

## Responses of temperate woody seedlings to shade and drought: do trade-offs limit potential niche differentiation?

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Diversity in seedling responses to combined shade and drought can drive species niche differences, and thus natural forest and scrub establishment dynamics and diversity. However, inherent trade-offs between shade tolerance and drought tolerance, as hypothesized in the literature, would constrain potential niche differentiation. For thirteen species of European trees and shrubs the impacts were determined of moderate and extreme drought on the growth and survival of first-year seedlings in a given soil volume, in irradiances in the range typical for temperate forest and scrub understories (3% daylight) and large gaps (30% daylight). Pots were watered differentially each second day to equalize soil water content across species and irradiances. Comparisons within and across species supported independent tolerances of shade and drought rather than trade-offs. For all species, drought reduced relative growth rate in dry mass by the same proportion in 3% daylight and in 30% daylight. Consequently, drought generally reduced final dry mass significantly more strongly in 30% daylight than in 3% daylight. Extreme drought led to earlier mortality in 30% daylight than in 3% daylight for nine of the eleven species tested, to earlier mortality in 3% daylight for one species, and to equal mortality rate in both irradiances for one species. For each species, growth-based shade tolerance was quantified as the ratio of absolute growth in low irradiance to that in high irradiance, and growth-based drought tolerance as the ratio of absolute growth in low water supply to that in high water supply. Across species, growth-based shade tolerance varied  $\approx$  9-fold, and growth-based drought tolerance  $\approx$  2-fold; species' tolerances correlated respectively with indices of field establishment in shade and drought. Growth-based drought tolerance correlated with survival time in extreme drought. Experimentally quantified shade and drought tolerances varied independently for the 13 species tested, indicating the potential for extensive species niche differentiation in combinations of irradiance and water supply.

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In forest and scrub, where irradiance and water supply are patchy, differences in the responses of woody seedlings to shade and drought drive establishment patterns, especially in combination with variation in responses to nutrient supply and biotic factors (Streng et al. 1989, Burslem 1996, Grubb et al. 1996, Kollmann and Grubb 1999, Caspersen and Kobe 2001). Understanding seedling responses becomes critical as droughts occur with increasing frequency and severity in forests

worldwide (Fearnside 1995, Karl et al. 1995, Peñuelas et al. 1998, Siwecki and Ufnalski 1998).

One fundamental question is whether shade and drought have interactive effects on plant performance. An intraspecific trade-off hypothesized several times in the literature holds that drying soil will have a stronger impact on plants of a given species that are growing in deeper shade (Smith and Huston 1989, Kubiske et al. 1996). One hypothesized mechanism is via biomass

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allocation: plants of a given species in deeper shade have greater allocation to shoot, and especially to leaf area, rather than to root, increasing their light capture at the expense of water capture (Smith and Huston 1989). However, another hypothesis predicts the opposite pattern – a weaker impact of drought in deeper shade, because shaded plants are protected from factors which can aggravate the impact of drought, such as high leaf and air temperatures, high vapour pressure deficit, and oxidative stresses (Holmgren 2000). A third, null, hypothesis predicts that dry soil should have a proportional impact across irradiances, i.e. that the effects of shade and drought are orthogonal (Sack and Grubb 2002). There has also been separately hypothesized an interspecific trade-off between shade and drought tolerances, such that species with greater shade tolerance are more vulnerable to drought than more light-demanding species (Smith and Huston 1989). Biomass allocation patterns have been proposed to underlie this trade-off too; shade tolerant species might be selected for a strong allocation to shoot, and especially leaf area, rather than to root (Smith and Huston 1989). An alternative hypothesis is that shade and drought tolerances would vary independently across forest and scrub species (Coomes and Grubb 2000, Sack and Grubb 2002).

Both intra- and inter-specific trade-offs would have important implications for species dynamics and diversity. If an intraspecific trade-off exists, then droughts will impact especially strongly in forest understories, because shaded plants are inherently more susceptible to dry soil. If an interspecific trade-off exists, then potential niche differentiation would be constrained to a limited set of combinations of irradiance and water supply (Smith and Huston 1989). A species that adapted to effectively establish in deep shade could do so only in moist soil; no species could tolerate combined strong shade and drought. On the other hand, if shade and drought tolerances are independent, species could in principle compete optimally at any combination of irradiance and water supply. In this case there may be extensive niche differentiation, especially as combinations fluctuate in space and time (Grubb 1977, Latham 1992, Wright 2002).

In the field soil dryness can vary across irradiances in different ways in different systems (reviewed by Sack and Grubb 2002). Controlled studies are thus needed for analysing seedling responses to irradiance  $\times$  water supply combinations. In a recent study of four shade-tolerant species, drought reduced relative growth rates proportionally in deep shade and in high irradiance, and species' growth-based shade and drought tolerances varied independently (Sack and Grubb 2002). The findings of previous work, from early (Kozłowski 1949, Keever 1950), to recent (Canham et al. 1996), are consistent, but many did not equalize drought intensity across irradiances, and no controlled study considered

impacts on growth for more than four species, or tested for differences in survival of extreme drought across irradiances. In this study two experiments were performed on thirteen temperate woody species grown one season in a given soil volume, in irradiance levels typical for temperate forest understorey and large gaps. The first experiment tested the impact of moderate drought on growth; the second experiment tested the impact of extreme drought on survival. Impacts were also tested for biomass allocation traits potentially linked with tolerance.

## Methods

### Species, site, seedling culture and irradiance treatments

Species were selected among tree and shrub species that overlap in geographic range in northern, central and mediterranean Europe (Table 1). The species were diverse in growth form, architecture, leaf phenology, and the irradiance and soil moisture regimes of typical establishment. Three species were included that have been observed to tolerate combined deep shade and drought during establishment (Table 1). Published information was gathered for shade and drought establishment indices, seed dry mass and embryo-cum-endosperm dry mass (Table 1).

In the spring of 1999 a poly-tunnel of 80 m<sup>2</sup> ground area (Fordingbridge Ltd, West Sussex, UK) was set up at the University of Cambridge Botanic Garden. To produce two irradiance regimes, half the tunnel was covered with one layer of neutral shade mesh, and the other half with three layers. The whole tunnel was covered with waterproof polythene, except 2.5 m at both ends, allowing ventilation. The diffuse photosynthetically active radiation at seedling level was measured on a cloudy day at 8 points in each shade tunnel half, and outside in an open area, using quantum sensors (Skye SKP 200/215, Skye Instruments Ltd, Llandindod Wells, Powys, UK). The halves allowed  $2.9 \pm 0.1\%$  and  $29.9 \pm 1.5\%$  full daylight. The impacts of neutral shade might differ to a degree from those of natural shade, with low red: far-red ratio; however, many species of woody seedlings reportedly respond only marginally in growth and biomass allocation to red: far-red ratio (Kitajima 1994, Lei and Lechowicz 1998, Sack and Grubb 2002).

Experimental soil was a 1:1:1 (by volume) mixture of sifted clay loam garden soil: peat (Levington Horticulture Ltd, Ipswich, UK): sharp sand (Pioneer Ltd., Warwickshire, UK), with a pH of 6.0–6.5. *Hedera* fruit was collected from >3 large plants outside Cambridge. Seeds were extracted by hand, and along with seeds of *Crataegus*, *Hedera*, *Prunus*, *Rosa* spp.,

Table 1. Species in the study (all dicots but *Ruscus aculeatus*, a monocot), and characteristics. EEM = embryo-cum-endosperm dry mass. Shade and drought establishment indices based on the irradiance and moisture conditions in which the species establish in the wild. Shade establishment index: 4 = establishes in understories with evergreen shade; 3 = establishes in understories with deciduous shade; 2 = intermediate; 1 = light demanding; Drought establishment index: 4 = tolerates Mediterranean drought; 3 = tolerates dry sites in temperate deciduous forest; 2 = intermediate; 1 = water demanding.

Species*	Family*	Growth form and typical height at maturity*	Deciduous/evergreen	Mean seed dry mass (mg) <sup>†</sup>	Mean EEM (mg) <sup>†</sup>	Shade establishment index <sup>‡</sup>	Drought establishment index <sup>‡</sup>	Criteria for death in the extreme drought experiment	
								3% daylight	30% daylight
<i>Buxus sempervirens</i>	Buxaceae	Shrub or small tree, to 8 m	E	13.3	8.2	4	4	Leaves desiccated; gentle tug uproots n/a	Leaves shrivelled; gentle tug uproots n/a
<i>Crataegus monogyna</i>	Rosaceae	Shrub or small tree, to 10 m	D	9.0	7.6	1	2		
<i>Hedera helix</i>	Araliaceae	Woody climber, to 30 m	E	20		4	4	Leaves desiccated; petioles bent	Leaves desiccated; petioles contorted
<i>Ilex aquifolium</i>	Aquifoliaceae	Shrub or small tree, to 10 m	E	32		2	3	Leaves discoloured; leaf and stem collapsed	Leaves desiccated
<i>Prunus spinosa</i>	Rosaceae	Shrub, to 4 m	D	240	39.9	1	2	Leaves and stem apex desiccated, buds flake off easily	As in 3% daylight
<i>Rosa canina</i>	Rosaceae	Shrub to 4m	D	9.4	3.2	1	2	''	''
<i>Rosa pimpinellifolia</i>	Rosaceae	Shrub to 1 m	D	16		1	2	''	''
<i>Rubus fruticosus</i> agg	Rosaceae	Shrub	D	2.5		1	2	''	''
<i>Ruscus aculeatus</i>	Ruscaceae	Herb or shrub, to 1 m	E	170		4	4	Phylloclades flattened; stem bent	Phylloclades desiccated; stem bent
<i>Sambucus nigra</i>	Caprifoliaceae	Shrub or small tree, to 10 m	D	1.3		2	1	Leaves and stem apex desiccated	Leaves and stem apex desiccated
<i>Tilia cordata</i>	Tiliaceae	Tree, to 30 m	D	25		3	3	n/a	n/a
<i>Viburnum lantana</i>	Caprifoliaceae	Shrub, to 6 m	D	44	16.8	3	3	Leaves and stem apex desiccated	Leaves and stem apex desiccated
<i>Viburnum opulus</i>	Caprifoliaceae	Shrub, to 4 m	D	42	16.7	3	1	''	''

\*from Tutin et al. (1964–1980).

<sup>†</sup>from Salisbury (1974), Grime et al. (1981), Herrera (1987), Pigott (1991), Grubb et al. (1996), original data for *Buxus* (mean for 10 seeds).

<sup>‡</sup>from Pigott (1991), Grubb et al. (1996), Kollmann and Grubb (1999), Kollmann and Grubb (2002), Sack and Grubb (2002), Sack et al. (2003).

*Rubus*, *Sambucus* and *Tilia* (from Forestart, Church Farm, Hadnall, Shropshire, UK) were germinated in soil in trays on greenhouse benches, covered with green plastic mesh. The emergent seedlings (with cotyledons, or first true leaves expanded) were transferred to the deeply shading half of the shade tunnel. These seedlings, and first-season seedlings of *Buxus*, *Ilex*, *Viburnum lantana* and *Viburnum opulus* (from Forestart), were transplanted into 9 cm pots. First-season seedlings of *Ruscus* were collected under UCBG shrub and tree canopies, and were likewise transplanted. In the tunnel, pots were suspended > 10 cm above the ground in the tunnel, in plastic plant-carrying trays (Plantapak-Cookson, Maldon, UK) with well bottoms cut out, supported by wood slat frames, allowing excess water to drain away from the roots. Seedlings were watered every 1–3 days until the beginning of the watering treatments.

