Oecologia (2002) 131:175–185
DOI 10.1007/s00442-002-0873-0

ECOPHYSIOLOGY

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# The combined impacts of deep shade and drought on the growth and biomass allocation of shade-tolerant woody seedlings

Received: 7 May 2001 / Accepted: 28 November 2001 / Published online: 1 March 2002

**Abstract** To test whether the impact of drought on the growth and biomass allocation of first-season shade-tolerant woody seedlings in low irradiance differs from that in high irradiance, seedlings of *Viburnum lantana*, *V. opulus*, *V. tinus* and *Hedera helix* were grown in pots at two watering frequencies × three irradiances. Hypotheses in the recent literature variously predict that drought will have a stronger, weaker or equal impact on seedling relative growth rate (RGR) in deep shade relative to that in moderate shade. Experimental irradiance levels were selected in the typical range for temperate deciduous forest seedlings in either understorey or clearings: 3–4% daylight (low red: far-red shade), 3–4% daylight (neutral shade), and 30–40% daylight (neutral shade). Watering was ‘frequent’ (every 3–4 days) or ‘infrequent’ (five times during the 8-week experiment), producing soil matric potentials as low as –0.03 MPa, and –2 MPa. To prevent the interaction of irradiance and watering treatments, each seedling was grown in a ‘shade tower’ that was surrounded by an uncovered sward of grass (*Festuca rubra*), which depleted pot water at the same rate regardless of the species of seedling, or its irradiance treatment. Shading affected all species: seedlings in 3.5% daylight grew at 56–73% of their dry-mass RGR in 35% daylight. Low red: far-red shade reduced the RGR of *Hedera* to 68% of its value in neutral shade. Infrequent watering significantly reduced the RGR of only *V. lantana* and *V. opulus*, by approximately the same proportion across irradiance treatments. Infrequent watering did not significantly alter any species’ biomass allocation across irradiance treatments. Such orthogonal impacts of deep shade and drought on seedling growth and biomass allocation indicate a large potential for niche differentiation at combinations of irradiance and water supply for species of forest seedlings, and suggest a multiplicative-effects approach for modelling seedling performance in microsites with different combinations of irradiance and water supply.

**Keywords** Red: far-red ratio · Leaf nutrients · Mediterranean climate · Plasticity · Stress tolerance

## Introduction

A knowledge of woody seedling growth responses to combined effects of shade and drought is important to explain species niche differentiation in many forest and scrub systems (e.g. Streng et al. 1989; Barton 1993; Burslem 1996; Walters and Reich 1997; Kollmann and Grubb 1999). Given information of survival rates (see, for example, Kobe 1999), this knowledge will allow prediction of seedling performance at given microsites. One fundamental question is whether a given drought (i.e. a given reduction of soil matric potential) has a stronger impact on seedling growth in deep shade or at higher irradiance. In the recent literature there are five divergent predictions.

The influential *trade-off hypothesis* predicts that drought has a stronger impact on individuals of a species grown in deep shade than on those in higher irradiance. This trade-off might arise if shaded plants have a high specific leaf area (lamina area/plant dry mass) and leaf area ratio (lamina area/total dry mass), for efficient irradiance capture at the expense of their root allocation, resulting in a greater sensitivity to drought (Smith and Huston 1989). Additional mechanisms for a trade-off have been indicated in specific cases (Marshall 1986; Vance and Zaerr 1991; Kubiske et al. 1996). On the other hand, two hypotheses predict that drought has a *weaker* impact on plants of a given species in deep shade. According to the *primary-limitation hypothesis* (Canham et al. 1996) this pattern occurs because the deeper the

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shade, the less water limits growth, so the less the impact of drought. According to the *above-ground facilitation hypothesis* (Holmgren 2000), this same pattern results from the fact that shade reduces leaf and air temperatures, vapour-pressure deficit, and the oxidative stresses that can aggravate the impact of drought at higher irradiance (Valladares and Pearcy 1997). Indeed, moderate shade (down to 20–40% daylight) often improves plant performance relative to plants in full daylight, during drought (see Callaway 1995; Rousset and Lepart 2000) – but the degree to which deep shade (i.e. <5% daylight) can be facilitative is unclear. A fourth hypothesis, the '*interplay*' hypothesis (Holmgren et al. 1997) predicts that the impact of drought is relatively strong at high irradiance, weaker in moderate shade (because of facilitation), and strong in deep shade. Finally, a null, *independent-effects* model (Nobel 1999) predicts that drought reduces relative growth rate (RGR) by a given proportion at any irradiance – i.e. that the impacts of deep shade and drought are orthogonal.

Several field studies have been made of seedling performance in different irradiance regimes during natural drought (e.g. Fisher et al. 1991; Sipe and Bazzaz 1995; Veenendaal et al. 1996), but the results often conflict, apparently because soil dryness varies differently across irradiance regimes in different systems (e.g. Abrams 1986; Vitousek and Denslow 1986; Ellsworth and Reich 1992; Poorter and Hayashida-Oliver 2000). Controlled studies are therefore needed for further progress, and there have been several (Kolb et al. 1990; Papavassiliou 1991; Dale and Causton 1992b; Canham et al. 1996; Groom and Lamont 1997; Van Hees 1997; Baruch et al. 2000; Holmgren 2000). However, few studies have included deep shade treatments (<5% daylight), or species that occur naturally in deep shade. Further, some studies apparently imposed a stronger drought treatment on the seedlings at higher irradiance: drought is generally applied by allowing the seedlings to dry their own soil, and the seedlings at high irradiance deplete their soil water sooner due to their faster transpiration, and their progressively larger size (Abrams et al. 1992; Coomes and Grubb 2000).

In this study we applied independent irradiance and water treatments to test the impacts of combined shade and drought on shade-tolerant species, in terms of yield, RGR and biomass allocation. We compare seedlings grown in various irradiance × water supply combinations for a given time: the first season of growth, which is critical in determining establishment patterns (Grubb 1977). Each seedling was covered by an individual 'shade tower' and surrounded by an uncovered grass sward to deplete pot water uniformly across irradiance treatments (Papavassiliou 1991; Fig. 1). The experiment also tested for interaction between the effects of red: far-red ratio and water supply.

