

RESEARCH

Open Access



Biomass allocation between reproductive and vegetative organs of *Artemisia* along a large environmental gradient

Tumenjargal Tsogtsaikhan^{1,2}, Xuejun Yang^{1*}, Ruiru Gao³, Jiangrui Liu³, Wenqiang Tang³, Guofang Liu¹, Xuehua Ye¹ and Zhenying Huang^{1*}

Abstract

Background Biomass allocation reflects functional tradeoffs among plant organs and thus represents life history strategies. However, little is known about the patterns and drivers of biomass allocation between reproductive and vegetative organs along large environmental gradients. Here, we examined how environmental gradients affect biomass and the allocation between reproductive and vegetative organs. We also tested whether the allocation patterns conform optimal or allometric partitioning theory.

Methods We collected 22 *Artemisia* species along a large environmental gradient in China and measured reproductive (infructescences including seeds) and vegetative (leaves, stems and roots) mass for each plant. We then used standardized major axes regressions to quantify the relationships between reproductive and vegetative organs and linear mixed-effect models to examine the effect of environmental gradients (climate and soil) on biomass allocation patterns.

Results We found significant negative correlations between total biomass of *Artemisia* and the first principal component of climate, an axis that was negatively correlated with temperature and precipitation. Overall, there were significant isometric relationships between reproductive and vegetative mass. In addition, the ratio of reproductive to vegetative mass increased with the second principal component of climate (representing climate variability), but decreased with the second principal component of soil (representing bulk density and available water capacity). These patterns were consistent at the individual and interspecific levels, but were mixed at the intraspecific level.

Conclusions Our findings of the plastic responses of biomass allocation to environmental gradients support the optimal partitioning theory (OPT). The isometric relationships between reproductive and vegetative organs indicate that plant growth and reproduction are intricately linked. Furthermore, the plasticity of biomass ratios of reproductive to vegetative organs to climate variability and soil physical properties suggests that the flexible allocation between growth and reproduction is crucial for successful adaptation to diverse habitats.

*Correspondence:

Xuejun Yang
xjyang_jx@ibcas.ac.cn
Zhenying Huang
zhenying@ibcas.ac.cn

Full list of author information is available at the end of the article



© The Author(s) 2025. **Open Access** This article is licensed under a Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International License, which permits any non-commercial use, sharing, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if you modified the licensed material. You do not have permission under this licence to share adapted material derived from this article or parts of it. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by-nc-nd/4.0/>.

Keywords Allometric partitioning theory, *Artemisia*, Biomass allocation pattern, Environmental gradient, Optimal partitioning theory, Reproductive mass, Vegetative mass

Introduction

Biomass allocation, the process by which plants allocate finite biomass to different organs, determines plant performance along environmental gradients [1–4]. In specific, proper biomass allocations guarantee the functions of different plant organs: leaves perform photosynthesis to fix carbon, stems and branches act as transport corridors and mechanical support, roots take up nutrients and water and anchor the plant, and seeds/fruits execute sexual reproduction [5–7]. Therefore, the patterns of biomass allocation reflect functional tradeoffs among plant organs and hence life history strategies [8, 9]. At the ecosystem level, patterns of plant biomass allocation are critical for the functioning of terrestrial ecosystems, because they impact biomass distribution, carbon cycling, and vegetation responses to environmental changes [10–12]. To date, most studies on biomass allocation patterns have focused on vegetative organs such as leaves, shoots and roots [13].

However, an essential aspect of plant life history strategy is reproductive allocation, which refers to the proportion of the total resources devoted to reproductive structures [5, 14] and represents the cost of reproduction [15, 16]. Allocation between vegetative and reproductive organs influences seed quality and yield, which in turn determines plant fitness [17]. Variation in reproductive allocation typically indicates distinct plant strategies imposed by natural selection [14]. At a broad scale, environmental gradients (e.g., soil and climate) directly affect plant growth and reproduction, as well as biomass allocation between the two processes. For instance, in suitable environments, larger plants with higher growth rate allocate more resources to reproductive processes; however, in unsuitable environments, plants reduce their allocation to reproduction to cope with environmental constraints [18, 19]. In addition, the availability of essential resources such as light, water and nutrients influences biomass allocation among plant organs [20]. Yet it is still uncertain how biomass allocation between growth and reproduction shifts across large environmental gradients.

There are two prevailing theories on the patterns of biomass allocation among plant organs: The optimal allocation theory (OPT; also called the balanced growth theory) [11, 21, 22] and the allometric allocation theory (APT) [19, 23, 24]. The OPT states that plants allocate more biomass toward the organ with the greatest capacity to absorb limiting resources to maximize their performance [11, 21, 22]. According to the OPT, the ratio of reproductive biomass to total biomass does not change significantly with plant size [11, 21, 25]. Instead, plants

can adjust their resource allocation to favor growth or reproduction depending on the prevailing conditions, thereby maximizing their fitness [9]. In contrast, the APT posits a uniform allocation pattern for all plants, subject to allometric constraints that limit biomass partitioning to different organs [10, 26]. Based on the APT, biomass allocation depends solely on plant size rather than on environmental conditions [26, 27]. To date, most studies testing the two theories of reproductive allocation have focused on the flowering stage, during which time reproductive mass typically increases as vegetative mass decreases [11, 17, 23, 24, 26]. However, the studies at the flowering stage cannot provide us with a complete understanding of life history strategies, as plant fitness is more directly linked to seeds produced at a later stage.

Although many studies have investigated the allocation patterns of reproductive and vegetative organs separately [1, 7, 27–32], few studies have examined the allocation patterns between them simultaneously. Among them, some studies supported APT [24, 33, 34], while others supported OPT [9, 21, 35]. Hence, it is still unclear whether biomass allocation patterns conform APT or OPT. Furthermore, biomass allocation patterns between reproductive and vegetative organs have seldom been investigated along large environmental gradients or among closely related species.

Here, we sampled 22 *Artemisia* species to explore how biomass allocation between reproductive and vegetative organs varies along a broad environmental gradient in China. We chose this genus because: (1) It is a specis-rich genus, comprising 350–500 species; (2) It is widely distributed in the natural habitats across Asia, Europe, and North America; (3) Most species in this genus have similar life forms (perennial herbs), with a few annuals, semi-shrubs and small shrubs. These features make it an ideal genus to study allocation patterns along large environmental gradients [36–38]. We proposed three hypotheses. First, we hypothesize that plant size (total biomass) should vary along environmental gradients, because the environment provides plants with resources for growth and reproduction (Fig. 1). With respect to climate, temperature can alter physiological processes and consequently determine plant growth [39, 40]. In addition, plants in regions with high precipitation tend to grow larger than those in arid regions, while extreme precipitation and seasonal changes have negative effects on plant growth [41]. For soil conditions, nutrient availability strongly influences plant growth, as reported in natural *Pinus tabuliformis* forests [42]. Further, soil texture and

