

Stage-dependent Plasticity in Biomass Allocation and Allometry of *Abutilon Theophrasti* in Response to Population Density

Shu Wang (✉ lnbx625@163.com)

College of Forestry, Forest Ecology Research Center, Guizhou University <https://orcid.org/0000-0002-5982-8641>

Dao-Wei Zhou

Northeast Institute of Geology and Agroecology, Chinese Academy of Sciences

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Abstract

How plants respond to density via modular plasticity is obscure, probably because relevant studies using covariance and allometry analyses rarely focus on multiple stages of plant growth, and also the two approaches are seldom used simultaneously in a same study. To address this issue, a field experiment was conducted by subjecting plants of *Abutilon theophrasti* to low, medium and high densities and measuring the mass of various plant modules, before covariance and allometry analyses at three stages of plant growth. Results showed inconsistent responses in allocation traits and allometric relationships at each growth stage. At 30 d, high density increased root:stem, root:leaf and stem:leaf ratios, but did not affect any allometric relationships. At 50 d, density altered most allocation traits, but not for allometric exponents. At 70 d, density altered allometric relationships, with no effects on allocation traits. The stage-dependent allometric relationships and inconsistent results of allometric and covariance analyses suggested one-stage allometric plasticity might be apparent plasticity. In response to the increase of density, plants first altered the strategy of biomass partitioning, then growth rate or developmental stage, indicating 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 left 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 implications in plants.

Introduction

The optimization 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 & Coleman 1999; Thornley 1972). For example, plants will increase root:shoot ratio at low water or nutrient availability, while increase stem mass allocation when light is limited (Aerts 1999; Poorter et al. 2012). The increase of population density may result in variations in multiple above- and belowground resources simultaneously (Casper & Jackson 1997). It is unclear how plants may alter the pattern of biomass allocation with increased density, when more than one kind of resources become limited. Density-induced extra stem elongation is regarded as a typical example of adaptive plasticity (van Kleunen & Fischer 2005), whereas how increased density may affect other modules of leaves, roots, branches and reproductive ones is unclear (Cheplick 2020; Japhet et al. 2009; Navas & Garnier 2002; Wang et al. 2017; Wang et al. 2006; Weiner et al. 2009). Different conditions can induce inconsistent local responses in a module or even a trait, and plasticity at the whole-plant level is the sum of all modular responses and their interactions (de Kroon et al. 2005; Wang et al. 2017). Relevant studies produced mixed results (Cahill Jr 2003; Müller et al. 2000; Shipley & Meziane 2002), probably because that they: 1) examined responses of root:shoot ratio to competition, with little information available on responses in various modules; 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 during reproductive periods; 3) neglected effects of plant growth stages as they often focused on a single stage. Not only the pattern of biomass allocation varies significantly along the lifetime of plants (Harper 1977), but also the intensity of among-plant competition shifts over time in a dense population (Hutchings & Budd 1981). It entails studies

that focus on multiple stages of plant growth or longer growth periods (Rudgers et al. 2019; Thompson 2019; Tobler & Nijhout 2010), to better understanding on how plants respond to density via plasticity in biomass allocation.

Coincidentally, there is also a lack of focus on multiple growth stages in allometry studies. The prevalence of allometric analyses in plasticity studies derived from that the consideration of size-dependence in allocation patterns. OPT has been questioned as it regards plant allocation as size-independent (Coleman et al. 1994; McCarthy & Enquist 2007), whereas almost all plant allocation patterns are size-dependent (Ogawa 2003; Pino et al. 2002). Variations in biomass allocation thus may not be due to environmental effects (“true plasticity”), but simply a result of (plant) size effects (“apparent plasticity”)(Weiner 2004). Covariate variance and allometry analyses are both approaches frequently used to examine true plasticity, via removing effects of plant size from trait variations. However, both sets of analyses have generally focused on a single stage of plant growth (Hill & Roberts 2017; Vizcaíno-Palomar et al. 2016). Nevertheless, both size-dependent allocation patterns and allometric relationships vary with growth stages (Thompson 2019; Wang et al. 2017), and allometry analyses across all stages differ significantly from one-stage allometry (Li et al. 2013). It is necessary to incorporate multiple growth stages in these studies (Wang et al. 2017; Weiner & Thomas 1992).

