Sensitivity to Abscisic Acid Alters Plant Allometry and Above-Ground Biomass-Density Relationships in Arabidopsis Populations under Drought Stress

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Abstract: Biomass (M)-density (D) relationships is always a hot issue in ecology and has caused great debates in both theoretical and empirical studies. Mounting evidence from both controlled experiments and field investigations suggests the scaling exponent of M-D relationships varies along environmental gradients rather than being a constant, negating both -3/2 and -4/3 "law". As a kind of crucial stress response hormone in plants, abscisic acid plays essential roles in adjusting plant morphological and phenotypic plasticity in response to stress during their growth and development, influencing the mass-growth-density regulations in populations and communities. Certain *Arabidopsis thaliana* L. mutants (*abi1-1*, insensitive to ABA and *era1-2*, hypersensitive to ABA) provide an ideal model for testing the effects of ABA on these eco-physiological processes. We investigated the H-R, above-ground M-D allometric relationship in the *Arabidopsis* mutants and WTs under drought stress. The results suggest that sensitivity to ABA can alter the above-ground M-D scaling exponents by mediating H-R allometric growth in mutants and WTs, reflecting the hormonal effects on allometric growth and mass-density regulations with environmental stress.

Keywords: hormone effects, optimal partitioning, morphological and phenotypic plasticity, mass-density relationship, environmental stress, phytohormonal ecology

Introduction:

Biomass-Density (M-D) relationships, the phenomena that average individual biomass decreases with increasing densities in evenly aged populations, is an important density-dependent competition process, and always described by a log-log form equation: $\log M = K + \alpha \log D$, where α and K are the slope and coefficient of M-D relationships, respectively (Yoda *et al.* 1963; Morris 2002; Dai *et al.* 2009). M-D relationship is an essential link between the traits of individual organism and dynamics of population and community. Its application has provided substantial insight into 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). Despite of the long history of research on α in various populations, its generality is still called into questions and vexes the ecologists (Weller 1987; Lonsdale 1990; Enquist *et al.* 1998; Morris 2003; Deng *et al.* 2006; Dai *et al.* 2009). Based on a simple geometric model, α is suggested to take a value close to -3/2 (Yoda *et al.* 1963). The "-3/2" self-thinning rule has been widely accepted as "one of the most widespread of ecological regularities" in 1960-1980s (Damuth 1998). Nevertheless, according to a model of fractal-like networks of branching tubes, Enquist *et al.* (1998)

predicted the scaling exponent of biomass–density should be -4/3 rather than -3/2. Although both of these constant theories have got great supports, numerous laboratory experiments and field investigations demonstrate that α is not a constant, and can be regulated by both abiotic and biotic factors, such as light (Lonsdale 1990), nutrient fertility (Morris 2002;2003), water availability (Deng *et al.* 2006; Dai *et al.* 2009), marine intertidal (Sibomana and Wang 2013), hormone response (Zhang *et al.* 2005; Zhang *et al.* 2006) and arbuscular mycorrhizal fungi infection (Zhang *et al.* 2011). The realistic M-D relationship seems far more complicated rather than ideally supposed by pure models (Pretzsch 2006).

Many allometric growth models have been developed to illuminate the variety of above-ground α along environmental gradients, suggesting that the M-D relationships depend on the allometry between plant biomass and canopy dimensions such as height or radius (Miyanishi *et al.* 1979; Dai *et al.* 2009). Dai et al. (2009) have shown that the plant height–crown radius relationship (H–R) could account for the deviation of α from universal values. In their model, plant above-ground biomass (M) is proportional to its canopy volume:

$$M \propto R^2 H \qquad (1.1)$$

where R is the crown radius and H is the shoot height. There is mounting evidence that an allometric relationship exists between H and R (e.g. Osunkoya

et al. 2007), thus:

$$H \propto R^{\beta} \qquad (1.2)$$

If plant canopies do not overlap, plant density (*D*) can be expressed as a function of *R*:

$$D \propto R^{-2} \qquad (1.3)$$

In an evenly aged population, we can get the expression:

$$M \propto D^{\alpha} \qquad (1.4)$$

Incorporating expression (1.2), (1.3) and (1.4) into expression (1.1) yields:

$$M \propto D^{-1-\beta/2} \qquad (1.5)$$

Or

$$\alpha = -1-\beta/2 \qquad (1.6)$$

Height growth has often shown to be at the costs of investment in horizontal crown expansion for adapting to the environment (Poorter *et al.* 2006). The trade-off between height growth and crown expansion results in variant *β* under stress, leading to various above-ground *α* along environmental gradients. The acclimation is not simply an ecological course but involves complex physiological courses tightly controlled by intrinsic growth regulators, especially plant hormones (Popko *et al.* 2010). As the most characterized hormone, absicisic acid (ABA) exists ubiquitously in higher plants, regulating plant growth and development in every aspect. Regarded as an excellent target for improving stress tolerance, ABA is proved to regulate stomatal movements and photosynthetic adjustment (Chaves *et al.* 2009), change morphology structure and biomass allocation patterns (Zhang *et al.* 2005; Arend *et al.* 2009), maintain root growth and inhibit shoot growth (Cramer and Quarrie 2002), provide better dry matter accumulation and yield production (Farnsworth 2004). According to the roles of ABA in adjusting morphological and physiological plastic in plant adaptive growth, it is reasonable ABA optimizes the resource capture and use strategy by affecting individual allometric growth, leading to various *M-D* allometric relationship along stress gradients. Although ABA has received extensive attentions at multiple levels from biosynthesis pathways, signaling transductions to plant morphological and phenotypic plasticity alterations (Chaves *et al.* 2003; Zhang *et al.* 2005; Zhang *et al.* 2006), the effect of ABA on population-level processes, especially the population dynamics and construction, has rarely been discussed.

Certain *Arabidopsis* mutants with different sensitivities to ABA (*abi1-1*, insensitive to ABA and *era1-2*, hypersensitive to ABA) provide an ideal model for testing our hypothesis (Zhang *et al.* 2005). Protein serine/threonine phosphatases 2C (PP2C) encoded by the *Arabidopsis ABI1* gene is a negative regulator of ABA signaling and the *abi1* mutant confers a dominant ABA-insensitive *Arabidopsis* phenotype with impaired stomatal closure, reduced

seed dormancy and changes in seedling development (Meyer *et al.* 1994; Merlot *et al.* 2001). *ERA1* gene encodes for farnesyltransferase and is implicated in the negative regulation of guard cell ABA responses. The *era1* mutants show hypersensitivity to ABA and display enhanced drought tolerance during drought stress compared to the wild-type (Pei *et al.* 1998; Pei *et al.* 2000). Using these *Arabidopsis* mutants and their WTs, in this research we investigated the *H-R* allometric relationship and the above-ground *M-D* relationships respectively among the *Arabidopsis* mutants and WTs under drought stress. We aim to figure out: 1) whether different sensitivity to ABA causes different *H-R* and *M-D* allometric relationships across genotypes under drought stress; 2) if it does, whether the differences in *M-D* relationships are caused by *H-R* allometric relationships.

Materials and methods

Plant materials and growth conditions

Seeds of *Arabidopsis* thaliana genotypes, including *abi1-1* mutants (insensitive to ABA), *era1-2* mutants (hypersensitive to ABA), Ler-0 (corresponding background Wide Type of *abi1-1*) and Col-0 (corresponding background Wide Type of *era1-2*), were obtained from *Arabidopsis* Biological Resource Center, the Ohio State University, USA. The seeds were stored at 4℃ in the dark for one week, treated with 70% ethanol solutions for 30 min, rinsed with deionized water and sown in a random spatial pattern in 5cm diameter, 10cm height plastic pots filled with a 1:1 (v/v) mixture of pearlite and vermiculite.