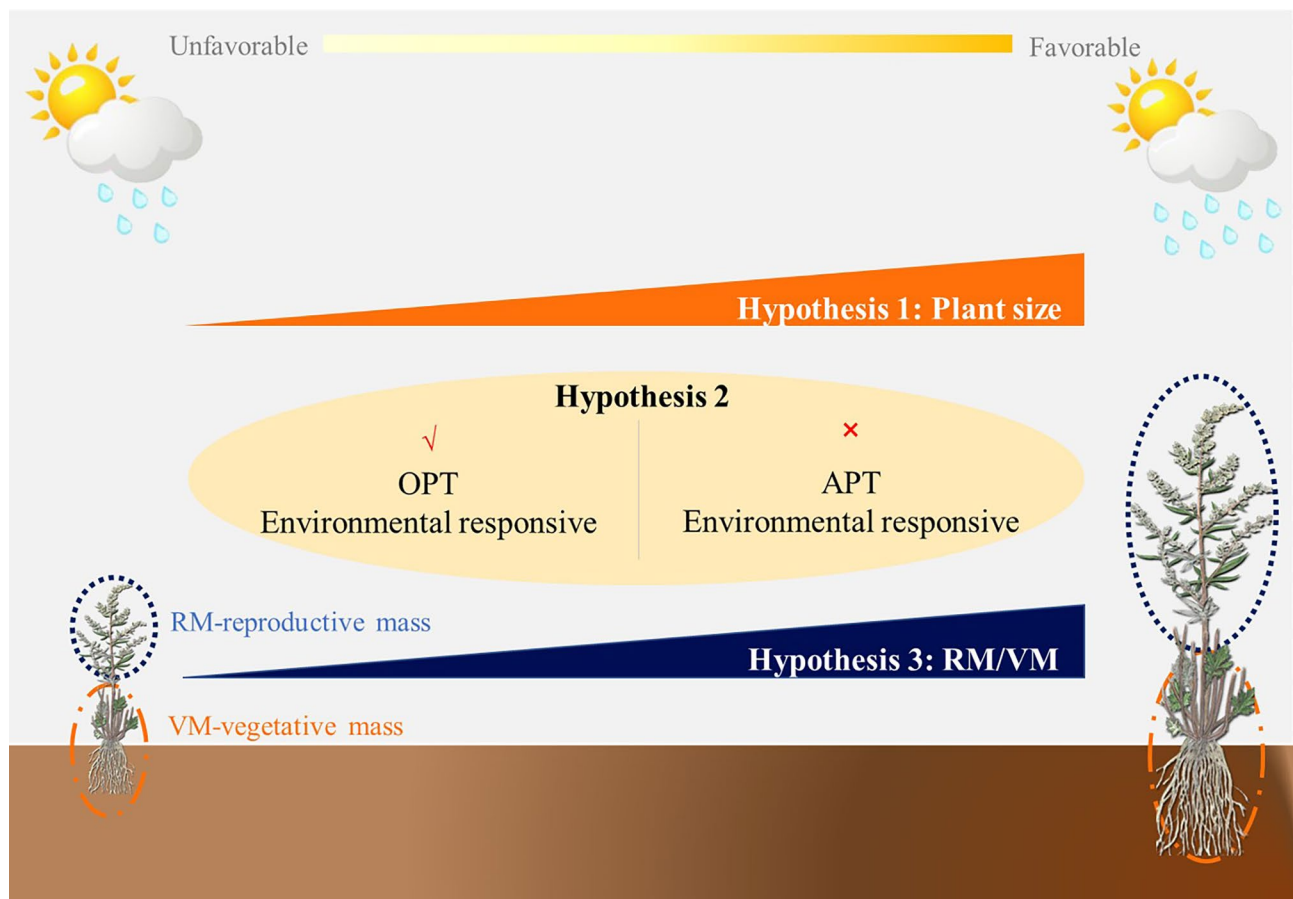


Fig. 1 Conceptual diagram illustrating the three hypotheses tested in this study. Hypothesis 1 is that plant size (total biomass) should vary along environmental gradients. Hypothesis 2 is that biomass allocation between reproductive and vegetative organs conforms optimal partition theory (OPT) rather than allometric partition theory (APT). Hypothesis 3 is that the allocation between reproductive and vegetative organs responds plastically to the environmental gradient

structure are also important determinants of plant size, as demonstrated in rhizomatous wetland plants [43].

Second, we hypothesize that biomass allocation between reproductive and vegetative organs conforms OPT (Fig. 1). Plants allocate resources differently to their reproductive and vegetative organs [44, 45], which results in OPT [25]. Some studies have already reported evidence to support OPT at small scales. For example, light exposure influences allocation patterns between growth and reproduction of *Plantago* species to optimize resource use [46, 47]. Perennial plants adjust their resource allocation to optimize growth and reproductive output, thereby maximizing fitness under varying conditions [9]. In addition, the optimal allocation of resources between growth and reproduction influences size of the plant at maturity [48]. Therefore, plants could adopt optimal partitioning strategies to balance growth and reproduction and thus maximize fitness.

Finally, we hypothesize that the allocation between reproductive and vegetative organs responds plastically to the environmental gradient (Fig. 1). Increased plant

growth in favorable environments has been reported to result in larger plants that can allocate more resources to reproduction [5, 19, 49]. Some large-scale studies also show apparent differences in the allocation between reproductive and vegetative biomass. For instance, environmental factors influence the allocation of reproductive and vegetative biomass of *Leymus chinensis* in northeastern China, with plants allocating more biomass to vegetative growth under nutrient-rich conditions, but more to reproductive structures under optimal climatic conditions to maximize reproductive success [50, 51]. In addition, soil temperature drives elevational patterns of reproductive allocation in the Gaoligong Mountains of China, with plants allocating more resources to reproductive structures at higher elevations to maximize reproductive success [52]. In grasslands, plants adjust their biomass allocation to optimize growth and reproduction along temperature and precipitation gradients [53].

To test the three hypotheses, we first quantified how the environmental gradient affects plant size of *Artemisia*;

then we determined whether biomass allocation between reproductive and vegetative organs conforms OPT or APT; finally, we assessed how biomass allocation changes along the environmental gradient. In addition, we identified these patterns at the individual, interspecific and intraspecific levels to determine whether the biomass allocation strategy was consistent across the three taxonomic levels.

Materials and methods

Plant sampling

We collected *Artemisia* species from 42 sites along a large environmental gradient in China in November, 2023 (Fig. 2A), when the seeds on most plants were fully matured. We focused on natural vegetation and established sites in areas with minimal human disturbance, avoiding those impacted by agriculture, urbanization, or significant habitat modification. Sites were located along a large environmental gradient in climate and soil to capture diverse conditions that influence *Artemisia* species. At each site, we recorded longitude, latitude and altitude, and four plots of 1 m × 1 m with distance > 5 m were established randomly. Then, all species of *Artemisia* were identified, and four reproductive individuals of each species were randomly sampled and put into separate paper bags. In total, we collected 376 individuals of 22 species

with fully matured seeds from all sites (Table 1). All species were formally identified by Associate Professor Ruiru Gao (The School of Life Sciences, Shanxi Normal University). The voucher specimens are preserved in the Herbarium of the School of Life Sciences, Shanxi Normal University.

Organ biomass determination

In the laboratory, we separated each individual into four modules, including one reproductive organ (infructescences including seeds) and three vegetative organs (leaves, stems and roots). The separated organs (infructescence, leaf, stem and root) were oven-dried at 65 °C for 48 h to constant weight and weighed to determine their dry mass. Reproductive mass (RM) was the weight of the infructescences of each individual, while vegetative mass (VM) was the sum of the mass of stems, leaves and roots.

Environmental variables

According to the geographical coordinates of the sampling sites, we extracted nineteen bioclimatic variables (eleven temperature and eight precipitation variables; Table 2) from the World Climate Information Database [54]. Our sampling sites covered a wide climate gradient, with annual mean temperature (AMT, ranging from

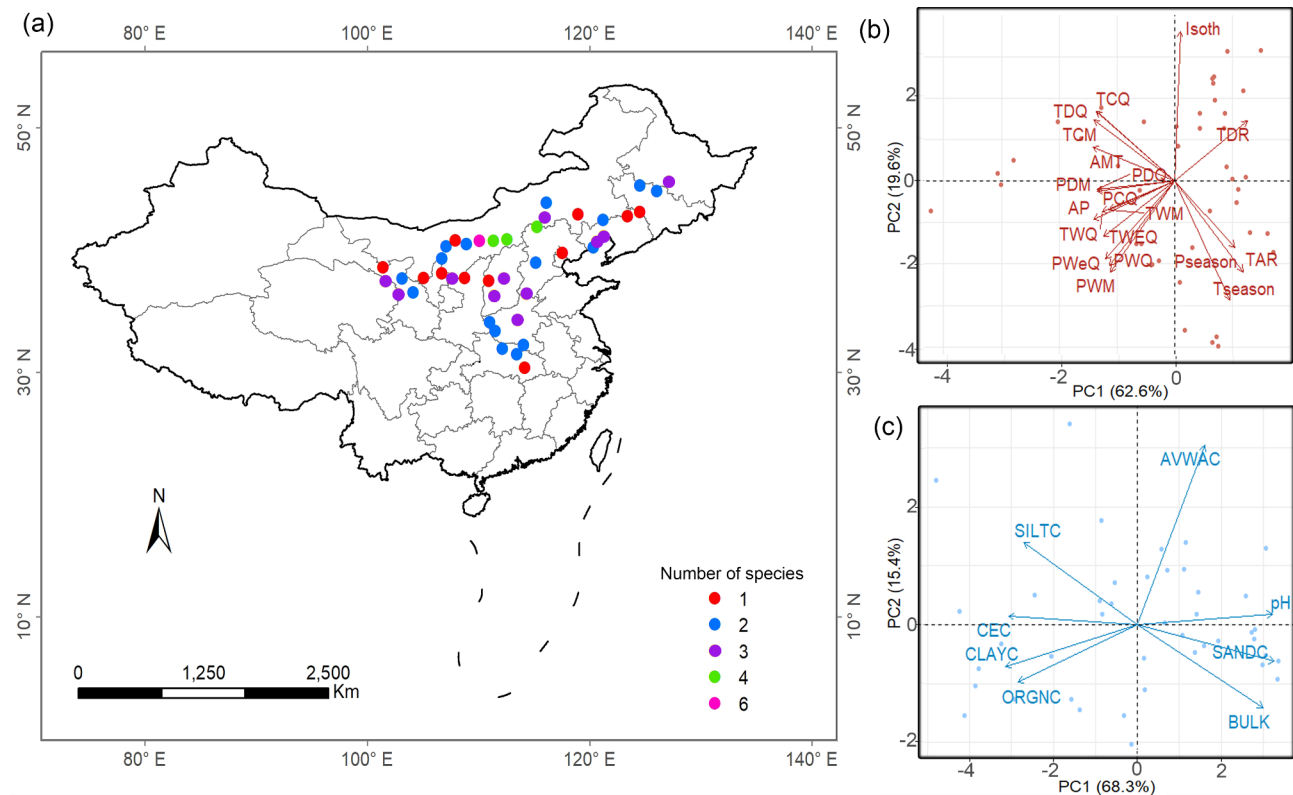


Fig. 2 The location and environmental gradients of 42 sampling sites across China. **(A)** The location of sampling sites. **(B)** The first two PC axes of 19 climate variables. **(C)** The first two PC axes of 8 soil variables

