Below-ground competition drives the self-thinning process of *Stipa purpurea* populations in northern Tibet

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Keywords

Above-ground biomass; Below-ground biomass; Competition; Density dependence; Harsh environments; Population self-thinning; Precipitation gradient

Abbreviation

AM = alpine meadow; AS = alpine steppe; ADS = alpine desert steppe; MAP = mean annual precipitation; MAT = mean annual temperature; R/S = root/shoot ratios

Nomenclature

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Introduction

As a process of density-dependent mortality in even-aged communities (Reynolds & Ford 2005), population self-thinning is commonly observed in natural and artificial plant populations (Han & Fang 2008). To describe this

Abstract

Questions: Above-ground, below-ground and individual mass–density relationships for perennial herbs were examined along a natural precipitation gradient in northern Tibet. We asked: (1) how do the self-thinning exponents respond to variation in precipitation; and (2) what mechanisms drive the observed population self-thinning?

Location: The alpine grassland of northern Tibet.

Methods: Forty-seven fenced sites along a precipitation gradient were established and surveyed in 2011 and 2012. Data (geographic coordinates, elevation, and vegetation information) were collected for *Stipa purpurea* populations at each site. Population self-thinning exponents were estimated using reduced major axis regression.

Results: The self-thinning exponents for below-ground (−1.27, −0.47) and individual biomass (−1.26, −0.46) increased with increasing mean annual precipitation, but those for above-ground biomass decreased with precipitation (0.18, −0.25). Soil resources (moisture and nutrients) are a more important constraining factor for below-ground components than light is for above-ground components. Root competition for below-ground resources dominated in *S. purpurea* population self-thinning. The driving force of density regulation changed from above-ground competition to below-ground competition with increased drought stress. Our results indicate that an increased root/shoot ratio was linked to enhanced below-ground competition and weakened above-ground competition. Our study further confirmed the hypothesis that plant populations in different environments exhibit different biomass allocation patterns, which, in turn, leads to different biomass–density relationships.

Conclusions: Our study revealed the mechanisms of population self-thinning for perennial herbs in the extreme environment of northern Tibet, where below-ground processes play a critical role in regulating population self-thinning. Our study also advances understanding of the interactions between above- and below-ground processes, providing baseline knowledge useful for local grassland management.

process, Yoda et al. (1963) put forward an empirical equation stated to hold for all plant species:

$$M = kN^{\gamma} \quad (1)$$

where M is mean plant biomass; N is population density; k and γ are, respectively, the intercept and exponent relating

biomass to population density (Osawa & Kurachi 2004). Considerable debate exists on the value of the self-thinning exponent (γ). The $-3/2$ law and $-4/3$ laws, proposed by Yoda et al. (1963) and Enquist et al. (1998), respectively, are considered by some as general rules in plant ecology. However, other ecologists consider these two laws as unsubstantiated hypotheses that lack theoretical and empirical justification (Lonsdale 1990; Kozlowski & Konarzewski 2004; Deng et al. 2006; Dai et al. 2009). It was suggested that γ could vary with environmental conditions, such as light availability (Hiroi & Monsi 1966; Lonsdale & Watkinson 1982), soil fertility (Morris 2002, 2003), water availability (Deng et al. 2006; Dai et al. 2009) or salt concentration (Chu et al. 2008). It is also notable that studies of mass–density relationships have largely focused on woody plants, with little attention given to herbaceous species.

In most studies of population self-thinning, M generally includes only above-ground biomass (Yoda et al. 1963; Enquist et al. 1998), reflecting methodological difficulties in the measurement of below-ground biomass (Ogawa 2005; Mokany et al. 2006). As a result, we still know little about the relationship between below-ground biomass and self-thinning (Zhang et al. 2011). A number of studies, conducted on herbs (Morris & Myerscough 1991; Morris 1999, 2002, 2003) tree seedlings (Ogawa 2005) and desert shrub communities (Deng et al. 2006; Bai et al. 2010), have proposed that below-ground competition may be a major factor in driving density-dependent mortality and hence self-thinning. However, despite progress so far, there is still a lack of comparison among above-ground, below-ground and individual self-thinning processes in plants, especially in herbaceous plants.

