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New challenges for sunflower ideotyping in changing environments and more ecological cropping systems[☆]

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Abstract – As a rainfed spring-sown crop, sunflower (*Helianthus annuus* L.) is increasingly exposed to negative impacts of climate change, especially to high temperatures and drought stress. Incremental, systemic and transformative adaptations have been suggested for reducing the crop vulnerability to these stressful conditions. In addition, innovative cropping systems based on low-input management, organic farming, soil and water conservation practices, intercropping, double-cropping, and/or agroforestry are undergoing marked in agriculture. Because of its plasticity and low-input requirements (nitrogen, water, pesticides), sunflower crop is likely to take part to these new agroecological systems. Aside from current production outputs (yield, oil and cake), ecosystem services (*e.g.* bee feeding, soil phytoremediation...), and non-food industrial uses are now expected externalities for the crop. The combination of climatic and societal contexts could deeply modify the characteristics of genotypes to be cultivated in the main production areas (either traditional or adoptive). After reviewing these changes, we identify how innovative cropping systems and new environments could modify the traits classically considered up to now, especially in relation to expected ecosystem services. Finally, we consider how research could provide methods to help identifying traits of interest and design ideotypes.

Keywords: ideotypes / ecosystem services / agroecology / climate change / breeding

Résumé – De nouveaux défis pour la conception d'idéotypes de tournesol pour des environnements changeants et des systèmes de culture plus écologiques. En tant que culture d'été non irriguée, le tournesol (*Helianthus annuus* L.) est davantage exposé aux impacts négatifs du changement climatique, et en particulier aux températures élevées et au stress hydrique. Des adaptations incrémentales, systémiques ou de rupture ont été suggérées pour réduire la vulnérabilité de la culture à ces conditions stressantes. Par ailleurs, des systèmes de culture innovants sont en fort développement qu'il s'agisse de systèmes à bas niveaux d'intrants, d'agriculture biologique, d'agriculture de conservation des sols, d'agroforesterie, ou de l'introduction d'associations de cultures et de doubles cultures. En raison de sa plasticité et de ses faibles besoins en intrants (eau, azote, pesticides), la culture de tournesol est amenée à s'insérer de manière privilégiée dans ces systèmes agro-écologiques. À côté de la production (grains, huile, tourteaux), de nouvelles externalités sont attendues comme la contribution aux autres services écosystémiques (pollinisateurs, phytoremédiation...) et de nouveaux usages non alimentaires. La conjugaison des contextes climatiques et sociétaux pourrait profondément changer les caractéristiques attendues des variétés cultivées dans les principales régions de production qu'elles soient traditionnelles ou en reconquête. Après une revue de ces changements, nous identifions comment systèmes innovants et changement climatique pourraient modifier les caractères phénotypiques considérés classiquement, en particulier dans la perspective de nouveaux services. Enfin, nous verrons comment la recherche pourrait fournir des méthodes pour faciliter l'identification de ces caractères d'intérêt et aider à la conception d'idéotypes.

Mots clés : traits / idéotypes / services écosystémiques / agroécologie / changement climatique / sélection variétale

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1 Opportunities for growing sunflower crop

Sunflower (*Helianthus annuus* L.) crop is grown worldwide in temperate, subtropical and tropical climates under a wide range of agro-environments. Among oilseeds, it ranked 3rd in 2018 behind soybean and rapeseed (4th after palm, soybean and rapeseed for edible oil) with an average annual world production of about 52 MnT (Oil World Annual, 2019). The EU-27 comes in 3rd position after Ukraine and Russia, the whole European continent producing 71% of the seeds on 67% of the acreage in sunflower worldwide.

Sunflower benefits from broad and established markets (Pilorgé, 2020). It is primarily grown for its edible oil but also for its achenes (confectionary types) both commonly used in human food. High-oleic varieties are widely appreciated by food industry because of oxidative and thermal oil stabilities (Dunford, 2015). After oil extraction, the residual cake becomes a high-protein meal for livestock (Peyronnet *et al.*, 2014). In addition, due to the properties of sunflower oil, green chemistry and energy are two potential outlets (Park *et al.*, 1997) while by-products utilizations have emerged in building industry (Borredon *et al.*, 2011).

In arid and semi-arid environments, sunflower is grown under irrigation or rainfed, whereas in temperate regions it is mainly a rainfed crop (García-Vila *et al.*, 2012). In France, where only 5% of the sunflower acreage receive supplemental irrigation, it needs only limited water amounts (~50 mm) with a good efficiency *i.e.* 0.5–1.5 q/ha of extra yield for each 10 mm applied around flowering (Champolivier *et al.*, 2011). As a warm-season and intermediate water-use crop, it can add diversity to dryland crop rotations (Anderson *et al.*, 1999; Johnston *et al.*, 2002). Being moderately drought-tolerant, it often brings satisfactory results when other crops are dramatically impacted by drought (Debaeke and Bertrand, 2008).

Agronomically, the crop is considered by farmers as versatile, cheap, rustic and easy to manage, with rotational benefits for winter crops (Lecomte and Nolot, 2011). It is largely labelled as “environmental-friendly” in relation with its low-input requirements in water, fertilizers and pesticides and due to limited greenhouse gas emissions (Debaeke *et al.*, 2017a, 2017b). Altogether, this makes sunflower the major oilseed crop grown in organic farms in France (Le Gall, 2019).

However, in spite of significant breeding efforts (Vear, 2016), its on-farm productivity is relatively low and stable because of a set of yield-limiting factors (*e.g.* birds, fungal diseases, low and uneven plant population, poor crop management) in the main production areas (Mercau *et al.*, 2001; Grassini *et al.*, 2009; Jouffret *et al.*, 2011; Hall *et al.*, 2013). Consequently, cultivated areas are stagnating or decreasing especially in Western Europe and the potential ecosystem services fulfilled by the crop do not compensate for the lack of economic competitiveness mainly attributed to low yields.

In addition, other sources of edible oil are now preferred for nutritional reasons: rapeseed and olive oils have increased their market share at the expense of sunflower oil as they provide more n-3 PUFA (polyunsaturated fatty acids) and among sunflower oils, more n-6 PUFA are provided by traditional linoleic varieties compared to high-oleic ones (Duru and Magrini, 2017; Duru, 2019). Other trade considerations have favoured the world extent of soybean and palm oils.

As stated, many breeding efforts by public and private research compensate for these drawbacks (oil quality, tolerance or resistance to fungal diseases, potential yield) and obvious genetic progress were reported in registration and demonstration trials (Vear *et al.*, 2003; Jouffret *et al.*, 2011; Vear, 2016).

However, the production context is now rapidly changing. New growing environments are open to sunflower with climate change (*e.g.* northern extension in Europe – Bellarby *et al.*, 2010). Societal demands for more ‘environmental-friendly’ agriculture using less or no chemicals and preserving environmental resources (*e.g.* water) are clearly asserted. Beyond production, agriculture must contribute to the provision of a package of ecosystem services. All these shifts could open new avenues for sunflower as the crop through its plasticity has many cards to play in various agricultural systems (Lecomte and Nolot, 2011; Debaeke *et al.*, 2017a, 2017b; Pilorgé, 2020). As crop management has to be deeply changed during agroecological transition, it will require a complete overhaul of the characteristics of the varieties that are currently grown (Meynard *et al.*, 1997). The expected new traits and ideotypes should draw a sunflower crop more adapted to these new challenges both in traditional and adoptive regions.

2 Are current varieties adapted to face these new challenges?

Advanced lines and hybrids developed by breeders are usually subjected to multi-environment trials to evaluate their relative performance for a target population of environments. Before its commercial release, each variety in the EU undergoes VCU (Value for Cultivation and Use) trials for at least two years before entering in the National List of Plant Varieties. Thereafter, at least in France, the registered varieties are widely tested for another 2–3 years (post-registration) to identify the best performing ones under local conditions and provide descriptions of their main agronomic and technological characteristics. These trials now result in the publication of Recommended Variety Lists (Terres Inovia, 2020).

Some limitations to this experimental system have been discussed previously for France (Debaeke *et al.*, 2011; Casadebaig *et al.*, 2016). Although this testing network covers the main regions of sunflower production, more diverse environmental conditions (soil, weather, management) would undoubtedly improve the assessment of yield stability and would be necessary to face the more stressful conditions observed with climate change, water restrictions and diversity of cropping systems. Moreover, no sound characterization of the physical environment (*e.g.* available soil water) and constraints perceived by plants (as water and nitrogen stresses, disease severity) is available routinely.

Meanwhile, only a few traits are measured to assess the performance of new sunflower varieties. They are restricted to final productivity, grain quality, earliness and tolerance to major diseases (Tab. 1) which is more or less the same in the other producing countries. Although sunflower is a summer crop, grown without irrigation in shallow to moderately deep soils, no evaluation of drought tolerance is achieved even if earliness to anthesis can be considered as a drought escape trait. Therefore, current evaluation criteria do not include yield stability *per se* and even exclude it indirectly because the

Table 1. Criteria available to growers in France to choose a sunflower variety. These criteria are presently included in the MyVar web tool (www.myvar.fr) developed by Terres Inovia (adapted from [Casadebaig *et al.*, 2016](#)).

Criteria	Entry	Levels	Details
General information	Breeding company	–	–
	Year of release	3	<2005, 2005–2010, >2010
	EU country of registration	2	France, abroad
Plant phenology	Anthesis earliness	5	Very early to late
	Maturity earliness	5	Very early to late
Plant morphology	Plant height	3	Short, medium, tall
Disease tolerance	Phomopsis stem canker	5	
	Sclerotinia head rot	4	
	Sclerotinia basal stalk rot	3	
	Verticillium wilt	4	
Downy mildew resistance	Resistance profile	3	RM9, RM8, other RMs
Herbicide tolerance	Technology used	3	None, Clearfield [®] , Express Sun [®]
Seed characteristics	Thousand kernel weight	3	Low, medium, high
	Oil concentration	4	Low, medium, high, very high
Oil characteristics	Oil quality	2	High oleic, linoleic (mid-oleic)
	Performance level	5	Scale depending on multi-location field trial

evaluation network has rather homogenous conditions that do not reflect the diversity of farming conditions such as the different water deficit scenarios observed in the vast majority of farming conditions ([Debaeke *et al.*, 2011](#)). Moreover, current procedures prevent the registration of varieties exhibiting higher yield stability in unfavorable grower-like conditions but with a similar or lower average performance compared to check varieties in the tested high-yielding conditions.