Table 1 List of species sampled, growth form, and number of sites of the occurrence of each species investigated in this study

No.	Latin name	Growth form	Number of sites
1	<i>Artemisia anethifolia</i>	Annual or biennial	1
2	<i>Artemisia annua</i>	Annual	6
3	<i>Artemisia capillaris</i>	Perennial	10
4	<i>Artemisia caruifolia</i>	Annual or biennial	1
5	<i>Artemisia demissa</i>	Annual or biennial	1
6	<i>Artemisia dubia</i>	Subshrub	2
7	<i>Artemisia edgeworthii</i>	Annual or biennial	3
8	<i>Artemisia freyniana</i>	Subshrub	1
9	<i>Artemisia frigida</i>	Perennial	3
10	<i>Artemisia giraldii</i>	Subshrub	3
11	<i>Artemisia incisa</i>	Perennial	1
12	<i>Artemisia indica</i>	Perennial	2
13	<i>Artemisia japonica</i>	Perennial	1
14	<i>Artemisia klementze</i>	Subshrub	1
15	<i>Artemisia lavandulaefolia</i>	Perennial	12
16	<i>Artemisia mongolica</i>	Perennial	2
17	<i>Artemisia ordosica</i>	Shrubs	7
18	<i>Artemisia sacrorum</i>	Subshrub	5
19	<i>Artemisia scoparia</i>	Perennial	14
20	<i>Artemisia sieversiana</i>	Annual or biennial	11
21	<i>Artemisia sphaerocephala</i>	Shrub	2
22	<i>Artemisia tangutica</i>	Perennial	1

0.29 °C to 17.1 °C) and annual precipitation (AP, from 146 mm to 1260 mm). Additionally, eight soil variables from the global SoilGrids250m database [55], including bulk density (BULK, ranging from 1044.8 to 1578.2 kg/m³) and cation exchange capacity (CEC, ranging from 2.4 to 32.56 cmolc/kg).

Statistical analysis

All analyses were conducted using R version 4.3.1 (<https://www.r-project.org/>). First, a principal component analysis (PCA) was carried out by applying the `prcomp` function in the `stats` package to determine the gradients in the climate and soil data separately. Before PCAs, the climate and soil data were centered and scaled.

To test the first hypothesis, we used linear mixed-effect models (LMMs) to determine how plant size (total biomass) varied with environmental gradients using the `lme4` package [56]. Plant size was log₁₀-transformed to enhance residual normality. We analyzed the data on three levels. On the individual level, we used pooled samples to determine overall patterns, with environmental gradients and species nested in sites as fixed and random effects, respectively. On the interspecific level, we used species means at each site to determine interspecific patterns, with environmental gradients and sites as fixed and random effects, respectively. On the intraspecific level, we used 10 species occurring in at least three sites to determine intraspecific patterns.

To test the second hypothesis, standardized major axes (SMA) regressions were performed to quantify the allometric power functions between RM and VM. The `sma` function in the `smart` package [57] was used. SMA regression is a standard allometric technique for calculating scaling exponents (α) and allometric constants (β) [10]. We also analyzed the data on three levels. First, we used the data of all individuals to determine overall patterns. Second, we used the means of the 22 species at each site to determine interspecific patterns. Third, we used species occurring in at least three sites to test intraspecific patterns. We also analyzed the allometric relationships between RM and each of the three vegetative organs (leaf, stem and root) separately.

To test the third hypothesis, we performed additional LMMs to examine the effects of climate and soil gradients on biomass allocation (the ratio of RM to VM). LMMs were also performed on three levels. First, we used the data from all individuals to determine overall patterns. Second, we calculated species means at each site, which were used to determine interspecific patterns. Third, at the intraspecific level, we used species occurring in at least three sites to determine intraspecific patterns. To determine whether the relationship was consistent across the three vegetative organs, we further carried out the analyses on the ratios of RM to stem, leaf and root mass separately.

Results

The effect of environmental gradients on plant size

PCAs of nineteen climate and eight soil variables revealed that the first two axes explained most of the variation in the climate (82.2%) and soil (83.7%) variables (Fig. 2B and C). Climate PC1 was a temperature and precipitation axis that was negatively correlated with AMT, AP and TCM, while climate PC2 was a climate variability axis that was positively correlated with Isoth but negatively correlated with Tseason and Pseason (Fig. 2B; Table 2). For soil gradients, PC1 was a chemical axis that was positively correlated with pH and SANDC but negatively with CEC, while PC2 was a physical axis that was correlated negatively with BULK but positively to AVWAC (Fig. 2C; Table 2).

LMMs showed that plant size decreased significantly with climate PC1 at the individual level (Fig. 3A). A similar trend was observed at the interspecific level (Fig. 3B), while the relationships were mixed at the intraspecific level (Fig. 3C; Table 3). In contrast, climate PC2, soil PC1 and soil PC2 had no significant effect on plant size at the individual, interspecific or intraspecific level.

The relationships between RM and VM

SMA analyses revealed significant isometric relationships between RM and VM at both individual and interspecific

Table 2 Principle components analysis of climate and soil variables across all sites

Variables	Description	PC1	PC2
Climate			
AMT	Annual mean temperature	-0.265	0.109
TDR	Mean diurnal range (Mean of monthly (max temp - min temp))	0.236	0.196
Isoth	Isothermality	0.017	0.485
Tseason	Temperature seasonality (standard deviation ×100)	0.179	-0.386
TWM	Max temperature of warmest month	-0.215	-0.093
TCM	Min temperature of coldest month	-0.262	0.197
TAR	Temperature annual range	0.222	-0.293
TWEQ	Mean temperature of wettest quarter	-0.231	-0.180
TDQ	Mean temperature of driest quarter	-0.255	0.225
TWQ	Mean temperature of warmest quarter	-0.236	-0.100
TCQ	Mean temperature of coldest quarter	-0.254	0.227
AP	Annual precipitation	-0.265	-0.125
PWM	Precipitation of wettest month	-0.209	-0.294
PDM	Precipitation of driest month	-0.253	-0.034
Pseason	Precipitation seasonality (coefficient of variation)	0.195	-0.214
PWeQ	Precipitation of wettest quarter	-0.225	-0.252
PDQ	Precipitation of driest quarter	-0.252	-0.027
PWQ	Precipitation of warmest quarter	-0.213	-0.273
PCQ	Precipitation of coldest quarter	-0.252	-0.027
Soil			
BULK	Bulk density of the fine earth fraction	0.366	-0.363
CEC	Cation exchange capacity of the soil	-0.374	0.038
CLAYC	Proportion of clay particles (< 0.002 mm) in the fine earth fraction	-0.383	-0.182
ORGNC	Organic carbon content	-0.347	-0.253
pH	Soil pH	0.392	0.047
SANDC	Proportion of sand particles (> 0.05 mm) in the fine earth fraction	0.398	-0.160
SILT	Proportion of silt particles (≥ 0.002 mm and ≤ 0.05 mm) in the fine earth fraction	-0.330	0.358
AVWAC	Available water capacity (%)	0.196	0.783

The first two PC axes were shown for the 19 climate variables and 8 soil variables

