







INVITED REVIEW

Dividing the pie: A quantitative review on plant density responses

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Abstract

Plant population density is an important variable in agronomy and forestry and offers an experimental way to better understand plant–plant competition. We made a meta-analysis of responses of even-aged mono-specific stands to population density by quantifying for 3 stand and 33 individual plant variables in 334 experiments how much both plant biomass and phenotypic traits change with a doubling in density. Increasing density increases standing crop per area, but decreases the mean size of its individuals, mostly through reduced tillering and branching. Among the phenotypic traits, stem diameter is negatively affected, but plant height remains remarkably similar, partly due to an increased stem length-to-mass ratio and partly by increased allocation to stems. The reduction in biomass is caused by a lower photosynthetic rate, mainly due to shading of part of the foliage. Total seed mass per plant is also strongly reduced, marginally by lower mass per seed, but mainly because of lower seed numbers. Plants generally have fewer shoot-born roots, but their overall rooting depth seems hardly affected. The phenotypic plasticity responses to high densities correlate strongly with those to low light, and less with those to low nutrients, suggesting that at high density, shading affects plants more than nutrient depletion.

1 | INTRODUCTION

Plants typically live with neighbours. These neighbouring plants may provide facilitation in various ways, for example, in the form of protection against grazing, support for climbing or provision of water (Brooker et al., 2008). At the same time, these neighbours also compete for the same available resources, such as light, nutrients or water, with the competition typically outweighing the facilitation. To some extent, this competition is asymmetric, with larger plants obtaining a disproportionately larger share of resources than smaller plants (Weiner, 1990). A clear case is a forest where mature trees may more easily obtain light than understory plants. In other

circumstances, plant size (height or biomass) will be more similar and competition, therefore, more symmetric. One of the more straightforward cases of competition is a stand of even-aged individuals of the same species (from here on ‘monostand’), where all plants are regularly spaced and start with similar seed mass or seedling mass. As density increases, the distance between plants is reduced and—given a more or less fixed supply of resources per unit ground area—the intra-specific competition becomes stronger. Density responses in such monostands, and the optimization of density, are highly relevant issues for productivity in agriculture and horticulture and have now been studied for over a century (e.g., Hickman, 1889). It is also a relevant topic in forestry, not only to maximize production but also to manage the shape of trees.

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At the same time, monostands also offer a relatively simple, elegant and reproducible experimental system to study a number of eco(physio)logical principles related to competition.

A range of interesting topics has been fruitfully studied in monostands of different densities. These relate to physiological aspects such as sensing of neighbours (Anten & Chen, 2020; Huber, Nieuwendijk, Pantazopoulou, & Pierik, 2020) and regulation of the vertical (re)distribution of leaves, roots and nitrogen (Niinemets, 2016; Pons, 2016). More ecologically oriented papers have focused on the size variability among individuals within a stand (Weiner & Thomas, 1986) and discussed the existence of laws about 'self-thinning', that is, the decreasing percentage of plants surviving when competition becomes more severe (Deng et al., 2012; Yoda, 1963). Here we examine the responses of biomass and productivity per unit ground area as a function of plant density, as well as trait plasticity of individual plants within the canopy. There are many studies on agronomic yield in response to density, and various authors have reviewed these with respect to a specific species (Mansfield & Mumm, 2014; Papadopoulos & Pararajasingham, 1997). A more conceptual approach was taken by, for example, Kira, Ogawa, and Shinozaki (1953), Drew

and Flewelling (1977) and Weiner and Freckleton (2010), who discussed the concept of what is known as 'constant final yield' (note that this term refers to biomass per ground area rather than to the more commonly used 'agronomic yield'). The basis for the idea of 'constant final yield' is the observation that the density response curves for standing crop will saturate, such that there is a broad range of plant densities that lead to the same above-ground or total biomass per ground area. Weiner and Freckleton (2010) also suggested that this would be different from the density response curve for seed output, which might decline at higher densities where total biomass would remain constant. In the first part of this paper, we investigate whether the law of 'constant final yield' has universal applicability and whether it also applies to the Leaf Area Index (LAI, Table 1). In the second part, we shift attention to the individual plant within stands of different densities and consider which environmental variables are affected by density and which ones are not, and how a monostand is composed of individuals of different sizes. We then broaden our analysis beyond biomass and present a meta-analysis of how the morphological, chemical and physiological traits of individual plants are affected by changes in density and how these phenotypic changes

TABLE 1 Glossary of terms and abbreviations. All biomass refers to dry biomass, unless indicated otherwise

Abbreviation	Variable	Explanation	Unit
GDM _A	Generative Dry Mass per Area	Reproductive biomass per ground area	g m ⁻²
GDM _I	Generative Dry Mass of an Individual	Reproductive biomass per individual plant	g plant ⁻¹
g _s	Stomatal conductance	Stomatal conductance measured in leaf cuvettes	mmol m ⁻² s ⁻¹
LAI	Leaf Area Index	Total leaf area per ground area	m ² m ⁻²
LDMC	Leaf Dry Matter Content	Leaf dry mass as percentage of leaf fresh mass	% w w ⁻¹
LMF	Leaf Mass Fraction	Leaf mass per total vegetative biomass	g g ⁻¹
[N] leaf	Leaf nitrogen concentration	Nitrogen concentration in leaf mass	mg g ⁻¹
[NO ₃] leaf	Leaf nitrate concentration	Nitrate concentration in leaf mass	mg g ⁻¹
PSa	Rate of photosynthesis	Light-saturated photosynthetic capacity per unit leaf area or in situ photosynthetic activity per unit leaf area	μmol m ⁻² s ⁻¹
RE	Reproductive Effort	Seed mass per plant biomass; equal to harvest index	g g ⁻¹
R:FR	Red to Far-Red light ratio	Ratio between light intensities in the red and far-red wavelength	mol mol ⁻¹
RDM _I	Root Dry Mass of an Individual	Total biomass of the roots per individual plant	g plant ⁻¹
RGR	Relative Growth Rate	Increase in plant biomass per unit current biomass per time	mg g ⁻¹ day ⁻¹
RLD	Root Length Density	Length of roots in a given soil volume	cm cm ⁻³
RMF	Root Mass Fraction	Root mass per total vegetative biomass	g g ⁻¹
SLA	Specific Leaf Area	Leaf area divided by leaf mass	m ² kg ⁻¹
slenderness	Slenderness Index	Height of plants over the diameter of the stems	m m ⁻¹
SMF	Stem Mass Fraction	Stem mass per total vegetative biomass	g g ⁻¹
SRL	Specific Root Length	Length of root system divided by its mass	m g ⁻¹
SSL	Specific Stem Length	Stem length divided by stem mass	m g ⁻¹
TDM _A	Total Dry Mass per Area	Total or shoot biomass per ground area	g m ⁻²
TDM _I	Total Dry Mass of an Individual	Total or shoot biomass per individual plant	g plant ⁻¹
TNC	Total Non-structural Carbohydrates	Sugar and starch concentrations in the leaf mass	g g ⁻¹
ULR	Unit Leaf Rate	Increase in plant biomass per leaf area per time	g m ⁻² day ⁻¹

alter the reproductive characteristics. Finally, we consider the extent to which these responses are triggered by density-dependent changes in the availability of light and nutrients.

2 | METHODOLOGY

In our analysis, we compiled data from 334 experiments from 229 publications where the density in monostands was manipulated through sowing or planting. References of data sources are included in the reference list, and citations by data are included in Data S1. These experiments included agronomic trials with unequal spacing patterns (e.g., varying row and inter-row distances) as well as experiments in pots. We considered only experiments where initial densities differed by at least two-fold. These data pertain to 163 species (listed in Table S1) and include mono- and dicotyledonous herbs as well as trees, and wild species as well as domesticated crops. Our analysis is across all these groups, but for comparison of the groups, see Tables S4–S6. For each experiment, we noted the starting and final plant density if data were provided, as well as three variables relevant at the stand level: Total Dry Mass per unit ground Area (TDM_A ; shoot or total plant biomass, with reproductive mass if given, otherwise without; for abbreviations and units see Table 1), Generative (reproductive) Dry Mass per unit ground Area (GDM_A ; seeds or fruits) and Leaf Area Index (LAI). If data of multiple harvests at different times were presented, we recorded TDM_A at the harvest that was closest to peak standing crop (usually the last harvest), GDM_A as the final reproductive yield and LAI at its peak value. If the moment of peak standing crop or peak LAI differed with density, we recorded the data at the time most densities peaked.

In addition to these three stand characteristics, we analyzed 33 phenotypic traits for individual plants related to their eco-physiological functioning (Poorter et al., 2019). For this analysis, we considered traits for which at least five experiments reported data. Several closely related variables were combined: Total and shoot Dry Mass of individual plants, with and without reproductive structures (TDM_i , Table 1); reproductive effort and harvest index based on either shoot or whole-plant data; number of tillers for grasses and side-shoots for dicots; and rates of photosynthesis determined at growth and saturating light levels. Experiments may have varied in their methodologies to measure a given trait, and variation in methodology may thus have contributed to the overall variation among experiments, on top of variations coming from species, experimental set-up, etc. Ideally, physiological, morphological and chemical data would be values measured across all leaves, stems and roots, but we also included values measured for specific canopy strata or single measurements on selected leaves, parts of stems or roots, because of the relative scarcity of such data in published experiments of density.

Following Poorter et al. (2019), we quantified the changes by calculating for every trait what the percentage change (PC) was in that trait given a doubling in density. For every experiment, we computed

$$PC = 100 * (2^{\text{slope}} - 1), \quad (1)$$

where ‘slope’ is the slope of the observed trait values against density on a log–log plot. For two densities, ‘slope’ is given by

$$\text{slope} = \frac{\log(Y_2) - \log(Y_1)}{\log(D_2) - \log(D_1)} \quad (2)$$

where Y_1 and Y_2 are the recorded trait values at plant densities D_1 and D_2 , respectively

For experiments with more than two densities, we used linear regression to estimate the mean slope across all densities reported. Actual densities may decline with time, as not all plants survive (Section 4). Most reports, however, did not include final densities and, therefore, we decided to analyse our data against initial plant densities only. These initial plant densities are often the counted number of plants, but in some cases these are the number of seeds sown. The distribution of the calculated response values over the various experiments and species were then characterized by boxplots, showing median, as well as 10, 25, 75, 90% quantiles, and statistically tested the mean for deviation from zero using one-sample *t*-tests.

