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# Complex plant interactions in heterogeneous material require the ecological rethinking of sowing density recommendations for bread wheat. A review

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## Abstract

Despite the growing concerns over the damages and unsustainability of conventional agriculture, arable farmers struggle to convert to organic cropping practices. In wheat farming, the lack of cultivars adapted to organic cropping has prompted a search for alternatives to better cope with unpredictability and stress. In that respect, heterogeneous material (HM) has attracted a lot of attention for its good performances and yield stability across years and environments. These benefits are thought to arise from facilitative plant interactions brought forth by intraspecific diversity, but much remains to be known about the mechanisms at play as well as their interactions with the other elements of the cropping system. Here, we review the literature on plant interactions within organic bread wheat crops through the successive scopes of (i) heterogeneous material, (ii) plant density, and (iii) their interaction. Our major findings are as follows: (1) optimizing heterogeneous material performance and evolutionary trajectories grossly amounts to tipping the balance between competitive and facilitative plant interactions toward the latter. (2) The stress gradient hypothesis applies to the competition/facilitation balance within HM: The more stressful the conditions, the more facilitation happens. (3) Plant density also affects this balance, and the relationship between net facilitation and plant density in HM follows a humped curve. (4) Therefore, the optimal plant density range for HM should be both narrower and lower than for pure lines, and also harder to predict. (5) High-tillering, high individual yielding plant types should probably be aimed for in HM, for two reasons: first, they perform better at the lower-than-the-recommendations plant densities at which HM are expected to best express their potential. Second, optimal plant densities of such plant types are more stable across environments, which should increase the probability of falling within the narrower optimal plant density range of HM, particularly in unpredictable and/or stressed environments.

**Keywords** Plant interactions · Organic heterogeneous material · Plant density · Bread wheat · Competition · Facilitation · Crop diversity · Organic farming

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## 1 Introduction

Once praised for the considerable yield improvements it brought, chemical and highly mechanized agriculture is now the subject of growing concerns over its lack of sustainability and resilience, and the damages it causes (Tilman 2001). As a result, a shift toward more sustainable agricultural practices is generally promoted, among which organic farming is especially in the spotlight. For example, the Farm to Fork Strategy aims to promote organic farming to at least 25% of the EU's agricultural land by 2030 (European Commission 2020). Yet, while the area under organic agriculture has been growing encouragingly (Eurostat 2020a), arable crops appear to be struggling the most to convert to organic agriculture, despite representing the largest share of utilized agricultural area in the EU-27 (61%; Eurostat 2020b). Indeed, while respectively 9.6 and 12% of permanent crops and permanent grassland area was organic, the share of organic arable land was only 5.8% in the EU-28 in 2018 (Eurostat 2020b, 2021). Cereals, which are the main arable crops in the EU (53% of total arable land; Eurostat 2020c), are particularly concerned as only 4% of the cultivated land area in 2019 was organic.

For now, the transition toward organic agriculture has mostly relied on the *input substitution* paradigm, which is still rooted in the conventional framework (Lamine and Bellon 2009). Mainstream and recommended organic practices for organic wheat cropping mostly rely on the substitution of mineral fertilizers by organic fertilization, and of herbicides by denser sowing densities and mechanical weeding operations. Failure of these cropping practices to provide sufficiently satisfying results may be a reason for the poor conversion rates (Xu et al. 2018). For instance, a known agronomic lock-in is the lack of cultivars adapted to organic practices (Lammerts van Bueren and Myers 2012), particularly for cereals (Murphy et al. 2007; Wolfe et al. 2008). This is a problem for farmers not only in terms of agronomic performance but also due to a higher difficulty to reach industrial quality standards with conventional cultivars

under organic conditions (Osman et al. 2012). Indeed, most of breeding work takes place under conventional conditions (Murphy et al. 2007; Vanloqueren and Baret 2008): A decade ago, it was estimated that 95% of organic production was based on wheat cultivars selected for conventional cropping systems (Lammerts van Bueren et al. 2011). However, empirical evidence shows that good cultivar performance under conventional cropping does not ensure good cultivar performance under organic cropping (Murphy et al. 2007). In wheat, the current conventional cultivar model grossly corresponds to Donald's ideotype (Donald 1968). Donald described an ideotype for wheat breeding where wheat plants should be short, with erect short leaves, few or no tillers and long spikes. This ideotype had two purposes. First, maximizing resource allocation toward reproductive parts, thereby increasing resource-use efficiency of single plants. Second, reducing plant competitive ability to its minimum in order to increase plant density and, in turn, maximize total resource uptake. Together, Donald believed that those characteristics would allow to further increase the amount of mineral fertilizer input that the crop could efficiently take up—the paradigm not being to spare fertilizer, but rather to inject as much fertilizer as possible without it being a waste. Meanwhile, the low competitiveness of crop plants could be compensated through the use of herbicides in order to control weeds. However, this model supposes environmental conditions which are not met in organic cropping. Besides, environmental conditions under organic cropping are much more variable (Döring et al. 2012; Lammerts van Bueren and Myers 2012): Between locations or years, nutrients may not be as available and biotic stresses not as readily controlled. Moreover, in the perspective of wider adoption of agroecological practices, organic farms may adapt to their local environmental conditions in very different ways, further strengthening environmental variability across locations (Wolfe et al. 2008).

This cultivar lock-in has prompted a search for alternative breeding strategies, among which evolutionary plant breeding (Wolfe et al. 2008) has gained sufficient attention in recent years for EU regulations to start including “heterogeneous material” (HM) for organic cropping (European Parliament 2018). Until then, only pure line cultivars could be legally sold for cereal cropping within member states. However, HM was shown to hold promise as early as the 1950s (Suneson 1956) but was not possible to develop under DVS regulation. Since then, further research appears to confirm and complement the benefits of within-crop intraspecific diversity for cereal cropping. Be it as pure line variety mixtures (Borg et al. 2018) or composite cross populations (CCPs, which are populations resulting from several individual lines being crossed and the bulking of the resulting progeny; Döring et al. 2011; see Fig. 1), diversity appears to have particular potential for

organic agriculture (Wolfe et al. 2008). Indeed, HM generally display higher yield stability than modern pure line cultivars across environments, thereby insuring both wider spatial and temporal adaptability (Phillips and Wolfe 2005; Döring et al. 2011). Besides, their evolutionary capacity across successive harvests, directly stemming from population genetic diversity, cannot only provide adaptability to changing environments (Döring et al. 2011) but is also compatible with participatory plant breeding. For instance, within a CCP, mass selection can be performed on-farm by the farmers themselves or in collaboration with breeders, so that breeding can better account for farmers' needs (Murphy et al. 2005). As such, by allowing them to have their own role and autonomy in breeding processes, HM can also be empowering for farmers (Ceccarelli and Grando 2007).

The good and stable performances of HM can be attributed to the facilitative plant interactions that are brought forth by intracrop diversity. In a similar fashion to intercrops, this diversity allows for facilitative interactions such as complementarity and compensation between the wheat genotypes (Döring et al. 2011; Barot et al. 2017). However, little is yet known as to the precise mechanisms and associations leading to those facilitative interactions, and there are no clear assembly rules for fostering them (Borg et al. 2018). Besides, as stressed by Duru et al. (2015), a challenge to the successful implementation of *biodiversity-based* practices such as the use of HM, which rely on complex interconnected ecological processes and interactions, is the lack of “knowledge about relations among practices, biodiversity, and associated

ecosystem services.” As HM brings drastic changes in the dynamics of plant–plant interactions within the crop, plant density should thus be a particular point of interest.

Although the effects of plant density on intraspecific competition within pure stands are well-known in conventional conditions, very little is known as to how plant densities affect plant interactions in HM, whether facilitation or competition. Furthermore, knowledge is also lacking on plant density under organic conditions, which has seldom been addressed in peer-reviewed literature except in the perspective of raising densities to better control weeds (Weiner et al. 2001; Olsen et al. 2005). However, the spectacular yield and income increases reported in India, Nepal, Afghanistan, and Mali after the implementation of the System of Wheat Intensification, which relies, inter alia, on drastic reductions of plant densities (Adhikari et al. 2018), put the spotlights on this additional knowledge gap (Baltazar et al. 2019).

This literature review digs deeper into plant–plant interactions in wheat organic cropping. First, we review the literature on both competitive and facilitative interactions in HM, and their impacts on HM performance. Second, we address the question of plant density and its effects on plant interactions and crop performance in organic cropping conditions for pure-line cultivars. Drawing from all of this, we finally address the overlap between the two themes: How does plant density interact with the diversity of plant interactions found in HM, and can we build new sowing density recommendations for HM from this?

**Fig. 1** A wheat composite cross population (CCP), several weeks before harvest. Intraspecific diversity is particularly apparent through the diversity of spike color, awnedness, height, and maturation stages of the spikes.



## 2 Crop intraspecific diversity

### 2.1 Plant–plant interactions within heterogeneous material

Instead of a homogeneous stand of crop plants each displaying the same suite of functional traits, HM is characterized by crop functional diversity (i.e., phenotypic diversity for traits that have an effect on ecosystem level processes; Petchey and Gaston 2006). Stemming from functional diversity, as compared to pure line cultivars in which all crop plants virtually have the same fitness, this is not the case anymore with HM. In HM, fitness can be dissected into two components: *environmental fitness*, referring to a crop plant being well adapted to its growing environment (i.e., overall soil conditions, climate, pests or diseases, exceptional stress conditions, ...), and *selfish fitness*, referring to a crop plant possessing competitive traits such as early vigor, tallness, or tillering capacity (Hoad et al. 2012; Lazzaro et al. 2019) which allows it to take over resources better and faster than its neighbors (Anten and Vermeulen 2016).

