Diverse Responses of Maple Saplings to Forest Light Regimes

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Seedlings of 11 species of forest maples (Acer L.) were grown outdoors from budburst to senescence under three light regimes: 'gap centre under clear skies' (approx. 20% open sky irradiance; red:far-red ratio = 1:12); 'gap centre under cloudy skies' (1.5%, ratio = 1:03); and 'gap edge' (2.5%, ratio = 0:6). Seedlings grown under the gap centre (clear sky) regime had significantly greater height growth, greater specific leaf mass, higher root:shoot ratio, greater investment in roots, higher leaf nitrogen concentrations, higher chlorophyll a:b ratio, lower photosynthetic rates under dim light, higher maximum photosynthetic rate, higher stomatal conductance, and lower leaf internal CO₂ concentrations compared with those grown in either gap edge or gap centre (cloudy) regimes. Responses to the gap edge vs. gap centre (cloudy) treatments differ little, suggesting that shade acclimation in forest maple seedlings is mainly a response to light intensity rather than spectral quality. The ubiquitous and, except for leaf internal CO₂ concentration, highly significant interspecific variation in traits was broad-ranging and continuous. These results suggest that (1) the responses to light quality found in shade intolerant herbaceous and woody species growing in more open habitats may not have a selective advantage in seedlings of shade tolerant forest trees, and (2) the adaptive plastic response to understorey vs. gap environments in forest maples, which is qualitatively consistent across species, is founded on co-ordinated, small shifts in sets of functionally inter-related traits.

Key words: Acer, forest gap heterogeneity, plasticity, specific leaf mass, photosynthesis, leaf chlorophyll, nitrogen, stomatal density, root growth, root:shoot ratio, growth form.

INTRODUCTION

The importance of treefall gaps and similar disturbances in the forest canopy for the growth, survival and reproduction of species of Acer (Canham, 1985, 1988; Peters et al., 1995) and many other tree seedlings is widely appreciated (Pickett and White, 1985; Attiwill, 1994). Under an intact forest canopy, maple saplings experience persistently low levels of diffuse and spectrally altered sunlight (Messier and Bellefleur, 1988; St. Jacques and Bellefleur, 1993) and are only occasionally exposed to sunflecks (Chazdon and Pearcy, 1991). Forest maples tolerate these shaded conditions as juveniles to varying degrees (Hoffmann, 1960; Kurata, 1974; Burns and Honkala, 1990), but all depend on the increased resources available in canopy gaps for their longer term survival and reproduction (Wilson and Fischer, 1977; Hibbs, Wilson and Fischer, 1980; Canham, 1985, 1988; Fried, Tappeiner and Hibbs, 1988; Peters et al., 1995). Interspecific differences in growth and survival of juvenile maples growing in shaded vs. more open environments are tied to diverse plastic changes in morphological and physiological traits (Eilsworth and Reich, 1992b; Sipe and Bazzaz, 1994, 1995; Walters and Reich, 1996; Lei et al., 1996; Lei and Lechowicz, 1997a, b). This paper concerns the ecological and evolutionary significance of these plastic responses to understorey vs. gap environments, responses that may or may not be adaptive (Lei and Lechowicz, 1990; Sultan, 1992, 1995).

While environmental plasticity is the norm, not the exception, among plants, its ecological and evolutionary significance remains a subject of debate (Sultan, 1992, 1995). Relatively few studies have considered whether such phenotypic changes in traits across environments are meaningful adaptive responses to environmental cues, especially for forest trees (Sultan, 1992, 1995). Two aspects of plastic responses by understorey tree seedlings to gap formation are at issue. First, what are the environmental cues that elicit and organize the plastic response. The possible adaptive value of a response requires a consistent relationship between a cue eliciting a plastic change and the environment in which the new phenotype will grow. Second, what is the functional significance of the response? If a plastic response does not contribute to more effective physiological function or greater survival and reproduction in the new environment, then the plasticity cannot be considered adaptive (Sultan, 1992, 1995). This paper focuses on the cues eliciting the plastic response of forest maples to gaps in the forest canopy, and makes an initial assessment of the adaptive significance of these responses.

