Stage-dependent plasticity in biomass allocation and allometry in response to population density in *Abutilon theophrasti*: a step forward to understanding the nature of phenotypic plasticity

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Abstract How plants respond to density via modular plasticity is obscure, probably because relevant studies using covariance analysis (ANCOVA) and allometric analysis rarely focus on multiple stages of plant growth, and also the two approaches are seldom used simultaneously. In this study, a field experiment evaluated the effects of three density levels on resource allocation traits in *Abutilon theophrasti* and tested the degree to which these were explained by indirect effects of density on biomass over time. Results showed inconsistent responses in allocation traits and allometric relationships at each growth stage. At 30 days of plant growth, high density increased root/stem, root/leaf, and stem/leaf, but did not affect any allometric relationships. At 50 days, density altered most mass and ratio traits, but not for allometric exponents. At 70 days, density altered allometric relationships, but did not affect plant allocation patterns. The stage-dependent allometric relationships and the fact that allocation plasticity and allometric plasticity did not coincide both suggested that one-stage allometric plasticity might be apparent plasticity. In response to the increase of density, plants first altered the strategy of biomass partitioning and then growth rate or developmental stage, indicating that density effects intensified over time. For plasticity in a modular trait, size effects can be regarded as a component of (indirect) environmental effects, with the residual variation after removal of size effects being the other component of plant (direct) active response. The insights into apparent plasticity of allometry and two components of plasticity should be of essential importance to investigating phenotypic plasticity and its ecological and evolutionary implications.

Keywords Allometric analysis · Apparent plasticity · Biomass allocation · Covariance analysis · Developmental stability · Growth stage · Plant size · True plasticity

Introduction

The optimal partitioning theory (OPT) predicts how plants will maximize the mass allocated to the organs that acquire the most limiting resources (Bloom et al. 1985; Müller et al. 2000; McConnaughay and
Coleman 1999; Thornley 1972). For example, plants will increase root:shoot ratio at low water or nutrient availability (Poorter et al. 2012). Or plants may increase stem mass allocation under limited light conditions (Aerts 1999; Poorter et al. 2012). When multiple above- and belowground resources become limited simultaneously, as a result of increasing population density (Casper and Jackson 1997), it is unclear how plants may alter the pattern of biomass allocation in response. Density-induced extra stem elongation is regarded as a typical example of adaptive plasticity (van Kleunen and Fischer 2005), whereas the adaptive value of how increased density may affect other modules (Table 1) of leaves, roots, branches, and reproductive ones is not well understood (Cheplick 2020; Japhet et al. 2009; Navas & Garnier 2002; Wang et al. 2017, 2006; Weiner et al. 2009). Relevant research on how plants respond to density via biomass allocation have produced mixed results (Cahill Jr 2003; Müller et al. 2000; Shipley and Meziane 2002). The lack of existing consensus on the effects of increasing density on resource allocation traits is likely due to most relevant studies having: (1) examined responses of root:shoot ratio to competition, with little information available on responses in other allocational relationships throughout the plant (Cahill Jr 2003; Murphy & Dudley 2007; but see Forster et al. 2011); (2) focused on the vegetative stages and thus responses in vegetative modules of plants, lacking attention to reproductive modules and relationships between reproductive modules and vegetative modules (Table 1) during reproductive periods (Li et al. 2016; Maliakal et al. 1999; but see Gersani et al. 2001); (3) neglected effects of plant growth stages as they often focused on a single stage (Gersani et al. 2001; Li et al. 2016; O’Brien et al. 2005).

A review by Poorter et al. (2012) showed an averaged decrease in root and leaf mass ratios, an increase in stem mass ratio in response to increasing density, and an increased root mass ratio with density at low nutrient availability (Berendse and Möller 2009), although root:shoot ratio does not always change with competition (Cahill Jr 2003; Casper et al. 1998). These suggested that the responses of modular mass to density can vary depending on specific circumstances in relation to the strength of competition among individuals due to factors such as abiotic conditions, experimental treatments, and plant growth stages (Wang and Callaway 2021; Wang et al. 2017, 2021). Not only does the pattern of biomass allocation varies significantly along with the lifespan of plants (Harper 1977), but also the intensity of among-plant competition shifts over time in a dense population (Hutchings and Budd 1981; Wang et al. 2017). It is unclear in which duration or growth stages over the lifespan of plants that a dense population may experience significant shifts in competition, neither is it known whether this principle applies to the situation of interspecific competition. However, it is known that as a dense population grows to reach its carrying capacity, intense competition may lead to mortality of smaller individuals, which is known as density-dependent mortality or ‘self-thinning’ (Morris 1999; Yoda et al. 1963). However, there are very few studies that have evaluated both biomass allocations and changing density effects over time. The combined effects of biomass allocation variation and competition variation over normalized time require studies that focus on multiple stages of plant growth or longer growth periods (Rudgers et al. 2019; Thompson 2019; Tobler and Nijhout 2010), in order to better understand how plants respond to density via plasticity in biomass allocation.

The OPT has predicted how plants may adjust biomass allocation pattern merely in response to external conditions, without considering that plant allocation can also be size-dependent (Coleman et al. 1994; McCarthy and Enquist 2007). Apart from environmental effects, a plant can also experience varying allocation over time due to its intrinsic ontogenetic effects. Therefore OPT has been questioned in the view of allometric growth (Table 1), which emphasizes that almost all plant allocation patterns are size-dependent (Ogawa 2003; Pino et al. 2002). By virtue of analyzing differences in the allometric relationships between a module and plant size or between different modules (Fig. 1b), researchers have been able to distinguish the “apparent plasticity,” defined as the variation in traits due to effects of plant size, from the “true plasticity,” which indicates the environment-induced variation in traits (Table 1; Weiner 2004). Covariance analysis (ANCOVA) is another widely used method to preclude the effects of plant size in variations of modules, by incorporating plant size (or other traits) as a covariance in the analysis of variance (ANOVA). For example, for a given module (Y), ANOVA on the environmental effects on the module may be
significant or insignificant due to complex effects of the environment and plant size; whereas the results from ANCOVA perhaps show similar or different environmental effects after removing effects of plant size (Fig. 1a). It is considered as true plasticity in module Y when the environmental effect is significant in ANCOVA and as apparent plasticity when environmental effect is insignificant in ANCOVA but significant in ANOVA. Both allometric analysis and covariance analysis are efficient approaches commonly used to distinguish true plasticity from apparent plasticity, but have been mostly employed in respective studies to investigate plant allocation strategies. In the rare studies applying both

