Universitat de Lleida

Document downloaded from:

<http://hdl.handle.net/10459.1/68411>

The final publication is available at:

<https://doi.org/10.1007/s00442-006-0379-2>

Copyright

(c) Springer-Verlag, 2006

**The role of below-ground competition during early stages of secondary
succession: the case of Scots pine (*Pinus sylvestris* L) seedlings in an
abandoned grassland**

Catherine Picon-Cochard^{1,4}, Lluís Coll^{2,3} and Philippe Balandier²

1. INRA, Agronomy Research Unit, Grassland Ecosystem Research Team, 234 Avenue du
Brézat, 63039 Clermont-Ferrand Cédex, France

2. CEMAGREF, DFCF Research Unit, Applied Ecology of Woodlands Research Team, 24
Avenue des Landais, BP 50085, 63172 Aubière Cédex, France

3. Present address: Groupe de Recherche en Écologie Forestière Interuniversitaire (GREFi),
Université du Québec à Montréal, C.P. 8888, Succ. Centre-Ville, Montréal, H3C3P8, Qc,
Canada

4. Corresponding author, E-mail: picon@clermont.inra.fr, tel: +33 4 73 62 45 84, fax: +33 4 73
62 44 57

5. Running headline: Scots pine performance in grassland

Abstract

In abandoned or extensively managed grasslands the mechanisms involved in pioneer tree species success are not fully explained. Resource competition among plants has been emphasised as one possible mechanism to explain variation of survivorship and growth. Asymmetric competition between grass vegetation and seedlings of tree species is expected because of aerial dominance of the former, while below-ground competition is generally considered symmetric. In this study we evaluated a number of mechanisms that may lead to successful survival and growth of seedlings of a pioneer tree species (Scots pine) in a grass-dominated ecosystem. Three year-old Scots pines were planted in an extensively managed grassland of the French Massif Central and for two years were either maintained in bare soil or subjected to aerial and below-ground interactions induced by grass vegetation. The tall grass canopy reduced light transmission by 77% at ground level and by 20% in the upper part of Scots pine seedlings. Grass vegetation presence also significantly decreased soil volumetric water content (Hv) and soil nitrate in spring and in summer. In these conditions the average tree height was reduced by 5% compared to trees grown in bare soil, and plant biomass was reduced by 85%. Scots pine intrinsic water-use efficiency (A/g), measured by leaf gas-exchange, increased when Hv decreased owing to a rapid decline of stomatal conductance (g). This result was also confirmed by $\delta^{13}C$ analyses of needles. A summer ^{15}N labelling of seedlings and grass vegetation confirmed the higher NO_3 capture capacity of grass vegetation in comparison with Scots pine seedlings. Our results provide evidence that these Scots pine seedlings experienced asymmetric competition from grasses for below-ground resources. Despite this, its success was linked to tolerance of resource depletion induced by grass vegetation based on morphological and physiological plasticity.

Key-words: light, soil water and N, $\delta^{13}C$, ^{15}N , asymmetric competition

Introduction

Understanding the mechanisms driving woody plant seedlings establishment and growth is an important first step in the comprehension of shifts from grass to woody plant domination during secondary succession caused by cessation of agricultural activities in grassland ecosystem. Natural patterns of seedling establishment (germination and emergence) in grasslands are well documented and have been related to different biotic (seed bank and dormancy, predation) and abiotic variables (climate change, fire regimes, livestock grazing frequency) (Van Auken 2000). In many cases seedling emergence can be severely restricted in an intact grass canopy and many species require gaps to establish (McConnaughay and Bazzaz 1991). Once established, survival and growth are further influenced by interactions with the grass vegetation (McConnaughay and Bazzaz 1991). The role of such interactions during succession is well documented (Connell and Slayter 1977; Tilman 1985; Wilson 1988). However these interactions are complex: they can be positive, negative or neutral, and they can change through time and space in relation to specific phenologies, resource availability and climatic conditions (Balandier et al. 2005a). Negative interactions are generally described by the word “competition”, even if used to describe such interactions at vastly different study levels (i.e. ecosystem, community, species or individuals; Grace and Tilman 1990). At the individual scale competition between plants occurs when the supply of shared resource is limited, leading to a reduction of growth, survival or reproduction (Begon et al. 1990). Here we used this term in accord with a functional meaning: resource competition occurs when plant individuals utilize the same pool of growth-limiting resources (Grime 2001).

One aspect of resource competition that has important consequences for individual and population dynamic is the degree to which the competition represents symmetrical or asymmetrical interaction (Schwinning and Weiner 1998; Freckleton and Watkinson 2001). Asymmetric competition means that the negative effect of a plant i on a plant j has a

disproportionate intensity compared to the effect of the plant j on the plant i . Competition for light between plants of unequal sizes can be a typical example of asymmetric competition (Rees and Bergelson 1997): the tallest plant intercepts much of the radiation resulting in reduced growth of the shorter plant, while shade caused by the latter has no influence on the former. In contrast, competition for below-ground resource is generally considered symmetric, in that resources are used equally or in proportion to the size of the root system (Weiner 1990; Schwinning and Weiner 1998; Bauer et al. 2004). Thus, in asymmetric competition few resource are available for the subordinate species. Consequently their success depends on the capacity to acclimate to resource depletion through morphological and physiological plasticity (e.g. lower tissue turnover, reduction of nutrient losses, lower stomatal conductance, etc) (Goldberg, 1990; Köchy and Wilson 2000; Connolly et al. 2001; Peltzer and Köchy 2001).

In the case of the grassland ecosystems, it has largely been shown that grasses (which are the dominant species) are highly competitive, and most have been determined to have the competitive strategy (C) or a combination of two or three strategies among the C-S-R (competitor, stress tolerator and ruderal, respectively) classifications of Grime (2001). Such grasses are generally assumed to be more competitive for below-ground resource (Grime et al. 1990; Harmer 1996), but their effect above ground is less evident. For example, the influence of grasses on light availability is unclear because most have thin erected leaves that may or may not significantly alter light penetration to ground level. However, in fertile grasslands characterised by a tall and dense grass canopy competition for light is more conspicuous (Soussana and Lafarge 1998). Others have also suggested that extreme temperature fluctuations, induced by grass vegetation, may have dramatic consequences for seedlings survival and growth (Ball et al. 1997; Ball et al. 2002). From these examples we can conclude that in many cases grasses are probably unfavourable to tree establishment and growth.

Pioneer tree species are characterized as having broad physiological responses to environmental variations (Bazzaz 1979; Sands and Nambiar 1984; Caldwell and Richards 1986; Casper and Jackson 1997). Their success despite the presence of grasses can only be realised if they survive and grow by avoiding or tolerating resource depletion. As they are smaller than grasses in their younger stages, it is likely that they must face an asymmetric competition for light and/or symmetric competition for soil resources. Both possibilities have yet to be truly determined, as well as the underlying competition mechanisms that enable seedlings to out compete grasses (Tilman 1987).

