LETTER

Do rock endemic and widespread plant species differ under the Leaf–Height–Seed plant ecology strategy scheme?

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Abstract

Westoby (1998) proposed the Leaf–Height–Seed (L–H–S) scheme, i.e. the use of three functional traits, specific leaf area (SLA), plant canopy height and seed mass, to describe plant ecological strategies. In this study, we examine whether endemic species from cliffs and rocky outcrops can be discriminated in a regional Mediterranean flora according to these three traits. First, we conducted a comparison across 13 pairs of rock endemic species and widespread congeners. Second, we performed a canonical discriminant analysis to compare the position in the L–H–S volume of these 13 pairs of endemic and widespread congeners with that of 35 phylogenetically unrelated widespread species taken from the same regional flora. Our results show that rock endemic species only differ from their widespread congeners in their smaller stature. However, when compared with the 35 unrelated widespread species, endemic species are discriminated by higher SLA and taller stature, and thus are not close to the stress-tolerant pole of ecological strategies (small stature, low SLA), as hypothesized in the literature.

Keywords

Endemism, functional traits, Leaf–Height–Seed scheme, Mediterranean, plant canopy height, plant ecological strategy, seed mass, specific leaf area.

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INTRODUCTION

The use of functional traits has repeatedly been advocated to understand and predict the distribution and abundance of plant species in natural habitats (Grime *et al.* 1988; Keddy 1992; Weiher *et al.* 1999). Recently, Westoby (1998) proposed that such questions could be addressed by using three fundamental traits: specific leaf area (SLA, i.e. light-intercepting area deployed per leaf dry mass) which captures the fundamental trade-off between resource acquisition and conservation in plants (Poorter & Garnier 1999; Reich *et al.* 1999), canopy height at maturity, which is related to competitive ability (Rösch *et al.* 1997) and fecundity (Aarssen & Jordan 2001), and seed mass, which strongly influences dispersal and establishment ability (Jakobsson & Eriksson 2000). This Leaf–Height–Seed (L–H–S) ecological strategy scheme is based on a similar perspective to vegetation as the Competitors–Stress-tolerators–Ruderals (C–S–R) scheme devised by Grime (1974) but does not preclude any combinations of traits as do the triangular C–S–R scheme. The L–H–S scheme proposes easily measurable traits that can be used in surveys involving large numbers of species, thereby allowing the development of a quantitative assessment of plant strategies. However, to our knowledge, no empirical test of whether the L–H–S scheme as a whole efficiently discriminates species with contrasting ecological affinities has been conducted as yet (reviewed by Westoby *et al.* 2002).

The aim of this study was to do so in the particular case of species with restricted geographical distributions. There is a long-lasting interest concerning the ecological conditions which provide a template for differentiation and/or persistence of restricted endemic species (Griggs 1940; Drury 1974; Murray *et al.* 2002). In Mediterranean land-scapes, numerous endemic plant species are found in sloping and rocky habitats with sparse vegetation (S. Lavergne *et al.*, unpublished data), as also observed in other regional floras (McVaugh 1943; Baskin & Baskin 1988; Matthews *et al.* 1993). Médail & Verlaque (1997) recently suggested that endemic species successfully persist in such harsh habitats because they present syndromes of stress-tolerator species. In the framework of the L–H–S plant

ecology strategy scheme, this should translate into lower values of both plant height and SLA (Westoby 1998) in endemic species as compared with widespread ones. Predictions concerning the propagule attributes of endemic species are less straightforward: restricted endemic species might have low dispersal ability or low establishment capacities, which may lead to contradictory effects on seed size (Aizen & Patterson 1990; Eriksson & Jakobsson 1998).

In this study, we asked whether, under the L–H–S plant ecology strategy scheme, endemic species of cliff and rocky habitats had different ecological strategies than species with wider geographic distribution. As variation of range size not only occurs at inter-specific level but also at higher taxonomic level (Edwards 1998), the question was addressed at two different phylogenetic scales, on species occurring in the French Mediterranean region: (i) endemic species were compared with congeneric widespread species on the three axes of the L–H–S volume; (ii) the position of endemic species and that of their widespread congeners was compared in the L–H–S volume with that of a set of phylogenetically unrelated widespread species.

