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Exploring the trade-off between individual fitness and community performance of wheat crops using simulated canopy shade

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Abstract

The genetic heritage of wheat (*Triticum* spp.) crops has been shaped by millions of years of predomestication natural selection, often driven by competition among individuals. However, genetic improvements in yield potential are thought to involve selection towards reduced competitiveness, thus enhancing adaptation to the crop environment. We investigated potential trade-offs between individual plant fitness and community performance using a population of introgression lines carrying chromosome segments of wild emmer (nondomesticated) in the background of an elite durum cultivar. We focused on light as a primary factor affecting plant–plant interactions and assessed morphological and biomass phenotypes of single plants grown in mixtures under sunlight and a simulated canopy shade, and the relevance of these phenotypes for the monoculture community in the field. We found that responses to canopy shade resemble responses to high density and contribute to both the individual and the community. Stepwise regressions suggested that grain number per spike and its persistence under shade are essential attributes of productive communities, advocating their use as a breeding target during early-generation selection. Overall, multiple phenotypes attained under shade could better explain community performance. Our novel, applicable, high-throughput set-up provides new prospects for studying and selecting single-plant phenotypes in a canopy-like environment.

KEYWORDS
biomass, grain number, phenotypic plasticity, wheat

1 | INTRODUCTION

Plant domestication and the start of an agricultural-based economy ~10 500 years ago in the fertile crescent altered human history and promoted the rise of modern civilization (Lev-Yadun et al., 2000). Ever since, crops have adapted to different environments, agronomy practices and deliberate breeding to improve yield, quality and ease of farming. One of the most significant drivers of crop evolution stems from the changes in the selection associated with the shift of plants from a highly heterogeneous and biodiverse natural environment into a homogeneous monoculture environment (Abbo et al., 2014; Harlan et al., 1973; Zohary, 2004). Competition for resources has been considered a prevalent force in structuring plant populations and natural selection, favoring the most competitive individual plants in a particular environment (Weiner, 1990). However, agricultural production evaluates collective population performance, measured as yield per unit area, which may conflict with individual competitiveness (Abbai et al., 2020; Denison, 2012; Denison et al., 2003; Weiner, 2019; Weiner et al., 2017).

To overturn the natural selection of competitive alleles towards the collective performance of the crop community, Donald (1968) suggested selections based on a theoretical ideotype, a phenotype designed to reduce the interplant competition among individuals in high-density stands. Such an ideotype was proposed to have a short stature, low tillering capacity, a highly fertile inflorescence and few erect leaves, which later was shown to increase grain yield by allowing higher light penetration into the canopy (Richards et al., 2019). Another critical feature of the like plant is its ability to allocate a maximal part of assimilation into the harvestable yield, resulting in less competitive genotypes with a high 'harvest index' (HI) (Donald, 1962). In fact, during the course of crop evolution, breeders have gradually and most likely unconsciously favoured genotypes with compromised individual competitiveness for enhanced yield potential (Cossani & Sadras, 2021; Lake et al., 2016; Reynolds et al., 1994; Sadras & Lawson, 2011; Sadras et al., 2019; Sukumaran et al., 2015), suggesting that genetic improvement of yield may be further achieved by intentionally aiming at the trade-off between individual plant fitness and community performance.

An essential feature of a high-yielding crop is its adaptation to high-density planting. For example, in maize (*Zea mays* L.), the genetic improvement in grain yield during the rise of the hybrid era is primarily attributed to improved tolerance to density, moving from 30 000 plants/ha in the 1950s to about 80 000 plants/ha (Gonzalez et al., 2018). Such change in sowing densities led to earlier canopy closure, which promoted weed suppression and light interception and, therefore, the crop dry matter accumulation per area. At the individual plant level, the increase in density results in a size reduction and, consequently, a less-than-proportionate increase in yield per area when density increases (Weiner & Freckleton, 2010). The reason for this is that allocation to different plant organs is generally allometric, that is, it changes with size; an increase in density is likely to trigger a shift in assimilate allocation from reproductive to more competitive structures like stems and leaves (Weiner, 2004), limiting yield increases. Nevertheless, maize breeders were able to mitigate the allometric growth problem by incorporating planting density as a constant source of stress in their trials and by selecting hybrids capable of maintaining efficient grain sets at high planting densities (Echarte et al., 2000; Gonzalez et al., 2018; Lee & Tollenaar, 2007).

Wheat (*Triticum* sp.) crops are usually planted in densely populated plots of 200–450 plants/m^2, providing up to 1000 grain-bearing heads/m^2. Consequently, from early developmental stages, young wheat seedlings detect alterations in the spectral distribution of the light (mainly reduction in red/far-red ratio) reflected from neighbouring plants. With the onset of stem elongation, the competition for resources between plants of the same row intensifies and broadens to the neighbouring rows, thereby creating a dense crop canopy around anthesis. At this time point, most of the individual wheat plants are largely covered or shaded by neighbouring plants, generating a steep illumination gradient towards the ground and stimulating an intense competition for photosynthetically active radiation (PAR) (Casal, 2013; Evers et al., 2006; Robles-Zazueta et al., 2022).

Depending upon the density-related signals perceived by the plant, a plant's response commonly affects a whole set of traits related to different domains, for example, biomass, physiology, reproduction, morphology, and patterning (Postma et al., 2021). In line with other plant species, cereal crops showed similar trait responses to high density. For example, in wheat, high density led to an increased area per leaf, a higher leaf area/weight, a reduced number of tillers and an overall drop in plant biomass (Puckridge & Donald, 1967). This reduction in the vegetative biomass is associated with a decrease in the number of spikes per plant, the number of spikelets per spike, a decrease in floret fertility and, therefore, fewer grains per spike (Darwinkel, 1978; Puckridge & Donald, 1967; Zhen-Wen et al., 1988). Importantly, density-induced trait responses correlate highly with responses to low light (Cossani & Sadras, 2021; Postma et al., 2021), implying that responses to the light environment play a significant role in modern agricultural set-ups. Studying responses to the canopy light environment may therefore provide prospects to better understand and improve the adaptability of wheat plants to dense canopies.

Here, we examined canopy shade responses and its relationship with the formation of individual plant fitness and community performance using a series of tetraploid wheat lines carrying various introgressions from wild emmer (the nondomesticated progenitor of wheat crops) in the background of an elite durum cultivar. The wild emmer introgressions, presumably shaped by natural selection, were hypothesized to alter plant architecture, plant–plant interactions and individual plant fitness of durum wheat grown in mixed stands under various levels of asymmetric competition. We focused on the light environment as the primary limiting resource in a canopy situation and examined the utility of single-plant phenotypes under sunlight and simulated canopy shade in predicting and comprehending genotypes' performance in high-density monoculture. We aimed to answer the following questions: (1) How does simulated canopy shade alter wheat plant architecture, and what are the key sources of variation for the response? (2) Can we draw similarities between proven density-induced responses and simulated canopy shade responses in wheat? (3) Are shade-induced responses adaptive under asymmetric competition, and what are the consequences for the crop environment? (4) Are there trade-offs between individual plant fitness and community performance, and what are the variables contributing to each of these? and (5) To what extent can we predict the performance of the crop community from individual plant phenotypes, and can we improve our estimates by simulating canopy shade in our trials? Our study furthers our understanding of the vital role of canopy shade responses in the crop environment.

