

## IMPACTS OF ROOT COMPETITION IN FORESTS AND WOODLANDS: A THEORETICAL FRAMEWORK AND REVIEW OF EXPERIMENTS

DAVID A. COOMES<sup>1,3</sup> AND PETER J. GRUBB<sup>2</sup>

<sup>1</sup>*Centre for Population Biology and Department of Biology, Imperial College at Silwood Park, Ascot, Berkshire, SL5 7PY, UK*

<sup>2</sup>*Department of Plant Sciences, University of Cambridge, Downing Street, Cambridge, CB2 3EA, UK*

**Abstract.** Light is widely considered to be the most important factor limiting the performance of plants on the floors of forests and woodlands, but the roles of nutrient availability and water supply remain poorly defined. We seek to predict the types of forest in which root competition affects seedling performance, and the types of plants that respond most strongly to release from root competition. We then test our predictions by reviewing experiments in which tree seedlings and forest herbs are released from belowground competition, usually by cutting trenches to sever the roots of surrounding trees.

First, we provide a worldwide review of changes in canopy form and fine-root mass along gradients of soil fertility and seasonal drought, keeping in mind the stages of forest development. Our review shows that penetration of light is least in forests on moist soils providing large amounts of major nutrients. The changes are far more complex than those considered by allocation models. Dry woodlands typically allow 20 times as much light to penetrate as do wet forests, but there is surprisingly little evidence that they have greater fine-root densities in the topsoil. Tropical rain forests on highly infertile soils have only slightly more open canopies than those on fertile soils, but much greater fine-root densities. Northern temperate forests on highly acidic peats and sandy soils are often dominated by early-successional, open-canopied conifers (generally pines), mostly as a result of recurrent fires, and transmit about five times as much light as surrounding deciduous forests. A review of trenching experiments shows that light alone limits seedling growth in forests on moist, nutrient-rich soils, but competition for belowground resources becomes important on infertile soils and in drier regions.

Secondly, we consider how root competition alters species' shade tolerances. Shade-house experiments demonstrate that species differ markedly in the minimum irradiance at which they respond to nutrient addition, but there generally tends to be a sizable response at >5% daylight and little response in <2% daylight. There is some evidence that species that have high potential growth rates and that respond markedly to increased irradiance are also most responsive to nutrient addition in 2–3% daylight. T. Smith and M. Huston have hypothesized that species cannot tolerate both shade and drought; this appears to be the case for species that tolerate shade chiefly by maximizing leaf area. However, many shade-tolerant woody plants in tropical and mediterranean-climate forests have thick, tough, long-lived leaves and a relatively high allocation to roots, and these species are much more drought tolerant. A few studies indicate that root trenching allows species to persist in deeper shade than that in which they are normally found and allows species from mesic sites to invade more xeric sites. Usually, the impact of trenching on growth rate is much greater in gaps than in the understory.

Finally, we discuss the ways in which life-form composition and population structure of plant communities are shaped by reduced water supply and reduced nutrient availability, emphasizing the inadequacy of models that consider the impact of "belowground resource availability" in a generic sense. Competition in a dry climate leads to widely spaced dominants, a lack of interstitial plants, high rates of seedling mortality in the understory, and a restriction of regeneration to patches where established matrix-forming plants have died. In contrast, vegetation on moist, infertile sites is characterized by closely packed, slender dominants, miniaturized interstitial plants, and slow rates of seedling growth in the understory, combined with relatively low rates of seedling mortality. Consequently, there is a continuum of sizes among the individuals of the dominant species, and a lack of reliance on gaps for establishment.

**Key words:** allocation; drought tolerance; forest types; leaf longevity; light penetration; nutrients; resource availability; root competition; shade tolerance; soil fertility; trenching; water supply.

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<sup>3</sup> Present address: Landcare Research, A Crown Research Institute, P.O. Box 69, Lincoln, New Zealand.

E-mail: CoomesD@landcare.cri.nz

## INTRODUCTION

The concept of shade tolerance is enormously influential among forest ecologists because interspecific differences in tolerance are widely believed to drive secondary succession in forests (Horn 1971, Bazzaz and Pickett 1980, Whitmore 1982, Shugart 1984, Pacala et al. 1996). Consequently, a great deal of effort has gone into characterizing the shade tolerances of species. In the early classifications, subjective field observations were used (Baker 1945, Ellenberg 1963). More recently, the parameterized relationships between growth rates and survival under a range of light conditions have been presented (Kobe et al. 1995, Kobe and Coates 1997). However, it is widely recognized that "shade tolerance" is not an immutable property of a species, but varies from site to site, depending on the availability of belowground resources (Toumey and Korstian 1937, Kozlowski 1949, Ellenberg 1963, Tilman 1988, Smith and Huston 1989, Kobe et al. 1995, Walters and Reich 1997).

The central aim of this paper is to make predictions about the impact of root competition on the dynamics of forests and woodlands, and then test these predictions by reviewing experiments that manipulate root competition in the field. Our first set of predictions concerns the identification of the types of forest in which root competition has an impact on the shade-tolerant herbs and tree seedlings found in the understory. The theory of multiple resource limitation predicts that the performance of such plants will depend on availability of water and nutrients as well as on the depth of shade cast by the established canopy (Chapin et al. 1987). We therefore attempt to provide a worldwide review of the trends in canopy structure and light transmission, and in the density and vertical placement of the fine roots, found along gradients of nutrient and water availability. The degree of shade cast does not depend simply on the annual allocation of biomass to leaves (cf. Tilman 1988). It depends on the stage of forest development (Ryan et al. 1997), the number of years for which the leaves remain in the canopy, the area produced per unit dry mass of leaf (the specific leaf area, SLA), the arrangement of the branches, and the size, shape, inclination, and clumping of the leaves (Aerts 1993). Likewise, the effectiveness of a given allocation to roots may depend on the length of time for which individual roots are active (Eissenstat and Yanai 1997), their degree of branching, fineness of division, and vertical stratification (Caldwell and Richards 1986), and the extent of mycorrhizal involvement (Smith and Read 1996). On the basis of the available observations, we put forward three hypotheses that concern the ways in which shade-tolerant plants are expected to respond to release from competition.

We make a second set of predictions that concern the impact of root competition on the shade tolerance of species. Ecologists have long recognized that species

tolerate deeper shade at sites where the risk of seasonal drought is low (Toumey and Korstian 1937), or where soils are more fertile (Ellenberg 1939, 1963). Explanations for such changes in shade tolerance have focused on the strategies by which plants obtain limiting resources. To varying degrees, plants growing in deep shade adjust leaf morphology, enzyme activity, branching patterns, and root-to-shoot allocation in ways that tend to maximize photosynthetic efficiency (Bjorkman 1981, Kohyama 1987, Ramos and Grace 1990, Pearcy and Yang 1996, Poorter and van der Werf 1998). Some of these adaptations may reduce a plant's capacity to capture and retain water and nutrients (Kramer and Kozlowski 1979), and limit the extent to which plants can tolerate drought or infertility in conjunction with deep shade (Tilman 1988, Smith and Huston 1989). However, surprisingly few studies have compared shade tolerance across various sites (Kobe et al. 1995, Kobe and Coates 1997, Walters and Reich 1997), or have sought to test whether species vary in their ability to tolerate shade in conjunction with drought and/or infertility. Our approach is to review studies that have considered the effects of combining different degrees of shade and different degrees of nutrient or water availability on the growth of plants under controlled conditions, and to review field studies on the impact of water shortage on plant survival. Four hypotheses are proposed about the ways in which root competition is expected to influence the shade tolerances of species.

The three hypotheses concerning forest types and the four hypotheses concerning the responses of species are tested by considering experiments that have manipulated root competition in the field, most commonly by cutting trenches around target plants to sever the roots of neighbors. We have found 47 such experiments reported in the literature, the earliest being that of Fricke (1904). A comprehensive review of recent work is lacking, although syntheses of earlier work are available for forests of the northern temperate region (Korstian and Coile 1938), boreal region (Walter and Breckle 1985), and the wet tropics (Coster 1933, Richards 1952).

Finally, we discuss the impact of root competition on the spacing of dominants, life-form composition, and age structure of forests and woodlands. The manifest differences between communities at drought-prone sites and those on highly infertile, but moist, soil are related to the different mechanisms by which competition affects the growth and survival of seedlings.

VARIATIONS IN AVAILABILITY OF RESOURCES  
AMONG FORESTS AND WOODLANDS

Simple models have predicted how foliage and root biomass change along gradients of belowground resource availability, deriving the predictions from optimal allocation theory (Tilman 1988). The availability of resources along these gradients is then predicted as a function of root and leaf mass. In this section, we describe the changes in canopy form and fine-root den-

sity that are actually observed along gradients of rainfall and soil fertility around the world. The changes in light transmission are more complicated than predicted by allocation theory, because light penetration is affected by leaf size, specific leaf area, canopy form, and deciduousness, as well as by leaf mass per se. Similarly, the availability of nutrients and water is affected by the number of fine-root apices and by total root length, as well as by the total mass of roots. We show that many of these attributes vary systematically along resource gradients and, for this reason, cannot be ignored. Furthermore, the changes that occur along rainfall gradients are very different from those found between forests on fertile and infertile soils.

Wherever possible, the light environment of the forest floor is given as the percentage of photosynthetically active radiation (PAR) penetrating under wholly overcast conditions; Anderson (1964) defined this as the diffuse site factor, dsf. A more comprehensive description would include the diurnal and annual variation in quantum flux to the forest floor, its spectral quality, and the proportion of flux transmitted as sunflecks (Anderson 1964, Jarvis and Leverenz 1983, Canham et al. 1994). Parent and Messier (1996) found that instantaneous measurements of dsf were effective predictors of total irradiance *within a given forest type*, and Ishida and Peters (1998) found that dsf was a better predictor of sapling growth than more complex measures of the light environment. However, such close correlation cannot be expected when different forest-types are compared (Eber 1972), or when there are discrete gaps in a canopy, and we accept that our comparisons of light climates using diffuse site factors are preliminary.

#### VARIATION IN AVAILABILITY OF RESOURCES AT VARIOUS STAGES OF STAND DEVELOPMENT

The process of forest development is continuous, but it is helpful to separate four distinct phases: pioneer, building, mature, and degenerate (Watt 1947). The pioneer phase occurs in treefall gaps, where the increased penetration of light may be paralleled by a reduction in fine-root density (Sanford 1989, Wilcynski and Pickett 1993, Denslow et al. 1998, Ostertag 1998) and an increase in soil water content during dry periods (Vitousek and Denslow 1986, Becker et al. 1988, Brujnzeel 1996, Veenendaal et al. 1996a, Ostertag 1998). An increase in nutrient availability might also be expected, but the evidence is less convincing. Vitousek and Denslow (1986) found no significant difference between natural gaps and understory soils in the steady-state concentrations of  $\text{NH}_4$  or  $\text{NO}_3$  or extractable P in a lowland rain forest in central America, but Denslow et al. (1998) found higher concentrations of  $\text{NO}_3$  and extractable P in artificially created gaps in the same forest, although the effects were restricted to the first year after gap formation.

Within stands containing only one tree species, the

building phase is the most productive of all the phases, casting the deepest shade and taking up mineral nutrients at the greatest rate. Ryan et al. (1997) give many examples of leaf area index (LAI) peaking during the building phase of monospecific forest stands. However, the gradual decline in LAI during the mature and degenerate phases may not result in a strong decline in light interception, due to the nonlinear relationship between LAI and light interception. For example, Smith et al. (1991) estimated that LAI declines from  $\sim 3.8$  to 2.3 between 35–50 and 90–100 yr in stands of *Pinus contorta*, but found little change in light penetration (25–28%). In forests composed of large numbers of species, e.g., tropical lowland rain forests, the light climate and state of the soil are probably less dependent on the stage of regeneration of the tallest species because of the many shorter trees growing below (cf. Kabakoff and Chazdon 1996).

The simplest hypothesis for soil nutrient availability is that it declines during forest development, as an increasingly large proportion of the total nutrient capital becomes bound in living wood (Tilman 1988). This was found to be the case in boreal larch forest (Schulze et al. 1995). In addition to living wood, a considerable proportion of the total nutrient capital may be locked up in dead wood that takes many years to decompose; Allen et al. (1997) found that the availability of soil cations was highest 25 years after a large-scale disturbance flattened forests of *Nothofagus solandri* var. *cliffortioides* in New Zealand. It was at this stage that the storage of cations in wood (both living and dead) was least, because much of the woody debris had decomposed but the mass of living stems remained relatively low.

Within a given forest type, there is also variation among tree species in the degree of light penetration at any given stage of forest development. In general, species that are most demanding of light to attain maximum growth rate cast the least shade as mature trees (cf. Ellenberg 1963). The most demanding species are also the fastest growing in height at the sapling stage; among species of deciduous forest in eastern North America, there is a positive relationship between the percentage of light penetrating through mature crowns and sapling growth rate in high light (Fig. 1; based on Canham et al. 1994 and Pacala et al. 1996). One result is that, when forest development after disturbance involves a succession of species, light penetration continues to decline during the mature phase as early-successional species are replaced by more deeply shading late-successional species. For example, Brown and Parker (1994) found that in mixed-species forest in Maryland, USA, the transmission of PAR declined from 2.5% in the building phase to 1.4% in the mature phase.

To summarize, we suggest that the intensity of shading is likely to be positively related to the intensity of root competition when different phases of forest development are compared in monospecific forests and secondary succession. These trends need to be borne

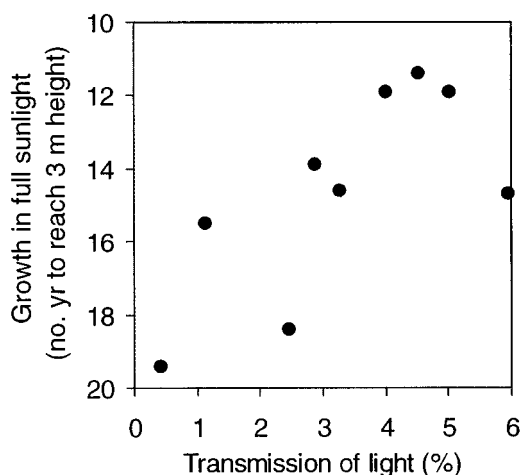


FIG. 1. The relationship between light transmission by crowns of mature individuals of nine North American tree species (average global light indices, from Canham et al. [1994]) and the growth rate of their saplings in high irradiance (from Pacala et al. 1994). Note that deeply shading tree species produce saplings with low growth rates in high irradiance.

in mind when assessing the published data on penetration of light through the canopies of forests along gradients of nutrient or water supply.

#### TRENDS IN VEGETATION STRUCTURE ALONG GRADIENTS OF NUTRIENT AVAILABILITY

##### *Canopy form*

The simplest case to consider is that of evergreen forests in the lowland wet tropics, where forests on moderately infertile soils can be compared with those

on extremely infertile white sands (avoided by shifting agriculturalists). The former allow penetration of 0.5–2% daylight in the mature phase, and the value is only modestly higher in forests on white sand (~1–3%. Table 1). For most lowland rain forest studies, LAI has been calculated as 7–9 (Alexandre 1981), but for the Amazonian caatinga (on white sand), LAI is 4.5–4.8 (Table 1). Beer's equation  $T = 100 e^{(-\lambda \text{LAI})}$  can be used to test whether the differences in percentage transmission ( $T$ ) among forest types are due only to differences in leaf area index, or whether changes in the extinction coefficient  $\lambda$  also occur. Based on the numbers reported, we estimate that  $\lambda = 0.7$ –1.0 for forests on white sand compared with  $\lambda = 0.5$ –0.8 for forests on more fertile soils, suggesting that the differences in transmission are principally the result of differences in LAI. This conclusion is supported by the observation that the spectrum of leaf sizes is similar in Amazonian caatinga and surrounding forests (Coomes and Grubb 1996).

There are several examples of light penetration increasing along gradients of decreasing soil fertility in the moister parts of the northern temperate zone, where evergreen and deciduous elements mix (Table 2). For example, in eastern Europe there is a sequence of dominant trees from *Tilia* and *Carpinus* to *Quercus* to *Pinus* along the gradient from loess-rich sand to pure sand (Walter 1974). In the central-northern United States, there is a similar sequence of dominant trees from *Acer* and *Tilia* to *Quercus* to *Pinus* along gradients from clayey- or silty-sand to pure sand (Curtis 1959). J. Pastor related light penetration to nitrogen supply rates in one such series of old-growth forests (Tilman 1988: 162). He showed that aboveground productivity was

TABLE 1. Leaf area index (LAI) and percentage transmission ( $T$ ) of daylight to seedling or sapling level in various tropical lowland forests. Stands are primary or very old secondary growth unless otherwise indicated.