### Experimental design

Each experiment was arranged into blocks in each irradiance regime, containing one seedling per species for each watering regime. In each irradiance regime there were 10 blocks of seedlings for the growth experiment, and 40 for the extreme drought experiment. Before random sorting into blocks, seedlings of each species were sorted into one to three classes of stem height and leaf number; each treatment contained equal numbers from each size-class. In the extreme drought experiment *Prunus* seedlings were sufficient for only 25 blocks per irradiance, *Ruscus* for only 15, and *Crataegus* and *Tilia* were not included. The two experiments involved 2060 seedlings.

The location of blocks in the shade-tunnel was re-randomised each two weeks. On 8 July, certain species had developed mild infections, particularly the Rosaceae (mildew), and *Sambucus* (aphids and whitefly), and all experimental plants were sprayed with Radar (active ingredient propiconazole; Zeneca Crop Protection, Surrey, UK) and Tumblebug (active ingredient heptenophos; Fisons, Suffolk, UK).

### Control of water supply

Water supply was controlled using gravimetric soil water content. Prior to the beginning of the treatments, soil was added or removed from the pots to achieve 365 g in each pot at field capacity (i.e. once watered to excess and 30 min had elapsed since water dripped from the bottom of the pots). Field capacity soil water content was determined from soil of 6 extra pots similarly prepared ( $36.4\% \pm 1.6$  SE).

Equal watering treatments were approximated across species and irradiances in each experiment, using a method refined from that of Canham et al. (1996).

Each second evening a sample of pots of each species was weighed in each treatment (5 pots per species per treatment) of the growth and extreme drought experiments). In each watering treatment the species that had highest soil water content in 3% daylight became the 'pace-setting' species for that watering treatment. The following morning, between 8:00 am–10:00 am, all the other seedlings in that watering treatment, in both irradiances, were brought up to same soil water content (to the nearest 5 ml).

For both experiments the trends of soil water supply were indicated by the trajectory of the all-species mean for soil water content, calculated from the weighed subsample in each treatment each second evening and the following morning after watering (Fig. 1a–c). In the growth experiment the water treatments were 'low water' expected to limit growth strongly, and 'high water'. In the low-water treatment (Fig. 1a), a hardening drought was applied, for 20 days, until soil was at 18% field capacity, at which point wilting began for all species, and pots were watered back to 49% field capacity. Subsequently, the pots cycled together between 18–28% and 49% field capacity. In the high-water treatment, all seedlings were watered each second day, to 95–100% field capacity. In the extreme drought experiment (Fig. 1b), seedlings in the drought treatment underwent a hardening drought for 12 days, to 37% field capacity; then, the pots were rewatered to 95% field capacity, and a progressive drought began on day 15. The high water treatment of the extreme drought experiment was imposed as in the growth experiment. A curve was determined relating soil matric potential to gravimetric water content using the filter-paper method (Fig. 2; Deka et al. 1995).

### Growth experiment – quantification of seedling traits and their plasticity

Dry mass relative growth rate (RGR) was calculated as  $(\ln(\text{final plant dry mass}) - \ln(\text{initial plant dry mass})) / \text{growth time}$  (Evans 1972). Initial dry mass was quantified on 1 June; five seedlings were harvested for each size-class used for each species. Final harvest was conducted on 22 August to 1 September, selecting blocks randomly. Excised shoots were hydrated overnight, covered with plastic, for measurement of leaf area (and for *Ruscus*, phylloclade area; using a leaf area meter, Delta-T Devices Ltd.), and then material was dried > 72 h above 70°C. Leaf loss was negligible for virtually all seedlings, and the presented results were calculated without including shed leaves (ANOVA results for final mass and RGR did not differ when shed leaves were included).

Root and leaf mass fractions (RMF and LMF) were calculated as dry mass of root and leaf laminae

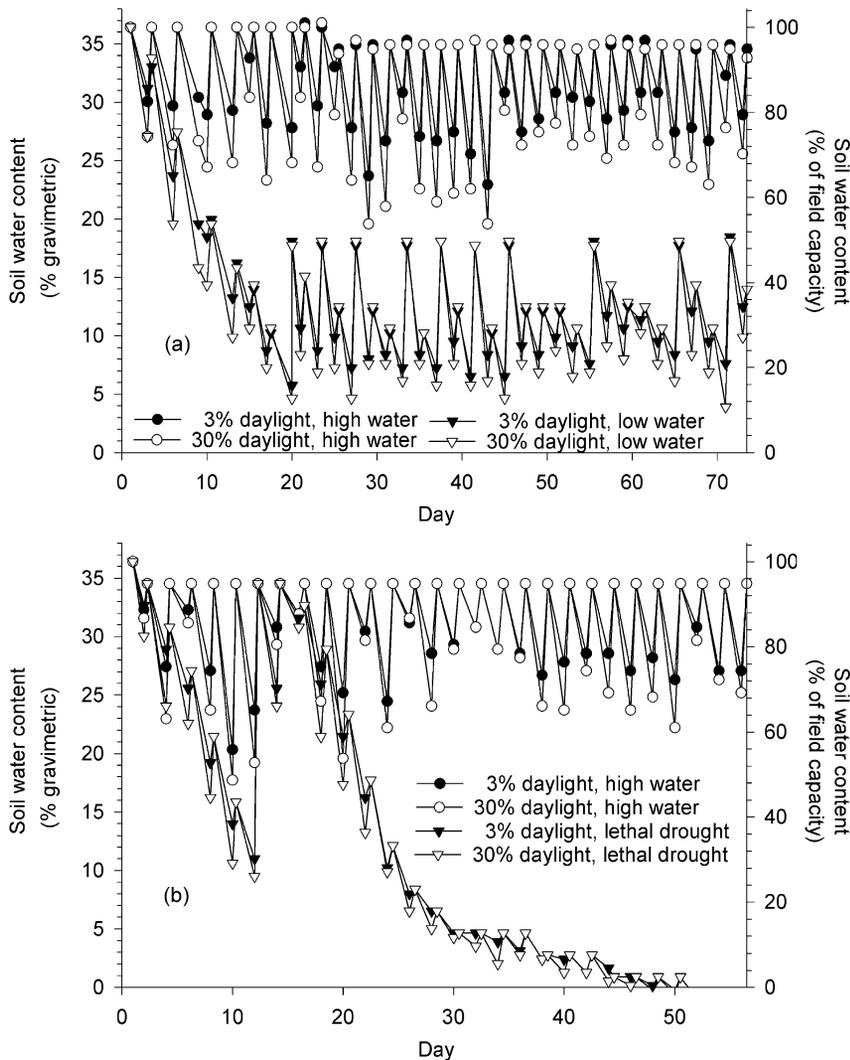


Fig. 1. Water supply treatments: soil water content (a) throughout the growth experiment, and (b) in the extreme drought experiment, until soil was dry (each point the mean for all species; 5 sample pots per species).

divided by plant dry mass, specific leaf area (SLA) as lamina area/lamina dry mass, and leaf area ratio (LAR) as lamina area/plant dry mass. Because growth and biomass allocation depend on seedling size (Evans 1972, Sack et al. 2002), treatment effects integrate size-related and size-independent effects, indicating overall impacts of shade and drought on first season traits (Coleman et al. 1994, Poorter and Nagel 2000).

The plasticities of biomass allocation traits were calculated using quotients (Table 2), so that a greater quotient typically corresponded to larger plasticity, according to patterns found in previous work (Veneklaas and Poorter 1998, Poorter and Nagel 2000, Valladares et al. 2002). Growth-based shade and drought tolerances were also assessed with quotients (Table 2; Fernandez and Reynolds 2000, Engelbrecht and Kursar 2003).

### Extreme drought experiment – quantification of stomatal conductance and survival time

To confirm progressive water shortage in the extreme drought experiment, stomatal conductance (using an AP4 porometer, Delta-T Devices, Cambridge, UK) was measured for three species between 9:00 am and 11:00 am, first on day 17, each second day for two weeks, and then weekly until negligible. Five average sized seedlings of *Rosa canina*, *Hedera* and *Viburnum lantana* were measured in each irradiance regime.

Seedlings were assessed as living or dead second day (by the criteria in Table 1). Seedlings assessed as dead were re-watered. For re-watered seedlings still erect in September, buds were tested for viability by fluorescein diacetate staining (Popov and Vysotskaya 1996). Seedling heights were recorded in extreme drought in 30% daylight to test for correlation with survival.

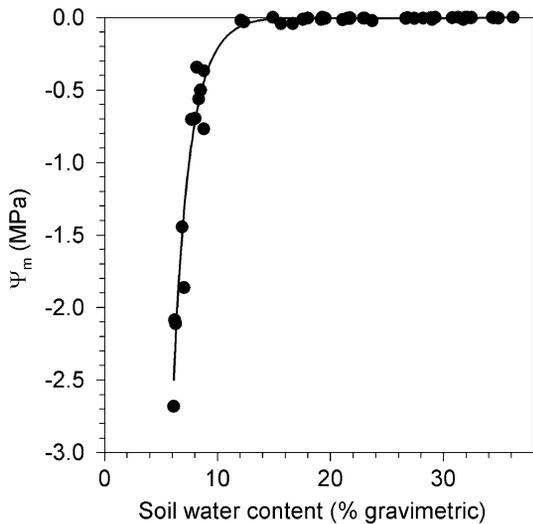


Fig. 2. Experimental soil gravimetric water content related to matric potential ( $\Psi_m$ ).

### Statistics

Because of the large number of seedlings and the resources required for controlling water supply, other aspects of experimental design were logistically constrained. All seedlings were grown in the two sides of a single shade-tunnel, thus pseudoreplicating the irradiance treatments (Hurlbert 1984). The randomised design allows testing for trait differences between seedlings in the two sides, which one can attribute to the 10-fold difference in irradiance, based on the findings of previous studies of the effects of irradiance (Grubb et al. 1996). For each plant trait measured in the growth

experiment a 3-way ANOVA was used (species  $\times$  irradiance  $\times$  water supply; using Minitab Release 13.32), and a 2-way ANOVA was used for each species (irradiance  $\times$  water supply); significance was tested at the all-species-wide 0.05 level using sequential Bonferroni testing (Rice 1989). ANOVA data were log-transformed to model multiplicative effects (Gilligan 1986). Trait correlations were tested with Spearman rank correlation and Pearson correlation ( $r_s$  and  $r_p$ , Zar 1999).

In the extreme drought, survival times were distributed non-normally for each species in each treatment. Mann–Whitney tests (Sokal and Rohlf 1995; Minitab Release 13.32) were used to detect species-differences in each irradiance regime, and Kruskal–Wallis tests to detect irradiance effects for each species. The findings were robust when dummy survival times were entered for the missing values arising from premature judgments of death – whether the substituted values were two days longer than the premature values, or whether they were the survival times of the longest surviving seedlings of the species in that irradiance regime.

