The functional morphology of juvenile plants tolerant of strong summer drought in shaded forest understories in southern Spain

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Abstract

It has been hypothesized that plants cannot tolerate combined shade and drought, as a result of morphological trade-offs. However, numerous plant species are reportedly widespread in shaded forest understories that face drought, whether seasonal or occasional. We studied juveniles of six plant species that cope with strong summer drought in the understoreys of mixed *Quercus* forests in southern Spain: the tall-shrubs *Phillyrea latifolia* and *Viburnum tinus*, the perennial herb *Rubia peregrina*, the small shrub *Ruscus aculeatus*, and climbers *Hedera helix* and *Smilax aspera*. All of these species persist in evergreen shade (c. 3% daylight). Two other species were studied as comparators, *Ruscus hypoglossum*, less tolerant of drought, and *Ceratonia siliqua*, less tolerant of shade. Morphological and chemical variables relevant to shade and drought tolerance were measured for juveniles in a range of sizes, and also for the leaves of mature plants. The species converge in features that confer tolerance of shade plus drought by reducing demand for resources. Demand for water is reduced through a moderate to high below-ground mass fraction and low to moderate specific leaf area (respectively 0.22–0.52 and 112–172 cm^2 g^{-1} at 1.00 g total dry mass). Demand for both irradiance and water is reduced through a low to moderate foliar nitrogen concentration and long-lived, physically protected leaves ($\geqslant$ 2 yr). The species also converge in features that confer tolerance of either low irradiance or drought through specialized capture of resource, without precluding the other tolerance. These features include deep roots relative to shoot size, moderately higher specific leaf area in shade (1.2–2.0 × that in sun) and higher chlorophyll:nitrogen ratio in shade. Foliar chlorophyll per unit mass was higher in shade, but chlorophyll was not necessarily synthesized in greater amounts; rather, it was higher apparently due to shade effects on structural features linked with specific leaf area. In contrast, N per unit mass was higher in sun leaves independently of specific leaf area. Despite these convergences, the species diverge considerably in their root mass allocation and architecture, leaf saturated water content, density of stomata and guard cell size. No single narrowly defined functional type is needed for tolerance of shade plus drought.

Introduction

Can plants tolerate combined shade and drought (specifically, dry soil)? Although shade can benefit droughted plants (reducing overheating, vapour-pressure deficit, and oxidative stress; Ludlow and Powles (1988) and Abrams and Mostoller (1995), Ellsworth and Reich (1992), Callaway (1995), Valladares and

Pearcy (1997)), droughted plants face mortality even in shade (Vance and Zaerr 1991; Veenendaal et al. 1995; Zavala et al. 2000). Further, Smith and Huston (1989) hypothesized that a trade-off makes drought tolerance impossible in shade. According to their hypothesis, shade tolerance is increased by a high allocation to shoot rather than root, and a high specific leaf area (lamina area/lamina dry mass), but drought

tolerance is reduced by these features, which entail a large evaporative surface, and reduced ability to capture water (Smith and Huston 1989). Many plants around the world, however, do tolerate drought in deep shade (say < 4% daylight; Wright et al. (1992) and Burslem (1996), Caspersen and Kobe (2001), Sack and Grubb (2002)). Understanding this tolerance is critical given the increasing incidence and severity of droughts affecting forests worldwide (Fearnside 1995; Karl et al. 1995; Peñuelas et al. 1998; Siwecki and Ufnalski 1998).

Functional morphology can confer tolerance of shade and drought in two separate ways. First, mechanisms might enhance the *specialized capture* of irradiance or water. For instance, mechanisms that enhance light-capture in shade include a high specific leaf area and a shade-acclimated photosynthetic apparatus (Lichtenthaler 1985; Givnish 1988), and mechanisms that increase water capture include deep roots with efficient architecture (Levitt 1980). Altogether different mechanisms might lead to *reduced demand* for resources. Mechanisms that reduce water demand during drought include reducing water loss and developing desiccation-resistant tissue. Mechanisms that reduce demand simultaneously for irradiance and water (and other resources) include long-lived parts, less frequently needing replacement (Grime 1966; Walters and Reich 1999; Lusk and Reich 2000). Such mechanisms are frequently grouped as a "stress-tolerator syndrome" (Grime 1979; Chapin et al. 1993). Mechanisms of this type might provide a way to overcome potential trade-offs between shade tolerance and drought tolerance such as that hypothesized by Smith and Huston (1989).

Juveniles establishing in the understories of sclerophyll-dominated, seasonally-dry forests in the Mediterranean Basin face evergreen shade combined with strong drought (Barbero et al. 1992). The proportion of daylight penetrating to plant level is often as low as 3% throughout the year (Baldy et al. 1987; Gratani 1997). Severe summer drought produces pre-dawn water potentials below −2 MPa in the leaves of deep-rooting canopy trees (Sala 1999; Save et al. 1999), and the soil occupied by the juveniles is probably drier, as upper layers of forest soil commonly dry out first (Zahner 1955; Veenendaal et al. 1995; Lopez et al. 1998; Poorter and Hayashida-Oliver 2000). We studied the functional morphology associated with tolerance for juveniles of six species. We measured biomass allocation, root form, leaf composition, the sun-shade plasticity of specific leaf area, and the con-

centrations of leaf chlorophyll and nitrogen. For several variables allometries were determined.

We determined the sun-shade plasticity of leaf features in mature plants to explore an ecological mechanism for shade tolerance. Mature shade-tolerators may show a relatively high plasticity in specific leaf area—which might contribute to casting deep shade that excludes juvenile light-demanders (Canham et al. 1994; Grubb 1998).

Methods

Study areas and species

Three forests in southern Spain were sampled in this study. The first (hereafter, 'Aljibe') is located in the Sierra del Aljibe (36°31′ N, 5°38′ W), province of Cádiz; the second (hereafter, 'Grazalema') is located on the south-facing slope of Sierra del Pinar (36°46′ N, 5°26′ W), also province of Cádiz; and the third (hereafter, 'Cazorla') is located in the Sierra de Cazorla (37°58′ N, 2°51′ W), province of Jaén. The forests differ in soil type and soil nutrient concentrations. Aljibe is set on sandstone with acidic soil, Grazalema on Jurassic limestone with basic soil, and Cazorla on Jurassic and Cretaceous limestone with basic soil (Table 1). Consequently, the soil at Aljibe is sandy, and poor in nutrients relative to those at Grazalema and Cazorla (Table 1). At Aljibe, the mean annual precipitation ranges among sites from 665 to 1210 mm (Ojeda et al. 1995), at Grazalema from 516 to 2223 mm (Aparicio and Silvestre 1996), and the value for a representative site at Cazorla is 1527 mm (Herrera et al. 1994). At all three forests precipitation is highly seasonal. At Aljibe, as little as 5 mm commonly occurs between June and September; in mid-July of a typically dry summer the water potential of soil 1 at 10 cm depth reaches −2 to −4 MPa (T. Marañón, unpublished data). At Cazorla, mean summer precipitation is 15 mm. Below the mountain peaks in all three study areas, the vegetation consists primarily of mixed evergreen-deciduous forest, varying from dense forest to open woodland. At Aljibe, the canopy is dominated by semi-deciduous *Quercus canariensis* (Fagaceae; nomenclature follows Tutin et al. (1964–1980)) and evergreen species *Arbutus unedo* (Ericaceae) *Phillyrea latifolia* (Oleaceae), *Quercus suber*, and *Viburnum tinus* (Caprifoliaceae). At Grazalema and Cazorla, the canopy is dominated by semi-deciduous *Quercus faginea* and by evergreen species *Phillyrea*

and *Quercus rotundifolia*. At Grazalema, additional evergreen canopy dominants include *Ceratonia siliqua* (Fabaceae) and *Pistacia lentiscus* (Anacardiaceae); at Cazorla, *Arbutus* and *Viburnum* are common instead. At Aljibe the forest is locally managed for cork production.

Eight species of juveniles were sampled in this study, of which six persist in the shaded understorey in soil prone to drought. These species have divergent life histories with respect to irradiance. Tall-shrub *Phillyrea latifolia* persists as saplings for many years in the understorey, apparently suppressed until the shade is relieved, whereas saplings of tall shrub *Viburnum tinus* achieve larger sizes in the understorey. Both species need moderate irradiance for flowering. *Rubia peregrina* (Rubiaceae), a scrambling herb that produces widely creeping rhizomes, establishes both in understorey and open sites. *Ruscus aculeatus* (Ruscaceae), a phylloclade-bearing monocotyledonous small shrub that forms tight clumps of shoots, is a *shade-demander*, flowering and fruiting only in the shade. *Hedera helix* (Araliaceae), a root-climber, and *Smilax aspera* (Smilacaceae), a tendril-climber, are observed establishing in deeply-shaded understories; *Hedera* can persist many years in deep shade. Both climbers flower under high irradiance in the mid- to upper-canopy. Juveniles of two species not generally tolerant of deep shade plus drought were also sampled, as comparators. *Ceratonia siliqua* a small tree species, establishes in well-lit patches in open woodland. *Ruscus hypoglossum* has a similar growth form to *Ruscus aculeatus*, but with larger, non-spiny phylloclades; it grows in moister shady sites.

In addition to the juveniles, at each study site we sampled sun and shade leaves from the mature plants of the dominant evergreen overstorey species. Hereafter generic names are used, except for the different species of *Quercus* and *Ruscus*.

Collection of understorey juveniles, and leaf samples from exposed plants

In each forest, one to three sites were selected, where abundant juveniles of the study species were located in a range of sizes, in observably deep shade. Adjacent clearings were also sampled. Sampling at Aljibe took place on 2–4 April 1998 at sites that had an understorey left apparently undisturbed by managers for at least several years. In our abbreviations for the sites, the first letter represents the forest; the second letter is 'U' (understorey) or 'O' (open); the third letter refers to the specific site, as needed. At Aljibe, two understorey sites were sampled: site AUa (600 m altitude), 20 to 30 m upslope from a river, and site AUb, 8 km from site AUa, on rocky terrain. One open site was sampled, site AO, a grazed clearing, at the edge of the forest, 50 to 70 m from site AUa. Sampling at Grazalema took place on 2 February 1999. One understorey site was sampled, site GU, and one open site, GO, 50 to 100 m away. Sampling at Cazorla took place on 9–10 February 1999. Three sites were sampled, CUa, CUb and CUc. Site CUa is at 790 m elevation, and is moister than the other sites, though the soil dries in summer. CUa is least susceptible to frost. Higher-altitude sites CUb (1150 m elevation) and CUc (2 km from site CUb, 1200 m elevation) are described by Herrera et al. (1994), respectively as *Hoyos de Muñoz* (tall scrub, to 4.5 m in height) and *Agracea* (forest, 5–18 m).