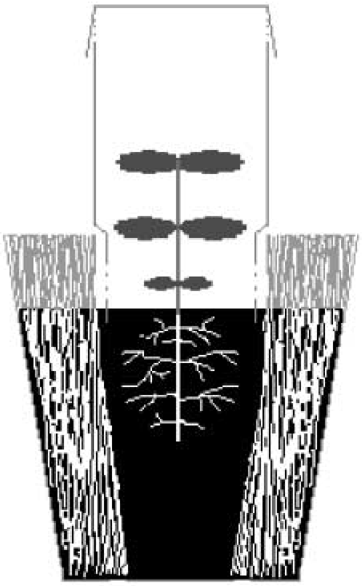


**Fig. 1** The experimental unit: a seedling in its shade tower, surrounded by a grass sward, soon after transplanting the seedling. In later stages of the experiment there was ingrowth of the grass roots into the seedling's soil. Gaps in the shade tower indicate pathways of air exchange. Shade tower dimensions: 10–11 cm diameter main body; 8 cm diameter base; 18 cm height

Three *Viburnum* species were selected that range in drought tolerance: in central and northern Europe *V. opulus* occurs at moist sites, and *V. lantana* at drier sites, while in forests of the Mediterranean Basin *V. tinus* persists through strong seasonal drought, as does *Hedera helix*. *Hedera* is also native to forest and scrub in central and northern Europe, along with *V. opulus* and *V. lantana* (Rodwell 1991). These species' relative performances in the field probably depend on irradiance, soil nutrient concentrations and water supply (Grubb et al. 1996; Kollmann and Grubb 1999).

## Materials and methods

### Site, soil and plant material

In April 1998 a rain-out shelter of 20 m$^2$ ground area with a roof of transparent plastic was set up at the University of Cambridge Botanic Garden (UCBG), running east to west. The soil under the shelter was levelled, sprayed with RoundUp Proactive herbicide, and covered with one layer of black polythene and sheets of corrugated plastic to raise pots and facilitate run-off of excess water.

The soil for the experiment was a clay loam with a pH of 6.0–6.5. Pots (18 cm) were filled with 2.6 kg of sieved and mixed soil, which reached to ca. 5 cm below the rims. On 14 May, 15 ml of *Festuca rubra* seed (Herbiseed, Billingbear Park, Wokingham, UK) was sown on the surface of the soil in each pot, leaving clear a central disk of 9 cm diameter, which was covered with an inverted plastic cup to keep the grass from invading. The pots were placed under the shelter and covered with green plastic mesh. The grass began to emerge 1 week later, and was cut to the level of the pot at least once per week until the end of the experiment, to maintain a consistent height of ca. 5 cm, adequate for the grass to deplete soil resources (Wang 1989).

Fruits of *Hedera helix* (Araliaceae; nomenclature follows Tutin et al. 1964–1980) were collected from large plants on two large trees outside Cambridge, on 28 February, and seeds were extracted by hand. Along with seeds of *Viburnum lantana* (Caprifoliaceae; supplied by Forestart, Church Farm, Hadnall, Shropshire, UK) they were sown for germination on trays, in soil at a depth of ca. 1 cm, and the trays were covered with green plastic mesh. On 14 April, the trays of emergent seedlings were transferred to 3% daylight (neutral shade). On 18–22 May, these seedlings, and first-season *V. opulus* seedlings (3.5–5 cm height; supplied by Forestart), were transplanted into 60 mm pots of soil and placed in 3% daylight (neutral shade). First-season *V. tinus* seedlings were collected from the shaded understorey of forest on the Sierra Aljibe, south of Sevilla, Spain (described in Ojeda et al. 1995), on 20 May, and on arrival in Cambridge they were likewise transplanted into soil in 60 mm pots, in 3% daylight (neutral shade). All seedlings were watered every 1–2 days.

Immediately prior to the experiment, the seedlings from each species were sorted into size-class groups, and equal numbers of seedlings from each group were randomly sorted into treatments for each block. On 4–7 July, each seedling was transplanted to one of the large pots with a grass sward; a standard volume of soil was removed from the centre of the large pot and the seedling with the soil from the 60 mm pot was inserted. The large pots were then placed under the shelter, and the seedlings were covered with the appropriate ‘shade towers’ (individual irradiance treatments; Fig. 1).

## Irradiance treatments

Shade towers were of three types: 3–4% daylight (low red: far-red shade), 3–4% daylight (neutral shade), and 30–40% daylight (neutral shade). These treatments are hereafter referred to as 3.5% low red: far-red, 3.5% neutral and 35%. For each shade tower, rectangles of lighting filter and taffeta (for the 3.5% treatments) were wrapped around a chicken wire frame, and held with a rubber band; squares of lighting filter and taffeta were stapled to the top. Shaded openings at the top rim and around the base permitted ventilation and heat exchange (Fig. 1). Two types of cellophane lighting filters (Lee Colortron International, Ladbroke Hall, London, UK) were used: Lee 130 Green (3.5% low red: far-red), and Lee 130 Clear (3.5% neutral and 35% treatments). Layers of taffeta were added as follows: 2 layers (low red: far-red), 5 layers (3.5% neutral), and none (35% neutral).

Transmittance spectra were determined using a scanning spectrophotometer (Unicam Helios, Unicam, Cambridge, UK). The clear lighting filter and taffeta absorbed evenly over the visible spectrum, whereas for the low red: far-red filter the ratio of transmittance at 660 nm (±10 nm) to 730 nm (±10 nm) was 0.35 (cf. Smith 1982). The degree of daylight penetration through the shade towers to seedling level was measured on a flat area in the UCBG on a cloudy day, using a quantum sensor (Skye SKP 200/215, Skye Instruments, Powys, UK). The shading from the roof of the rain-out shelter varied throughout the shelter from 68 to 76%. The mean of 24 readings (72%) was multiplied by the shade factor provided by the shade towers in calculating the overall shading provided by the irradiance treatments.

Specimen readings of the temperature of the air surrounding randomly-chosen seedlings from each irradiance treatment were made on 1 September, a sunny day with light wind and fluctuating cloud cover and temperature, repeatedly over the course of two hours beginning at noon (using a thermocouple type K with digital readout, R.S. Components, Corby, Northamptonshire, UK). The readings ranged from 18.8°C to 27.7°C, and at any time only very small differences (<1.0°C) were found between shade towers, or between the shade towers and outside.

