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**Drought affects abortion of reproductive organs by exacerbating developmentally-driven processes, via expansive growth and hydraulics**

Running title: Ovary or grain abortion, carbon and hydraulics

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## Highlight

Water deficit primarily impacts grain set through interaction between reproductive organs and hydraulics, before the carbon status of reproductive organs is affected

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## Abstract

Abortion of reproductive organs is a major limiting factor of yield under water deficit, but is also a trait selected for by evolutionary processes. Youngest reproductive organs must be prone to abortion so older organs can finish their development in case of limited resources. Water deficit increases natural abortion via two developmentally-driven processes, namely a signal from the first fertilized ovaries and a simultaneous arrest of the expansive growth of all ovaries at a precise stage. In maize (*Zea mays*) subjected to water deficits typically encountered in dryland agriculture, these developmental mechanisms account for 90 % of drought-associated abortion and are irreversible three days after silk emergence. Consistently, transcripts and enzyme activities suggest that the molecular events associated with abortion affect expansive growth in silks whereas ovaries keep a favourable carbon status. Abortion due to carbon starvation is only observed for severe drought scenarios occurring after silking. Both kinetic and genetic evidence indicate that vegetative and reproductive structures share a partly common hydraulic control of expansive growth. Hence, the control of expansive growth of reproductive structures probably has a prominent effect on abortion for mild water deficits occurring at flowering time, while carbon starvation dominates in severe post-flowering drought scenarios.

**Key-words:** carbon status, expansive growth, grain abortion, grain set, hydraulics, maize, ovary abortion, water deficit

## Introduction

The development of reproductive organs (fruits, seeds and their precursors, ovaries and ovules) plays a dominant role in global crop production (Liu *et al.*, 2013). Among the top fifteen major crops worldwide, ten are consumed as fruit or grain (Ross-Ibarra *et al.*, 2007) and 75% of the total worldwide crop yield comes from fruit and grain crops (Ruan *et al.*, 2010). Fruit and grain abortion under water deficit is a major limiting factor for achieving crop yield potential (Boyer and McLaughlin, 2007; Patrick and Stoddard, 2010; Ruan *et al.*, 2010). Indeed, abiotic stresses during early reproductive stages often result in failure of fertilization or abortion of fruits and seeds (Thakur *et al.*, 2010), thereby dramatically decreasing crop yield (Setter *et al.*, 2011; Kakumanu *et al.*, 2012). For example, drought at the flowering stage causes severe grain abortion in maize (*Zea mays*) (McLaughlin and Boyer, 2004) and heat stress can cause up to 80% flower abortion in tomato (*Solanum lycopersicum*) (Ruan *et al.*, 2010). Hence, reducing the sensitivity of fruit and seed set to abiotic stresses is a viable option for sustaining crop yield in the face of climate change.

In the plant life cycle, the early stages of fruit and grain development are the most sensitive to abiotic stresses such as heat, drought or cold (Barnabas *et al.*, 2008; Hedhly *et al.*, 2009; Thakur *et al.*, 2010). The period with maximum risk of abortion extends, in most species, from the beginning of flowering time to the end of cell division in the embryo or endosperm (Hedley and Ambrose, 1980; Ney *et al.*, 1993; Patrick and Stoddard, 2010). No abortion occurs any more after the latter stage so the risk of abortion occurs during a very limited period of time in a wide range of species including crops and non-cultivated trees or herbs (Stephenson, 1981). The failure of reproductive organs during this period can occur before and after fertilization, and is termed 'abortion' here for simplicity. Recent reviews on this topic have focused on the importance of hormones (Sotelo-Silveira *et al.*, 2014) or of carbon metabolism (Ruan *et al.*, 2010; Liu *et al.*, 2013) during this short period of time. The present paper examines the role of developmental processes, in particular the interaction between reproductive organs of different ages in the same plant and the role of the superposition of controls at organ and at plant level. This involves mechanisms such as expansive growth, hydraulics and carbon metabolism at the reproductive organ and whole-plant levels.

From an evolutionary point of view, youngest reproductive organs should be the most prone to abortion to ensure that older reproductive organs that are already developing have access to sufficient resources and can result in viable seeds. Indeed, reproductive organs of different ages usually coexist in a plant or an inflorescence (Stephenson, 1981), suggesting that interactions between them may act as feedbacks that result in a developmental control of abortion. Even in crop plants, grain abortion can be favorable in very dry climates by securing full development of a limited number of grains. In wheat (*Triticum aestivum*), an allele causing reduction in grain number has a highly positive effect on yield under severe water deficit but not in milder scenarios in which yield is associated with high grain number (Parent *et al.*, 2017). The hypothesis proposed in this paper is that, whereas the evolutionary trend to favour abortion in dry conditions is observed in most species, carbon availability to developing ovaries is not always the triggering mechanism of abortion. We present evidence from previously published studies for a role of developmental processes, which can avoid carbon shortage in reproductive organs by ‘mimicking’ carbon-starvation-driven abortion before any carbon stress occurs at the plant or ovary level.