METHODS

Study species

In a previous work (S. Lavergne *et al.*, unpublished data), we had selected 20 congeneric pairs of restricted endemic and widespread species (the two species of each pair having the same life-form, pollination and dispersal type) to study ecological and biological differentiation between endemic and widespread related species occurring in the Mediterranean. For the purpose of the present study, 13 pairs were extracted from this sample of 20 pairs on the basis of the following 'within pair' habitat differences (Table 1): the 13 endemic species occur in habitats with significantly steeper slope, higher percentage of bedrock and block cover, lower vegetation canopy height, lower cover of herbaceous plus woody species, and fewer coexisting species (Table 2a). Each of the 13 pairs of species therefore diverges on the same environmental gradient, which corresponds to the design called for by Westoby (1998) to test the L–H–S scheme.

The second comparison aimed at comparing each of the two samples of 13 endemic and 13 congeneric widespread species with a set of phylogenetically unrelated species ('unrelated widespread species' hereafter), which have a large geographic distribution and are representative of diverse successional Mediterranean plant communities from old fields to *Quercus ilex* woodlands (see Braun-Blanquet *et al.* 1952). This set of species was selected from the 57 species studied by Garnier *et al.* (2001a), following three criteria: (i) to limit phylogenetic confounding, we excluded species from genera that were represented among the 13 congeneric pairs of

endemic and widespread species; (ii) we discarded phanerophytes of high stature (>2 m), which were absent from the 13 congeneric pair set (see Table 1), and (iii) we removed some hemicryptophyte and therophyte species (sensu Raunkiaer 1934) which were over-represented in the data set of Garnier *et al.* (2001a) as compared with the 13 congeneric pairs $[\chi^2_{(\text{d.f.}=4)} = 23.6; \; P < 0.001]$. Hemicryptophyte and therophyte were randomly removed until life-form distributions among unrelated widespread species and the 13 congeneric pairs become not significantly different $[\chi^2_{(\text{d.f.}=4)} = 9.4; \; P = 0.052;$ Table 1]. We ended up with a final sample of 35 phylogenetically unrelated widespread species, which spanned the same array of morphology and life-forms as the 13 congeneric pairs of endemic and widespread species.

The geographic ranges of the 13 endemic species are mainly the Western Mediterranean. The distributions of the congeneric and unrelated widespread species overlap with those of endemic species (Tutin *et al.* 1964–1993) and are syntopic with seven of the 13 endemic species. The congeneric and unrelated widespread species largely extend beyond the Western Mediterranean, northwards and/or eastwards, throughout and outside Europe, in Africa and Asia (S. Lavergne *et al.*, unpublished data).

Trait measurements

Measurements were taken over 2 years (2000, 2001), in 20 different sites (Table 1). As we were only interested in interspecific variation, a single population per species was sampled to measure the three L–H–S traits. This sampling strategy is justified on the findings that species ranking based on SLA is usually well conserved across years and sites within species, and that variation for this trait was within a 8–12% range among Mediterranean sites (Garnier *et al.* 2001a). Similarly, intraspecific variation in seed mass among sites was found to be less than 20% (E. Garnier, unpublished data), which is low compared with the usual interspecific variation recorded for this trait (Michaels *et al.* 1988, and see Table 1). As canopy height of each species may vary across different sites, we measured this trait on mature and reproductive individuals occurring in ecological conditions representative of their usual habitats. None of the species has been sampled at its range limits.

Thirty mature individuals per species were randomly sampled to measure plant canopy height. To determine SLA and seed mass, mature leaves and one to five mature fruits (or flower heads in *Centaurea* and *Phyteuma*) were harvested on 15 of these individuals. Canopy height and seed mass of the 13 pairs of endemic and widespread congeners were measured as described by Westoby (1998), while SLA was determined on water-saturated leaves following the protocol described in Garnier *et al.* (2001b). For the set of 35 unrelated widespread species, SLA data were taken from

Table 1 List of species studied (nomenclature follows Tutin *et al*. 1964–1993). Mean values of plant canopy height (cm), specific leaf area (SLA, m² kg⁻¹) and seed mass (mg). Life forms (Raunkiaer 1934) are Ch: chamaephyte; Ge: geophyte; He: hemicryptophyte; Ph: phanerophyte; Th: therophyte. SLA was not determined for *Genista pulchella* as this species has very small and short-lived leaves

