Contrasted responses of two understorey species to direct and indirect effects of a canopy gap

Jean-Philippe Pagès[1] and Richard Michalet[2],*

[1]Cemagref, Campus universitaire Grenoble 1, UR Ecosystèmes et Paysages Montagnards, 2 rue de la Papeterie, BP 76, 38402 Saint Martin d'Héres, France; [2]UMR 1202 BIOGECO INRA-Université Bordeaux 1, Laboratoire d'Ecologie des Communautés, avenue des Facultés, 33405 Talence, France; *Author for correspondence (e-mail: r.michalet@ecologie.u-bordeauxl.fr)

Abstract

Positive associations between adult trees and understorey species have been explained either by direct or indirect facilitation. We tested both models by comparing the performance of two understorey species with contrasted stress-tolerance abilities Galium odoratum and Deschampsia flexuosa. Individuals of both species were transplanted in the four combinations of two treatments (gap and removal of an herbaceous competitor, Molinia caerulea). Our experiment demonstrated that direct facilitation of adult trees may explain the restricted occurrence of the shade-demanding Galium within closed forest communities. In contrast, the shade-tolerant Deschampsia was subjected to additional competition within the forest, likely because adult trees had a higher negative effect on light availability and a similar negative effect on nitrogen availability within the forest than did Molinia in the gaps.

Introduction

Do understorey species need or tolerate trees? For at least semantic reasons, the answer could differ if you ask the question to a plant ecologist whose native language is Latin-derived or to an English-speaking scientist. For the former, understorey species are assumed to need shade (sciaphilous species) whereas for the latter, the common word characterizing the same plant is shade-tolerant species. Nevertheless, that's Clements (1916) in North-America who was the first to argue that interdependency among species was the driving mechanism of plant communities. In this holistic conception, the autogenic succession was explained by an alleviation of physical stress due to the positive canopy effect of early successional species, allowing the recruitment of shade-demanding late-successional species (Connell and Slatyer 1977; Finegan 1984). Although the leader of the European phytosociological school, Braun-Blanquet et al. (1932), also argued that dependency played an important role in the life of plant communities, he was considering that plant communities were primarily determined by niche complementary processes. Both of these theories differed strongly from the individualistic theory of Gleason (1926) who considered that species are distributed independently of one another in continua along environmental gradients. Species distributions are thought to be primarily determined by their tolerances to abiotic factors and the

negative effect of other species. Since the 1950s and the emergence of gradient analyses (Whittaker 1956; Mchitosh 1967; Austin 1985), most ecologists have embraced the individualistic concept of community organization and there has been an intense research emphasis on plant competition and species tolerances to abiotic factors over the last few decades. The effect of shade due to the canopy of dominant species is rather considered as negative for the subordinated species of the community, as well in forests (Bazzaz 1979; Reich et al. 1998) than in grasslands (Grime 1974; Tilman 1982).

However, in the last 10 years many experimental studies have demonstrated positive interactions in plant communities (see reviews by Callaway 1995) suggesting that species are not always independent of each other, and that the influence of facilitation on community level variables is at least as important as other factors (Bruno et al. 2003). Callaway (1997) and Lortie et al. (2004) argued that continuous correlations are not proof of fully independent communities because species can either compete, have no effect on each other, or have positive relationships depending on the environmental conditions at particular locations along environmental gradients (Brooker and Callaghan 1998; Choler et al. 2001; Michalet et al. 2002). Specifically, the direct positive of shade by dominant canopy species was demonstrated in a number of stressful environments (Callaway et al. 1996; Weltzin and McPherson 1999). However, the strength and the direction of direct interactions among plant species may be altered by indirect interactions involving additional species (Levine 1976; Berlow 1999) and a number of modelling studies concluded that increased species number could reduce the intensity of competition and eventually lead to indirect positive effects (Lawlor 1979; Vandermeer 1990; Stone and Roberts 1991). Levine (1999) argued that indirect facilitation can contribute to the coexistence of species in diverse communities which suggests that a number of positive correlations between overstorey and understorey species are likely to be explained by indirect rather than direct positive effects of shade. However, empirical studies on indirect effects among plants are too rare (Miller 1994; Pennings and Callaway 1996; Levine 1999; Tielbörger and Kadmon 2000) to determine the generality of this conclusion (Levine 1999).