In the present experiment we studied Scots pine (*Pinus sylvestris* L.), which is able to rapidly colonize open areas (Hansen et al. 2002; de Chantal et al. 2003) and during the second half of the past century has naturally established in abandoned pastures of the French Massif Central (Bazin et al. 1983; Prévosto et al. 2000). Our main objective was to understand why and how this species (considered a pioneer tree) succeeds in grasslands during secondary succession while other species like beech (*Fagus sylvatica*), a late successional species, does not (Coll et al. 2003; Balandier et al. 2005c). Determination of these mechanisms was achieved by measurements of aerial and below-ground resource acquisition and resource use efficiency of the different competitors. Evaluations were based on plant functional traits (leaf gas exchange, needles bulk $\delta^{13}\text{C}$, SLA, N%), plant growth (height, biomass) and short-term ^{15}N labelling experiments for N mineral acquisition.

Specific questions addressed were:

- To what extent was the intensity of aerial and below-ground resource depletion driven by grass vegetation?
- How did Scots pine seedlings respond to this resource depletion?
- Is the competition between Scots pine seedlings and grass vegetation asymmetric or symmetric and which resource is most affected (light, water or nutrients)?

Materials and methods

Site and experimental plots

In March 2000, a grassland dominated by herbaceous species (mainly grasses) and extensively grazed by sheep prior the experiment was fenced (20 x 20 m²) to prevent predation by wild animals. The experiment was situated in the southern part of the 'Chaîne des Puys' in the French Massif Central (900m a.s.l.; 45°43' N, 2°59' E), where the montane climate experiences oceanic influences (820 mm annual rainfall, 7°C annual mean air temperature). Soil is developed on a substrate of basaltic ash-fall deposits or lava blocks. It is characterised by a loamy silt texture (pH_{water} = 6) with a rich-organic upper horizon (average thickness of 23cm). Scorias appear between 40 and 60 cm deep, which constitute a well-drained layer, whereas the upper horizon presents risk of rapid summer dehydration.

Thirty-six small plots (2 x 2 m²) were established to create four experimental treatments: (1) 'bare soil' created by a glyphosate application (*RoundUp*, Monsanto) and thereafter maintained by manual weeding (six replicates), (2) 'pine (P)' by planting 3 year-old bare rooted Scots pine (*Pinus sylvestris*, St-Bonnet-le-Château Provenance, France) in bare soil (ten replicates), (3) 'pine+vegetation (P+veg)' by planting Scots pine within the grass vegetation (ten replicates) and (4) 'vegetation' corresponding to the natural grass vegetation of the plot (ten replicates).

In the two treatments with pines, five individuals were planted per replicate. The planting occurred late in the season (May 2001) because the first planting (November 2000) failed due to the winter dryness (only 16.4 mm in December 2000).

The replicates were randomly assigned to the four treatments within the site.

Vegetation composition and management

The botanical composition of the vegetation was evaluated in June 2001 in order to quantify the proportion of herbaceous groups. All the species observed in a circle of 50cm diameter in the central area of each replicate were recorded. The vegetation was composed of 61% grasses

(mainly *Arrhenatherum elatius*, *Agrostis capillaris*, *Festuca heterophylla*, *Holcus latanus*, *Dactylis glomerata*, *Poa pratensis*), 26% non N-fixing dicots (*Achillea millefolium*, *Galium verum*, *Taraxacum officinale*) and 13% legumes (*Vicia sativa*, *Trifolium pratense*, *Lathyrus pratensis*, *Lotus corniculatus*).

The herbaceous vegetation was cut with manual battery powered clippers at 6cm height in November 2000 and in March 2002 in order to promote development of grasses that are considered to be the most competitive vegetation group (Grime et al. 1990).

Resources measurements

Soil water content

In February 2001, thin-walled plastic TDR tubes (80cm length, 4cm diameter) were inserted vertically in the soil at 20 cm away from the seedling located in the centre of the replicate. These were used to measure the profile of soil volumetric water content (Hv, %) with a TDR probe (Trime T3, IMKO, Ettlingen, Germany). Because the scoria layer at around 40cm depth disrupts too much the Hv measurement, values were only used from the 0-20 cm layer of the soil. Measurements were done weekly or every two weeks from day of year (DOY) 137 until DOY 225 in six to seven replicates of P, P+veg and vegetation treatments and in three replicates for the bare soil treatment. For each replicate, the mean of three measurements, performed in three different directions, was used for the calculation of Hv. Only the results of 2002 are shown in this paper because those of 2001 showed the same pattern of variation among treatments.

Soil nitrate availability

Ion-exchange resins bags were incubated in treatment soils in 2002 and NO₃⁻ captured on the resins was measured. According to Gloser et al. (2000), 6.19-6.205g of wet mixed bed resin (Amberlite IRN-150, Sigma, France) were placed in nylon mesh bags (5x10cm, mesh size 50 µm). Three (bare soil, P treatments) and four (vegetation, P+veg) bags were buried vertically at 15cm depth at a distance of 20cm from the stem of the central Scots pine seedling in five

replicates of P, P+veg and vegetation treatments and in three replicates of the bare soil treatment. Two sets of bags were incubated for 28 and 22 days, May to June (DOY 136-164, spring) and June to July (DOY 175-197, summer), respectively. After the incubation period, all bags for a given replicate were pooled and the resin washed with 50ml of de-ionised water. Inorganic N was extracted by shaking the resin for five minutes in 100ml of 2M NaCl in 0.1M HCl. The extract was filtered through ashless paper and frozen before determination of NO_3^- with a flow analyser (Aquatec, France). Nitrate exchanged in the resin bag was expressed in $\mu\text{g g}^{-1}$ resin for the two periods.

Light

The photosynthetic active radiation (PAR) was measured with a sunfleck ceptometer (Decagon Devices, Pullman, WA, USA) at three vertical heights, -10cm and -20cm from the apex of the pine and at ground level. The transmitted PAR was calculated as the ratio of PAR measured in the grass vegetation to the incident PAR above the grass vegetation. In the grass vegetation treatment, measurements were only performed at the ground level. Two vertical profiles were performed on either side of the Scots pine seedlings in an East-West orientation, and the mean of these two measurements was used. Measurements were performed at noon (solar time) on cloudless days four times during the 2002 growing season and on ten replicates for each treatment. No measurements were performed in P and bare soil treatments.

Growth measurements and functional traits

Growth and biomass

The heights of the pines and of the grass vegetation were measured weekly during the two growing seasons (April-August 2001 and 2002). For P+veg and grass vegetation treatments, height of the vegetation was measured with a sward stick in a square (25 contact points in 50 x 50 cm) around the central pine or in the centre of the replicate.

In July and December 2002, three and five Scots pine individuals per treatment, respectively, were harvested and oven-dried (60°C for 48 h) for needle, stem and root biomass determination. In the laboratory, needles were sorted by age class (current-, one and two-years old). Projected needle area was measured on sub sample of current- and one-year old needles with an electronic planimeter (LI 3100, Li-Cor, Lincoln, NE, USA). These measurements were used to calculate specific leaf area (SLA, $\text{m}^2 \text{kg}^{-1}$) after needles were oven-dried (60°C for 48 h) and weighed. Roots were washed and separated by diameter class (fine: <2mm; coarse: >2mm). Root to shoot ratio (R/S) was calculated as ratio of root to shoot dry biomass.