Forest type	LAI	$T$ (%)	References
Evergreen rain forest on oxisols/ultisols			
Pantropical	7–9		Alexandre (1981), Cannell (1982)
Malaysia		0.4	Kira (1975)
Costa Rica		0.0–0.9	Canham et al. (1990)
Singapore		0.6	Metcalf et al. (1998)
Northeastern Australia		0.4–2.0	Osunkoya et al. (1992)
Rain forest on white sand			
Amazonian caatinga†	4.5‡	1–3	Klinge and Herrera (1983), Heuvel dop (1978), Coomes and Grubb (1996)
Wallaba§		~1.5	Davis and Richards (1934)
Semi-evergreen and deciduous forest			
Pantropical	3–7 w		Murphy and Lugo (1986 <i>a</i> )
India		10 w, 54 d	Lee (1989)
West Mexico		5–6.4 w, 20–55 d	Maass et al. (1995)
Costa Rica¶		5–10 w, 30–40 d	Gerhardt and Fredriksson (1995)
Northeastern Australia		8 w	P. J. Grubb and J. M. G. Bloor ( <i>unpublished data</i> )

Note: Some data are identified as dry season (d) or wet season (w).

† On Rio Negro/Orinoco; soil waterlogged.

‡ LAI is 4.8 in short caatinga ("tall bana"), a closely related vegetation type (Bongers et al. 1985).

§ In the Guianas, on well-drained soil, probably influenced by seasonal drought as well as nutrient shortage.

|| Exploited for firewood.

¶ Secondary forest ~20–60 yr old.



TABLE 2. Percentage transmission ( $T$ ) of daylight to seedling or sapling level in various temperate forests of North America. Stands are primary or very old secondary growth and have grown for  $\geq 20$  yr since large-scale disturbance.

Vegetation type	Location	$T$	References
Warm-temperate evergreen coniferous forests on moist soils			
1) On richer soil			
<i>Sequoia sempervirens</i> on alluvium	California, USA	1–4	Pfitch and Percy (1989)
2) On poorer soil			
<i>Pinus elliotii</i> on sand	N. Florida, USA	18–42	Gholz et al. (1991)
Cold-temperate (boreal) evergreen forests†			
1) On richer soil			
<i>Picea glauca</i> (+ <i>Linnaea borealis</i> in HL)	Alberta, Canada	13–37	Ross et al. (1986)
<i>Picea glauca</i> (+ <i>Aralia nudicaulis</i> in HL)		12–18	
2) On poorer soil			
<i>Picea mariana</i> (+ <i>Ledum groenlandicum</i> in SL)	Alberta, Canada	10–60	Ross et al. (1986)
<i>Picea mariana</i>	Canada	20	Brooks et al. (1997)
<i>Pinus banksiana</i>		45	
Temperate deciduous forests			
1) On moister soil			
<i>Fagus grandifolia</i> and <i>Acer saccharum</i>	SW. Ohio, USA	0.3–1.8	Canham et al. (1990)
<i>Betula</i> – <i>Fagus</i> – <i>Acer</i>	Quebec, Canada	1.1–4.0	Messier and Bellefleur (1988)
<i>Carpinus</i> – <i>Carya</i> – <i>Liquidambar</i> – <i>Quercus</i>	Maryland, USA	1–3.7	Brown and Parker (1994)
<i>Fagus</i> and <i>Magnolia grandiflora</i>	N. Florida, USA	0.3–2.0	Canham et al. (1990)
2) On summer-dry soil			
<i>Carya</i> – <i>Quercus</i>	Tennessee, USA	2.9	Baldocchi et al. (1986)

† Abbreviations: SL, shrub layer; HL, herb layer.

positively correlated with the nitrogen supply rate of the soil (range 30–120 kg·ha<sup>-1</sup>·yr<sup>-1</sup>), and that the nitrogen supply rate was negatively related to light penetration through the canopy (range 30–150  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ). These results cannot be explained by allocation patterns

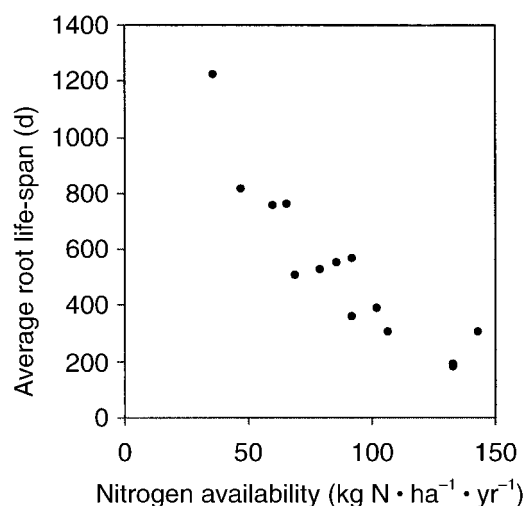


FIG. 2. The relationship between average root life-span and soil nitrogen availability for contrasting cool-temperate forests of North America. Data were taken from Eissenstat and Yanai (1997: Table 4), which was compiled from Aber et al. (1985) and Nadelhoffer et al. (1985). Root life-span was calculated as fine-root biomass divided by annual fine-root production; fine-root production was calculated from the nitrogen-budgeting approach.

alone, because the species found on soils with lower nitrogen availability tend to have longer root life-spans (Fig. 2; Eissenstat and Yanai 1997), and exploit a greater depth of soil in general (Gale and Gringal 1987). The increased penetration of light on infertile soils occurs despite a counteracting trend toward longer leaf life-span, i.e., toward a greater proportion of evergreen species in the canopy (Monk 1966, Chabot and Hicks 1982).

Why do forests on sandy soil in northeastern Europe and central North America allow greater penetration of light than the Amazonian caatinga? It is noteworthy that the temperate forests are dominated by *Pinus* spp., all of which are known to be light-demanding in their regeneration requirements (Fowells 1965). In contrast, the caatingas are dominated by *Eperua* spp., which are strongly shade-tolerant species (Coomes and Grubb 1996). Therefore, our question may be rephrased as “why are many cool-temperate forests on poor soils dominated by light-demanding species?” It is known that fires are relatively common under pine, in part because of the accumulation of highly flammable pine needles (Curtis 1959, Green 1981). It is also known that pines have the potential to live many hundreds of years, despite their “early-successional” status (Fowells 1965). Although some shade-tolerant trees may establish under pine, the process of succession is greatly slowed by the soil infertility, persistence of the early-successional species, and by fire and drought (Faliński 1994). We predict that if appropriate deeply shading species existed in the local flora, they could eventually

dominate on infertile soils where large-scale disturbance is very uncommon, and that the effects of fertility on light penetration would eventually become marginal. This is occurring in many North American oak forests on infertile soils, where *Acer saccharum* is invading as a result of fire suppression (C. D. Canham, *personal communication*). We believe that the dominance of shade tolerators in the Amazonian caatingas reflects, in part, a long history without major disturbance: there is little likelihood of fire because the forest is waterlogged for much of the year, and the region is tectonically stable and unaffected by hurricanes (Coomes and Grubb 1996). It is poignant to note that when humans clear these white-sand forests, they are replaced by open scrubland and woodland, which take many hundreds of years to revert to forest (Whitmore 1990).

Some areas in the northern temperate zone promise to show the effects of nutrient availability without the complication of drought or incidence of frequent fire, but few measurements of light have been made there. The evergreen swamp forest dominated by eastern white cedar *Chamaecyparis thyoides* (found on highly oligotrophic peats in eastern North America) and the related "bay" forests (dominated by evergreen *Magnolia*, *Persea*, and *Gordonia*) in the southeast are clear examples. These forests certainly intercept more light than forests dominated by pines (Korstian and Brush 1931).

Canopy closure and succession are exceptionally slow in the center of waterlogged raised bogs, extensive mounds of peat receiving nutrients only in the rain. Bog forest dominated by *Picea mariana* in Alberta still allowed 60% light transmission after 70 years of regeneration; only after 140 years was mean transmission reduced to 9.6% (Ross et al. 1986). Similarly, bog forest in northeastern Europe, dominated by *Pinus sylvestris*, remains very open for many years after disturbance (Szafer 1966, Faliński 1994). As in the case of well-drained, extremely nutrient-poor soils in the cool-temperate zone, no shade-tolerant, shade-casting tree is able to establish on bogs.

#### *The rooting layer*

Several studies demonstrate that the density of fine roots (in the upper 20–30 cm of topsoil) is greater in forests on infertile soils, when fertility is judged by the nutrient content of litterfall. In tropical rain forests on infertile soils, there is a negative relationship between the biomass of fine roots (mostly defined as <5 mm diameter) and the amount of P or Ca in the litterfall (Gower 1987). The root densities in most forests considered by Gower (300–700 g/m<sup>2</sup>) are much smaller than the 4900 and 8300 g/m<sup>2</sup> (<6 mm diameter), respectively, reported in the top 50 cm of forests on an exceedingly leached oxisol and on a spodosol in the Venezuelan Amazonas (Klinge and Herrera 1978, 1983, Uhl and Jordan 1984). In the northern temperate zone, the density of fine roots is negatively related to nitrogen

availability in both evergreen conifer forests (Keyes and Grier 1981, Vogt et al. 1983) and deciduous forests (Walters and Reich 1997).

Research in southern Venezuela has provided one of the few detailed studies of above- and belowground biomass among forest types in one climate on soils of differing fertility (Medina and Cuevas 1989). Although only a small patch was destructively sampled in each forest type, and the values for total biomass must be regarded as preliminary, there can be no doubt that there is a very marked increase in root mass fraction RMF (root mass/total mass) along the gradient of reduced supply of N (or of major cations), and a similarly marked increase in the absolute amount of root mass in the topsoil (Table 3).

The potential for nutrient uptake is more likely to be related to the surface area of roots, or the number of active apices, than to the mass of roots per se (Andrews and Newman 1973, Caldwell and Richards 1986). Unfortunately, it seems that no critical information has been published on any trend in diameter or degree of branching of fine roots along gradients of nutrient supply. Virtually all tree species are infected by mycorrhizae (Read 1997), but it remains difficult to contrast their activity between sites. In the northern temperate zone, the trees most strongly associated with nutrient-poor soils, species of *Pinus* and *Quercus*, have sheathing mycorrhizae; the same is true of *Eucalyptus*, which dominates on very poor soils in Australia from the cool-temperate regions to the tropics (Smith and Read 1996). However, in the Amazon region, the trees on both spodosols and exceedingly leached oxisols almost all have vesicular-arbuscular mycorrhiza (Moyersoen 1993).

It is now appreciated that the layer of soil in which roots are concentrated varies with soil type and depends upon which nutrient is most limiting. For example, it is currently believed that either P or one of the basic cations is the primary limiting nutrient for growth in most lowland rain forests (Vitousek and Sanford 1986, Burslem et al. 1996), whereas forests on spodosols are limited by N (Medina and Cuevas 1989, Coomes 1997). Where Ca and Mg are extremely scarce, roots "forage" in the fresh litter (L layer) and in fallen trunks and standing dead trees, but where N is scarce, fine roots are concentrated in the F layer of the mor humus, where N release is likely to be maximal, and do not penetrate the L layer (Medina and Cuevas 1989).

In summary, there is evidence from both tropical and temperate regions that the percentage of daylight penetrating the forest canopy is greater on infertile soils, whereas the fine-root density is greatest on these soils. There seems to be no consistent change in fineness of the fine roots or in the form of the mycorrhizae, although the literature is sparse. On infertile soils in temperate regions, recurrent fire, slow rates of regeneration, and a lack of shade-tolerant species in the available flora lead to many forests having open canopies.

TABLE 3. Measurements of biomass and root mass fraction (root/total) along gradients of decreasing nutrient availability in adjacent tropical lowland evergreen rain forests in southern Venezuela (various sources summarized by Medina and Cuevas [1989]).

Forest type	Biomass (Mg/ha)			Root mass fraction
	Total	Below-ground	Above-ground	
"Guaco" forest on grey ultisol	465	42	423	0.09
Mixed forest on oxisol (K-, Ca-, and Mg-starved) <sup>†</sup>	(a) 310	49	261	0.16
	(b) 292	57	234	0.20
Tall caatinga on spodosol (N-starved) <sup>†,‡</sup>	356	119	237	0.33
Short caatinga <sup>§</sup>	310	128	182	0.41

<sup>†</sup> These forests are also very short on P (Coomes 1997). Rows (a) and (b) denote different sample plots.

<sup>‡</sup> Sensu Coomes and Grubb (1996) on waterlogged sand (groundwater spodosol).

<sup>§</sup> Sensu Coomes and Grubb (1996), differing in lower stature and more waterlogging (Bongers et al. 1985).

In such areas, where the dominants being compared are shade-tolerant dicotyledons on the more fertile soils and light-demanding pines on the least fertile, there may be a four- to fivefold increase in penetration of light. The roughly twofold difference between forests on relatively fertile and highly infertile soils in the wet tropics is less pronounced.

#### TRENDS IN VEGETATION STRUCTURE ALONG GRADIENTS OF WATER AVAILABILITY

##### *Canopy form*

Plants respond to water shortage by closing stomata, the signal in some species being lowered humidity around the stomata, and in others lowered water potential in the leaf or root tissues (Schulze and Hall 1982, Dodd et al. 1996). Closure not only conserves water, but also increases water use efficiency (WUE) at a given vapor pressure deficit between the leaf interior and the air outside (i.e., increases carbon gain per unit water lost). Influx of CO<sub>2</sub> is less sensitive to stomatal closure than efflux of water, because of the large resistance to its influx resulting from the carboxylation process. It might be supposed that the compensatory effect of increased WUE would diminish the impact of rainfall on productivity, but the closure of stomata does not conserve water effectively in dry regions. Areas with low rainfall also have low air humidity in the middle of the day (high vapor pressure deficit), which greatly increases the rate of transpiration for a given wind speed. In fact, the actual WUE is often observed to decrease within species with increasing aridity, despite stomatal closure, as shown for *Acacia koa* stands in Hawaii (Harrington et al. 1995). Thus, water conservation in low-rainfall regions requires one of the following: a reduced LAI, the development of specialized leaves with thick cuticles and increased cytoplasmic tolerance of desiccation, or deciduousness during dry spells. All of these features incur a loss in productivity, so we expect little compensation for the effects of water shortage. Besides conserving water, plants in dry areas commonly develop deep root systems that make use of

water stored in the subsoil between rainfall events, and roots that run far outside the crown and capture water from the intercanopy areas. Greater allocation to root development comes at the cost of reduced allocation to leaves and/or stems.

In reporting on how canopy form changes along gradients of decreasing water supply, we first consider regions where the woody plants are evergreen along the whole length of the gradient, and then cases where evergreen plants give way to deciduous plants, or vice versa.

In the northwestern United States, evergreen conifers are dominant over a huge range of rainfall. The mean leaf area index has been estimated to fall by a factor of five along a gradient of total rainfall from 2500 to 300 mm/yr (Grier and Running 1977), and as forest gives way to woodland, the spatial variability of light transmission greatly increases (Peet 1988, Riegel et al. 1995). Parallel reductions in soil water potential and the extent of shading have been quantified along an elevation gradient farther south in the western United States by Barton (1993).

Most woody vegetation in the warm-temperate zones is also evergreen. Rain forests in areas of high summer rainfall give way to evergreen sclerophyll communities in mediterranean-climate regions with dry summers. The general reduction in LAI with decreasing water supply is very marked, as is the increase in light penetration (Table 4), and is clearly related to the maximum leaf area that a stand can maintain during the dry season in an average year (Woodward 1987). It should be noted that the five regions with a mediterranean-type climate display a huge variety of sclerophyll vegetation types. In the Mediterranean Basin, central California, and central Chile, densely shading forest formed the late-successional vegetation type over large areas until very recently, whereas in the Cape region of South Africa, such forest has long been confined to sites protected from frequent fire (gullies and large-block screes), and the fynbos heathland (0.5–3.0 m tall) predominates. In southern Australia, there is chiefly

TABLE 4. Canopy height, leaf area index (LAI), and percentage transmission of daylight (*T*) in woody communities of the warm-temperate zones.

