDVI) are commonly highlighted because of their usefulness, low cost, and high-throughput characteristics (Olivares-Villegas et al., 2008; Araus et al., 2008; Pinto et al., 2010). Under drought-prone environment with available water at depth, the ability to extract the water through a deeper root system corresponds to the main possible mechanism of adaptation (Lopes and Reynolds, 2010). This enhanced water extraction ability was robustly associated with cooler canopy and increased yield (Olivares-Villegas et al., 2007; Lopes and Reynolds, 2010; Pinto et al., 2010). Under heat stress conditions with water available in the soil, the ability to cool its canopy through an increased water uptake and transpiration can be considered as one of the main heat-adaptation mechanism in wheat (Reynolds et al., 1994). NDVI is an integrative measure of the green area, the photosynthetic capacity, and the nitrogen content of the canopy (Pietragalla and Madrigal Vega, 2012; Pietragalla et al., 2012). NDVI scoring at diverse stages of the crop cycle can inform on other physiological process. For example, the study of the dynamics of the NDVI decrease during the grain filling stage can provide an estimation of the stay-green capacity (Lopes and Reynolds, 2012). Under drought or heat-stress, the maintenance of green canopy, i.e., higher value of NDVI, was interpreted as a tolerance to stress (Olivares-Villegas et al., 2007; Pinto et al., 2010; Pietragalla and Madrigal Vega, 2012). Significant associations were found with grain yield (Raun et al., 2001; Olivares-Villegas et al., 2007; Pinto et al., 2010), the accumulation of the biomass during the crop cycle (Araus, 1996; Gutiérrez-Rodríguez et al., 2004; Babar et al., 2006a; b; Cabrera-Bosquet et al., 2011), but also the senescing rate (Lopes and Reynolds, 2012). Stem water soluble carbohydrates (WSC) also belongs to the frequently reported physiological traits despite its relative time- and cost-consuming feature (Blum, 1998; Yang et al., 2007; Rebetzke et al., 2008b). Indeed, under drought and heat stress conditions, when grain filling photosynthesis is inhibited, remobilization of WSC can represent up to 80 % of grain dry matter (Zhang et al., 2013).CT, NDVI, WSC and associated traits (e.g., early vigor, senescence, biomass at maturity, *etc.*) have been already scored on mapping populations in order to dissect their

genetic determinism under irrigated, drought, or heat-irrigated conditions (Yang et al., 2007; Olivares-Villegas et al., 2008; Rebetzke et al., 2008b; Pinto et al., 2010).

Pinto et al. (2010) reported the co-location of QTL for yield under drought and heat stress on 5A, respectively accounting for 27 and 14 % of the yield variation. At the same locus, a QTL for CT explained 28 % of the CT variation under heat stress. A QTL for CT on 3B explained 14 % of the CT variation under drought. Repeatable QTL for WSC were found by Rebetzke et al. (2008b) in wheat with small genetic effect (<10%) and frequently associated with phenology and architecture traits. Genomic regions associated with the NDVI and the evolution of the biomass along the crop cycle were previously reported under different water and temperature regimes in various genetic backgrounds of bread and durum wheat: (i) for early vigor (Rebetzke et al., 2001; Bennett et al., 2012a; b), (ii) for biomass under various water regimes (Kirigwi et al., 2007; Peleg et al., 2009; Bennett et al., 2012a; Edae et al., 2014) and under heat stress condition (Mason et al., 2013), (iii) for leaf area under various water regimes (Edae et al., 2014) and under heat stress conditions (Kumar et al., 2010), (iv) for NDVI at different development stages under Australian Mediterranean conditions (Bennett et al., 2012b), under various drought stress (Olivares-Villegas et al., 2008; Edae et al., 2014), and also under heat stress (Pinto et al., 2010), (v) for canopy photosynthesis related traits under different water regimes (Diab et al., 2008; Czyczyło-Mysza et al., 2011) and under high temperature regime (Vijayalakshmi et al., 2010), (vi) spike photosynthesis under irrigated conditions (Molero et al., 2014), and (vii) for senescence under different water regimes (Verma et al., 2004; Edae et al., 2014) and under heat stress (Vijayalakshmi et al., 2010). Most of the wheat chromosomes were harboring QTL for at least one of the previously cited traits. Accordingly, QTL for yield under various water stress regimes, heat stress, and Australian Mediterranean conditions were reported on the whole wheat genomes except on 2D chromosome within the sixteen studies already cited.

In most of the QTL study under drought or heat stress, significant QTL have relatively low effects. Theoretically, breeders need to take into account all QTL found within different genetic backgrounds and environments to improve their germplasm. However, two issues may hinder the expected benefits: interactions with the genetic background and, more importantly, with the environment. To quantify the former one,

different genetic backgrounds have to be tested in the same environments. For the latter one, difficulties encountered in anticipating QTL sensitivities to a given environmental condition have led the breeding community to focus its effort on robust QTL on a wide range of environment. Therefore, a wide part of the available genetic variability is ruled out. Environmental characterization is of paramount importance to make a better use of multi-environmental trial network (Brancourt-Hulmel, 1999; Voltas et al., 2005; Malosetti et al., 2013; Bouffier et al., 2014). The general idea supported by our previously reported environmental characterization (Bouffier et al., 2014) is that for a given trial, the environment is not seen as 'location x year' or 'treatment x year' combination anymore, but as a serie of constraints, which combined together, contribute to the achievement of the trait of interest (Bouffier et al., 2014). An efficient environmental characterization must provide explicit environmental covariates based on stresses experienced by plants (Brancourt-Hulmel, 1999; Campbell et al., 2004; Bouffier et al., 2014). Their interest was demonstrated at the genotypic level as they helped in dissecting the genotype-by-environment interaction (Campbell et al., 2004; Zheng et al., 2010). The use of such explicit environmental covariates can lead to the identification of QTL effect sensitivity to specific stress. With this information, a bigger proportion of the QTL identified could be used in specific area where their potential can be used.

In this paper, three elite crosses mapping populations were studied under irrigated, drought, and heat-irrigated conditions. Yield and yield components were evaluated. NDVI measurements were also performed along the whole crop cycle within the network enabling the estimation of various NDVI derivative traits. These traits allow dissecting NDVI response function regarding early vigor and development, biomass and chlorophyll content.

The objectives of our study were (i) to identify QTL associated with agronomic and physiological traits under a multi-environmental abiotic stress network, (ii) to dissect the NDVI response function under irrigated, drought, and heat-irrigated conditions into early vigor and development, maximum biomass and chlorophyll, and chlorophyll loss, and finally (iii) to analyze the sensitivity of the QTL identified regarding specific abiotic stresses.

MATERIALS AND METHODS

Mapping populations, experimental designs and trial managements

Three bread wheat recombinant inbred line (RIL) populations were assessed: (i) Population 1 consisted of a set of 196 F7:8 RILs from the Pastor//hxl7573/2*Bagula (PA) x Weebill1 (WB) cross (PW), (ii) Population 2 consisted of a set of 228 F7:8 RILs from the Sokoll (SO) x Weebill1 (WB) cross (SW), and (iii) Population 3 consisted of a set of 266 F5:8 RILs from the Vorobey (VB) x Parus/Pastor (PP) cross (VP). Parents of the populations are CIMMYT elite lines combining interesting physiological traits to tolerate both drought and heat stress. The parents do not segregate for dwarfing *Rht* genes. They are spring types (Dominant-spring alleles Vrn-B1 and Vrn-D1 for all parents and sensitive-winter allele vrn-A1 for all parents). Parents do not segregate for the *Ppd1-D1a* gene (all parents have the insensitive allele), but for the *Ppd-B1* gene parents displayed a different haplotypic profile (WB has alleles 2, 3, 4, 5, and 6; VB has alleles 2, 3, and 4; PA, SO, and PP has alleles 5 and 6). These profiles are associated with the wms682 microsatellite (SSR) marker for which six different alleles were reported. Alleles 1, 3, and 4 were reported as insensitive. Sensitivity of alleles 2, 5, and 6 were reported as unknown. PA carries the T1BL.1RS (rye) translocation.

These populations were sown in the northwestern Mexican desert of Sonora, Mexico, in 2011, 2012 and 2013 and under three different environmental scenario: winter sowing under Irrigated (IR) or limited irrigation, i.e., Drought (DR) conditions, and spring sowing inducing heat stress and under irrigated conditions (HI). A trial is defined as a combination of population x treatment x year (e.g. Pastor//… x Weebill1 population in 2012 winter sowing irrigated: PW12IR). Altogether the trial network represented fifteen trials in seven different environments (year x treatment: 11IR, 11DR, 11HI, 12IR, 12DR, 12HI, and 13DR). For more details, refer to Bouffier et al. (2014).

Environmental covariates

A complete environmental characterization of the trial network was performed as described in Bouffier et al. (2014). The fifteen environments of the different trials were grouped into six different environmental stress scenarios. For each scenario, a representative environmental covariate was extracted and named ECx, with xϵ[1;6] (see

(Bouffier et al. (2014) for more details). The subset of six representative environmental covariates represented 90.3 % of the total environmental variance for grain yield. A description of the six environmental scenarios is presented in Supplementary Data 1.

Phenotypic data

Within each trial, a maximum of 23 traits was scored. They are grouped into agronomic, architectural, phenological, and physiological traits.

Phenological traits

Crop cycles were divided into three developmental phases: (1) vegetative (VG), from emergence (Z1.2) to booting (Z4.1), (2) grain set (GS), from booting (Z4.1) to anthesis+7days (Z6.1) and (3) grain filling (GF), from anthesis+7d to physiological maturity (Z9.2) (Zadoks et al., 1974; Tottman, 1987; Slafer, 2012). Phenological data were expressed in growing degree days (GDD) using the formula described in McMaster and Wilhelm (1997) with a base temperature of 4.5°C (Dhillon and Ortiz-Monasterio, 1993). Anthesis and physiological maturity data were available for all plots within the network. The grain filling period (GFp) trait corresponds to the relative length of the ANT to PM period compared with the whole crop cycle, i.e., from emergence to PM.

Agronomic and architectural traits

Grain yield at 0% moisture (GY), thousand kernel weight (TKW), number of spikes per m² (SM2), plant height (PH), and peduncle length (PL) were scored. The average number of grains per spike (GSP) and number of kernels per m² (KM2) were derived from above variables. For more details, see Bouffier et al. (2014).

Physiological traits

Several traits were derived from the normalized difference vegetation index (NDVI) kinetics curve. NDVI was scored [NDVI = $(RF_{900}-RF_{680})/(RF_{900}+RF_{680})$, where RF_X is the spectral reflectance of wavelength X (nm)] using a 'N-Tech Industries manufactured GreenSeeker® Handheld sensor' (Trimble, USA). Scorings were performed roughly once a week during the whole crop cycle. Phenological stage effect was removed within each NDVI series before drawing a dynamical NDVI curve for each genotype with the 'loess' R function, implemented in the R 'Stats' package (R Development Core Team, 2011). Eight traits were derived from NDVI dynamic curves

and were considered for the analyses (Supplementary Data 2): (i) the slope of the phase of exponential growth (PEG) within the vegetative phase (NDVIpeg), (ii) the second inflexion point indicating the end of the PEG (NDVIinf2), (iii) the area under the curve during the PEG (NDVIApeg), (iv) the NDVI value at anthesis (NDVIant), (v) the area under the curve between the end of the PEG until anthesis, i.e., the stationary phase (SP) (NDVIAsp), (vi) the slope of senescence between anthesis and physiological maturity (NDVIsen), (vii) the NDVI value at physiological maturity (NDVIpm), and (viii) the area under the curve during the senescence phase (NDVIAsen).

The canopy temperature (CT) was scored using a calibrated infrared thermometer 'Hand-Held Infrared Thermometer Sixth Sense LT300' (Instrumart, USA) during VG (CTvg), GS (CTgs), and GF (CTgf). An average CT on the whole crop cycle was also estimated (CTcycle). Each trait encompassed at least two series of CT scorings. Stem water soluble carbohydrate (WSC) accumulation peak was targeted. WSC were scored on some PW trials and data were processed as presented in Bouffier et al. (in prep).

Phenotypic data statistical analyses

Phenotypic traits were adjusted to field effects as presented in Bouffier et al. (in prep). Significant correlations were observed between anthesis and physiological maturity, and most of the other traits (data not shown). Therefore, Pearson correlations were calculated between all traits. Principal component analyses (PCA) were performed per trial with all adjusted phenotypic traits to display relationship existing between agronomic, physiological, phenological, and architectural traits. Significance of the differences between parents was computed for each trait except GFp within each trial of the network. All statistical analyses were performed using R2.13.2 (R Development Core Team, 2011).

Genetic analyses

DNA extraction

Genomic DNA of each genotype was extracted from five to ten individual young seedling leaves using a CTAB method as described by (Saghai-Maroof et al., 1984) and modified according to CIMMYT laboratory protocols (Dreisigacker et al., 2013). DNA

extraction was performed by the CIMMYT's genotyping laboratory. The genotyping was performed using the KASPar SNP Genotyping System (http://www.lgcgroup.com/) using SNP markers from the CIMMYT) and from Limagrain Europe by the Limagrain Europe's genotyping laboratory.

Genetic maps construction

The maps of populations PW, SW, and VP were built using MAPMAKER software version 3.0 (Lander et al., 1987) using a minimum LOD score of 3.0, a recombination fraction of 0.5, and Kosambi genetic distance formula. Previous analyses revealed wide genomic area with segregation distortion within each population. In order to cope with wide distorted genomic regions, some markers were chosen as anchors from the Limagrain Europe reference map (data not shown) Secondly, markers order within each linkage group and the names of the linkage groups were defined according to the reference map. Finally, genetic distances were estimated. Seven genotypes from PW were removed because of bad quality or missing DNA. Five genotypes from SW were also removed and seven from VP for the same reasons. Therefore, 189 progeny genotypes were considered for PW, 223 for SW, and 259 for VP for QTL analyses.

Quantitative trait analyses

QTL analyses were performed using GenStat for Windows 16th edition (VSN International, Hemel Hempstead, UK). Firstly, raw phenotypic data were adjusted, trait by trait within a trial. Data adjustment was performed using two types of models based on the better AIC value (Akaike, 1974): either an incomplete block design or a spatial design in regular grid (order-1 auto-regressive model), as implemented in GenStat. Within both models, the effect of the subblock nested into repetition was considered as random. The effect of the repetition was considered as random in the former one, but as fixed in the latter one. Whatever the model performed, the effect of the genotype was first tested as random to estimate variance parameters and heritability, and then as fixed to get predicted genotype means (Best Linear Unbiased Predictors, BLUPs). Broad sense heritability (H^2) was estimated per trait per trial using formula implemented into GenStat as proposed by (Cullis et al., 2006):

$$H^2 = 1 - \frac{mean(pev(g_i))}{\sigma_g^2}$$

Where g_i is the i^{th} predicted genotype means (BLUPs), pev(g_i), the prediction error variance, and σ^2_g, the estimated genetic variance component.

For a given trait and population, two QTL mapping approaches were considered depending on the number of environments available: (1) With more than four environments available, the multi-environment single trait analysis of GenStat was performed and (2) with four and less environments a genome-wide scan was performed per trial. To perform QTL analysis, the following parameters were used: (i) step size of 2 cM, (ii) minimum cofactor proximity of 50 cM, (iii) minimum separation for selected QTLs of 30 cM, and (iv) -log10P threshold at α=0.05 genome-wide significance level (Li and Ji, 2005), as implemented in GenStat (Malosetti et al., 2013), resulting in a -log10P threshold of 3.63 for population PW, 3.66 for SW, and 3.67 for VP.

The mixed-model approach presented in Boer et al. (2007), Mathews et al. (2008), and Malosetti et al. (2013) was followed. For a given trait and population, it consisted in (i) selecting the best variance-covariance model for multiple-environment based on adjusted phenotypic data for all environments, (ii) a genome-wide scan using simple interval mapping (SIM), (iii) two consecutive rounds of composite interval mapping (CIM) using cofactors established at the step preceding the considered run, and finally (iv) a final QTL model was chosen based on backward selection on selected cofactors. It enables the estimation of the effect of the alleles of each QTL per environment, the effect of the QEI, and the part of phenotypic variance explained. For more details on the whole methodology, see Malosetti et al. (2013).

For a given trait, QTLs belonging to the same linkage group were declared as unique if the position of their peaks were different within a given population whatever the environment where they were detected. Any QTL which peak was located in a more-or-less 5 cM windows around a given QTL peak were declared as co-located. QTL with significant effect was named as follow: “Q” + “trait” + “population” + “chromosome” + “environment” + a number order was finally attributed (1, 2, 3, *etc*.) if more than one QTL with identical previous features was discovered. Unique QTL was named similarly without the environment feature as they encompass all environments where a same QTL of the same trait, chromosome and location was discovered.

Hotspots of QTL were identified within each population. A QTL hotspot was declared if it contained more than 7 QTL peaks within a maximum 20cM-window on a given linkage group. They were name as following: (i) one hotspot on a given population "HS" + "Population name" + "chromosome", and a number order (1, 2, 3, *etc.*) if more than one hotspot was found for the same reason than the one explained previously, (ii) hotspot common to various populations "HS" + "chromosome". A given unique QTL was classified: (i) stress QTL (STRESS) if it appeared at least twice, once per stress treatment, or twice in a given stress treatment, (ii) irrigated QTL (IRR) if it appeared only twice in irrigated treatment, (iii) constitutive QTL (CONS) if it appeared at least one year in every treatment. All other QTL were classified as "other".

RESULTS

Population and parental phenotypes

A significant genotype effect was detected in all trials for the 23 traits that were observed. All of them displayed a Gaussian-shape distribution within the entire trial network (Supplementary Figure 4). The range of variation for phenological and architectural traits is very similar whatever the treatment. However, in average, lower values are observed under stressed treatments than under irrigated treatment. Concerning physiological traits, a wide variation was usually observed whatever the treatment. However, some traits such as NDVIinf2 and NDVIApeg had really restricted variation under drought and heat stress (Supplementary Data 3, 4).

Transgressive expressions beyond parents were observed for all the traits. A few significant differences between parents appeared within the network (Table 1; Supplementary Data 3, 4). Concerning grain yield, significant differences were observed only within the VP population. Vorobey had lower yield than Parus/Pastor in 2011 ($p<0.01$), but higher yield in 2012 ($p<0.05$). In 12HI, Parus/Pastor had lower yield than Vorobey ($p<0.05$). In terms of precocity, Vorobey was significantly earlier than Parus/Pastor in DR and HI (991 *vs.* 1023 GDD). Pastor was earlier than Weebill1 in all three treatments (1013 *vs.* 1061). Sokoll was similar to Weebill1 in IR and DR but earlier in HI. Under drought conditions, Weebill1 was significantly cooler than Pastor in PW13DR ($p<0.01$) and Sokoll in SW12DR and SW13DR ($p<0.05$). Under Heat-

Irrigated conditions, Weebill1 was cooler than Pastor in 2011 ($p<0.05$), and Vorobey, cooler than PP in 2012 ($p<0.05$).

Broad sense heritability for physiological traits is relatively high. Concerning CT traits, broad sense heritability ranged from 0 (e.g., PW13DR - CTvg) to 0.74 (VP11DR – CTgs) with an averaged at 0.45 within the whole network. Heritability of NDVI traits ranged from 0.27 (VP12HI - NDVIpm) to 0.91 (PW11HI – NDVIAsp) and averaged at 0.68. Heritability of the stem water soluble carbohydrate content averaged at 0.51 and ranged from 0.16 (PW12HI) to 0.79 (PW11HI). Heritability of phenological and agronomic traits was detailed on Bouffier et al. (in prep).

Table 1: Table showing the parent with the highest value for each trait within each trial of the network. PA: Pastor//hxl7573/2*Bagula; SO: Sokoll; VB: Vorobey; WB: Weebill1; PP: Parus/Pastor. Female are indicated in green; Male are indicated in blue. The significance between the both parents of a cross for a given trait within a given trial is also indicated. *, **, and *** Significant at the 0.05, 0.01, and 0.001 level of probability. Dash symbol means data not available. Trait abbreviations are given with Figure 1.

Trait	Unit	Trial														
	Population	PW						SW					VP			
	Treatment	IR		DR		HI		IR	DR		HI		DR		HI	
	Year	2011	2012	2012	2013	2011	2012	2012	2012	2013	2011	2012	2011	2012	2011	2012
PH	cm	PA	PA	WB	WB	PA	PA*	SO***	SO	SO/WB	SO*	SO	PP***	VB	VB*	PP*
PL	cm	PA/WB	PA	WB	WB	WB	WB	SO	SO	SO/WB	WB	WB	-	-	PP	VB
CTvg	°C	-	PA	WB	WB	PA*	PA	SO	WB	WB*	SO	WB	-	-	PP	PP
CTgs	°C	-	-	WB	WB**	PA	PA	-	WB	-	SO	WB	PP	-	VB	PP*
CTgf	°C	PA	PA	WB	WB	PA	PA	WB	WB*	WB	SO/WB	SO	-	VB	VB	PP
CTcycle	°C	-	PA	WB	WB	PA	PA	SO/WB	WB	WB	SO	SO/WB	-	-	VB	PP*
NDVIpeg	°	-	PA	WB	WB	PA/WB	WB	SO	SO	WB	WB	WB	VB**	-	-	-
NDVIinf2	GDD	-	PA	WB**	PA	WB	PA	WB	WB	WB	SO	SO	PP**	-	VB	VB
NDVIApeg	GDD	-	WB	WB	PA	WB	WB	WB	WB	WB	SO*	SO	PP*	-	-	-
NDVIAsp	GDD	-	WB	WB	WB	WB*	WB	SO	SO/WB	WB	WB**	WB	PP*	-	PP	PP
NDVIant	-	WB	PA	PA	PA	PA	WB	SO*	WB*	SO	SO	SO	PP	-	PP	VB*
NDVIpm	-	-	-	-	PA	PA***	PA	-	-	SO	SO	-	-	PP	PP	PP**
NDVIsen	°	-	-	WB	PA/WB	PA*	PA*	-	SO	WB	WB	SO/WB	VB***	PP	VB	PP
NDVIAsen	GDD	-	-	-	PA	PA**	PA	-	-	WB	SO	-	-	-	VB	VB
ANT	GDD	WB*	WB*	WB*	WB	WB***	WB	WB	WB	WB	WB**	SO	PP***	PP**	PP*	PP*
PM	GDD	WB*	WB	WB	WB	WB	WB	WB	WB*	WB*	WB	SO	VB	PP	VB	PP
GFp	-	PA	PA/WB	PA	PA/WB	PA	PA	SO/WB	WB	SO/WB	SO	SO/WB	VB	VB	VB	VB
WSC	%	PA	-	PA	-	PA	PA/WB	-	-	-	-	-	-	-	-	-
SM2	spikes.m-2	-	PA	PA	WB	PA*	PA	SO	SO	SO	SO	SO	-	-	VB	VB**
GSP	grains.spike-1	-	WB	PA	WB	WB*	WB	WB	WB	WB	WB	WB	-	-	PP	PP
KM2	grains.m-2	WB	WB	PA	WB	WB	WB	WB	SO	SO	WB	WB	PP***	VB***	PP	VB
TKW	g	PA	WB	WB*	WB	PA	PA	SO	WB	WB	WB	SO	VB	PP***	VB	VB
YLD	g.m-2	WB	WB	PA	WB	WB	WB	WB	SO	WB	WB	SO	PP**	VB*	VB	VB*

Relationship between grain yield and other agronomic traits

PCAs were built per trial with all phenotypic data available (Figure 1). On the first axis, the percentage of total variance explained ranged from 20.8 (SW11HI) to 43.9 % (VP12DR). On the second axis, it ranged from 12 (PW13DR) to 22.6 % (PW11HI).

In total, the percentage of explanation of the total variance ranged from 38.5 (SW11HI) to 64.6 % (VP12DR) (Figure 1).

As previously detailed in Bouffier et al. (in prep), grain yield was mainly correlated with the number of grains per square meter and the number of grains per spike, whatever the population considered. The thousand kernel weight was almost exclusively positively correlated with grain yield in population SW ($p<0.001$).

In Bouffier et al. (in prep), frequent and significant correlations were reported between phenological traits and both agronomic and physiological traits. Five out of six DR trials displayed a significant negative correlation with anthesis and physiological maturity. Only PW11IR was positively and significantly correlated to both phenological traits. SW11HI and VP11HI were the only trials not significantly correlated to any of the phenological traits. A significant impact of the phenology was also observed on physiological traits, i.e., canopy temperature, NDVI, and water soluble carbohydrate concentration. NDVIinf2, NDVIAsp, and NDVIApeg were positively correlated with the anthesis date while NDVIAsen and NDVIpeg were negatively correlated to it. The sense of the correlation for NDVIant, NDVIsen, and NDVIpm depended on the trial considered (Figure 1; Supplementary Data 5).

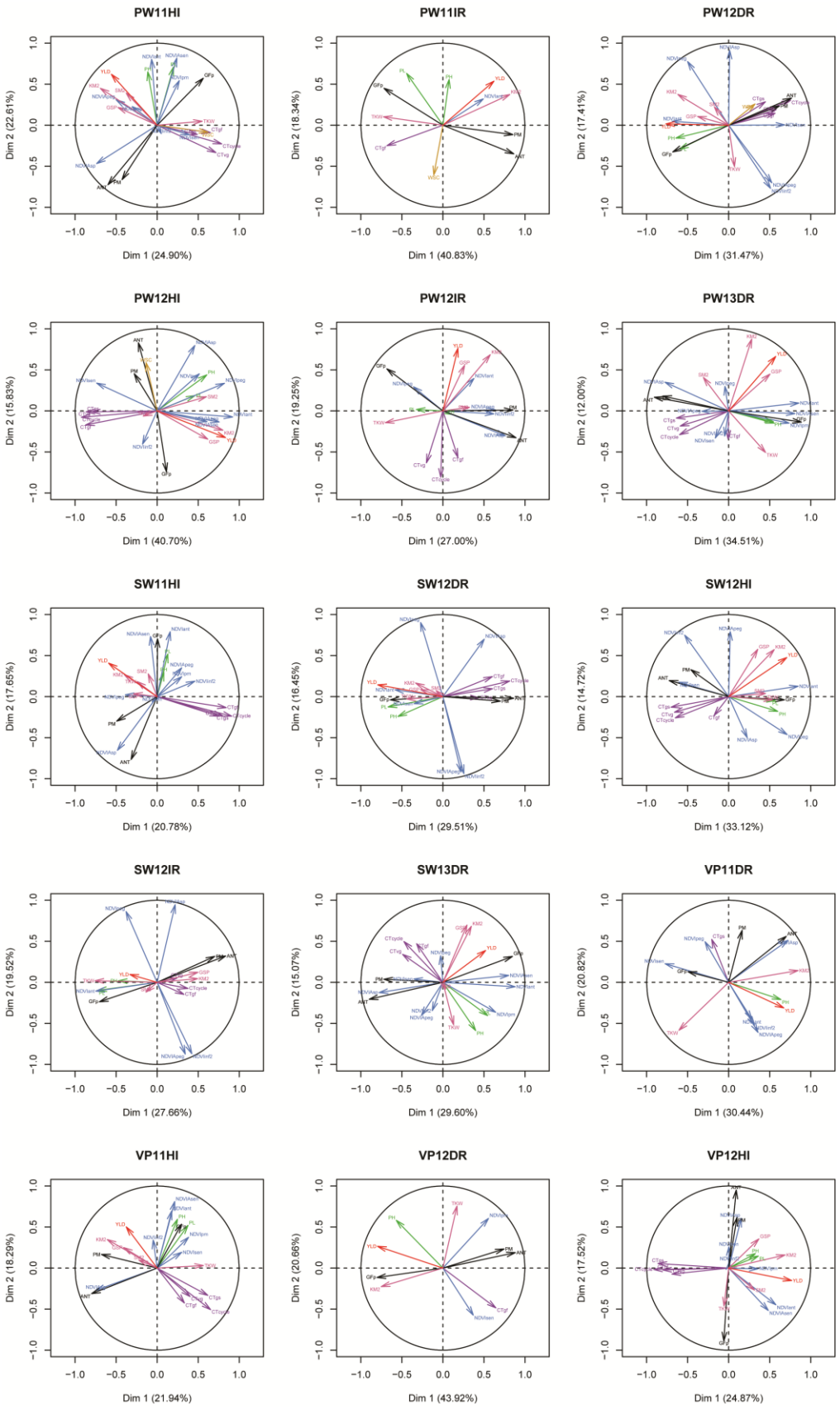

PW11HI
Dim 2 (22.61%)
Dim 1 (24.90%)
PW11IR
Dim 2 (18.34%)
Dim 1 (40.83%)
PW12DR
Dim 2 (17.41%)
Dim 1 (31.47%)
PW12HI
Dim 2 (15.83%)
Dim 1 (40.70%)
PW12IR
Dim 2 (19.25%)
Dim 1 (27.00%)
PW13DR
Dim 2 (12.00%)
Dim 1 (34.51%)
SW11HI
Dim 2 (17.65%)
Dim 1 (20.78%)
SW12DR
Dim 2 (16.45%)
Dim 1 (29.51%)
SW12HI
Dim 2 (14.72%)
Dim 1 (33.12%)
SW12IR
Dim 2 (19.52%)
Dim 1 (27.66%)
SW13DR
Dim 2 (15.07%)
Dim 1 (29.60%)
VP11DR
Dim 2 (20.82%)
Dim 1 (30.44%)
VP11HI
Dim 2 (18.29%)
Dim 1 (21.94%)
VP12DR
Dim 2 (20.66%)
Dim 1 (43.92%)
VP12HI
Dim 2 (17.52%)
Dim 1 (24.87%)

Figure 1: Principal component analyses of all traits scored within each trial. In red, the grain yield (YLD); in pink, the yield components (SM2, KM2, TKW, and GSP); in blue, all NDVI derivative traits (NDVIinf2, NDVIpeg, NDVIApeg, NDVIAsp, NDVIant, NDVIsen, NDVIAsen, and NDVIpm); in green, architecture traits (PH and PL); in gold, the WSC; in purple, all CT traits (CTvg, CTgs, CTgf, and CTcycle).

ANT: anthesis; PM: physiological maturity; GFp: Grain filling period; PH: plant height; PL: peduncle length; CT: canopy temperature during vegetative phase (CTvg), grain set phase (CTgs), grain filling phase (CTgf), or during the whole cycle (CTcycle); NDVIpeg: NDVI slope during the phase of exponential growth (peg) during vegetative phase; NDVIinf2: Time to which peg end during vegetative phase; NDVIApeg: area under the curve during the peg; NDVIAsp: Area under the NDVI curve between NDVIInf2 and ANT; NDVIant: NDVI value at ANT; NDVIsen: Slope of NDVI during the senescence phase during grain filling; NDVIpm: NDVI value at PM; NDVIAsen: Area under the NDVI curve during the senescence phase; WSC: Stem water soluble carbohydrate; SM2: Number of spikes per square meter; GSP: Number of grains per spikes; KM2: Number of kernel per square meter; TKW: thousand kernel weight; YLD: grain yield

Relationships between physiological traits and the yield and its components

Canopy temperature traits were usually positively correlated with each other, whatever the developmental stage (Figure 1). Moreover, we observed a strong, significant, and frequent negative correlation between grain yield and its components with CT traits (68 % of the 234 correlations available), ranging from r=-0.69 ($p<0.001$; PW12HI; CTcycle and YLD) to r=-0.12 ($p<0.05$; VP11DR; KM2 and CTgs) (Supplementary Data 5).