Leaf gas exchange

In June (DOY 170 and 177) and July (DOY 200) 2002, leaf net CO_2 assimilation rate (A , $\mu\text{mol m}^{-2} \text{s}^{-1}$) and stomatal conductance for water vapour (g_w , $\text{mmol m}^{-2} \text{s}^{-1}$) were measured *in situ* in natural light conditions (full light conditions, mean PAR = $1527 \pm 36 \mu\text{mol m}^{-2} \text{s}^{-1}$, $n=28$) with an open gas-exchange system (LiCor6400, Lincoln, NE, USA). At noon (solar time), measurements were performed on one-year old needles (11-33 cm^2 projected leaf area) from a lateral shoot. Values were recorded five times during the 20 to 30 minutes period following chamber closure. Thus the mean of five measurements was used for each of the three individuals per treatment. The same individuals were used for each date.

On DOY 177, leaf gas-exchange was also measured on the grass *Dactylis glomerata* located in the replicates of the P+veg treatment. Measurements were performed with the same chamber after the pine measurements. Two fully expanded leaves were chosen (2-4 cm^2) in the vicinity of the pine used in each of three replicates per treatment.

Scots pine isotopic composition of ^{13}C ($\delta^{13}\text{C}$)

Pine needles collected in July and December 2002 were sorted by age class (current-, one- and two-years old), oven-dried (48h, 60°C) and finely milled. Five to seven mg were weighed and

used for carbon isotope composition determination by mass spectrometry (FISONS/ISOCHROM). Results are expressed in δ notation (equation 1), i.e. relative to the Pee Dee Belemnite (PDB) standard:

$$\delta = \left(\frac{R_s}{R_{st}} - 1 \right) \times 1000 \text{ (‰)} \quad (1)$$

where R_s and R_{st} are the molar fractions of ^{13}C to ^{12}C for the sample and the standard, respectively.

Plant N measurements

At the end of June 2002 (DOY 179), one day after a 21mm rainfall, 500mL of $^{15}\text{NH}_4^{15}\text{NO}_3$ (10% isotopic excess) were applied to a 40cm square area centred on a target pine seedling in three replicates each of the P, P+veg and vegetation treatments. This amount of N corresponds to a supply of $0.1875\text{g}^{15}\text{N m}^{-2}$. Twenty-six days later (DOY 205), Scots pine seedlings were collected as well as the vegetation within the labelled area. Most of the pine roots were excavated in each treatment, especially for P+veg where the root system was confined in the first 20cm. However, in P treatment roots expanded horizontally and into deeper layers, thus it was impossible to get the whole root system. For the grass vegetation of each treatment, the roots of the first 40cm of in the soil were collected and washed. All organs of the Scots pines and the grass vegetation were oven-dried (48h, 60°C) and finely milled, and 5-7mg of each sample were analysed for total nitrogen concentration (mass basis) and ^{15}N by mass spectrometry (FISONS/ISOCHROM). Results are expressed as isotopic excess (%), which corresponded to the difference between sample ^{15}N abundance and air ^{15}N abundance (0.3663%). The quantity of absorbed ^{15}N was calculated at the plant level ($\mu\text{g }^{15}\text{N g}^{-1} \text{DW}$).

Data analysis

With a complete random experimental design, variance analysis (ANOVA) was performed using a General Linear Model (Statgraphics Plus, v 4.1, Manugistics, Inc., USA) for all variables to test treatment effects with one (vegetation presence) or two factor(s) (species, vegetation presence). Means were separated from least square deviation method (LSD). Root-to-shoot ratio was log-transformed before ANOVA.

Results

Resources availability

Soil water

Seasonal fluctuations of soil volumetric water content (Hv) of the upper horizon (0-20 cm) were observed with maximum and minimum values in spring and summer periods, respectively (Fig. 1). The bare soil treatment, without or with pine (bare soil and P, respectively), exhibited the highest values of Hv from DOY 176 to 225 ($P < 0.05$) and did not differ from each other except on DOY 212. The presence of grass vegetation (P+veg and vegetation) significantly decreased Hv values on three dates in summer (DOY 176, 204, 225; $P < 0.05$) in comparison with P and bare soil treatments. The two grass vegetation treatments (P+veg, vegetation) had statistically similar values of Hv throughout the 2002 growing season.

Soil NO₃ in ion exchange resin (IER)

The quantity of NO₃⁻ captured by IER was significantly higher ($P < 0.05$) in the bare soil treatment than in other treatments, both in spring and summer, with higher values being recorded in summer (Table 1). Values measured in the P treatment were about 30% lower than in bare soil but six to 13-fold higher than in the treatments with grass vegetation ($P < 0.05$). The P+veg and grass vegetation treatments had similar values of soil IER captured NO₃.

Light

In early spring, PAR transmitted through the vegetation was higher than 85% of incident sunlight even at the ground level (Fig. 2). Thereafter transmitted PAR values measured in the upper part of the Scots pine canopy (-10 and -20cm below stem tip) remained above 70%, while at ground level it decreased to as low as 20% in July (DOY 203). The decline of PAR availability was similar in P+veg and vegetation treatments.

Scots pine and grass vegetation development

Shoot growth occurred from May (DOY 129-136) to June-July (DOY 177-185) for both years (Fig. 3). Pines in the P and P+veg treatments exhibited the same height after growth cessation in 2001, but in 2002 P individuals were slightly taller (+6%, $P<0.05$). In 2001, grass vegetation reached a height of 60cm in June and remained taller than pines through the end of the growing season. This was not observed in 2002, due to grass vegetation being cut in spring and to new Scots pine shoot growth. Thus, Scots pine was smaller than grass vegetation in 2001 but not in 2002.

One year after Scots pines were planted (July 2002), plant biomass was significantly ($P<0.05$) lower by 51% in the P+veg treatment in comparison with the P treatment (Table 2). Five months later, this disparity was even more pronounced (an 85% difference, $P<0.001$). All Scots pine tissues had lower biomass in P+veg treatments than in P treatments, with the exception of roots and two-year old needles in July, however the root-to-shoot ratio was unaffected. Only root biomass increased from July to December in P+veg, mainly because of fine roots biomass increment (almost doubled), whereas in P treatments the biomass markedly increased for all plant tissues (three to five fold) during this period.

Specific leaf area was unaffected by the presence of grass vegetation (Table 2).

Functional traits of Scots pines and grass vegetation

Leaf gas-exchange

Positive relationships were observed among A , g and H_v , while intrinsic water-use efficiency (A/g) increased in response to soil dehydration (Fig. 4). From an absolute viewpoint and for the days of measurement, CO_2 assimilation rate and stomatal conductance in the P+veg treatment were significantly ($P<0.05$) lower than those measured in the P treatment, but the P+veg individuals also experienced lower soil H_v . In contrast, A/g was higher in P+veg seedlings than in P treatment seedlings. For similar H_v values, *Dactylis glomerata* exhibited higher values of A and g whereas A/g was lower than in seedlings of the P+veg treatment.