3 | RESPONSES OF THE WHOLE STAND

3.1 | Density–response curves for total biomass per area (TDM_A)

In a monostand, the total biomass per unit ground area is strongly determined by the plant density. A nice example is that of Li et al. (2015) who grew *Zea mays* at 12 densities, ranging from 1.5 to 18 plants per square metre. Total Dry Mass per unit ground Area (TDM_A , $g\ m^{-2}$) at the end of the experiment varied 2.8-fold among densities, and the response curve continued to rise, up to a density of 15 plants per square metre, after which it plateaued (Figure 1a). Generative Dry Mass per ground Area (GDM_A ; in most cases seed production) reached its peak at a lower density of 12 plants per square metre (Figure 1a). The rate of increase in shoot biomass is less than in density, therefore individual plant mass (TDM_i) decreased monotonically over the full range of densities (Figure 1b). It is noteworthy that the highest seed mass per area (yield) corresponded to a relatively low number of seeds produced per seed sown and that the reduction in seed production was even stronger than the reduction in individual plant biomass (Figure 1b). These curves demonstrate the gains in biomass production made possible by increasing plant density, but also by the competitive cost for the individual plant in terms of reduced growth and reproduction.

The lack of an age structure (variation in age) causes the monostand to develop over time as the individuals do (Figure 1c). When seeds start to germinate, there is no interaction among the seedlings. However, as soon as seedlings grow into each other's above- and

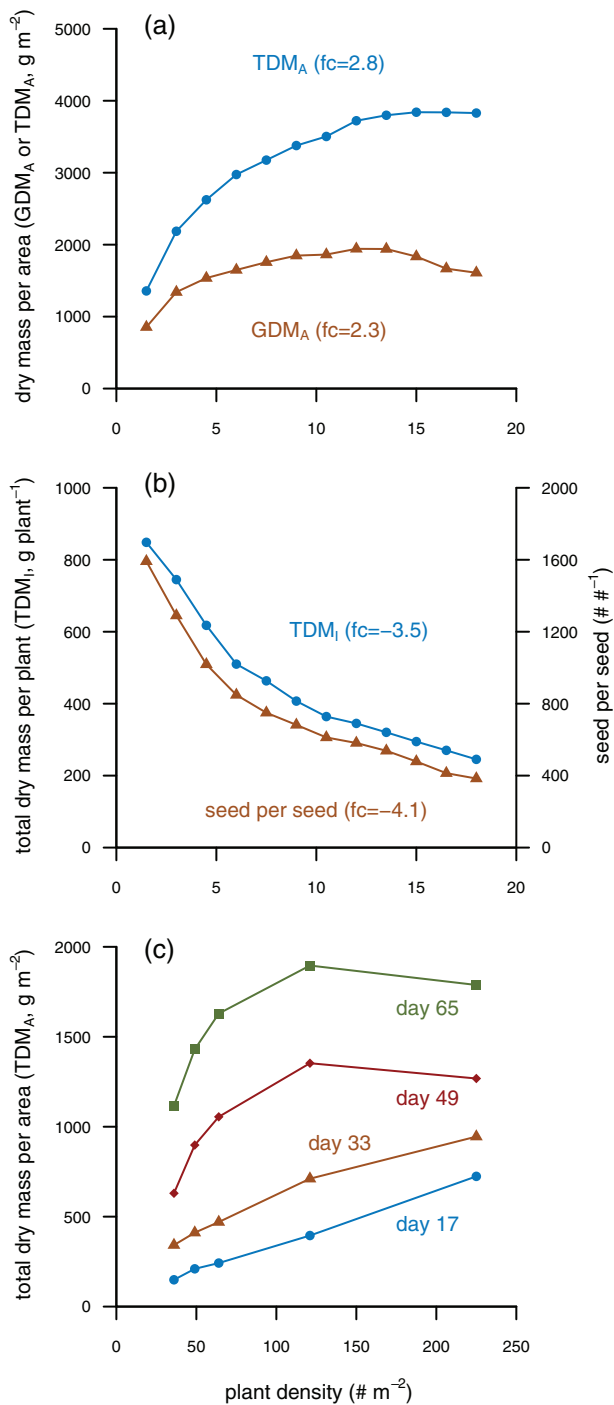


FIGURE 1 Exemplary response curves to plant population density for (a) *Zea mays* shoot and seed mass per unit land area (TDM_A and GDM_A respectively; data from Li et al., 2015). (b) Shoot mass per plant (TDM_I) and number of seeds produced per seed planted from the same experiment. (c) Time-series data of shoot mass per area (TDM_A) of *Allium cepa* at different plant densities (data from Li, Weiner, Wang, Wang, & Zhou, 2016). Numbers in panels (a) and (b) indicate the fold-change (fc) difference between the highest and lowest mean values across densities [Colour figure can be viewed at wileyonlinelibrary.com]

below-ground space, competition starts, with an intensity that increases with size and the proximity to neighbours. At higher densities (given constant resource availability), competition begins sooner and the resources

per individual are lower. This means that the nature of the competition and facilitation is changing continuously, with more pronounced concave density response curves as stands develop over time (Figure 1c).

Our meta-analysis encompasses 334 density experiments with starting densities ranging from less than 0.01 m⁻² for trees (Benomar, DesRochers, & Larocque, 2012) up to 49,000 individuals per square metre for small herbs (Li, Weiner, Zhou, Huang, & Sheng, 2013). In Figure 2a, we have plotted the total biomass per area against plant density (note the log scales). The general pattern is that of increasing TDM_A with increasing density, with evidence of a declining increase in TDM_A with density in many cases. For each experiment, we then calculated the percentage change in TDM_A for each doubling in density (Section 2, Equation ((1)). At very low densities, where plant-plant interactions remain absent, we may expect that a doubling in density leads to a 100% increase in TDM_A. In most experiments, however, plants in the lowest densities were already experiencing competition, and so the values were lower than 100%. Over all densities and experiments, the median increase in TDM_A with a doubling of density was 21%, with 85% of responses greater than 5% (Figure 2d, for means see Table S2). The law of ‘constant final yield’ says that this percentage should decline to zero at higher densities. Although various authors have provided nice examples in which TDM_A saturates at the highest densities (Figure 1a,c, and Harper, 1977), we note that our literature compilation actually shows relatively few such responses. To better quantify the responses at the outer ends of the curves, we computed—for all experiments with at least three density levels—the percentage change in biomass for a doubling in density based on either the lowest or the highest two densities. As expected, the median slope was higher between the two lowest density levels than between the two highest ones (Figure 2d, $p = .002$). Furthermore, the slope was positive at the highest densities ($p = .005$), with only 23% of the experiments having a near-zero response ($-5% < \text{TDM}_A < 5%$). We conclude that the densities where a ‘constant final yield’ may be observed are not reached in many of the density experiments published and that ‘constant final yield’ may not be as broadly applicable as previously suggested (see Weiner & Freckleton, 2010).

What might explain the observation that many experiments do not show a broad range of constant total mass? A simple possibility would be that many researchers focused only on a limited range of densities. Many experiments have an agricultural background, and extreme high densities are not agronomically relevant as they do not maximize seed production (Figure 1b). However, densities were high enough such that many experiments reached TDM_A values greater than 1,000 g m⁻², which suggests that densities were not particularly low either. A somewhat related issue is that the seminal experiments of Donald (1951); as presented in Harper, 1977) and Kays and Harper (1974); as presented in Weiner & Freckleton, 2010) apply designs where plant density is increased exponentially, yet the graphical results are presented on a linear axis. This may exacerbate the perception that there is a ‘broad constant final yield’. A second explanation could be that the seminal examples mentioned above are all done with clonal species. They may be ‘cheaters’ among the species considered, as over time they can bring in new vegetative