Finally but not the least importantly, covariance and allometry analyses have been most employed separately in respective studies. Studies using both variance and allometry analyses revealed inconsistent results, and often relied on explanations from the latter one (Huang et al. 2010; Müller et al. 2000). To investigate how plants deal with increased density via plasticity in biomass allocation, we conducted a field experiment on an annual species of *A. theophrasti*, by subjecting plants to three density treatments, and measuring or calculating mass ratio between various modules before covariance and allometry analyses at three stages of plant growth. We aimed to answer the following questions: 1) is there true plasticity in response to density in mass allocation and allometric relationships for various modules? 2) will responses of modular mass allocation and allometric relationships to density vary with different growth stages? 3) will the two sets of analyses provide consistent explanations for plant response to density?

Materials And Methods

Study species

Abutilon theophrasti Meic. (Malvaceae) is an old-field annual weedy species, which grows to a height of up to 1-1.5 m (Gleason & Cronquist 1991), reaching reproductive maturity within 90 days, and complete its life cycles in about five months (McConnaughay & 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 & Bazzaz 1992),

Experimental design

The experiment was conducted in 2007 at the Pasture Ecological Research Station of Northeast Normal University, Changling, Jilin province, China (44°45' N, 123°45' E). 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 . The nutrient contents of experimental field soil (aeolian sandy soil, $\text{pH} = 8.3$): organic C $3.1 \text{ mg}\cdot\text{kg}^{-1}$, available N $21.0 \text{ mg}\cdot\text{kg}^{-1}$, available P $1.1 \text{ mg}\cdot\text{kg}^{-1}$ during the growth season of 2007 (Zhao et al. 2010). Solid soluble grainy fertilizers ($(\text{NH}_4)_2\text{HPO}_4$, N: P = 18:46) were added before sowing at a rate of $20\text{g}\cdot\text{m}^{-2}$, to eliminate the uneven nutrient conditions of the experimental plots. The field was also covered with a layer of 5-10 cm virgin soil (meadow soil, $\text{pH} = 8.2$) transported from the nearby meadow to the north of the research station, to improve the quality of the soil conditions. With no cultivation history, the soil was naturally fertile (organic C $18.7 \text{ mg}\cdot\text{kg}^{-1}$, available N $47.5 \text{ mg}\cdot\text{kg}^{-1}$, available P $4.0 \text{ mg}\cdot\text{kg}^{-1}$) in the summer of 2007 (Zhang 2013).

A complete randomized block design was implemented, with three density treatments and three blocks. Density treatments included low, medium and high densities, 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 $121 \text{ plants}\cdot\text{m}^{-2}$. Each density had three blocks, randomly distributed into nine $2 \times 3 \text{ m}$ plots. Seeds were sown at initial densities that were a little higher than the target ones on June 7, 2007. Most seeds emerged four to five 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.

Data collection

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 to six individual plants were randomly sampled per replicate per density, making a maximum total of $6 \text{ individuals} \times 3 \text{ replicates} \times 3 \text{ densities} \times 3 \text{ stages} = 162 \text{ samplings}$. Each individual plant was separated into roots, stems, petioles, leaves, branches and reproductive organs (if available), oven-dried at 75°C for two days and weighed. Branches appeared at the third stage only, and were not incorporated in analyses. Plant total biomass and mass ratios between different modules were calculated (Table 1).

