

Dynamic architectural responses of morphological traits to emergence time in *Abutilon theophrasti* (Malvaceae)

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Research Article

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Abstract

How plants respond to the complex environmental changes via phenotypic plasticity has not been well documented. Dynamic architectural analysis provides a valuable approach to understanding the strategies of plants in response to variation in emergence time. To investigate how plants respond to emergence time via dynamic architectural plasticity, we conducted a field experiment by sowing plants of *Abutilon theophrasti* at different dates to make them emerge in different growth periods, and measured a series of mass and morphological traits in different vertical layers of plants at different stages. Plant architecture can vary over time, and branches played a significant role in modifying the distribution of modules long different layers. The layers with greatest total mass went up higher over time, a delay of emergence time caused more upper layers with the greater total layer mass than lower layers. The layers with the greatest total layer mass were mainly ascribed to greater allocation of leaf and reproductive mass. Plants of *A. theophrasti* tended to allocate greater mass to leaf and reproductive mass in higher layers with later emergence at day 50 and had petiole length decreasing with higher layers day 70. Results suggested plants can avoid the shading of its upper leaves and branches through additional elongation of petioles, and branches play a significant role in modifying the distribution of modules long different layers. Plants are able to optimize the sunlight acquirement though modifying architectural traits over time, and allocating more energy to the leaves and reproductive branches in the top layers is the most efficient strategy for maximizing light acquirement.

Introduction

Emergence time can have substantial influences on plant growth and reproduction subsequently, since plants that germinate in different periods can be exposed to different environments of great complexity. How plants respond to the complex environmental changes via phenotypic plasticity, defined as the ability of a genotype to produce different phenotypes under different environmental conditions (Bradshaw 1965), has not been well documented. The plasticity in plant architecture is an important strategy of adaptation towards environmental challenges (Sarlikioti et al. 2011; Teichmann & Muhr 2015). Architectural analysis provides a valuable approach to understanding the strategies of plants in response to variation in emergence time.

Either advanced or delayed emergence may have both advantages and disadvantages, there may be an optimal emergence timing for plants in terms of overall performance in adaptation to unpredictable environments (Gremer et al. 2020; ten Brink et al. 2020). A number of traits can respond to emergence time, contribute to the adaptation of plants in different subsequent environments (unpublished data). However, we know little about how plants emerging at different times improve performance through modulating different morphological traits. Since plasticity often occur at scales smaller than an individual (Stark 1994; Wilson 2000), or at the level of modules. Modules at different positions are probably exposed to varying abiotic conditions, and phenotypic response at the whole-plant level constitutes integrated responses of plant modules and characters (de Kroon et al. 2005), the local responses may be different and even contrary (Wang & Zhou 2021). Shifts in emergence time is very

likely to induce different responses in different modules and cause cascading effects on fitness (Gremer et al. 2020), and different local responses may interact to determine the final phenotype of plants. The responses of different modules and their interactions have been the central focus of investigation on plasticity in plant architecture. It is reported season is the more important driver of plant architecture of white clovers than neighbor or genetic basis (Nölke et al. 2021), suggesting significant effects of emergence time on plant architecture, but has not been empirically proved.

Plant architecture is an important trait influencing crop growth, yield, and stress resistance (Guo et al. 2020; Wang & Li 2006), and it has become an important research field in evolutionary plant ecology (Barthélémy & Caraglio 2007), providing the basis for more advanced research in plant sciences (Fourcaud et al. 2008; Guo et al. 2011). The architecture of a plant characterizes the nested hierarchical distribution of modular units over the entire course of growth (Barthélémy & Caraglio 2007; de Kroon et al. 2005). Investigation on plasticity in plant architecture, however, has mainly been used for agronomic purposes, such as enhancing crop yield and stress resistance (Gao et al. 2019; Kaggwa-Asiimwe et al. 2013; Reta-Sánchez & Fowler 2002; Yang et al. 2019). Few studies have focused on theoretical investigation with this tool. Also the approach of architectural analysis to separating endogenous developmental processes from environment-induced plasticity (Barthélémy & Caraglio 2007) coincides with the needs of differentiating true plasticity from apparent plasticity (Coleman et al. 1994; McCarthy & Enquist 2007; McConnaughay & Coleman 1999; Weiner 2004). Studies on architectural plasticity based on multiple stages of plant growth can provide even more detailed dynamic information, as plants at different stages may stay in contrasting developmental states due to changes in vigor (Carlsson & Callaghan 1991; Falinska 1985).

To investigate how plants respond to emergence time via dynamic architectural plasticity, we conducted a field experiment by sowing *Abutilon theophrasti* plants at different dates to make them emerge in different growth periods. Then we divided each sampled plant into different vertical layers, and measured a series of mass and morphological traits in different layers on the plant for each treatment of emergence time at different stages, to answer the following questions: 1) is there any difference among different layers in modular traits for plants that emerge in different periods? 2) do variations in these traits due to layer effects vary with different growth stages or emergence times?