The optimal partitioning theory suggests that low soil nutrient availability and low light supply would result in increased allocation to roots and leaves, respectively (Thornley 1972; Bloom et al. 1985), and that there might be a relationship between self-thinning exponents and biomass allocation (Bai et al. 2010). Consistent with these suggestions, it has been reported that above-ground competition for light drives the process of self-thinning for forest communities in the absence of drought stress (Hiroi & Monsi 1966; Xue & Hagihara 1999), and that root competition drives the process of density-dependent mortality for desert shrubs in arid regions (Deng et al. 2006). Moreover, the extent of environmental stress is known to affect the nature of species interactions, such that competitive interactions that tend to dominate in benign environments could turn into facilitative interactions in stressed habitats (stress gradient hypothesis; Bertness & Callaway 1994; Callaway et al. 2002). The balance between facilitation and competition might thus influence plant biomass–density relationships. Few studies, however,

have investigated how facilitative and competitive interactions combine to influence population self-thinning along environmental gradients (but see Chu et al. 2008).

The Northern Tibetan Plateau vegetation ecosystems exist under extreme environmental conditions, including intense radiation, strong winds, low temperatures, low soil nutrients and drought stress (Li et al. 2011; Yu et al. 2012). There are three main natural vegetation types: alpine meadow (dominated by *Kobresia pygmaea*), alpine steppe (dominated by *Stipa purpurea*) and alpine desert steppe (dominated by *Stipa subsessiliflora*) (Li et al. 2011), and all plants are perennial herbs. *S. purpurea* alpine steppe is one of the most important grassland types in northern Tibet, providing the main food source for local livestock (Hu et al. 2012). A natural precipitation gradient exists from east to west in northern Tibet (Wu et al. 2012), accompanied by relatively small variations in mean annual temperature and soil properties across the gradient (Cao & Wang 2012), providing a rare opportunity to examine the mass–density relationship for perennial herbs along a precipitation gradient under extreme environments. We hypothesize that, (1) self-thinning exponents will vary across the rainfall gradient, and (2) the variation in biomass allocation mode will change biomass–density relationships. We further asked what mechanisms drive the observed population self-thinning.

Methods

Study area

The Northern Tibetan Plateau (locally named Changtang) is in the hinterland of the Qinghai–Tibet Plateau (Cincotta et al. 1991; 29°53′–36°32′ N, 78°41′–92°16′ E), covering an area of 597 000 km² (Fig. 1). We set up a west–east alpine grassland transect (the Northern Tibetan Plateau Alpine Grassland Transect, NTPAGT) in May 2009 (Wu et al. 2012). The NTPAGT covers 79.71–92.03° E and 30.50–33.45° N, and is ca. 1200-km long and 400-km wide (Li et al. 2011). The NTPAGT traverses three main natural vegetation types: alpine meadow (AM, dominated by *K. pygmaea*), alpine steppe (AS, dominated by *S. purpurea*) and alpine desert steppe (ADS, dominated by *S. subsessiliflora*) (Li et al. 2011). Alpine steppe, dominated by *S. purpurea* (growth period May to September, about 120 d), is the most widely distributed vegetation type on the Northern Tibetan Plateau (Chinese Academy of Sciences, Intergrative Expedition Team to Qinghai–Tibet Plateau 1988). The mean annual precipitation (MAP) for alpine steppe varies from 120 to 500 mm, and mean annual temperature (MAT) ranges from -0.89 to -0.32 °C (Table 1). The elevation of the sample sites was from 4374 to 4953 m. According to distribution area of *S. purpurea* populations, we divided mean annual precipitation (120–500 mm) into

Fig. 1. Distribution of the 47 study sites along the Northern Tibetan Plateau Alpine Grassland Transect.

Table 1. The geographic and climatic conditions and characteristics of soil and natural vegetation along a precipitation gradient in northern Tibet. Mean $\pm$ SD

Parameters	Precipitation Gradient				
	120–180 mm	180–260 mm	280–360 mm	360–440 mm	440–500 mm
Altitude (m)	4406–4814	4374–4877	4494–4953	4533–4666	4548–4803
MAT (°C)	−0.89	−0.59	−0.32	−0.41	−0.45
Soil Moisture Content (%)	2.36–9.94	3.80–14.38	7.38–21.42	10.41–23.52	10.73–26.28
Vegetation Cover (%)	28 $\pm$ 2.15	35 $\pm$ 3.28	38 $\pm$ 2.84	43 $\pm$ 3.55	48 $\pm$ 4.86
Mean Root/Shoot Ratio	23 $\pm$ 5.35	20 $\pm$ 5.54	15 $\pm$ 3.48	11 $\pm$ 2.16	8 $\pm$ 2.25

five levels: 120–180, 180–260, 280–360, 360–440 and 440–500 mm.

