VARIATION OF FUNCTIONAL CLONAL TRAITS ALONG ELEVATION IN TWO FERN SPECIES

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Abstract

Phenotypical plasticity is generally considered among adaptive strategies by which plants can cope with environmental variation in space and time. Although much is known about plasticity in seed plants in terms of functional clonal traits while little is known about ferns. Variation of functional clonal traits of two ferns *Dicranopteris dichotoma* and *Diplopterygium glaucum* among plots differing in elevation in a subtropical evergreen broad-leaved forest in southern China was investigated. Along with elevation increasing the two fern species showed similar variation pattern of functional clonal traits: stable spacer length, increasing specific spacer length and decreasing spacer weight per ramet and specific spacer weight. The two ferns species had similar variation pattern of ramet performance traits but different variation pattern of ramet population properties. These results suggest an evolutionary trade-off between functions of foraging for and storing of resources in the two ferns, with a functional preference for the foraging in response to environmental change.

Key words: *Dicranopteris dichotoma, Diplopterygium glaucum,* Clonal plants, Ramet population.

Introduction

Phenotypic plasticity has been considered one adaptive strategy by which plants cope with environmental variation in space and time (Sultan, 1987; Hutchings & de Kroon, 1994; Valladares *et al*., 2007; Bell & Galloway, 2008; Tamkoe & Arslan, 2011). Clonal plants are able to deal with environmental heterogeneity (Dong, 1996; Dong *et al.*, 1997) not only by ramet-level responses which are similar to those of non-clonal plants, but also by genet-level responses which are unique for clonal plants (Hutchings & de Kroon, 1994). Clonal plants, therefore, possess a higher level of plasticity as compared to nonclonal ones (Hutchings & de Kroon, 1994;Yu & Dong, 2003).

Previous studies revealed, in response to reducing resources like shading and nutrient shortage, clonal plants may elongate their horizontal spacers like rhizomes and/or stolons and vertical spacers like stem and/or petioles between "feeding sites" like leaves for capturing essential resources like water, light and nutrients in patches. Such responses have been named plant foraging behavior (Slade & Hutchings, 1987) for resources essential for plant growth and reproduction. Meanwhile, the spacers weight per ramet indicating storage function for energy of ramet, which indicates increasing individual regeneration, may decrease population recruitment (de Kroons & Hutchings, 1995; Dong, 1996; Yu & Dong, 2003). These responses may influence interactions among the coexisting organisms (Sawada, 1999), community assembly and ecosystem functions (de Bello *et al.*, 2011). Plant traits, that are caused by clonality and related to genet fitness and/or ecosystem functioning, can be defined as functional clonal traits. Using plasticity of such functional clonal traits, clonal plants can effectively exploit the heterogeneous environment (Niva *et al*., 2006; Cornelissen *et al*., 2014), mitigating or overcoming the difficulty encountered in the process of exploration of essential resources, and consequently maintaining or increasing fitness (Dong, 1996).

In addition to sexual reproduction by spores, many fern species are able to propagate through clonal growth (Silander, 1985; During, 1990), some of which, for instance, are rhizomatous and very strong in clonal growth, such as *Pteridium aquilinum* (Wolf *et al.*, 1988; Parks & Werth, 1993). However, in the past decades, ecological researches of plant clonality for fern species were few and mostly with focus on species diversity (Guo *et al*., 2003) and genetic diversity (Parks & Werth, 1993; Gamperle & Schneller, 2002), instead of clonal traits (Rünk & Zobel, 2007) that are related functionally to foraging for and storing of essential resources like nutrients, water and carbohydrates. In fact, very little is known about plasticity of pteridophytes in terms of functional clonal traits.

The species: *Dicranopteris dichotoma* (Thunb.) Bernh. and *Diplopterygium glaucum* (Thunb.) Ching (syn. *Hicriopteris glauca*) (hereinafter referred to as *Dicranopteris* and *Diplopterygium*, respectively), belongs to Gleicheniaceae, are perennial herbaceous fern. They possess evergreen simple pinnate leaves with monomorphic lamina. They are distributed in southern China, Japan, India and Vietnam (Ching, 1959). They form horizontal rhizomes whereby they propagate new ramets asexually, being typical clonal plants. *Dicranopteris* is a heliophyte, usually inhabiting acid soil and dominating in forest gaps or heavily degraded forests. *Diplopterygium* is an understory species, mainly inhabiting the understory beneath canopy of evergreen broad-leaved forests in mountain ravines at elevations below 1500 m. They may separately or jointly form the thick layer of understory, acting as the important ecological filter for individual regeneration and population recruitment in the forests (George & Bazzaz, 1999).