2 | MATERIALS AND METHODS

2.1 | Plant material and experimental set-up

The introgression lines (ILs) were developed in the Distelfeld lab (Haifa University, Israel) by backcrossing recombinant inbred lines of the Svevo × Zavitan population (Avni et al., 2014) three times to the Svevo durum background and selfed over four generations, as previously described (Bacher et al., 2021). The ILs, along with the parental lines, were grown in two glasshouses containing natural loamy soil, which had two open, nonglassed sides each with porous metal netting to enable air circulation. Canopy shade was simulated by mounting a green plastic filter (Lee122 Fern green; LEE filters) on the roof inside of the glasshouse. As for genuine foliar shade, the green filter reduced irradiation of the blue light (450–470 nm) and the red light (655–685 nm) by ~80%, resulting in a reduction of the red/far-red (715–745 nm) ratio from 1.13 to 0.28 under the green filter. The PAR under the simulated canopy shade was reduced by ~55%. A similar reduction in the light intensity under a high-density wheat canopy resulted in a comparable red/far-red ratio of ~0.3–0.4 (Evers et al., 2006), which declined to 0.1 near canopy closure. The sunlight treatment of the wheat plants was conducted in a glasshouse with identical dimensions but without a green filter and was directly adjacent to the shaded glasshouse (Figure 1a,b). Fifty-three ILs and two parental lines were sown in jiffy pots in a controlled environment in March 2020, and 7 days later, eight jiffy pots per IL and 16 of each parental line were transplanted in incomplete blocks (nine plants per block) to account for the spatial effects in the glasshouse. We used approximately 10–15 cm distance between plants within a 1-m row and 20–25 cm between rows in the glasshouses. Six ILs that showed poor germination or brittle rachis were excluded from further analysis.

To study the community performance of each genotype, the ILs and Svevo were sown in IPK fields (51°49′23″ N, 11°17′13″ E, 112 m altitude) in three replications of six-rowed monoculture plots (~1.5 m^2) in an α-lattice design, containing 60 grains per meter row (~240 grains/m^2). Alleys surrounded the plots except for one side, which had a 0.5 m distance from an adjacent plot. Two rows on each side of the plot were used as border rows, and the data were recorded from the two most inner rows of the plots (excluding 30 cm borders) to estimate vegetative and reproductive biomass per area (Figure 1c).

2.2 | Phenotypic measurements

All single-plant phenotypes were recorded from the main culm (MC), except for the number of tillers and the spike biomass per plant, which we refer to in our study as individual plant fitness. Tiller count was recorded 8 weeks after sowing when the plants were in an early booting stage. Plant height and stem internodes length were measured at maturity and included the length of the peduncle (P) and the internodes below the peduncle, from the uppermost (P-1) to basal (P-3). Floret number was recorded from three central spikelets at anthesis. The number of grains per spikelet was derived by dividing the number per spike by the number of spikelets. Spike length

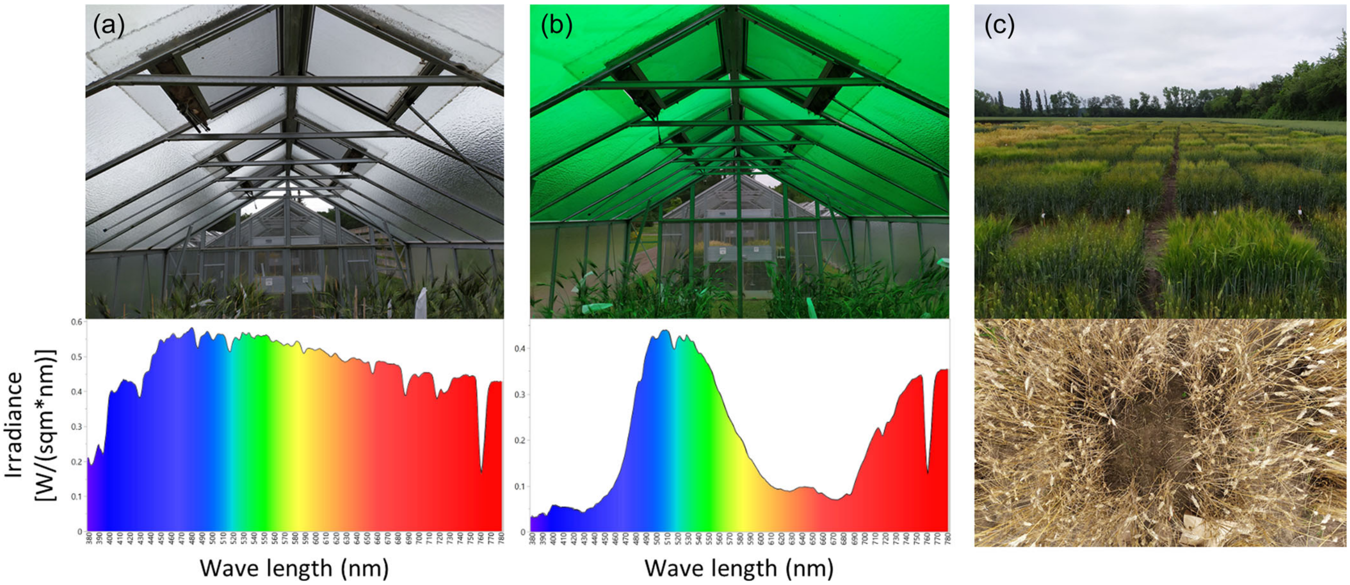


FIGURE 1 Experimental set-up used to study individual fitness, response to canopy shade and community performance. (a) Soil-grown plants grown in a mixture under natural sunlight spectrum and PAR. (b) Soil-grown plants grown in a mixture under simulated canopy shade, which reduces irradiance of the blue and red light and the overall PAR. (c) Monoculture plots of the ILs and an example of the sampling, using the most inner rows of the plot. IL, introgression line; PAR, photosynthetically active radiation.

(without awns) was measured at anthesis, and the rachis internode length was calculated by dividing spike length by the number of rachis nodes. The number of grains per spike, the average weight per grain (hereafter referred to as thousand grain weight [TGW]), grain width and grain length were determined using a digital seed analyser 'Marvin' (GTA Sensorik GmbH). All biomass measurements used the dry weight at maturity. The specific vegetative shoot length (SVSL) measured in cm/g was calculated by dividing the MC height (without spike) by its vegetative biomass.