| Term                          | Definition                                                                 | Source                                      |
|-------------------------------|---------------------------------------------------------------------------|---------------------------------------------|
| Phenotypic plasticity (or plasticity) | The ability of a genotype to produce different phenotypes in response to different environmental conditions | Bradshaw (1965), Pigliucci (2005)             |
| Canalization                  | The ability of a genotype to produce consistent phenotypes regardless of environmental and genetic variabilities | Waddington (1942)                           |
| Developmental stability       | The tendency of traits to resist “developmental errors,” evaluated using fluctuating asymmetry (FA, random deviation from perfect bilateral symmetry) | Palmer and Strobeck (1986), Debat and David (2001) |
| Modules                       | The repeated often semiautonomous structural and functional subunits produced by plants | de Kroon et al. (2005)                      |
| Vegetative modules            | The modules used for plant vegetative growth                              | de Kroon et al. (2005)                      |
| Reproductive modules          | The modules used for plant reproductive growth                             | de Kroon et al. (2005)                      |
| Modular plasticity            | Plastic responses that occur at the modular levels of a plant             | de Kroon et al. (2005)                      |
| Allocation                    | The process of partitioning or dividing resources among different structures or activities | Weiner (2004)                               |
| Allometry (or allometric growth) | The property of plant growth that modules grow with plant size at a varying rate | Weiner (2004)                               |
| Isometry (or isometric growth) | The property of plant growth that modules grow with plant size at a constant rate | Weiner (2004)                               |
| Allometric plasticity         | Variation in allometric relationships or allometric trajectory due to environmental effects | Weiner (2004)                               |
| Allometric relationship       | The relationship between two structures or modules (or modular traits) of a plant is allometric | Weiner (2004)                               |
| Allometric trajectory         | The growth of a plant over lifetime follows an allometric pattern          | Weiner (2004)                               |
| Allometric analysis           | An analysis conducted to evaluate whether there is any allometric relationship between two traits | Weiner (2004)                               |
| Covariance analysis (ANCOVA)  | An analytical method to preclude the effects of a variable on other variables in the analysis of variance | –                                           |
| True plasticity               | The variation phenotypic expression due to environmental effects, independent of plant size | McConnaughay and Coleman (1999), Wright and McConnaughay (2002) |
| Apparent plasticity (or passive plasticity) | The variation in phenotypic expression dependent of plant size | McConnaughay and Coleman (1999), Wright and McConnaughay (2002) |
| Adaptive plasticity           | A plasticity that results in the production of a phenotype that is in the same direction as the optimal value favored by selection in the new environment | Conover and Schultz (1995), Ghalambor et al. (2007) |
| Non-adaptive plasticity       | Compared to the ancestral phenotype, the environmentally induced phenotype in the new environment has on average reduced fitness or is further away from the optimal value favored by selection. It is a form of plasticity arising as a ‘passive’ consequence to environmental stress | van Kleunen and Fisher (2005), Ghalambor et al. (2007) |
approaches, they often primarily rely on the conclusions from allometric analyses when the two sets of analytical results are inconsistent (Huang et al. 2010; Müller et al. 2000).

Another problem is that either covariance analysis or allometric analysis has been conducted generally using the data at a single stage of plant growth (Hill and Roberts 2017; Vizcaíno-Palomar et al. 2016), lacking analyses based on multiple growth stages. However, both size-dependent allocation patterns and allometric relationships vary with growth stages (Thompson 2019; Wang et al. 2017), and allometric analyses across multiple stages differ significantly from allometry based on one stage (Fig. 2; Li et al. 2013). To ensure that the results will not be biased by the analyses based on any single stage, it is necessary to take multiple growth stages into account in analyses of relevant studies (Wang et al. 2017; Weiner and Thomas 1992).

To investigate how plants deal with increased density via plasticity in biomass allocation, we conducted a field experiment on an annual species, *Abutilon theophrasti* Meic. We subjected plants to three density treatments, and measured six variables of biomass in different portions of the plant, and tested showing inconsistent analytical results and conclusions on true plasticity or apparent plasticity in module Y in a same study.

*Fig. 1* The three hypothetical cases (①–③) of plasticity in a given module Y in response to environment (A, B) when both covariance analysis (a) and allometric analysis (b) are applied.

Materials and methods

Study species

*Abutilon theophrasti* Meic. (Malvaceae), native to China and India, is an invasive species and now spreads worldwide. It is an annual weedy species erect
with stout stems, grows to the maximum height between 1 and 1.5 m (Gleason and Cronquist 1991), reaching reproductive maturity within 90 days and complete its lifecycle in about 150 days (McConnaughay and Coleman 1999). It is typically found in open fields and waste places and colonizes relatively nutrient-rich habitats, grows rapidly, and displays intermediate plasticity (McConnaughay and Bazzaz 1992).

Experimental design

The experiment was conducted between June and August, 2007 at the Pasture Ecological Research Station of Northeast Normal University, Changling, Jilin province, China (44°45′ N, 123°4′ E). The region has a semi-arid and semi-humid temperate continental monsoon climate, dry and windy in spring and hot and wet in summer, with average annual air temperature of 4.6–6.4 °C, average annual amount of precipitation of 400–500 mm, and average annual amount of evaporation of 1000–2000 mm. The primary growing season occurs between June and August when the average air temperature exceeds 20 °C and peaks in July, while average precipitation during this time accounts for 70–80% of the total precipitation of the whole year.

Seeds of *A. theophrasti* were collected from local wild populations near the research station in the late August of 2006 and were dry stored at −4 °C. We labeled the density treatments as low, medium, and high densities, which were created by growing plants with inter-planting distances of 30, 20, and 10 cm, respectively, to reach the target densities of 13.4, 36, and 121 plants m⁻², respectively. Each density had three blocks, randomly distributed into nine 2 × 3 m plots. Seeds were sown at initial densities that were a little higher than the target ones on June 7, 2007. Most seeds emerged 4–5 days later. When almost all seedlings reached four-leaf stage, they were thinned to the target densities. Plots were hand weeded when necessary and regularly irrigated to prevent drought. The original soil of experimental field at the station had been used annually for many years (aeolian sandy soil), with low nutrient contents during the growth season of 2007 (Wang et al. 2017). To improve the soil quality of the experimental plots, we covered the other large plot with 5–10 cm virgin soil transported from a nearby meadow with no cultivation history (meadow soil). To keep the soil and resource amounts as even as possible, we crushed the blocky soil into very small bits and mingled them adequately, before spreading them over the entire plot and compaction. Seeds were sown into all plots at the same burial depth and sowing rate.

