

DIRECT AND INDIRECT EFFECTS OF SHADE ON FOUR FOREST TREE SEEDLINGS IN THE FRENCH ALPS

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Abstract. A number of authors have documented a higher occurrence of tree seedlings below the canopy of adult trees than in openings, particularly in mesic conditions, where increases in resources in openings stimulate the growth of competing shade-intolerant forbs. These patterns may be explained by indirect facilitation. Indirect facilitation has been mainly explored using models, and too few experimental studies have been conducted to understand the conditions under which it is likely to occur. We test here the indirect facilitation model in natural openings of subalpine forests and explore the relationship that may exist between species response to indirect interactions and life-history traits of target seedlings. Two evergreen conifers (*Picea abies* and *Abies alba*) and two deciduous broad-leaved angiosperms (*Fagus sylvatica* and *Acer pseudoplatanus*) that dominate the mixed mesic forests of the northern external French Alps were planted in a tall forb community invading natural forest openings. Seedlings were grown for three growing seasons, with and without competing forbs, and with and without a 50% shade cloth, simulating the relatively open canopy of the surrounding forests. The direct effects of shade were negative for all four species, but the conifers were much more negatively affected by shade than the angiosperms. Shade strongly reduced aboveground biomass of competing forbs, which improved the availability of nitrogen for the tree seedlings. However, because the indirect positive effect of competition release was outweighed by the direct negative effect of light reduction, the net effect was negative for all four species. Species' responses to the indirect effects of shade were correlated with species traits; additional competition was the highest for the most conservative and shade-intolerant species, *Picea*, and the lowest for the most nutrient-demanding and shade-tolerant species, *Acer*. We conclude that species traits may determine how a species responds to indirect interactions, but that further studies are needed to explore the real potential of indirect facilitation to determine patterns of tree seedling distribution.

Key words: additional competition; competition intensity; forest communities; French Alps; indirect facilitation; life-history strategies; light; nitrogen; regeneration; understory.

INTRODUCTION

Light is recognized as the prevalent factor that drives forest successional dynamics (Loach 1970, Bazzaz 1979, Bormann and Likens 1994, Kobe et al. 1995, Henry and Aarssen 1997, Koike 2001, but see Hubbell et al. 1999), and a number of studies have documented the positive effects of canopy gaps on shade-intolerant species (Denslow 1980, Runkle 1981, Beaudet and Messier 1998, Denslow et al. 1998, Le Duc and Havill 1998, Dalling et al. 2001, Davies 2001). Furthermore, both natural and experimental shade have been shown to decrease growth and survival of shade-tolerant species, at least in mesic environments (Canham 1988, Gray and Spies 1996, Walters and Reich 1996, Kne-

shaw et al. 1998, De Grandpré and Bergeron 2000). In dry or cold environments, the effects of shade can be positive (Finegan 1984, Callaway et al. 1996, Holmgren et al. 1997, Callaway 1998, Anderson et al. 2001, Michalet et al. 2003).

Canopy openings increase light levels and affect other characteristics of the environment such as nutrient availability, which increases in gaps in wet or seasonally wet climates (Bormann and Likens 1994, Denslow et al. 1998) but not in dry or cold climates (Bellingham et al. 2001, Chambers 2001, Michalet et al. 2001, Pugnaire and Luque 2001). Increases in light and nutrients in mesic gaps stimulate the growth of competing shrubs and fast-growing herbaceous plants (Maguire and Forman 1983, Ruel 1992, Humphrey and Swaine 1997, Takahashi 1997, Archambault et al. 1998, Messier et al. 1998, Lautenschlager 1999). Competition from these species may induce a higher occurrence and sur-

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vivorship of tree seedlings below adult tree species than in the openings (Wardle 1959, Van Auken and Bush 1991, Ruel 1992, Li and Wilson 1998, Kubota 2000, Slocum 2001). These patterns, which contradict the expected negative effects of shade from adult trees on survival and growth of tree seedlings, may be explained by indirect interaction mechanisms; the addition of a third competitor can modify the competitive interaction between two species into indirect facilitation (Levine 1976).

Indirect facilitation has been mainly explored using models (Levine 1976, Lawlor 1979, Vandermeer 1990, Stone and Roberts 1991), and few studies have examined indirect interactions in the field (Davidson 1985, Miller 1994, Pennings and Callaway 1996, Levine 1999, Tielbörger and Kadmon 2000). Levine (1999) argued that indirect facilitation may occur among three species when the different pairs of competitors involved in the system compete for different resources or have different mechanisms to acquire resources. For example, herbaceous species may compete for nutrients with tree seedlings, whereas adult trees may compete with herbaceous species and tree seedlings for light. The indirect facilitation model assumes that for the tree seedlings the negative effect of shade induced by the canopy of the adult trees is lower than the positive effect of increased nutrient availability induced by the lower nutrient uptake of the herbaceous species leading to a net positive effect (Levine 1999). Conversely, if the negative effect of additional shade is higher than the positive effect of nutrient availability, then the net interaction will be negative.