In all PCAs, NDVI traits were spread within all the quadrants. They were diversely correlated with grain yield and its components. NDVIpeg, NDVIant, and NDVIAsen were always positively and significantly correlated with grain yield.

For PW and SW, NDVIApeg, NDVIAsp, and NDVIinf2 was negatively correlated with grain yield under drought stress. Under heat stress, PW and SW displayed positive correlation with NDVIApeg and NDVIAsp, but negative with NDVIinf2. Concerning VP, correlations between grain yield and NDVIApeg, NDVIinf2, and NDVIAsp were atypical under drought as they were significant and positive correlations (VP11DR). NDVIsen was significantly and negatively correlated with grain yield whatever the population and the stress treatment (r=-0.78 ($p<0.001$; PW12HI) to r=-0.20 ($p<0.01$; SW13DR)) except in SW12DR where a positive correlation was reported (r=0.23; $p<0.001$) (Figure 1; Supplementary Data 5).

WSC was significantly and negatively correlated with grain yield whatever the trial ranging from r=-0.35 ($p<0.001$; PW11HI) to r=-0.15 ($p<0.05$; PW12DR). Similar correlations were observed with the number of grains per spike, the number of grains per square meter, and the number of spikes per square meter. Correlations between WSC and TKW were positive ($p<0.01$) in PW11HI and PW12HI.

Genetic maps

In total, 298 SNP were mapped on population PW, 327 on SW, and 318 on VP. Forty-nine markers are shared between the three populations. PW and SW shared 130 common SNP, PW and VP, 95 SNP, and SW and VP, 83 SNP. In PW, 49 % of mapped SNP were show a segregation distortion at $P<0.05$, 63 % in SW and 36 % in VP. During map constructions, some distorted markers (less than 1%; data not shown) appeared isolated and were removed because representing artifacts; distorted markers were shared within the whole genome and occurred in wide chromosome region. The average number of missing data was 7 % in PW and 9 % in SW and VP (data not shown). All three genetic maps displayed 21 linkage groups (Supplementary Data 6). The PW map covers 2596 cM, SW 2732 cM, and VP 2907 cM. Genomes A and B concentrated the majority of mapped markers (87 % in population PW, 82 % in SW, and 79 % in VP) and map size (79 % in PW, 70 % in SW, and 72 % in VP).

Mapping QTL with significant effects

A summary of QTL features per population is presented in Tables 2, 3, and 4 and the complete Figure of QTL positions in Supplementary Data 7. A total of 1487 QTL was detected considering all the populations, environments and traits. Seven hundred and thirty-three QTL were identified in all population PW trials, 624 in SW and 130 in VP.

A same QTL peak for a given trait within a given population was usually found for more than one environment where was tested the population. A notion of unique QTL corresponding to “1 peak x 1 trait x 1 pop” was then defined. Therefore, 623 QTL were considered as unique, with 244 QTL in population PW, 255 in SW, and 124 in VP. On the three populations, a total of 134 QTL for agronomic traits were found, 142 for

phenological traits, 289 for physiological traits, and 58 for architectural traits. In average, 27 QTL were found per trait within the network ranging from 1 (e.g., GSP in population VP) to 40 (ANT in SW). The highest number of QTL detected was for anthesis date in SW with 40 QTL found. Whatever the population, more QTL were found in HI than DR and IR. For example, in population PW, 208 QTL were found in IR, 250 in DR, and 275 in HI (Table 2).

Table 2: Summary table describing the different QTL by population. QTL refers to all QTL found with a significant effects ((1 trait x 1 peak x 1 population x 1 environment). uQTL refers to unique QTL across environment (unique QTL: 1 trait x 1 peak x 1 population). Trait abbreviations are given in Figure 1.

Type of QTL			Populations			Total
			PW	SW	VP	
QTL	Treatment	IR	208	122	-	330
		DR	250	247	42	539
		HI	275	255	88	618
	Total		733	624	130	1487
uQTL	Trait	YLD	11	9	11	31
		SM2	3	5	2	10
		GSP	5	5	1	11
		KM2	10	9	12	31
		TKW	14	18	19	51
		ANT	15	40	15	70
		PM	13	14	11	38
		GFp	11	13	10	34
		NDVIpeg	12	8	2	22
		NDVIinf2	8	11	2	21
		NDVIApeg	9	9	1	19
		NDVIAsp	15	12	3	30
		NDVIant	14	15	2	31
		NDVIpm	11	7	3	21
		NDVIsen	10	9	3	22
		NDVIAsen	15	13	4	32
		CTvg	6	13	2	21
		CTgs	6	9	2	17
		CTgf	8	6	3	17
		CTcycle	5	9	5	19
		WSC	17	-	-	17
		PL	15	13	3	31
		PH	11	8	8	27
	Total		244	255	124	623

Less QTL were found on genome D (130), than on genome A (275) and B (218) whatever the population considered. Considering all the populations together,

chromosomes 1B (54 QTL), 4A (73 QTL), and 5A (72 QTL) were the richest in QTL; 2D and 5D were the poorest (Data not shown).

CONS (27 %), i.e., constitutive QTL which appeared at least one year in every treatment and STRESS (14 %), i.e., stress QTL which appeared at least two years within exclusively stress treatments, QTL represented together 41 % of all unique QTL found. The mayor class was the "other" QTL with 58 % of total unique QTL. In PW and SW, CONS and STRESS QTL represented similar proportion (CONS: 35 and 33%; STRESS: 18 and 15% for PW and SW respectively (Table 3).

Table 3: Number of unique QTL (1 trait x 1 peak x 1 population) by classes within each population; STRESS: QTL appearing at least twice, once per stress treatment, or twice in a given stress treatment; IRR: QTL appearing only twice in irrigated treatment; CONS: QTL appearing at least one year in every treatment. Other: others QTL

QTL classes	Population			Total
	PW	SW	VP	
CONS	85	84	-	169
IRR	2	-	-	2
STRESS	45	38	6	89
other	112	133	118	363
Total	244	255	124	623

Hotspot of genomic regions within and between populations

Some genomic regions are particularly rich in QTL. They are so called hot spots (Marathi et al., 2012). Combined, they covered around 17 % of the genetic maps but represented 47 % of the total QTL. Sixteen are specific to population PW and 11 to SW. The number of QTL included within the 30 hot spots ranged from 7 (HS_PW_2A.2) to 94 (HS_1B) (Table 4). Only two hot spots did not contain either architectural or phenological traits: HS_PW_2A.2 and HS_PW_3A.1. Eight hotspots contained at least traits from each category, i.e., phenological, architectural, agronomic, and physiological traits (Table 4).

Three hot spots were common among populations. The first one was on 1B between PW and VP (HS_1B) where 94 QTL were grouped. The other ones were between PW and SW, on 2A (HS_2A) with 36 QTL and on 5A (HS_5A) with 55 QTL. The HS_1B on population PW may be associated with the T1BL.1RS rye translocation

present in Pastor//hxl7573/2*Bagula. All traits have a QTL in the HS-1B hot spot, except WSC and GFp. Pastor//hxl7573/2*Bagula carrying the rye translocation displayed the highest value allele for ANT, PM, TKW, NDVIinf2, NDVIsen, and all CT traits, and the lowest value allele for YLD, SM2, GSP, KM2, NDVIpeg, NDVIAsp, NDVIant, NDVIpm, NDVIAsen, PL, and PH. For NDVIApeg, Pastor//hxl7573/2*Bagula consistently provided the highest value allele under drought treatment, and the lowest one under non-limited water conditions, i.e., HI and IR (Supplementary Data 8).

On the 1487 QTL, 1319 had a –log10P higher than 3. For further analyses we considered only QTL explaining more than 5% of the variation: 755 QTL remained and 415 were defined as unique QTL (1 pop x 1 trait x 1 peak). Out of these 415 QTL that will then be used, 145 are in population PW, 168 in SW, and 102 in VP.

Table 4: Summary table of the population-specific and population-common QTL hotspots found in the genome of the three populations indicating: the population carrying the hotspot, the chromosome involved, the mapping position interval, the name of the hotspot, and the type of trait found within each hotspot

Population	Map position		HotSpot	Type of trait				Total QTL
	Chromosome	Interval (cM)		Agronomic	Architecture	Phenological	Physiological	
PW	1D	47.3-66.87	HS_PW_1D.1	2	2	6	5	15
		138.74-146.5	HS_PW_1D.2	-	-	15	13	28
	2A	55.2-67.1	HS_PW_2A	6	-	-	1	7
	3A	101.03-111.59	HS_PW_3A.1	6	-	-	9	15
		138.5-147.4	HS_PW_3A.2	12	3	4	1	20
	3B	29.72-49.1	HS_PW_3B	3	8	-	3	14
	4A	19.54-38.28	HS_PW_4A.1	-	2	-	14	16
		139.02-154.7	HS_PW_4A.2	9	-	6	13	28
	5A	75.08-94.4	HS_PW_5A.1	-	-	5	3	8
		116.23-127.9	HS_PW_5A.2	5	6	1	-	12
	6B	35.9-45.74	HS_PW_6B	-	3	11	6	20
	7A	0-13	HS_PW_7A.1	-	12	-	6	18
		57-68.93	HS_PW_7A.2	-	-	16	14	30
	7B	12.67-30.22	HS_PW_7B.1	3	-	12	11	26
		70.5-84.5	HS_PW_7B.2	6	-	6	3	15
	7D	9.71-27.15	HS_PW_7D	-	2	-	8	10
SW	1D	30.4-42.97	HS_SW_1D	5	5	-	2	12
	3A	0-0	HS_SW_3A	6	7	1	-	14
	3B	99.3-119.1	HS_SW_3B	5	-	1	17	23
	3D	0-20.52	HS_SW_3D	23	7	5	27	62
	4A	0-18.78	HS_SW_4A.1	3	5	6	7	21
		57.3-67.83	HS_SW_4A.2	2	-	1	14	17
		115.8-121.73	HS_SW_4A.3	-	10	-	-	10
	4B	20.5-39.72	HS_SW_4B	7	-	5	5	17
	5B	155.2-176.98	HS_SW_5B	5	-	3	11	19
	6A	51.83-62.54	HS_SW_6A	9	3	1	1	14
	7A	55.6-63.2	HS_SW_7A	4	2	8	13	27
PW	1B	0-18.4	HS_1B	27	7	8	42	84
VP		0-6.1		2	3	2	3	10
PW	2A	18.87-37.47	HS_2A	2	6	2	10	20
SW		11-29.47		5	1	10	-	16
PW	5A	140.3-158.6	HS_5A	-	9	11	14	34
SW		136.1-156.6		5	-	11	5	21

Genetic dissection of the agronomic traits

In PW and SW populations, only few loci were found to control grain yield. In PW, eleven loci were found to control it on chromosomes 1B, 2A, 2B, 3D, 4A (2 QTLs), 4B, 4D, 5B, and 7B (2 QTLs). Four of them were highly stable, i.e., CONS QTL which appeared in all environment tested, on chromosomes 1B, 2A, 5B and 7B. The high value allele on 1B, 2A, and 7B was brought by Weebill1 and by Pastor//hxl7573/2*Bagula concerning the CONS QTL on 5B. The seven yield QTL remaining, two were heat-stress specific which Weebill1 brought the high value allele. One strongly interacted with the environment on 4B. Indeed, under 13DR, 11HI, and 12HI, Weebill1 brought the high value allele, but under 11IR and 12DR, Pastor//hxl7573/2*Bagula displayed the high value allele. In SW, nine QTL were found for yield. Six of them were constitutive but only four appeared in all environments tested (Supplementary Data 7).

Some of these QTL for yield in PW and SW co-located with QTL for yield components. Concerning the QTL for yield found on the 1B of PW, QTL for each yield component co-located. All of them were CONS QTL which Weebill1 brought the high value allele for SM2, GSP and KM2, but Pastor//hxl7573/2*Bagula the high value allele for TKW. Only one QTL co-located between SM2 and grain yield in PW, an only two in SW. On 5A of PW, two CONS SM2 QTL which high value allele is brought by Weebill1 for the first one and by Pastor//hxl7573/2*Bagula for the second one seems co-localized with QTL found in SW on 5A. However, they did not belong to the same hotspot (Table 4). Concerning KM2 and GSP, some QTL co-located with yield QTL in PW and SW. QTL co-location were found between GSP and KM2 in PW but none in SW.

Genetic dissection of the NDVI response function

Early vigor and development

The early vigor developmental stage is characterized through different traits derived from NDVI measurements (Supplementary Data 2): the growth rate during the exponential phase (NDVIpeg), the second inflexion point indicating the end of this phase (NDVIinf2), and the area under the curve during this phase (NDVIApeg).

In PW, 11 QTL were found for these traits, 22 in SW, and 3 in VP (Table 5; Supplementary Figure 7). They collocated with many other traits as previously mentioned. In PW, four of them were co-located with the HS_1B hotspot associated with the rye translocation, and another one with the HS_PW_7A.2. Four QTL were identified for NDVIApeg on 1B, 5A, 5D, and 7A, two for NDVIinf2 on 1B and 5D, and four for NDVIpeg on 1B, 2B, 5B, and 5D. The highest phenotypic explained variances were associated with QTL belonging to the HS_1B ranging from 9.0 to 43.5 %. High value alleles were carried by Pastor//hxl7573/2*Bagula for NDVIApeg and NDVIinf2 but by Weebill1 for NDVIpeg. All QTL were classified as either STRESS or CONS. Most of the time, the high value allele was carried by WB. Only the QTL on 5D did not co-locate with a phenology trait QTL, but with other NDVI traits related to early vigor and development but also to maximum biomass.

Concerning population SW, QTL for NDVIApeg were located on chromosomes 1D, 3D, 4A, 4B, 5A, 6D, 7A, and 7D, for NDVIinf2 on 1B, 2B, 3B, 3D, 4A, 4B, 7D, and for NDVIpeg, on 1B, 3B, 3D, 4A, 4B, 5A, and 7A. The percentage of explained variance ranged from 5.4 to 31.9 %. Several of the highest values of explained variance were associated with chromosome 3D. Among the QTL which were mainly classified as CONS or STRESS, 18 did not co-locate with phenology-traits QTL, but frequently with canopy temperature traits, other NDVI traits, yield and yield components, and architecture (Table 5).

No QTL were found on the VP population for NDVIpeg. QTL for the other traits were located on chromosomes 5B, 5D, and 6D for which, the high value parent allele was brought by Parus/Pastor. The explained variance ranged from 5.2 to 20.1%. QTL collocated with CT traits, NDVIAsp, and also the number of grains per m^2 and TKW (Table 5).

Among all the QTL targeting that development stage, only three displayed a significant QTL-by-environment interaction with the environmental covariates developed in (Bouffier et al., 2014). The corresponding QTL are Q.NDVIApeg.PW.5A, Q.NDVIApeg.SW.4A, and Q.NDVIApeg.SW.7D. They displayed significant linear interaction ($p<0.05$) with EC2 ($r=0.89$), EC5 ($r=-0.93$), and EC5 ($r=0.92$), respectively (Supplementary Data 9).

Table 5: Summary of the QTL found on the three population concerning the early vigor and development. Are indicated, the population, the trait, the name of the unique QTL, the chromosome location, the hotspot to which they belong, the parent carrying the high value allele, the phenotypic explained variance (PEV; %), the effect of the QTL, the –log10P, and all other QTL co-localizing. Trait abbreviations are given in Figure 1.

Population	Trait	Unit	QTL	Chromosome	HotSpot	High value parent allele	Environment	Effect	PEV	-log10(P)	Co-location at ±5 cM of the QTL peak
PW	NDVIApeg	GDD	Q.NDVIApeg.PW.1B	1B	HS_1B	WB	12IR	6.4	9.0	28.9	ANT; CTcycle; CTgf; CTgs; CTvg; GSP; KM2; NDVIant;
						WB	12HI	7.0	19.0	28.9	NDVIApeg; NDVIAsen; NDVIAsp; NDVIinf2;
						PA	12DR	9.0	29.3	28.9	NDVIpeg; NDVIpm; NDVIsen; PH; PM; SM2; YLD
			Q.NDVIApeg.PW.5A	5A		WB	13DR	2.2	8.5	3.8	NDVIApeg; NDVIinf2; NDVIpm; PM
			Q.NDVIApeg.PW.5D	5D		PA	11HI	2.2	7.0	4.6	NDVIant; NDVIApeg; NDVIAsp; NDVIinf2; NDVIpeg
						WB	12DR	4.0	5.8	4.6	
			Q.NDVIApeg.PW.7A	7A	HS_PW_7A.2	WB	11HI	2.2	7.0	7.4	ANT; GFp; NDVIant; NDVIApeg; NDVIAsp; NDVIpm;
						WB	13DR	2.2	9.0	7.4	TKW
	NDVIinf2	GDD	Q.NDVIinf2.PW.1B	1B	HS_1B	PA	12DR	17.7	28.0	15.5	ANT; CTcycle; CTgf; CTgs; CTvg; GSP; KM2; NDVIant;
						PA	13DR	5.2	13.0	6.4	NDVIApeg; NDVIAsen; NDVIAsp; NDVIinf2; NDVIpeg; NDVIpm; NDVIsen; PH; PM; SM2; YLD
			Q.NDVIinf2.PW.5D	5D		WB	12DR	8.9	7.1	4.3	NDVIant; NDVIApeg; NDVIAsp; NDVIpeg
	NDVIpeg	°	Q.NDVIpeg.PW.1B	1B	HS_1B	WB	12HI	0.007	43.5	30.4	ANT; CTcycle; CTgf; CTgs; CTvg; GSP; KM2; NDVIant;
						WB	12DR	0.005	26.5	14.3	NDVIApeg; NDVIAsen; NDVIAsp; NDVIinf2; NDVIpeg; NDVIpm; NDVIsen; PH; PM; SM2; YLD
			Q.NDVIpeg.PW.1B.2	1B	HS_1B	WB	13DR	0.001	8.8	4.6	ANT; CTcycle; CTgf; CTgs; CTvg; GSP; KM2; NDVIant; NDVIApeg; NDVIAsen; NDVIAsp; NDVIinf2; NDVIpeg; NDVIpm; NDVIsen; PH; PM; SM2; YLD
			Q.NDVIpeg.PW.2B	2B		WB	13DR	0.001	6.2	3.4	KM2; NDVIpm
			Q.NDVIpeg.PW.5B	5B		WB	13DR	0.001	10.3	3.4	-
			Q.NDVIpeg.PW.5D	5D		PA	12DR	0.002	5.9	3.6	NDVIant; NDVIApeg; NDVIAsp; NDVIinf2; NDVIpeg
SW	NDVIApeg	GDD	Q.NDVIApeg.SW.1D	1D		WB	11HI	3.5	9.0	4.292	CTcycle; NDVIApeg
			Q.NDVIApeg.SW.3D	3D	HS_SW_3D	WB	12IR	5.1	7.7	16.3	CTvg; GSP; NDVIant; NDVIApeg; NDVIpeg; PL; SM2; TKW; YLD
						WB	11HI	2.7	5.4	16.3	
						SO	12HI	8.1	29.8	16.3	
						WB	12DR	7.5	31.9	16.3	
						WB	13DR	2.5	13.0	16.3	
			Q.NDVIApeg.SW.4A	4A	HS_SW_4A.2	SO	13DR	2.0	8.4	3.7	CTcycle; CTgs; NDVIApeg; NDVIinf2; NDVIpeg
			Q.NDVIApeg.SW.4B	4B		WB	12IR	5.2	7.7	7.7	NDVIApeg; NDVIpeg
						SO	13DR	2.1	8.9	7.7	
			Q.NDVIApeg.SW.5A	5A	HS_5A	WB	12DR	3.2	5.9	3.6	NDVIApeg; NDVIpeg
			Q.NDVIApeg.SW.6D	6D		WB	11HI	3.0	6.5	5.9	KM2; NDVIApeg; NDVIinf2; TKW
			Q.NDVIApeg.SW.7A	7A		WB	11HI	2.9	6.0	3.0	ANT; NDVIApeg
						WB	13DR	2.9	17.0	3.0	
			Q.NDVIApeg.SW.7D	7D		SO	11HI	5.9	25.6	6.6	NDVIApeg
	NDVIinf2	GDD	Q.NDVIinf2.SW.1B	1B		SO	12HI	12.4	6.9	4.3	NDVIinf2; PM
			Q.NDVIinf2.SW.2B	2B		WB	12DR	8.6	11.1	4.7	NDVIinf2

Table 5 (continued)

Population	Trait	Unit	QTL	Chromosome	HotSpot	High value parent allele	Environment	Effect	PEV	-log10(P)	Co-location at ±5 cM of the QTL peak
SW	NDVIinf2	GDD	Q.NDVIinf2.SW.3B.1	3B		WB	11HI	3.4	5.4	3.1	NDVIinf2
						WB	13DR	3.4	5.8	3.1	
			Q.NDVIinf2.SW.3D	3D	HS_SW_3D	WB	12IR	11.2	5.8	14.4	
						WB	11HI	7.8	28	14.4	CTcycle; CTgf; CTgs; CTvg; GSP; KM2; NDVIant;
						WB	12DR	13.2	26.2	14.4	NDVIAsp; NDVIinf2; NDVIpm; PH; PL; PM; SM2; YLD
						WB	13DR	5.2	13.5	14.4	
			Q.NDVIinf2.SW.4A	4A	HS_SW_4A.2	SO	12HI	11.4	5.8	4.8	CTcycle; CTgs; NDVIApeg; NDVIinf2; NDVIpeg
						SO	13DR	5.1	12.6	4.8	
			Q.NDVIinf2.SW.4B	4B	HS_SW_4B	WB	12IR	20.4	19.5	7.9	NDVIAsp; NDVIinf2
			Q.NDVIinf2.SW.7D	7D		SO	11HI	8.0	29.6	5.8	CTcycle; NDVIinf2
	NDVIpeg	°	Q.NDVIpeg.SW.1B.1	1B		WB	12HI	0.004	13.4	6.873	CTgs; CTvg; NDVIpeg
			Q.NDVIpeg.SW.3B	3B	HS_SW_3B	WB	12HI	0.003	6.0	3.4	ANT; CTgs; NDVIant; NDVIinf2; NDVIpeg; NDVIsen; TKW
			Q.NDVIpeg.SW.3D	3D	HS_SW_3D	SO	12IR	0.002	11.6	6	CTvg; GSP; NDVIant; NDVIApeg; NDVIpeg; PL; SM2;
						SO	12DR	0.003	21.6	6.0	TKW; YLD
			Q.NDVIpeg.SW.4A	4A	HS_SW_4A.2	WB	13DR	0.001	9.8	6.0	CTcycle; CTgs; NDVIApeg; NDVIinf2; NDVIpeg
			Q.NDVIpeg.SW.4B	4B		SO	12IR	0.003	18.4	8.9	
						SO	12HI	0.003	5.8	8.9	NDVIApeg; NDVIpeg
						WB	13DR	0.001	6.5	8.9	
			Q.NDVIpeg.SW.5A	5A	HS_5A	SO	12DR	0.002	11.6	8.4	NDVIApeg; NDVIpeg
					HS_5A	SO	13DR	0.001	11.1	8.4	
			Q.NDVIpeg.SW.7A	7A		SO	12IR	0.002	6.7	5.1	NDVIinf2; NDVIpeg
						WB	11HI	0.002	8.9	5.1	
VP	NDVIApeg	GDD	Q.NDVIApeg.VP.5D	5D		PP	11DR	3.6	20.1	3.8	-
	NDVIinf2	GDD	Q.NDVIinf2.VP.5B	5B		PP	11HI	2.9	5.2	3.6	CTcycle; CTvg; KM2
			Q.NDVIinf2.VP.6D	6D		PP	12HI	8.7	6.1	4.1	NDVIAsp; TKW

Maximum biomass

The NDVI value at anthesis (NDVIant) and the area under the curve during the stationary phase (NDVIAsp) are used to characterize the maximum biomass and chlorophyll content. In total, 18 QTL were found for these traits in population PW, 24 in SW, and 5 in VP (Table 5; Supplementary Figure 7). Eight QTL co-located with QTL of phenology in PW. However, for all remaining QTL, co-localizations with grain yield and yield component were observed (GSP in Q.NDVIant.PW.2A, Q.NDVIAsp.PW.1D.1, and Q.NDVIAsp.PW.2A; KM2 in Q.NDVIant.PW.7B.1), with WSC (Q.NDVIant.PW.6B), and with other NDVI traits in general (e.g., Q.NDVIant.PW.5A). As during early vigor and development, two QTL found were co-located with the HS_1B hotspot displaying the highest explained variance observed in that stage (PEV=47.2 % in Q.NDVIant.PW.1B in 12HI). Many QTL belong to hotspots as to the three hotspots which are common between populations (HS_1B, HS_2A, and HS_5A), but also to specific hot spots on chromosomes 1D, 3A, 4A, 7A, and 7B. For QTL which belong to the HS_1B hot spot, Weebill1 brought always the high allele value (Table 6).

In population SW, similarly to PW, QTL co-located to phenology QTL on 3D, 4A, 5A, 5B, and 7A. Co-location with other interesting traits appeared as with canopy temperature (e.g. Q.NDVIant.SW.3D), agronomic traits such as yield (e.g., Q.NDVIant.SW.7B), and in most cases, with other NDVI traits (e.g.). The explained variance ranged from 5.0 % (Q.NDVIant.SW.5D) to 61.4 % (Q.NDVIant.SW.3D). Concerning that last QTL that explained a very large amount of the phenotypic variation, it was located in a hotspot with many other QTL on 3D (HS_SW_3D), and Sokoll carried the high allele value.

Population VP, with 5 QTL, of which 3 were co-located with phenology traits, had an explained variance ranging from 7.6 to 12.2 %. On chromosome 2B, the QTL Q.NDVIant.VP.2B which high allele value was brought by Parus/Pastor under heat stress conditions co-located with a CTgf and an NDVIant traits. On 6D, Q.NDVIAsp.VP.6D, Vorobey brought the high value allele and was associated with TKW and NDVIinf2.

Five QTL with QTL-by-environment interaction (QEI) were identified in PW, ranging from $r=0.84$ ($p<0.05$) to $r=0.97$ ($p<0.01$) and seven in SW. Significant QEI was

established with drought stress environmental covariates, i.e., EC1, EC3, and EC6, heat stress ones, i.e., EC2, and radiation ones, i.e, EC4 (Supplementary Data 9).

Chlorophyll loss and senescence

The senescence phase was dissected in rate of senescence (NDVIsen), NDVI value at physiological maturity (NDVIpm), and the area under the curve during the senescence phase (NDVIAsen). In total, 51 QTL were found of which 26 belong to population PW, 16 to SW, and 9 to VP. Only 13 QTL in PW did not collocated with phenology traits, but with agronomic traits such as yield (e.g., Q.NDVIpm.PW.3D), other NDVI derivative traits (e.g., Q.NDVIpm.PW.5A.1), and also CT traits (e.g. Q.NDVIsen.PW) on chromosomes 2A, 4A, and.6A. In SW, all QTL founds co-located with a phenology trait QTL. In VP, only three QTL did not co-locate with phenology traits, but with agronomic (e.g., Q.NDVIsen.VP.4A) and architectural traits (e.g., Q.NDVIsen.VP.5A). During the senescence phase, no QTL with significant QEI were found (Supplementary Data 9).

Table 6: Summary of the QTL found on the three population concerning the maximum biomass and development. Are indicated, the population, the trait, the name of the unique QTL, the chromosome location, the hotspot to which they may belong, the parent carrying the high value allele, the phenotypic explained variance (PEV; %), the effect of the QTL, the –log10P, and all other QTL co-localizing. Trait abbreviations are given in Figure 1.