Species	Family	Sampling site	Latitude/longitude	Life-form	SLA (m² kg⁻¹)	Height (cm)	Seed mass (mg)
Endemic species							
Alyssum pyrenaicum	Brassicaceae	Nohèdes	42°37′ N; 2°15′ E	Ch	14.90	5.5	0.58
Aquilegia viscosa	Ranunculaceae	La Séranne	43°52′ N ; 3°38′ E	He	23.80	12.1	3.08
Centaurea corymbosa	Asteraceae	La Clape	43°08′ N; 3°05′ E	He	14.30	18.4	2.24
Cistus varius	Cistaceae	Col St Pierre	44°08′ N; 3°50′ E	Ch–Ph	8.37	27.3	2.15
Cyclamen balearicum	Primulaceae	St Jean du Gard	44°05′ N; 3°56′ E	Ge	27.83	3.9	2.91
Genista pulchella	Fabaceae	L' Etoile	43°46′ N; 3°42′ E	Ch	.	8.6	2.59
Lilium pyrenaicum	Liliaceae	Bouillousses	42°33′ N; 2°00′ E	Ge	30.96	115.6	9.58
Lonicera pyrenaica	Caprifoliaceae	Galamus	42°50′ N; 2°28′ E	Ph	17.60	75.7	2.04
Lysimachia ephemerum	Primulaceae	Maury	42°50′ N; 2°38′ E	Ge	20.15	98.0	0.32
Melica bauhinii	Poaceae	Gorniès	43°53′ N; 3°37′ E	He	18.72	31.6	1.43
Phyteuma charmelii	Campanulaceae	Pic d'Anjeau	43°55′ N; 3°37′ E	He	35.60	7.8	0.04
Reseda jacquinii	Resedaceae	Graissessac	43°41′ N; 3°04′ E	Th	25.40	18.2	1.43
Thymus nitens	Lamiaceae	Jontanels	44°10′ N; 3°30′ E	Ch	17.80	18.7	0.12
Congeneric widespread species							
Alyssum spinosum	Brassicaceae	La Séranne	43°52′ N; 3°38′ E	Ch	8.80	16.0	1.18
Aquilegia vulgaris	Ranunculaceae	Bez	43°58′ N; 3°31′ E	He	28.50	66.6	1.95
Centaurea maculosa	Asteraceae	Navacelles	43°53′ N; 3°30′ E	He	14.90	32.5	2.36
Cistus monspeliensis	Cistaceae	Mireval	43°30′ N; 3°46′ E	Ph	4.86	103.9	1.07
Cyclamen repandum	Primulaceae	St Tropez	43°15′ N; 6°37′ E	Ge	30.90	4.7	3.75
Genista pilosa	Fabaceae	Pic d'Anjeau	43°55′ N; 3°37′ E	Ch	19.84	29.5	2.48
Lilium martagon	Liliaceae	Mont Aigoual	44°07′ N; 3°33′ E	Ge	23.52	41.7	5.64
Lonicera xylosteum	Caprifoliaceae	Pic d'Anjeau	43°55′ N; 3°37′ E	Ph	28.30	199.2	6.01
Lysimachia vulgaris	Primulaceae	St Jean de Buèges	43°49′ N; 3°36′ E	Ge-He	20.71	100.9	0.38
Melica ciliata	Poaceae	La Séranne	43°52′ N; 3°38′ E	He	16.49	36.0	0.62
Phyteuma orbiculare	Campanulaceae	Pic d'Anjeau	43°55′ N; 3°37′ E	He	36.10	33.8	0.29
Reseda phyteuma	Resedaceae	Villemagne	43°37′ N; 3°06′ E	Th	16.10	16.2	1.74
Thymus pulegioides	Lamiaceae	Jontanels	44°10′ N; 3°30′ E	Ch	16.30	9.5	0.11
Unrelated widespread species							
Aegilops geniculata	Poaceae	Cazarils	43°46′ N; 3°42′ E	Th	22.6	8.6	8.32
Anagallis arvensis	Primulaceae	''	''	Th	28.7	10.0	0.69
Aristolochia rotunda	Aristolochiaceae	''	''	Ge	20.6	15.0	8.24
Avena barbata	Poaceae	''	''	Th	25.2	18.0	5.25
Avenula bromoides	Poaceae	''	''	He	16.4	11.9	0.59
Brachypodium distachyon	Poaceae	''	''	Th	28.2	9.0	2.26
Brachypodium phoenicoides	Poaceae	''	''	He	12.9	37.5	2.47
Bromus erectus	Poaceae	''	''	He	12.8	24.1	3.41
Bupleurum rigidum	Umbelliferae	''	''	He	11.3	20.0	4.30
Calamintha nepeta	Lamiaceae	''	''	Ch	25.7	3.9	0.21
Carex halleriana	Cyperaceae	''	''	He	17.1	5.6	1.22
Convolvulus arvensis	Convolvulaceae	''	''	Ge	24.2	3.8	12.99
Crataegus monogyna	Rosaceae	''	''	Ph	10.6	154.0	4.07
Dactylis glomerata	Poaceae	''	''	He	18.3	13.3	0.55
Daucus carota	Umbelliferae	''	''	He	18.0	9.7	0.98
Dorycnium hirsutum	Fabaceae	''	''	Ch	23.3	10.2	4.54
Dorycnium pentaphyllum	Fabaceae	''	''	Ch	11.4	15.0	3.23
Eryngium campestre	Umbellifereae	''	''	Ge	8.60	15.0	0.72
Helianthemum nummularium	Cistaceae	''	''	Ch	14.7	10.6	1.24
Lavandula latifolia	Lamiaceae	''	''	Ch	11.7	22.6	0.95