Statistical analysis

All data was 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 other traits were conducted first, with growth stage and density as main effects, 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, with total mass as a covariate in ANCOVA. Since regarding total mass as a covariate in ANCOVA has been questioned because total mass contains modular mass, we also conducted one-way ANCOVAs for each modular, with density or growth stage as effects, and another module as a covariate (Cahill Jr, 2003; Weijsschedé et al., 2006). Multiple comparisons used 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 & Coleman 1999; Weiner 2004; Wright & 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 of among the mass of various modules, including root mass, stem mass, petiole mass, lamina mass and reproductive mass (if available), were estimated by $\log_{10}$ -transformed regressions for each density and stage combination. Model Type II (reduced major axis [RMA]) regression analysis was used to determine scaling exponent, with $a_{\text{RMA}} = a_{\text{OLS}}/r$, where a_{OLS} is the ordinary least square scaling exponent and r is the ordinary least squares correlation coefficient. This regression is recommended when the variables of interest are biologically interdependent, subject to unknown measurement error (Nicklas, 1994; Wang et al., 2006). Effects of density or growth stage on allometric exponents (a) 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).

Results

Allocation

At the first stage, density had no effects on total mass; for the latter two stages, compared to low density, high and medium densities reduced total mass by average 58.15% and 46.95% respectively (LSD, $P < 0.001$ and $P < 0.01$; Table 2 and Fig. 4). Size effects contributed significantly to variations of most traits, while density still had significant effects on traits after removal of size effects (Table 2). Responses of allocation traits to density varied with different stages (Table 2, Fig. 1 and 5). At 30 d of growth, medium density relative to low density increased root mass ($P < 0.05$; Fig. 5), and medium and high densities increased root:stem ratio, root:leaf and stem:leaf ratios ($P < 0.05$; Fig. 1). At 50 d, compared to low density, high density increased stem mass ($P < 0.001$), decreased petiole, lamina and reproductive mass ($P < 0.05$) (Fig. 5); high density also decreased root:stem ratio ($P < 0.01$), petiole:lamina ratio ($P < 0.001$), reproductive:stem ratio and reproductive:lamina ratio ($P < 0.05$), increased stem:lamina and stem:petiole ratios ($P < 0.001$; Fig. 1). Little density effects were found on these traits at 70 d (Fig. 1 and 5).

Allometry

Allometric relationships among modules varied with different densities and stages (Table 3-6; Fig. 2 and 3). At 30 d and 50 d of growth, density had no or little effects on allometric relationships (Table 3, 5, 6 and Fig. 2). At 70 d, however, 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 (Fig. 2 and 3). 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 (Table 4).

Comparisons on allocation and allometry

Analyses of covariance (ANCOVA) and allometry revealed inconsistent results on responses of biomass allocation to density (Table 2, 3, 5, 6; Fig. 1-3). Allocation traits responded significantly to density but

allometric relationships did not at 30 d and 50 d, while only allometric relationships showed significant responses at 70 d. Comparisons on the r^2 of models for the two sets of analyses also varied with stages. At 30 d, the adjusted r^2 s for ANCOVAs were higher than those for allometric analyses, with 89.38% (ANCOVA) vs. 31.81% (allometry), 69.78% vs. 52.31% and 95.24% vs. 64.63% for the relationships between root mass and stem mass, root mass and leaf mass and stem mass and leaf mass respectively. At the latter two stages, allometric analyses had higher adjusted r^2 than ANCOVAs for all relationships, with average $88.54 \pm 1.91\%$ (allometry) vs. $44.91 \pm 11.02\%$ (ANCOVA) for relationships among vegetative modules and $66.56 \pm 2.72\%$ vs. $25.91 \pm 5.45\%$ for relationships between vegetative and reproductive modules at 50 d, and average $89.69 \pm 1.57\%$ vs. $30.47 \pm 6.25\%$ and $59.14 \pm 2.53\%$ vs. $9.83 \pm 2.20\%$ for these relationships at 70 d.