### Results

#### Efficacy of watering treatments in the growth and extreme drought experiments

In both the growth and survival experiments, the watering treatments produced strongly contrasting water supplies (Fig. 1a, b Table 3). In the high-water treatments, soil matric potential ( $\Psi_m$ ) was always above  $-0.1$  MPa (Fig. 1a, 2). In low-water supply,  $\Psi_m$  declined to c.  $-1.5$  to  $-2$  MPa between re-watering events. In

Table 2. Abbreviations and formulae for plasticity of biomass allocation traits and for growth-based shade and drought tolerances. For each species, plasticity in biomass allocation across irradiances was averaged for both watering supplies, and plasticity across water supplies was averaged across both irradiances. Growth-based shade tolerances were calculated for plants in high water supply; growth-based drought tolerances for plants in 30% daylight.

Trait quantified	Abbreviation	Calculated as:
Plasticity across irradiances		
In root mass fraction	$P_{RMF}^{irradiance}$	$RMF_{30\% \text{ daylight}}/RMF_{3\% \text{ daylight}}$
In leaf mass fraction	$P_{LMF}^{irradiance}$	$LMF_{3\% \text{ daylight}}/LMF_{30\% \text{ daylight}}$
In specific leaf area	$P_{SLA}^{irradiance}$	$SLA_{3\% \text{ daylight}}/SLA_{30\% \text{ daylight}}$
In leaf area ratio	$P_{LAR}^{irradiance}$	$LAR_{3\% \text{ daylight}}/LAR_{30\% \text{ daylight}}$
Plasticity across water supplies		
In root mass fraction	$P_{RMF}^{water}$	$RMF_{low \text{ water}}/RMF_{high \text{ water}}$
In leaf mass fraction	$P_{LMF}^{water}$	$LMF_{high \text{ water}}/LMF_{low \text{ water}}$
In specific leaf area	$P_{SLA}^{water}$	$SLA_{high \text{ water}}/SLA_{low \text{ water}}$
In leaf area ratio	$P_{LAR}^{water}$	$LAR_{high \text{ water}}/LAR_{low \text{ water}}$
Growth-based shade tolerance		
In terms of relative growth rate (dry mass)	$T_{RGR}^{shade}$	$RGR_{3\% \text{ daylight}}/RGR_{30\% \text{ daylight}}$
In terms of final dry mass	$T_{final \text{ mass}}^{shade}$	$final \text{ mass}_{3\% \text{ daylight}}/final \text{ mass}_{30\% \text{ daylight}}$
Growth-based drought tolerance		
In terms of relative growth rate (dry mass)	$T_{RGR}^{drought}$	$RGR_{low \text{ water}}/RGR_{high \text{ water}}$
In terms of final dry mass	$T_{final \text{ mass}}^{drought}$	$final \text{ mass}_{low \text{ water}}/final \text{ mass}_{high \text{ water}}$

the extreme drought treatment,  $\Psi_m$  fell below  $-1.5$  MPa on day 26–30 for all species, and then continued to decline (Fig. 1b, 2). Within each watering treatment the different species faced statistically similar soil water contents averaged throughout the experiment (Table 3). Although soil drying was faster in 30% than in 3% daylight between rewatering events (Fig. 1a, b, Table 3), the divergence was minimal, accounting for only 0.8% of the total variance in soil water content throughout the growth experiment, while the different watering treatments accounted for 93% (from data in Table 3).

Stomatal conductance declined continuously with decreasing morning soil water content for all three species tested, *Hedera*, *Rosa canina* and *Viburnum lantana*, in both irradiance treatments (Fig. 3), indicating that morning soil water content was meaningful for indicating water supply to the plants.

All seedlings in the extreme drought experiment were assessed as dead during the drought, except two *Ruscus* seedlings, which died while still receiving high water supply (i.e. before 7 July). The great majority of the seedlings assessed as dead, and then kept in moist soil until September, collapsed and began to decompose. Only 5% of seedlings were assessed as dead prematurely, with buds re-greening, and/or leaves expanding on re-watering; only these seedlings had buds that tested positive for viability. In the high-water treatment only one *Ruscus* and two *Rubus* seedlings died.

### Growth experiment: responses of individual species to irradiance and water supply

As expected, the ten-fold reduction in irradiance decreased growth for all species, as did reduction of water supply for all species except *Ruscus* (Fig. 4a, b, Table 4) *Ruscus* evidently performed as affectively in drying soil as in ever-moist soil. For all species, the impact of drought on RGR was equivalent across irradiances (Fig. 4c; no significant interaction between effects of irradi-

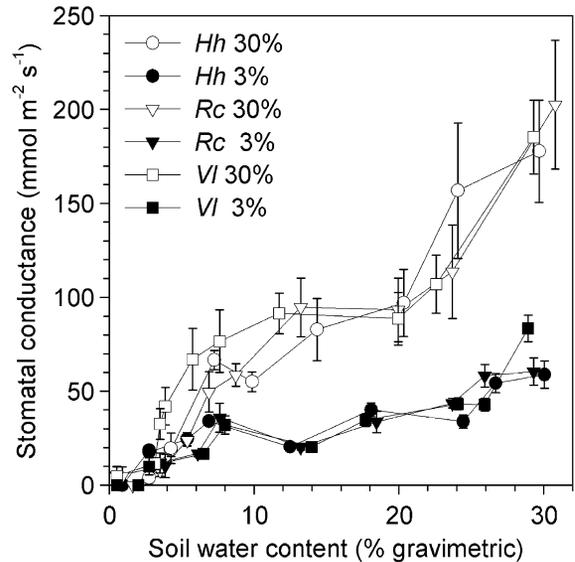


Fig. 3. Stomatal conductance for three study species as morning soil water content declined in 3% and 30% daylight irradiance (each point is a mean value for five seedlings  $\pm$  SE). Species symbols are initials of genus and species as in Table 1.

ance and water supply; Table 4). However, final mass was reduced by drought more strongly in 30% than in 3% daylight (Fig. 4d, Table 4; up to  $\approx 2 \times$  more strongly, for *Crataegus*).

### Growth experiment: plasticity of biomass allocation due to irradiance and water supply

The plasticity of biomass allocation to root and leaf across water supplies was statistically similar in both irradiances for 10–11 of 13 species ( $I \times W$  interaction not significant; Fig. 5; Table 4). Additionally, for nine species the plasticity of SLA and LAR across water supplies was statistically similar in both irradiances; for

Table 3. Mean soil water content during the growth experiment (averaged for all species)  $\pm$  SE, and 3-way ANOVA results for the effects of water-supply (W), irradiance treatment (I), species, and interactions (df = degrees of freedom; MS = mean squares).

	3% daylight, low water	3% daylight, high water	30% daylight, low water	30% daylight, high water
Mean soil water content (%)	13.4 $\pm$ 0.12	32.2 $\pm$ 0.14	12.0 $\pm$ 0.14	30.3 $\pm$ 0.24
3-way ANOVA results	Factor	df	MS	P
	W	1	22163	< 0.001
	I	1	178	< 0.001
	Species	12	3.29	0.926
	W $\times$ I	1	4.72	0.409
	W $\times$ Species	12	2.92	0.953
	I $\times$ Species	12	0.40	1.000
	I $\times$ W $\times$ Species	12	0.57	1.000
	Error	206	6.89	

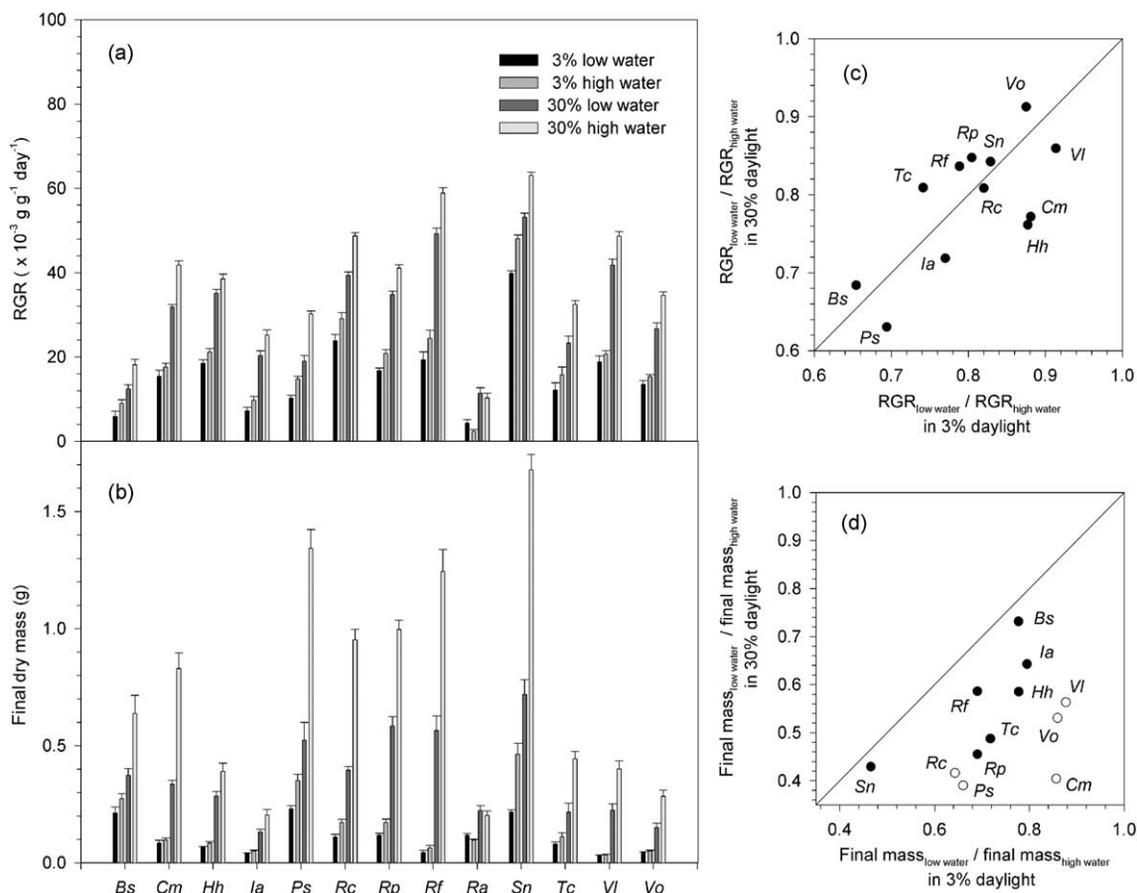


Fig. 4. Mean (a) dry-mass relative growth rates (RGR), and (b) final mass  $\pm$  SE of seedlings in the growth experiment and (c) and (d) the ability to maintain RGR and final dry mass under decreased water supply in 30% vs 3% daylight. For RGR (c) no species significantly departs from the 1:1 line; for final mass (d) open symbols represent species significantly distant from the line at  $P < 0.05$ , when considered individually (Table 4). Species symbols are initials of genus and species as in Table 1.

four species there was a 10–20% difference between irradiances (Fig. 6a, b, Table 4). Because of the typical lack of interaction, in presenting the plasticity of biomass allocation across irradiances, plasticity quotients were averaged for both water supplies, and for the plasticity across water supplies, plasticity quotients were averaged across both irradiances (Table 2).