Population	Trait	Unit	QTL	Chromosome	HotSpot	High value parent allele	Environment	Effect	PEV	-log10(P)	Co-location at ±5 cM of the QTL peak
PW	NDVIant	-	Q.NDVIant.PW.1B	1B	HS_1B	WB	13DR	0.007	5.0	60.0	ANT; CTcycle; CTgf; CTgs; CTvg;
						WB	11HI	0.013	13.5	60.0	GSP; KM2; NDVIant; NDVIApeg;
						WB	12HI	0.033	47.2	60.0	NDVIAsen; NDVIAsp; NDVIinf2;
						WB	11IR	0.015	16.0	60.0	NDVIpeg; NDVIpm; NDVIsen; PH;
						WB	12IR	0.009	18.0	60.0	PM; SM2; YLD
			Q.NDVIant.PW.2A	2A	HS_2A	PA	11HI	0.012	11.0	11.2	GSP; NDVIant; NDVIAsp
						PA	11IR	0.012	9.1	11.2	
			Q.NDVIant.PW.3A	3A	HS_PW_3A.1	PA	12DR	0.007	11.3	6.8	NDVIant; NDVIAsp; NDVIsen
						PA	11IR	0.009	6.0	6.8	
			Q.NDVIant.PW.4A	4A		WB	13DR	0.010	10.9	6.8	ANT; CTcycle; CTvg; GSP; KM2; NDVIant; NDVIAsen; NDVIAsp; NDVIpm; PH; PL; PM; TKW; YLD
			Q.NDVIant.PW.4D	4D		WB	12DR	0.007	9.2	9.1	NDVIant; NDVIAsp
						WB	12IR	0.005	6.0	9.1	
			Q.NDVIant.PW.5A	5A	HS_5A	PA	13DR	0.007	5.9	7.0	NDVIant; NDVIAsen; NDVIAsp;
						PA	11HI	0.014	14.4	7.0	NDVIinf2; NDVIpm
			Q.NDVIant.PW.6B	6B		PA	13DR	0.011	13.4	6.2	NDVIant; WSC
			Q.NDVIant.PW.7A.2	7A	HS_PW_7A.2	PA	13DR	0.009	8.4	6.9	ANT; GFp; NDVIant; NDVIApeg; NDVIAsp; NDVIpm; TKW
			Q.NDVIant.PW.7B.1	7B	HS_PW_7B.1	WB	12DR	0.010	19.1	7.2	KM2; NDVIant; NDVIpeg
						WB	13DR	0.015	24.5	7.2	
						WB	11HI	0.009	6.0	7.2	
	NDVIAsp	GDD	Q.NDVIAsp.PW.1B	1B	HS_1B	WB	12DR	8.5	6.9	12.4	ANT; CTcycle; CTgf; CTgs; CTvg;
						WB	12HI	10.1	9.8	12.4	GSP; KM2; NDVIant; NDVIApeg; NDVIAsen; NDVIAsp; NDVIinf2; NDVIpeg; NDVIpm; NDVIsen; PH; PM; SM2; YLD
			Q.NDVIAsp.PW.1D.1	1D		WB	13DR	6.3	5.0	6.8	GSP; NDVIAsp
						WB	12IR	6.3	5.2	6.8	
			Q.NDVIAsp.PW.1D.2	1D	HS_PW_1D.2	WB	12DR	9.8	9.2	9.6	ANT; GFp; NDVIAsp; PM
						WB	13DR	9.8	12.1	9.6	
						WB	11HI	9.8	7.9	9.6	
						WB	12HI	9.8	9.2	9.6	
						WB	12IR	9.8	12.7	9.6	
			Q.NDVIAsp.PW.2A	2A	HS_2A	PA	12DR	7.3	5.1	7.9	GSP; NDVIant; NDVIAsp
						PA	13DR	9.5	11.4	7.9	
						PA	12HI	8.3	6.6	7.9	
						PA	12IR	6.3	5.3	7.9	

Table 6 (continued)

Population	Trait	Unit	QTL	Chromosome	HotSpot	High value parent allele	Environment	Effect	PEV	-log10(P)	Co-location at ±5 cM of the QTL peak
PW	NDVIAsp	GDD	Q.NDVIAsp.PW.4A	4A	HS_PW_4A.2	PA	12DR	10.0	9.6	21.6	ANT; CTcycle; CTvg; GSP; KM2; NDVIant; NDVIAsen; NDVIAsp; NDVIpm; PH; PM; TKW; WSC; YLD
						PA	13DR	11.7	17.4	21.6	
						PA	11HI	18.2	27.1	21.6	
						PA	12HI	13.4	17.1	21.6	
						PA	12IR	11.8	18.5	21.6	
			Q.NDVIAsp.PW.5A.1	5A		WB	12DR	9.7	9.0	15.7	ANT; CTcycle; GFp; NDVIAsen; NDVIAsp; NDVIpeg
						WB	13DR	13.5	23.0	15.7	
						WB	11HI	15.3	19.1	15.7	
						WB	12HI	13.9	18.5	15.7	
						WB	12IR	8.7	10.0	15.7	
			Q.NDVIAsp.PW.5A.2	5A	HS_5A	WB	12HI	7.8	5.7	5.6	NDVIant; NDVIAsen; NDVIAsp; NDVIinf2; NDVIpm
						WB	12IR	6.6	5.7	5.6	
			Q.NDVIAsp.PW.5D	5D		PA	12HI	9.0	7.7	5.2	NDVIant; NDVIApeg; NDVIAsp; NDVIinf2; NDVIpeg
			Q.NDVIAsp.PW.7A	7A	HS_PW_7A.2	WB	12DR	8.9	7.7	17.3	ANT; GFp; NDVIant; NDVIApeg; NDVIAsp; NDVIpm
						WB	13DR	9.6	11.7	17.3	
						WB	11HI	10.8	9.5	17.3	
						WB	12IR	11.4	17.1	17.3	
SW	NDVIant	-	Q.NDVIant.SW.1A	1A		WB	13DR	0.007	5.3	6.0	NDVIant
						WB	11HI	0.009	10.8	6.0	
						WB	12HI	0.011	8.9	6.0	
						WB	12IR	0.006	8.6	6.0	
			Q.NDVIant.SW.1B	1B		WB	11HI	0.008	8.2	8.1	NDVIant; NDVIAsen
			Q.NDVIant.SW.2B.1	2B		WB	12HI	0.010	6.8	5.8	NDVIant; NDVIsen
			Q.NDVIant.SW.2B.2			SO	11HI	0.010	13.3	5.0	NDVIant
			Q.NDVIant.SW.3D	3D	HS_SW_3D	SO	12HI	0.030	61.4	17.2	CTgs; CTvg; GSP; NDVIant; NDVIApeg; NDVIAsp; NDVIinf2; NDVIpeg; PH; PL; SM2; TKW; YLD
			Q.NDVIant.SW.4A	4A		WB	13DR	0.011	11.6	5.9	ANT; NDVIant; NDVIAsen
			Q.NDVIant.SW.4D	4D		SO	13DR	0.008	5.9	2.9	CTgf; NDVIant; NDVIpm
			Q.NDVIant.SW.5B	5B		SO	12DR	0.012	14.1	5.5	ANT; NDVIant
						SO	12IR	0.005	8.1	5.5	
			Q.NDVIant.SW.5D	5D		WB	13DR	0.016	25.5	12.8	GFp; NDVIant
						SO	11HI	0.006	5.0	12.8	
			Q.NDVIant.SW.7A.1	7A	HS_SW_7A	SO	12IR	0.005	7.7	4.8	ANT; CTgs; GSP; KM2; NDVIant; NDVIAsp; NDVIpm; PM
			Q.NDVIant.SW.7A.2	7A		SO	12HI	0.013	11.4	5.7	NDVIant
			Q.NDVIant.SW.7A.3	7A		WB	12DR	0.008	5.3	9.4	CTcycle; CTvg; NDVIant
						WB	12HI	0.014	13.4	9.4	
			Q.NDVIant.SW.7B	7B		SO	13DR	0.011	12.6	8.1	NDVIant; NDVIAsen; YLD

Table 6 (continued)

Population	Trait	Unit	QTL	Chromosome	HotSpot	High value parent allele	Environment	Effect	PEV	-log10(P)	Co-location at ±5 cM of the QTL peak
	NDVIAsp	GDD	Q.NDVIAsp.SW.1B	1B		WB	11HI	6.8	7.5	5.0	GFp; NDVIAsp
				1B		WB	12HI	9.0	5.8	5.0	
			Q.NDVIAsp.SW.2B	2B		SO	12DR	7.1	7.4	2.4	NDVIAsp
				2B		SO	12IR	12.1	6.9	2.4	
			Q.NDVIAsp.SW.3D	3D	HS_SW_3D	SO	11HI	6.2	6.1	8.8	CTcycle; CTgf; CTgs; CTvg; GSP; KM2; NDVIant; NDVIAsp; NDVIinf2; NDVIpm; PH; PM
			Q.NDVIAsp.SW.4A.1	4A	HS_SW_4A.1	SO	11HI	5.7	5.4	6.6	NDVIAsp
			Q.NDVIAsp.SW.4A.2	4A		SO	13DR	7.9	9.1	7.0	ANT; GFp; NDVIAsen; NDVIAsp
				4A		SO	12IR	13.9	9.1	7.0	
			Q.NDVIAsp.SW.4B	4B	HS_SW_4B	SO	12IR	15.7	11.6	6.5	NDVIAsp; NDVIinf2
			Q.NDVIAsp.SW.5A	5A		SO	13DR	6.0	5.2	4.9	ANT; NDVIAsp
			Q.NDVIAsp.SW.5B.1	5B	HS_SW_5B	SO	12DR	8.7	11.0	4.0	CTgf; NDVIAsp; SM2; YLD
						SO	13DR	8.7	10.9	4.0	
						SO	11HI	8.7	12.2	4.0	
						SO	12HI	8.7	5.3	4.0	
			Q.NDVIAsp.SW.5B.2	5B		SO	12IR	13.1	8.1	7.2	NDVIAsp
			Q.NDVIAsp.SW.7A	7A	HS_SW_7A	WB	12DR	13.6	27.2	16.8	ANT; CTcycle; CTgs; GSP; KM2; NDVIant; NDVIAsp; NDVIpm; PL; PM
						WB	13DR	14.0	28.5	16.8	
						WB	11HI	6.4	6.7	16.8	
						WB	12IR	17.4	14.3	16.8	
			Q.NDVIAsp.SW.7D	7D		SO	12DR	8.7	11.1	5.2	NDVIAsp
						SO	13DR	8.7	11.0	5.2	
						SO	11HI	8.7	12.2	5.2	
						SO	12HI	8.7	5.3	5.2	
VP	NDVIant	-	Q.NDVIant.VP.1B	1B	HS_1B	VB	11HI	0.010	12.2	7.6	ANT; GFp; KM2; NDVIAsen; NDVIpm; PH; PL; TKW
			Q.NDVIant.VP.2B	2B		PP	11HI	0.008	7.6	4.5	CTgf; NDVIant
						PP	12HI	0.005	8.8	4.6	
	NDVIAsp	GDD	Q.NDVIAsp.VP.4A	4A		VB	11HI	6.1	8.3	4.8	ANT; GFp; KM2; TKW
			Q.NDVIAsp.VP.4D	4D		PP	11DR	6.1	6.6	4.2	ANT; TKW
			Q.NDVIAsp.VP.6D	6D		VB	12HI	9.0	7.4	4.9	NDVIinf2; TKW

Table 7: Summary of the QTL found on the three population concerning the loss of chlorophyll phase. Are indicated, the population, the trait, the name of the unique QTL, the chromosome location, the hotspot to which they may belong, the parent carrying the high value allele, the phenotypic explained variance (PEV; %), the effect of the QTL, the –log10P, and all other QTL co-localizing. Trait abbreviations are given in Figure 1.

Population	Trait	Unit	QTL	Chromosome	HotSpot	High value parent allele	Environment	Effect	PEV	-log10(P)	Co-location at ±5 cM of the QTL peak
PW	NDVIpm	-	Q.NDVIpm.PW.1B	1B	HS_1B	WB	12HI	0.011	16.6	8.2	ANT(6); CTcycle(5); CTgf(6); CTgs(2); CTvg(5); GSP(5); KM2(6); NDVIant(6); NDVIApeg(5); NDVIAsen(2); NDVIAsp(5); NDVIinf2(2); NDVIpeg(3); NDVIsen(4); PH(6); PM(6); SM2(5); YLD(6)
			Q.NDVIpm.PW.3D	3D		PA	12HI	0.013	23.3	4.2	YLD(6)
			Q.NDVIpm.PW.4A.1	4A	HS_PW_4A.2	WB	13DR	0.011	25.8	11.1	ANT(6); CTcycle(5); CTvg(5); GSP(5); KM2(6); NDVIant(6); NDVIAsen(2); NDVIAsp(5); PH(6); PM(6); TKW(6); WSC(1); YLD(6)
			Q.NDVIpm.PW.4A.2	4A	HS_PW_4A.3	WB	11HI	0.016	22.6	5.7	
			Q.NDVIpm.PW.5A.1	5A		PA	13DR	0.007	11.0	4.2	NDVIApeg(5); NDVIinf2(2)
			Q.NDVIpm.PW.7D	7D		WB	13DR	0.005	5.1	2.4	ANT(6); GFp(6); PL(6)
	NDVIsen	°	Q.NDVIsen.PW.1B	1B	HS_1B	PA	12DR	0.002	8.8	56.7	ANT(6); CTcycle(5); CTgf(6); CTgs(2); CTvg(5); GSP(5); KM2(6); NDVIant(6); NDVIApeg(5); NDVIAsen(2); NDVIAsp(5); NDVIinf2(2); NDVIpeg(3); NDVIpm(1); NDVIsen(3); PH(6); PM(6); SM2(5); YLD(6)
				1B	HS_1B	PA	12HI	0.003	50.1	56.7	ANT(6); CTcycle(5); CTgf(6); CTgs(2); CTvg(5); GSP(5); KM2(6); NDVIant(6); NDVIApeg(5); NDVIAsen(2); NDVIAsp(5); NDVIinf2(2); NDVIpeg(3); NDVIpm(1); NDVIsen(3); PH(6); PM(6); SM2(5); YLD(6)
			Q.NDVIsen.PW.2A	2A		WB	11HI	0.002	7.4	3.4	NDVIsen(3)
			Q.NDVIsen.PW.3A	3A	HS_PW_3A.1	WB	13DR	0.001	5.9	4.6	NDVIant(6); NDVIAsp(5); NDVIsen(3)
			Q.NDVIsen.PW.3B.3	3B	HS_PW_3B	PA	12HI	0.001	6.2	9.2	NDVIpeg(1); NDVIsen(3); PH(6); PL(6)
			Q.NDVIsen.PW.5A	5A		PA	13DR	0.001	8.3	3.5	NDVIsen(3); SM2(5)
			Q.NDVIsen.PW.6A	6A		PA	12DR	0.002	7.3	4.4	CTcycle(5); CTvg(5); GFp(6); NDVIAsen(1); NDVIsen(3)
			Q.NDVIsen.PW.7A	7A		WB	12DR	0.004	41.7	9.9	NDVIsen(3)
				7A		WB	12HI	0.003	30.2	9.9	NDVIsen(3)
			Q.NDVIsen.PW.7D	7D		WB	12DR	0.001	5.9	5.7	NDVIAsp(5); NDVIsen(3); PH(6)
	NDVIAsen	GDD	Q.NDVIAsen.PW.1A	1A		WB	11HI	6.3	6.5	3.8	
			Q.NDVIAsen.PW.1B.1	1B	HS_1B	WB	11HI	7.1	8.0	5.6	ANT(6); CTcycle(5); CTgf(6); CTgs(2); CTvg(5); GSP(5); KM2(6); NDVIant(6); NDVIApeg(5); NDVIAsen(1); NDVIAsp(5); NDVIinf2(2); NDVIpeg(3); NDVIpm(1); NDVIsen(4); PH(6); PM(6); SM2(5); YLD(6)

Table 7 (continued)

Population	Trait	Unit	QTL	Chromosome	HotSpot	High value parent allele	Environment	Effect	PEV	-log10(P)	Co-location at ±5 cM of the QTL peak
PW	NDVIsen	GDD	Q.NDVIAsen.PW.1B.2	1B	HS_1B	WB	12HI	15.4	36.5	19.9	ANT(6); CTcycle(5); CTgf(6); CTgs(2); CTvg(5); GSP(5); KM2(6); NDVIant(6); NDVIApeg(5); NDVIAsen(1); NDVIAsp(5); NDVIinf2(2); NDVIpeg(3); NDVIpm(1); NDVIsen(4); PH(6); PM(6); SM2(5); YLD(6)
			Q.NDVIAsen.PW.2A	2A	HS_2A	PA	12HI	7.7	9.1	6.2	CTvg(5)
			Q.NDVIAsen.PW.4A.1	4A	HS_PW_4A	WB	13DR	4.0	5.3	2.5	CTcycle(5)
			Q.NDVIAsen.PW.4A	4A		WB	11HI	5.9	5.6	3.3	ANT(6); CTcycle(5); CTvg(5); GSP(5); KM2(6); NDVIant(6); NDVIAsen(1); NDVIAsp(5); NDVIpm(1); PH(6); PM(6); TKW(6); YLD(6)
			Q.NDVIAsen.PW.4A.2	4A	HS_PW_4A.4	WB	13DR	3.9	5.0	2.4	ANT(6); CTcycle(5); CTvg(5); GSP(5); KM2(6); NDVIant(6); NDVIAsen(1); NDVIAsp(5); NDVIpm(1); PH(6); PM(6); TKW(6); WSC(1); YLD(6)
			Q.NDVIAsen.PW.5A.2	5A		PA	11HI	8.6	11.9	5.2	ANT(6); CTcycle(5); GFp(6); NDVIAsp(5); NDVIpeg(1)
			Q.NDVIAsen.PW.5A.4	5A	HS_5A	PA	11HI	8.2	10.7	6.4	NDVIant(6); NDVIAsen(1); NDVIAsp(5); NDVIinf2(2); NDVIpm(1)
			Q.NDVIAsen.PW.5A.5	5A	HS_5A	PA	13DR	4.3	6.2	3.4	ANT(6); GFp(6); PH(6); PL(6)
			Q.NDVIAsen.PW.6A	6A		WB	13DR	4.4	6.5	3.7	CTcycle(5); CTvg(5); GFp(6); NDVIsen(4)
			Q.NDVIAsen.PW.7D.1	7D	HS_PW_7D	WB	12HI	6.0	5.4	3.2	PL(6)
SW	NDVIpm	-	Q.NDVIpm.SW.3D	3D	HS_SW_3D	WB	13DR	0.005	7.1	4.2	CTcycle(5); CTgf(5); CTgs(1); CTvg(2); KM2(5); NDVIAsp(5); NDVIinf2(5); PH(5); PM(5)
			Q.NDVIpm.SW.5A	5A	HS_5A	SO	11HI	0.008	7.7	5.0	ANT(3); GFp(5); PM(5)
			Q.NDVIpm.SW.6A	6A		WB	11HI	0.014	23.1	6.1	GFp(5); KM2(5); PH(5); TKW(5)
			Q.NDVIpm.SW.7A	7A	HS_SW_7A	SO	13DR	0.009	22.6	14.6	ANT(2); CTgs(1); GSP(5); KM2(5); NDVIant(5); NDVIAsp(5); PM(5)
	NDVIsen	°	Q.NDVIsen.SW.1A.1	1A		SO	13DR	0.001	10.4	6.0	PM(5)
			Q.NDVIsen.SW.1A.2	1A		SO	11HI	0.002	19.7	6.8	PM(5)
			Q.NDVIsen.SW.2B.1	2B		SO	12HI	0.003	18.1	8.0	NDVIant(5)
			Q.NDVIsen.SW.3D	3D	HS_SW_3D	WB	12HI	0.002	14.8	5.8	ANT(1)
			Q.NDVIsen.SW.5B	5B		WB	11HI	0.002	23.1	6.0	
			Q.NDVIsen.SW.6A	6A	HS_SW_6A	WB	11HI	0.002	21.7	6.3	PL(5)
			Q.NDVIsen.SW.6B	6B		SO	12HI	0.001	6.3	3.4	ANT(3); GFp(5)
	NDVIAsen	GDD	Q.NDVIAsen.SW.1B.1	1B		SO	11HI	7.8	13.7	3.1	
			Q.NDVIAsen.SW.2B	2B		SO	11HI	5.6	7.1	2.1	
			Q.NDVIAsen.SW.4A.1	4A	HS_SW_4A.1	WB	13DR	5.6	11.3	4.2	ANT(1); CTgs(1); GFp(5); PH(5); TKW(5)
			Q.NDVIAsen.SW.4A.2	4A		WB	13DR	5.9	12.4	6.3	ANT(1); NDVIant(5); NDVIAsp(5)
			Q.NDVIAsen.SW.5D	5D		WB	13DR	12.6	56.7	13.3	

Table 7 (continued)

Population	Trait	Unit	QTL	Chromosome	HotSpot	High value parent allele	Environment	Effect	PEV	-log10(P)	Co-location at ±5 cM of the QTL peak
VP	NDVIpm	-	Q.NDVIpm.VP.1B	1B	HS_1B	VB	12DR	0.004	7.5	4.4	ANT(1); GFp(1); KM2(1); NDVIant(1); NDVIAsen(1); PL(2); TKW(1)
			Q.NDVIpm.VP.2D	2D		PP	11HI	0.011	13.9	4.6	
			Q.NDVIpm.VP.4A	4A		VB	11HI	0.009	9.1	4.3	PM(1)
	NDVIsen	°	Q.NDVIsen.VP.4A	4A		VB	12DR	0.002	16.6	5.7	YLD(1)
			Q.NDVIsen.VP.5A	5A		PP	11HI	0.001	8.4	3.9	PH(1)
			Q.NDVIsen.VP.7B	7B		VB	12HI	0.001	7.8	4.1	PM(1); TKW(2)
	NDVIAsen	GDD	Q.NDVIAsen.VP.1B	1B	HS_1B	VB	11HI	9.3	16.5	10.1	ANT(1); GFp(1); KM2(1); NDVIant(1); NDVIpm(1); PL(2); TKW(1)
			Q.NDVIAsen.VP.3D	3D		VB	12HI	4.3	6.4	4.3	GFp(1); KM2(1); YLD(1)
			Q.NDVIAsen.VP.4A	4A		PP	11HI	10.6	21.4	4.2	

Interdependence of traits

Among the 415 unique QTL found with more than 5% of the phenotypic variance explained and a –log10P higher than 3, 136 QTL do not collocate neither with phenology nor architecture traits. In total, 47 belong to PW, 55 to SW, and 34 to VP

On the QTL hot spot HS_SW_5B, there was a co-location of QTL for yield, NDVIAsp, and CTvg. The range of the phenotypic variance explained for the QTL for yield (Q.YLD.SW.5B) underneath ranged from 18.4 (SW11HI) to 33.6 % (SW12HI). However, at that location, QTL for yield was constitutive.

Some QTL colocations were found between yield component and NDVI, CT, and WSC traits. Some of them displayed a significant interaction with the environment. For example, the Q.NDVIant.PW.2A collocated with QTL for grains per spike and NDVIAsp. The phenotypic variation explained ranged from 9.1 (PW11IR) to 11 % (PW11HI).

Some QTL of the NDVI response function co-located with canopy temperature and WSC QTL.

DISCUSSION

New genetic regions were detected for NDVI traits

In this study, new genomic regions were discovered for early vigor and development on chromosomes 1B, 5A, and 5D (Table 5). In the literature, QTL for early vigor have been reported on chromosomes 2B, 3B, 3D, 4A, 4B, 5B, 6A, 6B, 7A, and 7B (Rebetzke et al., 2001; Bennett et al., 2012a; b). The main QTL on 1B is probably the result of the T1BL.1RS rye translocation. This major translocation has been associated to an increase in grain yield on wheat (Shearman et al., 2005) but with a poorer bread-making quality due to a reduction of some bread-making feature: the dough strength and the stickiness (Dhaliwal and MacRitchie, 1990). The translocation was also found to be associated with increased resistance to some pathogens as the yellow rust (Worland and Snape, 2001; Foulkes et al., 2006).

We found QTL on 20 out of the 21 wheat chromosomes for the maximum biomass stage (Table 6) and literature reported QTL on all of them (Kirigwi et al., 2007; Olivares-Villegas et al., 2008; Peleg et al., 2009; Pinto et al., 2010; Bennett et al., 2012a;

b; Mason et al., 2013; Edae et al., 2014). However, QTL discovered on chromosome 1B cannot be associated with the one discovered and reported within the literature. Indeed, all the QTL we found on 1B co-located with the HS_1B hot spot located at the T1BL.1RS rye translocation.

The senescing part of the crop cycle enabled to discover QTL on 17 chromosomes in our study (Table 7). Indeed, no QTL were discovered only on chromosomes 1D, 4B, 4D, and 6D. However, most genomic regions were different than the ones reported in the literature (Verma et al., 2004; Vijayalakshmi et al., 2010; Edae et al., 2014). Indeed, new genomic regions were discovered on chromosomes 1A, 1B, 2D, 3D, and 5B. For the same reasons previously mentioned, chromosome 1B should be considered with care. The new QTL found for these traits could be explained by the use of the new NDVI derived traits that were proposed by Lopes and Reynolds (2012) to characterize the senescing phase.

Interestingly, as expected in view of the phenotypic correlations reported in the PCA (Figure 1), each NDVI trait shared genetic regions with the other ones, but also had its own specific determinant regions. Moreover, some of NDVI traits QTL co-located with QTL for agronomic traits which confirm phenotypic correlation observed between these traits.

Significant interactions of these QTL with the environment were highlighted

A significant QEI was found for several QTL during the early development phase and also during the maximum biomass phase. Most QEI were identified with heat stress covariates, i.e., EC2 and EC5, and then with drought stress covariates, i.e., EC1, EC3, and EC6. Fifteen of the 18 QEI detected for NDVI traits were observed for population SW, within which more heat stress covariates were of influence. At the GEI level, the very high sensitivity of SW to heat stress was already reported using the same experiments (Bouffier et al. in prep.). This study at the genetic level enabled to confirm this result as exemplified with a QTL for NDVIAsp on 2B and EC4 (Figure 2; Supplemental Data 9). Although several significant QEI were found within the network, the power of detection was quite low because only a few environments were available, and most environmental covariates behave as discrete variables. Such design enabled to

detect only the strongest relationships between environmental covariates and QTL effects. With more environments tested a continuous distribution of environmental covariates would probably be observed which could ease determining the QTL sensitivity to environmental stresses.

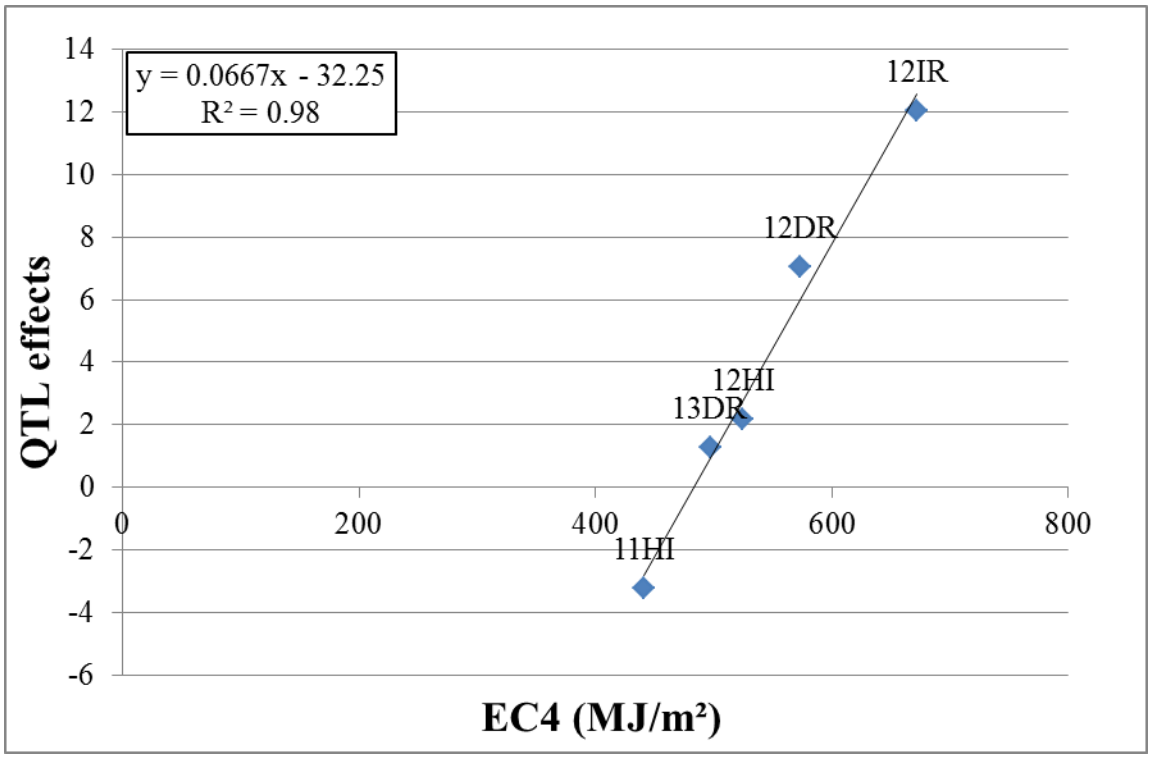


Figure 2: Plot of the effects of the QTL 'Q.NDVIAsp.SW.2B' as a function of the environmental covariate EC4 which is the amount of solar radiation received by the canopy during the grain set phase. Each point corresponds to the effects in population Sokoll/Weebill1 of the QTL in a given environment (IR = irrigated, DR = drought, HI = heat irrigated). The solid line represents the linear regression. A positive effect means that Sokoll brought the high value allele.

Use of relevant QTL in a breeding program

Many QTL were found during the dissection of the NDVI dynamics during each phase of development. Numerous QTL that explained an important part of the phenotypic variation were associated to the T1BL.1RS rye translocation (Table 5, 6, and 7). For all traits except WSC and GFp, QTL were found around that location on chromosome 1B. Identifying the parents carrying the high value allele for the translocation, we were able to determinate its positive or negative impact on grain yield. The translocation had a negative impact on yield, number of spikes per square meter,

number of grains per spike, and number of grains per m², but a positive effect on TKW whatever the environment, i.e., what we called CONS QTL. Worland and Snape (2001) reported that the translocation was initially introgressed for diseases resistance brought from rye to wheat. However, several studies revealed that such translocation had a negative impact on the wheat flour quality (Dhaliwal and MacRitchie, 1990). As wheat quality largely structures the world wheat market, the introgression of such translocation should be considered with care.

QTL co-localizations show a strong impact of phenology, mainly during the maximum biomass and senescence phases. Later genotypes tended to have increased yield under irrigated conditions, but lower yield whatever the stressed conditions and population considered. This was expected as the parents were known to be diverse for the main photoperiod and vernalization genes, and this was observed in the field with the wide range of phenology within each population (Supplementary Data 3). Nevertheless, several genomic regions were found that did not collocate with phenology QTL. Particularly interesting is a region on chromosome 5B of SW where a co-localization was found between grain yield, NDVI, and CT traits. This let the opportunity to a breeder to beneficiate to the new alleles found without modifying phenology.

Co-location of QTL was also found between NDVI traits during the period of senescence and canopy temperature traits. This result enables to establish a link between both traits at the genetic level and it highlights the dependence of the stay-green process to the access of water by roots, in DR and HI treatments. Moreover, the differential associations between grain yield and its components with NDVI, but also with CT and WSC traits at each phase of development, leads to the conclusion that the tolerance is partly common to drought and heat stress. (Suzuki et al., 2014) also hypothesized partly similar bases for adaptation to drought and heat stress considering studies of unique or combined stress on Arabidopsis and Tobacco. Negative correlations were found between WSC and yield within our network. This could be the results of scoring the traits too late during the grain filling phase, after the WSC peak level (Pietragalla and Pask, 2012). As a consequence, higher yielding genotypes were the ones which were able to remobilize more carbohydrates into their grains at the date of the WSC scoring. In general, WSC measurement is done around seven days after anthesis. In our case, such measurement

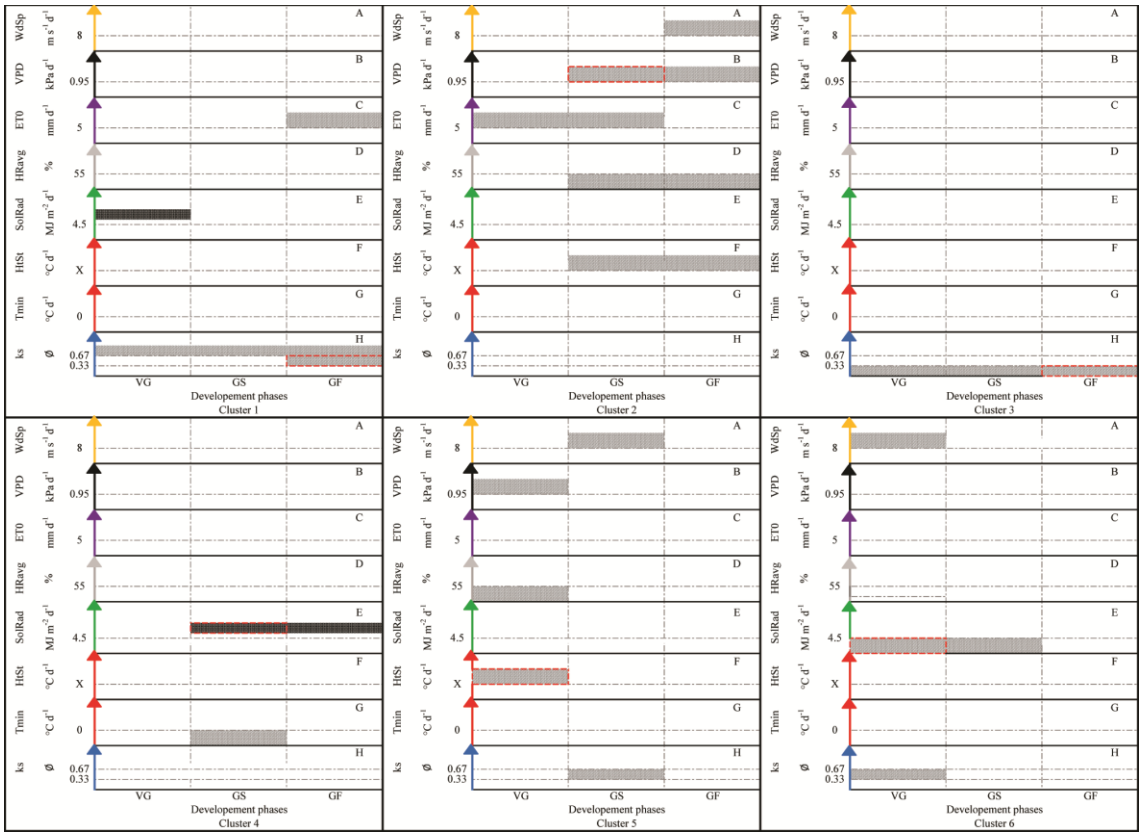
was done from anthesis+10 to anthesis+20. The measurement should been performed again in order to check the interest of WSC in that material and conditions.