Data collection

Field surveys were conducted in late July to early August 2011 and 2012. The sampled vegetation is composed mainly of *S. purpurea* with low species diversity; other less common, but frequently observed species include *Poa annua*, *Koresia macrantha*, *Carex moorcroftii*, *Festuca ovina*, *Oxytropis microphylla*, *Potentilla bifurca*, *Leontopodium nanum* and *Saussurea stella*. Forty-seven fenced sites along a precipitation gradient were established and surveyed (Fig. 1). We recorded geographic coordinates, elevation, soil moisture content (TDR300, Spectrum, California, CA, USA) and vegetation type for each site. Five 1 $\times$ 1-m quadrats were laid out randomly within each 100 $\times$ 100-m site and all vascular plant species were recorded. The number of species, number of individual plants (genets and ramets), canopy cover, above-biomass and below-ground biomass were measured in

each quadrat. All above-ground biomass was clipped to ground level. The sites were surveyed in 2011 and 2012, and the data were averaged over the 2 yr. The below-ground biomass was sampled by randomly taking a 7-cm diameter soil core to 50-cm depth within each of the five quadrats (depth intervals: 0–5, 5–10, 10–20, 20–30, 30–50 cm). Six soil samples were collected from 0 to 5 cm and from 5 to 10 cm; three soil samples were collected from 10 to 20 cm and from 20 to 30 cm; two soil samples were collected from 30 to 50 cm. Soil was rinsed from roots under running water over a 1-mm screen. Above- and below-ground samples were weighed after removing dead parts and oven-dried at 65 °C for 72 h to a constant weight. In Tibetan grasslands, about 90% of total root biomass occurs in the top 30 cm of soil (Yang et al. 2009). We calculated the below-ground biomass across the five depth intervals. The above-, below-ground and total biomass at each site was averaged across the five quadrats. Mean above-, below-ground and total biomass for each individual plant was calculated by dividing the population

biomass of its species by its population size. We then calculated root/shoot (R/S) ratios for all sampling sites.

Daily air temperatures and rainfall throughout each year from 1982 to 2011 were obtained from the National Meteorological Information Centre of China Meteorological Administration. Mean annual precipitation and temperature for each site were extrapolated using a geographic information system-based multiple regression method (Bai et al. 2007) in ArcGIS 9.2 (ERSI, Redlands, CA, US).

Data analysis

As observed vegetation cover is only 28–48% over the rainfall gradient, the plant canopy is not closed at all sites, thus plant biomass may be at a maximum for this environment (Fowler 1986). Specifically, plant stands may maintain a relatively steady structure and energy balance under limited resources during the thinning process. The log M –log N regression lines may therefore reflect the self-thinning process (Deng et al. 2006). The allometric exponents or slopes (γ) and the intercept (k) in the allometric equation ($M = kN^\gamma$) were estimated using reduced major axis (RMA) regression of the log-transformed data. In analysing the exponents, statistical significances were tested based on 95% CIs. The additional calculated variables were: $N = n/s$, $B = b/s$, $M = B/N$, where N , B , M , n , b and s represent population density, above-/below-ground biomass per area,

mean above-/below-ground biomass, number of individuals, total above-/below-ground biomass and sample area, respectively. The R/S ratios for each of the five precipitation levels were used as independent variables in linear regression models, and with above-ground, below-ground M – N allometric exponents (γ) as dependent variables. All statistical analyses were conducted in SPSS (v 13.0; SPSS Inc., Chicago, IL, US).

Results

The slopes of self-thinning lines for above-ground plant parts became steeper with increasing mean annual precipitation (MAP; Fig. 2). When MAP was 360–500 mm, the above-ground allometric exponents were negative; there was no significant relationship between above-ground biomass and density (i.e. zero slope) when MAP was 180–360 mm ($P > 0.05$); when MAP was <180 mm, the exponent for above-ground biomass was significantly positive (Table 2, Fig. 2), i.e. above-ground biomass significantly increased with increasing population density.