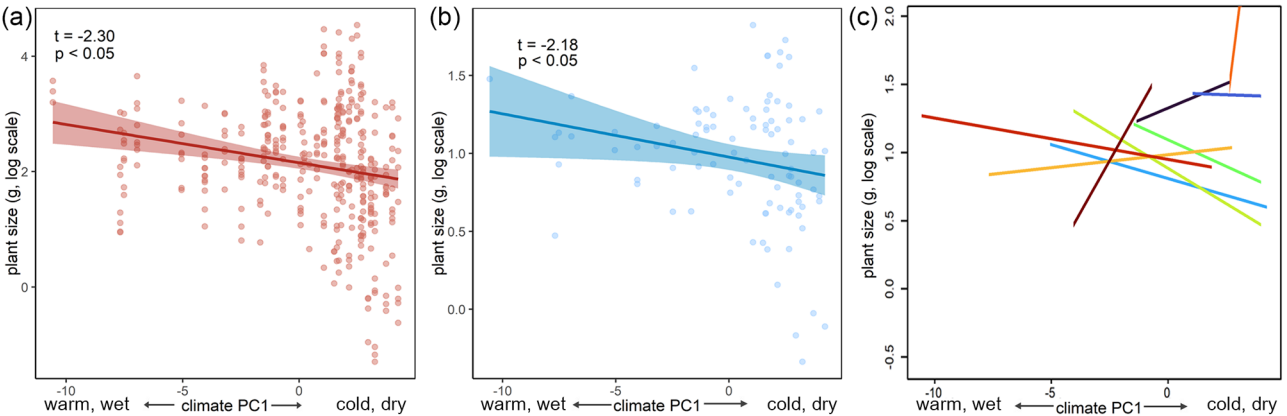


Fig. 3 Relationships between plant size of *Artemisia* species and environmental gradients. **(A)** The individual level. **(B)** The interspecific level. **(C)** The intraspecific level, where different colour lines represent all relationships of the 10 different species. Species names are provided in Table 3. *t* and *p* values are from linear mixed models

levels (Fig. 4A and B). Additionally, most relationships at the intraspecific level were similar to those at the individual level (Fig. 4C, Table S1).
For the three vegetative organs, the relationship between RM and leaf mass was not significant at both

individual and interspecific levels (Figs S1A and B). However, the relationship between RM and stem mass was isometric (Figs. S1D and E), but that between RM and root mass was allometric (Figs S1G and H). At the

Table 3 Linear mixed models for analyses of the relationships between plant size of *Artemisia* species occurring in at least three sites and environmental gradients

Species name		Climate				Soil			
		Estimate	SE	t-value	p	Estimate	SE	t-value	p
<i>A.sacrorum</i>	Intercept	1.31	0.14	9.13	0.01	1.54	0.20	7.68	0.02
	PC1	0.07	0.06	1.16	0.37	0.01	0.10	0.13	0.91
	PC2	-0.04	0.09	0.46	0.69	-0.21	0.16	-1.36	0.31
<i>A.ordosica</i>	Intercept	1.43	0.45	3.20	0.03	1.13	0.49	2.29	0.08
	PC1	-0.01	0.16	-0.04	0.97	0.15	0.18	0.86	0.44
	PC2	0.05	0.11	0.41	0.70	0.17	0.43	0.39	0.72
<i>A.scoparia</i>	Intercept	0.80	0.06	12.28	< 0.001	0.81	0.07	12.14	< 0.001
	PC1	-0.05	0.02	-2.03	0.06	-0.03	0.03	-0.87	0.40
	PC2	-0.06	0.03	-2.26	0.04	-0.10	0.05	-1.93	0.07
<i>A.edgeworthii</i>	Intercept	-2.62	6.48	-0.40	0.70	1.07	0.79	1.35	0.21
	PC1	-3.21	8.63	-0.37	0.72	-0.17	0.30	-0.57	0.58
	PC2	3.35	8.24	0.41	0.69	-0.39	0.39	-1.00	0.34
<i>A.sieversiana</i>	Intercept	1.08	0.09	11.88	< 0.001	1.05	0.06	17.01	< 0.001
	PC1	-0.08	0.03	-2.55	0.03	-0.11	0.04	-2.60	0.03
	PC2	-0.05	0.03	-1.36	0.21	-0.15	0.05	-2.85	0.02
<i>A.capillaris</i>	Intercept	0.87	0.08	10.95	< 0.001	0.91	0.08	10.84	< 0.001
	PC1	-0.10	0.03	-3.19	0.02	-0.21	0.08	-2.76	0.03
	PC2	-0.08	0.05	-1.38	0.21	-0.10	0.11	-0.94	0.38
<i>A.annua</i>	Intercept	0.97	0.18	5.46	0.01	0.87	0.18	4.89	0.02
	PC1	0.02	0.04	0.48	0.66	0.07	0.09	0.81	0.48
	PC2	0.24	0.63	0.39	0.72	-0.26	0.37	-0.71	0.53
<i>A.frigida</i>	Intercept	-2.08	0.61	-3.38	0.01	0.16	0.38	0.41	0.69
	PC1	1.35	0.31	4.28	< 0.001	-0.02	0.28	-0.07	0.95
	PC2	2.18	0.41	5.26	0.00	1.46	0.27	5.46	< 0.001
<i>A.lavandulaefoliada</i>	Intercept	0.94	0.09	9.97	< 0.001	0.91	0.13	7.25	< 0.001
	PC1	-0.03	0.02	-1.57	0.15	-0.06	0.04	-1.41	0.19
	PC2	-0.06	0.04	-1.70	0.12	-0.02	0.05	-0.39	0.71
<i>A.giraldii</i>	Intercept	1.69	0.39	4.37	0.00	1.64	1.28	1.28	0.23
	PC1	0.30	0.15	2.06	0.07	1.40	2.41	0.58	0.58
	PC2	0.30	0.16	1.85	0.10	1.67	2.82	0.59	0.57

The bold values mean the effects of environmental gradients are significant

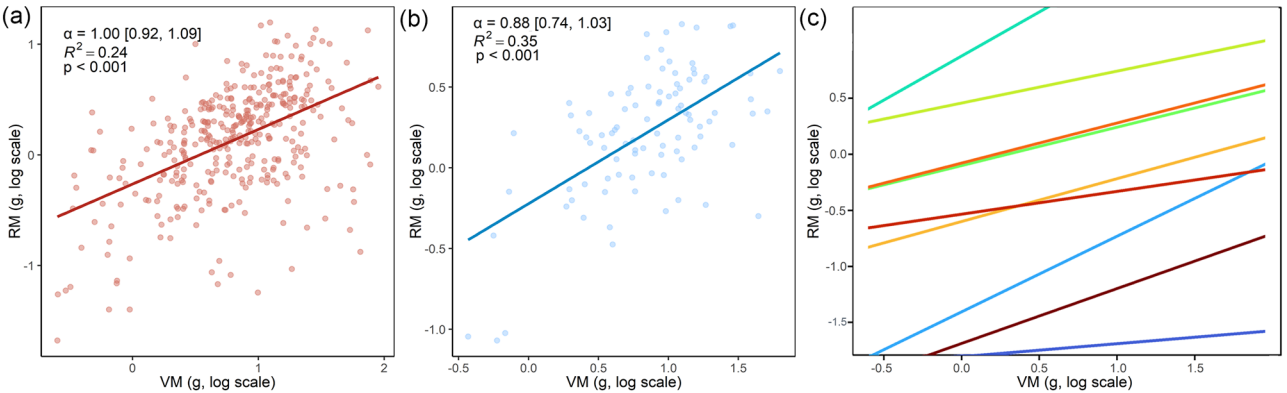


Fig. 4 Standardized major axis (SMA) regressions between reproductive mass (RM) and vegetative mass (VM) of *Artemisia*. **(A)** The individual level. **(B)** The interspecific level. **(C)** The intraspecific level, where different color lines represent all relationships of the 10 different species. Species names are provided in Table S1. α is the observed allometric exponent, and numbers in square brackets are the lower and upper 95% confidence intervals. All data are \log_{10} -transformed before analysis

intraspecific level, these relationships differed among species (Figs S1C, F and I, Table S1).

The patterns of biomass allocation between reproductive and vegetative organs along environmental gradients

LMMs showed that climate PC1 (individual level: $t=1.07$, $p=0.28$; interspecific level: $t=0.87$, $p=0.38$) and soil PC1 (individual level: $t=1.44$, $p=0.15$; interspecific level: $t=1.28$, $p=0.20$) did not significantly affect the ratio of RM to VM, but climate PC2 and soil PC2 did (Fig. 5). In specific, the ratio of RM to VM increased with climate PC2 (Fig. 5A and B), but decreased with soil PC2 (Fig. 5D and E). These trends were consistent at both interspecific and individual levels (Fig. 5). At the intraspecific level, however, the relationships were mixed (Fig. 5C and F; Table 4).