Discussion

Allocation plasticity

Our results showed plasticity of modular mass allocation in response to density varied with different stages of plant growth, and true plasticity mainly occurred at the earlier two stages. At the first stage, medium density increased root mass, root:stem and root:leaf ratios, consistent with other studies ([Gersani et al. 2001](#); [O'Brien et al. 2005](#)), indicating low to intermediate interactions is more likely to facilitate root growth, and root interactions occurred before aboveground interactions. In spite of no response in leaf mass, the significant increases of root:leaf and stem:leaf ratios by high relative to low density indicated a relatively lower investment of resource into leaves, than into stems and roots under competition. As plants grew larger at 50 d, they began to interfere with each other and competing for aboveground resources, when greater mass allocated to stems was required for an extra elongation ([Bell & Galloway 2007](#); [Weiner & Fishman 1994](#)). Greater stem mass and smaller mass allocated to other modules led to increased ratios of stem mass to other modular mass by high versus low density. Meanwhile, because of the greater importance of laminae to reproductive organs ([Cheplick 2006](#)), lamina:petiole and lamina:reproductive ratios also increased with density. The decreases in leaf mass and reproductive mass might be a cost of extensive stem elongation. 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 was found in root mass at this stage, consistent with some studies ([Cahill Jr 2003](#); [Casper et al. 1998](#)), but not with others ([Huang et al. 2010](#)). Under both competition and limited belowground resources, root allocation usually decreased, as resource deficiency aggravated belowground competition. However, the sufficient soil nutrients in this study may ameliorated root competition, leading to no response in root mass.

There has been less studies on responses of reproductive modules to density, which showed inconsistent results. Reduction of productive mass can be due to competition ([Gersani et al. 2001](#); [Japhet et al. 2009](#); [Murphy & Dudley 2007](#)), or just an effect of plant size ([Arenas et al. 2002](#); [Wang et al. 2006](#)). We found both decrease and canalization in reproductive mass and its ratios to other modular mass, indicating reproductive plasticity depends on specific stages. At the initial stage of reproduction, a trade-off occurs during resource distribution at the physiological level, either towards vegetative growth or towards reproduction ([Fox 1995](#)), as plant resource allocation or development is limited ([Karlsson & Méndez 2005](#);

Levins 1968). Increased vegetative mass was at the cost of reproductive mass, consistent with other studies (Álvarez-Cansino et al. 2010; Matsuyama & Sakimoto 2008).

At 70 d, we did not find responses in any modular mass or allocation traits. This may be due to attenuated competition and its effects over time. As plants grew, competition increases and then decreases over time in a dense population (Hutchings & Budd 1981), resulting in shifts in resource availability and plant-plant interactions (Bouvet et al. 2005; Zhou et al. 2005). As plants continued to grow in the dense populations, reaching its carrying capacity, smaller individuals may be obsoleted (Hutchings & Budd 1981), and competition attenuated again.

Allometric plasticity

Our results showed plasticity in mass allocation and allometric relationships did not coincide. We found true plasticity in allocation after removal of size effects in covariance analyses, as well as the growth-dependence in allometric relationships. Growth period or duration can significantly affect the pattern of allometry (Thompson 2019; Tobler & Nijhout 2010), results from allometry analyses based on single stages differs from those across difference 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 true plasticity. If the one-point allometric plasticity is apparent plasticity, plasticity of developmental trajectory might also be apparent plasticity per se. Because differences in developmental trajectories should be caused by shifts in allometric relationships at one or multiple points. Therefore allometric plasticity might be only a function of plant size or developmental rate.

An organism is capable to buffer developmental pathways against genetic or environmental perturbations (Kitano 2004; Masel & Siegal 2009; Mestek Boukhibar & Barkoulas 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 & Lens 2000). Once the equilibrium is broken, deviation from developmental trajectory due to mis-regulation of allometry might be lethal (Vea & Shingleton 2020) and prevented as best as possible. The ability to maintain developmental stability is thereby 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) and the highly stabilized allometric pattern between size and shape of *Drosophila* wings over 40 million years (Houle et al. 2019). Voje et al. (2013) analyzed over 300 empirical estimates of allometry, and also 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).

Plant strategy revealed by stage-dependent allocation and allometry plasticity

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: 1) at the first and second stages when allocation traits responded to density but allometry remained stable at the earlier stages, plants altered strategy of resource partitioning without changing growth rate or ontogenetic trajectory; 2) at the third stage 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.

Two components in trait plasticity

The definition of plasticity did not define but explicitly 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 & 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 plasticity of a given trait. In this study, we are 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 density. If the response of plant size can reflect whether an environmental effect is benign or malignant and its extent, then the effect of plant size in the variation of a given trait can be considered as an indirect environmental effect, and the left proportion of variation after removal of 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 and consequences of plasticity.

