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ORIGINAL ARTICLE

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Plasticity and ontogenetic drift of biomass allocation in response to above- and below-ground resource availabilities in perennial herbs: a case study of *Alternanthera philoxeroides*

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Abstract Changes in plant biomass allocation in response to varying resource availabilities may result from ontogenetic drift caused by allometric growth (i.e., apparent plasticity), a true adjustment of ontogenetic trajectories (true plasticity) or both (complex plasticity). Given that the root allocation of annual species usually decreases during the growth, the developmentally explicit model predicts that annual herbs will exhibit true plasticity in root allocation under above-ground resource limitation and apparent plasticity for moderate stress of below-ground resource. For perennial species, the root allocation of which increases during growth, the reverse patterns would be expected. In this study, we tested the developmentally explicit model with a perennial weed, *Alternanthera philoxeroides* (Mart.) Griseb. We report its adaptive changes and ontogenetic drift of root allocation in response to different resource levels (i.e., light, water and nutrient availability) by comparing root allocation on both an age and a size basis. The root allocation of *A. philoxeroides* increased with the size (i.e., ontogenetic drift) during the growth, and exhibited significant changes in response to different resource availabilities. Furthermore, the root allocation in response to water or nutrient availability exhibited typical complex plasticity, while the light stress only slowed down the growth, with the ontogenetic trajectory unchanged (apparent plasticity). The contrasting responses to above-ground and below-ground stresses were consistent with the prediction of the developmentally explicit model.

Keywords Biomass allocation · Plasticity · Ontogenetic drift · Perennial · *Alternanthera philoxeroides*

Introduction

Biomass allocation is the central concept in life history theory (Stearns 1992). The pattern of biomass allocation influences the performance of plants, including growth (Osone and Tateno 2005), reproduction (Schmid and Weiner 1993), competitive ability (Grime 1979; Tilman 1982) and shoot size hierarchy (Suzuki and Hara 2001). Plants may allocate their biomass to different organs or different functions in response to varying resource availabilities in an economical manner (Bloom et al. 1985). For example, plants may invest more resources in roots in dry or infertile environments, but allocate more to shoots when more water and nutrients are available. This flexibility of allocation is thought to be an important strategy for plants to maximize growth rate and fitness in the environments with variable resource availabilities (Hirose 1987; Rice and Bazzaz 1989a; Sultan 2000).

However, the changes in biomass allocation may also result from ontogenetic drift (Evans 1972) since biomass allocation usually changes as a function of plant size (e.g., total biomass) during the course of growth and development (Hunt 1990; Coleman et al. 1994; Coleman and McConnaughay 1995). Commonly, the size of the plant grown under resource stresses would be smaller than that under favorable conditions; thus, allocation patterns exhibited under resource stresses may be only the result of a slower growth along a fixed ontogenetic trajectory and not an actual adjustment of resource allocation. Therefore, when compared at the same age

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(e.g., a certain day following germination), the changes in allocation patterns, highly responsive to different resource levels, may result from ontogenetic drift (i.e., apparent plasticity) or adjustment of ontogenetic trajectory (true plasticity) or both (complex plasticity) (Rice and Bazzaz 1989a; McConnaughay and Coleman 1999; Wright and McConnaughay 2002; Weiner 2004).

The further question is: when do plants show which kind of plasticity? McConnaughay and Coleman (1999) developed a 'developmentally explicit model', which predicts that plants exhibit variable responses with respect to the type of resource stresses. In most annual herbs, the root allocation usually decreases during the course of growth and development (Hunt 1990), meaning that, in stressful environments, ontogenetic drift itself enables plants to maintain a higher root allocation because of a slow growth. Taking the effects of ontogenetic drift into account, the developmentally explicit model predicts that annual herbs exhibit true plasticity under above-ground resource limitation, while apparent plasticity might suffice in the case of moderate stress of below-ground resource (McConnaughay and Coleman 1999; Wright and McConnaughay 2002). However, some perennial species have the opposite ontogenetic trajectory, that is, their root allocation usually increases during growth and development (Bond 2000; Niinemets 2004; Moriuchi and Winn 2005). Thus, according to the mechanism underlying the model, the reverse patterns are expected in such perennial species: apparent plasticity for above-ground resource limitation and true plasticity for below-ground resource limitation.