### **Developmental control of abortion**

*Abortion occurs at preferential locations within or among inflorescences.*

In pea (*Pisum sativum*), a steep gradient of development exists within a single plant: oldest basal pods begin seed filling whereas apical reproductive organs are still at early stages in the shoot apex, with all intermediate stages between them (Fig. 1A; Ney and Turc, 1993). The same occurs in the maize ear, in which basal ovaries are older than apical ovaries (Kiesselbach, 1949), and in the sunflower (*Helianthus annuus*) capitulum in which central akenes are the youngest because of centripetal initiation of floret primordia (Palmer and Steer, 1985; Dosio *et al.*, 2006). In these three cases, a clear localization of aborted ovaries is observed in regions carrying the youngest ovaries, i.e. at the shoot apex in pea (Fig. 1A), at the ear apex in maize (Fig. 2A) and at the capitulum centre in sunflower (Connor and Sadras, 1992; Sinsawat and Steer, 1993; Alkio *et al.*, 2003). Water deficit does not change this pattern, but essentially extends the region of shoot/inflorescence in which ovaries abort (Fig. 1; Fig. 2). This suggests that a link may exist between position, age, water deficit and abortion frequency. This link is also observed in other species in which the spatial gradients

of abortion frequency coincide with an opposite gradient of pollination or fertilization (see review by Stephenson (1981)), for ovaries located within a fruit (Rocha and Stephenson, 1991; Susko, 2006), in different fruits of an inflorescence (Cawoy *et al.*, 2007) or in different inflorescences of a plant (Ney *et al.*, 1994; Egli and Bruening, 2006).

#### *Spatial gradients of ovary abortion as a result of developmental sequences in maize and pea*

The maize ear is a coalesced inflorescence composed of spikelet pairs arranged in rings sequentially initiated at the ear apex (Bonnett, 1940; Kiesselbach, 1949). These rings are therefore cohorts of ovaries that are initiated simultaneously. Styles and stigma of female flowers, called silks, must rapidly elongate at flowering time to emerge from bracts and collect pollen originating from the apical male inflorescences (or tassels) (Weatherwax, 1916; Kiesselbach, 1949). The first silks to emerge originate from basal spikelets, and the last ones from apical spikelets. Two mechanisms account for early ovary abortion and result in the typical distribution of aborted ovaries at the ear tip (Fig. 2A), which contrast with the random distribution observed with later carbon-starvation-based grain abortion under severe drought (Fig. 2B).

- The fertilization of basal, oldest, ovaries is sufficient to stop the development of younger, apical, ovaries and cause their abortion. This happens, for example, when fertilization occurs at two different dates, either naturally or via an artificial a-synchronous pollination (Freier *et al.*, 1984; Cárcova and Otegui, 2001). In this case, young ovaries located at the tip of the ear abort, even in the absence of carbon deficiency or water deficit (Fig. 2A, "GP"). This suggests that ovaries progressively lose competence to develop into grains after the fertilization of the first older ovaries, probably because of a signalling process. This explains why aborting ovaries are located at the ear tip, where youngest ovaries are located, but probably not the increased abortion in case of water deficit. The nature of the signal remains unknown but may involve cytokinins synthesized during the early development of grains needed for the development of starchy endosperm (Brugiére *et al.*, 2003). Other hormones have been hypothesized to contribute to this systemic signal, such as ABA (Wang *et al.*, 2002; Setter and Parra, 2010; Setter *et al.*, 2011) or ethylene (Cheng and Lur, 1996; Habben *et al.*, 2014).
- The temporal pattern of ear development can also cause abortion of ovaries located close to the ear tip. In our analysis, abortion rate is accounted for by the superposition of (a) the

sequential emergence of silks originating from ovaries of different cohorts along the ear with (b) one event occurring on a single day for the whole ear, namely the simultaneous arrest of the growth of silks originating from all ovary cohorts. Abortion occurs in all ovaries that are not pollinated two days before silk growth arrest (Fig. 2C). This superposition of events explains why aborting ovaries are located at the ear tip, which cannot be pollinated before silk growth arrest because they are younger than basal ovaries. In contrast with the signalling process presented above, this temporal process also explains why the aborted region of the ear increases in size when silk growth rate decreases with water deficit (Fig. 2A, "WD"). Indeed, the decreased silk growth rate due to water deficit delays silk emergence so the time from silk emergence to silk growth arrest is shorter in water deficit (typically 2-3 days) than in well-watered plants (typically 7-8d, Oury *et al.*, 2016b). A greater number of ovary cohorts therefore cannot be pollinated before silk growth arrest, and eventually abort. The link between silk growth arrest and abortion may be due to the ability of pollen tubes to grow into the silks. Indeed, during the normal pollination process, tissue stiffening occurs along the silk after the passage of the first pollen tube, thereby blocking the progression of additional pollen tubes (Kapu and Cosgrove, 2010). If tissue stiffening accompanies the early arrest of silk growth in water deficit, as it does in growing leaves (Chazen and Neumann, 1994; Vincent *et al.*, 2005) or roots (Zhu *et al.*, 2007), it may block the progression of the first pollen tube therefore impeding fertilization. The limit of 2 days before silk growth arrest might be linked to the necessary time for a pollen tube to reach the ovule through the silk (Miller, 1919). Alternatively, it could correspond to the end of the period of sensitivity of ovaries to plant water status which occurs when ovary tissues become hydraulically isolated from the mother tissues a few days after fertilization (Westgate and Thomson Grant, 1989; Bradford, 1994). Overall, 90 % of drought-associated abortion was already irreversible three days after the emergence of the first silk, when silk emergence stopped in plants subjected to water deficit (Fig. 3; Oury *et al.*, 2016b).