At each understorey site, ten juveniles were selected of each study species that occurred abundantly. Juveniles were selected in a range of sizes, from newly-germinated seedlings to plants several years of age. While in the studied forests there was pronounced herbivory, the selected understorey juveniles showed minimal damage or none at all (i.e., 0 to 10% of above-ground parts affected by herbivory or mechanical damage), with the exception of moderately-grazed large juveniles of *Ruscus* species collected at sites AUb and GU (ca. 10–30% of shoots eaten).

Irradiance levels were measured at the study sites, and soils were sampled. Soil samples were collected from several spots at each study site, from above and below 20–25 cm depth (Table 1). Soil analysis followed Allen (1989). As an index of the light environment, the diffuse site factor of Anderson (1964) was calculated as the percent daylight photosynthetically active radiation. During cloudy conditions (i.e. during sampling at Aljibe and Cazorla), irradiance was measured for each sampled juvenile, and simultaneously in a fully open area (using a Skye SKP 200/215 PAR quantum sensor, Skye Instruments Ltd, Llandrindod Wells, Powys, UK). During sampling at Grazalema measurements were made for 25 understorey juveniles during 30 min in which small clouds obscured the sun's disc.

The understorey juveniles were excavated in entirety, and brought back to the lab in sealed plastic bags with moist paper towel. From open sites AO and GO, shoot samples (> 3 leaves) were collected from the ungrazed parts of juvenile plants to allow sun-

Table 1. Soil characteristics of the study sites. Concentrations of N are total (Kjeldahl) concentrations and concentrations of P, K, Ca and Mg are available concentrations. Mean values given when n > 1

Site	depth of sample, (cm), n	pH	CaCO$_3$ (%)	% loss on ignition	N (%)	P (μg g^{-1})	K (μg g^{-1})	Ca (μg g^{-1})	Mg (μg g^{-1})	Sand (%)	Silt (%)	Clay(%)
Aljibe												
Understorey site AUa	0–20, n = 3	5.3	0	8.5	0.30	3.9	136	1365	288	67.7	24.3	8.0
Understorey site AUa	20–30, n = 1	5.3	0	3.3	0.11	0.5	85	505	140	66.7	18.8	14.5
Understorey site AUb	0–20, n = 3	5.6	0	6.7	0.30	2.5	260	1595	405	52.6	31.3	16.0
Understorey site AUb,	20–30, n = 2	5.6	0	3.5	0.15	0.6	149	833	315	55.2	26.6	18.3
Open site AO	0–20, n = 3	5.8	0	6.1	0.26	4.5	167	1317	253	67.5	21.0	11.5
Open site AO	20–30, n = 3	5.8	0	3.4	0.12	0.8	155	713	190	64.9	18.4	16.7
Grazalema												
Understorey site GU	0–20 cm*	6.5	0	14	0.819	10	744	5080	328	20.3	33.7	46.0
Open site GO	0–20 cm*	6.9	0	12	0.381	5	580	3600	318	21.6	25.7	52.7
Cazorla												
Understorey site CUa	0–20 cm*	7.2	24	18	0.495	8	333	6740	115	35.4	36.7	27.9
Understorey site CUa	20–30 cm*	7.5	38	14	0.323	5	223	5940	73	34.8	38.6	26.6
Understorey site CUb	0–25 cm*	7.3	3.3	9.9	0.612	11	415	4260	48	48.7	20.0	31.3
Understorey site CUc	0–25 cm*	6.7	1.3	14	0.305	9	200	3700	75	56.8	29.2	14.0

* 'mixed sample' = samples from three spots, mixed in the field.

shade comparison of leaf features with the understorey juveniles. For each available study species, ten open-grown juveniles were sampled, with mean lamina area values in the same range as the collected understorey juveniles. At site AO, four *Ruscus aculeatus* plants were sampled at the forest edge, partially shaded by crowns of *Quercus*.

Processing of plant material

Leaf chlorophyll per unit area (Chl/area) was measured with a SPAD-502 chlorophyll meter (Minolta Co., 2–30 Toyotsu-Cho, Sulla-shi, Osaka 641, Japan). Each plant's value was calculated as the mean of the values for the three top leaves, with each leaf value the mean of three abaxial readings, centrally, to the right of the midvein. For a given species SPAD measurements are linearly related to total chlorophyll (a + b) per unit area (Marquard and Tipton 1987; Singha and Townsend 1989; Fanizza et al. 1991; Manetas et al. 1998). Sun and shade leaves for a given species can be compared directly in their SPAD values. It is unresolved whether the SPAD-chlorophyll relationship differs for leaves of different species (Marquard and Tipton 1987; Gratani 1992; Castelli et al. 1996), so we did not compare SPAD values *across* species. Leaf chlorophyll per unit mass (Chl/mass) was calculated as Chl/area × SLA (in units SPAD × cm^2 g^{-1}).

In the lab, the excavated juveniles were separated into leaf, stem, rhizome and root for subsequent measurements. The plant sections were saturated in beakers of water, inside plastic bags, at least 24 hours, and then saturated mass values were determined, as well as lamina areas (Skye Leaf Area meter, Skye Instruments Ltd., Landrindod Wells, Powys, UK). Dry mass was measured after oven-drying 48 hours at 70 °C. Leaf water mass concentration was calculated as (leaf saturated mass – leaf dry mass) /leaf dry mass × 100%. Fresh leaf and root tissues were preserved in formalin-acetic acid, for three juveniles from each species sampled at site CUa. Stomatal densities and guard cell lengths were determined from nail varnish impressions of the abaxial lamina immediately to the right of the midvein.

Mean nitrogen concentrations (N/mass) were determined for 4–10 pooled-leaf samples for randomly selected juveniles of each species from at least two study sites. Concentrations of total nitrogen were determined from Kjeldhal digests of samples (38 °C for 3 h in concentrated sulphuric acid with mercuric oxide and hydrogen peroxide) with a continuous flow colorimeter (ChemLab Scientific Products, Hornchurch, RM12 4EH). Standard leaf samples provided by Dr E.V.J. Tanner, and previously analysed in several international laboratories, were used as a check.

Data analysis

Several plant variables that were quantified change during ontogeny. Variables were log-transformed and regressed against log plant dry mass, for each species at each site, using least squares:

$$log\,y = a \cdot \log \text{plant dry mass} + b, \qquad (1)$$

where *y* is a variable, and *a* and *b* are parameters of the linearized power law (Niklas 1994). The regressions allowed testing of species and site differences, controlling for differences in plant dry mass.

The regression approach was also used to estimate sun-shade plasticity in SLA. SLA is often inversely related to lamina area during ontogeny (Veneklaas and Poorter 1998), so it is important to compare SLAs for sun and shade leaves of similar area. SLA was regressed against lamina area for the leaves of understorey juveniles ('shade leaves') of each species, using Equation (1). Next, a shade leaf SLA was estimated from the regression, for leaves of the same lamina area as the mean value for the leaves of open-grown juveniles ('sun leaves') in the adjacent clearing. The sun-shade plasticity for SLA was calculated as 'estimated shade SLA' / mean sun SLA. This analysis was not done for *Hedera* and *Smilax*, because sun leaves had much larger mean area than shade leaves.

Regressions were also used to investigate the sun-shade plasticity of leaf chlorophyll and nitrogen concentrations. These features often vary with SLA for both sun and shade leaves of a given species (Stewart et al. 1990; Evans 1998). Leaf chlorophyll and nitrogen concentrations were regressed against SLA, for the sun leaves of each species, and for shade leaves. The sun and shade leaf regressions were then compared. This analysis indicates whether sun-shade differences in Chl/mass and N/mass might arise simply from differences in SLA-linked structural features, without modulation of leaf chemistry.

For each regressed variable, regressions were fitted for each species at each site. Regressions were tested for differences in slopes and intercepts ((Zar 1999); Genstat 5 Release 4.1, Rothamsted Experimental Station, UK). For each variable, first, regressions were fitted for each species at each individual

site, and these site-specific regressions were compared. When for a given species the site-specific regressions for a given forest coincided, the data were pooled, for a forest-specific regression. Next, the forest-specific regressions for that species were compared. When these coincided, the data were pooled, and a single regression was fitted for the species. Finally, the *different* species' regressions were compared. When, for a given species, site- or forest-specific regressions were non-significant, a pooled-site regression was fitted, and, if significant, it was compared with other species' regressions. Regressions were tested at an all-species-wide Type-I error rate of 0.05 for each relationship, using the sequential Bonferroni technique (Rice 1989).

From the regressions, values for given variables were estimated for plants of dry mass 100 mg and 1.00 g. Confidence intervals were derived for 95% confidence for each species (Snedecor and Cochran 1989; Sokal and Rohlf 1995; Zar 1999). The regression parameters are provided to allow estimation for plants in the sampled mass range, and, for chlorophyll and nitrogen concentrations, for leaves of SLA in the sampled range. We note that leaf characteristics change seasonally (Eliáš and Masarovičová 1986; Gratani et al. 1992) and the values provided describe the study species during late winter to early spring.

A separate analysis was performed to determine 'allometric' slopes—i.e. the precise ontogenetic changes in given plant variables with plant dry mass, or SLA. The least-squares regression approach described above is useful for estimation, and for determining differences among sites, forests or species (Ricker 1984; Kohyama and Grubb 1994; Yamada et al. 2000), but it typically underestimates the magnitude of allometric slopes (Ricker 1984). For allometric slopes, standard major axes were used (Rayner 1985). In cases in which a common least-squares slope held for two or more sites or species, a common standard major axis was calculated analogously, as $\Sigma_{i=1}^{k} s(y_i)/\Sigma_{i=1}^{k} s(x_i)$, where k is the number of pooled species, and $s(x_i)$ and $s(y_i)$ are the standard deviations of the x- and y-data of species i (cf. Zar (1999)). We tested whether allometric slopes depart from geometric scaling. Geometric scaling holds when an object maintains a constant shape and bulk density as it increases in size (Niklas 1994). The departure from geometric scaling quantifies a change in shape and/or bulk density.

Studies of the plasticity of leaves of mature trees

We conducted two different studies of the sun-shade plasticity of leaves of mature plants. In the first study, adjacent to site AUa, five trees each of *Arbutus*, *Phillyrea*, *Quercus suber*, and *Viburnum* were used. Five leaves from each tree were collected from the outer exposed canopy along the southern side; five leaves also were collected from the inner, shaded canopy along the northern side. Data for SLA, lamina area, and chlorophyll concentrations were analysed by two-way repeated-measures ANOVA, blocked for given trees, with species and sun-shade as factors (Sokal and Rohlf 1995). For the second study we sampled the dominant tree species at the other sites, and determined the differences between the most-exposed set of forest sun leaves and the most-shaded set of shade leaves. For each species ≥ 3 (usually 10) exposed leaves were collected from each of 5–10 forest-edge trees, and ≥ 3 (usually 10) lower-canopy leaves from each of 5–10 forest-interior trees. Data were analysed by three-way ANOVA, with species, site, and sun-shade as main factors. In both studies differences were tested as orthogonal constrasts (Gilligan 1986). Prior to running ANOVAs, all data were log-transformed, to increase homoscedasticity, and to model for multiplicative effects (Gilligan 1986). Statistics were calculated using Minitab Release 12 and Genstat 5.