The phenotypic plasticity index (PI) for each trait was calculated as follows:

$$\mathrm{PI}= 1 + [(\text{simulated canopy shade} - \text{sunlight})/\text{sunlight}].$$

2.3 | Data analysis

Statistical analyses were performed with JMP 16 software (SAS Institute) and Genstat (VSN International). The phenotypic data were analysed using the following mixed linear model (restricted maximum likelihood [REML]):

$$y = \mu + \mathrm{env} + g + g \times \mathrm{env} + b + e$$

to evaluate the intercept, and the effects of the light environment (env, fixed), the genotype (g, random), the genotype by light environment interaction ($g \times$ env, random), the block (b, random) and the residual term.

We analysed the allometric relationship (Niklas, 1994) between the main culm shoot biomass and the grain weight at harvest using individuals grown in both light environments. Linear regression analysis was used to determine the allometric slope and intercept according to the equation described below, where $\log \beta$ is referred to as the intercept and α as the allometric slope

$$\log \text{ grain weight} = \log \beta + \alpha \log \textit{main} \text{ culm } \textit{shoot} \text{ weight}.$$

For the full analysis, we used a mixed model (REML) to predict the effects of the genotype (random), the block (random), the light environment (fixed), MC shoot biomass (fixed), and the genotype by shoot biomass interaction (fixed) on grain weight.

The genotypic values (best linear unbiased estimations [BLUEs]) for each trait in each environment were calculated using the two-step mixed-model analysis implemented in Genstat. In the first step, the genotype and the block were fitted as random to estimate the variance components used in the second step, with the genotype (g) fitted as a fixed term and the block (b) as random as indicated below:

$$y = \mu + g + b + e.$$

We used stepwise regressions to estimate the contribution of the variables from each environment to individual plant fitness and community performance. We employed an alternate forward and backward selection to determine the model's variables, including the most significant term to enter and the least significant term to remove ($p < 0.1$), as implemented in jmp.

3 | RESULTS

3.1 | Sources of variation in plant architecture under sunlight and simulated canopy shade

As wild plants were assumed to have a significant competitive nature compared to crops, we used crosses of durum × wild emmer wheat as a source for genetic variation in our study. We hypothesized that wild introgressions would confer a more competitive plant architecture contributing to fitness in mixed stands. Phenotypic examination of the two parental lines in the glasshouses under sunlight and simulated canopy shade demonstrated that overall, wild emmer accession Zavitan (Avni et al., 2017) allocates a significantly higher proportion of assimilates to competitive structures such as stems, tillers and leaves, resulting in taller, high-biomass plants with reduced allocation to reproduction under both light environments (Supporting Information: Figure S1). Two-way analysis of variance confirmed significant differences in response to the light environment between Svevo and Zavitan depicted in the reaction norms. Zavitan showed a reduction in plant height mainly due to a decrease in the peduncle length under the simulated canopy shade associated with a lower increase in the SVSL (cm vegetative shoot/vegetative shoot biomass) than Svevo (Supporting Information: Figure S1 and Table S1). Under canopy shade, Svevo showed a significant reduction in floret number, grain number per spike (GPS) and the TGW compared to sunlight conditions. Zavitan, in comparison, had a lower grain yield potential and was more resistant to the simulated canopy shade. The significant reduction in the chaff weight of Zavitan spikes under a canopy shade may indicate a shift in allocation from the chaff to the grains, minimizing the adverse effects of shade on the grain filling (Supporting Information: Figure S1).

The wild introgressions introduced significant genetic variation for all the investigated traits. Likewise, the light environment considerably contributed to phenotypic variation in most traits. Interestingly, canopy shade had no significant effect on the number of spikelets per spike and on the final plant height at maturity, which generally increases in shade-avoiding species. Nevertheless, we observed elongation in basal stem internodes (P-3), but rather a reduction in the length of the peduncle and P-1, suggesting that shade-induced elongation is mainly limited to the early stages of stem growth, a response shown to be regulated by the wheat phytochrome (Casal, 1993). We detected significant genotype (G) × environment (E) interaction for most internode length traits, suggesting that wild introgressions may alter some stem length responses to canopy shade (Supporting Information: Tables S2 and S3).

We used the BLUEs within each light environment in a principal component analysis to identify the major sources of variation among the 24 investigated traits (Supporting Information: Figure S2a). PC1 (38.6%) illustrated a clear distinction between light environments. Plants grown under sunlight were associated with high spike and vegetative biomass, with a higher number of florets and grains per spikelet, grains per spike and grain size compared to shaded plants. On the other hand, shaded plants were associated with longer second leaf (L2) laminas, a delay in heading the spike and a significant increase in the SVSL. PC2 explained ~21% of the variation and was positively loaded with plant-height-related traits and negatively loaded with the culm spike mass fraction (SpMF), which positively contributed to PC1. The number of tillers, number of days to heading, the number of spikelets per spike and the rachis internode length, traits related to the developmental rate of the plants, were the major factors contributing to PC3 (Figure 2a and Supporting Information: Figure S2).

We quantified the response of the ILs to simulated shade by calculating a PI for each trait based on the BLUEs differences between the light environments (Figure 2a). To maximize light interception, the shaded plants increased laminas length and the SVSL, which indicates an increase in height per unit of vegetative shoot biomass (Figures 2a and S2). Previous studies suggested that density-induced increase in specific stem length (cm stem/stem biomass) enables plants to maintain elevated leaf positions without an increase in allocation to stem growth (Poorter et al., 2012; Postma et al., 2021). Although not equal, the substantial increase (27%) in the SVSL under canopy shade also points to the maintenance of height at the expense of the shoot sturdiness, resulting in more slender plants. Drastic reductions under simulated canopy shade were recorded for the number of tillers (33%) and biomass of the vegetative shoot (22%) and spike (30%), which overall reduced spike biomass per plant (45%) (Figure 2a).

To better understand whether the plant biomass reductions similarly alter the allocation of individual plants to reproduction, we examined the allometric relationship between the log biomass of the main shoot and the grains. Using a linear regression, we show that the shoot biomass may explain up to 93% of the variation in grain yield per spike with an overall allometric slope of 1.12 (Supporting Information: Figure S3). An allometric slope >1 indicates a shift in assimilate allocations from the spike to the stem, leaves and roots when plants become smaller (e.g., under high density). A full analysis of the relationship using a mixed linear model showed that although the shoot biomass was the most important factor in accounting for variation in grain yield per spike, the light environment, the genotype, and the genotype × shoot biomass interaction also had significant effects (Supporting Information: Table S4). The significant biomass × genotype interaction implies that the ILs differed in their allometric