For the three vegetative organs, the ratio of RM to stem and root mass increased significantly, but that of RM to leaf mass decreased, with climate PC2 at both individual and interspecific levels (Fig. S2, Table S2). Although soil PC2 had no significant effect on the ratio of RM to leaf or root mass at all three levels, it had a significant positive effect on the ratio of RM to stem mass at both individual and interspecific levels (Fig. S3, Table S3). At the

intraspecific level, the relationships were mixed; while some species had positive relationships, others were negatively correlated with climate PC2 and soil PC2 (Figs S2 and S3, Tables S2 and S3).

Discussion

Temperature and precipitation strongly affect plant size of *Artemisia*

In support of our first hypothesis, we found that plant size was negatively correlated with climate PC1 (Fig. 3), an axis that was negatively correlated with temperature and precipitation (Fig. 2B; Table 2). These results suggest that high temperature and precipitation favor plant growth and biomass accumulation of *Artemisia* species. Three main mechanisms could explain such positive effects. (1) Favorable climatic conditions enhance plant metabolic processes during growth [20, 58, 59]. For instance, an adequate precipitation is essential to maintain plant productivity, whereas water deficit can impair metabolic processes such as photosynthesis and respiration, resulting in reduced plant growth [60, 61]. For *Artemisia* species, a previous study also highlighted the significant role of precipitation in determining biomass accumulation across northern China [62]. (2)

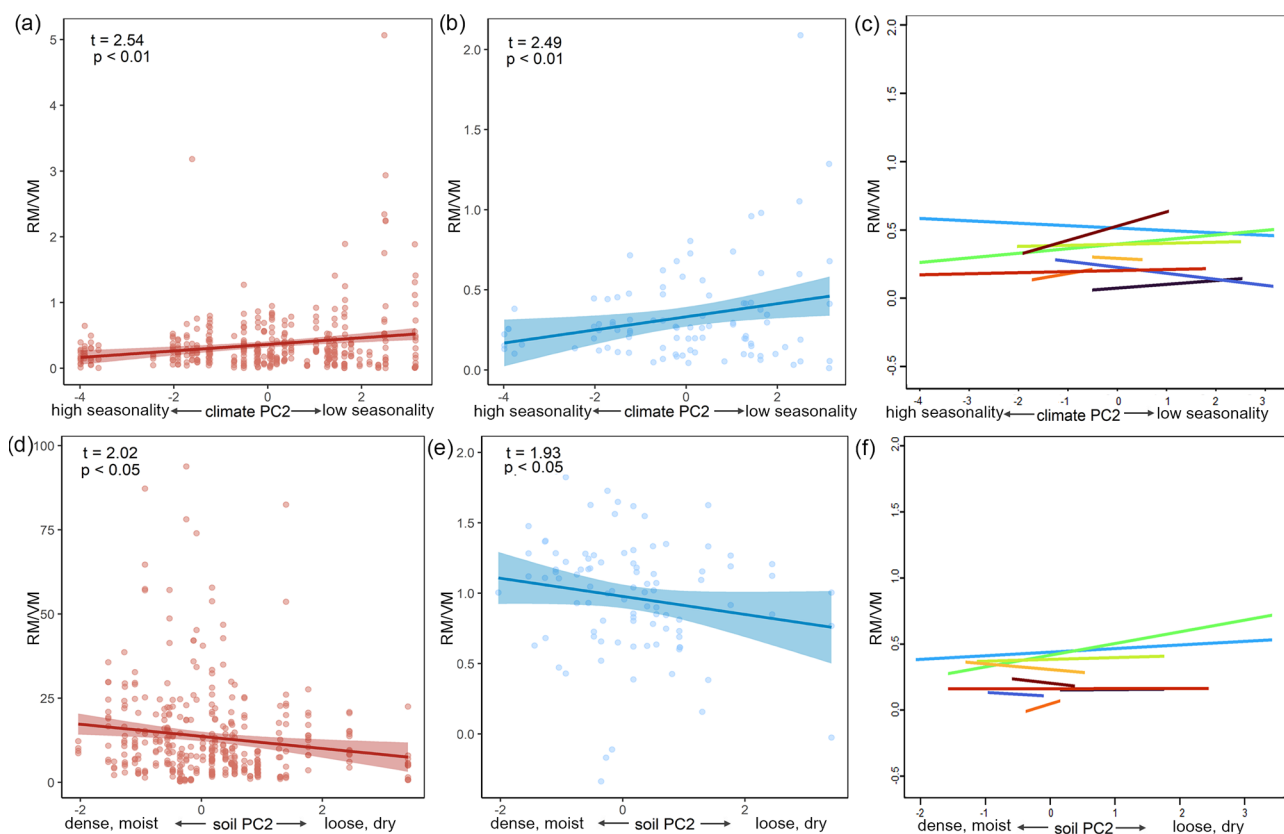


Fig. 5 Relationships between the ratio of reproductive mass to vegetation mass (RM/VM) of *Artemisia* and environmental gradients. (A, D) The individual level. (B, E) The interspecific level. (C, F) The intraspecific level, where different colored lines represent all relationships for the 10 species analyzed. Species names are provided in Table 4. t and p values are from linear mixed models

Table 4 Linear mixed models for analyses of the relationships between the ratio of reproductive to vegetation mass (RM/VM) of *Artemisia* species occurring in at least three sites and environmental gradients

Species name		Climate				Soil			
		Estimate	SE	t-value	p	Estimate	SE	t-value	P
<i>A.sacrorum</i>	Intercept	0.07	0.05	1.45	0.28	0.16	0.11	1.53	0.27
	PC1	0.03	0.02	1.34	0.31	0.00	0.05	0.08	0.94
	PC2	0.04	0.03	1.39	0.30	-0.03	0.08	-0.31	0.79
<i>A.ordosica</i>	Intercept	0.23	0.09	2.66	0.06	0.12	0.12	0.98	0.38
	PC1	-0.05	0.03	-1.49	0.21	-0.03	0.04	-0.67	0.54
	PC2	-0.04	0.02	-1.81	0.14	-0.10	0.10	-0.95	0.40
<i>A.scoparia</i>	Intercept	0.52	0.04	4.13	< 0.001	0.45	0.05	9.34	< 0.001
	PC1	-0.02	0.01	-1.32	0.21	0.03	0.02	1.30	0.21
	PC2	0.07	0.02	4.52	< 0.001	0.07	0.04	1.92	0.07
<i>A.edgeworthii</i>	Intercept	2.91	28.02	0.10	0.92	4.22	5.06	0.83	0.43
	PC1	-4.81	37.31	-0.13	0.90	-1.09	1.93	-0.56	0.59
	PC2	2.93	35.63	0.08	0.94	-0.63	2.47	-0.26	0.80
<i>A.sieversiana</i>	Intercept	0.40	0.14	2.88	0.02	0.42	0.07	5.68	< 0.001
	PC1	0.03	0.05	0.74	0.48	0.09	0.05	1.79	0.08
	PC2	0.01	0.05	0.24	0.82	0.06	0.06	0.94	0.35
<i>A.capillaris</i>	Intercept	0.40	0.04	9.64	< 0.001	0.39	0.04	9.57	< 0.001
	PC1	0.01	0.02	0.46	0.66	0.01	0.04	0.36	0.73
	PC2	0.04	0.03	1.45	0.19	0.07	0.05	1.38	0.21
<i>A.annua</i>	Intercept	0.29	0.09	3.12	0.05	0.32	0.10	3.18	0.05
	PC1	-0.02	0.02	-0.93	0.42	-0.04	0.05	-0.87	0.45
	PC2	0.02	0.33	0.07	0.95	0.04	0.21	0.17	0.87
<i>A.frigida</i>	Intercept	0.24	0.38	0.64	1.00	0.05	0.22	0.25	0.81
	PC1	0.06	0.19	0.33	1.00	0.15	0.16	0.95	0.36
	PC2	0.20	0.26	0.77	1.00	0.25	0.15	1.60	0.14
<i>A.lavandulaefoliada</i>	Intercept	0.20	0.03	6.01	< 0.001	0.17	0.04	3.85	< 0.001
	PC1	0.01	0.01	1.14	0.28	0.00	0.02	0.04	0.97
	PC2	0.01	0.01	1.17	0.27	0.01	0.02	0.60	0.56
<i>A.giraldii</i>	Intercept	0.53	0.19	2.86	0.02	0.21	1.12	0.19	0.85
	PC1	0.11	0.07	1.50	0.17	-0.06	2.10	-0.03	0.98
	PC2	0.19	0.08	2.38	0.04	0.18	2.45	0.07	0.94

The bold values mean the effects of environmental gradients are significant

Climatic conditions impact plant growth by determining how plants acquire resources. In particular, an increase in temperature enhances the availability of water and nutrients in the soil, causing plants to grow and develop faster [63]. (3) Climate affects plant growth by shifting the timing of life cycle events (phenology; e.g., seedling emergence, flowering and fruiting) and subsequently the timing for biomass accumulation [61].