Pea is a species with indeterminate flowering in which each phytomere, from the first reproductive phytomere and above, carries an inflorescence originating from an axillary bud (Fig. 1A). The stage "open flower", synchronous with pollination, occurs first at the most basal reproductive phytomere and then progresses sequentially towards apical positions. The duration of flowering, and therefore the developmental lag time between the



fertilization of basal and apical organs, is typically 12-20 days in well-watered plants (Ney and Turc, 1993; Ney *et al.*, 1994; Guilioni *et al.*, 2003), i.e. much longer compared with maize. As in the case of maize, abortion occurs in youngest organs: abortion frequency is 100% in the most apical reproductive organ regardless of watering treatments (Fig. 1B). When plants are subjected to soil water deficit during flowering, abortion occurs at more basal positions than in well-watered plants (Ney *et al.*, 1994; Guilioni *et al.*, 2003; Fig. 1). The final number of reproductive phytomeres that emerge from the apical bud is also reduced by water deficit due to an early arrest of phytomere initiation (Ney *et al.*, 1994; Guilioni *et al.*, 2003). This event is synchronous with a simultaneous cessation of growth and development of all the phytomeres located in the apical bud (Kelly and Davies, 1988; Roche *et al.*, 1998). Leaf emergence and flowering therefore stop simultaneously, 4-10 days (2-5 phyllochrones) earlier in plants subjected to soil water deficit compared to well-watered plants (Ney *et al.*, 1994; Guilioni *et al.*, 2003). As in the case of maize, the abortion frequency of the reproductive organs is explained by the organ age (days from pollination) at this critical stage (Fig. 1C). Abortion occurs in all reproductive organs that are pollinated less than 1d before apex growth arrest, whereas all reproductive organs that have been pollinated since more than 7 days at that date complete their development (Fig. 1C). A common relationship between organ age and abortion rate was observed for various levels of soil water deficit and different genotypes (Fig. 1C, data from Ney *et al.* (1994) and Guilioni *et al.* (2003)).

Abortion occurring in pea and maize therefore present striking similarities, shared with other species (i) The presence of fertilized reproductive organs affects the development of young, non-fertilized ovaries in maize, pea (Guilioni *et al.*, 1997) and other species (Stephenson, 1981), even in the absence of any carbon limitation or abiotic stress. (ii) The distribution of abortion frequency in the youngest ovaries under water deficit is associated with an early arrest of growth that occurs simultaneously for all the silks of the maize ear or for all the phytomeres in the pea apical bud. A similar situation is observed in sunflower, in which one observes a synchronous cessation of the development of all youngest organs located in the centre of the capitulum, due to the arrest of capitulum meristem growth (Dosio *et al.*, 2006). In these three species, a gradient of reproductive organ age in the shoot or inflorescence results in abortion for organs younger than a threshold at a given date, associated with

cessation of growth. The effect of water deficit is mainly to amplify these effects, in relation with the expansive growth of silks, capitulum or shoot apex.

### **Is ovary/grain abortion in water deficit caused by carbon starvation or by developmental processes?**

The mechanisms presented above are at first sight contradictory with the well-accepted theory that abortion in maize is linked to carbon starvation in young ovaries, based on a series of experiments showing that sucrose feeding can partly reverse the effect of water deficit on abortion (Boyle *et al.*, 1991; Zinselmeier *et al.*, 1995a; Zinselmeier *et al.*, 1999; McLaughlin and Boyer, 2004). In these experiments, the sucrose flux to ovaries decreases to near-zero but is partly restored upon sucrose feeding (Makela *et al.*, 2005). Enzyme activities and gene expressions of cell wall invertases increase 5-8 days after silking in ovaries of well-watered plants, whereas they remain low under water deficit (Zinselmeier *et al.*, 1995b; Zinselmeier *et al.*, 1999; McLaughlin and Boyer, 2004). This has led several authors to consider cell wall invertases, in particular *INCW2*, as a causal link between water deficit, sugar availability to ovaries and ovary abortion (Boyer and McLaughlin, 2007; Ruan *et al.*, 2010). It was recently demonstrated that the targeted overexpression in developing maize ovaries of a gene involved in sugar signalling improves maize yield under water deficit by reducing grain abortion (Nuccio *et al.*, 2015). This was interpreted as an evidence for the central role of sucrose sensing and carbon metabolism in grain set and abortion (Smeekens, 2015; Griffiths and Paul, 2017).

Several arguments lead us to consider that “developmental” and “carbon-starvation-based” abortion might correspond to events occurring at two separate phenological stages during maize reproductive development. First, it is important to note that all experiments with sucrose perfusion reported in the former paragraph follow a common protocol, in which a water deficit is imposed for six days following silk emergence (Zinselmeier *et al.*, 1999). As a consequence, mechanisms occurring earlier, such as silk growth arrest, cannot be observed in the protocol followed by Boyle *et al.* (1991) and in further studies. Secondly, this protocol causes a drastic reduction in photosynthesis, which is not the case in natural drought scenarios in which photosynthesis is in most cases at least partially maintained. Finally, this protocol involves artificial synchronous pollination 5-7 days after silk emergence, so the

consequences of asynchronous pollination cannot be observed. The protocol of Boyle *et al.* (1991) and further studies is, therefore, appropriate to characterize carbon-starvation-associated processes leading to abortion but, by its characteristics, cannot account for other causes. It is noteworthy that this protocol results in a random abortion on the ear (Fig. 2B), whereas water deficits in natural conditions result in abortion at the ear tip, in both field and controlled conditions (Fig. 2A). This reinforces the possibility that carbon-starvation-based and development-based abortion may coexist.