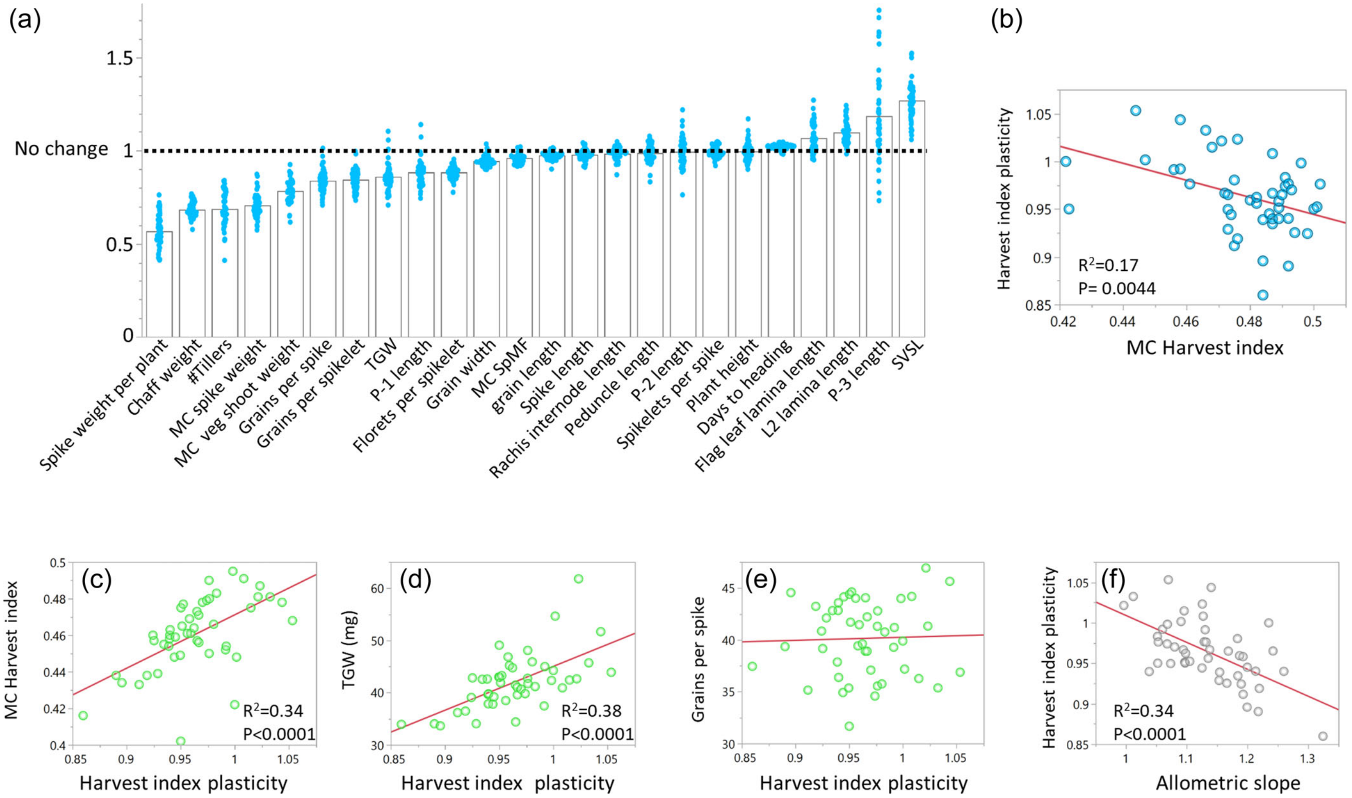


FIGURE 2 Effect of simulated canopy shade on plant architecture, biomass and resource allocation. (a) Plasticity indices of the ILs calculated for each trait based on differences between BLUEs calculated for each environment. A plasticity index of 1 (dotted horizontal line) indicates no phenotypic plasticity. A plasticity index larger or smaller than 1 indicates an increase or decrease in the phenotype. (b) Relationship between the main culm harvest index under sunlight conditions (blue circles) and the harvest index plasticity. (c) Relationship between the plasticity of the harvest index and harvest index under simulated canopy shade (green circles). (d) Relationship between harvest index plasticity and the thousand grain weight under shade. (e) Relationship between harvest index plasticity and the grain number per spike under shade. (f) Relationship between the allometric slope and the plasticity of the harvest index. BLUEs, best linear unbiased estimations; IL, introgression line. [Color figure can be viewed at wileyonlinelibrary.com]

slope so that some lines were able to attenuate the common shift in allocation, favoring reproduction under canopy shade.

To gain further insights into allocation dynamics in response to shading, we measured the plasticity of the MC HI (the ratio of grains to above-ground biomass) between the two light environments. The HI plasticity was negatively correlated with the HI under sunlight (Figure 2b). Genotypes showing low HI under sunlight (e.g., tall genotypes) tended to allocate relatively more biomass to the grains when shaded (higher PI). In contrast, genotypes with higher HI respond to shading by allocating more biomass to competitive structures such as the leaves and the stem, indicating a significant G × E interaction for HI among the ILs (Figure 2c). Interestingly, under canopy shade, the high PI was significantly and positively correlated with TGW (R^2= 0.38; Figure 2d), while there was no significant effect on GPS (Figure 2e). These findings indicate that shade-induced plasticity for HI is mainly related to resource reallocation at the late stages of plant development and the grain-filling period. Examination of the relationship between HI plasticity and the allometric slope of the ILs demonstrated a significant negative correlation (Figure 2f; R^2 = 0.34), indicating that allometric growth can partly explain shade-induced allocation. Genotypes with low HI tended to allocate biomass to the spike when their biomass was reduced under canopy shade. In contrast, genotypes with a relatively high proportion of reproductive biomass diverted assimilate to the vegetative parts. Natural selection favours competitive genotypes with low HI that, when suppressed by neighbouring plants, drive allocation to reproduction to maintain at least some grains with a proper size for establishment. Such behaviour is likely to bring about stability in grain yield, mainly at the expense of yield potential (Du et al., 2020; Weiner et al., 2021), and such a trade-off is likely to impose complexities in yield improvement through increases in sowing density.

3.2 | Formation of individual plant fitness

The underlying hypothesis was that there is a trade-off between the competitiveness of individual plants and the collective performance of a monoculture because 'selfish' phenotypes and trait responses that increase individual plant fitness are detrimental to crop yield. The current study examined the development of single-plant phenotypes or response traits that were scored in a mixture of genotypes grown under sunlight and simulated canopy shade. Then, we estimated their relationship with biomass and reproductive yield per area measured in monoculture field plots to differentiate between behaviours that fuel individual plant fitness and those that promote productive communities.