The allometric exponents for below-ground and individual biomass, however, showed an opposite trend with MAP. Specifically, both slopes of self-thinning lines became flatter as MAP increased (Figs 3 and 4). Note that only when rainfall was 120–180 mm were the allometric exponents for below-ground and individual biomass–density relationships close to $-4/3$; their 95% CIs (-1.57 ,

Fig. 2. M – N relationships between above-ground biomass and plant density of *Stipa purpurea* populations along a natural precipitation gradient in northern Tibet. (a) 120–180 mm; (b) 180–260 mm; (c) 280–360 mm; (d) 360–440 mm; (e) 440–500 mm.

Table 2. Slopes and intercepts of linear relationships between mean above-ground, below-ground and individual biomass and population density along a precipitation gradient as estimated from the reduced major axis method.

Regression $M:D$	MAP (mm)	Slope	95% CI	Intercept	95% CI	R^2	n	P -value
Above-Ground Biomass	440–500	−0.25	−0.31, −0.17	0.39	0.29, 0.48	0.13	55	<0.001
	360–440	−0.17	−0.24, −0.11	0.37	0.26, 0.44	0.22	45	<0.001
	280–360	−0.15	−0.20, −0.12	0.34	0.26, 0.37	0.10	50	>0.05
	180–260	−0.10	−0.15, −0.07	0.32	0.25, 0.38	0.08	45	>0.05
	120–180	0.18	0.09, 0.21	−0.12	−0.18, −0.07	0.15	40	<0.05
Below-Ground Biomass	440–500	−0.47	−0.60, −0.35	1.49	1.18, 1.80	0.21	55	<0.001
	360–440	−0.67	−0.83, −0.51	2.00	1.62, 2.38	0.39	45	<0.001
	280–360	−0.83	−1.03, −0.64	2.36	2.01, 2.71	0.39	50	<0.001
	180–260	−1.20	−1.53, −0.87	2.75	2.30, 3.24	0.17	45	<0.001
	120–180	−1.27	−1.57, −0.96	2.83	2.36, 3.30	0.35	40	<0.001
Individual Biomass	440–500	−0.46	−0.58, −0.35	1.47	1.17, 1.78	0.21	55	<0.001
	360–440	−0.65	−0.82, −0.50	2.00	1.62, 2.38	0.40	45	<0.001
	280–360	−0.83	−1.03, −0.64	2.36	2.01, 2.71	0.39	50	<0.001
	180–260	−1.18	−1.51, −0.85	2.72	2.28, 3.23	0.16	45	<0.001
	120–180	−1.26	−1.55, −0.95	2.82	2.35, 3.30	0.35	40	<0.001

Fig. 3. $M-N$ relationships between below-ground biomass and plant density of *Stipa purpurea* populations along a natural precipitation gradient in northern Tibet. (a) 120–180 mm; (b) 180–260 mm; (c) 280–360 mm; (d) 360–440 mm; (e) 440–500 mm.

−0.96 and −1.55, −0.95, respectively), however, included both $-4/3$ and $-3/2$ (Table 2).

Mean vegetation cover was 28–48% across all sites, and increased with increasing MAP (Table 1). This variable exhibited a negative relationship with the R/S ratio, which decreased with increasing MAP (Table 1). Across the five precipitation regions, the allometric exponents for the above-ground biomass–density relationship increased with increasing R/S ($R^2 = 0.69$, $P < 0.001$; Fig. 5), while for the

below-ground biomass–density relationship it decreased with R/S ($R^2 = 0.96$, $P < 0.001$; Fig. 5).

Discussion

Responses of above- and below-ground exponents to precipitation variations

Studies on the responses of self-thinning exponents to precipitation variations are more common in arid and

Fig. 4. $M-N$ relationships between individual biomass and plant density of *Stipa purpurea* populations along a natural precipitation gradient in northern Tibet. (a) 120–180 mm; (b) 180–260 mm; (c) 280–360 mm; (d) 360–440 mm; (e) 440–500 mm.

Fig. 5. The relationships between root/shoot ratios (R/S) and above-ground (a) and below-ground (b) $M-N$ allometric exponents (γ) for the five precipitation levels along the precipitation gradient.

semi-arid regions (Deng et al. 2006; Dai et al. 2009; Bai et al. 2010). In the present study, the largest difference in mean annual temperature (MAT) is less than 1 °C, which is trivial compared to the wide range of the precipitation gradient. We consequently focused on the effects of the precipitation gradient on the exponents. The slopes of

self-thinning lines for below-ground parts became flatter as MAP increased, while the opposite trend was observed for above-ground parts. Several other studies in arid regions also reported that slopes of self-thinning lines for above-ground plant parts become steeper as MAP increases (Deng et al. 2006; Dai et al. 2009).