## Watering treatments

Until the beginning of the experiment, 22 July, the pots were watered every 4 days. During the experiment, two watering frequencies were used, ‘frequent’ (FW), i.e. soil watered to field capacity each 3–4 days, such that the soil surface always remained moist, and ‘infrequent’ (IW), i.e. five times during the 8-week experiment. The watering of all the IW pots was cued once five seedlings of *V. lantana* (intermediate in drought tolerance among the study species) had begun to wilt in each irradiance treatment. The aim was to impose a strong cyclic drought to simulate a natural pattern, but without killing seedlings.

To estimate soil water status throughout the experiment, a sample of 22 IW pots and 22 FW pots was selected randomly at the start of the experiment, two pots from each species × irradiance treatment combination. These sample pots were weighed with a spring balance before and after each watering session. The mean whole-pot soil water content was estimated for each treatment at each watering session (Fig. 2a), by subtracting from the mean total mass of the sample pots a mean mass for the shade tower and pot, the grass and the soil, dividing by the soil dry mass, and multiplying by 100%. The mean dry mass of soil in the pots was determined by weighing pots at field capacity, and then weighing soil samples from 20 extra pots at field capacity, and then after oven-drying for 72 h at 70°C. Soil was held to be at field capacity after being watered to saturation, once 30 min had elapsed after water stopped dripping from the pot. The fresh mass of grass was determined at the end of the experiment for four pots randomly selected from each watering treatment. The soil was watered to field capacity, the grass was left to saturate overnight; before weighing, the shoots and roots were washed free of soil and blotted dry. A curve relating soil matric potential to soil water content (Fig. 2b) was constructed for the garden soil using the filter-paper technique (Deka et al. 1995).

## Blocking

For *V. lantana*, *V. opulus*, and *Hedera*, 12 plants were grown in each treatment. The limited number of *V. tinus* seedlings available permitted only 8 plants per treatment, with the 3.5% low red: far-red shade treatments omitted. Pots from all treatments were randomly allocated to four blocks under the shelter, to prevent treatment aggregation (see Hurlbert 1984). The locations of the four blocks under the shelter were randomised each 2 weeks, and within each block the 50% of the pots close to the inside of the shelter were alternated with those close to the edge, and within these groups the pots were randomised.

## Initial and final harvests

At the time of transplanting newly-emergent seedlings into 18 cm pots ($t_o$) the fresh mass of each experimental seedling was determined, as were the fresh mass values of 6–20 extra seedlings for each species. These extra seedlings were harvested when the experimental seedlings were transplanted to the grass pots ($t_o'$), and a least-squares regression was plotted for each species, for $t_o'$ dry mass versus $t_o$ fresh mass ($R^2$=0.48–0.77, $P$<0.05), and a $t_o$ dry mass was estimated for each experimental seedling.

The blocks were harvested from 20 September to 1 October, in random sequence, 1 each 3 days. The seedlings were washed free of soil, and then leaves, stem and roots were weighed, and the remaining parts were weighed again after oven-drying for >48 h at 70°C. Before drying, seedling total leaf lamina areas were determined (leaf area meter, Delta-T Devices).

Nutrient analyses were performed on Kjeldhal digests (380°C for 3 h in concentrated sulphuric acid with mercuric oxide and hydrogen peroxide) of pooled-leaf samples (two to four samples, as volume allowed; Table 1). Concentrations of total nitrogen and total phosphorus were determined by continuous-flow colorimetry (ChemLab Scientific Products, Hornchurch, UK) and concentrations of total potassium by flame emission spectrophotometry (Corning Flame Photometer 410, Corning, New York).

## Analysis

RGR was calculated as [ln (final total dry mass)–ln ($t_o'$ dry mass)]/growth time. Mean values for root mass fraction (RMF), stem mass fraction (SMF), and leaf mass fraction (LMF) were calculated

**Fig. 2 a** Mean gravimetric pot soil water content (SWC) throughout the experiment for sample experimental pots frequently (*FW*) and infrequently watered (*IW*). *Error bars* indicate standard error. The initial sample pot *n* was 22 in each treatment; by the end of the experiment *n* was 21 and 19 for the IW and FW treatments respectively, due to removal of sample pots when seedlings died. **b.** Soil matric potential (Ψ) versus SWC, determined for the experimental soil using the filter paper method

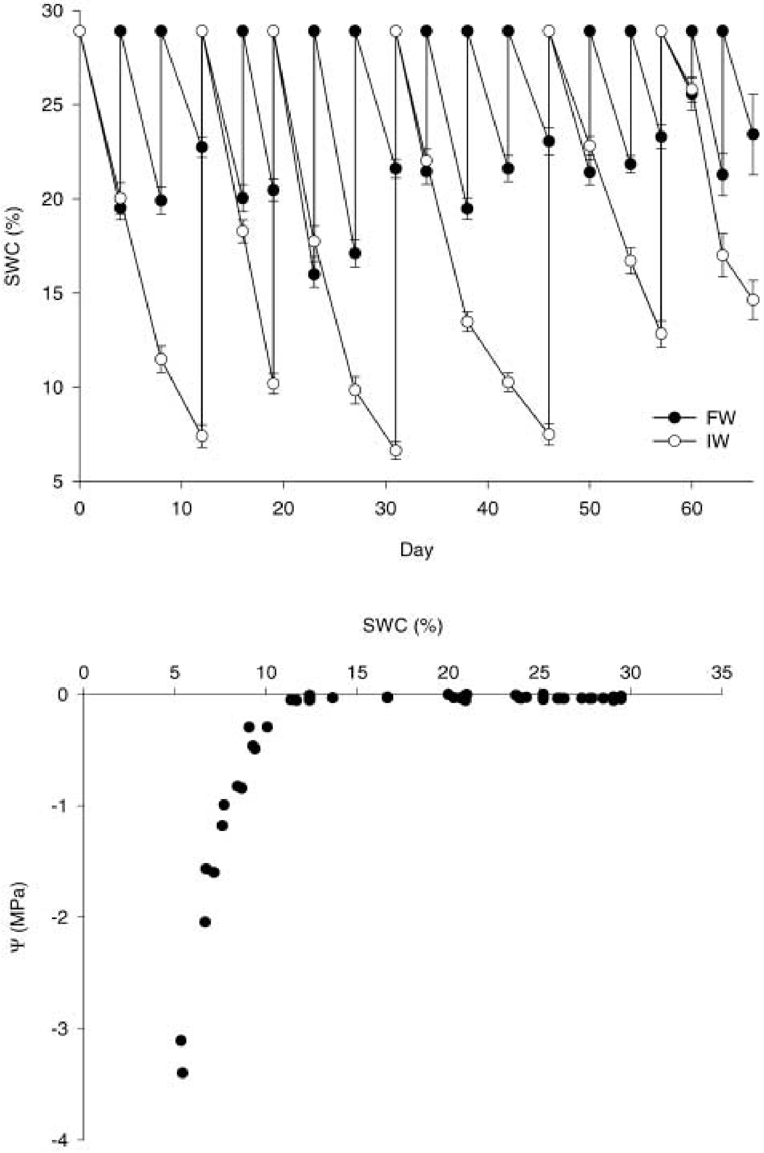


**Table 1** Mean final dry mass values of experimental seedlings in each treatment at final harvest, number of seedlings dead, and mean foliar nutrient concentrations. *FW* and *IW* indicate, respectively, frequent watering, and infrequent watering