As a result, crop functional diversity gives rise to new types and dynamics of plant–plant interactions. For one, competitive interactions between crop plants become asymmetric. Asymmetric competitive interactions will benefit those plants with the highest fitness. Depending on what defines the fitness advantage, the outcomes of this new competition dynamic may both be positive or negative for the whole crop (Weiner et al. 2017). In conventional breeding, it is considered that selfish fitness is negatively related to yield performances at crop level (Donald 1968; Fasoula and Fasoula 2002; Andrew et al. 2015). If the fitness differential between genotypes is mostly determined by selfish fitness, it may hence favor less-productive genotypes. On the other hand, if the fitness differential between genotypes is mostly determined by environmental fitness, this can enhance crop performance through a mechanism described by Döring et al. (2011) as *compensation*. Compensation relates to the fact that the yield loss incurred by genotypes which are poorly adapted to local conditions can be compensated by the adapted genotypes taking over part of the resources that could not be used by their less-adapted counterparts (Frey and Maldonado 1967; Phillips and Wolfe 2005; Borg et al. 2018).

Second, crop functional diversity may also lead to the presence of complementary traits resulting in facilitative interactions. For example, complementarity might occur when the genotypes constituting the population display different resource-use profiles (e.g., root and aerial architecture or phenology) that complement each other (Dahlin et al. 2020), in a similar fashion to what has been documented at the species level for intercropping (Bessler et al.

2009; Postma and Lynch 2012; Li et al. 2014). Barot et al. (2017) refer to this type of positive interactions as “complementarity effects.”

### 2.2 Evidence of facilitative interactions in HM

Facilitative interactions are hence considered to enhance HM performances: Compensation is expected to lead to productive stability across environments in both time and space as well as overyielding (i.e., HM being more productive than the average of its components grown as monocultures), while complementarity effects can be expected to lead to overyielding, even transgressive overyielding (i.e., HM being more productive than its most productive individual component grown as a monoculture; Barot et al. 2017), or enhanced yield-sustaining benefits, such as stimulation of ecosystem services.

Cases of transgressive overyielding have been reported in oats (Frey and Maldonado 1967); in spring barley (Kiær et al. 2012); and in wheat (Chapman et al. 1969) and spring pea (Tarhuni and McNeilly 1989). These cases are however not the most frequent, and simple overyielding, where one or several components of HM still remain more productive when grown in pure stands, is the most commonly observed benefit of HM. Two meta-analyses found that mixtures significantly overyield, with an average 3.5% (Borg et al. 2018) and 2.2% (Reiss and Drinkwater 2018) yield increase compared to the mean of their component cultivars. In CCPs, Döring et al. (2015) showed similar results in a paper comparing CCPs and same-parent mixtures with their parent lines. Furthermore, the same study found higher yield stability of both CCPs and the mixtures over both the mean of parent lines and the highest-yielding single parent line, across contrasting environments.

#### 2.2.1 Compensation

Such figures reveal how HM are “safe bets” in terms of cultivar choice. More importantly, this is particularly the case in unpredictable and harsh environments, where the best-yielding cultivar may be more difficult to predict. Several papers indeed report that overyielding of HM is particularly significant within environments where individual parent lines display higher yield variability (Döring et al. 2010; Kiær et al. 2012), and that the degree of overyielding increases under stress conditions, confirming the relevance of HM to cope with environmental variability. Remarkably, this indicates that this type of facilitation in HM—and hence its benefits, including overyielding—follows the stress-gradient hypothesis, which states that facilitative interactions become more frequent as conditions become more stressful (Bertness and Callaway 1994). In their meta-analyses, Borg et al. (2018) report higher overyielding of mixtures

under high disease pressure but fail to find any effect of abiotic stresses—possibly due to lack of information—while Reiss and Drinkwater (2018) found increased overyielding under both high disease pressure and some abiotic stresses, in this case lower soil organic matter, lower soil pH, and absence of fertilization. In oat, Frey and Maldonado (1967) also reported higher overyielding of mixtures for a later (and suboptimal) sowing date when compared to optimal sowing date. The higher overyielding in harsher conditions is coherent with the mechanism behind compensation which, by definition, occurs when conditions are suboptimal for at least part of the individual components of HM.

### 2.2.2 Complementarity effects

Complementarity effects can however also explain this phenomenon of stronger overyielding under harsher conditions. Indeed, higher overyielding under high disease pressure is most probably the result of a better disease resistance of HM, as observed in mixtures (Finckh et al. 2000) and CCPs (Costanzo and Bàrberi 2016). This better disease resistance stems from diverse mechanisms pertaining to intergenotypic complementarity. The dilution effect, for example, arises from the presence of resistant genotypes within the population which lowers the probability of the disease spreading by reducing the density of susceptible plants. Another example is the more complex premunition effect: Wheat population diversity may lead to more diverse pathogen populations in which avirulent spores might be found. Those might stimulate plant defenses without causing any harm, inducing a better plant resistance against virulent spores (Borg et al. 2018). Diversity in plant architecture, such as plant height, may also provide better canopy aeration and thereby reduce risks of disease contamination (Finckh 2008; Vidal et al. 2017).

Higher overyielding under abiotic stresses can also be explained by resource-use complementarity, which is expected to be all the more beneficial where resources are scarcer (Reiss and Drinkwater 2018; Dahlin et al. 2020). In barley, Dahlin et al. (2020) report reduced intraspecific competition in mixtures, evidenced by a longer vegetative growth phase and shorter plants in mixtures as compared to pure lines—where strong competition rather leads to a “race” for light and an earlier onset of the reproductive phase and taller plants (see 3.3.1). Resource-use complementarity for nitrogen can also be evidenced through higher protein yield of mixtures over the average of its components (Lazzaro et al. 2018), which can be explained by complementary belowground resource exploration by the cultivars (Sarandon and Sarandon 1995), although this may not be systematic (Döring et al. 2015).

There are also complementarity effects regarding weed competition. Indeed, Lazzaro et al. (2018) investigated mixtures of various diversity levels, both in terms of genotypic

(i.e., number of cultivars in the mixture) and functional diversity, and found that weed biomass was 65% lower for the most diverse mixture (both genotypically and functionally), as compared to the average of the other entries (i.e., less diverse mixtures and mixture components grown as pure stands) in a year of higher weed infestation. Yet, other mixtures did not suppress weed significantly better than the average of their components in pure stands.

Finally, other ecosystem services of HM have been reported concerning crop-associated biodiversity. Chateil et al. (2013) compared crop arthropod and wild plant diversity in pure lines and in HM of bread wheat in an organic farm over one growing season. Although they did not find any effect on wild plant diversity—which could be expected as those would be strongly influenced by soil seed banks and other environmental factors—they did find significantly richer arthropod communities in HM, especially in springtails and spiders but also in predatory carabids. In barley, Ninkovic et al. (2011) found that a polyphagous ladybird preferred a variety mixture over its two single components both before aphid arrival and after their emigration, apparently due to the mixed scents of the barley genotypes. Although Chateil et al. (2013) did not report changes in wild plant diversity over only 1 year, such changes may take place over the longer term, as noticed with more diverse crop rotations (Neyret et al. 2020). Also, although not yet investigated for HM, cultivars have been reported to affect soil arbuscular mycorrhiza fungi (AMF) community composition (Ellouze et al. 2018), as well as AMF colonization rates and mycorrhizal responsiveness (Zhu et al. 2019) in correlation with cultivar root traits (Behl et al. 2003). Functional root diversity may thus also foster more diverse symbiotic soil communities, which may be beneficial to the crop. Further research is however required to confirm this.

## 2.3 Evolutionary trajectories of HM

Because of their genetic diversity, a second major specificity of HM compared to pure line cultivars is their capacity to evolve over successive harvests. Indeed, when seeds from previous harvests are saved and re-sown on the following year, the genetic structure of populations can change in the course of generations in response to natural selection or anthropic selection. This can lead to local adaptation and continuous population improvement, which is at the core of evolutionary plant breeding (Wolfe et al. 2008; Ceccarelli and Grando 2020). Here, also, plant–plant interactions play an important role.

### 2.3.1 Natural selection

According to Darwinian evolution, natural selection should favor the genotypes associated with higher fitness. In barley,

Allard and Jain (1962) indeed showed that the evolution of a CCP led to increased average fitness of individual genotypes, measured as the total number of seeds produced by the progeny of random individual genotypes from the population. Regarding crop performance, however, the outcomes of natural selection depend on which components of fitness determine the evolutionary trajectory of the population.

A preponderance of environmental fitness as a driver of natural selection leads to local adaptation of the population, both to local environment and to cropping practices. For instance, Rhoné et al. (2010) reported significant divergences in flowering time after several generations of a same wheat population evolving in different climate regions of France: After 12 generations, in a common garden experiment, flowering time was earlier for the southern population, thus reducing exposure to drought and heat stresses, but later for the northern population, thereby reducing the exposure to late frosts and allowing longer maturation. In another example, in just one generation after an event of serious frost-killings, Thomas and Schaalje (1997) showed that the composition of a cultivar mixture evolved at the advantage of the most winter-hardy cultivars. Diseases may also be an important selection pressure. After 10 years of evolution of a same population in contrasting environments, it was observed that resistance to powdery mildew (*Blumeria graminis* f. sp. *tritici*) had been significantly selected for in locations where pathogen pressure was high, but not where pathogen pressure was low (Paillard et al. 2000a, b). Cropping practices also exert environmental pressures, and Vijaya Bhaskar et al. (2019) observed that a same population evolved toward higher seedling seminal root length and root dry weight but lower total root length after 6 generations of organic cropping, whereas such changes had not happened under conventional cropping. As suggested by the authors, seedling vigor is particularly essential in organic agriculture, where nutrient availability is lower, especially so early in the growing season when mineralization processes are hindered by the low temperatures.