Location	Height (m)	LAI	<i>T</i>	References
Rain forest				
Japan	23	5.4–8.9	0.5–1.0	Kira (1975), Yoda (1978)
Mediterranean-climate forest (sclerophyll)				
France	10–20	4.5		Lossaint (1973)
Italy	10–20	4.5	1.1–1.5†	Baldi et al. (1987), Gratani et al. (1992)
Mediterranean-climate shrubland (sclerophyll)				
California	2–3	2	11–22	Miller and Poole (1980)
Chile	2–3	2.0–3.6	...	Rundel (1982)
	2–3	1.3–2.1	18–50‡	Roberts and Miller (1977)
		1.7–2.2	42–66§	
	2–5	0.9–4.4	...	Rundel (1982)
South Africa (fynbos invaded by <i>Acacia</i> )	3	...	8–9	Holmes and Cowling (1997)
South African fynbos				
1) sandy	1	...	1) 46	Holmes and Cowling (1997)
2) sandy loam			2) 14–18	

Note: Ellipses indicate that no data were available.

† Values quoted are for January–October; inexplicably, values of 6.9% and 15% were obtained for November and December.

‡ A species with leaves uniformly distributed in the canopy.

§ A species with leaves around the periphery only.

*Eucalyptus* forest, woodland, or scrub (all of which allow through a very high percentage of daylight), and heathland (kwongan). In southern California, where the effective drought is greater than farther north, there is extensive low scrubland (1–3 m tall). Toward the coast it is replaced by deciduous low scrub “coastal sage,” but at the junction with semidesert inland it remains evergreen and the shrubs become widely spaced (Hanes 1977, Mooney 1977). In Chile there is also deciduous low scrub in an extensive low-rainfall area near the coast (Rundel 1981). It is hardly surprising that greatly varying values for LAI and light penetration have been recorded in mediterranean-climate regions.

A consistent trend in mediterranean-climate communities is for vegetation on pole-facing slopes to have a greater LAI than that on adjacent equator-facing slopes, and to have dry topsoil to a greater extent. This trend has been reported in California for comparisons in chaparral (Ng and Miller 1980), coastal sage scrubland (Ng and Miller 1980), and sclerophyll woodland in a moister area (Giffin 1973); it has also been noted in eucalypt forests in southern Australia (Martin and Specht 1962). The greater LAI on pole-facing slopes is consistent with the fact that these communities receive less radiation, and therefore have a lower transpiration load.

In the tropics and subtropics, on average soils, a decline in total rainfall and/or an increase in length of the dry season is associated with a transition from evergreen forest through semi-evergreen forest to deciduous forest or woodland (Groves 1981, White 1983, Bullock et al. 1995). On deep, infertile soils, even the dry-climate vegetation types are evergreen, as in the cerrado of central Brazil (rainfall 750–1500 mm/yr; Eiten 1978) and the mulga (*Acacia aneura*) woodlands

of Australia (200–500 mm/yr; Beadle 1981). The drier woodlands grade into savannas dominated by graminoids, but with scattered trees or shrubs; in such areas the tree density is strongly dependent on recent fire history, as is the balance between shrubs and grasses in the understory, grasses being favored by more frequent fires. The few data available for semi-evergreen and deciduous forests show a marked drop in LAI and a marked increase in daylight penetration (in the wet season) when compared with evergreen forests of moist regions (Table 1). The increase in penetration is more than that found in the forests on the most infertile soils with secure water supply (up to 8% vs. 2%; Table 1). The deciduous trees may be leafless for up to six months (Holbrook et al. 1995). However, seedlings of deciduous species cannot utilize the periods when the taller trees are leafless, and those of evergreen species may be able to make limited use (if any) because of water shortage in their tissues (Holbrook et al. 1995, Gerhardt 1996). It follows that the differences in shade cast during the wet season are most consequential, and these differences are less pronounced. In contrast to the position in temperate deciduous forests, the lower growing plants in tropical deciduous forests do not leaf out before the taller growing plants, and thus there is no period analogous to the “spring window” in which lower growing plants can make a significant carbon gain.

In the northern temperate zone, we often find the opposite of the trend in deciduousness seen in the tropics. In other words, evergreen species take over from deciduous species at topographically dry sites. The trend in the temperate zone reflects the dominance of conifers on shallow soils. Although a few of the conifers concerned are deciduous (*Larix* spp.; Walter



TABLE 5. The root mass fraction, RMF (root dry mass/total dry mass) along gradients of increasing dryness in three temperature zones, based on Reichle (1981) unless otherwise indicated.

Vegetation type	RMF§
Tropical lowland forests†	
Rain forest (Ivory Coast, Brazil, Ghana)	0.09, 0.14, 0.19 <sup>e</sup>
Deciduous forests (Mexico, Puerto Rico)	0.30 <sup>f</sup> , 0.34 <sup>g</sup>
Warm-temperate evergreen communities	
Moist-site broad-leaved (rain forest)	
<i>Castanopsis-Quercus</i> (three plots, S. Japan)	0.16, 0.19, 0.20 <sup>a</sup>
Moist-climate dry-site conifer forest	
<i>Pinus densiflora</i> (C. Japan)	0.20
Mediterranean-climate sclerophyll communities	
<i>Quercus ilex</i> (France)	0.15 <sup>b</sup>
<i>Protea fynbos</i> tall-heath (S. Africa)	~0.2 <sup>c</sup>
<i>Eucalyptus obliqua</i> (Australia)	0.19
Temperate lowland deciduous forest	
Moist-site forests	
<i>Fagus sylvatica</i> (Germany, Denmark, Sweden)‡	0.12, 0.14, 0.14
<i>Quercus-Tilia-Sorbus-Corylus</i> (Sweden)	0.16
<i>Quercus-Tilia-Carpinus</i> (Poland)	0.17
<i>Quercus-Tilia-Acer-Ulmus</i> (two plots, Russia)	0.20, 0.29
<i>Quercus-Carpinus-Acer</i> (Belgium)	0.22
Dry-site deciduous forests	
<i>Quercus-Carya</i> (Tennessee)	0.19
<i>Quercus-Prunus</i> (Wisconsin)	0.20
Dry-site coniferous forests	
<i>Pinus sylvestris-Quercus robur</i> (Poland)	0.22
<i>Pinus sylvestris</i> (Spain)	0.21
<i>Pinus contorta</i> (Wyoming), three less dry sites	0.22, 0.23, 0.22 <sup>d</sup>
<i>Pinus contorta</i> (Wyoming), three drier sites	0.21, 0.31, 0.33

† Excluding those on exceptionally infertile soils.

‡ A montane species brought into the lowlands by human activity.

§ References: (a) Karizumi (1978); (b) Lossaint (1973); (c) Higgins et al. (1987); (d) Pearson et al. (1984); (e) Greenland and Kowal (1960); (f) Castellanos et al. (1991); (g) Murphy and Lugo (1986b).

1974, Ellenberg 1988), most are evergreen, e.g., species of *Juniperus*, *Pinus*, and *Thuja* (Fowells 1965, Knapp 1965, Shidei 1974, Ellenberg 1988).

#### The rooting layer

Extrapolating from experiments in which individual species are grown with different degrees of soil drying (Bradford and Tsiao 1982, Burslem et al. 1996, Canham et al. 1996), we expect the root mass fraction (RMF) of whole communities to increase along gradients of increasing dryness, whether determined by climate or soil type. The few data available from the tropical lowlands do show a consistent increase in RMF from evergreen forest to deciduous, but no convincing trend is found in the warm-temperate or cool-temperate regions (Table 5). At the moister end of the spectrum in the northern cool-temperate zone, only forests dominated by *Fagus* have consistently low RMF values (Table 5); *Fagus* species are typically montane (Peters 1997), and *Fagus sylvatica* has become widespread and abundant in European lowlands only under human influence (Godwin 1975). The lack of trend came as a surprise to us, and may reflect a sampling bias. Drier forests

and woodlands generally have deeper roots (Canadell et al. 1996), and a lesser proportion may have been sampled than in moister forests (Jackson et al. 1996), but it remains possible that drier forests have deeper roots without having a greater mean RMF.

Considering the intensity of competition for water experienced by a seedling, the RMF is likely to be less important than the absolute amount of root in the topsoil (e.g., the top 30 cm). Not all of the authors that we cite have given values for the top 30 cm, and we have had to make some interpolations from data for the top 20 and 40 cm. Along gradients of increasing dryness, there is no convincing trend for topsoil root dry mass to increase in either the warmer temperate regions or in the tropics, though the few data for the cooler temperate regions are suggestive (Table 6). However, fine-root mass is likely to be more important in competition than is total root mass. Using data from three disparate studies in the tropics, Cuevas (1995) has found evidence of an increase in fine-root mass from 440 g/m<sup>2</sup> at a site with rainfall of 1260 mm/yr to 1350 g/m<sup>2</sup> at rainfall of 710 mm/yr in the wet season, and from 310 to 950 g/m<sup>2</sup> in the dry season.

TABLE 6. The dry mass of roots in the top 30 cm of soil in different vegetation types. Unless otherwise indicated, data are from Jackson et al. (1996), who averaged values from a variable (small) number of sites for each vegetation type.

Vegetation type	Root dry mass (kg/m <sup>2</sup> )†
Tropical lowland	
Rain forest	3.4
Deciduous forest (Mexico, Puerto Rico)	~1.7 <sup>a</sup> , ~3.7 <sup>b</sup>
Warm temperate	
Rain forest (two sites, Japan)	2.1, 4.4 <sup>c</sup>
Dry-site conifer ( <i>Pinus densiflora</i> , Japan)	3.0 <sup>c</sup>
Mediterranean-type sclerophyll	3.2
Cool temperate	
Deciduous forests	2.7
Dry-site conifer (three sites of <i>Pinus contorta</i> , Wyoming)	3.9 <sup>d</sup> (mean)

† References: (a) Castellanos et al. (1991); (b) Murphy and Lugo (1986b); (c) Karizumi (1978); (d) Pearson et al. (1984).

It is the surface area of “active” root, rather than dry mass, that should determine the rate of water uptake, along with the difference in water potential between leaf and root and the internal resistances to flow (Andrews and Newman 1968, Caldwell and Richards 1986). The proportion of the root surface that is suberized and inactive in uptake of water is unknown for most trees and shrubs. Furthermore, we remain ignorant of the extent to which mycorrhizal hyphae are effective channels for uptake of water (Smith and Read 1996).

Quantitative information on trends of specific root length along gradients of dryness is not available, but it is notable that many of the dicotyledonous families of the wet tropics have “magnolioid” roots (Baylis 1975) with thick terminal branchlets (e.g., Annonaceae, Lauraceae, Magnoliaceae, Monimiaceae, and Myristicaceae), whereas families prominent in drier forests tend to have finer ultimate branchlets (e.g., Anacardiaceae, Burseraceae, and Meliaceae). Additionally, tree-forming monocots (palms, pandans) have notably coarse “fine roots” (Corner 1966) and they, too, are concentrated in the wetter forests. It is perhaps significant that, in the warm-temperate zone, the Lauraceae are among the dominants in most natural warm-temperate rainforests, but (apart from Chile; Oberdorfer 1960) are absent from most mediterranean-climate vegetation or are confined to sites with a reliable ground-water supply (e.g., *Laurus nobilis* and *Umbellularia californica*; Walter 1968).

It is undoubtedly the case that grasses have much finer roots than most trees and, consequently, have a much greater surface area per unit root mass. In savannas, the trees have a far smaller root length in the topsoil than do the grasses, but have extensive roots at greater depths. For example, Knoop and Walker (1985) found that the average length of grass roots in the top 50 cm of soil was 70 times greater than that of tree roots under isolated trees in an *Acacia nilotica*–*A. tortilis* savanna in South Africa (rainfall 630 mm/yr). As a result of their “spendthrift” nature, grasses in tropical savannas tend to use much of the rain that falls during

the wet season. According to the hypothesis of H. Walter (1939, 1973) the transition down the rainfall gradient from tree savanna via shrub savanna to pure grassland on sandy soils in the summer-rainfall region of southern Africa results from the grasses allowing decreasing amounts of rain to penetrate to the subsoil. Woody plants depend on subsoil water to support their transpiration during the dry season, and when the amount remaining in the subsoil at the end of the wet season decreases, woody plants are first reduced in stature and density, and finally fail altogether. In support of this hypothesis, Knoop and Walker (1985) found a much greater penetration of water to the subsoil of savanna after removal of the grass.

To summarize, there is clear evidence that light penetration increases with decreasing rainfall or increased length of dry season. The root mass fraction of the whole-forest biomass is greater in drier regions than in moister regions in the tropical lowlands, but apparently not in warm- or cool-temperate regions. There is no substantial body of information on the most important variable for uptake of water, the surface area of roots or the number of living apices per unit volume of topsoil. From a taxonomic perspective, we suspect that woody species have finer roots in dry regions, but this requires thorough investigation. There is certainly an increase in root surface area in the dry woodlands in which grasses become abundant. In general, trees become more dependent on deep roots where the annual rainfall is lower.

#### RESPONSES OF SEEDLINGS TO NUTRIENT ADDITIONS AND WATER SUPPLY IN VARIOUS DEGREES OF SHADE

So far we have discussed how above- and below-ground resources vary in their availability along environmental gradients and with stand development. Whether or not seedlings respond to removal of root competition will depend partly on which resources are in scarce supply and partly on the inherent responsiveness of the target species.

TABLE 7. A spectrum of shade tolerances with examples from temperate deciduous forest, taken from Fowells (1965), Canham (1989), and Pacala et al. (1996). In the first column, numerals 1–2 represent light-demanding categories; 3–4, intermediate; and 5–6, shade-tolerant categories.

Deepest shade in which seedlings found	No. years that seedlings persist in deep shade	Examples in North American temperate deciduous forest
1) Edges and very large gaps		Paper birch <i>Betula papyrifera</i>
2) Single treefall gaps		Tuliptree <i>Liriodendron tulipifera</i>
3) Understory	1–5	Various oaks including <i>Quercus rubra</i>
4) Understory	5–10	Black cherry <i>Prunus serotina</i>
5) Understory	20–50	Sugar maple <i>Acer saccharum</i>
6) Understory	>50	Beech <i>Fagus grandifolia</i>

In this section, we consider the extent to which responsiveness to soil resources is related to the shade tolerance of a species. There is no uniquely satisfactory definition of shade tolerance, partly because of the negative correlation between rate of growth in deep shade and rate of survival (Kitajima 1994, Kobe et al. 1995, Kobe and Coates 1997, Walters and Reich 1997, Grubb 1998). The rate of survival is more closely related to traditional foresters' estimates of "tolerance" (Pacala et al. 1996). However, it is arguable that, among tree species that regularly regenerate in deep shade, there is a spectrum from those enabled to do so chiefly by a very high rate of survival, to those that have only a moderate rate of survival but a relatively high rate of height growth in the shade (Kohyama 1987, Grubb 1998). The best known systems of "tolerance" are the five-point scales used by Baker (1945) and Ellenberg (1963) to characterize North American and European tree species, respectively. These early systems were based largely on subjective observations, and failed to take account of how tolerances change with tree size (Oldeman 1990). It will be many years before more objective methods are applied generally. Meanwhile, we adopt a six-point scale taking into account (1) the conditions under which seedlings become established, and (2) the longevity of seedlings in deep shade (Table 7; cf. Canham 1989). In this review, we simplify the six-point scale to one with only three categories: light-demanding, intermediate, and shade-tolerant (Table 7).

#### RESPONSIVENESS OF TREE SEEDLINGS AND FOREST HERBS TO RATE OF NUTRIENT SUPPLY

In the following section, we consider how far species differ in the minimum irradiance at which they respond positively to nutrient addition, and we relate our findings to species traits. The basic physiological responses of plants to irradiance and nutrient supply are relatively well understood. Most plants respond to a greater supply of nutrients in full sunlight by increasing their growth rate (Chapin 1980), but many respond at very low irradiance by reducing growth rate or dying more quickly (Hutchinson 1967, Grubb et al. 1996). There is no proven explanation for the negative effect of nu-

trient supply on survival and growth at very low irradiance, but the most likely explanation is that an increased uptake of nutrients is followed by an increase in respiration rate without any compensating increase in photosynthetic rate; in many plants, respiration rate parallels the concentration of N in the tissues (Lambers and Poorter 1992, Reich et al. 1996).