Consistent with previous work, higher irradiance generally led to significantly higher values for RMF (11 species;  $P_{RMF}^{irradiance}$  highest at 2.1 for *Sambucus*), lower values for each of LMF (9 species;  $P_{LMF}^{irradiance}$  highest at 1.6 for *Sambucus*), SLA (all species;  $P_{SLA}^{irradiance}$  highest at 3.2 for *Rubus*) and LAR (all species;  $P_{LAR}^{irradiance}$  highest at 4.0 for *Sambucus*; Fig. 5, 6a, b, Table 4). Responses to drought were weaker, and occurred only in certain species. Drought increased RMF (3 species;  $P_{RMF}^{water}$  highest at 1.5, for *Hedera*), reduced LMF (4 species;  $P_{LMF}^{water}$  highest at 1.4, for *Ilex*), increased SLA (3 species; by up to 12%, in *Crataegus*), and variously reduced LAR

(three species;  $P_{LAR}^{water}$  highest at 1.2, for *Viburnum lantana*) or increased it (by 20% in *Rubus*; Fig. 5, 6a, b, Table 4).

### Growth experiment: species-differences in growth, biomass allocation and growth-based shade and drought tolerances

Species varied  $\approx$  7-fold in both RGR and final dry mass (averaged across treatments; Fig. 4a, b, Table 4),  $\approx$  2.5-fold in each of RMF and LMF, and  $\approx$  5-fold in both SLA and LAR (Fig. 5, 6a, b, Table 4). Species' RGRs were tightly correlated among the four treatments ( $r_s = 0.94$  to  $0.98$ ;  $r_p = 0.89$  to  $0.99$ ;  $P < 0.001$ ). Species also differed in growth-based shade tolerance and drought tolerances. Species varied  $\approx$  3-fold in  $T_{RGR}^{shade}$  (from 0.23 for *Ruscus* to 0.76 for *Sambucus*) and  $\approx$  9-fold in  $T_{final\ mass}^{shade}$  (from 0.05 for *Rubus*, to 0.48 for *Ruscus*;

Table 4. Mean squares (MS) from ANOVAs of log-transformed variates for individual species (\*0.05 > P ≥ 0.01; \*\*0.01 > P ≥ 0.0038; \*\*\*0.0038 > P; P = 0.0038 is the all-species-wide full Bonferroni 0.05 significance level), and for all species' data (\*0.05 > P ≥ 0.01; \*\* 0.01 > P ≥ 0.001; \*\*\*P < 0.001). Only six seedlings died in the growth experiment (one seedling of each of *Crataegus*, *Prunus*, *Rosa canina* and *Ruscus*, and two *Tilia*) and another *Prunus* shed all its leaves and died back several cm; these seedlings were excluded from the analyses.

Species	Factor	Final mass	RGR	RMF	LMF	SLA	LAR
<i>Buxus</i>	Irradiance	<b>0.912***</b>	<b>1.29***</b>	<b>0.121***</b>	<b>0.0890***</b>	<b>0.411***</b>	<b>0.117***</b>
	Water	0.292***	0.478***	0.0114	0.00515	0.00046	0.00252
	I × W	0.0242	0.214	0.00233	0.00832	0.00176	0.00243
	Residual MS, df	0.0184, 36	0.0380, 36	0.00558, 36	0.00366, 36	0.00397, 36	0.00707, 36
<i>Crataegus</i>	Irradiance	<b>5.88***</b>	<b>1.22***</b>	<b>0.293***</b>	<b>0.00007</b>	<b>0.946***</b>	<b>0.930***</b>
	Water	0.539***	0.0828***	0.00031	0.0341	0.0292***	0.00018
	I × W	0.220***	0.00637	0.00009	0.0306	0.0112**	0.0788*
	Residual MS, df	0.0136, 35	0.00561, 35	0.0242, 35	0.0160, 35	0.00130, 35	0.0165, 35
<i>Hedera</i>	Irradiance	<b>4.22***</b>	<b>0.737***</b>	<b>0.0867**</b>	<b>0.0675***</b>	<b>0.742***</b>	<b>1.26***</b>
	Water	0.135***	0.0237**	0.311***	0.0287***	0.00451	0.0105
	I × W	0.0015	0.00090	0.00482	0.000205	0.00008	0.00003
	Residual MS, df	0.0104, 36	0.00251, 36	0.00882, 36	0.00111, 36	0.00291	0.00393, 36
<i>Ilex</i>	Irradiance	<b>3.03***</b>	<b>2.07***</b>	<b>0.0316</b>	<b>0.0105</b>	<b>0.733***</b>	<b>0.919***</b>
	Water	0.197***	0.125*	0.226**	0.103***	0.00548	0.0613**
	I × W	0.0193	0.00348	0.0186	0.000662	0.00079	0.00001
	Residual MS, df	0.0169, 36	0.0188, 36	0.0103, 36	0.00339, 36	0.00312, 36	0.00686, 36
<i>Prunus</i>	Irradiance	<b>1.82***</b>	<b>0.751***</b>	<b>0.0456*</b>	<b>0.815***</b>	<b>0.900***</b>	<b>3.43***</b>
	Water	0.988***	0.371***	0.00433	0.406*	0.00756	0.303*
	I × W	0.206***	0.00936	0.00216	0.354*	0.00431	0.280
	Residual MS, df	0.0076, 34	0.00537, 34	0.00766, 34	0.0705, 34	0.00348, 34	0.0720, 34
<i>Rosa canina</i>	Irradiance	<b>4.22***</b>	<b>0.500***</b>	<b>0.425***</b>	<b>0.0175*</b>	<b>1.89***</b>	<b>2.27***</b>
	Water	0.816***	0.0798***	0.0332	0.00106	0.00162	0.00529
	I × W	0.0786**	0.00004	0.00171	0.0189*	0.00004	0.0207*
	Residual MS, df	0.0086, 35	0.00390, 35	0.0103, 35	0.00348, 35	0.00167, 35	0.00376, 35
<i>Rosa pimpinellifolia</i>	Irradiance	<b>5.36***</b>	<b>0.951***</b>	<b>0.896***</b>	<b>0.0144***</b>	<b>2.19***</b>	<b>3.45***</b>
	Water	0.386***	0.0683***	0.107***	0.0277*	0.00757	0.0063
	I × W	0.0172	0.00112	0.100***	0.00300	0.00721	0.0195*
	Residual MS, df	0.0084, 36	0.00210, 36	0.00469, 36	0.00406, 36	0.00203, 36	0.0035, 36
<i>Rubus</i>	Irradiance	<b>15.1***</b>	<b>1.68***</b>	<b>0.970***</b>	<b>0.0681***</b>	<b>2.48***</b>	<b>3.38***</b>
	Water	0.718***	0.0872**	0.00102	0.00667	0.0237**	0.0555**
	I × W	0.0748	0.00236	0.00005	0.00236	0.00104	0.0003
	Residual MS, df	0.0355, 36	0.00919, 36	0.00701, 36	0.00172, 36	0.00274, 36	0.0062, 36
<i>Ruscus</i>	Irradiance	<b>0.801***</b>	<b>4.68***</b>	<b>0.0960***</b>	<b>0.180***</b>	<b>0.0337***</b>	<b>0.370***</b>
	Water	0.0329	0.0326	0.00614	0.00122	0.0124	0.0325
	I × W	0.00251	0.0101	0.0116	0.0469	0.00208	0.0687*
	Residual MS, df	0.0137, 35	0.191, 35	0.00767, 35	0.0122	0.00333, 35	0.0158, 35
<i>Sambucus</i>	Irradiance	<b>2.94***</b>	<b>0.148***</b>	<b>1.10***</b>	<b>0.412***</b>	<b>1.55***</b>	<b>3.56***</b>
	Water	1.22***	0.0612***	0.0262	0.00092	0.0134*	0.0073
	I × W	0.100	0.000100	0.0413	0.00068	0.00637	0.0029
	Residual MS, df	0.0101, 36	0.000518, 36	0.00700, 36	0.00305, 36	0.00310, 36	0.0064, 36
<i>Tilia</i>	Irradiance	<b>2.69***</b>	<b>1.13***</b>	<b>0.146***</b>	<b>0.102**</b>	<b>0.558***</b>	<b>1.14***</b>
	Water	0.550***	0.226*	0.0308	0.00031	0.00606	0.00914
	I × W	0.109	0.00014	0.0265	0.00210	0.00626	0.0156
	Residual MS, df	0.0347, 34	0.0347, 34	0.0102, 34	0.0122, 34	0.00170, 34	0.0111, 34
<i>Viburnum lantana</i>	Irradiance	<b>9.46***</b>	<b>1.33***</b>	<b>0.962***</b>	<b>0.0844***</b>	<b>1.13***</b>	<b>1.84***</b>
	Water	0.275***	0.0328*	0.214***	0.0230***	0.00971	0.0625***
	I × W	0.0934*	0.00099	0.0183	0.00107	0.00898	0.0162
	Residual MS, df	0.0211, 36	0.00476, 36	0.0167, 36	0.00133, 36	0.00402, 36	0.00418, 36
<i>Viburnum opulus</i>	Irradiance	<b>3.91***</b>	<b>1.07***</b>	<b>0.0259*</b>	<b>0.00781</b>	<b>0.542***</b>	<b>0.420***</b>
	Water	0.342***	0.0821***	0.0264	0.0141	0.00666	0.0402
	I × W	0.128*	0.00751	0.000430	0.0133	0.00992	0.00025
	Residual MS, df	0.0172, 36	0.00543, 36	0.00411, 36	0.0135, 36	0.00472, 36	0.0135, 36
All species	Species	2.83***	2.92***	0.645***	0.905***	1.23***	1.20***
	Irradiance	<b>52.2***</b>	<b>15.5***</b>	<b>3.09***</b>	<b>0.858***</b>	<b>12.4***</b>	<b>19.7***</b>
	Water	5.21***	1.20***	0.414***	0.267***	0.0103	0.173***
	S × I	0.657***	0.174***	0.174***	0.0967***	0.142***	0.282***
	S × W	0.108***	0.0465*	0.0460***	0.0325**	0.00982***	0.0348**
	I × W	0.736***	0.0003	0.0316	0.0232	0.0242**	0.00001
	S × I × W	0.0214	0.0053	0.0163	0.0384***	0.00299	0.0422***
	Residual MS, df	0.0166, 461	0.0245, 461	0.00954, 461	0.0110, 461	0.00294, 461	0.0129, 461