Table 1 (*continued*)

Species	Family	Sampling site	Latitude/longitude	Life-form	SLA ($m^2 kg^{-1}$)	Height (cm)	Seed mass (mg)
Lotus corniculatus	Fabaceae	''	''	He	18.2	10.0	1.32
Medicago minima	Fabaceae	''	''	Th	21.2	5.0	0.92
Phleum pratense	Poaceae	''	''	He	22.2	15.7	0.42
Plantago lanceolata	Plantaginaceae	''	''	He	10.6	7.0	0.87
Prunus spinosa	Rosaceae	''	''	Ph	10.7	26.0	22.6
Psoralea bituminosa	Fabaceae	''	''	He	15.0	15.0	16.7
Rosa micrantha	Rosaceae	''	''	Ph	11.6	146.0	13.6
Rubia peregrina	Rubiaceae	''	''	Ch	13.8	9.4	17.5
Rubus fruticosus	Rosaceae	''	''	Ph	14.4	44.0	2.17
Scabiosa atropurpurea	Dipsacaceae	''	''	He	11.4	35.0	0.84
Stachys officinalis	Lamiaceae	''	''	He	13.4	5.0	1.28
Teucrium chamaedrys	Lamiaceae	''	''	Ch	11.3	5.5	0.71
Trifolium angustifolium	Fabaceae	''	''	Th	15.6	11.0	1.22
Urospermum dalechampii	Asteraceae	''	''	He	21.6	10.0	1.11
Viola scotophylla	Violaceae	''	''	He	15.9	10.0	2.10

Table 2 Results of pairwise tests for a general difference in habitat characteristics (a) and species traits (b) across the 13 pairs of endemics and widespread congeners. For habitat characteristics, tests are unilateral Wilcoxon signed rank test. For SLA, height and seed mass, tests are bilateral paired *t*-tests (after logarithmic transformation)

	P-value	Difference
(a) Habitat characteristics		
Bedrock + rock cover (%)	**0.0001**	E > W
Slope (%)	**0.0017**	E > W
Woody species cover (%)	**0.0447**	E < W
Woody + herbaceous species cover (%)	**0.0071**	E < W
Vegetation height (m)	**0.0236**	E < W
Number of coexisting species	**0.0095**	E < W
(b) Species traits		
Specific leaf area (SLA, $m^2 kg^{-1}$)	0.2931	NS
Plant canopy height (m)	**0.0451**	E < W
Seed mass (mg)	0.5286	NS

P-values below 0.05 are in boldface.
The column Difference indicates the direction of the general difference, if significant, between endemic and widespread congeners with: E, Endemic; W, Widespread; NS, no significant difference.

Garnier *et al*. (2001a) while plant height and seed mass were measured with the same protocol as above (E. Garnier *et al*., unpublished data).