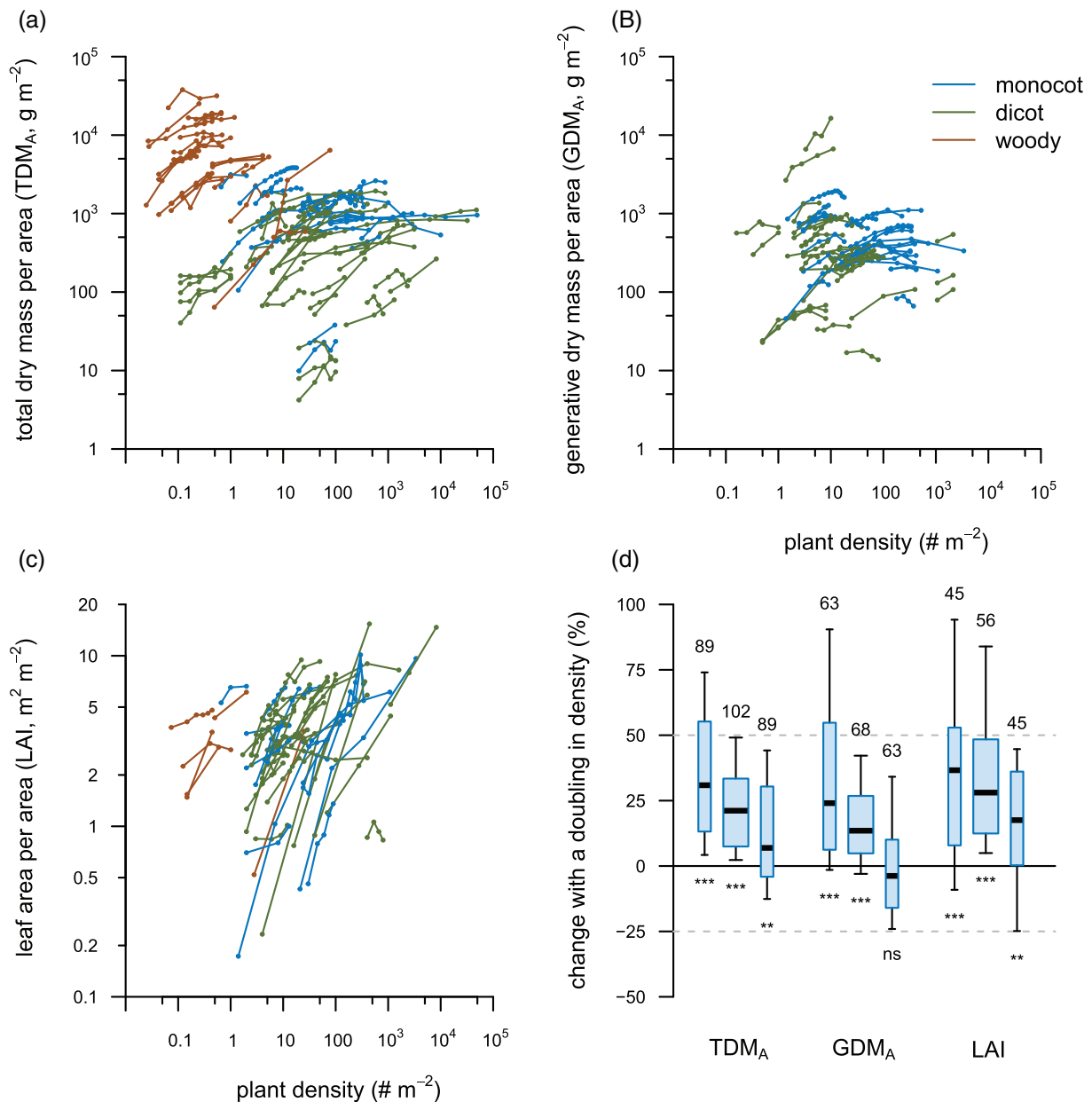


FIGURE 2 Density-response curves (a)–(c) and statistics on the number of experiments and their individual responses in (d). (a) Shoot or total plant biomass per unit ground area (TDM_A); (b) generative (seed or reproductive) biomass per unit ground area (GDM_A); (c) Leaf Area Index (LAI). (d) Box plots of the distribution of the percentage change per doubling in density for the three variables. In (a)–(c), points connected by a line represent one species or genotype within a given experiment. In (d), wide boxplots indicate % change per doubling of density across the whole range of densities. The narrow boxes at the left and right from the wide boxes indicate the slope between the two lowest densities and the slope between the two highest densities, respectively. *, **, ***, $p < .05$, .01, .001 in a t -test for deviation from zero

offspring into positions that were previously not occupied. For single-stemmed species that have to rely on stem tillers or branches, it will be more difficult to occupy all spaces where no neighbours are present (anymore) and probably at higher costs. Thirdly, time may be an issue. Even for the clonal species of Donald (1951), 130 days into the experiment ‘constant final yield’ was not reached. Most experiments with crops are of shorter duration, which could be too little time to occupy all available space. Apart from problems with time and space, the absence of ‘constant final yield’ could mean that sparse

monostands are not as good as dense stands at capturing all resources. Especially early in the season, increased density could lead to faster canopy closure and, consequently, greater light capture and TDM_A (e.g., Westgate, Forcella, Reicosky, & Somsen, 1997). A final possibility is that in high density stands plants may improve resource utilization efficiency, possibly through facilitative mechanisms (Sections 6 and 7).

Density levels can also be supra-optimal, although this is not often reported. An example is shown in Figure 1c at the last time

series, the example of Kays and Harper (1974) mentioned above, and also in data of, for example, Hiroi and Monsi (1966) and Morano et al. (2017). This decline in TDM_A may be due to early growth and capturing of nutrients, followed by excessive self-thinning or leaf senescence, and was modelled to occur more prominently when all individuals are of equal size (Fibich, Lepš, & Weiner, 2014).

3.2 | The generative biomass per area (GDM_A)

In accordance with the postulations of Westoby (1984) and Weiner and Freckleton (2010), the response of Generative Dry Mass per Area (GDM_A) does not completely follow TDM_A (Figure 2b). The overall response is lower than for TDM_A (median = 13% vs. 21%), and the average slope at the two highest density levels is not different from zero ($p = .6$). In fact, in 60% of the experiments, the highest density is supra-optimal, with a slope smaller than zero. The underlying reasons are discussed in Section 6.

3.3 | The leaf area index (LAI)

The leaf area index (LAI, $m^2 m^{-2}$) describes the total leaf area per unit ground area and generally varies far less among different types of vegetation (crops, grasslands and forests) than TDM_A . We anticipated that plants in stands with low starting densities would quickly fill up all available space with leaf area by growing faster than plants at high densities, and that—more than for TDM_A —LAI would become independent of starting densities (i.e., saturate) soon after the vegetation would close.

On the contrary, many studies report large increases in LAI with plant density (Figure 2c). The median response of LAI to a doubling in density is a 28% increase, whereas that for TDM_A is 21% (Figure 2d; for means and test of their difference from zero, see Table S2). We may assume that almost all available light is captured by a monostand when the LAI is greater than $4 m^2 m^{-2}$. We note that at high densities the LAI may go significantly beyond and that, when we include only data with $LAI > 4$, we still get a 17% increase of the median with a doubling in density. We may wonder why this is, given that further increases in LAI do not increase light capture very much. One explanation comes from a game-theoretic model, which predicts that plants with more leaf area have a competitive advantage, leading to vegetations with a high LAI (Schieving & Poorter, 1999).

4 | HOW PLANT DENSITY SHAPES THE ABIOTIC ENVIRONMENT

We have described how competition intensifies during the development of the monostand. Space itself is not the commodity of interest, rather the resources that can be captured in that space (Wilson, Steel, & Steel, 2007). In the course of stand development, plants are not only subjected to what we may see as external abiotic

environmental factors but they also actively or passively alter these factors themselves. How then are the above- and below-ground environmental factors changing with the density of a canopy?

4.1 | The above-ground environment

In this section, we describe the vertical profiles that exist within canopies, and which are critical for the physiological functioning of the plant. We do so by some examples, considering canopy height relative to the top of the canopy and environmental variables relative to the highest value anywhere in the canopy. The light intensity (photosynthetic photon flux density, PPFD) strongly decreases with the relative depth in the canopy, the more so in denser stands (Figure 3a). The profiles measured here were determined on an overcast and windstill day. With direct sunlight and vegetation moving in the wind, sun flecks may penetrate deeper into the canopy and make the profile more variable (Burgess, Gibbs, & Murchie, 2019). Plant density determines the total light capture of the stand mainly through its effect on LAI. Leaf angle influences the light penetration depth and, especially when LAI is low, co-determines the total light capture (Flénet, Kiniry, Board, Westgate, & Reicosky, 1996; Monsi & Saeki, 1953).

Chlorophyll, responsible for most light absorption, characteristically has high absorption in the blue and red part of the light spectrum but low absorption in the green part. Nonetheless, due to scattering and re-absorption, individual leaves will absorb ~80% of green light, and dense canopies could absorb even more than 95% of green light (Paradiso et al., 2011). Leaves are, however, relatively transparent and reflective to far-red light (700–800 nm, Ustin & Jacquemoud, 2020). Hence, the ratio between red and far-red light (R:FR) strongly decreases through the canopy, and more so at high plant densities (Figure 3b). Plants are very sensitive to these differences in R:FR ratios through the canopy and are even able to detect slight differences in R:FR ratios in the light reflected by neighbours some distance away (Ballaré & Pierik, 2017).

For the other micro-climatic factors we were not able to find data for monostands at different densities, so we rather compared data from a relatively open stand of *Zea mays* (Desjardins et al., 1978), a more closed stand of *Hordeum vulgare* (Ney & Graf, 2018) and a profile through a tropical forest (Kumagai et al., 2001), all measured around noon. The profile of aerial CO_2 concentration is hardly affected by the vegetation (Figure 3c). At midday and in the afternoon, concentrations at the top of the canopy are, due to CO_2 uptake, somewhat lower than tropospheric, and tend to rise towards ground level as a result of soil respiration. At night until early morning, CO_2 concentrations can accumulate to higher than tropospheric levels. However, this mostly small variation in space and time will have little effect on plant function.

Wind speed above the canopy varies both diurnally and with the weather, but the relative wind speed profile is generally similar for the three stands, with strong reductions lower in the canopy (Figure 3d). Temperature budgets of canopies are complicated, but in open, sparse canopies, especially those of crops with large inter-row distances,