We used a completely randomized design including three densities (15, 150, 1500 seeds per pot yielding ca. 2000, 20000 and 200000 seedlings per square metre), and three replicates per genotype, density, and harvest combination. For the lower and intermediate densities the seeds were counted, whereas for the highest density they were weighed based on n=150 counted samples (mean ± s.e. =0.003247 ± 0.000075, 0.002860 ± 0.000236, 0.003317 ± 0.000086, 0.003467 ± 0.000045 mg for *abi1-1*, *era1-2*, Ler-0 and Col-0, respectively). The pots were placed in a controlled environment chamber with a day/night temperature of 23/20℃, 70% atmosphere relative humidity and 16h photoperiod of artificial light (incandescent lamps with photon fluence rate of 240 μmol m^{-2} s^{-1}). Pots were irrigated with PNS mineral nutrient solution, and the mutants were allowed to germinate and grow to a 4-leaves stage (about ten days after seedling) before drought treatments.

Drought treatments

In this study, the soil water contents (SWCs)

were determined gravimetrically everyday by weighing pots at the start and end of the photoperiod throughout the whole drying period (Xiong *et al.* 2006). During the drought treatment, the SWC was maintained about 30-40%. All drying treatments lasted 40 days (the whole growth period lasted 50 days). Various volumes of PNS mineral nutrient solutions were added to the pots to maintain the SWCs at the designed level.

Biomass measurements

The harvest was carried out 50 days after sowing. To avoid edge effect, a 3.5cm-radius PVC pipe was positioned in the center of each pot, with only the inside plants sampled. The final numbers are counted for calculating densities. The population density yields as (no. of individuals, g)/(area, m^2). The above-ground parts of the plants were collected with great caution, then put into envelops and dried at 80℃ to a constant weight. Mean biomass of the plants was calculated as (total biomass, g)/(no. of individuals). A random sub-sample of 3 individuals was chosen from each mesocosm to measure the plant canopy radius (Morris 1996), and the maximum diameter of the canopy (the rosette) for each individual plant was recorded. As the rosette is the main organ involving in light, space and water competitions, the radius (*R*) was defined as half the diameter and the plant height (*H*) as the height from the bottom to the highest point of rosette, both of which were recorded concomitantly.

Data analysis

The allometric scaling exponents or slopes and the intercepts were estimated by the standardized major axis (SMA; SMATR Version 2.0; Warton *et al.* 2006) regression on log-transformed data. Comparisons of slopes of *M-D* relationship, *H-R* relationship between the genotypes were performed in SMATR. The R^2 statistic for each line was used to report the amount of variance explained. The 95% confidence intervals of SMA were used to assess whether an empirically determined power of self-thinning complied with that of control, and for the comparison of difference between slopes (Niklas 1994).

Results

The *H-R* allometric scaling exponent (*β*) decreased with increasing sensitivity to ABA in genotypes (Table 1; Figure 1), and the differences between genotypes were significant (p=0.001). The regression slope of *abi1-1* mutants (1.086) was significantly higher than all the other genotypes, while that of *era1-2* mutants (0.504) was significantly lower than the others (Table 1). Ler-0 and Col-0 genotypes remained intermediate with no statistic difference between each other (0.808, 0.843). The 95% confidence intervals of *β* were 0.957 to 1.233, 0.601 to 0.861, 0.692 to 0.957 and 0.410 to 0.619 for *abi1-1*, Ler-0, Col-0 and *era1-2* ecotypes, respectively. The predicted above-ground *M-D* allometric scaling exponent (*α*), according to the equation (1.6), were resulted as -1.543 (*abi1-1*), -1.360 (Ler-0), -1.407 (Col-0) and -1.252 (*era1-2*) respectively, showing an increasing trends with increasing sensitivity to ABA.