In the experiments reported in Fig. 4, where plants were subjected to a moderate water deficit (soil water potential between -0.25 and 0.30 MPa), the analysis of transcript abundance suggests no carbon deficiency in either ovaries or silks (Fig. 4). The amount of sugars and starch in ovaries even tended to be higher in water deficit than in well-watered plants (Oury *et al.*, 2016a), as it did in other experiments including soil water shortage (Andersen *et al.*, 2002; Nuccio *et al.*, 2015) or osmotic stress due to salt (Henry *et al.*, 2015). The most striking changes in gene expression were observed in silks rather than ovaries, and were related to genes involved in cell wall mechanical properties, such as expansins, pectinases, pectinesterases, cellulases or wall-associated kinases. A counter example could be the higher vacuolar acid invertase activity in well-watered than in droughted plants. However, the latter was probably associated with high tissue expansion rate, as it does in several studies involving pea epicotyl, maize roots and silks, *Arabidopsis thaliana* roots and cotton (*Gossypium hirsutum*) fibers (Morris and Arthur, 1984; Sturm and Tang, 1999; Tang *et al.*, 1999; Kohorn *et al.*, 2006; Wang *et al.*, 2010). A favourable carbon status of ovaries and silks in droughted plants is also suggested by the level of trehalose-6-phosphate (T6P), which acts as a signalling intermediate for reporting the cellular sucrose status (Lunn *et al.*, 2006; Yadav *et al.*, 2014). T6P content is increased in maize ovaries during salt stress (Henry *et al.*, 2015) and water deficit (Nuccio *et al.*, 2015). The reduction of transcript abundance of trehalose-6-phosphate phosphatase (TPP), the enzyme converting T6P to trehalose, observed in silks of plants subjected to a moderate water deficit (Oury *et al.*, 2016a) suggests an increased level of T6P in silks.

In ovaries, the main changes in carbon-related transcript amounts and enzyme activities occur only 5-8 days after silk emergence (e.g. Andersen *et al.*, 2002; Oury *et al.*, 2016a), i.e.

when ovaries had already engaged in the abortion process for several days (Fig. 3). The same conclusion applies to changes in concentrations and amounts of sugars in ovaries. Hence, it has been proposed that these late changes in carbon metabolism of ovaries are a consequence rather than a cause of the beginning of ovary abortion (Oury *et al.*, 2016a). The absence of appreciable effect of moderate water deficit on carbon status is consistent with studies indicating that moderate water deficits induce a carbon satiation because expansive growth of sink organs, including peach (*Prunus persica*) and tomato fruit, sunflower capitulum, arabidopsis expanding leaves, is more affected than photosynthesis (Hummel *et al.*, 2010; Dosio *et al.*, 2011; Muller *et al.*, 2011; Pantin *et al.*, 2013). Hence, plants subjected to moderate water deficit show ovary abortion that is probably not linked to carbon deprivation, in opposition to the later and intense water deficit imposed in the protocol of Boyle *et al.* (1991) and further studies of the Boyer's group.

The above paragraphs suggest that two successive periods of sensitivity of reproductive organs coexist in maize. The first period is associated to developmental processes (arrest of silk growth and first fertilization), characterized by abortion located near the ear tip (Fig. 2A). The second period, linked to carbon deprivation occurs after fertilization, is only observed under severe water deficit that drastically decreases photosynthesis and results in a random distribution of abortion on the ear (Fig. 2B).

### **Vegetative and reproductive structures share a partly common hydraulic control of expansive growth**

The developmental controls presented above suggest a major role for expansive growth on grain abortion in maize, pea and sunflower. In maize, the control of silk elongation might be a key for grain abortion, consistent with the fact that the anthesis-silking interval (ASI) is closely correlated with yield in water deficit, both phenotypically and genotypically (Bolaños and Edmeades, 1996; Ribaut *et al.*, 1997; Bruce *et al.*, 2002). Drought-induced ASI is linked to silk growth because the rates of silk elongation and of cell division are both reduced by water deficit, resulting in a delayed silk emergence, whereas anthesis is essentially unaffected by water deficit (Fuad-Hassan *et al.*, 2008). Expansive growth, defined as an increase in organ volume via water entry into growing cells, depends on the interplay of cell wall extensibility and of gradients of water potential and hydraulic conductance on the

water pathway from the xylem to cells (Lockhart, 1965). It is loosely coordinated with carbon accumulation, in particular via the contribution of sugars to osmotic adjustment (Hummel *et al.*, 2010). However, a limited contribution of carbon supply to expansive growth is usually observed under water deficit (Hummel *et al.*, 2010; Muller *et al.*, 2011; Tardieu *et al.*, 2011; Fatichi *et al.*, 2014).