We used stepwise regressions to model the contribution of morphological and biomass traits to individual plant fitness (spike biomass per plant) in each environment (Table 1). Under natural sunlight (Model a), the MC spike dry weight explained the most significant

TABLE 1 Stepwise regressions for individual fitness (spike weight per plant) in sunlight and simulated canopy shade using 23 traits BLUEs and 10 adjusted plasticity indices

Model	Glasshouse light environment	Fitness component	Estimate	Percentage of squares	*F* ratio	Prob > *F*	R^2 adj.
a	Sunlight	MC spike weight	9.603	42.903	84.960	<0.0001	
		# Tillers	0.952	25.621	50.736	<0.0001	
		P-1 length	−0.493	3.640	7.207	0.0104	
		Grain length	4.542	4.976	9.855	0.0031	
		Days to heading	−0.442	2.156	4.270	0.0452	
		Total		79.296			0.767
b	Simulated canopy shade	MC spike weight	4.822	36.750	46.536	<0.0001	
		# Tillers	0.587	20.048	25.387	<0.0001	
		Flag leaf lamina length	0.174	5.224	6.615	0.0138	
		P-1 length	−0.367	2.708	3.429	0.0713	
		P-3 length	0.358	2.892	3.662	0.0627	
		Total		67.622			0.636
c	Simulated canopy shade	Increased SVSL	−8.31	11.317	8.336	0.0062	
		Elongation of L2 lamina	13.234	9.133	6.728	0.0132	
		Delay in heading time	38.54	6.949	4.349	0.0434	
		Total		27.39			0.223

Note: Model a: The significant variables contributing to fitness under sunlight. Model b: The significant variables contributing to fitness under simulated canopy shade. Model c: The significant adjusted plasticity responses contributing to fitness under canopy shade.

Abbreviations: adj., adjusted; BLUEs, best linear unbiased estimations; L2, second leaf; MC, main culm; SVSL, specific vegetative shoot length.

TABLE 2 Stepwise regressions of AGDM per area, spike mass fraction and spike biomass per area of monoculture field plots using single-plant phenotypes (BLUEs) recorded in the glasshouse under natural sunlight conditions

Glasshouse light environment	Single plant phenotypes	Estimate	Percentage of squares	*F* ratio	Prob > *F*	R^2 adj.	Community attributes
Sunlight	Grains per spike	6.100	22.247	14.902	0.0004		
	MC shoot weight	111.617	7.275	4.873	0.0327		
	L2 lamina length	−22.854	6.282	4.208	0.0464		
	Total		35.804			0.313	AGDM per area (g/m^2)
	P-1 length	−0.004	40.350	40.03	<0.0001		
	Grains per spikelet	0.047	10.946	10.859	0.002		
	Rachis internode length	−0.226	3.113	3.088	0.0861		
	MC shoot weight	−0.04	3.255	3.229	0.0795		
	Total		57.66			0.536	Spike mass fraction
	Grains per spike	6.243	31.010	21.228	<0.0001		
	L2 lamina length	−13.356	4.714	3.227	0.0793		
	Total		35.724			0.328	Spike biomass per area (g/m^2)

Abbreviations: adj., adjusted; AGDM, above-ground dry matte; BLUEs, best linear unbiased estimations; L2, second leaf; MC, main culm.

proportion of the variation in individual plant fitness (43%, $p < 0.0001$), followed by tiller number (25.6%, $p < 0.0001$), and grain length (4.9%, $p = 0.003$). Internode P-1 length (3.6%, $p = 0.01$) and the number of days to heading (2.15%, $p = 0.045$) had negative associations with individual plant fitness in the multivariable model. The negative association with days to heading may arise due to the low fertility of a few late flowering genotypes and might be specific to the current study. The effect of P-1 may be related to its negative effect on the allocation to reproduction which promoted fitness among the adapted ILs, where variation in plant height is limited (most of the lines were between 70 and 85 cm tall). Similarly, MC spike dry weight was the most significant variable under simulated canopy shade (Model b) (36.7%, $p < 0.0001$), followed by tiller number (20%, $p = 0.0002$), flag leaf length (5.2%, $p = 0.013$), P-3 length (2.9%, $p = 0.06$) and the P-1 length (2.7%, $p = 0.07$). Thus, in adapted elite varieties, genotypes producing many high-biomass tillers with long internodes during early stem elongation and long flag leaves are likelier to be most fitted among the genotypes under competition.

The risk for plant survival by light constraint has driven the evolution of plastic responses in morphology, phenology and physiology to avoid or tolerate shading by neighbouring plants. Here, we aimed to address whether elongation responses of the stem and the leaves, the delay in flowering time and the reduction in tillering contribute to the fitness of shaded plants. Correlation analysis between sunlight and simulated canopy shade phenotypes (Supporting Information: Figure S4) demonstrated that the variation under shade could be primarily attributed to the variation under sunlight (i.e., genotype effect). The relationship between PI and sunlight phenotypes (Supporting Information: Figure S5) suggested that the genotype response to simulated canopy shade considerably depends on the genotype performing under sunlight. For example, lines with a long flag leaf under sunlight elongated less under simulated shade than lines with short leaves. Similarly, lines that flower early under sunlight show a more significant delay in heading time and thus a higher PI (Supporting Information: Figure S5). To distinguish actual shade-induced plasticity from the plasticity arising due to the general growth capacity of the genotype, we followed Filiault and Maloof (2012) and used the residuals from the sunlight-versus-PI regression as a new, adjusted PI, which is highly correlated with the initial PI (Supporting Information: Figure S6). Positive residuals from the regression represent high shade-induced plasticity, whereas negative residuals correspond to genotypes with a lower response than predicted. We utilized the adjusted PI to examine the effect of canopy shade responses on the fitness of the individual plant under competition for light (Table 1c). Stepwise regression suggested that elongated L2 laminas (9.1%, $p = 0.013$) and delayed heading time (6.94%, $p = 0.04$) contributed significantly to the plant's fitness under canopy shade. In contrast, the increase in the SVSL (11.3%, $p = 0.006$) was maladaptive for plant fitness under simulated canopy shade (Table 1c). The results suggest that although wheat plants' morphology and phenology under a canopy are primarily genotype-related, the G × E response to shading has significant implications for the ability to occupy superior canopy positions and support reproductive success under asymmetric competition.

3.3 | Formation of community performance

We then examined the relevance of the 24 single-plant phenotypes recorded in each light environment (Figure 1a,b) to the variation in the performance of monoculture field plots (Figure 1c) using stepwise regressions. For the above-ground dry matter (AGDM) per area, the MC vegetative shoot weight (7.3%, $p = 0.03$) and the number of grains per spike (22.2%, $p = 0.004$) in glasshouse sunlight conditions were the most contributing factors. In addition, the L2 lamina length (6.3%, $p = 0.04$) (Table 2) was associated with the AGDM of the community. The positive effect of GPS on AGDM may involve an increase in radiation use efficiency due to an enlarged sink size that increases the demand for photosynthesis in the late stages of plant development (Reynolds et al., 2005). The association of long L2 laminas with biomass production per area may arise due to its effect on competitiveness during early developmental stages but also due to an association with lengths of the successive leaves on the stem, together intensifying mutual shading in the community. For the SpMF of the community, the stem internode P-1 length in the glasshouse explained 40.3% of the variation ($p < 0.0001$), where genotypes with short P-1 length and smaller vegetative shoot (3.25%, $p = 0.07$) allocated more to the spike under field conditions. In addition, the number of grains per spikelet (11%, $p = 0.002$) positively correlated with the SpMF. The slight association (3.1%, $p = 0.08$) with the rachis internode length may arise due to its negative correlation with spikelet number, which contributes directly to the spike size (Supporting Information: Figure S7). Notably, for the spike dry weight per area, the number of grains per spike contributed almost solely (31%, $p < 0.0001$), followed by an adverse effect associated with L2 lamina length (Table 2).