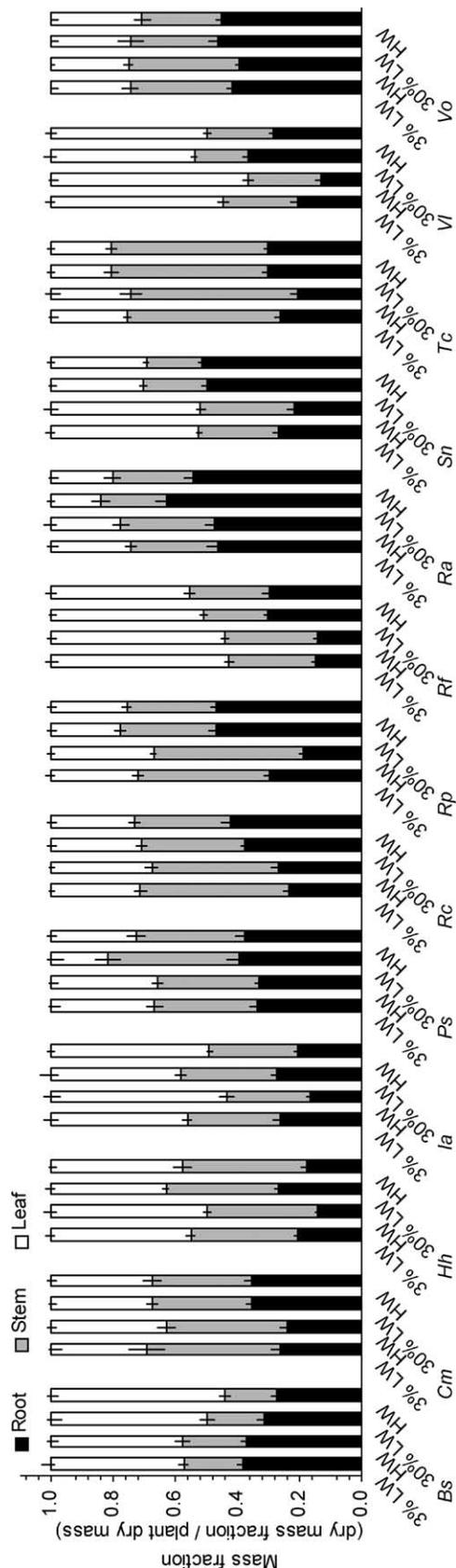


Fig. 5. Mean mass fractions of root, leaf and stem at final harvest for the treatments of the growth experiment. Species symbols are initials of genus and species as in Table 1.

calculated from data in Fig. 4a, b). While *Ruscus* was not affected by the drought, the other species varied  $\approx 1.5$ -fold in  $T_{RGR}^{drought}$  (from 0.63 for *Sambucus* to 0.91 for *Hedera*) and  $\approx 2$ -fold in  $T_{final\ mass}^{drought}$  (from 0.39 for *Prunus* to 0.73 for *Hedera*; calculated from data in Fig. 4a, b).

### Relationship among RGR, biomass allocation and experimental shade and drought tolerances

Across species, growth, biomass allocation and seed size were inter-related. RGR in 30% daylight, high water correlated with SLA and LAR averaged across treatments (Table 5), and RGR in all treatments correlated negatively with log EEM ( $r_s = -0.71$  to  $-0.79$ ,  $r_p = -0.78$  to  $-0.82$ ;  $P < 0.01$ ). Log EEM correlated negatively with LAR averaged across treatments (Table 5).

$T_{final\ mass}^{shade}$  and  $T_{final\ mass}^{drought}$  were linked with slow RGR in 30% daylight, high water supply, as was survival time in extreme drought (for  $T_{final\ mass}^{drought}$  and survival time only the rank-correlation or parametric correlation was significant; the other was marginally insignificant; Table 5). Slow RGR in high resource supply was further linked with low SLA and/or LAR and low plasticity in biomass allocation across irradiance regimes (i.e. a low  $P_{RMF}^{irradiance}$ ,  $P_{SLA}^{irradiance}$  and  $P_{LAR}^{irradiance}$ ; Table 5). RGR in high resource supply was not linked with plasticity in biomass allocation across water supplies (Table 5).

$T_{final\ mass}^{shade}$  and  $T_{final\ mass}^{drought}$  were thus also sometimes associated with the correlates of slow RGR in high resource supply, i.e. a high RMF, a low SLA and LAR, and a low plasticity in these traits across irradiances (in each case only the rank-correlation or parametric correlation were significant; Table 5).

### Extreme drought experiment: survival times in low and high irradiance

In the extreme drought, nine of the 11 species tested survived significantly longer in 3% than 30% daylight (Fig. 7) – by up to 8 days, in the case of *Hedera* (comparing medians). *Viburnum lantana* survived an equal time in both irradiances. *Ilex* survived 8 days longer in 30% daylight. In fact, in 30% daylight *Ilex* had a survival time second only to that of *Ruscus*, but it died earliest of all species in 3% daylight (Fig. 7). For *Ilex* in 3% daylight, but not in 30% daylight, seedling leaves and stem were soft, and collapsed on desiccation. Species differed significantly in survival time, in each irradiance regime (Fig. 7; Kruskal–Wallis tests,  $P < 0.001$ ). When excluding *Ilex*, the species' survival times in both irradiances were correlated ( $r_s = 0.82$ ;  $P < 0.01$ ;  $r_p = 0.89$ ;  $P < 0.001$ ).

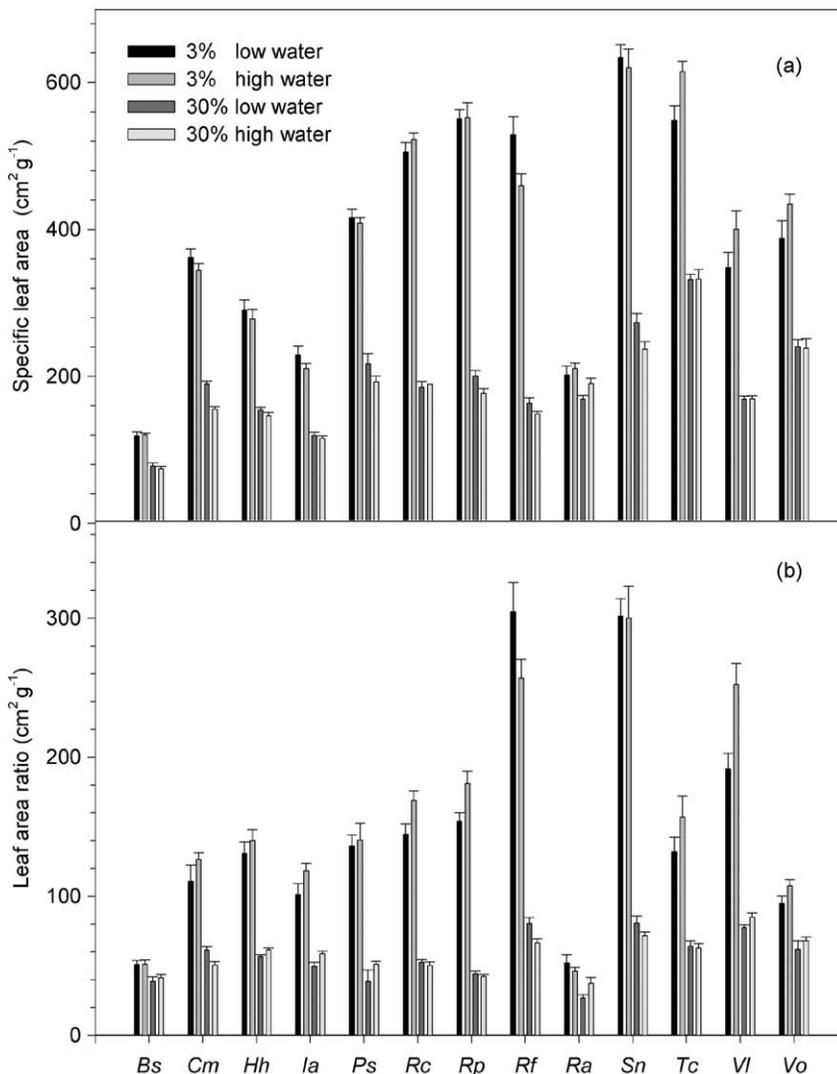


Fig. 6. Mean (a) specific leaf area, and (b) leaf area ratio  $\pm$ SE at final harvest for the treatments of the growth experiment. Species symbols are initials of genus and species as in Table 1.

Only for *Viburnum lantana* the seedling survival times in 30% daylight correlated positively with stem heights ( $r_s = 0.54$ ;  $r_p = 0.52$ ;  $n = 40$ ;  $P < 0.001$ ).

#### Association of tolerances with field establishment indices, and the independence of shade and drought tolerance

Shade and drought tolerances based on final mass, but not on RGR, were overall consistent with field establishment indices.  $T_{\text{final mass}}^{\text{shade}}$  correlated positively with shade establishment index ( $r_p = 0.58$ ;  $P < 0.05$ ).  $T_{\text{final mass}}^{\text{drought}}$  correlated positively with drought establishment index (as given in Table 1;  $r_p = 0.67$ ;  $P = 0.01$ ).  $T_{\text{final mass}}^{\text{drought}}$  also correlated with survival time in extreme drought (Fig. 8a), which also correlated with drought establishment index ( $r_p = 0.85$ ;  $P = 0.001$ ). However,  $T_{\text{RGR}}^{\text{shade}}$  and  $T_{\text{RGR}}^{\text{drought}}$

were unrelated to shade and drought establishment indices ( $r_s$  and  $r_p$  ranged  $-0.45$  to  $0.32$ ;  $P > 0.12$ ).

On the whole, the findings of both experiments were not consistent with an interspecific trade-off between shade and drought tolerance. Across species, shade and drought establishment indices were positively correlated ( $r_p = r_s = 0.68$ ;  $P = 0.02$ ), due to the inclusion of the species tolerant of deep shade plus drought, *Buxus*, *Hedera* and *Ruscus*. When excluding these species, shade and drought establishment indices were uncorrelated for the remaining ten species ( $r_p = r_s = 0.20$ ;  $P = 0.59$ ). Similarly, across all species,  $T_{\text{final mass}}^{\text{shade}}$  and  $T_{\text{final mass}}^{\text{drought}}$  were parametrically correlated ( $r_p = 0.60$ ;  $P = 0.03$ ), though they were not rank-correlated ( $r_s = 0.22$ ;  $P = 0.47$ ; Fig. 8b), and the positive parametric correlation did not hold when *Buxus*, *Hedera* and *Ruscus* were excluded ( $r_p = 0.50$ ;  $P = 0.15$ ).  $T_{\text{final mass}}^{\text{shade}}$  and  $T_{\text{final mass}}^{\text{drought}}$  were likewise uncorrelated when considering only the 8 of 13 species

Table 5. Correlation matrix for species' traits (Pearson coefficients in normal type; Spearman rank coefficients in italics). Bold values significant at  $P < 0.05$  for both Pearson and Spearman correlations; log EEM = log-transformed embryo-cum-endosperm dry mass (from Table 1; log seed mass substituted when log EEM not available); RMF, LMF, SLA and LAR = mean values across treatments for root and leaf mass fraction, specific leaf area and leaf area ratio;  $P^{irr}$  and  $P^w$  represent plasticity values across respectively irradiance and water supply treatments (Table 2).