We tested the indirect facilitation model by manipulating artificial shade in natural forest openings of the subalpine belt of the northern French Alps. Foresters have documented very little regeneration of the dominant tree species of the surrounding closed forests in openings dominated by tall ferns and forbs. We used four species as target seedlings: two evergreen conifers (*Picea abies* (L.) Karsten and *Abies alba* Miller) and two broad-leaved deciduous angiosperms (*Fagus sylvatica* L. and *Acer pseudoplatanus* L.). Their contrasting leaf traits suggest that they may have strong differences in shade tolerance and nutrient requirements. We also explored how variations in species response to the direct and indirect effects of shade may be related to differences in physiological and life-history traits of the seedlings.

MATERIALS AND METHODS

Study area and species

The experiment was performed in the forest of La Ruchère (1450 m above sea level, 45°20' N, 5°45' E) in the Chartreuse Massif. In this oceanic part of the northern French Alps the climate is characterized by heavy precipitation (3150 mm/yr at this elevation) and buffered thermal conditions (Pache et al. 1996). La

Ruchère is made up of a mosaic of relatively closed (~70% cover) and open (~30% cover) forest communities, the former located on convex slopes and the latter on concave slopes. All experimental sites are located on gentle concave slopes (~15°) where water availability is never limiting during the growing season (Pache 1998) and litter decay is very efficient in these mesic conditions (mesomulls, RPE 1995) with a low C/N ratio (12.7 ± 0.8 ; all $N = 6$; Pache 1998). *Acer* is the only species occurring in both the tree strata and the understory. Foresters have documented very little regeneration by the three other species codominating the surrounding closed forests. In particular, *Picea* has been shown to regenerate poorly in a number of forest communities of the northwestern Alps (Ponge et al. 1994). The understory is dominated by 120 cm tall, shade-intolerant, fast-growing forbs (*Rubus idaeus*, *Adenostyles alliariae*, *Cicerbita alpina*), ferns (*Athyrium filix-femina*, *Dryopteris carthusiana*), and small, shade-tolerant forbs (*Stellaria nemorum*, *Lysimachia nemorum*).

Distribution patterns during forest succession have been used by foresters to assign tree species strategies. Among the four species *Abies* and *Fagus* are considered to be more shade tolerant, and *Picea* and *Acer* to be less shade tolerant (Rameau et al. 1993, Brzeziecki and Kienast 1994). Although experimental studies have not compared the nutrient requirements of the four species being studied, the differences in leaf life span between the evergreen conifers and the deciduous angiosperms suggest that they differ in nutrient acquisition (Reich et al. 1998).

Experimental design and data collection

A 2×2 factorial field experiment involving shade and competition was conducted during three growing seasons (1999–2001) to assess the direct effect of shade on the tree seedlings, and to analyze how shade may alter competition with the tall shade-intolerant fast-growing forbs. We used artificial shade to simulate the effect of an adult tree to test the indirect facilitation mechanism because the very sparse natural tree cover did not allow us to remove the tree strata. We selected four similar sites, at least 100 m apart from each other, as replicates for a block effect. The four experimental sites were located in at least 0.1 ha wide patches of open forest communities with ~30% cover of *Acer*. In May 1999 we delimited a 20×20 m area in the center of each of the four sites and these areas were fenced 1.5 m high to avoid herbivory by deer. In each site the fenced area was subdivided into sixteen 4×4 m plots with 1-m buffers between them. Shade was systematically applied to the eight plots on the northeast side of the sites, to avoid a likely edge effect coming from the southwest. We used a 50% shade cloth to reduce light to the level approximately occurring below the canopy of the surrounding relatively closed forests (~70% cover). The nets were fixed at 1.5 m directly

TABLE 1. Regression formulas used to biomass transform basal stem diameter values of the four tree species from the French Alps.

Species	Formula	R	P	N
<i>Picea abies</i>	$Y = 0.28X^{2.03}$	0.783	0.001	65
<i>Abies alba</i>	$Y = 0.22X^{2.02}$	0.789	0.001	64
<i>Fagus sylvatica</i>	$Y = 0.25X^{2.00}$	0.714	0.001	61
<i>Acer pseudoplatanus</i>	$Y = 0.01X^{2.58}$	0.92	0.001	61

Notes: X is basal stem diameter in mm, and Y is total biomass in g; R are Pearson correlation coefficients, P are probability values, and N are number of seedlings.

above the plots and extended down to 10 cm above the ground on all sides except the northeast where the nets stopped 50 cm above the ground to allow lateral aeration. The nets were installed each year (1999, 2000, and 2001) at the beginning of the growing season (early June) and removed in early November because of the heavy snowfalls of the Chartreuse Massif. The mesh of the shade cloth allowed the rain to pass easily.