To compare with the leaves of the juvenile *Hedera* and *Smilax*, 3–5 shaded leaves were collected from 5–10 many-year-old individuals at sites AUa and GU.

Results

Maximum depth of shade for understorey juveniles

The study forests cast moderate shade on average. The mean light readings for each species ranged from 4.9 to 7.3% daylight in forest A, and 4.2% to 8.5% in forest C (Table 2), and at forest G, the mean ± SE of all 25 readings was 7.2% ± 0.54. However, juveniles persist in shade much deeper than the average level. In forest G, the three lowest values for seedlings ranged from 3.7 to 4.3% daylight. In forests A and C, numerous juveniles of significant size of all six species occurred at ca. 3% daylight or below (Table 2).

Table 2. Replication of the six study species, and the two comparator species, their mass and height ranges, and microsite diffuse site factors (dsf).

Species	Understorey site, number of seedlings sampled	Range in plant dry mass (mg)	Range in height of tallest stem (cm)	Mean dsf ±SE for all sampled seedlings (% daylight)	Dsf range (% daylight) of three seedlings sampled in deepest shade, their ranges in mass (mg), and in height of tallest stem (cm)
Phillyrea	GU, 10	35.6 – 128	4.0 – 9.5	—	—
	CUa, 10	73.1 – 775	5.2 – 16.8	8.5 ± 1.4	5.4 – 6.6; 124 – 218; 7.0 – 7.7
	CUb, 10	102 – 722	5.2 – 15.9	6.4 ± 1.7	2.2 – 3.0; 104 – 280; 5.2 – 9.1
	CUc, 10	73.6 – 1780	8.7 – 23.8	—	—
Viburnum	AUa, 10	13.5 – 1180	3.0 – 23.0	7.3 ± 0.93	3.7 – 6.5; 30.2 – 401; 3.0 – 13.0
	CUa, 10	42.1 – 939	1.3 – 13.0	6.3 ± 0.44	4.6 – 5.3; 59.5 – 939; 2.0 – 5.5
	CUb, 10	81.5 – 343	3.6 – 10.4	6.3 ± 1.8	2.2 – 3.0; 81.5 – 343; 4.3 – 9.6
Rubia	AUa, 10	9.10 – 7560	5.5 – 19.0	4.9 ± 0.67	3.2 – 3.5; 418 – 584; 14.0 – 19.0
	GU, 10	34.9 – 888	4.2 – 17.0	—	—
	CUa, 10	13.2 – 221	4.0 – 12.5	6.1 ± 0.50	3.6 – 5.3; 70.0 – 130; 6.5 – 12.5
Ruscus	AUa, 10	94.0 – 27500	9.5 – 59.0	6.3 ± 0.41	4.1 – 5.6; 262 – 1140; 11.0 – 36.0
	AUb, 4	4180 – 26000	16.0 – 33.0	—	—
	GU, 4	373 – 5290	6.4 – 12.5	—	—
	CUa, 10	115 – 1930	3.7 – 17.5	5.7 ± 1.1	2.8 – 3.6; 153 – 1010; 6.0 – 17.5
Hedera	GU, 10	29.6 – 366	1.8 – 10.5	—	—
	CUa, 10	28.3 – 89.1	2.0 – 5.8	4.4 ± 0.61	2.9 – 3.0; 28.3 – 77.9; 3.2 – 5.3
Smilax	AUb, 6	14.1 – 160	3.2 – 13.0	—	—
	GU, 10	18.8 – 179	4.5 – 10.2	—	—
	CUa, 10	17.6 – 170	4.0 – 15.5	4.2 ± 0.30	3.1 – 3.3; 30.6 – 60.0; 5.1 – 9.8

Comparator species

Species	Understorey site, number of seedlings sampled	Range in plant dry mass (mg)	Range in height of tallest stem (cm)	Mean dsf ±SE for all sampled seedlings (% daylight)	Dsf range
Ceratonia	GU, 7	54.0 – 106	4.0 – 7.5	—	—
Ruscus hypoglossum	AUb, 10	93.9 – 71200	10 – 106	—	—

SE = standard error of the mean.

Table 3. Intercepts *b* and slopes *a* for regressions of log root dry mass (mg) vs log plant dry mass (mg). Italics indicate that the regression for an individual site was significant at $P < 0.05$. Parentheses indicate that when sites within a forest were pooled the regression was significant at $P < 0.05$. For each species juveniles at different sites and in different forests had coincident regressions. Excepting *Rubia*, species' pooled-site regressions had coincident slopes; intercepts *b* allow prediction for each species.

Species	Understorey site(s)	$b \pm SE$
Phillyrea	*GU*, (*CUa*, *CUb*, *CUc*)	−0.359 ± 0.057
Viburnum	*AUa*, (*CUa*, *CUb*)	−0.431 ± 0.058
Rubia	*AUa*, *GU*, *CUa*	−0.410 ± 0.193($a = 0.710 \pm 0.082$; $R^2 = 0.78$***)
Ruscus aculeatus	(*AUa*, *AUb*), *GU*, *CUa*	−0.198 ± 0.063
Hedera	*GU*, *CUa*	−0.491 ± 0.061
Smilax	*AUb*, *GU*, *CUa*	−0.582 ± 0.059
Comparator species		
Ruscus hypoglossum	*AUb*	−0.436 ± 0.078
Ceratonia	*GU*	−0.629 ± 0.068
Common least-squares slope $a \pm SE$		0.961 ± 0.023†
R^2		0.97***†
Common allometric slope $a \pm$ 95% CL		1.02 ± 0.045†

SE = standard error of mean; CL = confidence limits. n.s. = not significant at $P = 0.05$. ***: $P < 0.001$, *F*-ratio test. †Common slope for all species but *Rubia*.

Allocation below ground

For all the species, allocation to root dry mass followed clear ontogenetic trends. For all species, the pooled-site regressions for log root dry mass vs log plant dry mass were significant (R^2 range 0.63–0.98; $P < 0.05$). Except for *Rubia* the species' regressions had coincident slopes, and differed significantly only in intercepts ($P < 0.001$; *F*-ratio test; Table 3). Further, except for *Rubia*, the allometric slope ≈ 1, so root mass fraction remained about the same for each species as plant size increased, as previously reported for herbs and for temperate tree species up to c. 20 g dry mass (Pearsall 1927; Monk 1966). For *Rubia*, allocation to root decreased with increasing plant size (Table 3; allometric slope 0.806 ± 0.169, 95% CL).

The species' root mass fractions estimated for plants of 100 mg and 1.00 g dry mass ranged from very low to very high (Figure 1). The values ranged from 0.10 and 0.05 for *Rubia* to 0.53 and 0.48 for *Ruscus aculeatus*. The outstandingly high root mass fractions of the *Ruscus* spp. reflect relatively massive, fleshy roots. The shade tolerators *Viburnum* and *Phillyrea* had root mass fractions (respectively 0.29–0.33 and 0.34–0.39, 95% CI, at 100 mg plant dry mass) notably high relative to the light-demander *Ceratonia* (0.19–0.20, 95% CI), and relative to light-demanding tropical evergreen rainforest tree juve-niles, though only moderate relative to the juveniles of temperate deciduous trees and shrubs (Figure 1).

In *Rubia* and the *Ruscus* species, allocation below ground also includes considerable allocation to rhizome, in contrasting ways. *Rubia* develops a long, thin (leptocaul) creeping rhizome in the size range sampled, and the *Ruscus* spp. develop short, fat (pachycaul) rhizomes (see Bell (1991), p. 131). *Rubia* increases its allocation to rhizome at it develops, making possible its wide-spreading habit (Figure 1; allometric slope for log below-ground dry mass vs log plant dry mass was 1.30 ± 0.178, 95% CL). Including its rhizome, *Rubia* has a below-ground mass fraction in the same range as the root mass fractions for the other study species, even at 100 mg plant dry mass (Figure 1). For *Rubia*, the smallest sampled juvenile with a distinct rhizome was 70 mg dry mass, and the largest plant sampled had a rhizome 1.4 m in length, linking distinct clumps of shoots (Table 4). By contrast, allocation to rhizome in the *Ruscus* species does not increase ontogenetically, but rather simply keeps pace with allocation to shoot and root, forming the foundation for a cespitose architecture (for the two *Ruscus* spp. the common allometric slope for log below-ground dry mass vs log plant dry mass was 0.992 ± 0.072, 95% CL). Despite this conservative allocation pattern, the *Ruscus* rhizome becomes large. The smallest *Ruscus aculeatus* juvenile with distinct rhizome was 180 mg dry mass. In the largest *Ruscus*
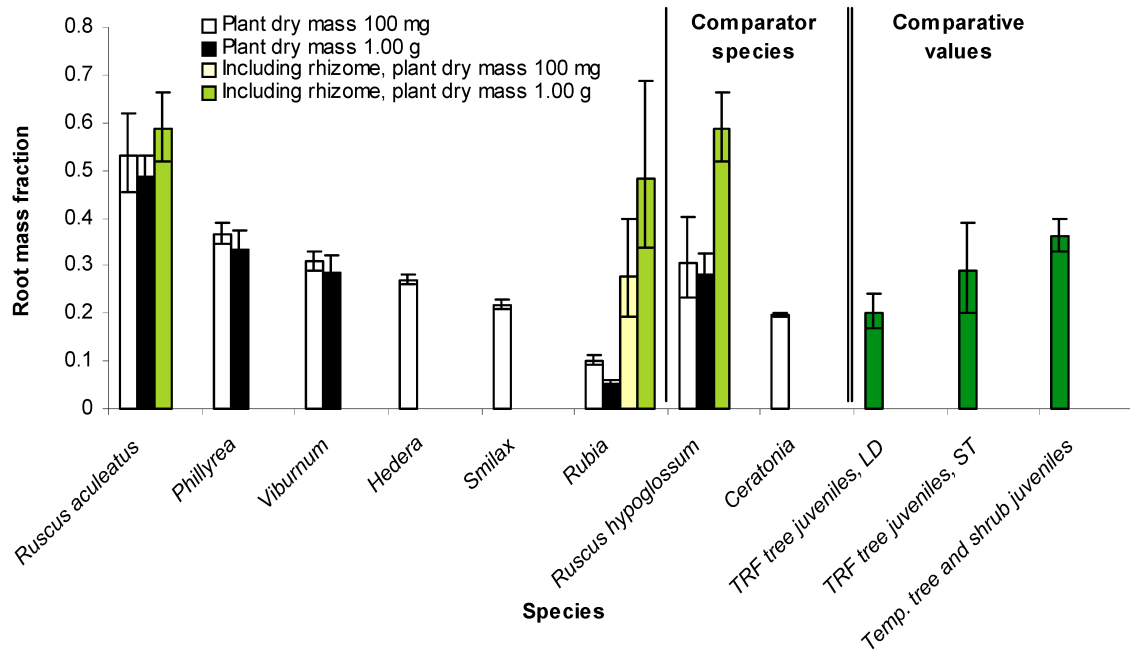
Figure 1. Mean root mass fractions for collected juveniles, and, for *Rubia* and *Ruscus* species, below-ground mass fractions including rhizome. Values estimated for plants of 100 mg and 1.00 g dry mass from regression equations (Table 3, and in text). Error bars = 95% confidence limits (Bonferroni-adjusted for each species). Comparative data: median root mass fractions with interquartile ranges for juveniles experimentally grown in <5% daylight. 'TRF' = tropical rainforest; 'Temp.' = temperate deciduous forest or scrub. Sources: TRF species data for 52 shade-tolerant tree species (ST) and 29 light-demanding tree species (LD; the 'intermediate' species in that study) summarized in Veneklaas and Poorter (1998); Temp. species data for 21 tree and shrub species grown one season, from Loach (1970) and Latham (1992), Canham et al. (1996), Grubb et al. (1996), and Walters and Reich (1996).

juveniles sampled, the rhizome reached 25 cm in total length and c. 3 cm in diameter (Table 4). *Ruscus aculeatus* allocates significantly more to root and less to rhizome than moist site comparator *Ruscus hypoglossum* (Figure 1). The two *Ruscus* species have nearly identical total below-ground allocation (Figure 1).