	log EEM	RGR in 30% daylight, high water treatment	Growth-based tolerance		shade		Growth-based drought tolerance				Biomass allocation				Plasticity of biomass allocation across irradiances				Plasticity of biomass allocation across water supplies				Survival time in extreme drought	
			$T_{f\ mass}^{shade}$	$T_{RGR}^{shade}$	$T_{f\ mass}^{drought}$	$T_{RGR}^{drought}$	RMF	LMF	SLA	LAR	$P_{RMF}^{irr}$	$P_{LMF}^{irr}$	$P_{SLA}^{irr}$	$P_{LAR}^{irr}$	$P_{RMF}^w$	$P_{LMF}^w$	$P_{SLA}^w$	$P_{LAR}^w$	3% daylight	30% daylight				
log EEM			<i>0.39</i>	<i>-0.43</i>	<i>0.45</i>	<i>0.06</i>	<i>0.08</i>	<i>-0.36</i>	<i>-0.36</i>	<b>-0.58</b>	<i>-0.58</i>	<i>0.19</i>	<b>-0.63</b>	<i>-0.41</i>	<i>0.34</i>	<i>0.57</i>	<i>0.51</i>	<b>0.85</b>	<i>0.46</i>	<i>0.66</i>				
RGR in 30% daylight, high water treatment	<b>-0.83</b>		<b>-0.62</b>	<i>0.39</i>	<i>-0.50</i>	<i>0.21</i>	<i>-0.25</i>	<i>0.37</i>	<b>0.57</b>	<b>0.88</b>	<b>0.86</b>	<i>0.16</i>	<b>0.86</b>	<b>0.72</b>	<i>-0.19</i>	<i>-0.37</i>	<i>-0.43</i>	<i>-0.54</i>	<i>-0.52</i>	<i>-0.62</i>				
Growth-based shade tolerance																								
$T_{f\ mass}^{shade}$	<i>0.46</i>	<b>-0.74</b>			<i>0.22</i>	<i>-0.14</i>	<i>0.50</i>	<i>-0.39</i>	<i>-0.21</i>	<i>-0.49</i>	<i>-0.46</i>	<i>0.26</i>	<b>-0.65</b>	<i>-0.30</i>	<i>0.09</i>	<i>-0.02</i>	<i>0.28</i>	<i>0.14</i>	<i>0.26</i>	<i>0.29</i>				
$T_{RGR}^{shade}$	<i>-0.73</i>	<i>0.63</i>	<i>-0.15</i>	<i>0.16</i>	<i>-0.25</i>	<i>-0.09</i>	<i>0.10</i>	<i>-0.04</i>	<i>0.46</i>	<i>0.44</i>	<i>0.26</i>	<i>0.16</i>	<i>0.32</i>	<i>0.46</i>	<i>0.04</i>	<i>-0.08</i>	<i>-0.15</i>	<i>-0.36</i>	<i>-0.30</i>	<b>-0.67</b>				
Growth-based drought tolerance																								
$T_{f\ mass}^{drought}$	<i>0.69</i>	<i>-0.64</i>	<i>0.60</i>	<i>-0.60</i>		<b>0.63</b>	<i>-0.10</i>	<i>0.00</i>	<i>-0.47</i>	<i>-0.38</i>	<i>-0.29</i>	<i>-0.09</i>	<i>-0.44</i>	<i>-0.40</i>	<i>0.66</i>	<i>0.22</i>	<i>0.50</i>	<i>0.36</i>	<i>0.43</i>	<b>0.69</b>				
$T_{RGR}^{drought}$	<i>0.29</i>	<i>-0.09</i>	<i>0.21</i>	<i>-0.35</i>	<b>0.80</b>		<i>-0.10</i>	<i>0.12</i>	<i>-0.08</i>	<i>0.24</i>	<i>0.42</i>	<i>0.33</i>	<i>0.18</i>	<i>0.22</i>	<i>0.44</i>	<i>0.06</i>	<i>0.24</i>	<i>0.11</i>	<i>0.25</i>	<i>-0.38</i>				
Biomass allocation																								
RMF	<i>0.32</i>	<i>-0.40</i>	<i>0.59</i>	<i>-0.20</i>	<i>0.39</i>	<i>0.29</i>		<b>-0.67</b>	<i>0.19</i>	<i>-0.28</i>	<i>-0.18</i>	<i>0.29</i>	<i>-0.31</i>	<i>-0.10</i>	<i>-0.37</i>	<i>-0.06</i>	<i>0.19</i>	<i>0.05</i>	<i>0.02</i>	<i>-0.26</i>				
LMF	<i>-0.38</i>	<i>0.32</i>	<i>-0.31</i>	<i>-0.09</i>	<i>-0.14</i>	<i>-0.06</i>	<b>-0.67</b>		<i>-0.38</i>	<i>0.32</i>	<i>0.20</i>	<i>-0.28</i>	<i>0.37</i>	<i>0.15</i>	<i>0.25</i>	<i>0.07</i>	<i>-0.32</i>	<i>-0.12</i>	<i>-0.16</i>	<i>0.16</i>				
SLA	<i>-0.39</i>	<b>0.63</b>	<i>-0.41</i>	<i>0.51</i>	<i>-0.51</i>	<i>-0.16</i>	<i>0.02</i>	<i>-0.41</i>		<b>0.70</b>	<b>0.60</b>	<i>0.46</i>	<i>0.50</i>	<b>0.63</b>	<i>-0.21</i>	<i>-0.43</i>	<i>-0.08</i>	<i>-0.26</i>	<i>-0.53</i>	<b>-0.84</b>				
LAR	<b>-0.69</b>	<b>0.93</b>	<i>-0.63</i>	<i>0.53</i>	<i>-0.51</i>	<i>-0.02</i>	<i>-0.40</i>	<i>0.41</i>	<b>0.62</b>		<b>0.90</b>	<i>0.46</i>	<b>0.85</b>	<b>0.88</b>	<i>-0.00</i>	<i>-0.33</i>	<i>-0.32</i>	<i>-0.37</i>	<i>-0.42</i>	<i>-0.61</i>				
Plasticity of biomass allocation across irradiances																								
$P_{RMF}^{irr}$	<i>-0.53</i>	<b>0.82</b>	<i>-0.57</i>	<i>0.35</i>	<i>-0.27</i>	<i>0.28</i>	<i>-0.16</i>	<i>0.18</i>	<b>0.61</b>	<b>0.85</b>		<i>0.52</i>	<b>0.85</b>	<b>0.84</b>	<i>-0.03</i>	<i>-0.38</i>	<i>-0.35</i>	<i>-0.46</i>	<i>-0.26</i>	<i>-0.42</i>				
$P_{LMF}^{irr}$	<i>0.07</i>	<i>0.28</i>	<i>0.06</i>	<i>0.25</i>	<i>0.02</i>	<i>0.22</i>	<i>0.17</i>	<i>-0.26</i>	<i>0.53</i>	<i>0.45</i>	<i>0.49</i>		<i>0.28</i>	<b>0.68</b>	<i>0.07</i>	<i>-0.01</i>	<i>-0.03</i>	<i>0.11</i>	<i>0.07</i>	<i>-0.24</i>				
$P_{SLA}^{irr}$	<b>-0.70</b>	<b>0.82</b>	<b>-0.71</b>	<i>0.45</i>	<i>-0.58</i>	<i>-0.13</i>	<i>-0.38</i>	<i>0.26</i>	<i>0.50</i>	<b>0.73</b>	<b>0.80</b>	<i>0.19</i>		<b>0.87</b>	<i>-0.19</i>	<i>-0.13</i>	<i>-0.57</i>	<i>-0.44</i>	<i>-0.41</i>	<i>-0.62</i>				
$P_{LAR}^{irr}$	<i>-0.55</i>	<b>0.78</b>	<i>-0.50</i>	<i>0.53</i>	<i>-0.47</i>	<i>-0.03</i>	<i>-0.21</i>	<i>0.10</i>	<i>0.66</i>	<b>0.80</b>	<b>0.86</b>	<b>0.63</b>	<b>0.88</b>		<i>-0.07</i>	<i>-0.08</i>	<i>-0.48</i>	<i>-0.31</i>	<i>-0.35</i>	<i>-0.63</i>				
Plasticity of biomass allocation across water supplies																								
$P_{RMF}^w$	<i>0.30</i>	<i>-0.07</i>	<i>-0.12</i>	<i>-0.07</i>	<i>0.31</i>	<i>0.23</i>	<i>-0.50</i>	<i>0.46</i>	<i>-0.27</i>	<i>0.06</i>	<i>0.06</i>	<i>0.04</i>	<i>-0.11</i>	<i>-0.05</i>		<i>0.41</i>	<i>0.19</i>	<i>0.37</i>	<i>0.03</i>	<i>0.30</i>				
$P_{LMF}^w$	<i>0.52</i>	<i>-0.38</i>	<i>0.07</i>	<i>-0.16</i>	<i>0.05</i>	<i>-0.22</i>	<i>-0.11</i>	<i>0.02</i>	<i>-0.34</i>	<i>-0.34</i>	<i>-0.35</i>	<i>0.13</i>	<i>-0.26</i>	<i>-0.14</i>	<i>0.49</i>		<i>-0.07</i>	<b>0.63</b>	<i>0.15</i>	<i>0.23</i>				
$P_{SLA}^w$	<i>0.47</i>	<i>-0.38</i>	<i>0.30</i>	<i>-0.30</i>	<i>0.44</i>	<i>0.29</i>	<i>0.38</i>	<i>-0.33</i>	<i>0.01</i>	<i>-0.31</i>	<i>-0.22</i>	<i>-0.10</i>	<i>-0.49</i>	<i>-0.46</i>	<i>-0.02</i>	<i>-0.16</i>		<b>0.60</b>	<i>0.20</i>	<i>0.42</i>				
$P_{LAR}^w$	<b>0.76</b>	<i>-0.58</i>	<i>0.27</i>	<i>-0.35</i>	<i>0.36</i>	<i>0.04</i>	<i>0.17</i>	<i>-0.20</i>	<i>-0.28</i>	<i>-0.49</i>	<i>-0.43</i>	<i>0.02</i>	<i>-0.55</i>	<i>-0.44</i>	<i>0.40</i>	<b>0.70</b>	<b>0.60</b>		<i>0.05</i>	<i>0.42</i>				
Survival time in extreme drought																								
3% daylight	<i>0.56</i>	<i>-0.50</i>	<i>0.46</i>	<i>-0.44</i>	<i>0.73</i>	<i>0.51</i>	<i>0.14</i>	<i>-0.12</i>	<i>-0.50</i>	<i>-0.43</i>	<i>-0.32</i>	<i>0.12</i>	<i>-0.49</i>	<i>-0.36</i>	<i>0.16</i>	<i>-0.00</i>	<i>0.15</i>	<i>0.09</i>		<i>0.54</i>				
30% daylight	<i>0.58</i>	<i>-0.56</i>	<i>0.35</i>	<b>-0.68</b>	<b>0.77</b>	<i>0.54</i>	<i>-0.16</i>	<i>0.29</i>	<b>-0.78</b>	<i>-0.41</i>	<i>-0.42</i>	<i>-0.19</i>	<i>-0.58</i>	<i>-0.59</i>	<i>0.43</i>	<i>0.15</i>	<i>0.20</i>	<i>0.25</i>	<i>0.66</i>					

