Agroecological genetics of biomass allocation in wheat uncovers genotype interactions with canopy shade and plant size

Guy Golan[1] (iD), Jacob Weiner[2] (iD), Yusheng Zhao[1] (iD) and Thorsten Schnurbusch[1,3] (iD)

[1]Leibniz Institute of Plant Genetics and Crop Plant Research (IPK), OT Gatersleben, 06466, Seeland, Germany; [2]Department of Plant and Environmental Sciences, University of Copenhagen, DK-1871, Frederiksberg, Denmark; [3]Martin Luther University Halle-Wittenberg, Faculty of Natural Sciences III, Institute of Agricultural and Nutritional Sciences, 06120, Halle, Germany

Author for correspondence:
Guy Golan
Email: golan@ipk-gatersleben.de

Summary

- How plants distribute biomass among organs influences resource acquisition, reproduction and plant–plant interactions, and is essential in understanding plant ecology, evolution, and yield production in agriculture. However, the genetic mechanisms regulating allocation responses to the environment are largely unknown.
- We studied recombinant lines of wheat (*Triticum* spp.) grown as single plants under sunlight and simulated canopy shade to investigate genotype-by-environment interactions in biomass allocation to the leaves, stems, spikes, and grains. Size-corrected mass fractions and allometric slopes were employed to dissect allocation responses to light limitation and plant size.
- Size adjustments revealed light-responsive alleles associated with adaptation to the crop environment. Combined with an allometric approach, we demonstrated that polymorphism in the DELLA protein is associated with the response to shade and size. While a gibberellin-sensitive allelic effect on stem allocation was amplified when plants were shaded, size-dependent effects of this allele drive allocation to reproduction, suggesting that the ontogenetic trajectory of the plant affects the consequences of shade responses for allocation.
- Our approach provides a basis for exploring the genetic determinants underlying investment strategies in the face of different resource constraints and will be useful in predicting social behaviours of individuals in a crop community.

Introduction

Plants fix carbon during photosynthesis, and the biomass produced is allocated to different organs and tissues to support growth and reproduction. Biomass allocation is not fixed and may vary across environments and during the growth and development of the plant. Optimal partitioning theory (OPT) predicts that plants will shift biomass allocation to the organ that acquires the most limiting resource to increase growth (Bloom *et al.*, 1985). For example, when plants sense that light is limiting growth, OPT predicts a shift in allocation to leaves. Similarly, under low nutrient conditions plants should increase biomass allocation to the roots. Thus, the abiotic conditions within the crop microenvironment will affect the allocation patterns among the individuals in the community. In agriculture, such changes in the allocation patterns are also likely to alter the source-sink balance, directly affecting crop yields (Lafitte & Edmeades, 1994; Igartua *et al.*, 1995; Edmeades *et al.*, 1999; Assefa *et al.*, 2013).

Several studies have suggested that plasticity in allocation in response to resource limitation is a result of allometric growth (Müller *et al.*, 2000; Cahill Jr, 2003; Weiner, 2004; Peng & Yang, 2016; Eziz *et al.*, 2017; Liu *et al.*, 2021). The principal assumption of the allometric approach is that biomass allocation to plant organs is primarily a function of plant size and will,

therefore, follow a program associated with the ontogenetic trajectory of the plant (Niklas, 1994; Enquist & Niklas, 2002; Poorter *et al.*, 2015). Therefore, comparisons should be made at common size or size corrected (Coleman *et al.*, 1994), or across sizes (Weiner, 2004), to understand whether plants also shift their allocation patterns in a direct response to an environmental factor. Previous studies have focused on the allometric relationships between plant size and plant growth rate in *Arabidopsis thaliana*, thereby providing a genetic link between life history variation and strategies for leaf resource use (Vasseur *et al.*, 2012), with consequences for environmental adaptation (Vasseur *et al.*, 2018, 2023). Yet, the genetic regulation of size-dependent resource allocation among organs and their implications for the crop environment remain unknown.

Resource allocation implies trade-offs between the growth and function of different organs, and the relative amount of biomass in the various organs determines the plant's fitness and reflects its investment strategy (Weiner, 2004; Veresoglou & Peñuelas, 2019). Thus, the allocation pattern of the plant will determine, to a large extent, resource acquisition and inter-plant competition, which are of fundamental importance in plant ecology, evolution, agriculture, and plant breeding (Donald, 1968; Schwinning & Weiner, 1998; Denison *et al.*, 2003; Weiner, 2004, 2019; Denison, 2012; Poorter *et al.*, 2012). A plant's

ability to gather resources is highly influenced by its morphology. For example, larger leaves and longer stems may increase light interception, and a prolific root system will promote nutrient and water uptake. Allocation to resource-foraging organs such as leaves, stems, and roots entails reduced allocation to reproductive growth and intensifies competition for resources, which may lead to the so-called 'Tragedy of the Commons' (Hardin, 1968; Rankin *et al.*, 2007), in which increases in individual plant fitness reduce population yield.

Although ecological knowledge accumulated on biomass allocation and its response to resource limitation has vast implications for agricultural production, it has rarely been recognized and applied in crop plant research. Given the significant influence that abiotic factors and resource limitation have on agricultural yields (Boyer, 1982; Mittler, 2006), investigating the distribution of biomass in an ecological-genetic framework could provide valuable insights for increasing yields. Such an analysis would take into account not only the genotype effect but also the impact of environmental factors, plant size, and their interactions with the genotype (Weiner, 2004; Poorter *et al.*, 2012).

Increases in crop density have played a major role in increasing cereal yields in recent decades. Because active competition among crop plants uses resources that could be used for yield, yield production will benefit from less 'selfish' and more 'cooperative' resource acquisition behaviours (Weiner, 2017, 2019; Abbai *et al.*, 2020; Zhu *et al.*, 2022). Natural selection favours the most fit/competitive individuals in the population; however (Denison *et al.*, 2003; Denison, 2012), making 'cooperative' behaviours evolutionary unstable and implying that modern crop plants have inherited competitive alleles from their wild progenitors (Zhang *et al.*, 1999). Recognizing this, Donald (1968) suggested selection based on a theoretical wheat plant 'ideotype' designed to minimize active inter-plant competition and optimize resource allocation at the population level. It was proposed that such an ideal plant architecture would feature a compact form with a limited number of upright leaves and a productive inflorescence growing on a single stem. This configuration would prioritize reproductive allocation while sacrificing resources that would be used for competitive structures such as leaves and stems.

Numerous studies have provided compelling evidence that a genotype's reaction to competition from neighbours is a critical determinant of its yield potential. Specifically, low-yielding genotypes show greater plasticity in response to competition than their high-yielding counterparts, indicating that the former are less suited to the resource constraints in a high-density crop environment (Reynolds *et al.*, 1994; Sadras & Lawson, 2011; Sukumaran *et al.*, 2015; Lake *et al.*, 2016). Recent studies have shown a strong correlation between responses to plant density and to low light, indicating that the scarcity of light is often a limiting factor in high-density crop communities (Poorter *et al.*, 2019; Postma *et al.*, 2021). The performance of individual plants cultivated under simulated shade shows stronger correlations with the performance of the monoculture community than individuals grown under natural sunlight conditions (Golan *et al.*, 2023). Practices such as tillage, fertilizing the soil, and regulating the water supply can reduce competition for water and

nutrients, but they amplify competition for light. These observations suggest that studying the genetic basis of plant responses to changes in the intensity and spectrum of light due to competition from neighbouring plants will advance our understanding of adaptation to the crop environment.

Here, we apply a new approach that combines principles from plant ecology and quantitative genetics to identify genetic determinants underlying biomass allocation responses. We used a recombinant inbred lines (RIL) population developed from a cross between a wild emmer genotype and an elite durum wheat cultivar showing contrasting biomass allocation patterns. Mixed linear models were employed to detect genetic loci that control biomass allocation among the leaves, stem, spike, and grains, and to measure the influence of these loci on allocation responses to light. We take an allometric approach to differentiate between alleles promoting direct responses to light and those changing allocation due to plant size (allometric loci).

In summary, our study aims to provide a framework for investigating the genetics of biomass allocation and growth in the face of resource constraints that is particularly useful for distinguishing between alleles that exhibit cooperative vs competitive behaviours for resource acquisition.

Materials and Methods

Experimental approach

To elucidate the genetic basis underlying the investment strategy of individual wheat plants and how it is influenced by canopy shade, we grew recombinant inbred lines in a mixture under natural sunlight and simulated canopy shade (Golan *et al.*, 2023) to obtain the biomass of the leaves, stems, spikes, and grains. Two complementary approaches were employed using organ masses to investigate the genetic factors influencing plasticity in biomass allocation: The first approach involved calculating mass fractions and utilizing a residual method to account for plant size effects. The size-corrected mass fractions (MF) were then incorporated into a multi-environment quantitative trait locus (QTL) model to identify allocation loci and examine their interactions with the light environment. The second approach explored size-induced allocation responses by analysing the slopes of plant mass vs organ mass regressions in a similar QTL model. By combining these two lines of investigation, our experimental approach allows us to identify the genetic determinants of a response to the limiting resource (light quantity and quality in the present study) as well as any response to plant size (Fig. 1).