The most striking environmental shift in a newly created gap compared to the previously shaded understorey is in the light regime, which is altered both quantitatively and qualitatively. Understorey irradiance is typically only 1–5% of that at the forest canopy, and the red to far-red (R:FR) ratio declines from the values of 10–12 typical of sunlight, to only 0.1–0.5 (St. Jacques and Bellefleur, 1993; Turnbull and Yates, 1993). Traditional views emphasize responses to the quantitative changes in light regime following gap formation (e.g. Björkman, 1981), but recently there has also...
been considerable interest in tree responses to the qualitative shift in the gap light regime (Kwesiga and Grace, 1986; Kwesiga, Grace and Sandford, 1986; Warrington et al., 1989; Riddoch, Lehto and Grace, 1991; Lee et al., 1996). Irradiance alone may not be the only cue for the location of a new gap as the R:FR ratio also varies somewhat independently within and around the gap (Endler, 1993; Turnbull and Yates, 1993). Furthermore, in some situations such as coastal fog forest and montane cloud forest (e.g. Vogelmann, 1973; Cavelier and Goldstein, 1989), young maples will often be exposed to low photon flux density (PPFD) but high R:FR similar to that of direct sunlight (Gates, 1980). In these situations, and perhaps more generally, R:FR may be a more reliable indication of position in or near a gap than increase in light quantity. An increased PPFD is ultimately an important cause of accelerated growth in gaps, but an increased R:FR may provide an essential stimulus to the coordinated physiological and morphological responses of shade-adapted plants that allow their effective exploitation of a gap event. We have therefore compared the responses of diverse maple species to different combinations of PPFD and R:FR to decide which environmental signals govern seedling responses to gaps in the forest canopy.

Whatever the environmental cues for a particular plastic response may be, an ancillary concern is the significance of the morphological and physiological changes from one environment to another. If a set of maples have differing plastic responses, do those differences represent species-specific adaptations? For example, does the shift in a trait contribute to more effective physiological function in the environment or demonstrably enhance survival or reproduction? If a set of maples all show a similar plastic response, is that response some sort of universal adaptation or simply a reflection of a genetically fixed trait? Interspecific patterns of plastic responses mapped onto maple phylogeny could reveal such a constraint on the evolution of adaptation to forest light regimes. To begin answering such questions, we need to compare a fairly broad sample of forest maple species grown in contrasting forest environments.

We grew seedlings of 11 species of forest maples under three light regimes that simulated: (1) a forest gap centre under clear skies; (2) a gap edge; and (3) a gap centre under cloudy skies. The three light regimes were selected to represent the range of light environments that forest maples might encounter, and to separate the possible effects of light quantity and light quality on the plastic responses of seedlings. The sampled maples (Table 1) originate from three continents, represent the major lines of phylogenetic divergence within this well defined genus (van Gelderen, de Jong and Oterdoom, 1994), and differ in their heights at maturity and associated reproductive ecology (Hoffmann, 1960; Kurata, 1974; Burns and Honkala, 1990). Their diversity provides a test of the generality of earlier comparisons among maple species (Lei and Lechowicz, 1990, 1997a, b; Sipe and Bazzaz, 1994, 1995) and an opportunity for an initial assessment of the ecological and evolutionary significance of plastic responses to contrasting forest light regimes.