Conclusions

Our results showed the stage-dependent allometry and the inconsistency between results from two sets of analyses, suggesting one-stage allometric plasticity might be apparent 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 after removal of the 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 implications in plants.

Declarations

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Compliance with ethical standards

Conflict of interest No conflict of interests have been declared.

Authors' contributions

Both authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Shu Wang. The first draft of the manuscript was written by Shu Wang and both authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Tables

Table 1. Abbreviations for traits and measurement stages (1st, 2nd and 3rd stages). LM was leaf mass, including lamina and petiole mass for the first stage and across all stages.

Abbrev.	Trait	Stage
TM	Total mass	1 st , 2 nd , 3 rd
RM	Root mass	1 st , 2 nd , 3 rd
SM	Stem mass	1 st , 2 nd , 3 rd
LM	Lamina (leaf) mass	1 st , 2 nd , 3 rd
PM	Petiole mass	2 nd , 3 rd
REM	Reproductive mass	2 nd , 3 rd
R/S	Root:stem ratio	1 st , 2 nd , 3 rd
R/L	Root:lamina (leaf) ratio	1 st , 2 nd , 3 rd
S/L	Stem:lamina (leaf) ratio	1 st , 2 nd , 3 rd
R/P	Root:petiole ratio	2 nd , 3 rd
S/P	Stem:petiole ratio	2 nd , 3 rd
P/L	Petiole:lamina ratio	2 nd , 3 rd
RE/R	Reproductive:root ratio	2 nd , 3 rd
RE/S	Reproductive:stem ratio	2 nd , 3 rd
RE/L	Reproductive:lamina ratio	2 nd , 3 rd
RE/P	Reproductive:petiole ratio	2 nd , 3 rd

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. Abbreviations for all traits are in Table 1. Significance levels: * P < 0.05, ** P < 0.01, *** P < 0.001.

1 st stage				2 nd stage			3 rd stage		
Trait	TM		PD	TM		PD	TM		PD
	N	(Df = 1)	(Df = 2)	N	(Df = 1)	(Df = 2)	N	(Df = 1)	(Df = 2)
TM	42		1.30	50		13.46***	41		14.75***
RM	42	28.25***	3.64*	50	460.23***	2.27	41	190.63***	0.70
SM	42	109.53***	0.87	50	1228.89***	23.45***	41	1634.31***	1.92
LM	42	4478.93***	0.82	50	3392.04***	11.77***	41	666.70***	3.44*
PM				50	2577.90***	33.71***	41	538.60***	0.50
REM				39	88.12***	3.04	41	45.65***	0.17
BM							31	194.49***	3.07
R/S	42	12.25**	143.36***	50	1.81	9.56***	41	3.70	0.66
R/L	42	0.23	38.76***	50	0.09	0.04	41	5.41*	2.19
S/L	42	15.71***	350.97***	50	6.61*	22.53***	41	0.31	4.39*
R/P				50	21.05***	2.28	41	2.16	1.79
S/P				50	46.80***	35.74***	41	16.91***	1.61
P/L				50	67.90***	10.71***	41	37.90***	0.36
RE/R				39	4.70*	1.56	41	0.67	0.12
RE/S				39	10.75**	5.13*	41	2.22	0.06
RE/L				39	6.01*	2.28	41	2.34	0.35
RE/P				39	1.12	1.18	41	0.13	0.31