Diel kinetics of silk elongation rate strongly suggest a hydraulic control for silk elongation (Turc *et al.*, 2016): (i) the half times of change in silk elongation rate is about 30 min upon changes in soil water potential (Fig. 5B) or evaporative demand (Fig. 5A), (ii) maximum silk elongation rate is observed during the dark period when photosynthesis is arrested but plant water status is most favourable because of a low evaporative demand (Fig 5A), (iii) silk elongation rate largely decreases with evaporative demand, even when ear and silk transpiration is impeded, so it is the whole-plant water status that affects silk growth (Turc *et al.*, 2016). These characteristics are similar to those in leaves, in which the half times of changes in elongation rate are 20-30 min upon changes in soil water potential or evaporative demand, the elongation rate is maximum during nights and the day-time elongation rate is closely related to evaporative demand (Caldeira *et al.*, 2014). Consistently, both leaves and silks are maternal tissues directly connected to the xylem (Heslop-Harrison *et al.*, 1984; Tao *et al.*, 2006), whereas the embryo is largely isolated hydraulically from maternal tissues (Felker and Shannon, 1980; Miller and Chourey, 1992). The genetic variability of the sensitivity of silk elongation rate to water deficit is related to that of leaves. It was estimated in 8 maize inbred lines carrying QTL alleles for contrasting sensitivity of leaf elongation rate to soil water potential (Fig 5C). This has allowed identification of the soil water potential that stops elongation of both silks and leaves of each line (Fig. 5C). Strikingly, the values corresponding to silks were closely related to those in leaves in this set of lines (Fig. 5D), thereby suggesting that alleles affecting leaf elongation also affect silk elongation. Consistently with Westgate and Boyer (1985), silks were more sensitive than leaves because the regression line was above the 1:1 line meaning that, for a given maize line, silks stopped elongation at soil water potentials higher than leaves (Fig. 5D).

Taken together these elements suggest a commonality of mechanisms controlling the response of elongation in leaves and silks. This conclusion cannot be extended to the growth

of the endosperm and of the embryo that are weakly connected hydraulically to the stem, with a disruption of vascular elements in the ovary pedicel (Kiesselbach, 1949; Felker and Shannon, 1980; Miller and Chourey, 1992), resulting in lower symptoms of water deficit than in maternal tissues (Yu and Setter, 2003).

Recent studies propose that the diurnal time courses of leaf elongation rate closely follows that of xylem water potential over changes in evaporative demand (Caldeira *et al.*, 2014; Tardieu *et al.*, 2015). The response curve of leaves and silks elongation rates to soil water potential during the night can be interpreted as a response to xylem water potential because water potentials equilibrate in silks, leaves, in the xylem and in the soil during the night, in the absence of transpiration. The model of Tardieu *et al.* (2015) uses this relationship to simulate the time course of leaf elongation rate during the day, in such a way that diurnal variations in elongation rate reflect those of xylem water potential following changes in evaporative demand and soil water potential. This conclusion can probably be extended to silks that are also directly connected to the stem xylem. The similarity of time courses of silk and leaf elongation rates, but also the genetic correlation between them, lead us to propose that silk elongation rate also follows xylem water potential, in spite of the fact that these are two different organs carried by plants at different phenological stages. The expansive growth of leaves and silks may therefore be governed by common alleles that control cell wall mechanical properties (Cosgrove, 2005) or the water entry into growing cells via changes in hydraulic conductance as modelled in Tardieu *et al.* (2015). Expansins may be involved in the common control, via their effect on cell wall properties (Zhang *et al.*, 2014). This is consistent with the fact that transcript amounts of genes involved in water movements (aquaporins) and in cell wall properties (expansins, XET) are more expressed in silks of well-watered than of droughted plants (Oury *et al.*, 2016a).

The link between the sensitivities of leaf elongation rate and silk elongation rate via hydraulic processes probably explains the common genetic control observed between leaf elongation and anthesis-silking interval (Welcker *et al.*, 2007). Anthesis-silking interval has long been considered as a trait associated with maintenance of maize yield in water deficit, so hydraulic processes may eventually have a role on grain abortion via silk elongation. This may explain the unexpected result that the sensitivity of grain number to water deficit in the

field has a high genetic correlation with the sensitivity of leaf growth to water deficit in young plants assessed in a phenotyping platform (Chapuis *et al.*, 2012).

### Concluding remarks

Grain or ovary abortion is, from an evolutionary point of view, a feedback mechanism that allows plants to produce at least a few viable seeds, whereas there would be a risk that no seed is viable if all ovaries continued development after flowering time under unfavourable conditions. Plants carrying such alleles have therefore not been able to reproduce during very dry years. In agronomic conditions, a favourable effect of abortion on yield can be observed in extreme drought scenarios by ensuring adequate grain filling in spite of limited resources (Parent *et al.*, 2017). However, a maximum grain number, involving minimum abortion rate, is a favourable trait in most drought scenarios (Millet *et al.*, 2016; Parent *et al.*, 2017), so breeding for limited abortion under water deficit is needed.

In this context it would be tempting to consider that carbon availability to ovaries is the triggering mechanism causing abortion, whereas it is proposed here that developmental mechanisms “mimic” an effect of carbon supply before any carbon starvation is sensed in reproductive organs. These mechanisms involve the effect of fertilized reproductive organs on the development of younger organs, the superposition of a gradient of ovary development with a “stop” signal occurring on a given day and, in maize, hydraulic processes that affect silk elongation rate. However, carbon-starvation-based and water-fluxes-based abortion are not mutually exclusive, and probably correspond to different phenological stages in maize. Early developmental abortion is prominent when the water deficit is moderate during flowering time, as it is in more than 40% drought scenarios in Europe (Harrison *et al.*, 2014). Carbon-starvation-based abortion occurs later, in particular when a severe water deficit at flowering time causes a drastic reduction in photosynthesis. This case is estimated as 18% of drought scenarios in Europe (Harrison *et al.*, 2014).

The results reviewed here have large consequences for both modelling and breeding.

- The timing and preferential location of abortion can be accounted for by models of reproductive organogenesis, which simulate the distribution and hierarchy of organs at any time of the reproductive period (e.g. Ney and Turc, 1993; Moreau *et al.*, 2007; Chenu *et al.*, 2009). Coupled with rules of assimilate partitioning, these models allow one to account for spatial and temporal distribution of abortion in inflorescences (Mathieu *et al.*, 2009; Egli, 2010; Jullien *et al.*, 2011).