Here, a field investigation with rhizomatous *Dicranopteris* and *Diplopterygium* was conducted to examine the variation of functional clonal traits of fern species. In this study, functional clonal traits, ramet performance traits and ramet population properties in plots differing in elevation were compared. Specifically, the attempt was made to understand how functional clonal traits varied with elevation and whether the two species have different functional clonal traits to cope with elevation.

Material and Methods

Filed investigation: The investigation was carried out on the Gutianshan National Nature Reserve (29°10'19.4"N - 29°17'41.4"N; 118°03'49.7″E - 118°11'12.2″E), Zhejiang province, China, where is mountainous, with elevation range from 200 m to 1258 m above sea level, is subtropical moist monsoon climate, complex topology and diverse microhabitats. The mean annual precipitation is ca. 1963 mm, mean annual temperature is 15.3 °C, with 38.1 °C the mean for the warmest month (July), and with -6.8 °C the mean for the coldest month (January). Total annual insolation hours is 1334.1 h, frost-free period is 250 days. The insolation hours and precipitation take parabolic change with increasing elevation, and heat decreasing linearly (Shi, 1987).

On July 2007, for each of the two species, six plots of 1 m × 1 m were randomly set up at low (340 m asl), medium (620 m asl) and high (860 m asl) elevation, respectively. In total, there were 36 plots. The forests are dominated by *Castanopsis eyrei* (Champ.) Tutch. (Yu *et al.*, 2001). Factorial design with elevation (three levels: low, medium versus high elevation) and species identity (*Dicranopteris* versus *Diplopterygium*) as main factors was used, resulting in 6 treatments, 6 replicates per treatment and, in total, 36 plots.

Measurements and analyses: In each of the plots, number of ramets was counted and then harvested all above-ground and below-ground plant parts ramet by ramet. Length of spacer (rhizome interconnecting adjacent ramets) of each ramet was measured. The plant materials were separated into leaf, rhizome and stem and dried to constant weight under 70 °C in the oven before weighed on the scale as precisely as 0.1 g. The functional clonal traits (McLetchie & Puterbaugh, 2000; Halassy *et al.*, 2005; de Bello *et al.*, 2011) (spacer length, specific spacer length, spacer mass, specific spacer weight), ramet performance traits (ramet biomass and biomass allocation to spacer), and ramet population properties (ramet population density and ramet population biomass) were measured or derived.

Two-way ANCOVA with ramet population property as covariate was used to test for the effect of elevation and species identity and their interactions on functional clonal traits and ramet performance traits (SPSS 13.0). When needed, data were logarithmically or square-rootedly transformed.