Figures

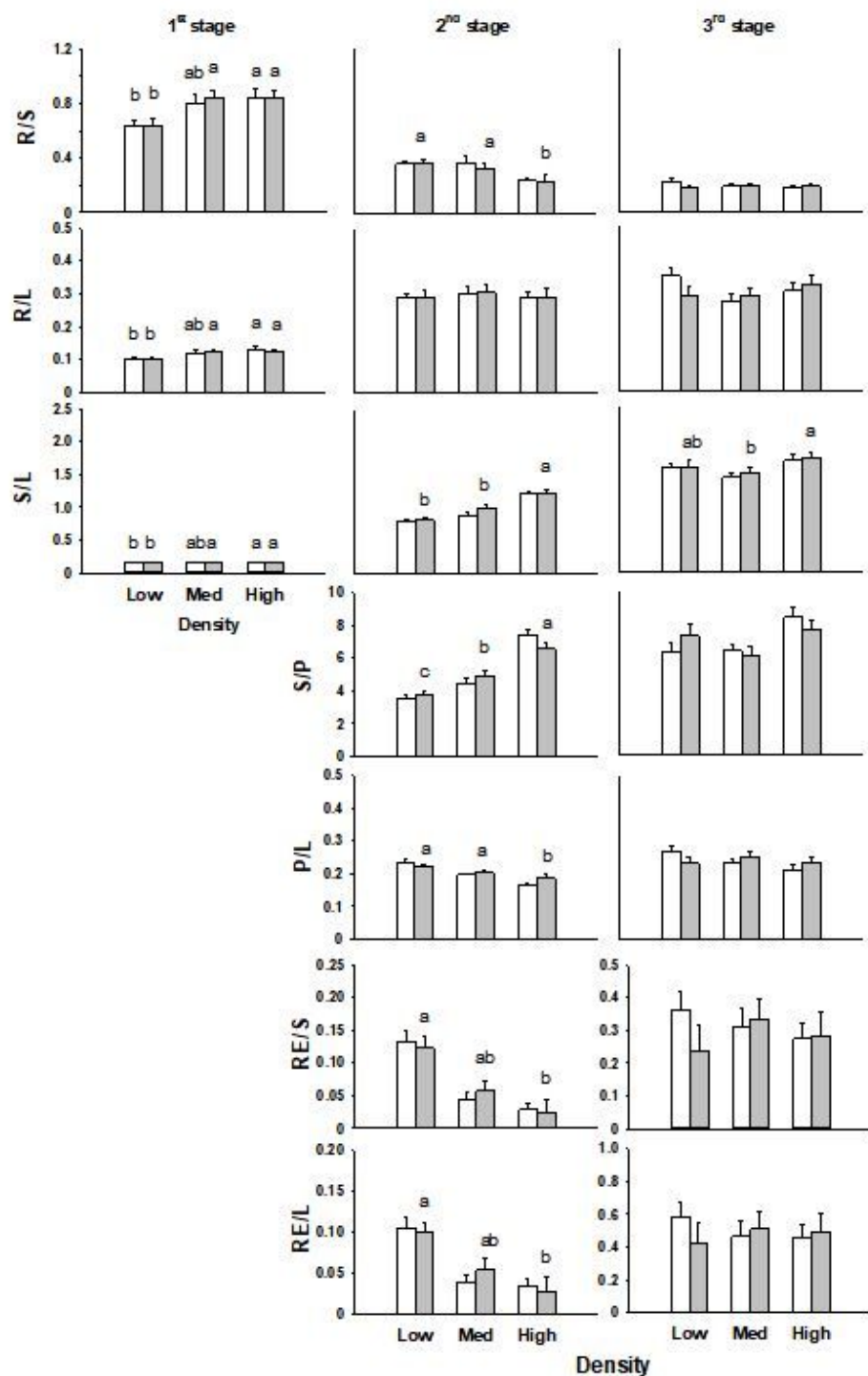


Figure 1

True (white) and adjusted (gray) mean values of the mass ratios ($\pm$ SE) between various modules in response to population density for plants at the 1st, 2nd and 3rd stages. Different letters indicate significant differences among density treatments within each stage in ANCOVA ($P < 0.05$). Abbreviations for all traits are in Table 1.