CONCLUSION

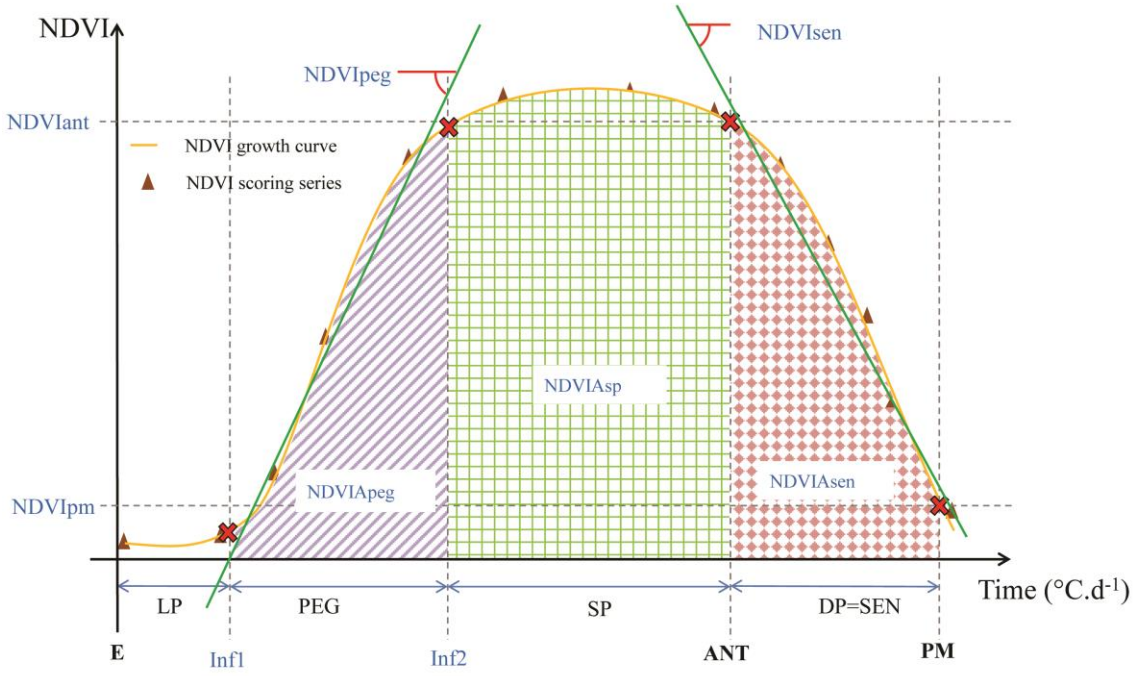
This study on a wide trial network testing the tolerance to both drought and heat stress on bread wheat led to the identification of common and differential genetic bases between traits involved in the tolerance to drought and heat stress experienced in Northern Mexico. It enabled to investigate stress adaptive strategies and demonstrated the value of NDVI at different periods of the crop cycle. Moreover, it allowed displaying the interdependence between stay-green feature and the access to water by roots under drought and heat stress conditions. As both NDVI and CT may be measurable through high-throughput technics it opens the possibility to breed for higher adaptation to heat and drought.

Aknowledgement: Bruno Bouffier would like to thank all the staff of the CIMMYT for their welcoming, their help, availability and advices, especially in the bread wheat physiology group, with firstly all the engineer and technical staff (Araceli, Eugenio, Mayra, Pimi, Syhara, Nayeli, Abisai, Edgar, Chema, Jazmin, Israel, Arturo, Raymundo, Manuel, Gilberto, Geras, Martha, Joaquin, Roman, Don Bicho…) and the post-docs and PhD students (Julian, Mariano, Gemma, Alistair, Maria, Perla, Arnaud, Carolina, Eliseo, Francisco, Suzuky, Alejandro, Oscar, Sean, Ruth…). Moreover, Bruno Bouffier wants to thank Norma Hernandez and Eloisa Carillo. The authors are also grateful to Aurélien Audes and Jordi Comadran for her help, availability and advices in the analyses. Authors also thank the Native Trait team of Limagrain Europe, especially Philippe Dufour for their important and very useful comments and advices on the analyses and discussion. This work was partly funded by the ANRT (Association Nationale de la Recherche et de la Technologie) through a CIFRE contract n° 2011/0550. Authors would also thanks the anonymous reviewers for their helpful comments on the manuscript.

SUPPLEMENTARY DATA



Supplementary Data 1: Diagram of the environmental covariates grouped into six different clusters. Per cluster, limiting factors are on the y-axis and development phases on x-axis. On x-axis are found the following developmental phases: vegetative (VG), grain set (GS) and grain filling (GF). On y-axis are found WdSpeed (A), the average wind speed, VPD (B), the average vapour pressure deficit, ET0 (C), the reference evapotranspiration, HRavg (D), the average relative air moisture, SolRad (E), the solar radiation received by crop, HtSt (F), the high temperature stress, Tmin (G), the minimum temperature, and ks (H), the drought stress coefficient. The darkest cells filled for the SolRad subplot correspond to the SumSolRad EP. For HtSt, threshold "X" represents "Tmax>33°C" + "30<Tmax≤33°C & ks<1". Red dotted outlined cell are the representative environmental covariates of each cluster.



Supplementary Data 2: Scheme of a theoretical NDVI curve. Such curve can be assimilated to microorganism growth curve in which usually five phases can be chronologically identified: (1) the lag phase (LP), (2) the phase of exponential growth (PEG), (3) the slowdown phase (SdP), (4) the stationary phase (SP) and (5) the decline phase (DP). The biological significance of all phases described for microorganism growth curve is not adapted for plant. The SP better corresponds to the maximum greenness due to a continued accumulation and the lack of sensitivity of the tool used which reach saturation. DP may be better named senescence phase (SEN) for plants. In our situation, to simplify computation, neither LP nor SdP were considered. SdP was split between PEG and SP. The PEG started at the inflexion point abscissa between LP and PEG (Inf1, not shown). This is the starting point of each curve) and ended at the inflexion point abscissa between PEG and SP (Inf2), where SP started. It ended then at anthesis (ANT) of the considered plot, where SEN begun. Finally, SEN ended when PM was reached. Several traits were estimated based on NDVI growth curve. Estimating a trait during a whole phase as previously defined required using both boundaries of the considered phase and all scorings between them. First of all, specific points were established. For a given plot, the abscissa of the boundaries of the PEG, called Inf1 and Inf2 were computed to determine its own PEG phase. As usually Inf1 did not vary within a trial. It was not considered. Then, a prediction of NDVI value at ANT and physiological maturity (PM) was calculated. During the PEG, the slope (NDVIpeg) and the area under the curve (NDVIApeg) were estimated. Similar traits were computed during SEN called respectively NDVIsen and NDVIAsen. Finally, the area under the curve during the SP was estimated (NDVIAsp)

Supplementary Data 3: Summary table of all the phenotypic traits scored within the trial network shared between the offspring and the parents. Offspring: the lowest value (Min), the highest value (Max), the mean (Mean), the standard error (sd); Parents: value of the female of the cross (Female; either PA, Pastor//hxl7573/2*Bagula, SO, Sokoll, or VB, Vorobey, in PW, SW, and VP population respectively), value of the male of the cross (Male; either WB, Weebill1 in PW and SW population, or PP, Parus/Pastor in VP population). The broad sense heritability (H^2) is also indicated. The significance between the both parents of a cross for a given trait within a given trial is also indicated. *, **, and *** Significant at the 0.05, 0.01, and 0.001 level of probability; ns: non-significant at the 0.05 level of probability. Dash symbol means data not available. Trait abbreviations are given with Figure 1.

Trait	Unit	Statistics	Trial															
			PW11IR	PW12IR	SW12IR	VP11DR	PW12DR	SW12DR	VP12DR	PW13DR	SW13DR	PW11HI	SW11HI	VP11HI	PW12HI	SW12HI	VP12HI
PH	cm	Min	84	95	92	50	69	67	62	65	61	75	70	81	60	59	73
		Mean	98	107	112	69	80	82	75	75	72	84	85	93	69	71	82
		Max	114	130	132	80	89	95	90	84	84	98	96	103	82	84	90
		sd	4	4	5	4	4	5	5	4	4	3	4	4	4	5	3
		H^2	0.76	0.75	0.91	0.65	0.8	0.77	0.61	0.73	0.42	0.72	0.75	0.79	0.76	0.81	0.78
		Female	98	106	108	67	75	84	76	74	70	86	88	90	72	74	80
		Male	95	104	100	72	78	78	74	76	70	84	79	89	70	68	82
		Signif.	WB<PA ns	WB<PA ns	WB<SO ***	VB<PP ***	PA<WB ns	WB<SO ns	PP<VB ns	PA<WB ns	WB<SO ns	WB<PA ns	WB<SO ns	PP<VB ns	WB<PA ns	WB<SO ns	VB<PP ns
PL	cm	Min	31	36	37	-	21	22	-	18	17	25	25	33	20	17	22
		Mean	37	40	43	-	26	29	-	22	23	30	33	37	23	24	29
		Max	44	50	49	-	30	36	-	25	27	36	37	42	29	30	34
		sd	2	2	2	-	2	2	-	1	2	2	2	2	1	2	2
		H^2	0.74	0.7	0.84	-	0.81	0.78	-	0.43	0.71	0.77	0.82	0.8	0.7	0.74	0.61
		Female	37	43	45	-	26	30	-	21	23	30	31	36	22	25	30
		Male	37	40	40	-	27	28	-	22	23	32	34	36	26	26	29
		Signif.	WB<PA ns	WB<PA ns	WB<SO ns	-	PA<WB ns	WB<SO ns	-	PA<WB ns	WB<SO ns	PA<WB ns	SO<WB *	PP<VB *	PA<WB *	SO<WB ns	PP<VB *
CTvg	°C	Min	-	20.5	21	-	24	25.2	-	21.4	20.6	22.5	21.9	21.3	21.5	21.9	19.7
		Mean	-	21.3	21.6	-	25	26	-	22.4	21.5	23.4	23.1	22.1	23.3	23.5	20.9
		Max	-	22	22.3	-	25.9	26.6	-	24	22.7	24.1	24.2	22.9	25.1	26	22.2
		sd	-	0.3	0.3	-	0.3	0.2	-	0.5	0.4	0.3	0.4	0.3	0.8	0.7	0.5
		H^2	-	0.63	0.57	-	0.52	0.1	-	0	0.29	0.66	0.56	0.25	0.66	0.55	0.38
		Female	-	21.2	21.4	-	25.1	25.9	-	22.1	21.2	23.2	22.9	22.2	23.1	22.6	20.3
		Male	-	20.9	21.1	-	25.8	26.1	-	22.7	21.7	22.9	22.6	22.3	22.2	23.1	21.4
		Signif.	-	WB<PA ns	WB<SO ns	-	PA<WB ns	SO<WB ns	-	PA<WB ns	SO<WB *	WB<PA *	WB<SO ns	VB<PP ns	WB<PA ns	SO<WB ns	VB<PP ns
CTgs	°C	Min	-	-	-	26.7	22.7	19.5	-	19.8	-	25.9	22.1	24.8	24.1	27.2	23.5
		Mean	-	-	-	27.8	23.9	20.7	-	20.9	-	27.3	23.1	25.8	25.8	28.4	24.9
		Max	-	-	-	28.9	25.5	22	-	21.9	-	28.2	24.5	27.2	27.8	29.9	26
		sd	-	-	-	0.4	0.4	0.4	-	0.4	-	0.4	0.4	0.4	0.7	0.4	0.5
		H^2	-	-	-	0.74	0.36	0.49	-	0.14	-	0.02	0.56	0.5	0.66	0.44	0.71
		Female	-	-	-	27.8	24.4	20.7	-	20.8	-	27.6	23	26	25.9	27.8	24.3
		Male	-	-	-	27.9	25.3	21.4	-	21.6	-	25.9	22.6	25.7	24.9	28.5	25
		Signif.	-	-	-	VB<PP ns	PA<WB ns	SO<WB ns	-	PA<WB **	-	WB<PA ns	WB<SO ns	PP<VB ns	WB<PA ns	SO<WB ns	VB<PP *

Supplementary Data 3 (continued)

Trait	Unit	Statistics	Trial														
			PW11IR	PW12IR	SW12IR	VP11DR	PW12DR	SW12DR	VP12DR	PW13DR	SW13DR	PW11HI	SW11HI	VP11HI	PW12HI	SW12HI	VP12HI
CTgf	°C	Min	23.6	22	22.9	-	26.4	26.9	30.2	24.8	23.4	28.8	26.5	28.6	29.1	28.2	28.2
		Mean	24.7	22.6	23.9	-	27.2	28	32	26	24.8	29.7	27.4	29.5	30.9	30.2	29.3
		Max	25.7	23.6	24.7	-	28.3	29.5	33.8	27	26.1	30.3	28.3	30.1	33.3	32.7	30.7
		sd	0.3	0.3	0.3	-	0.3	0.4	0.7	0.4	0.5	0.3	0.3	0.3	0.9	0.8	0.5
		H²	0.62	0.3	0.23	-	0.55	0.35	0.63	0.06	0.26	0.24	0.58	0.24	0.6	0.03	0.59
		Female	24.6	22.9	24.1	-	27.2	28.1	32.8	25.7	24.3	29.8	27.2	29.9	30.9	30.6	28.8
		Male	24.5	22.7	24.3	-	27.4	28.6	32.3	26.2	24.6	29.6	27.2	29.5	29.8	29.3	29.5
		Signif.	WB<PA ns	WB<PA ns	SO<WB ns	-	PA<WB ns	SO<WB *	PP<VB ns	PA<WB ns	SO<WB ns	WB<PA ns	WB<SO ns	PP<VB ns	WB<PA ns	WB<SO ns	VB<PP ns
CTcycle	°C	Min	-	21.5	22	-	24.7	24	-	22.2	22.2	26.1	23.7	25.2	25.1	26.3	24
		Mean	-	21.9	22.7	-	25.4	24.9	-	23.1	23.1	26.8	24.5	25.8	26.7	27.3	25
		Max	-	22.4	23.3	-	26.2	25.7	-	24	24.3	27.5	25.7	26.3	28.6	29.2	26.2
		sd	-	0.2	0.2	-	0.2	0.3	-	0.3	0.3	0.3	0.3	0.2	0.7	0.5	0.4
		H²	-	0.64	0.48	-	0.52	0.62	-	0	0.38	0.42	0.68	0.47	0.74	0.44	0.74
		Female	-	22	22.7	-	25.6	24.9	-	22.9	22.8	26.9	24.4	26	26.7	27	24.5
		Male	-	21.8	22.7	-	26.1	25.4	-	23.5	23.2	26.1	24.1	25.8	25.6	27	25.3
		Signif.	-	WB<PA ns	WB<SO ns	-	PA<WB ns	SO<WB ns	-	PA<WB ns	SO<WB ns	WB<PA ns	WB<SO ns	PP<VB ns	WB<PA ns	SO<WB ns	VB<PP *
NDVIpeg	°	Min	-	0.052	0.058	0.103	0.073	0.079	-	0.087	0.092	0.071	0.068	-	0.054	0.054	-
		Mean	-	0.058	0.075	0.124	0.099	0.096	-	0.097	0.099	0.105	0.096	-	0.078	0.075	-
		Max	-	0.066	0.092	0.144	0.112	0.111	-	0.103	0.108	0.117	0.109	-	0.097	0.099	-
		sd	-	0.002	0.006	0.008	0.007	0.005	-	0.002	0.003	0.006	0.006	-	0.009	0.009	-
		H²	-	0.47	0.56	0.58	0.8	0.63	-	0.36	0.36	0.77	0.81	-	0.82	0.75	-
		Female	-	0.057	0.08	0.134	0.093	0.111	-	0.096	0.099	0.105	0.1	-	0.074	0.073	-
		Male	-	0.056	0.072	0.126	0.095	0.101	-	0.1	0.105	0.105	0.102	-	0.091	0.077	-
		Signif.	-	WB<PA ns	WB<SO ns	PP<VB **	PA<WB ns	WB<SO ns	-	PA<WB ns	SO<WB ns	PA<WB ns	SO<WB ns	-	PA<WB ns	SO<WB ns	-
NDVIinf2	GDD	Min	-	877	660	616	506	500	-	609	613	553	587	602	553	584	479
		Mean	-	941	766	637	554	556	-	641	640	575	622	635	595	686	579
		Max	-	1036	854	665	661	634	-	682	668	617	675	672	682	801	664
		sd	-	15	40	9	28	22	-	13	11	7	13	12	23	39	28
		H²	-	0.56	0.56	-	0.73	0.66	-	0.52	0.58	0.74	0.8	0.57	0.56	0.63	0.57
		Female	-	949	724	631	537	518	-	636	631	573	617	649	610	711	612
		Male	-	934	797	645	580	532	-	614	635	576	604	628	582	693	527
		Signif.	-	WB<PA ns	SO<WB ns	VB<PP **	PA<WB **	SO<WB ns	-	WB<PA ns	SO<WB ns	PA<WB ns	WB<SO ns	PP<VB ns	WB<PA ns	WB<SO ns	PP<VB ns
NDVIApeg	GDD	Min	-	314	227	176	175	185	-	193	193	152	172	-	117	161	-
		Mean	-	380	272	194	210	219	-	207	207	172	211	-	162	201	-
		Max	-	462	311	219	260	247	-	223	220	188	250	-	198	232	-
		sd	-	19	16	8	14	11	-	6	6	7	10	-	13	13	-
		H²	-	0.75	0.48	0.33	0.59	0.59	-	0.47	0.56	0.85	0.78	-	0.67	0.55	-
		Female	-	370	261	190	189	205	-	206	205	171	220	-	159	220	-
		Male	-	377	288	196	227	208	-	201	207	176	199	-	169	209	-
		Signif.	-	PA<WB ns	SO<WB ns	VB<PP *	PA<WB ns	SO<WB ns	-	WB<PA ns	SO<WB ns	PA<WB ns	WB<SO *	-	PA<WB ns	WB<SO ns	-

Supplementary Data 3 (continued)

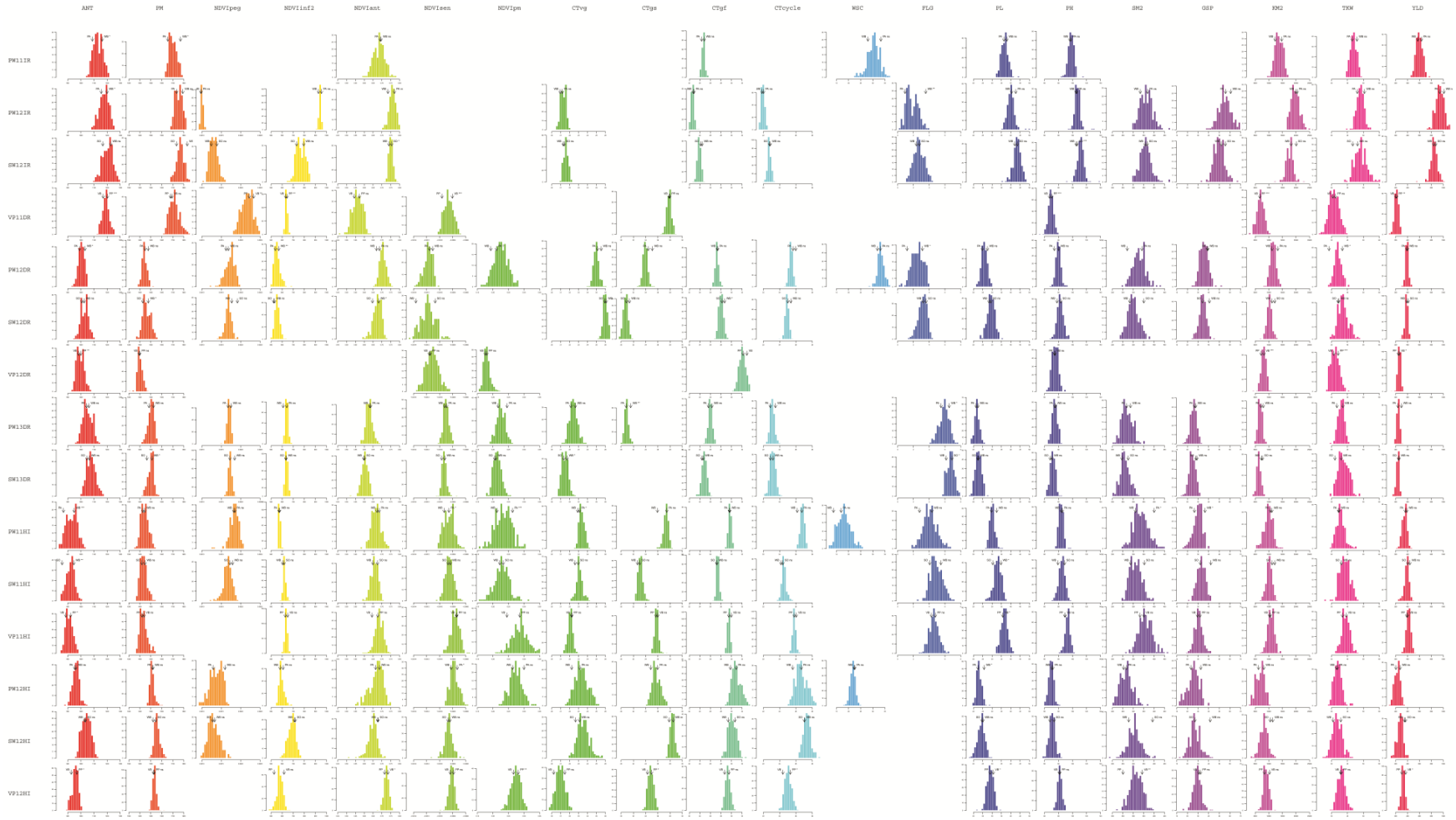
Trait	Unit	Statistics	Trial														
			PW11IR	PW12IR	SW12IR	VP11DR	PW12DR	SW12DR	VP12DR	PW13DR	SW13DR	PW11HI	SW11HI	VP11HI	PW12HI	SW12HI	VP12HI
NDVIAsp	GDD	Min	-	114	238	354	225	304	-	241	271	183	152	152	147	174	218
		Mean	-	188	355	401	355	369	-	303	323	259	213	201	251	250	284
		Max	-	244	469	466	422	423	-	364	377	345	278	252	331	351	358
		sd	-	25	43	21	27	24	-	26	23	31	23	20	28	30	26
		H²	-	0.83	0.64	0.78	0.82	0.78	-	0.89	0.84	0.91	0.81	0.65	0.75	0.43	0.54
		Female	-	164	366	393	342	388	-	301	311	217	181	165	228	238	238
		Male	-	208	348	404	357	388	-	339	320	278	242	212	275	251	328
		Signif.	-	PA<WB ns	WB<SO ns	VB<PP *	PA<WB ns	SO<WB ns	-	PA<WB ns	SO<WB ns	PA<WB *	SO<WB **	VB<PP ns	PA<WB ns	SO<WB ns	VB<PP ns
NDVIant	-	Min	0.586	0.709	0.701	0.436	0.649	0.579	-	0.558	0.458	0.574	0.568	0.591	0.554	0.482	0.666
		Mean	0.684	0.76	0.75	0.562	0.705	0.674	-	0.628	0.604	0.668	0.658	0.684	0.669	0.647	0.725
		Max	0.769	0.805	0.786	0.629	0.758	0.756	-	0.708	0.671	0.743	0.724	0.756	0.747	0.709	0.76
		sd	0.033	0.018	0.017	0.029	0.02	0.03	-	0.026	0.028	0.03	0.024	0.025	0.039	0.033	0.015
		H²	0.67	0.69	0.73	0.62	0.72	0.79	-	0.83	0.84	0.87	0.73	0.8	0.9	0.86	0.77
		Female	0.677	0.77	0.767	0.547	0.697	0.659	-	0.637	0.617	0.707	0.702	0.654	0.668	0.676	0.741
		Male	0.708	0.738	0.733	0.565	0.665	0.685	-	0.628	0.609	0.666	0.639	0.671	0.686	0.668	0.711
		Signif.	PA<WB ns	WB<PA ns	WB<SO *	VB<PP ns	WB<PA ns	SO<WB *	-	WB<PA ns	WB<SO ns	WB<PA ns	WB<SO ns	VB<PP ns	PA<WB ns	WB<SO ns	PP<VB *
NDVIpm	-	Min	-	-	-	-	-	-	0.154	0.173	0.173	0.155	0.165	0.199	0.221	-	0.213
		Mean	-	-	-	-	-	-	0.18	0.225	0.214	0.233	0.229	0.286	0.273	-	0.273
		Max	-	-	-	-	-	-	0.231	0.268	0.259	0.308	0.324	0.362	0.345	-	0.321
		sd	-	-	-	-	-	-	0.013	0.019	0.017	0.03	0.026	0.028	0.022	-	0.017
		H²	-	-	-	-	-	-	0.62	0.43	0.65	0.62	0.6	0.58	0.66	-	0.27
		Female	-	-	-	-	-	-	0.172	0.255	0.221	0.271	0.228	0.241	0.294	-	0.262
		Male	-	-	-	-	-	-	0.181	0.206	0.204	0.213	0.22	0.292	0.259	-	0.287
		Signif.	-	-	-	-	-	-	VB<PP ns	WB<PA ns	WB<SO ns	WB<PA ***	WB<SO ns	VB<PP ns	WB<PA ns	-	VB<PP **
NDVIsen	°	Min	-	-	-	-0.06	-0.081	-0.084	-0.078	-0.06	-0.058	-0.058	-0.062	-0.054	-0.053	-0.066	-0.054
		Mean	-	-	-	-0.049	-0.068	-0.067	-0.064	-0.052	-0.053	-0.049	-0.049	-0.044	-0.044	-0.049	-0.046
		Max	-	-	-	-0.038	-0.056	-0.048	-0.049	-0.045	-0.041	-0.036	-0.037	-0.032	-0.032	-0.034	-0.04
		sd	-	-	-	0.005	0.005	0.007	0.006	0.002	0.002	0.005	0.004	0.004	0.004	0.005	0.002
		H²	-	-	-	0.76	0.78	-	0.7	0.69	0.79	0.7	0.7	0.71	0.85	-	0.73
		Female	-	-	-	-0.045	-0.067	-0.059	-0.066	-0.052	-0.056	-0.047	-0.05	-0.041	-0.042	-0.052	-0.048
		Male	-	-	-	-0.057	-0.059	-0.078	-0.065	-0.052	-0.052	-0.054	-0.048	-0.043	-0.046	-0.052	-0.045
		Signif.	-	-	-	PP<VB ***	PA<WB ns	WB<SO ns	VB<PP ns	PA<WB ns	SO<WB ns	WB<PA *	SO<WB ns	PP<VB ns	WB<PA *	WB<SO ns	VB<PP ns
NDVIAsen	GDD	Min	-	-	-	-	-	-	-	161	116	190	191	221	200	-	266
		Mean	-	-	-	-	-	-	-	199	175	243	246	272	280	-	318
		Max	-	-	-	-	-	-	-	239	218	304	302	322	322	-	353
		sd	-	-	-	-	-	-	-	16	15	22	19	20	22	-	14
		H²	-	-	-	-	-	-	-	0.8	0.79	0.84	0.7	0.7	0.82	-	0.72
		Female	-	-	-	-	-	-	-	203	173	298	286	264	302	-	328
		Male	-	-	-	-	-	-	-	201	185	231	243	250	285	-	299
		Signif.	-	-	-	-	-	-	-	WB<PA ns	SO<WB ns	WB<PA **	WB<SO ns	PP<VB ns	WB<PA ns	-	PP<VB ns

Supplementary Data 3 (continued)