We will compare the responses of two understory species to a canopy gap and the removal of herbaceous neighbours in a temperate hardwood forest to analyse the respective roles of direct and indirect effects of canopy trees in explaining the higher occurrence of these two understory species within the forest than in the openings. We choose as target species two common perennials herbaceous species with contrasted 'phytosociological status', *Galium odoratum* (L.) Scop. and *Deschampsia flexuosa* (L.) Trin. *Galium* is almost completely restricted to closed forest communities and considered as a 'characteristic species' of nutrient-rich broad-leaved or mixed temperate forests from low to middle-high elevation in Europe *(Galeobdolon-Galium-Asarum* union Lippmaa 1938, *Galio-Fagion* Tuxen 1955), whereas *Deschampsia* occurs on nutrient-poor soils, irrespectively of elevation, and as well in forest communities than in grasslands or heaths (Ellenberg 1953; Rameau et al. 1993; Michalet and Philippe 1995). The latter is often used by phytosociologists to distinguish nutrient-poor forest communities on acidic soils from nutrient-rich ones on weakly acid or neutral soils. These contrasted distribution patterns clearly indicate that *Deschampsia* is more stress-tolerant than *Galium*. Because of its strictly occurrence within closed forest communities, we hypothesized that *Galium* may require the shade of the adult trees to avoid physical stress and should be directly facilitated in our experiment. In contrast the stress-tolerant *Deschampsia* is more likely to tolerate the shade of adult trees and we hypothesized that indirect facilitation should explain its higher occurrence within the forest than in open areas. Canopy trees are expected to indirectly facilitate *Deschampsia*, through the shading of the fast-growing herbaceous competitor, *Molinia caerulea* ssp. *arundinacea* (Schrank) K. Richt, invading natural gaps (Taylor et al. 2001; Pages and Michalet 2003).

Materials and methods

Study site

The experimental site is located at 650 m a.s.l in the region of Dauphiné (northern French Alps) in a temperate deciduous forest., co-dominated by sessile oak (*Quercus petraea* (Mattus.) Liebl.),

sweet chestnut (*Castanea saliva* Mill.) and European beech (*Fagus sylvatica* L.). The site is included in the National Forest of Chambaran which is exploited by French National Office of Forest every 50 years for firewood. The climate is characterized by mesic conditions, with 1000 mm of rainfalls per year and an annual average temperature of 10.3 °C. The topography of the study site is flat with deep silty soils. C:N ratio in the upper part of the of soil is 15 and pH varies from 3.5 to 5 (Joud 1997). The purple moor-grass (*Molinia caerulea* ssp. *arundinacae*) is the dominant herbaceous species within the forest with an average cover of 40%. Other main understorey species (< 5% cover) are wavy hair-grass (*Deschampsia flexuosa*, honeysuckle (*Lonicera periclymenum* L.) and wood sage (*Teucrium scorodonia* L.). Sweet woodruff (*Galium odoratum*) is only present as a rare species in this forest community because of the low nutrient availability of the acidic soils (Joud 1997).