Data collection and analysis

Plants were harvested at 30, 50, and 70 days of growth, which represented vegetative stage, early reproductive stage, and middle reproductive stage.
respectively. For each stage, five–six individual plants were randomly sampled per replicate per density, making a maximum total of 162 samplings. Each individual plant was separated into roots, stems, petioles, leaves, branches, and reproductive organs (if available), oven-dried at 75 °C for 2 days, and weighed. Branches appeared at the third stage only and were not incorporated in analyses. Plant total biomass, shoot mass, and mass ratios between different modules were calculated, and consequently we used all the mass traits and mass ratio traits as follows: total mass, root mass, shoot mass, stem mass, leaf or lamina mass, petiole mass, reproduction mass, branch mass, root/shoot, root/stem, root/leaf(lamina), stem/leaf(lamina), root/petiole, stem/petiole, petiole/lamina, reproduction/root, reproduction/stem, reproduction/petiole, and reproduction/lamina (Table 2).

All data were log-transformed to minimize variance heterogeneity before analyses. Analyses were conducted with SAS statistical software (SAS Institute 9.0 Inc. 2002). Two-way ANOVA for total mass and two-way ANCOVA for modular mass and ratio traits were conducted first, with growth stage and density as fixed effects and log-transformed total mass as a covariate in ANCOVA. Then one-way ANOVAs or ANCOVAs were used to analyze the effects of density on total mass and other traits at each stage, with total mass as a covariate in ANCOVA. Since regarding total mass as a covariate in ANCOVA has been questioned because the total mass contains all modular mass, we also conducted one-way ANCOVAs for each module, with density or growth stage as effects and another module as a covariate (Cahill Jr 2003; Wejschedé et al. 2006). Multiple comparisons used Least Significant Difference (LSD) method in all analyses. Whenever total biomass explained significant variation in a trait in response to density, the trait was regarded to exhibit apparent plasticity (McConnaughay and Coleman 1999; Weiner 2004; Wright and McConnaughay 2002). By contrast, any variation in trait expression independent of total biomass (size) was considered as an indication of true plasticity (Weiner 2004). Adjusted mean values and standard errors were produced through LSD method of General Linear Model (GLM) program.

The relationships among the mass of various modules, including root mass, stem mass, petiole mass, lamina mass, and reproductive mass (if available), were estimated by log10-transformed regressions for each density and stage combination. Model Type II [reduced major axis (RMA)] regression analysis was used to determine scaling exponent, with

\[ z_{\text{RMA}} = \frac{z_{\text{OLS}}}{r}, \]

where \( z_{\text{OLS}} \) is the ordinary least squares scaling exponent and \( r \) is the ordinary least squares correlation coefficient. This regression is recommended when the variables of interest are biologically interdependent, subjected to unknown measurement error (Nicklas 1994; Wang et al. 2006).

Effects of density or growth stage on allometric exponents (\( x \)) for all relationships were detected by significant interactions between covariate and density or stage in ANCOVAs on modules with other modules as covariates (Müller et al. 2000). We also compared the proportions explained by covariance and allometric analysis models in the variation of a dependent variable, by evaluating the \( R^2 \) values of both models. The \( R^2 \) value for each analysis (model), or multiple regression coefficient, was calculated by dividing the sum of squares of the model with the corrected total sum of squares.

Results

Density-induced variations in plant size

Effects of density on plant size (total biomass) varied with different stages of plant growth (Table 2; Fig. 5 in the Appendix). At 30 days, density had no effects on total mass; at 50 days and 70 days, compared to low density, high and medium densities reduced total mass by average 58.15% and 46.95%, respectively (LSD, \( P < 0.001 \) and \( P < 0.01 \); Fig. 5 in the Appendix), indicating greater effects of high density than medium density.

Density-induced variations in modular mass allocation

Effects of plant size contributed significantly to the variations in all mass traits and most mass ratio traits of modules, whereas density still had significant effects on these traits after the removal of size effects (Table 2). Responses to density in the mass of different modules varied with different stages (Table 2; Appendix Fig. 6). At 30 days of growth, compared to low density, medium density increased root mass (\( P < 0.05 \)). At 50 days, compared to low density,
high density increased stem mass \((P < 0.001)\) and decreased petiole, lamina, and reproductive masses \((P < 0.05)\). No density effect was found on any trait at 70 days.

Density-induced variations in mass ratios

Responses to density in mass ratios among different modules also varied with different stages (Table 2, Fig. 3). At 30 days of plant growth, compared to low density, medium and high densities increased root/stem ratio, root/leaf, and stem/leaf \((P < 0.05)\). At 50 days, compared to low density, high density also decreased root/stem \((P < 0.01)\), petiole/lamina \((P < 0.001)\), reproductive/stem, and reproductive/lamina \((P < 0.05)\), and increased stem/lamina and stem/petiole \((P < 0.001)\). No density effect was found on any mass ratio at 70 days.

Density-induced variations in allometric relationships

Increasing density significantly affected allometric relationships among modules (Table 3; Appendix Table 4, Figs. 7, 8, 9). At 30 days and 50 days, density had no or little effects on allometric relationships (Table 3; Appendix Table 4, Figs. 7, 8). However, density had significant effects on much more allometric relationships at 70 days (Table 3; Appendix Table 4, Fig. 9). Compared to low and medium densities, high density steepened slopes of stem-petiole and petiole-lamina relationships and relationships between the mass of vegetative modules and reproductive mass (Table 3; Appendix Fig. 9). For example, the scaling exponent for the regressive relationship between stem mass and petiole mass was 0.662 at low density, but increased to an average of 0.930 at medium and high densities \((P = 0.027)\); high density also increased the scaling exponents from

### Table 2 One-way ANCOVA on log-transformed mean values of traits with population density (PD) as main effect and total mass (TM) as a covariate at 1st stage, 2nd stage, and 3rd stage