A preponderance of selfish fitness as a driver of natural selection will, on the other hand, tend to favor those genotypes that are best able to suppress their neighbors or tolerate competition. In a wheat CCP, Knapp et al. (2020) found an evolution toward wild-type competitive alleles leading to increased plant height and later heading after 10 generations of natural selection, regardless of either location or farming system. As stated earlier, individual performance is however not necessarily synonym to group or population performance (Donald 1968; Weiner et al. 2017). For example, both Khalifa and Qualset (1974) and Thomas and Schaalje (1997) found that, with only natural selection pressures, more competitive (i.e., taller) but lower-yielding cultivars tended to dominate cultivar mixtures, leading to grain yield reduction of those mixtures

over time. Over time, an “arms race” for competitive resource-harvesting organs may thus lead to a population investing more resources in resource-harvesting organs for the same total amount of resource uptake at population-level and hence lead to a decline of population performance, a phenomenon sometimes described as a tragedy of the commons (Anten and Vermeulen 2016). However, selfish fitness might also be an interesting trait to select for in organic cropping if it contributes to weed suppressiveness. Besides, intergenotypic competition can also stimulate niche differentiation or fitness equality between genotypes, which may lead to reductions in overall net competitive interactions over time (Schöb et al. 2018).

Finally, facilitative interactions may have a stabilizing effect on the evolutionary trajectory of HM. In the case of mixtures, for instance, an increase in the frequency of one genotype will reduce overall facilitative intergenotypic interactions while increasing intragenotypic competition, which will have a negative impact on that genotype's fitness. As such, facilitative interactions may rather favor the stable coexistence of different genotypes (Chesson 2000).

To sum up, evolution toward higher environmental fitness should lead to improved crop performance overall, while the outcomes of more direct plant interactions (i.e., competition and facilitation) are less predictable. Evolution guided by higher selfish fitness, being blind to overall population performance, may in some cases be antagonistic to overall crop performance, but could also stimulate niche differentiation and, thereby, complementarity effects. Facilitative interactions could also lead to stabilization of population diversity. Therefore, depending on the relative importance of these components in natural selection (which may vary according to the stress gradient hypothesis), its resulting effects on the evolutionary trajectory of a population can be expected to vary. In turn, the balance between these evolutionary forces and, hence, the outcome of natural selection, depend not only on the distribution of the population's genotypes but also on the conditions in which the population evolves (Wade and Kalisz 1990). Hypothetically, Allard and Jain (1962) may have found plant height to decrease over time due to low-density planting (approximately 12 plants/m<sup>2</sup>) as well as thorough weeding which may have prevented light competition to be an agent of selection, while Knapp et al.'s (2020) observation of increased plant height may have the opposite explanation.

In the end, natural selection can be a pathway for increased population performance, but may also lead to its gradual decline, depending on the selective agents at play. Natural selection may however also lead to the loss of other important traits through genetic hitchhiking (Goldringer et al. 2001) and because it is blind to traits such as end-use quality.

### 2.3.2 Anthropic selection

In order to both counterbalance these negative aspects of natural selection as well as to select for specific traits of interest, anthropic selection can be implemented by the farmers themselves. Moreover, the trait associations found in genetically diverse populations implying crosses (such as simple crosses or CCPs) makes them able to provide single lines outyielding their parents (Khalifa and Qualset 1975), hinting at the potential for further improvement of populations through selection. As shown by Rivière et al. (2015), mass selection within populations can lead to significant positive selection responses on traits such as plant height, earliness, spike weight, or thousand kernel weight within as little as two generations. Although the same paper also showed significant deteriorations for some traits including baking-quality traits, it shows mass selection can be a powerful tool to shape population evolution on-farm. Past experiences of participatory plant breeding have shown that farmers are perfectly able to improve populations and varieties through mass selection (Ceccarelli and Grando 2007; Goldringer et al. 2019).

Coming back to the scope of this review, mass selection may hence as well shape the evolution of plant–plant interaction dynamics within HM. Further research may want to assess the impact of mass selection practices on this matter, as well as investigate the potential for including new criteria for the promotion of facilitative interactions.

Across Section 2, we have seen that compensation and complementarity effects in HM could lead to enhanced yield stability, overyielding, and yield-sustaining ecosystem services through a diversity of mechanisms encompassing compensation, improved disease resistance, resource-use complementarity, or enhanced weed competitiveness. But intraspecific diversity could also foster strong asymmetric competitive interactions which could be deleterious to crop performance and HM evolutionary trajectories. Overall, the balance between facilitative and competitive interactions thus determines the outcome of intraspecific diversity, and optimizing this balance is thus key to making the most out of HM. This objective can be reached through increasing the total amount of facilitative interactions, minimizing competitive interactions, or both. Both components are largely determined by the composition of intraspecific diversity, the growing conditions of HM (e.g., facilitative interactions are most expressed under harsher condition), and their interactions (Wade and Kalisz 1990). While partly out of our grasp (meteorological conditions, landscape-level pest population dynamics, ...), the growing conditions of a crop can be shaped to some extent through cropping practices. In the next sections, we address how plant density, through

its direct impact on the intensity of plant interactions, has a role to play in this.

## 3 Plant density and plant-plant interactions

### 3.1 A brief history of sowing density recommendations

Contemporary sowing recommendations for wheat cropping are to sow in high densities: In Belgium, for instance, current sowing density recommendations for winter wheat start at 200 seeds/m<sup>2</sup> (Blanchard et al. 2019). The use of high sowing densities predates the Green Revolution: In 1943, Sauvageot and Grillo report common seeding rates of 200 kg/ha (around 400 seeds/m<sup>2</sup>) in France. With the onset of modern conventional agriculture, with its new cultivar types and abundant chemical inputs, seed density for wheat cropping was reevaluated (Puckridge and Donald 1967; Darwinkel et al. 1977; Darwinkel 1978) and, despite finding constant yield over a wide range of densities, including much lower densities than common practice, these papers came to the same conclusion: Wheat should be sown in high densities. Part of the explanation for this lies in the description of Donald's ideotype for wheat (Donald 1968), as mentioned earlier (see section 1). Another explanation is to exaggerate sowing density in anticipation of bad emergence or winter frost killings, for example. For organic cropping, sowing density recommendations tend to be even higher than for conventional cropping, due to later recommended sowing dates, and with the aim of establishing early competitiveness against weeds (Weiner et al. 2001; Olsen et al. 2005) or to anticipate plant mortality during mechanical weeding operations.

The system of wheat intensification (SWI) is based on the opposite paradigm. Instead of dense crop stands, it promotes careful seed selection and treatment, precision seeding, careful weeding, abundant organic fertilization and, last but not least, drastically reduced sowing density (as low as 25 grains/m<sup>2</sup>; Adhikari et al. 2018; Baltazar et al. 2019). The objective of reducing plant density is to substantially reduce competition between crop plants in order to promote, jointly with the other specific treatments, the establishment of robust individual wheat plants that tiller abundantly. This method, which also includes the use of organic amendments and good soil aeration in order to improve soil structure and efficient organic matter decomposition, has demonstrated spectacular yield and income increases in India, Nepal, Afghanistan, and Mali (Adhikari et al. 2018). Although temperate agroecosystems are drastically different from African or South-Asian agro-ecosystems both in climate, pedological and socio-technical aspects, SWI was successfully implemented under Western-European conditions by at least one Dutch

farmer with precision and conservation farming techniques (Baltazar et al. 2019), and a similar method was described in France in the 1940s, claiming significant yield increases over common practices of the time (Sauvageot and Grillo 1943).

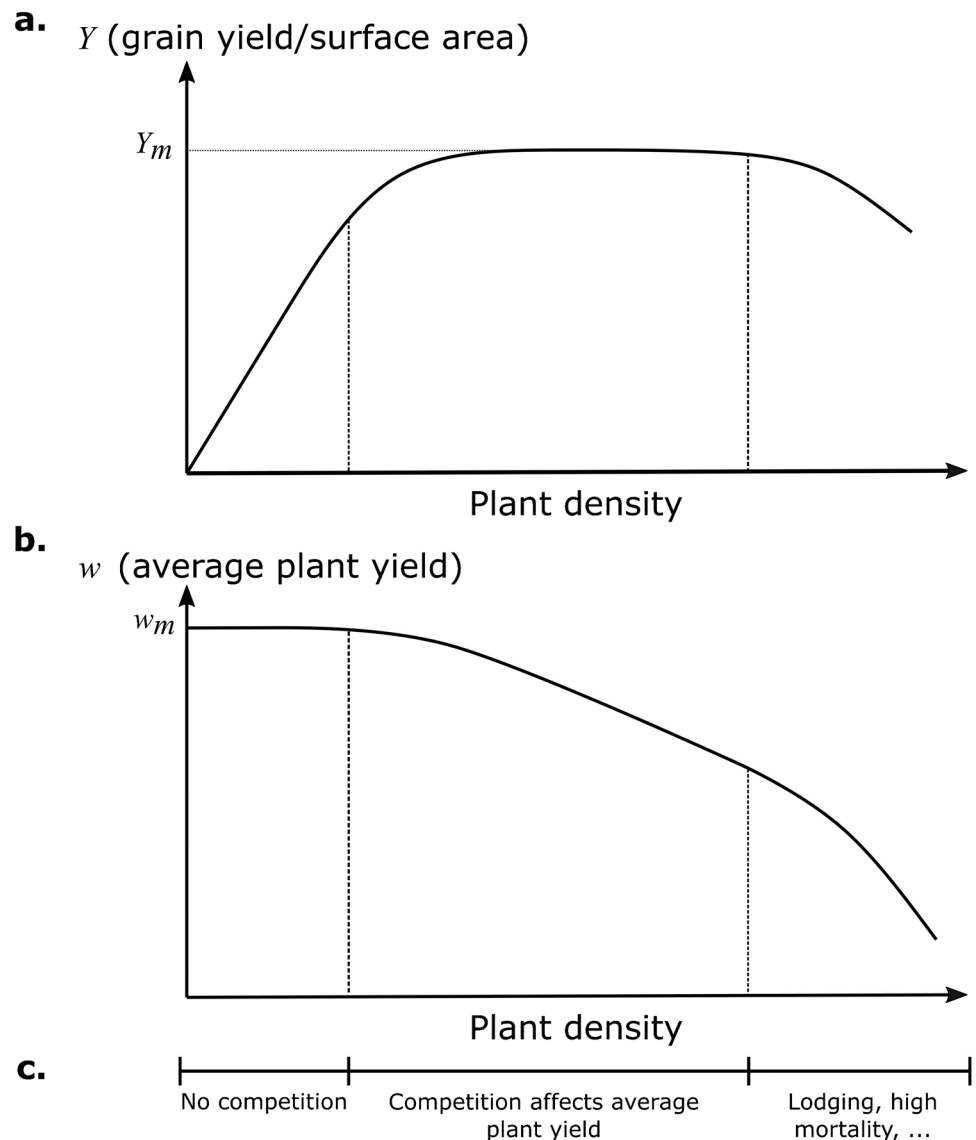
### 3.2 Plant density and the law of constant final yield