Plant material and experimental set-up

Recombinant inbred lines (F_8 generation) were developed from a cross between the durum (*Triticum turgidum* ssp. *durum*) cultivar Svevo (Maccaferri *et al.*, 2019) and the wild emmer accession Zavitan (*Triticum turgidum* ssp. *dicoccoides*) (Avni *et al.*, 2017) using the single-seed descent approach. Genotypic profiling of the RILs was conducted using the Illumina iSelect 90 K single nucleotide polymorphism assay (Avni *et al.*, 2014; Wang
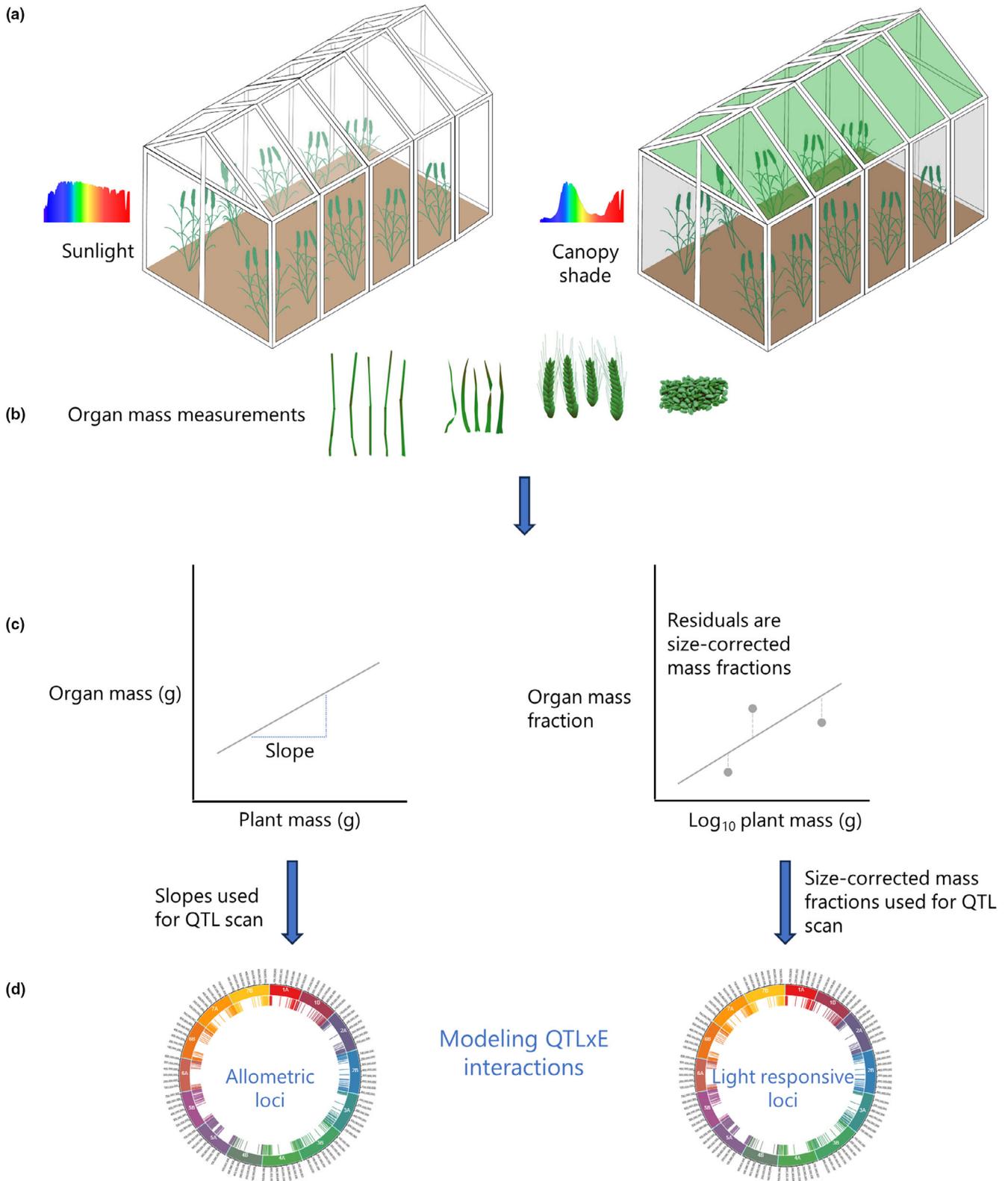
Fig. 1 The experimental approach employed for the genetic dissection of plasticity in biomass allocation into responses to light properties and plant size. (a) Under natural sunlight and simulated canopy shade (low red and blue light), a total of 131 wheat recombinant inbred lines (RIL) were cultivated ($n = 4$) in soil in two glasshouses with open sides, arranged in an incomplete block design. (b) Plants were harvested at maturity to obtain the mass of the main tiller leaves, stems, and spikes, as well as the vegetative mass, spikes, and grains of the entire plant. (c) Mass fractions were corrected for plant size using a residual approach and organ mass was plotted against plant mass to determine the allometric slope of each genotype in each environment. (d) Allocation loci were mapped and the interaction of the loci with the light environment was modelled.

et al., 2014) and the linkage map was constructed as previously described (Nave *et al.*, 2016). Since the initial linkage map was created before assembling the reference genome for tetraploid wheat, we reviewed the map and replaced markers that exhibited inconsistencies with their physical positions with markers that shared a similar genetic position, aligning with the physical position in the Zavitan reference genome V2 (see updated map in Supporting Information Table S1). Two glasshouses were used to cultivate the RILs, using natural loamy soil supplemented with 140 l of substrate2 (Klasman-Deilmann, Geeste, Germany) each. The glasshouses had two open sides with porous metal netting to allow air circulation. Canopy shade was simulated using a green plastic filter (Lee122 Fern green; LEE filters, Andover, UK), as previously described (Golan *et al.*, 2023), reducing the irradiation of blue and red light by *c.* 80% and resulting in a reduction of the red/far-red (715–745 nm) ratio from 1.13 to 0.28. The photosynthetically active radiation (PAR) under the simulated canopy shade was reduced by *c.* 55%. While the green filter altered the light environment notably between the glasshouses, we cannot dismiss the possibility that variation in other abiotic factors, like temperature and soil conditions, potentially influencing plant growth. However, incorporating these extra factors would have been impractical for a thorough genetic screening. Hence, we opted for a more direct approach that allows screening of large populations throughout their complete life cycle and could potentially serve as a method for individual plant selections in breeding.

At the end of March 2021, 131 RILs were sown in jiffy pots under controlled environmental conditions (photoperiod: 16 h : 8 h, 20°C : 16°C, light : dark). After 12 d (Zadok's scale11–12), the seedlings were transplanted in the glasshouse in an alpha lattice design with incomplete blocks of nine plants per block arranged in four replications (Table S2). To facilitate single-plant phenotyping, *c.* 10–15 cm spacing was maintained between plants within a 1-m row and 20–25 cm between rows. The plants were watered three times a week and fertilized during the stem elongation phase with 300 g of calcium ammonium nitrate.

Due to a technical error, the current study did not include the parental lines. However, we have recently published a comprehensive analysis comparing the responses of Svevo and Zavitan to shade, under conditions similar to those described in the present study (Golan *et al.*, 2023).

Phenotypic measurements

All phenotypes (Table S3) were evaluated from single plants and harvested at the soil surface when they reached maturity (108 d after sowing, Zadok's scale 94–95). Biomass was measured following a seven-day drying period at 40°C. Leaf number was recorded at anthesis (Zadok's scale 65) and tiller number during stem elongation (Zadok's scale 33–34). We used the main tiller (Mt) for phenotyping final leaf number, leaf mass, plant height, stem mass, and spike mass. Plant height was measured as the distance between the soil and the spike base (the junction between the spike and the peduncle). Leaf mass fraction (LMF), stem mass fraction (StMF), and main tiller spike mass fraction (SpMF)

were calculated by dividing the organ mass by the total main tiller mass. We also measured the whole plant vegetative mass, spike mass, and grain mass to calculate SpMF and the grain mass fraction (Harvest index, hereafter HI).

Phenotypic analysis

We used a mixed linear model to examine the effects of the light environment, plant size (mass), and the genotype on biomass allocation to the leaves, the stem, the spike, and the grains using mass fractions (the proportion of the total mass that is organ mass) as

$$\text{Mass fraction} = \mu + E + S + (E \times S) + G + R + B + e$$

Eqn 1

where the intercept (μ), the light environment (E), plant size (S), and light × size interactions ($E \times S$) are fixed effects and the genotype (G), the replication (R), and the block (B) are random effects.

Genetic analysis

To understand how the light environment affects the allocation of biomass in a genotype-dependent manner, we examined the genetic factors affecting mass fractions while controlling for size effects. The mass fractions were size-corrected by associating them with the logarithmically transformed plant size (g) data (Poorter & Sack, 2012) and considering the residuals from the regression analysis (Fig. S1) as size-corrected mass fractions. The relationships between the Mt_StMF and the Mt_SpMF to the Main tiller total mass showed dynamic trends across plant size and were fitted using the LOESS (locally estimated scatterplot smoothing smother) function in JMP 16 software (SAS Institute). The LOESS curve was fitted with α = 0.5 using a locally linear functional form. Robustness weights were incorporated in the fitting process, which was repeated four times.

Before performing the QTL analysis, we used the two-step mixed model analysis in Genstat (VSN International, Hemel Hempstead, UK) to obtain the within-environment unit error and calculate the Best Linear Unbiased Estimation (BLUE) for each genotype in each environment to be used in subsequent QTL analysis. The first step involved fitting the genotype and the replication and block as random factors to determine the variance components. In the second step, the genotype (G) was fitted as a fixed term, and the replication (R) and the block (B) were fitted as random, as

$$Y = \mu + G + R + B + e$$

Eqn 2

Detection of QTL and their interaction with the environment was conducted in Genstat using the multi-environment trial model (Malosetti *et al.*, 2013). The best variance–covariance model describing the variation between genotypes, both within and between environments, was selected based on Schwarz information criterion (SIC) and subsequently used to denote the

phenotypic data structure in a genome-wide scan by applying single QTL models across the genome at marker and inter-marker positions (simple interval mapping, SIM) using a maximum step size of 10 cM. In total, 483 genetic predictors were tested. Significant QTLs were then used as co-factors in composite interval mapping (CIM) until the significant QTLs profile stabilized. Significant QTLs determined using backward selection were included in the final multi-QTL model using a minimum co-factor proximity of 50 cM and a minimum separation of 30 cM between selected QTLs. Genome-wide QTL significance was assessed at $\alpha = 0.05$ (LOD = 3.653) based on the number of effectively independent tests (Li & Ji, 2005). The final model for each trait enabled exploration of the consistency of QTL effects across different environments by decomposing the QTL effects into main effects and effects due to QTL-environment interactions (QEI), as

$$Y = \mu + E + G + \sum QTL + \sum (QTL \times E) + e \qquad \text{Eqn 3}$$

where μ is the intercept, E is the light environment effect, G is the random genetic effect, $\sum QTL$ is the total additive effect of each QTL, $\sum (QTL \times E)$ represents the total QTL effects × environment interactions, and e is the residual term (including the QEI residual) modelled by the variance–covariance matrix.