Smilax juveniles develop rhizomes at sizes larger than those sampled.

Rooting depth

Rooting depth at a given plant dry mass was statistically the same for all the species. The pooled-site regressions for log rooting depth vs log plant dry mass were significant for all species but comparator *Ceratonia* ($R^2 = 0.26$–0.77; $P < 0.05$), and coincided in slope, and intercept ($a = 0.223 \pm 0.015$ SE; $b = 0.538 \pm 0.037$ SE; $R^2 = 0.55$; $P < 0.001$). For these species, mean rooting depth at 100 mg and at 1.00 g plant dry mass was 9.6 cm (95% CI 9.1–10.2) and 16.1 cm (95% CI 15.0–17.2) respectively. *Ceratonia* had a

similar mean rooting depth, 8.9 cm ± 2.5 SE (mean plant dry mass 82.9 mg ± 6.38). If the rooting depth function holds for larger juveniles then the species root as deeply as deciduous *Quercus* species noted for deep roots, c. 25 cm for plants of 4 to 7.4 g dry mass (Pallardy and Rhoads 1993). *Rubia* and the *Ruscus* species were sampled at that size (Table 2) and root that deeply. One difference in rooting depth was found between sites: for *Phillyrea*, juveniles from drier forest G had deeper roots than those of moister forest C; the regression of log rooting depth vs log plant dry mass had a higher intercept ($P = 0.025$; $b_{site\ G} = 0.239 \pm 0.0549$; $b_{site\ C} = 0.111 \pm 0.135$; common slope $a = 0.384 \pm 0.056$; $R^2 = 0.48$; $P < 0.001$).

The species' rooting depth allometry favors rapid soil penetration. The common allometric slope for log rooting depth vs log plant dry mass for all species except *Ceratonia* was 0.301 ± 0.030 (95% CL). This slope differs negligibly from geometric scaling (1/3, the scaling of a length versus a volume), indicating that allocation to depth is maintained even as roots increasingly branch, thicken, and suberize. Despite

Table 4. Seedling root architecture and development for the understory study species. Values with same superscript letters are not significantly different at $P < 0.05$ (planned orthogonal contrasts).

Species	Root architecture and rhizome development	Diameter of fine root, 5 mm from tip (mm) ±SE
Viburnum	One primary root extends vertically with many short, finer branches, some of which develop into prominent horizontal secondaries with lateral branches.	0.38 ± 0.033[a]
Phillyrea	Root system like that of *Viburnum*, but the main roots are often thicker, and horizontal secondaries are commonly unbranched.	0.33 ± 0.068[a]
Rubia	Smallest seedlings have one fine descending root with few branches. From the second growing season the strongly woody rhizome develops and dominates below-ground growth, reaching c. 5 to 6 mm diameter. Fine adventitious roots arise in tufts along the rhizome at intervals of 2 to 5 cm.	0.37 ± 0.12[a]
Ruscus aculeatus	Smallest seedlings have a single, thick root. During early growth a new vertical root is initiated for each new shoot. Growing roots can bifurcate, involving bifurcation of stele (Arber 1925). By the third growing season, the succulent/woody rhizome develops (c. 5 mm diameter), and initiates new roots and shoots. In larger seedlings fleshy, coarsely-branched roots radiate diffusely from the central rhizome system (1.5 to 3 cm diameter). Direction of root growth ranges from vertically downward to nearly horizontal.	0.71 ± 0.034[b]
Hedera	Root system of small seedlings is similar to that of *Viburnum*, but the main roots are often slender. Larger juveniles (beyond the range of study seedlings) root adventitiously from the nodes of the above-ground creeping stem. Still larger plants use adventitious roots for climbing.	0.45 ± 0.030[a]
Smilax	Smallest seedlings have roots similar to those of *Hedera*, but often more branched. Larger juveniles (beyond the range of study seedlings) possess a strongly woody rhizome, up to 2 cm diameter, sometimes spiny, along which arise roots. Many-year-old plants possess a rhizome that can extend below ground for several metres, connecting spiny above-ground vine-like stems.	0.42 ± 0.062[a]

SE = standard error of mean.

this allocation pattern, the roots of all but the largest of the sampled juveniles were in the top 30 cm of soil, which holds c. 80% of the overstorey tree fine roots (Lopez et al. 1998; Canadell et al. 1999).

Root architecture

Not all species have a highly dissected root architecture. While the roots of *Hedera* and *Smilax* juveniles were highly dissected, those of *Phillyrea*, *Viburnum*, and *Rubia* were notably less so, and those of *Ruscus aculeatus* were coarsely branched (Table 4). The fine root diameter 5 mm from the tips was similar for all species (c. 0.35–0.45 mm) except *Ruscus aculeatus*, which had strikingly thicker roots (Table 4).

Specific leaf area

SLA was strongly linked with seed size, across species, and with plant size in each species' ontogeny. Excluding phylloclade-bearing *Ruscus aculeatus*,

SLA was negatively related to seed dry mass (Figure 2), as reported for diverse sets of species of seedlings (Marañón and Grubb 1993; Hunt and Cornelissen 1997). SLA declines ontogenetically with increasing plant dry mass. For all species but comparator *Ceratonia*, the pooled-site regressions for log SLA vs log plant dry mass were significant (R^2 range 0.21–0.71; $P < 0.05$), coincided in slope, and differed in intercepts (intercept difference $P < 0.001$; F-ratio test; Table 5).

The species' SLA values were low to moderate, relative to values for species of moister forests (Fig. 3a). The estimated mean SLA values at 100 mg plant dry mass ranged from 154 cm^2 g^{-1} for *Phillyrea*, to 236 cm^2 g^{-1} for *Smilax* (Fig. 3a). The values for shade-tolerant *Phillyrea* and *Viburnum* at 100 mg plant dry mass were close to that of light-demanding comparator *Ceratonia* (154 ± 14.0 SE). By 1.00 g plant dry mass the study species' SLAs range from from 112 cm^2 g^{-1} for *Phillyrea*, to 172 cm^2 g^{-1} for
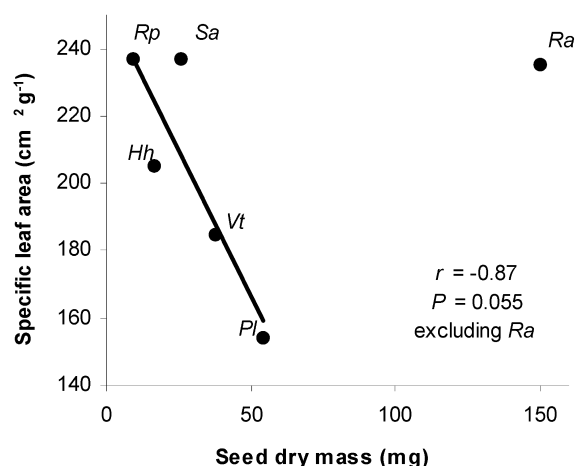
Figure 2. Mean values for specific leaf area, estimated at 100 mg plant dry mass, versus seed dry mass (seed data from Herrera (1987)): *Hh, Hedera helix*; *Pl, Phillyrea latifolia*; *Ra, Ruscus aculeatus*; *Rp, Rubia peregrina*; *Sa, Smilax aspera*; *Vt, Viburnum tinus*.

Rubia (Fig. 3a). Moist-site comparator *Ruscus hypoglossum* had a relatively high initial SLA (Fig. 3a).

The allometry of SLA vs plant dry mass indicates a changing of proportions during leaf ontogeny, which is relevant to light capture. If the leaf proportions and density remained constant with increasing size, SLA would decline with increasing plant mass with an allometric slope of $-1/3$, because SLA represents an area/mass. Leaf density might increase during ontogeny, and this would tend to produce a still steeper decline of SLA. However, the species' allometric slope is *weaker* than $-1/3$. Thus, as plants of the study species increase in size, a less than proportionate increase in leaf thickness retards the decline of SLA.

The species show similar sun-shade plasticity in SLA to the juveniles of many tropical trees and temperate trees and shrubs (Table 6). The species' shade leaf regressions for log SLA vs log lamina area, significant except for *Phillyrea* ($R^2 = 0.33$–0.76; $P < 0.05$), coincided in slope, but differed in intercepts (*F*-ratio test; $P < 0.001$; Table 6). The SLA plasticity quotients were typically moderate, in the range 1.7 to 1.9, but low for *Rubia* at one site (1.2; Table 6). All the species' values are low, however, relative to those of some shade-tolerant herbs of moist sites (Table 6).

Leaf water mass concentration

For all the study species, leaf water mass concentration declined ontogenetically with increasing plant dry mass (Fig. 3b). For the relationship log leaf water mass concentration vs log plant dry mass, the species' pooled-site regressions were significant for all species but *Ceratonia* (R^2 range 0.24–0.60; $P < 0.05$; Table 5), coincided in slope, and differed in intercepts ($P < 0.001$, *F*-ratio test). The species' leaf water mass concentrations at 100 mg and at 1.00 g plant dry mass varied considerably (Fig. 3b). All values were well below the ranges for 'all-leaf-cell succulent' shrubs of semi-desert, and for temperate herbs (Fig. 3b). Excepting *Phillyrea*, the species' leaf water mass concentrations were within the range for mature non-succulent shrubs of semi-desert, and higher than values for temperate deciduous and tropical rainforest trees (Fig. 3b). *Phillyrea* at 1.00 g dry mass had a lower value, in the range for temperate trees (Fig. 3b). *Rubia* and *Ruscus aculeatus* had the highest values, similar to that of comparator species *Ceratonia* (Fig. 3b). Comparator species *Ruscus hypoglossum* had an even higher value (Fig. 3b). In the *Ruscus* species, a special leaf anatomy may facilitate water storage. Under microscopic inspection swollen achlorophyllous cells were observed in the phylloclade mesophyll.