| Trait                  | 30 days | 50 days | 70 days |
|------------------------|---------|---------|---------|
|                        | \(N\) | TM \((Df = 1)\) | PD \((Df = 2)\) | \(N\) | TM \((Df = 1)\) | PD \((Df = 2)\) | \(N\) | TM \((Df = 1)\) | PD \((Df = 2)\) |
| Total mass             | 42     | 1.30    | 50      | 46.46*** | 41     | 14.75*** |
| Root mass              | 42     | 28.25*** | 3.64*   | 50      | 460.23*** | 2.27    | 41     | 190.63*** | 0.70    |
| Shoot mass             | 42     | 12.262.90*** | 4.93* | 50      | 22.091.60*** | 2.23    | 41     | 18.53*** | 12.67*** |
| Stem mass              | 42     | 109.53*** | 0.87    | 50      | 1228.89*** | 23.45*** | 41     | 1634.31*** | 1.92    |
| Lamina (leaf) mass     | 42     | 4478.93*** | 0.82    | 50      | 3392.04*** | 11.77*** | 41     | 666.70*** | 3.44*   |
| Petiole mass           | 42     | 577.90*** | 33.71*** | 50      | 538.60*** | 0.50    | 41     | 194.49*** | 3.07    |
| Reproduction mass      | 39     | 88.12*** | 3.04    | 41      | 45.65*** | 0.17    |        |         |         |
| Branch mass            | 31     | 194.49*** | 3.07    |        |         |         |        |         |         |
| Root/shoot             | 42     | 1.42    | 6.14*** | 50      | 1.20    | 0.74    | 41     | 0.09    | 0.42    |
| Root/stem              | 42     | 12.25** | 143.36*** | 50      | 1.81    | 9.56*** | 41     | 3.70    | 0.66    |
| Root/lamina (leaf)     | 42     | 0.23    | 38.76*** | 50      | 0.09    | 0.04    | 41     | 5.41*   | 2.19    |
| Stem/lamina (leaf)     | 42     | 15.71*** | 350.97*** | 50      | 6.61*   | 22.53*** | 41     | 0.31    | 4.39*   |
| Root/petiole           | 50     | 21.05*** | 2.28    | 41      | 2.16    | 1.79    |
| Stem/petiole           | 50     | 46.80*** | 35.74*** | 41      | 16.91*** | 1.61    |
| Petiole/lamina         | 50     | 67.90*** | 10.71*** | 41      | 37.90*** | 0.36    |
| Reproduction/root      | 39     | 4.70*   | 1.56    | 41      | 0.67    | 0.12    |
| Reproduction/stem      | 39     | 10.75** | 5.13*   | 41      | 2.22    | 0.06    |
| Reproduction/petiole   | 39     | 6.01*   | 2.28    | 41      | 2.34    | 0.35    |
| Reproduction/lamina    | 39     | 1.12    | 1.18    | 41      | 0.13    | 0.31    |

Significance levels: \(*P < 0.05, **P < 0.01, ***P < 0.001\)
average 0.290 at low and medium densities to 0.779 for the relationship between root mass and reproductive mass \((P = 0.016)\), from average 0.400 at low and medium densities to 0.608 for the relationship between stem mass and reproductive mass \((P = 0.030)\), and from average 0.230 to 0.629 for the relationship between lamina mass and reproductive mass \((P = 0.002)\).

Variations in allometric relationships due to growth stage

The allometric relationships among modules not only varied with different densities, but also with different stages of plant growth (Table 5, Fig. 11 in the Appendix). The scaling exponents of allometric relationships for plants at each density varied with growth stages, and stage effects were significant for more relationships across all densities than for each density. Besides, density induced variations in allometric relationships based on the data within a single stage significantly differed from those based on the data across three stages (Table 3; Appendix Table 4, Figs. 7, 8, 9, and 10).

Stage-dependent plasticity in response to density

The covariance analyses (Table 2, Fig. 3; Fig. 6 in the Appendix) and allometric analyses (Table 3; Appendix Table 4, Figs. 7, 8, 9, and 10) showed significant responses to density of modular mass ratios and allometric relationships among modules did not coincide. And comparisons on the \(r^2\) of models for the two sets of analyses varied with different growth stages (Fig. 3; Figs. 7, 8, and 9). At 30 days, \(r^2\) for ANCOVAs on mass ratios were generally higher than \(r^2\) for allometric analyses, with 0.89 (root/stem) vs. 0.32 (root-stem relationship), 0.70 (root/leaf) vs. 0.52 (root-leaf relationship), and 0.95 (stem/leaf) vs. 0.65 (stem-leaf relationship), respectively, except for the comparison on \(r^2\) for root/shoot (0.37) and root-shoot relationship (0.52; Fig. 3; Appendix Fig. 7). At the latter two stages, \(r^2\) for allometric analyses were higher than that for ANCOVAs for all relationships: at 50 days, it was average 0.88 ± 0.02 (for relationships among vegetative modules) vs. 0.40 ± 0.11 (for ratios between vegetative modules) and average 0.67 ± 0.03 (for relationships between vegetative and reproductive modules) vs. 0.26 ± 0.05 (for ratios between vegetative and reproductive modules); at 70 days, it was average 0.89 ± 0.01 vs. 0.27 ± 0.06 and 0.59 ± 0.03 vs. 0.10 ± 0.02, respectively (Fig. 3; Appendix Figs. 8, 9).

Consequently, plant plasticity in biomass growth in response to increasing density varied significantly with different growth stages (Table 2, 3; Fig. 3; Appendix Table 4, Figs. 7, 8, and 9). At 30 days and 50 days, plants mainly responded to density via changes in modular mass allocation, with no shifts in allometric relationships among modules; whereas at 70 days, they responded to density via modifying allometric relationships, with no changes in biomass allocation.

Discussion

Density-induced plasticity in biomass allocation

How plants respond to increasing density is a complicated situation when both above- and belowground resources become limited for competitors, which the “optimal partitioning theory” did not predict (Aerts 1999; Donald 1958; Dybzinski et al. 2011; Tilman 1988). Poorter et al. (2012) reviewed some experimental studies and found there was generally a decrease in root and leaf mass allocations and an increase in stem mass ratio in response to increasing density, although root/shoot does not always change with competition (Cahill Jr 2003; Casper et al. 1998). The review also reported an increased root mass allocation with density at low nutrient availability (Berendse and Möller 2009). It suggested the conditionality of plant response to increasing density, depending on the strength of competition among neighbors. By virtue of dynamic observations, we were able to show how plant response to increasing density can vary, essentially with competition intensity. We found stage-dependent responses of modular mass and allocation traits to density, and true plasticity mainly occurred at the earlier two stages:
Table 3  Scaling exponents ($a_{RMA} \pm SE$) in allometric regression models ($Y = bX^a$) for relationships between different modules for individuals at low, medium, high densities, and across all densities, at 30, 50, and 70 days of growth and across all stages.