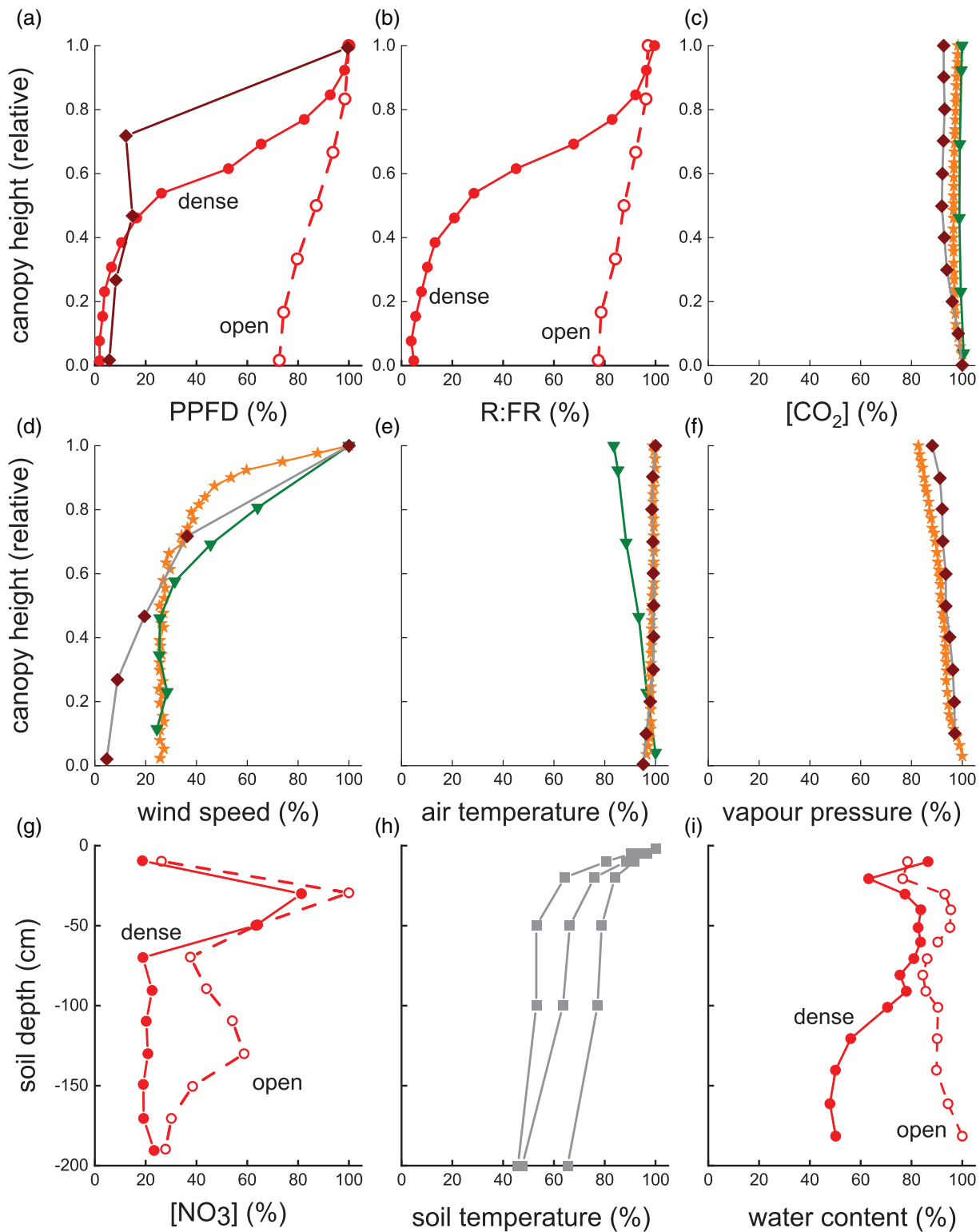


FIGURE 3 Change in environmental variables within a canopy (a)–(f) and in the soil (g)–(i). All values are relative to the highest value as experienced by the leaves or roots at any position in the canopy or soil. In all cases, canopy height was scaled relative to the top. (a) Photosynthetic photon flux density (PPFD) for an open and dense stand of *Lysimachia vulgaris* and a tropical forest; (b) red-to-far-red ratio for the open and dense stands of (a). (c) Aerial CO_2 concentration for a monostand of *Zea mays* (green triangles), *Hordeum vulgare* (orange stars) and a tropical forest (brown diamonds). (d) Wind speed for the same stands as (c). (e) Aerial temperature for the same stands as (c). (f) Vapour pressure for a monostand of *H. vulgare* and a tropical forest. Change in environmental conditions with depth in the soil. (g) Nitrate profile in an open and dense stand of *Triticum aestivum*. (h) Some temperature profiles early, middle and late in the growing season. (i) Water profile under an open and dense stand of *Salix psammophila*. Density data for (a) and (b) are based on Pons (2016), for (g) on Fu et al. (2012) and for (i) on Gao et al. (2009). *Zea mays* data are from Desjardins, Allen, and Lemon (1978), tropical forest data from Kumagai et al. (2001). *H. vulgare* data from Ney and Graf (2018). Soil temperature data are from the website of the PIK (<https://www.pik-potsdam.de/services/climate-weather-potsdam/climate-diagrams/ground-temperature>) [Colour figure can be viewed at wileyonlinelibrary.com]

sunlight heats the soil surface and convective transfer warms the air lower down in the canopy. In dense canopies, however, where most of the radiation is intercepted by the upper leaves, convective heating of the air is likely to happen higher in the canopy, and the resulting profile will be slightly different from the open canopy (Figure 3e). Overall, however, no strong gradients in air temperature will develop in the canopy. It should be noted that the profile of leaf temperatures may deviate from the air temperature profile, as leaf temperature is raised by sunlight but reduced by transpiration (Lambers & Oliveira, 2019).

4.2 | The below-ground environment

In terms of relative distribution, the below-ground environment is less predictable and general, but we plotted example distributions in Figure 3g–i. Soil resources, notably nutrients and water, are often replenished from the top, for example, through rain, fertilization or litter deposition. This initially increases their availability in the topsoil. After a rain, water moves down, often relatively quickly. Nutrients move through advection (with the water) and diffusion. Nutrients distinguish themselves in their rate of movement, mostly because of sorption. Slow-moving nutrients, like phosphorus, reside much longer in the topsoil, whereas fast-moving ones, like nitrate, may move down more rapidly. Roots can deplete both water and nutrients to very low levels, thereby locally preempting the resources for competing roots. This prevents roots of competing plants from accessing those resources and possibly discourages growth of competing roots into these zones. Figure 3g,i demonstrates how a soil profile may be more depleted of nitrogen and water under high plant density compared to low plant density, even to a depth of 2 m or more. Interestingly, the relative depletion of water and nitrogen is greater deeper down, in the 1–2 m zone, than in the 0–1 m zone. The soil temperature deeper down is typically more stable and less influenced by density or other surface processes, but in the topsoil we expect it to vary with plant density as it depends on how much light penetrates the canopy (Figure 3a,e). We were not able to locate measurements of soil temperature under dense and sparse stands. But Song et al. (2013) simulated the effect by placing dried reed stalks at various densities. This resulted in cooler soil temperatures and less of a difference between day and night temperatures, with more pronounced effects at 5 than at 20 cm depth. We expect stronger cooling from a transpiring crop. For reference, Figure 3h shows three exemplary soil temperature profiles.

Rhizosphere research reports the various ways the soil environment in the vicinity of roots is different from that further away. Roots may modify their environment, such that the chemistry and biology become more favourable to them. *Oryza sativa*, for example, exudes organic acids, especially citrate, to increase zinc uptake. The necessary changes in soil environment are more easily achieved at high plant density, and rice growth on a low zinc soil is one of few studies where crowding plants lead to increased individual plant mass (Hoffland, Wei, & Wissuwa, 2006). Similarly, but at a much longer time scale and

with many more interacting processes contributing, a remarkable increase in soil fertility was achieved in dense compared to sparse *Coffea* stands (Pavan et al., 1999). Concurrently, plants protect the soil against erosion, and this is better achieved at higher plant density (Halim & Normaniza, 2015). We may thus conclude that dense stands may improve soil fertility, especially at longer time scales (i.e., those relevant to acquisition by future monostands), but more typically deplete soil resources faster at shorter time scales (i.e., those relevant to resource acquisition by contemporary competitors), and these processes vary quantitatively with depth. The balance between enrichment and depletion will also depend on the extent to which plant material (and thus nutrients) are removed in harvest versus remaining to decompose in situ.

5 | THE INDIVIDUAL PLANT INSIDE A MONOSTAND

5.1 | Variability among individuals

Right after germination, the space per individual plant may well be sufficient for ample access to resources, even at relatively high densities. However, as plants grow, their zone of influence expands, and crowding effects develop, with competition for resources becoming more intense. At an early stage of competition, all plants will be able to reach the top of the canopy. As competition increases, smaller plants may be out-grown by larger plants and subjected to a subordinate growth trajectory (Nagashima, Terashima, & Katoh, 1995). This leads to variation in plant size increasing, both with greater density and over time (Weiner & Thomas, 1986). The reported variation is usually measured using either the Gini coefficient or the coefficient of variation, and thus relative to the total plant size discussed below. As competition becomes increasingly fierce in the higher densities, the individuals that have been outcompeted will begin to die (Westoby, 1984; White, 1980). The ‘self-thinning rule’ describes that with increasing stand biomass, fewer individuals survive, and in very crowded stands 80–95% of the individuals may have died within months after starting the experiment (DeBell & Harrington, 2002; Li et al., 2013; Puckridge & Donald, 1967). This loss of the smallest individuals leads to a more homogeneous size distribution over time as demonstrated by the Gini coefficient for forest trees, which drastically declined over a 200-year period (Weiner & Thomas, 1986).

While self-thinning is a general phenomenon observed across many species (Weiner & Freckleton, 2010), it may be of less relevance in an agricultural setting, as density in crop canopies aims at maximizing GDM_A (cf. Figure 1a), where self-thinning is still marginal (Deng et al., 2012). Nevertheless, even in a crop stand, variation in size will develop among individuals. This may be due to many reasons including variation in seed mass or germination time, or variation in local soil conditions or distances among plants. Contrary to what we may expect from asymmetric competition, this variation does not always increase over time (Rossini, Maddonni, & Otegui, 2011). Asymmetric competition would suggest that below-average sized plants are

neighbouring by an above-average sized plant. The opposite, however, has been observed: Large individuals have large neighbours and, consequently, the size of neighbouring plants correlates positively (e.g., Kira et al., 1953). In these studies, large individuals did not out-grow smaller ones, but rather large individuals arise in the same neighbourhood, reflecting locally favourable growth conditions. In particular, if plants are unevenly spaced, for example, due to poor germination or self-thinning, plants on all sides of a void may benefit (Wyszomirski & Weiner, 2009).

We conclude that the data is not always consistent with asymmetric competition and that other processes are working concurrently. First, a larger fraction of plants may become subordinate in the canopy, but are still able to survive (Nagashima et al., 1995). Second, a larger size may have its disadvantages. In artificially created stands, where some *Chenopodium* plants were purposely positioned higher in the canopy than others, those that were placed higher actually did not take advantage of that situation, and all plants converged to the same height (Nagashima & Hikosaka, 2011). Shibuya, Takahashi, Endo, and Kitaya (2013) confirmed this convergence in height for *Cucumis* plants but only in those that could physiologically sense the decrease in R:FR ratio induced by the shading of neighbouring plants (Figure 3b). This could mean that growing out of the canopy can also be risky for plants, supposedly because it exposes them more to wind or predation, and that this risk outweighs the benefit of additional light capture. Removing the risk of wind by anchoring plants, Nagashima and Hikosaka (2012) observed that anchored plants grew higher than the surrounding un-anchored ones.

