Abiotic and Biotic Factors Affecting Plant Mass-Density Relationship in Self-Thinning Populations

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Abstract: Self-thinning scaling relationship emerges as a consequence of the trade-off between growth and survival in crowed populations with resource limitations. As an essential link between the organism- and population-level traits of species, it is crucial for predicting ecosystem patterns, dynamics and construction. Despite a long research history, it remains controversial whether the scaling exponent is constant or if it is, what value it takes. The long-term debate always revolves around a dichotomous distinction between the exponent of -3/2 predicted by Euclidean geometry model and -4/3 derived from the fractal network of branching tubes. Evidence emerging recently suggests that the exponent traverses across any single value with the influence caused by biotic and abiotic factors. From a long-term systematic research combined with theoretical analysis, field investigation and experimental observation, our group summarizes that the biotic and abiotic factors are especially noticeable in self-thinning process ascribed to their roles in mediating plant architecture (i.e., allometric growth in height (H) and radius (R)) as well as above- and below-ground allocation, which alters the intensity and pattern of plant interaction (competition and facilitation) and results in variable self-thinning trajectory. To better understand how body mass and density are related in self-thinning process in relation to affecting factors, we describe the self-thinning phenomena, review the theoretical and empirical -3/2 and -4/3 self-thinning rule, discuss the various factors affecting the self-thinning trajectory, analyze the possible mechanism underlying the formation of self-thinning relationship and propose novel directions for future mass-density research.
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Introduction:

Mass-density relationship has been received great attentions in theoretical and quantitative ecology as an essential link between the organism- and population-level traits of species and the structure and dynamics of ecosystems (White EP *et al.* 2007). The most focused mass-density form is the self-thinning relationship. Self-thinning relationship describes a phenomenon in density-dependent mortality populations that the density of survivors (D, number per square meter) is related to their mean biomass (M, in grams) by a power equation $M=kD^\alpha$, where k and α are constants. When transformed to logarithms, the equation turns to be $\log M= k'+\alpha\log D$, where α is the allometric exponent of biomass and density and k' is the coefficient. This allometric relationship has been considered "one of the most widespread of ecological regularities" (Damuth 1998), and extended to predict growth and biomass across ecological communities (Niklas *et al.* 2003). Despite a long and eminent research history in ecology, debates over whether α is a universal constant or if it is, what value should it take remain controversial. The most famous "-3/2" self-thinning rule suggests α should take a value close

to -3/2 based on the traditional Euclidean surface-area-to-volume geometry model (Yoda *et al.* 1963). This rule has been recognized as the "first principle" in plant ecology during 1960s to 1980s (Hutchings 1983). In contrast, the recent metabolic scaling theory predicts that the scaling relationship between individual metabolic rate and biomass (β) is 3/4 according to a fractal-branching model and the scaling exponent between individual biomass and maximum population density (α) should inversely be -4/3, instead of -3/2 (West *et al.* 1997, 1999a, 1999b; Enquist *et al.* 1998; Brown *et al.* 2005; Price *et al.* 2012). Although both of the universal "laws" have gained considerable support in a general sense (Yoda *et al.* 1963; Hutchings 1983; Enquist *et al.* 1998; Enquist and Niklas 2001; Enquist and Niklas 2002; Brown *et al.* 2004; West and Brown, 2004), suspicion and criticism on their assumption and applicability present the theories big challenges (Weller 1987; Lonsdale 1990; Dodds *et al.* 2001; Sack *et al.* 2002; Bokma 2004; Kozłowski and Konarzewski 2004; Coomes 2006; Muller-Landau 2006). Although these simple and general rules are prone to reduce complexity, they cannot avoid the risk of neglecting individual species