^{13}C isotopic composition

Values of $\delta^{13}C$ were significantly ($P<0.05$) higher (less negative) in July than in December, for all treatments (Table 3). One-year old needles of the P+veg seedlings had significantly ($P<0.05$) higher (less negative) values of $\delta^{13}C$ in July and December than the P seedlings. For the current year's needles, P+veg pines had higher values only in July (difference of 2.06‰, $P<0.01$).

N uptake

Plant nitrogen concentration, plant excess ^{15}N and ^{15}N -mass of Scots pines were similar between P+veg and P treatments (Table 4). Grass vegetation had more than ten fold greater excess ^{15}N and ^{15}N -mass than pines. Grass vegetation grown in the P+veg treatment had 36% more ($P<0.001$) ^{15}N -mass than grass vegetation grown in the grass vegetation treatment, (i.e., without Scots pine seedlings).

Discussion

Competitive ability of grass vegetation to deplete resources

The effects of grass vegetation on depletion of soil resources have been well documented, especially for water (Caldwell and Richards 1986; Davis et al. 1998; Collet et al. 1996; Calvet

2000; Picon-Cochard et al. 2001; Coll et al. 2003; Coll et al. 2004). In our study the grass vegetation took up most of the available soil water to the detriment of pine seedlings, as indicated by similar P+veg and grass vegetation Hv curves (Fig. 1). Grass vegetation also took up most of the soil nitrogen as demonstrated by their substantially greater $E^{15}N$ values (Table 4). A representative grass species (*D. glomerata*) from these experimental plots also maintained a high CO_2 assimilation rate for low values of Hv in comparison with Scots pine seedlings, enabling a high growth rate under soil water depletion and possibly the ability to continue foraging for new resources.

Certain plant traits contribute greatly to the higher competitive ability for resource acquisition. For grasses, the finely branched, 'herringbone' architecture enables more efficient mobile nutrient acquisition than 'dichotomous' root systems found in species like Scots pine (Fitter 2002). Grasses also exhibit high values of specific root length (SRL, ratio of root length to root mass, data not shown), meaning that they are able to build longer roots for a given dry mass investment. This is achieved by constructing roots of thin diameter or low tissue density (Fitter et al. 1991; Lambers and Poorter 1992; Reich et al. 1998). SRL values of herbaceous species can reach 700 m g^{-1} (Ryser 1996; Arredondo and Johnson 1999; Atkinson 2000; Craine et al. 2001; Nicotra et al. 2002), while that of tree species hardly reached 10-15 m g^{-1} in the case of *Pinus sylvestris* (Curt et al. 2005). This difference of SRL, coupled with differences in root architecture, results in higher root density (per soil volume unit) and spatial distribution of active roots in the upper horizon (Casper and Jackson 1997; Coll et al. 2003; Balandier et al. 2005b). These differences may, in part, explain why grasses are more competitive for soil resources than young trees. Our results for Hv, soil and plant N supported this point of view (Fig. 1, Tables 1 and 4) as well as those reported by other authors (Staples et al. 1999; Hangs et al. 2003; Coll et al. 2004).

By contrast the effect of grass vegetation on competition for light is less clear because of their thin erected leaves and their vertical canopy structure (high leaf angle, $>60^\circ$, Sonohat et al. 2002). Thus, in comparison with shrubs or trees, grasses are often not considered to be strong light competitors (Tournebise and Sinoquet 1995). However, in fertile grasslands, tall and dense vegetation (high LAI) induced competition for light leading to biomass reduction (Teyssonneyre et al. 2002). In our experiment the presence of grass vegetation in the vicinity of Scots pine seedlings greatly reduced light availability (transmitted PAR=20%) in the lower part of the pine (Fig. 2), as also reported by Köchy and Wilson (2000) and Peltzer and Köchy (2001). However, the upper part of pine seedlings received more than 70% of incident PAR.

Growth and functional traits response of Scots pine to depletion of resources

Due to the pre-determined growth of Scots pine (initiation of leaf primordia the year before their elongation) the effect of light competition on growth was delayed by one year (Junttila and Heide 1981). This growth pattern may explain why height of pines in P+veg were unaffected in the first year (2001) (Fig. 3, Table 2). De Chantal et al. (2003) showed that the ratio of height to stem biomass was significantly greater in low light conditions than in high light. Similar results were found in the second year of the present experiment: 0.5 and 2.6 cm g⁻¹ in P (full light) and P+veg (lower light) treatments, respectively (Fig 3 and Table 2). Both light quantity and quality may affect this shift (de la Rosa et al. 1998). Stem morphology is primarily affected by lateral far red-to-red ratio (Aphalo and Lehto 2001) while light quantity may mostly modify leaf morphology and photosynthetic capacity. The upper part of Scots pine (about half of needle surface) received more than 70% of incident PAR, i.e., 1400 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for sunny days conditions. This value is close to the photosynthetic light saturation value for this species measured in field situation (1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$; Luoma 1997). Moreover increase of SLA in response to shade was often reported (Percy and Sims 1994), while in our experimental conditions no statistical differences between treatments were observed (Table 2). Therefore, the

modification of the height-to-stem biomass ratios of our three year-old Scots pines seems to have been more affected by lateral light quality than by light quantity.

Leaf gas-exchange measurements demonstrated the sensitivity of Scots pine to soil dehydration (Fig. 5) as expected in drought avoiding species (Picon et al. 1996). Stomatal closure enabled the species to limit water stress (Fig. 4) and possibly xylem embolism (Cochard 1992) but to the detriment of C gain and growth (Fig. 5, Table 2). Nevertheless stomatal conductance decreased faster than CO₂ assimilation rate and therefore increased intrinsic leaf water-use efficiency (Fig. 5). This result is consistent with measurements of $\delta^{13}\text{C}$ that increased (less negative) in P+veg treatment (Table 3), as expected in response to reduced soil water availability (Farquhar et al. 1989). Carbon isotopic composition may also be modified by soil nitrogen availability because ^{13}C discrimination occurs both during diffusion of CO₂ through stomata and during Rubisco carboxylation. However some authors either reported no change (Hubick 1990) or a decrease of $\delta^{13}\text{C}$ (more negative values) in response to N fertilisation (Bender and Berge 1979; Guehl et al. 1995). In the case of PAR availability, several studies have reported a decrease of $\delta^{13}\text{C}$ (more negative) when PAR was reduced (Vora et al. 1989; Forseth et al. 2001; Staples et al. 2001). However, as pointed out by Farquhar et al. (1989), interpreting the influences of light on $\delta^{13}\text{C}$ under field conditions is confounded by the fact that plants, especially those in the shaded understory, may recycle respired CO₂ that has a different $\delta^{13}\text{C}$ signature than that of the atmosphere (-8‰). As seen in the nitrogen effect on $\delta^{13}\text{C}$ measured in Scots pine of this study, it appears that the PAR effect we measured was also opposite that expected or had no effect at all.