Materials And Methods

Plant materials

Abutilon theophrasti Meidicus (Malvaceae) is native to China and India but is now distributed worldwide. It is an annual semi-shrub herbaceous species, with alternate and round hearted leaves of 5–10 cm in length, petioles of 3–12 cm, yellow solitary flowers of 5 lobes, and hemispheric capsules (Appendix Fig. 7). It grows rapidly, usually to a height of up to 1–1.5 m (Gleason & Cronquist 1991). It also produces abundant branches with several leaves, flowers, and fruits on them, especially when entering the stage of reproduction. It reaches reproductive maturity within 90 days, and completes its life cycle in ~ 5 months

(McConnaughay & Coleman 1999). It colonizes relatively nutrient-rich habitats, being ubiquitous in open fields, on roadsides, and in gardens, with substantial plasticity in allocation, morphology, and architecture in response to varying environmental factors (McConnaughay & Bazzaz 1992).

Experimental design

We conducted the field experiment in 2007 at the Pasture Ecological Research Station of Northeast Normal University, Changling, Jilin province, China (44°45' N, 123°45' E). The original soil of experimental field (aeolian sandy soil, pH = 8.3) at the station had been used annually for many years, thereby low in nutrients availability (organic C 3.1 mg kg⁻¹, available N 21.0 mg kg⁻¹, and available P 1.1 mg kg⁻¹) during the growth season of 2007 (Zhao et al. 2010). Seeds of *A. theophrasti* were collected from local wild populations near the research station in late August 2006 and dry stored at -4°C. We applied a complete randomized block design, with four treatments of emergence time (ET) and three blocks (Table 1). The whole plot was divided into twelve 2 × 3 m sub-plots, which were randomly assigned with ET treatments and blocks. Seeds of *A. theophrasti* were sown at an inter-planting distance of 10 cm on June 7, June 27, July 17 and August 7, as four ET treatments of spring (ET1), late spring (ET2), summer (ET3) and late summer (ET4). The treatments of emergence timing accorded with the time range of emergence of *A. theophrasti* in its nature habitats in northeast of China. Most seeds emerged four days after sowing. Seedlings were thinned at four-leaf stage and plots were hand-weeded when necessary and watered regularly.

Table 1
The information on treatments of emergence time, and planting date and sampling time in this study.

Emergence time	Abbreviation	Planting date	Sampling	Growth period (d)
Spring	ET1	Jun. 7	I	50
			II	80
			III	110
Late spring	ET2	Jun. 27	I	50
			II	70
			III	90
Summer	ET3	Jul. 17	I	30
			II	50
			III	70
Late summer	ET4	Aug. 7	I	30
			II	40
			III	50

Data collection

For each treatment, we arranged three to four times of sampling, according to their growth stages and the lengths of life cycle, and generally sampled them at the stages of vegetative growth, late vegetative or early reproductive growth, and middle to late reproductive growth respectively (Table 1). For individuals that emerged in spring (ET1), we took an additional sample at their early vegetative growth stage as an extra sample (EX), as a second reference (the first one is the vegetative growth stage) for comparison with the first samplings of other treatments, since the plants emerged early had a prolonged vegetative growth. At each harvest, five to six individual plants were randomly chosen from each plot, making a maximum total of $6 \text{ replicates} \times 3 \text{ blocks} \times 4 \text{ treatments} \times 3 \text{ harvests} + 6 \text{ replicates} \times 3 \text{ blocks} \times 1 \text{ treatments (SP)} \times 1 \text{ harvest} = 234 \text{ samplings}$. Each individual was divided into different vertical layers along the main stem from bottom to top with an inter-layer distance of 10 or 20 cm (according to the total stem length of a plant), before the following traits were measured (if applicable): main root length, diameter at the basal of the main root, length and number of lateral roots (above or equal to 1 mm in diameter along the main root), the length of stem, diameter at the base of stem, petiole length and angle, leaf number, lamina width (leaf size; abbreviations for all traits are in Table 2). For individuals from ET1 and ET4 treatments, some traits were unavailable for measurement at early growth stages due to small plant sizes. Each plant individual was then separated into roots, stems, petioles, laminas, reproductive modules and branches (if there were any), oven-dried at 75°C for two days and weighed. Reproductive modules consisted of flowers and fruits produced along the main stem and branches, and branches included the stems and leaves on branches. Total mass and mass allocation traits were calculated.

Table 2

Abbreviations for all traits, emergence treatments and measurement stages in this study.

Trait	Unit	Abbreviation	Emergence time	Growth stage (d)
Total mass	g	TM	ET1-4	I, II, III
Total layer mass	g	TLM	ET1-4	I, II, III
Main root mass	g	MRM	ET1-4	I, II, III
Lateral root mass	g	LRM	ET1-4	I, II, III
Stem mass	g	SM	ET1-4	I, II, III
Petiole mass	g	PM	ET1-4	I, II, III
Lamina mass	g	LM	ET1-4	I, II, III
Reproductive mass	g	REM	ET1-4	I, II, III
Branch stem mass	g	BSM	ET1-3	II, III
Branch leaf mass	g	BLM	ET1-3	II, III
Branch reproductive mass	g	BREM	ET1-3	II, III
Main root length	cm	MRL	ET1-4	I, II, III
Main root diameter	mm	MRD	ET1-4	I, II, III
Lateral root length	cm	LRL	ET1-4	I, II, III
Stem length	cm	SL	ET1-4	I, II, III
Stem diameter	mm	SD	ET1-4	I, II, III
Petiole length	cm	PL	ET1-4	I, II, III
Petiole angle	°	PA	ET1-4	I, II, III
Branch length	cm	BL	ET1-3	II, III
Branch angle	°	BA	ET1-3	II, III