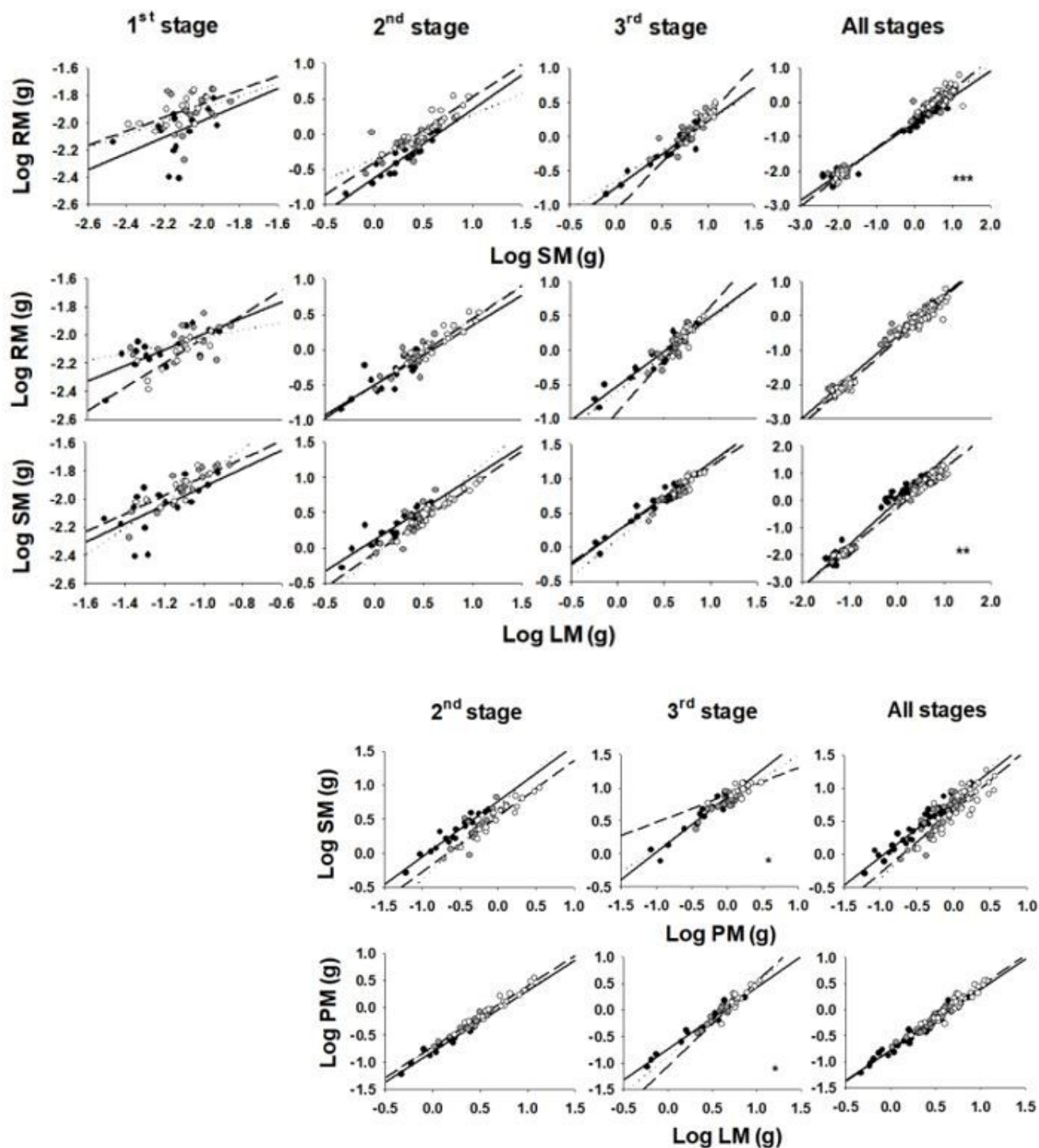


Figure 2

Log10-log10 regression on the mass of vegetative modules in response to density at the 1st, 2nd and 3rd stages. White (dashed line), gray (dotted line) and black (solid line) circles represent trait values of plants at low, medium and high densities respectively. Significant differences in these relationships between densities were denoted as: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Abbreviations for all traits are in Table 1. LM means leaf mass for the first stage and across all stages.