**MATERIALS AND METHODS**

The 2- or 3-year-old seedlings of 11 *Acer* species used in the experiment (Table 1) were raised from seed in the McGill University Phytotron. The glasshouse compartment where the seedlings were grown was programmed to track outdoor conditions, except that in winter air temperature was held just above freezing; insolation was reduced throughout the year with 50% neutral density shade cloth. Seedlings were grown in cylindrical Plexiglas ‘rhizotrons’ (61 cm deep; volume 28 l) filled with commercial top soil (Fafard et Frères Ltée, St. Guillaume, Quebec, Canada) and covered with an opaque plastic wrapping that could be removed to assay root characters. The seedlings were watered as necessary and fertilized weekly during the growing season.
with Hoagland’s solution (Dunn and Arditti, 1968, Version 2). In early spring (April) 1990, the seedlings were transferred to a lath house at the university’s Mont St. Hilaire Research Centre (45° 33’ N, 73° 09’ W) where leafing out took place in the gap centre (clear), gap centre (cloudy) and gap edge treatments described below. The seedlings were randomly assigned to the three light treatments. Leaf morphology in *Acer* is strongly determined by irradiance level during leaf expansion (Isanogle, 1994; Goulet and Bellefleur, 1986) and, unlike *Fagus* (Eschrich, Burchart and Essiamah, 1989), little affected by light regime during development of leaf primordia the preceding season; we therefore expect the influence of the experimental light regimes to dominate the seedling responses. There was minimum shading from neighbouring plants. During the experiment, seedlings were fertilized once a week, and watered regularly. All plants were harvested late in September 1990 as the normal growing season ended.

**Experimental design and light treatments**

Three treatments were selected to approximate the contrasting combinations of light quality and quantity found in the centre of forest gaps under clear and under cloudy skies, and at the edge of gaps under clear skies (Lee, 1987; Messier and Bellefleur, 1988; Canham *et al.*, 1990; Lawton, 1990; St. Jacques and Bellefleur, 1993; Turnbull and Yates, 1993; Endler, 1993). The gap centre (clear) treatment simulated the light regimes in a moderate size (approx. 10 m diameter) forest gap; plants were grown in a lath house, which had 37% open area in a latticed pattern, at a lath to plant distance sufficient (Yates, 1989) to yield fairly uniform irradiance at about 20% open sky values and a red to far-red ratio (R:FR) of 1:10. The forest edge light regime was simulated by covering the lath roof and sides to 1 m from the ground with a spectral filter; the lowest metre of the compartment was shielded with 32% transmittance shade cloth (Les Industries Harnois Inc., St-Thomas-de-Joliette, Québec, Canada). The spectral filter consisted of alternating strips of filter pigments (17 cm) and clear (2.5 cm) bands on polyurethane sheet (CIL Durafilm 1, from Les Industries Harnois Inc. Québec, Canada). The banding pattern, perpendicular to the solar track, created alternating sunflecks and shade lasting 2 and 13 min, respectively. The filter pigment mixture follows Lee (1985) but without the carbon black. This arrangement yielded a gap edge regime with about 2.5% open sky irradiance and a R:FR of 0.60, occasionally punctuated by simulated sunflecks with higher irradiance and R:FR ratio. The gap centre (cloudy) treatment was designed to simulate the natural light properties of low PPFD and high R:FR prevailing during continuous cloud cover or fog (Gates, 1980). It consisted of 10% transmittance shade cloth on the roof (without lath) and 17% transmittance shade cloth on all four sides. Irradiance under this treatment was about 1:5% of open sky but R:FR was 1:03. This treatment allows an evaluation of any independent effects of light quality and quantity on *Acer* seedlings by comparison to the gap centre (clear) and cloudy regimes.

**Light chamber design for gas exchange determination**

Photosynthesis, leaf internal CO₂ and stomatal conductance were measured twice on each plant with a LiCor 6200 Portable Photosynthesis System (Lincoln, Nebraska, USA) on 23–30 Jul., 1990. Both dynamic and steady-state gas exchange measurements were made under artificial lights in the Mont St. Hilaire Research Centre near the lath house. Plants were brought inside (by random block and treatment) and acclimated for at least 1 h under an array of fluorescent tubes and incandescent bulbs, giving a mean PPFD of 29 μmol m⁻² s⁻¹ and R:FR of 0.95. After acclimation, gas exchange was measured under this dim light on one randomly selected leaf per plant. Seedlings were then moved under a GE Cool Beam Flood Lamp (300W PAR 56/2MFL) suspended over a thermal barrier; mean PPFD was 1260 μmol m⁻² s⁻¹ and R:FR was 1:90. Gas exchange of the same leaf measured under dim light was determined after 0.5 min and 24.5 min of exposure to this bright light. This procedure simulates the initial stage (at 0.5 min) and steady state (at 24.5 min) photosynthetic inductive response of a dim-light-acclimated leaf to a saturating sunfleck. Photosynthesis at 24.5 min is referred to as $A_{max}$, based on preliminary determinations that the seedling response curves began to plateau at approx. 10 min in all the *Acer* species. Repeated handling of the same leaf at these time intervals had no affect on gas exchange characteristics.