Allelic differences within the sequences of candidate genes were identified using the two reference genomes of the parental lines (Avni *et al.*, 2017; Maccaferri *et al.*, 2019).

Results

Effects of light and plant size on biomass allocation in the RIL population

The phenotypic analysis of each mass fraction with mixed linear models showed that the genetic constituents of the RILs accounted for most of the variation in biomass allocation in the random effects models (Table S4), indicating that the genetic program largely determines biomass allocation. The LMF was 9% higher under simulated canopy shade, due to the effects of both the light environment and plant size (Fig. 2a; Table S4). The significant effect of the light environment indicates that shading increased LMF in addition to effects caused by size differences. The LMF was negatively associated with the total weight of the main tiller ($F = 230.29$, $P < 0.0001$) in both light environments, indicating that when plants are smaller, allometric growth shifts allocation to the leaves in a manner consistent with OPT. The nonsignificant interaction between the main tiller size and the light environment indicates that an increase in tiller size
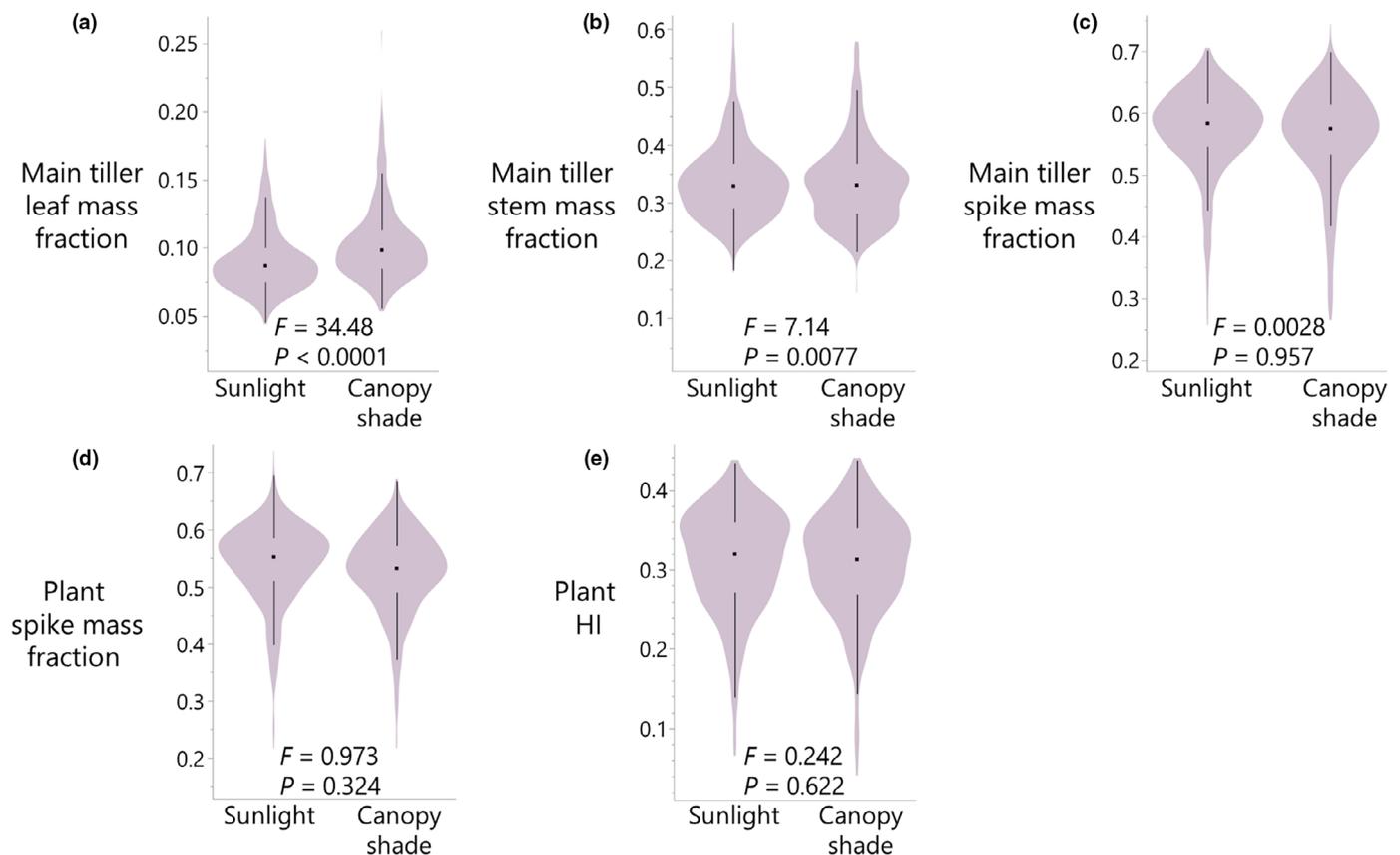
Fig. 2 Biomass distribution per plant under natural sunlight and simulated canopy shade in the wheat recombinant inbred line (RIL) population. (a–e) phenotypic recordings of mass fractions. Median and whiskers extending to the expected minimum and maximum are indicated. The effects of light on mass fractions is presented using the F statistics and P-values obtained from a mixed linear model (Supporting Information Table S4).

results in comparable decrease in LMF in both light environments. The StMF decreased slightly (*c.* 2%) in response to canopy shade (Fig. 2b, $F = 7.14$, $P = 0.007$) and was affected by the main tiller weight and its interaction with the light environment (Table S4). For small individuals (Mt mass between 1 and 3 g), an increase in size implies reduced allocation to the stems, while the opposite trend is observed for larger individuals (Fig. S1). The significant interaction between the Mt weight and the light environment indicates that the effects of tiller size on StMF were light-dependent.

The SpMF was not affected by shading but was influenced by the main tiller weight ($F = 68.32$, $P < 0.0001$) and its interaction with the light environment ($F = 11.28$, $P = 0.0008$). Allocation to the spike increased with size in small individuals and decreased in larger plants. The whole plant SpMF and the grain mass fraction (HI) were reduced when plant biomass was reduced, and the effects were larger under shade (Fig. S1), indicating plasticity in reproductive allometry in response to canopy shade. Light had no significant main effect on whole plant allocation to reproduction (Table S4). In summary, the mixed linear models show that, at the RIL population level, the direct effect of light is mainly on biomass allocation to leaves and, to a lesser extent, to the stems. However, size and size × light interactions significantly affected resource allocation, not only to the leaves and stems but also to reproduction.

Accounting for plant size effects reveals QTL × light interactions

QTL mapping of the size-corrected mass fractions associated with different organs identified six loci on chromosomes 3A, 4B, and 5A (Table S5). The *Reduced-height-B1* (*Rht-B1*) locus (chr 4B), encoding a DELLA protein that suppresses GA-mediated growth, was the most dominant factor in determining resource allocation in the RIL population. Wild emmer Zavitan (parental line) carries the GA-sensitive allele (*rht-B1a*), while Svevo contains an early stop codon (Fig. S2a), giving rise most likely to an N-terminally truncated Rht-B1b protein (Peng *et al.*, 1999) conferring the dominant semi-dwarfism associated with low StMF and high allocation to the spike, leaves and grains.