No significant reduction of plant nitrogen concentration was observed between P and P+veg treatments in July (Tables 2, 4) and N absorption, based in ^{15}N excess data, was similar in July for P and P+veg treatments (Table 4). The lack of difference between treatments and the slow N uptake observed in summer could be linked to the fact that the most intensive period of Scots

pine root growth occurs at the end of the growing season (early autumn) after shoot growth ceases (Livonen et al. 2001). Thus in spring and summer Scots pine must acquire soil resources with few new (coarse) roots, and thereby must develop either morphological and/or physiological plasticity to maintain N plant levels. This may be achieved through a number of mechanisms, including the development of more fine roots to increase foraging capacity (but which may be to the detriment of coarse root development; Table 2), increased activity of mycorrhiza which are associated with the finest roots (Eissenstat and Yanai 1997), or increased N recycling from reserves (Temperton et al. 2003). Whatever the involved mechanisms, an adequate nitrogen supply was maintained as indicated by the nitrogen concentration of pine needles ($>1.4\%$) remaining above the value determined by Ingestad and Kähr (1985) to be critical for growth (0.91%), and in the range for optimal growth ($1.2 < N\% < 1.5$) as defined by Bonneau (1988).

Is competition between Scots pine seedlings and grass vegetation asymmetric or symmetric?

Scots pine is considered a high-light requiring species (Keeley and Zedler 1998), while some other authors have suggested dramatic reduction in root growth under low light conditions may make seedlings more vulnerable to additional stresses such as drought (Rundel and Yoder 1998). As such, one might hypothesise that light competition would exist between Scots pine seedlings and surrounding grass vegetation. However, at the development stage of Scots pine considered in this study (3-4 year-old), light was not reduced to a point that compromised pine photosynthesis and growth. Thus only a slight competition for light between pines and grasses could occur. Moreover a morphological acclimation, as indicated by the ratio of height-to-stem biomass (higher for P+veg), suggests also that Scots pine is able to escape competition for light by sensing lateral reflected far red light before the onset of competition for light (Aphalo and Lehto 2001).

Below-ground resources depletion induced by grass vegetation and its effects on pine growth reduction was more evident (Tables 1 and 4, Fig 1). Moreover similar soil volumetric water content in P+veg and grass vegetation treatments (Fig 1) indicates that Scots pine had only a small effect on water availability. The same pattern was recorded for NO₃ captured in IER (Table 1). From these observations we can say that Scots pine had no effect on grasses and at the opposite grasses had a strong effect on pine seedlings. Consequently the competition for below-ground resources between Scots pine seedlings and grass vegetation was asymmetric. Few data on below-ground asymmetric competition have been reported, possibly because below-ground competition is not as intensively studied as aboveground effects such as light (Rajaniemi 2003).

Tolerance of Scots pine to water depletion by physiological plasticity (effective stomatal closure) is one strategy used to overcome below-ground competition. Another strategy that we did not assess here is the capture of resources at different periods of the growing season between competitors owing to differential phenology (Kimberley and Richardson 2004). For example, at certain times of the year, evergreen tree species, like Scots pine, have an advantage over broadleaved species because they can activate during autumn and winter if favourable temperatures are encountered (Ryypö et al 1997, 1998). This is particularly true in extensively managed or abandoned grassland where shading by grasses in winter time is reduced due to important senescent leaves accumulation and therefore a lower canopy height.

Conclusions

Survival and growth of a young pioneer tree species (Scots pine) in grassland vegetation, 3 or 4 years after emergence, was mainly related to its capacity to tolerate marked soil resource depletion, especially for water. If pines succeed in growing through the grass vegetation, the grasses will then be progressively shaded by Scots pine leading to their reduction and

asymmetric competition between grass vegetation and Scots pine will be reversed. However in order to better understand the full dynamics of this secondary succession process, we need more information about the first stage of pioneer tree species development, i.e., emergent seedling (less than one-year old) development. The driver of competition for this stage is generally assumed to be light, but some authors point out that a stable soil moisture regime for radicle development is most critical (Hille and den Ouden 2004). Both have yet to be tested in field conditions.

Acknowledgements:

This project was funded by FNADT and Auvergne Region through the project: “Gestion durable de la végétation dans les espaces de moyenne montagne en cours de colonisation par les ligneux”. We would like to thank JM Vallée, F Landré and A Marquier for their technical assistance and site maintenance, as well as the students C Alexandre and A Gutknecht. We also acknowledge R Falcimagne for the meteorological logistic. Darren Sandquist is greatly acknowledged for useful comments on an earlier version of the manuscript.

References

- Aphalo PJ, Lehto T (2001) Effect of lateral far-red light supplementation on the growth and morphology of birch seedlings and its interaction with mineral nutrition. *Trees* 15: 297-303
- Arredondo JT, Johnson DA (1999) Root architecture and biomass allocation of three range grasses in response to non uniform supply of nutrients and shoot defoliation. *New Phytol* 143: 373-385
- Atkinson D (2000) Root characteristics: why and what to measure In: Smit AL, Bengough AG, Van Noordwijk M, Pellerin S, Van De Geijn SC (eds) *Root methods*. Springer-Verlag, Berlin, pp 1-32
- Balandier P, Collet C, Miller JH, Reynolds PE, Zedaker SM (2005a) Designing forest vegetation management strategies based on the mechanisms and dynamics of crop tree competition by neighboring vegetation. *Forestry* submitted
- Balandier P, De Montard FX, Curt T (2005b) Root competition for water between trees and grass in a silvopastoral plot of ten-year-old *Prunus avium*. In: Batish D (ed) *Agroforestry: Tree-Crop Interactions* Haworth Press, USA, in press
- Balandier P, Guitton JL, Prévosto B (2005c) Forest restoration in the French Massif Central mountains In: Stanturf J, Madsen P (eds) *Restoration of Boreal and Temperate Forests*. CRC Press, pp 355-369
- Ball MC, Egerton JJG, Leuning R, Cunningham RB, Dunne P (1997) Microclimate above grass adversely affects spring growth of seedling snow gum (*Eucalyptus pauciflora*). *Plant Cell Environ* 20: 155-166
- Ball MC, Egerton JJG, Lutze JL, Gutschick VP, Cunningham RB (2002) Mechanisms of competition: thermal inhibition of tree seedling growth by grass. *Oecologia* 133: 120-130