In addition, on each site, a single crop management system is applied, independently of variety-specific requirements (*e.g.* plant density), which impedes the proposal of specific “variety-management” pairs per type of environment.

More information at least on plant architecture and response to water constraint would improve the characterization of past and future varieties and their response to a wider range of environments. This was developed in sunflower for calibrating a variety-based simulation model (SUNFLO) ([Casadebaig *et al.*, 2011](#)). For over 100 commercial varieties, additional parameters were measured in dedicated fields (Terres Inovia) and semi-controlled platforms (INRAE) such as: leaf area index (LAI) dynamics, harvest index, response of transpiration and leaf expansion to soil water deficit ([Debaeke *et al.*, 2010](#); [Casadebaig *et al.*, 2008, 2016](#); [Gosseau *et al.*, 2019](#); [Pinochet *et al.*, 2020](#)). This phenotypic database is regularly updated with new accessions.

As argued before, sunflower ideotypes have to be designed for changing environments, new cropping systems and ecosystem services. This implies that new trait measurement protocols must complete the current routine characterization done in the VCU (and post-registration) trials. They should assess non-productive ecosystem services provided by the crop

with possible intra-specific variation such as melliferous potential ([Cerrutti and Pontet, 2016](#)) and test a wider range of growing conditions (water-limited conditions, organic farming). A multicriteria approach combining several breeding targets such as adaptation to environments, cropping systems, markets, and non-productive ecosystem services should be proposed for designing and evaluating the multi-performance of a variety as illustrated on [Figure 1](#). The end-use of sunflower achenes and oil is actually determinant in the variety decision at farm level. In Europe, it concerns mainly the choice of a linoleic (classic) *versus* (high) oleic type, in relation with a premium paid for quality by the market. In other countries, choosing an oilseed or a confectionary type could be an option too. Among oilseed varieties, different fatty acids profiles and the content in minor components as tocopherols and phytosterols could orientate the choice towards specific varieties ([Nolasco *et al.*, 2006](#); [Ayerdi-Gotor *et al.*, 2015](#)).

Hulls are a by-product of sunflower oil processing and of confectionary seeds dehulling process. The hullability and protein concentration traits are now more important to consider for meal production in animal nutrition and some variability was observed among commercial varieties ([Dauguet *et al.*, 2016](#)). All these outcomes and the market access will orientate the information included in the recommended list of varieties with some absolute requirements (seed composition) or some preferences

In the following sections, we will discuss traits to be considered and ranked by breeders and advisers regarding new sets of constraints expected in a close future in relation with climate change ([Sect. 3](#)) and innovative cropping practices ([Sect. 4](#)). We will also propose expected outcomes of sunflower

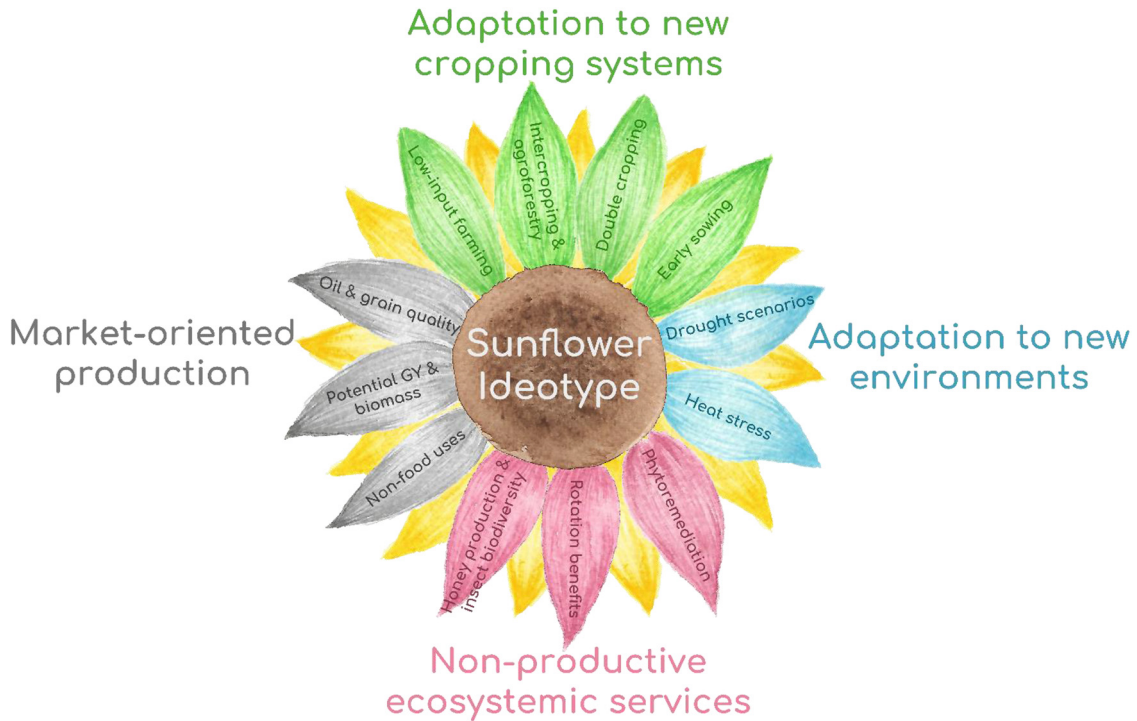


Fig. 1. Multicriteria design and evaluation of sunflower ideotypes.

varieties in delivering ecosystem services (Sects. 5 and 6). Finally, we will discuss new research approaches to identify and screen adapted traits and design ideotypes for specific climate, cropping management and ecosystemic needs (Sect. 7).

3 Varietal adaptation to climate change

3.1 New climatic constraints for sunflower production

Climate change (CC) is characterized by higher temperatures, elevated atmospheric CO₂ concentrations, extreme climatic hazards, reduced water availability in some regions, waterlogging in others (IPCC, 2014). With ongoing climate change, sunflower, as a spring-sown rainfed crop, could be more exposed to the direct effect of heat stress at anthesis or during grain filling and to different and unpredictable drought scenarios during its growing cycle, both factors resulting in severe yield losses, oil content decrease and alterations of fatty acid composition (Moriondo and Bindi, 2007; Moriondo *et al.*, 2011; Donatelli *et al.*, 2015; Andrianasolo *et al.*, 2016). In the present and future climatic context, sunflower cropping offers a wide range of options for attenuating or preventing the negative impacts of climate change (Debaeke *et al.*, 2017b; Awais *et al.*, 2018). Adaptations through crop management (*e.g.* modifying sowing dates), breeding (earliness, stress tolerance) and shifting growing areas could be introduced, assessed and combined at field level to partly cope with CC negative impacts. At farm level, diversification of crop management systems (*e.g.* range of sowing dates and/or maturity groups) could be a way to adapt to more variable and unexpected weather conditions. Climate change could also offer some new opportunities with warmer winters and longer

growing periods allowing sunflower to be cultivated as a double crop after a winter cereal or as a winter crop itself.

Current varieties could probably be part of the solution. But their potential in more constrained conditions will have to be explored by combining field networks with sufficient water deficits and platforms to mimics water constraints. Breeding will be necessary as well to reinforce some under-represented maturity groups (*e.g.* very early hybrids) and to develop hybrids more tolerant to drought and heat under higher CO₂ (Miladinović *et al.*, 2019; Attia *et al.*, 2021).

3.2 Early sowing (as an escape strategy)

3.2.1 Description of the practice

By anticipating the timing of critical growth stages, the exposure of sunflower crop to the most stressful abiotic factors (heat and drought) can be minimized. Therefore, sowings in early spring (about 1 month earlier than the common practice, once soils have warmed up to 7–9°C) have been tested in temperate regions from Western and Southern Europe to escape the risk of high temperatures and water stress during flowering period (*e.g.* Alline *et al.*, 2008). However, the risk of losing the plant stand increases as sowing date is anticipated because of cold or frost damage to seedlings and young plants but also because of greater exposure to predation by soil insects, slugs or birds and infection by soilborne diseases when emergence phase is too long. Additionally, difficult germination and weak plant establishment combined with slow development of plants could delay the canopy closure and favor the growth of weeds. Cold stress can impact dramatically the root system development with consequences on water and nutrient uptake later in the season.

In some Mediterranean regions (*e.g.* South of Spain and Italy, Morocco) or in Asia (India, Pakistan) characterized by mild winters, sunflowers can even be planted in late autumn or winter with good results in water use efficiency and yield (Gimeno *et al.*, 1989; Boujghagh, 1993; Gosset and Vear, 1995; Flagella *et al.*, 2002; Barros *et al.*, 2004; Tariq *et al.*, 2018). With such very early sowings, more of the growing cycle takes place under low evaporative demand (and cooler conditions), so water productivity is higher, and high summer temperatures during flowering and grain filling are partly avoided (Soriano *et al.*, 2004).

In addition, sunflower production area is often expanding to marginal regions with suboptimal growing conditions (*e.g.* southwestern Argentina). In Europe, the cultivation area of sunflower could move northward with climate change exposing the crop to more frequent low temperatures during the first part of the crop cycle (Debaeke *et al.*, 2017b).

However, early sowing could be more than an escape strategy when combined with deep soils or supplemented by irrigation. Associated to late maturing cultivars, it could be an option to take advantage of the increasing heat units and CO₂ with global warming (Donatelli *et al.*, 2015). In this case, varieties should be tolerant to fungal diseases (*e.g.* phomopsis) as the risks might increase with early sowing (Debaeke *et al.*, 2014).

Anticipating (or delaying) sowing dates will change incident radiation and thermal conditions during the critical periods for yield components and oil determination. This could change the grain number per unit area, the unit grain weight or the oil composition depending on the time and intensity of the constraints as was reported by Cantagallo *et al.* (2004), Izquierdo *et al.* (2008) and Echarte *et al.* (2010).