Statistical analysis

Statistical analyses were conducted using SAS statistical software (SAS Institute 9.0 Incorporation, 2002). All measured and calculated traits were used for analysis (Table 2). To minimize variance heterogeneity, all data was log-transformed (petiole angles and branch angles were square root-transformed) before statistical analyses. Firstly, a one-way ANOVA was used to test the effect of density on total mass. Then four-way (three-way) ANOVAs were performed to test the effects of growth stage, emergence time, (module type), plant layer, and their interactions on mean values of modular traits. For each stage, the effects of plant layers on all traits within each of the other factors in combination were

analyzed by a one-way ANOVA, and the effects of emergence time on all traits per layer were analyzed by a one-way ANCOVA with total biomass as a covariate. For a given trait, significant contribution of total biomass (plant size) to its variation in response to emergence timing indicates an occurrence of apparent plasticity (McConnaughay & Coleman 1999). When effects of total mass were removed, the variation due to emergence time in trait expression was an indication of true plasticity (Weiner 2004). Multiple comparisons used the Least Significant Difference (LSD) method in the General Linear Model (GLM) program, which produced adjusted mean values and standard errors in one-way ANCOVA.

Results

Plants emerging in late spring (ET2) had the greatest total mass at the second and third stages (LSD, $P < 0.05$; Appendix Fig. 8). Plants emerging in spring (ET1) and late spring (ET2) also had greater stem mass and allocation and stem length than others ($P < 0.05$), while late-emerging plants (ET3 and ET4) showed higher petiole and lamina mass allocation than others ($P < 0.05$), and ET2 and ET3 had the greatest reproductive mass and allocation ($P < 0.05$; Appendix Figs. 9, 10).

For the modular mass per layer, effects of emergence time, growth stage, modular type and layer and their interactions were significant in most cases (Table 3; Appendix Table 5). Generally for plants in all treatments at all stages, stem mass decreased with higher layers, and main root mass and lateral root mass decreased with lower layers (Fig. 1–4). For those emerged in spring (ET1), they had the greatest petiole and lamina mass, with the greatest total layer mass in the top layer (at the height of 40 cm) than in other layers at day 50 (ANOVA, $P < 0.001$), but had the greatest petiole, lamina and reproductive mass, with the greatest total layer mass in the layer of 60 cm at day 80 ($P < 0.05$), and the layer with greatest total layer mass (also with greater branch leaf mass than layer of 60 cm) became 80 cm at day 110 ($P < 0.05$; Fig. 1). For plants that emerged in late spring (ET2), compared to that in other layers, they had higher total layer mass in layers of 40–50 cm at day 50 ($P < 0.05$), in layers of 40–60 cm at day 70 ($P < 0.05$), and in layers of 60 and 80 at day 90 ($P < 0.05$; Fig. 2). The plants that emerged in summer (ET3) had the highest lamina mass and total layer mass in the layer of 30 cm at day 50 ($P < 0.05$), had higher total layer mass from 20 to 40 cm at day 70 ($P < 0.05$; Fig. 3). The plants that emerged in late summer (ET4) had the highest total layer mass in the layer of 20 cm at day 40 ($P < 0.05$), and in the layer of 30 cm at day 50 ($P < 0.05$; Fig. 4).

Table 3
Four-way ANOVA on modular mass per layer of plants, with emergence time (ET), growth stage (GS), module component (MC), and layer (LA) as effects.

Source of variation	<i>df</i>	<i>F</i>	<i>p</i>
ET	3	46.523	< 0.001
GS	2	80.945	< 0.001
MC	8	45.109	< 0.001
LA	4	9.650	< 0.001
ET × GS	3	3.264	0.021
ET × MC	21	11.287	< 0.001
ET × LA	9	3.948	< 0.001
GS × MC	13	29.435	< 0.001
GS × LA	6	15.463	< 0.001
MC × LA	21	4.387	< 0.001
ET × GS × MC	15	5.001	< 0.001
ET × GS × LA	9	0.573	0.820
ET × MC × LA	27	2.459	< 0.001
GS × MC × LA	14	2.709	0.001
ET × GS × MC × LA	14	0.596	0.870

For the morphological traits per layer, effects of emergence time, growth stage and layer and their interactions were mostly significant for stem diameter, petiole length and angle (Table 4; Appendix Table 5). Generally across all treatments, stem diameter of plants decreased with higher layers, and this trend became more pronounced at later stages ($P < 0.05$; Fig. 5). They also had petiole length decreasing with higher layers at the second stage ($P < 0.05$; Fig. 6b, g, l, o), but not at the first stage (Fig. 6a, f, k), or had even increasing petiole length with higher layers at the third stage ($P < 0.05$; Fig. 6c, h, m, p). The petiole angle did not differ among different layers for all ET treatments and stages (data not shown).