Leaf water mass concentration and SLA were interrelated. The two traits were strongly correlated across species at a given plant dry mass (the intercepts of the species' regressions for log SLA vs log plant dry mass and those for log leaf water mass concentration vs log plant dry mass were correlated; $r = 0.91$; $P = 0.004$ including comparator *Ruscus hypoglossum*; $r = 0.90$; $P = 0.013$ without). Such a relationship is typical for leaves of sets of species at maturity, given a relatively narrow range of leaf succulence (Stewart et al. 1990; von Willert et al. 1990; Roderick et al. (1999a, 1999b)).

Chlorophyll concentrations

For the study species, chlorophyll concentrations were strongly linked with SLA. The pooled-site regressions of log Chl/area vs log SLA, and log Chl/mass vs log SLA were significant for sun and shade leaves of all species except the comparator *Ruscus hypoglossum* (Table 7). As plants increase in size, and leaves of lower SLA are produced, higher Chl/area values occur, probably due to increasing mesophyll layers. Notably, the allometric slopes for log Chl/area

Table 5. Intercepts (*b* values) and slopes (*a*) of regressions for log specific leaf area (SLA; cm^2 g^{-1}) vs log plant dry mass (mg) and log leaf water mass concentration (%) vs log plant dry mass (g). Italics indicate that the regression for an individual site was significant at $P < 0.05$. Parentheses indicate that when sites within a forest were pooled the regression was significant at $P < 0.05$. For each species but *Hedera*, no differences were found among juveniles at different sites and in different forests. For the relationship log SLA vs log plant dry mass, *Hedera* at more xeric site GU had significantly lower mean SLA values than *Hedera* of moister site CUa ($P = 0.032$; $b_{site\ GU} = 2.62 \pm 0.021$ SE; $b_{site\ CUa} = 2.66 \pm 0.065$ SE; common $a = -0.184 \pm 0.038$ SE; $R^2 = 0.69$; $P < 0.001$). Species' pooled-site regressions had coincident slopes; intercepts *b* allow prediction for each species.

Species	Understorey site(s)	(i) *b* ±SE, log SLA vs log plant dry mass	Understorey site(s)	(ii) *b* ±SE, log leaf water mass concentration vs log plant dry mass
Phillyrea	*GU*, (*CUa*, CUb, CUc)	2.47 ± 0.030	GU, (*CUa*, CUb, CUc)	2.36 ± 0.025
Viburnum	*AUa*, *CUa*, CUb	2.55 ± 0.031	*AUa*, *CUa*, CUb	2.60 ± 0.026
Rubia	*AUa*, GU, *CUa*	2.65 ± 0.031	*AUa*, GU, *CUa*	2.78 ± 0.026
Ruscus aculeatus	(*AUa*, AUb), GU, CUa	2.65 ± 0.034	*AUa*, GU, CUa	2.67 ± 0.030
Hedera	*GU*	2.53 ± 0.037	GU, CUa	2.61 ± 0.031
	CUa	2.59 ± 0.033		
Smilax	AUb, GU, CUa	2.65 ± 0.062	AUb, GU, CUa	2.65 ± 0.026
Comparator species				
Ruscus hypoglossum	*AUb*	2.93 ± 0.044	*AUb*	2.92 ± 0.042
Ceratonia	GU	n.s.	GU	n.s.
Common least-squares slope *a* ±SE		−0.139 ± 0.012		−0.113 ± 0.013
R^2		0.66***		0.77***
Common allometric slope *a* ±95% CL		−0.219 ± 0.024		−0.229 ± 0.027

SE = standard error of mean; CL = confidence limits. n.s. = not significant at $P = 0.05$. ***: $P < 0.001$, *F*-ratio test.

vs log SLA were weaker than predicted from geometric scaling (−1, a mass/area vs an area/mass). The slower than expected increase in Chl/area presumably arises at least in part because Chl/area is diluted by additional cell wall thickening and vascularisation. Consistent with these patterns, Chl/mass declines with declining SLA (Table 7).

Strikingly, we found no sun-shade plasticity in chlorophyll concentrations except for that predicted by sun-shade differences in SLA. To evaluate sun-shade plasticity in chlorophyll concentrations, the regressions for sun leaves were compared with the regressions for shade leaves, for log Chl/area vs log SLA and for Chl/mass vs log SLA. The regressions for sun and shade leaves were fully coincident for *Hedera*, *Rubia*, *Ruscus*, *Smilax* and *Viburnum* for one or both of the relationships (Fig. 4a for *Viburnum* and *Smilax*). Differences between sun- and shade-leaf regressions occurred only for *Rubia* leaves; sun leaves from plants at site AO had higher regression intercepts than shade leaves from plants at site AUa for both relationships ($P < 0.001$; F-ratio test), but also higher than those at other sites, including open site

GO (Table 7). The bulk of this evidence indicates that sun-shade differences in leaf chlorophyll concentrations may arise simply from structural differences linked to sun-shade differences in SLA, without any greater chlorophyll synthesis.

Nitrogen concentrations

The species' N/mass values ranged widely. The values ranged from 12.0 mg g^{-1} ± 0.16, 95% CL for *Phillyrea* to 20.4 mg g^{-1} ± 0.24, 95% CL for *Smilax* (Fig. 4b), and in shade leaves were linked with SLA (Figure 5; $r = 0.84$; $P = 0.018$), as previously found for sets of species within and across biomes (Field and Mooney 1986; Stewart et al. 1990; Reich et al. 1999). Understorey *Smilax* falls above the regression.

Sun leaves have higher N/mass than shade leaves, after controlling for SLA. The sun leaves showed a distinct N/mass vs SLA relationship from that of the shade leaves (Fig. 4b). Even excluding outliers *Ruscus aculeatus* and leguminous comparator *Ceratonia*, the sun leaves' non-significant regression for N/mass vs SLA lay above the shade leaves' regression (Fig.
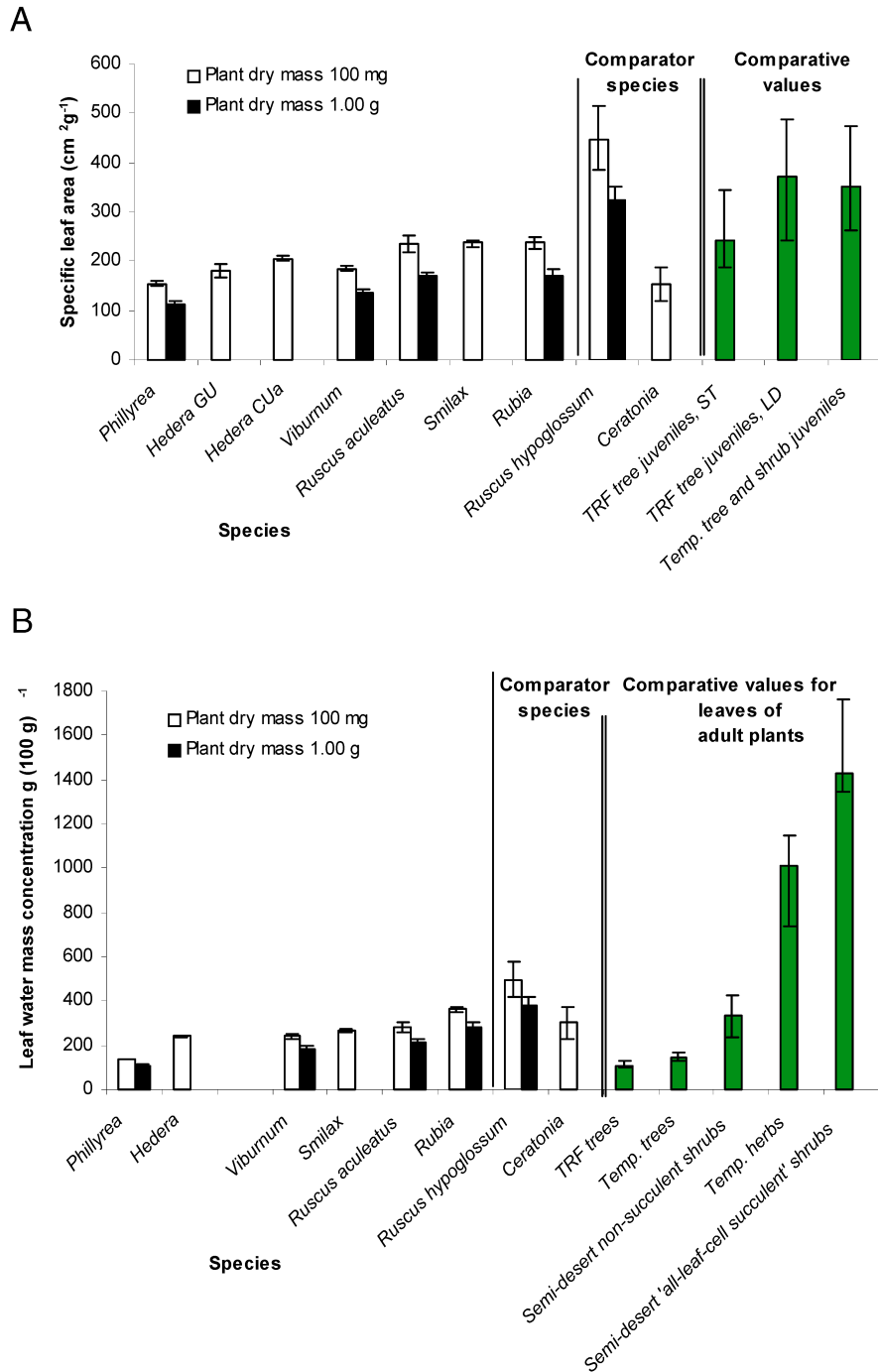
Figure 3. Mean properties for fully expanded leaves estimated from regressions for plants of 100 mg and 1.00 g dry mass (Table 5), except for *Ceratonia* for which simple means are given (mean total plant dry mass 83 mg): (a) specific leaf area, and (b) leaf water mass concentration. Error bars show 95% confidence intervals, Bonferroni-adjusted for each species. Comparative data: median values with interquartile ranges, in (a) for juveniles experimentally grown in <5% daylight (TRF, tropical rainforest; Temp, temperate deciduous forest or scrub); sources: for TRF species, Veneklaas and Poorter (1998) for 69 shade-tolerant tree species (ST), and 51 light-demanding tree species (LD; 'intermediate' species in their study), and for Temp. species as in Figure 1. In (b) for leaves of adult plants sampled in the field; sources: von Willert et al. (1990) for saturated leaves of non-succulent and 'all-leaf-cell succulent' semi-desert shrubs (10 and 6 species respectively) and Ricklefs and Matthew (1982) and Shipley (1995), and Turner et al. (2000) respectively for fresh (not saturated) leaves of 34 Temp. trees, 34 herbaceous angiosperms of well-lit habitats, and 25 species of TRF trees (values reported for heath forest and mixed dipterocarp forest did not differ significantly and are pooled here).