peculiarities. In addition, extensive evidence from filed investigations and laboratory experimentations has demonstrated that the allometric exponents for the metabolic rate could vary significantly with some biotic and abiotic factors (Ricklefs 2003; Kozłowski and Konarzewski 2004; Pretzsch 2006; Reich *et al.* 2006; Duncan *et al.* 2007; White CR *et al.* 2007), just as the slopes of self-thinning lines change as a function of water or nutrient limitations (Morris 2002, 2003; Deng *et al.* 2006; Dai *et al.* 2009), saline (Zhang H *et al.* 2010b), shade tolerance (Lonsdale and Watkinson 1982), marine intertidal (Sibomana and Wang 2013), spatiotemporal scales (Dunham and Vinyard 1997), arbuscular mycorrhizal fungi infection (Zhang Q *et al.* 2011a, b), ontogeny stages (Sack *et al.* 2002), species-specific traits (Pretzsch 2006; Deng *et al.* 2008), forest types (Zhang WP *et al.* 2011) and taxonomic levels (Isaac and Carbone 2010). The existence of heterogeneous self-thinning relationships implies that some factor or combination of factors is acting to limit population density. As the "actual slopes convey valuable information about species and habitats that should not be cast away" (Zeide 1987), to identify the causal factors and underlying mechanisms for the deviation of self-thinning lines is essential for the assessment and understanding of the dynamics of organisms, populations or ecosystems (Lobón-Cerviá and Mortensen 2006; Pretzsch 2006). In this paper, we analyzed the causal factors and underlying mechanisms of heterogeneous scaling relationships to make a better understand towards the mass-density regulations in self-thinning populations, while a detailed review of constant theories of self-thinning phenomenon was beyond the scope of this paper.

The abotic or biotic factors affecting the mass-density relationship

The mass-density relationship in self-thinning process often reflects the consequence of intraspecific competition, which is greatly related to plant strategies of resources allocation and utilization across body size. The analysis of a broader range of competitive states and stand densities of individual plants demonstrates that allometry for self-thinning conditions is one special borderline-case in a continuum of growing conditions. Emerging laboratory experiments and field investments have suggested various biotic or abiotic factors can influence the population dynamics by determining plant allometric growth and patterns of plant interactions. We have summarized the evidence against the universal self-thinning rules in eminent literatures in this research field and classified the affecting factors as follows.

Environmental factors

The physical environment is the primary determinant of net primary production. In natural stressful environments, plants have to cope with several limiting factors, such as water shortage, nutrient sterility, salinity and shade, which may influence plant competitive potential and consequently population dynamics and construction (Niinemets and Valladares 2006; Valladares and Niinemets 2008). In benign environments with abundant water and nutrient, plants primarily compete for light or space via stretching the shoots; in harsh conditions with limited water and nutrient, they always increase root allocations to compete for the below-ground resources preferentially. The magnitude and pattern of competitions is supposed to shift along environmental gradients, resulting in deviation in slopes of self-thinning lines (Jia *et al.* 2011). Lonsdale and Watkinson (1982) investigated the effects of shade on self-thinning in *Lolium perenne* populations grown under various shade regimes, and found that populations thinned along a line of slope -1 to -3/2 from deep shade to un-shaded growth conditions. This phenomenon could be explained via the higher shoot/root ratios in shaded than in un-shade populations. Consequent studies discussed the roles of light competitions in driving the self-thinning process and draw the same conclusions (Xue and Hagihara 1999). Westoby (1984) found that mono species grown under heterogeneous resource level conditions would have different intercepts of self-thinning lines. These differences caused great deviation of slopes for the same self-thinning lines. Zeide (1985) deduced the same conclusion that the slope was habitat-specific. In addition, the slope was defined as the survival ability under intraspecific competitions. Morris (2002, 2003) investigated the effect of fertility level of the substrate on the self-thinning lines in the *Ocimum basilicum* populations. He pointed out the slope of self-thinning line was the ultimate manifestation of intraspecific competition. He also proposed that the differences in the slopes of the self-thinning lines were due to the differences in the radial extension of the canopy versus shoot mass relationships of individual plants at each fertility level, and/or to an increase in root competition at the lower fertility level. Wang *et al.* (2004) agreed that competition was the dominant factor that restricted the self-thinning process. The growth pattern of individuals in the plant population was supposed to change from isometry to allometry with the self-thinning exponents ranging from -2.5 to -1 accompanied with the increase of competition intensity from the beginning as he observed. Deng *et al* (2006) analyzed data obtained from plant communities along a natural gradient of moisture and latitude in north-west China, figuring out the above-ground mass-density scaling exponents decreased (absolute value increased)

with increasing natural moisture and plant cover. Dai *et al.* (2009) observed the similar phenomenon and proposed that the scaling relationship was determined by another two allometric relationships, i.e., plant height with crown radius (φ) and canopy coverage with density (θ). The equation could be expressed as $\alpha=(2+\varphi)(\theta-1)/2$, where φ was allometric exponent of the shoot height with the crown radius and θ was the exponent of canopy coverage with plant density. The equation was matched with the investigated data. Zhang H *et al.* (2010b) investigated the mass-density relationship in *Suaeda salsa* populations grown in heterogeneous salinity conditions and found that the mass-density allometric exponent increased with decreasing salinity level. The alteration resulted from the distinguished geometric morphologies and resource utilization in response to salinity stress. An individual-based "zone-of-influence" model analysis demonstrated the mass-density relationship shifted from monotonic to humped when the mimic salinity stress increased (Chu *et al.* 2008). The conclusion was consolidated with a field experiment on the clonal grass *Elymus nutants* in an alpine meadow, showing that facilitation would increase in harsh environment and the mass-density relationship was determined by the balance between facilitation and resource competition.