These contradictory recommendations, as well as the findings of constant yield over wide ranges of plant densities, are to be attributed to wheat plasticity and the known phenomenon of “Constant Final Yield.” Constant final yield (CFY) is a common pattern in plant ecology describing the relationship between plant density and yield (i.e., total and/or harvestable biomass produced per surface area), which has been described and modeled since the beginning of the twentieth century (Montgomery 1912). Here, we focus on the developments proposed by Weiner and Freckleton (2010) in a recent

literature review. The pattern of CFY, which is exposed in Fig. 2a, can be summed up as follows: Starting at low densities, crop yield first increases linearly with plant density, before leveling out to a plateau at which further increases in plant density do not increase yield (Weiner and Freckleton 2010). At very high densities, yield (particularly harvestable yield, i.e., grains in cereals) can even tend to decrease due to a shift in resource allocation leading to a lower harvest index, lodging or increased disease pressure, for example (Gallandt and Weiner 2015). CFY applies equally to biological yield (total biomass) and grain yield, but we will be focusing on grain yield in the following.

To explain this pattern, it is helpful to examine its consecutive parts, as exposed by Weiner and Freckleton (2010). At very low densities, plants are sufficiently far apart not to experience any competition: Each plant acts as an isolated individual and is able to fully exploit the environment’s resources

**Fig. 2** (a) Grain yield per unit area ( $Y$ ) as a function of density.  $Y_m$  is the maximal grain yield. (b) Average yield per plant ( $w$ ) as a function of density.  $w_m$  is the maximal plant yield and corresponds to the yield of an isolated plant. (c) Factors affecting total grain yield and average plant yield according to plant density (adapted from Weiner and Freckleton 2010).



within its neighborhood. At this stage, changes in density does not affect average yield per plant, as shown in Fig. 2b, hence, the linear relationship of Fig. 2a. At higher densities, plant ecological neighborhoods eventually begin to significantly overlap and plants start competing with each other for resources (see Fig. 2c), resulting in a decrease of the average yield per plant. At this stage, increases in density still result in increases of yield per surface area but at an ever-decreasing rate: The curve starts flattening. Finally, the pattern may reach the point where further increases in density are exactly compensated by the decrease of average yield per plant or even, at some level, plant mortality, so that the curve reaches a plateau of maximum grain yield per unit area. This maximum yield can be interpreted as the stage at which the crop fully exploits its environment's resources. Before the plateau, adding more plants allows to "fill in the space" and exploit resources that are still available. When all the space is "filled in" by the crop, adding more plants does not increase yield anymore. In the following, two values will be particularly useful in order to describe this pattern and make ecological sense out of it: individual isolated plant yield (i.e., individual grain yield per plant in the absence of competition, which corresponds to the maximal attainable grain yield for a plant of a given genotype in a given environment), and maximum grain yield per unit area (i.e., yield per unit area when the plateau is reached). For the sake of clarity and readability, we will further refer to those values as  $w_m$  and  $Y_m$ , respectively.

### 3.3 Evidence of constant final yield in wheat

The law we just described is of course an ideal representation, which assumes absence of competition from weeds and considers intraspecific competition as the only type of interaction between crop plants. The vast majority of peer-reviewed research on plant density in wheat being in conventional conditions, this law paints a good picture of what has been observed for the wheat crop in the literature, as we will expose in the present subsection. Along section 3.3, the literature cited refers to trials with full weed and pathogen control and non-limiting water and nutrient status, so that the main interaction between plants is light competition. In section 3.4, we will then review how several parameters (cultivar, sowing date, suboptimal conditions, ...) affect the CFY pattern, which will allow us to better understand the yield–density relationship in organic conditions, which has not been studied as extensively.

#### 3.3.1 Effects of plant density on individual plants

The observed effects of increasing plant densities on individual plants of wheat reported in the literature match the described pattern of gradual decrease of individual plant

yield as a result of increasing competition. Indeed, competition is seen to impede growth rate (Whaley et al. 2000; Baccar et al. 2011) as well as to shorten some growth phases: As plant density increases, the tillering phase is shortened (Puckridge and Donald 1967; Whaley et al. 2000), leaf and tiller senescence start earlier (Puckridge and Donald 1967; Darwinkel 1978), and heading (Geleta et al. 2002; Hansen et al. 2005) as well as maturity (Hansen et al. 2005; Nakano and Morita 2009) are reached earlier. Tillering is also significantly impacted by competition, as higher plant density is associated with lighter (Puckridge and Donald 1967) and fewer tillers per plant (Puckridge and Donald 1967; Whaley et al. 2000; Beres et al. 2010; Baccar et al. 2011; Gross et al. 2012), seemingly as a result of the shorter tillering phase in spring (Puckridge and Donald 1967; Whaley et al. 2000). Later in the season, stronger competition also leads to higher tiller mortality. This tiller mortality is however not fully responsible for the lower tiller abundance per plant at higher plant densities, which is also a consequence of lower tiller development as shown by Darwinkel (1978), who reported a peak tillering of around two tillers per plant at 800 plants/m<sup>2</sup> compared to approximately 17 tillers per plant at 25 plants/m<sup>2</sup>, before the onset of tiller mortality in both cases. Besides, hastened heading and maturity resulting from higher plant densities possibly make the crop more vulnerable to late frost events (Whaley et al. 2004).

Finally, although the literature is relatively poor on this matter, probably due to the technical difficulties of root analyses, plant density appears to have similar impacts on root development as what we described for aboveground plant parts. For instance, Berry et al. (2000) report that root plate spread (horizontal diameter of the root system where the majority of rigid root portions terminates) as well as structural rooting depth are larger as sowing density is lowered from 500 to 250 seeds/m<sup>2</sup>, while Dai et al. (2014) report an increase in the number of nodal roots per plant as plant density decreases.

#### 3.3.2 Effects of plant density on crop yield

The effects of plant density on grain yield components illustrate even better the mechanisms responsible for CFY. As a reminder, the relationship between total grain yield and yield components is as follows:

$$\text{Yield (g/m}^2\text{)} = \text{Ear density (ears/m}^2\text{)} \times \text{Grains/ear} \times \frac{\text{Thousand kernel weight (g)}}{1000}$$

First, as described earlier, competition is detrimental to tiller production, tiller survival, and tiller fertility rates. Yet, in terms of ear density (ears/m<sup>2</sup>) at crop level, ear density is systematically—yet not proportionally—increased when increasing plant density (Darwinkel 1978; Easson et al.

1993; Whaley et al. 2000; Nakano and Morita 2009; Beres et al. 2010). On its own, this first effect of competition is thus not enough to explain CFY. However, ear weight is also affected by competition: Spikelet initiation and survival are negatively correlated with plant density, leading to fewer fertile spikelets per ear at higher densities (Puckridge and Donald 1967; Darwinkel 1978; Whaley et al. 2000; Gross et al. 2012), which in turn leads to fewer grains per ear (Puckridge and Donald 1967; Darwinkel 1978; Easson et al. 1993; Whaley et al. 2000; Nakano and Morita 2009; Lazzaro et al. 2017). Finally, the impact of plant density on thousand grain weight (TGW) is not as evident. Despite broad density ranges in all cases, some authors report no significant differences with plant density (Puckridge and Donald 1967; Whaley et al. 2000), others observe a reduction of TGW with higher plant densities (Darwinkel 1978; Easson et al. 1993; Baltazar et al. 2019) and one study even reports a positive effect of plant density on TGW, presumably due to late tillers producing smaller grains as compared to main stems (Geleta et al. 2002). It is thought that generally, TGW is strongly controlled by genotype (Hansen et al. 2005; Xie et al. 2015) and is mainly affected by grain sink size (i.e., how much assimilates a grain is able to accumulate) rather than assimilate availability at the moment of filling (Jenner et al. 1991), which might explain the inconsistency of plant density impact on TGW. Overall, the combination of fewer kernels per ear and either equal or inferior TGW leads to lighter ears (Puckridge and Donald 1967; Darwinkel et al. 1977; Darwinkel 1978; Gross et al. 2012), which combined to fewer fertile tillers per plant, thus, leads to lower grain yield per plant at higher plant densities (Puckridge and Donald 1967). At even higher densities, strong competition ends up leading to a less efficient use of resources as density reaches an excessive level due to higher plant (Puckridge and Donald 1967) and tiller (Darwinkel 1978; Whaley et al. 2000; Spink et al. 2000) mortality, lower harvest index (Darwinkel 1978; Whaley et al. 2000) and increased frequency of lodging events (Easson et al. 1993).