There are marked differences among species in their responses to light and nutrient supply, as reported in comparative growth rate studies of seedlings of temperate woody plants (Latham 1992, Canham et al. 1996, Grubb et al. 1996). The minimum amount of light at which these plants responded to nutrient addition varied among species, from 2–3% to >45% daylight in each of the studies (Table 8). Generally, these studies agree, but there are a few inconsistent results to mention. Although *Quercus rubra* is consistently unresponsive to N addition in deep shade, Latham (1992) found it responsive to added nutrients in 30% daylight (in agreement with an earlier study by Phares (1971) using NPK fertilizer), whereas Canham et al. (1996) found it unresponsive at even 45% daylight. Similarly, *Acer saccharum* did not respond in 20% daylight (Canham et al. 1996), or in 8% daylight (Walters and Reich 1996), but its growth in the forest understory was found to be positively correlated with N mineralization rates (Walters and Reich 1997).

Marked differences among species in the minimum amount of light in which they will respond to nutrients have recently been established for trees of tropical lowland rain forest. In Singapore, seedlings of the shade-tolerant *Antidesma cuspidatum* (grown on granite-derived forest soil) were found to respond to nutrient addition (notably Mg) in <1% daylight (Burslem et al. 1995, 1996), whereas those of *Shorea curtisii* (a widespread dipterocarp species of intermediate tolerance) were not responsive to nutrient addition in the shade of the understory, but were in a natural forest gap (Burslem 1996). In northern Queensland, seedlings of two fast-growing species (*Dendrocnide cordata* and *Solanum dallachii*) of forest on basalt-derived soil need slight gaps in the canopy for establishment; they responded appreciably to nutrient addition (N, P, K, Ca,

TABLE 8. Experimental determination of the minimal percentage daylight at which species respond to the addition of nutrients, using potted plants under shade screens.

Soil type	Fertilizer	Percentage of full daylight under screens				Unresponsive	Reference
		2–4%	5–11%	20–30%	> 45%		
North American tree species							
Artificial mix	N, P, K, Mg, Ca, S	<i>Liriodendron tulipifera</i>	<i>Nyssa sylvatica</i>	None	<i>Castanea dentata</i> , <i>Fagus grandifolia</i> , <i>Quercus rubra</i>	<i>Carya tomentosa</i>	Latham (1992)
Artificial mix	N		<i>Acer rubrum</i>	<i>Pinus strobus</i> †	<i>Acer saccharum</i> †	<i>Quercus rubra</i>	Canham et al. (1996)
European shrubs							
Grass- and shrub-land soil	Natural differences in N+P supply	<i>Viburnum lantana</i>	<i>Cornus sanguinea</i> , <i>Rhamnus catharticus</i> , <i>Rosa canina</i> , <i>Viburnum opulus</i>	None	<i>Ligustrum vulgare</i>	<i>Crataegus monogyna</i> , <i>Euonymus europaeus</i> , <i>Juniperus communis</i>	Grubb et al. (1996)

† Responded only when supplied with additional water.

and Mg) in 2% daylight, whereas seedlings of several species that routinely become established in the understory did not respond to nutrient addition in 2% daylight, but did so in 5% (P. J. and E. A. A. Grubb, unpublished data).

In general, we expect species with the highest relative growth rates at a moderate level of nutrient supply to be most responsive to nutrient addition. This result was obtained for 34 Mexican tropical deciduous forest species (Fig. 3, based on Huante et al. 1995), and 10 European tall-shrub species (Grubb et al. 1996), but not for 15 Ghanaian evergreen and semi-evergreen forest species (Veenendaal et al. 1996b). Insofar as the species that are most responsive to increased light are

also the ones with the highest maximum relative growth rates, we expect that, among forest trees found naturally on average to highly fertile soils, the species most responsive to light will be the ones that show the greatest sensitivity to nutrient supply. This generalization is supported by the fact that the species that were most able to respond to additional nutrients in relatively low irradiance were *Liriodendron* and *Nyssa* in the study of Latham (1992), *Acer rubrum* and *Pinus strobus* in that of Canham et al. (1996), and *Dendrocnide cordata* and *Solanum dallachii* in the Australian tropical rain forest study. Denslow et al. (1998) found that a light-demanding species of *Miconia* responded to nutrient addition in artificial treefall gaps in a Costa Rican rain forest, but that three shade-tolerant species of *Miconia* were unresponsive.

All of the published experiments on combined effects of shade and nutrient supply concern growth rate rather than survival, but Ellenberg (1939) and, more recently, Kobe et al. (1995) demonstrated that some species penetrate deeper shade on soils of higher pH. Peace and Grubb (1982) argued that the most probable explanation of this phenomenon is that faster growth of seedlings in response to a greater of supply of nutrients enables them to resist hazards such as short-term drought, physical disturbance, or herbivory.

What mechanisms underpin the observed differences in responsiveness to nutrient supply in various degrees of shade? This question is instructively explored by considering the relative growth rate RGR of a plant (in grams per gram per day) as the product of two components: (1) unit leaf rate ULR (rate of dry matter gain per unit leaf area, in grams per square meter per day), and (2) leaf area ratio LAR (leaf area per unit of whole plant dry mass, in square meters per gram). This subdivision allows the relative importance of morphology and photosynthetic processes to be ascertained (Evans

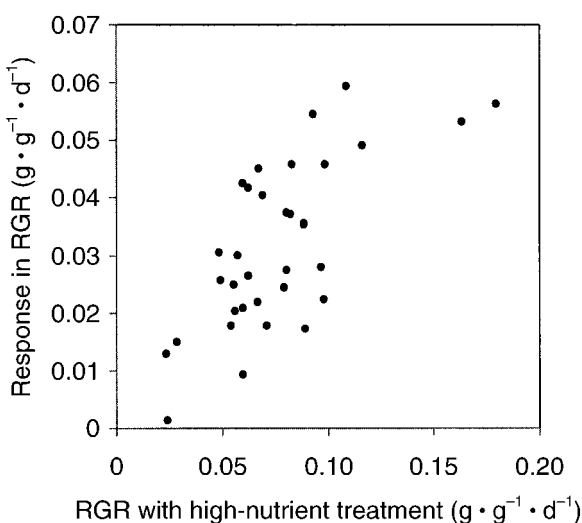


FIG. 3. The relationship between the responsiveness to nutrient addition (difference between the relative growth rates, RGR, attained under high- and low-nutrient treatments) and the RGR attained under the high-nutrient treatment for 34 Mexican species (based on Huante et al. 1995).



TABLE 9. Growth analysis using LAR, ULR, LMF, SLA,  $T$ , and  $P_{\max}$  to identify the causes of increased relative growth rates in response to nutrient additions in growth cabinet experiments.

Species	Type of plant and habitat	4–5% of full daylight	25–70% of full daylight	Notes	Author(s)
<i>Impatiens parviflora</i>	Annual herb of gaps in European temperate forest	+ LAR	+ LAR† + ULR	+ LMF (not SLA) → + LAR – R (not + $P_{\max}$ ) → + ULR	Peace and Grubb (1982)
<i>Festuca gigantea</i>	Perennial grass of gaps in European temperate forest	+ LAR	+ LAR† + ULR	+ LMF (not SLA) → + LAR	Peace (1984)
<i>Mansonia altissima</i>	Non-pioneer light-demanding tree of West African rain forest	+ LAR	+ LAR‡ + ULR		Veenendaal et al. (1996b)
<i>Triplochiton scleroxylon</i>	Pioneer tree of West African rain forest		+ ULR‡		Veenendaal et al. (1996b)
<i>Toona australis</i>	Light-demanding tree of Australian rain forest	+ ULR‡	+ ULR‡	+ $P_{\max}$ (not –R) → + ULR	Thompson et al. (1992a,b)
<i>Argyrodendron</i> spp.	Shade-tolerant trees of Australian rain forest	§	§	$P_{\max}$ not affected by nutrient additions	Thompson et al. (1992a,b)

Notes: LAR, ratio of leaf area to whole plant mass ( $\text{m}^2/\text{g}$ ); ULR, unit leaf rate ( $\text{g}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ ); LMF, leaf mass fraction ( $\text{g}/\text{g}$ ); SLA, specific leaf area ( $\text{m}^2/\text{g}$ );  $T$ , percentage transmission of daylight;  $P_{\max}$ , maximum rate of photosynthesis. Positive (+) and negative (–) responses to nutrient addition are indicated, and arrows (→) denote “resulted in.”

† Percentage daylight values were 40% penetration.

‡ Percentage daylight values were 27–66%.

§ Irradiances in growth cabinets of 30 and 535  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  over a 12-h day.

1972). Furthermore, the LAR of a plant can be expressed as the product of two components: the LMF, or leaf mass fraction (leaf dry mass/total dry mass), and SLA, or specific leaf area (leaf area per unit dry mass, in square meters per gram). This subdivision makes it possible to assess the importance of changes in resource allocation among plant parts relative to changes in leaf structure.

Experiments under controlled conditions show that species generally respond to increased nutrient availability in deep shade by increased LAR, and not by increased ULR (Table 9). It follows that species that are most responsive to nutrient addition in deep shade are those that are most flexible in LAR in deep shade. This supports our prediction that relatively fast-growing species are most responsive to nutrient addition in shade, because a recent review of 194 species has demonstrated that light-demanding species were able to increase their LAR greatly when grown in low light conditions (1–5% daylight), but that shade-tolerant species were far less flexible (Veneklaas and Poorter 1998).

Work carried out under controlled conditions shows that species respond to increased nutrient availability in bright light by increasing ULR and/or LAR, and that the increases in ULR result from increases in the maximum rate of photosynthesis  $P_{\max}$  rather than decreases in respiration  $R$  (but see Peace and Grubb 1982). For example, plants of *Atriplex patula* (a light-demanding herb) responded to additional N by increasing their maximum rate of photosynthesis in bright light but not

in shade (Medina 1971). Essentially similar results were reported for light-demanding and moderately shade-tolerant species by Osmond (1983, 1987), Evans (1989), and Bungard et al. (1997). The minimum shade at which plants respond to nutrient addition by increasing  $P_{\max}$  is very dependent on species. For example, seedlings of *Toona australis* (a light-demanding tree) responded positively in very low irradiance, whereas species of *Argyrodendron* (strongly shade tolerant) did not respond at any irradiance tested (Thompson et al. 1992a, b). However, changes to the  $P_{\max}$  of a species will have little impact in deep shade.

In studies of the shade relations of plants of the temperate zones, shade-requirement is rarely discussed (cf. Spurr and Barnes 1980, Ellenberg 1988). There are records of shade-tolerant species performing much less well in high irradiance than in low. For example, Sipe and Bazzaz (1995) reported much lower survival of seedlings of *Acer saccharum* in large canopy gaps than in small gaps or in the understory. A preliminary study has been published relating shade tolerance to the potential for dissipation of excess excitation energy via the xanthophyll cycle in 22 species of British herbs (Johnson et al. 1993). Among those working on plants of the lowland wet tropics (Murray and Nichols 1966, Hadfield 1968, 1974, Mulkey et al. 1996), however, there is a much longer established concern with shade requirement. On moderately fertile soils, yields of crops such as cocoa and coffee are deleteriously affected by irradiance of >50% daylight unless addi-

tional NPK fertilizer is added (Murray and Nichols 1966), and high irradiances may even cause the death of young plants (Nunes et al. 1993). The deleterious effects of high irradiance are caused largely by photoinhibition, i.e., a reduction in photosynthetic rate resulting from damage to the light-absorbing system when the production of high-energy compounds in light reactions exceeds their usage in dark reactions (Long et al. 1994). The dark reactions are greatly slowed by a shortage of N (Ferrar and Osmond 1986, Thompson et al. 1992a, Nunes et al. 1993) and by the desiccation and overheating of leaves (Gamon and Pearcy 1990, Mulkey and Pearcy 1992), and it follows that root competition for nutrients and/or water in treefall gaps may significantly decrease photosynthesis via photoinhibition. Far more research is needed into the deleterious effects that high irradiance has on the physiology of the juveniles of forest trees (cf. Turner and Newton 1990, Lovelock et al. 1994, Scholes et al. 1996, Watling et al. 1997).

To summarize, plants tend to be substantially more responsive to nutrient supply when grown in irradiances typical of gaps and edges in natural forests (>5% daylight) than when grown in irradiances typical of the understory (<2%), but species differ markedly in the minimum irradiance at which they respond. We predict that, in general, the species most responsive to nutrient supply will prove to be (1) those with relatively high growth rates at moderate levels of nutrient supply, and (2) those most responsive to increased irradiance.

#### RESPONSIVENESS OF TREE SEEDLINGS AND FOREST HERBS TO SOIL WATER SUPPLY

In contrast to the case for nutrient supply in different levels of shade, little is known from experiments about the combined effects of water shortage and shade. We first review the little experimental work that has been published on the combined effects on growth rate, and then consider the evidence from field studies on survival. It is in the latter context that we discuss the trade-off between shade tolerance and drought tolerance hypothesized by Smith and Huston (1989).

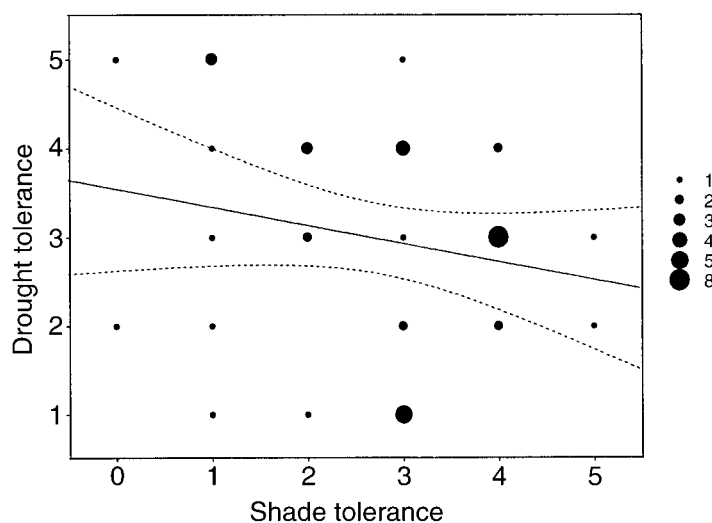
Of the few relevant experiments that have been published, some are flawed. The standard means of imposing a range of water availability on container-grown seedlings is to apply different frequencies of watering, and at each watering to return the rooting medium to field capacity (e.g., Kozlowski 1949). Such experiments fail to provide the same degree of drying across the range of shading treatments, because plants grown in deep shade are generally smaller and have lower transpiration rates than those grown in bright light, and thereby dry the soil to a lesser extent. This difficulty can be lessened by maintaining each pot at near-constant soil moisture (i.e., varying the amount of water applied so that the mass of the pot remains nearly constant). By this method, Canham et al. (1996) showed that *Acer rubrum*, *Acer saccharum*, *Pinus strobus*, and

*Quercus rubra* were unresponsive to watering treatment (50% and 100% of field capacity) at 2% daylight, whereas *Acer rubrum* responded at 9% daylight, and all responded strongly in 20%, 45%, and 100% daylight. Thus, despite the very different niches of these species, the minimum irradiance at which they responded to water treatment was similar, making it difficult to distinguish among them by this criterion.

Field studies have left no doubt that desiccation is a major source of seedling mortality in the understory of a wide range of forest types, including rain forests. For example, the dry-season mortality for first-year seedlings was 72–93% for *Shorea* spp. in Malaysia (Turner 1990). Under forests that cast deep shade, dry-season mortality is much lower in treefall gaps than in the understory in rainforests in Malaysia, Panama, and Ghana (Turner 1990, Fisher et al. 1991, Veenendaal et al. 1996a). *Acer saccharum* has higher mortality on drier sites, shown by Caspersen et al. (*in press*) using maximum likelihood modeling. Along similar lines, irrigation reduces mortality to a greater extent in the understory than in gaps (Mulkey et al. 1991). Reduced root density in the centers of large gaps means that soil water content may remain relatively high, more than compensating for the increased transpiration associated with higher irradiance, greater midday vapor pressure deficit, and any drying of the soil surface that is exposed to direct sunlight. The simplest explanation for a deleterious interaction of shade and drought on survival in the deep shade is that seedlings do not grow fast enough to develop roots of adequate depth to maintain contact with moist soil in dry spells. This effect is compounded by any reduction in allocation to roots that results from growth in deep shade, or from any reduction in carbohydrate supply so that the needs for root respiration are no longer met (Marshall 1986). It was along these lines that Kozlowski (1949) explained the death of *Pinus taeda* seedlings where they become established in shade. Seedlings have a greater chance of surviving drought once they have developed a sizeable taproot. Bragg et al. (1993) showed that 4–5 yr-old seedlings of *Quercus macrocarpa* and *Q. muehlenbergii* (species in the gallery forest of the tall-grass North American prairie) maintained higher xylem water potentials than did 1–2 yr-old seedlings during drought, the reason being that they had developed long taproots.