The LMF was regulated by three loci, one on chromosome 4B (associated with *Rht-B1*) and two on chromosome 5A, one of them associated with the *VERNALIZATION-A1* (*VRN-A1*) locus. The allelic effects were similar in both environments, indicating a lack of genetic variation for LMF plasticity in the studied RIL population (Fig. 3a; Table S5). The wild allele in the *VRN-A1* locus on chromosome 5A increased LMF, most likely due to its promoting effect on leaf number (Table S5). Furthermore, our analysis revealed that the wild allele (*vrn-A1*) stimulates tiller number and delays the heading time of the spikes (Table S5). The observed effects on the size-corrected LMF, leaf number, tiller number, and heading time indicate that the wild allele enhances the genotype's competitive nature by increasing tiller number, and promoting light interception through higher investments in leaves. The *VRN-A1* locus encodes APETALA1 (AP1), a MADS-box transcription factor that modulates the requirement for cold temperatures for flowering. In line with our QTL mapping, a comparison of the gene sequence at *VRN-A1* in the parental lines showed that the durum cv Svevo carries a large deletion (*c.* 7.4 kb) within the gene's first intron (Fig. S2b), which is assumed to eliminate vernalization requirements (Fu *et al.*, 2005).
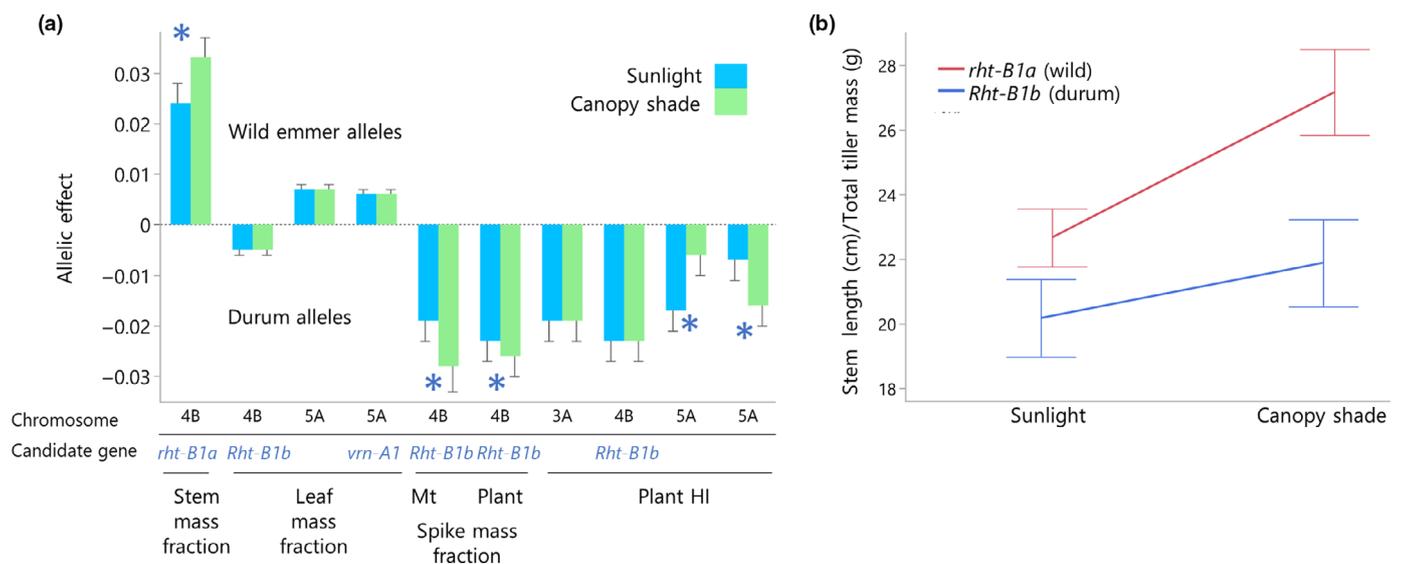
Fig. 3 Genetic basis of wheat allocation responses to light. (a) Additive effects (+SE) of size-corrected mass fractions alleles for the stem (StMF), the leaves (LMF), the spikes (SpMF) and the grains (HI) calculated from the main tiller (Mt) or the whole plant under sunlight (blue) and simulated canopy shade (green). Asterisks indicate loci exhibiting a significant interaction with light. The *Y*-axis is absolute values, where the positive values indicate increasing alleles contributed by Zavitan and negative values indicate alleles contributed by Svevo. The chromosome and the underlying candidate gene and increasing allele of the QTL peak marker are indicated below. (b) The effect of *Reduced-height-B1* (*Rht-B1*) alleles on the stem length per unit mass under sunlight and canopy shade. Error bars are 95% confidence intervals of the mean.

We detected a significant QEI for StMF, where the effect of the wild *rht-B1a* allele increased by 39% in the shaded environment compared to natural sunlight (Fig. 3a). This result suggests a substantial light effect on StMF mediated by *Rht-B1*. Analysis of the spike mass fractions showed that the dominant *Rht-B1b* allele, increases allocation to the spike, and this effect is increased by 47% and 13% for the main tiller and the whole plant, respectively, under shaded conditions. These results suggest that the allelic status at the *Rht-B1* locus determines biomass allocation between the stem and the spike and its effect is light-dependent. It also demonstrates the increasing advantage of the durum allele to promote reproduction in a dense population where plants experience mutual shading. The wild allele, however, enhances 'selfish' behaviour under shade by augmenting its promoting effect on StMF, thus reinforcing the drive for light competition.

Durum alleles promoted the HI at four loci on chromosomes 3A, 4B, and 5A. The QTL on chromosome 4B showed a double peak in the QTL analysis; one peak associated with *Rht-B1* and another peak *c.* 12 cM away from *Rht-B1* showed a higher significance and was included in the final QTL model (following backward selection) (Table S5). While the QTL on chromosomes 3A and 4B showed no interaction with the light environment, the QTL on chromosome 5A (*c.* 53 cM proximal to *VRN-A1*) was effective only under sunlight conditions (Fig. 3a, Table S5). Another QTL at the distal end of chromosome 5A had an effect only under simulated canopy shade. Overall, wild emmer alleles promoted the growth of competitive structures such as leaves and stems, whereas alleles from durum wheat favoured reproductive growth, potentially reducing competition among plants.

We then examined possible mechanisms underlying the increased effect of the wild *rht-B1a* allele on StMF when plants are shaded. We hypothesize that the allelic status at the *Rht-B1* locus impacts stem elongation in response to canopy shade. subsequently influencing biomass distribution. Notably, we observed no significant increase in the final plant height under shade when analysing the plant's response to canopy shade (Table S6). In fact, there was a minor reduction in plant height, indicating that the larger effect on resource allocation towards the stem in shaded environments is not associated with a general rise in final plant height. Nevertheless, there was variation in the relative height of the main tiller, measured as the length of the main stem divided by the overall mass of the tiller. Genotypes that possessed the wild *rht-B1a* allele exhibited greater stem lengths relative to their biomass, and this effect was amplified in shaded conditions (Fig. 3b). The increase in shaded environments may imply an increase in StMF to maintain height under low light, as revealed by our analysis of QEI.

We investigated the phenotypic and genetic relationships between phenology and allocation patterns to ask whether variation in phenology resulting from shading or genetic factors impact allocation patterns. Simulated canopy shade had a negligible effect on the number of days to heading (DTH; Fig. S3a). However, we observed positive associations between the size-corrected LMF and DTH, and negative associations between the size-corrected StMF and DTH, regardless of the light environment (Fig. S3b,c). These associations could partly be explained by the genotype effects. Two DTH QTL were associated with the allocation loci. The late heading allele of *vrn-A1* (wild) was associated with a higher LMF, and an early heading allele associated with *rht-B1* (wild) promoted StMF and decreased LMF (Table S5). These findings suggest possibly genetic pleiotropic links between phenology and biomass allocation patterns.

After identifying the allelic effects that contribute to the size-corrected mass fractions, in which the presence of QEI signifies a response to light, we compared these effects with those influencing the observed mass fractions when they were not corrected for plant size. The uncorrected mass fractions encompass both the responsiveness to light and the plasticity resulting from changes in plant size. This comparison should indicate the distinct plant size effects of different alleles on allocation. For example, the increasing allele related to LMF on chromosome 4B (associated with the semi-dwarf allele) showed an additive effect of 0.005 when adjustments for size were considered and an effect of 0.009 without any size correction (Fig. S4a; Table S5). This comparison suggests that a considerable portion of the allele's effect stems from its capacity to diminish size. Similarly, QTL mapping of the uncorrected LMF could not detect the *VRN-A1* locus, suggesting its increasing effect on the total tiller mass eliminated its influence on biomass allocation to the leaves (Table S5). For StMF, we see that the promoting effects of the *rht-B1a* (wild) allele are lower when adjusted for size (Fig. S4a; Table S5), suggesting that the promoting effect of the allele on the total tiller mass contributes to its effect on StMF.

We found that the *Rht-B1* locus shows a more significant QEI for StMF and SpMF with size correction (Table S5; Fig. S4b). These results indicate a contrasting influence of size and light on allocation associated with the *Rht-B1* locus, implying that the growth consequences of responses to light, such as shade avoidance responses, are conditioned by plant size. Additionally, size corrections exposed a QTL for HI on the distal end of chromosome 5A, which was not detected using the uncorrected data, and the durum allele for this QTL had the strongest effect under shade (Fig. 3a; Table S5). Overall, differences in QEI and in the set of QTLs detected when size corrections were used imply genetic variation for size effects on biomass allocation.

Rht-B1 links reproductive allocation and sensitivity to plant mass

To pinpoint the genetic loci that influence biomass allocation in a size-dependent manner, we investigated the relationships between the mass of the different organs and the mass of either the whole plant or the main tiller. The slopes for each RIL in each environment were then utilized in a QTL analysis. We detected two loci underlying the main tiller mass-main stem mass regressions slopes. One QTL was associated with *Rht-B1*, and another locus on chromosome 2B was associated with the *Photoperiod-B1* (*PPD-B1*) locus. Genotypes possessing the wild *rht-B1a* allele exhibit steeper slopes than those with the durum allele (Fig. 4a; Table S5). Consequently, when plants are small, biomass allocation to the stem will be more reduced in genotypes
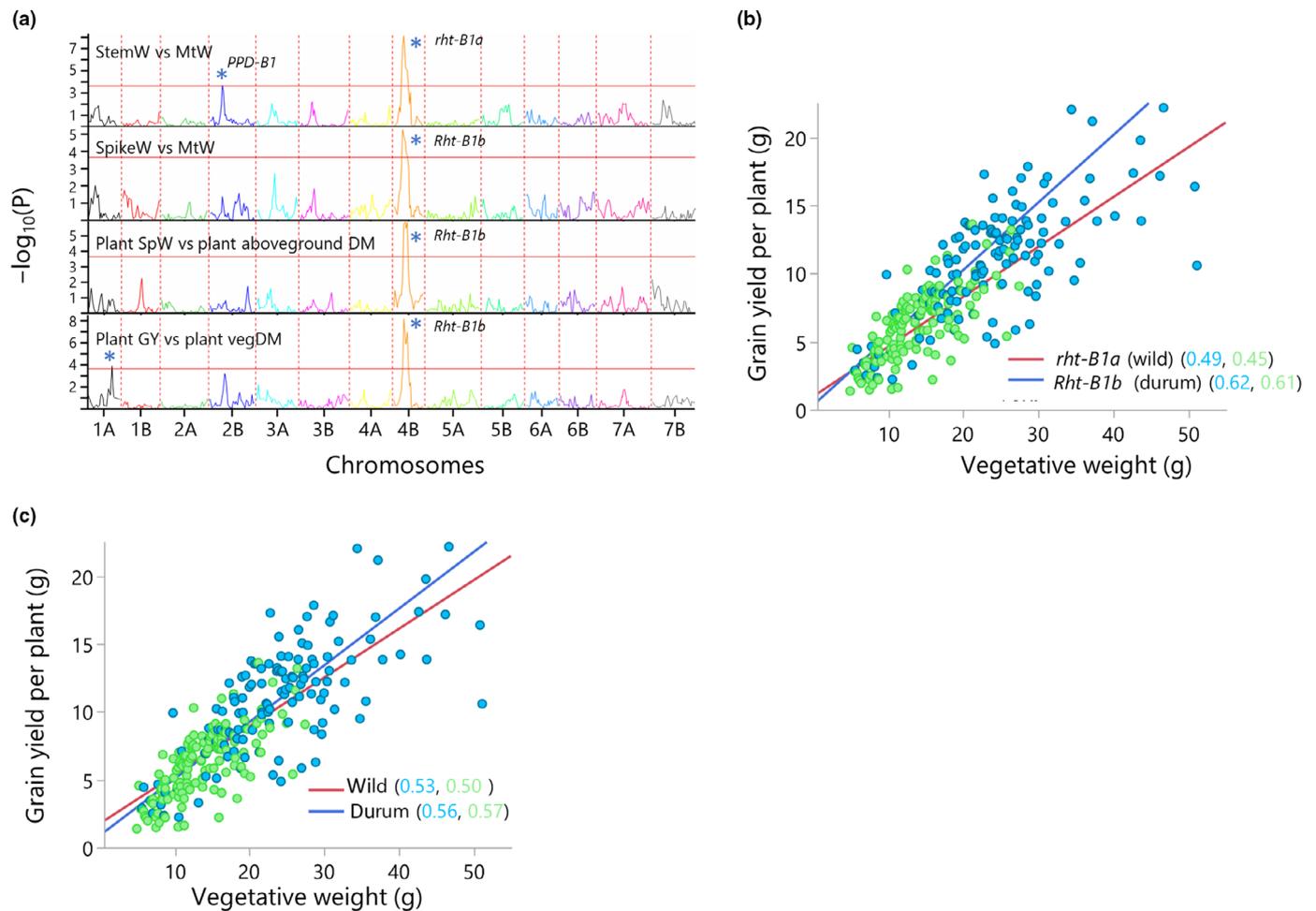
Fig. 4 *Reduced-height-B1* (*Rht-B1*) exerts significant control over the plasticity of wheat biomass allocation in response to differences in plant size. (a) Using regression slopes, a genome-wide analysis identified loci that significantly influence the effects of size on biomass allocation. These loci are marked with asterisks (see Supporting Information Table S5 for a detailed description of the QTL parameters). (b) Effects of the vegetative weight (BLUE values) on grain yield associated with the different *Rht-B1* alleles. (c) Effects of vegetative weight on grain yield associated with the different 1A QTL alleles. The average intra-genotype slope for each allele in each environment is indicated in brackets. Blue and green indicates plants under sunlight and simulated canopy shade, respectively.