The result of this mechanism is that, when finally looking at total grain yield per unit area, although the response to plant density varies from one reviewed study to another, all of them report that CFY is met at some point. Indeed, reviewed papers either find no significant effect of plant density (Nakano and Morita 2009; Gross et al. 2012; Auskalniene et al. 2018), find a linear yield increase with plant density up to a plateau (Darwinkel 1978; Whaley et al. 2000; Spink et al. 2000; Hansen et al. 2005), or find the same plateau followed by a yield decrease at the highest plant densities (Puckridge and Donald 1967; Easson et al. 1993; Beres et al. 2010; Popovic and Malesevic 2011). The differences between papers is simply ascribable to differences in the density ranges which were tested, resulting in different papers observing different parts of the full pattern. Indeed, the papers finding an initial

linear increase report the lowest starting plant densities, ranging from 1 to 20 plants/m<sup>2</sup>. The plateau is then typically reached at around 100 to 150 plants/m<sup>2</sup>, although Puckridge and Donald (1967) find their plateau to start at 34 plants/m<sup>2</sup>, and Nakano and Morita (2009) found no effect of plant density on yield despite their plant density range starting as low as 50 plants/m<sup>2</sup>. Accordingly, the studies that did not observe this initial yield increase had starting plant densities typically ranging from 160 to 300 plants/m<sup>2</sup>. Likewise, post-plateau yield decrease is found in studies in which the upper limit of the sowing density range is extremely high, ranging from 600 to 1600 seeds/m<sup>2</sup>. When reported, the start of this yield decline is observed at sowing densities of 100 (Easson et al. 1993), 600 (Beres et al. 2010), and 900 seeds/m<sup>2</sup> (Popovic and Malesevic 2011). The decrease at 100 seeds/m<sup>2</sup> reported by Easson et al. (1993) requires some nuance though, as this study is characterized by extremely high lodging occurrence which is a result of particularly high spring N fertilization (178 kg N/ha) combined with the absence of growth-regulator use. Besides, several papers reported no significant yield reductions despite including plant densities superior to 600 plants/m<sup>2</sup> (Spink et al. 2000; Weiner et al. 2001; Olsen et al. 2005; Auskalniene et al. 2018).

### 3.4 Interacting parameters

Yet, what parameters define the CFY curve? Although the observation of CFY is consistent across the cases cited until now, the lower and higher density limits of the plateau vary. For instance, the density at which yield starts to plateau ranges from 34 plants/m<sup>2</sup> (Puckridge and Donald 1967) to 139 plants/m<sup>2</sup> (Spink et al. 2000) in the cases we have cited until now—when the investigated range of plant densities goes low enough as to precede the plateau. Besides, all of those studies were performed in relatively similar conditions, with standard modern cultivars grown in their optimal nutrient and water supply conditions, and weed infestation and pathogens controlled for with chemical control. Stronger divergences would be expected with more diverse environments or cultivars.

The focus of this review, however, is HM in organic and low-input environments, straying quite afar from the case of standard modern cultivars grown under conventional practices. In order to gain a better understanding of the interaction between HM and plant density and, ultimately, make sowing density recommendations, one must be able to predict—to some extent—the general allure of its yield-plant density relationship in the target environment. For this, acknowledging the specificities of the target environment and cropping practices, and understanding their effects on the yield-density relationship is essential.

Despite very limited literature on the yield–density relationship in organic cropping, the available evidence appears to indicate that a CFY pattern is maintained under organic conditions (Weiner et al. 2001; Kristensen et al. 2008). Although it may at times lead to oversimplifications of the interactions at play, it is helpful to conceptualize the effects of the (organic) environment and cropping practices as modifications to the main parameters of the CFY pattern. Schematically, the CFY pattern can vary in three ways: (a) the slope of the linear section, (b) the height of the plateau, and (c) the upper density limit of the plateau. The first two are conceptually easy to apprehend: The slope of the linear section is directly proportional to the yield of an isolated plant,  $w_m$ , while the height of the plateau corresponds to the maximum yield potential of a given cultivar/genotype/population in a given environment,  $Y_m$ , which is defined by the resource availability of the environment and the capacity of the cultivar/genotype/population to convert those resources into yield (Weiner and Freckleton 2010). The upper density limit of the plateau may not be as readily conceptualized, however. Changes in environmental conditions or cropping practices are expected to affect both  $w_m$  and  $Y_m$  and, hence, the CFY pattern. In the following, we review the factors influencing these parameters.

### 3.4.1 Sowing date

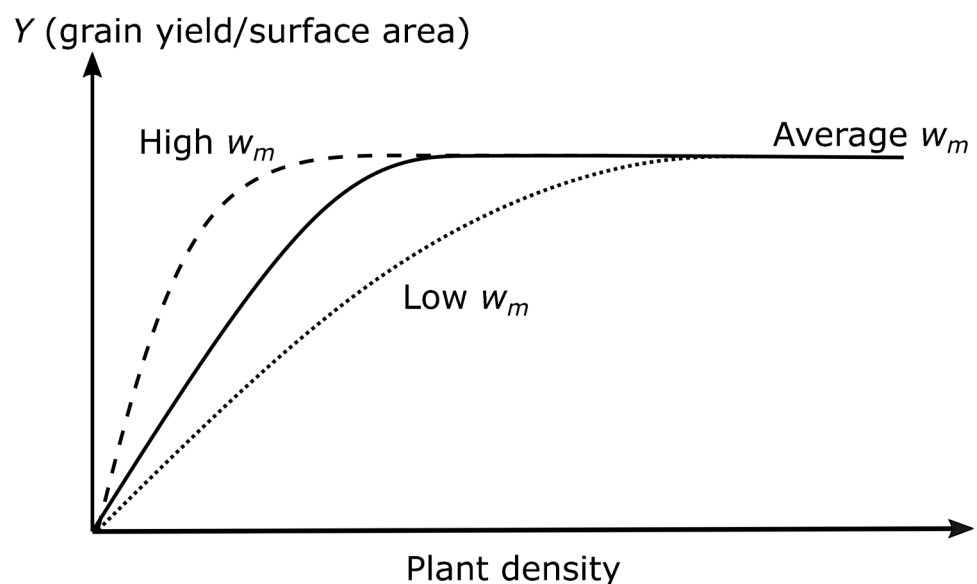
In a way, because wheat reproductive phenology is largely defined by photoperiod and vernalization requirements (Hyles et al. 2020), sowing date defines the length of vegetative growth, including tillering, thus impacting  $w_m$ . Therefore, the earlier the sowing date, the lower the density at which CFY is reached (Darwinkel et al. 1977; Spink

et al. 2000). Indeed, at a given plant density, later sowing leads to fewer fertile tillers per plant (Darwinkel et al. 1977; Spink et al. 2000), equal (Spink et al. 2000) or fewer (Darwinkel et al. 1977) grains per ear, lower TGW (Darwinkel et al. 1977; Spink et al. 2000) and, thus, lower individual plant yield. A similar behavior appears to occur for root development, as indicated by the results of Rasmussen and Thorup-Kristensen (2016) showing deeper roots, denser root systems in autumn, and enhanced N absorption in earlier sown wheat stands despite plant density adjustments to the sowing date according to local (Denmark) standard recommendations. As sowing date clearly affects  $w_m$ , it indirectly affects the linear slope too, as illustrated in Fig. 3: The earlier the sowing, the steeper the slope. Besides, literature examining the interaction between sowing date and density reports a tendency for lower  $Y_m$  at later sowing dates under conventional conditions (Darwinkel et al. 1977; Spink et al. 2000), which may be attributed to the crop being photosynthetically active for a shorter period at later sowing dates (Darwinkel et al. 1977). In organic conditions, later sowing date may also lead to increased nutrient leaching or runoff in winter hence further decreasing  $Y_m$ , which may be avoided if plants are better developed when entering winter.

### 3.4.2 Resource availability

Across section 3.3, we discussed cases in which the density–yield relationship was mostly structured by light competition. In cases where water or nutrient become limiting, the general rule appears to be that “the lower the yield potential of a given environment (i.e., the more limiting the conditions), the lower the optimal density”

**Fig. 3** Variations of the yield–plant density relationship according to  $w_m$  (average individual plant weight in the absence of competition) for the same environment.  $w_m$  may be lower in cases such as later sowing dates or varieties with a lower tillering potential, as well as cases of low varietal weed suppressiveness or higher weed pressure in which higher plant densities are required to raise the crop weed suppressiveness, and vice versa.



(Gooding et al. 2002; Fang et al. 2010; Tokatlidis 2014). This is the result of two co-occurring mechanisms: first,  $Y_m$  is reduced when conditions become limiting, so that for an equal linear slope CFY is reached at a lower plant density (see Fig. 4). Second, a more limiting environment may not sustain denser populations, and hence the post-plateau decrease tends to occur at lower plant densities.

Indeed, focusing on water resources, Tokatlidis (2014) noted that denser populations cannot be sustained, and optimal plant densities tend to drop when water resources become limiting. In fact, and as also reported by Fang et al. (2010), yield even decreases with increases in plant density when water resources are scarce. For nutrient supply, Gooding et al. (2002) report similar results when investigating a wide range of plant densities under various mineral nitrogen fertilization levels. For instance, looking at the effect of plant density on total crop biomass, they found that instead of the initial linear increase followed by a plateau found under fertilized conditions, cutting out nitrogen fertilization canceled the effect of density on crop biomass although the starting plant density was 28 plants/m<sup>2</sup>. Yields actually even decreased when increasing plant density, mostly because of a steeper decrease of grains per ear with increasing densities.