Table 6. Sun-shade plasticity of juvenile specific leaf area (SLA) for four study species. Mean SLA values of open-grown juveniles ('sun leaves') compared with estimated values for understorey juveniles ('shade leaves') of the same mean lamina area (LA) as the sun leaves. Shade leaf values were estimated from log SLA (cm² g⁻¹) vs log LA (cm²) regressions. Italics indicate that the regression for an individual site was significant at $P < 0.05$. Parentheses indicate that when sites were pooled the regression was significant at $P < 0.05$. Except for *Phillyrea*, the pooled-site regressions were significant; common slope $a = -0.382 \pm 0.056$ SE ($R^2 = 0.56$; $P < 0.001$); intercept b is provided for each species. For *Phillyrea* the regression for understorey seedlings was non-significant; the 'estimated' SLA is the mean value. Different superscript letters indicate differences between *Rubia* sun leaves at different sites ($P = 0.05$; *t*-test).

Species	Understorey *vs* open sites compared	Mean SLA (cm² g⁻¹) of sun leaves ± SE	Mean lamina area (cm²) of sun leaves ±SE	$b \pm$ SE, log SLA vs log LA for understorey seedlings	Estimated SLA (cm² g⁻¹) for shade leaves with the same mean lamina area as sun leaves (95% CI)	Plasticity: shade SLA/ sun SLA
Phillyrea	GU *vs* GO	94.7 ± 4.99	1.44 ± 0.185	n.s.	174 (150, 198)	1.8
Viburnum	AU*a vs* AO	98.5 ± 6.3	3.72 ± 0.893	2.49 ± 0.049	184 (168, 202)	1.9
Rubia	(AU*a*, GU) *vs* AO,	134 ± 5.02ᵃ	1.71 ± 0.121ᵃ	2.29 ± 0.022	158 (140, 177)	1.2
	vs GO	90.9 ± 9.50ᵇ	1.31 ± 0.149ᵇ		174 (159, 192)	1.9
Ruscus aculeatus	(AU*a*, AU*b*) *vs* AO*	78.5 ± 2.91	2.62 ± 0.151	2.29 ±0.037	134 (121, 148)	1.7

Comparative values

Tropical rainforest tree seedlings (>120 species) raised in <5% and >25 % daylight†;					median for 'shade-tolerators'	1.6
					median for 'light-demanders'	1.8
Temperate shrub and tree seedlings of 21 species harvested after one season in 2–3% and 17–65% daylight†;					median	1.7
					interquartile range	1.5 to 2
Shade-tolerant temperate herbs of moist sites, *Lamiastrum galeobdolon* and *Oxalis acetosella*, raised in 6% and 100% daylight‡						c. 2.5

CI = confidence interval. Sources of comparative values: * *Ruscus aculeatus* juveniles at site AO were semi-shaded. † Sources as in Fig. 3a; ‡ Packham and Willis (1977, 1982).

Table 7. Intercepts b and slopes a of linear regressions describing seedling characteristics: log chlorophyll per area (Chl/area; SPAD) vs log specific leaf area (SLA; cm^2 g^{-1}), log Chl/mass (SPAD cm^2 g^{-1}) vs log SLA and log N/mass (mg g^{-1}) vs log SLA. For each relationship parameters allow prediction for each species. Italics indicate that the regression for an individual site was significant at $P < 0.05$. Parentheses indicate that when data were pooled for sites within a forest, or for all understorey sites, or for open sites, the regression was significant at $P < 0.05$. When regressions for leaves of understorey and open-grown juveniles were significantly different, they had a coincident slope and differed in intercepts. Species-differences in Chl/area-related regressions were not investigated (see Methods).

Species	Understorey and open site(s)	log Chl/area vs log SLA			Understorey and open site(s)	log Chl/mass vs log SLA			Understorey and open site(s)	Log N/mass vs log SLA		
		Least-squares slope a ± SE, R^2	b ± SE	Allometric slope a ± 95% CL		Least-squares slope a ± SE, R^2	b ± SE	Allometric slope a ± 95% CL		Least-squares slope a ± SE, R^2	b ± SE	Allometric slope a ± 95% CL
Phillyrea	GU, (CUa, CUb, CUc), GO	−0.731 ± 0.080; 0.68***	3.10 ± 0.171	0.88 ± 0.24	GU, (CUa, CUb, CUc), GO	0.269 ± 0.0805; 0.21***	3.10 ± 0.171	0.56 ± 0.24	GU, CUa, CUb, GO	n.s.		
Viburnum	AUa, AO, (CUa, CUb)	−0.347 ± 0.059; 0.75***	2.41 ± 0.125; 2.31 ± 0.020	0.53 ± 0.18	(AUa, CUa, CUb), AO	0.594 ± 0.074; 0.64***	2.59 ± 0.161; 2.59 ± 0.161	0.68 ± 0.22; 0.68 ± 0.22	(AUa, CUa), AO	Common a, Common b for *Viburnum* undestorey and *Rubia*:		0.73 ± 0.19
Rubia	(AUa, GU, CUa), GO, AO	−0.352 ± 0.046; 0.69***	2.40 ± 0.022; 2.52 ± 0.101	0.45 ± 0.14	(AUa, GU, CUa), GO; AO	0.648 ± 0.046; 0.82***	2.40 ± 0.022; 2.52 ± 0.101	0.75 ± 0.14	(AUa, GU, CUa); (GO, AO)	−0.477 ± 0.0319		
Ruscus aculeatus	((AUa, AUb), GU, CUa), AO	−0.600 ± 0.069; 0.73***	3.02 ± 0.151	0.70 ± 0.21	(AUa, AUb), GU, CUa, AO	0.400 ± 0.069; 0.54***	3.02 ± 0.151	0.54 ± 0.21	AUa, GU, CUa; AO	0.717 ± 0.0925; 0.54***	for open sites: −0.233 ± 0.190	
Hedera	GU, CUa, AO, GO	−0.607 ± 0.072; 0.74***	3.01 ± 0.089	0.70 ± 0.22	GU (AO, GO); CUa	0.554 ± 0.073; 0.74***	2.67 ± 0.021; 2.60 ± 0.173	0.58 ± 0.23	GU, CU,	n.s.		
Smilax	GU, CUa, (AO, GO)	−0.656 ± 0.0401; 0.88***	3.06 ± 0.089	0.70 ± 0.12	(GU, CUa), (AO, GO)	0.344 ± 0.040; 0.66***	3.06 ± 0.089	0.42 ± 0.12	GU, CUa; AO	n.s.		
Comparator species												
Ceratonia	GU	−0.592 ± 0.097; 0.86***	3.05 ± 0.210	0.63 ± 0.46	GU	0.408 ± 0.097; 0.74***	3.05 ± 0.211	0.46 ± 0.46	GU	n.s.		

SE =standard error of mean; CL = confidence limits (Bonferroni-adjusted). n.s. = not significant at $P = 0.05$. ***$P < 0.001$, F-ratio test.
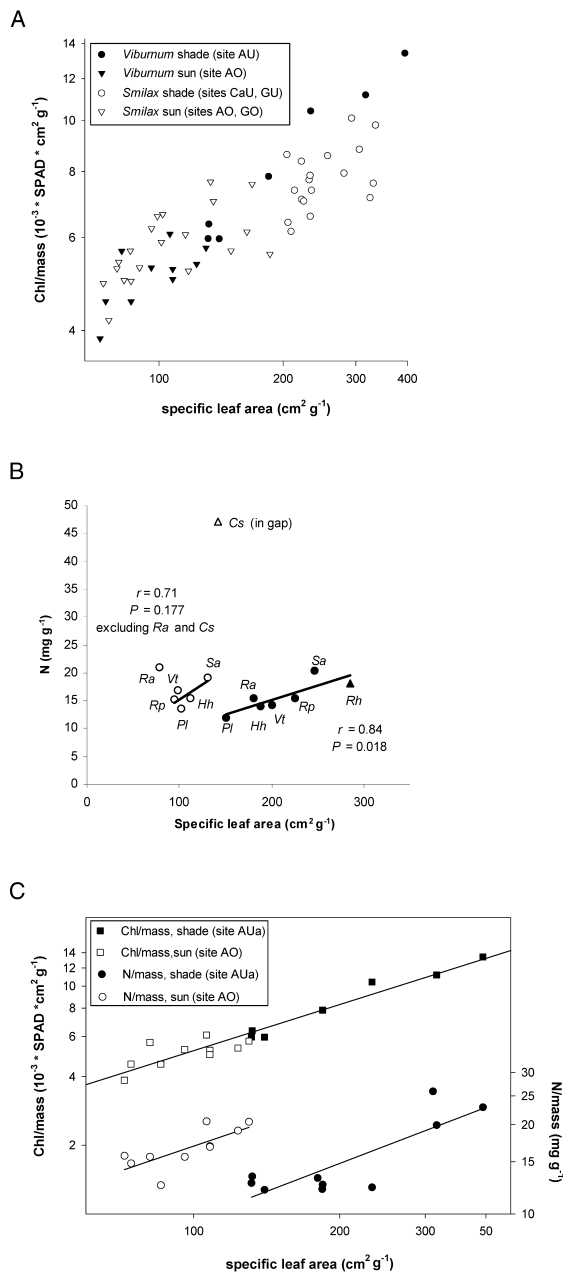
A

B

C

Figure 4. Three plots of leaf chemical properties on specific leaf area (SLA) for sun and shade leaves: (a) double-log plot of chlorophyll per dry mass (Chl/mass) on SLA for two species (for each species the sun and shade regressions are coincident), (b) N/mass versus SLA, for subsampled juveniles; circles for study species, triangles for comparators; filled symbols for juveniles in understorey sites; open symbols for juveniles at open sites (*Ruscus aculeatus* juveniles were semi-shaded); symbols for species as in Figure 2, plus *Cs*, *Ceratonia siliqua* and *Rh*, *Ruscus hypoglossum*, and (c) double-log plots of the concentrations of Chl/mass and N/mass versus SLA for *Viburnum*.
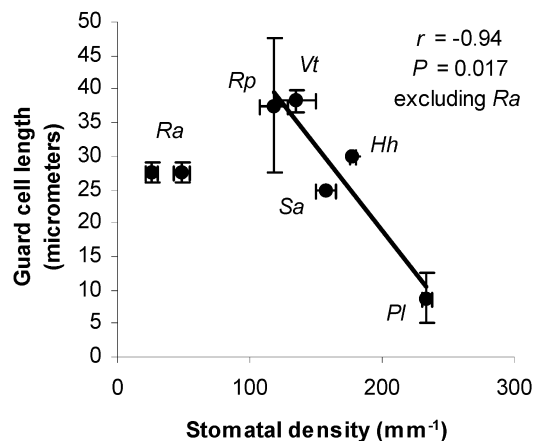

Figure 5. Guard cell length versus stomatal density for the study species; means with standard errors (symbols for species as in Figure 2). For *Ruscus aculeatus* one point represents the lower surface of the phylloclade, as for the leaves of the other species; the other point represents the upper and lower surfaces together.