Trait	Unit	Statistics	Trial														
			PW11IR	PW12IR	SW12IR	VP11DR	PW12DR	SW12DR	VP12DR	PW13DR	SW13DR	PW11HI	SW11HI	VP11HI	PW12HI	SW12HI	VP12HI
ANT	GDD	Min	1048	1087	1103	1126	940	944	939	966	999	831	851	850	882	963	891
		Mean	1129	1177	1203	1188	1003	1028	995	1050	1078	931	920	911	962	1041	957
		Max	1210	1253	1299	1250	1047	1100	1067	1138	1175	1035	1005	982	1048	1124	1006
		sd	36	36	38	26	22	29	28	35	34	41	31	27	25	33	23
		H²	0.93	0.93	0.9	0.78	0.95	0.94	0.88	0.96	0.94	0.91	0.78	0.72	0.86	0.85	0.87
		Female	1088	1155	1167	1170	989	1007	982	1043	1046	868	857	885	953	1035	927
		Male	1162	1200	1227	1202	1031	1025	1000	1061	1065	948	946	922	962	1029	969
		Signif.	PA<WB *	PA<WB *	SO<WB ns	VB<PP ***	PA<WB *	SO<WB ns	VB<PP **	PA<WB ns	SO<WB ns	PA<WB ***	SO<WB **	VB<PP *	PA<WB ns	WB<SO ns	VB<PP *
PM	GDD	Min	1628	1685	1681	1625	1388	1373	1299	1424	1425	1363	1375	1370	1468	1496	1484
		Mean	1702	1755	1768	1714	1442	1462	1402	1502	1501	1444	1432	1433	1512	1558	1533
		Max	1790	1823	1854	1858	1528	1558	1468	1557	1574	1533	1531	1543	1598	1631	1627
		sd	34	32	34	44	21	36	22	27	26	34	31	34	20	25	17
		H²	0.84	0.85	0.86	0.82	0.77	0.87	0.82	0.88	0.91	0.87	0.89	0.86	0.8	0.77	0.77
		Female	1655	1735	1734	1692	1447	1427	1395	1483	1464	1427	1419	1439	1517	1545	1524
		Male	1771	1792	1832	1678	1476	1477	1399	1525	1510	1444	1447	1420	1519	1522	1530
		Signif.	PA<WB *	PA<WB ns	SO<WB ns	PP<VB ns	PA<WB ns	SO<WB *	VB<PP ns	PA<WB ns	SO<WB *	PA<WB ns	SO<WB ns	PP<VB ns	PA<WB ns	WB<SO ns	VB<PP ns
GFp	-	Min	0.28	0.28	0.3	0.23	0.27	0.24	0.25	0.24	0.2	0.3	0.3	0.31	0.27	0.25	0.3
		Mean	0.31	0.31	0.33	0.28	0.29	0.28	0.28	0.28	0.26	0.34	0.34	0.35	0.31	0.28	0.32
		Max	0.36	0.34	0.38	0.33	0.34	0.32	0.31	0.34	0.31	0.39	0.39	0.39	0.35	0.32	0.36
		sd	0.02	0.01	0.02	0.02	0.01	0.01	0.01	0.02	0.02	0.02	0.02	0.01	0.01	0.01	0.01
		H²	0.87	0.83	0.87	0.8	0.85	0.65	0.72	0.91	0.87	0.84	0.7	0.54	0.79	0.76	0.76
		Female	0.33	0.31	0.34	0.29	0.31	0.28	0.29	0.28	0.27	0.37	0.38	0.37	0.32	0.28	0.34
		Male	0.31	0.31	0.34	0.26	0.29	0.29	0.28	0.28	0.27	0.33	0.33	0.33	0.31	0.28	0.31
		Signif.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
WSC	%	Min	21.8	-	-	-	28.6	-	-	-	-	12.2	-	-	17.5	-	-
		Mean	30.3	-	-	-	33.3	-	-	-	-	18.1	-	-	21.7	-	-
		Max	37.2	-	-	-	37.7	-	-	-	-	25.5	-	-	24.6	-	-
		sd	2.8	-	-	-	1.4	-	-	-	-	2.8	-	-	1.2	-	-
		H²	0.79	-	-	-	0.3	-	-	-	-	0.79	-	-	0.16	-	-
		Female	33.8	-	-	-	32.7	-	-	-	-	18.1	-	-	22.4	-	-
		Male	25.3	-	-	-	32.4	-	-	-	-	13.4	-	-	22.4	-	-
		Signif.	WB<PA ns	-	-	-	WB<PA ns	-	-	-	-	WB<PA ns	-	-	WB<PA ns	-	-
SM2	spikes.m-2	Min	-	288	294	-	243	235	-	202	202	244	240	264	205	170	218
		Mean	-	362	358	-	328	300	-	269	260	336	311	358	266	305	314
		Max	-	472	480	-	430	384	-	365	326	449	399	471	371	418	393
		sd	-	31	28	-	30	28	-	27	23	36	28	33	29	33	29
		H²	-	0.38	0.06	-	0.34	0.46	-	0.45	0.46	0.62	0.3	0.17	0.58	0.29	0.19
		Female	-	363	369	-	343	354	-	265	277	399	357	346	267	392	348
		Male	-	344	359	-	267	283	-	291	243	311	284	334	253	275	249
		Signif.	-	WB<PA ns	WB<SO ns	-	WB<PA ns	WB<SO ns	-	PA<WB ns	WB<SO ns	WB<PA *	WB<SO ns	PP<VB ns	WB<PA ns	WB<SO ns	PP<VB **

Supplementary Data 3 (continued)

Trait	Unit	Statistics	Trial														
			PW11IR	PW12IR	SW12IR	VP11DR	PW12DR	SW12DR	VP12DR	PW13DR	SW13DR	PW11HI	SW11HI	VP11HI	PW12HI	SW12HI	VP12HI
GSP	grains.spike-1	Min	-	36	36	-	27	24	-	17	13	16	21	21	12	14	16
		Mean	-	55	50	-	36	34	-	26	25	30	33	31	26	27	29
		Max	-	72	68	-	52	44	-	34	32	40	42	41	41	44	43
		sd	-	6	5	-	4	3	-	3	3	4	4	4	6	5	4
		H²	-	0.44	0.4	-	0.52	0.45	-	0.46	0.62	0.7	0.57	0.49	0.84	0.58	0.46
		Female	-	55	53	-	39	35	-	27	28	26	32	29	23	27	30
		Male	-	63	57	-	38	41	-	28	30	37	42	32	32	41	33
		Signif.	-	PA<WB ns	SO<WB ns	-	WB<PA ns	SO<WB ns	-	PA<WB ns	SO<WB ns	PA<WB *	SO<WB ns	VB<PP ns	PA<WB ns	SO<WB ns	VB<PP ns
KM2	grains.m-2	Min	10182	15816	13635	1884	8709	6575	4139	5144	3951	5945	6811	7480	2574	3157	6285
		Mean	13707	19723	17661	6909	11569	10220	8116	6825	6344	9888	10142	10790	6796	8184	9054
		Max	18757	24828	23792	11374	14229	13214	10884	8883	8349	14752	12690	14453	10576	12062	12322
		sd	1698	1992	1518	1559	1078	976	1041	768	820	1572	1082	1242	1730	1523	990
		H²	0.76	0.78	0.76	0.75	0.78	0.78	0.79	0.65	0.77	0.82	0.65	0.79	0.94	0.75	0.73
		Female	13415	19856	19400	6153	13498	12382	8467	7043	7653	10397	11458	10066	6049	10476	10051
		Male	14375	21565	20017	7487	10857	11221	7110	8042	7542	11230	11989	10596	7944	11273	8532
		Signif.	PA<WB ns	PA<WB ns	SO<WB ns	VB<PP ***	WB<PA ns	WB<SO ns	PP<VB ***	PA<WB ns	WB<SO ns	PA<WB ns	SO<WB ns	VB<PP ns	PA<WB ns	SO<WB ns	PP<VB ns
TKW	g	Min	37.3	40.2	37.3	19.4	28.7	28.2	26.8	28.8	29.5	29.1	26.2	32.6	27.8	22.6	30.1
		Mean	43.8	48	48.4	31.6	34	37.3	32.2	36	37.5	35.7	38.4	39	33.9	33.6	36.2
		Max	48.9	55.6	60.8	45.1	40.3	46.7	40.9	41.2	47.4	44.8	46.5	46	42.1	43.6	42.6
		sd	2.4	3	4.3	4.5	2.3	3.4	2.6	2.1	3.4	2.8	3.3	2.6	2.7	3.5	2.6
		H²	0.77	0.85	0.96	0.83	0.86	0.88	0.89	0.88	0.94	0.85	0.89	0.89	0.92	0.93	0.91
		Female	44.8	47.3	45.5	33.1	28.7	34.5	31.3	34	32.9	35.3	35.6	39.8	34.5	35.4	36.8
		Male	43.6	48.3	44.2	31.6	36.7	34.7	34.1	36.4	35.5	34.5	36.7	36.7	33.4	29.4	35.6
		Signif.	WB<PA ns	PA<WB ns	WB<SO ns	PP<VB ns	PA<WB *	SO<WB ns	VB<PP ***	PA<WB ns	SO<WB ns	WB<PA ns	SO<WB ns	PP<VB ns	WB<PA ns	WB<SO ns	PP<VB ns
YLD	g.m-2	Min	472	751	638	82	308	240	132	188	141	238	238	317	108	92	238
		Mean	596	942	849	214	392	380	260	245	236	349	387	417	227	275	326
		Max	751	1177	1007	310	467	455	335	311	291	463	490	530	335	400	416
		sd	58	74	65	36	28	33	28	25	26	42	41	36	52	56	30
		H²	0.69	0.71	0.73	0.71	0.66	0.78	0.72	0.64	0.63	0.75	0.71	0.7	0.93	0.76	0.7
		Female	603	937	878	202	399	423	265	238	250	363	406	400	204	361	370
		Male	627	1043	891	237	386	388	242	294	266	388	438	386	268	331	304
		Signif.	PA<WB ns	PA<WB ns	SO<WB ns	VB<PP **	WB<PA ns	WB<SO ns	PP<VB *	PA<WB ns	SO<WB ns	PA<WB ns	SO<WB ns	PP<VB ns	PA<WB ns	WB<SO ns	PP<VB *



Supplementary Data 4: Frequency distributions of non-normalized adjusted traits values organized by trial (rows) and by traits (columns). Each vertical axis indicates the number of lines per trait value class; each horizontal axis, the different trait value classes. Within a column, the abscissa is the same. Parents of each population are indicated: PW (PA: Pastor//hxl7573/2*Bagula; WB: Weebill1), SW (SO: Sokoll; WB: Weebill1), and VP (VB: Vorobey; PP: Parus/Pastor). Trait abbreviations are given with Figure 1.

Supplementary Data 5: Pearson correlation (r) table for all traits scored within the trial network. Dash symbol means data not available. *, **, and *** Significant at the 0.05, 0.01, and 0.001 level of probability; ns: non-significant at the 0.05 level of probability; Trait abbreviations are given with Figure 1.

Trial	Trait	PH	PL	CTvg	CTgs	CTgf	CTcycle	NDVIinf2	NDVIant	NDVIAsen	NDVIsen	NDVIpm	NDVIAsp	NDVIApeg	NDVIpeg	ANT	GFp	PM	WSC	GSP	KM2	SM2	TKW
PW11HI	PL	0.56***																					
	CTvg	-0.27***	-0.09ns																				
	CTgs	-0.22**	-0.03ns	0.35***																			
	CTgf	-0.16*	0.02ns	0.46***	0.37***																		
	CTcycle	-0.28***	-0.04ns	0.76***	0.8***	0.75***																	
	NDVIinf2	-0.02ns	-0.1ns	0.13ns	-0.01ns	-0.1ns	0.01ns																
	NDVIant	0.57***	0.45***	-0.23**	-0.11ns	-0.13ns	-0.2**	0.15*															
	NDVIAsen	0.46***	0.5***	-0.08ns	-0.03ns	0.06ns	-0.03ns	-0.01ns	0.76***														
	NDVIsen	-0.21**	-0.02ns	0.19**	0.13ns	0.16*	0.21**	-0.12ns	-0.42***	0.08ns													
	NDVIpm	0.42***	0.49***	-0.02ns	-0.04ns	0.02ns	-0.02ns	-0.03ns	0.4***	0.54***	0.47***												
	NDVIAsp	-0.08ns	-0.4***	-0.33***	-0.29***	-0.42***	-0.44***	-0.1ns	-0.23**	-0.52***	-0.23**	-0.3***											
	NDVIApeg	0.25***	-0.05ns	-0.4***	-0.18*	-0.36***	-0.39***	0.08ns	0.64***	0.23**	-0.43***	0.09ns	0.37***										
	NDVIpeg	0.22**	0.15*	-0.23**	-0.01ns	-0.12ns	-0.15*	-0.37***	0.14*	0.11ns	-0.1ns	0.02ns	0.34***	0.2**									
	ANT	-0.26***	-0.56***	-0.17*	-0.23**	-0.34***	-0.32***	0.09ns	-0.47***	-0.69***	-0.13ns	-0.4***	0.89***	0.15*	0.03ns								
	GFp	0.11ns	0.34***	0.18*	0.2**	0.31***	0.29***	0.01ns	0.42***	0.74***	0.2**	0.21**	-0.83***	-0.13ns	-0.09ns	-0.88***							
	PM	-0.35***	-0.64***	-0.1ns	-0.17*	-0.26***	-0.23**	0.18*	-0.37***	-0.38***	0ns	-0.5***	0.66***	0.12ns	-0.07ns	0.8***	-0.41***						
	WSC	-0.12ns	-0.03ns	0.44***	0.25***	0.28***	0.41***	0.02ns	0.01ns	0.07ns	0.16*	0.12ns	-0.3***	-0.13ns	-0.1ns	-0.27***	0.24***	-0.22**					
	GSP	-0.01ns	-0.03ns	-0.36***	-0.11ns	-0.19**	-0.27***	-0.11ns	0.05ns	-0.03ns	-0.14*	-0.16*	0.09ns	0.13ns	0.18*	-0.02ns	-0.03ns	-0.08ns	-0.37***				
	KM2	0.16*	0.1ns	-0.59***	-0.18*	-0.33***	-0.46***	-0.14*	0.26***	0.14ns	-0.24***	-0.06ns	0.17*	0.33***	0.29***	-0.02ns	-0.04ns	-0.09ns	-0.53***	0.75***			
	SM2	0.29***	0.21**	-0.4***	-0.12ns	-0.23**	-0.31***	-0.08ns	0.34***	0.28***	-0.16*	0.16*	0.13ns	0.31***	0.2**	0ns	-0.01ns	-0.02ns	-0.3***	-0.24***	0.45***		
	TKW	0.2**	0.24**	0.27***	0.05ns	0.1ns	0.17*	-0.05ns	0.08ns	0.16*	0.13ns	0.27***	-0.26***	-0.14*	-0.1ns	-0.25***	0.19**	-0.24***	0.55***	-0.49***	-0.7***	-0.35***	
	YLD	0.34***	0.26***	-0.59***	-0.19**	-0.37***	-0.48***	-0.21**	0.38***	0.29***	-0.24***	0.06ns	0.04ns	0.33***	0.31***	-0.19**	0.08ns	-0.27***	-0.35***	0.71***	0.88***	0.35***	-0.3***
PW11IR	PL	0.47***																					
	CTvg	-	-																				
	CTgs	-	-	-																			
	CTgf	-0.39***	-0.05ns	-	-																		
	CTcycle	-	-	-	-	-																	
	NDVIinf2	-	-	-	-	-	-																
	NDVIant	0.23**	-0.09ns	-	-	-0.24***	-	-															
	NDVIAsen	-	-	-	-	-	-	-	-														
	NDVIsen	-	-	-	-	-	-	-	-	-													
	NDVIpm	-	-	-	-	-	-	-	-	-	-												
	NDVIAsp	-	-	-	-	-	-	-	-	-	-	-											
	NDVIApeg	-	-	-	-	-	-	-	-	-	-	-	-										
	NDVIpeg	-	-	-	-	-	-	-	-	-	-	-	-	-									
	ANT	0.01ns	-0.44***	-	-	-0.57***	-	-	0.28***	-	-	-	-	-	-								
	GFp	-0.06ns	0.42***	-	-	0.46***	-	-	-0.23**	-	-	-	-	-	-	-0.93***							
	PM	-0.05ns	-0.37***	-	-	-0.6***	-	-	0.27***	-	-	-	-	-	-	0.84***	-0.58***						
	WSC	0ns	-0.22**	-	-	0.06ns	-	-	-0.13ns	-	-	-	-	-	-	0.11ns	-0.28***	-0.15*					
	GSP	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-				
	KM2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
	SM2	0.07ns	-0.27***	-	-	-0.49***	-	-	0.45***	-	-	-	-	-	-	0.46***	-0.3***	0.57***	-0.31***	-	-		
	TKW	0.11ns	0.42***	-	-	0.37***	-	-	-0.32***	-	-	-	-	-	-	-0.53***	0.41***	-0.57***	0.12ns	-	-0.66***	-	
	YLD	0.17*	-0.11ns	-	-	-0.41***	-	-	0.39***	-	-	-	-	-	-	0.27***	-0.14*	0.4***	-0.32***	-	0.9***	-	-0.27***

Supplementary Data 5 (continued)

Trial	Trait	PH	PL	CTvg	CTgs	CTgf	CTcycle	NDVIinf2	NDVIant	NDVIAsen	NDVIsen	NDVIpm	NDVIAsp	NDVIApeg	NDVIpeg	ANT	GFp	PM	WSC	GSP	KM2	SM2	TKW
PW12DR	PL	0.63***																					
	CTvg	-0.25***	-0.2**																				
	CTgs	-0.25***	-0.18*	0.37***																			
	CTgf	-0.59***	-0.55***	0.19**	0.13ns																		
	CTcycle	-0.51***	-0.44***	0.73***	0.75***	0.61***																	
	NDVIinf2	-0.19**	-0.07ns	0.14ns	0.05ns	0.14*	0.15*																
	NDVIant	0.53***	0.51***	-0.31***	-0.22**	-0.47***	-0.47***	-0.28***															
	NDVIAsen	-	-	-	-	-	-	-	-														
	NDVIsen	-0.31***	-0.24***	0.43***	0.24***	0.2**	0.41***	0.3***	-0.58***	-													
	NDVIpm	-	-	-	-	-	-	-	-	-	-												
	NDVIAsp	-0.03ns	-0.17*	0.15*	0.18*	0.01ns	0.16*	-0.72***	0.13ns	-	0.1ns	-											
	NDVIApeg	-0.15*	-0.07ns	0.14*	0.08ns	0.13ns	0.16*	0.96***	-0.22**	-	0.33***	-	-0.59***										
	NDVIpeg	0.24***	0.12ns	-0.16*	0.01ns	-0.17*	-0.14*	-0.93***	0.35***	-	-0.29***	-	0.76***	-0.85***									
	ANT	-0.39***	-0.43***	0.43***	0.33***	0.29***	0.5***	0.25***	-0.36***	-	0.6***	-	0.47***	0.34***	-0.16*								
	GFp	0.36***	0.47***	-0.3***	-0.27***	-0.33***	-0.43***	-0.18*	0.44***	-	-0.45***	-	-0.42***	-0.25***	0.13ns	-0.87***							
	PM	-0.31***	-0.25***	0.44***	0.3***	0.14ns	0.42***	0.25***	-0.16*	-	0.59***	-	0.37***	0.33***	-0.14ns	0.83***	-0.45***						
	WSC	-0.16*	-0.31***	0.26***	0.06ns	0.19**	0.23***	-0.03ns	-0.17*	-	0.17*	-	0.22**	-0.02ns	-0.01ns	0.32***	-0.31***	0.23**					
	GSP	0.2**	0.22**	-0.09ns	-0.17*	-0.18*	-0.21**	-0.13ns	0.11ns	-	-0.19**	-	0.02ns	-0.17*	0.16*	-0.16*	0.15*	-0.13ns	-0.09ns				
	KM2	0.26***	0.21**	-0.27***	-0.14ns	-0.25***	-0.31***	-0.39***	0.41***	-	-0.4***	-	0.21**	-0.4***	0.42***	-0.27***	0.24***	-0.22**	-0.13ns	0.65***			
	SM2	0.02ns	-0.06ns	-0.21**	0.06ns	-0.04ns	-0.08ns	-0.21**	0.31***	-	-0.19**	-	0.15*	-0.17*	0.21**	-0.1ns	0.09ns	-0.08ns	-0.03ns	-0.6***	0.2**		
	TKW	0.15*	0.21**	-0.04ns	-0.13ns	-0.12ns	-0.14*	0.21**	-0.05ns	-	0.18*	-	-0.25***	0.26***	-0.21**	-0.1ns	0.12ns	-0.04ns	0.03ns	-0.38***	-0.65***	-0.21**	
	YLD	0.48***	0.48***	-0.4***	-0.31***	-0.45***	-0.55***	-0.32***	0.52***	-	-0.39***	-	0.03ns	-0.28***	0.34***	-0.46***	0.45***	-0.33***	-0.15*	0.49***	0.71***	0.1ns	0.05ns
PW12HI	PL	0.56***																					
	CTvg	-0.42***	-0.25***																				
	CTgs	-0.44***	-0.28***	0.79***																			
	CTgf	-0.51***	-0.31***	0.69***	0.8***																		
	CTcycle	-0.5***	-0.31***	0.9***	0.94***	0.92***																	
	NDVIinf2	-0.16*	-0.07ns	0.19**	0.22**	0.21**	0.23**																
	NDVIant	0.55***	0.41***	-0.67***	-0.77***	-0.79***	-0.81***	-0.02ns															
	NDVIAsen	0.5***	0.35***	-0.59***	-0.68***	-0.64***	-0.69***	-0.02ns	0.87***														
	NDVIsen	-0.22**	-0.18*	0.5***	0.57***	0.57***	0.6***	-0.01ns	-0.76***	-0.46***													
	NDVIpm	0.64***	0.47***	-0.39***	-0.44***	-0.47***	-0.47***	-0.15*	0.47***	0.44***	-0.01ns												
	NDVIAsp	0.51***	0.26***	-0.33***	-0.38***	-0.54***	-0.46***	-0.61***	0.37***	0.17*	-0.18*	0.45***											
	NDVIApeg	0.35***	0.29***	-0.38***	-0.46***	-0.52***	-0.5***	0.56***	0.73***	0.57***	-0.54***	0.3***	0.08ns										
	NDVIpeg	0.57***	0.4***	-0.62***	-0.71***	-0.76***	-0.76***	-0.52***	0.75***	0.6***	-0.5***	0.5***	0.76***	0.38***									
	ANT	0.16*	-0.03ns	0.22**	0.25***	0.04ns	0.18*	-0.05ns	-0.28***	-0.43***	0.31***	0.13ns	0.59***	-0.07ns	0ns								
	GFp	-0.19**	-0.06ns	-0.15*	-0.18*	0ns	-0.11ns	0.1ns	0.24***	0.51***	-0.17*	-0.32***	-0.56***	0.07ns	-0.04ns	-0.89***							
	PM	0.01ns	-0.15*	0.21**	0.21**	0.08ns	0.18*	0.06ns	-0.16*	0.02ns	0.37***	-0.27***	0.27***	-0.01ns	-0.06ns	0.54***	-0.09ns						
	WSC	0.12ns	-0.06ns	0ns	0.04ns	0.02ns	0.02ns	-0.07ns	-0.14ns	-0.11ns	0.29***	0.17*	0.3***	-0.04ns	0.05ns	0.45***	-0.35***	0.34***					
	GSP	0.16*	0.19**	-0.41***	-0.41***	-0.45***	-0.46***	0.02ns	0.48***	0.26***	-0.67***	0.07ns	0.11ns	0.37***	0.35***	-0.21**	0.03ns	-0.41***	-0.3***				
	KM2	0.34***	0.31***	-0.57***	-0.58***	-0.6***	-0.64***	-0.05ns	0.64***	0.41***	-0.75***	0.21**	0.23**	0.45***	0.52***	-0.21**	0.03ns	-0.41***	-0.28***	0.9***			
	SM2	0.48***	0.33***	-0.5***	-0.52***	-0.5***	-0.55***	-0.16*	0.51***	0.44***	-0.34***	0.36***	0.33***	0.3***	0.49***	-0.06ns	0.02ns	-0.08ns	-0.04ns	0.02ns	0.44***		
	TKW	-0.13ns	-0.21**	0.04ns	-0.02ns	0.07ns	0.03ns	-0.02ns	0ns	0.19**	0.22**	-0.03ns	-0.15*	-0.01ns	0.01ns	-0.26***	0.39***	0.12ns	0.19**	-0.51***	-0.54***	-0.2**	
	YLD	0.31***	0.26***	-0.62***	-0.65***	-0.64***	-0.69***	-0.06ns	0.7***	0.51***	-0.78***	0.19**	0.18*	0.49***	0.57***	-0.35***	0.18*	-0.43***	-0.28***	0.87***	0.95***	0.4***	-0.27***

Supplementary Data 5 (continued)

Trial	Trait	PH	PL	CTvg	CTgs	CTgf	CTcycle	NDVIinf2	NDVIant	NDVIAsen	NDVIsen	NDVIpm	NDVIAsp	NDVIApeg	NDVIpeg	ANT	GFp	PM	WSC	GSP	KM2	SM2	TKW
PW12IR	PL	0.51***																					
	CTvg	-0.12ns	0.07ns																				
	CTgs	-	-	-																			
	CTgf	0.07ns	-0.11ns	0.1ns	-																		
	CTcycle	-0.04ns	-0.02ns	0.78***	-	0.71***																	
	NDVIinf2	0.12ns	-0.14*	0.01ns	-	0.08ns	0.06ns																
	NDVIant	0.32***	0.13ns	-0.38***	-	-0.1ns	-0.33***	0.38***															
	NDVIAsen	-	-	-	-	-	-	-	-														
	NDVIsen	-	-	-	-	-	-	-	-	-													
	NDVIpm	-	-	-	-	-	-	-	-	-	-												
	NDVIAsp	0.09ns	-0.24***	-0.01ns	-	0.21**	0.12ns	0.11ns	0.06ns	-	-	-											
	NDVIApeg	0.27***	-0.01ns	-0.28***	-	0.11ns	-0.12ns	0.41***	0.64***	-	-	-	0.43***										
	NDVIpeg	0.01ns	0.11ns	-0.03ns	-	-0.21**	-0.16*	-0.49***	0.03ns	-	-	-	-0.09ns	-0.42***									
	ANT	0.09ns	-0.29***	0.05ns	-	0.22**	0.18*	0.49***	0.09ns	-	-	-	0.91***	0.46***	-0.3***								
	GFp	-0.15*	0.22**	-0.12ns	-	-0.27***	-0.25***	-0.36***	-0.01ns	-	-	-	-0.84***	-0.42***	0.32***	-0.88***							
	PM	-0.03ns	-0.27***	-0.06ns	-	0.09ns	0.02ns	0.48***	0.16*	-	-	-	0.71***	0.35***	-0.17*	0.82***	-0.45***						
	WSC	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
	GSP	-0.15*	-0.17*	-0.19**	-	-0.09ns	-0.19**	0.11ns	0.13ns	-	-	-	0.05ns	0ns	0.04ns	0.08ns	0.09ns	0.26***	-				
	KM2	-0.08ns	-0.23**	-0.37***	-	-0.16*	-0.36***	0.31***	0.31***	-	-	-	0.2**	0.2**	0.03ns	0.27***	0.02ns	0.54***	-	0.7***			
	SM2	0.14ns	0ns	-0.18*	-	-0.06ns	-0.16*	0.21**	0.19**	-	-	-	0.18*	0.22**	-0.02ns	0.22**	-0.11ns	0.29***	-	-0.53***	0.23**		
	TKW	0.03ns	0.26***	0.17*	-	-0.16*	0.02ns	-0.44***	-0.28***	-	-	-	-0.36***	-0.3***	0.16*	-0.48***	0.22**	-0.64***	-	-0.34***	-0.62***	-0.29***	
	YLD	-0.05ns	-0.07ns	-0.34***	-	-0.31***	-0.44***	0.05ns	0.18*	-	-	-	-0.03ns	0.02ns	0.17*	-0.03ns	0.21**	0.2**	-	0.62***	0.78***	0.07ns	-0.01ns
PW13DR	PL	0.66***																					
	CTvg	-0.24***	-0.15*																				
	CTgs	-0.32***	-0.25***	0.54***																			
	CTgf	-0.21**	-0.17*	0.03ns	0.16*																		
	CTcycle	-0.36***	-0.26***	0.8***	0.79***	0.52***																	
	NDVIinf2	0.18*	0.07ns	0.01ns	0ns	-0.16*	-0.07ns																
	NDVIant	0.46***	0.43***	-0.41***	-0.48***	-0.03ns	-0.45***	-0.07ns															
	NDVIAsen	0.52***	0.51***	-0.35***	-0.45***	-0.11ns	-0.43***	0.1ns	0.89***														
	NDVIsen	0.07ns	0.12ns	0.17*	0.13ns	-0.08ns	0.11ns	0.27***	-0.39***	0ns													
	NDVIpm	0.45***	0.41***	-0.32***	-0.43***	0.03ns	-0.35***	-0.11ns	0.73***	0.7***	0.01ns												
	NDVIAsp	-0.32***	-0.38***	0.37***	0.4***	-0.14ns	0.32***	-0.36***	-0.55***	-0.61***	-0.09ns	-0.47***											
	NDVIApeg	0.08ns	-0.08ns	0.12ns	0.16*	-0.22**	0.03ns	0.72***	-0.17*	-0.08ns	0.19**	-0.25***	0.15*										
	NDVIpeg	-0.07ns	0.01ns	0.07ns	0.06ns	-0.03ns	0.05ns	-0.32***	0.04ns	0.06ns	0.05ns	0.07ns	0.23**	-0.15*									
	ANT	-0.33***	-0.42***	0.43***	0.46***	-0.19**	0.35***	0.06ns	-0.73***	-0.7***	0.09ns	-0.61***	0.89***	0.41***	0.06ns								
	GFp	0.34***	0.44***	-0.42***	-0.44***	0.14ns	-0.36***	0.02ns	0.73***	0.75***	-0.06ns	0.53***	-0.9***	-0.33***	-0.06ns	-0.97***							
	PM	-0.23**	-0.31***	0.4***	0.42***	-0.28***	0.28***	0.21**	-0.6***	-0.43***	0.22**	-0.69***	0.74***	0.51***	0.08ns	0.88***	-0.77***						
	WSC	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
	GSP	0.27***	0.25***	-0.24***	-0.16*	-0.02ns	-0.21**	-0.1ns	0.4***	0.32***	-0.19**	0.2**	-0.28***	-0.16*	0.02ns	-0.39***	0.4***	-0.32***	-				
	KM2	0.04ns	0.05ns	-0.2**	-0.12ns	-0.17*	-0.24***	-0.16*	0.28***	0.2**	-0.2**	0.05ns	-0.04ns	-0.02ns	0.15*	-0.18*	0.21**	-0.1ns	-	0.66***			
	SM2	-0.28***	-0.23**	0.06ns	0.07ns	-0.18*	-0.02ns	-0.01ns	-0.17*	-0.17*	0.03ns	-0.18*	0.3***	0.22**	0.12ns	0.29***	-0.27***	0.28***	-	-0.51***	0.29***		
	TKW	0.34***	0.31***	-0.27***	-0.33***	0.11ns	-0.24***	-0.07ns	0.29***	0.28***	-0.01ns	0.39***	-0.35***	-0.2**	-0.16*	-0.4***	0.34***	-0.44***	-	-0.14*	-0.42***	-0.3***	
	YLD	0.24***	0.25***	-0.39***	-0.33***	-0.12ns	-0.41***	-0.2**	0.48***	0.38***	-0.23**	0.28***	-0.25***	-0.13ns	0.07ns	-0.43***	0.43***	-0.37***	-	0.64***	0.85***	0.14*	0.12ns

Supplementary Data 5 (continued)