Results

Ramet population properties: Two-way ANCOVA indicated that ramet population density was significantly ($p<0.05$) affected by elevation (E), species identity (S) and E × S while ramet population biomass was significantly ($p<0.05$) influenced by E and E × S. In *Dicranopteris*, ramet population produced significantly less ramets and accumulated significantly less biomass at higher elevation (Fig. 1A, C). However, this pattern was not observed in *Diplopterygium* and actually whose ramet population properties hardly varied along elevation (Fig. 1B, D).
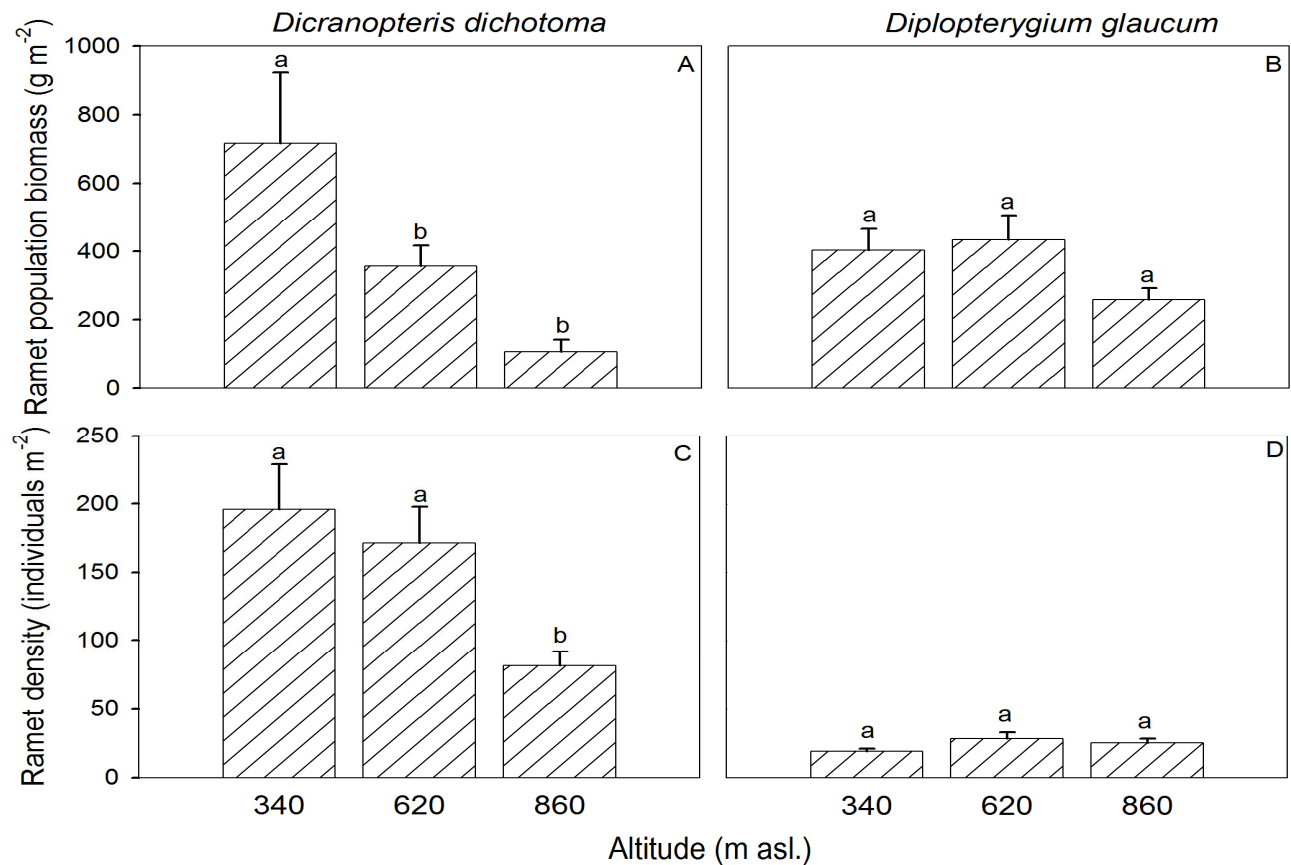

Fig. 1. Mean values (+1 SE) of ramet population properties including ramet population biomass (RPB) and ramet population density (RPD). The panels in left and right column are for *Dicranopteris dichotoma* and *Diplopterygium glaucum*, respectively. In each panel, figures sharing the same letter are not significantly different. Significance level is $p<0.05$.

Table 1. Results of ANCOVAs of the effects of ramet population density (RPD), elevation (E), species identity (S) and their interaction on plant traits. F and p are F-values and probability, respectively. Degree of freedom is (1, 29), (2, 29), (1, 29) and (2, 29) for the effect of RPD, Al, Si and their interaction, respectively. Significance level is $p < 0.05$ is in bold.