- Alleles related to the maintenance of processes of tissue expansion in both vegetative and reproductive organs may have a direct effect on yield maintenance under drought. Genetic variability exists in maize for this maintenance. Phenotyping silk elongation rate is a difficult task at a throughput compatible with genetic analyses, i.e. hundreds of genotypes, but is feasible in situ via a combination of robot-assisted image analysis and machine learning (Brichet *et al.*, 2017). The commonality of mechanisms controlling the responses of expansive growth to environmental constraints in both vegetative and reproductive structures, centered on hydraulic processes, has therefore potentially large consequences in breeding for plants adapted to changing environments, but also in understanding plant adaptive traits and in modeling plant-water interactions from the cell to the global scale. This is consistent with recent studies addressing the modeling and prediction of terrestrial carbon and water dynamics, which suggest to revise the hierarchy of plant growth control in the vegetation models (Fatichi *et al.*, 2014) by giving a pivotal role to plant hydraulics (Fatichi *et al.*, 2015; Pappas *et al.*, 2016).

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## Figure captions

**Fig. 1.** Abortion occurs in youngest apical ovaries in pea (*Pisum sativum* L), and water deficits reduce the number of fertile phytomerer. A, Schematic representation of pea plants during seed filling. The stem (vertical green bar) is made of successive phytomerer with an internode, a leaf (green) and an inflorescence. Youngest phytomerer are located in the apical bud at the top of the plant. WW: well-watered plant, WD: plant subjected to a moderate soil water deficit at flowering. Pods at later stages are represented in red. Black triangles: aborted reproductive organs. B, Abortion frequency is related to the spatial position of reproductive organs along the stem. It is calculated as  $(SN_{max} - SN_i)/SN_{max}$ , where  $SN_i$  and  $SN_{max}$  are the number of seeds counted, respectively, at the position  $i$  and at the oldest reproductive phytomerer. WW, closed symbols; WD, open symbols. Two water deficits were applied during flowering (Data from Ney et al., 1994). C, Abortion frequency is related to the time elapsed between the growth arrest of the apical bud and the stage 'open flower' (pollination) of the considered organ. (Data from Ney et al. (1994): circles, and Guillioni et al. (2003): triangles).

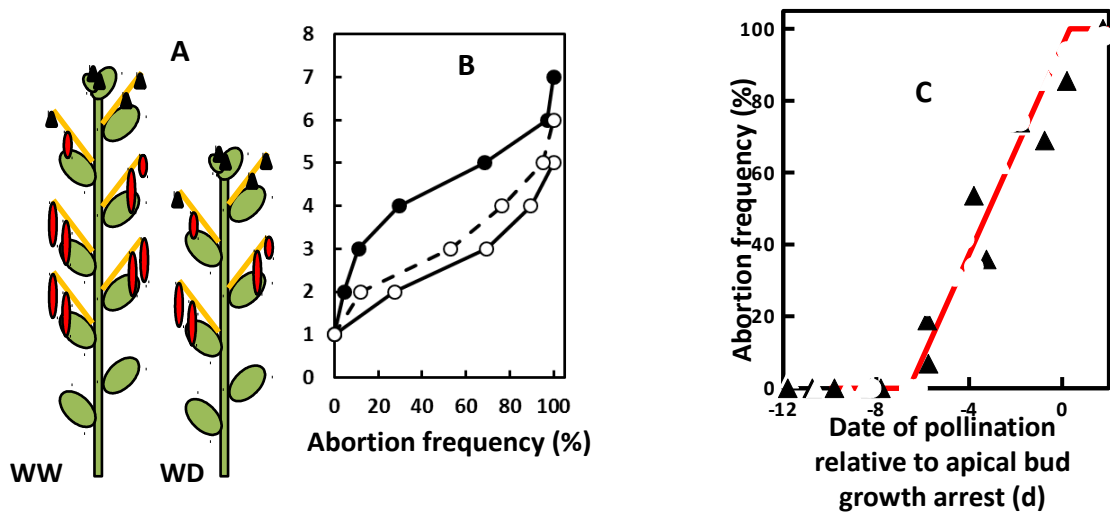
**Fig. 2.** A, Abortion is predominantly apical in maize (*Zea mays* L) ears, with an aborted region that increases in length in plants subjected to a moderate water deficit (WD) or to asynchronous pollination (GP). WW, well-watered plants. Adapted from Oury et al., 2016b. B, A severe water deficit after silking (SWP) induces a randomly distributed abortion which is partly reversed by sucrose (Suc) feeding (Mc Laughlin and Boyer, 2004). C, The abortion frequency of each ovary cohort is related to the time elapsed between silk growth arrest and silk emergence of the considered cohort. The relationship is common to 4 hybrids and 3 levels of soil water deficit at flowering (Oury et al., 2016b).

**Fig. 3.** More than 90% of drought-associated abortion is already irreversible at silk growth arrest, i.e. 2-3 days after the emergence of the first silk in water deficit. The relationship is common to 4 hybrids and 3 levels of soil water deficit at flowering (Oury et al., 2016b).

**Fig. 4.** The first molecular events associated with water deficit in reproductive organs occur in silks rather than in ovaries, and involve genes affecting expansive growth rather than sugar metabolism. SE: first silk emergence. +5d: five days later. WW: well-watered plants. WD: moderate water deficit at flowering. Colours represent the ratio of expression between WW and WD plants. Adapted from Oury et al., 2016a.