Table 4

F-values for three-way ANOVA on all morphological modular traits per layer, with growth stage (GS), population density (PD), and layer (LA) as effects. Abbreviations: SD stem diameter; PL petiole length; PA petiole angle; BL branch length; BA branch angle. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Source of variation	df	SD (mm)	PL (cm)	PA (°)	BL (cm)	BA (°)
ET	3	54.533***	28.703***	28.919***	0.063	0.585
GS	2	21.259***	22.908***	123.798***		
LA	4	72.572***	2.156	7.723***	0.451	0.478
ET × GS	3	11.687***	9.831***	13.578***		
ET × LA	8	5.715***	18.995***	1.355	0.556	1.749
GS × LA	6	15.047***	7.958***	2.270		
ET × GS × LA	9	0.895	3.398*	1.273		

Comparing the distributions of traits among layers of plants that emerged in different periods, we found that at day 50, plants tended to allocate greater mass to leaf and reproductive mass in higher layers (30–50 cm for ET1, 2 and 20–30 cm for ET3, 4), with later emergence (Fig. 1a, Fig. 2a, Fig. 3b, Fig. 4c). However, at day 70–80, plants of ET2 and ET3 had greater mass allocated to leaves, reproductive organs and branches in lower layers (40 cm for ET1 and ET2, and 20–40 cm for ET3), compared to those of ET1 (Fig. 1b, Fig. 2b, Figure 3c). In addition, plants of ET1 and ET2 had thicker stems in layers of 10–30 cm than those of ET3 and ET4 (Fig. 5), while plants of ET3 and ET4 at day 50 had similar distribution of petiole length among layers as ET1 and ET2 at day 70–80 (Fig. 6b, g, l, p). At the third stage, plants of ET2 had branches mainly in layers of 60–80cm, but those of ET1 and ET3 had branches distributed over more layers (Fig. 1c, d, Fig. 2c, d, Fig. 3c, d, Fig. 6e, j, n).

Discussion

Plant architecture can vary significantly over time and with environmental factors. By architectural analyses, we found plant strategies in light acquirement: the top-priority strategy and the trade-off strategy in energy allocation between layers, reflected by the time-over changes in plant architecture. Generally, across all treatments, results showed that the stem, leaf and reproductive organs of plants can grow in vertical and horizontal directions simultaneously. The delay of emergence led to an increase of leaf and reproductive mass in upper layers at earlier stages, which mainly contributed to the earlier initiation of reproduction at smaller sizes for late-emerged plants (Zhou et al. 2005).

The exact positioning of leaves inside the canopy of a plant is crucial for optimal photosynthesis. Mantilla-Perez et al. (2020) have shown that Sorghum has a “smart canopy” architecture with more vertical leaves on top and more horizontal lower leaves to optimize light interception over the entire plant (Mantilla-Perez et al. 2020). We did not find the differences in petiole angle between different layers of

leaves, but found significant differences between layers in petiole length. Results revealed the most vibrant layers were the top 2–3 ones, which tended to have longer petioles with lower positions. This may be because the leaves in the top 2–3 layers of a plant are able to avoid the shading of its upper leaves and branches, through additional elongation of petioles. It suggested the length of petioles is very important for plants to maximize light acquirement. However, as plants grew, the increase of branches can alter the distribution of petioles, probably due to the shading of branch leaves in upper layers and the withering main-stem leaves in lower layers. This implied that plant architecture can vary over time, and branches play a significant role in modifying the distribution of modules long different layers.

The transition to flowering typically releases the lateral buds from apical dominance, allowing short branching (Gaarslev et al. 2021). The branches generated in flowering periods should be reproductive branches. These branches and main-stem leaves and reproductive structures mainly distributed in the top three layers, with the leaves in lower layers gradually declining, as they were inefficient in light acquirement. However, plants that emerged in spring (ET1) also had branches and reproductive modules in the lower layers, suggesting a non-optimal architecture for light acquirement. Consequently, ET1 plants had lower final performance with a longer growth periods, than ET2 plants. Therefore, distributing energy evenly among different layers should be the inefficient for foraging light, and a delay of emergence can lead to accelerated growth of leaves and reproductive organs in upper layers. These demonstrated that plants are able to optimize the sunlight acquirement though modifying architectural traits over time. They tended to allocate energy to the layers or modules that were the most efficient in light-acquiring or shade-avoiding.

Declarations

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

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Conflict of interest No conflict of interests have been declared.