Plant traits	RPD		E		S		E × S	
	F	p	F	p	F	P	F	p
Ramet performance traits								
1. Ramet biomass [a]	4.14	0.051	**12.53**	**<0.001**	**154.05**	**<0.001**	0.02	0.985
2. Allocation to spacer	3.38	0.076	1.83	0.178	**10.16**	**0.003**	0.20	.0818
Functional clonal traits related to resource foraging								
3. Spacer length[a]	0.04	0.845	2.27	0.121	**33.64**	**<0.001**	2.74	0.081
4. Specific spacer length	0.01	0.939	**8.35**	**0.001**	1.09	0.306	0.12	0.887
Functional clonal traits related to resource storing								
5. Spacer weight per ramet[a]	0.03	0.868	**6.69**	**0.004**	**27.57**	**<0.001**	0.41	0.668
6. Specific spacer weight	0.41	0.528	**4.88**	**0.015**	0.81	0.376	0.13	0.880

Note: a, log transformation

Table 2. Results of ANCOVAs of the effects of ramet population biomass (RPB), elevation (E), species identity (S) and their interaction on plant traits. F and p are F-values and probability, respectively. Degree of freedom is (1, 29), (2, 29), (1, 29) and (2, 29) for the effect of population property, elevation, species identity and their interaction, respectively. Significance level $p < 0.05$ is in bold.

Plant traits	RPD		E		S		E × S	
	F	p	F	p	F	P	F	p
Ramet performance traits								
1. Ramet biomass [a]	**19.12**	**<0.001**	9.20	**0.001**	**584.47**	**<0.001**	0.58	0.566
2. Allocation to spacer	**4.25**	**0.048**	1.03	0.369	**10.31**	**0.003**	0.26	0.776
Functional clonal traits related to resource foraging								
3. Spacer length[a]	1.35	0.255	0.51	0.603	**204.70**	**<0.001**	2.85	0.074
4. Specific spacer length	0.05	0.832	**8.33**	**0.001**	**4.28**	**0.048**	0.14	0.870
Functional clonal traits related to resource storing								
5. Spacer weight per ramet[a]	0.17	0.687	**5.98**	**0.007**	**100.92**	**<0.001**	0.76	0.477
6. Specific spacer weight	0.30	0.587	**4.91**	**0.015**	**6.90**	**0.014**	0.11	0.894

Note: a, log transformation

Ramet performance traits: When the covariate was ramet population density, ramet biomass was significantly affected both by elevation and species identity (Table 1). In the same case, biomass allocation to spacer was affected only by species identity (Table 1). When the covariate was ramet population biomass, ramet biomass was significantly affected both by elevation and species identity (Table 2). Biomass allocation to spacer was affected significantly only by species identity (Table 2). For the two fern species, no trait was affected by interaction between elevation and species identity (Tables 1, 2).

In the two fern species, ramet biomass decreased significantly as elevation increased (Fig. 2A, B); biomass allocation per spacer did not change with elevational changes (Fig. 2C, D).

Functional clonal traits: When the covariate was the ramet population density, spacer length was significantly affected only by species identity and specific spacer length only by elevation (Table 1). In the same case, spacer weight per ramet was influenced by both elevation and species identity while specific spacer weight only by elevation (Table 1). When the covariate was ramet population biomass, spacer length was significantly affected only by species identity and specific spacer length by both elevation and species identity (Table 2). In the same case, spacer weight per ramet and specific spacer weight were influenced by both elevation and

species identity (Table 2). For the two fern species, no trait was affected by interaction between elevation and species identity (Tables 1, 2).

For the two fern species, spacer length kept unchanged along elevation (Fig. 3A, B), while specific spacer length was significantly greater at higher elevation (Fig. 3C, D). In the two fern species, spacer weight per ramet and specific spacer weight both were significantly smaller at higher elevation (Fig. 4).

Discussion

A number of empirical and theoretical studies have shown that clonal plants exhibit plasticity in functional clonal traits to cope with heterogeneous environments, which may provide advantage in capture of essential resources (Huber, 1996; Huber *et al*., 1998; Dong *et al*., 1997; van Kleunen *et al*., 2002; Fischer *et al*., 2004; Herben & Novoplansky, 2010). Recent study confirmed elevation was one of the most important environmental factors shaping variations of plant functional traits in this subtropical evergreen forest (Ding *et al*., 2011). In this study, the two fern species showed quite similar variation along elevation in functional clonal traits related to function of foraging for essential resources, i.e. unchanged spacer length and increased specific spacer length (indicating more slender spacers) as elevation increased. These are similar to what found for some