When the resource in question is not a shared resource, such as degree days or incident radiation, the implications are different. Bastos et al. (2020) indeed showed that a higher plant density was required to meet CFY in environments characterized mainly by colder winters and lower cumulative daily radiation. Here, the reasoning can be seen as analogous to that of the effect of sowing date: Environments in which photosynthesis is diminished lead to lower biomass accumulation of individual plants, hence,

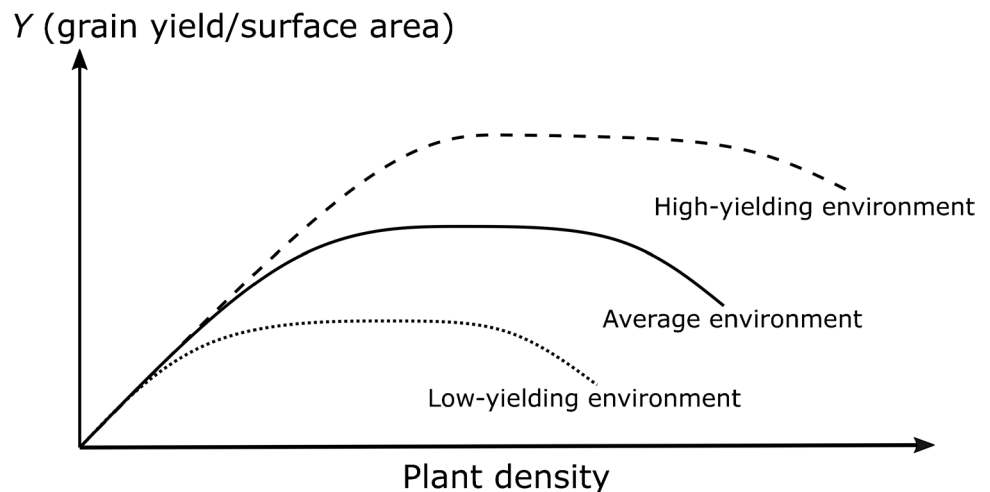
reducing  $w_m$ , and thus the linear slope. Besides, such environments also tend to have lower yield potential ( $Y_m$ ).

### 3.4.3 Weed competition

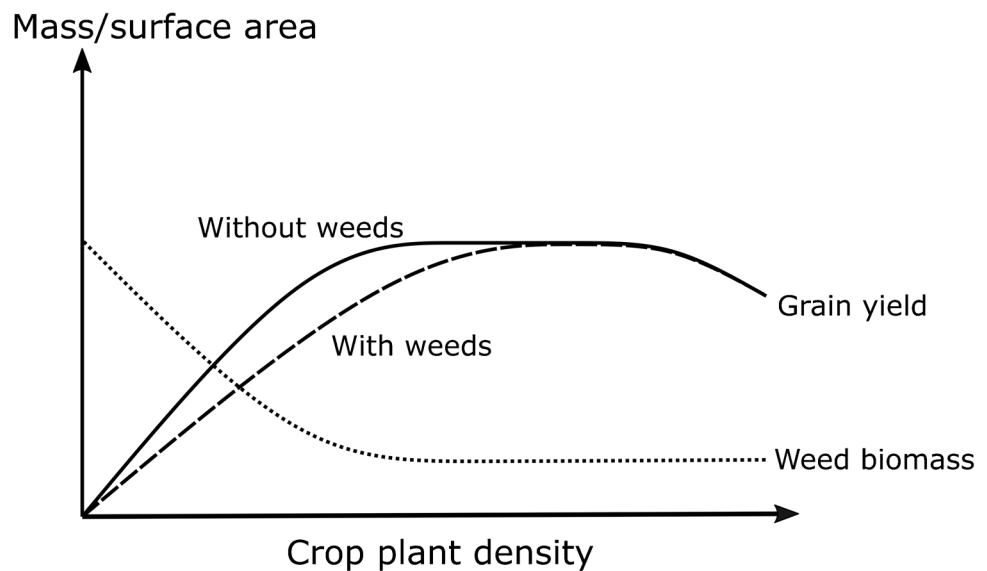
When abundant, some weed species compete with the crop for resources. In such cases, crop plants will experience interspecific competition, including at plant densities where they would normally avoid intraspecific competition. As a result, this may affect individual plant yield and thus decrease the linear slope compared to a weed competition-free scenario (see Fig. 5). Yet, competition works both ways: Weed growth is also hindered by the competition from crop plants. Thereby, a competitive crop will mitigate the potential damages of weeds. Just as increasing density increases competition between crop plants, it also inevitably leads to increased crop competition on weeds and, thus, weed suppression (Weiner et al. 2010, see Fig. 5). This is why increasing plant densities is investigated and recommended as a way to increase weed suppression for organic cropping (Weiner et al. 2001; Korres and Froud-Williams 2002; Yenish and Young 2004; Olsen et al. 2005; Kristensen et al. 2008; Auskalniene et al. 2018). As the critical period for crop-weed competition is generally early in the season (Zimdahl 2004; Gallandt and Weiner 2015), higher plant densities are expected to be all the more efficient at suppressing weeds despite falling far beyond the start of the CFY plateau in weed-free scenarios.

In weed-infested environments, the density at which CFY is reached can thus be expected to be higher compared to weed-free scenarios. Indeed, a tendency toward reduced weed biomass is observed when increasing plant density which, in turn, can lead to increased yields (Weiner et al. 2001; Yenish and Young 2004; Olsen et al. 2005;

**Fig. 4** Variations of the yield–plant density relationship for the same cultivar in environments of contrasting shared resource availability (e.g., nutrients or water).



**Fig. 5** Effect of plant density on grain yield in the presence (dashed line) and absence (solid line) of weeds. When present, weeds can compete with the crop and lead to crop yield reductions. On the other hand, the crop also competes with weeds, so that weed biomass (dotted line) is reduced with increasing crop plant density. However, weeds cannot be fully suppressed. Yet, total weed suppression is not necessary to achieve maximum grain yield (adapted from Weiner et al. 2010).



Beres et al. 2010). However, the true importance of plant density for mitigating weed-related yield loss must be tempered. Indeed, the above-mentioned studies achieved high weed pressures by sowing monospecific weed covers at very high densities. When weed pressure is lower and consists of naturally occurring weeds, plant density may still affect weed biomass without it having any impact on crop yield (Olsen et al. 2005; Lazzaro et al. 2017). Indeed, depending on weed density and community composition, sheer weed presence is not systematically detrimental to crop yield (Zimdahl 2004; Gaba et al. 2016).

Besides, there appears to be a limit to weed suppression: Olsen et al. (2005) report that, under lower, naturally occurring weed pressure, increasing plant density stops being effective on weed biomass past a sowing density of 449 seeds/m<sup>2</sup>. Cultivar may also affect the impact of plant density on weed-suppression, with weed-competitive cultivars being poorly reactive to plant density as compared to less competitive cultivars (Weiner et al. 2001). The impact of plant density on weed infestation may therefore be interpreted as analogous to CFY: Weed suppression increases with plant density until a plateau is reached, and the lower plant density limit of this plateau depends on the competitiveness of the cultivar as well as the level of weed pressure. Stemming from this, the impact of weed competition on the yield–density relationship is a complex matter, as it depends on cultivar and weed pressure, the latter of which depends on weed density, community composition, resource availability, and much more (Zimdahl 2004). As a general rule, weed-competition may push the CFY plateau toward higher densities, but weed presence does not systematically affect yield and, hence, the density–yield relationship.

#### 3.4.4 Cultivar

The most straightforward example of how cultivar may affect the yield–density relationship is that of cultivar adaptation to an environment, which allows better exploitation of the environment’s resources and hence leads to higher  $w_m$  (Weiner et al. 2017) and  $Y_m$ .

But, other cultivar traits may affect the CFY pattern. For equal environmental adaptations,  $w_m$  may still vary between cultivars. For instance, cultivars with higher tillering potential perform better at low densities than low-tillering cultivars (Otterson et al. 2007; Valério et al. 2009; Bastos et al. 2020). A higher tillering potential thus results in a steeper slope (Valério et al. 2009; Bastos et al. 2020) which, if compared to a cultivar of equal  $Y_m$ , implies that  $Y_m$  is reached at lower densities. This is coherent with the fact that tillering potential is a “selfish” trait (Hoad et al. 2012).

For the same reason, other selfish traits—such as plant height or early cover (Hoad et al. 2012)—will also have an impact on the relation between plant density and weed suppression: Taller and/or early-cover cultivars should be able to reach maximal weed suppression at lower plant densities than less selfish cultivars. This is suggested by the 2 year trial of Korres and Froud-Williams (2002), investigating weed suppressiveness of several cultivars at three sowing densities. On the first year, where sowing date was late and plant establishment was very low so that plant densities ranged from < 50 to > 150 plants/m<sup>2</sup> only, there was no interaction between plant density and cultivar: Increasing plant density enhanced weed suppressiveness in all cultivars. In the second year, however, establishment rates were much better, so that achieved plant densities ranged from 125 to 380 plants/m<sup>2</sup>. Besides, sowing date was earlier by

a month. Then, plant density no longer had a significant effect on weed suppression in the two tall heritage cultivars (i.e., more weed-competitive), but still did in the modern, semi-dwarf, less weed-competitive ones. Considering the CFY-like pattern of weed suppression described earlier (see 3.4.3), this suggests that the two tall heritage cultivars had reached maximal weed suppression at the lower density. Similarly, other papers investigating sowing densities starting at 200 plants/m<sup>2</sup>, found no effect of plant density on weed biomass for the most weed-competitive cultivars only (Weiner et al. 2001; Beres et al. 2010), suggesting a similar scenario where the most competitive cultivars reach maximum weed suppression at lower densities.

Finally, some cultivars—among which tall heritage cultivars—show a higher sensibility to lodging with increasing plant density (Easson et al. 1993; Lazzaro et al. 2017), which again may lower the higher density limit of the plateau.