We then tested the relevance of the phenotypes recorded on the shaded plants to community performance (Table 3). As for the AGDM per area, the number of grains per spike was the most significant variable explaining the phenotypic variation (26.3%, $p < 0.0001$). In addition, MC SpMF (5.9%, $p = 0.04$) and P-2 length (4.6%, $p = 0.07$) showed a positive association with AGDM, while rachis internode length (4.5%, $p = 0.07$) had a negative association.

For the SpMF of the community, a negative association with the MC vegetative shoot weight of single plants explained the most significant part of the variation in the multivariable model (46.5%, $p < 0.0001$) (Table 3). The number of grains per spike was positively associated with the SpMF (17.1%, $p < 0.0001$), while the spike length (3.8%, $p = 0.02$,), associated with vegetative shoot weight, was associated with a reduced SpMF. The number of days to heading associated with a higher spikelet number could also explain a small proportion of the variance (3.6%, $p = 0.02$).

Most importantly, under simulated canopy shade conditions, the number of grains per spike (37%, $p < 0.0001$), the rachis internode length (7.1%, $p = 0.01$, negative association), the flag leaf lamina length (4%, $p = 0.06$, negative association) and the MC SpMF (3.85%, $p = 0.07$) could explain more than 50% of the variation in the spike biomass per area (Table 3).

Overall, the stepwise regressions for community performance in the field using single plant phenotypes from the sunlight environment explained 35%, 58% and 35% of the AGDM, SpMF and spike biomass per area, respectively (Table 2). When simulated canopy shade

TABLE 3 Stepwise regressions of AGDM per area, spike mass fraction and spike biomass per area of monoculture field plots using single-plant phenotypes (BLUEs) recorded in the glasshouse under simulated canopy shade

Glasshouse light environment	Single plant phenotypes	Estimate	Percentage of squares	*F* ratio	Prob > *F*	R^2 adj.	Community attributes
Simulated canopy shade	Grains per spike	9.890	26.356	18.876	<0.0001		
	P-2 length	9.974	4.610	3.301	0.0764		
	MC SpMF	1048.984	5.876	4.208	0.0465		
	Rachis internode length	−483.744	4.514	3.233	0.0794		
	Total		41.355			0.357	AGDM per area (g/m^2)
	Grains per spike	0.006	17.149	24.979	<0.0001		
	Days to heading	0.003	3.660	5.332	0.0259		
	MC shoot weight	−0.104	46.550	67.803	<0.0001		
	Spike length	−0.016	3.805	5.543	0.0233		
	Total		71.165			0.684	Spike mass fraction
	Grains per spike	9.013	37.036	32.403	<0.0001		
	Rachis internode length	−315.499	7.122	6.231	0.0160		
	MC SpMF	802.445	3.857	3.375	0.0733		
	Flag leaf lamina length	−5.410	3.979	3.481	0.0691		
	Total		51.994			0.474	Spike biomass per area (g/m^2)

Abbreviations: adj., adjusted; AGDM, above-ground dry matte; BLUEs, best linear unbiased estimations; MC, main culm; SpMF, spike mass fraction.

phenotypes were used, they could increase the percentage of variance explained to 41%, 71% and 52% of the AGDM, SpMF and spike biomass per area, respectively (Table 3). These findings indicate that the response to canopy shade plays a role in the wheat crop environment.

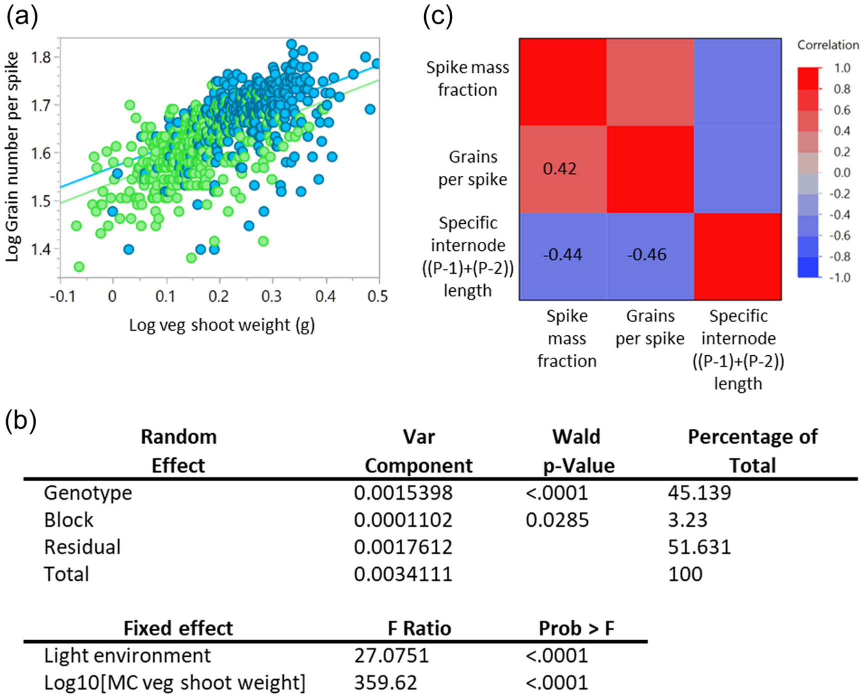
To further investigate the influence of canopy shade responses and identify the significant consequences for the community, we combined sunlight phenotypes with PIs (presented in Figure 2a) in a stepwise regression. Adding PIs to the sunlight model (Table 4) increased the explained variance of spike biomass per area from 35% to 53%, endorsing that canopy shade responses impact the wheat community performance. In the combined model (sunlight + PI), the number of grains per spike was the most significant variable (31%, $p < 0.0001$) contributing to spike biomass per area, followed by the PI of the number of grains per spike (9.8%, $p = 0.005$), rachis internode length (4.5%, $p = 0.05$, negative association), the PI of the SVSL (4%, $p = 0.06$) and PI of the floret number per spikelet (3.8%, $p = 0.07$). These results suggest that the genotype capability of maintaining grain number under limiting light conditions may be an essential feature of high-yielding cultivars.

Because our simulated canopy shade but also high density largely reduces plant biomass (Postma et al., 2021; Weiner & Freckleton, 2010), we examined the relationship between the vegetative shoot biomass and the number of grains per spike. The number of grains per spike was highly correlated with the vegetative shoot biomass, with larger plants having more grains per spike (Figure 3a). The vegetative shoot biomass could explain 24% and 27% of the variation under sunlight and simulated canopy shade, respectively. A linear mixed

TABLE 4 Stepwise regression of spike biomass per area of field plots using a model combining the 24 single-plant phenotypes (BLUEs) recorded under natural sunlight conditions and the corresponding PIs

Glasshouse light environment	Single plant phenotypes	Estimate	Percentage of squares	*F* ratio	Prob > *F*	R^2 adj.	Community attributes
Sunlight + PI	Grains per spike	8.336	31.010	27.173	<0.0001		
	Grains per spike_PI	380.084	9.874	8.652	0.0054		
	Rachis internode length	−351.340	4.473	3.920	0.0545		
	SVSL_PI	165.246	4.086	3.580	0.0656		
	# Florets per spikelet_PI	366.237	3.767	3.301	0.0766		
	Total		53.210			0.475	Spike biomass per area (g/m^2)

Abbreviations: BLUEs, best linear unbiased estimations; PI, plasticity index; SVSL, specific vegetative shoot length.