3.2.2 Varietal traits for this new practice

3.2.2.1 Physiological aspects of cold tolerance (and response to low temperatures)

Being able to sow early to maximize the growing season and escape drought and heat stress increases the importance of cold tolerance among varieties, especially during the vegetative period. In spite of global warming, climatic accidents are not excluded in early spring, and a low and fluctuating temperature regime (including several small frost events) is expected. Consequently, seedlings and young plants could be exposed to cold stress (low temperatures, frost) in the early stages of development (germination, emergence, 2–3 leaf stage). Cold stress, which includes both chilling ($T > 0^{\circ}\text{C}$) and freezing ($T < 0^{\circ}\text{C}$), modifies gene expression and plant metabolism with consequences on many biological functions (Alline *et al.*, 2010; Janmohammadi *et al.*, 2015; Hniličková *et al.*, 2017). The conditions of exposure (timing, intensity, duration) are to be considered to explain the final response. Cold conditions may affect duration and rate of emergence, plant survival and early growth.

3.2.2.1.1 Base temperature for germination

Base temperatures for germination (T_b) between 3.0 and 6.9°C have been reported in sunflower with intra-specific variability (Connor and Hall, 1997; Khalifa *et al.*, 2000; Trudgill *et al.*, 2000). González-Belo *et al.* (2014) observed T_b values between 0.7 and 3.3°C among 9 genotypes, the high-linoleic genotypes germinating earlier at low temperatures.

3.2.2.1.2 Frost damage (freezing stress)

During early growth stages, sunflower plants can withstand temperatures in the -3.3 to -3.8°C range for short periods (source: NSA of Canada). As the plants develop through the vegetative stages (V2 to V6) (Schneider and Miller, 1981), they become progressively more sensitive to frost. At the V2 stage, the lowest temperature plants can withstand is -2.7 to -3.3°C but, for the V4–V6 stages, -1.6 to -2.2°C is the lower limit. Alline *et al.* (2009) confirmed this information: at cotyledon stage, sunflower could resist to temperatures of -5 to -7°C but as soon as the first leaves appear, -3°C could provoke severe necrosis on young plants. Cool temperatures (0.5 to 1.1°C) over several days, coupled with wet soils and dew, help reduce frost damage but this process of hardiness is still poorly understood in sunflower (Hewezi *et al.*, 2006). Most damage can be expected if temperatures change rapidly between extremes. Frost damage can result in partial destruction of the terminal bud with a loss of apical dominance causing branching from axillary buds and multiple heads later in the season, affecting greatly yield and quality (Boujghagh, 1993). Hniličková *et al.* (2017) identified some physiological mechanisms of resistance and tolerance of young sunflower plants to overnight freezing temperatures.

3.2.2.1.3 Low temperature stress (chilling stress)

Each plant species, more particularly each genotype, has an optimum range of temperatures for its normal growth and development. These cardinal temperatures depend also on the growth and development stage for a given genotype. When temperature moves beyond this optimal range, temperature stress affects leaf development and photosynthesis and this can be modeled by SUNFLO (Casadebaig *et al.*, 2011). This approach allowed to estimate the grain yield loss due to chilling stress between 3 and 10% in a French multi-environment trial network (Mangin *et al.*, 2017). Early sowing (or sowing in marginal regions) increases the occurrence and duration of sub-optimal temperatures during vegetative stages.

3.2.2.2 Genetic variability and breeding

Breeding for cold tolerant genotypes should contribute to stabilizing sunflower cultivation in areas frequently exposed to early spring frosts and night chilling. Two directions have been explored (Vear, 2016): germination at low temperatures and plant resistance to frost, either by withstanding cold periods without developmental damages, or by the capacity to recover later without impacts on production. These different tolerance strategies still need to be characterized in the current varieties and the other genetic resources to ensure efficient optimization of G x E x M interactions.

Cold resistance should be improved in the early stages of growth and development, in order to enable successful plant establishment. Although less often evoked, cold resistance at maturation could enable sunflower growing at higher altitudes and in colder regions (Škorić, 2009).

Varieties with lower base temperatures, shorter thermal times for emergence and increased vigor should be targeted in early sowings (Houmanat *et al.*, 2016). For instance, such varieties adapted to autumn sowings have been selected in Morocco (cv. Ichraq – Nabloussi *et al.*, 2008) and improved germplasm has been evaluated (Houmanat *et al.*, 2016).

Chlorophyll content and specific leaf area among others have been genetically associated with cold tolerance, so they could be used as selection criteria in breeding programs (Alline *et al.*, 2009, 2010; Fabio *et al.*, 2016). From QTL analyses, it was illustrated that several putative genomic regions are involved in the variation of physiological traits under cold conditions (Alline *et al.*, 2009; Škorić, 2009; Tetreault *et al.*, 2016; Mangin *et al.*, 2017; Miladinović *et al.*, 2019).

Conventional breeding methods have moderately succeeded in improving the cold tolerance of major crop plants (Škorić, 2009; Sanghera *et al.*, 2011; Miladinović *et al.*, 2019). Therefore, wild populations of sunflower (*e.g. H. maximiliani*) growing in US mountains with harsh winters and cold springs could be a source of variability for improving the cold tolerance of *H. annuus* (Tetreault *et al.*, 2016; Seiler *et al.*, 2017). In Argentina, Gutierrez *et al.* (2016) pointed out that *H. petiolaris* could also be a useful genetic resource to explore.

Mangin *et al.* (2017) identified 9 genomic regions associated with oil yield plasticity in response to chilling stress in a core collection of cultivated and wild accessions. This genetic material together with the molecular markers constitute a valuable resource to improve this trait and decipher the physiological processes of importance for sunflower to tolerate cool nights. Hernandez *et al.* (2020) observed a wide genetic variation for the tolerance to freezing in the primary gene pool of sunflower and suggested that tolerance might be introgressed into elite germplasm without growth penalties.

Based on general physiological understanding of plant development and cropping issues in cold conditions, we can hypothesize that particular attention to vigor, root development and resistance to soilborne diseases such as downy mildew should be considered when ideotyping sunflower genotypes adapted to early sowing.

3.3 Moving to new environments

Moving to more favorable environments is a way to escape unsuitable conditions and exploit emerging opportunities for crop growing. New cultivation opportunities could be expected in northern parts of Europe, North America, Ukraine or Russia where sunflower is not grown presently and where it could usefully contribute to diversify cereal-based cropping systems (Tuck *et al.*, 2006; Deppermann *et al.*, 2018). This will require early maturing, cold-tolerant varieties with a low susceptibility to sclerotinia head rot, as this disease is more present in cool and wet environments. In the US, northward expansion of sunflower was limited by the lack of commercial hybrids with such early maturity. Hulke and May (2018) recently provided early-maturing restorer inbred germplasms with high yield potential. In Europe, new hybrids have been recently registered for northern conditions but their spread is still constrained by the limited use of these very early varieties in current cropping systems.

3.4 Double cropping

3.4.1 Description of the practice

Due to its short growing season together with the global warming context, sunflower becomes an attractive option for double cropping following the early harvest of winter crops (Salera, 1992; Lecomte, 2009; Gesch and Archer, 2013).

Numerous results have been reported from North and South America, France, Italy, Serbia, India, Iran and Turkey (Sojka *et al.*, 1989; Dragovic *et al.*, 1992; Salera, 1992; Bahrani *et al.*, 2009; Ada and Tamkoç, 2015; Akcay and Dagdelen, 2016; Ross, 2016). The practice however requires short-season cultivars, associated to minimum tillage and sowing soon after harvest, and sufficient irrigation for good establishment and minimization of climatic risks (cold, heavy rain) at the end of the season. Among cultivars adapted to second crop (<100 days), Dalchiavon *et al.* (2016) in Brazil obtained the highest yields with the latest and tallest varieties among a collection of hybrids. Double cropping is also used for energy (*e.g.* in Germany, Graß *et al.*, 2013) or silage (*e.g.* in USA, Sheaffer *et al.*, 1977; in Brazil, Tomich *et al.*, 2003) with different varietal objectives. In the US, double crop sunflower can be used as an emergency crop or when the season is too short to produce mature corn for silage.

3.4.2 Varietal traits for this new practice

Very early-maturing sunflowers are required for double cropping, growing degree days (GDD) ranging from 1300 to 1400 °C.days (Tb=6 °C). In Europe, these hybrids often come for the selection of very early materials intended for main sunflower cropping in the northern regions. Among these cultivars, 100–120 days varieties are adapted to sunflower cropping in the continental parts of eastern and central Europe. The reproductive period (from anthesis to physiological maturity) of such late-sown cultivars is proportionally longer than in conventional hybrids. They could be unadapted to late sowing and climatic conditions of southern Europe where hot and dry conditions are prevailing in summer. Indeed, delaying sowing date in early summer will change dramatically the radiative, water and thermal conditions during the most critical periods of yield determination. However, trials where cultivars are tested for their response to late sowing under double cropping conditions are not widespread and should be encouraged.

In France, for instance, hybrids less susceptible to sclerotinia head rot should be preferred because of irrigation around flowering and possible wet and cold conditions during ripening (Lecomte, 2009). Because of high temperature and low relative air humidity, fungal diseases as phomopsis should be less frequent in relation with a shorter vegetative period and lower leaf area index (LAI). Oleic cultivars are not recommended because of possible low night temperatures during grain filling which can reduce the biosynthesis of this fatty acid (Izquierdo *et al.*, 2002).

Double cropping, sowing in cool environments or northern regions, and escaping summer drought by early sowing all require early-flowering and/or early-maturing hybrids. As for many crops, flowering time is a quantitative trait, which has been crucial for the domestication and spread of sunflowers into new ecoclimatic regions (Blackman *et al.*, 2011). In breeding programs, flowering date (expressed as number of days from sowing or emergence) and seed moisture at harvest are the two characters regularly measured (Tab. 1) and used as indicators of earliness, in order to assign a genotype to a maturity group, and to discard very late-maturing materials (Vear, 2016). Generally, early-maturing hybrids are characterized by the shortening of the period from star bud to early anthesis growth stages resulting in lower LAI, total

evapotranspiration, and yield potential than later hybrids (Chervet and Vear, 1990; Fick and Miller, 1997).