| Trait                      | PD   | 30 days  |                      | 50 days  |                      | 70 days  |                      | All stages |                      |
|----------------------------|------|----------|----------------------|----------|----------------------|----------|----------------------|------------|----------------------|
|                            |      | SE     | 95%CI                | SE      | 95%CI                | SE      | 95%CI                | SE        | 95%CI                |
| Root-shoot                 |      |        |                      |          |                      |          |                      |            |                      |
| Low                        |      | 1.081  | 0.054–1.297          | 0.989   | 0.763–1.106          | 1.229   | 0.897–1.079          |            |                      |
| Medium                     |      | 0.716  | −0.109–0.651         | 0.999   | 0.488–1.163          | 1.332   | 0.418–1.340          |            |                      |
| High                       |      | 0.814  | 0.236–0.885          | 1.035   | 0.729–1.176          | 1.135   | 0.806–1.185          |            |                      |
| All                        |      | 0.933  | 0.313–0.712          | 1.033   | 0.873–1.087          | 1.195   | 0.809–1.120          |            |                      |
| All stages                 |      | 2.61   |                      | 0.31    |                      | 0.32    |                      |            |                      |
| Root-stem                  |      |        |                      |          |                      |          |                      |            |                      |
| Low                        |      | 1.272  | 0.170–1.464          | 1.006   | 0.720–1.134          | 1.600   | 0.344–1.605          |            |                      |
| Medium                     |      | 0.692  | −0.151–0.600         | 0.760   | 0.296–0.937          | 1.376   | 0.454–1.281          |            |                      |
| High                       |      | 0.586  | −0.090–0.512         | 1.031   | 0.776–1.168          | 1.151   | 0.776–1.186          |            |                      |
| All                        |      | 0.715  | 0.074–0.475          | 1.067   | 0.826–1.130          | 1.362   | 0.827–1.155          |            |                      |
| All stages                 |      | 2.74   |                      | 1.03    |                      | 1.25**  |                      |            |                      |
| Root-lamina (leaf)         | Low  | 1.029  | 0.487–1.235          | 1.005   | 0.753–1.128          | 1.967   | −0.093–2.033         | 1.248     | 0.190–1.286          |
| Medium                     |      | 0.710  | −0.105–0.164         | 1.337   | 0.533–1.353          | 1.653   | 0.551–1.561          | 1.241     | 0.171–1.281          |
| High                       |      | 0.798  | 0.254–0.875          | 1.012   | 0.562–1.134          | 1.166   | 0.784–1.228          | 1.223     | 0.114–1.265          |
| All                        |      | 0.812  | 0.318–0.702          | 1.012   | 0.819–1.045          | 1.304   | 0.843–1.161          | 1.226     | 0.118–1.243          |
| All stages                 |      | 2.42   |                      | 0.75    |                      | 1.25**  |                      |            |                      |
| Stem-lamina (leaf)         | Low  | 0.809  | 0.330–0.970          | 0.999   | 0.840–1.098          | 1.153   | 0.630–1.351          | 1.443     | 0.382–1.485          |
| Medium                     |      | 1.026  | 0.702–1.176          | 1.577   | 0.758–1.911          | 1.258   | 0.782–1.380          | 1.554     | 0.501–1.591          |
| High                       |      | 1.363  | 0.073–1.352          | 0.982   | 0.689–1.090          | 1.098   | 0.826–1.165          | 1.600     | 0.146–1.660          |
| All                        |      | 1.135  | 0.542–1.037          | 0.895   | 0.703–0.926          | 1.042   | 0.874–1.046          | 1.503     | 0.141–1.523          |
| All stages                 |      | 0.88   |                      | 1.27    |                      | 0.17    |                      |            |                      |
| Stem-petiole               | Low  | 0.871  | 0.655–0.978          | 0.662   | 0.285–0.755          | 1.124   | 0.706–1.164          |            |                      |
| Medium                     |      | 1.339  | 0.695–1.426          | 0.922   | 0.480–0.935          | 1.282   | 0.919–1.312          |            |                      |
| High                       |      | 0.853  | 0.700–0.940          | 0.928   | 0.680–0.986          | 0.899   | 0.769–0.954          |            |                      |
Table 3 continued

| Trait               | PD    | 50 days | 70 days | All stages |
|---------------------|-------|---------|---------|------------|
|                     |       | \(a_{\text{RMA}} \pm \text{SE}\) | 95%CI    | \(a_{\text{RMA}} \pm \text{SE}\) | 95%CI    | \(a_{\text{RMA}} \pm \text{SE}\) | 95%CI    |
| All                 |       | 0.730 ± 0.049 | 0.654–0.760\(^b\) | 0.866 ± 0.039 | 0.680–0.835 | 0.887 ± 0.040 | 0.714–0.872 |
| \(F\)               | 1.44  | 3.97*   |         |            |          | 4.21        |          |
| Petiole-lamina      |       | 1.147 ± 0.066 | 0.975–1.256 | 1.773 ± 0.222 | 1.110–2.068 | 1.283 ± 0.074 | 1.062–1.366 |
| Low                 |       | 1.151 ± 0.077 | 0.911–1.237 | 1.486 ± 0.121 | 1.137–1.649 | 1.280 ± 0.057 | 1.109–1.340 |
| Medium              |       | 1.135 ± 0.052 | 1.006–1.227 | 1.218 ± 0.069 | 1.014–1.314 | 1.199 ± 0.048 | 1.073–1.270 |
| High                |       | 1.210 ± 0.030 | 1.132–1.251\(^b\) | 1.282 ± 0.043 | 1.131–1.304\(^b\) | 1.248 ± 0.025 | 1.172–1.271\(^b\) |
| \(F\)               | 0.10  | 3.53    |         |          |          | 0.20        |          |
| Root-reproduction   |       | 0.595 ± 0.097 | 0.242–0.656 | 0.206 ± 0.157 | –0.304–0.372\(^b\) | 0.412 ± 0.063 | 0.089–0.345\(^b\) |
| Low                 |       | 0.606 ± 0.153 | –0.004–0.669 | 0.284 ± 0.076 | –0.097–0.224\(^b\) | 0.301 ± 0.051 | 0.017–0.228\(^b\) |
| Medium              |       | 0.758 ± 0.204 | –0.058–0.852 | 0.779 ± 0.156 | 0.102–0.781 | 0.499 ± 0.083 | 0.119–0.461 |
| High                |       | 0.651 ± 0.062 | 0.390–0.641 | 0.631 ± 0.071 | 0.149–0.437 | 0.478 ± 0.041 | 0.208–0.369 |
| \(F\)               | 0.16  | 4.58*   |         |          |          | 1.72        |          |
| Stem-reproduction   |       | 0.591 ± 0.100 | 0.225–0.648 | 0.418 ± 0.083 | –0.050–0.306 | 0.491 ± 0.050 | 0.302–0.506\(^b\) |
| Low                 |       | 0.617 ± 0.140 | 0.096–0.714 | 0.383 ± 0.063 | –0.057–0.212 | 0.378 ± 0.053 | 0.142–0.358 |
| Medium              |       | 0.706 ± 0.177 | 0.038–0.825 | 0.608 ± 0.154 | 0.079–0.749 | 0.511 ± 0.075 | 0.199–0.510 |
| High                |       | 0.543 ± 0.054 | 0.308–0.527\(^b\) | 0.512 ± 0.060 | 0.171–0.412\(^b\) | 0.476 ± 0.032 | 0.301–0.430\(^b\) |
| \(F\)               | 0.01  | 3.69*   |         |          |          | 1.45        |          |
| Petiole-reproduction|       | 0.679 ± 0.118 | 0.238–0.738 | 0.534 ± 0.123 | –0.043–0.490 | 0.285 ± 0.059 | 0.165–0.406 |
| Low                 |       | 0.505 ± 0.103 | 0.146–0.599 | 0.363 ± 0.078 | –0.089–0.241 | 0.191 ± 0.050 | 0.089–0.292 |
| Medium              |       | 0.878 ± 0.233 | –0.042–0.997 | 0.632 ± 0.161 | 0.190–0.892 | 0.374 ± 0.089 | 0.190–0.558 |
| High                |       | 0.768 ± 0.070 | 0.482–0.765 | 0.642 ± 0.074 | 0.225–0.522 | 0.553 ± 0.043 | 0.290–0.462 |
| \(F\)               | 0.13  | 4.83*   |         |          |          | 1.91        |          |
| Lamina-reproduction |       | 0.592 ± 0.099 | 0.232–0.650 | 0.255 ± 0.073 | –0.063–0.253\(^b\) | 0.340 ± 0.048 | 0.115–0.310\(^b\) |
| Low                 |       | 0.404 ± 0.097 | 0.034–0.459 | 0.196 ± 0.054 | –0.096–0.133\(^b\) | 0.236 ± 0.038 | 0.039–0.194 |
| Medium              |       | 0.795 ± 0.222 | 0.121–0.868 | 0.629 ± 0.137 | 0.152–0.749 | 0.483 ± 0.081 | 0.106–0.441 |
| High                |       | 0.635 ± 0.062 | 0.373–0.622\(^b\) | 0.503 ± 0.061 | 0.155–0.401\(^b\) | 0.444 ± 0.037 | 0.206–0.353|
| \(F\)               | 0.44  | 7.76**  |         |          |          | 1.91        |          |