Although overwhelming evidence has demonstrated environmental factors are determinate in mass-density regulations by influencing plant interactions, the quantitative effect is rarely discussed due to the difficulties in quantifying the stress intensity. The involvement of the Michaelis-Menten Equation ($R/(K_m+R)$) can solve this problem. For example, the effects of photosynthetic active radiation on the metabolic scaling relationship in marine autotrophs could be tested by the equation: $Y=\sigma M^{\alpha}(R/(K_m+R))$, where R was the resource availability (here photosynthetic active radiation) and K_m was the half-saturation constant that represented the amount of quanta at which half the maximum metabolic activity was reached for the metabolic rates of marine autotrophs   (López-Urrutia *et al.* 2006).

Ontogeny stage
Studies tracking herbaceous plants from seedlings to senescence have demonstrated that rates of photosynthesis, patterns of biomass allocation, relative growth rates, construction costs, leaf longevity, root: shoot ratios, plant architecture, levels of plasticity, and sensitivity to stress co-vary with plant age, or the varying levels of ontogenetic drift. The ontogenetic effects on structural and physiological traits are determinate in species competitive potentials in various environments. Sack *et al.* (2002) investigated series of biomass allometric partitioning relations and found that the scaling exponents were dramatically affected by

ontogeny stages. Examination of the juveniles of seven woody species showed that the specific leaf area (*SLA*) $\propto M_t^{-0.22}$, where M_t was the total plant dry mass. Noticeably, the scaling exponents changed from early to later ontogeny. For small plants, the proposed relations $M_L \propto M_S^{3/4} \propto M_R^{3/4}$ by Enquist and Niklas (2002), where was M_L standing leaf dry mass, M_S was stem dry mass and M_R was root dry mass, had also been rejected. The data supported the relations $M_L+M_S \propto M_R$ and $M_L \propto M_T$ only for the early stage, which constituted a crucial period for establishment. Cheng *et al.* (2009) analyzed a large dataset for Chinese forests covering six major forest biomes and a total of 17 forest types grown across a range of stand age (3 to 350 yrs), figuring out the scaling exponent of annual productivity with metabolic rate was unity (>1) at the early stage and systematically declined with the stand age. Using a forest biomass dataset including 1 266 plots of 17 main forest types across China, Li *et al.* (2005) explored the scaling exponents between tree productivity and tree mass and found no universal value across forest stands. The variations were probably caused by the large range of plant size and age of the samples. By measuring respiration of 271 whole plants spanning nine orders of magnitude in body mass, Mori *et al.* (2010) substantiated the allometric exponent varied continuously from 1 (in the smallest plants) to 3/4 (in large saplings and trees). It was possible that juveniles had higher growth rates in comparison to more mature conspecifics provided they produced disproportionately large foliage biomass (Niklas and Enquist 2001). Enquist *et al.* (2007) had made some modifications to their original WBE model and restated that scaling exponents were close to 1.0 for seedlings owing to the violation of WBE assumptions in seedlings and shifted to 3/4 in large plants.

Species-specific
Kozlowski and Konarzewski (2004) criticized the WBE model as neither mathematically correct nor biological relevant or universal. They claimed more biological realism and analysis to explain why scaling exponents differed between taxonomic groups. Pretzsch (2006) provided empirical evidence against the general and species-invariant scaling rule by analyzing the database including plots of pure common beech, Norway spruce, Scots pine and common oak stands which had been inventoried since 1870. The results demonstrated the $\ln(N)$-$\ln(D)$-relationships with a species-specific values of $\alpha=-1.789$ for European beech, $\alpha=-1.664$ for Norway spruce, $\alpha=-1.593$ for Scots pine and $\alpha=-1.424$ for Sessile oak. The heterogeneous allometric exponents indicated how strongly a species-specific structural

enforced self-thinning lines or the species' self-tolerance. Deng *et al.* (2008) examined the mass-density and metabolic scaling relationships in tree, desert shrubs and herbage communities spanning a size range of 11 orders of magnitude, suggesting the continually variable scaling relationships was species-specific and dependent on environmental conditions. Zhang *et al.* (2012) analyzed the standing stem, branch and leaf biomass-density relationships across a range of forest community in China, concluding that the scaling exponents for the components of plants might vary across different forest types. Isaac and Carbone (2010) provided the first estimate of the variance among taxa and found the scaling was dependent on the taxonomic level. According to the variation, they suggested the expression of "universal" should be modified as "3/4 scaling of metabolism is the central tendency". All the observed developments of plant structure and stand self-thinning dynamics seem to result from a general allometric partitioning, as a species-specific structural allometry and plasticity is an adaptation and acclimation to selective pressure (Pretzsch *et al.* 2012).