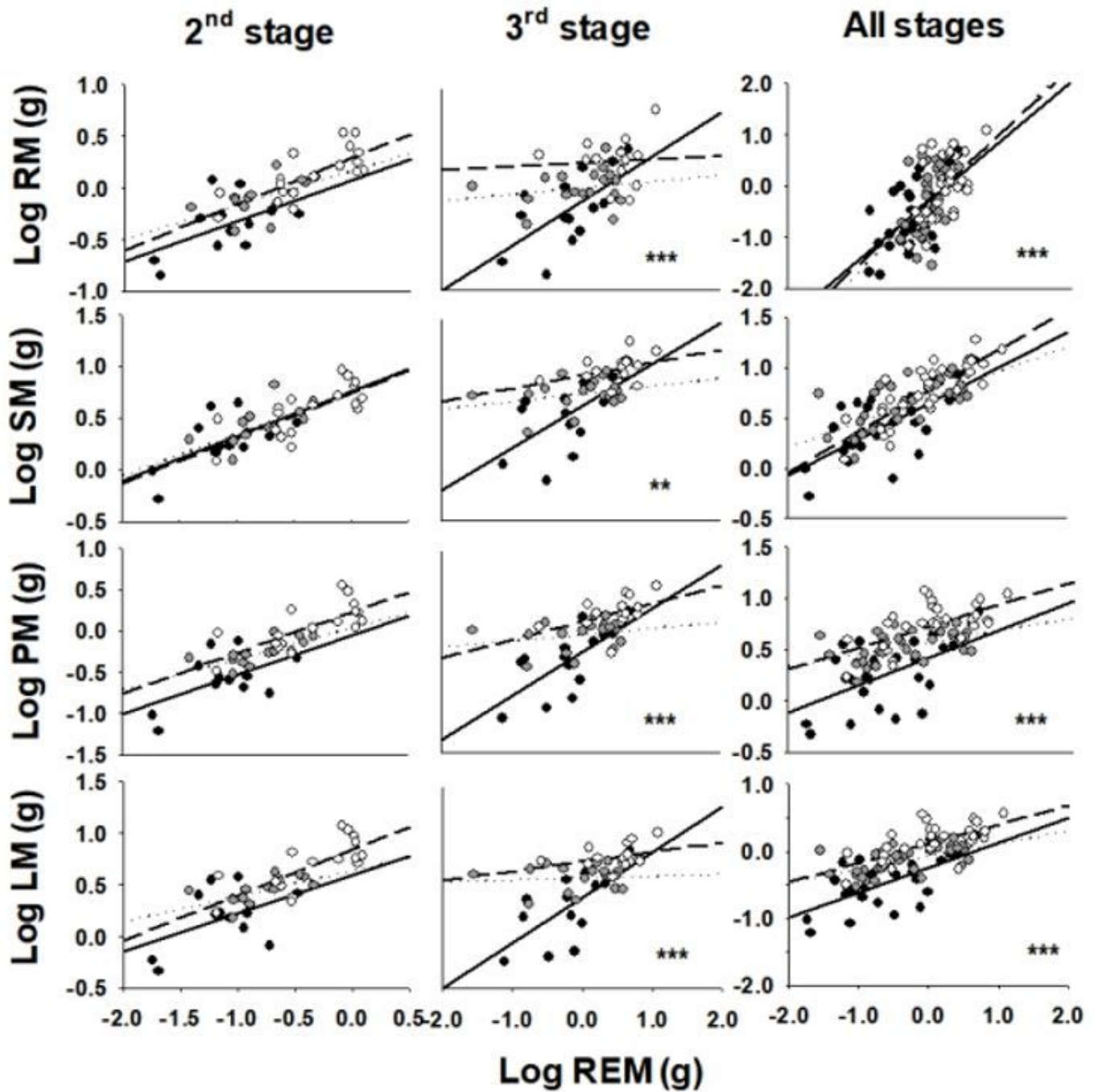


Figure 3

Log10-log10 regression on the mass of various vegetative modules against reproductive mass in response to density at the 2nd and 3rd stages. White (dashed line), gray (dotted line) and black (solid line) circles represent trait values of plants at low, medium and high densities respectively. Significant differences in these relationships between densities were denoted as: * P < 0.05, ** P < 0.01, *** P < 0.001. Abbreviations for all traits are in Table 1. LM means leaf mass for the first stage and across all stages.