4b). The data for *Rubia* and *Viburnum* could be analysed in more detail. For both species the regression of log N/mass vs log SLA was significant for both sun and shade leaves ($P < 0.001$; Table 7). For each species, the regressions for sun and shade leaves coincided in slope ($P < 0.001$; Table 7), but the regression for sun leaves had a higher intercept ($P < 0.001$ for each species; Table 7), indicating higher N/mass relative to SLA Fig. 4c for *Viburnum*). Since for each species the regressions for log Chl/mass vs log SLA for sun and shade leaves coincided (Fig. 4, a and c), but the regression for log N/mass vs log SLA for sun leaves had a higher intercept than that for shade leaves (Fig. 4c), the sun leaves had a higher nitrogen:chlorophyll ratio.

Ruscus aculeatus apparently increases its sun leaf N more than the other study species. This finding is consistent with that in a previous study, in which the leaf N concentration in semi-shaded adult *Ruscus aculeatus* was a notably high 34 mg g^{-1} (de Lillis and Fontanella 1992).

Stomatal density

The study species ranged widely in stomatal density. *Phillyrea* had a relatively high value, 234 ± 3.8 stomata mm^{-2}, while *Viburnum*, *Rubia*, *Hedera*, and *Smilax* had lower values, 118–178 stomata mm^{-2} (Figure 5). The stomatal density for *Ruscus aculeatus*, 25.8 ± 4.6, was outstandingly low, even when doubled to account for both surfaces; the phylloclades

have stomata on each surface, unlike the leaves of the other study species. Across species, when *Ruscus aculeatus* was excluded, guard cell length was negatively correlated with stomatal density ($r = -0.94$; $P = 0.017$; Figure 5).

Leaf form and plasticity for older plants

SLA declined from juveniles to mature plants. The SLA values for mature *Viburnum* and *Phillyrea* were substantially lower than those for the sun and shade leaves of juveniles (Tables 6, 8a, 8b). The same trend was found for *Hedera* and *Smilax*; mean values for many-year-old plants were respectively 146 ± 7.72 SE and 106 ± 4.19 SE (cf. juvenile values in Figure 3a.

Mature plants showed significant sun-shade plasticity in SLA, lamina area and Chl/mass (Tables 8a, 8b). The plasticities of SLA and lamina area were about the same as in many previously studied temperate and tropical trees and shrubs, 1.2 to 1.5 × (Table 8a). Species that are shade-tolerant during establishment, such as *Phillyrea* and *Viburnum*, did not have consistently higher plasticity in SLA than species that are light-demanding during establishment, such as *Arbutus*, *Ceratonia*, *Pistacia*, and *Quercus rotundifolia* (Tables 8a, 8b). As in the case of juvenile leaves (see above), the sun-shade plasticity in mature plant leaf Chl/mass was apparently linked to the plasticity in SLA (the values for PQ$_{SLA}$ and PQ$_{Chl/mass}$ in Tables 8a, 8b, were typically about the same).

Discussion

The six study species persist, despite repeated drought, in irradiance ca. 3% of full sunlight or less. Such deep shade presumably excludes species of open sites, though it is only moderately deep compared with the shade that occurs in the understories of moister temperate deciduous forests (0.3% to 4% daylight; reviewed in Coomes and Grubb (2000)). Notably, the shade reported in this study is evergreen shade, and still deeper shade may occur in the growing season (April–May), when the semi-deciduous *Quercus* species leaf out completely; during this study they had partially expanded foliage.

The six study species tolerate deep shade plus drought, in forests varying in soil types. We propose that tolerance occurs as a result of reduced resource demand, combined with specialized resource capture.

Mechanisms for reduced resource demand

The species converge in features that reduce the demand for water or, in general, for growth resources (Table 9). All species have moderate to high below-ground mass fractions (0.22–0.59), sometimes above the range of shade-tolerant tropical rainforest juveniles (Figure 1). A high below-ground allocation reduces aerial evaporative surface relative to plant mass, and though it entails allocation away from irradiance capture, it is compatible with shade tolerance. Moreover, it reduces demand for resources (including irradiance) by protecting much of the plant from mechanical damage. Shade-tolerant juvenile trees of tropical rainforests allocate more belowground than do light-demanders (Veneklaas and Poorter 1998); the shade-tolerators presumably benefit from a reduced demand, as well as from increased capture of soil resources due to high root allocation (see below). The morphology of below-ground parts can further reduce resource demand; the relatively thick roots of *Viburnum* and *Phillyrea* are likely to have relatively long lifespans, in the way argued by Eissenstat (1992). The rhizome of *Rubia* and the fleshy roots and rhizome of *Ruscus* apparently store water and/or carbon (Antonielli et al. 1989). Finally, underground parts can support a protective plant architecture. For understorey *Rubia*, the wide-spreading "guerilla form" (*sensu* Lovett Doust (1981) and Navas and Garnier (1990)) might reduce the risk of destruction by separating shoots in space. *Ruscus aculeatus* has a compact cespitose "tank" form, with hard, spiny phylloclades.

The species' values for specific leaf area (leaf area/ leaf dry mass; SLA) imply a reduced demand for water, and simultaneously for other resources. Low SLA values imply water retentiveness (i.e., low surface area: mass). The species' decrease of SLA with increasing plant size suggests increasing water-retentiveness. The species' SLAs range from low to moderate, relative to species of moister forest (Fig. 3a) and are probably associated with relatively long leaf lifespans ($\geq$ 2 yrs; unpub. obs.), as discussed by Reich et al. (1991, 1999) and Walters and Reich (1999). Similarly, shade-tolerant tree juveniles in tropical rainforest might achieve a benefically reduced demand for resources, with their low SLAs relative to light-demanders.

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Table 8a. Characteristics of sun and shade leaves of trees at Aljibe: lamina area (LA), specific leaf area (SLA), chlorophyll per area (Chl/area), and chlorophyll per mass (Chl/mass). PQ = plasticity quotient, shade value/sun value. ANOVAR = repeated-measures ANOVA. Species-differences (for LA and SLA) and sun-shade differences tested as orthogonal contrasts with F-ratio tests. Same lowercase letters signify no significant difference between species means at $P = 0.05$.

	LA_{su} cm²	LA_{sh} cm²	species differences	PQ_{LA}	SLA_{su} cm² g⁻¹	SLA_{sh} cm² g⁻¹	species differences	PQ_{SLA}	$Chl/area_{su}$	$Chl/area_{sh}$	$PQ_{Chl/area}$	$Chl/mass_{su}$	$Chl/mass_{sh}$	$PQ_{Chl/mass}$
Arbutus	10.3 ± 1.33	14.5 ± 1.92	ab	1.4[**]	79.0 ± 8.23	108 ± 14.1	a	1.4[*]	49.5 ± 2.7	46.9 ± 1.8	0.95	3.83 ±0.18	5.07 ± 0.70	1.3[*]
Phillyrea	7.18 ± 0.687	8.57 ± 1.06	a	1.2	77.8 ± 4.64	96.1 ± 6.34	a	1.2	47.2 ± 3.6	43.8 ± 1.7	0.93	3.63 ± 0.22	4.17 ± 0.16	1.1
Quercus rotundifolia	11.5 ± 1.29	16.6 ± 1.49	b	1.4[**]	66.1 ± 5.39	90.8 ± 4.79	a	1.4[*]	39.4 ± 1.2	38.4 ± 0.96	0.97	2.60 ± 0.22	3.47 ± 0.11	1.3[*]
Viburnum	24.2 ± 2.60	34.0 ± 1.72	a	1.4[**]	68.9 ± 5.78	117 ± 12.1	a	1.7[***]	46.8 ± 1.8	46.3 ± 0.65	0.99	3.22 ± 0.27	5.41 ± 0.58	1.7[***]
ANOVAR:														
species	[***]				n.s.				[**]			[**]		
sun-shade	[***]				[***]				n.s.			[***]		
Comparative values														
Temperate deciduous trees and shrubs[†]				1.3				1.2						
Tropical rainforest trees and shrubs				1.5[‡]				1.4[‡]						2.0[§]

Significance levels: [*]: $0.05 \geqslant P \geqslant 0.01$; [**]: $0.01 > P \geqslant 0.001$; [***]: $P < 0.001$. n.s. = not signicant at $P = 0.05$. Mean values given ±SE. Comparative values: [†]Values for Estonian species (Niinemets and Kull 1994); for PQ_{LA} the mean value is provided for the 22 out of 67 species sampled that had shade leaves larger than sun leaves; for PQ_{SLA} the mean value is given for the 55 species sampled that had shade leaves with higher SLA than sun leaves; [‡]Mean values for 61 Mexican species; Bongers and Popma (1988). [§]Mean value for two Costa Rican species (Poorter et al. 1995). The "species * sun-shade" interaction in the ANOVAR was not significant for any variable.

Table 8b. Characteristics of sun and shade leaves of edge and interior trees at four study sites: lamina area (LA), specific leaf area (SLA), chlorophyll per area (Chl/area), and chlorophyll per mass (Chl/mass). PQ = plasticity quotient, shade value/sun value. Species differences and sun-shade differences tested as orthogonal contrasts by *F*-ratio. Same lowercase letters signify no significant difference between species means at *P* = 0.05.