with the wild *rht-B1a* allele than those with the durum *Rht-B1b* allele. Similarly, the presence of the durum allele in the *PPD-B1* locus increased the steepness of the slopes, implying that genes responsible for the speed of development may affect allometric growth.

Size-dependent allocation to spikes on the main tiller and the whole plant was promoted by *Rht-B1b*, which conferred steeper allometric slopes (Fig. 4a; Table S5). This means that smaller plant size will affect spike growth more in semi-dwarf genotypes than in tall genotypes. When we examined the relationship between the vegetative biomass and the grain yield of the plant, we found that the *Rht-B1b* semi-dwarf allele confers steeper slopes than the tall allele, thus compromising yield potential relatively more when plants are small. In addition, we detected another QTL on chromosome 1A, where the durum allele confers steeper slopes, similarly implying greater sensitivity of grain yield to overall size (Fig. 4a; Table S5).

Rht-B1 was found to mediate a trade-off in the sensitivity of the stem and spike growth to plant mass, the most significant trade-off in allocation in our study. In case of the wild *rht-B1a* allele, reductions in size primarily impact stem growth, with a lesser effect on spike growth. Conversely, when the durum *Rht-B1b* allele is present, the opposite effect is observed: smaller size affects spike growth more prominently and having a lesser impact on stem growth. Overall, the contribution of the durum alleles underlying reproductive allometry to the production of grain yield is most pronounced when plants are large, and its effectiveness diminishes when a plant is small, shifting allocation more towards vegetative biomass (Fig. 4b,c). The steeper allometric slopes of these alleles are associated with a higher size-corrected HI adapted to canopy shade (Fig. S5), suggesting that genotypes with a higher HI are more sensitive to changes in plant size.

We also detected interactions of the QTL underlying reproductive allometry (*Rht-B1* and the 1A QTL) with the light

environment, indicating genotype-dependent plasticity in allometry due to canopy shade. The durum allele of *Rht-B1b* exhibited steeper allometric slopes under canopy shade compared to sunlight conditions. The wild allele showed the opposite trend, with smaller allometric slopes under shade. Thus, the effect of the *Rht-B1* locus on spike growth allometry was larger under shade (Fig. S6a,b). The 1A QTL showed similar patterns for the allometric slope of grain yield (Fig. S6c), together suggesting that the differences between wild and durum alleles in the sensitivity of reproductive growth to size are greater in a shaded environment.

Basis for plant size responses to limited light intensity and quality

Size-corrected mass fractions correspond to the portion of organ mass resulting from resource allocation to that particular organ. These fractions can account for *c.* 52% of the differences in leaf weight per culm and 21–32% of the variation in stem weight under sunlight and simulated canopy shade (Fig. 5a). Allocation to the main tiller spike accounted for 14–16% of the variation in spike mass on the main tiller under both sunlight and canopy shade. Moreover, biomass allocation could only account for 6% of the plant spike weight and *c.* 16–20% of the grain yield per plant. The variation in organ mass not accounted for by allocation is probably due to differences in plant size, determined by the genotype's ability to convert resources to biomass, which is measured in our study as the total aboveground dry matter (AGDM) of the main tiller or the whole plant. In general, plant size accounted for most of the variation in organ mass. Nevertheless, under canopy shade, where plants are small, allocation patterns play a more important role in organ growth (Fig. 5a).

We identified four loci associated with plant size. Wild alleles at the *Rht-B1* and *VRN-A1* governing biomass distribution in the RILs promoted the main tiller mass and were major contributors to the total plant mass. A wild allele on chromosome 1A, which was associated with allometry, and a durum allele on chromosome 5B, which did not affect allocation, also promoted whole plant mass (Fig. 5b,c). The light environment conditioned the allelic effects of the plant size loci, as we observed reduced allelic effects of these loci under simulated canopy shade. The most substantial QEI was related to the effect of *rht-B1a* on plant size. The allelic effect was reduced by 68% compared to under sunlight conditions. The wild *vrn-A1* allele exhibited comparable effects on the main tiller mass in both environments, but its influence on the whole plant mass was diminished by 32% under canopy shade, most likely due to a compromised impact on tillering (Table S5).

The 1A QTL and the 5B QTL effects were reduced by 44% and 56% under simulated canopy, respectively. This suggests that the impact of the identified plant size loci (chr 1A, 4B, 5A, 5B) was influenced by the amount of radiation intercepted, and the different loci were associated with different growth rate responses to such limitation. Modelling plant size QEI makes it possible to identify alleles more suitably adapted to canopy shade conditions associated with high-density stands.

Discussion

Competition among plants limits the resources available to individuals and plays an important role in crop production (Donald, 1968; Zhang *et al.*, 1999; Weiner & Freckleton, 2010; Denison, 2012; Weiner, 2019). This is especially important in high-density cereal crop stands, which have been the basis for increased cereal yields over recent decades. When considering a density series spanning very low to very high density, the total biomass produced per area demonstrates a linear increase with density when density is low but reaches a plateau and remains relatively stable as densities increase (Weiner & Freckleton, 2010). The explanation is that, at very low densities, there is no competition among individuals, and an increase in plant density will entail a higher biomass per area. However, further increases in density result in and amplify inter-plant competition, which reduces the individual plant size, primarily caused by decreases in light availability (Poorter *et al.*, 2019; Postma *et al.*, 2021) in high-resource crop production. Furthermore, in wheat, the light spectrum, specifically the decrease in the red/far-red light ratio due to competition for light, directly impacts potential yield (Evers *et al.*, 2006; Chelle *et al.*, 2007; Ugarte *et al.*, 2010; Dreccer *et al.*, 2022).

Plant responses to their environment are largely expressed in changes in the allocation of resources among different organs (Poorter *et al.*, 2012, 2019), which has significant consequences on yield production. For example, HI, an important determinant of grain yield, changes in response to plant density (Donald & Hamblin, 1976; Vega *et al.*, 2000; Echarte & Andrade, 2003; Qin *et al.*, 2013). Changes in the plant HI due to crowding reflect the degree of competition among plants in the field (Denison, 2012), and identifying the genetic factors responsible for such responses in resource allocation can facilitate the development of high-yielding cooperative genotypes. Although previous studies have looked into HI from a genetic point of view (Molero *et al.*, 2019, 2023; Dreisigacker *et al.*, 2021; Sierra-Gonzalez *et al.*, 2021; Ruiz *et al.*, 2023), as far as we know, no genetic investigation has been carried out to analyse the plasticity in resource allocation.

It is essential to understand whether a change in allocation is a direct response to the limiting resource, a result of plant size, or both. In the context of crop improvement, previous studies have indicated that tolerance of different crops to abiotic factors, such as water, nitrogen, and salinity are primarily related to the allocation patterns under these limiting conditions (Lafitte & Edmeades, 1994; Igartua *et al.*, 1995; Edmeades *et al.*, 1999; Assefa *et al.*, 2013). However, studies of the tolerance of crops to abiotic factors usually neglect size-driven allocation, described by allometric relationships and shown to account for much of the variation in the allocation response to abiotic factors in ecological studies (Müller *et al.*, 2000; Cahill Jr, 2003; Weiner, 2004; Peng & Yang, 2016; Eziz *et al.*, 2017; Liu *et al.*, 2021).