Significance levels: * \(P < 0.05\), ** \(P < 0.01\), *** \(P < 0.001\)

\(^b\) Denote scaling exponents that significantly deviate from 1

\(^*\) F values produced from ANCOVAs on effects of density and covariate interaction
At 30 days of plant growth, medium density increased root mass, root/stem, and root/leaf, consistent with other studies (Gersani et al. 2001; O’Brien et al. 2005), indicating that low to intermediate interactions are more likely to facilitate root growth, and root interactions as proxied by density occurred before aboveground interactions (Wang and Callaway 2021; Wang et al. 2021). In spite of no response in leaf mass, the significant increases of root/leaf and stem/leaf by high vs. low density indicated a relatively lower investment of resource into leaves, than into stems and roots under competition. And we may also deduce that at this stage, plant growth in the dense populations had not yet been limited by resource deficiency due to competition.

As plants grew larger at 50 days, they began to interfere with each other and compete for aboveground resources when greater mass allocated to stems was required for an extra elongation (Bell and Galloway 2007; Weiner and Fishman 1994). Greater stem mass and smaller mass allocated to other modules lead to increased ratios of stem mass to other modular mass by high relative to low density. It suggested at this stage, the increase of density mainly resulted in the limitation of light availability, which led to an extra increment of stem mass, according to the prediction of OPT. Meanwhile, the extensive stem elongation might be at the cost of leaf mass and reproductive mass, although lamina/petiole and lamina/reproductive increased with density due to the greater importance of laminas to reproductive organs (Cheplick 2006). However, the decrease of leaf mass may also be a direct effect of density, as it is reported that root mass and leaf mass were still decreased by high vs. low density despite the induced stem elongation has been suppressed (Maliakal et al. 1999).

No response to density was found in root mass allocation or root/shoot at this stage, consistent with some studies (Cahill Jr 2003; Casper et al. 1998). But it is also reported that root/shoot decreased with increased density under less fertile soil conditions (Wang et al. 2021). This is potentially explained by root allocation typically decreasing in response to competition in absence of belowground resources (Poorter et al. 2012), as belowground competition can be aggravated by resource deficiency, but be ameliorated under sufficient resources, leading to no response to density in root/shoot (Wang et al. 2017, 2021).

There have been fewer studies on responses of reproductive modules to density, which showed inconsistent results. There are multiple drivers of reproductive allocations. Reduction of reproductive mass can be due to competition (Gersani et al. 2001; Japhet et al. 2009; Murphy and Dudley 2007) or just an effect of plant size (Arenas et al. 2002; Wang et al. 2006). We found both a decrease and no change in reproductive mass and its ratios to other modular mass, indicating that reproductive plasticity depends on specific stages. At the initial stage of reproduction, a trade-off occurs during resource distribution at the physiological level, either toward vegetative growth or toward reproduction (Fox 1995), as plant resource allocation or development is limited (Karlsson and Méndez 2005; Levins 1968). Increased vegetative mass was correlated with the cost of reproductive mass, consistent with other studies (Álvarez-Cansino et al. 2010; Matsuyama and Sakimoto 2008). Due to the trade-off between reproduction and growth or survival, inferring effects on fitness from the connections between traits and vital rates can be misleading and identifying traits that determine fitness remain an important empirical challenge (Laughlin et al. 2020).

Increasing density enhanced the mass allocated to stems and reduced the mass allocation of petioles, laminas, and reproduction, implying a translocation of energy investment away from leaves, further leading to a reduced reproduction. Under the abiotic conditions that limit plant growth, surplus photosynthates can be produced or translocated from leaves to roots (Prescott et al. 2020). When competing for resources with intraspecific neighbors, plants may also have surplus photosynthates translocated from leaf mass to root or stem mass, as a result of reduced accessibility to resources. This can explain both the increase in root mass and relevant ratio traits at 30 days and the extensive
growth in stem mass at 50 days in response to increasing density.

(3) At 70 days, we did not find responses to density in any modular mass or allocation traits. This may be explained by that competition intensity and its effects attenuated over time for individuals grown with neighbors. In a dense population, as plants grow, the strength of competition first increases then decreases over time (Hutchings and Budd 1981; Wang et al. 2017), resulting in shifts in resource availability and plant–plant interactions (Bouvet et al. 2005; Zhou et al. 2005). When plants continued to grow in the dense populations, reaching its carrying capacity, intense competition may lead to mortality (Hutchings and Budd 1981) in the process known as density-dependent mortality or ‘self-thinning’ (Morris 1999; Yoda et al. 1963). And the competition strength may attenuate again due to the elimination of small plants, leading to the alleviation of resource competition and allocation responses (Wang et al. 2017).