Experimental design and layout

A 2 × 2 × 2 factorial field experiment involving species, gap and competition treatments was designed to analyse the responses of the two herbaceous species, *Deschampsia* and *Galium*, to the opening of the forest canopy and the removal of herbaceous neighbours. Four forested sites (150×75 m-large) were initially selected as replicates for a block effect with at least 100 meters apart between them. All sites were surrounded with wire netting (1.5 m high) to limit the herbivory due to wild herbivores such as deer. In November 1999, half of each forested site was clear-cut with caution not to disturb soil and understorey vegetation. In the center of each plot (75×75 m-large), six 4×4 m-large subplots were delimited with at least 3 m-large buffered area between them, and the competition treatment was applied on three of the six subplots with a regular alternation of the treatment (Hurlbert 1984). *Molinia* and other neighbouring species were treated chemically with glyphosate (Round Up 360 mg l^{-1}) at the beginning of the growing season in the competition-free subplots. The chemical treatment was applied at ground level around target individuals protected with plastic pots. All re-growth was clipped at ground level every 3–4 weeks and we removed the clipped biomass.

We transplanted randomly three individuals of the two target species in each of the subplot in all sites, at the beginning of the experiment, in March 2000. Target individuals were collected in the same forest community, in the vicinity of the experimental sites, just before transplantation. All transplants of both *Deschampsia* and *Galium* were chosen as isolated plants with 2–3 leaves.

Data collection and compilation

We measured total height and number of leaves of all individuals at the beginning of the experiment, March 2000, and at the end of the experiment, late October 2000. Survival was also recorded late October 2000. Total initial biomass (above and belowground) was determined on at least 81 extra individuals of each species, March 2000. At the end of the experiment, all plant material of all individuals who survived (root system and aboveground biomass) were harvested, washed to separate root system from soil, dried 7 days at 70 °C, and then weighed. Growth was calculated per individual as the proportional change in biomass during the course of the experiment: [(Biomass in October 2000)−(Biomass in March 2000)]×(Biomass in March 2000)$^{-1}$. Individual values of proportional change in biomass were averaged per subplot, prior statistical analyses. Survival was expressed in percent of survival per block, for each treatment (gap × competition) and each species. We did not analyse growth data of *Galium*, because of the high mortality of this species in the gaps.

We measured light penetration, total biomass of *Molinia*, and collected soil samples for measurements of available forms of nitrogen to analyse changes occurring during the course of the experiment. On a sunny day in September 2000, we measured Photosynthetic Photon Flux Density (PPFD in μmol photon m^{-2} s^{-1} at ground level within 1 h of solar noon (1400 French Standard Time) with 12 replicates per combination of the two treatments (opening × competition) with a LI-COR (LI-188b) radiometer (LI-COR, Lincoln, Nebraska, USA). Results were expressed in percentage of average PPFD measured in full light (subplots without neighbours in the gaps). In each combination of the two treatments (gap × competition), eight replicates of soil samples (two per

block) were collected June 2000, at the beginning of the growing season and October 2000, 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 peformed immediately and then soils were dried at 105 °C for 4 days for water content measurements. NO_3^- and NH_4^+ were extracted respectively in water and in KCl 1 M, and then stored at −18 °C (Wheatley et al. 1989). NO_3^- was determined by ionic chromatography (Dionex 4500i) and NH_4^+ with the blue indophenol method (Dorich and Nelson 1983). In September 2000, we measured total (aboveground and belowground) biomass of herbaceous neighbours competing with understorey species in 0.5 × 0.5 m quadrates randomly located within each canopy treatment of each block (four replicates). The belowground biomass of *Molinia* was obtained by washing away the soil and separating the roots by hand. Aboveground biomass was harvested at the same time, and all plant material was dried for 7 days at 70 °C and then weighed.

Quantification of direct and indirect interactions

The competitive effect of *Molinia* on the survival of the two target species, and on the growth of *Deschampsia* only, were quantified with Relative Competitive Intensity ($RCI_{Molinia}$) indices (Wilson and Keddy 1986; Grace 1995). The absolute difference in mean performance between target individuals of the subplots with and without neighbours was weighted by the mean performance of the target of the subplots without neighbours for competition and by the mean performance of the target of the subplots with neighbours for facilitation (Markham and Chanway 1996), which makes RCI values included between −1 (for facilitation) and +1 (for competition). $RCI_{Molinia}$ for survival was calculated per plot whereas $RCI_{Molinia}$ for growth was calculated by paired subplots, using the regular alternation of the competition treatment to pair the subplots. The direct effect of the forest canopy (without herbaceous neighbours) on the survival of the two target species, and on the growth of *Deschampsia*, were determined by calculation of RCI_{Forest}. To measure the indirect effect of the forest canopy on both target species (i.e. the alteration of the