By accounting for size in the analysis of mass fractions, we see that the *Rht-B1* locus encoding a DELLA protein is responsive to light (Fig. 3a, significant QEI). In this locus, the presence of the wild (emmer) allele leads competitive behaviour, which reduces
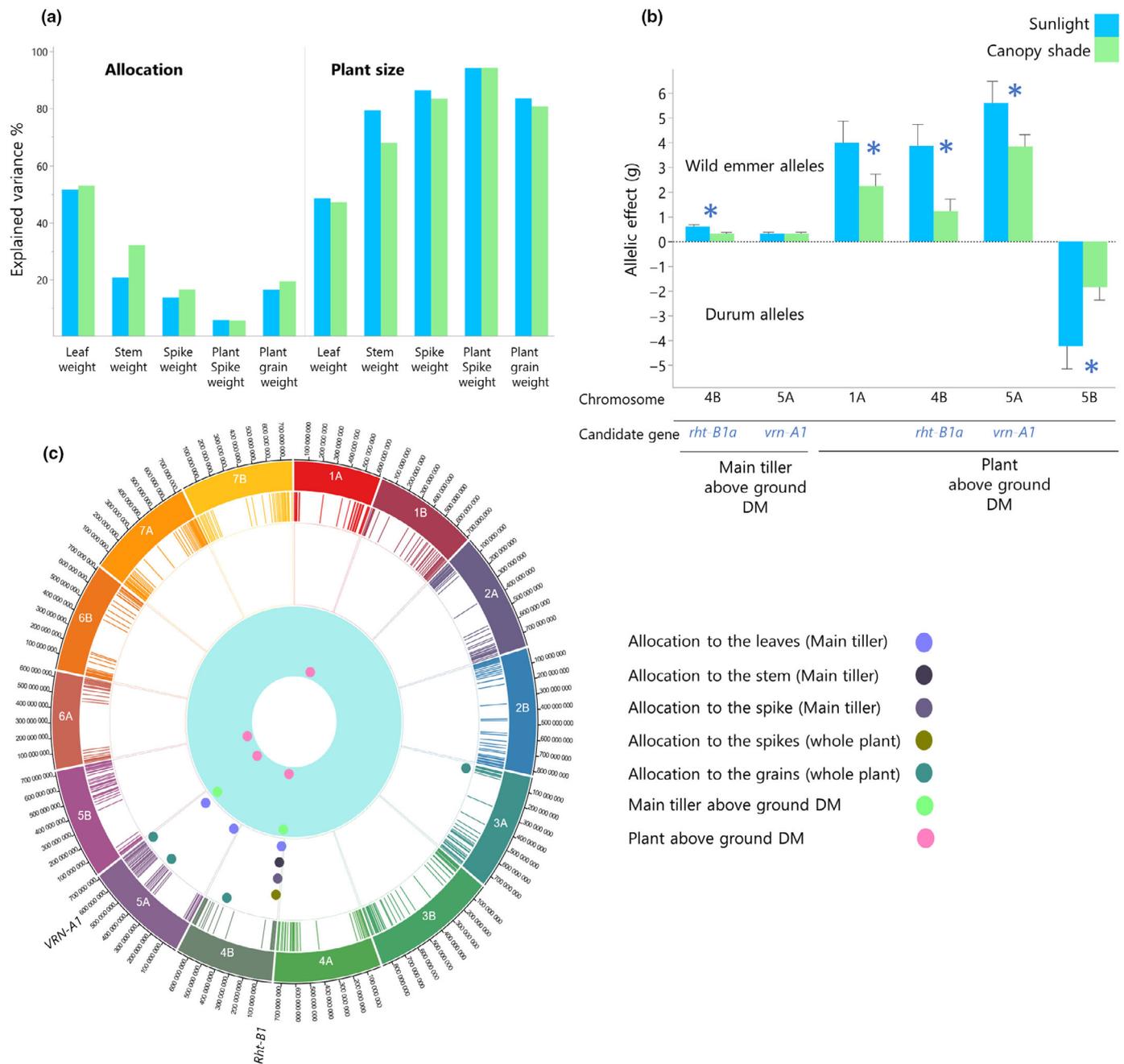
Fig. 5 The genetic basis of wheat organ growth and plant size responses to light limitations. (a) Variation in organ mass accounted for by biomass allocation and by the biomass of the main tiller and whole plant above ground. (b) Additive effects (+SE) of plant size alleles for the main tiller (Mt) and the whole plant under sunlight (blue) and simulated canopy shade (green). Asterisks indicate loci exhibiting a significant interaction with light. The *Y*-axis is absolute values, where the positive values indicate increasing alleles contributed by Zavitan and negative values indicate alleles contributed by Svevo. The chromosome and the candidate gene underlying the QTL peak marker are indicated below. (c) Circos plot depicting the physical (most outer track) and genetic positions (rectangles) of the allocation loci and the plant size loci (inner, blue track) and their co-localization in the *Reduced-height-B1* (*Rht-B1*) and *VERNALIZATION-A1* (*VRN-A1*) loci.

population yield by promoting a relatively higher resource allocation to the stem and away from the spike. This finding aligns with the GA-mediated degradation of DELLA proteins when red/far-red light ratio is low to enable the growth of the hypocotyl and the petiole of *Arabidopsis* plants as a means to avoid being shaded (Achard *et al.*, 2007; Djakovic-Petrovic *et al.*, 2007). But

Rht-B1 also affects allocation responses through allometry in directions that may oppose the response to light. Genotypes carrying the wild *rht-B1a* allele exhibit greater tolerance to smaller size than those carrying the semi-dwarf allele, as the reduction in reproductive growth associated with the wild *rht-B1a* allele is comparatively smaller (Fig. 4). The opposing effect of canopy

shade and plant size on biomass allocation may be due to the dual effect of the green filter on light spectra and light intensity. For example, in genotypes carrying the GA-sensitive wild allele, the low red/far-red ratio may increase the stem mass fraction through stem elongation (Colombo *et al.*, 2022), while the lower light intensity induces a more significant restriction on stem growth due to the allometric trajectory of the genotypes carrying the wild allele.

The introduction of semi-dwarf genotypes during the 1960s Green Revolution was pivotal in increasing crop grain yields. This achievement was largely possible due to the extensive adoption of chemical fertilizers, pesticides, and controlled irrigation. Creating optimal conditions for cultivating the semi-dwarf varieties, which possess resistance against lodging but require significant amounts of nitrogen fertilizers to maximize their productivity per unit area, played a crucial role (Wu *et al.*, 2020; Liu *et al.*, 2022; Song *et al.*, 2023). The intensification of crop production, especially the substantial increase in fertilizer usage, resulted in enhanced plant growth per unit area. This intensification also led to a higher degree of mutual shading among plants in the field, and the new varieties selected had to perform well in this new crop environment. Our findings indeed show that semi-dwarf genotypes carrying the *Rht-B1b* allele are more adapted to the modern crop environment, as they exhibit allocation patterns favourable for the crop population (less allocation to the stems and more to reproduction), which become even more advantageous under shade (Fig. 3).

On the other hand, under limiting conditions like drought, semi-dwarf varieties typically do not outperform their taller counterparts (Jatayev *et al.*, 2020), as well as (Butler *et al.*, 2005; Lanning *et al.*, 2012; Sanad *et al.*, 2016; Keser *et al.*, 2017). These observations are consistent with our allometric analyses, which reveal that semi-dwarf lines are more sensitive to smaller size (Fig. 4). Our analysis highlights the benefit of the semi-dwarf *Rht-B1b* allele in facilitating spike growth in larger plants, whereas this advantage is much smaller in smaller plants. Under drought conditions, the semi-dwarf genotypes are limited in size, and growth in these plants may prioritize roots, not reproductive parts (Eziz *et al.*, 2017). Consistent with these findings, it has been proposed that allometry regulates the trade-off between yield potential, assessed under favourable conditions, and yield stability in limiting environments (Weiner *et al.*, 2021). However, a study in maize indicated that yield potential does not conflict with tolerance to density (Gonzalez *et al.*, 2018), suggesting that yield potential and allometry could be selected independently. We encourage genetic investigations into reproductive allometry in crops to identify favourable genetic variation for allocation. By integrating these findings into breeding programs, we may be able to enhance the ability of crops to withstand resource limitations.

The capacity of a genotype to convert resources into biomass largely determines organ growth, and the major improvement in grain yield potential during wheat breeding has largely been attributed to notable increases in aboveground biomass per unit area (Shearman *et al.*, 2005; Sadras & Lawson, 2011; Aisawi *et al.*, 2015). However, it is important to select beneficial plant size alleles that do not impair the reproductive allocation patterns of the plant (Rivera-Amado *et al.*, 2019). Ideally, favourable alleles should exhibit minimal interaction with the environment and not decrease reproductive allocation, even under limited resources and conditions resulting in smaller plant sizes. In our RIL population, the increases in plant AGDM were predominantly attributed to the presence of wild emmer alleles, indicating their potential as a valuable resource for enhancing biomass in elite varieties. Of the four loci detected, only one (chromosome 5B), originating from Svevo was not related to the allocation patterns of the plants (Fig. 5c), indicating it is useful for increasing plant potential and was, therefore, selected during crop evolution and breeding.

The *Rht-B1b* allele and the durum allele on chromosome 1A may also contribute to yield potential as they increase allometric slopes for grain yield, promoting grain production when plants are less limited in size. Selection of the wild alleles associated with *Rht-B1* and *VRN-A1* may affect allocation patterns and increase inter-plant competition in the crop community, as these alleles prioritize the growth of competitive structures such as stems, leaves, and tillers (Fig. 3; Table S5).

Our methodology facilitates the identification of plant size/ growth rate (see Weiner, 2004) and allocation loci that can potentially be combined to reduce competition among plants and maximize grain yield production. Additionally, by investigating the response of these QTLs to variation in light and plant size, we enhance our understanding of the adaptability of these loci to densely populated agricultural settings, where resources, especially light, are limiting. Identifying known loci, such as *Rht-B1* and *VRN-A1*, and several unidentified loci influencing biomass allocation in wheat, validates our approach and opens new possibilities for future genetic research into biomass allocation in crops.