| Species | Irradiance treatment | Mean final dry mass (mg); number of seedlings dead, if >0 | | Foliar nutrient concentration (mg/g dry mass) | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Sample *n* | | N | | P | | K | |
| | | FW | IW | FW | IW | FW | IW | FW | IW | FW | IW |
| *Viburnum lantana* | 3.5% low red: far-red | 37.6±1.30 | 33.8±2.01; 3 | 4 | 4 | 17.5±1.0 | 13.8±2.0 | 4.10±0.75 | 3.38±0.55 | 27.6±3.0 | 29.1±2.2 |
| | 3.5% neutral | 39.5±2.28; 2 | 35.7±1.36 | 4 | 4 | 13.0±1.4 | 14.4±0.60 | 2.84±0.75 | 3.25±0.21 | 24.2±3.0 | 26.2±1.1 |
| | 35% | 81.2±4.36 | 67.3±4.76; 3 | 4 | 4 | 5.16±1.0 | 5.34±1.7 | 1.24±0.19 | 1.90±0.43 | 9.88±0.51 | 11.5±0.51 |
| *V. opulus* | 3.5% low red: far-red | 189±23.3 | 148±10.5 | 4 | 2 | 16.4±0.69 | 16.6±0.23 | 4.00±0.71 | 4.47±0.24 | 26.7±0.64 | 26.4±0.64 |
| | 3.5% neutral | 211±21.0 | 160±11.3 | 3 | 4 | 15.9±0.56 | 13.9±2.3 | 4.00±0.46 | 3.84±0.88 | 27.6±2.8 | 25.5±1.3 |
| | 35% | 278±10.5 | 222±12.5 | 4 | 4 | 7.41±0.80 | 8.40±1.3 | 2.59±0.64 | 2.79±0.64 | 21.8±0.71 | 22.6±2.6 |
| *V. tinus* | 3.5% neutral | 66.5±7.50; 3 | 63.7±3.68 | 3 | 4 | 13.7±0.97 | 10.3±1.3 | 1.74±0.27 | 1.10±0.24 | 15.3±6.5 | 12.2±1.5 |
| | 35% | 107±5.61; 2 | 101±6.49; 4 | 2 | 4 | 8.80±2.4 | 8.59±2.3 | 2.14±1.30 | 1.36±0.30 | 9.78±1.4 | 11.4±5.5 |
| *Hedera helix* | 3.5% low red: far-red | 66.9±3.16 | 62.9±4.45 | 4 | 3 | 17.7±0.68 | 16.7±1.0 | 1.65±0.22 | 1.42±0.090 | 29.1±1.5 | 33.4±2.6 |
| | 3.5% neutral | 93.5±5.11 | 89.2±7.02 | 4 | 3 | 14.5±0.77 | 15.5±0.67 | 1.28±0.054 | 1.59±0.13 | 28.1±0.54 | 35.5±1.2 |
| | 35% | 134±6.56 | 130±9.48 | 4 | 4 | 6.08±0.31 | 7.60±0.40 | 0.71±0.028 | 0.68±0.025 | 14.5±1.1 | 16.8±0.66 |

**Table 2** Results of ANOVAs and MANOVAs on log-transformed data for dry-mass relative growth rates (RGR) and biomass allocation variables. Mean squares (MS) are reported for ANOVAs, and *F*-values for Wilk's test statistics for MANOVAs. Tests for the effect of irradiance quantity (3.5%N vs 35%) and irradiance quality (3.5%N vs 3.5%LR:FR) were made by planned orthogonal contrast for all species but *V. tinus*. Significance levels: * 0.05> $P \geq 0.01$; ** 0.01> $P \geq 0.001$; *** $P<0.001$. †Two *V. opulus* seedlings and two *V. tinus* seedlings were excluded from RGR determination as $t_o'$ values were not available ($t_o$ values were outside the range of those sampled for the $t_o'$ versus $t_o$ calibration curve). Two *V. lantana* seedlings were excluded from mean SLA determination as their leaves were desiccated; two *V. opulus* seedlings that sensesced their leaves before the end of the experiment were excluded from all biomass allocation analyses. Interactions of block and other factors, and three-way interactions were never significant, and are omitted