Random Effect	Var Component	Wald p-Value	Percentage of Total
Genotype	0.0015398	<.0001	45.139
Block	0.0001102	0.0285	3.23
Residual	0.0017612		51.631
Total	0.0034111		100

Fixed effect	F Ratio	Prob > F
Light environment	27.0751	<.0001
Log10[MC veg shoot weight]	359.62	<.0001

FIGURE 3 Determinants of grain number per spike. (a) Relationship between the log main culm vegetative shoot biomass, the light environment and the log number of grains per spike recorded on single plants grown in the glasshouses. Blue circles denote phenotypes obtained under natural sunlight and green circles denote phenotypes obtained under simulated canopy shade. Lines of fit describe the response to shoot weight within each light environment. (b) Mixed linear model (REML) to dissect the effects of the genotype, the block, the light environment and the main culm vegetative shoot weight. Adjusted R^2 for the model is 0.727. (c) Relationships between the specific internode length $\frac{(P-1)+(P-2)\ (cm)}{\text{Shoot biomass}\ (g)}$ and the spike mass fraction of the community and its association with grain number per spike. MC, main culm; REML, restricted maximum likelihood; Var, variance. [Color figure can be viewed at wileyonlinelibrary.com]

model indicated a significant effect also to the light environment, where canopy shade reduces grain number (Figure 3b). These findings suggest that the number of grains per spike, shown in our study to be a significant determinant of community performance, is considerably shaped by the light environment in the plot, reducing plant size and directly limiting yield potential.

Stepwise regressions (Table 3) indicated that GPS under simulated canopy shade is associated with a higher SpMF in the community, implying a link between high GPS and reduced allocation to competitive structures like stems and leaves. However, what is the mechanism connecting GPS with competitiveness?

Examination of the relationship between the length of the stem internodes and plant height to GPS showed no significant correlation (Supporting Information: Figure S7). However, we found a significant negative correlation ($r = -0.46$, $p = 0.001$) between GPS and the specific length of stem internodes P-1 and P-2, that is, the length of P-1 and P-2 divided by the MC shoot biomass (Figure 3c). The specific internode length under shade was also negatively correlated ($r = -0.44$, $p = 0.001$) with the SpMF in the field (Figure 3c), providing a link between GPS and biomass allocation, and suggesting that elongation of stem internodes P-1 and P-2 per shoot biomass promotes stem length but compromises fertility. These findings suggest that even though GPS is not a cooperative trait per se, genotypes with high fertility are likely to have low competitive ability relative to their biomass.

4 | DISCUSSION

4.1 | Different reproductive strategies between wild emmer and durum wheat under competition

Following the domestication of cereal crops, a great deal of adaptation in human-managed environments is believed to result in a reduction of individual plant competitiveness, enabling efficient use of resources by the crop community. In line with this hypothesis, analysis of the phenotypes of wild emmer accession Zavitan and the durum cultivar Svevo demonstrated Zavitan's competitive nature of tall plants with many tillers and a large vegetative mass fraction, most likely adaptive under asymmetric competition for light. Under simulated canopy shade, Zavitan showed a reduction in height, which was not evident in Svevo. The reduction in height was associated with a smaller increase in the SVSL (Supporting Information: Figure S1), suggesting that Zavitan maintains a relatively higher vegetative biomass per centimeter shoot. As for the reproductive part, Zavitan showed high spike biomass associated with high chaff weight but smaller grain size and GPS compared to Svevo.

Interestingly, Zavitan showed less plasticity in grain number and weight, maintaining comparable phenotype values even when light became a limiting resource. Such phenotypic stability could be attributed to the competitive nature of Zavitan, capable of occupying superior positions in the canopy under asymmetric competition. Shifts in allocation under simulated canopy shade may have also contributed to more stability in the GPS and the weight of the grains (Supporting Information: Figure S1). For example, Zavitan showed a substantial reduction in the chaff biomass, which may have facilitated increased allocation to the grain. Furthermore, the height reduction in Zavitan under canopy shade may have promoted assimilate divergence from stem to spike growth (Sadras & Denison, 2009), aiding floret development. Zavitan showed the lowest allometric slope (0.67) among the genotypes in the experiment, indicating an increase in allocation to reproduction when plant biomass reduces under competition. Indeed, we found that a low allometric slope promotes resource allocation to reproduction when plants are shaded (Figure 2f) to support grain filling (Figure 2d). This reflects a bet-hedging reproductive strategy that enables a more stable reproductive output across environments, often at the expense of yield potential (Du et al., 2020; Weiner et al., 2021).

4.2 | Simulated canopy shade resembles high population density and may therefore enhance early-generation selection during breeding

Postma et al. (2021) have conducted a meta-analysis of the phenotypic responses to population density and found reductions in individual plant biomass to be the most significant outcome of an increase in density, mainly because of a reduced rate of photosynthesis in a dense canopy. In our study, we also found biomass traits being the most affected. In line with Postma et al. (2021), we found that the reductions in biomass under canopy shade are associated with a reduction in tiller number, a reduction in the reproductive effort, a delay in flowering time, a reduction in grain number and size, and an unchanged plant height at maturity (Figure 2 and Supporting Information: Tables S2 and S3). The similar responses found for density and canopy shade, and the higher percentage of variance explaining the community performance when multiple phenotypes from simulated canopy shade were considered, enforce our experimental set-up as a manageable solution for studying a plot-like situation but using soil-grown single-plants. Studying single plants under simulated canopy shade may also help understand the genetic basis of 'selfish' and 'cooperative' traits using various mapping populations, enabling the identification of adaptive alleles for the crop environment.

Moreover, breeding new wheat varieties often involve early generation (F2–4) selections of individual plants. Adopting simulated canopy shade may support the rapid identification of density tolerant genotypes mainly through screening for high GPS, which evidently can be verified in monoculture plots during later stages of the breeding programme.

4.3 | Early generation selections for yield potential

The selection of individual plants in early generations may pose a problem because 'selfish' traits promoting individual plant fitness are likely to be selected and compromise yield improvement in high-density monoculture plots, where 'cooperative' plant behaviours are instrumental (Abbai et al., 2020; Cann et al., 2022; Fasoula, 1990; Fischer & Rebetzke, 2018). To avoid such a problem, Fasoula (1990) proposed selection for grain yield per plant under zero competition, as he found it positively correlated with yield under intraplant competition and therefore is a good predictor of yield in monoculture stands. More recently, Fischer et al. (2019) highlighted that under favourable, irrigated growth conditions, optimal sowing densities were as low as 20 plants/m^2. Since significant density × genotype interactions are not likely to arise when moving from zero competition to 20 plants/m^2, Fischer (2020) advocated reinvestigating Fasoula's idea.