The competition treatment was applied four times within each light treatment in each site in a systematic design with a regular alternation of the treatment (Hurlbert 1984). In early June 1999, we clipped all above-ground biomass at ground level in all the plots free of competition and removed the clipped biomass. All regrowth of neighboring plants was cut back every 3–4 weeks.

We planted 24 seedlings of each of the four species in each light treatment of each site in early June 1999. The seedlings were taken from a local nursery (Robin Pépinières, Saint Laurent de Cros, France) and grown from seeds from the northern French Alps. The two conifers were grown for three years in-nursery and for one year in-pot, whereas the two deciduous angiosperms were grown for only one year in-nursery and for one year in-pot because of their higher growth rates. Because there were small differences in initial size among the 192 individuals of each species, all individuals were first measured to equally distribute the size variability between sites and treatments. Within each light treatment of each site the 24 individuals of each species were grouped in 12 pairs with similar individual sizes within each pair. Three numbered seedlings of each species were randomly planted, 30 cm apart from each other, in the center of each plot, in order to distribute the paired individuals of each species in adjacent paired plots along the slope.

We measured the basal stem diameter and the total height of all individuals at the beginning of the experiment in early June 1999. We harvested biomasses (above- and belowground biomass) of seedlings at the end of the experiment in late May 2002. Initial total biomasses were measured for 61–65 extra seedlings of each species to analyze the relationship between biomass and our initial growth measurements. For the four species there was a highly significant correlation between total biomass and basal stem diameter (Table 1),

but total biomass was not significantly correlated to seedling height. Using the formulas of the regressions (Table 1), initial basal stem diameter values were converted to biomass. Growth was calculated as the proportional change in biomass during the course of the experiment: $[(\text{biomass in May 2002}) - (\text{biomass in June 1999})] \times (\text{biomass in June 1999})^{-1}$. Survival was determined at the end of the experiment and expressed in percentage of survival per site for each treatment (shade \times competition) and each species.

We calculated relative competition intensity (RCI) to analyze the effect of herbaceous neighbors on survival and growth of the four species (Wilson and Keddy 1986). For each treatment and each species, RCI for survival was calculated per site, and RCI for growth per paired plots, using the following formula: $RCI_{\text{survival or growth}} = (\text{survival or growth}_{\text{without neighbors}} - \text{survival or growth}_{\text{with neighbors}}) \times (\text{higher value})^{-1}$. The absolute difference in performance between target individuals with and without neighbors is weighted by the performance of the target without neighbors for competition and by the performance of the target with neighbors for facilitation, so that the RCI index will take values between -1 (facilitation) and $+1$ (competition). To measure the effect of artificial shade on competition between tree seedlings and herbaceous neighbors we calculated a relative indirect effect intensity index (RIEI): $RIEI_{\text{survival or growth}} = (\text{survival or growth}_{\text{with neighbors without shade}} - \text{survival or growth}_{\text{with neighbors with shade}}) \times (\text{higher value})^{-1}$. Although our shade was only a simulation of the canopy of an adult tree, this index measures the direction and the strength of the indirect interaction due to the addition of a third species in a system that previously consisted of two interacting species. If the addition of shade decreases the performance of the species competing with neighbors, RIEI is positive, indicating additional competition. Conversely, if the addition of shade increases the performance of the species competing with neighbors, RIEI is negative, indicating indirect facilitation. RIEI may also be negative in the case of direct facilitation; however the indirect facilitation mechanism assumes that, without neighbors, shade (induced by the canopy of an adult tree or experimentally simulated) decreases the performance of the seedling (Levine 1999).

In order to analyze environmental changes occurring during the course of the experiment, as well as changes in understory biomass and composition, we collected soil samples to assess available forms of nitrogen, measured light penetration, and determined the above-ground biomass of the competing neighbors. In each combination of the two treatments (shade \times competition) four replicates of soil samples (one per site) were collected in June 2001 (i.e., at the beginning of the growing season) and eight replicates were taken in September 2001 (i.e., at the end of the growing season). Soil samples were collected 5–10 cm deep and then stored at 4°C. Extractions of NO_3^- and NH_4^+ were per-

formed immediately and then the soil was dried at 105°C for 4 d and water content was quantified. NO_3^- and NH_4^+ were extracted as described in Wheatley et al. (1989), in water and in 1 mol/L KCl respectively, and then stored at -18°C . NO_3^- was determined by ionic chromatography (4500i, Dionex, Sunnyvale, California, USA) and NH_4^+ by the blue indophenol method (Dorich and Nelson 1983). On a sunny day in September 2000, we measured total photosynthetically active radiation (PAR; 400–700 nm) at ground level within 1 h of solar noon (1400 French Standard Time) with 16 replicates per combination of the two treatments (shade \times competition) with a LI-COR (LI-188b) radiometer (LI-COR, Lincoln, Nebraska, USA). Without neighbors, photosynthetic photon flux density was 36.1 ± 1.5 and $10.3 \pm 0.8 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (mean \pm 1 SE) in the 100% and 50% light treatments, respectively. In September 2001 we measured aboveground biomass of all of the understory species competing with tree seedlings in 1×1 m quadrats randomly located within each light treatment with four replicates (one per site). All aboveground parts of the understory species were harvested, dried for 4 d at 70°C , and weighed. Prior to statistical analyses, aboveground masses were gathered per functional group for each sampling; three functional groups were distinguished: tall forbs (height > 30 cm), small forbs and grasses (height < 30 cm), and ferns.