5.2 | The declining biomass of individual plants

Knowing that the population density may decrease over time, we now discuss how density impacts mean plant biomass. We have seen that TDM_A generally increases with density (Figure 2a). These increases in biomass per area are, however, small compared to the increases in plant numbers. Hence, the biomass per plant generally decreases, even if self-thinning is taken into account (Figures 1b and 4a; White, 1980).

In the log-log plot of Figure 4a, most lines are approaching linearity. The percentage change (Section 2) is thus a good estimator over the full width of an experiment. Therefore, we did not further analyse the slopes at the lowest and highest densities as we did in Figure 2d. Across all experiments, a doubling in density decreases plant mass by 35% (Figure 4b). To make this insightful, an average decrease of 35% would imply that over a 10-fold range in density, the average plant becomes 5-fold smaller. Ignoring self-thinning, the law of the 'constant final yield' predicts that a doubling in density would halve the plant size, but individual plant biomass is reduced significantly less than 50% ($p = .001$).

Casually multiplying TDM_I with the starting plant density, we get a median TDM_A response of 29%, significantly ($p = .002$) higher than the 21% found for TDM_A . The difference likely indicates self-thinning, but could also reflect biases towards sampling the largest and best

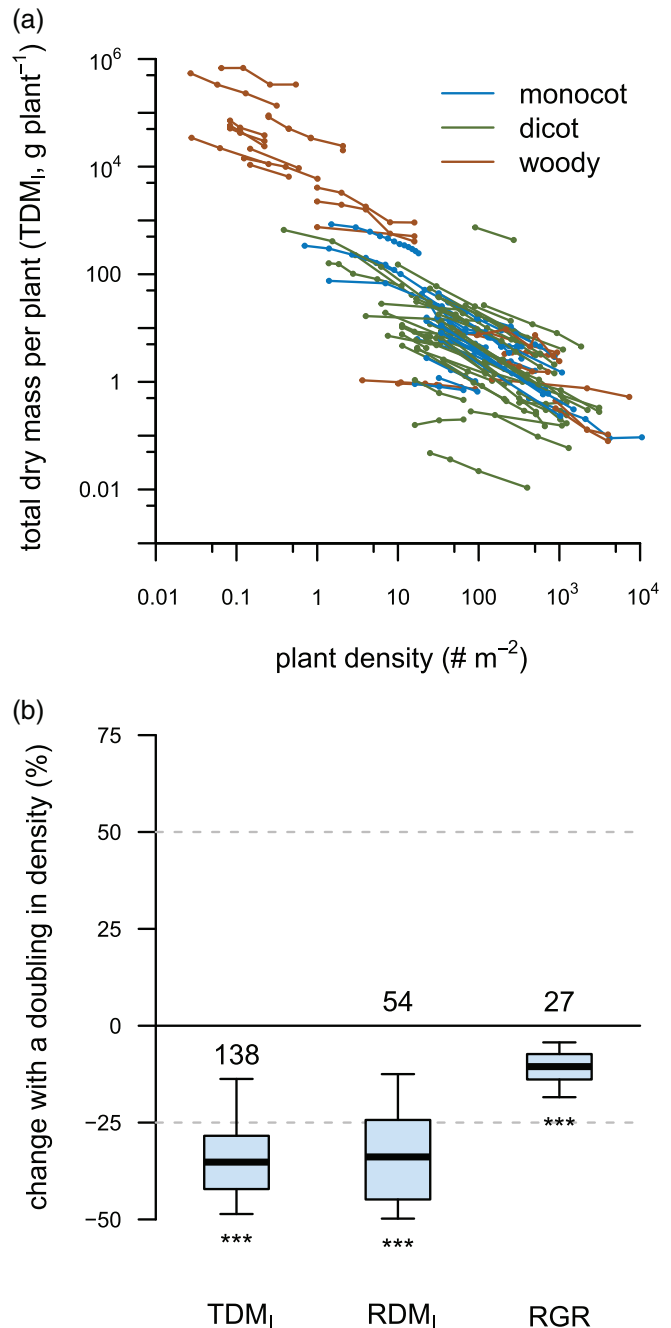


FIGURE 4 Density-response curves (a) and statistics on the number of experiments and their individual responses in (b). (a) Shoot or total plant biomass per living individual (TDM_I). (b) Boxplots indicating the distribution of the percentage change in TDM_I , Root Dry Mass (RDM_I) and Relative Growth Rate (RGR) with a doubling in plant density across all experiments. For abbreviations see Table 1. *, **, ***, $p < .05, .01, .001$ in a t -test for deviation from zero [Colour figure can be viewed at wileyonlinelibrary.com]

looking plants. We conclude that plant biomass decreases strongly with density, and that this is a result of high competition pressure, but also that the decrease is less than the reduction in area and resources per plant. Thus competition increases resource use efficiency, and it thereby becomes pertinent to understand how plants respond morphologically and physiologically under such competitive conditions.

6 | COMPETING FOR LIGHT: PLASTICITY IN SHOOT TRAITS

6.1 | Morphology and allocation

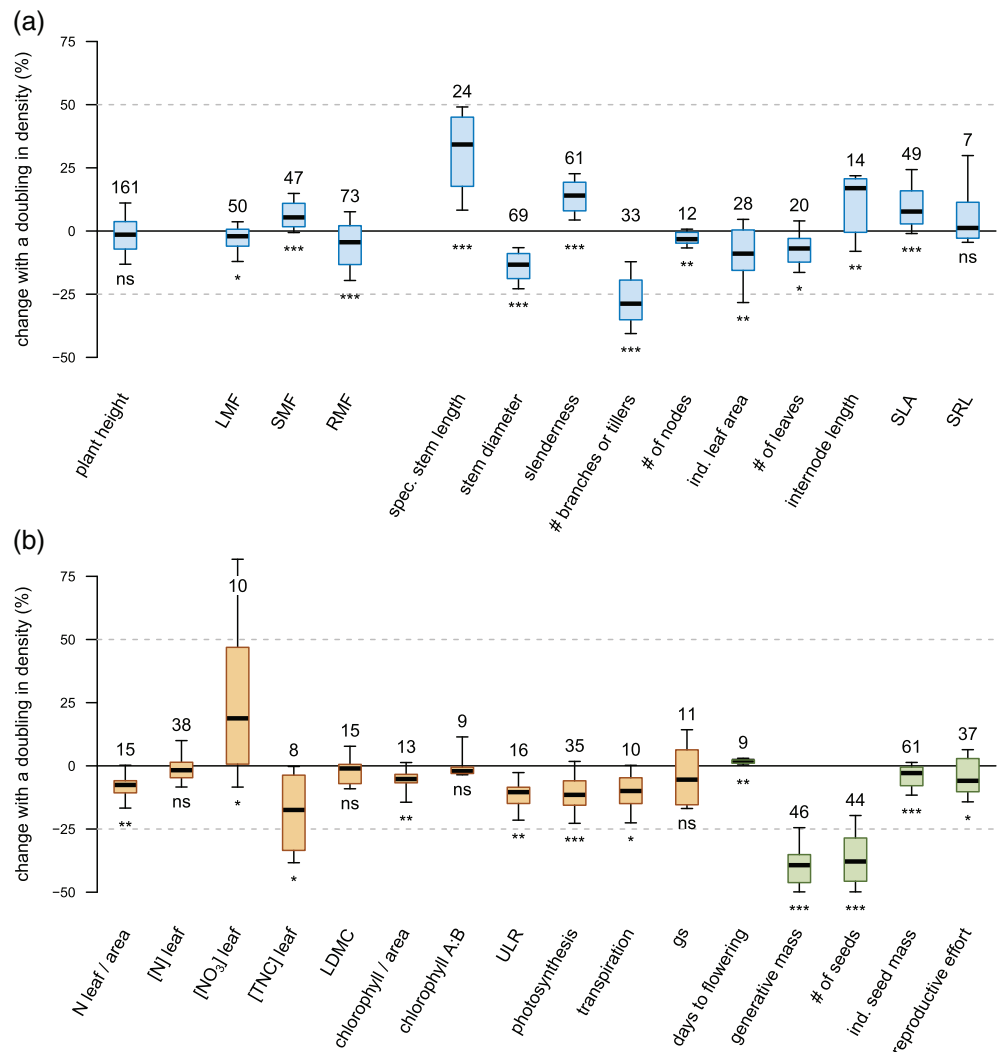
From the last two sections, it transpires that high densities lead to smaller plants, which compete with each other for even lower quantities of light, nutrients and water available per plant. How do plants respond phenotypically to this increased pressure? Analogous to the biomass response, we analysed the responses of a range of phenotypic traits to an increase in plant density (Figure 5). We endeavoured to maintain a whole-plant perspective, and therefore (as much as possible) used average values over all the leaves, stems or roots of a plant.

One of the more fascinating results of this analysis is that plant (or vegetation) height is not affected by density (Figure 5a, mean ~ -1%, $p = .24$). This is remarkable, as similar height among stands of different densities is achieved notwithstanding large differences in the average whole plant biomass (Figure 4). Two factors play a role here. First, plants at high density will increase the allocation to stems.

That is, the fraction of biomass invested in stems is increased, at the expense mainly of roots and somewhat of leaves (Figure 5a). Our analytical approach does not enable a proper allometric analysis to check whether the observed differences are indeed an active acclimation to high densities, rather than an indirect effect of plant size per se (Enquist & Niklas, 2002). Smaller plant size, however, generally goes with a low stem mass fraction (Poorter et al., 2015). Thus, with high-density plants being so much smaller, the observed increases in stem mass fraction would be even more pronounced if the allometric size effect was taken into account.