competitive effect of the herbaceous neighbours on understorey species), we calculated a Relative Indirect Effect Intensity index (RIEI) for Survival and growth: RIEI = (performance$_{with neighbours in the gaps}$−performance$_{with neighbours within the forest}$) × (higher value)$^{-1}$ (Pages et al. 2003). When the performance of the species competing with herbaceous neighbours is decreased by the forest, RIEI is positive, which means an additional competition; conversely, when the performance of the species competing with herbaceous neighbours is increased by the forest, RIEI is negative, which means an indirect facilitation. However, because RIEI may also be negative in the case of direct facilitation, there is an indirect facilitation only when RCI_{Forest} is also positive.

Statistical analysis

Survival was analysed with chi-square likelihood ratio (logistic regression, SAS institute, Cary, North Carolina) with species, gap and competition as treatments. For the growth of *Deschampsia*, we conducted a split plot ANOVA on proportional changes in biomass, with gap treatment as main effect and competition as subplot effect. We conducted a split plot ANOVA on $RCI_{Molinia}$ for survival with gap treatment as main effect and species as subplot effect. We conducted one-way ANOVAs to analyse the effects of species on RCI_{Forest} and RIEI for survival. All ANOVAs were conducted with SPSS (1997) and multi-ways ANOVAs were followed by Tukey's HSD test.

Results

The gap treatment had a strong positive effect on *Molinia* ($F_{1,6} = 147.9$, $p < 0.0001$): total biomass increased from 320 ± 33 g m^{-2} within the forest to 1227 ± 67 g m^{-2} in the gaps. The decrease in light due to *Molinia* was much lower within the forest than in the gaps ($F_{1,6} = 569.0$, $p < 0.0001$, Table 1). However, the lowest light level was found with neighbours within the forest (% PPFD = 2.1 ± 0.1), because the shading effects of the forest canopy and of *Molinia* were additive. Total available nitrogen in soil strongly increased in the gaps, only when *Molinia* was excluded ($F_{1,6} = 28.2$, $p < 0.0001$, in June 2000 and

Table 1. ANOVA table of *F*-values for the effects of neighbours and gap, and their interactions on light penetration and total available nitrogen in soil, in June 2000 and September 2000.

	PPFD (%)	Total available nitrogen (mg N g^{-1} of dried soil)	
		June 2000	September 2000
F-values			
Neighbours	593.5****	17.4***	21.8***
Gap	1032.8****	10.9**	20.3***
Neighbours × gap	569.0****	28.2****	24.3****
% SS	98.7	82.5	84.6
Treatment means			
Forest with neighbours	2.1 a	11.6 a	6.9 a
Forest without neighbours	3.0 a	10.4 a	6.0 a
Gap with neighbours	16.4 b	9.4 a	5.4 a
Gap without neighbours	100.0 c	19.7 b	39.3 b

% SS : sum of squares explained by the model. Treatment means: forest with neighbours, forest without neighbours, opening with neighbours and opening without neighbours. Different letters indicate significant differences between means ($p < 0.05$, Tukey's HSD). ****$p < 0.0001$, ***$p < 0.001$, **$p < 0.01$.

$F_{1,6} = 24.3$, $p < 0.0001$, in September 2000, Table 1). This suggests that the nutrient uptake of *Molinia* was much higher in the gaps than within the forest; however, in the presence of *Molinia*, nitrogen availability was not significantly higher within the forest than in the gaps (Table 1).