Table 1. Scaling Exponents (*β*) and Intercepts (IT) of *H-R* Relationships in All the Ecotypes, as Estimated by the SMA Regression of Log-transformed data. Predicted *α* was Calculated According to Equation (1.6)

Ecotypes	*β*	95%CIs	IT	95%CIs	R^2	Number	Pre *α*
abi1-1	1.086	0.957,1.233	0.033	-0.019,0.086	0.905	27	-1.543
Ler-0	0.720	0.601,0.861	0.157	0.109, 0.206	0.808	27	-1.360
era1-2	0.504	0.410,0.619	0.125	0.091,0.160	0.747	27	-1.252
Col-0	0.814	0.692,0.957	0.167	0.114,0.220	0.843	27	-1.407
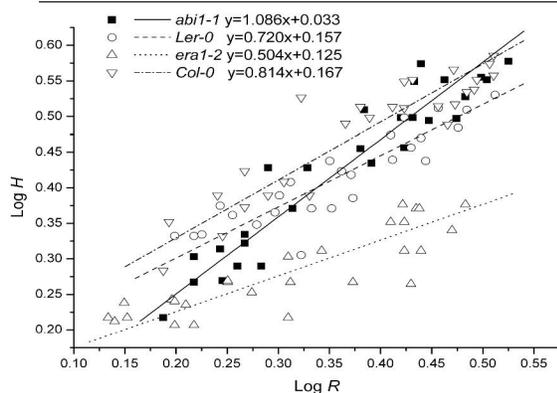
Figure 1. *H-R* relationships in all the genotypes under drought stress, as estimated by the SMA regression of log-transformed data. The slopes of regressions in *abi1-1* and *era1-2* mutants were significantly different from each other (p=0.001). The slope of regressions in *abi1-1* mutants was significantly different from both that of Ler-0 (p=0.001) and Col-0 (p=0.007), respectively. *era1-2* mutants had the significantly different slope with Ler-0 (p=0.013) and Col-0 (p=0.001) as well. While the slopes of two WTs, Ler-0 and Col-0, shared no statistic difference (p=0.285). Parameters estimates are given in Table 1.

The observed above-ground *M-D* allometric scaling exponent (*α*) showed the same trend with the predicated *α* (Table 1, Table 2; Figure 2), and significant differences (p=0.018) existed between genotypes. *abi1-1* mutants had the steepest regression line (*α*= -1.544) and the absolute value of *α* was significantly higher than the other genotypes (Ler-0, p=0.007; Col-0, p=0.007; *era1-2*, p=0.001), which had no statistic difference from each other (Ler-0,

α=-1.245; Col-0, *α*=-1.266; *era1-2*, *α*= -1.123). The confidence intervals of above-ground *α* were -1.755 to -1.358, -1.378 to -1.124, -1.287 to -0.980 and -1.416 to -1.132 for *abi1-1*, Ler-0, Col-0 and *era1-2* genotypes, respectively. More importantly, the predicted *α* for all the mutants were within the 95% confidence intervals of the direct estimate and statistically indistinguishable from their observed values (Table 1, Table 2; Figure 2).

Table 2. Scaling Exponents (*α*) and Intercept (*K*) of the Above-ground *M-D* Relationships in All Mutants and WTs, as Estimated by the SMA Regression of the Log-transformed Data.