Surprisingly, we found that soil conditions did not significantly affect plant size of *Artemisia* species. A possible reason could be that the gradients in soil chemical and physical properties in our study are not large enough to influence plant size. The weak effect of soil on plant growth has also been reported in several previous studies. For instance, a meta-analysis demonstrates that soil properties have a weaker effect on plant growth compared to elevated atmospheric CO₂ levels [64]. Similarly, compared to seasonal climatic conditions, soil properties, also have a minor effect in determining net ecosystem

production in C₃ grasslands, highlighting the dominant role of climate in determining plant size [65].

The consistent trends at the interspecific level suggest the generalizability of the effect of climate across species along the environmental gradient (Fig. 3B). These results align with the report that temperature and precipitation significantly influence plant biomass in *Leymus chinensis* along a large-scale gradient in northeastern China [51]. This consistency between our study and others underscores the strong influence of climate on plant growth across different species. However, at the intraspecific level, we observed mixed relationships between plant size and environmental gradients (Fig. 3C; Table 3). This suggests that while climatic gradients may consistently influence plant size across species, within-species variability may be influenced by additional factors such as genetic diversity or microenvironmental conditions [66].

Biomass allocation between reproductive and vegetative organs conforms OPT

In line with our second hypothesis, we found significant isometric relationships between reproductive and vegetative mass at both individual and interspecific levels (Fig. 4A and B), supporting the prediction of OPT. In addition, the consistent interspecific patterns suggest that different species follow a similar biomass allocation strategy, possibly due to evolutionary pressures that favor consistent reproductive investment across broad environmental conditions. The isometric relationships suggest an underlying strategy of balanced biomass allocation between reproduction and growth to optimize fitness. Our findings are consistent with the isometric allocation pattern, with a slope close to 1, in cereal-legume intercropping systems [67] and the consistent reproductive allocation of *Gentiana* species across elevation gradients on the Yunnan-Guizhou Plateau, China [68]. However, other studies have found an allometric relationship between plant reproductive and vegetative mass [19, 24, 69–71]. These studies focused on different species, life-forms, environmental contexts, nutrient additions or land-use changes, which may result in the different results from our study. Furthermore, *Artemisia* species, being well-adapted to diverse and sometimes harsh environments, may have evolved a strategy to maintain an isometric resource allocation to balance growth and reproductive success under variable conditions.

Furthermore, our study on *Artemisia* species revealed distinct patterns of reproductive allocation in relation to different vegetative organs, with the relationships between reproductive mass and root mass being allometric, but that between reproductive mass and stem mass being isometric (Fig. S1). The different allocation patterns could be attributed to the different roles among plant organs. Leaves and roots are directly involved in photosynthesis and nutrient uptake, which are critical for supporting reproduction. These findings are consistent with the allometric models of seed plant reproduction, which posited that plants allocate resources to maximize reproductive success while maintaining essential vegetative functions [72]. In addition, our findings align with the dynamic optimization theory, which suggests that plants dynamically adjust their growth and resource allocation to balance immediate growth with reproductive success [8]. The isometric relationship between reproductive mass and stem mass (Fig. S1D and E) indicates that reproductive output also increases proportionately with increasing stem growth to maintain structural integrity and efficient nutrient transport. Conversely, the allometric relationship between reproductive mass and root mass (Fig. S1G and H) indicates that *Artemisia* species prioritize reproductive investment over root growth during reproduction. Similar results have been reported in

Tibetan alpine grasslands, where reproductive mass allocation varies allometrically with root mass in response to environmental conditions, reflecting an adaptive response to maximize reproductive output while maintaining sufficient root function [69].

It is important to distinguish between the intra- and interspecific biomass allocation patterns, as they can differ significantly [24]. In our study, the allocation patterns within species (i.e., the intraspecific level) are largely consistent with the general patterns observed at the individual level and the overall trends seen across different species (i.e., the interspecific level), whereas the relationships differed among species at the intraspecific level (Figs S1C, F and I, Table S1), highlighting the potentially diverse intraspecific adaptations to environmental gradients. Similarly, in cereal-legume intercropping systems, both interspecific and intraspecific factors play crucial roles in determining biomass allocation patterns [67]. Also, life forms (e.g., annual, perennial and semi-shrub) have different reproductive allocations at the intraspecific and interspecific levels. For instance, an experiment with fifteen species showed that long-lived iteroparous species typically exhibit very low reproductive allocation, whereas species with shorter lifespans exhibit relatively high reproductive allocation [73]. For two *Plantago* species, reproductive allocation of *P. major* decreases with vegetative mass, but there is no consistent relationship between reproduction allocation for *P. asiatica* [46, 47].

Biomass allocation between reproductive and vegetative organs is plastic to environmental gradients

In accordance with our third hypothesis, we found that biomass allocation between reproductive and vegetative organs was plastic in response to environmental gradients (Fig. 5). Our findings align with those of previous studies reporting significant effects of climatic factors and soil water availability on plant reproductive strategies [17, 74]. In North American, biomass allocation to reproduction of sunflowers varied with climate and soil variables [75]. With regard to climate, we found a significant increase in the ratio of reproductive to vegetative mass with climate variability (Fig. 5A and B). Because climate variability axis (PC2) was positively associated with isothermality but negatively with Tseason and Pseason (Fig. 2), our results suggest that plants invest more in reproduction under lower climate variability (i.e., more stable climatic conditions). However, an earlier study on *Artemisia* reported that climate has a weak effect on biomass allocation among vegetative organs [66]. The key difference between the present study and that study is that they focused on biomass allocation in different ontogenetic stages of *Artemisia*. Therefore, our results suggest that allocation patterns differ fundamentally between growth and reproduction stages.

For the three vegetative organs, our analysis revealed significant increases in the ratio of reproductive mass to stem and root mass with climate variability, while the ratio to leaf mass decreased (Fig. S2). Our findings partially support the general trend that plants often decrease allocation to reproductive structures, but increase that to roots, under climatic stresses [76]. The disparate responses among the organs may be indicative of organ-specific allocation mechanisms. For *Artemisia*, a robust stem structure may be essential for maintaining the health and function of reproductive organs under stressful conditions. The promotion of reproduction by the stem has also been documented in other Asteraceae herbs, in which the increased stem allocation is associated with enhanced reproductive success across varying soil depths and water availability [77]. Conversely, we found the biomass allocation to leaves exhibited a contrasting pattern, indicating a trade-off where resources are redirected from leaves to reproductive and supportive structures including stems, roots and fruits. Furthermore, the reduction in leaf allocation of *Artemisia* could minimize water loss and enhance resource use efficiency under stressful conditions. Similarly, *Vallisneria spirulosa* has been observed to reduce leaf mass in favor of reproductive success when resources are limited [74].

With regard to the soil, we found a significant change in the biomass ratio of reproductive to vegetative organs with physical properties (Fig. 5D and E). This points to a potentially unique role of soil conditions in influencing structural growth components such as stems, which may be of particular importance for supporting reproductive structures. Soil physical properties, including texture and water availability, are critical factors influencing nutrient uptake, plant health, structure and reproductive success [34]. In a semi-arid grassland, an increase in soil water and nutrient availability causes plants to invest less in belowground biomass, with a corresponding increase in allocation to reproduction [63]. Under high nutrient conditions, *Plantago lanceolata* maximizes fitness by increasing root biomass to enhance nutrient uptake and allocating more resources to reproductive organs [35]. Similarly, soil water availability significantly affects reproductive strategies in Asteraceae herbs by influencing biomass allocation, reproductive phenology and seed production [77].

At the intraspecific level, the relationships were mixed. While some species had positive relationships with climate variability and soil physical properties, others had negative relationships (Fig. 5C and F; Table 4), suggesting that species-specific adaptive strategies significantly influence how biomass allocation responds to environmental gradients. Reproductive allocation is known to vary significantly among species with different life forms and even among populations of a species growing in

different environmental conditions [15, 18, 19, 78]. For example, semelparous annual species allocate a greater proportion of their resources to reproduction than iteroparous perennials [78]. Similarly, distinct biomass allocation patterns have been observed in different sunflower species growing in diverse soil pH, organic matter content, cation exchange capacity across North America [75]. Together, our findings of diverse intraspecific responses indicate that genetic diversity and micro-environmental conditions may play an important role in shaping species-specific responses. However, further research is needed to explore these factors in a broader range of species groups and environmental gradients.