Genetic and environmental controls of flowering in sunflower are complex and mostly undefined. Photoperiod and temperature are the primary environmental factors regulating the transition to flowering in sunflower (Goyné *et al.*, 1989). Three classes of photoperiod response (day neutrality, short-day response, and long-day response) were observed in *H. annuus* (Wien, 2008; Blackman *et al.*, 2011). QTLs and/or mutations involved in the control of flowering time in the cultivated sunflower were identified (Leon *et al.*, 2000, 2001; Cadic *et al.*, 2013) and the genetic network controlling flowering time including 475 genes could be reconstructed based on similarity to *A. thaliana* (Badouin *et al.*, 2017). Recently, Todesco *et al.* (2020) identified major haplotypic variations in wild *Helianthus* species (*H. annuus*, *H. petiolaris* and *H. argophyllus*) driving flowering time. Such haploblocks are present in cultivated hybrids and certainly impact the capacity to introduce favorable alleles in their vicinity due to modified recombination rates.

3.5 Breeding for drought-resistant and/or water use efficient genotypes

3.5.1 Description of the practice

When compared to other field crops, sunflower has moderate water requirements, can tolerate short-term drought and partly recovers from water stress (García-Vila *et al.*, 2012). Reducing water consumption results in moderate yield reduction ($K_y < 1$) because sunflower forms a deep root system, extracts water from the deeper soil layers and can efficiently regulate water transpiration from leaves when submitted to water deficit. However, long-term water deficits can severely affect grain yield, oil content and quality, and other important yield traits (Ahmad *et al.*, 2014; Hussain *et al.*, 2018; Debaeke and Izquierdo, 2021). Although water shortage affects all phenological phases, the maximum yield reduction is observed when drought occurs during the reproductive phase (García-Vila *et al.*, 2012). Therefore, irrigation around flowering stage is advised to maximize yield response (Goksoy *et al.*, 2004; Champolivier *et al.*, 2011).

In the near future, sunflower could be increasingly exposed to water deficit due to higher evapotranspiration and less effective rainfall with global warming (García-Vila *et al.*, 2012; IPCC, 2014; Donatelli *et al.*, 2015; Debaeke *et al.*, 2017b; Awais *et al.*, 2018). Therefore, it is essential to identify the physiological, molecular and genetic components of sunflower tolerance and resilience to water stress in this emerging context (Hussain *et al.*, 2018; Miladinović *et al.*, 2019).

In water-limited environments, the optimal crop management must ensure a rapid canopy closure, avoid excessive LAI at anthesis, maintain a green canopy throughout the grain filling period while fully deplete the root zone to exhaust the soil reservoir at maturity (Feres *et al.*, 1986; Merrien and Grandin, 1990; García-Vila *et al.*, 2012; Lisanti *et al.*, 2013). Management decisions, through choice of cultivars (characterized by phenology, potential leaf area, response of leaf expansion and transpiration to water deficit) and optimal sowing dates, are crucial in this context as they will play on the

environmental patterns of water supply and demand (Casadebaig and Debaeke, 2011; Casadebaig *et al.*, 2016). Shifting the cropping season to less evaporative periods may reduce the crop exposure to drought (Soriano *et al.*, 2004), while the choice of early maturing cultivars may increase the fraction of water used after anthesis leading to greater harvest index and yield (Sadras and Connor, 1991). Crop population density adjusted to the maturity group ensures an adequate exploitation of available water resources while preventing excessive and inefficient crop transpiration (Villalobos *et al.*, 1994). In addition, N-fertilization practices (rates, splitting) adapted to available water for irrigation will maximize input efficiency (García-López *et al.*, 2016).

3.5.2 Varietal traits for this new practice

Drought tolerance in breeding programs could be achieved following two main directions: (i) stress avoidance which includes reduced transpiration and water conservation and (ii) increased water uptake from the soil by optimizing root architecture and functioning. We previously indicated the importance of drought escape strategies (*cf.* Sects. 3.2–3.4).

3.5.2.1 Stress avoidance

When subjected to soil drying, sunflower plants immediately adapt their transpiration by two reversible physiological processes (Connor and Hall, 1997; Debaeke and Izquierdo, 2021): (i) leaf wilting, which saves soil water and protects leaves from thermal stress and high radiation loads (Velázquez *et al.*, 2012) and (ii) stomatal closure, which increases the resistance to gaseous loss and saves water for the plant (Hernández and Orioli, 1985; Gimenez and Fereres, 1986; Kiani *et al.*, 2007). After anthesis, the most efficient adaptation is provided by stomatal closure (Connor and Jones, 1985; Maury *et al.*, 1996). Leaf senescence may be hastened also but with less impact on plant transpiration as it affects in priority basal leaves, which are less active and smaller (Sadras *et al.*, 2000). Leaf wilting can be observed before and after anthesis (Guiducci, 1988). After anthesis, due to complex interactions between leaf senescence, wilting, and reduced stomatal conductance, it is difficult to identify a predominant factor of adaptation to water deficit (Connor and Hall, 1997). In contrast, before anthesis, the main adaptation strategy to maintain plant water status is to reduce leaf size with delayed consequences on both radiation interception and evaporative demand (Takami *et al.*, 1981; Connor and Jones, 1985; Cox and Jolliff, 1986; Guiducci, 1988; Sadras *et al.*, 1991).

The possible large genotypic variability in leaf expansion and stomatal closure responses to water deficits has not been extensively explored in sunflower. Pereyra-Irujo *et al.* (2008) reported genetic variability for the response of leaf growth to water deficit among 18 inbred lines. Casadebaig *et al.* (2008) compared these responses for 25 hybrids subjected to a progressive soil dry-out in greenhouse. No impact was observed on leaf expansion until the fraction of transpirable soil water (FTSW) in the root zone declined below 0.6, but it had to decline below 0.4 to induce stomatal closure. Two contrasted adaptive strategies were observed among genotypes, either conservative (decreasing water loss) or productive (maintaining water uptake). Conservative genotypes have a

gradual response to water deficit (stomatal closure for low soil water deficit) and might be most suited to environments with severe water deficits where survival is the priority. However, this strategy may not be the most efficient for environments with short, frequent and moderate soil water deficits alternating with well-watered periods. In such conditions, a steeper response (“productive” strategy), maintaining organ expansion, photosynthesis and biomass production, could result in better yield maintenance in such conditions (Casadebaig and Debaeke, 2011).

Water uptake maintenance is facilitated within plant cells by osmotic adjustment (OA), a biochemical mechanism that helps plants to acclimatize to dry conditions. A large intraspecific variability in OA was observed for sunflower (Chimenti and Hall, 1993), the genotypes with a high capacity for OA having also leaf expansion less reduced by drought (Chimenti and Hall, 1994). Chimenti *et al.* (2002) observed that genotypes with high OA could extract twice as much water from the soil during a drought period occurring between V11 and R5.5.

To screen and develop sunflower hybrids better adapted to water stress, several indicators at field level and protocols in dedicated platforms should be associated (*e.g.* plant and leaf growth, senescence, transpiration, OA potential, leaf temperature...) (Vannozi *et al.*, 1999; Pereyra-Irujo *et al.*, 2007; Rauf, 2008; Gosseau *et al.*, 2019).

Obviously, cultivated sunflower has a narrow genetic base and is deficient in drought-survival mechanisms which were lost during the selection process towards high yields. However potential sources of drought resistance were identified in wild sunflower relatives such as *H. anomalus* and *H. deserticola*, native to drought-prone environments (Kantar *et al.*, 2015; Seiler *et al.*, 2017). Up to now, *H. argophyllus* was the most often used species for such purpose, as it can be easily crossed with cultivated *H. annuus* (Hussain *et al.*, 2019).

3.5.2.2 Root system and water capture

As compared with other crops, sunflower is known to have a well-developed and deeply penetrating root system which is capable of fully depleting the water (and nutrients) present in subsoil layers. This was extensively reported by comparative field studies (Bremner *et al.*, 1986; Cox and Jolliff, 1987; Hattendorf *et al.*, 1988; Rachidi *et al.*, 1993; Dardanelli *et al.*, 1997; Cabelguenne and Debaeke, 1998; Stone *et al.*, 2001; Merrill *et al.*, 2002). Sunflower’s root system is “explorative” of large soil volumes with a combination of thick and thin roots, small average specific root length, and small root length density, which explains why sunflower can extract more water than most other crops, especially from deep soil layers (Connor and Hall, 1997). However, in undisturbed soils with hard layers in depth or compacted in sub-surface, the potential of deep rooting of sunflower could be dramatically reduced with consequences on plant height and growth (Scapinelli *et al.*, 2016).

Some variations in root depth were observed among sunflower genotypes in relation with plant height and maturity group, long-season and tall varieties exploring deeper the soil layers and extracting water from drying soil more efficiently (Gimenez and Fereres, 1986; Angadi and Entz, 2002; Radanielson *et al.*, 2012). Genotypes with longer roots can also explore deeper soil layers and hence exhibit higher level of

tolerance to drought stress conditions (Angadi and Entz, 2002). When applying water deficit, Rauf *et al.* (2009) observed longer root length for drought tolerant inbred lines (and a reduced length for susceptible ones) and higher values of root-to-shoot ratio in almost all genotypes regardless of their drought tolerance. Pre-anthesis drought also increases the proportion of roots in depth mainly by reducing the amount in the uppermost layers (Connor and Jones, 1985).