Ecotypes	*M: D*	*α*	95%CIs	*K*	95%CIs	R^2	Number
abi1-1	M_A:D	-1.544	-1.755,-1.358	3.985	3.279,4.691	0.979	9
Ler-0	M_A: D	-1.245	-1.378,-1.124	2.993	2.530,3.455	0.987	9
era1-2	M_A: D	-1.123	-1.287,-0.980	2.547	1.981,3.113	0.977	9
Col-0	M_A: D	-1.266	-1.416,-1.132	3.064	2.546,3.582	0.984	9
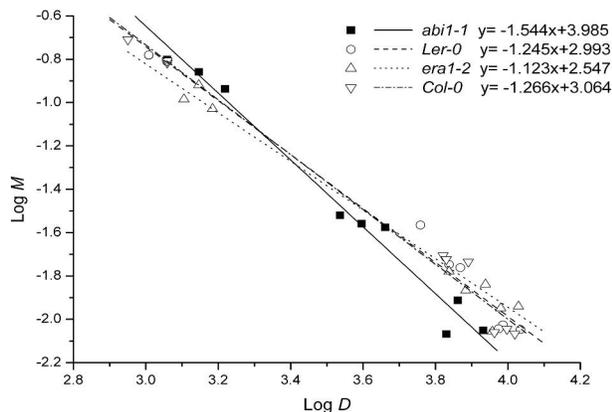
Figure 2. *M-D* relationships between average above-ground biomass in all the genotypes under drought stress, as estimated by the SMA regression of log-transformed data. The slope of regression in *abi1-1* mutants was significantly different from that of Ler-0 (p=0.007), Col-0 (p=0.007) and *era1-2* mutants (p=0.001), respectively. The WTs and *era1-2* mutants shared no statistically different slopes. Parameters estimates are given in Table 2.

Discussion

Sensitivity to ABA and plant allometric growth

Plant allometric growth is usually an adaptive trait to maximize the uptake of limiting resources in response to environmental constrains (Dai *et al.* 2009). Plants always 'evolve towards the optimal allometric trajectory' and adjust the trajectory adaptively (Weiner 2004). Our results showed that *β* decreased with increasing sensitivity to ABA in genotypes under drought stress, which meant that as plants grew larger, they tended to have less height growth for a given amount of radial extension in the increasing sensitivity mutants. These results suggest the altered ABA

sensitivity can change plant allometry under stress. Morphological alterations with enhanced shoot growth, retarded leaf and root development are observed evidently in *abi1*-expressing poplars transformed with the dominant *Arabidopsis* mutant *abi1* genes, indicating that growth processes in these plant organs are differently affected by altered ABA sensitivities (Arend *et al.* 2009). ABA has also been demonstrated to adjust the relative growth rates of various plant organs by inhibiting the leaf area development and plant height (Zhang and Davies 1991), as synthesis and accumulation of ABA in different organs may determine the final morphology of plants. Altering scaling relationships of plant height and biomass, as well as adjustments of height and leaf area growth have also been observed in the same material models (Zhang *et al.* 2005; Zhang *et al.* 2006), which co-indicate the mediation roles of ABA in plant developmental plasticity with our results.

Sensitivity to ABA, environmental stress and M-D relationships

Results from the experiments confirm our model prediction that *H-R* relationships (i.e. *β*) determine the above-ground *M-D* relationships (i.e. *α*) in stressful environments (equation 1.6), which consolidate the allometric growth model proposed by Dai *et al.* (2009). Furthermore, *α* is not invariant, but decrease with increasing ABA sensitivity under drought stress (Table1, 2; Figure1, 2), which demonstrate that above-ground *M-D* relationships as a consequence of altered individual allometric growth could be regulated by sensitivity to ABA. It's noticeable that Zhang *et al.* (2006) also find that reduced resource transport distance (i.e. *H*) and amplified resource utilization area (i.e. leaf area) could lead to increased above-ground *α* in hypersensitive mutants than insensitive ones, which comply with the metabolic theory instead of individual

allometric model, illustrating the influence of response to ABA on population regulations at an eco-physiological level. Other environmental factors are proved to participate in *M-D* relationship regulations as well, as the plant architecture is determined by the interaction between hormone signals and environmental stimuli such as light distribution, nutrient regimes and soil water (Guo *et al.* 2011). Flatter self-thinning lines have been observed in environments with low light (Lonsdale and Watkinson 1982), nutrient availability (Morris 2003), salinity contamination (Zhang *et al.* 2010) and water deficit (Deng *et al.* 2006; Dai *et al.* 2009), which is supposed to be consistent with our results. As plant growth and development are controlled by both external cues and intrinsic growth regulators (Depuydt and Hardtke 2011), and the osmotic stress caused by environmental stress will originate ABA synthesis and accumulation to adjust plant growth in response to stress and enhance stress tolerance, we are concerned that the physiological and morphological mediation roles of ABA on plant growth is the mechanism explaining the various above-ground scaling exponent of *M-D* regulated by environmental factors.