**Plant characters**

In June 1990, fine root (< 2 mm diameter) density was estimated by counting the number of fine roots intercepted along six circumferences (24 cm each) of the ‘rhizotron’ at 5, 8, 26, 29, 47 and 50 cm depths. A record of the root positions along the transects was kept on an acetate sheet and 1 month later a second census was taken at the same positions. Fine root density was estimated as the number of roots intercepting the six transect lines and is expressed as number of fine roots per cm. Mean fine root density of two censuses (July and August) is reported. *Acer* root growth is maintained at a steady rate from June to senescence (Millard and Proe, 1991) and root production rates determined in this study are representative of summer below-ground growth activities.

On 22–23 Sep. 1990, abaxial leaf (*Acer* is a hypostomatous genus; Powers, 1967) impressions were made with clear nail polish for stomatal density and pore diameter measurements (Lei and Lechowicz, 1990). Impressions were taken from three randomly chosen leaves per plant. We made three stomatal density counts and four stomatal pore diameter measurements per impression. Immediately after leaf impressions were collected, all leaves from each plant were harvested. A random subsample of ten discs (each 20 mm²) from five leaves was used to determine specific leaf mass (SLM); the remaining tissue was kept in a −18 °C freezer for subsequent chlorophyll determination. A LiCor Area Meter (Li-3100) was used to measure total leaf area on each seedling. Lengths and number of shoots on each plant were recorded. Leaf, twig and roots were separated and oven-
FIG. 1. Norm of reaction diagrams and associated ANOVA results summarizing responses of the different species of *Acer* seedlings grown under three light regimes (see Methods). This figure summarizes responses related to the growth and architecture of the seedlings. Lines connect the mean response of each species to the three contrasting light regimes; note that the x-axis is ordinal, the y-axis quantitative. The species acronyms are given in Table 1. Trait abbreviations: Fig. 1C, Shoot dry weight-based Leaf Display Index; D, shoot length-based Leaf Display Index; E, relative growth rate of vertical plant height; F, RGR of total twig length. ANOVA results appear above each graph: Treat, treatment main effect; Sp, species main effect; T*S, treatment by species interaction; NS, no significant difference; *P < 0.05; **P < 0.01; ***P < 0.001.
dried for biomass determination. Plant height and basal diameter were measured in May and again in September.

Chlorophyll a and b levels were determined on freshly frozen leaves (one pooled sample per tree) using a DMSO extraction method adapted from Barnes et al. (1992). Chlorophyll levels were estimated from absorption values using formulae for 80% Acetone in Barnes et al. (1992). No chlorophyll degradation products were evident during this procedure. Leaf N was determined by a Kjeldahl analysis (Bradstreet, 1965) using a pooled sample of oven-dried (70 °C) leaves for each plant. Ground leaf samples (0 ± 100 g each) were digested for approx. 90 min with six selenium catalyst granules, 0 ± 5 g K₂SO₄ and 5 ml concentrated H₂SO₄; the digest was Nesslerized and assayed colorimetrically.

Fig. 2. Norm of reaction diagrams and associated ANOVA results summarizing responses of the different species of Acer seedlings grown under the three light regimes: responses in traits related to gas exchange. The format and coding of the diagrams are given in the caption to Fig. 1.
Fig. 3. Norm of reaction diagrams and associated ANOVA results summarizing responses of the different species of *Acer* seedlings grown under the three light regimes: responses in traits related to the structure and composition of leaves. The format and coding of the diagrams are given in the caption to Fig. 1.