#### 4 Designing sowing density recommendations for HM in agroecology

The question of appropriate sowing density clearly cannot have a universal answer, as a number of environmental and technical factors interact with the plant density–yield relationship, sometimes in opposite ways. Rather, the question of appropriate sowing density is a complex equation, in which cultivar and cropping system are important parameters.

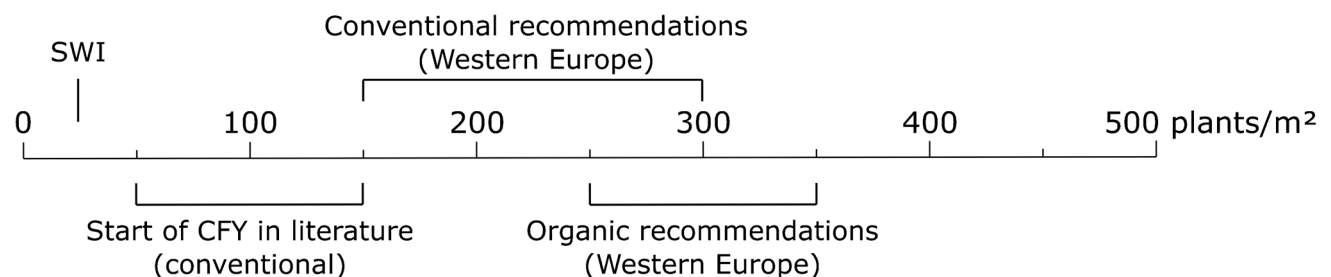
Conventional sowing density recommendations were designed in coherence with modern short-strawed, high harvest index cultivars allowing for the intensive use of chemical fertilizers without lodging. Besides, cultivar competitive traits were not a real priority owing to the better weed-control opportunities offered by herbicides and mechanization (Gallandt and Weiner 2015). On top of this, recommended densities for conventional cropping are usually double those necessary to reach CFY (see Fig. 6), rather aiming at the end of the plateau, which may be a form of insurance policy against unpredictable extreme events (Geleta et al. 2002; Valério et al. 2009).

In the frame of this review, we address two major twists to these parameters: HM as cultivar type and organic cropping as a cropping system, which requires us to solve this equation anew. Before us, other researchers have made attempts at solving this sowing density equation for organic cropping or suboptimal environments, coming up with strategies combining new cultivar ideotypes and their appropriate plant densities. Before jumping to the resolution of our own equation, we need to detail some of those strategies, as their reasoning are relevant to the thinking of appropriate sowing recommendations for HM in organic cropping.

##### 4.1 Transition to organic cropping: business as usual

Organic conditions bring forth two main changes to the previous (conventional) situation. On the one hand, nutrients are usually scarcer as chemical inputs are no longer an option. Besides, their release depends on mineralization processes, complexifying precise timing of fertilization. In the CFY framework, this leads to a reduction in  $Y_m$ , and may also lower the density at which post-plateau yield losses are reached (see 3.4.2), hence, drawing optimal sowing densities toward lower values. On the other hand, weed pressure is higher as fewer weed-control options are available. We saw that, depending on the level of weed pressure, this could rather push CFY toward even higher densities, albeit not systematically. These contradictory constraints make recommendations less straightforward than in the conventional case, and several strategies may be valid.

Mainstream practice and recommendations for organic wheat cropping in Europe do not stray far from the conventional model. Chemical inputs are substituted by organic inputs and mechanized weeding, and the rotation may differ. However, wheat is still cropped mainly as a sole crop, and cultivars are of the same type as those used in conventional cropping. With these cultivars that tolerate high densities and have a low weed competitiveness, the recommendations



**Fig. 6** Wheat plant density scale with some reference points. SWI: “System of Wheat Intensification” and CFY: “Constant Final Yield.” Plant densities lower than 200 plants/m<sup>2</sup> would generally be consid-

ered as low, while plant densities higher than 300 plants/m<sup>2</sup> would generally be considered as high.

are clearly oriented toward tackling the weed problem. Indeed, sowing is usually recommended to be later than in conventional cropping as a way to avoid autumn-germinating weeds as well as virus transmission by aphids. Sowing density recommendations are also pushed higher (see Fig. 6), both as a way to compensate for the later sowing, and also in order maximize weed suppressiveness early in the season and provide some insurance against damages incurred by tine-weeding.

This solution amounts to reusing the same building blocks as those used in conventional agriculture and making slight adaptations for it to work in organic conditions, rather than a redesign taking the specificities of organic cropping into account. As exposed in the introduction, one of the deficient building blocks of this system are the cultivars.

## 4.2 Communal plants for high densities

Weiner et al. (2010) have sought to refine the mainstream organic model in order to make it more efficient through an approach they call “Evolutionary Agroecology.” Their model is still anchored on high densities as a way to control weeds, but the objective is to get around its main drawbacks through two core ideas: enhancing the weed-suppressive effect of increased densities and reducing the yield losses caused by intraspecific competition. First, they advocate for a uniform sowing pattern as a way to increase the weed/intraspecific competition ratio. Crowded rows indeed lead to high intraspecific competition, while interrows are left to the weeds, so that increasing plant density becomes counter-productive at some point. And indeed, different authors have found uniform sowing pattern to be more effective at suppressing weeds (Weiner et al. 2001; Olsen et al. 2005; Kristensen et al. 2008) while reducing intraspecific competition, as evidenced by slightly higher yield with uniform sowing pattern in weed-free environments (Olsen et al. 2005), albeit not always significant (Kristensen et al. 2008). However, such practice may hamper the use of inter-row cultivators for mechanized weeding.

The second core idea is about cultivar type: Weiner et al. (2010) plead for an ideotype inspired from Donald’s later concept of a “communal plant” (Donald 1981). In order to win the “race for resources,” plants will generally shorten some growth phases (including tillering), grow taller (Franklin 2008), and overall decrease their harvest index (Weiner et al. 2010, 2017). Their ideotype for wheat breeding would be stripped of these plastic responses to plant competition in order to eliminate yield losses at high densities (Weiner et al. 2010). Overall, the idea is thus to maximize plant densities while optimizing sowing pattern and cultivar traits in order to maximize weed-suppression by the crop and minimize the

drawbacks of high plant density resulting from high intraspecific competition.

## 4.3 High individual yielders for low densities

In his review focusing on water scarcity, Tokatlidis (2014) has the opposite approach. His scope being conventional farming, the weed problem is not predominant, but his reasoning revolves around the problem of yield losses at high densities when a resource becomes limiting (see section 3.4.2). The issue that is raised is that resource availability may not always be predictable, especially for those that depend on meteorological conditions to come, which will become ever less predictable with climate change. As a result, the choice of the appropriate sowing density can be challenging as both under- and over-estimation can result in significant yield losses. To answer this problem, Tokatlidis proposes a strategy to increase the odds of falling within the optimal plant density range. He reports that cultivars displaying the highest  $w_m$  not only tend to have the lowest optimal plant density but also that their optimal plant density varies less across environments with contrasted resource availability (see Fig. 7). As a result, combining the use of such cultivars with relatively low plant densities maximizes the chances of falling into the CFY plateau whatever happens to the crop.

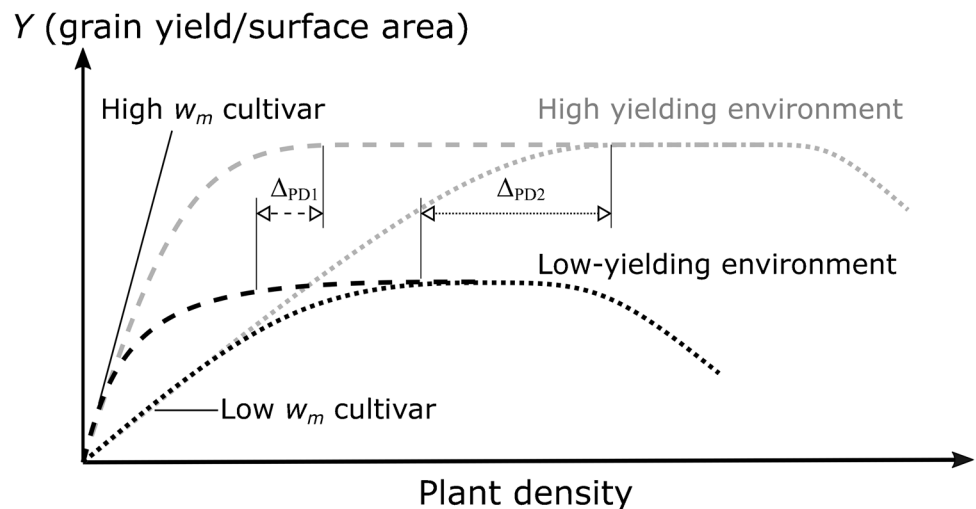
Besides, this strategy also fits well that of the SWI, which promotes low densities in order to obtain strong and resilient crop plants (see section 3.1). Indeed, on top of Tokatlidis’ idea of making a “safer bet” for optimum plant density, this strategy may also lead to more resilient crop plants and, hence, a more resilient crop (Dhar et al. 2016). What is more, some traits associated to high  $w_m$  are also weed-competitive traits, such as tillering potential or rapid early growth (Hoad et al. 2012; Lazzaro et al. 2019). Hence, this ideotype may help compensate the loss of crop weed-suppression incurred by the reduction of plant density (see sections 3.4.3 and 3.4.4). Depending on the level of weed-pressure, this strategy may still have to be complemented by other weed management strategies.

## 4.4 Designing sowing density recommendations for heterogeneous material

Finally, heterogeneous material brings a new dimension into the balance of plant–plant interactions. Instead of the near-homogeneous intraspecific competition that is found within pure-line crop stands, different types of plant–plant interactions come into play and are no longer homogeneously distributed nor symmetric across crop plants.