One interesting result with regard to the above-ground $M-N$ allometric exponent is a declining trend with increasing MAP. Specifically, it was significantly positive for the lowest precipitation, not different from zero for intermediate precipitation and significantly negative for the highest precipitation; i.e., in the extreme environment of northern Tibet, population self-thinning occurred only when rainfall was relatively abundant, and above-ground biomass actually increased with population density under drought stress. These results could potentially be explained through the stress gradient hypothesis (Bertness & Callaway 1994; Callaway 2007), which emphasizes the relative importance of competition and facilitation along environmental stress gradients. Applying this hypothesis to our study system, we suggest that competition may be important and drive self-thinning in regions that receive abundant rainfall, and that facilitation may be important in regions with relatively little rainfall. Facilitation may occur in this extreme environment, as observed for (non-thinning) populations (Chu et al. 2008). Plants with higher population densities can improve local temperature, slow wind and create a relatively stable soil environment, such that plants provide mutual support to withstand adverse conditions (Callaway 2007). An alternative explanation, if the populations are truly self-thinning, is that root competition is so severe that surviving plants show negative growth responses in above-ground biomass (Morris 1999).

Mechanisms of population self-thinning

Newman (1973) proposed that below-ground competition becomes more important with increasing abiotic stress in plant populations. Bai et al. (2010) also proposed that the driving forces of density regulation might shift from canopy to root competition under environmental stress. The Northern Tibetan Plateau is a system under extreme abiotic environmental conditions. The slopes of self-thinning lines for above-ground parts become flatter under drought stress, while for below-ground parts lines become steeper with drought stress. Hence, the intensity of density-dependent regulation of above- and below-ground biomass changed during drought stress: it decreased with stress for above-ground biomass and increased with stress for below-ground biomass (Li & Zhou 2011).

The optimal partitioning theory suggests that lower nutrient supply increases allocation to roots, and lower light supply increases allocation to leaves (Bloom et al. 1985). Therefore, when water supply is limited, accompanied by lower nutrient availability, plants preferentially allocate more biomass to below-ground parts, and the R/S ratio increases (Brown & Lugo 1982). Our study corroborates these predictions. Dai et al. (2009) proposed that the slopes of self-thinning lines for above-ground

parts become flatter with declining MAP, and this might be interpreted in decreasing above-ground biomass with increasing drought stress, as plants allocate more biomass to below-ground parts. In the present study, the R/S ratio was positively correlated with the self-thinning exponents for above-ground biomass and negatively with below-ground biomass (Fig. 5). An increased R/S ratio with increasing drought stress indicates that plants allocated more biomass to below-ground parts as they grew larger to maximize uptake of water and nutrient resources (Bloom et al. 1985). The resultant higher below-ground competition under increased drought stress presumably led to smaller exponents for below-ground biomass; the resultant weaker above-ground competition under increased drought stress presumably led to larger exponents for above-ground biomass. Our results further confirmed the hypothesis that plant populations in different environments exhibit different biomass allocation patterns, which, in turn, lead to different biomass–density relationships (Bai et al. 2010).

Below-ground competition regulates population self-thinning

Above- and below-ground and individual biomass were influenced by density regulation ($\gamma < 0$), the result of both intraspecific and interspecific competition (Ogawa 2005). As the γ -value reflects the magnitude of density dependence (the smaller the value, the higher the intensity of density dependence; Li & Zhou 2011), we conclude that the effect of density-dependent regulation on below-ground biomass was greater than that on above-ground biomass. In this study area, solar radiation is 5000–8000 MJ·m⁻²·yr⁻¹, mean soil moisture content is 2.36–26.28% (0–20 cm) and mean N content is 0.05–0.12% (0–20 cm; our data). We thus inferred that light limitation for above-ground parts was not important, while soil moisture and nutrients were limited for below-ground plant parts. Consequently, root competition for below-ground resources dominated *S. purpurea* population self-thinning. Other recent studies also recognized that root competition can play an important role in regulating plant populations (Morris 1999, 2002, 2003; Deng et al. 2006; Li et al. 2012). Our results identified the importance of below-ground competition on plant population regulation in environmentally stressed regions.

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