| Species | Factor | MANOVA | ANOVAs | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | Final biomass | RGR | SLA | RMF | SMF | LMF |
| *Viburnum lantana* | Irradiance (total effect) | 18.9*** | 0.606*** | 0.471*** | 0.276*** | 0.165*** | 0.00332 | 0.0147* |
| | 3.5%N vs 35% | | 0.953*** | 0.779*** | 0.435*** | 0.223*** | 0.00906 | 0.0129* |
| | 3.5%N vs 3.5%LR:FR | | 0.00509 | 0.000458 | 0.00560 | 0.0121 | 0.000069 | 0.000375 |
| | Watering frequency | 4.71** | 0.0546** | 0.0902** | 0.00548 | 0.0247 | 0.00225 | 0.00159 |
| | Block | 1.15 | 0.00221 | 0.00723 | 0.00188 | 0.0394 | 0.00942* | 0.00461 |
| | I×W | 0.550 | 0.00241 | 0.00245 | 0.000226 | 0.00069 | 0.000922 | 0.00149 |
| | Residual MS, df | | 0.00613,–40 | 0.00813,–40 | 0.00316,–38† | 0.0157,–40 | 0.00276,–40 | 0.00316,–40 |
| *Viburnum opulus* | Irradiance (total effect) | 13.52*** | 0.229*** | 0.338*** | 0.0949*** | 0.0350*** | 0.0711*** | 0.00042 |
| | 3.5%N vs 35% | | 0.246*** | 0.339*** | 0.148*** | 0.0540*** | 0.119*** | 0.000716 |
| | 3.5%N vs 3.5%LR:FR | | 0.0228 | 0.0400 | 0.000037 | 0.0000013 | 0.000297 | 0.000642 |
| | Watering frequency | 4.17** | 0.176** | 0.345*** | 0.000206 | 0.00358 | 0.000042 | 0.00184 |
| | Block | 0.897 | 0.00666 | 0.0111 | 0.000766 | 0.00865 | 0.0155 | 0.0112 |
| | I×W | 1.17 | 0.00070 | 0.00788 | 0.000038 | 0.000240 | 0.00257 | 0.00042 |
| | Residual MS, df | | 0.0168,–48 | 0.0163,–46† | 0.00169–46† | 0.00372,–46† | 0.00757,–46† | 0.0132,–46† |
| *Viburnum tinus* | Irradiance | 16.9* | 0.177*** | 0.164** | 0.0836*** | 0.0606*** | 0.0411** | 0.00339 |
| | Watering frequency | 0.417 | 0.000004 | 0.00278 | 0.000295 | 0.000396 | 0.00125 | 0.000365 |
| | Block | 0.680 | 0.0110 | 0.00639 | 0.000163 | 0.000114 | 0.00142 | 0.000892 |
| | I×W | 1.16 | 0.000351 | 0.00137 | 0.000177 | 0.00269 | 0.00899 | 0.00149 |
| | Residual MS, df | | 0.00387, 10 | 0.00574, 8† | 0.00196, 10 | 0.00257, 10 | 0.00383, 10 | 0.00375, 10 |
| *Hedera* | Irradiance (total effect) | 35.0*** | 0.572*** | 0.638*** | 0.383*** | 0.0548** | 0.0218* | 0.0942*** |
| | 3.5%N vs 35% | | 0.316*** | 0.242*** | 0.567*** | 0.0732* | 0.0375* | 0.146*** |
| | 3.5%N vs 3.5%LR:FR | | 0.257*** | 0.403*** | 0.000095 | 0.000906 | 0.000849 | 0.000195 |
| | Watering frequency | 0.766 | 0.0129 | 0.00496 | 0.000189 | 0.0129 | 0.00204 | 0.00334 |
| | Block | 1.26 | 0.0123 | 0.0111 | 0.00233 | 0.0207 | 0.00696 | 0.00153 |
| | I×W | 0.326 | 0.000327 | 0.000033 | 0.000276 | 0.00037 | 0.00176 | 0.00150 |
| | Residual MS, df | | 0.00694,–48 | 0.00660,–48 | 0.00181,–48 | 0.0104,–48 | 0.00592,–48 | 0.00248,–48 |
| All species | Species | 96.0*** | 2.70*** | 0.533*** | 0.347*** | 1.04*** | 0.0999*** | 0.539*** |
| | Irradiance quantity | 128*** | 1.15*** | 1.05*** | 0.806*** | 0.316*** | 0.0464** | 0.0631** |
| | Watering frequency | 2.29* | 0.0583* | 0.0797** | 0.00158 | 0.0155 | 0.00322 | 0.00220 |
| | Block | 0.679 | 0.00194 | 0.00412 | 0.000304 | 0.00610 | 0.00679 | 0.00186 |
| | S×I | 6.86*** | 0.0502** | 0.0337* | 0.0281*** | 0.0140 | 0.0524*** | 0.0269** |
| | S×W | 1.18 | 0.0152 | 0.0263* | 0.000805 | 0.00221 | 0.000342 | 0.000328 |
| | I×W | 0.503 | 0.00145 | 0.00265 | 0.000074 | 0.00157 | 0.00278 | 0.000024 |
| | Residual MS, *df* | | 0.00919,–107 | 0.00858,–103 | 0.00216,–104 | 0.00830,–105 | 0.00540,–106 | 0.00557,–106 |

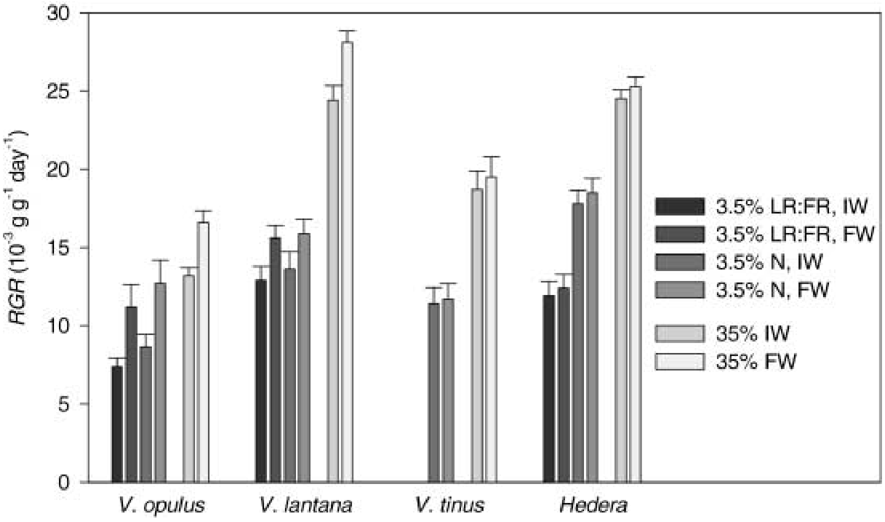


**Fig. 3.** Dry mass relative growth rates over the whole of the experiment for the seedlings in the different treatments. *LR:FR*, *N*, *FW* and *IW* indicate respectively low red: far-red shade, neutral shade, frequent watering, and infrequent watering

as the dry mass of respectively root, stem (including petioles) and leaf laminae divided by the total dry mass, averaged for all seedlings in a treatment. Specific leaf area (SLA) was calculated as lamina area/lamina dry mass. We note that since biomass allocation often depends on seedling size (Evans 1972), 'treatment' effects in this study integrate size-related and size-independent treatment effects. Our aim was to test whether the overall impacts of shade and drought are orthogonal on RGR and biomass allocation, as determined at the end of a first growth season (Coleman et al. 1994; Poorter and Nagel 2000). Allometric analysis can provide detail by separating treatment effects into size-related effects and size-independent effects. However, such analysis is weak using the data of single-harvest experiments; weakly-significant 'static allometries' are found, which do not necessarily reflect ontogeny (see Smith 1981; Strauss 1993).