In contrast, Donald (1968) suggested that early generation selection should target cooperative plant traits to minimize competition under high density rather than selecting for yield. Disregarding some instances where a communal trait was not realized (Moeller & Rebetzke, 2017), or trait-based selection was not superior to yield-based selection (Yuan et al., 2011), Donald's idea of a 'communal' plant for grain yield improvement has been mostly accepted (Fischer, 2020) and references within.

4.4 | Selfish and cooperative behaviours in plant–plant interactions

Following the evolutionary approach suggested by Donald and later by Denison and Weiner (Denison, 2012; Denison et al., 2003; Donald, 1968; Weiner, 2019), we examined the relevance of single-plant phenotypes in a mixture to the production of monoculture communities. We distinguish between single-plant phenotypes increasing individual plant fitness under competition and those reducing competitiveness, thus promoting communal plants. We also highlight the importance of phenotypes that increase tolerance to shading/density without suppressing neighbouring plants.

The biomass of the MC spike (highly associated with the vegetative shoot weight) and the number of tillers during stem elongation were the most significant traits fuelling individual plant fitness/competitiveness under both light environments. When the plants experienced competition under the simulated canopy shade, where light becomes the most limiting resource, elongation of leaf laminas and a delay in heading time contributed to improved light interception to boost fitness/competitiveness (Table 1c). The adverse effect of the increase in SVSL suggests that a high proportion of vegetative biomass per height promotes individual plant fitness/competitiveness. Long leaves lamina, which promotes individual plant fitness/competitiveness, showed adverse effects on the crop community, possibly by intensifying mutual shading among individuals in the plot and generating steeper illumination gradients under the canopy (Donald, 1968; Richards et al., 2019).

As for cooperative traits, we found the size of the vegetative shoot as an essential factor in determining intraplant competition in the community. In particular, the P-1 stem internode measured in both light environments was negatively correlated ($r = -0.63$ and -0.6 in sunlight and canopy shade, respectively) with the allocation of resources to competitive versus reproductive organs in the field (Supporting Information: Figure S7). This finding is in line with (Rivera-Amado et al., 2019; Sierra-Gonzalez et al., 2021), who found a significant negative correlation between biomass partitioning to P-1 and P-2 (termed Int2 and Int3 in their studies) and resource allocation to the spike. Similarly, in our study, reduced elongation of P-1 and P-2 relative to the culm biomass resulted in a higher SpMF and higher GPS (Figure 3c). As floret development takes place in a period coinciding with stem elongation (Miralles et al., 2000; Slafer et al., 2001), increased allocation to the stem during this period is likely to result in the reduction of assimilates allocated to the spike and consequently lower grain numbers.

Stepwise regressions suggested that the increase in SVSL, which was maladaptive for the individual plant, is a beneficial plasticity response for the community (Table 4), possibly by reducing resource allocation to competitive structures like stems and leaves. In addition, the rachis internode length came up in the multivariable models as having minor adverse effects on community performance. Such an effect may be due to the negative association of this trait with heading time and spikelet number, which directly affect the GPS.

Another essential aspect of community performance we did not address in the current study relates to below-ground competition. Reduced root competition was shown to be associated with cooperation and higher production among *Arabidopsis* and wheat plants (Li et al., 2022; Wuest et al., 2022; Zhu et al., 2019); thus, future studies on community performance will likely benefit from investigating the architecture and biomass allocation to roots. Taken as a whole, we found that individual plant fitness and community performance are associated with distinct and conflicting plant behaviours.

4.5 | High fertility under simulated canopy shade is an essential feature of productive communities

Although GPS may not directly promote cooperation among individuals, we and others (Lichthardt et al., 2020; Voss-Fels et al., 2019; Würschum et al., 2018) found it as an essential component for increasing the grain yield of the community. As GPS reduces significantly under shade but also under high density, screening for genotypes with high grain numbers under simulated canopy shade may be a promising path for identifying high-yielding genotypes for high-density stands.

This prime effect of GPS is in line with previous work in maize, suggesting that the remarkable improvement in maize grain yield during the rise of the hybrid era was, and most likely still is, highly associated with an increase in grain number per area in high-density stands (Tollenaar et al., 1992). Grain number per area in maize is a function of plant growth rate during a period around silking. Since plant growth rate during this period varies little among old and new hybrids, it was deduced that the genetic improvement in grain number per area is associated with a higher allocation to the inflorescences under high-density planting (Lee & Tollenaar, 2007). For wheat, we found GPS to be positively correlated with the shoot biomass and the SpMF, suggesting that selection for high GPS may bring together traits that are usually negatively correlated. Variance analysis also indicated an important role of the light environment, suggesting a direct effect of the light on sink organs (Figure 3). This notion is in line with the finding of (Dreccer et al., 2022; Ugarte et al., 2010), which demonstrated the effect of far-red light on floret development and grain number determination in wheat. The reductions in PAR and the red/far-red light ratio attained in our simulated shade have altered floret development resulting in reduced spikelet fertility and GPS, which may also be due to a reduction in the spike photosynthesis under shade (Molero & Reynolds, 2020).

5 | CONCLUDING REMARKS

Wheat plants respond to simulated canopy shade in patterns similar to those found for increased plant density. Our analysis implies that in the wheat field, where plants grow in high densities, the fitness responses of the genotype to increase its light capture, its allocation patterns under shade, and its ability to withstand reductions in PAR and changes in the light spectrum are significant to the overall community performance. Our analysis further implies that the like-genotype in the monoculture community will have short leaves, a reduced allocation to the stem, a significant SpMF and a high number of grains per spike. These communal attributes were most likely adopted during the evolution of domesticated wheat through the selection of beneficial alleles, contributing to reduced individual plant fitness and high community performance.

However, it is important to mention that our experimental set-up might have possible drawbacks. For example, the intensity and duration of the simulated canopy shade may have triggered rather severe reductions in biomass which could be refined by a more targeted application, starting from stem elongation (Dreccer et al., 2022). Furthermore, the use of unique genetic material containing wild emmer alleles may limit the generalization of our findings in the breeding context. Moreover, the six-rowed plots used in our field experiment may not have been large enough to eliminate possible suppressing effects of the border on interior rows (Rebetzke et al., 2014). To minimize the possible border effect, we used only the two most inner rows of the plot. Nevertheless, environmental effects associated with plot size may have still played a role in our study. Therefore, we would like to encourage breeders to reassess the use of simulated canopy shade for early-generation selections using an extensive array of breeding material and elite varieties and its relevance for on-farm yield in different environments.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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