Trial	Trait	PH	PL	CTvg	CTgs	CTgf	CTcycle	NDVIinf2	NDVIant	NDVIAsen	NDVIsen	NDVIpm	NDVIAsp	NDVIApeg	NDVIpeg	ANT	GFp	PM	WSC	GSP	KM2	SM2	TKW
SW11HI	PL	0.57***																					
	CTvg	-0.01ns	-0.04ns																				
	CTgs	0.09ns	0.03ns	0.58***																			
	CTgf	-0.06ns	0.01ns	0.58***	0.75***																		
	CTcycle	0.02ns	0ns	0.84***	0.9***	0.87***																	
	NDVIinf2	0.21**	0.09ns	0.14*	0.22***	0.23***	0.23***																
	NDVIant	0.2**	0.3***	-0.04ns	-0.05ns	0.02ns	-0.03ns	0.28***															
	NDVIAsen	0.11ns	0.23***	-0.1ns	-0.21**	-0.22***	-0.2**	0ns	0.66***														
	NDVIsen	0.15*	0.06ns	0.03ns	-0.04ns	-0.13*	-0.05ns	-0.14*	-0.36***	0.23***													
	NDVIpm	0.46***	0.37***	0.17*	0.19**	0.17*	0.2**	0.13ns	0.27***	0.21**	0.48***												
	NDVIAsp	0.03ns	-0.25***	-0.16*	-0.15*	-0.33***	-0.23***	-0.34***	-0.37***	-0.36***	0.02ns	-0.06ns											
	NDVIApeg	0.31***	0.21**	0.04ns	0.1ns	0.06ns	0.08ns	0.72***	0.54***	0.13*	-0.21**	0.19**	-0.19**										
	NDVIpeg	-0.03ns	0.05ns	-0.16*	-0.16*	-0.19**	-0.19**	-0.66***	0.05ns	0.06ns	-0.09ns	-0.03ns	0.33***	-0.46***									
	ANT	0.02ns	-0.32***	-0.07ns	-0.07ns	-0.25***	-0.14*	0ns	-0.52***	-0.49***	0.09ns	-0.07ns	0.86***	-0.02ns	-0.09ns								
	GFp	-0.13ns	0.13ns	-0.08ns	-0.17**	-0.11ns	-0.14*	-0.04ns	0.44***	0.77***	0.11ns	-0.18**	-0.68***	0ns	0.03ns	-0.77***							
	PM	-0.14*	-0.34***	-0.22***	-0.33***	-0.52***	-0.39***	-0.06ns	-0.24***	0.21**	0.27***	-0.36***	0.48***	-0.04ns	-0.11ns	0.58***	0.07ns						
	WSC	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-				
	GSP	-0.11ns	-0.01ns	-0.18**	-0.1ns	-0.06ns	-0.13*	-0.23***	-0.06ns	-0.04ns	-0.09ns	-0.15*	0.04ns	-0.22**	0.19**	-0.09ns	0ns	-0.13ns	-				
	KM2	-0.12ns	-0.04ns	-0.32***	-0.25***	-0.14*	-0.28***	-0.23***	0.17*	0.05ns	-0.22***	-0.09ns	0ns	-0.15*	0.26***	-0.18**	0.03ns	-0.23***	-	0.69***			
	SM2	0.01ns	-0.04ns	-0.15*	-0.18**	-0.08ns	-0.16*	0.02ns	0.28***	0.13*	-0.13*	0.1ns	-0.05ns	0.08ns	0.06ns	-0.1ns	0.05ns	-0.08ns	-	-0.49***	0.28***		
	TKW	0.51***	0.34***	-0.26***	-0.19**	-0.36***	-0.3***	0.12ns	0.03ns	0.1ns	0.19**	0.13ns	0.11ns	0.24***	-0.02ns	0.16*	-0.01ns	0.23***	-	-0.31***	-0.39***	-0.06ns	
	YLD	0.29***	0.25***	-0.52***	-0.4***	-0.41***	-0.51***	-0.14*	0.18**	0.12ns	-0.06ns	0.01ns	0.08ns	0.02ns	0.25***	-0.05ns	0.03ns	-0.04ns	-	0.44***	0.69***	0.23***	0.4***
SW12DR	PL	0.67***																					
	CTvg	-0.06ns	-0.19**																				
	CTgs	-0.29***	-0.22***	0.26***																			
	CTgf	-0.62***	-0.58***	0.13*	0.22***																		
	CTcycle	-0.54***	-0.51***	0.53***	0.75***	0.74***																	
	NDVIinf2	-0.01ns	-0.11ns	0.08ns	0.08ns	-0.02ns	0.05ns																
	NDVIant	0.13ns	0.28***	-0.16*	-0.28***	-0.18**	-0.3***	-0.17**															
	NDVIAsen	-	-	-	-	-	-	-	-														
	NDVIsen	0.09ns	0.19**	-0.12ns	-0.18**	-0.03ns	-0.15*	-0.01ns	0.11ns	-													
	NDVIpm	-	-	-	-	-	-	-	-	-	-												
	NDVIAsp	-0.22***	-0.25***	0.17*	0.33***	0.29***	0.4***	-0.56***	-0.3***	-	-0.33***	-											
	NDVIApeg	0.05ns	-0.03ns	0.07ns	0.09ns	-0.05ns	0.04ns	0.96***	-0.17*	-	0.03ns	-	-0.51***										
	NDVIpeg	-0.01ns	0.11ns	-0.08ns	-0.04ns	0.01ns	-0.04ns	-0.91***	0.19**	-	0.05ns	-	0.49***	-0.85***									
	ANT	-0.3***	-0.46***	0.29***	0.45***	0.33***	0.52***	0.23***	-0.63***	-	-0.39***	-	0.66***	0.24***	-0.26***								
	GFp	0.19**	0.35***	-0.22***	-0.3***	-0.3***	-0.4***	-0.12ns	0.5***	-	0.23***	-	-0.5***	-0.11ns	0.18**	-0.73***							
	PM	-0.26***	-0.35***	0.21**	0.41***	0.23***	0.42***	0.23***	-0.48***	-	-0.35***	-	0.53***	0.24***	-0.22***	0.83***	-0.22***						
	WSC	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-				
	GSP	-0.09ns	0.05ns	-0.21**	-0.23***	-0.02ns	-0.2**	-0.06ns	0.13**	-	0.09ns	-	-0.08ns	-0.06ns	0.07ns	-0.18**	0.12ns	-0.14*	-				
	KM2	-0.16*	-0.03ns	-0.28***	-0.14*	-0.09ns	-0.21**	-0.08ns	0.2**	-	0.17**	-	-0.17**	-0.07ns	0.23***	-0.31***	0.2**	-0.26***	-	0.56***			
	SM2	-0.05ns	-0.06ns	-0.08ns	0.09ns	-0.08ns	-0.03ns	-0.02ns	0.07ns	-	0.1ns	-	-0.11ns	-0.02ns	0.17*	-0.16*	0.09ns	-0.14*	-	-0.49***	0.44***		
	TKW	0.56***	0.57***	-0.13ns	-0.22***	-0.36***	-0.37***	-0.19**	0.19**	-	0.03ns	-	-0.02ns	-0.14*	0.08ns	-0.22***	0.19**	-0.16*	-	-0.17**	-0.52***	-0.34***	
	YLD	0.38***	0.53***	-0.41***	-0.37***	-0.45***	-0.59***	-0.28***	0.4***	-	0.23***	-	-0.22**	-0.21**	0.32***	-0.56***	0.42***	-0.44***	-	0.43***	0.53***	0.1ns	0.44***

Supplementary Data 5 (continued)

Trial	Trait	PH	PL	CTvg	CTgs	CTgf	CTcycle	NDVIinf2	NDVIant	NDVIAsen	NDVIsen	NDVIpm	NDVIAsp	NDVIApeg	NDVIpeg	ANT	GFp	PM	WSC	GSP	KM2	SM2	TKW
SW12HI	PL	0.59***																					
	CTvg	-0.27***	-0.19**																				
	CTgs	-0.45***	-0.4***	0.53***																			
	CTgf	-0.09ns	-0.16*	0.16*	0.23***																		
	CTcycle	-0.33***	-0.32***	0.76***	0.71***	0.71***																	
	NDVIinf2	-0.39***	-0.26***	0.21**	0.21**	-0.05ns	0.15*																
	NDVIant	0.45***	0.36***	-0.61***	-0.54***	-0.09ns	-0.52***	-0.34***															
	NDVIAsen	-0.22**	-0.38***	0.29***	0.29***	0.05ns	0.27***	0.4***	-0.49***														
	NDVIsen	-	-	-	-	-	-	-	-	-													
	NDVIpm	-	-	-	-	-	-	-	-	-	-												
	NDVIAsp	0.3***	-0.02ns	-0.15*	-0.06ns	0.01ns	-0.09ns	-0.71***	0.21**	-	0.01ns	-											
	NDVIApeg	0.02ns	0.06ns	-0.15*	-0.11ns	-0.12ns	-0.18**	0.63***	0.19**	-	0.09ns	-	-0.35***										
	NDVIpeg	0.48***	0.31***	-0.4***	-0.41***	-0.01ns	-0.34***	-0.83***	0.6***	-	-0.38***	-	0.74***	-0.34***									
	ANT	-0.31***	-0.49***	0.33***	0.43***	-0.01ns	0.3***	0.44***	-0.53***	-	0.66***	-	0.24***	0.16*	-0.38***								
	GFp	0.31***	0.41***	-0.32***	-0.44***	0.02ns	-0.28***	-0.31***	0.59***	-	-0.43***	-	-0.22***	-0.04ns	0.34***	-0.87***							
	PM	-0.18**	-0.39***	0.19**	0.23***	0ns	0.17*	0.42***	-0.22***	-	0.68***	-	0.16*	0.25***	-0.26***	0.74***	-0.31***						
	WSC	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
	GSP	0.03ns	0.21**	-0.18**	-0.18**	-0.09ns	-0.19**	0.07ns	0.29***	-	-0.19**	-	-0.03ns	0.29***	0.13ns	-0.11ns	0.14*	-0.02ns	-				
	KM2	0.12ns	0.19**	-0.39***	-0.29***	-0.05ns	-0.31***	-0.01ns	0.52***	-	-0.27***	-	0.03ns	0.3***	0.26***	-0.21**	0.24***	-0.07ns	-	0.82***			
	SM2	0.23***	0.04ns	-0.41***	-0.28***	0.03ns	-0.27***	-0.15*	0.5***	-	-0.19**	-	0.12ns	0.07ns	0.31***	-0.23***	0.25***	-0.1ns	-	-0.2**	0.36***		
	TKW	0.48***	0.24***	-0.24***	-0.38***	0.02ns	-0.23***	-0.26***	0.52***	-	-0.11ns	-	0.18**	0.12ns	0.4***	-0.34***	0.46***	-0.02ns	-	0.02ns	0.07ns	0.16*	
	YLD	0.32***	0.27***	-0.44***	-0.42***	-0.03ns	-0.36***	-0.13ns	0.68***	-	-0.25***	-	0.1ns	0.3***	0.4***	-0.33***	0.4***	-0.07ns	-	0.71***	0.89***	0.37***	0.5***
SW12IR	PL	0.62***																					
	CTvg	0.23***	0.04ns																				
	CTgs	-	-	-																			
	CTgf	-0.23***	-0.24***	0.16*	-																		
	CTcycle	-0.02ns	-0.15*	0.71***	-	0.81***																	
	NDVIinf2	-0.15*	-0.17**	0.02ns	-	0.12ns	0.1ns																
	NDVIant	0.25***	0.45***	-0.24***	-	-0.14*	-0.24***	-0.26***															
	NDVIAsen	-	-	-	-	-	-	-	-														
	NDVIsen	-	-	-	-	-	-	-	-	-													
	NDVIpm	-	-	-	-	-	-	-	-	-	-												
	NDVIAsp	0.03ns	-0.19**	0.12ns	-	-0.06ns	0.03ns	-0.72***	-0.28***	-	-	-											
	NDVIApeg	-0.12ns	-0.11ns	-0.05ns	-	0.1ns	0.04ns	0.95***	-0.18**	-	-	-	-0.71***										
	NDVIpeg	0.07ns	0.14*	-0.07ns	-	-0.14*	-0.14*	-0.93***	0.24***	-	-	-	0.7***	-0.91***									
	ANT	-0.14*	-0.49***	0.23***	-	0.08ns	0.19**	0.15*	-0.76***	-	-	-	0.57***	0.1ns	-0.12ns								
	GFp	-0.07ns	0.33***	-0.35***	-	-0.14*	-0.31***	-0.15*	0.7***	-	-	-	-0.5***	-0.1ns	0.15*	-0.89***							
	PM	-0.37***	-0.54***	-0.03ns	-	-0.04ns	-0.05ns	0.1ns	-0.55***	-	-	-	0.45***	0.05ns	-0.03ns	0.77***	-0.39***						
	WSC	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
	GSP	-0.44***	-0.37***	-0.04ns	-	0.01ns	-0.01ns	0.1ns	-0.16*	-	-	-	0.12ns	0.08ns	-0.08ns	0.29***	-0.12ns	0.43***	-				
	KM2	-0.56***	-0.42***	-0.16*	-	0.06ns	-0.06ns	0.16*	-0.12ns	-	-	-	0.05ns	0.12ns	-0.07ns	0.25***	-0.01ns	0.49***	-	0.69***			
	SM2	0ns	0.05ns	-0.1ns	-	0.04ns	-0.03ns	0.03ns	0.08ns	-	-	-	-0.11ns	0.02ns	0.03ns	-0.13ns	0.15*	-0.05ns	-	-0.61***	0.15*		
	TKW	0.42***	0.57***	-0.13*	-	-0.27***	-0.27***	-0.28***	0.35***	-	-	-	-0.11ns	-0.19**	0.21**	-0.49***	0.4***	-0.43***	-	-0.41***	-0.6***	-0.1ns	
	YLD	-0.14*	0.19**	-0.35***	-	-0.28***	-0.41***	-0.16*	0.29***	-	-	-	-0.05ns	-0.11ns	0.19**	-0.28***	0.46***	0.07ns	-	0.3***	0.41***	0.03ns	0.47***

Supplementary Data 5 (continued)

Trial	Trait	PH	PL	CTvg	CTgs	CTgf	CTcycle	NDVIinf2	NDVIant	NDVIAsen	NDVIsen	NDVIpm	NDVIAsp	NDVIApeg	NDVIpeg	ANT	GFp	PM	WSC	GSP	KM2	SM2	TKW
SW13DR	PL	0.57***																					
	CTvg	-0.27***	-0.34***																				
	CTgs	-	-	-																			
	CTgf	-0.32***	-0.29***	0.38***	-																		
	CTcycle	-0.36***	-0.37***	0.78***	-	0.87***																	
	NDVIinf2	0.02ns	0.02ns	-0.03ns	-	0.02ns	0ns																
	NDVIant	0.33***	0.5***	-0.33***	-	-0.23***	-0.33***	0.02ns															
	NDVIAsen	0.2**	0.35***	-0.3***	-	-0.21**	-0.3***	-0.01ns	0.9***														
	NDVIsen	-0.13ns	-0.29***	0.11ns	-	0.08ns	0.11ns	-0.05ns	-0.48***	-0.16*													
	NDVIpm	0.49***	0.39***	-0.28***	-	-0.24***	-0.31***	0.02ns	0.65***	0.53***	-0.12ns												
	NDVIAsp	-0.16*	-0.24***	0.27***	-	0.01ns	0.14*	-0.18**	-0.61***	-0.59***	0.15*	-0.43***											
	NDVIApeg	0.04ns	0.1ns	0.04ns	-	0ns	0.02ns	0.82***	-0.05ns	-0.12ns	-0.09ns	-0.03ns	0.14*										
	NDVIpeg	-0.17**	-0.16*	0.19**	-	0.17**	0.21**	-0.26***	-0.02ns	-0.03ns	-0.03ns	0.04ns	0.05ns	-0.13*									
	ANT	-0.21**	-0.33***	0.28***	-	0.06ns	0.19**	0.19**	-0.74***	-0.69***	0.24***	-0.5***	0.91***	0.38***	-0.08ns								
	GFp	0.1ns	0.25***	-0.25***	-	-0.05ns	-0.17*	-0.18**	0.74***	0.79***	-0.18**	0.33***	-0.85***	-0.37***	0.05ns	-0.94***							
	PM	-0.34***	-0.34***	0.24***	-	0.05ns	0.16*	0.17**	-0.5***	-0.28***	0.33***	-0.66***	0.73***	0.29***	-0.11ns	0.8***	-0.57***						
	WSC	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
	GSP	-0.18**	0.04ns	-0.04ns	-	0.03ns	0ns	-0.2**	0.18**	0.26***	-0.11ns	-0.16*	-0.17**	-0.22***	0.02ns	-0.25***	0.33***	-0.03ns	-				
	KM2	-0.22***	0.01ns	-0.11ns	-	-0.01ns	-0.06ns	-0.1ns	0.25***	0.33***	-0.13*	-0.06ns	-0.21**	-0.13ns	0.1ns	-0.26***	0.34***	-0.05ns	-	0.78***			
	SM2	-0.06ns	-0.06ns	-0.09ns	-	-0.06ns	-0.08ns	0.18**	0.05ns	0.06ns	0.01ns	0.15*	-0.06ns	0.14*	0.12ns	0.01ns	-0.02ns	-0.04ns	-	-0.42***	0.22***		
	TKW	0.35***	0.32***	-0.1ns	-	-0.16*	-0.16*	-0.16*	0.09ns	0.01ns	-0.05ns	0.19**	0.03ns	-0.05ns	-0.13ns	-0.06ns	0ns	-0.15*	-	-0.38***	-0.54***	-0.22***	
	YLD	0.03ns	0.28***	-0.21**	-	-0.14*	-0.21**	-0.25***	0.37***	0.4***	-0.2**	0.07ns	-0.23***	-0.19**	0.01ns	-0.37***	0.41***	-0.19**	-	0.62***	0.73***	0.07ns	0.17*
VP11DR	PL	-																					
	CTvg	-	-																				
	CTgs	-0.39***	-	-																			
	CTgf	-	-	-	-																		
	CTcycle	-	-	-	-	-																	
	NDVIinf2	0.13*	-	-	-0.16**	-	-																
	NDVIant	0.26***	-	-	-0.39***	-	-	0.16**															
	NDVIAsen	-	-	-	-	-	-	-	-														
	NDVIsen	-0.44***	-	-	0.2***	-	-	-0.23***	-0.55***	-													
	NDVIpm	-	-	-	-	-	-	-	-	-	-												
	NDVIAsp	0.34***	-	-	0.07ns	-	-	-0.17**	0.2**	-	-0.53***	-											
	NDVIApeg	0.15*	-	-	-0.12*	-	-	0.8***	0.28***	-	-0.34***	-	-0.05ns										
	NDVIpeg	-0.17**	-	-	0.06ns	-	-	-0.4***	-0.25***	-	0.25***	-	-0.03ns	-0.71***									
	ANT	0.27***	-	-	0.19**	-	-	0.09ns	-0.18**	-	-0.35***	-	0.85***	0.05ns	-0.08ns								
	GFp	-0.3***	-	-	0.09ns	-	-	-0.14*	0.2***	-	0.33***	-	-0.28***	-0.11ns	0.13*	-0.42***							
	PM	-0.04ns	-	-	0.26***	-	-	-0.06ns	0.03ns	-	0ns	-	0.51***	-0.06ns	0.05ns	0.51***	0.56***						
	WSC	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
	GSP	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-				
	KM2	0.47***	-	-	-0.12*	-	-	0.16**	0.06ns	-	-0.55***	-	0.51***	0.11ns	-0.01ns	0.52***	-0.38***	0.11ns	-	-			
	SM2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
	TKW	-0.18**	-	-	-0.17**	-	-	-0.07ns	0.14*	-	0.23***	-	-0.59***	0.03ns	-0.09ns	-0.7***	0.16**	-0.48***	-	-	-0.71***	-	
	YLD	0.54***	-	-	-0.35***	-	-	0.15*	0.21***	-	-0.57***	-	0.21***	0.18**	-0.1ns	0.13*	-0.38***	-0.26***	-	-	0.78***	-	-0.14*

Supplementary Data 5 (continued)

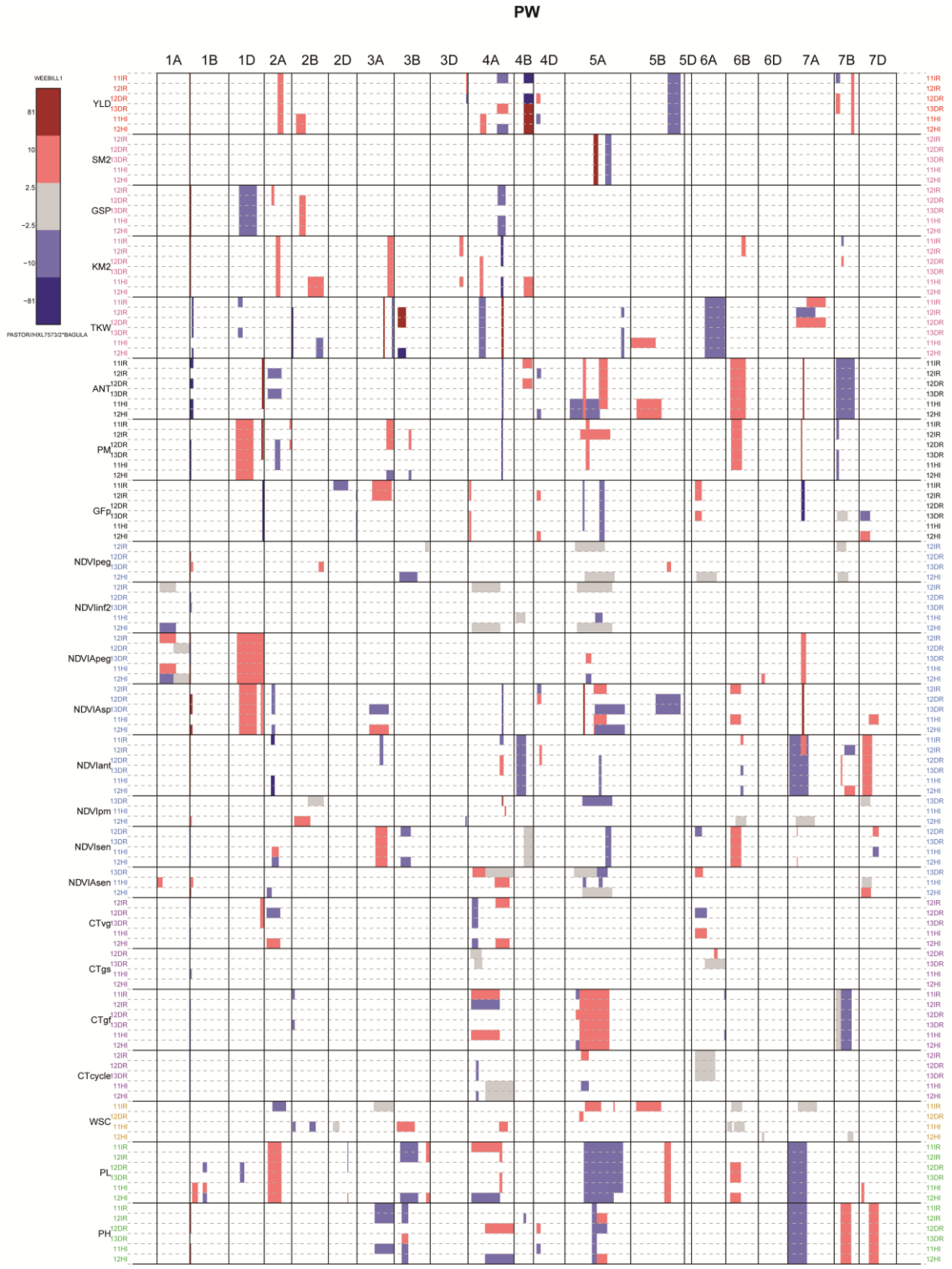
Trial	Trait	PH	PL	CTvg	CTgs	CTgf	CTcycle	NDVIinf2	NDVIant	NDVIAsen	NDVIsen	NDVIpm	NDVIAsp	NDVIApeg	NDVIpeg	ANT	GFp	PM	WSC	GSP	KM2	SM2	TKW
VP11HI	PL	0.61***																					
	CTvg	-0.14*	-0.01ns																				
	CTgs	0.02ns	0.09ns	0.26***																			
	CTgf	-0.21***	-0.06ns	0.22***	0.31***																		
	CTcycle	-0.13*	0.02ns	0.65***	0.8***	0.68***																	
	NDVIinf2	0.13*	0.15*	0.01ns	-0.15*	-0.05ns	-0.1ns																
	NDVIant	0.41***	0.37***	-0.11ns	-0.05ns	-0.03ns	-0.09ns	0.61***															
	NDVIAsen	0.37***	0.32***	-0.12*	-0.16**	-0.22***	-0.23***	0.18**	0.63***														
	NDVIsen	0.17**	0.2**	0.04ns	0.06ns	-0.15*	-0.01ns	-0.4***	-0.29***	0.33***													
	NDVIpm	0.49***	0.48***	0.05ns	0.11ns	-0.04ns	0.07ns	0.1ns	0.29***	0.27***	0.54***												
	NDVIAsp	-0.11ns	-0.24***	-0.2**	-0.33***	-0.16**	-0.33***	-0.19**	-0.27***	-0.36***	-0.16**	-0.14*											
	NDVIApeg	-	-	-	-	-	-	-	-	-	-	-	-										
	NDVIpeg	-	-	-	-	-	-	-	-	-	-	-	-	-									
	ANT	-0.18**	-0.29***	-0.15*	-0.37***	-0.17**	-0.34***	0.09ns	-0.3***	-0.44***	-0.25***	-0.2**	0.9***	-	-								
	GFp	0.1ns	0.11ns	-0.04ns	-0.07ns	-0.16**	-0.12*	-0.03ns	0.3***	0.75***	0.28***	-0.16**	-0.55***	-	-	-0.63***							
	PM	-0.13*	-0.25***	-0.23***	-0.53***	-0.38***	-0.55***	0.07ns	-0.06ns	0.24***	-0.01ns	-0.42***	0.54***	-	-	0.58***	0.27***						
	WSC	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
	GSP	-0.03ns	0.04ns	-0.12ns	-0.14*	-0.03ns	-0.14*	0.06ns	0.11ns	0.03ns	-0.14*	-0.09ns	0.14*	-	-	0.13*	-0.04ns	0.12ns	-				
	KM2	0ns	-0.02ns	-0.22***	-0.26***	-0.1ns	-0.28***	0.1ns	0.14*	0.08ns	-0.14*	-0.04ns	0.23***	-	-	0.24***	-0.1ns	0.2**	-	0.71***			
	SM2	0.03ns	-0.08ns	-0.13*	-0.14*	-0.08ns	-0.17**	0.04ns	0.04ns	0.06ns	0ns	0.08ns	0.12ns	-	-	0.14*	-0.08ns	0.09ns	-	-0.45***	0.3***		
	TKW	0.26***	0.25***	0.11ns	0.19**	-0.06ns	0.13*	-0.08ns	0.09ns	0.07ns	0.14*	0.2***	-0.24***	-	-	-0.33***	0.11ns	-0.28***	-	-0.42***	-0.68***	-0.29***	
	YLD	0.2**	0.17**	-0.21***	-0.2**	-0.19**	-0.28***	0.07ns	0.27***	0.17**	-0.09ns	0.09ns	0.11ns	-	-	0.06ns	-0.02ns	0.04ns	-	0.64***	0.81***	0.16**	-0.13*
VP12DR	PL	-																					
	CTvg	-	-																				
	CTgs	-	-	-																			
	CTgf	-0.59***	-	-	-																		
	CTcycle	-	-	-	-	-																	
	NDVIinf2	-	-	-	-	-	-																
	NDVIant	-	-	-	-	-	-	-															
	NDVIAsen	-	-	-	-	-	-	-	-														
	NDVIsen	-0.41***	-	-	-	0.35***	-	-	-	-													
	NDVIpm	0ns	-	-	-	0.1ns	-	-	-	-	-0.14*												
	NDVIAsp	-	-	-	-	-	-	-	-	-	-	-											
	NDVIApeg	-	-	-	-	-	-	-	-	-	-	-	-										
	NDVIpeg	-	-	-	-	-	-	-	-	-	-	-	-	-									
	ANT	-0.38***	-	-	-	0.47***	-	-	-	-	0.1ns	0.55***	-	-	-								
	GFp	0.39***	-	-	-	-0.45***	-	-	-	-	-0.11ns	-0.49***	-	-	-	-0.91***							
	PM	-0.26***	-	-	-	0.37***	-	-	-	-	0.06ns	0.47***	-	-	-	0.84***	-0.54***						
	WSC	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
	GSP	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-				
	KM2	0.27***	-	-	-	-0.3***	-	-	-	-	-0.35***	-0.47***	-	-	-	-0.48***	0.42***	-0.43***	-	-			
	SM2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
	TKW	0.26***	-	-	-	-0.25***	-	-	-	-	-0.14*	0.41***	-	-	-	0.13*	-0.08ns	0.16**	-	-	-0.58***	-	
	YLD	0.51***	-	-	-	-0.54***	-	-	-	-	-0.52***	-0.29***	-	-	-	-0.5***	0.46***	-0.42***	-	-	0.8***	-	0.03ns

Supplementary Data 5 (continued)

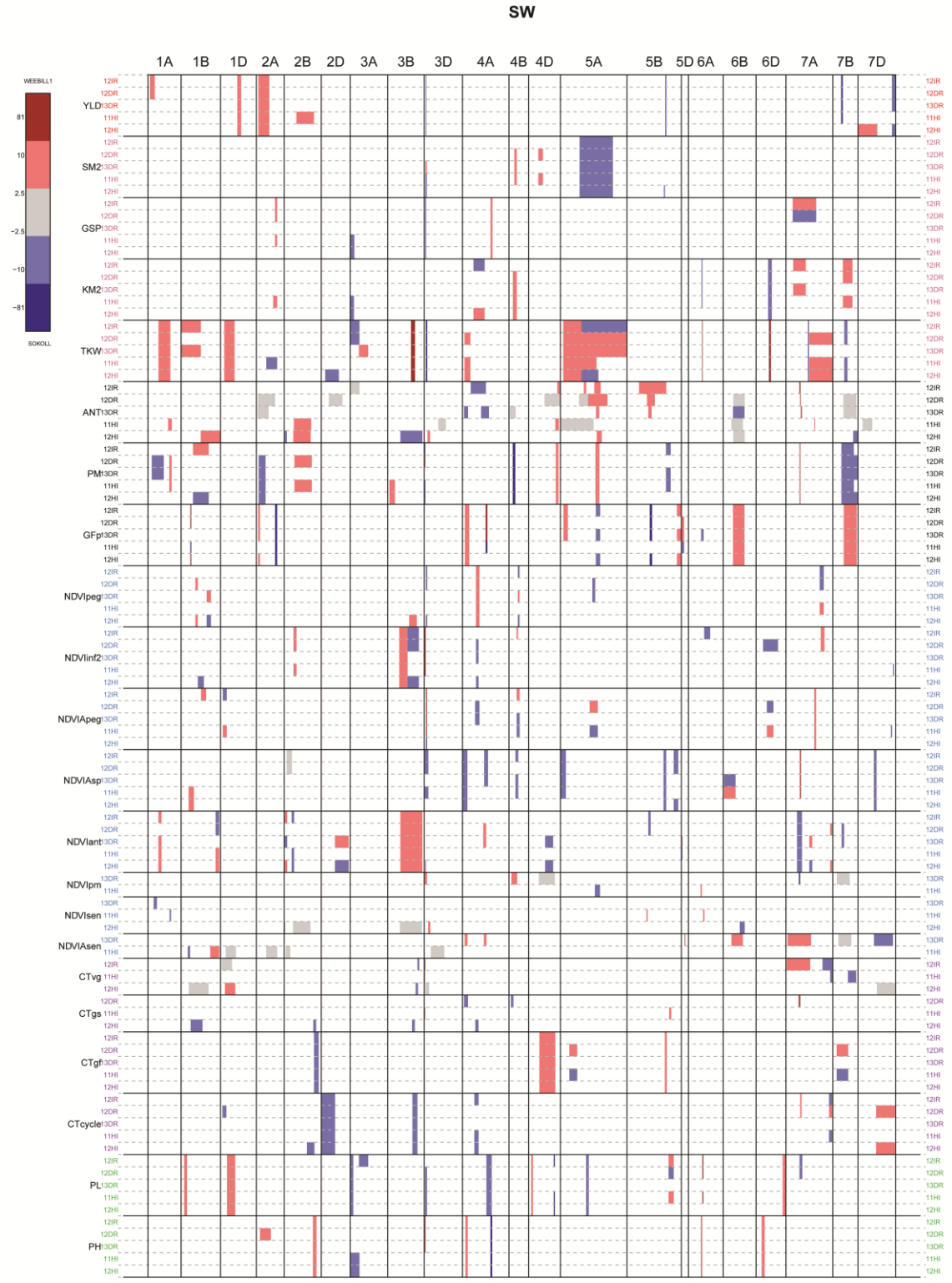
Trial	Trait	PH	PL	CTvg	CTgs	CTgf	CTcycle	NDVIinf2	NDVIant	NDVIAsen	NDVIsen	NDVIpm	NDVIAsp	NDVIApeg	NDVIpeg	ANT	GFp	PM	WSC	GSP	KM2	SM2	TKW
VP12HI	PL	0.64***																					
	CTvg	-0.06ns	-0.09ns																				
	CTgs	-0.2**	-0.19**	0.6***																			
	CTgf	-0.15*	-0.15*	0.49***	0.71***																		
	CTcycle	-0.16**	-0.17**	0.83***	0.9***	0.85***																	
	NDVIinf2	0.06ns	0.04ns	-0.02ns	-0.02ns	0ns	-0.02ns																
	NDVIant	0.31***	0.31***	-0.18**	-0.43***	-0.38***	-0.38***	-0.03ns															
	NDVIAsen	0.27***	0.24***	-0.18**	-0.32***	-0.36***	-0.33***	-0.04ns	0.66***														
	NDVIsen	0.21***	0.16**	-0.06ns	0.03ns	-0.07ns	-0.04ns	0.1ns	-0.39***	0.2**													
	NDVIpm	0.28***	0.3***	-0.18**	-0.28***	-0.27***	-0.28***	-0.1ns	0.2***	0.32***	0.5***												
	NDVIAsp	0.19**	0.17**	-0.07ns	-0.09ns	-0.16**	-0.13*	-0.66***	-0.04ns	-0.18**	0.06ns	0.15*											
	NDVIApeg	-	-	-	-	-	-	-	-	-	-	-	-										
	NDVIpeg	-	-	-	-	-	-	-	-	-	-	-	-	-									
	ANT	0.21***	0.15*	-0.1ns	-0.05ns	-0.13*	-0.11ns	0.18**	-0.29***	-0.4***	0.22***	0.05ns	0.59***	-	-								
	GFp	-0.12ns	-0.13*	0.08ns	0.04ns	0.08ns	0.08ns	-0.12ns	0.33***	0.55***	-0.13*	-0.21***	-0.56***	-	-	-0.91***							
	PM	0.27***	0.13*	-0.1ns	-0.02ns	-0.14*	-0.1ns	0.22***	-0.09ns	0.06ns	0.29***	-0.26***	0.35***	-	-	0.68***	-0.33***						
	WSC	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
	GSP	0.04ns	0.09ns	-0.2***	-0.22***	-0.16**	-0.23***	0.1ns	0.08ns	-0.06ns	-0.14*	-0.09ns	0.1ns	-	-	0.24***	-0.22***	0.15*	-				
	KM2	0.04ns	0.15*	-0.4***	-0.46***	-0.41***	-0.49***	0.08ns	0.27***	0.13*	-0.17**	0.02ns	0.06ns	-	-	0.12*	-0.13*	0.03ns	-	0.65***			
	SM2	-0.01ns	0.04ns	-0.19**	-0.26***	-0.28***	-0.28***	-0.06ns	0.22***	0.22***	-0.03ns	0.14*	-0.04ns	-	-	-0.16**	0.12ns	-0.15*	-	-0.52***	0.28***		
	TKW	0.05ns	-0.02ns	0.07ns	-0.11ns	-0.03ns	-0.03ns	-0.13*	0.14*	0.21***	-0.01ns	0.13*	-0.11ns	-	-	-0.33***	0.32***	-0.21***	-	-0.32***	-0.54***	-0.16**	
	YLD	0.08ns	0.16**	-0.42***	-0.63***	-0.5***	-0.6***	0ns	0.42***	0.31***	-0.21***	0.12ns	-0.02ns	-	-	-0.1ns	0.07ns	-0.12*	-	0.53***	0.78***	0.21***	0.09ns

Supplementary Data 6: Number of single nucleotide markers (SNP) mapped and size (cM) of each linkage group per population. The total number of SNP and cumulative size of each linkage group is displayed per population.