We quantified specific leaf area (SLA: area of leaf per unit dry mass) and carbon and nitrogen content in the leaves or needles of each species; the area of mature leaves or needles was measured for extra seedlings of each species (one leaf of 25 seedlings for angiosperms and five needles of five seedlings for conifers) with an area meter (Mk2, Delta-T, Cambridge, UK) and biomass was weighed after drying leaves or needles for 4 d at 70°C . Total carbon and nitrogen content in two leaves or needles of 10 extra seedlings per species were determined in ground dry samples with a CHONS microanalyzer (1500 Carlo Erba, Rodano, Italy).

Statistical analyses

The Shapiro-Wilk W tests done prior to analyses showed that proportional changes in biomass, as well as RCI and RIEI values, meet the assumptions of normality. We conducted one-way ANOVAs for each species and each treatment (shade \times competition) to test for differences in proportional changes in biomass by sites (block effect). Because ANOVA results indicated no significant site effects ($P > 0.146$), data from the four sites were pooled for the following ANOVAs analyses. Individual data on proportional changes in biomass were averaged per plots and means were analyzed with two-way ANOVAs with shade and species as independent variables; two separate ANOVAs were conducted, one for the plots without neighbors and one for the plots with neighbors, with the plots as unit of replication. All ANOVAs were conducted with SPSS (1997). For survival, we tested shade and species ef-

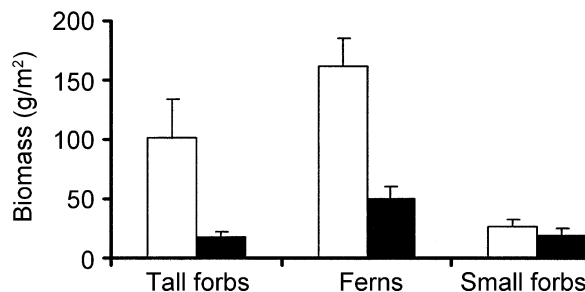


FIG. 1. Means (\pm 1 SE, $N = 4$ sites) of aboveground biomass of the three functional groups of competing understory species (tall forbs, ferns, and small forbs) without (white bars) and with shade (black bars).

fects and their interactions with a chi-square likelihood ratio using two separate logistic regression models (SAS Institute 1990), one for the plots without neighbors and one for the plots with neighbors. RCI for survival and RCI for growth were analyzed with two-way ANOVAs with shade and species as independent variables. Differences among species in RIEI for survival and RIEI for growth were analyzed with one-way ANOVAs, followed by Tukey hsd tests. Data of *P. abies* were excluded from the ANOVAs on RCI and RIEI for growth because of the very low survivorship of this species in some treatments.

Changes in understory aboveground biomasses were analyzed with one-way ANOVA on total mass, followed by Tukey hsd test for each functional group. Environmental variables, including light penetration and available forms of nitrogen, were also analyzed with two-way ANOVAs with shade and competition as independent variables. Differences among species in SLA and C/N values were analyzed with one-way ANOVAs, followed by Tukey hsd tests.

RESULTS

Changes in understory composition, light, and nitrogen

Shade reduced total aboveground biomass of the neighboring vegetation by 70% ($F_{\text{shade}} = 9.0$, $\text{df} = 1, 7$, $P = 0.005$). Although individual t tests for functional groups were nonsignificant, this general trend was likely determined by the strong decrease in biomass of the tallest species (tall forbs and ferns groups, Fig. 1). Neighbors reduced light more than shade treatment (Fig. 2), and the effect of neighbors on light was much stronger in the control plots than in the shaded plots ($F_{\text{shade} \times \text{neighbors}} = 414.8$, $\text{df} = 1, 63$, $P < 0.0001$). The lowest light level was observed in the shaded plots with neighbors. Differences in total available nitrogen among treatments were not significant at the beginning of the growing season, June 2001. However, at the end of the growing season, September 2001, there was slightly but significantly more total available nitrogen in the shade than in the sun for the plots with neighbors (Fig. 3). Although the effect of shade was only mar-