Density-induced plasticity in allometric relationships

Our results showed plasticity in mass allocation and allometric relationships did not coincide. We found true plasticity in allocation by covariance analyses and allometric plasticity at different stages, respectively, as well as the growth dependence in allometric relationships. Growth period or duration can significantly affect the pattern of allometry (Thompson 2019; Tobler and Nijhout 2010), and results from allometric analyses based on single stages differ from those across different stages (Li et al. 2013; Wang 2006). The discrepancy in the two sets of results and stage dependence of allometric relationships (Table 3) implied that allometric plasticity might be apparent plasticity, rather than generally recognized true plasticity. If the allometric plasticity within one growth stage is apparent plasticity, then the variation in developmental trajectory might also be apparent plasticity per se, since the entire developmental trajectory consists of countless allometric relationships at each moment along development.

An organism is capable of buffering developmental pathways against genetic or environmental perturbations (Kitano 2004; Masel and Siegal 2009; Mestek and Barkoula 2016; Wilkins 1997) to maintain developmental stability and make sure the precision of developmental progression, in order to produce an “ideal” form regardless of different circumstances (Auffray et al. 1999; Palmer 1994; Van Dongen and Lens 2000). Once the equilibrium is broken, deviation from the developmental trajectory due to mis-regulation of allometry might be lethal (Vea and Shingleton 2020) and needs to be prevented as best as possible. The ability to maintain developmental stability is therefore regarded as a premise for plants surviving different stressful environments (Elgart et al. 2015). Consequently, the occurrence of real significant deviations from a programmed development should be very difficult and rare. Evidences come from the little effects of phenology on leaf-shoot and other scaling relationships in woody species (Smith 2020). Voje et al. (2013) analyzed over 300 empirical estimates of allometry and found limited evidence for microevolutionary changes in allometric slopes for allometric relationships among morphological traits of animals (Voje et al. 2013). This is probably because there is a lack of genetic variation of allometry or genetic constraints to allometry (Lines et al. 2012), due to a potentially large number of pleiotropic effects (Houle et al. 2019). The relative consistency in ontogenetic trajectory may have constrained the variation among populations within a species, and thus the rate of intraspecific trait change, reflecting plastic and/or adaptive changes across populations, is limited and prevents species from adjusting to environmental gradients as quickly as interspecific changes resulting from community assembly (Sides et al. 2014).

When we consider allometric plasticity as apparent plasticity, the following conclusions can be made: (1) at the early two stages of 30 days and 50 days, plants in the dense populations produced active responses but did not suffer from the limitation of resources initially and then began to make substantial adjustments in allocation patterns in response to increasingly pronounced effects of resource competition, before any response in allometric growth; (2) when plants continued to grow at 70 days, competition led to mortality in the dense populations and had been severe enough to cause the lag of development in the surviving small
individuals, consequently leading to changes in their allometric relationships; (3) the variation or plasticity in allometric relationships, although regarded as apparent plasticity, may have implied the most intense effects of increasing density. Therefore, at 70 days, although the biomass allocation pattern of plants was unaffected by density, plant sizes had diverged into different classes, with disparate developmental states at different densities.

Two components in plasticity

The definition of plasticity did not define but implies that the difference in phenotype is a complex result of environmental effects (positive or negative) and active responses of organisms (Nicotra et al. 2010; Pigliucci 2005; van Kleunen and Fischer 2005). In other words, phenotypic plasticity intrinsically comprises two components of plant responses and environmental effects. In spite of its great significance to relevant investigations, no studies have attempted to disentangle the two components in the plasticity of a given trait. In this study, we have been trying to address this by virtue of covariance analysis. In covariance analyses, the variation in a given trait includes effects of both plant size and environment. If the response of plant size can reflect whether an environmental effect is benign or detrimental and the extent of such effect, then the effect of plant size in the variation of a given trait can be considered as an indirect environmental effect, and the remaining proportion of variation after removing the size effect indicates the direct response of the trait. For example, when plant size decreased in response to high vs. low density, it suggested high density was less beneficial than low density for plants. In the responses of modular traits to density, effects of plant size can be considered as an indirect effect of density (which was mostly adverse), while the variation in adjusted mean trait values reflected their actual responses. By discerning the two components in plasticity, we may be able to evaluate relative extents of environmental effects versus plant responses, which should be essential for understanding the nature of plasticity and its implications and consequences, as well as driving the progress of investigations on many associated issues that are of important ecological and evolutionary significances.

Stage-dependent plasticity in response to density

If we take both sets of analytical results into account and regard allometric plasticity as apparent plasticity, then uniform conclusions on plant response density in module Y can be reached for each stage as: (1) plants

Fig. 4 The three hypothetical cases (1–3) of conclusions on plasticity in a given module Y in response to environment (A, B) from both covariance analysis (a) and allometric analysis (b) in this study

![Fig. 4](image-url)
show true plasticity when results of ANCOVA show significant effects of density (whatever those of ANOVA are), but allometric analyses do not (Fig. 4 Case ①); (2) plants show apparent plasticity when results from ANOVA and allometric analysis show significant effects of density, but those from ANCOVA do not (Fig. 4 Case ②); (3) plants show both true and apparent plasticities when results of ANCOVA and allometric analysis show significant effects of density (whatever those of ANOVA are; Fig. 4 Case ③). Comprehensively, the two sets of results demonstrated the transition of the strategy of plants dealing with increased density. If plasticity in allocation traits and allometric relationships were true plasticity and apparent plasticity, respectively, then the stage dependence of plasticity in biomass allocation of A. theophrasti revealed the temporal shifts in effects of increased population density and plant growth strategy as: (1) at the 30 days and 50 days of plant growth when allocation traits responded to density but allometry remained stable, plants altered strategy of resource partitioning without changing growth rate or ontogenetic trajectory; (2) at 70 days when allometry responded to density but allocation traits did not, plants began to alter growth rate or developmental trajectory, leading to divergent developmental stages at different densities; and (3) stage-dependent plasticity in allocation traits and allometry suggested density effects became increasingly severe over time, as delayed developmental processes should be more detrimental than altered allocation strategy.

The model of growth allometry can also be successfully applied in understanding the diversity of leaf form and function (Price et al. 2007), and variation in growth allometry contributes to local adaptation to contrasting environments (Vasseur et al. 2018). Our results demonstrated that both optimal partitioning theory (OPT) and allometric growth play an important role in explaining how plants deal with complex density effects, depending on plant growth stage. Allometric plasticity, although regarded as apparent plasticity, represented a shift in developmental phase or state, indicating intensified effects of increasing density and weaker responsive ability of plants. By differentiating true plasticity and apparent plasticity that occurred at different stages, we were able to reveal the increasingly pronounced effects of density on plant individuals with later stages. The principles of metabolic production and biomass partitioning among different modules at the level of the individual plant and their responses to environmental factors can help understand connections between plant performance and ecosystem functioning (Enquist and Niklas 2001; Kost et al. 2005). The dynamic patterns in plant biomass allocation and growth allometry in response to biotic and abiotic environments should be useful in bridging the organismal ecology with the ecology at the population, community, and ecosystem levels (Enquist and Niklas 2001; Hulshof et al. 2012; Sides et al. 2014; Vasseur et al. 2018).