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Figures

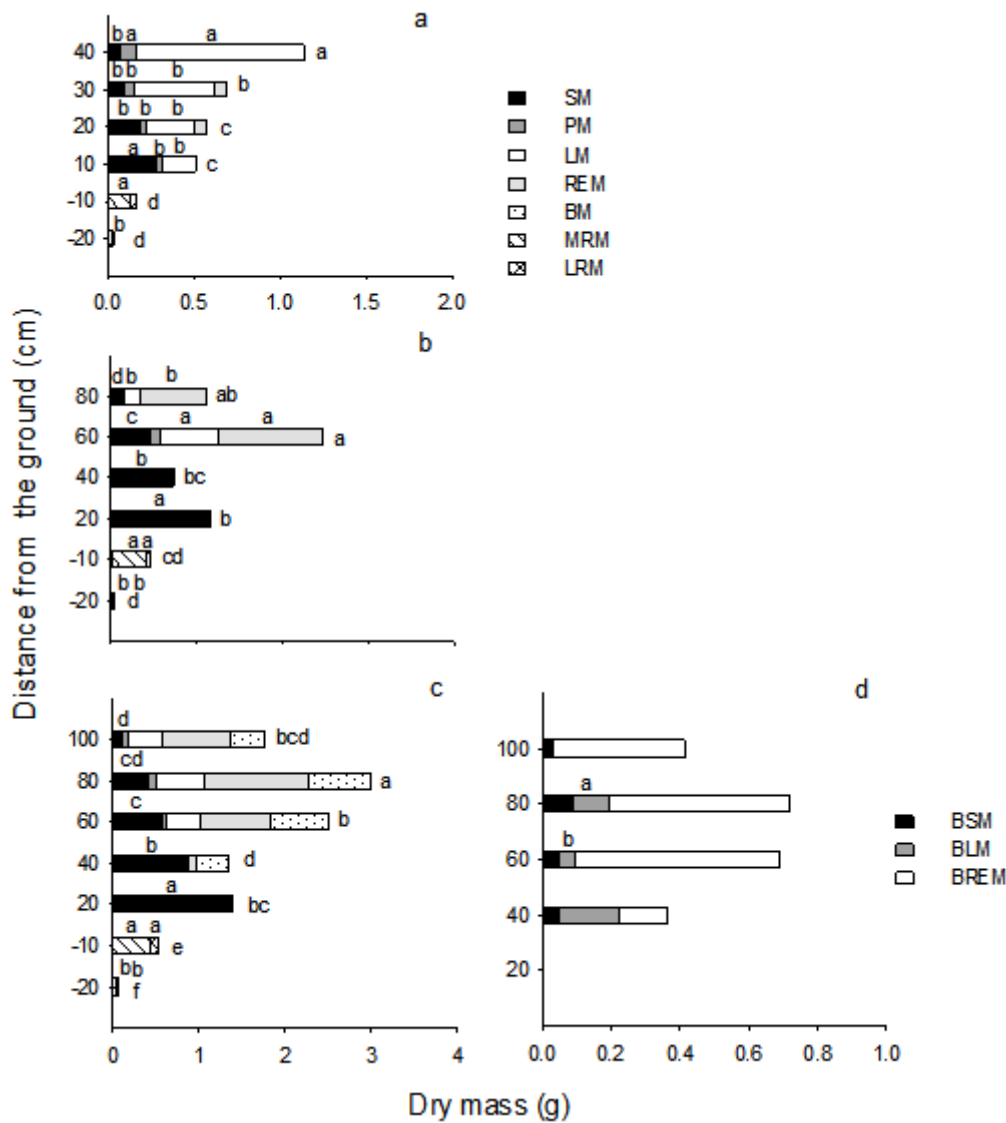


Figure 1

Biomass allocation in different layers (divided every 10 or 20 cm along the vertical direction of the main stem) of plants that emerged in spring (ET1) at day 50 (a), 80 (b) and 110 (c, d) of growth. The values in layers of -10 and -20 cm indicate the main and lateral root mass. Different lowercase letters denote significant differences among layers for each module (above the bars) and among layers for total layer mass (to the right of bars), compared by the Least Significant Difference (LSD) method from ANOVA ($p < 0.05$). SM stem mass; PM petiole mass; LM lamina mass; REM reproductive mass; BSM branch stem mass; BLM branch leaf mass; BREM branch reproductive mass; MRM main root mass; LRM lateral root mass.