rhizomatous seed plant species. Their rhizome length had very small or even no response to enviromental change (Lovett-Doust, 1987; de Kroon & Knops, 1990; Dong & Pierdominici, 1995; Dong *et al.*, 1996; Clevering & Hundscheid, 1998). The unresponsive spacer lengths permit a continuious search of habitat space rather than a selective placement of ramets (de Kroon & Hutchings, 1995). Habitat conditions are generally more unfavorable for plants at higher elevation. Thus, a relatively stable spacer length in response to environmental change may benefit the plants to keep a persistent function of foraging for essential resources in heterogeneous environments. A greater specific spacer length at higher elevation may help maintain spacer length. This would be particularly true in the situation of this study that as elevation increasing the ramet biomass decreased and the biomass allocation to spacer kept unchanged.

Rhizomes of clonal plants often store nutrients, especially carbohydrates (Dong & Pierdominici, 1995; Liu *et al.*, 2007; Miller *et al.*, 2003; Kinmonth-Schultz & Kim, 2011; Shad *et al.*, 2011). Accordingly, spacer weight per ramet and specific spacer weight may be seen as indicator for the ability to store resources. In this study the two fern species showed similar variation along elevation in spacer weight per ramet (indicator of capacity of storing of resources by ramet) and specific spacer weight (indicator of capacity of storing resources by unit

length of spacer) and decreasing as elevation increasing, which indicates the plants reduced their resource storing function in response to elevation. This is particularly ecologically meaningful as ramet biomass decreased and biomass allocation to spacer kept stable. Whereby, the plants are able to allocate or reallocate more resources to maintain their growth and reproduction as encountering worse environments. This implicates that the two fern species are able to plastically regulate their function of storing of essential resources by rhizomes in response to environmental change.

Stolons and/or rhizomes are usually regarded having both functions of foraging for and/or storing of resources essential for plants (Dong & de Kroon, 1994; Marshall & Price, 1997; Brooker *et al.*, 1999; Stuefer & Huber, 1999; Suzuki & Stuefer, 1999; Song *et al.*, 2013). These results show a clear pattern that, when habitat conditions became unfavorable due to elevation increasing, the fern plants strived to stabilize function of foraging for resources and to reduce function of stroring of resources. The results show a tendency to maintain foraging on the cost of reduced resource storage along the elevational gradient, since spacer length remained stable but at the same time ramet biomass decreased. Such a trade-off between foraging for and storing of resources could have been a product of adaptation and might help the plants adapt to heterogeneous environments.
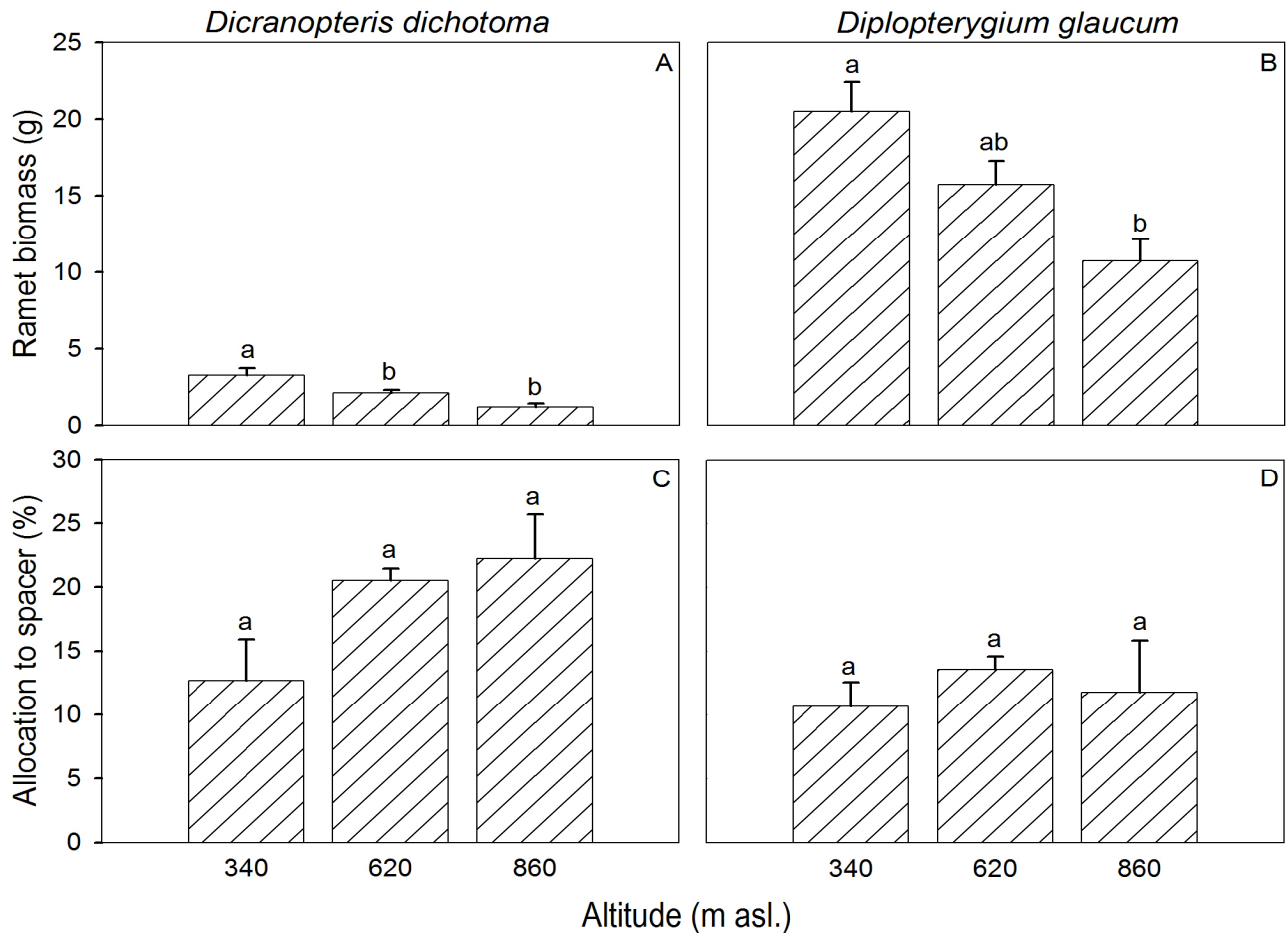