Mechanistically, a minimal plant density is necessary for some facilitative effects to occur (Zhang and Tielbörger

**Fig. 7** Relationship of grain yield per unit area to plant density for cultivars with different  $w_m$  in a low- (black) and a high-yielding (gray) environments. Two double-headed segments show the difference in optimal plant density between environments for the high  $w_m$  cultivar (dashed lines),  $\Delta_{PD1}$ , and low  $w_m$  cultivar (dotted lines),  $\Delta_{PD2}$ , which is greater for the latter.  $w_m$  is the average individual plant weight in the absence of competition.



2020). Indeed, compensation effects mainly rely on the ability of better-adapted genotypes to take over the resources and compensate for the losses of less-adapted genotypes. For this resource takeover to happen, plant density must thus be sufficiently high (Barot et al. 2017). Similarly, resource-use complementarity effects require some level of overlap in the plants' ecological neighborhoods in order to happen. In that respect, Chapman et al. (1969) do indeed report the overyielding of a wheat two-cultivar mixture to increase with plant density, and to be null at very low densities (the sowing density range of the experiment being approximately 13 to 160 seeds/m<sup>2</sup>).

However, we have seen extensively that increasing plant density also amounts to increasing the intensity of intraspecific competition. Meanwhile, within HM, heterogeneity in selfish fitness across plants can result in fiercer competitive interactions. As a result, high plant densities may have a negative impact on yield.

Besides, the intensity of facilitative interactions may not increase linearly with plant density, contrarily to intraspecific competition. In consequence, there may be a certain plant density past which further increases result in increased competition more than facilitation and thus increase the proportion of competition in the balance of plant interactions (Tarhuni and McNeilly 1989). Research in ecology actually found the relationship between net plant interactions and plant density to follow a humped shape curve, with peak facilitative interactions occurring at intermediate densities in populations of *Arabidopsis thaliana* (Zhang and Tielbörger 2020) and *Elymus nutans* (Chu et al. 2008). Sowing pattern may also affect this balance, as uniform sowing pattern can decrease competition (Weiner et al. 2010) and could hypothetically lead to a better distribution of facilitative interactions. In that perspective, low sowing densities may be of interest in that lowering density for a same interrow distance

leads to a more uniform pattern (until intra-row distance equals the inter-row distance).

This relationship between plant density and plant interactions is also susceptible to affect natural selection in HM. The prominence of selfish fitness as a driver for natural selection at high densities may have the undesirable outcome of favoring unwanted genotypes over higher-yielding genotypes (Khalifa and Qualset 1974; Thomas and Schaalje 1997), although it may also stimulate niche differentiation (Schöb et al. 2018). On the other hand, facilitative interactions may favor the stable coexistence of different genotypes (Chesson 2000) and, thus, the maintenance of those facilitative interactions over generations. Adequate plant density may thus be crucial to ensure favorable evolution of HM. Besides, phenotypic diversity of HM has been observed to be best expressed under lower sowing densities (Baltazar et al. 2019), presumably as a result of lower intraspecific competition. Shade avoidance (Franklin 2008) resulting from intraspecific competition might play a role in this: In the presence of light competition, plants tend to grow taller in order to escape this competition, for example. In barley, Dahlin et al. (2020) indeed show a tendency for adaptive similarity (plant height of different cultivars becoming more similar when grown in mixtures). High plant densities would be expected to emphasize this phenomenon. Besides, reductions in plant tiller number when increasing plant density must also make differences in tillering potential less apparent. Furthermore, lowering plant density allows individual plants to occupy a larger portion of their environment, thus reducing the impact of small-scale environmental heterogeneity on genotype  $\times$  environment interactions (Fasoula and Fasoula 2002). The stronger expression of plant traits is particularly relevant for farmers' breeding efforts as it makes contrasts between plants more visible, easing mass selection (Fasoula and Fasoula 2002; Baltazar et al. 2019). Furthermore, increased adaptive similarity may also reduce

niche differentiation and hence resource-use complementarity effects (Dahlin et al. 2020).

Considering the previous elements, the yield–density relationship of HM should resemble a CFY-curve, tweaked by the facilitative interactions. As stated earlier, several facilitative interactions require some level of overlap in plants' ecological neighborhoods; hence, we can assume that peak facilitative interactions occur past the linear part of the curve (i.e., after the start of competitive interactions as well) or, otherwise stated, on or just before the plateau. Optimal plant density for HM should thus target the density at which facilitative interactions peak.

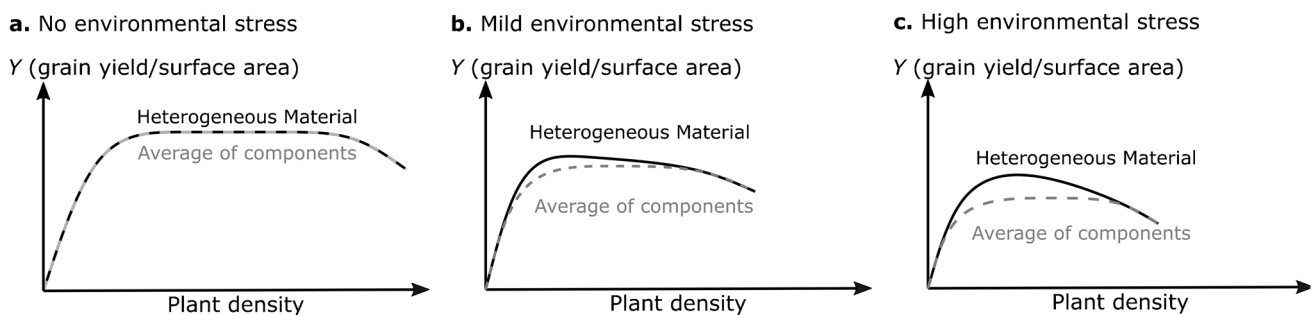
Available evidence suggests that this peak may vary according to environmental conditions. For instance, results obtained by Zhang and Tielbörger (2020) go in the sense of the stress-gradient hypothesis, which states that facilitative interactions are amplified in stress conditions. Accordingly, the peak of facilitative interactions may never be observed under optimal conditions but become more pronounced as conditions degrade (see 2.2.1). More interestingly, they also found the plant density for peak facilitative interactions to shift according to the stress gradient. In their case, the stress gradient was a gradient of salinity, and this shift was toward higher densities, which they explain by the fact that “at higher stress levels, more neighbors are required for ameliorating habitat conditions.” (Zhang and Tielbörger 2020). Yet, not all facilitative interactions can be expected to follow that logic. For example, we showed in section 3.4.2 that stresses caused by resource scarcity rather pushed optimal plant densities toward lower values and it thus seems unlikely that the density of peak facilitative interactions would increase with increasing resource-related stresses. Figure 8 summarizes our findings: Under optimal conditions, the yield–density relationship of HM is a classic CFY curve which should be close to that followed by the average of its components. Along a gradient of increasing stress, compensation and facilitation should gain importance, and we expect the CFY

plateau to take an increasingly humped shape. As current evidence is still scarce to predict or discuss potential shifts of peak facilitative interactions according to stress gradients, we do not account for this in this figure.

Overall, the evidence gathered until now suggests that high plant densities are best avoided for HM, and that optimal plant density may rather be near the beginning of the CFY plateau. Furthermore, environmental conditions may doubly affect optimal plant density: first, through the general interactions with the CFY curve explained in section 3.4; second, by affecting the balance between facilitation and competition. This not only narrows the range of target plant densities but also makes it harder to predict, especially in agroecological cropping, although the stabilizing effects of HM may arguably help mitigate the variations of optimal plant densities across environments (see section 2.2.1). The “Communal plants for high densities” appear ill suited to HM, as maintaining a “communal plant” ideotype in a genetically diverse population evolving at very high plant densities is expected to be challenging. Considering the low optimal plant densities expected and the need to anticipate unpredictable environmental variations, the most relevant sowing density strategy for HM may be to combine it with the “High individual yielders for low densities” strategy (see section 4.3).

## 5 Conclusion

The evidence reviewed along this paper has led us to the conclusion that the optimal plant density range for HM in organic cropping may not only be narrower than in the case of pure lines but may also be hard to predict. To answer for this, and accounting for the evidence indicating that benefits of HM are best harnessed under low-to-intermediate plant densities, we suggest that designing HM with a high average  $w_m$  should reduce the environment-induced variability of



**Fig. 8** Conceptual and hypothetical representation of the relationship between grain yield and plant density for heterogeneous material (solid black line) compared to the average of its components grown in monoculture (dashed gray line) in increasingly stressful environments. According to the stress-gradient hypothesis, the yield

advantage of heterogeneous material is increased under increasingly stressful environments. The precise position of peak yield for heterogeneous material may vary according to the types of stresses involved (not represented).

optimal plant density, and that such HM should be combined to lower plant densities than mainstream recommendations. Besides high average  $w_m$ , heterogeneous material should obviously be designed to include diversity for functional traits involved in facilitative interactions, but a lot remains to be uncovered on that matter. A potential weakness of this strategy may however be insufficient weed-suppression early in the season, especially in cases of high weed pressure. As a result, populations should also preferably include weed-competitive traits and be combined with additional weed management strategies.

These hypotheses however rest on numerous interacting factors, and may be difficult to prove or disprove without answering underlying questions. For instance, to which extent does facilitation affect optimal densities in actual field conditions? Does the stress-gradient hypothesis entail that HM can only bring significant benefits in marginal environments? Which trait associations are linked to density-dependent plant interactions, and in which direction? More than anything, we stress that more attention should be given to plant density as well as the cropping environment when evaluating HM, as some of its benefits may have been underestimated in previous research. When using HM in organic environments, a lot of “closed cases” in agronomic research may need to be reopened. One of them is plant and sowing density.

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## Declarations

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