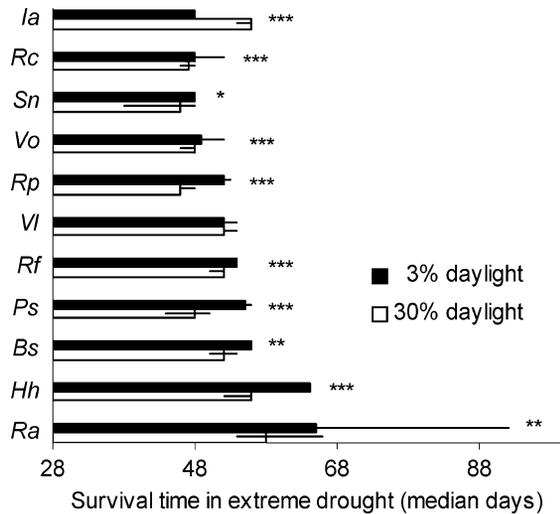


Fig. 7. Median survival time in the extreme drought experiment  $\pm$  interquartile ranges. Mann – Whitney tests: \* $0.05 > P \geq 0.01$ ; \*\* $0.01 > P \geq 0.001$ ; \*\*\* $P < 0.001$ . All differences significant at all-species-wide 0.05 (sequential Bonferroni test). Species symbols are initials of genus and species as in Table 1.

that were cultured identically from seed ( $r_s = 0.06$ ;  $P = 0.89$ ;  $r_p = -0.12$ ;  $P = 0.78$ ), or the five species within Rosaceae (Table 1;  $r_s = -0.50$ ;  $P = 0.39$ ;  $r_p = -0.15$ ;  $P = 0.81$ ). While  $T_{RGR}^{shade}$  was negatively correlated with survival time in extreme drought in 30% daylight, as seen above  $T_{RGR}^{shade}$  was not a good indicator of shade tolerance in the field, and further, it was not correlated with survival of extreme drought in 3% daylight.  $T_{final\ mass}^{shade}$  was independent of survival time in extreme drought in both irradiances (Table 5).

## Discussion

### Does drought have a stronger impact on a given species' performance in shade than in high irradiance?

To eventually predict field establishment patterns it is important to understand the combined impacts of deep shade and drought on the growth of given species of woody seedlings. According to the intraspecific trade-off between shade tolerance and drought tolerance hypothesized in the literature, dry soil should have a stronger impact on the growth and survival of seedlings of a given species grown in deeper shade (Introduction). This study did not support such a trade-off. For 12 of the 13 species significantly affected by drought, drought reduced RGR proportionally in low and high irradiance, consistent with a previous study of four shade tolerant species, and with data for other studies of small species sets, analysed in different ways (reviewed by Sack and Grubb 2002). The orthogonal effects of shade and drought on RGR were associated with largely orthogonal effects of shade

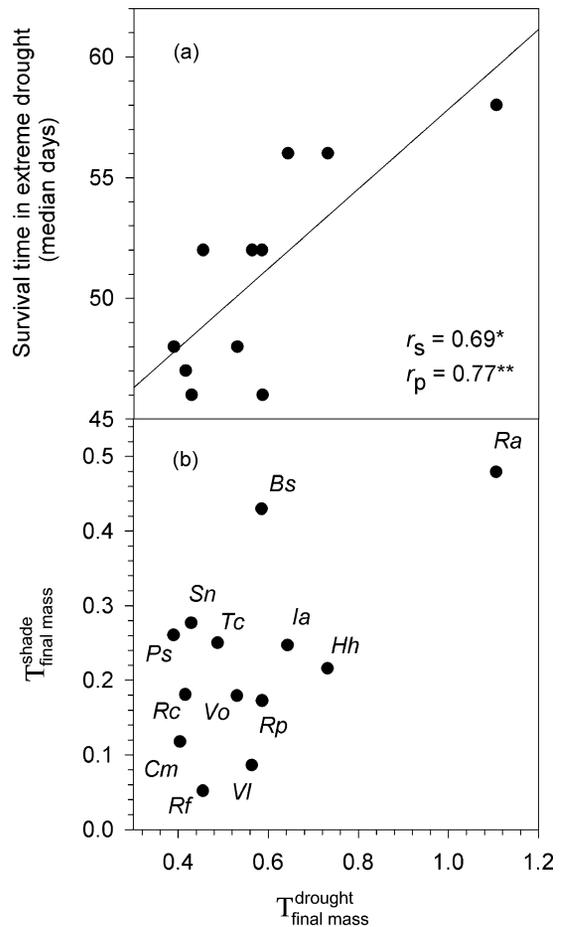


Fig. 8. Tolerances of shade and drought in terms of absolute growth and survival. (a) correlation of survival time in extreme drought (in high irradiance) and  $T_{final\ mass}^{drought}$ ; (b) independence of  $T_{final\ mass}^{shade}$  and  $T_{final\ mass}^{drought}$  (definitions in Table 2). \* $P < 0.05$ ; \*\*\* $P < 0.001$ . Species symbols are initials of genus and species as in Table 1.

and drought on biomass allocation. Notably, despite the proportional impact of drought on RGR in low and high irradiance, there was frequently a substantially stronger impact of drought on absolute growth in higher irradiance (Fig. 4c, d). This interaction is expected as a mathematical consequence of proportional impacts of drought on RGR at low and high irradiance, because absolute growth is an exponential function of RGR (Evans 1972). The interaction is especially likely when RGR is high, i.e. for fast-growing species (Corré 1983, Sack and Grubb 2002).

Whereas moderate drought had a proportional impact on RGR in deep shade and in higher irradiance, extreme drought generally reduced survival more strongly in higher irradiance. The equivalent (proportional) impact of drought on RGR at 30% as at 3% daylight, despite the higher daytime leaf and air temperatures and vapour pressure deficit in 30% daylight (Sack 2000), and

possibly greater oxidative stresses (Callaway 1995), indicates that seedlings in 30% daylight can compensate for these factors without suffering inhibition. However, such factors might aggravate the effects of drought at higher, photoinhibitory irradiances (i.e. beginning > 30% daylight; Valladares and Pearcy 1997), and at moderate irradiances, during extreme drought. In extreme drought, nine of eleven species died faster in 30% irradiance. *Ilex* was the one species to die sooner in deep shade, as previously reported for *Andropogon virginicus* and *Pinus ponderosa*; for these species foliage and stem of shade-grown plants have an apparently reduced ability to withstand drought (Keever 1950, Vance and Zaerr 1991). For the bulk of species, shade apparently played a protective, “facilitative” role for seedlings in lethal drought, reducing the evaporative demand, and the impact of stresses associated with high irradiance. Notably, plants in deeper shade were smaller than those in higher irradiance, and thus had lower total leaf area. However, this difference probably did not account for their greater survival. For seedlings tested in 30% daylight, seedling size was not linked with sensitivity to extreme drought; in fact, for one species, *Viburnum lantana*, larger plants survived longer. Similarly, survival of drought was unrelated to pre-drought total leaf area for the 28 species of tropical seedlings studied by Engelbrecht and Kursar (2003).

Notably, one mechanism for an intraspecific trade-off between shade and drought tolerance was not tested in this study. One might hypothesize that in the field seedlings in high irradiance might access greater soil volumes through their greater size. In this study, plants accessed a given volume of soil, to reflect the situation in which species germinate together at the start of a growth season, and root into a standard volume of soil of the same dryness. In the first season, seedlings typically root within the top 30 cm of soil, in which the bulk of tree fine roots drive the soil drying, in the understorey, and sometimes in gaps (Coomes and Grubb 2000). When soil drying is thus uniform across irradiances, the findings of this study suggest that the impact of drought on RGR is proportional across irradiances.

In such a scenario, the findings of this study have implications for modeling of seedling growth. Given orthogonal effects of shade and drought on RGR, plant growth in response to irradiance × water combinations would be predictable from a simple multiplicative model of responses to irradiance and to water supply individually (Nobel 1999, Sack and Grubb 2002). This finding has practical implications for combining light and water-supply response functions for modelling seedling establishment dynamics (Pacala et al. 1994, Kobe et al. 1996). This finding can also be used for interpreting forest plant responses during drought. In systems in which the soil dries evenly in the understorey and in gaps, or faster in gaps, it is expected that plant survival and absolute

growth will be more strongly reduced in the gaps (Ellsworth and Reich 1992, Sipe and Bazzaz 1995). However, plant survival and growth are often observed to decline during drought more strongly in the understorey, or equally across irradiances (Fisher et al. 1991, Veenendaal et al. 1996, Poorter and Hayashida-Oliver 2000, Valladares and Pearcy 2002). One conclusion of this study is that such a pattern does not arise from a greater sensitivity of understorey plants to drought due to physiology or morphology. Rather, the upper soil layers in the understorey are probably drier than in gaps, due to root competition from overstorey trees (Coomes and Grubb 2000, Valladares and Pearcy 2002). Alternatively, the seedlings in the gap may have exploited a larger volume of soil, and accessed soil moisture at depth.

### Growth-based tolerance and its linkage with slow RGR in high-resource conditions

Growth-based shade and drought tolerances were quantified in two ways. A novel finding of this study was that  $T_{\text{final mass}}^{\text{shade}}$  and  $T_{\text{final mass}}^{\text{drought}}$  correlated respectively with field establishment indices, whereas  $T_{\text{RGR}}^{\text{shade}}$  and  $T_{\text{RGR}}^{\text{drought}}$  did not.  $T_{\text{final mass}}^{\text{drought}}$  also correlated with survival time in extreme drought, which itself correlated with drought establishment index. Notably,  $T_{\text{final mass}}^{\text{shade}}$  and  $T_{\text{final mass}}^{\text{drought}}$  were linked with slow RGR in the 30% daylight, high water supply treatment. The linkage between  $T_{\text{final mass}}^{\text{shade}}$ ,  $T_{\text{final mass}}^{\text{drought}}$  and RGR in high resource supply is in fact expected by their mathematical definitions (Evans 1972). In the case of growth-based shade tolerance:

$$\begin{aligned} T_{\text{final mass}}^{\text{shade}} &= \text{final mass}_{\text{shade}} / \text{final mass}_{\text{high irradiance}} \\ &= m_0 e^{t \cdot \text{RGR}_{\text{shade}}} / m_0 e^{t \cdot \text{RGR}_{\text{high irradiance}}} \\ &= e^{t (\text{RGR}_{\text{shade}} - \text{RGR}_{\text{high irradiance}})} \\ &= e^{t (1 - T_{\text{RGR}}^{\text{shade}}) (-\text{RGR}_{\text{high irradiance}})} \end{aligned} \quad (1)$$

Similarly, for drought tolerance,

$$T_{\text{final mass}}^{\text{drought}} = e^{t (1 - T_{\text{RGR}}^{\text{drought}}) (-\text{RGR}_{\text{high water supply}})} \quad (2)$$

where  $m_0$  represents initial dry mass, and  $t$  represents growth time. Thus, from Eq. 1,  $T_{\text{final mass}}^{\text{shade}}$  (a species’ ability to maintain its absolute growth in shade) is potentially dependent on two factors.  $T_{\text{final mass}}^{\text{shade}}$  is (a) positively related to  $T_{\text{RGR}}^{\text{shade}}$ , the species’ ability to maintain its RGR in shade, related to physiology and morphology, and (b) negatively related to  $\text{RGR}_{\text{high irradiance}}$  per se. Thus, for two species with the same  $T_{\text{RGR}}^{\text{shade}}$ , the species with higher  $\text{RGR}_{\text{high irradiance}}$  will have a lower  $T_{\text{final mass}}^{\text{shade}}$ , often dramatically so. Which factor is most important in driving  $T_{\text{final mass}}^{\text{shade}}$  in a set of species will depend on how variable each factor is across the species set (Shipley 2002). Likewise,  $T_{\text{final mass}}^{\text{drought}}$  can be driven by a slow  $\text{RGR}_{\text{high water supply}}$  and/or a high  $T_{\text{RGR}}^{\text{drought}}$  (Eq. 2).