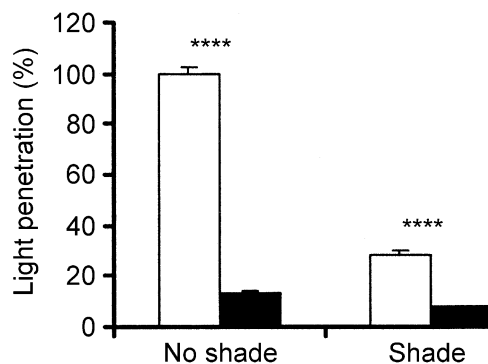


FIG. 2. Means (± 1 SE, $N = 16$, i.e., four measurements for each of the four sites) of light penetration in each combination of the two treatments (shade \times competition). White bars are for plots without neighbors, and black bars for plots with neighbors. Asterisks indicate significant effect of neighbors for each shade treatment: **** $P < 0.0001$.

ginally significant in the plots without neighbors, the significant interaction among treatments ($F_{\text{shade} \times \text{neighbors}} = 7.3$, $df = 1, 31$, $P = 0.012$), in September, showed that the presence of neighbors altered the general trend of decreasing nitrogen availability due to shade (Fig. 3). Results for nitrates were very similar to the results for total available nitrogen, whereas differences among treatments were not significant for ammonium (data not shown).

Species traits and direct effects of shade

There were strong differences in both C/N and SLA between conifers and angiosperms, with conifers having the highest C/N and the lowest SLA (Table 2). Within each group there were also significant differences for C/N, but not for SLA; *Picea* had the lowest nitrogen content and *Acer* the highest.

In the absence of neighbors, shade decreased survival of the two conifers. In particular, *Picea* survived half as much in the shade as in the sun. In contrast, shade did not affect survival of the two angiosperms ($\chi^2_{\text{species} \times \text{shade}} = 34.9$, $df = 3$, $P < 0.0001$; Fig. 4A). With neighbors, the overall effect of shade was negative ($\chi^2_{\text{shade}} = 140.2$, $df = 1$, $P < 0.0001$; Fig. 4B). However, although the species \times shade interaction was not significant, the lowest survival in the shade with neighbors was observed for conifers, *Picea* in particular, and this

TABLE 2. Means (± 1 SE) of specific leaf area (SLA), carbon/nitrogen (C/N) ratio, and sampling number (N) for the four tree species.

Species	SLA (cm ² /g)	C/N	N
<i>Picea abies</i>	55.24 ^a \pm 1.40	40 ^a \pm 0.26	25
<i>Abies alba</i>	51.32 ^a \pm 0.88	37 ^b \pm 0.39	25
<i>Fagus sylvatica</i>	172.02 ^b \pm 2.78	16 ^c \pm 0.21	25
<i>Acer pseudoplatanus</i>	186.49 ^b \pm 28.73	12 ^d \pm 0.27	25

negative effect of shade was not significant for *Acer* (Fig. 4B). To summarize, the ranking in shade tolerance of the four species was similar to the ranking in nitrogen content of leaves or needles with the highest differences in shade tolerance occurring between conifers and angiosperms, and between *Picea* and *Abies* (i.e., *Acer* $>$ *Fagus* $>>$ *Abies* $>>$ *Picea*). Unlike the results on survival, the effect of shade was negative for the growth of all four species, both without neighbors ($F_{\text{shade}} = 38.6$, $df = 1, 127$, $P < 0.0001$; Fig. 5A) and with neighbors ($F_{\text{shade}} = 51.6$, $df = 1, 95$, $P < 0.0001$; Fig. 5B). However, with neighbors, *Picea* was excluded from the two-way ANOVA on growth because of its very low survivorship in the shade.

Indirect interactions

For survival, shade increased RCI of all four species ($F_{\text{shade}} = 41.4$, $df = 1, 31$, $P < 0.0001$), but this effect was not significant for *Acer* ($F_{\text{species} \times \text{shade}} = 2.9$, $df = 3, 31$, $P < 0.1$; Fig. 6A). Conversely, for growth, shade decreased RCI of *Abies* and the two angiosperms ($F_{\text{shade}} = 14.2$, $df = 1, 95$, $P < 0.0001$; Fig. 6B), *Picea* being excluded from this analysis because of its very low survivorship in the shade with neighbors. However this decrease was again not significant for *Acer* ($F_{\text{species} \times \text{shade}} = 4.6$, $df = 2, 95$, $P < 0.05$; Fig. 6B). RIEI for survival were the highest for conifers and the lowest for angiosperms with an opposite ranking to the rankings in shade tolerance and in nitrogen content in leaves or needles: *Acer* $<$ *Fagus* $<$ *Abies* $<$ *Picea* ($F_{\text{species}} = 14.5$, $df = 3, 15$, $P < 0.001$; Fig. 7A). Differences in RIEI for growth between the three species surviving in the shade with neighbors were significant ($F_{\text{species}} = 3.7$, $df = 2, 47$, $P < 0.05$), and the lowest value was observed for *Acer*. The high RIEI values for survival of both conifers indicate that the additional shade induced a