Because individual irradiance treatments were applied with the shade towers, each seedling is a true replicate (see Hurlbert 1984). For each species, all growth and biomass allocation variables together (see Table 2) were tested for the effects of block × irradiance treatment × watering frequency, by MANOVA, and then each variable was tested separately for the effects of the factors by three-way ANOVA. For each species excluding *V. tinus*, a test was made for the effect of irradiance *quantity* (using a comparison of the 35% treatment with the 3.5% neutral treatment), as well as the effect of irradiance *quality* (using a comparison of the 3.5% neutral treatment with the 3.5% low red: far-red treatment). Comparisons were made using planned orthogonal contrasts (Gilligan 1986; Sokal and Rohlf 1995). Finally, the data for *all species together* were tested (excluding data for the 3.5% low red: far-red treatment, since such data were not available for *V. tinus*) for the effects of species, irradiance, water, and block. The effects of all factors and their interactions on all variables together were tested by MANOVA, and the effects on individual variables were tested by four-way ANOVA, excluding four-way interactions for increased power (Zar 1999). Prior to analyses, all data were log-transformed, to model for multiplicative effects (Gilligan 1986). For any variable, a significant irradiance × water interaction would indicate that the proportional impact of infrequent watering differed across the irradiance treatments (and, equally, that the proportional impact of deeper shade differed across watering treatments). Statistics were calculated using Minitab Release 12.1, and Genstat 5.

## Results

### Efficacy of treatments and design

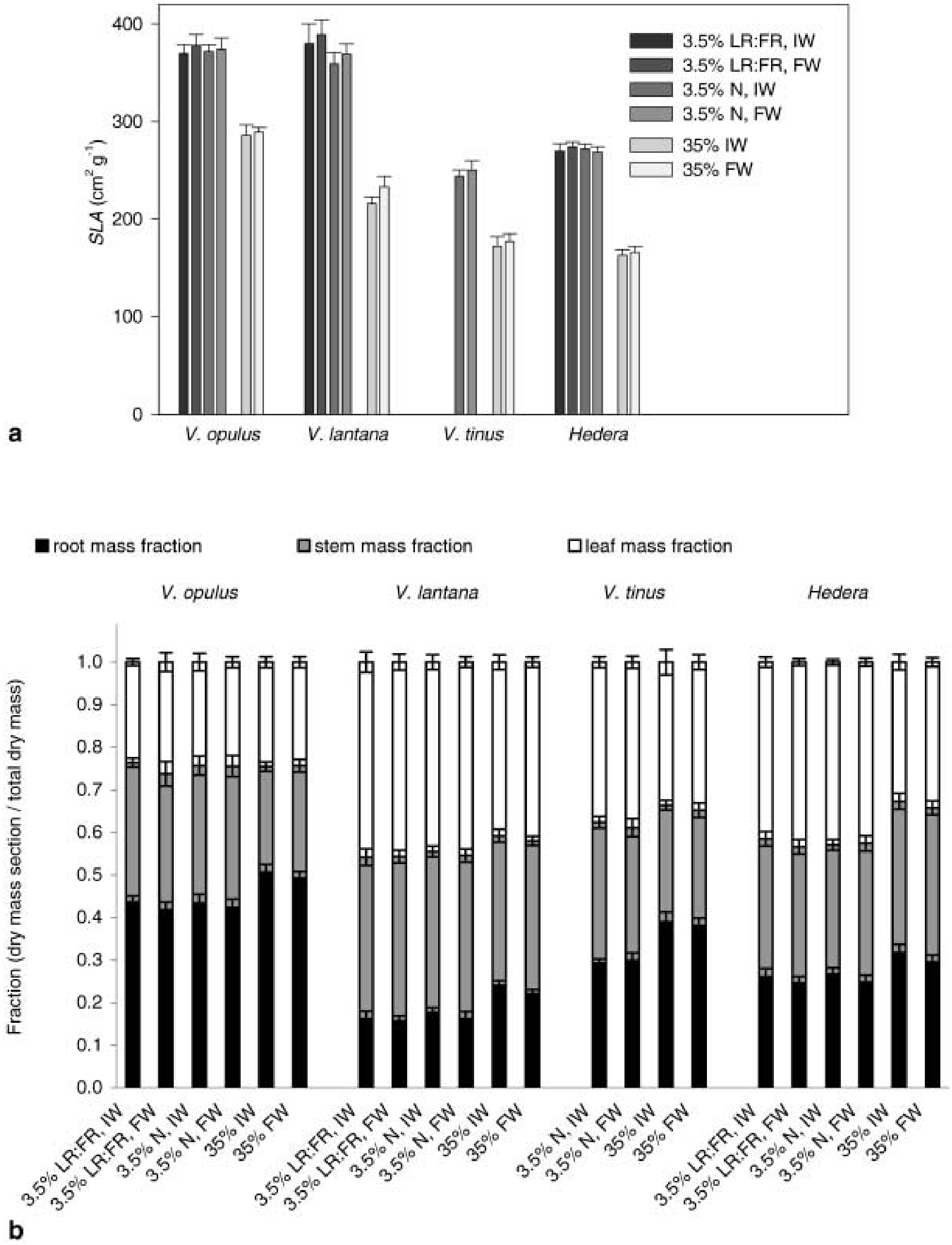
The grass swards were effective in drying the soil in the pots evenly across irradiance treatments. There was no significant effect of irradiance treatment on the sample pot soil water contents throughout the experiment, and no significant interaction between irradiance treatment and time (repeated-measures ANOVA; effect of irradiance treatment $F_{\mathrm{FW};\,1,20}=0.14$; $F_{\mathrm{IW};\,1,\,20}=2.3$; $P>0.05$; effect of irradiance treatment × time $F_{\mathrm{FW};\,15,\,259}=1.05$; $F_{\mathrm{IW};\,15,\,282}=1.3$; $P>0.05$). Further, the different *species* were subjected to the same soil drying (repeated-measures ANOVA; effect of species $F_{\mathrm{FW};\,3,18}=2.7$; $F_{\mathrm{IW};\,3,\,18}=1.6$; $P>0.05$; effect of species×time $F_{\mathrm{FW};\,45,\,229}=1.0$; $F_{\mathrm{IW};\,45,\,252}=1.3$; $P>0.05$). A pooled sample pot soil water content was calculated for each of the FW and IW treatments at each watering session (Fig. 2a): matric potentials fell as low as –0.03 MPa and –2 MPa respectively (Fig. 2a, b).