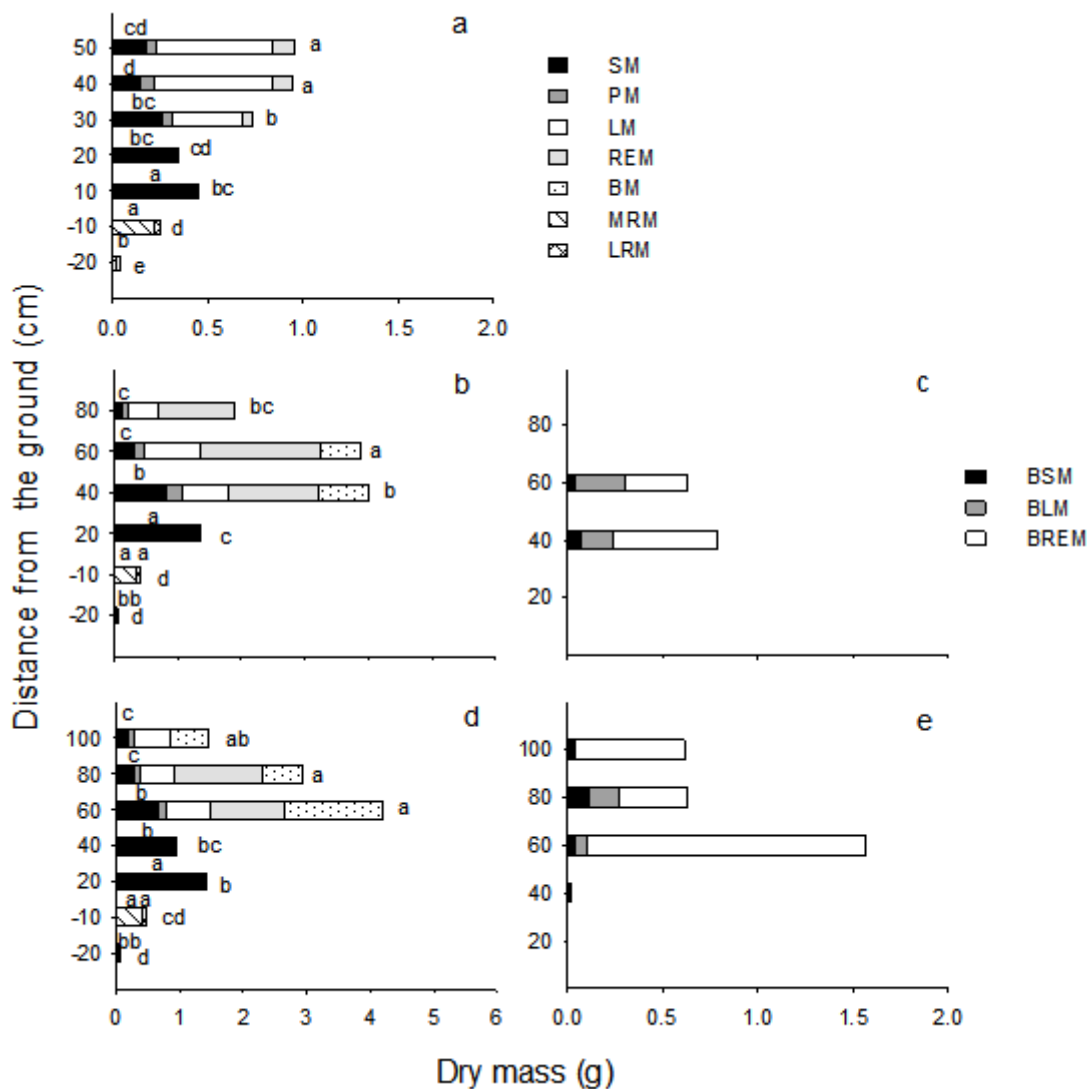


Figure 2

Biomass allocation in different layers (divided every 10 or 20 cm along the vertical direction of the main stem) of plants that emerged in late spring (ET2) at day 50 (a), 70 (b, c) and 90 (d, e) of growth. The values in layers of -10 and -20 cm indicate the main and lateral root mass. Different lowercase letters denote significant differences among layers for each module (above the bars) and among layers for total layer mass (to the right of bars), compared by the Least Significant Difference (LSD) method from ANOVA ($p < 0.05$). SM stem mass; PM petiole mass; LM lamina mass; REM reproductive mass; BSM branch stem mass; BLM branch leaf mass; BREM branch reproductive mass; MRM main root mass; LRM lateral root mass.