Smith and Huston (1989) stated that the shade-tolerating strategy of plants is diametrically opposed to that for tolerating drought. In the first case, plants are supposed to maximize the efficiency of photosynthesis by producing thinner leaves and by allocating more assimilates to leaves and fewer to roots. In the second case, they are supposed to maximize water use efficiency by producing thick leaves and by allocating more assimilates to roots. Smith and Huston (1989) maintain that it is thus impossible to tolerate both shade and drought.

FIG. 4. The drought tolerance and shade tolerance of European trees species, as assessed by Ellenberg (1988). Note that there is no evidence of a negative correlation, in contrast to the predictions of Smith and Huston (1989). Circle sizes indicate the number of species represented by a combination of drought and shade tolerance values.



It is important to distinguish between intra- and interspecific effects (L. Sack, *personal communication*). We know that many species increase SLA and LMF and decrease RMF when grown in low irradiance (Lambers and Poorter 1992). Thus, we should expect to find that, in many species, a given degree of drought induces greater mortality where the shading is greater, just as we have documented. The position is substantially different in comparisons between species. Although it is true that some very abundant, well-known drought-tolerant conifers are highly intolerant of shade, e.g., *Juniperus virginiana* (Knapp 1965), *Pinus densiflora* (Shidei 1974), and *Pinus sylvestris* (Ellenberg 1988), other conifers can tolerate both drought and shade, e.g., *Tsuga canadensis*. Caspersen et al. (*in press*) found, using a maximum likelihood technique, that *T. canadensis* had the same chance of mortality irrespective of soil moisture supply (at a given growth rate). Furthermore, the supposed trade-off is not supported by the ratings of Ellenberg (1988) for 42 tree species in central Europe (Fig. 4). In addition, strongly shade-tolerant understory species are found in the evergreen sclerophyll forests of regions with mediterranean-type climates, e.g., *Asparagus acutifolius*, *Hedera helix*, *Rubia peregrina*, *Ruscus aculeatus*, and *Viburnum tinus* in the Mediterranean Basin (de Lillis and Fontanella 1992, Gratani et al. 1992), *Asparagus scandens* and *Knowltonia vesicatoria* in South Africa (Adamson and Salter 1950), and *Heteromeles arbutifolia* and *Rhus (Toxicodendron) diversiloba* in California (Thomas 1961).

Most plants that endure both shade and drought have long-lived, relatively thick leaves of low SLA, and do not show marked changes in SLA or RMF when grown in different irradiances (L. Sack and P. Grubb, *unpublished data*). Possession of low SLA values and low flexibility is important for shade-tolerant trees in general, including huge numbers of species in tropical rain forests, because death from desiccation during rainless spells is a major hazard for plants that spend decades

growing slowly in the undergrowth before release in a treefall gap (Burslem et al. 1996, Grubb et al. 1996, Grubb 1998). Only on reliably moist soils do we find shade-tolerant plants with low RMF values and high flexibility in SLA (Grubb 1998).

An issue that is difficult to assess is the impact of soil drying on the nutrient supply to plants. It is well known that the microbial release of nutrients is sensitive to the water potential of the soil (Black 1968). Also, the ability of root cells to take up nutrients can be greatly reduced at low water potentials, the exploration of new soil by root growth is reduced, and, in the extreme case, the rates of supply to root surfaces by mass flow and diffusion are reduced (Dunham and Nye 1976, Mackay and Barber 1985, Kuchenbuch et al. 1986). The position is particularly complicated when the uptake of one nutrient is reduced more than that of another. For example, Wang (1989) found, using a glasshouse experiment with five species of short-lived perennial herbs in a chalk-derived soil, that the sensitivity to soil drying was consistently much greater for uptake of P than for uptake of N. On the other hand, it is possible that a major characteristic of plants that inhabit very dry regions is an ability to maintain the rates of uptake of major nutrients even when the roots are suffering considerable desiccation. Such an ability has been established for the semidesert shrub *Artemisia tridentata* by Matzner and Richards (1996).

In the section on seedling responses to nutrients, we discussed the fact that many species of the lowland wet tropics have a "shade requirement." Shade requirements may also be important in drought-prone forests, woodlands, and semidesert (Holmgren et al. 1997). Seedlings stand a higher chance of survival under some shade in forests or scrub growing at dry sites, as reported for mixed *Nothofagus* forest in New Zealand (Wardle 1991), pine woodland in the western United States (Barton 1993), scrub on dunes in the Netherlands (De Jong and Klinkhamer 1988), and scrub on lime-

stone in Germany (Kollmann and Reiner 1996). None of these communities casts deep shade, and it seems that the protection afforded against direct sunlight more than outweighs any loss in productivity due to shade. During dry spells, seedlings may perhaps benefit from "hydraulic lift," i.e., transfer of water during the night from subsoil into the dry topsoil via "leaky" roots that provide a low-resistance conduit (cf. Dawson 1993, Caldwell et al. 1998). It remains to be seen whether such facilitative effects are commonly of benefit to seedlings when compared with the negative impact of tree roots drying the topsoil.

To summarize, field observations indicate a strong interaction between shade and water shortage on mortality, but less is known about the effects of combinations of shade and water shortage on growth. Conflicting strategies for shade tolerance and drought tolerance make some species less tolerant of shade on seasonally droughted soils. However, other species have a relatively inflexible low-SLA, low-LAR strategy that allows them to persist in deep shade, and we predict that the shade tolerance of such species will be less affected by drought.

#### REVIEW OF ROOT-TRENCHING EXPERIMENTS: HYPOTHESES CONCERNING THE EFFECTS OF ROOT TRENCHING

Based on results of the experiments and observations just reported, we propose the following hypotheses.

##### *Impact of root competition on growth*

*Hypothesis 1: where soils are relatively nutrient rich and drought is uncommon, root trenching will have no impact in the understory on either growth rate or survival.*—This hypothesis is based on the inability of most plants tested to respond to added nutrients when grown in deep shade on such soils.

*Hypothesis 2: on infertile soils, root trenching will have a positive effect on growth rate in the understory.*—The basis for this hypothesis is that the dominant plants bring the concentrations of limiting nutrients down to exceedingly low levels and cast slightly less shade than those on moist fertile soils. Our prediction is made despite our expectation that a large proportion of species in these vegetation-types will be slow growing.

*Hypothesis 3: where there is seasonal drought, root trenching will have a positive effect on growth rate in the understory.*—Our reasoning is similar to that given under (2), except that water is the resource in short supply, and the shade cast by the dominant trees is less than on moist, infertile soils.

##### *Modification of shade tolerance by root competition*

*Hypothesis 4: where there is seasonal drought, root trenching will have a greater positive effect on survival of young seedlings in the understory than in small tree-fall gaps.*—This hypothesis can be addressed only by

comparing seedlings of similar age in gaps and understory. It is based on the slow growth of seedlings under shade and the presumed positive relationship between seedling size (and rooting depth) and survival.

*Hypothesis 5: the effects of root trenching on growth rate will be greater in treefall gaps than in the understory and greater under lightly shading than deeply shading species, and this interaction will be more marked in more light-demanding species.*—This hypothesis is based on the nature of the shade  $\times$  nutrient interaction found for most species tested, and on the trend found on comparing different species.

*Hypothesis 6: species not usually regarded as shade tolerant will be enabled by root trenching to grow in deep shade.*—The basis of this hypothesis is that, in nature, the distribution of a species is set by the interactions between shade and the supply of water and nutrients, and not simply by the degree of shade.

*Hypothesis 7: root trenching on dry and/or infertile sites will make possible invasion by species otherwise found only at moister or less infertile sites.*—The basis for this hypothesis is that, in nature, the limits to distribution with respect to soil drying and nutrient paucity are set by interactions with shade, and not simply by the lack of soil resources.

#### METHODS FOR MANIPULATING BELOWGROUND COMPETITION

Most experiments on root competition have attempted to quantify the impact of belowground competition by cutting deep trenches around plots, thereby severing the lateral roots of surrounding trees. The plots may either contain already established target plants (e.g., Fricke 1904), or seeds/seedlings that are sown in (e.g., Shirley 1945). The steel tubes inserted to various depths around grass seedlings planted in grassy woodland by Cook and Ratcliff (1984) served an identical purpose, as did the baked clay tubes used by Callaway et al. (1991).

With regard to competition for water, the technique of trenching does not provide any serious problem. Only an infinitesimal part of the increase in soil water content that follows trenching can possibly arise from movement of moisture out of the dead roots, and any such effect will be short lived. The extent of the increase in soil water content can be considerable (at least twofold), as shown by the records of Fricke (1904), Craib (1929), Ellison and Houston (1958), and Dillenberg et al. (1993). Only rarely has the increase in soil water potential been documented (Slavíková 1958; Riegel et al. 1995). Also, few studies in forests or woodlands have used measures of pre-dawn and midday xylem potential in the target plants, and of stomatal conductance, to confirm that inhibition of growth has been correlated with shortage of water in the plant tissues (Bowman and Kirkpatrick 1986, Riegel et al. 1995).

With regard to competition for mineral nutrients, there is no doubt that trenching can lead to an increase



in the availability of mineral N, as shown in various forests dominated by deciduous dicotyledons or by evergreen conifers in North America (Vitousek et al. 1982), in spruce plantations in Europe (Harmer and Alexander 1985), and in tropical lower montane forest in the Caribbean (Silver and Vogt 1993). A concomitant increase in foliar N concentration has been shown in trenched plants by Watt and Fraser (1933), N. V. Dylis and A. N. Utkin (summarized by Walter and Breckle 1985: 167), Walker et al. (1986), Riegel et al. (1992), Chapin et al. (1994), and Coomes and Grubb (1998). However, the source of mineralized nutrients is more open to question: does it arise principally from the cessation of competition with surrounding trees, or from decaying severed roots (Berendse 1983)? Limited evidence suggests that the supply by root decay is relatively small during the time period in which many experiments are conducted. It is known that the N content of leaf litter often *increases* in the early stages of decay (Will 1967), and the same may well be true of many roots, especially as they tend to have lower N concentrations than leaves when alive (Edwards and Grubb 1982, Grubb and Edwards 1982). Moreover, as Walter and Breckle (1985) have pointed out, the increase in the growth of root-trenched plants and in the depth of their greenness can be very rapid, whereas the release of N from cut roots, if it occurs, is likely to be slow. Nevertheless, Putz and Canham (1992) recommended compensating for the effects of decomposing roots (whether positive or negative) by adding severed roots to untrenched plots.

A direct test of the net change in competition from the roots of other plants plus microorganisms was made by V. G. Karpow on saplings of spruce, *Picea abies*, in two forests dominated by birch, *Betula pubescens* ssp. *tortuosa*, in the boreal zone (summarized by Walter and Breckle 1985: 166–167). Karpow added  $^{32}\text{P}$  to the soil around the test plants, and about five times as much was taken up by the root-trenched individuals of *Picea* as by the control plants. No difference in water content was found between trenched and control plots. Björkman and Lundberg (1971) also used  $^{32}\text{P}$  to study competition between species in boreal forest.

Recent studies using  $^{13}\text{C}$  and  $^{14}\text{C}$  isotopes have shown that significant amounts of carbon may be transferred between seedlings of *Betula papyrifera* and *Pseudotsuga menziesii* via ectomycorrhizal fungi that are not host specific (Read 1997, Simard et al. 1997a). It has been suggested that mycorrhizal bridges may provide a mechanism enabling seedlings to persist in the deeply shaded understory through C transfer from the adult trees, but it is unlikely that such transfers will compensate ultimately for the large competitive impact of shading. Trenching severs mycorrhizal links and may lead to marked differences in the identity of the mycorrhizal fungi on seedlings, as reported by Simard et al. (1997b) for seedlings of *Pseudotsuga menziesii* at three sites. Gadgil and Gadgil (1975) reported that

trenching increased the rates of litter decomposition under *Pinus radiata*, and suggested that the mycorrhizae were normally able to suppress the activities of decomposers.

An alternative approach to quantifying the impact of root competition is to insert into the forest floor seedlings that are growing in pots, with and without holes, and to allow ingrowth of the roots of competitors into the root-free soil of the pot (Jones et al. 1989, Jones and Sharitz 1990). Such experiments are clearly relevant to plants invading soil in which all fine roots have died, but it may be that properties conveying success in root-free soil are quite different from those required to invade soil containing a steady-state quantity of fine roots (Grubb 1994, Goldberg and Novoplansky 1997). A potential advantage of the holed-pot technique is that one might be able to regress the target plant's performance on the mass or length of invading roots in the pot, rather than having simply + and – treatments. However, Jones et al. (1989) and Jones and Sharitz (1990) found a great deal of scatter in their results for individual species, and therefore few significant regressions.

To summarize, the technique of root trenching has no serious drawback in studying competition for water, but theoretically poses problems in studying competition for nutrients. Nevertheless, various arguments lead one to accept that the undoubtedly greater supply of nutrients received by plants in root-trenched plots is primarily a result of the removal of competition rather than an extra supply from decaying roots. The planting of seedlings in the forest in holed and non-holed tubes of forest soil avoids the problem of a potentially increased supply from decaying roots, but fails to mimic adequately the position in which a seedling invades soil saturated with fine roots.

#### TESTS OF SEVEN HYPOTHESES ON THE EFFECTS OF ROOT TRENCHING

We test each of our hypotheses against the results of trenching experiments that are summarized in Table 10. When other experiments provide relevant information, we review them in the appropriate section.

*Hypothesis 1: where soils are relatively nutrient rich, and drought is uncommon, root trenching will have no impact in the understory on either growth rate or survival.*—Support for the hypothesis is provided by experiments in the temperate region. No increase in growth after trenching was found in experiments at relatively fertile sites for any of the following tree species: *Fagus sylvatica* (Burschell and Schmalz 1965), *Acer saccharum* (C. E. Olmsted in Kozlowski 1949, C. D. Canham et al. in Pacala et al. 1996), *Acer rubrum*, and *Fraxinus americana* (Putz and Canham 1992). N. V. Dylis and A. N. Utkin (summarized by Walter and Breckle 1985: p.167) found that shade-tolerant herbs were unresponsive to trenching in “the deep shade” under mixed *Picea*–deciduous forest.

TABLE 10. Impact of root trenching (TR) on the growth of test plants in moist regions (ordered according to risk of summer drought) and dry regions. Effects of trenching on seedling survival (*S*), emergence (*E*), and growth in biomass ( $G_m$ ), height ( $G_h$ ), leaf area ( $G_a$ ), leaf number or leaf area ( $G_l$ ), stem diameter ( $G_d$ ), and branch length ( $G_b$ ), cover (*C*), or density (*D*) are summarized as: ++ strongly positive, + positive, – no effect, — negative effect.