The development of more productive and drought-tolerant lines in breeding programs requires the knowledge of root traits and functions and their effect on productivity (Miladinović *et al.*, 2019). Traits such as root length and diameter, root length density, root volume, fresh and dry root weight, and total dry matter were recognized as significant indicators of drought tolerance (Rauf, 2008; Nagarathna *et al.*, 2012; Comas *et al.*, 2013). However, in spite of previous studies, very few explorations of the genetic variation in root traits have been published in sunflower. Phenotyping root traits is extremely difficult at field level, because the root system of field-grown plants is impossible to extract completely (Nagarathna *et al.*, 2012). The architecture of the root system can be studied during the very early stages in controlled conditions providing relevant information (Aguirrezábal and Tardieu, 1996). Masalia *et al.* (2018) revealed in growth room a substantial variation for seedling root morphology and growth traits among 288 lines, resulting in no tradeoffs between aboveground and belowground biomass which is promising for the selection of deep-rooting genotypes.

A wide range of genetic variation for root morphology was described by Seiler (1994) among annual *Helianthus* species. An increased percentage of deep roots in response to water deficits was found with *H. petiolaris* (Sobrado and Turner, 1986). As for shoot traits, these desirable traits from wild species could be introgressed into cultivated sunflower by interspecific hybridization process resulting in substantial genetic variability in root growth (Seiler, 2008).

3.5.2.3 Water-use efficiency

Water-use efficiency (WUE) is the ratio of total carbon in the plant and the total loss of water due to transpiration (Blum, 2005). Creating high-WUE genotypes is often the most efficient and cheapest strategy to deal with the problem of water deficit (Rauf, 2008). Selecting for high harvest index will most likely result in genotypes with high WUE. Differences in WUE were observed among sets of hybrids or inbred lines (Lambrides *et al.*, 2004; Adiredjo *et al.*, 2014; Canavar *et al.*, 2014). These authors suggested that leaf carbon isotope discrimination could be an indirect tool for breeding for WUE in sunflower. Strong negative correlations were observed between whole plant WUE (or intrinsic WUE) and leaf carbon isotope discrimination with decreasing water availability.

3.6 Breeding for heat tolerance

In spite of early sowing, climate change will expose more and more sunflower crop to high temperatures during the reproductive phase (Moriondo *et al.*, 2011) with dramatic consequences for pollination, fertilization, seed set, rate and duration of seed growth, seed weight and oil characteristics (Connor and Hall, 1997; Chimenti and Hall, 2001; Chimenti *et al.*, 2001; Astiz and

Hernandez, 2013; Andrianasolo *et al.*, 2016). The temperature of 35 °C was mentioned as a stressful threshold for sunflower at least during early- to mid-grain filling (Rondanini *et al.*, 2003, 2006). According to Terzic *et al.* (2017), temperatures above 27 °C reduce nectar production, while those above 33 °C completely stop it. Chabert *et al.* (2020) observed that nectar sugar mass per floret increased with air temperature over the range of 16–32 °C and appeared to decrease beyond 32 °C on the overall range of cultivars sampled.

Avoiding adverse conditions (Sect. 3.2) or breeding varieties with increased resistance to heat shocks are two complementary adaptive strategies. Higher air temperature can negatively affect sunflower growth by inducing shorter phenological phases. Resulting shorter crop duration could be compensated for by sowing early long-cycle cultivars (Debaeke *et al.*, 2017b). The increased temperatures could also lead to rapid senescence and diminish oxidative protection in sunflower primary leaves (de la Haba *et al.*, 2014). Fortunately, increasing transpiration should keep the leaves relatively cool if enough water is supplied by a deep and well-developed root system (*cf.* Sect. 3.5).

Other traits related to plant architecture could be efficient to avoid heat stress. For instance, the orientation of the capitulum could be optimized. Ploschuk and Hall (1995) found that restraining a capitulum in a vertical position increases temperature by 10 °C during a sunny day and reduces the duration of grain filling by 2–6 days. Through modelling, Guillioni and Lhomme (2006) found that plants around 2 m high, with small LAI and a capitulum inclination between 45° and 90°, should experience lower temperatures. In addition, Kalyar *et al.* (2013) demonstrated that a genotype with upward inclined leaves was superior to that with downward inclined leaves as it maintained lower post-noon temperature and heat injury. Leaf temperature adjustment over time was proposed as a useful trait for selecting heat-tolerant genotypes. In addition, root type, head position, tolerance to high atmospheric demand for water vapor, increased capacity of a plant to produce more pollen, high seed filling rate, and rapid synthesis of oil under hot conditions were suggested as important criteria for selecting accessions tolerant to high temperatures (Miladinović *et al.*, 2019).

A wide genetic variation for the tolerance to heat exists in the primary gene pool of sunflower (Hernandez *et al.*, 2020). These authors found no evidence of a growth-tolerance trade-off. Regarding germplasm, *H. argophyllus* was suggested as a useful source of heat tolerance traits due to its silver leaves that reflect sunbeams and reduce transpiration (Warburton *et al.*, 2017). In addition, Seiler (2012) recommended several wild relatives as *H. anomalus* Blake, *H. deserticola*, *H. nuttallii*, and *H. petiolaris* as possible germplasms for heat stress studies.

4 Adaptation of variety offer for production in agroecological cropping systems

4.1 New context for crop production

Agroecological cropping systems in the wider sense (incl. organic farming) are characterized by the application of a limited amount of exogenous inputs (agrochemicals, fertilizers), the actions of which are partly compensated by the intensification of ecological processes (through cover crops,

diversified rotations, legumes...) (Duru *et al.*, 2015). Such systems could rely on intercropping and agroforestry which associates several species with different outcomes and functions. Soil tillage can be drastically reduced especially when considering conservation agriculture which combines reduced tillage, crop rotations and more or less permanent soil covering (Govaerts *et al.*, 2009). In such systems, varieties must be more resistant to biotic factors and have to capture more efficiently resources (water, nutrients, light) at soil and canopy level.

4.2 Low-input management and organic farming

4.2.1 Description of the practice

As a cash crop, sunflower is mostly grown for grain production in low-input (rainfed) cropping systems where it brings some yield stability (Debaeke *et al.*, 1998; Silvestri *et al.*, 2000; Mazzoncini *et al.*, 2006). Sunflower may be attractive to organic grain crop farmers, who often rely on diversified crop rotations to manage insect pests and fungal diseases (Mohler and Johnson, 2009). Grain yield of organically-grown sunflower was lower by 41%, 17% and 44% in 2002, 2003 and 2004 respectively when compared to the conventional practice in Italy (Mazzoncini *et al.*, 2006). In a 5-year survey in France, average organic yield may reach up to 82% of conventional one (Le Gall and Lecomte, 2019). Mechanical weed control being feasible as row widths are greater than 50 cm, inter-row tillage is practised in more than 40% of the fields in France. However, in such low-input systems, nutrient stresses, weed infestation and disease attacks may limit grain yield and possibly oil concentration but the literature on management practices for organic and low-input sunflower production is extremely limited.

4.2.1.1 Weed management

Ineffective weed suppression is one major reason of lower yields in organic cropping systems (Ryan *et al.*, 2009; Seufert *et al.*, 2012). Weeds that emerge and establish during sunflower germination can compete with the crop and reduce sunflower yield. Sunflower seed yield is maximized when the crop is kept weed-free for 4–6 weeks after sowing (Johnson, 1971). Cultivating with a tine weeder in the two weeks after sowing has been shown to control weeds as effectively as herbicides, but cultivating can also reduce sunflower plant density. Previous research has shown that high seeding rates can facilitate weed suppression in organic sunflower (Mouillon *et al.*, 2020). However, high sunflower density can also lead to disease attacks such as white mold and phomopsis stem canker (Debaeke *et al.*, 2014), as well as crop lodging which can reduce seed harvestability. In order to limit weed emergence in the early stages, organic farmers often decide to plant later than conventional ones in order to have time for a false sowing and thus mechanically control the first flush of weed emergence before sunflower planting (Le Gall and Lecomte, 2019).

4.2.1.2 Nutrient stress

N deficiency is often mentioned as a limiting factor in organic farming (Stockdale *et al.*, 2001). In spite of the moderate N rate applied to sunflower in conventional systems,

and the use of legumes in the rotation, crop growth could be limited by N deficiency during the vegetative phase with direct consequences on radiation interception and photosynthesis. At the same time, this could reduce pre-anthesis leaf development and evapotranspiration which could be favorable for preserving water during grain filling in drought-prone environments (Sadras and Connor, 1991).

4.2.1.3 Disease attacks

As fungicides are not widely used in sunflower, the use of tolerant varieties combined to less favorable microclimate for the infection of plants by fungi (due to lower nitrogen nutrition index and lower LAI) should not increase much the risk of diseases (e.g. phomopsis, phoma, sclerotinia) in sunflower as compared to conventional systems (Debaeke *et al.*, 2014).

4.2.2 Varietal traits for this new practice

Currently, there is no strong difference between the characteristics desired for organic and conventional production systems, and yields are often well correlated between the two systems. Contrary to wheat, there is no specific network to assess the performance of sunflower varieties in organic farming. Generally, varieties used in organic farming are rather old and less diverse than in conventional systems (Le Gall and Lecomete, 2019).

4.2.2.1 Competitiveness against weeds

Weeds compete with sunflower for moisture, nutrients, and depending on species for light and space. Weed competition cause substantial yield losses in sunflower, with reports ranging from 20 to 70% (Zimdahl, 2004). Weeds are usually a problem because sunflower does not cover ground rapidly enough to prevent them from becoming established. The critical period of weed competition was found to occur from 25 to 43 days after sowing (Wanjari *et al.*, 2000). However, once well established, sunflower is a good competitor with weeds due to its shoot height, extinction coefficient between 0.8 and 0.9 and deep rooting system (Onofri and Tei, 1994). In spite of the use of mechanical weeding (which doesn't guarantee a complete weed control on the row), competitiveness against weeds will be important to consider in such low-input systems.

Using cultivars with high competitive ability against weeds is one of the effective strategies for sustainable weed management which has been explored in other major crops (e.g. cereals).

Zarch *et al.* (2017) showed that rapid emergence and plant height increasing rate at first 53 days after sowing and leaf area development rate between 17 to 53 days after sowing were the most important effective factors that increase sunflower competitiveness against *Amaranthus albus*. They observed a significant difference between the 6 cultivars under study for Competitive Index. Latify *et al.* (2017) suggested that combining highly competitive cultivars with proper living mulch species would be a feasible weed management that should be modulated by the dominant weed spectrum.