Statistical analyses

To perform the analyses, the three axes of the L–H–S scheme were log transformed to conform to normality (Westoby 1998). As suggested for phylogenetically independent comparisons, we performed pairwise tests (Felsenstein 1985) to assess the significance of a general difference in L–H–S traits between endemic and widespread congeners. To do so, bilateral paired *t*-tests were performed with SAS (version 8.02).

To perform the second comparison, the two sets of 13 endemic species and the 13 widespread congeners were separately compared with the sample of 35 unrelated widespread species by performing a canonical discriminant analysis, using the procedure CANDISC in SAS (version 8.02). The aim of this analysis was to determine the linear combination of the three log-transformed quantitative variables (SLA, height, seed mass) that maximize variance between the two groups (e.g. endemic vs. unrelated widespread species), which we tested with a multivariate *F*-test (Wilk's Lambda *F*-test). Canonical coefficients were displayed for each of the three original variables in order to quantify their own contribution to the canonical variable and to determine the most discriminant original variables.

RESULTS

In the first comparison, endemic species exhibited significantly smaller stature than their widespread congeners (Table 2b), but we found no significant differences in SLA and seed mass between endemic and widespread congeners (Table 2b). In the second comparison, the canonical analysis significantly discriminated endemic species from unrelated widespread species [Wilk's Lambda $F_{(3;43)} = 4.34$; $P = 0.0093$]. This discrimination was mainly accounted for by a higher SLA in endemic species, and to a lesser extent by a higher stature (as shown by the canonical structure, Fig. 1a). The 13 widespread congeners were also significantly discriminated from the unrelated widespread species [Wilk's Lambda $F_{(3;43)} = 6.10$; $P = 0.0015$], by a higher stature and SLA (Fig. 1b).

(a)

(b)
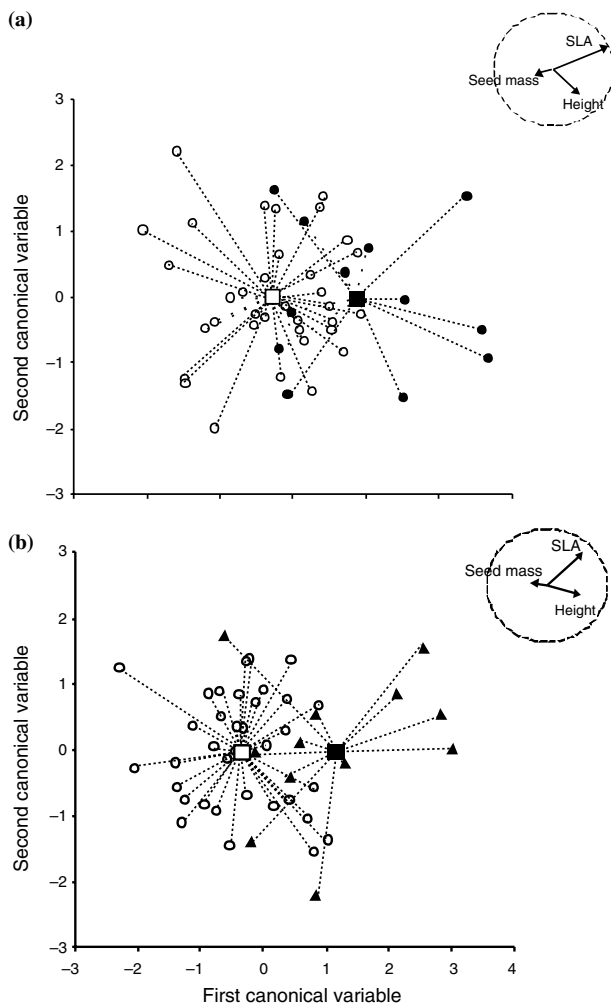
Figure 1 Plots of species on the plane defined by the first two canonical variables fitted by the two discriminant analysis. Only the first canonical variables discriminate the two groups of species, i.e. unrelated widespread species (open circles) vs. endemic species (filled circles) for graph (a), and unrelated widespread species (open circles) vs. widespread congeneric species (filled triangles) for graph (b). The second canonical variable is represented only to facilitate graphical interpretation but has no discriminant function. In each graph, the open square represents the mean position of unrelated widespread species on the first canonical plane; the filled squared represents the mean position on the canonical plane of endemic species (a), and of their widespread congeners (b). The structure of the two canonical variables is represented on the diagram by a unity circle: coordinates of the three vectors SLA, height and seed mass are equal to their canonical coefficients.