Vegetation type and location	P and E† (mm)	Species in trenched plots‡	Understory irradiance (%)§
<b>Wet tropics</b>			
<b>A) Relatively fertile soil</b>			
1) E. Costa Rica	P 4000 E 2200	Transplanted seedlings: (a) <i>Inga fagifolia</i> (ST) (b) <i>Inga peizizifera</i> (ST), Legum- inosae	1.3
2) E. Costa Rica (a) Treefall gaps (b) Understory	P 4000 E 2200	<i>Hampea appendiculata</i> (LD), Malvaceae	CO (a) 7.3 (b) 3.9
3) E. Costa Rica, with 1-yr-old sap- lings (a) <i>Cedrela odorata</i> (b) <i>Cordia alliodora</i> (c) <i>Hyeronima alchorneoides</i>	P 4000 E 2200	Transplants: (1) <i>Piper auritum</i> (LD) (2) <i>Piper phytolaccaefolium</i> (IT- ST), Piperaceae	LAI (a) 0–2.5 (b) 0–2.0 (c) 2.2–5.4
4) N. Queensland, Australia	P 3500 E ?	<i>Beilschmiedia tooram</i> (ST) <i>Endiandra monothrya</i> (ST), Lauraceae	0.4–1.5
5) Java, Indonesia	P > 2500	<i>Tectona grandis</i> (teak, LD) Ver- benaceae	100
<b>B) Relatively infertile soil</b>			
6) Amazonas state, S. Venezuela Caatinga forest on waterlogged white sand	P 2600 E 1700	13 common species (IT–ST)	1.6–3.0
7) Amazonas State, S. Venezuela Palm-rich terra firme forest	P 2600 E 1700	<i>Protium crassipetalum</i> (ST), Burseraceae	0.5–1.0
8) Manaus, Amazon State, Brazil Lecythidaceae-dominated forest on terra firme (oxisol)	P 2186 E 1642	(a) <i>Aspidosperma carapanauba</i> (ST), Apocynaceae (b) <i>Dinizia excelsa</i> (IT), Legu- minosae	1.0
9) Vanikoro Island, Santa Cruz	P 6250 E 2020	<i>Agathis macrophylla</i> (ST), Ar- aucariaceae	...
10) N. Queensland, Australia On granite	P 3500 E ?	<i>Chrysophyllum</i> sp. (ST), Sapo- taceae	...
11) Sabah, E. Malaysia Forest dominated by dipterocarps	E 3140 P 1760	Mixed seedlings (ST), Diptero- carpaceae	...
12) Sabah, E. Malaysia Regrowth on ultisol, 13–14 yr after logging; mostly <i>Macaranga</i> spp.	P 2800	<i>Shorea parviflora</i> (IT), Diptero- carpaceae	CO 11–15
<b>Dry tropics</b>			
<b>A) Dry forest</b>			
13) W. Costa Rica secondary forests (a) Deciduous, poor soil (b) Semi-evergreen, richer soil	P 780–985 E ?	Transplanted seedlings of <i>Cedre- la odorata</i> (IT) and <i>Swietenia macrophylla</i> (IT), Meliaceae, and <i>Hymenaea courbaril</i> (IT). Leguminosae	7
14) Sierra Madre, NW Mexico Drought-deciduous <i>Lysiloma divari- cata</i> woodland (a) Shrubs left in understory (b) Shrubs removed	P 530–670 E ?	Sown seeds of <i>L. divaricata</i> (IT), Leguminosae	...
<b>B) Savannas</b>			
15) Tsavo Park, Kenya (a) Wetter region (b) Drier region	(a) P 767 E 917 (b) P 450 E 1864	Savanna grasses near <i>Acacia tortilis</i> trees: (1) under trees (2) edge of crowns (3) away from trees	...

TABLE 10. Extended.

Dura- tion (mo)	Repli- cates (no.)	Results of trenching			Additional notes	Author(s)
23	80	(a) $G_m$ (b) —	$G_1$ —	$G_h$ —	Trenched plots adjoined un- trenched plots.	Denslow et al. (1991)
12	4	(a) $G_h$ (b) —	—	—	Same site as Denslow et al. (1991) and another consid- ered more fertile.	Ostertag (1998)
12	3	(a) $G_m$ (b) — (c) —	(1) — + —	(2) — — —	Root density (g/m <sup>2</sup> ) (a) 42 (b) 85 (c) 363	Gerwing (1995)
24	10	$G_h$ —	$G_1$ —	—	—	P. J. Grubb and E. A. A. Grubb ( <i>unpublished</i> <i>data</i> )
?	1	$G_h$ +	—	—	Long trench cut between young and mature planta- tions.	Coster (1933)
12	~6	$G_a$ +	$G_h$ +	—	Soils very infertile. Trench- ing effect no greater in higher irradiance.	Coomes and Grubb (1998)
18	6	$G_a$ —	$G_h$ —	—	—	Coomes and Grubb (1998)
6	?	(a) $G_h$ (b) +	$G_1$ + ++	—	Forests on soils of marginal agricultural use. Effect of TR greatest in high irradi- ance.	Lewis and Tanner ( <i>in</i> <i>press</i> )
12	?	$G_h$ +?	—	—	Height ~0.8–2.4 cm. No sta- tistics.	Whitmore (1966)
?	?	$S$ —	—	—	—	Connell (1970)
8	1	$G_h$ +?	—	—	$G_h$ increased 1.3-fold to 37 cm/yr. No statistics possi- ble.	Fox (1973)
12	~3 5	$G_h$ —	$S$ —	—	Growth related to canopy openness.	Pinard et al. (1998)
18	5	(a) $S$ (b) ++	$G_h$ + +	—	Survival after 1 yr in con- trols: 40% under (a) and 70% under (b).	Gerhardt (1996)
12	4	(a) $E$ (b) —	$S$ + ++	—	Survival improved by TR and shrub removal. Seed predation a major limita- tion to regeneration.	Goldberg (1985)
1 yr	5	(a) (1) (b) —	$G_m$ (2) — —	(3) — — —	TR had (surprisingly) no im- pact in dry savanna. Sug- gests intense competition for nutrients under trees in wet savanna.	Belsky (1994)

TABLE 10. Continued.

Vegetation type and location	P and E† (mm)	Species in trenched plots‡	Understory irradiance (%)§
Moist-climate moist-site temperate			
A) Soils not strongly acidic or nutrient deficient, dicot trees dominant			
16) North Carolina, USA (a) Mostly <i>Quercus</i> spp. (b) Mixed deciduous, with <i>Carpinus</i> understory	P 1072 E 806	Naturally regenerating herbs and tree seedlings	NR (a) = 6 × (b)
17) Wisconsin, USA Oak–maple forest	P 640 E 600–800	<i>Acer saccharum</i> (ST)	?
18) Minnesota, USA Stands of <i>Populus tremuloides</i>	P 500–750 E 480–640	Transplanted seedlings of <i>Pinus resinosa</i> (LD), <i>Pinus strobus</i> (LD), and <i>Picea glauca</i> (IT)	21
19) Chippenham Fen, S. England <i>Alnus glutinosa</i> : (a) Alder–birch–ash wood (b) Single tree in meadow	P 760 E 607	Seedlings of <i>Alnus</i> (LD)	...
20) Central Germany <i>Fagus sylvatica</i>	E 663 P 657	Seedlings of <i>Fagus</i> (ST)	...
21) North Carolina, USA Mixed forest on the Piedmont	P 1072 E 806	Transplanted seedlings: (a) <i>Acer rubrum</i> (IT) (b) <i>Cornus florida</i> (IT) (c) <i>Oxydendron arboreum</i> (LD), Ericaceae	2–5
22) Tanana floodplain, Alaska (a) <i>Alnus tenuifolia</i> (b) <i>Populus balsamifera</i>	P 1400 E 450	Natural seedlings of <i>Picea glauca</i> IT	(a) 30 (b) 30
23) Glacier Bay, Alaska, USA Deglaciated soil, stands of (a) <i>Alnus sinuata</i> (b) <i>Picea sitchensis</i>	P 1400 E 450	Transplanted seedlings: (1) <i>Alnus sinuata</i> (LD) and (2) <i>Picea sitchensis</i> (IT)	(a) 7 (b) 8
24) Connecticut, USA Mixed mesic forest	P 1360 E 668	Tree seedlings of six species (LD–ST)	?
25) New York, USA <i>Cornus racemosa</i> thicket Soil fertility and water retention: (a) high, (b) intermediate, (c) low	P 1020 E 717	Seedlings of <i>Acer rubrum</i> (IT) and <i>Fraxinus americana</i> (IT), Oleaceae	CO (a) 3.9 (b) 4.5 (c) 5.8
26) New York, USA Recently abandoned old fields: (a) Canopy intact (b) Surrounding leaves held back	P 750–1500 E 600–800	Transplanted seedlings of <i>Acer rubrum</i> (IT), <i>Cornus racemo- sa</i> (IT), <i>Pinus strobus</i> (LD), and <i>Rhamnus catharticus</i> (IT)	10
27) South Carolina, USA Isolated loblolly pine trees (~7 m tall) in secondary succession on loamy sand	P 1000–1500 E 1000–1200	Natural regeneration, measuring affects on: (a) perennials (b) annuals	17
28) Maryland, USA Vines of: (a) <i>Lonicera japonica</i> (b) <i>Parthenocissus quinquefolia</i>	P 1036 E 800	Saplings of <i>Liquidambar styraci- flua</i> (LD), Hamamelidaceae	100
B) Soils nutrient deficient but not strongly acidic; conifers or eucalypts dominant			
29) North Carolina, USA Four stands of <i>Pinus taeda</i> and <i>Pinus echinata</i> (see also [16])	P 1072 E 806	Naturally regenerating herbs and tree seedlings under each forest type	20 × that under dicots
30) New Hampshire, USA Stands of <i>Pinus strobus</i>	P 800–1200	Natural regeneration of seed- lings of: (a) LD spp. (e.g., <i>Pinus stro- bus</i> ), (b) ST spp. (e.g., <i>Tsuga cana- densis</i> )	...
31) Tasmania, Australia Montane forest of <i>Eucalytus dele- gatensis</i>	P 652–740 E 650–690	Transplanted seedlings of <i>E. delegatensis</i> , (LD) Myrtaceae	...



TABLE 10. Continued. Extended.

Dura- tion (mo)	Repli- cates (no.)	Results of trenching			Additional notes	Author(s)	
6 yr	1	(a) (b)	$C$ + —	$G_h$ + —	Response to TR far less than under pine. SMC increased after TR, but soil [NH <sub>4</sub> ] and [NO <sub>3</sub> ] unaffected.	Korstian and Coile (1938)	
?	?		$G_h$ —			C. E. Olmsted in Kozlowski (1949)	
4 yr	12		$G_m$ +	$S$ —	Despite drought, $S$ unaffected by TR, but greatest in shade. Removing herbs under aspen had large effect, as did canopy thinning.	Shirley (1945)	
11	1	(a) (b)	$G_h$ — +?	$G_l$ — —		McVean (1956)	
24	?		$G_h(?)$ —		Particularly wet summers.	Burschel and Schmalz (1965)	
2.5	4	(a) (b) (c)	$S$ — + +	$G_a$ + + +	$G_h$ + — —	Soil water content higher in TR plots. Leaf area of <i>Cornus</i> correlated to light only in TR plots.	Horn (1985)
24	5	(a) (b)	$G_m$ + —		Foliar [N] and [P] (a) + — (b) + +	Walker et al. (1986)	
36	10		$G_b$ (1)(2) ++ +—	$G_h$ (1)(2) —+ —	TR caused increases in foliar [N] and [P]. Growth rate under (b) less than under (a)	Chapin et al. (1994)	
?	?		$G$ —	$S$ —	Possibly influenced by industrial pollution.	C. D. Canham et al. ( <i>unpublished data</i> ) in Pacala et al. (1996)	
2.5	8	(a) (b) (c)	$G_m$ — + +		Effect of canopy manipulation (increased light to ~80%) on $G_m$ (a) +, (b) +, and (c) —. No TR $\times$ L interaction.	Putz and Canham (1992)	
13	18	(a) (b)	$G_b$ — ++		Small effect of increased irradiance in untrenched plots, but large effect in trenched plots.	Gill and Marks (1991)	
24	4	(a) (b)	$C$ ++ —		Annuals responded strongly to litter removal.	Monk and Gabrielson (1985)	
24	6	(a) (b)	$G_b$ ++ +		Climbers' root competition much stronger than shoot competition.	Dillenberg et al. (1993)	
5 yr	1		$C$ ++	$G_h$ ++	Herbs typical of mesic sites invaded. SMC, but not soil N, responded to TR.	Korstian and Coile (1938)	
8 yr 19 yr	1	Density 8 yr 19 yr	(a) ++ — $G_h$ +?	(b) + ++	Early invasion by light demanders; only shade tolerators persisted in the longer term.	Toumey and Kienholz (1931), Craib (1929), Lutz (1945)	
12	6		$G_h$ +?		Significance not correctly determined in paper.	Bowman and Kirkpatrick (1986)	

TABLE 10. Continued.

Vegetation type and location	P and E† (mm)	Species in trenched plots‡	Understory irradiance (%)§
C) Soils nutrient-deficient and strongly acidic (mor humus), mostly with conifers dominant			
32) Bavaria, Germany	P 687	Seedlings of <i>Picea</i> (IT)	...
Mature stand of <i>Picea abies</i>	E 655		
33) Bavaria, Germany	P 687	Seeds of <i>Picea</i> , <i>Abies</i> , <i>Larix</i> , <i>Pinus</i> , and <i>Fagus</i> sown in open and in understory	...
Forests of <i>Pinus sylvestris</i> and <i>Picea abies</i>	E 655		
34) North Island, New Zealand	P 1600	Seedlings (15–30 yr old) podocarps	...
Seral vegetation ( <i>Kunzea ericoides</i> )	E ?		
(a) Intact			
(b) Removed			
35) Aberdeenshire, Scotland	P 800	Annual ground layer harvest, mainly:	...
(a) Stand of <i>Pinus sylvestris</i>	E 611	(1) <i>Deschampsia flexuosa</i> (ST),	
(b) Trees of <i>Fagus sylvatica</i>		(2) <i>Oxalis acetosella</i> (ST),	
		(3) <i>Vaccinium myrtillus</i> (ST, only under <i>Fagus</i> )	
36) Minnesota, USA		Transplanted seedlings of <i>Pinus resinosa</i> (LD), <i>Pinus strobus</i> (LD), and <i>Picea glauca</i> (IT)	23
Stands of <i>Pinus banksiana</i>			
37) Former USSR		Naturally regenerating seedlings of <i>Picea abies</i> (IT)	?
Stands of <i>Betula pubescens</i> in boreal region			
38) Former USSR	P100–500	Natural cover of:	?
<i>Abies sibirica</i>		(1) <i>Oxalis acetosella</i> (ST)	
		(2) <i>Hylocomium splendens</i> (moss)	
39) Montana, USA	P 630–1160	Understory herbs (ST)	...
Old-growth bottomland forest of <i>Abies grandis</i>	E 593		
40) Central Oregon, USA	P 2400	Seedlings of <i>Tsuga heterophylla</i> (ST)	...
<i>Pseudotsuga menziesii</i> ; <i>Rhododendron macrophyllum</i> below	E ?		
41) British Columbia, Canada	P 670	Seedlings of <i>P. menziesii</i>	...
<i>Pseudotsuga menziesii</i> with <i>Betula papyrifera</i>	E 200–600		
Moist-climate dry-site temperate			
42) S. Germany	P 600–750	Seeds of <i>Fagus</i> , <i>Picea</i> , <i>Pinus</i> , and <i>Quercus</i>	...
Young stand of <i>Pinus sylvestris</i>	E 400–600		
43) Czech Republic	P 500–700	Undergrowth plants	...
<i>Fagus sylvatica</i> forest	E 600		
Dry-climate temperate			
44) Utah, USA	P 580–700	Sown seeds of <i>Bromus carinatus</i> and <i>Elymus glaucus</i> , Poaceae; <i>Heracleum lanatum</i> , Apiaceae; and <i>Rudbeckia occidentalis</i> , Asteraceae	...
<i>Populus tremuloides</i>	E 1200–1400		
45) Central California, USA	P 540	<i>Bromus diandrus</i> growing under isolated trees that appeared to (a) suppress and (b) facilitate grass productivity	~45
<i>Quercus douglasii</i> "savanna"	E 1400		
46) E. Oregon, USA	P 605	<i>Carex geyeri</i> , Cyperaceae; and <i>Symphoricarpos alba</i> , Caprifoliaceae	NR
<i>Pinus ponderosa</i>	E 1000–1200		
47) E. Oregon, USA	P 605	Natural ground cover, including 103 spp. of graminoids, forbs, shrubs, and tree seedlings	NR
<i>Pinus ponderosa</i>	E 1000–1200		

Note: Ellipses indicate that values were not determined.

† Mean annual precipitation (P) and potential evapotranspiration (E) are interpolated from the nearest stations in Müller (1982) unless explicitly stated in the paper.

‡ Wherever possible, each target species is identified as light demanding (LD), intermediate (IT), or shade tolerant (ST).

TABLE 10. Continued. Extended.