Emergence rate, rapid root growth, seed vigor, development rate of leaves, rapid root and shoot biomass accumulation, rapid canopy closure and plant height are important traits

in relation to the competitive ability between different cultivars of crops. These characters have been seldom evaluated among sunflower cultivars.

4.2.2.2 Increasing nutrient uptake and use efficiencies

Varieties highly tolerant to suboptimal levels of nutrients (N, P, K) or efficiently using limited resources from the soil or the fertilizers are welcome in low input crop management systems.

In breeding programs, the following plant properties should be taken into account: (a) the ability to produce near-maximum yields on low-level soil nutrients and (b) the root system that efficiently uses large amounts of soil nutrients, in order to create varieties with high NUE, PUE, or KUE that can contribute positively to environment (Clark and Duncan, 1991; Miladinović *et al.*, 2019).

At least three ratios could be calculated to compare the different genotypes regarding nutrient capture and utilization efficiencies (Dalla Costa and Giovanardi, 1996): the apparent N recovery (ANR: plant N uptake/N fertilizer applied); the physiological N efficiency (PE: grain yield/plant N uptake) and the agronomic efficiency (AE: increase in grain yield of the fertilized crop compared to the unfertilized crop per unit of N fertilizer applied). Sunflower has lower PE and decreased ANR at high N fertilizer rates than maize, resulting in an overall lower AE.

Most of the studies were concerned by NUE ignoring the other nutrients but very few studies compared the previous ratios for a wide range of inbred lines or hybrids by contrast with other highly-fertilized crops (e.g. wheat, maize, oilseed rape). ANR, PE or AE were not identified as priorities for breeding in sunflower. However, Montemurro and De Giorgio (2005) observed differences in NUE for 2 cultivars at field level and recently Keipp *et al.* (2019) in a pot experiment obtained significant differences for the three nutrient-utilization efficiencies (NUE, PUE, and KUE) among 25 sunflower hybrids.

The potential for the creation of varieties with superior nutrient-utilization efficiencies depends largely on: (i) the genetic variability in the species present for that particular NUE (or PUE or KUE)-regulated property and (ii) the development of a methodology for the precise quantification of physiological parameters reflecting an effective NUE, PUE or KUE (Baligar *et al.*, 2001; Miladinović *et al.*, 2019). In sunflower, the evaluation of nutrient uptake in grain and vegetative parts requires heavy sampling at field level and thus is relatively inaccurate for discriminating small differences among genotypes. Dense root system is probably a favorable trait in sunflower for capturing most efficiently P and K, two nutrients with a low mobility in soils (Fernandez and Rubio, 2015).

4.2.2.3 Breeding for disease resistance

Sunflower diseases causing the highest damages worldwide are Sclerotinia head rot and stalk rot, Phomopsis stem canker, rust, and downy mildew (Markell *et al.*, 2015). Breeding for fungal disease resistance or tolerance is a continuous and renewed challenge in sunflower both in conventional and low-input systems because of the reduction

of fungicide applications, the absence of satisfactory chemical or cultural control methods exist for some potentially yield-reducing fungal diseases and the regular emergence of new pathotypes which threaten the efficacy of efficient genetic control (Vear, 2016; Miladinović *et al.*, 2019).

Increasing durable genetic tolerance or resistance to the dominant fungal diseases is one of the basic tasks of sunflower breeders, in a double context of more ecological production and changing climate. Currently genetic resistance exists to diseases such as *P. halstedii* and *Verticillium*, high level of tolerance has been selected for *Phomopsis*, satisfactory tolerance exists for *Phoma macdonaldii* and *Sclerotinia sclerotiorum*, and partial disease tolerance exists against *Botrytis cinerea* (Vear, 2016). Resistant varieties should be optimally used to maintain the resistance sustainability and multiresistant varieties should be encouraged to face the diversity of pathogens.

Variety mixture is often recommended in cereals in order to reduce the use of fungicides and increase crop resilience (Barot *et al.*, 2017). In sunflower, this practice has not been reported in the literature and only empirical approaches have been tested (Debaeke *et al.*, 2017a). However, Tourvieille de Labrouhe *et al.* (2010) mixed different major resistance genes (PI) to downy mildew using multi-hybrids during 5 years of continuous cropping. This obviously contributed to a more durable control of downy mildew by delaying the appearance of new races.

4.3 Intercropping

4.3.1 Description of the practice

Sunflower was reported as a serious candidate for strip, row and relay intercropping systems (Robinson, 1984). Its desirable agronomic characteristics such as erect growth habit, harvestable head, relative resistance to lodging and drought, and minimal land cover makes sunflower an excellent component to intercrop with a short stature and/or duration crop.

The sunflower-soybean intercrop has emerged as a popular option that increases land productivity in the southern Pampas of Argentina, compared with sole crops, because of complementary use of resources between species (Echarte *et al.*, 2011; Andrade *et al.*, 2012; de la Fuente *et al.*, 2014). More results were given for West Africa (Olowe and Adebimpe, 2009) for different varieties of sunflower and soybean. In France, this system is only profitable in very low-input systems where sunflower growth is reduced and benefits from the soybean complementarity for N (Landé *et al.*, 2012; Tribouillois *et al.*, 2012).

In the tropics, sunflower can be intercropped with a wide range of crops (groundnut, maize, mungbean, sesame, cowpea...) (e.g. Olowe and Adebimpe, 2009). In the US, vegetable legumes (vetch, clover, alfalfa, medic, lentil...) were intercropped with sunflower with the objective of increasing soil cover, reducing soil erosion and adding nitrogen and organic matter to the soil (Kandel *et al.*, 1997). Sunflower yield was reduced by 15% when it was sown at the same time than the legumes.

4.3.2 Varietal traits for this new practice

The optimal variety type for successful intercropping has not been extensively examined, as this system is not widespread. Kandel *et al.* (1997) did not observe significant yields for two contrasted hybrids (standard-height and – maturity hybrid vs early-maturing dwarf hybrid) intercropped with legumes. In Nigeria, Olowe and Adebimpe (2009) and Olowe and Adebimpe (2009) comparing the performance of 3 open pollinated sunflower varieties intercropped with sesame and soybean respectively, observed significant differences among the tested varieties relatively to the sole crops. From these limited experiences, it is impossible to indicate which varietal traits should be selected in priority for maximizing the performance of sunflower grown in intercropping.

4.4 Reduced tillage

Ploughing is still widely used as primary tillage (60% in 2017 in France, Le Gall and Lecomte, 2019) because sunflower needs uncompacted soils for the establishment of its tap root system (Scapinelli *et al.*, 2016). The situation is quite different in Argentina where about 80% of the sown area is conducted under no-tillage system for economic and agronomic reasons (Rodríguez and Brihet, 2019).

Several studies were conducted to evaluate the relative performance of sunflower under conventional and reduced tillage as main or double crop (Murillo *et al.*, 1998; Halvorson *et al.*, 1999; Lopez-Bellido *et al.*, 2002; Bahrani *et al.*, 2009; Seddaiu *et al.*, 2016). Minimum or reduced tillage often appeared to be a more suitable strategy for rainfed agriculture in areas with frequent periods of scarce rainfall where sunflower is often sown and where most of the long-term tillage studies were conducted.

Little information was available on how hybrids of different maturity groups respond or interact with various tillage systems and no significant effect of tillage x hybrid interaction was generally found on grain yield (Deibert, 1989; Halvorson *et al.*, 1999).

Quiroz *et al.* (2008) in Argentina demonstrated that the combination of no tillage and genetic resistance reduced the effect of *Verticillium* wilt of sunflower and the production of microsclerotia in stem pith to very low values. The choice of a cultivar could be modulated by the biotic risks associated to the tillage system.

4.5 Agroforestry

The agroforestry systems consist of associating forest trees with annual crops simultaneously, resulting in less dependence on inputs, greater food security and allowing the achievement of a greater number of products in the same area (Torralba *et al.*, 2016). However, the forestry component may adversely affect the yield of agricultural crops in the agroforestry systems. Furthermore, the reduction in photosynthetically active radiation during the grain filling causes a decrease in oil production in sunflower (Aguirrezábal *et al.*, 2003). In spite of

the societal interest for such sustainable production systems, very few papers reported successful tree-sunflower intercropping results (e.g. Ramshe *et al.*, 1994 for India).

de Oliveira *et al.* (2012) evaluated the effect of shading, caused by eucalyptus, on sunflower yield for 3 cultivars in an agroforestry system in Brazil. The shading caused by the trees created ideal conditions for the increased incidence of sclerotinia white rot in sunflower and induced a negative effect on the mean LAI, both resulting in a decline of sunflower yield of ca. 60%. Therefore, intercropping with sunflower can be feasible only in the first years of implementation of the agroforestry system. Disease tolerance, adaptation to shading, rooting depth, response to plant density should be relevant traits to consider when evaluating the potential interest of a sunflower genotype for agroforestry.

5 Ecosystem services other than production delivered by sunflower crop

As was stated by several authors, sunflower has a potential for providing multiple ecosystem services (ES) in diverse cropping systems (Jones and Sieving, 2006; Franco *et al.*, 2016; Debaeke *et al.*, 2017a). In the absence of monetization, these ES should be widely emphasized to give more attractiveness to this low-input oilseed crop. We identified several services that could be filled by sunflower: (i) sustainment of biodiversity, by providing nutritional resources to pollinators; (ii) environment protection by a contribution to phytoremediation in heavy-metal polluted soils; (iii) pest regulation by a break effect in cereal rotations and by contributing to weed control in succeeding crops through allelopathy. The contribution of sunflower fields to the aesthetic value of landscapes should be also highlighted although this cultural service looks difficult to evaluate properly. Genetics could contribute to this service but, obviously, it doesn't deserve such an effort.

5.1 Sunflower as a source of pollen and nectar for pollinators

5.1.1 Description of the service

Beneficial insects, such as *Apis mellifera* (honey bees) and *Bombus* sp. (bumble bees), play important roles as sunflower pollinators. As well as being a service, pollination is a determinant process for successful seed set and yield in sunflower (Chabert *et al.*, 2019).