Which of the factors are most important in driving  $T_{\text{final mass}}^{\text{shade}}$  and  $T_{\text{final mass}}^{\text{drought}}$ ? *Prunus* and *Sambucus* achieved considerable  $T_{\text{final mass}}^{\text{shade}}$  through a high  $T_{\text{RGR}}^{\text{shade}}$ , despite relatively very rapid high-resource RGR (Fig. 4a, 8b). However, across the bulk of the species,  $T_{\text{RGR}}^{\text{shade}}$  was not important in driving  $T_{\text{final mass}}^{\text{shade}}$ ; a slow RGR in high resource supply was the key determinant of  $T_{\text{final mass}}^{\text{shade}}$ . Indeed, *Ruscus*, an extreme shade tolerator in the field (Sack et al. 2003) had the lowest  $T_{\text{RGR}}^{\text{shade}}$ , yet the highest  $T_{\text{final mass}}^{\text{shade}}$ , due to its distinctively slow RGR in high resource supply (Fig. 4a, 8b). On the other hand,  $T_{\text{final mass}}^{\text{drought}}$  was driven more by  $T_{\text{RGR}}^{\text{drought}}$  than by slow high-resource RGR, indicating the importance in drought tolerance of features that contribute to water-use efficiency of RGR, such as, by hypothesis, stomatal water use-efficiency, resistance to xylem embolism, and tolerance of tissue desiccation (Tyree et al. 2003). Similarly, in a previous study of eight grass species,  $T_{\text{final mass}}^{\text{drought}}$  was unrelated to high-resource RGR (Fernandez and Reynolds 2000) and thus driven entirely by differences in  $T_{\text{RGR}}^{\text{drought}}$  (Eq. 2).

Why should growth-based shade and drought tolerances ( $T_{\text{final mass}}^{\text{shade}}$  and  $T_{\text{final mass}}^{\text{drought}}$ ) correlate with field establishment indices for shade and drought? First, the correlation may be partly due to linkage with slow high-resource RGR. ‘Slow-growing’ species (i.e. those with low high-resource RGRs), which tend to have higher  $T_{\text{final mass}}^{\text{shade}}$  and  $T_{\text{final mass}}^{\text{drought}}$ , as seen above, also tend to have morphological and physiological traits conferring higher survival rates in resource shortage than ‘fast-growing’ species (Kitajima 1994, Walters and Reich 2000). Such traits may confer additional resistance against other resource shortages, herbivory, pathogens and mechanical damage during early establishment. These traits include large seed, high RMF, and low SLA and LAR, low foliar nitrogen concentrations, respiration rates and long tissue lifespans (Kitajima 1994, Grubb 1998, Walters and Reich 1999, 2000). In this study too, for instance, survival of extreme drought was linked with low SLA and LAR, traits associated with slow growth. It has also been hypothesized that in the longer term, species with relatively slow high-resource RGR may, in low resource conditions, out-compete species with relatively rapid high-resource RGR. Such RGR rank-changes between low and high resource supplies tend not to occur during the first season; here, species-rankings in RGR in all treatments are typically driven by seed size, as found in this study, because the first season small seed size is allometrically linked with a high initial LAR, which initially drives species differences in absolute growth and RGR (Marañón and Grubb 1993, Sack and Grubb 2001). However, the seed size-LAR linkage decreases over time. For older seedlings (>20 weeks old) and saplings, RGR rank hierarchies in shade at least partially reflect, or drive,

commonness in deep shade (Pacala et al. 1994, Sack and Grubb 2001, Lin et al. 2002, Lusk and Del Pozo 2002).

Additionally,  $T_{\text{final mass}}^{\text{shade}}$  and  $T_{\text{final mass}}^{\text{drought}}$  might in themselves confer tolerance of shortage in the field. A species’ robustness to stressors, and its resilience in the field might depend on the proportion it achieves of an ‘optimal’ growth rate attainable at high, though not inhibitory resource levels (Rosen 1967). Further, species with high  $T_{\text{final mass}}^{\text{shade}}$  and  $T_{\text{final mass}}^{\text{drought}}$  are by definition resistant to suppression by shade and drought respectively, and as they encroach on limited resources, they may increasingly suppress other species. These hypotheses require further investigation. We note that alone none of RGR, survival,  $T_{\text{final mass}}^{\text{shade}}$  or  $T_{\text{final mass}}^{\text{drought}}$  is likely to fully explain field shade and drought tolerance. Species’ relative commonness in conditions of shade and drought depend both on RGR and survival throughout establishment as well as their responses to other resource shortages, and to mechanical damage, herbivores and pathogens, different across systems (Kobe 1996, Sack and Grubb 2003).

Biomass allocation and its plasticity were not found to be a significant general basis for  $T_{\text{final mass}}^{\text{shade}}$  and  $T_{\text{final mass}}^{\text{drought}}$  in ways previously hypothesized. According to one hypothesized mechanism for a trade-off between shade tolerance and drought tolerance (Introduction) shade tolerance would be associated with high light capture ability, conferred by a low RMF, and high SLA, LMF and LAR, as well as by a plant’s ability in deeper shade to reduce RMF, and to increase SLA, LMF and LAR via a high plasticity. Further, according to this hypothesis, drought tolerance would be associated with the opposite set of traits, a high RMF, and low SLA, LMF and LAR, as well as the ability to increase RMF, and to reduce SLA, LMF and LAR in dry soil. According to this view, tolerance is thus primarily achieved through specialized resource capture, with a trade-off arising between capture of irradiance and capture of water. However, as seen above, across species,  $T_{\text{final mass}}^{\text{shade}}$  and  $T_{\text{final mass}}^{\text{drought}}$  were apparently linked with slow high-resource RGR, and with traits potentially conferring a reduced resource demand, such as low SLA and LAR, which are linked with long leaf lifespans (Walters and Reich 1999, Sack et al. 2003).  $T_{\text{final mass}}^{\text{shade}}$  was also generally linked with low plasticity in these traits, consistent with previous work on trees and shrubs (Grubb et al. 1996, Veneklaas and Poorter 1998, Valladares et al. 2000).  $T_{\text{final mass}}^{\text{drought}}$  was not generally linked with the plasticity of biomass allocation across water supplies.

### The independence of shade tolerance and drought tolerance: potential for niche differentiation

No evidence was found to support any absolute interspecific trade-off between shade tolerance and

drought tolerance. Shade and drought tolerances experimentally quantified in terms of growth and survival varied considerably and independently. Notably, species were not included in this study to represent every expected combination of expected shade/drought tolerance (Table 1). Thus, the possibility remains that if numerous shade-tolerant, drought-sensitive species had been included, a weak overall negative trend might have arisen. However, the lack of any trade-off signal despite strong variation in species' shade and drought tolerances stands against any absolute, inherent interdependence of shade and drought tolerance as previously hypothesized (Smith and Huston 1989). As noted above, the fact that seedlings were grown in a given soil volume leaves a trade-off mechanism untested: shade tolerant species might root less deeply than light demanding species, and thus achieve less drought tolerance. However, such a trade-off is very unlikely to be inherent or absolute, given the improbability of any strict correspondence of light demand and rooting depth across species. In Mediterranean forest, shade tolerant seedlings have been found to root as deeply, relative to plant mass, as light demanding species (Sack et al. 2003).

Consistent with the finding of independent shade and drought tolerances for this species set, qualitative indices of shade and drought establishment varied independently for 42 tree species of Central Europe (Coomes and Grubb 2000, data of Ellenberg 1988). Independent tolerances of shade and drought implies a strong potential for species niche differentiation across combinations of irradiance and water supply in the field (Latham 1992, Wright 2002). Certain species have apparently considerable tolerance of combined shade and drought, such as *Buxus*, *Hedera* and *Ruscus*. Species with strong dual tolerance may in fact occur relatively frequently among forest understorey species in temperate and tropical systems (Wright et al. 1992, Caspersen and Kobe 2001, Engelbrecht and Kursar 2003, Sack et al. 2003). These species may be advantaged in understorey dry sites, especially as climates become drier.

### Limitations of the study and future work

The method used to approximate equal drought across species and irradiances was effective, though it allowed transient minimal divergences in water supply. Notably, total soil water content used as a variable does not account for the regions of localised high supply that occurred near the surface after re-watering, which drive some degree of rehydration, and possibly growth. However, the small pots contained relatively sandy soil; water permeated rapidly, and in the drought treatments, stomatal conductance declined progressively with soil water content.

In this study, each experiment tested the impacts of two different irradiances, and two water supplies. In future work, the finding of orthogonal impacts of shade and drought on RGR would usefully be confirmed for a continuum of irradiances and water supplies. Similarly, the plasticity of biomass allocation across irradiances and water supplies would usefully be characterized over a range of resource supplies. If experimental resource supplies are well replicated and quantified, accurate comparisons may be made between studies conducted at geographically and climatically disparate sites.

As in other pot studies, these experiments relied on the assumption that pot-grown plants can provide a sound indication of seedling growth patterns in the field, despite potentially altered root allocation and morphology. There is recent support for this assumption (Bloor 2003). Further, the experiments focused only on seedlings in their first season, critical for establishment. However, as plant size increases, absolute growth rates increase, and biomass partitioning patterns change; relative growth rates decline, and shade and drought tolerances may increase or decrease (Evans 1972, Walters et al. 1993, Cavender-Bares and Bazzaz 2000, Sack and Grubb 2001). Thus, experiments on seedlings of larger sizes and saplings will be essential to extend the findings of this study. Larger plants may show additional drought tolerance by accessing deeper water (Kozlowski 1949, Fisher et al. 1991). An exciting challenge is to investigate the contribution of differential rooting depths to drought response, in different irradiances (Donovan and Ehleringer 1994, Sack et al. 2003).

An overall objective is to mechanistically link seedling responses with field dynamics, especially as more data become available from large forest plots, to understand the maintenance of species-richness. In the field there are many additional axes of variation; irradiance and water fluctuate temporally (e.g. via sunflecks and short rainfall events), and plants access varying nutrient supplies, interact with mycorrhizae, and face mechanical damage, pathogens and herbivores (Fitter 1988, Grubb et al. 1996, Ackerly 1997, Robison and McCarthy 1999). Compounded by the variation in these factors, species differences in shade and drought responses have potential to contribute extensively to dynamics during establishment, and to co-existence.

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