The second and quantitatively more important factor in this height convergence is that plants at high density increase their ‘Specific Stem Length’ (SSL, Table 1). They do so by forming more narrow stems with smaller diameters. This may in part be triggered by lower wind speeds inside dense canopies (Anten, Casado-Garcia, & Nagashima, 2005), by lower availability of sugars or through increased stem elongation triggered by lower R:FR ratios (Hussain et al., 2019). A constant height and a reduced stem diameter result in an increased ‘slenderness index’, which is plant height over stem diameter (Table 1). This is a highly consistent response, shown for all species

FIGURE 5 Meta-analysis of the response of individual plant traits to a doubling in density. (a) Traits related to morphology and allocation. (b) Traits related to physiology, chemistry and reproduction. Box plots show the distribution of means across the different studies, with the line inside the box showing the 50th percentile, the lower and upper part of the boxes the 25th and 75th percentiles, and the whiskers the 10th and the 90th percentiles. *, **, ***, $p < .05, .01, .001$ in a t -test for deviation from zero. The number of experiments on which the distribution is based is shown above the boxes. Further details are given in Tables S2 and S3 [Colour figure can be viewed at wileyonlinelibrary.com]



considered. While being advantageous in terms of accessing the upper canopy, the trade-off is that such plants are more sensitive to lodging or buckling (Shi et al., 2016; Zhang et al., 2014).

One of the strongest effects of high population density is the suppression of tillering in grasses and branches in herbs and trees (Figure 5a). Foresters desire unbranched tree stems and achieve this by planting the trees at high densities. To increase stem diameter, foresters thin the stand at later growth stages. In *Poaceae*, tiller counts may be reduced because of both reduced tiller production and early tiller senescence (e.g., Hecht et al., 2019). High-density plants have a reduced total leaf area because they have both fewer and smaller leaves (Figure 5a). For many species, fewer leaves may come with reduced branching and tillering. However, fewer leaves were also counted in non-branching and tillering maize and may be associated with a reduced number of internodes (Figure 5a; Bos, Vos, & Struik, 2000). The leaf area-to-leaf mass ratio (specific leaf area, SLA, Table 1) is increased somewhat. SLA is a hallmark of shade acclimation (Poorter et al., 2019) and may be expected to be higher in the lower strata of a dense stand. However, the increase in SLA is seen not only below but also at the top for newly formed leaves (Boonman et al., 2007; Hirose, Werger, Pons, & van Rheeën, 1988). This may point to developmental signalling from these older leaves to developing ones (Yano & Terashima, 2001).

6.2 | Chemistry and physiology

The effect of plant density on the chemistry and physiology of plants is extremely understudied, and most of the following results are based on data from only a few experiments. With more biomass per ground area, we might expect lower N concentrations in plant dry mass. Leaf nitrogen content per unit leaf area is indeed reduced (Figure 5b), but this is more a consequence of higher SLA than reduced nutrient supply. Leaf nitrogen expressed on a per mass basis is not significantly affected. This result may be due to a bias in our data towards experiments with ample nutrient supply. Leaf chemistry is also affected through decreased total non-structural carbohydrates (TNC, Table 1) concentrations in the leaves of the dense canopies and increasing nitrate levels (though this result is based on a small number of reports). There is a somewhat lower chlorophyll content per unit leaf area in dense stands, but the chlorophyll *a:b* ratio seems unaffected.

We found the relative growth rate (RGR, Table 1) to be lower in high-density plants, which leads to a smaller individual biomass (TDM_i; Figure 4). The RGR can be computed as a product of leaf mass fraction (LMF), specific leaf area (SLA) and unit leaf rate (ULR). ULR is the rate of increase in biomass per unit of leaf area and thereby closely related to rates of whole-plant photosynthesis (Poorter & Van der Werf, 1998). ULR and photosynthesis both show similar responses to density (Figure 5b). With the small increase in SLA and a minor decrease in LMF (Figure 5a), the main factor why RGR is lower is likely to be the ULR. Indeed, RGR, ULR and photosynthesis decrease at similar magnitudes (Figures 4b and 5b). We suppose that reductions in ULR are mainly driven by reduced photosynthesis per unit area caused by

increased shading at higher densities. Hence, we consider it likely that reduced photosynthesis is the main factor causing lower growth rates, and hence smaller size, in plants grown at high densities.

The decreases in transpiration rates are quantitatively comparable to those of photosynthesis. We expected this in part to be due to stomatal closure in the lower parts of the vegetation, but the limited data we found were variable in this respect. Reduced transpiration may also reflect reduced vapour pressure lower in the vegetation (Figure 3i) as well as a higher boundary layer resistance due to the lower wind speeds (Figure 3d; Pons, 2016).

6.3 | Reproductive characteristics

There is some indication that density slightly increases the days to flowering (2%, Figure 5b), which may well be related to reduced levels of available carbohydrates. As the size of the plants is reduced, along with a decreased number of tillers and side branches, plants will be strongly reduced in the number of flowers and seeds (−38%). Plants do form seeds of slightly smaller size with a doubling in density (3%), and also the reproductive effort (the proportion of plant mass present in seeds or generative organs, also harvest index) is reduced (−6%). However, the main reason why the reproductive output of individual plants is so much lower is because of the strong reduction in plant size (−35%, Figure 4).

6.4 | Scaling down to the organ level

So far we have considered traits at the crop and whole plant scale. For some of the traits presented, we may expect significant variation within the plant, in part because of the vertical variation in environmental conditions presented in Figure 3, but also because of ontogenetic reasons. For example, leaves at different positions in the canopy will experience different environmental conditions, especially for light. In trees, where the light profile is relatively stable through the season, new leaves may already be pre-acclimated to their local conditions (Uemura et al., 2000). In stands of herbaceous plants, however, leaves are often formed as sun-leaves at the top of the canopy. As the canopy grows, there is a transition for these leaves from being fully exposed to being shaded, with a rate of change that will be faster and more pronounced in denser stands. This induces shade acclimation in these leaves followed by senescence when the canopy continues to grow. Here, we will not focus on these temporal changes experienced by individual leaves; for recent reviews the reader is referred to Pons (2016) and Niinemets (2016).

7 | COMPETING FOR NUTRIENTS AND WATER: ROOT TRAITS

7.1 | Root length, architecture and morphology

Few plant density studies have reported root traits, and fewer still report root length. This limits our options for a meta-analysis. The

evidence that we have, so far, is that roots respond little to plant density, except for their size (length and mass) and traits that are known to be strongly size-related (allometry). This is surprising, as roots are generally considered very plastic to environmental change (Hodge, 2004).

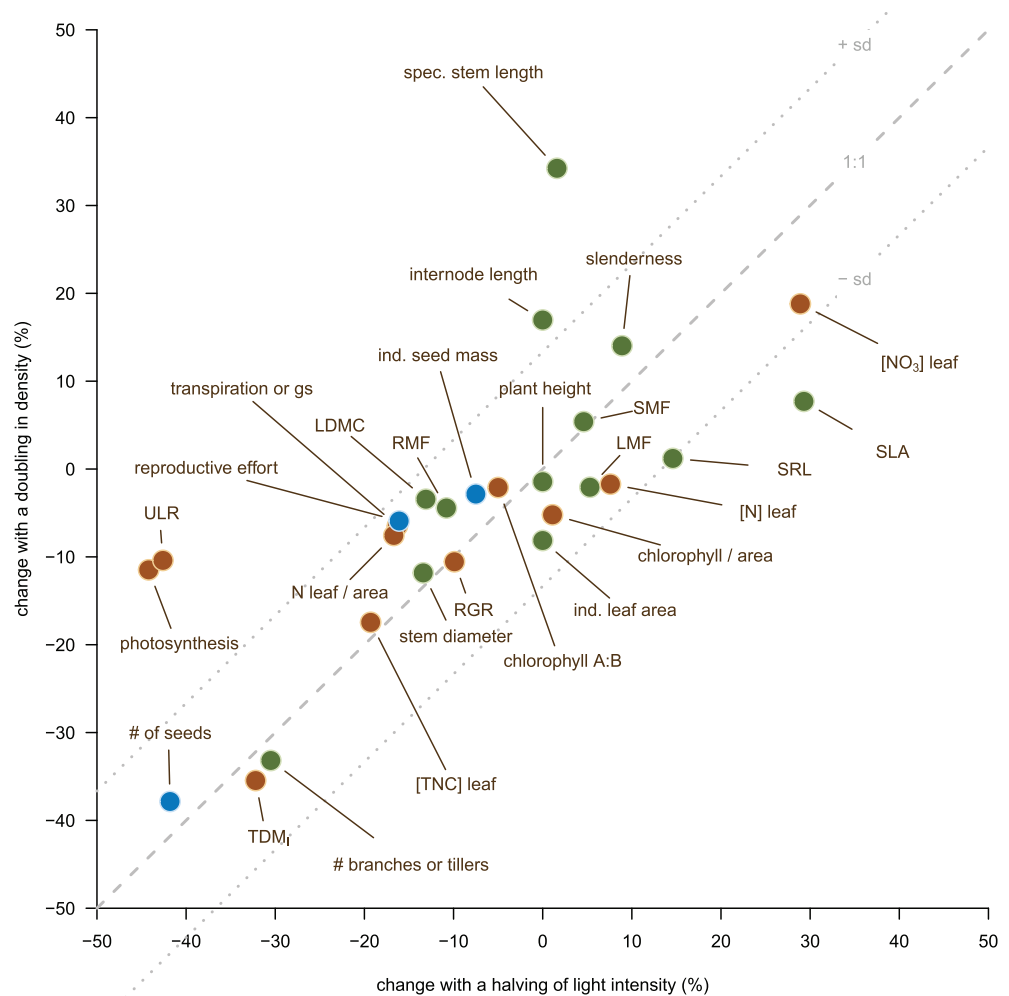
Our meta-analysis of the root mass fraction (RMF, Table 1) response shows a small decline with density (-4% , Figure 5a). RMF was one of the few traits that differed significantly between field (-9%) and lab (-3%) experiments (Tables S4 and S6). It also differed between crops (-11%) and wild species (0%), which may reflect less intense below-ground competition resulting from higher levels of soil fertility in agronomic field experiments. Given the decline in TDM_i noted earlier, this should correspond to an even stronger decline in total root mass. The decline in total root dry mass (RDM_i , -32% , Figure 4b), however, is on average less than -50% , suggesting that the root mass per ground area increases. Specific root length (SRL) seems little affected, therefore we expect root length per area to increase along with root mass per area. Rooting depth is minimally affected by density (Atkinson, 1976; Dai et al., 2014; Grimes, Miller, & Wiley, 1975; Mason, Rowse, Bennie, Kaspar, & Taylor, 1982; Sadras, Hall, Trapani, & Vilella, 1989). This means that stands with different densities explore a more or less similar volume of soil, but with

different intensity, as root length density (RLD) increases with plant density (Hecht, Temperton, Nagel, Rascher, & Postma, 2016; Li et al., 2017).