**Fig. 5.** Hydraulic control of expansive growth in maize silks and leaves. A, Silk elongation rate is more rapid during nights than days, with a rapid transition ( $t_{1/2}$  : half time,). B, Recovery of silk elongation rate is also rapid upon soil rehydration. C, The relationship between elongation rate and soil water potential is linear in both leaves and silks in two maize lines introgressed with alleles conferring contrasting sensitivities. D, Leaf and silk sensitivities are closely correlated in a panel of 8 lines. They are estimated by the soil water potential (SWP) causing growth arrest (x-intercept of response curves in C). *Adapted from Turc et al., 2016.*

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**Figure 1**

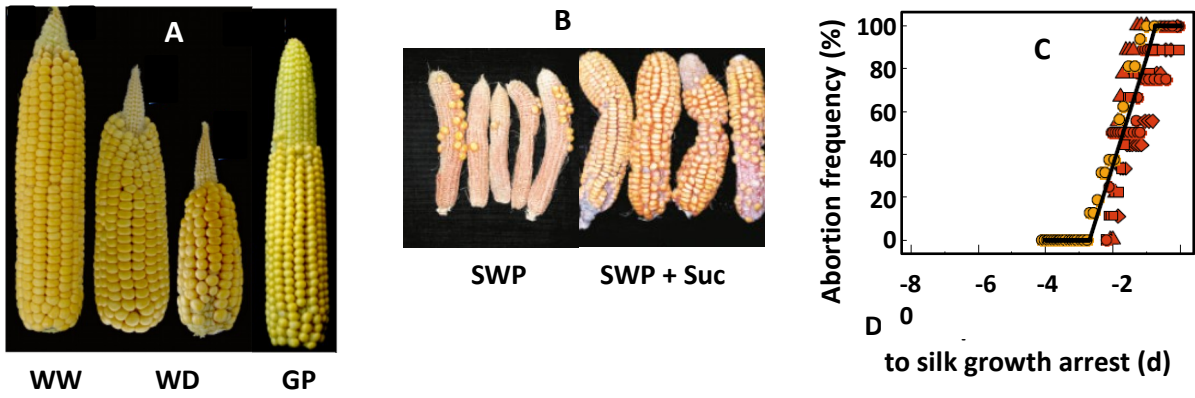


Figure 2

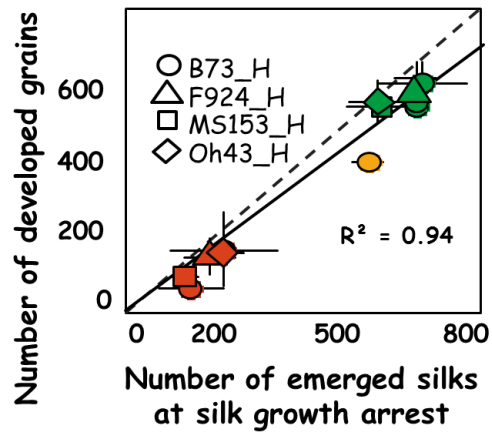


Figure 3

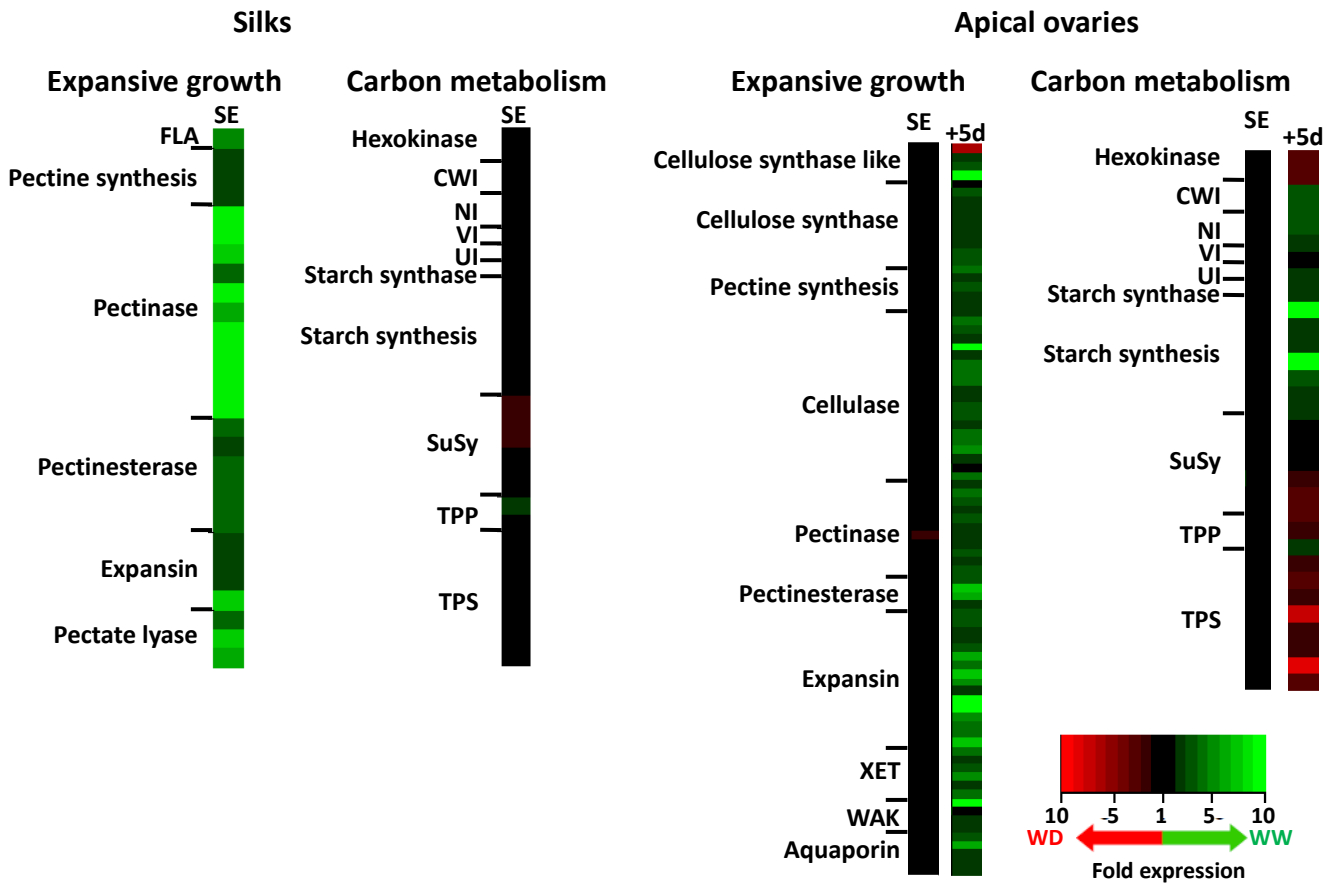


Figure 4

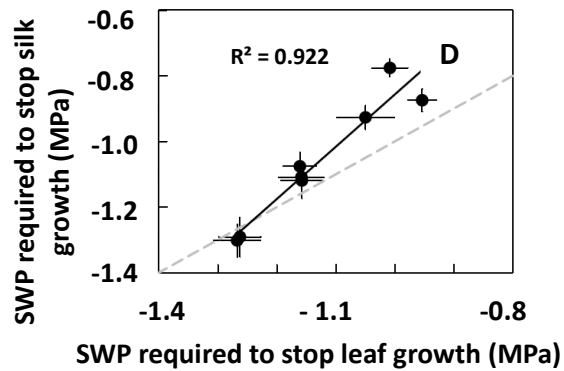
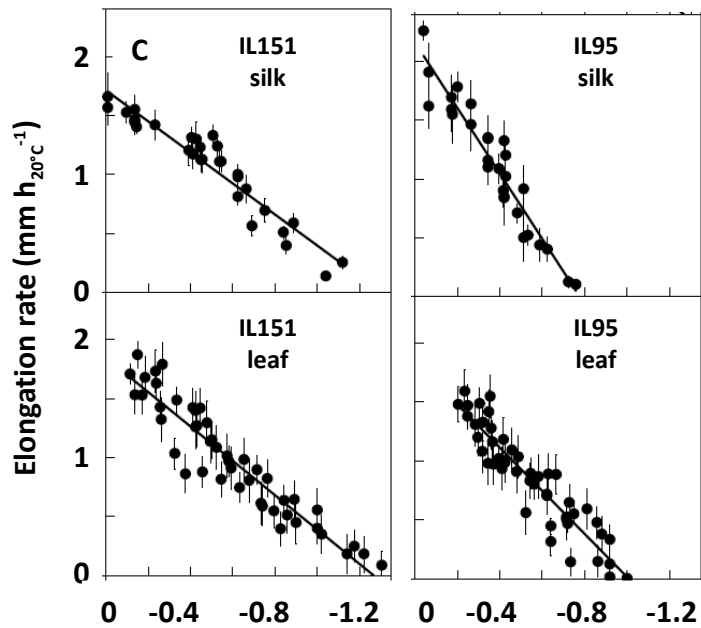
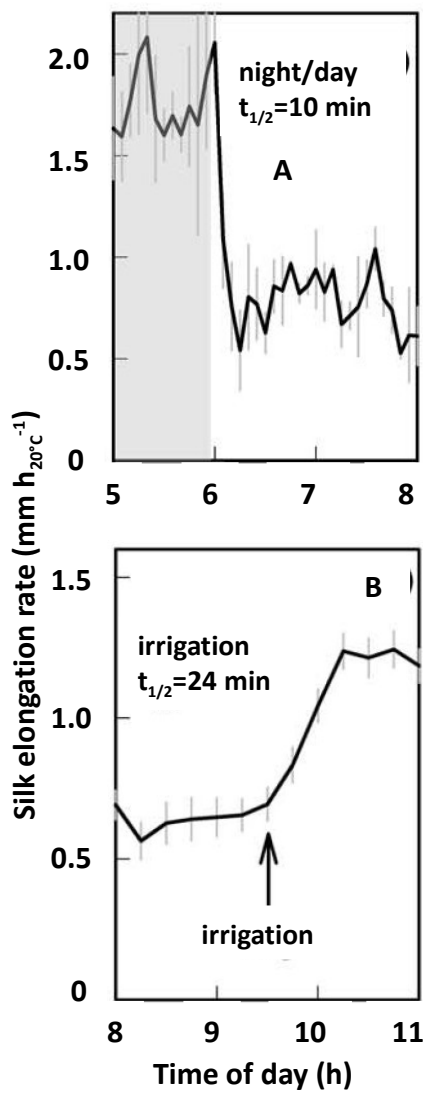


Figure 5