**Conclusion**

Our results showed that stage-dependent allometry did not coincide at the same stage as allocation plasticity and allometric plasticity, thereby suggesting one-stage allometric plasticity might be apparent plasticity, rather than traditionally assumed true plasticity. Plasticity in both allocation traits and allometric relationships in response to density varied with different growth stages. In response to increased density, plants initially altered the strategy of biomass allocation (true plasticity), then the allometry or growth rate (apparent plasticity), indicating density effects intensified over time. Plasticity in a given trait can be divided into two components of the indirect environmental effect (size effect) and the direct plant response (trait variation without size effect). The insights into apparent plasticity of allometry and two components of plasticity should be of essential importance to investigating phenotypic plasticity and its ecological and evolutionary implications, which may further drive investigations on functional traits in relation to community and ecosystem processes.

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**Author contributions** Both authors contributed to the study conception and design. SW conducted the experiment, collected the data, and performed statistical analyses. The first draft of the manuscript was written and edited by SW. All authors read and approved the final manuscript.

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Declarations

Conflict of interest No conflict of interests have been declared.

Appendix

See Table 4
See Table 5

Table 4 One-way ANCOVAs on log-transformed mean values of the mass of different modules, with population density (PD) as effect, and another module as a covariate (CV) at 30, 50, and 70 days of plant growth and across all stages

| Trait            | CV    | 30 d PD | 50 d PD | 70 d PD | All stages PD |
|------------------|-------|---------|---------|---------|---------------|
| Root             | Shoot | †       | †       | †       |               |
| Root             | Stem  | †       | ***     | †       |               |
| Root             | Lamina (leaf) | †     |         |         |               |
| Stem             | Lamina (leaf) |       | †       | ***     | ***           |
| Root             | Petiole | –      | –       | –       |               |
| Stem             | Petiole | –      | –       | ***     |               |
| Petiole          | Lamina | –      | –       | **      |               |
| Root             | Reproduction | –    | –       | ***     |               |
| Stem             | Reproduction | –    | –       | **      |               |
| Petiole          | Reproduction | –    | –       | *       |               |
| Lamina           | Reproduction | –    | –       | †       | ***           |

Significance levels: † P < 0.10, * P < 0.05, ** P < 0.01, *** P < 0.001

Table 5 One-way ANCOVAs on log-transformed mean values of the mass of different modules, with growth stage (GS) as effect, and another module as a covariate (CV) at low, medium, and high densities and across all densities

| Trait            | CV    | Low GS | Low GS × CV | Medium GS | Medium GS × CV | High GS | High GS × CV | All densities GS | All densities GS × CV |
|------------------|-------|--------|-------------|-----------|----------------|---------|--------------|------------------|-----------------------|
| Root             | Shoot | ***    | ***         | †         | **             | †       |              |                  |                       |
| Root             | Stem  | **     | ***         | **        | ***            | **      | **           | **               |                       |
| Root             | Lamina (leaf) | *    | ***         | *         | ***            | ***     | **           | **               |                       |
| Stem             | Lamina (leaf) | *** | ***         | ***       | ***            | ***     | ***          | ***              |                       |
| Root             | Petiole |       | ***         | *         | ***            | *       | **           | **               |                       |
| Stem             | Petiole | ***    | *           | ***       | †              | *       | ***          |                  |                       |
| Petiole          | Lamina | *      | *           | **        | **             | **      |              |                  |                       |
| Root             | Reproduction | *    | *           | **        | *              | **      |              |                  |                       |
| Stem             | Reproduction | *    | *           | **        | *              | **      |              |                  |                       |
| Petiole          | Reproduction | *    | †           | †         | †              | **      |              |                  |                       |
| Lamina           | Reproduction | *    | †           | †         | †              | **      |              |                  |                       |

Significance levels: † P < 0.10, * P < 0.05, ** P < 0.01, *** P < 0.001
Fig. 5  Mean total biomass (± SE) for plants at low (rectangle), medium (gray-filled rectangle), and high (black-filled rectangle) densities at 30, 50, and 70 days of growth. Different letters indicate significant differences among density treatments (LSD, $P < 0.05$).

Fig. 6  Mean values of root, stem, petiole, lamina (or leaf), reproduction, and branch mass for plants at low, medium, and high densities at 30, 50, and 70 days of growth. Different letters indicate significant differences among density treatments (LSD, $P < 0.05$).
Fig. 7 The log10–log10 regressive relationships among the mass of different modules for individuals at low (green square), medium (red triangle), and high (black circle) densities at 30 d of plant growth. *F* values with significance levels (*P* < 0.10; **P** < 0.05; ***P*** < 0.01; from ANCOVAs on effects of density on a module with another module as a covariate) denote the significant differences between densities.
Fig. 8 The $\log_{10}-\log_{10}$ regressive relationships among the mass of different modules for individuals at low (green square), medium (red triangle), and high (black circle) densities at 50 d of plant growth. $F$ values with significance levels ($^*P < 0.10; ^**P < 0.05; ^***P < 0.01$; from ANCOVAs on effects of density on a module with another module as a covariate) denote the significant differences between densities.
Fig. 9 The log₁₀–log₁₀ regressive relationships among the mass of different modules for individuals at low (green square), medium (red triangle), and high (black circle) densities at 70 d of plant growth. *F* values with significance levels (*P < 0.10; **P < 0.05; ***P < 0.01; from ANCOVAs on effects of density on a module with another module as a covariate) denote the significant differences between densities.
Fig. 10 The log_{10}–log_{10} regressive relationships among the mass of different modules for individuals at low (green square), medium (red triangle), and high (black circle) densities across all growth stages. $F$ values with significance levels (*$P < 0.10$; **$P < 0.05$; ***$P < 0.01$; from ANCOVAs on effects of density on a module with another module as a covariate) denote the significant differences between densities.
Fig. 11 The log10–log10 regressive relationships among the mass of different modules for individuals across all densities at 30 days (black circle), 50 days (red triangle), and 70 days (green square) of growth. $f$ values with significance levels (*$P < 0.10$; **$P < 0.05$; ***$P < 0.01$; from ANCOVAs on effects of density on a module with another module as a covariate) denote the significant differences between densities.

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