In many plant species, the number of shoot-born roots (for classification see Freschet et al. (2020)) scales with plant size. This trait is the root equivalent of the above-ground trait 'number of branches or tillers'. The number of shoot-born roots seems to be the root architectural trait that is most sensitive to density (Dai et al., 2014; Hecht et al., 2019; Liu, Song, Liu, Zhu, & Xu, 2012). Other architectural traits, such as root angles and inter-branching distances (for definitions see Freschet et al., 2020), seem little affected (Hecht et al., 2019; Liu et al., 2012; Shao et al., 2019).

Increased Total Dry Mass per Area (TDM_A , Figure 2) and stable nutrient concentrations in that biomass (Figure 5a) with increased density imply increased nutrient uptake, and since the explored soil volume does not change dramatically, faster depletion of the nutrients in that soil volume must occur (Section 4.2). The faster depletion could casually be associated with the greater root length density, analogous to LAI and light interception. We note, however, that this association is not as straightforward and, in non-density experiments, not supported by the data (Dybzinski et al., 2018).

FIGURE 6 Plot of the mean percentage change of 26 phenotypic traits for plants subjected to a doubling in plant density and, for individually grown plants, to halving of the light intensity integrated over the day. The dashed line indicates a 1:1 relationship, and the dotted lines show a plus or minus the standard deviation (SD = 13.5) of the residuals of the model 'density response = light response'. Light response data are from Poorter et al. (2019) and are based on daily light integral levels of 20 and 10 mol m⁻² day⁻¹, respectively. Abbreviations are given in Table 1. The color scheme is as in Figure 5 [Colour figure can be viewed at wileyonlinelibrary.com]



7.2 | Decreased nutrient uptake through mycorrhizae

The percentage of root length colonized by mycorrhizal fungi usually declines with increasing plant density (Ayres, Gange, & Aplin, 2006; Koide & Dickie, 2002; Li, Smith, Dickson, Holloway, & Smith, 2008; Zhang, Zhang, Weiner, Tang, & Chen, 2011). Koide and Dickie (2002) provide several explanations: one is that at high plant density mutual shading reduces the growth rate, and thereby the individual plant's demand for P, such that uptake by the root system is already sufficient. Mycorrhizal colonization becomes then less critical for P uptake and the concomitant higher carbon requirements costly to a partly shaded plant. In accordance with this statement, inoculation had much less effect on plant growth at high densities (Moora & Zobel, 1996). In some cases, high-density inoculated plants stayed smaller than those without mycorrhizae (Schroeder-Moreno & Janos, 2008). Reduced mycorrhizal colonization and plant-benefit from it in dense monostands are in agreement with shading experiments that report similar responses to low light (Fellbaum et al., 2014; Zheng, Ji, Zhang, Zhang, & Bever, 2015).

8 | ARE PLANTS AT HIGH DENSITIES RESTRICTED MORE BY LIGHT OR BY NUTRIENTS?

We described how increasing stand density can increase biomass per unit ground area while reducing the availability of light and nutrients per individual as well as individual plant mass. We would improve our understanding of this system if we could determine whether light or nutrients are most limiting plant growth. One approach is to compare the trait responses discussed in Sections 6 and 7 with those of individual plants grown at different light or different nutrient levels.

Recently, generalized dose–response curves for light intensity were established for a wide range of plant traits (Poorter et al., 2019). From these dose–response curves, we calculated for 26 traits how much they would be affected if the daily light integral would be halved, reasoning that for an individual plant this would be more or less similar to a doubling in density. Unfortunately, we do not have similar dose–response curves for halving nutrient availability. Nevertheless, the results are very instructive (Figure 6). For many of the traits, responses to halving light intensity are quantitatively similar to doubling density. This is especially clear for leaf nitrate concentration, which responds strongly positively in both cases, and the number of branches or tillers per plant, number of seeds or fruits per plant, TDM_i , as well as the starch and sugar concentration in the leaves (TNC), which all responded strongly negatively. Specific stem length is much more sensitive to doubling density than to halving light levels, which may be explained by the fact that stem elongation, although sensitive to light at very low light levels, is known to be effectively triggered by reduced R:FR within crowded stands (Ballaré & Pierik, 2017). SLA and ULR, on the other hand, are more sensitive to light than density. This may reflect the difference between an overall reduction in light for all leaves in different light treatments and the case where the upper leaves still experience high light when density is changed.

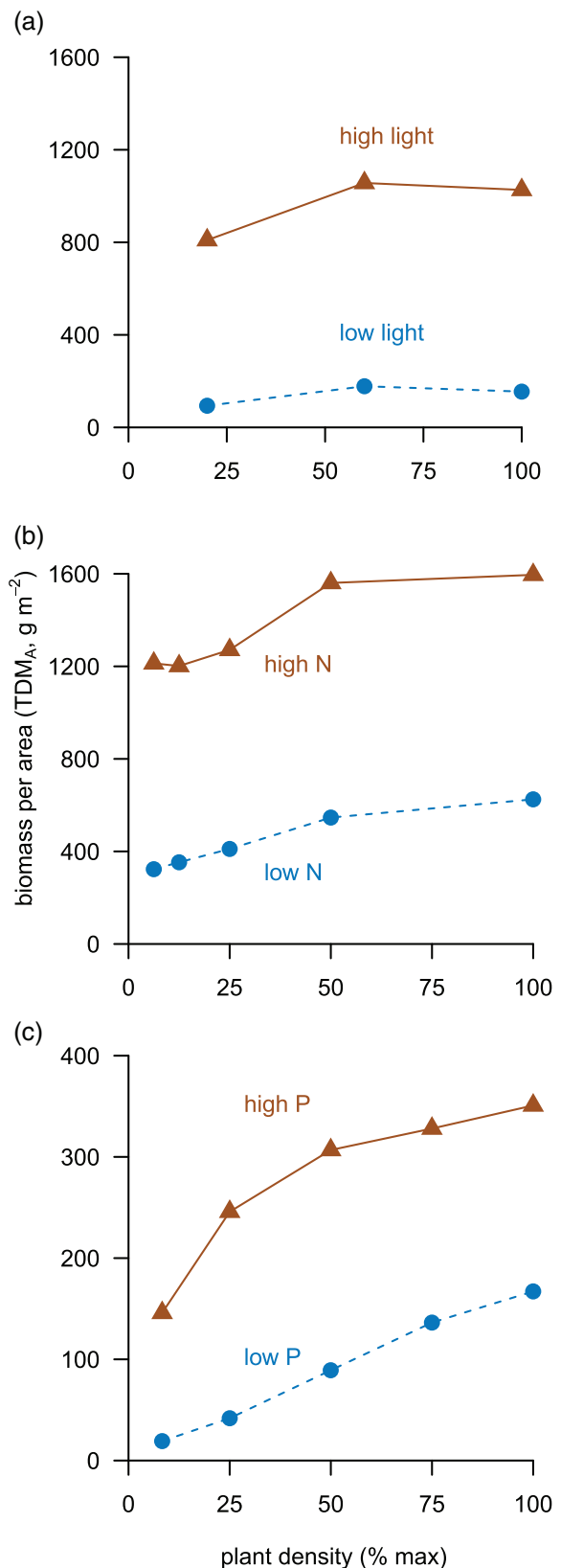


FIGURE 7 Biomass response curves to density under low and high resource availability: (a) Low and high light levels (data for *Lamium maculatum* from Barišić et al., 2006); (b) low and high nitrogen (data for *Plantago lanceolata* from Berendse & Möller, 2009); (c) low and high phosphorus (data for *Trifolium subterraneum* from McLachlan, Haling, Simpson, Flavel, & Guppy, 2020) [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.com)]

TABLE 2 Median response (% change with a doubling in density) for plants with either above- and below-ground competition ('full') or just above-ground ('shoot'). Shoots were allowed to compete but roots were in separate compartments. ., *, **, *** $p < .1, .05, .01, .001$ in a two-sided t -test for differences between means. For means see Table S5. n -values are number of experiments in each group

Trait	Full, median	Shoot, median	t -test	Full, n	Shoot, n
Biomass per individual plant (TDM _I , g plant ⁻¹)	-36.1	-17.0	**	125	13
Photosynthesis/leaf area ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	-10.5	-11.8	NS	27	7
N leaf/area (g m ⁻²)	-7.0	-7.9	NS	6	8
Root mass fraction (RMF, g g ⁻¹)	-3.2	-8.1	NS	63	10
Leaf nitrogen concentration ([N], mg g ⁻¹)	-2.8	8.3	**	31	7
Plant height (cm)	-2.6	9.7	**	142	14
Leaf mass fraction (LMF, g g ⁻¹)	-2.0	-3.1	NS	43	7
Stem mass fraction (SMF, g g ⁻¹)	4.7	11.9	.	40	7
Specific leaf area (SLA, m ² kg ⁻¹)	5.3	16.2	**	38	10
Leaf area index (LAI, m ² m ⁻²)	22.2	87.8	**	49	6
Specific stem length (SSL, m g ⁻¹)	37.1	24.7	NS	18	6

Although reduced TDM_I and height, reduced branching or tillering, and reduced ULR or photosynthesis are not only characteristic for low-light but also low-N plants, we would expect opposing trends for other traits. In the case of low-N plants, we would expect higher TNC levels, lower leaf nitrogen concentrations, lower plant heights, higher levels of stomatal conductance and possibly lower SLAs. These are largely contrary to our observations (Figure 6). Only the reduced leaf size fits more with a low-nutrient than a low-light phenotype, although severely shaded plants also decrease their leaf size (Barišić, Stojković, & Tarasjev, 2006; Poorter et al., 2019). Considering the responses of all traits, we conclude that high-density plants have many more characteristics of low-light than nutrient-stressed plants.