Concluding remarks

Understanding and predicting crop yield production is a major challenge due to the many factors and interactions that determine it, including numerous genomic loci, the cultivation environment, plant–plant interactions, and the complex interplay between these factors and the environment. Predicting genotype-by-environment interactions is especially demanding as it requires extensive datasets encompassing the targeted populations and environmental conditions.

From a physiological perspective, crop yield can be simplified and described as the total biomass generated per unit area multiplied by the harvest index. Understanding allocation responses in crops and identifying the underlying genetic factors can improve our ability to predict genotype performance in different environments.

Given that numerous studies have emphasized the role of plant size in allocation under resource limitations and climatic variables, an allometric approach can help predict genotype performance in new environments. In addition, by investigating genotype responses to limiting resources using size-adjusted data, we can uncover alleles that promote optimal responses to resource

limitations for yield production. These alleles may have an impact on a genotype's performance across diverse environments, although not necessarily in the same direction as allometry. In summary, our new approach combining principles from plant ecology and quantitative genetics sheds light on essential constituents of G × E interactions, increasing our understanding of crop yield formation and offering the possibility of identifying genes that underlie both yield potential and stability of crop plants.

Competing interests

None declared.

Author contributions

GG: funding, conceptualization, data acquisition, analysis, and interpretation, preparation of the first draft. YZ: experimental design and support in data analysis. JW: manuscript review and editing. TS: funding, supervision, manuscript review and editing.

ORCID

Guy Golan https://orcid.org/0000-0002-5255-393X
Thorsten Schnurbusch https://orcid.org/0000-0002-5267-0677
Jacob Weiner https://orcid.org/0000-0002-0736-7943
Yusheng Zhao https://orcid.org/0000-0001-6783-5182

Data availability

The data that supports the findings of this study are available in the Supporting Information of this article.

References

Abbai R, Singh VK, Snowdon RJ, Kumar A, Schnurbusch T. 2020. Seeking crops with balanced parts for the ideal whole. *Trends in Plant Science* 25: 1189–1193.

Achard P, Liao L, Jiang C, Desnos T, Bartlett J, Fu X, Harberd NP. 2007. DELLAs contribute to plant photomorphogenesis. *Plant Physiology* 143: 1163–1172.

Aisawi KAB, Reynolds MP, Singh RP, Foulkes MJ. 2015. The physiological basis of the genetic progress in yield potential of CIMMYT spring wheat cultivars from 1966 to 2009. *Crop Science* 55: 1749–1764.

Assefa T, Beebe SE, Rao IM, Cuasquer JB, Duque MC, Rivera M, Battisti A, Lucchin M. 2013. Pod harvest index as a selection criterion to improve drought resistance in white pea bean. *Field Crops Research* 148: 24–33.

Avni R, Nave M, Barad O, Baruch K, Twardziok SO, Gundlach H, Hale I, Mascher M, Spannagl M, Wiebe K *et al.* 2017. Wild emmer genome architecture and diversity elucidate wheat evolution and domestication. *Science* 357: 93–97.

Avni R, Nave M, Eilam T, Sela H, Alekperov C, Peleg Z, Dvorak J, Korol A, Distelfeld A. 2014. Ultra-dense genetic map of durum wheat × wild emmer wheat developed using the 90K iSelect SNP genotyping assay. *Molecular Breeding* 34: 1549–1562.

Bloom AJ, Chapin FS III, Mooney HA. 1985. Resource limitation in plants-an economic analogy. *Annual Review of Ecology and Systematics* 16: 363–392.

Boyer JS. 1982. Plant productivity and environment. *Science* 218: 443–448.

Butler JD, Byrne PF, Mohammadi V, Chapman PL, Haley SD. 2005. Agronomic performance of Rht alleles in a spring wheat population across a range of moisture levels. *Crop Science* 45: 939–947.

Cahill JF Jr. 2003. Lack of relationship between below-ground competition and allocation to roots in 10 grassland species. *Journal of Ecology* 91: 532–540.

Chelle M, Evers JB, Combes D, Varlet-Grancher C, Vos J, Andrieu B. 2007. Simulation of the three-dimensional distribution of the red:far-red ratio within crop canopies. *New Phytologist* 176: 223–234.

Coleman JS, McConnaughay KDM, Ackerly DD. 1994. Interpreting phenotypic variation in plants. *Trends in Ecology & Evolution* 9: 187–191.

Colombo M, Montazeaud G, Viader V, Ecarnot M, Prosperi J-M, David J, Fort F, Violle C, Fréville H. 2022. A genome-wide analysis suggests pleiotropic effects of Green Revolution genes on shade avoidance in wheat. *Evolutionary Applications* 15: 1594–1604.

Denison RF. 2012. *Darwinian agriculture*. Princeton, NJ, USA: Princeton University Press.

Denison RF, Kiers ET, West SA. 2003. Darwinian agriculture: when can humans find solutions beyond the reach of natural selection? *The Quarterly Review of Biology* 78: 145–168.

Djakovic-Petrovic T, Wit M, Voesenek LACJ, Pierik R. 2007. DELLA protein function in growth responses to canopy signals. *The Plant Journal* 51: 117–126.

Donald CM. 1968. The breeding of crop ideotypes. *Euphytica* 17: 385–403.

Donald CM, Hamblin J. 1976. The biological yield and harvest index of cereals as agronomic and plant breeding criteria. *Advances in Agronomy*, 28: 361–405.

Dreccer MF, Zwart AB, Schmidt R-C, Condon AG, Awasi MA, Grant TJ, Galle A, Bourot S, Frohberg C. 2022. Wheat yield potential can be maximized by increasing red to far-red light conditions at critical developmental stages. *Plant, Cell & Environment* 45: 2652–2670.

Dreisigacker S, Burgueño J, Pacheco A, Molero G, Sukumaran S, Rivera-Amado C, Reynolds M, Griffiths S. 2021. Effect of flowering time-related genes on biomass, harvest index, and grain yield in CIMMYT elite spring bread wheat. *Biology* 10: 855.

Echarte L, Andrade FH. 2003. Harvest index stability of Argentinean maize hybrids released between 1965 and 1993. *Field Crops Research* 82: 1–12.

Edmeades GO, Bolaños J, Chapman SC, Lafitte HR, Bänziger M. 1999. Selection improves drought tolerance in tropical maize populations: I. Gains in biomass, grain yield, and harvest index. *Crop Science* 39: 1306–1315.

Enquist BJ, Niklas KJ. 2002. Global allocation rules for patterns of biomass partitioning in seed plants. *Science* 295: 1517–1520.

Evers JB, Vos J, Andrieu B, Struik PC. 2006. Cessation of tillering in spring wheat in relation to ligh tinterception and red:far-red ratio. *Annals of Botany* 97: 649–658.

Eziz A, Yan Z, Tian D, Han W, Tang Z, Fang J. 2017. Drought effect on plant biomass allocation: a meta-analysis. *Ecology and Evolution* 7: 11002–11010.

Fu D, Szűcs P, Yan L, Helguera M, Skinner JS, von Zitzewitz J, Hayes PM, Dubcovsky J. 2005. Large deletions within the first intron in *VRN-1* are associated with spring growth habit in barley and wheat. *Molecular Genetics and Genomics* 273: 54–65.

Golan G, Abbai R, Schnurbusch T. 2023. Exploring the trade-off between individual fitness and community performance of wheat crops using simulated canopy shade. *Plant, Cell & Environment* 46: 3144–3157.

Gonzalez VH, Tollenaar M, Bowman A, Good B, Lee EA. 2018. Maize yield potential and density tolerance. *Crop Science* 58: 472–485.

Hardin G. 1968. The tragedy of the commons. *Science* 162: 1243–1248.

Igartua E, Gracia MP, Lasa JM. 1995. Field responses of grain sorghum to a salinity gradient. *Field Crops Research* 42: 15–25.

Jatayev S, Sukhikh I, Vavilova V, Smolenskaya SE, Goncharov NP, Kurishbayev A, Zotova L, Absattarova A, Serikbay D, Hu Y-G et al. 2020. Green revolution 'stumbles' in a dry environment: dwarf wheat with Rht genes fails to produce higher grain yield than taller plants under drought. *Plant, Cell & Environment* 43: 2355–2364.

Keser M, Gummadov N, Akin B, Belen S, Mert Z, Taner S, Topal A, Yazar S, Morgounov A, Sharma RC et al. 2017. Genetic gains in wheat in Turkey: winter wheat for dryland conditions. *The Crop Journal* 5: 533–540.

Lafitte HR, Edmeades GO. 1994. Improvement for tolerance to low soil nitrogen in tropical maize III. Variation in yield across environments. *Field Crops Research* 39: 27–38.

Lake L, Li Y, Casal JJ, Sadras VO. 2016. Negative association between chickpea response to competition and crop yield: phenotypic and genetic analysis. *Field Crops Research* 196: 409–417.

Lanning SP, Martin JM, Stougaard RN, Guillen-Portal FR, Blake NK, Sherman JD, Robbins AM, Kephart KD, Lamb P, Carlson GR et al. 2012. Evaluation of near-isogenic lines for three height-reducing genes in hard red spring wheat. *Crop Science* 52: 1145–1152.

Li J, Ji L. 2005. Adjusting multiple testing in multilocus analyses using the eigenvalues of a correlation matrix. *Heredity* 95: 221–227.

Liu Q, Wu K, Song W, Zhong N, Wu Y, Fu X. 2022. Improving crop nitrogen use efficiency toward sustainable green revolution. *Annual Review of Plant Biology* 73: 523–551.

Liu R, Yang X, Gao R, Hou X, Huo L, Huang Z, Cornelissen JH. 2021. Allometry rather than abiotic drivers explains biomass allocation among leaves, stems and roots of *Artemisia* across a large environmental gradient in China. *Journal of Ecology* 109: 1026–1040.

Maccaferri M, Harris NS, Twardziok SO, Pasam RK, Gundlach H, Spannagl M, Ormanbekova D, Lux T, Prade VM, Milner SG et al. 2019. Durum wheat genome highlights past domestication signatures and future improvement targets. *Nature Genetics* 51: 885–895.