In this study, we tested the developmentally explicit model with a perennial weed, *Alternanthera philoxeroides* (Mart.) Griseb, in which we observed increasing root allocation during its growth. *A. philoxeroides* rarely produces viable seeds in the field (Julien et al. 1995) and reproduces mainly through vegetative structures such as broken stems and roots. In terrestrial habitats with a cold winter, most of the above-ground parts are killed by frost (Zhang et al. 2004). The thickened taproots, which store large amounts of resources, are likely to escape from frost injury and become the major resource pool to support the early growth and population regeneration in the following spring (Li 1998). Therefore, in terrestrial habitats, root allocation is a remarkably functional character for *A. philoxeroides* in determining its performance.

Here, we report a study of the dynamics of root allocation under different resource levels in *A. philoxeroides*. We examined the overall growth and pattern of root allocation in *A. philoxeroides* as a function of plant age and plant size in response to the resource levels of light, nutrient and water. We addressed two questions: (1) how does *A. philoxeroides* change the root allocation in response to different resource levels, and (2) are the changes consistent with the prediction of the developmentally explicit model (i.e., apparent plasticity in the case of light stress but true plasticity for nutrient or water limitation)?

Materials and methods

Materials

In the autumn of 2002, 50 clones were sampled as stems from a natural population in Zhuji, Zhejiang Province (E120° 20′, N 29° 40′). Although these clones were physically separated from each other in the field, molecular marker analysis revealed that these clones were developed from a single genet (i.e., multi-locus genotype, unpublished data). All clones had been grown under greenhouse conditions for more than 1 year to remove possible environmental effects resulting from heterogeneous microhabitats from which the clones had been collected. Four clones were randomly selected and vegetatively propagated during the summer of 2004 to produce sufficient ramets.

The whole experiment was performed in the greenhouse with a natural photoperiod (August–November 2004). We used asexual offsprings from stem fragments instead of seedlings from seeds since *A. philoxeroides* rarely produce viable seeds and reproduce mainly through vegetative organs in the field. We used two different lengths of stem fragments to test whether the initial size of stem fragment had a significant effect on the root allocation dynamics under different resource availability conditions. Two different lengths of stem fragments were cut from the ramets of similar diameter to produce individual clones, i.e., 5–6 cm versus 10–12 cm, which consisted of two nodes versus three nodes, respectively (hereafter referred as small versus large groups). Plants were grown in plastic pots (25 cm in diameter×30 cm deep) containing mixtures of sterilized sand and vermiculite (1:1). Peter's fertilizer (N:P:K = 20:20:20, Scotts Company, USA) was used to supply nutrients (3 g per pot). Watering by hand was performed every other day to keep the mixture moist. Once the first two leaves appeared (6–10 days), plants were thinned to one in each pot and treatments of different resources were then implemented separately.

Treatments

Three independent resource treatments were created, i.e., light, nutrient and water. The light treatments included two levels: high (full sun) and low light (30% full sun, which was created using neutral shade cloth). The nutrient treatments also included two levels: high (4 g of Peter's fertilizer per pot per week) and low (0.5 g per pot per week). Water treatments included two levels: high (at field capacity, water was added every day) and low (plants were monitored twice each day, 100 ml water was added per pot when wilting was first observed). While the availability of one resource was manipulated, that of the other two was kept at high or moderate level (i.e., full sun for all pots except those in the light treatment, 3 g of fertilizer per pot per week except for those in the nutrient treatment, and soil was kept moist except in the water treatment) so that they would not limit the growth of plants.

In this study, there were six groups of treatments in total. Each group consisted of two subgroups (small versus large). In each subgroup, 21 individuals were used and 252 individuals in total for the whole experiment (3 resources × 2 levels × 2 initial size × 21 individuals = 252). The first harvest (one individual per subgroup per treatment per level per harvest) was performed 2 days after treatments (25 August 2004). The other harvests were made at varying intervals: 7 harvests at 2-day intervals, 8 at 4-day intervals, and 5 at 7-day intervals. The last harvest was performed in mid-November (81 days after treatments, at plant age 86–90 days). This multi-harvest protocol was a regression design, in which we increased the times of harvest in cost of decreasing the number of replicates at each harvest to examine the time trend of root allocation during the whole growth period. Previous studies have found that the low number of replicates at each harvest has little effect on the overall ontogenetic trajectory (Gedroc et al. 1996; McConnaughay and Coleman 1999).