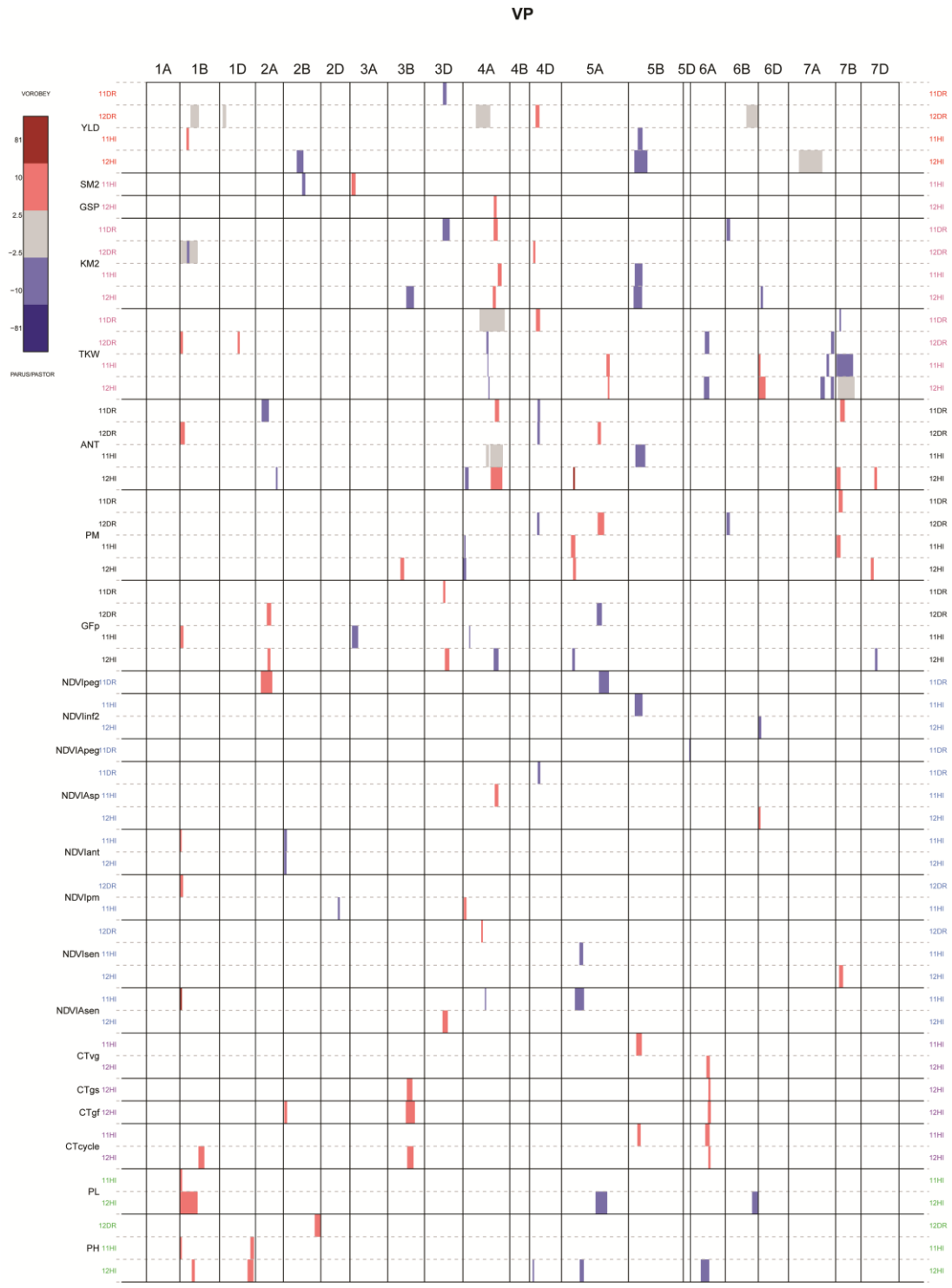
Chromosome		PW		SW		VP	
		SNP	Size	SNP	Size	SNP	Size
1A		17	136	14	98	12	119
1B		26	85	26	162	24	143
1D		12	147	11	84	25	228
2A		27	114	23	89	20	112
2B		16	133	24	142	19	182
2D		6	55	9	112	6	83
3A		13	162	11	76	11	130
3B		26	149	18	180	22	171
3D		5	174	7	111	13	119
4A		19	238	13	124	27	205
4B		11	80	10	47	2	50
4D		5	35	8	130	3	44
5A		26	248	26	272	29	250
5B		15	207	20	223	19	189
5D		1	0	7	58	6	63
6A		16	168	15	118	11	84
6B		14	89	18	94	14	144
6D		3	51	10	161	4	100
7A		21	159	27	192	16	190
7B		13	88	24	106	25	135
7D		6	81	6	155	10	167
Total		298	2596	327	2732	318	2907
	A	139	1223	129	968	126	1090
	B	121	831	140	953	125	1014
	D	38	542	58	811	67	804



Supplementary Data 7



Supplementary Data 7



Supplementary Data 7: Heat-map showing the -log10P profiles of the scored traits QTL found within the network. Each column corresponds to the chromosomes of the genome. Each row corresponds to the traits ordered by trial (11IR, 12IR, 11DR, 12Dr, 13DR, 11HI, and 12HI). First sheet correspond to PW QTL, the second one, to SW's, and the third one to VP's. Colour scale: stronger the colour, higher the absolute value of -log10P is. In PW and SW, red colour indicates a positive effect on the trait value from Weebill1, blue colour indicates a positive effect on the trait value from Pastor//hxl7573/2*bagula (PW) or Sokoll (SW). In VP, red indicates a positive effect of Vorobey and blue colour indicates a positive effect of Parus/Pastor. Grey colour corresponds to QTL with -log10P less than 2.5 in absolute values. Bar width indicates the significance of the confidence interval.

Supplementary Data 8: Summary table of the QTL found on PW for the hotspot "HS_1B". Each row correspond to a QTL with significant effect (p<0.05). Each bloc of QTL corresponds to a unique QTL. The nearest QTL peak marker is indicated as the nearest markers for both the lower and upper limit of the confidence interval with between parentheses, first the position in cM of the marker on the genetic map, and then the distance to the QTL peak. Environment, as a combination of year and treatment (IR, DR, and HI), the parents carrying the high value allele (WB: Weebill1; PA: Pastor//hxl7573/2*Bagula), the effects of the QTL, the phenotypic explained variance (PEV), the -log10P, the standard error and the p-value of the effect. Dash symbols mean "not tested".

Unique QTL	QTL peak nearest marker	Lower limit nearest marker	Upper limit nearest marker	Environment	High value parents	Effect	PEV	-log10(P)	s.e.	Pvalue
Q.YLD.PW.1B	W_00096908 (1.5; 0)	Ws_01000060 (0; 0)	W_00094325 (4.8; 0.82)	12DR	WB	6.0	3.3	51.2	2.173	0.006
				13DR	WB	11.5	16.2	51.2	1.946	0
				11HI	WB	29.8	37.3	51.2	2.563	0
				12HI	WB	45.5	53.8	51.2	2.969	0
				11IR	WB	20.1	8.9	51.2	3.946	0
				12IR	WB	32.2	14.9	51.2	5.562	0
Q.SM2.PW.1B	Ws_01000060 (0; 0)	Ws_01000060 (0; 0)	W_00094325 (4.8; -0.12)	12DR	WB	10.1	8.8	22.7	2.242	0
				13DR	WB	6.1	3.8	22.7	2.16	0.005
				11HI	WB	19.4	22	22.7	2.587	0
				12HI	WB	19.2	28.4	22.7	2.309	0
				12IR	WB	11.6	10.6	22.7	2.534	0
Q.GSP.PW.1B	W_00096908 (1.5; -1.65)	Ws_01000060 (0; 0)	W_00094325 (4.8; -3.11)	12DR	WB	0.9	3.9	22	0.307	0.004
				13DR	WB	0.8	4.6	22	0.273	0.003
				11HI	WB	0.8	2.6	22	0.329	0.02
				12HI	WB	3.7	29.3	22	0.397	0
				12IR	WB	1.0	1.9	22	0.503	0.047
Q.KM2.PW.1B	W_00096908 (1.5; -1.65)	W_00096605 (0.6; 0.06)	W_00094325 (4.8; -0.96)	12DR	WB	595.6	22.6	53	78.908	0
				13DR	WB	439.4	24.9	53	56.119	0
				11HI	WB	864.9	24.7	53	95.71	0
				12HI	WB	1451.1	51.1	53	94.885	0
				11IR	WB	698.8	13.3	53	111.73	0
				12IR	WB	986.8	19.7	53	136.061	0
Q.TKW.PW.1B	W_00094200 (11.3; 0)	W_00094325 (4.8; 0.03)	wsnp_BE494527B_Ta_2_1 (18.4; 0.57)	12DR	PA	1.2	22.1	20	0.152	0
				13DR	PA	0.9	14.3	20	0.125	0
				12HI	PA	0.4	1.9	20	0.14	0.003
				11IR	PA	0.7	6.4	20	0.164	0
				12IR	PA	0.9	7.9	20	0.185	0
Q.ANT.PW.1B	W_00096908 (1.5; 0)	Ws_01000060 (0; 0)	W_00099249 (26; -1.3)	12DR	PA	6.6	6.8	13	1.343	0
				11HI	PA	7.6	2.7	13	2.506	0.002
				12HI	PA	8.2	7.9	13	1.763	0
				11IR	PA	4.9	1.6	13	1.995	0.014
Q.PM.PW.1B	W_00096908 (1.5; 0)	Ws_01000060 (0; 0)	W_00094200 (11.3; 1.41)	12DR	PA	8.4	12.6	18.2	1.177	0
				13DR	PA	6.2	4.3	18.2	1.575	0
				11HI	PA	9.4	6.1	18.2	2.278	0
				12HI	PA	9.9	17.8	18.2	1.424	0
Q.NDVIpeg.PW.1B	W_00096908 (1.5; 0)	Ws_01000060 (0; 0)	W_00094325 (4.8; -2.01)	12DR	WB	0.005	26.5	14.3	0.001	-
				12HI	WB	0.007	43.5	30.4	0.001	-
Q.NDVIpeg.PW.1B.2	W_00096908 (1.5; -1.65)	Ws_01000060 (0; 0)	W_00099249 (26; 1.27)	13DR	WB	0.001	8.8	4.6	0	-
Q.NDVIinf2.PW.1B	W_00096908 (1.5; 0)	Ws_01000060 (0; 0)	W_00094325 (4.8; -1.7)	12DR	PA	17.7	28	15.5	1.97	-
				13DR	PA	5.2	13	6.4	0.988	-

Supplementary Data 8 (continued)

Unique QTL	QTL peak nearest marker	Lower limit nearest marker	Upper limit nearest marker	Environment	High value parents	Effect	PEV	-log10(P)	s.e.	Pvalue
Q.NDVIApeg.PW.1B	W_00096908 (1.5; 0)	Ws_01000060 (0; 0)	W_00094325 (4.8; -1.46)	12DR	PA	9.0	29.3	29	1.001	0
				13DR	PA	1.3	3.2	29	0.506	0.009
				11HI	WB	1.8	4.5	29	0.571	0.002
				12HI	WB	7.0	19	29	1.03	0
				12IR	WB	6.5	9	29	1.407	0
Q.NDVIAsp.PW.1B	W_00096908 (1.5; 0)	Ws_01000060 (0; 0)	wsnp_BE494527B_Ta_2_1 (18.4; -1.46)	12DR	WB	8.5	6.9	12.4	1.798	0
				13DR	WB	3.2	1.3	12.4	1.402	0.024
				12HI	WB	10.1	9.8	12.4	1.7	0
Q.NDVIant.PW.1B	W_00096908 (1.5; 0)	Ws_01000060 (0; 0)	W_00094325 (4.8; 0.46)	12DR	WB	0.003	2.2	60	0.001	0.011
				13DR	WB	0.007	5	60	0.002	0
				11HI	WB	0.013	13.5	60	0.002	0
				12HI	WB	0.033	47.2	60	0.002	0
				11IR	WB	0.015	16	60	0.002	0
				12IR	WB	0.009	18	60	0.001	0
Q.NDVIpm.PW.1B	W_00096908 (1.5; -1.65)	Ws_01000060 (0; 0)	W_00094200 (11.3; -0.99)	12HI	WB	0.011	16.6	8.2	0.002	-
Q.NDVIsen.PW.1B	W_00096908 (1.5; 0)	Ws_01000060 (0; 0)	W_00094325 (4.8; 0.63)	12DR	PA	0.002	8.8	56.7	0	0
				13DR	PA	0	2.6	56.7	0	0.015
				11HI	PA	0.001	3.1	56.7	0	0.011
				12HI	PA	0.003	50.1	56.7	0	0
Q.NDVIAsen.PW.1B.1	W_00096908 (1.5; 0)	Ws_01000060 (0; 0)	W_00099249 (26; -0.69)	11HI	WB	7.1	8	5.6	1.453	-
Q.NDVIAsen.PW.1B.2	W_00096908 (1.5; -1.65)	Ws_01000060 (0; 0)	W_00094325 (4.8; -2.09)	12HI	WB	15.4	36.5	19.9	1.463	-
Q.CTvg.PW.1B	W_00096908 (1.5; 0)	Ws_01000060 (0; 0)	W_00094325 (4.8; 0.1)	12DR	PA	0.1	3.4	53.2	0.026	0.005
				11HI	PA	0.3	42.2	53.2	0.022	0
				12HI	PA	0.5	36	53.2	0.049	0
				12IR	PA	0.2	29.6	53.2	0.022	0
Q.CTgs.PW.1B.1	Ws_01000060 (0; 0)	Ws_01000060 (0; 0)	W_00096908 (1.5; -1.18)	12HI	PA	0.6	49.9	28.4	0.043	-
Q.CTgs.PW.1B.2	W_00096605 (0.6; 0)	Ws_01000060 (0; 0)	wsnp_BE590634B_Ta_2_5 (15.2; 1.49)	11HI	PA	0.2	12.4	6	0.03	-
Q.CTgf.PW.1B	W_00096908 (1.5; 0)	Ws_01000060 (0; 0)	W_00094325 (4.8; 0.35)	12DR	PA	0.1	3.7	44	0.026	0.004
				13DR	PA	0.1	2.2	44	0.032	0.037
				11HI	PA	0.1	14.3	44	0.022	0
				12HI	PA	0.7	45.6	44	0.053	0
				12IR	PA	0.1	7.9	44	0.022	0
Q.CTcycle.PW.1B	W_00096908 (1.5; 0)	Ws_01000060 (0; 0)	W_00094325 (4.8; 0.94)	12DR	PA	0.1	5.8	80.5	0.02	0
				13DR	PA	0.1	3.7	80.5	0.023	0.005
				11HI	PA	0.2	34.1	80.5	0.017	0
				12HI	PA	0.6	56.3	80.5	0.04	0
				12IR	PA	0.1	32.7	80.5	0.015	0
Q.PL.PW.1B.1	wsnp_BE494527B_Ta_2_1 (18.4; 0)	Ws_01000060 (0; 0)	W_00099249 (26; -22.42)	11HI	WB	0.5	7.3	5.4	0.118	0
				12HI	WB	0.3	4.6	5.4	0.103	0.002

Supplementary Data 8 (continued)

Unique QTL	QTL peak nearest marker	Lower limit nearest marker	Upper limit nearest marker	Environment	High value parents	Effect	PEV	-log10(P)	s.e.	Pvalue
Q.PH.PW.1B	W_00096908 (1.5; 0)	Ws_01000060 (0; 0)	W_00094325 (4.8; -3.18)	12DR	WB	0.6	2.5	16.7	0.248	0.011
				11HI	WB	1.7	22.2	16.7	0.219	0
				12HI	WB	1.5	14.1	16.7	0.232	0
				11IR	WB	0.9	5	16.7	0.267	0
				12IR	WB	0.5	1.8	16.7	0.224	0.029

Supplementary Data 9: Summary of the significant QEI reported between NDVI traits QTL and environmental covariates. Blue cells correspond to drought stress related covariates; orange ones, to heat stress related covariates; Green cells referred to radiation related covariates.

QTL name	Correlation coefficient (r)	Signif	EC involved in the correlation
Q.NDVIant.PW.2A	-0.85	*	EC6
Q.NDVIant.PW.5A	0.88	*	EC5
Q.NDVIant.PW.7B.1	0.84	*	EC1
Q.NDVIant.SW.1B	-0.94	*	EC2
Q.NDVIant.SW.2B.2	-0.89	*	EC3
Q.NDVIant.SW.4A	0.90	*	EC1
Q.NDVIant.SW.5D	-0.98	**	EC6
Q.NDVIant.SW.7B	0.89	*	EC3
Q.NDVIApeg.PW.5A	0.89	*	EC2
Q.NDVIApeg.SW.4A	-0.93	*	EC5
Q.NDVIApeg.SW.7D	0.92	*	EC5
Q.NDVIAsp.PW.4A	0.97	**	EC5
Q.NDVIAsp.PW.5A.2	0.95	*	EC3
Q.NDVIAsp.SW.1B	-0.97	**	EC2
Q.NDVIAsp.SW.2B	0.99	***	EC4
Q.NDVIAsp.SW.5B.2	0.94	*	EC4
Q.NDVIAsp.SW.7A	0.96	**	EC2
Q.NDVIinf2.SW.7A	-0.98	**	EC4

CHAPTER VI: General discussion and conclusion

At the beginning of the report, we were wondering if this study could answer to some important questions dealing with breeding for tolerance to drought and heat:

- Is there a differential tolerance to drought and heat stress within the germplasm studied?

- What do physiological traits bring in the explanation of the tolerance to such abiotic stress?

- Is the protocol followed the most adapted to tackle such a long term issue like the improvement of European winter bread wheat? Will these results be readily transferable into a European context?

The general discussion will highlight all these questions.

I. General conclusions

The collaborative project established between the CIMMYT and Limagrain Europe aimed to study the genetic determinism of the tolerance to drought and heat stress in various spring bread wheat genetic backgrounds. The heart of the thesis was the study of the phenotypic variation of bread wheat mapping populations observed in an abiotic stress multi-environmental trial (MET) network. In a MET network, the effect of the phenotype can be dissected into an effect of (i) the environment, (ii) the genotype, and (iii) the genotype-by-environment interaction. These three terms were the three pillars of this study.

a. Importance of the environmental characterization in MET network

The first pillar, i.e. the comprehensive environmental characterization, at the basis of the whole study, was the first main result of the thesis. Our work allowed the dissection of the different type, period, and relative intensity of the stresses experienced by the different genotypes within the network which, in turn, enabled the understanding of their performance in the light of what they had experienced in the field. First, it resulted in the establishment of a relatively easy-to-use and -to-adapt environmental characterization methodology whatever the MET network considered. It is based on traits which are commonly available or routinely scored in each experimental station, excepted core soil samples. Secondly, it leads to the identification

of six environmental scenarios within the studied MET from which one representative environmental covariate was extracted. They were as followed: (EC1) zero to light drought stress from vegetative to grain filling stages with moderate drought stress in grain filling, (EC2) heat stress during grain set and grain filling phase, (EC3) strong drought stress from vegetative to grain filling phases, (EC4) frost in grain set and solar radiation amount during grain set and grain filling phases, (EC5) heat stress during vegetative phase associated with moderate drought stress during grain set phase, and (EC6) deficit of solar radiation in vegetative and grain set phases and moderate drought during vegetative phase. The six representative and informative environmental covariates were then used in the analysis of the other pillars. This work was submitted to Agronomy Journal for publication (Paper 1) and is under revision prior to publication.

The establishment of an environmental characterization should lead to a better use of the MET data. The environment is not seen as 'location x year' or 'treatment x year', but rather as a series of constraints, which, combined, contribute to crop performance.

b. Importance of the physiological phenotyping approach in the understanding of the drought and heat stress tolerance in wheat

The efficiency of the physiological trait breeding approach used by the CIMMYT was demonstrated in practice with the release of more advanced lines from the physiology breeding than using a conventional breeding methods (Reynolds et al., 2009).

Several physiological traits were scored and studied: (i) canopy temperature, (ii) NDVI (several traits were extracted from NDVI dynamical scoring along the whole crop cycle), (iii) stem water soluble carbohydrate content, and (iv) flag leaf glaucousness. The physiological breeding enables the dissection of the plant response to the experienced environmental conditions. Therefore, the use of physiological phenotyping allows the identification of specific habit and mechanism useful in a given climatic scenario. The literature already widely reported these features: (i) in Australia, with the improvement of transpiration efficiency in a dry environment without available water at depth (Richards et al., 2001), (ii) in Northern Mexico, in dry environment where a deeper root system may enhance uptake of water available in depth (Olivares-Villegas et al., 2007).

The physiological traits scored and established during this study enabled the dissection of the plant response to environmental stressed conditions. For example, the NDVI traits at a given developmental phase inform on the capacity of the genotypes to produce biomass. In chapters V and VI, we showed that (i) significant correlation exists between these traits and both the grain yield and its components, (ii) these traits are only partially correlated among them, (iii) they are in general more sensitive to the environment than agronomic traits, i.e., physiological traits have a larger proportion of GEI than agronomic traits, and (iv) there are different but also common genetic regions involved in NDVI traits, but also important agronomic traits within each population, thus confirming the phenotypical correlations.

As previously described in the literature, in a given environment experiencing drought with limited water available in the soil, a strategy to improve the tolerance to water deficit could be a quick early establishment and a full ground cover to limit water loss by evaporation. To help this strategy, our work resulted in the identification of genomic regions involved in the control of NDVI traits measured during the vegetative establishment and related to biomass, i.e., NDVIpeg, representing the slope of the phase of exponential growth (PEG), NDVIApeg, representing the amount of biomass established during the PEG phase, and NDVIinf2, representing the end of the PEG phase. These genomic regions could help to the establishment of a molecular markers' assisted program aiming at improving crop establishment.

The approach is further elaborated by the study of the QTL-by-environment interaction. Indeed, knowledge about the sensitivity of the QTL to given environmental conditions may allow breeders to target the most interesting and useful genes for a given target population of environment.

c. Dissection of the genotype-by-environment interaction using environmental covariates revealed the stress sensitivity of the germplasm

The second pillar of the study concerned the dissection of the genotype-by-environment interaction using a factorial regression approach and the six informative

environmental covariates representative of the whole trial network and previously established. This study aimed to (i) the identification of the main grain yield agronomic and physiological determinants under abiotic stress conditions, (ii) the estimation and the dissection of the GEI for all grain yield determinants using environmental covariates, and finally (iii) the quantification of the stability of the genotypes regarding the stress experienced, i.e., environmental covariates.

The dissection of the total genetic variance of grain yield and its main agronomic and physiological determinants revealed a higher contribution of the GEI variance for physiological traits (68 %) than for agronomic traits (46 %). The factorial regression method enabled the dissection of most of GEI (from 64 to 100 % depending on the trait considered) using environmental covariates. The GEI dissection highlighted differential stress sensitivity between populations.

d. Genetic dissection of the traits involved in the control of drought and heat stress tolerance in wheat can lead to a wider use of the QTL-by-environment interaction

The last pillar of the study consisted in the genetic dissection of the traits involved in the control of the tolerance of drought and heat stress. The QTL detection methodology used enabled the study of QTL for agronomic, phenological, architectural, and physiological traits. It resulted in the detection of 1487 QTL, highlighting the complex genetic bases of the control of drought and heat stress tolerance in the wheat germplasm studied. The methodology also permitted the estimation of the QTL-by-environment interaction, i.e. the effects of a QTL at a given locus was estimated within the trial network and then compared with the informative environmental covariates. It resulted in the identification of 92 unique QTL displaying a significant interaction with specific environmental covariates. This is highly valuable information as it may allow a wider and more efficient use of the QTL. Indeed, nowadays, among the huge amount of QTL detected, only the robust ones with a large proportion of phenotypic variance explained are potentially introgressed within the elite material. The study of the QEI combined with informative environmental covariates gives the opportunity to target the introgression of QTL whose usefulness in different environments will be documented.

II. General discussion

a. Need for standard protocols

The thesis led to the establishment and design of new traits: NDVI traits derived along the crop cycle as the area under the curve, rate of establishment, rate of senescence, and particular inflexion points. These traits have revealed their potential, i.e., high-throughput and robust field NDVI scorings, high heritability, good correlations observed with grain yield and yield components, complementary in the genetic dissection of adaptive strategies under drought and heat stress, access to useful information about the evolution of the green biomass along the crop cycle. However, for their establishment, i.e., from the NDVI raw data to the NDVI derivative traits, several difficulties had been surpassed. Most difficulties came from establishing a common set of decision rules for all trials in order to automate the computing process.

Three treatments, i.e., irrigated, drought, and heat irrigated, were experimented. The frequency of scorings, roughly once a week, within each treatment enabled the access to some traits. The Figure II-1 represents the evolution of NDVI along the crop cycle under each treatment in 2012 for all the genotypes of the population Pastor//hxl7573/2*Bagula/3/Weebill1. Irrigated and drought conditions were sown in winter. Their crop cycles' durations were therefore longer than the heat-irrigated spring sowing treatment. Around the same number of NDVI series were taken in each environment. However, after analyses, it appeared that some key developmental stages required further scorings to model the curve of each genotype within each treatment. For example, under drought condition, the early vigor can be observed (Figure II-1). Indeed, it constituted an important tolerance mechanisms to protect soil water loss under water deficit environment (Rebetzke et al., 2001) and with more scorings during the crop establishment phase, a better characterization could probably have been done for early vigor. As a general rule, every inflexion point of the curve should be carefully and frequently scored. Inversely, the saturation phase of the NDVI during the time when the biomass is at its highest does not require so many points. During that stage, measurement steps may be more delayed in time.