**Statistical methods**

The total number of seedlings used in the experiment was 168 (four replicates per species-population per treatment). The experimental plants were arranged in four blocks in each light treatment, one seedling per species-population per block. Differences between light treatments, species and treatment by species interaction were analysed using Procedure GLM in SAS (1989) for a two-factor fixed effects model. ANOVA showed no significant block effect in the traits measured and block effects will not be considered in subsequent analyses. The s.e. associated with data presented...
in Figs 1–3 was in the order of 5–15% of the mean. Readers wanting more quantitative detail on the patterns reported in these summary figures are invited to request the full data set from the authors.

RESULTS
For all the diverse traits that we investigated, there were significant differences among the various maple species in their response to the three combinations of light quantity and quality (Figs 1–3). The species responses generally fall on a continuum of greater or lesser range, occasionally with one or two slightly more extreme responses (compare, for example, Fig. 2A and C). Many traits showed significantly different responses to the three experimental light regimes, but these differences were most often founded on light quantity [between gap centre (clear) and gap edge], not light quality (between gap edge and gap centre: cloudy) (cf. Figs 1A, B, E; G; 4C, D; 5A, C, D–F). The nature of the relationships among species sometimes changed across the treatments; in statistical terms, there were some significant interactions between species and treatment responses (cf. Figs 1B–D, F, G; 5C, E). These interactions arise from differences among treatments in the spread of species values and/or changes in species ranks among the treatments. We also analysed these traits with an additional growth form factor (in ANOVA) which separates large tree (canopy diameter growth under the gap treatment. However, the relative growth rates were not separated as species of different growth forms.

Shoot growth and plant structure

All the plants grown in gap centre (clear) had higher root:shoot ratio and greater numbers of fine roots than those grown in the two low PPFD environments (Fig. 1A and B). Root:shoot ratio was highest in A. ginnala, but this singularity does not arise from unusually high root density (Fig. 1B). Acer rubrum has notably high root density in all three light regimes.

Light regime had no effect on the display of leaves along branches, despite substantial interspecific differences in this measure of canopy architecture (Fig. 1C). Acer nigrum consistently had the greatest leaf area per unit branch length and A. ginnala most often had the least. The woody tissue invested in branch per unit leaf area shows a similar lack of response to light regime, but in this instance there is also a significant interaction between species and treatment (Fig. 1D). This interaction arises from the tendency for only three of the species ([A. nigrum, A. spicatum, and A. buergerianum]) to increase the leaf area supported per unit branch wood.

Gap-grown plants showed marginally higher relative growth rate (RGR) in vertical height, with the highest growth rates found in the two closely related species of A. saccharum and A. nigrum (Fig. 1E). RGR in total twig length shows a significant interaction between treatment and species (Fig. 1F). Those species that reach maturity as part of the canopy crown (i.e. A. saccharum, A. macrophyllum, A. plantanoides and A. nigrum) maintained similar twig growth in all three treatments, while those that mature as subcanopy or small trees (i.e. A. buergerianum, A. ginnala, A. spicatum, A. rufinerve and A. pensylvanicum) exhibit a substantial decrease in growth from gap centre (clear) to the two low PPFD treatments. The lack of discernible variation in twig growth between gap edge and gap centre (cloudy) treatments in all species indicates that R:FR has little effect on growth rates. The RGR in stem basal diameter of all species showed an increase in basal diameter growth under the gap treatment. However, the relative growth rates were not separated as species of different growth forms.

Gas exchange

Both photosynthesis (A) and stomatal (g s) conductance under saturating light (A max and g s at A max respectively) showed strong PPFD-dependent patterns for all species (Fig. 2A and B). In these two gas exchange traits, the similarity between gap edge and gap centre (cloudy) indicates a lack of light quality effect. The obvious exception was A. macrophyllum, where A and g s measured under both saturating and dim light were the highest among the species in all three treatments. The large drop in both g s and A by A. macrophyllum in the gap centre (cloudy) treatment (Fig. 2A, B, D) suggests that the photosynthetic capacity of this coastal Pacific species can respond to variations in R:FR light alone. It is interesting that A. macrophyllum, which is the only sampled species that frequently occurs in foggy coastal forests, is the only species to show a marked difference in response to overcast vs. shaded growth regimes. In all species, variation in g s at A max is strongly correlated with A max under the three treatments (Fig. 2A and B), but the coupling between these two traits is not apparent under dim light (Fig. 2C and D). A. rufinerve appears to be particularly poor in dim light photosynthesis, perhaps due to unusually high dark respiration rates. A. pensylvanicum and A. saccharum showed consistently low gas exchange performance in all three treatments under both saturating and dim light conditions (Fig. 2A–D).