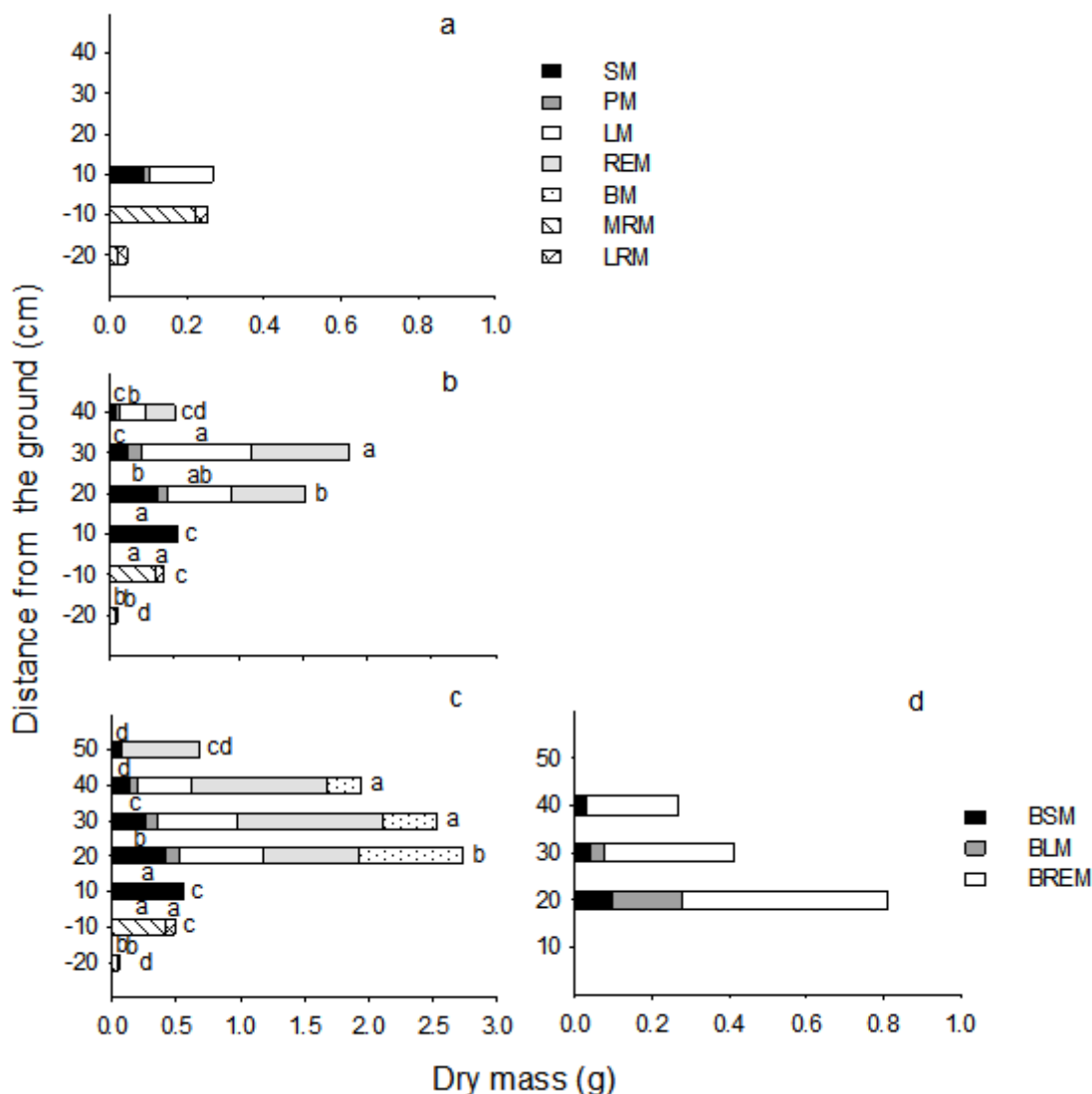


Figure 3

Biomass allocation in different layers (divided every 10 or 20 cm along the vertical direction of the main stem) of plants that emerged in summer (ET3) at day 30 (a), 50 (b) and 70 (c, d) of growth. The values in layers of -10 and -20 cm indicate the main and lateral root mass. Different lowercase letters denote significant differences among layers for each module (above the bars) and among layers for total layer mass (to the right of bars), compared by the Least Significant Difference (LSD) method from ANOVA ($p < 0.05$). SM stem mass; PM petiole mass; LM lamina mass; REM reproductive mass; BSM branch stem mass; BLM branch leaf mass; BREM branch reproductive mass; MRM main root mass; LRM lateral root mass.

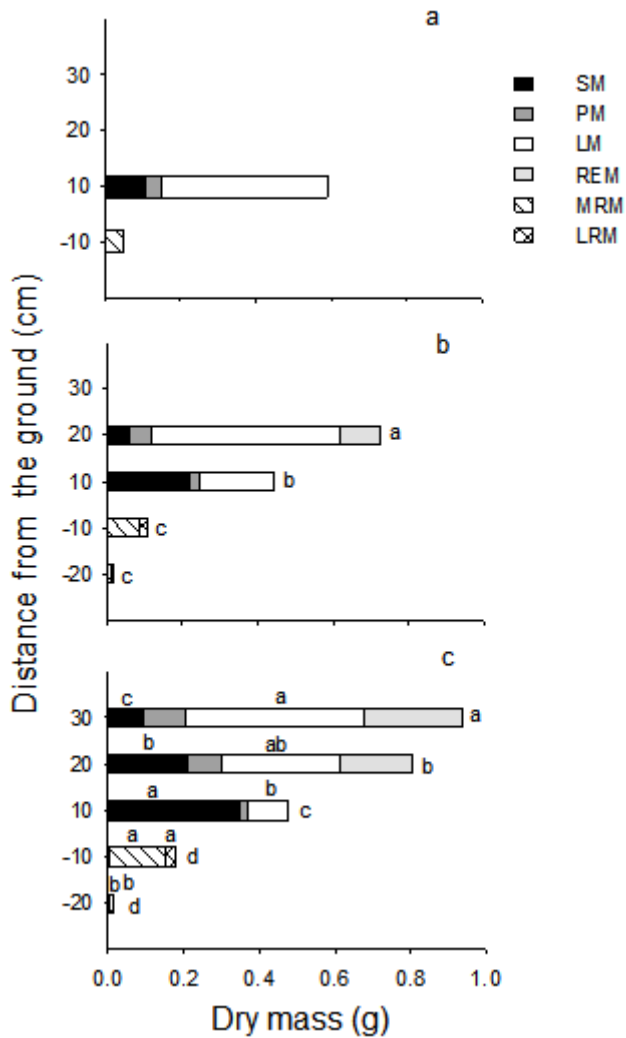


Figure 4

Biomass allocation in different layers (divided every 10 or 20 cm along the vertical direction of the main stem) of plants that emerged in late summer (ET4) at day 30 (a), 40 (b) and 50 (c) of growth. The values in layers of -10 and -20 cm indicate the main and lateral root mass. Different lowercase letters denote significant differences among layers for each module (above the bars) and among layers for total layer mass (to the right of bars), compared by the Least Significant Difference (LSD) method from ANOVA ($p < 0.05$). SM stem mass; PM petiole mass; LM lamina mass; REM reproductive mass; MRM main root mass; LRM lateral root mass.