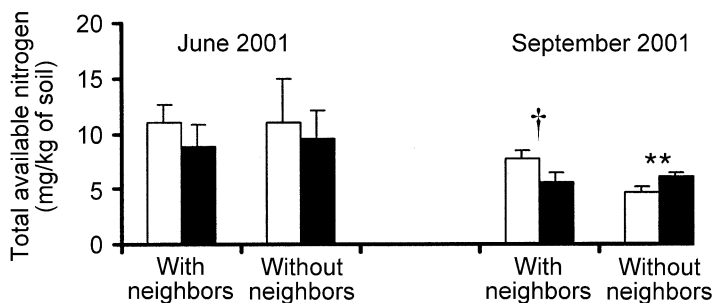


FIG. 3. Means (± 1 SE, $N = 4$ sites in June and $N = 8$ sites in September, i.e., two measurements for each of the four sites) of total soil available nitrogen in each combination of the two treatments (shade \times competition) in June and September 2001, without (white bars) and with shade (black bars). Symbols indicate a significant effect of shade for each competition treatment: † $P < 0.1$; ** $P < 0.01$.

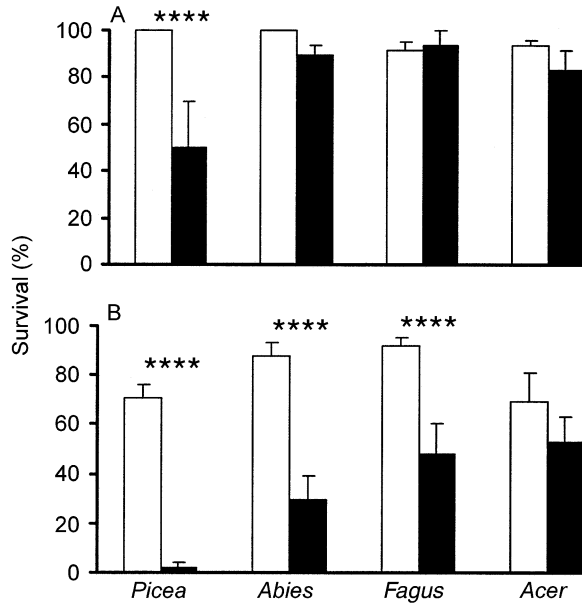


FIG. 4. Means (± 1 SE, $N = 4$ sites) of percentage of survival for *Picea abies*, *Abies alba*, *Fagus sylvatica*, and *Acer pseudoplatanus* without (white bars) and with shade (black bars). (A) Data without neighbors. (B) Data with neighbors. Asterisks indicate significant effect of shade for each species: * $P < 0.05$; **** $P < 0.0001$.

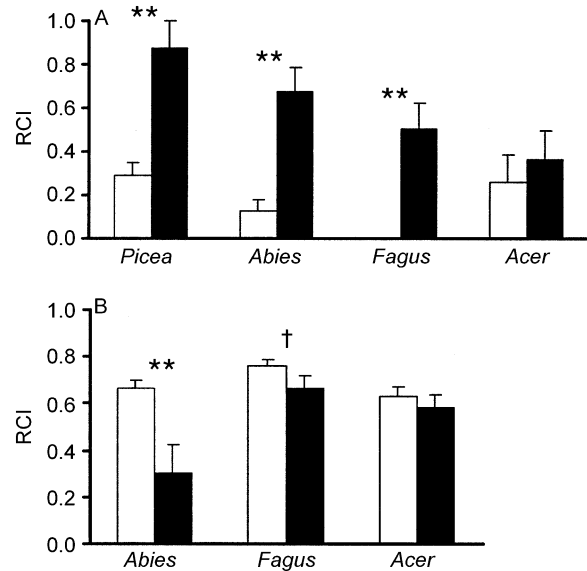


FIG. 6. (A) Means (± 1 SE, $N = 4$ sites) of relative competition intensity index (RCI) for survival of *Picea abies*, *Abies alba*, *Fagus sylvatica*, and *Acer pseudoplatanus* without (white bars) and with shade (black bars). (B) Means (± 1 SE, $N = 16$) of relative competition intensity index (RCI) for growth of *Abies alba*, *Fagus sylvatica*, and *Acer pseudoplatanus* without (white bars) and with shade (black bars). Symbols indicate significant effect of shade for each species: † $P < 0.1$; ** $P < 0.01$.