Fig. 2. Mean values (+1 SE) of ramet performance traits including ramet biomass and biomass allocation to spacer. The panels in left and right column are for *Dicranopteris dichotoma* and *Diplopterygium glaucum*, respectively. In each panel, figures sharing the same letter are not significantly different. Significance level is *p* < 0.05.
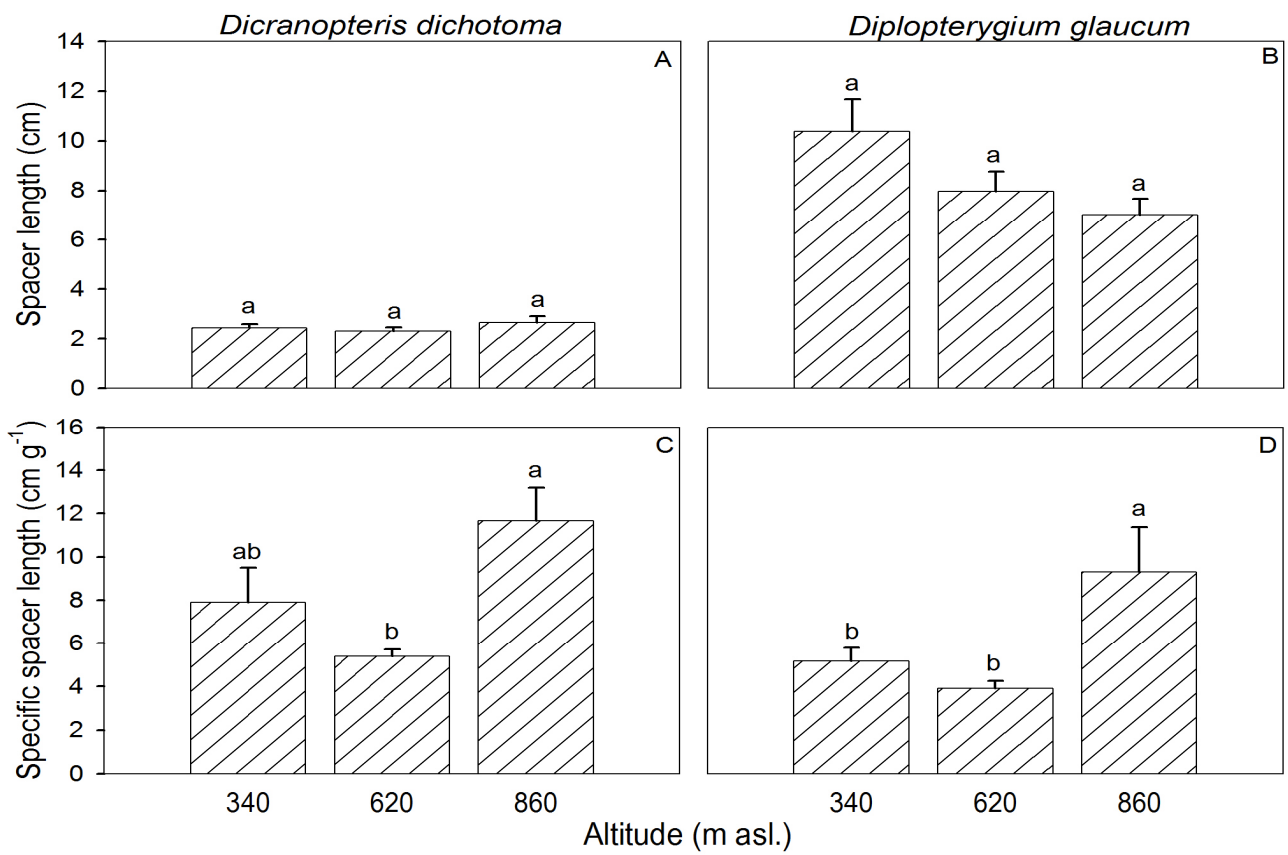