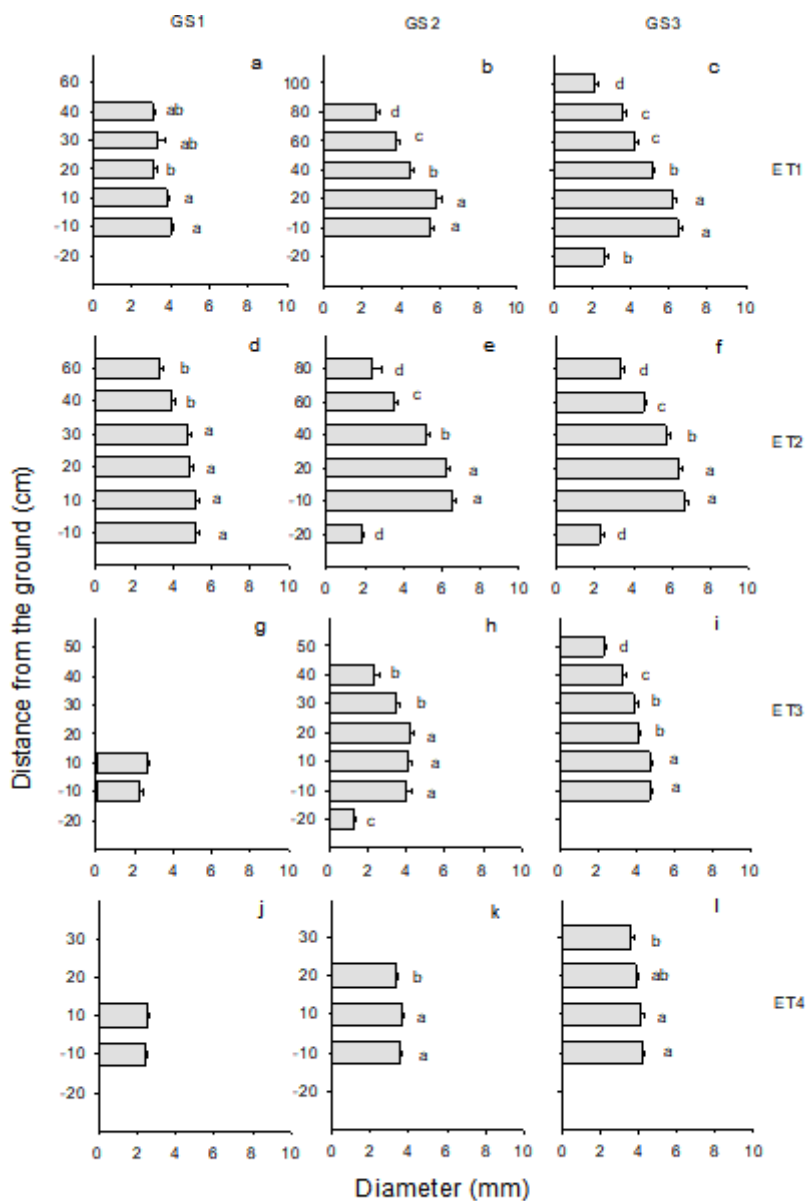


Figure 5

Mean values ($\pm$ SE) of stem diameter in different layers (divided every 10 or 20 cm along the vertical direction of the main stem) of plants that emerged in spring (ET1; a-c), late spring (ET2; d-f), summer (ET3; g-i) and late summer (ET4; j-l) at three stages (GS1-3). The values in layers of -10 and -20 cm indicate the main root diameter. Different letters in lowercase denote significance among layers compared by the Least Significant Difference (LSD) method from ANOVA ($p < 0.05$).

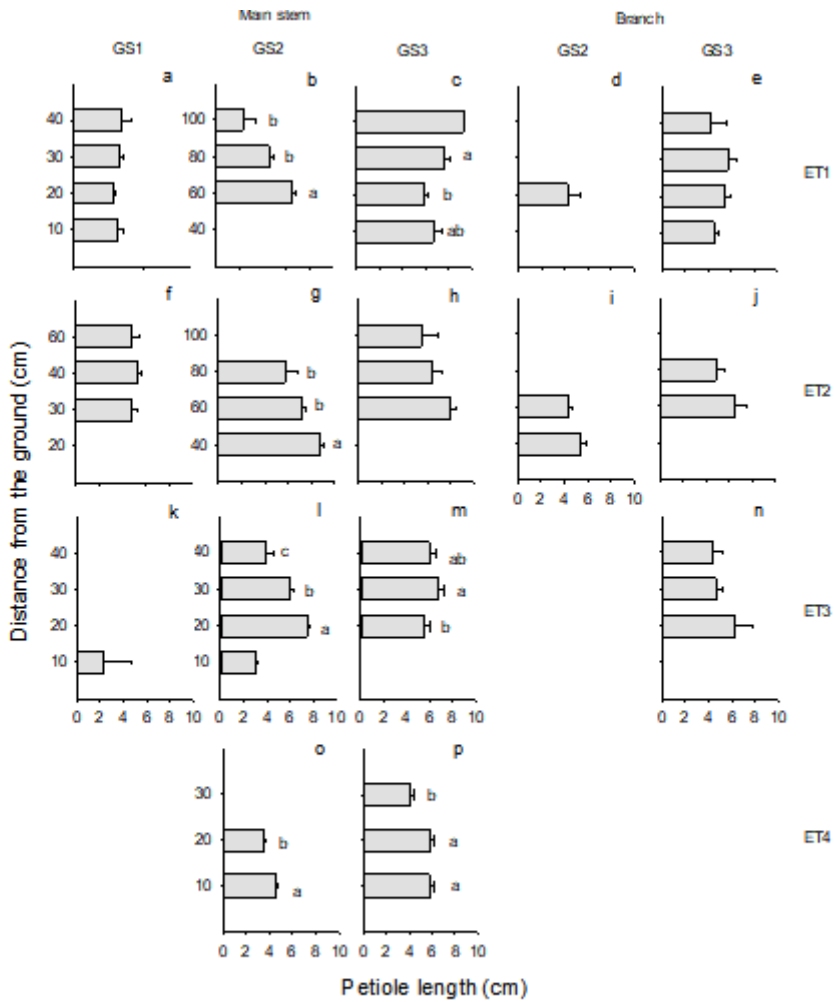


Figure 6

Mean values ($\pm$ SE) of petiole length (a-c, f-h, k-m, o, p) and branch length (d, e, i, j, n) in different layers (divided every 10 or 20 cm along the vertical direction of the main stem) of plants that emerged in spring (ET1; a-e), late spring (ET2; f-j), summer (ET3; k-n) and late summer (ET4; o, p) at three stages (GS1-3). Different letters in lowercase denote significance among layers compared by the Least Significant Difference (LSD) method from ANOVA ($p < 0.05$).

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [AppendixGTarch2022.3.docx](#)