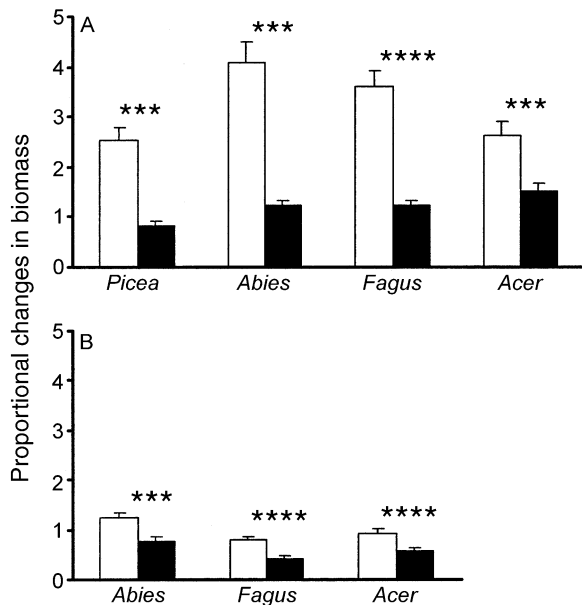


FIG. 5. Means (± 1 SE, $N = 16$) of proportional changes in biomass for *Picea abies*, *Abies alba*, *Fagus sylvatica*, and *Acer pseudoplatanus* without (white bars) and with shade (black bars). (A) Data without neighbors. (B) Data with neighbors (no bars are shown for *Picea abies*, because of its too low survivorship in the shade with neighbors). Asterisks indicate significant effect of shade for each species: *** $P < 0.001$; **** $P < 0.0001$.

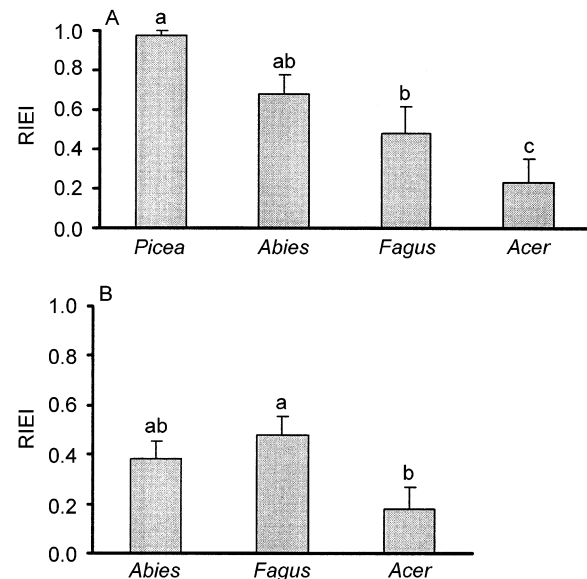


FIG. 7. (A) Means (± 1 SE, $N = 4$ sites) of relative indirect effect intensity index (RIEI) for survival of *Picea abies*, *Abies alba*, *Fagus sylvatica*, and *Acer pseudoplatanus*. (B) Means (± 1 SE, $N = 16$) of relative indirect effect intensity index (RIEI) for growth of *Abies alba*, *Fagus sylvatica*, and *Acer pseudoplatanus*. Different letters indicate significant differences among species ($P < 0.05$, Tukey's hsd test).

strong additional competition for these species, particularly for *Picea*.

DISCUSSION

The indirect facilitation model (Levine 1976, 1999) assumes that the direct negative effect of adult trees on fast-growing competitors induces an indirect positive effect on tree seedlings, which overrides the direct negative effect of adult trees on the seedlings. To test this model in natural openings of a subalpine forest, we compared the performance of the seedlings of four tree species, planted in the sun and below a 50% artificial shade, with and without tall herbaceous competitors. Our shade treatment produced a strong decrease in biomass for the herbaceous neighbors, which correlated with a significant increase in nitrogen availability for the seedlings. Conversely, light was more available in the sun with neighbors than in the shade with neighbors. Although competition for growth with herbaceous neighbors was lower in the shade than in the sun for the three species who sufficiently survived, this competition release (Keane and Crawley 2002) was strong and significant only for *Abies*. This shows that our shade treatment had only a weak indirect positive effect on the growth of the target species, likely through the indirect increase in nitrogen availability. Furthermore, this effect was weaker than the direct negative effect of shade for the growth of these three species, so the net effect of shade was negative. For *Picea*, *Abies*, and *Fagus* the addition of shade increased competition intensity for survival; so overall the net effect was strongly negative for these species.

Indirect facilitation has been mainly explored using models (Levine 1976, Lawlor 1979, Vandermeer 1990, Stone and Roberts 1991) and few studies have examined indirect interactions in the field (Davidson 1985, Miller 1994, Pennings and Callaway 1996, Levine 1999, Tielbörger and Kadmon 2000). Davidson (1985) found evidence of indirect facilitation among three species of harvester ants differing in body size. The addition of the largest species decreased the competitive effect of the intermediate species on the smallest species because of diet overlap related to body size; the magnitude of this indirect positive effect was higher than the direct negative effect because competition was the least between the largest and the smallest species. Pennings and Callaway (1996) showed that *Cuscuta* infection of a *Salicornia* species induced an indirect facilitation for other salt marsh species, otherwise suppressed by the *Salicornia* in the absence of the parasite. Levine (1999) tested the indirect facilitation model for three focal species competing with the monkey-flower, *Mimulus guttatus*, below the canopy of a sedge in a northern California riparian community; he found evidence of indirect facilitation for a liverwort species, but no significant indirect interaction for a moss and a forb. He argued that indirect facilitation occurred for the liverwort species because the sedge inhibited the