If light is the most limiting factor, we expect that reducing the light intensity above the crop causes even stronger competition and reduction in biomass. Indeed, in a density experiment carried out at different light levels, reduced light decreased the TDM_A response to density (Figure 7a). Do nutrients then never limit growth at high plant densities as plants compete for light? Figure 7b,c shows that nutrients (nitrogen and phosphorus alike) can clearly affect TDM_A of both high- and low-density plants. The TDM_I of the low-nutrient plants (not shown) decreased with density in all these (and many other) experiments, suggesting that competition for nutrients can play a role especially when nutrient availability is low.

How can we resolve this apparent conflict? One way would be to simply assume that the intensity of below-ground competition depends on the level of fertilization, and assume that our database consists mostly of data from highly fertilized plants. Another way would be to compare plants that experience both root and shoot competition with those that have only shoot competition. The latter is achieved by planting each individual plant in a separate pot with its own individual supply of nutrients. Plant density treatments are then accomplished by placing the narrow pots closer or further apart. We split our database into two groups accordingly: a shoot-competition only group and a full-competition group. We computed the response to doubling in density for the traits in each group and compared the

responses using a t -test (Table 2). The result is insightful: Plants with shoot-only competition respond to competition by growing taller, whereas the below-ground competing ones do not ($p = .004$). In addition, the percentage decrease in TDM_I with doubling density of the shoot-competition-only plants is only half of that of full-competition ones. These results suggest that below-ground competition still plays an important role in plant density experiments and that the phenotype of high-density plants that we reported is a result of plants striking a balance between above- and below-ground competition. However, the possibility of pot-size effects limiting growth under low-density conditions may partly explain the result as well (Poorter, Bühler, van Dusschoten, Climent, & Postma, 2012). In the pot studies, TDM_I of high and low-density plants may have been more similar as they received the same, possibly low, amount of nutrients. More detailed experimentation under low nutrient conditions, especially in the field, is necessary to gain understanding of how plant density and nutrition interact.

9 | AN AGRONOMIC IDEOTYPE FOR PERFORMANCE AT HIGH DENSITIES

We have seen that seed production per ground area is often optimal at a specific density (Figures 1a and 2d). Farmers will aim to plant accordingly. Crops in modern agriculture are typically planted at much higher densities than in traditional farming. For example, the density at which *Zea mays* is planted in the United States has increased from 3 to 8 plants per square metre over the last century (Mansfield & Mumm, 2014). Although improved crop management, including increased fertilization, may explain part of the shift, modern cultivars have been bred for high tolerance to plant density. Figure 8 shows how cultivars from nearly a century ago have a maximum seed production at 3, whereas modern cultivars peak at 8 plants per square metre. Mansfield and Mumm (2014) list several hybrids that have their peak production at 12 plants per square metre, similar to the data in Figure 1a.

We expected that this tolerance to high plant density might be reflected in a different trait-response to plant density between wild and domesticated species. For example, we expected less of a decline in reproductive effort (harvest index) as it has been a breeding target.

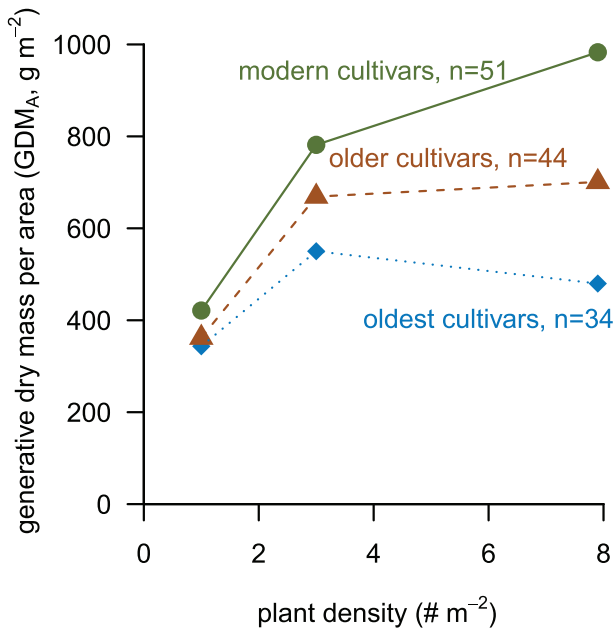


FIGURE 8 Density-response curve for seed mass per unit area (GDM_a) for 129 *Zea mays* cultivars released in different decades. Old, intermediate, and modern cultivars were released between 1930-1950, 1950-1970, and 1970-2000, respectively (data from Duvick, 2005) [Colour figure can be viewed at wileyonlinelibrary.com]

Increased allocation to stems, a high LAI and a high RLD have all been associated with a so-called tragedy of the commons: an overproduction of vegetative growth at the cost of reproduction and are thereby an undesirable response in agriculture (Anten & Vermeulen, 2016; McNickle, Gonzalez-Meler, Lynch, Baltzer, & Brown, 2016). To test the hypothesis that crops differ from wild species in their response to density, we split the database into agricultural and wild species (Table S6). The median reproductive effort response to density is for crops indeed closer to zero, but not significantly different from that of wild species. We found thus no proof that human selection has significantly reduced the ‘tragedy of the commons’.

Whether the shift from generative towards vegetative biomass is truly a tragedy from an ecological perspective remains a question (Bongers, Pierik, Anten, & Evers, 2018). Individual plants may do so to win the asymmetric competition, and the true tragedy may be represented by those individuals that did not survive (self-thinning). It is important to note here that evolution selects for fitness of the individual, whereas human selection is for productivity of the whole stand (Weiner, Andersen, Wille, Griepentrog, & Olsen, 2010). This difference in selection criteria combined with the highly altered environment created by modern production systems is an important reason why cultivated crops today have so much greater production than their wild counterparts or their historic antecedents. These factors may also explain why crop species are rarely invasive in natural habitats.

10 | CONCLUDING REMARKS

High plant density reduces individual plant mass dramatically, mainly because of a reduced rate of photosynthesis (Figure 9). Plants at high

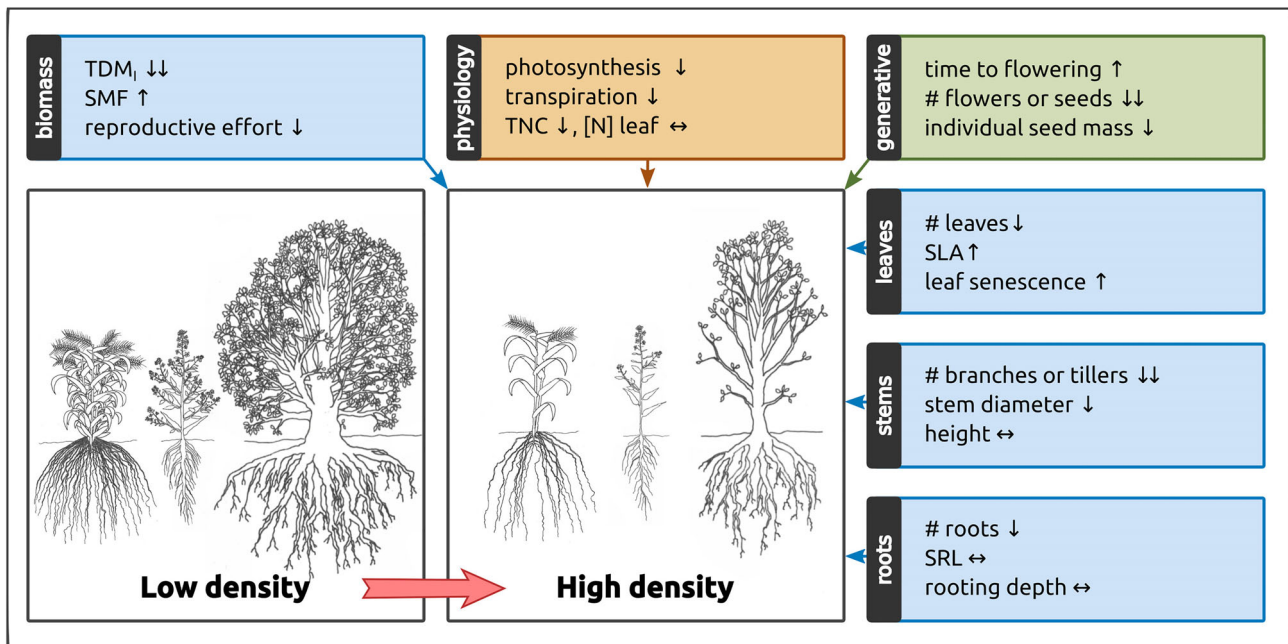


FIGURE 9 Schematic drawing of a monocot, dicot and tree, illustrating the individual plant responses to low and high plant density. Significant responses are indicated by vertical arrows: (↑) increase (0 to 25%), (↑↑) strong increase (>25%), (↓) decrease (0 to -25%), (↓↓) strong decrease (<-25%). Horizontal arrows (↔) indicate no significant change in the trait values in response to a doubling in density. For values and tests, see Figure 5 and Tables S2 and S3 [Colour figure can be viewed at wileyonlinelibrary.com]

density maintain height and rooting depth, and likely to reach heights and depths where competition is less strong. The high-density phenotype is more like that of shaded plants than that of low nutrient ones, but both low light and low soil fertility may reduce the biomass across a range of densities. There is, however, still a poor understanding of how the phenotypic and physiological responses to density influence competition for light and nutrients differentially. So far, root phenotypic responses have only been sparingly characterized; and this is also true for many traits related to plant chemistry and physiology. Although strictly our study pertains only to monostands, we think that many of the here reported trait responses to density will be similar in mixed-species stands as they arise from reduced light and nutrient availability per plant.

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CONFLICTS OF INTEREST

The authors declare no conflict of interest.

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

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