The leaf internal CO 2 at A max (C i) of plants grown in gap centre (cloudy) was higher than those in gap centre (clear) and gap edge light regimes. The similarity between the latter two regimes where PPFD and R:FR were both high (gap centre (clear)) or both low (gap edge) suggest an effect of an interaction (i.e. low PPFD and high R:FR ratio) on leaf internal CO 2. In the gap centre (clear) treatment, seven of 12 species had a C i between 230 and 265 ppm. This could be the range of stable CO 2 partial pressure which all species maintain through stomatal regulation under saturating light conditions. The high C i and low A max in A. saccharum suggests a relatively ineffective conversion of light energy to carbon uptake in this species. At the other extreme, A. pensylvanicum was notably conservative in managing its gas exchange with low g s and modest A max associated with low C i. This is the only trait among those examined with no significant differences among species.

The maple species differ significantly in the speed with which they attain steady state photosynthesis when exposed to high irradiance, but these differences do not depend on light regime (Fig. 2F). Photosynthetic induction rate is
calculated as the percent ratio of transient photosynthesis after a 30 s exposure to saturating light: steady state rate (after 245 min). Higher values, such as in *A. saccharum*, may be interpreted as a more rapid response to the onset of sunflecks in shade-acclimated plants (Chazdon and Pearcy 1985, but see Lei and Lechowicz, 1997a). Photosynthetic induction appears not to be strongly correlated with $A_{\text{max}}$, since both *A. macrophyllum* (high $A_{\text{max}}$) and *A. pensylvanicum* (low $A_{\text{max}}$) showed low rates of induction (Fig. 2A, F).

Leaf structure and composition

There were significant differences in specific leaf mass (SLM) among the maples, and all the maples had greater SLM when grown in the gap centre (clear) regime compared to gap edge or gap centre (cloudy) (Fig. 3A). *Acer ginnala* had notably high SLM in all growth regimes, and *A. spicatum* had especially low SLM in the two low PPFD regimes.

There were significant differences among the maples in their leaf area-based nitrogen concentrations with lower concentrations in plants grown in gap centre (clear) compared to those in gap edge or gap centre (cloudy) (Fig. 3C). *Acer saccharum* has extremely high leaf nitrogen concentrations and *A. rubrum* notably low concentrations. These concentration data can be converted to an estimate of areal investments in nitrogen by combining with SLM data for each seedling (Fig. 3D). The high investment in leaf nitrogen by *A. saccharum* then remains clear on an areal basis, but a notably low investment by *A. spicatum* also becomes apparent.

Leaf chlorophyll concentration varied significantly among treatments and among species (Fig. 3E). Most species showed an increase in chlorophyll level with decreasing PPFD [i.e. from gap centre (clear) to gap edge], with *A. ginnala* being the exception. There was also a tendency for chlorophyll level to peak at the gap edge regime where R:FR was lower than the other two treatments. The ratio of chlorophyll $a$ to chlorophyll $b$ decreased from high PPFD to low PPFD treatments and showed significant differences among species (Fig. 3F). *Acer saccharinum* and *A. saccharum* have fairly high chlorophyll $a:b$ ratios and *A. spicatum* has a consistently low chlorophyll $a:b$ ratio.

Finally, there are substantial interspecific differences and treatment effects in stomatal density (Fig. 3B). Except for *A. saccharum* and *A. rubrum*, stomatal density decreases from gap centre (clear) to gap edge-grown plants. The three Asian species: *A. ginnala*, *A. rufinerve* and *A. buergerianum* have consistently high stomatal density and *A. spicatum*, along with low SLM, tends also to have low stomatal density.