In addition, it has been recognized for a long time that sunflower crop is a crucial source of pollen and nectar in early summer for the activity of the pollinators (Delaplane and Mayer, 2000). It generally offers abundant and accessible pollen and constitutes an additional source of pollen while floral nectar and other reward facilitate crop pollination (Nicolson and Human, 2013). Jones and Gillett (2005) indicated that sunflower sowings within rows of vegetable crops may be an effective way to attract beneficial insects into organic cropped fields in addition to bees.

Unfortunately, the pollinators are directly affected by agronomical practices, such as pesticide spraying or the selection of crop cultivar. Consequently, in France, sunflower

honey production has decreased since the nineties and beekeepers reported important honey yield variability between years and locations (Cerrutti and Pontet, 2016). The nutritional needs of bees received renewed attention in the context of declining abundance and diversity of the insect populations and changes in land use that threaten floral resources. Giacomini *et al.* (2018) discovered that sunflower pollen dramatically reduced a protozoan pathogen (*Crithidia bombi*) infection in bumble bees (*Bombus impatiens*) and also reduced a microsporidian pathogen (*Nosema ceranae*) of the European honey bee (*A. mellifera*), indicating the potential for broad anti-parasitic effects. Given consistent effects of sunflower in reducing pathogens, sowing more sunflower in agroecosystems may provide a simple solution to reduce disease and improve the health of economically and ecologically important pollinators.

Therefore, all sunflower growers, and more especially producers of hybrid seeds, are concerned by pollinating insects. Wild and managed bees are needed to move sunflower pollen, both to create hybrid seed and to encourage high and consistent yields from these hybrids. Both for effective pollination and for nutritional value, the pollinators should be encouraged to visit sunflower at flowering. Specific traits should be evaluated for that. If differences among cultivars exist, farmers' choice concerning cultivars at a territory scale could contribute to enhance nectar resource for pollinators and to increase viability of apicultural activity.

5.1.2 Varietal traits for this service

Beekeepers have suggested that modern sunflowers would be less attractive than varieties grown 30 years ago. Therefore, pollinator attractivity is an important quality trait to be considered in sunflower breeding and registration programs (Terzic *et al.*, 2017). For insect-pollinated crops, identifying and breeding for attractive floral traits may increase yields as well.

Cerrutti and Pontet (2016) assessed the attractiveness for honeybees of 13 current cultivars at blooming during 3 years. They concluded that sunflower genetics was a major and consistent factor influencing honeybee attendance on plots. Discrepancy between most and least visited cultivars reached a factor of 3 in this study. Similar results were obtained by Stejskalová *et al.* (2018). This could be potentially related to melliferous characteristics (Chabert *et al.*, 2020) but also to other floral traits (Prasifka *et al.*, 2018). Nicolson and Human (2013) indicated that the protein content of sunflower pollen is relatively low and the cultivars of such mass-flowering crops may also vary in value for pollinators.

For seriously addressing these questions, a lot of additional phenotyping would be necessary: pollen and nectar composition and secretion, tubular floret length (Vear, 2016; Chabert *et al.*, 2020). Pollinators make foraging decisions based on numerous floral traits, including nectar and pollen rewards, and associated visual and olfactory cues (Mallinger and Prasifka, 2017). These authors observed that bee visits significantly increased with nectar sugar amount and decreased with corolla length, but appeared unaffected by nectar sugar composition. Portlas *et al.* (2018) concluded that among influential floral traits, floret size may be critical, as the depth of the corolla affects the accessibility of nectar. Therefore, production of

inbreds and hybrids with smaller florets could enhance sunflower pollination. Genetic markers for key floral traits are needed to facilitate selection, and an understanding of potential trade-offs between traits is also required. Selecting for these traits could thus increase sunflower crop yields while providing greater floral resources for bees.

5.2 Soil phytoremediation

Accumulation of heavy metals (HMs) in soils as a result of various industrial and anthropogenic activities has reduced soil fertility significantly in some regions. It contributes to the contamination of agricultural crops then to the transfer of HMs into the food chain. Phytoremediation (or phytoextraction of HMs) is an emerging method of remediating metal-contaminated soils which can improve soil fertility and provide inexpensive feedstock for biorefineries (Awa and Hadibarata, 2020).

Sunflower can be used efficiently for phytoextraction thanks to its high biomass production, its capacity for metal accumulation and because its oil can be used for non-food purpose thus improving the economic balance of the process (Angelova *et al.*, 2016; Rizwan *et al.*, 2016; Alaboudi *et al.*, 2018). Sunflowers can tolerate the toxic effects of certain HMs through different mechanisms, this tolerance varying with variety, soil type, metal type, dose, and duration of metal exposure. The hyperaccumulation capacity of sunflower biomass was experimentally demonstrated by cultivating the plants in various concentrations of HMs. Nehnevajova *et al.* (2005) observed highly significant differences for metal accumulation and extraction efficiency among 15 cultivars grown on metal-contaminated soil. In this field-based screening, the authors found enhanced cumulative Cd, Zn, and Pb extraction efficiency by a factor 4.4 for cv. Salut.

Prior to any breeding attempt, a careful screening of various genotypes should be done to select the cultivars with the naturally highest metal uptake as an effective strategy for the phyto-management of soils contaminated with HMs. This hyperaccumulation activity could also be used to extract and concentrate essential elements (*e.g.* selenium) through bio-fortification in order to improve human nutrition (Garousi *et al.*, 2018).

5.3 Break crop for pests, weeds and diseases and contribution to useful biodiversity

Growing sunflower in rotation with other crops is of first importance for the sustainability of the cropping system. In making the decision to include sunflower in their rotations, farmers will have to consider impact on subsequent crop yields, as well as costs of production, market value of crop, impact on pest problems, and total productivity of all crops in the rotation (Nielsen *et al.*, 1999).

Sunflower is usually grown in 3–4 year rotations with cereals (*e.g.* wheat, barley, maize, sorghum), soybean, oilseed rape and grain legumes (Johnston *et al.*, 2002; Lecomte and Nolot, 2011). However, it should not be grown too frequently to prevent the setting up of fungal diseases inoculum (*e.g.* phoma, phomopsis, downy mildew). Risks of sclerotinia could be enhanced also when increasing the proportion of some host

plants in the rotation (*e.g.* pea, oilseed rape and soybean) (Debaeke *et al.*, 2014).

The benefits of sunflower in nutrient cycling are well-known. It acts as a “scavenger” crop as its deep root system can recover some of the nitrogen applied to the previous shallow-rooted crop that has been leached to below its root zone (Angadi and Entz, 2002). Residual water left in the subsoil by previous crops can also be exploited by sunflower (Feres *et al.*, 1993; Cabelguenne and Debaeke, 1998). Sunflower reduces the potential for saline-seep development in dry environments (Halvorson *et al.*, 1999). However, sunflower which extracts more water from the profile than other crops, leaves less water in the soil for the next crop which could be detrimental for yield in dry conditions (Cabelguenne and Debaeke, 1998; Anderson *et al.*, 1999; Nielsen *et al.*, 1999).

The fast degradation of sunflower cultural debris can deliver nutrients rapidly into the next crop (Rodriguez-Lizana *et al.*, 2010; Babu *et al.*, 2014) but N residual amount after sunflower is lower than after legumes (McEwen *et al.*, 1989).

As a late spring-sown crop, sunflower could break winter crop rotations with benefits for the non-chemical control of weeds and soilborne diseases in winter cereals and oilseed rape (Colbach *et al.*, 1994; Anderson *et al.*, 1999). It proved to be effective in alleviating the “corn monoculture yield depression” (Porter *et al.*, 1997). According to Jones and Sieving (2006), the addition of sunflower intercrops in organic vegetables proved to be an effective habitat modification for augmenting the number of avian insectivores and their insect-foraging time. Intercropping sunflower with wheat contributed to the reduction of stripe rust and powdery mildew on wheat through a barrier effect (Cao *et al.*, 2015).

The break potential of sunflower which is related to several plant characteristics has not been evaluated at the genotype level so far.

5.4 Allelopathy

The strategy of using allelopathic crop residues and water extracts for weed control seems to be a sustainable and friendly option to reduce dependence on herbicides. In addition to controlling weeds, residues of allelopathic crops positively affect soil health. Since the pioneer work of Leather (1983), numerous papers (about 40 in Web of Science) reported the allelopathic potential of sunflower plants and tissues in controlling weeds in sunflower and next crops with possible unwanted effects on subsequent crop species. This high allelopathic activity could be exploited more than currently done to reduce chemical weed control in sustainable agriculture. Several papers reviewed these effects (*e.g.* Gawronska *et al.*, 2007; Albuquerque *et al.*, 2011; Jabran, 2017) indicating that sunflower contains bioactive allelochemicals, especially phenolics and terpenoids, which would be involved in this suppressing effect.

Sunflower shows inhibitory effects on a relatively wide range of weeds (dicots and grasses) as assayed under laboratory, greenhouse and field conditions. Allelopathy could be exploited for biocontrol in several ways, among others as biologically active mulch either scattered over the soil surface or mixed into the soil. Sunflower root exudates also inhibit weed seedling growth, but are less effective than leaf and stem

Table 2. Morpho-physiological traits of interest for choosing varieties or breeding according to priorities: market-oriented production, adaptation to new environments or new cropping systems, provision of ecosystem services.