Survival of *Deschampsia* was relatively high in all combination of treatments, with no significant differences between subplots (Figure 1); however the gap × competition interaction was marginally significant because survival of *Deschampsia* decreased in the gaps when *Molinia* was excluded, but increased in the gaps in the presence of *Molinia* (Chi-square = 3.4, $p < 0.1$; Figure 1). The removal of the forest canopy was strongly negative for *Galium* (Chi-square = 191.1, $p < 0.0001$; Figure 1); in the gaps, only one individual (2.8%)

survived without neighbours and two individuals (5.6%) with neighbours, versus respectively 67.5 and 80% within the forest. For growth, the effect of the gap was very positive for *Deschampsia* when *Molinia* was excluded, but this effect was not significant with neighbours (interaction gap × competition: $F_{1,6} = 5.5$, $p < 0.05$; Figure 2). Data for growth were not analysed for *Galium*, because of its very low survival in the gaps.

For survival, there was no significant differences between both species in their response to the direct effect of *Molinia*, which was weak, as well within the forest than in the gaps (RCI$_{Molinia}$ was close to zero for both species, data not shown). In contrast, there was a highly significant difference in species response to the direct effect of the forest on survival, with a very low value of RCI$_{Forest}$ (cal-
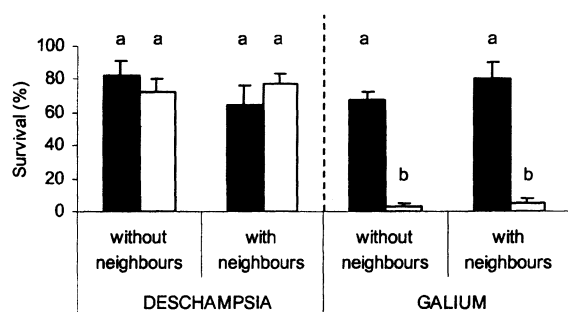

Figure 1. Survival (Means ± SE, *n* = 4) of *Deschampsia* and *Galium* without and with herbaceous neighbours. Black bars represented survival within the forest and white bars survival in the gaps. Different letters indicate significant differences between means ($p < 0.05$, Tukey's HSD).
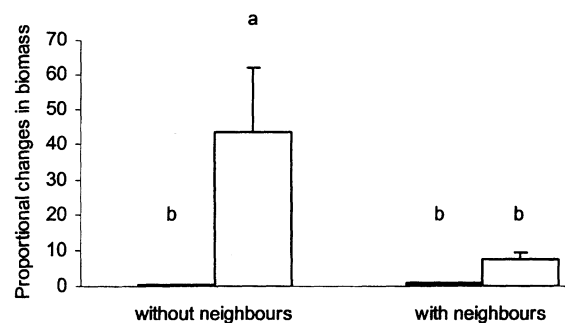

Figure 2. Means (± SE, *n* = 12) of proportional changes in biomass for *Deschampsia* without and with herbaceous neighbours, within the forest (black bars) and in the gaps (white bars). Different letters indicate means were significantly different ($p < 0.05$, Tukey's HSD).

culated in the subplots without herbaceous neighbours) for *Galium* only ($F_{1,6}$ = 33.3, $p < 0.001$; Figure 3). RIEI for survival were also significantly different ($F_{1,6}$ = 66.7, $p < 0.0001$; Figure 4), with a very low value for *Galium*.

For the growth of *Deschampsia*, there was a highly significant effect of the gap treatment on the competitive effect of *Molinia* ($F_{1,6}$ = 35.2, $p < 0.0001$): $RC_{molinia}$ was much higher in the gaps (0.67 ± 0.11) than within the forest (-0.07 ± 0.10). However, because the negative effect of the forest canopy was stronger ($RCI_{Forest} = 0.97 \pm 0.01$) than the negative effect of *Molinia* in the gaps, the net effect of adult trees was negative for the growth of *Deschampsia* (RIEI = 0.81 ± 0.06). In other words, in the presence of *Molinia*, the growth of *Deschampsia* was much higher in the gaps than in the forest.