**DISCUSSION**

Forest maples respond primarily to changes in light quantity associated with canopy gaps, and most traits do not respond to concordant changes in light quality. All forest maples show essentially the same responses to low irradiance, regardless of whether the R:FR ratio is characteristic of open sky or gap values. The canopy species, whose maturation is so strongly dependent on release growth during gap events (Canham, 1985, 1988; Fried *et al.*, 1988; Peters *et al.*, 1995), do not show any greater sensitivity to the increase in R:FR than subcanopy species. This general indifference of forest maples to R:FR levels existing within and around canopy gaps is true for a variety of morphological, biochemical and physiological traits, including measures of growth. Studies of tropical tree seedlings show a comparable lack of sensitivity to light quality for shade tolerant species (Kwesiga and Grace, 1986; Lee *et al.*, 1996). Given the well-documented responses of shade intolerant trees to light quality as well as quantity (Kwesiga and Grace, 1986; Warrington *et al.*, 1989; Lee *et al.*, 1996), some of the more ruderal maples like *A. negundo* (Maeglin and Ohmann, 1973) and *A. campestris* (Küppers, 1984) may respond to changing R:FR ratio under high irradiance. In general though the forest maples respond primarily to the quantitative increases in irradiance associated with gap light patches and not to any associated changes in R:FR ratio.

The sole importance of quantitative changes in irradiance does not preclude the possibility for adaptive, interspecific differences in response to gaps among maple species. Quantitative variation in the light regime within gaps, which has been recognized by earlier authors (e.g. Runkle, 1985; Canham, 1988; Wayne and Bazzaz, 1993a, b), is complex and substantial. Over a 5-m distance in a gap from edge to centre and from the forest floor towards the crown, both direct-beam and diffuse irradiance typically differ more than five-fold (Nakashizuka, 1985; Canham *et al.*, 1990; Lawton, 1990). Such gradients extend beyond the limits of the vertical projection of the gap itself and can influence seedlings growing in the adjacent understory. While PPFD decreases with increasing clouds, light intensity may remain the same or even increase from gap edge to the closed forest (Endler, 1993; Lee *et al.*, 1998) due to stronger diffused radiation. Within a gap, the seasonal and daily tracks of the sun cast a gradation of direct beams (i.e. sunflecks of different intensities and durations) through the gap into the adjacent forest. The gradient of PPFD between gap centre and closed canopy is also enhanced by differences in forest structure. For example, in more open woodlands with large areas of open sky not in the path of direct sunlight, the contrast between gap and closed canopy conditions blurs (Endler, 1993). Endler’s comments on the nature of woodland shade also apply to places where topography (e.g. north-facing slopes, stream bank), substrate (shallow, poor or flooded soils) or exposure (ridgetops) reduce the density or height of forest canopy and increase the amount of open sky. These effects of weather, topography, forest density, gap geometry and solar movement create a spatially heterogeneous light regime around a canopy gap (Lieberman, Lieberman and Peralta, 1989; Canham *et al.*, 1990; Runkle, 1990), with consequent effects on the spatial distribution and growth of sapling trees (Wayne and Bazzaz, 1993a, b; Sipe and Bazzaz, 1994, 1995). All these sources of variation within and among gap environments provide ample opportunity for the ecological and evolutionary diversification of forest maples on gap-related environmental gradients (Lei and Lechowicz, 1990; Sipe and Bazzaz, 1994, 1995).
While forest maple species do differ significantly in their responses to light regime (Sipe and Bazzaz, 1994, 1995; Lei and Lechowicz, 1997a, b), these differences do not fall into neat ecological or evolutionary categories. Although the 11 species investigated had distinctive morphological, biochemical and physiological characteristics (Figs 1–3), these were not tied to species differences in size at maturity (Table 1) as we expected initially (Lei and Lechowicz, 1990). For example, a canopy species like A. saccharum has gas exchange characteristics more like the subcanopy species A. pensylvanicum than another canopy species, A. macrophyllum. In terms of seedling growth and demography, juvenile Acer macrophyllum, which is a large canopy tree at maturity, also behaves more like the subcanopy species A. pensylvanicum (Wilson and Fischer, 1977; Hibbs et al., 1980; Fried et al., 1988) than like canopy species such as A. saccharum or A. mono (Canham, 1985, 1988; Peters et al., 1995). Nor do these complicated patterns of interspecific variation fall on phylogenetic lines, at least not by our present understanding of phylogenetic relationships within Acer (cf. Table 1; van Gelderen et al., 1994). Acer saccharum and A. macrophyllum are closely related, yet have strongly contrasting morphological and physiological characteristics. In other words, the pattern of interspecific variation in these forest maples defies simple categorization. The different characteristics of each species fall on continuous quantitative gradients of variation, not into qualitatively distinct subsets on ecological or phylogenetic lines. Some of this continuous variation may be related to specialized adaptation to contrasting forest environments, but we cannot be certain as the ecology of these species is too poorly quantified.