Fig. 3. Mean values (+1 SE) of functional clonal traits related to resource foraging, including spacer length and specific spacer length. The panels in left and right column are for *Dicranopteris dichotoma* and *Diplopterygium glaucum*, respectively. In each panel, figures sharing the same letter are not significantly different. Significance level is $p < 0.05$.
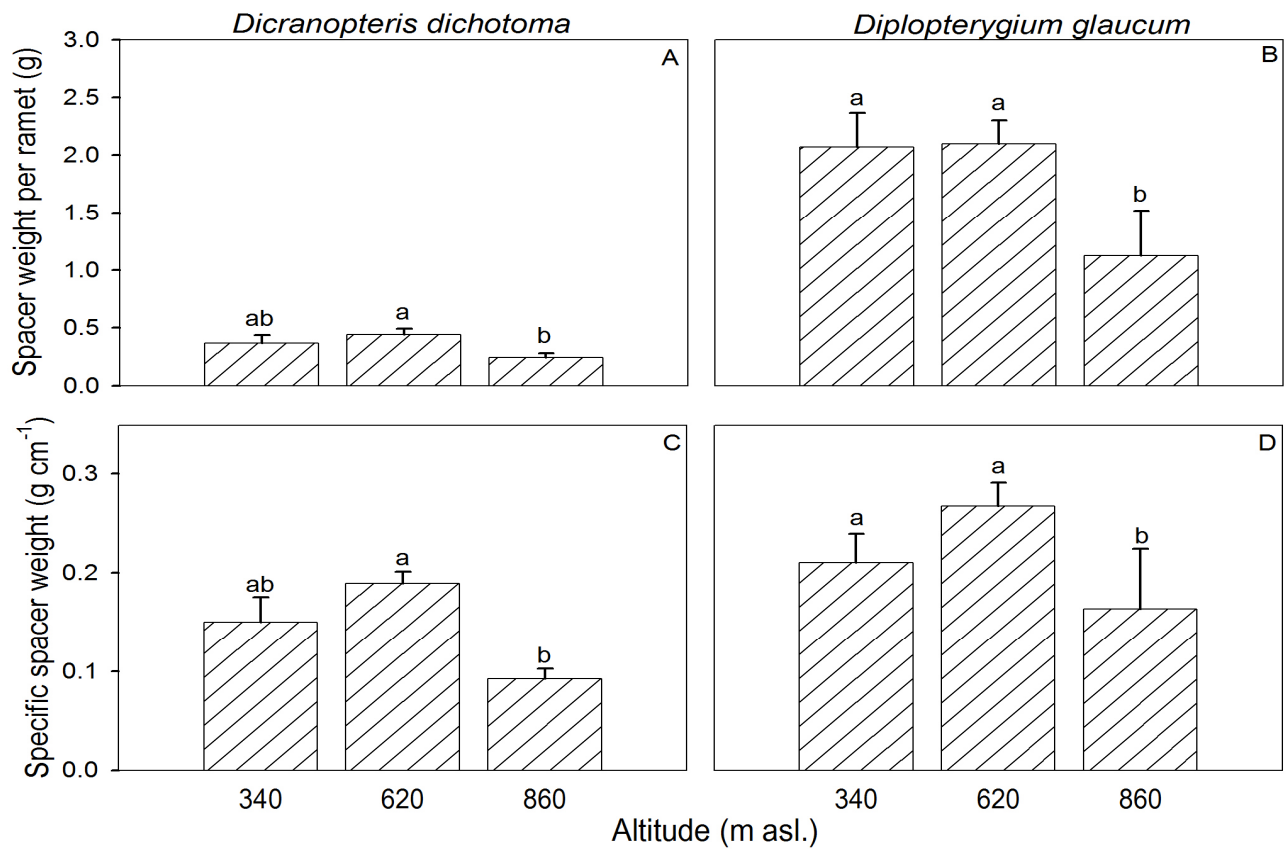