Discussion

Our first hypothesis that direct facilitation of adult trees may explain the restricted occurrence of

Figure 3. Means ($\pm$ SE, n = 4) of RCI $_{Forest}$ for survival of the two understorey species, *Deschampsia* and *Galium*.

Figure 4. Means ($\pm$ SE, n = 4) of RIEI for survival of the two understorey species, *Deschampsia* and *Galium*.

Galium within closed forest communities was confirmed. The removal of the tree canopy induced a dramatic mortality for this species and this pattern was observed in all subplots, as well with the competitor *Molinia* than without neighbours. We can conclude that the restricted occurrence of *Galium* in closed forest communities (Lippmaa 1939; Rameau et al. 1993) is not due to an indirect effect (alleviation of competition) but to a direct positive effect (alleviation of stress) of the adult trees. Shade has been shown to be a driving mechanism of positive interactions in stressful environments (Callaway et al. 1996). The responses of plants to the decrease in light level may be nutrient or moisture dependent (King et al. 2001). Trees can either buffer temperatures and increase moisture (Weltzin and McPherson 1999; Pages and Michalet 2003), increase nutrient availability (Li and Wilson 1998; Peltzer and Köchy 2001) or decrease photoinhibition (Henry and Aarssen 1997; Murchie and Horton 1998). Although *Galium* is a nutrient-demanding species (Ellenberg 1953; Rameau et al. 1993), we suggest that the direct positive effect of adult trees on this species in our experiment was not nutrient-dependant, because nitrogen availability was the highest in the gaps without herbaceous neighbours where *Galium* dramatically died. Alleviation of light-stress and microclimatic buffering were more likely to be the driving mechanisms for this shade-demanding species.

Our second hypothesis was that *Deschampsia*, known to occur the most in forest communities but also in open areas (Rameau et al. 1993; Michalet and Philippe 1995), should be considered as a shade-tolerant rather than a shade-demanding species and that adult trees may indirectly facilitate this herbaceous species by inhibition of the fast-growing herbaceous competitor, *Molinia*. In our experiment, *Deschampsia* was certainly shade-tolerant because its highest growth was observed in the gaps without neighbours and its mortality was low in these subplots. However the marginally significant effect of the competition × gap interaction observed for survival indicated that there was a tendency for *Molinia* to decrease the negative effect of the gap on the survival of *Deschampsia*. This effect was marginally significant likely because physical conditions were not harsh in this hardwood temperate forest but increasing stress might trigger this tendency. Thus, Michalet
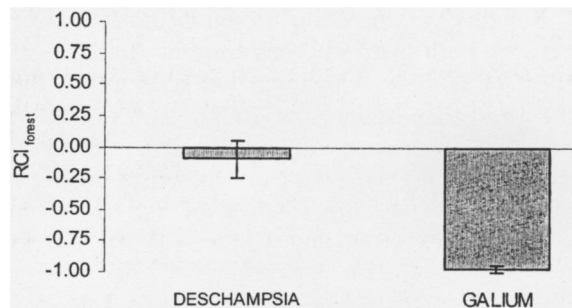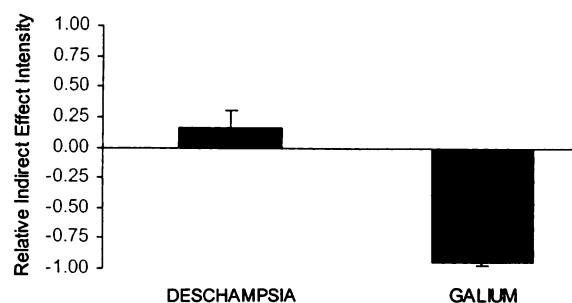
et al. (2002) have shown with multivariate analyses that associations between understorey species (including *Deschampsia*) and tree species increase with stress along the rainshadow gradient opposing the external Alps (mild and wet climate) to the inner Alps (cold and dry climate). Whittaker (1960) and del Moral and Watson (1978) have shown similar patterns in other mountain ranges. This suggests, after Holmgren et al. (1997), that a same species can switch from a shade-tolerant behaviour to a shade-demanding one along a gradient of increasing physical stress.