Most of the studies on *M-D* relationship in the previous research are referred to the above-ground parts, while the below-ground *M-D* relationship is far less discussed due to methodological difficulties in root excavation, observation, measurement as well as equation built between root biomass and soil volume occupied (Zhang *et al.* 2011). However, it is ecologically irrational to discuss *M-D* relationships omitting the below-ground parts (Ogawa 2005), for the two parts may have different mechanisms during competition in self-thinning process (Zhang *et al.* 2011). ABA is also essential in establishing a root system. It has been proved to stimulate elongation of the main root, promote lateral root formation and increase relatively dry-matter allocation into the root fraction, leading to a significant rise of root/shoot ratio and fine root/ total root ratio under drought stress (De Smet *et al.* 2006; Peleg and Blumwald 2011). This mediation role conforms to the optimal partitioning theory which regards the variance of root: shoot ratio as an acclimation strategy acquires the most limiting resource to survive under stress (Bloom *et al.* 1985; McCarthy and Enquist 2007; Zhang *et al.* 2011). Additionally, variation in root: shoot ratio has been demonstrated to alter the above- and below-ground *M-D* relationships under resource-limited conditions (Morris 2002; Bai *et al.* 2010; Zhang *et al.* 2011). Therefore, the roles of ABA in mediating below-ground *M-D* relationships and the different mechanisms from the above-ground parts will cause more attentions in our future work.

The rise and prospect of phytohormonal ecology

Our study reveals the plant mass-growth-density regulations involve complex ecological and physiological processes mediated by the external stress stimuli and internal hormonal system. Environmental stress is indispensable part in influencing population dynamics, as various scaling exponents of *M-D* relationships have been observed along environmental gradients. Of great concern is that these stresses become increasingly important due to global warming, land degradation, water deficit and population expansion (Depuydt and Hardtke 2011). Plants have evolved great plasticity to enhance tolerances to abiotic stresses, which are typically complex quantitative traits influenced by a number of hormone signaling and environmental interactions. Phytohormonal ecology is thus emerging as an integrative approach to testing the role of interactions between hormonally signaled responses on ecologically important traits (Farnsworth 2004). Information on the effects of ABA on the expression of specific genes in different plant species reveals a central role of ABA in the regulation of plant response to stress (Davies *et al.* 2005; Zhang *et al.* 2006). However, mounting evidence suggests a complex network with extensive cross-talk exists between the different hormone signaling pathways during the adaptive response courses (Chaves *et al.* 2003; Davies *et al.* 2005; Popko *et al.* 2010; Peleg and Blumwald 2011). It demonstrates that ABA regulates physiological processes in plant growth and development coordinately with other hormones, regardless of antagonistic or synergistic (Sharp and LeNoble 2002; Farnsworth 2004; Sharp *et al.* 2004; Fujita *et al.* 2006; Peleg and Blumwald 2011; Rivas-San Vicente and Plasencia 2011). The hormones, such as cytokinin, auxin, gibberellins, ethylene, and jasmonate, deserve increasing investigations to explore their implications on individual development and population dynamics, which will advance our information on plant-mass-regulations. Plants bearing mutations in hormone-biosynthetic pathways have provided a profound approach to integrated understanding of the biochemical and physiological basis of stress responses in plants (Finkelstein and Somerville 1990; Cramer 2002; Cramer and Quarrie 2002; Zhang *et al.* 2005; Arend *et al.* 2009; Depuydt and Hardtke 2011), bridging the gap of hormone effects and ecological processes.

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