Each harvested individual was partitioned into roots, leaves, stems and "old stems" (the original stem fragments). In our experiments, only three plants produced a single inflorescence. In this case, the small biomass of reproductive organs was included in that of stems. All plant materials were oven-dried at 80°C for 48 h and then weighed.

Growth analysis and statistical analysis

In this study, the root allocation was calculated as the root mass divided by the total newly produced biomass. The "old stems" were excluded from calculation because they made a considerable contribution to the total biomass for the first several harvests and, hence, significantly changed the root allocation. We used root allocation instead of root:shoot ratio, because the latter is more sensitive to small change in allocation (Poorter and Nagel 2000) and, therefore, is more sensitive to measurement error.

Statistical methods previously described by McConnaughay and Coleman (1999) were carried out. Linear regression was not suitable for our data (i.e., $P < 0.001$ for the null hypothesis that the second-order coefficient is zero in polynomial regression). Logistic equations were used for comparisons of (1) Ln total biomass versus time (days), and second-order polynomial regression equations were used for comparisons of (2) Ln root allocation versus time (days), and (3) Ln root allocation versus in total biomass. Biomass variables were log transformed to meet the assumptions of normality and homoscedasticity associated with model-I regression techniques. Log-transformed variables and their residuals were judged to be normally distributed and homoscedastic by a combination of histograms, normality statistics and normal probability plots. All curves were fitted using Statistica 6.0 (StatSoft Inc., Bedford, UK).

Fitted curves were compared statistically following the methods described by Mead and Curnow (1983) and Potvin et al. (1990). Briefly, for each comparison, the goodness-of-fit of a single curve (two subgroups or groups) was compared with the goodness-of-fit of two separate curves (one curve for each subgroup or group). Analysis of variance statistics (*F*) was computed from the sums of square of type-III residual, according to published equations (Potvin et al. 1990).

In our experiment, each group of treatments (six in total) consisted of two subgroups (small versus large). We first tested the sensitivity of root allocation to initial stem fragment size within each group. If the three functional relationships were all insensitive to initial size (i.e., there was no significant difference between large and small subgroups), the two subgroups were pooled, and then the effects of treatments were tested between two groups. This treatment may increase the power of comparison and decrease the number of simultaneous tests and the probability of type-I error (Kokoska and Johnson 1987). Otherwise, the effects of treatments were tested within large and small subgroups separately.

Results

Plant growth

In all treatments, the "large" subgroup accumulated more total biomass than the "small" one, but the differences were not significant ($F_{4,34} = 0.43$–2.20, $P > 0.05$, Fig. 1). Since biomass accumulation was insensitive to the initial size, we pooled the data of the two subgroups to test the effects of treatments. The total biomass of individuals in each treatment group increased steadily over the 81-day growth period. Resource availability had significant effects on biomass accumulation and relative growth rate in all three treatments. The dry weight of biomass reached 6.50 g versus 18.15 g (low versus high light), 4.47 g versus 25.45 g (low versus high water), and 3.50 g versus 32.5 g (low versus high nutrients), at the last harvest.

Biomass allocation

Similar to biomass accumulation, the size of initial stem fragments had no significant effects on the root allocation in both age-based ($F_{4,34} = 0.79$–2.44, $P > 0.05$) and size-based comparisons ($F_{4,34} = 0.95$–2.07, $P > 0.05$). Again, the two subgroups were pooled together to test the effects of treatments.