Priorities	Crop development				Increased plant growth and resource capture		Increased resource-use efficiency		Abiotic Stress Resistance		Disease resistance	Bird resistance	Non-kernel composition	Kernel composition (genotype)
	Maturity groups (MGs) or timing to anthesis	Plant vigor (Canopy cover, Leaf area index)	Shoot biomass	Plant height	Root biomass & depth	Nutrient-use efficiency	Water use efficiency	Floral biology	Cold	Heat				
Market-oriented production														
Oil %	* (late)	**	*	*	*	*	*	*	*	*	*	* (prevent low * (hull fraction) plant density)	***	***
Oleic acid %	*	*	*	*	*	*	*	*	*	*	*	*	***	***
Protein %													**	**
Other non-food by-products			**	*	*	*	*	*	** (early)	*	** (mildew)	** (sowing)	**	**
Early sowing (stress escape)	* (late)	**	*	*	*	*	**	**	** (early)	*	** (sclerotinia, phomopsis)	** (sowing)	**	**
Supplemental irrigation	* (late)	*	*	*	*	*	*	*	*	*	*	*	**	**
Adaptation to new environments														
Crop shift to northern areas	* (early)	*	*	*	*	*	*	*	* (early + lately)	*	*	** (sowing)	non-oleic types	non-oleic types
Increased cultivated diversity (field)	** mixture of MGs	*	*	*	**	*	*	*	**	**	** mixture of resistances	*	***	***
Increased cultivated diversity (farm) - yield stability	** different MGs	*	*	*	*	*	*	*	**	**	** (multi-resistant)	*		
Double cropping	** (very early)	**	*	*	*	*	**	**	* (lately)	**	*	*	non-oleic types	non-oleic types
Adaptation to new cropping systems														
Organic farming	Low-input late-sown	**	*	*	**	*	*	*	*	*	*	*	*	*
Reduced tillage	**	**	*	*	**	*	*	*	*	*	*	*	*	*
Agroforestry	*	*	*	*	*	*	*	*	*	*	** (soilborne diseases)	*	*	*
Biocontrol (allelopathy...)	*	*	*	*	*	*	*	*	*	*	*	*	** (allelochemicals)	**
Rotation fertility	*	*	*	*	**	*	*	*	*	*	*	*	*	*
Pollinators	** mixture of MGs	*	*	*	**	*	*	*	** small flowers	*	*	*	*	*
Provision of ecosystem services									** nectar + pollen	*	*	*	*	*
Phyto-remediation	**	**	**	**	**	*	*	*	**	*	*	*	**	**

tissue leachates (Leather, 1983). Results indicated that application of sunflower water extracts reduced weed density by 5–26% and weed biomass by 9–31%, while sunflower residue incorporation (4 to 6 t/ha) caused 44–57% reduction in weed density and 58–70% reduction in weed biomass compared with the control (Ullah *et al.*, 2018).

Genotypic variation, growing conditions, and various plant organs, such as leaves, stems and inflorescences may influence the allelopathic activity of sunflower, which can be both stimulatory (at low concentrations) and inhibitory (Gawronska *et al.*, 2007). Different allelopathic activities were observed among a small set of sunflower hybrids (Anjum and Bajwa, 2008; Silva *et al.*, 2009; Alsaadawi *et al.*, 2012; Ullah *et al.*, 2018). The total concentration of phytotoxins (phenolic compounds) was found to be higher in the most-suppressive potential genotypes compared with the least-suppressive ones.

6 Challenges for designing and breeding sunflower ideotypes to face new and multiple objectives

As climatic conditions, crop practices and cropping systems are changing markedly and because new ecosystem services are expected from sunflower crop, this requires a complete overhaul of the characteristics of the current varieties and justifies the exploration of new traits and the design and breeding of new ideotypes to make the crop better adapted to these emerging challenges.

In Table 2, we proposed a synthetic chart crossing priorities (targets) for management and breeding as described on Figure 1 and morpho-physiological traits of interest to consider and combine. From this table, we can conclude that some traits should be considered for a wide range of objectives (columns): root biomass and depth, canopy cover and plant vigor, phenology, disease resistance, drought-resistance. Some of them (phenology, disease resistance) have been already actively improved by breeders, but the other ones should be considered more for adapting sunflower to new environments and cropping systems. When looking at the rows, the main traits to combine when designing an ideotype for a given priority are suggested (see previous sections for more details). For instance, designing ideotypes for organic farming, double cropping or maximal oil production will have to optimize numerous criteria while phytoremediation or biocontrol will concentrate on specific plant characteristics.

Therefore, these changes in agricultural systems renew the potential interest of ideotype breeding (Gauffreteau, 2018). Donald (1968) first defined an ideotype as a “biological model which is expected to perform or behave in a predictable manner within a defined environment”. In ideotype breeding, the relation between crop yield and its determining factors is implicitly modeled. In this case, a crop ideotype is mainly defined at the plant level, focusing on plant traits desirable to achieve a given objective. Because of increased knowledge in crop physiology, and developments in crop modeling and operational research, ideotype breeding can be pursued with greater formalization, potentially giving this approach an edge over classical breeding to tackle crop adaptation to new contexts (Martre *et al.*, 2015).

Recent and diverse methodological approaches applied to sunflower (*e.g.* phenotyping, crop modeling, genomic prediction, multi-goal optimization, participatory breeding...) could be useful for the exploration and design of ideotypes (*e.g.* Picheny *et al.*, 2017a, 2017b; Vincourt and Carolo, 2018; Gosseau *et al.*, 2019; Debaeke *et al.*, 2020). The existence of important wild and cultivated genetic resources in sunflower should facilitate the adaptation to this new context as well (Vear, 2016; Seiler *et al.*, 2017; Terzić *et al.*, 2020).

In major crops, genomic prediction (GP) approaches are used to select best lines for complex traits (Heslot *et al.*, 2015). However, as genotyping and phenotyping technologies become available and cheaper, it creates new avenues for predictive approaches and enables their expansion to new crops and in smaller breeding programs (Ramstein *et al.*, 2019). Genomic prediction was successfully applied for sunflower hybrids in an incomplete factorial design to predict oil yield (Mangin *et al.*, 2017) and GP is now widely used in the main sunflower breeding companies.

A key challenge yet to solve is to predict the performance of novel hybrids in different pedo-climatic environments and with different crop practices. To achieve this, predictive approaches bridging quantitative genetics and crop modeling (Bustos-Korts *et al.*, 2016) are under development to scale traits from the molecular to the crop level. Such approaches provide a unique way forward in defining an ideotype as a combination of genetic markers and not only as an addition of desired morpho-physiological and phenological traits.

One option is to process in two steps: firstly, to use GP to estimate a set of component traits, and then use a crop simulation model to predict performance-related traits as a function of environmental data (*e.g.* Chenu *et al.*, 2009 for maize; Quilot-Turion *et al.*, 2016, for peach tree). Typically, the genetically studied traits should encompass variables from both the real and the modelled system. For sunflower, such analysis can be conducted using the Phenotoul-Heliaphen high-throughput phenotyping platform (www.inrae.fr/phenotoul, Gosseau *et al.*, 2019) that enables automatic estimation of the responses of leaf expansion and transpiration ratios to soil water deficit used as drought stress sensitivity proxies in the SUNFLO crop model (Casadebaig *et al.*, 2008). The genetic analysis of the input parameters of the model, either to estimate allelic effects of QTLs or to train a large population for GP, relies on the high-throughput genotyping and phenotyping capacities (Cobb *et al.*, 2013).

Breeding tools to select for the traits of interest have been revolutionized in the last decade with the first high-quality genomic sequence (Badouin *et al.*, 2017), the use of resequencing and high-throughput genotyping arrays and the identification of numerous markers associated to QTLs or even the first cloning by fine-mapping of an *Orobanche* resistance gene (Duriez *et al.*, 2019). New developments, including long-read sequencing and ever-cheaper short-read resequencing data are giving access to structural variations and genetic diversity in larger collections (Hübner *et al.*, 2019; Todesco *et al.*, 2020), that facilitates the identification of markers for breeding.

In the same time, the current revolution in phenomics is giving access to high-throughput automatic acquisition of images and 3D scans of sunflower plants and organs in

controlled conditions under different biotic or abiotic stresses but also in field conditions. However, image and signal processing pipelines to estimate most of the classical traits are yet to be developed and the evaluation of new traits are pending.

In this context, the challenges to move from the identification of candidate traits (the purpose of this article) to the cultivation of varieties fulfilling climate change and societal demands are multiple.

First, research efforts should be deployed in the phenomics field to automatically measure traits used in the current registration system (Tab. 1) on a wide range of genetic material and environmental conditions including new cropping systems. This should allow to develop more complete sets of genetic markers for breeding including haplotypic variants, but also to study the stability of these traits in response to different stresses. In addition, phenomics procedures should be developed to characterize new traits such as yield plasticities for abiotic and biotic stresses, attractiveness to pollinators or phytoremediation. Performed systematically on a large extent of the genetic resources and in the registration process, and supported by crop simulation, this would provide information for breeders and possibly farmers. This could also justify a reshaping of the current experimental networks by diversifying the testing environments and the crop management systems.

To exploit the increasingly large and complex phenotypic and genotypic data, we can clearly identify as well a challenge for the sunflower community to organize them under the FAIR principles. Initiatives from the French community to archive sequencing and phenotyping data (<https://sunrise-archive.toulouse.inra.fr/web/index.html>) should be consolidated and amplified to an international level. Thanks to the recently released sunflower Crop Ontology, an international database for both resources should be created and made available to public and private research.

The ambitious goal to better adapt the choice of varieties also necessitates to better characterize the biotic and abiotic environments of the registration and post-registration multi-environment trials using more systematically simulation models and sensors. This would enable the estimation of infra-specific yield plasticities (i.e. sensitivity to abiotic stresses) like in Mangin *et al.* (2017).

7 Conclusion

As was reviewed, many traits are possibly relevant when designing and breeding sunflower varieties better adapted to climate change, new ecological cropping systems and providing ecosystem services (Tab. 2). This implies to produce many different varieties adapted to contrasting and fluctuating environments or needs (markets, services) and to combine the desired traits by stacking faster and more efficiently.

Research and innovation will have to share their efforts between different and multiple breeding targets and agro-environmental conditions, in the context of a strong market segmentation (Pilorgé, 2020) and priorities will have to be established among the numerous and sometimes opposite breeding objectives identified for sustainable production (Kaya, 2016).

The challenges faced by the sunflower research community are important and include the development of resources and methods, their transfer to the breeding sector and also the improvement of the registration and recommendation devices to finally provide to farmers a larger panel of varieties with more complete and accessible information including possibly new traits related to stress tolerance and ecosystem services.

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