Very little mortality occurred (Table 1). The higher mortality for *V. tinus* reflected the death of those seedlings that were partly wilted at the outset of the experiment, probably from the shock of the colder, damper climate; the seedlings that survived to final harvest were conspicuously healthy. In the analyses of growth and biomass allocation (Table 2), there was no significant effect of block, or its interactions, except for a marginal block effect on SMF for *V. lantana* ($P=0.026$).

### Relative growth rates

All species responded in RGR to the different irradiance treatments (Fig. 3; Table 2), and differed significantly in final dry mass (Tables 1, 2). RGR was lower in 3.5% daylight (neutral shade) than in 35% daylight, with the reduction differing significantly across species ($P=0.001$), from 27% for *Hedera* to 44% to *V. lantana* (Fig. 3). However, only *V. lantana* and *V. opulus* were significantly affected by reduced watering frequency (IW relative to FW); their mean RGRs were reduced by 14% and 26% respectively. Neither of the two species naturally found in Mediterranean forest, *V. tinus* and *Hedera*, were significantly affected by watering frequen-

**Fig. 4** Values for **a** specific leaf area and **b** mass fraction of root, stem and leaf at final harvest for seedlings in the different treatments. Abbreviated treatment names are explained in the legend for Fig. 3



cy (Fig. 3; Table 2). Irradiance *quality* had an effect for only *Hedera*; mean RGR in low red: far-red shade was 68% the value of that in neutral shade (Fig. 3). There was no significant interaction between irradiance treatment and watering frequency on RGR or on final dry mass for any species (Table 2): the impact of decreasing water frequency was approximately proportional across irradiance treatments (Fig. 3). This finding implies independent impacts of shade and drought on RGR for each species.

Defining shade tolerance as the ability to maintain RGR and yield in deeper neutral shade (as a proportion of the value at higher irradiance) the species ranked *V. opulus*~*Hedera*>*V. tinus*>*V. lantana*. Defining drought tolerance as ability to maintain RGR and yield at lower watering frequency they ranked as expected from field distributions, *V. tinus*~*Hedera*>*V. lantana*>*V. opulus*. Strong interpretation of species' relative performance is permitted only for *V. lantana* and *Hedera*, which were identically cultured (see Materials and methods). *V. lantana* significantly outperformed *Hedera* in the 3.5% low red: far-red FW treatment ($P<0.001$; planned orthogonal contrast), but in no other treatment combination.

## Biomass allocation

The species differed significantly in biomass allocation and in form (Fig. 4; Table 2). Notably, SLA in high irradiance declined across species with increasing drought tolerance, from *V. opulus* to *V. lantana*, to *Hedera* and *V. tinus*.

In response to deeper shade each study species showed a higher mean SLA and a lower RMF, due to size-dependent and/or size-independent effects (Fig. 4a, b; $P<0.001$; Table 2). Species differed in the plasticity of their SLA ($P<0.001$) with *Hedera* most plastic (value in 3.5% daylight was 164% that in 35% daylight) and *V. opulus* least (130%). The species did not differ significantly in their plasticity in RMF (value in 3.5% daylight 73–86% of that in 35% daylight). Additionally, all species but *V. opulus* had higher LMFs when grown in deeper shade, with *Hedera* most plastic (LMF in 3.5% daylight was 130% the value in 35% daylight), and *V. lantana* least (LMF in 3.5% daylight was 110% the value in 35% daylight). All species but *Hedera* showed a significantly higher SMF in deeper shade (Fig. 4b, Table 2). Shade effects on biomass allocation did not vary across watering treatments (no significant I × W interaction, Table 2, Fig. 4b), indicating orthogonal impacts of shade and drought, as found for RGR, described above.

For the study species, differences in irradiance *quality* produced no significant changes in biomass allocation. Further, no significant plasticity in biomass allocation was found across the different watering treatments (Table 2). However, there were statistically non-significant but consistent trends for reduced watering frequency to reduce SLA, and to increase RMF (Fig. 4a, b).

### Foliar nutrient concentrations

Foliar nutrient concentrations differed significantly among species and irradiance treatments, but not among watering treatments (Table 1). The lower nutrient concentrations for plants grown at 35% daylight may have arisen partly from greater nutrient-limitation, especially given competition with the grass, but primarily it reflected the fact that autumn resorption was visibly underway for plants at 35% daylight, and not for plants at 3.5% daylight (conspicuous even for evergreen *Hedera* and *V. tinus*).

## Discussion

### Orthogonal impacts of shade and drought

Unsurprisingly, all four species were significantly affected by the ten-fold difference in irradiance quantity. Only *Hedera* was affected by irradiance *quality*, reducing its RGR in low red :far-red shade relative to that in neutral shade by an amount (32%) similar to that found previously for three *Veronica* spp. (Dale and Causton 1992a). The *Viburnum* species were perhaps more typical of shade tolerators in showing no sensitivity to low red: far-red ratio (Kwesiga and Grace 1986; Kitajima 1994). The two non-mediterranean species, *V. opulus* and *V. lantana*, were significantly affected in RGR and final dry mass by the imposed drought. Our study found no interaction between irradiance and water treatments on seedling final dry mass, RGR, biomass allocation, for any species (Fig. 2, Tables 1, 2).

These findings support the independent-effects model for the four study species. The independent-effects model is implicitly supported by two previous shade × drought experiments (Papavassiliou 1991; Baruch et al. 2000), but at first sight not by several others, in which drought had a stronger impact at higher irradiance on seedling final dry mass, for one or more of the species grown (Kolb et al. 1990; Canham et al. 1996; Groom and Lamont 1997; Van Hees 1997; Baruch et al. 2000; Holmgren 2000). However, these studies, analysing the data from differing perspectives, did not test whether the proportional impact of drought on RGR differed across irradiance treatments. Because dry mass yield is an exponential function of RGR (Evans 1972), a greater impact of drought on yield can arise at higher irradiance, even when resource-levels have independent, multiplicative effects on RGR (Corré 1983), especially when RGR is high, i.e. for fast-growing species. The above-ground facilitation effect (see Introduction) was notably absent in our study, though it is well-established for plants in moderate shade, relative to those in full daylight (Gamon and Pearcy 1990; Callaway 1995; Valladares and Pearcy 1997). Our findings suggest that at irradiances below the excessive range, shade and drought impact independently on growth and biomass allocation.