Arbuscular mycorrhizal fungi (AMF) infection

Allometry is determinate in the regulation of plant biomass-density relationships during self-thinning. AMF was reported to affect the importance of below-ground relative to above-ground interactions and change shoot/root biomass allocation. These changes would alter the allometric allocation of biomass and shift the self-thinning trajectory (Zhang Q *et al.* 2011b). Although AMF can affect the biomass-density relationship through mediating intraspecific competition, the effect is always resource-dependent in more complex environment. Zhang Q *et al.* (2011a) demonstrated that AMF status could shift the biomass-density relationship via effects on intraspecific competition with sufficient availability of water but could not when the water was insufficient. Yu *et al.* (2012) investigated the how interactions of salt stress and AMF acted to influence plant neighbor effects and self-thinning in *Medicago sativa* populations. They proved that AMF could increase competition, decrease survival rate and steepen the self-thinning line with the absence of salinity while its roles were buffered with the salt stress.

Hormonal regulation

Plants utilize phytohormone signaling systems to maintain their cellular and whole-body functions (Okamoto *et al.* 2012). Phytohormones participate in diverse fundamental physiological process, including developmental regulation and stress responses. In Arabidopsis, hypersensitivity to ABA reduces shoot branching, suggesting a role of ABA in

maintaining axillary bud dormancy and hence in shoot architecture (Pei *et al.* 1998). The plant architecture and canopy structure is supposed to be greatly involved in mass-density allometric relationships in crowed population. Zhang H *et al.* (2005, 2006, 2010a) found that sensitivity to ABA could affect self-thinning relationships and scaling of growth rate with body mass as well as plant interaction in *Arabidopsis* mutant populations via mediating resource utilization efficiency. They figured out that the hypersensitive mutant (*era1-2*) had larger total leaf area and shorter energy transportation distance according to the fractal distribution model, and thus was more advantageous in resource use than the insensitive mutant (*abi1-1*) in response to density stress. Series of physiological functions were altered accordingly, which ultimately led to variable scaling exponents of self-thinning and metabolism across the mutants. The involvement of hormonal regulation on mass-density relationships has linked the physiological and morphological process to the population and community functions. The coordinated regulations of hormone biosynthetic pathways have been demonstrated to play crucial roles rather than a single hormone (see the reviews by Acharya and Assmann 2009; Pinheiro and Chaves 2011), indicating more species of hormone are engaged in the regulation. Phytohormone ecology has developed as a new tool to explore the central role that hormones may have in population dynamics and construction (Farnsworth 2004).

Prospect

As an essential link between ecosystem function with evolutionary demography (Westoby 1984), self-thinning relationship is always a central issue in theoretical ecology (White EP *et al.* 2007). The self-thinning rules have been broadly applied in the development of density management diagrams, patterns of abundance (Enquist and Niklas 2001), energy partitioning patterns (Griffiths 1992; Dunham *et al.* 2000) and growth predictions across ecological communities (Niklas *et al.* 2003; Lobón-Cerviá and Mortensen 2006). Although -3/2-scaling derived from Euclidian geometric model or -4/3-scaling based on the metabolic scaling theory can meet human's innate propensity for generality and simplicity of pattern and processes in nature, the lack of support for a single exponent model suggests that there is no universal allometric scaling relationship, representing a significant challenge to any present model that predicts constant exponent. Emerging evidence suggests more and more physiological and ecological factors and phenomena are implicated in self-thinning process, which should be concerned in analyzing the mechanism underlying the variation of scaling exponents, meliorating the imperfect predicting models

or equations. The environmental factors are especially noticeable due to their roles in mediating plant architecture and above- and below-ground allocation. In further work, the combining of approaches of mathematic models, computer simulation, field investigations and the micro-level physiological and molecular experiment will shed light on the quantitative dynamics calculations in the mass-density regulations. This research area will offer a predictive framework for assessing and responding to global changes in the abundance, distribution and diversity of organisms, as well as the fluxes of energy and materials in ecological systems.

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