Malosetti M, Ribaut J-M, van Eeuwijk FA. 2013. The statistical analysis of multi-environment data: modeling genotype-by-environment interaction and its genetic basis. *Frontiers in Physiology* 4: 44.

Mittler R. 2006. Abiotic stress, the field environment and stress combination. *Trends in Plant Science* 11: 15–19.

Molero G, Coombes B, Joynson R, Pinto F, Piñera-Chávez FJ, Rivera-Amado C, Hall A, Reynolds MP. 2023. Exotic alleles contribute to heat tolerance in wheat under field conditions. *Communications Biology* 6: 21.

Molero G, Joynson R, Pinera-Chavez FJ, Gardiner L-J, Rivera-Amado C, Hall A, Reynolds MP. 2019. Elucidating the genetic basis of biomass accumulation and radiation use efficiency in spring wheat and its role in yield potential. *Plant Biotechnology Journal* 17: 1276–1288.

Müller I, Schmid B, Weiner J. 2000. The effect of nutrient availability on biomass allocation patterns in 27 species of herbaceous plants. *Perspectives in Plant Ecology, Evolution and Systematics* 3: 115–127.

Nave M, Avni R, Ben-Zvi B, Hale I, Distelfeld A. 2016. QTLs for uniform grain dimensions and germination selected during wheat domestication are co-located on chromosome 4B. *Theoretical and Applied Genetics* 129: 1303–1315.

Niklas KJ. 1994. *Plant allometry: the scaling of form and process.* Chicago, IL, USA: University of Chicago Press.

Peng J, Richards DE, Hartley NM, Murphy GP, Devos KM, Flintham JE, Beales J, Fish LJ, Worland AJ, Pelica F et al. 1999. 'Green revolution' genes encode mutant gibberellin response modulators. *Nature* 400: 256–261.

Peng Y, Yang Y. 2016. Allometric biomass partitioning under nitrogen enrichment: evidence from manipulative experiments around the world. *Scientific Reports* 6: 1–7.

Poorter H, Jagodzinski AM, Ruiz-Peinado R, Kuyah S, Luo Y, Oleksyn J, Usoltsev VA, Buckley TN, Reich PB, Sack L. 2015. How does biomass distribution change with size and differ among species? An analysis for 1200 plant species from five continents. *New Phytologist* 208: 736–749.

Poorter H, Niinemets Ü, Ntagkas N, Siebenkäs A, Mäenpää M, Matsubara S, Pons T. 2019. A meta-analysis of plant responses to light intensity for 70 traits ranging from molecules to whole plant performance. *New Phytologist* 223: 1073–1105.

Poorter H, Niklas KJ, Reich PB, Oleksyn J, Poot P, Mommer L. 2012. Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytologist* 193: 30–50.

Poorter H, Sack L. 2012. Pitfalls and possibilities in the analysis of biomass allocation patterns in plants. *Frontiers in Plant Science*, 3: 259.

Postma JA, Hecht VL, Hikosaka K, Nord EA, Pons TL, Poorter H. 2021. Dividing the pie: a quantitative review on plant density responses. *Plant, Cell & Environment* 44: 1072–1094.

Qin X-L, Weiner J, Qi L, Xiong Y-C, Li F-M. 2013. Allometric analysis of the effects of density on reproductive allocation and Harvest Index in 6 varieties of wheat (*Triticum*). *Field Crops Research* 144: 162–166.

Rankin DJ, Bargum K, Kokko H. 2007. The tragedy of the commons in evolutionary biology. *Trends in Ecology & Evolution* 22: 643–651.

Reynolds MP, Acevedo E, Sayre KD, Fischer RA. 1994. Yield potential in modern wheat varieties: its association with a less competitive ideotype. *Field Crops Research* 37: 149–160.

Rivera-Amado C, Trujillo-Negrellos E, Molero G, Reynolds MP, Sylvester-Bradley R, Foulkes MJ. 2019. Optimizing dry-matter partitioning for increased spike growth, grain number and harvest index in spring wheat. *Field Crops Research* 240: 154–167.

Ruiz A, Trifunovic S, Eudy DM, Sciarresi CS, Baum M, Danalatos GJN, Elli EF, Kalogeropoulos G, King K, dos Santos C et al. 2023. Harvest index has increased over the last 50 years of maize breeding. *Field Crops Research* 300: 108991.

Sadras VO, Lawson C. 2011. Genetic gain in yield and associated changes in phenotype, trait plasticity and competitive ability of South Australian wheat varieties released between 1958 and 2007. *Crop and Pasture Science* 62: 533–549.

Sanad MNME, Campbell KG, Gill KS. 2016. Developmental program impacts phenological plasticity of spring wheat under drought. *Botanical Studies* 57: 35.

Schwinning S, Weiner J. 1998. Mechanisms determining the degree of size asymmetry in competition among plants. *Oecologia* 113: 447–455.

Shearman VJ, Sylvester-Bradley R, Scott RK, Foulkes MJ. 2005. Physiological processes associated with wheat yield progress in the UK. *Crop Science* 45: 175–185.

Sierra-Gonzalez A, Molero G, Rivera-Amado C, Babar MA, Reynolds MP, Foulkes MJ. 2021. Exploring genetic diversity for grain partitioning traits to enhance yield in a high biomass spring wheat panel. *Field Crops Research* 260: 107979.

Song L, Liu J, Cao B, Liu B, Zhang X, Chen Z, Dong C, Liu X, Zhang Z, Wang W et al. 2023. Reducing brassinosteroid signalling enhances grain yield in semi-dwarf wheat. *Nature* 617: 118–124.

Sukumaran S, Reynolds MP, Lopes MS, Crossa J. 2015. Genome-wide association study for adaptation to agronomic plant density: a component of high yield potential in spring wheat. *Crop Science* 55: 2609–2619.

Ugarte CC, Trupkin SA, Ghiglione H, Slafer G, Casal JJ. 2010. Low red/far-red ratios delay spike and stem growth in wheat. *Journal of Experimental Botany* 61: 3151–3162.

Vasseur F, Exposito-Alonso M, Ayala-Garay OJ, Wang G, Enquist BJ, Vile D, Violle C, Weigel D. 2018. Adaptive diversification of growth allometry in the plant *Arabidopsis thaliana*. *Proceedings of the National Academy of Sciences, USA* 115: 3416–3421.

Vasseur F, Violle C, Enquist BJ, Granier C, Vile D. 2012. A common genetic basis to the origin of the leaf economics spectrum and metabolic scaling allometry. *Ecology Letters* 15: 1149–1157.

Vasseur F, Violle C, Enquist BJ, Vile D. 2023. Genetic variability and plasticity of plant allometry. *Functional Ecology* **37**: 1095–1105.

Vega CRC, Sadras VO, Andrade FH, Uhart SA. 2000. Reproductive allometry in soybean, maize and sunflower. *Annals of Botany* **85**: 461–468.

Veresoglou SD, Peñuelas J. 2019. Variance in biomass-allocation fractions is explained by distribution in European trees. *New Phytologist* **222**: 1352–1363.

Wang S, Wong D, Forrest K, Allen A, Chao S, Huang BE, Maccaferri M, Salvi S, Milner SG, Cattivelli L *et al.* **2014.** Characterization of polyploid wheat genomic diversity using a high-density 90 000 single nucleotide polymorphism array. *Plant Biotechnology Journal* **12**: 787–796.

Weiner J. 2004. Allocation, plasticity and allometry in plants. *Perspectives in Plant Ecology, Evolution and Systematics* **6**: 207–215.

Weiner J. 2017. Applying plant ecological knowledge to increase agricultural sustainability. *Journal of Ecology* **105**: 865–870.

Weiner J. 2019. Looking in the wrong direction for higher-yielding crop genotypes. *Trends in Plant Science* **24**: 927–933.

Weiner J, Du Y-L, Zhao Y-M, Li F-M. 2021. Allometry and yield stability of cereals. *Frontiers in Plant Science* **12**: 681490.

Weiner J, Freckleton RP. 2010. Constant final yield. *Annual Review of Ecology, Evolution, and Systematics* **41**: 173–192.

Wu K, Wang S, Song W, Zhang J, Wang Y, Liu Q, Yu J, Ye Y, Li S, Chen J *et al.* **2020.** Enhanced sustainable green revolution yield via nitrogen-responsive chromatin modulation in rice. *Science* **367**: eaaz2046.

Zhang D-Y, Sun G-J, Jiang X-H. 1999. Donald's ideotype and growth redundancy: a game theoretical analysis. *Field Crops Research* **61**: 179–187.

Zhu YH, Weiner J, Jin Y, Yu MX, Li FM. 2022. Biomass allocation responses to root interactions in wheat cultivars support predictions of crop evolutionary ecology theory. *Frontiers in Plant Science* **13**: 858636.

Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Linear regressions and Locally Estimated Scatterplot Smoothing depicting size effects on mass fractions at the population level.

Fig. S2 Polymorphism associated with the DELLA protein and *AP1* gene underlying the *Rht-B1* and *VRN-A1* loci.

Fig. S3 Relationships between days to heading and size-corrected mass fractions under sunlight and simulated canopy shade.

Fig. S4 Size correction alters allelic effects of allocation loci.

Fig. S5 Reaction norms depicting the size-corrected HI under sunlight and simulated canopy shade.

Fig. S6 Reaction norms depicting allometric plasticity between light environments underlying significant quantitative trait locus × E interactions.

Table S1 Linkage map and genotyping data of the RIL population used in the current study.

Table S2 Experimental design of the glasshouses.

Table S3 Phenotypic data (BLUEs).

Table S4 Mixed linear models of mass fractions.

Table S5 Quantitative trait locus analysis data.

Table S6 Analysis of variance of plant height.

Please note: Wiley is not responsible for the content or functionality of any Supporting Information supplied by the authors. Any queries (other than missing material) should be directed to the *New Phytologist* Central Office.