475 Bauer S, Wyszomirski T, Berger U, Hildenbrandt H, Grimm V (2004) Asymmetric competition
 476 as a natural outcome of neighbour interactions among plants: results from the field-of-
 477 neighbourhood modelling approach. *Plant Ecol* 170: 135-145
 478 Bazin G, Larrère GR, de Montard FX, Lafarge M, Loiseau P (1983) *Système agraire et pratiques*
 479 *paysannes dans les Monts Dômes*, INRA éditions, Paris
 480 Bazzaz FA (1979) The physiological ecology of plant succession. *Annu Rev Ecol Syst* 10: 351-
 481 371
 482 Begon M, Harper JL, Townsend CR (1990) *Ecology: individuals, populations, and communities*.
 483 2nd edn. Blackwell Science Publishing, Cambridge, UK
 484 Bender MM, Berge AJ (1979) Influence of N and K fertilization and growth temperature on
 485 $^{13}\text{C}/^{12}\text{C}$ ratios of Timothy (*Phleum pratense* L.). *Oecologia* 44: 117-118
 486 Bonneau M (1988) Le diagnostic foliaire. *Rev For Fr* 40: 19-28
 487 Caldwell MM, Richards JH (1986) Competing root systems: morphology and models of
 488 absorption. In: Givnish TJ (ed) *On the economy of plant form and function*. Cambridge
 489 University Press, Cambridge, UK, pp 251-271
 490 Calvet JC (2000) Investigating soil and atmospheric plant water stress using physiological and
 491 micrometeorological data. *Agric For Meteorol* 103: 229-247
 492 Casper BB, Jackson RB (1997) Plant competition underground. *Annu Rev Ecol Syst* 28: 545-570
 493 Cochard H (1992) Vulnerability of several conifers to air embolism. *Tree Physiol* 11: 73-83
 494 Coll L, Balandier P, Picon-Cochard C, Prévosto B, Curt T (2003) Competition for water between
 495 beech seedlings and surrounding vegetation differing in light availability and vegetation
 496 composition. *Ann For Sci* 60: 593-600
 497 Coll L, Balandier P, Picon-Cochard C (2004) Morphological and physiological responses of
 498 beech seedlings to grass-induced belowground competition. *Tree Physiol* 24: 45-54

499 Collet C, Frochot H, Guehl JM (1996) Growth dynamics and water uptake of two forest grasses
 500 differing in their growth strategy and potentially competing with forest seedlings. Can J Bot
 501 74: 1555-1561

502 Connell JH, Slayter RO (1977) Mechanisms of succession in natural communities and their role
 503 in community stability and organization. Am Nat 111: 1119-1144

504 Connolly J, Wayne P, Bazzaz FA (2001) Interspecific competition in plants: How well do
 505 current methods answer fundamental questions? Am Nat 157: 107-125

506 Craine JM, Froehle J, Tilman DG, Wedin DA, Chapin FS (2001) The relationships among root
 507 and leaf traits of 76 grassland species and relative abundance along fertility and disturbance
 508 gradients. Oikos 93: 274-285

509 Curt T, Coll L, Prévosto B, Balandier P, Kunstler G (2005) Plasticity in growth, biomass
 510 allocation and root morphology in beech seedlings as induced by irradiance and herbaceous
 511 competition. Ann For Sci: in press

512 Davis MA, Wragge KJ, Reich PB (1998) Competition between tree seedlings and herbaceous
 513 vegetation: support for a theory of resource supply and demand. J Ecol 86: 652-661

514 de Chantal M, Leinonen K, Kuuluvainen T, Cescatti A (2003) Early response of *Pinus sylvestris*
 515 and *Picea abies* seedlings to an experimental canopy gap in a boreal spruce forest. For Ecol
 516 Manage 176: 321-336

517 de la Rosa TM, Aphalo PJ, Lehto T (1998) Effects of far-red light on the growth, mycorrhizas
 518 and mineral nutrition of Scots pine seedlings. Plant Soil 201(1): 17-25

519 Eissenstat DM, Yanai RD (1997) The ecology of root lifespan. Adv Ecol Res 27: 1-60

520 Farquhar GD, Ehleringer JR, Hubick KT (1989) Carbon isotope discrimination and
 521 photosynthesis. Annu Rev Plant Physiol Plant Mol Biol 40: 503-537

522 Fitter AH, Stickland TR, Harvey ML, Wilson GW (1991) Architectural analysis of plant root
 523 systems 1 Architectural correlates of exploitation efficiency. New Phytol 118: 375-382

524 Fitter AH (2002) Characteristics and functions of root systems In: Waisel Y, Eshel A, Kafkafi U
525 (eds) Plant roots: the hidden half. Marcel Dekker Publisher, New York, pp 15-32

526 Forseth IN, Wait DA, Casper BB (2001) Shading by shrubs in a desert system reduces the
527 physiological and demographic performance of an associated herbaceous perennial. *J Ecol* 89:
528 670-680

529 Freckleton RP, Watkinson AR (2001) Asymmetric competition between plant species. *Funct*
530 *Ecol* 15: 615-623

531 Gloser V, Jezikova M, Lüscher A, Frehner M, Blum H, Nösberger J, Hartwig UA (2000) Soil
532 mineral nitrogen availability was unaffected by elevated atmospheric pCO₂ in a four year old
533 field experiment (Swiss FACE). *Plant Soil* 227: 291-299

534 Goldberg DE (1990) Components of resource competition in plant communities. In: Grace JB
535 and Tilman D (eds) *Perspectives on Plant Competition*. Academic Press, New York, pp 27-65

536 Grace JB, Tilman D (1990) Perspectives on plant competition: some introductory remarks. In:
537 Grace JB and Tilman D (eds) *Perspectives on Plant Competition*. Academic Press, New York,
538 pp 1-6

539 Grime JP, Hodgson JG, Hunt R (1990) *The abridged comparative plant ecology* Chapman &
540 Hall, London

541 Grime JP (2001) *Plant strategies, vegetation processes and ecosystems properties*. John Wiley &
542 sons Ltd, Chichester, England, 2nd Edition

543 Guehl JM, Fort C, Ferhi A (1995) Differential response of leaf conductance, carbon isotope
544 discrimination and water use efficiency to nitrogen deficiency in maritime pine and
545 pedunculate oak plants. *New Phytol* 131: 149-157

546 Hangs RD, Knight JD, Van Rees KCJ (2003) Nitrogen accumulation by conifer seedlings and
547 competitor species from (15)nitrogen-labelled controlled-release fertilizer. *Soil Sci Soc Am J*
548 67: 300-308

549 Hansen U, Schneiderheinze J, Rank B (2002) Is the lower shade tolerance of Scots pine, relative
 550 to pedunculate oak, related to the composition of photosynthetic pigments? *Photosynthetica*
 551 40: 369-374

552 Harmer R (1996) Growth of seedling tree root-systems in competition with grasses. *Asp Appl*
 553 *Biol* 44: 47-54

554 Hille M, den Ouden J (2004) Improved recruitment and early growth of Scots pine (*Pinus*
 555 *sylvestris* L.) seedlings after fire and soil scarification. *Eur J For Res* 123: 213-218

556 Hubick KT (1990) Effects of nitrogen source and water limitation on growth, transpiration
 557 efficiency and carbon isotope discrimination in peanut cultivars. *Aust J Plant Physiol* 17: 413-
 558 430

559 Ingestad T, Kär M (1985) Nutrition and growth of coniferous seedlings at varied relative
 560 nitrogen addition rate. *Physiol Plantarum* 65: 109-116

561 Junttila O, Heide OM (1981) Shoot and needle growth in *Pinus sylvestris* as related to
 562 temperature in northern Fennoscandia. *For Sci* 27: 423-430

563 Keeley JE, Zedler PH (1998) Evolution of life histories in pines. In: *Ecology and biogeography*
 564 *of Pinus*, DM Richardson (Ed.), Cambridge University Press, Cambridge, UK, pp 219-250