For *Deschampsia*, Relative Indirect Effect Intensity (RIEI) was very high for growth, whereas RIEI for survival was not significantly different from zero. These results indicate that, in opposition with our second hypothesis, the net indirect effect of adult trees was primarily negative for *Deschampsia*. The indirect facilitation model assumes that the direct negative effect of adult trees on fast-growing competitors should induce an indirect positive effect on understorey species, which should override the direct negative effect of adult trees on the latter (Levine 1976). Our results showed that the gap treatment strongly increased the biomass of *Molinia*, as well as its competitive effect on the growth of *Deschampsia*, which demonstrated that adult trees induced an indirect positive effect on this species. However, because adult trees had a higher direct negative effect on the growth *of Deschampsia* than did *Molinia* in the gaps, the indirect positive effect of decreasing competition with *Molinia* was lower than the direct negative effect of adult trees. Levine (1999) found evidence of indirect facilitation for a liverwort species, but not for two other target species, competing with *Mimulus gutatus* below the canopy of a sedge in a Californian riparian community. He argued that indirect facilitation might occur when species compete for different resources and specifically that indirect facilitation occurred for the liverwort species because the sedge inhibited *Mimulus gutatus* by shading, whereas the latter physically interfered with the shade-tolerant liverwort. Callaway and Pennings (1998) 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. In this latter example, like in the study of Levine (1999), the three species of the system were competing for different resources,

whereas Tielbörger and Kadmon (2000) found no evidence of indirect effects in a system including several annuals below a shrub and Miller (1994) only a null effect within a grassland community.

We suggest that the three species occurring in our system were sufficiently different to expect that they compete for different resources. It has been shown that shrubs and trees have lower competitive effects than herbaceous species (Li and Wilson 1998; Peltzer and Köchy 2001), likely because the latter are more efficient to uptake nutrients (Grime 1974). In our experiment the fast-growing shade-intolerant *Molinia* (Taylor et al. 2001) had a strong negative effect on nutrient availability in the gaps, but not within the forest. Thus, the negative direct effect of adult trees on *Molinia* was potentially to induce an indirect positive effect on the nutrient availability of *Deschampsia*. However, nutrient availability was not higher within the forest than with *Molinia* in the gaps, either because adult trees and *Molinia* had similar nitrogen uptakes or more likely because nitrogen mineralization was much lower within the forest than in the gaps (Rice and Pancholy 1973; Raschid and Schaeffer 1988), as suggested by previous studies conducted in temperate hardwood forests (Mladenoff 1987; Bormann and Likens 1994). We can conclude that the net indirect effect of adult trees was negative for *Deschampsia*, because nitrogen availability was not higher within the forest than in the gaps with *Molinia*, while light penetration was the lowest. This may be explained, either because species competed for the same resources (similar per-gram effect), according to Levine (1999), or because the effect of the forest was too strong, as compared to *Molinia* (mass effect). Indirect facilitation is likely to occur in more open forest communities, where a critical light transmission may allow indirect positive effects to override direct negative effects. Pages et al. (2003) have shown that nutrient-demanding deciduous tree species are better candidates for indirect facilitation than conservative conifers because of their higher sensitivity to the indirect positive effect of shade on nutrient availability. *Deschampsia* is known to tolerate a very low nutrient availability and this may also explain why we did not observe an indirect facilitation for this species. Although more experimental studies are needed to understand the real conditions under which indirect facilitation may occur in forest communities, our results demonstrated that this

model is very unlikely to explain at least the restricted occurrence within closed forest communities of species which are not stress-tolerant. Low tolerance of physical stress has also been shown to be a good predictive functional trait for direct facilitation in herbaceous communities (Liancourt et al. 2005).

Acknowledgements

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