Conclusions

Our study has demonstrated that climate has a more pronounced effect on plant size than soil conditions along the environmental gradient for pooled species. However, this does not rule out the important role of soil on plant growth of some species, because our study involved different species that may evolve according to environmental conditions. In addition, the allocation between reproductive and vegetative organs is isometric, which does not support the OPT, at both the individual and interspecific levels. This suggests a proportional allocation between reproductive and vegetative growth that transcends species-specific variation. Furthermore, our findings show the plasticity in biomass allocation between reproductive and vegetative organs along environmental gradients, aligning with the prediction of the OPT. Such plasticity is merged among individuals, across species and even within species, indicating a consistent adaptation in plant growth and reproduction across different taxonomic levels. These findings highlight the necessity of considering climatic and soil factors in understanding plant ecological strategies in growth and reproduction.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s12870-024-06030-3>.

Supplementary Material 1

Author contributions

X.Y. and Z.H. conceived the ideas and designed methodology; T.T., X.Y., R.G., J.L., W.T., G.L. and X.Y. collected the data; T.T. and X.Y. analyzed the data; T.T., X.Y. and Z.H. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Funding

This work was supported by the National Natural Science Foundation of China [grant numbers 31770514 and 32071524].

Data availability

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

Author details

¹State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China

²University of Chinese Academy of Sciences, Beijing 100049, China

³The School of Life Sciences, Shanxi Normal University, Taiyuan 030031, China

Received: 2 December 2024 / Accepted: 30 December 2024

Published online: 08 January 2025

References

- Poorter H, Nagel O. The role of biomass allocation in the growth response of plants to different levels of light, CO₂, nutrients and water: a quantitative review. *Aust J Plant Physiol.* 2000;27(6):595–607.
- Crosby SC, Ivens-Duran M, Bertness MD, Davey E, Deegan LA, Leslie HM. Flowering and biomass allocation in U.S. Atlantic coast *Spartina alterniflora*. *Am J Bot.* 2015;102(5):669–76.
- Crosby SC, Sax DF, Palmer ME, Booth HS, Deegan LA, Bertness MD, et al. Salt marsh persistence is threatened by predicted sea-level rise. *Estuar Coast Shelf Sci.* 2016;181:93–9.
- Husáková I, Weiner J, Münzbergová Z. Species traits and shoot-root biomass allocation in 20 dry-grassland species. *J Plant Ecol.* 2018;11(2):273–85.
- Bazzaz FA, Chiariello NR, Coley PD, Pitelka LF. Allocating resources to reproduction and defense. *Bioscience.* 1987;37:58–67.
- Kleyer M, Minden V. Why functional ecology should consider all plant organs: an allocation-based perspective. *Basic Appl Ecol.* 2015;16:1–9.
- Poorter H, Jagodzinski AM, Ruiz-Peinado R, Kuyah S, Luo Y, Oleksyn J, et al. How does biomass distribution change with size and differ among species? An analysis for 1200 plant species from five continents. *New Phytol.* 2015;208(3):736–49.
- Iwasa Y. Dynamic optimization of plant growth. *Evol Ecol Res.* 2000;2:434–55.
- Mironchenko A, Kozłowski J. Optimal allocation patterns and optimal seed mass of a perennial plant. *J Theor Biol.* 2014;354:12–24.
- Niklas KJ, Enquist BJ. Canonical rules for plant organ biomass partitioning and annual allocation. *Am J Bot.* 2002;89(5):812–9.
- McCarthy MC, Enquist BJ. Consistency between an allometric approach and optimal partitioning theory in global patterns of plant biomass allocation. *Funct Ecol.* 2007;21:713.
- Yan B, Ji Z, Fan B, Wang X, He G, Shi L, et al. Plants adapted to nutrient limitation allocate less biomass into stems in an arid hot grassland. *New Phytol.* 2016;211:1232–40.
- Kumordzi BB, Gundale MJ, Nilsson MC, Wardle DA. Shifts in aboveground biomass allocation patterns of dominant shrub species across a strong environmental gradient. *PLoS ONE.* 2016;11(6):e0157136.
- Bazzaz FA, Ackerly DD, Reekie EG. Reproductive allocation in plants. In: Fenner M, editor. *Seeds: The Ecology of Regeneration in Plant communities*. 2nd ed. CABI Publishing; 2005. pp. 1–29.
- Wilson AM, Thompson K. A comparative study of reproductive allocation in 40 British grasses. *Funct Ecol.* 1989;3:297–302.
- Wenk EH, Abramowicz K, Westoby M, Falster DS. Investment in reproduction for 14 iteroparous perennials is large and associated with other life-history and functional traits. *J Ecol.* 2017;106:1338–48.
- Tang L, Zhou QS, Gao Y, Li P. Biomass allocation in response to salinity and competition in native and invasive species. *Ecosphere.* 2022;13:e4027.
- Bazzaz FA, Grace J. *Plant Resource Allocation*. New York: Academic; 1997.
- Weiner J. Allocation, plasticity and allometry in plants. *Perspect Plant Ecol Evol Syst.* 2004;6(4):207–15.
- Poorter H, Niklas KJ, Reich PB, Oleksyn J, Poot P, Mommer L. Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytol.* 2012;193:30–50.
- Shipley B, Meziane D. The balanced-growth hypothesis and the allometry of leaf and root biomass allocation. *Funct Ecol.* 2002;16(3):326–31.
- Lugli LF. Digging deeper? Biomass allocation patterns in trees and lianas in tropical seasonal forests. *New Phytol.* 2020;226:639–40.
- Müller I, Schmid B, Weiner J. The effect of nutrient availability on biomass allocation patterns in 27 species of herbaceous plants. *Perspect Plant Ecol Evol Syst.* 2000;3(2):115–27.
- Weiner J, Campbell LG, Pino J, Echarte L. The allometry of reproduction within plant populations. *J Ecol.* 2009;97:1220–33.
- Gedroc JJ, McConaughay KDM, Coleman JS. Plasticity in root/shoot partitioning: optimal, ontogenetic, or both? *Funct Ecol.* 1996;10:44–50.
- Enquist BJ, Niklas KJ. Global allocation rules for patterns of biomass partitioning in seed plants. *Science.* 2002;295(5559):1517–20.
- Fang T, Rao M, Chen Q, Liu S, Lai J, Chen T, et al. Different biomass allocation strategies of geophytes and non-geophytes along an altitude gradient. *Ecol Indic.* 2023;146:110828.
- Yin Q, Tian T, Han X, Xu J, Chai Y, Mo J, et al. The relationships between biomass allocation and plant functional traits. *Ecol Indic.* 2019;102:302–8.
- Boonman CCF, Langevelde FV, Oliveras L, Couedon J, Luijken N, Martini D, et al. On the importance of root traits in seedlings of tropical tree species. *New Phytol.* 2020;227(1):156–67.
- Jin Y, Liu C, Qian SS, Luo Y, Zhou R, Tang J, et al. Large-scale patterns of understory biomass and its allocation across China's forests. *Sci Total Environ.* 2022;804:150169.
- Wang X, Wang R, Gao J. Precipitation and soil nutrients determine the spatial variability of grassland productivity at large scales in China. *Front Plant Sci.* 2022;13:996313.
- Carvalho RB, Pizo MA. Seed removal, seed dispersers, and the allocation of tissues in Myrtaceae seeds. *Biotropica.* 2023;55:719–28.
- Wang T, Zhou D, Wang P, Zhang H. Size-dependent reproductive effort in *Amaranthus retroflexus*: the influence of planting density and sowing date. *Can J Bot.* 2006;84:485–92.
- Zhang J, Zhao Y, Wang Y. The trade-off between growth and reproduction in an alpine herbaceous plant along an elevation gradient. *Pak J Bot.* 2019;51(3):533–9.
- Janeček S, Patáková E, Klimešová J. Effects of fertilization and competition on plant biomass allocation and internal resources: does *Plantago lanceolata* follow the rules of economic theory? *Folia Geobot.* 2013;49:49–64.
- Vallès J, García S, Hidalgo O, Martín J, Pellicer J, Sanz M, et al. Biology, genome evolution, biotechnological issues and research including applied perspectives in *Artemisia* (Asteraceae). *Advances in Botanical Research*. Academic; 2011. pp. 349–419.
- Yang X, Huang Z, Zhang K, Cornelissen JHC. C:N:P stoichiometry of *Artemisia* species and close relatives across northern China: unravelling effects of climate, soil, and taxonomy. *J Ecol.* 2015a;103(4):1020–31.
- Yang X, Huang Z, Zhang K, Cornelissen JHC. Geographic pattern and effects of climate and taxonomy on nonstructural carbohydrates of *Artemisia* species and their close relatives across northern China. *Biogeochemistry.* 2015b;125(3):337–48.
- Khodorova NV, Boitel-Conti M. The role of temperature in the growth and flowering of geophytes. *Plants.* 2013;2:699–711.
- Hatfield JL, Prueger JH. Temperature extremes: Effect on plant growth and development. *Weather Clim Extremes.* 2015;10:4–10.
- Zeppel MJB, Wilks JV, Lewis JD. Impacts of extreme precipitation and seasonal changes in precipitation on plants. *Biogeosciences.* 2014;11(11):3083–93.
- Gao J, Wang J, Li Y. Effects of soil nutrients on plant nutrient traits in natural *Pinus tabulaeformis* forests. *Plants.* 2023;12(4):735.
- Huang L, Dong BC, Xue W, Peng YK, Zhang MX, Yu FH. Soil particle heterogeneity affects the growth of a rhizomatous wetland plant. *PLoS ONE.* 2013;8(7):e76252.
- Poorter H, Sack L. Pitfalls and possibilities in the analysis of biomass allocation patterns in plants. *Front Plant Sci.* 2012;3:259.
- Cheplick GP. Life-history variation in a native perennial grass (*Tridens flavus*): reproductive allocation, biomass partitioning, and allometry. *Plant Ecol.* 2020;221(2):103–15.
- Reekie EG. An explanation for size-dependent reproductive allocation in *Plantago major*. *Can J Bot.* 1998;76:43–50.