Plants showed obvious ontogenetic drift in root allocation across resource levels in all treatments. The root allocation increased over the 81-day growth period

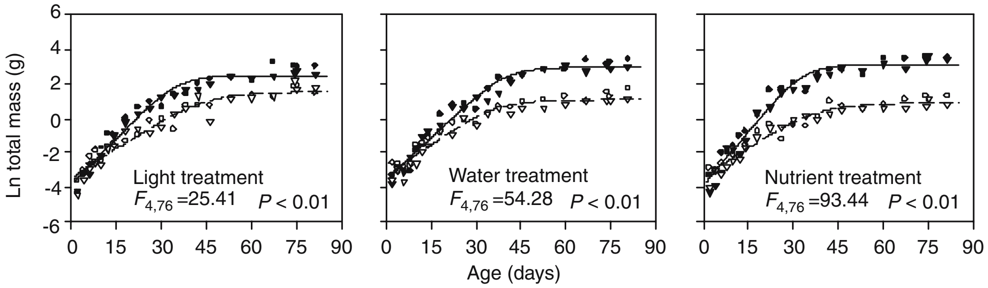

Fig. 1 Growth trajectory of *Alternanthera* individuals (large and small subgroups pooled), over an 81-day period, in response to varying light, nutrient or water availabilities. The results of comparisons between two resource levels are shown. *Filled circle* (large) and *filled triangle* (small): high resource level; *open circle* (large) and *open triangle* (small): low resource level

as a function of both plant age (Fig. 2) and total biomass (Fig. 3).

Resource availability significantly changed the root allocation in relation to all three resources when compared at the same age (Fig. 2). In general, the allocation to roots had been increased under low nutrient and low water conditions, while light limitation resulted in an increased allocation to shoots (i.e., decrease in root allocation) (Fig. 2).

However, size-based comparisons revealed different patterns. Although the differences between treatments remained significant for water and nutrients, there was no significant difference between light treatments (Fig. 3). Therefore, the low availability of below-ground resources (i.e., water and nutrients) resulted in a significant increment in root allocation when compared at both the same age (Fig. 2) and the same size (Fig. 3). In contrast, low light significantly reduced the total biomass (Fig. 1) and root allocation as a function of age (Fig. 2), but had no significant effect on the ontogenetic trajectory of root allocation (Fig. 3).

Discussion

In this study, we examined the dynamics of root allocation in *A. philoxeroides* grown at different resource levels to investigate the effects of ontogenetic drift on biomass allocation in response to different resource availabilities. Our results show that *A. philoxeroides* displayed obvious ontogenetic drift in root allocation and exhibited different types of plasticity (both apparent plasticity and true plasticity) with respect to the type of resource stress.

Root allocation of *A. philoxeroides* was also shown to increase with age and size over the whole growth period at all resource levels. In other words, this perennial species displayed a substantial ontogenetic drift in root allocation, but the trajectory is the opposite to that of annual herbs. Such ontogenetic drift resulted in a lower root allocation in plants under resource stress than under favorable conditions. From an economical viewpoint, plants would keep a higher root allocation in response to below-ground resource stress, but a lower root allocation in response to above-ground resource stress, to increase the capability of acquiring the most limited resources (Bloom et al. 1985). Thus, the effect of ontogenetic drift in *A. philoxeroides* was contrary to the adaptive changes needed in the case of below-ground resource stress. It is not surprising that the changes of root allocation in response to water or nutrient stresses resulted from a combination of ontogenetic drift and adjustment of ontogenetic trajectory (i.e., complex plasticity). In the case of light stress, however, the effect of ontogenetic drift itself may suffice to enable *A. philoxeroides* to maintain a lower root allocation to balance the absorption of above- and below-ground resources. As a result, light stress only slowed down the growth along an unchanged ontogenetic trajectory (i.e., apparent plasticity) in *A. philoxeroides*.

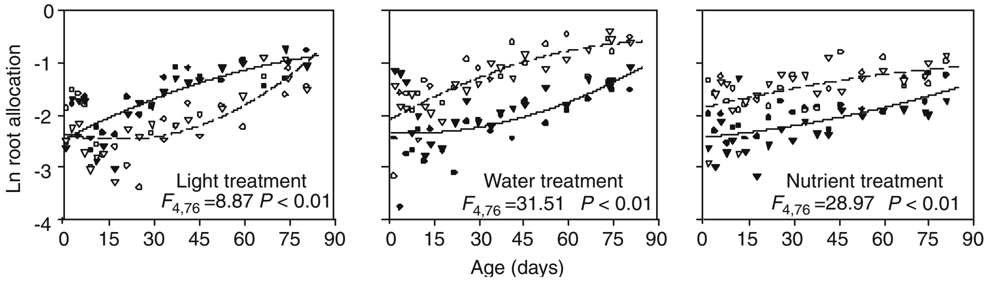

Fig. 2 Age-based comparisons of root allocation (large and small subgroups pooled), over an 81-day period, in response to varying light, nutrient or water availabilities. The results of comparisons between two resource levels are shown. *Filled circle* (large) and *filled triangle* (small): high resource level; *open circle* (large) and *open triangle* (small): low resource level