Dura- tion (mo)	Repli- cates (no.)	Results of trenching				Additional notes	Author(s)
?	1		$G_h$ ++			Darkening of leaves after TR suggests N limiting	Fabricsius (1927)
1	8		$G_h$ +			TR had strong effect on herb cover in first year. Species differed in response to light.	Fabricsius (1929)
4 yr	?	(a) (b)	$G_h$ + +			Removing <i>Kunzea</i> increased growth by 86%, but TR by only 28%.	Cameron (1960)
2 yr	1	(a) (b)	(1) + +	$G_m$ (2) —	(3) ... —	Irrigation had no effect. TR increased foliar [N] of <i>Deschampsia</i> (2.1–3.2%) under pine.	Watt and Fraser (1933)
4 yr	12		$G_m$ ++		$S$ —	Despite drought, $S$ was unaffected by TR and increased with shading.	Shirley (1945)
?	?		$G_m$ ++			TR resulted in 5–6 times greater uptake of added $^{32}\text{P}$ .	V. G. Karpov in Walter and Breckle (1986)
3 yr	?		(1) (2)	$C$ ++ --			N. N. Latschinski (1968) in Walter and Breckle (1986)
60	2		$C$ ++			<i>Clintonia uniflora</i> was most responsive. Herbivores ate many tree seedlings.	McCune (1986)
24	24		$G_b$ +	$G_h$ +	$G_d$ —	Canopy thinning (33% more light) had little effect. SMC not affected by TR.	Christy (1986)
16	?		$G_b$ —	$G_h$ —	$G_d$ —	TR reduced diversity and abundance of ectomycorrhizae and reduced photosynthetic rate.	Simard et al. (1997 <i>b</i> )
1 yr	>1		E +	$G_m$ +		TR caused 2–3 fold increase in SMC, and increased herb cover. Controls remained virtually bare.	Fricke (1904)
			$C$ ++			“Nudum” forest was near aridity limit of <i>Fagus</i> and had little understory, except in gaps.	Slavíková (1958)
3 yr	3 at 4 sites		$G_m$ ++			$G_m$ in TR plots similar to that in clearings.	Ellison and Houston (1958)
4	3 × 8 trees	(a) (b)	$G_m$ ++ —			Superficial fine-root density greater under (a) than (b) for reasons not fully understood.	Callaway et al. (1991)
3 yr	4 at 3		$G_m$ +			TR increased soil N, foliar nutrient and water potential. No effect of canopy thinning.	Riegel et al. (1992)
3 yr	20		$C$ +	$D$ +		10 species responded to canopy thinning. TR increased soil and xylem water potentials, soil mineralizable N, and pH.	Riegel et al. (1995)
			Responsive species were early- and mid-successional				

§ Percentage daylight values are given whenever possible, but some authors give canopy openness (CO), leaf area index (LAI), or flux measured in the understory without an external reference (NR).

|| Abbreviations: TR, treatment (root trenching); SMC, soil moisture content.

Evidence in support of the hypothesis for tropical rain forests is scanty. Seedlings of shade-tolerant species under forest in northeastern Australia were unresponsive in terms of growth (P. J. and E. A. A. Grubb, *unpublished data*). Denslow et al. (1991) found that *Inga* spp. were unresponsive in a Puerto Rican rain forest, but their experiment was seriously flawed because they root-trenched two quarters of each  $0.5 \times 0.5$  m<sup>2</sup> plot in a latin-square design so that the "control" plants had roots coming from only two sides. Recently, Ostertag (1998) found that transplanted seedlings of a strongly light-demanding species (*Hampea appendiculata*) were unresponsive to trenching in both the understory and gaps. Possibly the test species needs a higher irradiance to show appreciable sensitivity to nutrient supply. The plants were unresponsive at the site where Denslow et al. (1991) conducted their experiments and also at a nearby site that was inferred to be more fertile, based on greater concentrations of acid-ammonium-fluoride-extractable P in the soil.

*Hypothesis 2: on infertile soils, root trenching will have a positive effect on growth rate in the understory.*—The hypothesis is tested (1) by comparing the responsiveness of plants in soils of differing fertility within the same geographic area, and (2) by using the information given in the paper to judge whether a forest is growing on soil likely to be deficient in nutrients.

1. *Local differences in soil fertility.*—Coomes and Grubb (1998) found that competition for nutrients had a clear impact on the growth of 13 species in Amazonian caatinga (soil very deficient in N and P; Fig. 5), but had no impact on the highly shade-tolerant *Protonotaria crassipetalum* in an adjacent palm-rich forest on well-drained brown sand (soil less deficient in N and P). The result from caatinga is convincing because so many species were included, but we suspect that some positive results would have been observed in the infertile palm-rich forest if less strongly shade-tolerant species had been used. In fact, positive responses were found by Lewis and Tanner (*in press*) for two species on an infertile oxisol in central Brazil, despite penetration of <1% daylight. In the caatinga study, trenched plants had increased foliar concentrations of nutrients, whereas a shortage of water was ruled out.

Putz and Canham (1992) compared the responses of seedlings of *Acer rubrum* and *Fraxinus americana* under *Cornus racemosa* thickets on three contrasting soil types, which differed in both water and nutrient supply (dry infertile to moist fertile). *Cornus* cast the least shade on the driest/most infertile soil, and it was here that trenching had the greatest impact. No response was found under the deeply shading *Cornus* on the moist/most fertile soil.

2. *Forests on soils of inherently low nutrient availability.*—Fabricius (1927) found a large positive effect of root trenching on height growth of seedlings of *Picea abies* in mature closed forest of that species; such forests generally have low levels of available N (Ellenberg

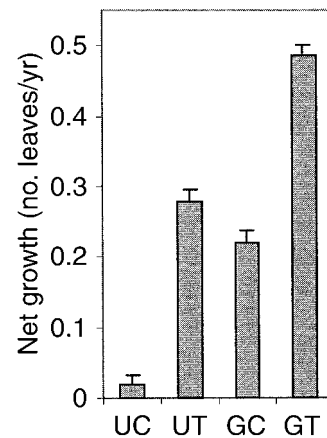


FIG. 5. Mean relative growth rates ( $\pm 1$  SEM) in the number of leaves of trenched (T) and untrenched (C) saplings of 13 species, measured in understory (U) and small treefall gaps (G) of an Amazonian rain forest growing on waterlogged white sand. Data are taken from Coomes and Grubb (1998).

1988). Fabricius (1929) reported similar large effects on the natural cover of subshrubs and herbs in the understory of such forest; he considered that competition for water played a considerable part in his experiments, in addition to competition for nutrients. Cameron (1960) recorded a 36% increase in the height growth of seedlings of podocarps (mainly *Dacrydium cupressinum* and *Podocarpus totara*) following trenching of plots containing 15–30 yr-old seedlings in the North Island of New Zealand. The seedlings were growing under a stand of *Kunzea ericoides*, an early-successional species found mainly on infertile soils. Two studies of root competition have been made in forests of *Pseudotsuga menziesii* in northwestern North America. Christy (1986) found that root competition had a marked impact on the growth of *Tsuga heterophylla* seedlings under forest (northwestern United States), but Simard et al. (1997b) found no effect on seedlings of *Pseudotsuga menziesii* at three sites in floristically similar forest farther north (in southwestern Canada). All of the forests were on infertile soils; Christy worked in the *Rhododendron–Berberis* variant (described by Zobel et al. 1976 as growing on infertile soil), whereas Simard worked on two spodosols and one dystic brunisol. Neither study found an increase in soil water content in trenched plots, even though, as emphasized by Waring and Franklin (1979), the summers in the area where Christy (1986) worked are warm and dry (only 100 mm of rainfall in June–August). Possibly the explanation of the contradictory results is that *Pseudotsuga* needs a higher irradiance to respond to increased nutrient supply.

Root trenching led to large increases in the growth of the extremely shade-tolerant herb *Oxalis acetosella* under *Fagus sylvatica* in Scotland, and of *Oxalis acetosella* and *Deschampsia flexuosa* under the less deeply shading *Pinus sylvestris* in the same area (Watt and



Fraser 1933). The leaves of both species were deeper green and had higher N concentrations in trenched plots. N. V. Dylis and A. N. Utkin (summarized by Walter and Breckle 1985: 167) obtained similar results for a wider range of herbs in mixed *Picea*-deciduous forest in Russia, where the N supply was shown to be limiting growth. Addition of 143 mm of water in June–July had no effect on growth, whereas addition of N at a rate of 75–200 kg/ha did increase growth; addition of N at only 40 kg/ha had no effect, possibly because tree roots took it all up, leaving none for the herbs. Trenching also resulted in increased growth of *Oxalis* under *Picea* in the boreal zone, but this result is not relevant here because the stand was rather open and admitted 20% daylight (V. G. Karpow, summarized by Walter and Breckle 1985: 165). Probably the same was true at a site studied by N. N. Latschinsky (summarized by Walter and Breckle 1985: 167) and dominated by *Abies sibirica*; again, *Oxalis* responded strongly to trenching.

The few root trenching experiments in the tropics, where we expect that soils were infertile but have no nearby sites for comparison, have provided only equivocal results: an apparently positive growth response in a single trenched plot (Fox 1973), an ostensibly positive effect on growth in a figure that is not supported by statistical analysis (Whitmore 1966), no response of survival in a single Latin-square experiment (Connell 1970), and a major response of growth in a well-replicated experiment involving two species (Lewis and Tanner, *in press*). Pinard et al. (1998) reported that trenching had no effect on dipterocarp seedlings sown under a stand of light-demanding species (mostly *Macaranga* spp.) reestablishing on an ultisol, 13–14 years after logging; the amount of daylight reaching the understory of *Macaranga* stands is undoubtedly greater than that under mature rain forest, making the lack of an effect of trenching even more remarkable.

*Hypothesis 3: where there is seasonal drought, root trenching will have a positive effect on growth rate in the understory.*—There is no study that wholly satisfactorily separates the effects of shortage of water and shortage of nutrients because, as previously pointed out, water shortage is likely to reduce the rate of microbial release of N and P and to inhibit the rate of nutrient uptake by the roots. In the three following studies, however, the seasonal shortage of water was severe, yet the soils were not known to be particularly nutrient deficient.

Ellison and Houston (1958) reported very large effects of trenching on the productivity of herbaceous understory plants (*Bromus carinatus*, *Elymus glaucus*, *Heracleum lanatum*, and *Rudbeckia occidentalis*) sown under *Populus tremuloides* in Utah. The growth rate in the trenched plots was similar to that in large clearings. The study area is drought-prone in summer, and the authors found soil moisture content to be greater in trenched plots during one of the summers investigated.

Gerhardt (1996) found a positive effect of trenching on both growth and survival of seedlings in tropical semi-evergreen and deciduous forest. In Californian oak “savanna,” under isolated trees of *Quercus douglasii*, the productivity of herbs is reduced in a patchy fashion; reduction occurs only where the topsoil contains large numbers of oak roots that extract water from the same layer as the herbs (Callaway et al. 1991). When tubes were inserted into the soil around newly planted grass seedlings, the inhibitory effect was prevented. The experiment of Putz and Canham (1992) has been discussed in the previous section; the result on a mesic–fertile soil was contrasted with that on a xeric–infertile soil, but it is unclear which was more important: the difference in water supply or that in nutrient supply.

Using fertilizer addition, Belsky (1994) showed that growth of herbaceous plants was limited by nutrient supply at both the high- and low-rainfall savanna sites where she worked. Rather surprisingly, severing roots of the trees (*Acacia tortilis*) did not increase productivity of the grasses at the low-rainfall site, even though many tree roots occurred in the same depth zone of the soil profile as the grass roots. The effect of the grasses on tree growth was not tested, but in another study with *Acacia tortilis* in South African savanna, (mean rainfall 635 mm/yr), removal of the aboveground parts of the herbs markedly increased productivity of the trees, more so in a dry than a wetter year (Knoop and Walker 1985).

*Hypothesis 4: where there is seasonal drought, root trenching will have a greater positive effect on survival of young seedlings in the deeply shaded understory than in treefall gaps.*—This hypothesis is supported by two studies that address it directly. Horn (1985) found in deciduous forest in eastern North America that the impact of root trenching on survival of first-year seedlings of both *Acer rubrum* and *Cornus florida* was much greater in the understory. Shirley (1945) found that trenching had no effect on the survival of pine seedlings under *Pinus banksiana* in Minnesota, USA, except under the most deeply shading stands (<20% daylight).

*Hypothesis 5: the effects of root trenching on growth will be greater in treefall gaps than in the understory and greater under lightly than deeply shading species, and this interaction will be more marked in more light-demanding species.*—Experiments are divided into those in which (1) light penetration was manipulated by holding back surrounding vegetation, (2) differences in growth were compared in treefall gaps and the understory, and (3) differences in growth were compared under trees of different shading ability. Not one of the experiments separates unequivocally the effects of above- and belowground competition; those in category (1) are subject to the criticism that increased self-shading among shoots that have been held aside might have led to decreased root competition.

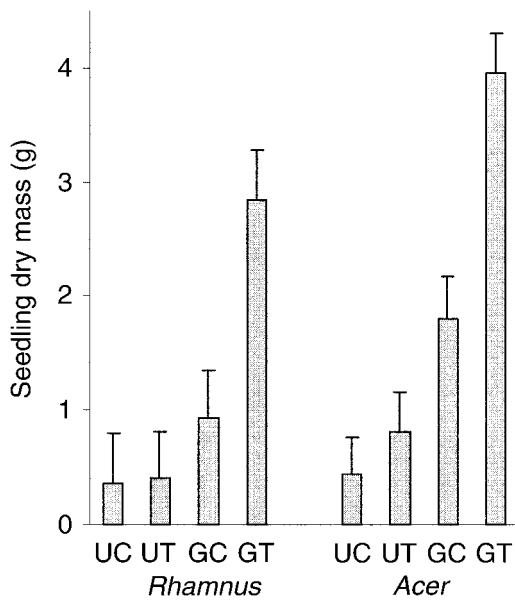


FIG. 6. Growth ( $\pm 1$  SEM) of seedlings of *Rhamnus cathartica* and *Acer rubrum* that were planted into a 2-yr-old field, in plots that were trenched (T) or untrenched (C), and that were in the shade of herbs (U) or had surrounding foliage held back (G); redrawn from Gill and Marks (1991).

1. *Artificial manipulation of light conditions.*—Gill and Marks (1991) manipulated above- and below-ground competition around woody seedlings in an old field in the northeastern USA. Seedlings were unresponsive to root trenching alone and responded weakly to the holding back of surrounding leaves, but showed a large increase in growth rate when both above- and below-ground competition were removed in conjunction (Fig. 6). As already noted, Putz and Canham (1992) manipulated above- and below-ground competition under *Cornus* thickets growing on three contrasting soil types. On soils of intermediate nutrient and water status, they found that root trenching in conjunction with canopy manipulation had a much greater effect than trenching or canopy manipulation alone. On a soil with a superior nutrient and water supply, they found that competition for light was of overriding importance, whereas only trenching had an effect on one with an inferior nutrient and water supply.

2. *Comparison of impact in gaps and understory.*—Lewis and Tanner (*in press*) found a positive interaction of irradiance (range 0.5–5% daylight) and root trenching in a study of Brazilian rain forest. In contrast, Coomes and Grubb (1998) found no interaction based on 13 species in caatinga; trenching had similar effects on growth in small treefall gaps (3–6% daylight) and in the understory (1–2%). Horn (1985) found that the leaf area attained by seedlings of *Cornus florida* in temperate deciduous forest was positively correlated with irradiance in trenched plots, but not in control plots.

3. *Comparison of impact under deeply and lightly shading trees.*—Gerwing (1995) found that root trench-

ing had a beneficial effect on seedlings of *Piper auritum* (a gap-demanding shrub) under 1-yr-old nursery trees of a species with a weakly shading crown and relatively dense surface roots, but no significant effect under two more deeply shading species. Walker et al. (1986) and Chapin et al. (1994) studied primary succession on an Alaskan floodplain and a deglaciated area, respectively. The N-fixing activities of *Alnus tenuifolia* allowed *Picea glauca* to grow more rapidly in early-successional stages on the floodplain, and the same process helped *Picea sitchensis* under *Alnus sinuata* on the deglaciated land. Nevertheless, the *Alnus* species competed strongly with *Picea* seedlings for both light and belowground resources (water or P, but not N), as demonstrated by shading experiments, canopy manipulation, and trenching. Seedlings of *Picea sitchensis* grew more slowly under stands of that species (which cast a deeper shade than *Alnus* does), and trenching had a smaller effect on growth.

*Hypothesis 6: species not usually regarded as shade tolerant will be enabled by root trenching to grow in deep shade.*—In *Fagus sylvatica* forest on shallow soil over limestone, with no herb layer, the “gap-demanding” *Galeopsis tetrahit* spontaneously invaded deeply shaded root-trenched plots (Slavíková 1958). The forest was seasonally droughted, with summer soil water contents falling below the conventional permanent wilting point in control plots but not in trenched plots; even so, Ellenberg (1988) has suggested that reduced competition for nutrients as well as for water might have been important. Competition for water and N inhibited the productivity of understory plants under *Pinus ponderosa* (Riegel et al. 1992), but only eight species of the 105 naturally occurring species were responsive to trenching. Riegel et al. (1995) noted that all of these were associated with early- to midsuccessional stands. Similarly, in boreal forest with a relatively open *Picea abies* canopy, the “gap-demanding” shrub *Rubus idaeus* invaded spontaneously in root-trenched plots (V. G. Karpow, summarized by Walter and Breckle 1985: 165); competition must have been for nutrients, because rainfall greatly exceeds potential evapotranspiration in the study area. In tropical semi-evergreen forest, Mulkey et al. (1991) showed, over 3.5 years, that irrigation during the dry season enabled the “gap-demanding” tall-herb species *Pleiostachya pruinosa* (Marantaceae) to persist for a longer time after gap closure.