47. Kobayashi T, Okamoto K, Hori Y. Variations in size structure, growth, and reproduction in Japanese plantain (*Plantago asiatica* L.) between exposed and shaded populations. *Plant Spec Biol*. 2001;16:13–28.
48. Kozłowski J. Optimal allocation of resources to growth and reproduction: implications for age and size at maturity. *Trends Ecol Evol*. 1992;7(1):9–15.
49. Samson DA, Werk KS. Size-dependent effects in the analysis of reproductive effort in plants. *Am Nat*. 1986;127(5):667–80.
50. Wang R, Qiong G, Quansheng C. Effects of climatic change on biomass and biomass allocation in *Leymus chinensis* (Poaceae) along the North-East China Transect (NECT). *J Arid Environ*. 2003;54(4):653–65.
51. Zheng Y, Xue J, Lv Y, Zhang C, Wang R. Plant mass variations of *Leymus chinensis* (Poaceae) and their relationships with environmental factors on a large-scale gradient, northeastern China. *Ecol Evol*. 2024;14:e11215.
52. Chen K, Liu Q, Chen ZH, Li ZL. Soil temperature drives elevational patterns of reproductive allometry in a biodiversity hotspot. *Plant Ecol*. 2020;221(10):979–88.
53. Skarpaas O, Meineri E, Bargmann T, Pötsch C, Töpper J, Vandvik V. Biomass partitioning in grassland plants along independent gradients in temperature and precipitation. *Perspect Plant Ecol Evol Syst*. 2016;19:1–11.
54. Fick SE, Hijmans RJ. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int J Climatol*. 2017;37(12):4302–15.
55. Hengl T, Mendes de Jesus J, Heuvelink GBM, Ruiperez Gonzalez M, Kilibarda M, Blagotić A, et al. SoilGrids250m: global gridded soil information based on machine learning. *PLoS ONE*. 2017;12(2):e0169748.
56. Bates D, Mächler M, Bolker B, Walker S. Fitting linear mixed-effects models using *lme4*. *J Stat Softw*. 2015;67(1):1–48.
57. Warton DI, Duursma RA, Falster DS, Taskinen S. *smatr smatr 3* – an R package for estimation and inference about allometric lines. *Methods Ecol Evol*. 2012;3(2):257–59.
58. Chaves MM, Pereira JS, Maroco J, Rodrigues ML, Ricardo CPP, Osório ML, et al. How plants cope with water stress in the field: photosynthesis and growth. *Ann Bot*. 2002;89:907–16.
59. Zhu XG, Long SP, Ort DR. Improving photosynthetic efficiency for greater yield. *Annu Rev Plant Biol*. 2010;61:235–61.
60. Chaves MM, Maroco JP, Pereira JS. Understanding plant responses to drought – from genes to the whole plant. *Funct Plant Biol*. 2003;30:239–64.
61. Morecroft MD, Paterson JS. Effects of temperature and precipitation changes on plant communities. In: Morison JIL, Morecroft MD, editors. *Plant Growth and Climate Change*. Academic; 2006. pp. 96–122.
62. Yang X, Huang Z, Venable DL, Wang L, Zhang K, Baskin JM, et al. Linking performance trait stability with species distribution: the case of *Artemisia* and its close relatives in northern China. *J Veg Sci*. 2016;27:123–32.
63. Mueller KE, LeCain DR, McCormack ML, Pendall E, Carlson M, Blumenthal DM, et al. Root responses to elevated CO₂, warming, and irrigation in a semi-arid grassland: integrating biomass, length, and lifespan in a 5-year field experiment. *J Ecol*. 2018;106(6):2176–89.
64. Poorter H, Navas ML. Plant growth and competition at elevated CO₂: on winners, losers, and functional groups. *New Phytol*. 2003;157:175–98.
65. Peichl M, Sonnentag O, Wohlfahrt G, Varlagin A, Merbold L, Nilsson M, et al. Convergence of potential net ecosystem production among contrasting C3 grasslands. *Ecol Lett*. 2013;16(4):502–12.
66. Liu R, Yang X, Gao R, Hou X, Huo L, Huang Z, et al. Allometry rather than abiotic drivers explains biomass allocation among leaves, stems, and roots of *Artemisia* across a large environmental gradient in China. *J Ecol*. 2021;109(2):1026–40.
67. Gaudio N, Violle C, Gendreau X, Dumora D, Jeuffroy M-H, Pellerin S, et al. Inter-specific interactions regulate plant reproductive allometry in cereal-legume intercropping systems. *J Appl Ecol*. 2021;58(11):2579–89.
68. Zhang J, Wang YZ, Gao HK, Zuo ZT, Yang SB, Cai CT. Different strategies in biomass allocation across elevation in two *Gentiana* plants on the Yunnan-Guizhou Plateau, China. *J Mt Sci*. 2020;17(11):2750–7.
69. Niu K, Choler P, Zhao B, Du G. The allometry of reproductive biomass in response to land use in tibetan alpine grasslands. *Funct Ecol*. 2009;23:274–83.
70. Guo H, Weiner J, Mazer SJ, Zhao Z, Du G, Li B. Reproductive allometry in *Pedicularis* species changes with elevation. *J Ecol*. 2012;100:452–8.
71. Tian D, Pan Q, Simmons M, Chaolu H, Du B, Bai Y, et al. Hierarchical reproductive allocation and allometry within a perennial bunchgrass after 11 years of nutrient addition. *PLoS ONE*. 2012;7(9):e42833.
72. Niklas KJ, Enquist BJ. An allometric model for seed plant reproduction. *Evol Ecol Res*. 2003;5:79–88.
73. Wenk EH, Falster DS. Quantifying and understanding reproductive allocation schedules in plants. *Ecol Evol*. 2015;5(23):5521–38.
74. Li L, Ding M, Lan Z, Zhao Y, Chen J. Light availability and patterns of allocation to reproductive and vegetative biomass in the sexes of the dioecious macrophyte *Vallisneria spirulosa*. *Front Plant Sci*. 2019;10:572.
75. Mason CM, Goolsby EW, Davis KE, Bullock DV, Donovan LA. Importance of whole-plant biomass allocation and reproductive timing to habitat differentiation across the north American sunflowers. *Ann Bot*. 2017;119:1131–42.
76. Tian D. Drought effect on plant biomass allocation: a meta-analysis. *Ecol Evol*. 2017;7(24):11002–10. Han W, Tang Z, Fang J.
77. Li S, Liu J, Li J, Deng Y, Chen J, Wang J, et al. Reproductive strategies involving biomass allocation, reproductive phenology, and seed production in two Asteraceae herbs growing in karst soil varying in depth and water availability. *Plant Ecol*. 2021;222:737–47.
78. Karlsson PS, Méndez M. The resource economy of plant reproduction. In: Reekie EG, Bazzaz FA, editors. *Reproductive allocation in plants*. San Diego: Elsevier Academic; 2005. pp. 1–49.

Publisher's note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.