	site	LA_{su} cm²	LA_{sh} cm²	species differences	PQ_{LA}	SLA_{su} cm² g⁻¹	SLA_{sh} cm² g⁻¹	species differences	PQ_{SLA}	$Chl/area_{su}$	$Chl/area_{sh}$	$PQ_{Chl/area}$	$Chl/mass_{su}$	$Chl/mass_{sh}$	$PQ_{Chl/mass}$
Ceratonia	GU	10.5 ± 1.85	11.5 ± 0.560		1.1	64.0 ± 3.16	100 ± 11.0		1.6^{**}	47.4 ± 2.06	48.3 ± 2.56	1.0	3.03 ± 0.162	4.77 ± 0.385	1.6^{***}
Phillyrea	GU	3.16 ± 0.882	8.34 ± 2.10	a	2.6^{***}	112 ± 13.7	109 ± 19.6	a	0.9	43.1 ± 2.84	47.5 ± 1.59	1.1	4.70 ± 0.439	5.21 ± 0.985	2.6
	CUa	4.04 ± 0.329	10.4 ± 0.767		2.6^{***}	86.2 ± 4.81	121 ± 5.40		1.4^{**}	40.0 ± 1.72	39.3 ± 2.59	0.99	3.39 ± 0.098	4.8 ± 0.286	1.4^{**}
	CUb	5.25 ± 0.529	9.08 ± 3.29		1.7^{x}	96.3 ± 3.31	120 ± 7.77		1.3^{*}	41.6 ± 1.96	48.0 ± 1.96	1.2^{**}	3.99 ± 0.210	5.76 ± 0.369	1.4^{***}
	CUc	3.89 ± 0.705	6.61 ± 0.829		1.7^{x}	82.2 ± 2.17	107 ± 11.1		1.3^{*}	48.2 ± 2.47	41.0 ± 1.88	0.85^{**}	3.95 ± 0.231	4.36 ± 0.455	1.1
Pistacia	GU	2.10 ± 0.368	2.59 ± 0.121	ab	1.2	59.0 ± 4.98	129 ± 11.9	ab	2.2^{***}	47.0 ± 3.03	48.9 ± 1.25	1.0	2.73 ± 0.150	6.33 ± 0.502	2.3^{***}
	GU	3.90 ± 0.515	3.93 ± 0.452		1.0	57.9 ± 1.78	68.1 ± 4.09		1.2	45.7 ± 1.25	49.5 ± 1.94	1.1	2.65 ± 0.111	3.35 ± 0.175	1.3^{x}
Quercus rotundifolia	CUa	3.33 ± 0.658	8.11 ± 0.841	a	2.4^{***}	58.8 ± 3.53	80.0 ± 3.32	a	1.4^{*}	41.5 ± 0.910	38.4 ± 1.46	0.93	2.45 ± 0.181	3.07 ± 0.214	1.2^{x}
	CUb	5.70 ± 1.28	7.78 ± 0.851		1.4	71.3 ± 3.18	71.7 ± 5.49		1.0	42.8 ± 0.341	43.2 ± 2.16	1.2	3.05 ± 0.137	3.06 ± 0.131	1.0
	CUc	4.32 ± 0.582	9.93 ± 0.705		2.3^{**}	60.2 ± 1.61	90.4 ± 9.57		1.5^{**}	43.1 ± 0.541	45.7 ± 0.708	1.1	2.60 ± 0.078	4.10 ± 0.381	1.6^{***}
Viburnum	CUa	17.1 ± 2.50	26.5 ± 2.13	b	1.6^{x}	106 ± 5.26	140 ± 6.54	b	1.3^{*}	41.5 ± 0.910	36.5 ± 1.06	0.88^{x}	4.38 ± 0.249	5.07 ± 0.085	1.2
	CUb	11.2 ± 1.24	12.4 ± 1.74		1.1	92.0 ± 4.95	116 ± 5.05		1.3^{*}	40.6 ± 1.58	36.5 ± 1.89	0.90^{x}	3.72 ± 0.214	4.29 ± 0.400	1.2
ANOVA:															
species				***		***				**			***		
site				*		n.s.				**			n.s.		
sun-shade				***		***				n.s.			***		
species*site				*		n.s.				n.s.			x		
species*sun-shade				n.s.		**				n.s.			**		

Significance levels: ^{x}: $0.1 \geq P > 0.05$; *: $0.05 \geq P > 0.01$; **: $0.01 \geq P > 0.001$; ***: $P < 0.001$. n.s. = not significant. n.s. = not signicant at $P = 0.01$. Higher order ANOVA interactions were not significant. Mean values given ± SE.

Table 9. Tolerance mechanisms of the study species.

Type of mechanism	For irradiance (I), water (W), or both (I, W)	Phillyrea	Viburnum	Rubia	Ruscus aculeatus	Hedera	Smilax
Reducing resource demand							
● high below-ground mass fraction	I,W	++	++	+++	+++	++	++
● low specific leaf area	I,W	+	+	++	++	+	++
● protected, long-lived parts[*]	I, W	+++	+++	+++	+++	+++	+++
● high water content (?storage)	W	++	+++	+++	+++	+++	+++
● low stomatal density	W	+	++	++	+	++	++
Specialized resource capture							
● higher specific leaf area in shade	I	++	++	++	++	?++	?++
● higher Chl/mass in shade	I	++	++	++	++	++	++
● high root mass fraction	W	++	++	+	+++	++	++
● deep roots	W	+++	+++	+++	+++	+++	+++
● fine, dissected roots[†]	W	++	++	++	+	+++	+++

+++, ++, and + respectively indicate high, moderate or low values relative to species of moister forest. Chl/mass = leaf chlorophyll per dry mass. Summarized from data in the text, and in Figures 1, 3a and 3b, and 5, and Tables 4, 6, and 7. [*]unpubl. obs. [†]For this trait comparative data were scant, and species are ranked relative to each other.

Water storage ability also reduces demand for soil water during drought. The leaf water mass concentrations of the study species may confer considerable drought tolerance in the shade. The leaf water mass concentrations are mostly in the range of semi-desert non-succulent shrubs, higher than those of temperate deciduous and tropical rainforest trees. Water storage also depends on the leaf water-retentiveness, which relates to SLA (see above), cuticle properties (Schreiber and Riederer 1996), and microclimate (Kerstiens 1996). A rough suggestion of the usefulness of stored water can be derived from the cuticular transpiration for adult *Hedera* leaves under high irradiance, c. 3 mg water per hour, per g fresh weight (Pisek and Berger 1938). If double this rate is extended to *Hedera* juvenile leaves (perhaps accounting for their higher SLA), the leaves would fall to 60% relative water content in two days under high irradiance. Given deep shade, and day-night cycles, the stored water might allow survival for weeks.

Other leaf traits reflect a reduced resource demand. The species have moderate or low stomatal densities, typical of shaded habitats (Salisbury 1927; Grubb et al. 1975; Peat and Fitter 1994), and reflecting a low water demand (Grubb 1984). While the inverse relationship between guard cell length and stomatal size (excepting *Ruscus aculeatus*) may to some degree balance water loss, *Phillyrea* and *Ruscus aculeatus*

have especially small guard cells, relative to stomatal density, compared with the other species, and with the general trend for 60 woody species of Japanese rainforest (Figure 1 in Grubb et al. (1975)). Finally, the species' N/mass ranged low to moderate, relative to the shade leaves of woody species in tropical lowland rainforest in Mexico (mean 18 mg g^{-1}; Bongers and Popma (1988)) and Singapore (range 11–26, mean 17 mg g^{-1}; Grubb et al. (1994)). Low to moderate N/mass is often linked with slow maximum photosynthesis in resource-poor habitats (Small 1972; Field and Mooney 1986; Aerts and Chapin 2000).

Although many of the species converge in features that reduce resource demand, there are strong divergences (Table 9). For example, *Phillyrea* has only 40–50% the leaf water mass concentration of *Rubia* or *Ruscus aculeatus*; *Phillyrea* is unlikely to depend as much on stored leaf water. Instead, *Phillyrea* probably reduces water loss, with its low SLA and small stomata. *Ruscus aculeatus* shows the most extreme development of mechanisms for reduced resource demand (Table 9).

Mechanisms for specialised resource capture

Several of the study species' features may confer tolerance through specialised resource capture (Table 9). The allometry of SLA vs plant size may contribute to

irradiance capture. Since SLA indicates the area for irradiance interception per unit mass, the relatively high initial SLA of seedlings is likely to benefit irradiance capture (Sack and Grubb 2001). Further, as plants increase in size, the leaf proportions change; the decline of SLA, and thus of irradiance capture per leaf mass, is slowed, relative to geometric scaling.

Moderate sun-shade plasticity in SLA may also contribute to the species' irradiance capture in shade (Givnish 1988). The production of leaves of higher SLA in shade apparently not only increases the photosynthetic surface per unit mass, but simultaneously increases the Chl/mass, and the chlorophyll:nitrogen ratio, all of which further improve irradiance capture efficiency (see Evans (1998)). Our results provide the first explicit indication that the commonly described increase in the chlorophyll:nitrogen ratio in shade leaves (e.g. Björkman and Holmgren (1963) and Seemann et al. (1987), Evans (1989), Kull and Niinemets (1998), Evans and Poorter (2001)) does not necessarily involve biochemical modulation of Chl/mass. Instead, it may result from a single allometric relationship of Chl/mass vs SLA across sun and shade leaves of a species, and an increased incorporation of N/mass in sun leaves, independently of SLA (Figs 4a, b and c). The data reported in other studies are consistent with this pattern (e.g. Stewart et al. (1990) and Evans (1998)). For *Phillyrea*, *Viburnum*, *Rubia* and *Ruscus*, the shade-driven increases in SLA (Table 6) correspond, given the equations in Table 7, to Chl/mass increases of 1.2–1.5 ×. Such increases in Chl/mass are low to moderate, when compared with values estimated from the plasticity of leaf chlorophyll *per fresh mass* provided for a range of British forest species (Murchie and Horton 1997). For these species, Chl/mass may increase 1.8 to 2.4 × in shade (given increases in fresh mass: dry mass in shade-grown plants of up to c. 1.5 to 2 times; Evans (1972)).

The species converge in having traits associated with specialised water capture. The species have moderate to high root mass fractions (excepting *Rubia*), and deep roots (comparable with deciduous *Quercus* juveniles) that scale geometrically with plant mass. *Ruscus aculeatus* allocates more to root than moist site congener *Ruscus hypoglossum*. *Hedera* and *Smilax* have dissected roots, probably efficient for water capture (Fitter and Stickland 1991). However, despite these features, a reduced water demand is critical, given the absolute shallowness of juvenile roots.

The species show divergence in several traits relevant to resource capture (Table 9). For instance, *Ru-bia* has a relatively high SLA, and its wide-spreading habit probably benefits resource acquisition; for larger juveniles, the shoots in higher irradiance may provide sugar to more deeply-shaded shoots, which may supply more water (Stuefer 1998). The relatively higher shoot allocation in *Hedera* and *Smilax* and the high N/mass of *Smilax* are consistent with exploitation of high irradiance patches; these species' dissected roots may benefit water capture. *Ruscus* also has a noteworthy mechanism for irradiance capture: all parts of the aerial stems are strikingly chlorophyllous.

Mature trees might also facilitate juvenile resource capture. A high sun-shade plasticity in mature plant SLA could help cast shade that excludes less shade-tolerant species (Canham et al. 1994; Grubb 1998). The study species did *not* show higher SLA plasticity at maturity than light demanders, perhaps due to additional constraints in a system prone to severe drought (Grier and Running 1977; Specht and Specht 1989; Sala et al. 1994; Coomes and Grubb 2000).

In sum, the studied species of juveniles differ strongly in functional morphology and growth form. However, these species converge in several mechanisms. Some of the mechanisms possessed by the study species also occur, to varying extents, among particular species of tropical rainforests and of temperate deciduous forests. This fact suggests that tolerance of shade plus drought, achieved in part through functional morphology, may contribute importantly to the ecology of many species in widely-varying forest systems throughout the world. This tolerance may thus play an increasingly important role, as droughts become stronger and more common worldwide.

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