Fig. 4. Mean values (+1 SE) of functional clonal traits related to resource storage, including spacer mass and specific spacer weight. The panels in left and right column are for *Dicranopteris dichotoma* and *Diplopterygium glaucum*, respectively. In each panel, figures sharing the same letter are not significantly different. Significance level is $p < 0.05$.

Plants growing at the high elevation are usually exposed to low temperature, strong winds, intense solar radiation and low atmospheric pressure as well as other unpredictable environmental changes (Billings & Mooney, 1968). This leads to decreasing productivity and diversity along elevational gradients (Körner, 2007; Khan *et al*., 2011). Previous study found, in herbaceous plant communities in an alpine Massif, clonal production decreased while the duration of clonal integration and bud-bank size increased with elevation increasing (Evette *et al*., 2009). A similar variation pattern was also observed for *Dicranopteris* in this study. Ramet population density and biomass both decreased with elevation increasing. However, *Diplopterygium* had a different pattern in this study. Its ramet population properties kept unchanged along elevation. This clearly suggest an interspecific difference in plasticity in response to environmental (elevation in this case) change.

With elevation increasing, environmental factors such as temperature and water availability could become more unfavorable for plant growth and development. As a result, biomass allocations could be modified (Körner, 2007). Water availability is ecologically critical for fern species, because they are inherently weak in maintaining individual water balance and thus need free water as intermediary for fertilization of gametophyte (Page, 2002; Lu, 2007). This may explain, at least in part, why ramet biomass decreased with the increase in elevation in both species. These data show an unchanged biomass allocation to spacer along elevation. This is different from results of previous studies in which clonal plants allocated more resources in clonal growth than in sexual reproduction at higher elevation (Stöcklin, 1999; Šťastná *et al*., 2012). In case of ramet biomass decreasing with elevation increasing, a relatively stable allocation of biomass to spacers may help to maintain strength of foraging and storing of resources essential for the plants (Dong & de Kroon, 1994; de Kroon & Hutchings, 1995).

Conclusions

In summary, these data found along an elevational gradient the two fern species showed similar variation pattern of functional clonal traits: stable spacer length, plastic specific spacer length, spacer weight per ramet and specific spacer weight. Meanwhile these data found the two ferns species had similar variation patterns of ramet performance traits but different variation patterns of ramet population properties. These results, particularly those of functional clonal traits, suggest the existence of an evolutionary trade-off between functions of foraging for and storing of resources as well as the functional preference for foraging of resources in response to environmental change.

Acknowledgements

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