565 Kimberley MO, Richardson B (2004) Importance of seasonal growth patterns in modelling
 566 interactions between radiata pine and some common weed species. *Can J For Res* 34: 184-194

567 Köchy M, Wilson SD (2000) Competitive effects of shrubs and grasses in prairie *Oikos* 91: 385-
 568 395

569 Lambers H, Poorter H (1992) Inherent variation in growth rate between higher plants : a search
 570 for physiological causes and ecological consequences. *Adv Ecol Res* 23: 189-261

571 Livonen S, Rikala R, Vapaavuori E (2001) Seasonal root growth of Scots pine seedlings in
 572 relation to shoot phenology, carbohydrate status, and nutrient supply. *Can J For Res* 31: 1569-
 573 1578

574 Luoma S (1997) Geographical pattern in photosynthetic light response of *Pinus sylvestris* in
 575 Europe. *Funct Ecol* 11: 273-281
 576 McConnaughay KDM, Bazzaz FA (1991) Is physical space a soil resource? *Ecology* 72(1): 94-
 577 103
 578 Nicotra AB, Babicka N, Westoby M (2002) Seedling root anatomy and morphology: an
 579 examination of ecological differentiation with rainfall using phylogenetically independent
 580 contrasts. *Oecologia* 130: 136-145
 581 Pearcy RW, Sims DA (1994) Photosynthetic acclimation to changing light environments: scaling
 582 from the leaf to the whole plant. In: *Exploitation of environmental heterogeneity by plants*,
 583 MM Caldwell and RW Pearcy (eds), Academic Press Inc., San Diego, California, pp 145-174
 584 Peltzer DA, Köchy M (2001) Competitive effects of grasses and woody plants in mixed-grass
 585 prairie. *J Ecol* 89: 519-527
 586 Picon C, Guehl JM, Ferhi A (1996) Leaf gas-exchange and carbon isotope composition
 587 responses to drought in a drought-avoiding (*Pinus pinaster*) and a drought tolerant (*Quercus*
 588 *petraea*) species under present and elevated atmospheric CO₂ concentrations. *Plant Cell*
 589 *Environ* 19: 182-190
 590 Picon-Cochard C, Nsourou-Obame A, Collet C, Guehl JM, Ferhi A (2001) Competition for
 591 water between walnut seedlings (*Juglans regia*) and rye grass (*Lolium perenne*) assessed by
 592 carbon isotope discrimination and $\delta^{18}\text{O}$ enrichment. *Tree Physiol* 21: 183-191
 593 Prévosto B, Curt T, Gueugnot J, Coquillard P (2000) Modeling mid-elevation Scots pine growth
 594 on a volcanic substrate. *For Ecol Manage* 131: 223-237
 595 Rajaniemi TK (2003) Evidence for size asymmetry of belowground competition. *Basic Appl*
 596 *Ecol* 4: 239-247
 597 Rees M, Bergelson J (1997) Asymmetric light competition and founder control in plant
 598 communities. *J Theor Biol* 184: 353-358

599 Reich PB, Walters MB, Tjoelker MG, Vanderklein D, Buschena C (1998) Photosynthesis and
 600 respiration rates depend on leaf and root morphology and nitrogen concentration in nine
 601 boreal tree species differing in relative growth rate. *Funct Ecol* 12: 395-405
 602 Rundel PW, Yoder BJ (1998) Ecophysiology of Pinus. In: Ecology and biogeography of Pinus,
 603 DM Richardson (Ed.), Cambridge University Press, Cambridge, UK, pp 296-323
 604 Ryser P (1996) The importance of tissue density for growth and life span of leaves and roots: a
 605 comparison of five ecologically contrasting grasses. *Funct Ecol* 10: 717-723
 606 Ryypö A, Sutinen S, Mäenpää M, Vapaavuori E, Repo T (1997) Frost damage and recovery of
 607 Scots pine seedlings at the end of the growing season. *Can J For Res* 27: 1376-1382
 608 Ryypö A, Iivonen S, Rikala R, Sutinen ML, Vapaavuori E (1998) Responses of Scots pine
 609 seedling to low root zone temperature in spring. *Physiol Plantarum* 102: 503-512
 610 Sands R, Nambiar EKS (1984) Water relations of Pinus radiata in competition with weeds. *Can J*
 611 *For Res* 14: 233-237
 612 Schwinning S, Weiner J (1998) Mechanisms determining the degree of size asymmetry in
 613 competition among plants. *Oecologia* 113: 447-455
 614 Sonohat G, Sinoquet H, Varlet-Grancher C, Rakocevic M, Jacquet A, Simon JC, Adam B (2002)
 615 Leaf dispersion and light partitioning in three-dimensionally digitized tall fescue-white clover
 616 mixtures. *Plant Cell Environ* 25: 529-538
 617 Soussana JF, Lafarge M (1998) Competition for resources between neighbouring species and
 618 patch scale vegetation dynamics in temperate grasslands. *Ann Zoo* 47: 371-382
 619 Staples TE, Van Rees KCJ, van Kessel C (1999) Nitrogen competition using ¹⁵N between early
 620 successional plants and planted white spruce seedlings. *Can J For Res* 29: 1282-1289
 621 Staples TE, Van Rees KCJ, Knight JD, van Kessel C (2001) Vegetation management and site
 622 preparation effects on C-13 isotopic composition in planted white spruce. *Can J For Res* 31:
 623 1093-1097

624 Temperton VM, Millard P, Jarvis PG (2003) Does elevated atmospheric carbon dioxide affect
625 internal nitrogen allocation in the temperate trees *Alnus glutinosa* and *Pinus sylvestris*? Global
626 Change Biol 9: 286-294

627 Teyssonneyre F, Picon-Cochard C, Soussana JF (2002) How can we predict the effects of
628 elevated CO₂ on the balance between perennial C₃ grass species competing for light ? New
629 Phytol 154: 53-64

630 Tilman D (1985) The resource-ratio hypothesis of plant succession. Am Nat 125: 827-852

631 Tilman D (1987) On the meaning of competition and the mechanisms of competitive superiority.
632 Funct Ecol 1: 304-315

633 Tournebise R, Sinoquet H (1995) Light interception and partitioning in a shrub/grass mixture.
634 Agric For Meteorol 72: 277-294

635 Van Auken OW (2000) Shrub invasions of North American semiarid grasslands. Ann Rev Ecol
636 Syst 31:197-215

637 Vora AB, Patel JA, Punjani BL (1989) Comparative photosynthesis and levels of metabolites in
638 leaves and chloroplasts of sun-adapted and shade-adapted plants of *Achyranthes aspera* Lin. J
639 Environ Biol 10: 159-164

640 Weiner J (1990) Asymmetric competition in plant populations. Tree 5: 360-364

641 Wilson JB (1988) Shoot competition and root competition. J App Ecol. 25: 279-296

Table 1 : Soil nitrate captured by ion exchange resin bags ($\mu\text{g NO}_3^- \text{ g}^{-1}$ resin) incubated (0-15cm) in bare soil, soil with young Scots pine grown without vegetation (P) and with grass vegetation (P+veg) and grass vegetation conditions in spring (DOY 136-164) and summer (DOY 175-197) 2002.