monkey-flower by shading it, whereas the monkey-flower physically interfered with the shade-tolerant liverwort. In all of these experiments indirect facilitation occurred in a model of three species when the different pairs of competitors involved in the system competed for different resources or had different mechanisms to acquire resources (Levine 1999). Other experiments testing indirect interactions within plant communities including only angiosperms and nonparasitic plants did not find significant indirect facilitation (Miller 1994, Tielbörger and Kadmon 2000). Increasing the number of competitors competing for the same resources generally induces positive indirect effects, which tend to decrease the strength of direct competitive effects (Miller 1994, Levine 1999, Tielbörger and Kadmon 2000), but the occurrence of indirect facilitation necessitates that indirect positive effects exceed negative direct effects (Levine 1976), which is unlikely when species compete for the same resources (Levine 1999).

We designed our experiment to check if species variations in response to the indirect effect of shade might be explained by differences in their physiological and life-history traits. We observed a negative correlation between the strength of additional competition intensity sustained by the target species for survival and the nitrogen content in leaves or needles; the highest value of RIEI was found for conifers, *Picea* in particular, and the lowest value for angiosperms, *Acer* in particular. Furthermore there was also a negative correlation between RIEI values and species ranking in shade tolerance, i.e., species responses to the direct effect of shade measured in the subplots without neighbors. There is a large consensus in the literature that nitrogen content in leaves, SLA, relative growth rate, and nutrient requirements of woody and herbaceous plants are all tightly positively correlated and negatively correlated to leaf life span (Monk 1966, Grime and Hunt 1975, Chabot and Hicks 1982, Lambers and Poorter 1992, Huante et al. 1995, Cornelissen et al. 1996, Reich et al. 1998, Ryser and Wahl 2001; but see Marañón and Grubb 1993). We can conclude that additional competition was the highest for the most conservative and shade-intolerant species, *Picea* and the lowest for the most nutrient-demanding and shade-tolerant species, *Acer*. Our results suggest that shade-intolerant conservative tree species are poor candidates for positive indirect interactions; the addition of shade for the two conifers, and in particular *Picea*, produced a strong additional competition because the negative effects of decreasing light were much higher than the positive effects of increasing nutrient availability. Conversely, shade-tolerant exploitative tree species, such as *Acer*, may hold the essential traits for indirect facilitation.

In the Chartreuse Massif, indirect facilitation did not occur for *Acer*, either because light was by far the most contested resource among the competitors, or because the increase in nutrient availability due to the addition of shade was insufficient to produce a higher positive

effect than the negative effect of decreasing light availability. Our artificial addition of shade may not have completely mimicked the effect of the canopy of an adult tree, and in the tall forb community of the Char treuse Massif the natural increase in shade, occurring under adult maples during forest succession, may induce a higher nitrogen availability than our artificial shade through the decomposition process of nutrient-rich maple leaves. Results of Peace and Grubb (1982) on the forb *Impatiens parviflora* suggest that the shade-tolerant and nutrient-demanding maple seedlings are more likely to respond positively to this natural nutrient addition than shade-intolerant competing species, which are weakened by the decrease in light. Conversely, additional competition may be higher below a natural tree canopy because our artificial shade did not include the effect of root competition from adult trees on tree seedlings. In addition to resource competition, effective nutrient supply to tree seedlings in closed forests may also be negatively affected by changes in factors that promote mineralization of nutrients (Cater and Chapin 2000). Both effects may explain why canopy openings have been shown to increase nutrient availability in mesic conditions (Bormann and Likens 1994, Denslow et al. 1998). However, other studies conducted in open savanna forests (Callaway et al. 1991, Belsky 1994, Köchy and Wilson 1997, Li and Wilson 1998, Weltzin and McPherson 1999) and in general in dry and/or cold climates (Bellingham et al. 2001, Chambers 2001, Michalet et al. 2001, Pugnaire and Luque 2001) have shown that soils under trees tend to have more available nitrogen than soils under adjacent open areas.

Our experiment indicated that canopy shade weakly reduced the effect of competition by understory forbs on tree seedlings and that the negative effect of shade outweighed the indirect positive effect, raising doubts about whether the indirect model can explain patterns of seedling distribution. Because the strength of indirect interactions is likely to vary predictably among species, future studies should explicitly consider variation among potential target species when studying indirect effects. Our experiment had potential weaknesses: it did not manipulate tree roots, and it was of relatively short duration. Further experiments that overcome these limitations are needed to fully address the role of indirect interactions in explaining the distribution of tree seedlings. However, we suggest that the major contribution of this experiment was to demonstrate that the strength of indirect interactions was correlated with plant traits.

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