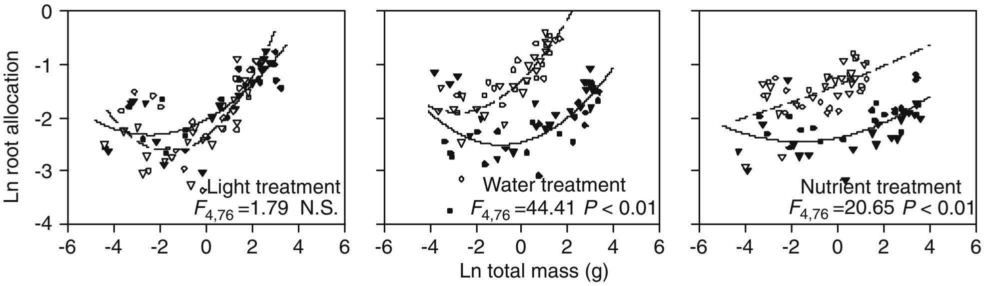

Fig. 3 Size-based comparisons of root allocation (large and small subgroups pooled), over an 81-day period, in response to varying light, nutrient or water availabilities. The results of comparisons between two resource levels are shown. *Filled circle* (large) and *filled triangle* (small): high resource level; *open circle* (large) and *open triangle* (small): low resource level

Such different responses to above-ground (apparent plasticity) and below-ground (complex plasticity) stresses are consistent with the prediction of the developmentally explicit model (McConnaughay and Coleman 1999; Wright and McConnaughay 2002). Although the original version of the model concerns only annual species in which the root allocation decreases with the growth and development, the results from *A. philoxeroides* suggest that the model is also valuable in predicting the behavior of perennial species. In a recent study, Moriuchi and Winn (2005) found the developmental trajectory of root:shoot ratio of a perennial species, *Viola septemloba*, to be significantly different between favorable and stressful environments in which both water and nutrient availabilities were manipulated simultaneously. The size-based comparison showed that plants grown at high resource level have significantly lower root:leaf ratio than those grown at low resource level. Given that the root:leaf ratio increased during the growth of this perennial species, the true plasticity in response to below-ground resource limitation was consistent with the prediction of the developmentally explicit model (Moriuchi and Winn 2005). Furthermore, the field measurements made by the same authors have revealed that the responses to stressful environments in the field are qualitatively similar to those observed in glasshouse experiments, suggesting that ontogenetic drift might also contribute to phenotypic variation in the field (Moriuchi and Winn 2005).

Similar patterns have also been found in woody species. For example, Ledig et al. (1970) applied allometric analyses in the growth of loblolly pine (*Pinus taeda* L.) seedlings and found that the slope of the allometric relationship between shoot and root remained unchanged under varying light availability (apparent plasticity), while the slope decreased under moisture stress (true plasticity). In another study of the seedling of loblolly pine, Gebauer et al. (1996) found that CO_2 (above-ground resource) affected biomass allocation indirectly through accelerating growth (i.e., apparent plasticity), while N availability (below-ground resource) had a direct effect on biomass allocation.

It is important to distinguish the true plasticity from the apparent plasticity since ontogenetic drift can obscure the degree and nature of adaptive changes of plants in response to variable growth conditions (Rice and Bazzaz 1989b; Pigliucci and Schlichting 1995; Wright and McConnaughay 2002). Our results highlight the differences between annual and perennial herbs in ontogenetic trajectory of root allocation. The case study of *A. philoxeroides* presented here, together with data from other studies with perennial herbs or woody species, suggest that the developmentally explicit model can be used to explain the plastic changes in biomass allocation of perennial herbs in response to above- and below-ground resource availabilities.

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