	Bare soil	P	P+veg	Vegetation
Spring	551.1 $\pm$ 66.0 a	378.4 $\pm$ 58.8 b	37.5 $\pm$ 25.4 c	28.9 $\pm$ 12.6 c
Summer	866.2 $\pm$ 19.8 a	257.0 $\pm$ 35.4 b	32.1 $\pm$ 8.4 c	39.9 $\pm$ 11.5 c

Values are means $\pm$ SE. n=5 for P, P+veg and vegetation; n=3 for bare soil. For a given period mean values not sharing the common letters are significantly different (LSD separation, $P \leq 0.05$).

Table 2: Biomass (g) of Scots pine needles age classes, stem, root (fine and coarse) and total plant. Also shown are root shoot ratios (R/S) and specific leaf areas (SLA, m² kg⁻¹) of one year-old and current needles. Comparisons are for Scots pine seedlings grown without vegetation (P) and with grass vegetation (P+veg) in July and December 2002.

	July			December		
	P	P+veg	ANOVA	P	P+veg	ANOVA
Biomass						
Two years old needles	2.8 ± 1.0	3.6 ± 0.6	NS	3.0 ± 0.5	1.2 ± 0.4	*
One-year old needles	5.6 ± 0.5	2.9 ± 0.9	0.06	16.3 ± 2.5	3.9 ± 0.6	**
Current needles	35.1 ± 5.6	12.2 ± 1.9	*	112.4 ± 19.3	12.4 ± 1.6	***
Total Needles	43.5 ± 6.7	18.7 ± 2.6	*	131.7 ± 22	17.5 ± 2.3	***
Stem	37.1 ± 5.7	18.4 ± 1.5	*	112.5 ± 12.3	19.7 ± 3.4	**
Fine root (<2mm)	5.8 ± 1.2	3.3 ± 1.0	NS	21.1 ± 3.3	5.9 ± 1.8	***
Coarse root (>2mm)	10.0 ± 1	7.3 ± 1.1	NS	56.8 ± 7.4	6.8 ± 1.9	***
Total Root	15.8 ± 2.1	10.6 ± 1.7	NS	77.9 ± 9.9	12.7 ± 3.1	*
Plant	96.4 ± 13.9	47.7 ± 4.2	*	322.1 ± 41.4	49.9 ± 8.6	***
R/S	0.20 ± 0.03	0.30 ± 0.06	NS	0.32 ± 0.02	0.34 ± 0.03	NS
SLA _{One-year old needles}	3.23 ± 0.19	3.40 ± 0.17	NS	2.21 ± 0.14	2.73 ± 0.18	NS
SLA _{Current needles}	3.81 ± 0.14	3.29 ± 0.14	0.06	2.31 ± 0.15	2.92 ± 0.38	NS

Values are means ± SE. n=3 and 5 in July and December, respectively. (ANOVA, NS: P>0.05, *: P≤0.05, **: P≤0.01, ***: P≤0.001).

Table 3: Carbon isotope ratios ($\delta^{13}\text{C}$, ‰) of three age classes of needles of young Scots pine grown without vegetation (P) and with grass vegetation (P+veg) in July and December 2002.

	July			December		
	P	P+veg	ANOVA	P	P+veg	ANOVA
Two years old needles	-26.70 ± 0.21	-26.55 ± 0.11	NS	-28.08 ± 0.27	-27.67 ± 0.27	NS
One-year old needles	-26.18 ± 0.36	-24.72 ± 0.2	*	-27.98 ± 0.28	-26.74 ± 0.45	*
Current needles	-26.84 ± 0.03	-24.75 ± 0.34	**	-27.94 ± 0.36	-27.06 ± 0.71	NS

Values are means $\pm$ SE. n=3 and 5 in July and December, respectively. (ANOVA, NS: $P>0.05$, *: $P\leq 0.05$, **: $P\leq 0.01$).

Table 4: Nitrogen concentration (N, %), ^{15}N isotopic excess ($E^{15}\text{N}$, %) and ^{15}N mass ($\mu\text{g } ^{15}\text{N g}^{-1}$ DW) calculated (1) at the plant level (needles, stem and roots) for Scots pine seedlings grown without vegetation (P) and with grass vegetation (P+veg) and (2) at the labelled plot level (0.16m^2) for the surrounding grass vegetation including leaf blades, sheaths and roots. The plots were labelled with $^{15}\text{NH}_4^{15}\text{NO}_3$ (^{15}N excess = 10%) in June 2002 (DOY 179) and harvested 26 days later.

	species	P	P+veg	vegetation	ANOVA
N (%)	Scots pine	1.04 ± 0.04 b	0.90 ± 0.07 b	-	***
	vegetation	-	1.43 ± 0.06 a	1.25 ± 0.05 a	
$E^{15}\text{N}$ (%)	Scots pine	0.074 ± 0.029 b	0.043 ± 0.007 b	-	***
	vegetation	-	0.756 ± 0.034 a	0.619 ± 0.093 a	
^{15}N mass ($\mu\text{g g}^{-1}\text{DW}$)	Scots pine	7.73 ± 3.40 c	3.63 ± 0.61 c	-	***
	vegetation	-	102.82 ± 4.32 a	75.86 ± 11.31 b	

Values are means $\pm$ SE. n=3. For a given parameter mean values not sharing the common letters are significantly different. (LSD separation and ANOVA, ***: $P \leq 0.001$).

Figure legends

Figure 1:

Soil volumetric water content (0-20cm) measured in bare soil, in soil with young Scots pine grown without vegetation (P) and with grass vegetation (P+veg) and in soil with grass vegetation only during the 2002 growing season. Values are means $\pm$ SE, n=6 or 7 for P+vegetation, vegetation and P and n=3 for bare soil.

Figure 2:

Percentage of transmitted photosynthetic active radiation (PAR) measured as ratio of incident PAR above canopy to three height levels from the apical part of the pine to ground level (P+veg) and at ground level for grass vegetation plots during the 2002 growing season. Values are means $\pm$ SE. n=10.

Figure 3:

Height (cm) of Scots pine seedlings grown without vegetation (P) and with grass vegetation (P+veg) and of grass vegetation only of the P+veg treatment during the 2002 growing season. Values are means $\pm$ SE. n=10. Arrow corresponds to the annual cut of the grass vegetation in early spring.

Figure 4:

Relationships between leaf carbon dioxide assimilation rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$), leaf conductance ($\text{mmol m}^{-2} \text{s}^{-1}$), leaf intrinsic water use efficiency (mmol mol^{-1}) and soil volumetric water content at 0-20cm (%) in Scots pine seedlings grown without vegetation (P) and with grass vegetation (P+veg) and for one of the most abundant grass species of the plot (*Dactylis glomerata*). Measurements were performed on DOY 170, 177 and 200 in year 2002 for Scots pine and on

741 DOY 177 for grass species. Each symbol corresponds to one replicate, with three replicates per
742 treatment.

Figure 1

Figure 2

Figure 3 :

777 Figure 4 :

778