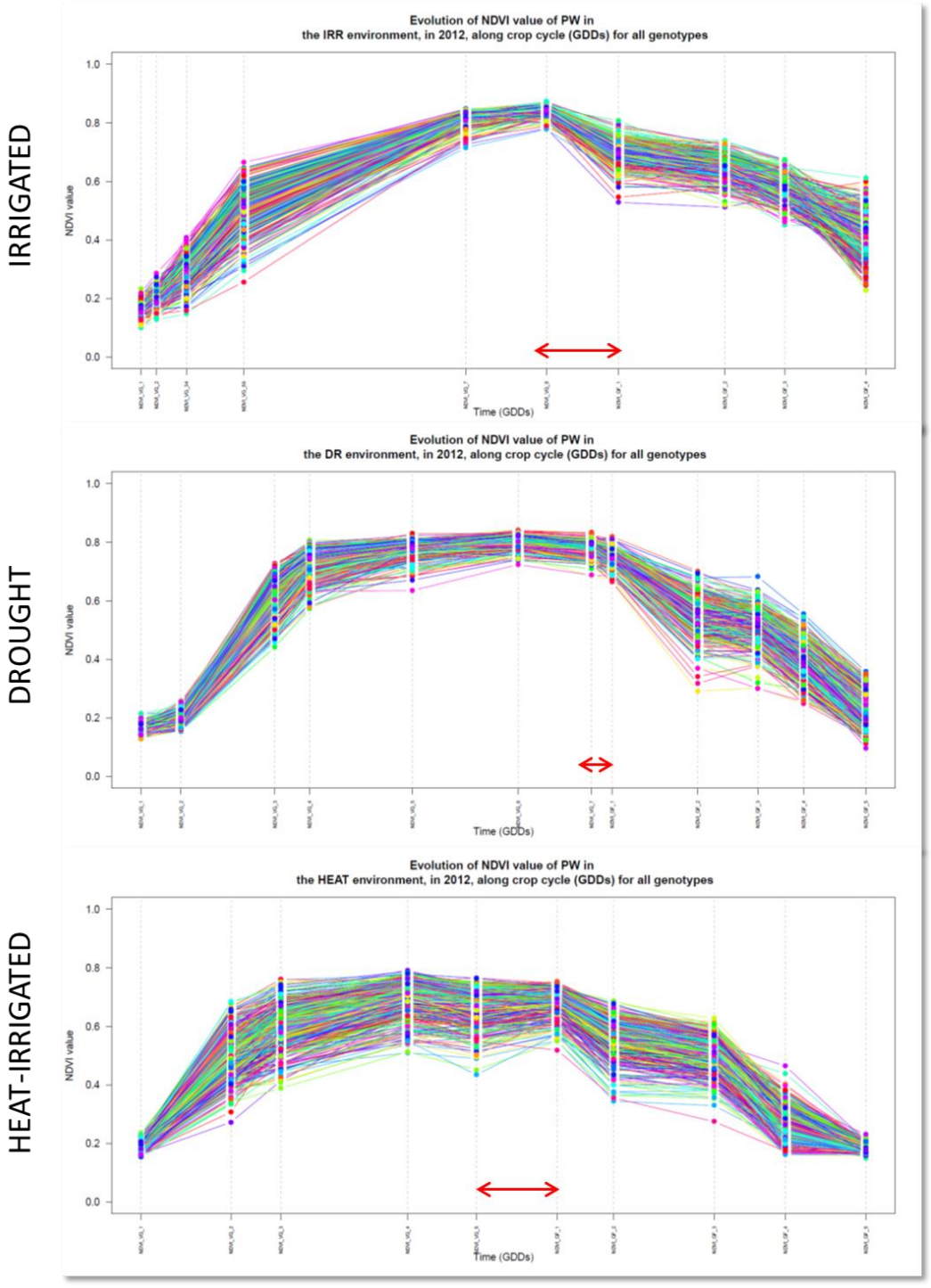


Figure II-1: Dynamic curves of NDVI performed on the PASTOR//HXL7573/2*BAGULA/3/WEEBILL1 population in 2012, in irrigated, drought, and heat-irrigated treatments. The x-axis is the thermal time of each NDVI scoring date while the y-axis represents the NDVI values (no unit). Within each plot, each color line corresponds to the evolution of the NDVI for a given genotype. Red arrows indicate the anthesis range within each treatment.

The recommended protocol for a good estimation and ease of the automation of the data processing requires frequent NDVI scorings along the crop cycle (3 times a week) in areas where the crop cycle lasts less than 130 days as in northern Mexico for spring wheat. In Europe, where crop cycles are not so short, less frequent scorings should be enough for winter wheat. Moreover, in a European context, during this slower rhythm of wheat development (crop cycle around 275 days), other NDVI features appeared (Pers. Comm. Jeremy Derory). Indeed, a pre-senescing phase appears after anthesis where the NDVI starts to decrease slowly before entering in a more active phase of senescence later on. In that case, another computation process and a new set of rules should be established as for example proposed by Bogard et al. (2011).

b. New phenotyping methods

During years and years, the development was focused on genotyping tools and fine phenotyping was left behind. Consequently, today it remained the bottleneck of all breeding programmes. There is a huge need of high throughput phenotyping methods enabling the evaluation of thousands of plots repetitively, with precision and at a reduced cost. This topic will be approached through the presentation of an example experienced during the thesis.

Our study revealed that the physiological phenotyping can be quite difficult to manage partly due to its sensitivity to the environment. Access to available water at depth by a deeper root system represents the main drought-adaptive mechanisms of wheat in dry areas where water is available at depth in the soil (Olivares-Villegas et al., 2007; Pinto et al., 2010). Under heat conditions, where water is non-limiting, the ability to uptake and evaporate more water represents a very successful mechanism of tolerance to heat stress (Reynolds et al., 1998). The canopy temperature scorings were therefore one of the most important physiological traits scored despite its strong sensitivity to environmental conditions (Pietragalla, 2012). Heritabilities found ranged from 0.00 to 0.74 within the network, and averaged at 0.45 (Chapter V).

CIMMYT protocols (Pask et al., 2012) suggest a minimum of four scorings per development phase to have a relevant estimation of plant canopy temperature differences. Only for a couple of trial x development stage combinations, enough CT series were

scored in our study. This is due to the numerous experiments and the narrow time windows available to score it, i.e., between 11am to 1pm, without cloud and wind, with full sun, and plants experiencing the desired stress conditions.

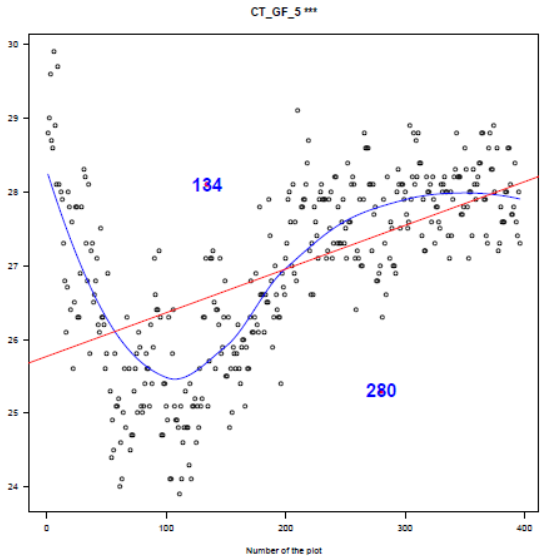


Figure II-2: Evolution of a canopy temperature series within a trial during grain filling in Pastor//hxl7573/2*Bagula/3/Weebill1 under heat stress condition in 2011 at Ciudad Obregon, Sonora, Mexico. The red line represents the linear regression line. The blue line represents a local fitting curve. The x-axis represents the number of the plot and in the y-axis, the value of canopy temperature. Number in blue represents outliers that were removed.

Due to the size of the mapping populations studied, at least 20 minutes were required to score the CT of a whole trial. During that time, meteorological conditions evolved more than likely and plant reacted to them (Figure II-2). The quality of the data is therefore negatively impacted. Even if statistics enabled a certain correction of field effects, it will never improve data better than what they are. The quality of the data taken is of first importance because everything depends on them later on.

A great step was done with the use of remote sensing tools such as for example the GreenSeeker© or the infrared thermometer to phenotype plants. However, another step is currently jumped with the adaptation of such remote sensing tools on mobile platforms which should improve the throughput of the measures performed enabling to tend to be freer from the environmental effect. At this end, a “phenomobile” was first developed by the High Resolution Plant Phenomics Centre (HRPPC) by Tatura Engineering and integrate three main remote sensing technologies to take phenotypic measurements at the plot scale: (i) spectral reflectance radiometer system (350nm-

2500nm), (ii) an infrared thermal imaging system for monitoring canopy temperature and a 3D imaging reconstruction tool to estimate biomass accumulation over time and plant height (CSIRO, 2014). The speed of that tool is nevertheless very limited. In parallel, remote sensing tools were also adapted on unmanned vehicle (UAV) as the so-called 'Pheno-copter' (Chapman et al., 2014). The UAVs have the great advantage to be programmed, automated and thousands of plots can be scored at the same time which enables repetitive daily measurements. Their low autonomy and the need of image processing tools to extract the data can however be seen as a limit to their development. CIMMYT and Limagrain Europe, among others, are currently working on that kind of phenotyping tools to improve their phenotyping capabilities.

This need for improvement of phenotyping methods is a global awareness. In France, the 'Phenome' project aimed to establish a national phenotyping facility able to phenotype agronomical and physiological traits on plants experiencing various climatic scenarios and trial managements associated with climate change. It is leaded by the French National Institute of Agronomical Research (INRA) and started on April 2013 (INRA, 2013).

c. Interest of the genetic material studied

This PhD is part of a long term objective of improvement of the European bread wheat tolerance to drought and heat stress.

The genetic material studied within this project comes from crosses of CIMMYT elite lines tolerant to drought and heat stress. These lines have been produced following different steps as described. First of all, parental lines were characterized for several traits which may be of interest in the targeted environments. GEI was exploited to benefit from the best of the traits available, i.e., a trait which is better expressed and useful in a given treatment will be targeted for that environment. Then crosses are made in order to enable the widest combination of useful traits for the targeted environment. At F2 stage, lines are screened for disease resistance, plant height and phenology. Finally, under drought conditions, a canopy temperature screening is done on early bulk generations to keep usually the coolest genotypes (Reynolds et al., 2009).

The parents of the three mapping populations displayed specific features for the studied field conditions. Even if the stresses experienced in a given treatment are not the same between years, each parent displayed interesting habits depending on the type of stress experienced. Pastor//HXL7573/2*Bagula and Sokoll used in PW and SW crosses were superior to Weebill1 in drought conditions. Under heat-irrigated conditions, Weebill1 and Parus/Pastor used in PW and VP crosses tended to be better than the other parents.

Within each population and whatever the trait considered an important proportion of genotypes displayed transgressive expression. This suggests that some individuals within the progeny were able to combine the best, but also the worst, from their parents. For example, under drought condition with available water at depth, several genotypes of each population displayed cooler canopy than their respective parents. This suggests that parents had different cooling canopy temperature strategy involving different genomic regions.

d. Relevant genomic regions directly usable in breeding

Before targeting genomic regions to introgress within the European germplasm, this latter one should be tested in European drought and heat stress conditions in order to check if the genomic regions involved in northern Mexico are also expressed under that environment.

Considering that this first step was confirmed, the European environment should be characterized in order to identify where these introgression must be the most beneficial, i.e., if there are different drought and heat stress scenarios occurring in Europe. Indeed, although Brisson et al. (2010) identified the pre-anthesis drought stress and the end of grain filling heat stress as the abiotic stresses responsible for the yield stagnation in Europe, some European regions might not benefit from the alleles brought by this CIMMYT germplasm, i.e., for example in drought conditions where there is no water available at depth. Finally the new source of germplasm that constitutes the CIMMYT material should be compared with the European material and check if the new germplasm brought significantly improved habits of tolerance.

Once the targeted environments are identified, the robustness of QTL found in European conditions checked, and the interest of the CIMMYT germplasm verified, several genomic regions identified may be of great interest. Within the BreedWheat project, crosses have been already conducted between CIMMYT elite lines and European elite lines. As seen in paper III, there was a strong influence of the phenology. However, some regions helped in improving grain yield and yield components. As already described for the identification of specific biomass components (I-b), some traits could be of interest in a European context. For example, to avoid the terminal heat stress damages, an increased senescence rate could be very useful. To this aim, seven genomic regions located on chromosomes 2A, 3B, 4A, 5A, 6A, 7A, and 7D were found, and especially the regions on the chromosome 7A of PW, the 6A of SW, and the 4A of VP because they explained a large part of the phenotypic variation (>16 %) (Table II-1). The 3B genomic region of PW may probably be avoided as it co-locates with a QTL for height brought by the same parent, Pastor//HXL7573/2*Bagula. This QTL might be the same one found by Bonneau et al. (2013). However, further investigations are necessary to confirm this last hypothesis as only a few markers are common to the two studies. Increasing the plant height may lead to a decreased lodging resistance very detrimental in European conditions. Moreover, in top of such a strategy, these QTL should be used with care because an accelerated senescence could decrease yield under favorable European conditions.

Table II-1: Genomic regions potentially interesting to increase the senescence rate

Population	QTL_ID	Chromosome	Hotspot	Parents carying the high value allele	Environment	effects	PEV	-log10P	QTL co-located at ±5cM
PW	Q.NDVIsen.PW.2A	2A		WB	11HI	0.002	7.4	3.4	NDVIsen(3)
PW	Q.NDVIsen.PW.3B.3	3B	HS_PW_3B	PA	12HI	0.001	6.2	9.2	NDVIpeg(1); NDVIsen(3); PH(6); PL(6)
PW	Q.NDVIsen.PW.5A	5A		PA	13DR	0.001	8.3	3.5	NDVIsen(3); SM2(5)
PW	Q.NDVIsen.PW.6A	6A		PA	12DR	0.002	7.3	4.4	CTcycle(5); CTvg(5); GFp(6); NDVIAsen(1); NDVIsen(3)
PW	Q.NDVIsen.PW.7A	7A		WB	12DR	0.004	41.7	9.9	NDVIsen(3)
PW		7A		WB	12HI	0.003	30.2	9.9	NDVIsen(3)
PW	Q.NDVIsen.PW.7D	7D		WB	12DR	0.001	5.9	5.7	NDVIAsp(5); NDVIsen(3); PH(6)
PW	Q.NDVIAsen.PW.4A.1	4A	HS_PW_4A	WB	13DR	4.003	5.3	2.5	CTcycle(5)
PW	Q.NDVIAsen.PW.6A	6A		WB	13DR	4.428	6.5	3.7	CTcycle(5); CTvg(5); GFp(6); NDVIsen(4)
SW	Q.NDVIpm.SW.6A	6A		WB	11HI	0.014	23.1	6.1	GFp(5); KM2(5); PH(5); TKW(5)
VP	Q.NDVIsen.VP.4A	4A		VB	12DR	0.002	16.6	5.7	YLD(1)

III. Perspectives

This thesis focused on the study of three bread wheat mapping populations in a three-treatment (winter sowing irrigated, winter sowing rainfed, and spring sowing heat-irrigated) and three-year (2011-2013) trial network. In total 15 trials constituted the trial network instead of 27 theoretically, i.e., 3 populations x 3 treatments x 3 years (Figure III-2, Chapter II). Every first semester from 2011 to 2013, phenotyping was performed in northern Mexico. Traits scored can be classified into agronomical, architectural, phenological, and physiological traits. Most of the traits of the three first classes were scored routinely in all trials and correspond to standard references. Physiological traits constituted by canopy temperature, NDVI, stem water soluble carbohydrates, and visual traits should be scored every year but their relevance for a given cycle should be carefully considered. Indeed, due to their environmental dependency, these traits may not be relevant every year, within a given population and treatment. So, it is highly important to be sure of the quality of the data. Through the experiences of the work performed, two points were identified as highly important to beneficiate from the physiological phenotyping: (i) the need of standard protocols and (ii) the use of high-throughput remote sensing methods.

a. A new experimental design to tackle the long term objective of the thesis

If this work should be done from now in order to deliver genomic regions for the improvement of the tolerance of European winter wheat to drought and heat stress, we would focus on the Pastor//hxl7573/2*Bagula/3/Weebill1 population because of the contrast existing between the parents in the tolerance to drought and heat stress (Pastor//hxl7573/2*Bagula better in drought; Weebill1 better in heat-irrigated conditions). The trial network would be constituted by several locations in different countries such as Mexico (Ciudad Obregon, Mexicali), Spain or Israel in order to experience different climatic scenario of drought, heat, and irrigated conditions, during two years. Through the use of a new experimental design, we will prefer to have more diverse environments and less repetition per environment.

Due to the size of the population, an unreplicated row-column experimental design would be sown including more checks widely distributed within the trials (Clarke and Stefanova, 2011). These checks should be partly common among each trial (the parents for example) and partly locally adapted elite lines to permit comparison with the local material. To have a better estimation of yield, larger plots would be required. Appropriate fertilization, weed, disease, and pest control would be required to avoid or minimize any yield limitations other than the desired ones. Concerning the "management" of the treatments (irrigated, drought, and heat-irrigated), some trials as the ones in the Ciudad Obregon platform should be managed to experience severe drought and severe heat-stress in order to have a kind of extreme scenario. Then, experimentations in various environments should lead to the establishment of a range of drought and heat stress scenarios. The objective of such network is to get access to a wide range of combinations of environmental conditions and plant reactions.

Each trial would be equipped with a set of meteorological sensors enabling a fine characterization of these environments. At the beginning of each cycle, a set of core soil samples would be taken to estimate the amount of water available in the soil in order to start the parameterization of the dynamical water balance. An environmental characterization would then be performed within the whole trial network.

The phenotyping within each location should include measurements at plot level. Figure III-1 summarizes the evolution of the plots within the crop cycle:

- 1- A phenological characterization of the plants within each location
- 2- The use of unmanned vehicle equipped with remote sensing in the thermal and reflectance wavelengths should allow the measurement of:
    - NDVI values at a frequency of three times per week within each location to establish well-shaped NDVI dynamic curves, starting at sowing and ending after having reached the physiological maturity.
    - CT at diverse periods along the crop cycle, in the morning (11am-12pm) and in the afternoon (12:30pm to 2:30pm), at least twice in the morning and in the afternoon separated by 30 minutes. This measurement needs to be taken at least six times during each development phase to ensure robustness of the plant responses. The morning measurement should reveal the most sensitive genotypes already hot when the stress is low or absent, and the afternoon scoring should reveal the most tolerant plants, i.e., the coolest plants with the more intense stress.
        - During vegetative stage when the stress is impacting plants and the plots are displaying full ground cover
        - During the grain set stage, before plants start to head
        - During grain filling, after full anthesis have been reached and before plant wilting
    - Stem water soluble carbohydrate content and biomass at anthesis
    - Before physiological maturity, the yield components within each plot must be evaluated as follows: at one end of the plots, the plant height and yield are estimated. A grain sample is taken to estimate the grain moisture within each plot and adjust grain yield from all plots within the network.

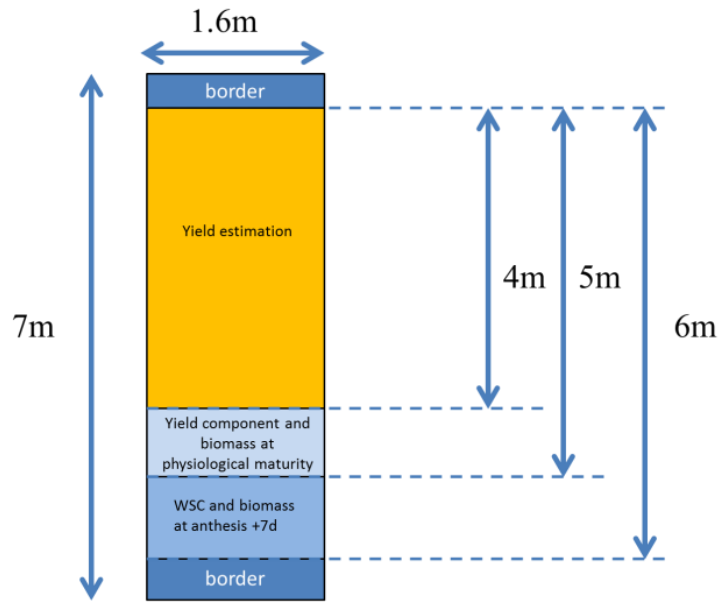


Figure III-1: Description of a typical plot in the trial network and its use during the crop cycle

The genotyping would then be performed in order to get a high density genetic map. A pipeline of data analysis would first lead to the data cleaning, the field effect adjustment, and finally to the QTL detection. The availability of a wide range of environmental data and plant responses within each trial should lead to the estimation of the effects of the QTL x Environment interaction and allows easy identification of genomic regions of interest in a given environmental conditions.

These interesting QTLs would then be addressed by breeders in order to stack them into European elite wheat lines.

b. Use of the environmental characterization methodology developed to characterize the bread wheat trial network

Limagrain Europe and the CIMMYT have a trial network worldwide where plants experienced diverse environmental conditions. To benefit from most of the alleles discovered within genetic resources, the sensitivity to the environment must be tackled. Therefore, specific alleles could be targeted to specific environments. At this end, the environmental characterization should be the first step of any multi-environmental trial network in order to determine what plants have experienced in the field

The paper 1 (Chapter III) aimed to establish a methodology to characterize an abiotic stress trial network. Its flexibility enables its wide use whatever the stress considered and the trial network. The methodology can therefore be applied to any testing sites as long as some basic data are available. To be performed, this environmental characterization requires:

- The phenological characterization of the plant material, i.e., the identification of the main phases of development.
- Meteorological data relevant for the area considered (Bouffier et al., 2014). A daily step is sufficient.
    - In the case where drought should be characterized, a water balance is required on the same time-step than the meteorological data. The methodology proposed by (Allen et al., 1998a) is very useful and easy to follow.
- Knowledge about any other potential grain yield limitations if not controlled (disease for example)
- Threshold from which an abiotic factor impact plants

The environmental characterization was performed following four steps. Indeed, within the same germplasm, if not the stress thresholds could be different, it is necessary to:

- 1/ (i) Identify all the environmental factors varying within and between each trial of the network and (ii) Determine from the literature or arbitrarily or from experiments, as many thresholds as potential stresses are expected within the network. The stress thresholds are then combined with their corresponding environmental factors (e.g., a threshold of 30°C applied to the maximum daily temperature) leading to the establishment of the limiting factors
- 2/ The occurrence of each limiting factor is computed within each developmental phase established within the whole trial network (e.g., the number of growing degree days during the grain set phase where the limiting factor ‘30°C over the maximum daily temperature’ is observed). This step

corresponds to the establishment of the environmental covariates within the whole network. Each developmental phase within each trial of the network is then characterized for the whole range of limiting factors. A matrix is then obtained with in rows, all the trial of the network, and in columns, each environmental covariate

- 3/ Run a hierarchical clustering in order to identify common stress scenario experienced by plants within the network.
- 4/ Establish a certain number of clusters respecting the parsimony principle (i.e., number of cluster cannot exceeds the number of trials within the network minus one). At that step, an environmental covariate is then selected to represent its cluster.

The analysis can be easily automated and new covariates can be therefore determined every year to analyze the MET network results. A probabilistic approach can also be performed to help breeder with the characterization of the environment. It corresponds to the environmental characterization method proposed by Chenu et al. (2011). However, to our sense, both methods are complementary. The method proposed by Chenu et al. (2011) is of wide help to calibrate the trial network, i.e., to estimate whether the locations within the Target Population of Environments represent the major stress types structuring the market. Then, the methodology proposed in Bouffier et al., (2014) is of more practical use for breeders during a given crop cycle as it enables the estimation of the actual stresses plants really experienced in the field in order to understand their behavior.

c. Winter x spring wheat crosses

In Europe, most of cultivated wheat is classified as winter wheat whereas northern Mexican CIMMYT wheat is almost exclusively spring wheat. The long term objective of this work is the improvement of the tolerance of winter European bread wheat to drought and heat stress. However, Limagrain Europe has also a spring wheat breeding program. Tolerance sources or genomic regions to drought and heat stress found in this study could be used to improve this germplasm. The two following steps would therefore be necessary before the diffusion of CIMMYT QTL into Limagrain

Europe germplasm: (i) the validation of the robustness of the QTL found in Mexican conditions in an European context, for example in the south of Spain, at Limagrain Iberica's experimental station (Carmona, SP), and (ii) winter x spring wheat backcrosses to check the expression of spring wheat QTL for drought and heat stress tolerance introgressed into a winter genetic background.

The first point has already been anticipated. Indeed, in 2011, the germplasm studied in northern Mexico was sent to southern Spain for seed multiplication in order to evaluate this material under European drought and heat stress conditions. The first yield trials were harvested during the summer 2014 and analyses are in progress. QTL detection would be performed soon in order to compare QTL robustness with northern Mexican experiments.

The second point should start the next season if valuable genotypes appeared within the analyses. Preliminary analyses done in the Spanish nursery indicated that several genotypes displayed a good agronomic level. As a consequence, backcrosses using the elite European line as recurrent parent, either in spring or winter material, could be done with the best lines. However, as seen in Paper 3, parents of the populations segregate for the Ppd-B1 and probably for some *Vrn* genes. The use of such marker information should ease the selection of genotypes harboring the desirable photoperiod and vernalization combinations.

d. To go further on genetics

With the actual advance of genotyping, the number of markers mapped within each genetic map could be considered as really low. Densifying the genetic maps with more SNP markers would open numerous opportunities such as (i) the use of genomic selection approach which would be very relevant especially when our QTL analysis revealed that the majority of QTL found displayed low effects and circumvent some pitfalls such as (ii) the impact of the segregation distortion (Wang et al., 2005).

Moreover, a point we could not exploit during the study is the existing connection between populations. Indeed, the parent Weebill1 is the male of the populations Pastor//hxl7573/2*Bagula/3/Weebill1 and Sokoll/Weebill1. Moreover, the

line Pastor is shared between the Pastor//hxl7573/2*Bagula/3/Weebill1 and Vorobey//Parus/Pastor population. A consensus map between the three populations could be build which may allow the comparison of the genomic regions involved in the tolerance to drought and heat stress between the different populations. For this purpose, the software MC-QTL (Jourjon et al., 2005) could therefore be used.

To finish with, there is an interesting QTL hotspot on 5B of SW. I would suggest starting a project in order to clone this QTL by "positional cloning". More recombinations in the area of interest on the 5B of SW should be obtained with near isogenic lines and allow a finer identification of the QTL in the area of interest. To this end, the newly published chromosome-based draft sequence (International Wheat Genome Sequencing Consortium (IWGSC), 2014) could be of great help.

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Annexes

Annex 1: The water balance equations and methodology used to follow the amount of water available in the soil during the crop cycle of each trial within the trial network (source: Allen et al., 1998b)

- **[$ET_{c,i}$]:** Evapotranspiration of a spring wheat crop at Ciudad Obregon, Son., in optimum conditions (mm/day):
  - (1) $ET_{c,i} = k_{c,i}.ET_{0,i}$
    - $k_{c,\,i}$ => (Allen et al., 1998c); Values for spring wheat along crop cycle; (no unit)
    - $ET_{0,\,i}$ => Daily data from the meteorological station at Ciudad Obregon, Son.; (mm/day)
- **[$Z_{r,i}$]:** Daily roots depth (m) ⇔daily volume of soil explored by roots (m^3)
  - (2) $Z_{r,i}$
    - $Z_{r,\,i}$ => putative linear growth from sowing data ($Z_{r,sowing}$=-0.03m) to mid anthesis ($Z_{r,\,anthesis}$=-1.20m). Then, 1.20m until end of crop cycle; (m)
- **[TAW_i]:** Daily theoretical Total Available Water for plant (mm of water column)
  - (3) $TAW_i = 1000.\left(\frac{\theta_{FC}}{100} - \frac{\theta_{PWP}}{100}\right).Z_{r,i}$
    - θ_{FC} => Point of field capacity per layer known (Pedological studies of the CIMMYT) – Constant per layer; (%)
    - θ_{PWP} => Permanent wilting point per layer known (Pedological studies of the CIMMYT) – Constant per layer; (%)
    - $Z_{r,\,i}$ => Known at the step (2); (m)
- **[p_i]:** Average fraction of TAW_i that can be depleted from the root zone before reaching moisture stress (no unit)
  - (4) $p_i = p_{table\ 22} + 0.04(5 - ET_{c,i})$
    - $p_{table\ 22}$ => ; Values for spring wheat considering $ET_{c,i}$=5mm/day; (no unit)
    - $ET_{c,\,i}$ => given at the step (1); It is used in order to fit the the "$p_{table\ 22}$" value for 5mm/day at any daily ET_c;(mm/day)
- **[RAW_i]:** Daily readily available water (mm)
  - (5) $RAW_i = p_i.TAW_i$
    - p_i => given at the step (4); (no unit)
    - TAW_i => given at the step (3); (mm)
- **[$D_{r,\,i-1}$]:** Initial depletion (in order to start the water balance) (mm)
  - (6) $D_{r,i-1} = 1000\left(\frac{\theta_{FC}}{100} - \frac{\theta_{i-1}}{100}\right)Z_{r,i-1}$
    - θ_{i-1} => The average soil water content for the effective root zone; Given by the first soil sampling; (%)
    - θ_{FC} => Given by pedological studies of the CIMMYT; (%)
    - $Z_{r,\,i-1}$ => Given at the step (2); (m)
- **[$D_{r,\,i}$]:** Daily water balance expressed in terms of depletion at the end of the day (mm)

- (7) $D_{r,i} = D_{r,i-1} - (P - RO)_i - I_i - CR_i + ET_{c,i} + DP_i$
  - $D_{r,i}$ => Root zone depletion at the end of the day "i"; (mm)
  - $D_{r,i-1}$ => Water content in the root zone at the end of the previous day, "i-1"; (mm)
    - To start the water balance, need the Dr, initial: given at the step (6)
  - P_i => Precipitation on day "i"; (mm)
    - Known with meteorological data at Ciudad Obregon, Son.
  - RO_i => Runoff from the soil surface on day "i"; (mm)
    - As the slop of the field at Cd. Obregon is close to 0, rain during crop cycle were not heavy rain ➔ non-significant term
  - I_i => Net irrigation depth on day "i" that infiltrates the soil (mm)
    - Known with crop management records or soil sampling
  - CR_i => Capillary rise from the groundwater table on day "i"; (mm)
    - As the water table is deeper than 1m to the bottom of the crop at Cd. Obregon ➔ non-significant term (Allen et al., 1998e)
  - $ET_{c,i}$ => Crop Evapotranspiration on day "i"; (mm)
  - DP_i => Water loss out of the root zone by deep percolation on day "i"; (mm)
    - DP_i >0 if more water input than what the soil can stock for plant

[$k_{s,i}$]: Water stress coefficient: transpiration reduction factor dependent on available water [0 ; 1]; (no unit)

- (8) $if\ D_r \geq TAW, \quad k_s = 0$
- (9) $if\ D_r \geq RAW, \quad k_s = \frac{TAW - D_r}{(1-p)TAW}$
- (10) $if\ D_r < RAW, \quad k_s = 1$
  - TAW => given at the step (3); (mm)
  - D_r => given at the step (7); (mm)
  - p => given at the step (4); (no unit)

[$ET_{c,adj}$]: Real Evapotranspiration of the crop (=adjusted crop Evapotranspiration); (mm)

- (11) $ET_{c,adj,i} = (k_{s,i}k_{cb,i} + k_{e,i})ET_{0,i}$ *or* (12) $ET_{c,adj,i} = k_{c,i}k_{s,i}ET_{0,i}$
  - Dual crop coefficient approach: (11)
    - Comments: higher precision but more complicated
    - $k_{s,i}$ => given at the steps (8), (9) or (10)
    - $k_{cb,i}$ => basal crop coefficient => Coefficient to estimate the transpiration component of the ET (Allen et al., 1998d); Values for spring wheat along crop cycle
    - $k_{e,i}$ => soil evaporation coefficient => Coefficient to estimate the evaporation component of the ET (Allen et al., 1998d); Values given depending on the wetness of the soil, …
    - $ET_{0,i}$ => Daily data from the meteorological station at Ciudad Obregon, Son.; (mm/day)

- Single crop coefficient approach : (12)
  - Comments: less precision but accessible
  - $k_{s,\ i}$ => given at the step (8), (9) or (10)
  - $k_{c,\ i}$ => (Allen et al., 1998c); Values for spring wheat along crop cycle; (no unit)
  - $ET_{0,\ i}$ => Daily data from the meteorological station at Ciudad Obregon, Son.; (mm/day)