DISCUSSION

In this study, we focused on cliff dwelling endemic species from the Mediterranean region. These endemic species are found in habitats with a relatively harsh topography (sloping

and rocky habitats), lower and less dense vegetation, and fewer coexisting species than geographically widespread congeneric species (Table 2). Endemic species may therefore experience lower competition for light and space and fewer competitive interactions, possibly because of fewer colonization events in these habitats (Foster 2001).

Within the studied genera, rock endemic species have a significantly lower plant canopy height than their widespread congeners. Given the importance of individual height in competitive hierarchies in plants (Rösch *et al.* 1997), the smaller stature of narrow endemic species suggests that these species have a lower competitive ability. However, endemic species may not differ from their widespread congeners in terms of resource acquisition and establishment ability (as far as these functions are appropriately captured by SLA and seed mass, respectively). Direct measurements of net photosynthetic rate on six of these 13 pairs have confirmed that endemic species do not have a lower capacity to acquire atmospheric carbon (S. Lavergne & E. Garnier, unpublished data). Recent works on temperate floras also failed to show consistent differences in seed size between geographically restricted and widespread related species compared in varying phylogenetic contexts (Eriksson & Jakobsson 1998). Together, our results suggest that rock endemic species do not differ from widespread congeners in terms of stress-tolerance, which should be translated into both small stature and low resource acquisition potential (Grime *et al.* 1988). In cliff and rocky habitats where the studied endemic species occur, resources may not limit establishment and growth, but the number of 'micro-sites' favourable for installation may be low, which results in fewer coexisting species and sparse vegetation, and thus in a low level of above-ground competition.

Restricted endemic species are generally non-randomly distributed among families or genera in regional floras (Edwards 1998). Then, the position of endemic species in the L–H–S volume spanned by the whole regional flora may be at least partly determined by their phylogenetic origin. In our study, both the 13 rock endemics and the 13 widespread congeners were discriminated from the 35 unrelated widespread species by a relatively higher SLA and a taller stature. Rock endemic species thus tend to belong to genera with larger light-intercepting area per unit leaf dry mass and higher above-ground biomass. These genera do not exhibit traits which would classify them as particularly stress-tolerant in the regional spectrum of ecological strategies. Clearly, the rock endemic species and their widespread congeners may have a taller stature because they mostly occur in later successional stages than the 35 unrelated widespread species. Although the set of unrelated widespread species is representative of the main plant communities and dominant families of the French Mediterranean,

the comparison outlined in this study should be enlarged to a larger set of species.

This study is the first to address the relevance of the L–H–S plant ecology strategy scheme proposed by Westoby (1998). The L–H–S variables reflect fundamental features of growth and regeneration capacity in plants, and then may be useful to understand how plants respond to the selective forces undergone by a group of species with particular ecological affinities. However, the L–H–S might capture less variation in ecological behaviour than C–S–R scheme: 'soft' attributes such as L–H–S traits may not be sufficient to capture the actual functional diversity of plant assemblages with mixed life-forms (e.g. Walker & Langridge 2002). Westoby et al. (2002) thus recently suggested that it may be worth adding other dimensions or different quantitative traits to the L–H–S scheme. In agreement with this, we found that additional reproductive traits such as female fertility and pollen/ovule ratio discriminated better endemic and widespread species than seed mass did (S. Lavergne et al., unpublished data).

The occurrence of endemic plants in sloping and rocky habitats with sparse vegetation has frequently been reported (Baskin & Baskin 1988), but little effort had been invested in understanding whether endemic species constitute a homogeneous or a random assemblage of ecological strategies (e.g. Lloyd et al. 2002). This study shows that endemic species from cliffs and rocky glades have a smaller stature, and then possibly have a lower competitive ability than widespread congeneric species exploiting less harsh habitats. However, such endemic species can occur in many different phylogenetic contexts, and not necessarily in lineages prone to stress-tolerance as proposed elsewhere (Médail & Verlaque 1997). On the contrary, emergence or persistence of endemic species in cliffs or rocky glades tend to have mainly occurred in lineages with higher stature and SLA.

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