There is also evidence that trenching increases the persistence of seedlings of some tree species in the understory, although not sufficiently for long-term survival. In lowland rain forest in Brazil, *Dinizia excelsa*, a species of intermediate tolerance, loses leaves too quickly relative to the rate of production and is doomed in the understory. Nevertheless, Lewis and Tanner (*in press*) have shown that trenching allows *Dinizia* to persist longer in the understory by increasing the rate at which leaves are produced. Possibly the same mech-

anism explains the increased persistence of *Lysiloma* in the understory of montane forest in a subtropical region after trenching (Goldberg 1985). Transplants of *Alnus sinuata* responded positively to trenching under stands of *Alnus* and *Picea sitchensis*, but growth remained very slow compared with that found in the open (Chapin et al. 1994).

A more complex result was recorded in a trenched plot of  $1.5 \times 2.7$  m in a stand of *Pinus strobus* in New Hampshire, USA. In the years immediately following trenching, recruitment of seedlings of *Pinus* and of gap-demanding herbs such as *Potentilla canadensis* was hugely increased, but so was the recruitment of slow-growing seedlings of the strongly shade-tolerant and strongly shading *Tsuga canadensis* (Toumey and Kienholz 1931). Nineteen years after trenching, the *Tsuga* had come to dominate the understory, and most of the more light-demanding species had been eliminated (Lutz 1945).

*Hypothesis 7: root trenching on dry and/or infertile sites will make possible invasion by species otherwise found only at moister or less infertile sites.*—This effect has been reported only in temperate forests. It was shown in Fricke's (1904) classic study of *Pinus sylvestris* woodland that, after trenching, trees that normally occur on moister soils (such as *Fagus*) invaded spontaneously. The effect was also seen in the plots of Korstian and Coile (1938), who found that root trenching in pine stands enabled "moist-site species" to invade. However, an analogous effect was far less marked under deciduous forest on nearby sites, where the soil dried out less in summer; perhaps the key difference was a greater drying of the topsoil by pine than by deciduous species on a given soil type.

## DISCUSSION

### *Overview of impacts of root competition in forests and woodlands*

Limitation of growth and survival of forest herbs and juvenile trees by soil resources as well as by shade has been shown in most of the trenching experiments reported in the literature. These positive results are concentrated on soils deficient in nutrient supply or water. For example, saplings of 13 species in tropical lowland rain forest on exceedingly nitrogen-poor soil were able to increase their relative (net) growth rate of leaf number by five times as a result of trenching, even while receiving only 1–3% daylight (Fig. 5). Likewise, when small areas were protected from root competition in a beech forest on shallow soil in central Europe, the strongly shade-tolerant herb *Galium odoratum* spontaneously invaded an otherwise bare plot and built an 80% cover in two years (Slavíková 1958). More remarkably, the "canopy-gap-demonstrator" *Galeopsis tetrahit* became established. These and other examples show how effective root competition can be in deep shade. There are two main ways in which the growth

rates of juveniles of many plants can respond to extra soil resources while in deep shade: by decreasing the root mass fraction when given extra nutrients, and by increasing the unit leaf rate when given an increased water supply.

Wilson (1988) reviewed pot experiments in which fast-growing herbaceous plants were allowed to compete either above or belowground, and showed that belowground competition had the greater impact in 33 of the 47 studies. Our review is not directly comparable with that of Wilson (1988), because we focus on plants that grow relatively slowly in the deep shade of forest floors and we do not have a random sample of community types from forests and woodlands around the globe. Nevertheless, we find that 40 of 47 root-trenching experiments resulted in positive plant response, emphasizing the general importance of belowground competition in many community types.

### *Comments on models that lump the effects of drought with those of nutrient paucity*

Several recent reviews, notably those of Twolan-Strutt and Keddy (1996) and Goldberg and Novoplansky (1997), have considered the relative magnitude of the impacts of competition along gradients of productivity, thus lumping the effects of nutrient paucity and water shortage. This is remarkable when we consider the manifestly contrasted effects of drought and nutrient shortage. Along gradients of decreasing rainfall, plants become more spaced out, whether trees along the forest–woodland transition, bunchgrasses passing from natural grassland in high-rainfall areas to semidesert grassland, or shrubs in semideserts with increasingly severe droughts (Walter 1968, 1973). Interstitial perennial plants (particularly dicotyledonous herbs) within the matrix of dominants are lost, most notably on passing from "meadow–steppe" to *Stipa*–steppe in western Asia (Walter 1968), or from tallgrass prairie (or palouse prairie) to shortgrass prairie in North America (Sims 1988). Similarly, forest on very shallow soils (e.g., over flat-bedded rock) may have almost no understory other than where exceptionally drought-tolerant herbs or shrubs can maintain themselves (e.g., bromeliads in some forests in South America; Vareschi 1980). It is virtually certain that increased root competition between the dominants is leading to their increased spacing, as supported by the results of experimental root trenching in woodland by Riegel et al. (1992) and in semidesert by Robberecht et al. (1983) and Ehleringer (1984). It is also virtually certain that an increased impact of root competition from the dominants is eliminating the interstitial species in the transition from dicot-rich grassland to dicot-poor grassland (cf. Sala et al. 1997) and in the transition from forest with understory to forest without understory (Slavíková 1958). The only significant exception to this trend toward loss of interstitial perennial plants is seen in the phenomenon of "nursing" of slower growing and/

or more palatable species inside some semidesert perennials, both shrubs and bunchgrasses (Callaway 1995, Holmgren et al. 1997).

Competition for nutrients on reliably moist soil leads to a completely different suite of effects. Basically, in a given climatic regime, all of the plants are thinner-stemmed and more closely packed, not increasingly separated as in the case of increasing water shortage. The trend is very clear in comparing tropical lowland forest on average soils with that on exceedingly leached oxisol or nitrogen-starved caatinga (Medina and Cuevas 1989, Coomes and Grubb 1996), or with "wallaba" or "kerangas" on exceedingly nutrient-poor, well-drained sands (Richards 1952). In all of the poor-soil forests, the trees are thin-stemmed, making "pole forest" that may contain the odd "superplant" able to grow taller and thicker (e.g., *Agathis* in southeast Asia; Richards 1952). The most impoverished forests are not devoid of interstitial perennial plants, but instead have miniaturized plants of all the main life-forms: thin-stemmed climbers instead of thick-stemmed, small-leaved herbs instead of large-leaved, and epiphytes confined to the lower trunks where sufficient leachates from the crowns have accumulated to support them (Coomes and Grubb 1996). They may also have extra kinds of perennial interstitial plants that are rare or absent in forests on more nutrient-rich soils, e.g., insectivorous plants (*Nepenthes* in southeast Asia), and non-green epiparasites ("saprophytes") such as Gentianaceae and Orchidaceae. Here, the competitive effects between dominants stop any one gaining enough nutrients to outgrow the others readily, and thus self-thinning of the stand is greatly slowed down. Similarly, competition between dominants and interstitials appears to keep the interstitials to small sizes, but because shortage of nutrients does not kill in the way that drought does, the suppressed plants can persist. Our work in caatinga (Coomes and Grubb 1998) is the only work showing the strength of competitive inhibition by dominant plants on juveniles in such communities.

In summary, extreme competition on nutrient-poor soil with an assured water supply leads to a dense array of miniaturized plants, whereas extreme competition in a dry climate leads to widely spaced dominants and a lack of interstitial plants, except for some species that are nursed, and when pulses of rainfall allow the interdominant spaces to be filled in by ephemerals.

#### *Root competition and population structure*

Again, the effects of extreme nutrient shortage and extreme water shortage are quite different. In the floristically rich tropics, we find a continuum of sizes among individuals of the dominant species on soils that are starved of nutrients but have a plentiful water supply (e.g., *Eperua* spp. in caatinga; Coomes and Grubb 1996). Indeed, that is also true where there is a less secure water supply on well-drained, nutrient-deficient sands (Davis and Richards 1934). In contrast, in wood-

lands and semideserts there is a lack of smaller trees, saplings, and established seedlings among larger individuals of the dominant species (e.g., in *Pinus ponderosa* woodlands and even drier woodlands of *Juniperus occidentalis* in the northwestern USA; Franklin and Dyrness 1969, Peet 1988). Only when a tree dies as a result of extreme drought or fire, or (more often) when trees are cut down, do we see young trees able to establish. The gap needed for regeneration by these species has to come from the death of an established matrix-forming plant; the interdominant spaces suffer too much root competition (Riegel et al. 1995). Essentially the same is true in semideserts dominated by such celebrated species as *Larrea tridentata* or *Encelia farinosa* and in shortgrass prairie dominated by *Bouteloua gracilis* (Aguilera and Lauenroth 1993). Thus, where water is in very short supply, competition has a huge impact on the population structure of species that are (for the sites concerned) "late successional," but not at sites in species-rich areas with assured water supply but extreme nutrient paucity.

#### *Competition in the context of pulsed resources*

Eber (1972) argued that the mechanism of competition between herbs on the floor of a temperate forest will vary between years. In a dry summer, competition for water between herb and tree roots will dominate, but in a wet year, competition between adjacent individual herbs for light will be critical. Grubb (1992) extended this idea to plants in drier climates, i.e., those in woodlands and semideserts, arguing that one should expect them to experience an alternation between (1) periods of competition for nutrients and light after heavy rainfall, and (2) periods of competition for water as the soil dries out in the interpulse period. Goldberg and Novoplansky (1997) also drew attention to the importance of pulsed water and nutrient supply, but did not suggest explicitly an alternation between periods of competition for water and competition for other resources. They suggested that drying out of the soil after a period of rainfall will normally occur at much the same rate, whether or not plants are present. However, the data of Robberecht et al. (1983) indicate that this is not always the case; in the major rooting horizon, the difference in soil water potential between control plots and plots from which the dominant bunchgrass *Hilaria rigida* had been removed persisted for at least two months. Up to that time, the values were still diverging. Similarly, Fonteyn and Mahall (1978) found for the shrubs *Larrea tridentata* and *Ambrosia trifida* that differences in the leaf water potential between control plants and plants from which neighbors were removed increased up to three months after the last rain. Likewise, Ehleringer (1984) found for the shrub *Encelia farinosa* that the leaf water potential of plants from which neighbors had been removed was significantly and appreciably higher than in the leaves of control plants three months after the last rain.



We also need to know how soil drying affects nutrient uptake in regions that receive widely separated pulses of rainfall. For example, in a forest of *Quercus ilex* in the Mediterranean Basin, it was found that soil drying more strongly affected nitrate uptake by roots than its rate of release by microorganisms, resulting in a build-up of topsoil nitrate during the dry season (Lossaint 1973). Is this a general phenomenon in dry woodlands and semideserts?

A final complication that is especially obvious in dry-climate vegetation is the balance between "nurse" effects and competitive effects of one species on another. For example, Franco and Nobel (1990) estimated that in an average year (over a period of 15 years) the adult bunchgrass *Hilaria rigida* reduced the water uptake of seedling *Agave deserti* by 38%, and yet had a net favorable effect over the year through prevention of overheating. Similar balanced relationships have been reported for savanna by Belsky (1994) and Callaway et al. (1991), and may be found in many woodlands and shrublands (Callaway 1995, Pugnaire et al. 1996).

#### *Predicting how shade tolerances are modified by nutrient supply and drought*

Few studies have specifically investigated the influence of belowground processes on the shade tolerance of plants under natural conditions (Carter and Klinka 1992, Kobe et al. 1995, Kobe and Coates 1997). There is no doubt that some forest plants have greater shade tolerance on soils that provide greater quantities of available nutrients, but the most compelling examples are understory herbs. Peace (1984) documented the effect for 9 out of 10 species of forest herbs studied in southwest Germany, and Wiser et al. (1998) demonstrated that the alien weed *Hieracium lepidulum* invaded the more fertile microsites in mountain beech forests in New Zealand. Furthermore, we have provided several examples of herbaceous vegetation invading trenched plots. The evidence is less convincing for trees: Kobe et al. (1995), who contrasted forest on richer and poorer soils in the eastern United States, found a definite effect for only one of six tree species and a possible effect in one other. However, the fact that the impact of root competition for nutrients on the growth of seedlings is greater on nutrient-poor soils implicates root competition in the determination of shade tolerance, especially as plants probably endure somewhat deeper shade on the more fertile sites. In other words, the inherent tendency of invaders to fail in deep shade on nutrient-poor soils is greatly exacerbated by the presence of the plants already established.

Although we suggest that the shade tolerance of many species will depend on the impact of root competition, we are unable to predict with confidence the types of species that are most likely to exhibit plasticity in this attribute. In the short term, shade-house studies indicate that species with high potential growth rate

are most responsive to nutrient addition in semi-shade, but we do not know enough about the factors regulating whole-plant compensation points (sensu Givnish 1988) to make a persuasive argument about long-term survival in deep shade.

There is very little precise information on the extent to which shade tolerance of wide-ranging species varies with water supply. It is apparent that acute droughts cause saplings to die from the immediate effects of desiccation rather than from any reduction of whole-plant compensation point and growth rate (Kobe and Coates 1995). Regional differences in annual rainfall are likely to affect the growth rates of most such species, because net rates of assimilation are almost universally affected by plant water status (Carter and Klinka 1992). Again, the competition from already established plants will greatly exacerbate the shortage of the limiting resource, and will play a key part in determining the realized value for shade tolerance.

Although we have demonstrated that shade tolerance is likely to be affected by root competition, we recognize that the performances of regenerating trees depend upon other factors that may vary systematically along gradients of resource supply. First, the nutritional quality of leaf litter for soil microbes tends to be poorer among species predominating on infertile or droughted sites, and this in turn leads to slow decomposition, thereby reducing the pool of soil nutrients available for plants (Wardle 1997). Secondly, there is some evidence that herbivory has a differential impact on communities growing on fertile and infertile soils (Proulx and Mazumder 1998). Thirdly, understory herbs and shrubs vary considerably in cover and composition between sites and can restrict the availability of regeneration sites when sufficiently dense; examples include bamboos along a gradient in the Andes (Veblen 1989) and ferns in New Zealand (Wardle 1991). Although these factors are not the focus of this review, we recognize that the ability of a species to survive and grow under a given amount of shade may be strongly influenced by such factors.

#### CONCLUDING REMARKS

The extent to which shade tolerances are modified by belowground competition remains a challenging and largely unexplored area of research that will require a combination of laboratory and field experiments to address satisfactorily. On highly infertile and droughted soils, the increase in irradiance in canopy gaps is not all-important in controlling growth rates, as it is on fertile soils free of water shortage. It therefore becomes less straightforward to characterize woody species by shade tolerances, and more illuminating to understand the ways in which species respond to the availability of nutrients and to pulses of water availability. One topic that demands particular attention is the extent to which utilization of nutrients is uncoupled from utili-



zation of water in areas with long dry spells between rainfalls.

This review underscores how little is known about changes in root form along gradients of water and nutrient availability. Because trenching experiments have demonstrated the impact of root competition on regeneration in many natural communities, there is a need to develop a clearer perspective on how root morphologies vary between community types, on how the regeneration niches of species are influenced by their rooting systems, and on how these changes in morphology influence competitive interactions.

One barrier to the understanding of competitive interactions has been an excessive pre-occupation with grasslands and other communities of herbs, whereas valuable and rather obvious lessons emerge from working with forests, woodlands, and semideserts. We have documented trends in the structure of woody vegetation, and have emphasized the differences between rainfall and fertility gradients and the differences among gradients in various parts of the world. For each gradient, the observed trends can be interpreted in terms of adaptations to the local environment, but the global situation cannot be replicated by any single theoretical model founded upon a few life history traits.

Flexible models such as SORTIE (Pacala et al. 1996) have greatly assisted in the integration of above- and belowground competitive processes into a cohesive framework within forest types, and should make a substantial contribution to our understanding of vegetation dynamics on a regional scale. On a global scale, we argue that advances in understanding will emerge from putting together (often fragmentary) studies in a way that takes account of natural history observations, evolutionary histories, and well-founded physiological work.

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