The general functional value of many of the plastic responses that are consistent among these forest maple species is more straightforward. For example, although levels of total chlorophyll differ among the studied species, the plastic response in total chlorophyll is consistent and functionally sensible. Total chlorophyll levels increase for all these forest maples when seedlings are grown at low irradiance, as we would expect given the role of increased chlorophyll content in improving light harvesting capacity in the shade (Chow et al., 1990a, b). Similarly, the chlorophyll a:b ratio is lower for all the maples in low light regimes (Fig. 3F), which is consistent with the expected greater investment in chlorophyll b to enhance photosystem II function under low irradiance (Lei et al., 1996). Most maple species showed no indication of altering chlorophyll investment in response to light quality alone (i.e. gap centre cloudy vs. gap edge. Fig. 3E and F). This lack of response to light quality in regulation of chlorophyll investment is consistent with reports for tropical tree seedlings of different successional status (Turnbull, 1991) and tropical vines (Lee, 1988). It is noteworthy that there is a suggestion of a qualitative response in some of the canopy maples: A. saccharum, A. nigrum and A. planotooides (cf. Fig. 5E and F). In general though, the plastic response of chlorophyll to light regime follows the same pattern regardless of interspecific differences in the amount of chlorophyll.

We can note other examples of a generalized adaptive response in all these maples to low vs. high irradiance growth regimes. Gap-grown plants consistently have a higher root:shoot ratio and a greater density of fine roots (Fig. 2A and B), which is consistent with the greater evaporative demand characteristic of the sunnier gap environment. The greater photosynthetic capacity (Fig. 1A) and associated nitrogen investments (Fig. 3D) of leaves from the sunnier gap environment is commensurate with the higher irradiance in the sunny gap. On the other hand, adaptation to the shaded regimes is less certain (Fig. 1C and F; Lei and Lechowicz, 1997a). It should be noted here that some of the treatment effects on whole plant characters may have been dampened by the growth environment prior to the experiment, but the overall patterns of responses should prevail, even if a second year of treatments were imposed. What remains interesting is the quantitative variation among these maple species, despite the frequent qualitative similarity of their responses to contrasting growth regimes. The challenge is to identify the functional basis for the interspecific differences in traits and their plastic responses for the many other traits that we know to be important to seedling growth and survival in forest trees.

Efforts have been made to relate patterns of variation in functionally important traits to plant performance in herbs (Farris and Lechowicz, 1990) and also in trees (Atipanumpai, 1989; Ceulemans, 1990). These investigations suggest that, as would be expected, intraspecific variation in a given trait is usually functionally co-ordinated with variation in other traits. Selection does not work on traits in isolation, as known to both plant breeders and evolutionary ecologists. The continuous variation evident in all the traits we have compared here across different species of Acer suggest that similar patterns of co-ordination among traits can prevail at the generic level. It appears that there is an underlying template that organizes variation among traits in forest maples, but that within the constraints of that template species can find individualistic combinations of traits that are functionally viable and perhaps better suited to one or another environment. Such co-ordinated and constrained variation in a set of functionally interrelated traits may be the basis for ecological differentiation among forest maple species.

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