One implication of orthogonal impacts of shade and drought is that simple methods may be used to predict seedling performance at given microsites. For example, if a given degree of shade reduces RGR of plants at optimal water supply to S% of maximum, and a given drought reduces RGR of plants at optimal irradiance to D% of maximum, then RGR in the combination of that degree of shade and that drought can be estimated as S%–D% of maximum. Such an ‘independent-effects model’ can be used for accurately predicting growth, as shown by Nobel and co-workers for cacti and agaves at combinations of resource-supplies in the ranges experienced in the field, when they scaled up from gas exchange measurements (Nobel 1984, 1999; Nobel and Hartsock 1986). Our study suggests that the model may be usefully applied to woody seedlings in irradiance and water-supply combinations.

There are more possibilities for niche differentiation under the ‘independent effects’ model than would occur under a trade-off between shade tolerance and drought tolerance: species may specialise on a broad range of irradiance × water combinations. It is notable in this study that *V. lantana* significantly outperformed *Hedera* only on moist soil in low red: far-red shade, and not at other treatment combinations. Also notable is the finding that *V. tinus* and *Hedera* were markedly tolerant both of deep shade and drought. Such tolerance explains these species’ persistence through months of drought in the understories of deeply-shading evergreen forests of the Mediterranean Basin. *Hedera* establishes even in typically moist forests in western Europe, and might be favoured relative to other species as climates become drier (see, for example, Karl et al. 1995), in areas where overstorey shade remains strong.

## Seedling tolerance of deep shade combined with drought

How can seedlings tolerate deep shade plus drought? According to the trade-off hypothesis, sun-shade plasticity should lead to a stronger impact of drought in deep shade (Smith and Huston 1989; see Introduction). However, that pattern was not found, even though all species had higher SLAs and lower RMFs when grown in deeper shade. The study species' SLAs and RMFs in 3.5% daylight were respectively 130–164% and 73–86% of those in 35% daylight, which reflect a moderate degree of plasticity if compared with those of 19 species of temperate woody deciduous seedlings raised a single season in 2–3% daylight and 17–65% daylight (mean values 155% and 82% for the increase of SLA and the reduction of RMF respectively; references for SLA and RMF values provided below). Such moderate morphological plasticity is typical for shade-tolerators (Grime 1979; Grubb 1998; Valladares et al. 2000). It is possible that the lower vapor-pressure deficit in deeper shade compensates to a degree for the greater evaporative load resulting from a higher leaf area ratio.

How is the dual tolerance of *Hedera* and *V. tinus* possible, given that a plant cannot preferentially allocate both to shoot and root, i.e. both to specialised irradiance-capture and water-capture? One solution is that specialised resource-capture is not the only mechanism for maintaining yield in a resource shortage. Tolerance can alternatively depend on reducing demand for the scarce resource(s). Many traits can contribute to a reduced demand for irradiance and water simultaneously, such as small size, low respiration rates (Grime 1966), long-lived leaves of low SLA (Small 1972; Orians and Solbrig 1977; Walters and Reich 1999), and a high below-ground allocation (L. Sack, T. Marañón, P.J. Grubb, to be published). The study species had moderate to low SLAs in deep shade (247–374 $cm^2g^{-1}$, in 3.5% daylight, averaged across treatments), and only *V. lantana* showed a low below-ground allocation (its RMF was 0.16, in 3.5% daylight, averaged across treatments) if compared with 19 species of temperate woody deciduous seedlings, raised a single season in 2–3% daylight (mean SLA±95% confidence intervals 372±63; mean RMF 0.36±0.06; Loach 1970; Latham 1992; Canham et al. 1996; Grubb et al. 1996; Walters and Reich 1996). The high RMF of *V. tinus* may also contribute to specialised water-capture (Grubb 1998), but this trait does not necessarily drive differences in drought tolerance (see, for example, *Hedera* versus *V. opulus*). There are other traits that confer drought tolerance by reducing demand for water, such as high cuticular resistance (Schreiber and Riederer 1996), conservative stomatal behaviour (i.e. modulating gas exchange according to leaf water status for a high overall water-use efficiency; Oren et al. 1999; Mencuccini et al. 2000), a low SLA, and in some cases tissue water storage, and/or tolerance of tissue desiccation (Levitt 1980).

## Limitations of the study and future work

The shade tower + grass sward method, while very effective as used, is not ideal. One concern is that by the end of the experiment, the FW soil probably had lower nutrient concentration than the IW soil, due to faster-growing grass and microbes. However, this greater depletion would have been consistent across irradiances, and therefore it does not affect the evaluation of the impact of drought across irradiances.

This study concerns overall impacts on seedlings in their first season; longer-running studies are needed to confirm orthogonal impacts of shade and drought across different seasons and growth stages, since tolerances of shade and drought can change (Walters et al. 1993; Grubb 1998; Sack and Grubb 2001). Multiple-harvest experiments and allometric analyses are needed to allow detailed dissection of treatment effects on biomass allocation into size-related and size-independent effects. Future work is also needed to test the limitations of pot experiments. Whereas in this study water supply was controlled across irradiances, in the field seedlings in high irradiance may root more extensively than shaded seedlings, and in this way they might access more soil water. Controlled testing for the effect of variation in soil resources across soil strata presents an exciting challenge. Other experiments are needed to determine whether *lethal* drought differs across irradiances. Finally, studies are needed to understand the impact of drought combined with field sunfleck regimes (see Wayne and Bazzaz 1993; Ackerly 1997; Robison and McCarthy 1999), and with mycorrhizae (e.g. Fitter 1988), pathogens and herbivores.

**Acknowledgements** Thanks to Jessica Smith, Teo Marañón, Alex Goodall, Ken Marr, Glyn Jones, and Geoff Holmes for logistic support, to Bill Davies, Taylor Feild, Michael Huston, Ed Tanner, and to editor Robin Chazdon and her two anonymous referees for their helpful comments on the manuscript, and to NSERC Canada, the Cambridge Commonwealth Trust, and the Department of Plant Sciences, University of Cambridge (Frank Smart Fund) for scholarships.

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