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## RESEARCH ARTICLE

# Response of *Araucaria angustifolia* seedlings to root competition in three different plant communities of southern Brazil

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The mixed rainforests in southern Brazil are characterised by the presence of a canopy-emergent conifer, *Araucaria angustifolia*. Experiments were conducted to test the hypotheses that root competition reduces establishment and growth of *A. angustifolia* in a grassland, *Pinus* plantation and native forest, and that root competition is more pronounced in the two former communities than in the latter. Seedlings were grown in grassland under three neighbourhood conditions: no neighbours; neighbour roots; and neighbour shoots and roots. In the native forest and *Pinus* sites, soil trenching was used to alleviate root competition. Plant survival was little affected by treatments and was higher in the *Pinus* site (77%) than in the others, where ant herbivory (grassland) and pathogens (native forest) caused low survival (46% and 43%, respectively). Plant growth was increased by relief from shoot competition in the grassland and by trenching in the *Pinus* site.

**Keywords:** Brazilian pine; forest regeneration; *Pinus elliottii*; seedling ecology; seedling growth; tree establishment

## Introduction

Plant–plant interactions influence the ultimate outcome of establishment and survival of tree species in plant communities (Buckley et al. 1998; Lewis & Tanner 2000; Vandenberghe et al. 2006), and represent a mechanism of maintenance of species diversity (Chesson 2000). These interactions are complex, comprising a mixture of positive and negative effects, and involving several mechanisms (Holmgren et al. 1997; Maestre et al. 2003; Weigelt et al. 2007). Plant competition, an interaction with mutual negative effects (Connell 1990), may operate belowground through depletion of soil resources (Tilman 1990; Shainsky & Radosevich 1992). In order to study belowground competition among plants, one needs to examine the neighbour negative effects on the availability of a given soil resource and the response of the target plant to the depletion of this resource (Goldberg 1990).

In the southern highland plateaus of Rio Grande do Sul, Brazil, the native vegetation is mostly represented by a mosaic of forest islands and surrounding grasslands and, less often, by continuous forests. The grasslands are relicts of a cooler and drier climate in that region, where managed fires and cattle grazing are common present-day practices (Behling & Pillar 2007). The forest component of this vegetation has *Araucaria angustifolia* (Bertol) Kuntze (Araucariaceae) as its more conspicuous tree species, because of its great number and size and its emergent status in the upper canopy. Such forests are known as mixed ombrophylous forests (Pastore et al. 1986), mixed rain forests or, simply, *Araucaria* forests. The high-quality wood of *A. angustifolia* was heavily exploited, mainly in the first half of the twentieth century. This almost decimated this species within Brazil (Koch & Corrêa 2002), and, because of the small size and high degree of

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fragmentation of the remaining populations, this species is today classified as Critically Endangered (Farjon 2006). Because it is wind pollinated, the reduction in population size and the increased distance among populations has led to a reduction in genetic diversity (Patreze & Tsai 2010). Restoring populations will require introducing new individuals to degraded forests and deforested areas. The success of such an action will depend, among other factors, on a profound knowledge of ecological and physiological aspects that are relevant for the natural regeneration and establishment of planted individuals.

The expansion of the *Araucaria* forests into adjacent grasslands is currently a natural process (Oliveira & Pillar 2004), and Klein (1960) indicated that *A. angustifolia* is one of the first tree species to colonise grasslands. More recently, isolated trees growing in grasslands have been shown to play an important role as nurse plants for other forest species (Duarte et al. 2006; Korndörfer et al. 2014). In the colonisation process, tree–grass competition seems to be a limiting factor to the establishment of trees. Such competition can be particularly intense when trees are still seedlings (Davis et al. 1999; Espigares et al. 2004), because seedlings explore mostly the upper layers of soil, where grasses display higher rooting densities (Knoop & Walker 1985; Scholes & Archer 1997). The dense and thin root system and the high root:shoot ratio of grasses can confer on them a competitive advantage for soil resources over tree seedlings, which typically have coarser and less dense root systems and also lower root:shoot ratios (Caldwell & Richards 1986; Tilman 1988). Indeed, grasses were shown to reduce tree seedling survival and growth through belowground competition in abandoned tropical pasture, semi-arid and savanna environments (Davis et al. 1999; Espigares et al. 2004; Wakeling et al. 2014). Aboveground competition from grasses depends largely on grassland management (e.g. grazing and burning), as well as on grass life form. Shading of tree seedlings by tussock grasses has resulted in strong reductions of tree growth (Holl 1998). At the seedling stage, the abundant seed reserves of *A. angustifolia* have fundamental importance in promoting early and fast stem elongation (Einig et al. 1999) and in escaping from aboveground competition

from tussock grasses (Laharrague 1967). However, there is little background information on plant–plant interactions in this ecosystem, and the responses of *A. angustifolia* to the competitive interactions with grasses, as forest encroachment takes place, are mostly unknown.

Other ongoing human activities are also resulting in major vegetation and landscape changes in the focus ecosystem. Deforested areas and adjoining grasslands have been extensively planted with the exotic, fast-growing tree species *Pinus taeda* L. and *P. elliottii* Engelm., two invasive species (Rejmánek & Richardson 1996). Because of their high demand for soil resources (La Bastide & Van Goor 1970; Cuevas et al. 1991), these exotic pines are expected to exert strong competitive effects on *A. angustifolia*. Besides competing with native species (Walck et al. 1999; Corbin & D'Antonio 2004), exotic tree plantations can also act as nurse crops for the colonisation of indigenous plants (Harrington & Ewel 1997). In fact, in the area where the present study was conducted, forest management allowed the colonisation of a great number of native tree species in *Pinus* plantations, including *A. angustifolia* (Duarte et al. 2002; Garbin et al. 2006). However, the impact of belowground interactions with these exotic species on the establishment and growth of native species has not yet been addressed.

Besides colonising these two different environments (grasslands and *Pinus* plantations), *A. angustifolia* also exhibits some degree of self-regeneration in native forests. Its regeneration follows the pattern of recalcitrant-seeded species (Augsburger 1984): early and fast seed germination, and establishment of a seedling bank of shade-tolerant, slow-growing individuals, which will grow quickly to the upper canopy as soon as a gap is formed and light becomes more highly available (Duarte et al. 2002). Many studies have emphasised the importance of light to seedling survival in tropical forests (Augsburger 1984; Denslow et al. 1990, 1991). However, despite the low regeneration of *A. angustifolia* in native forests, Duarte et al. (2002) did not find an association between the degree of regeneration and the level of irradiance when comparing different understory environments. Competition for

belowground resources can also play an important role on tree regeneration in the forest understory, as demonstrated in some trenching studies in temperate (Horn 1985; Riegel et al. 1992), subtropical (Verkaik et al. 2007) and tropical (Coomes & Grubb 1998; Lewis & Tanner 2000) forests. No study up to this date has looked at the intensity of root competition and its effects on the establishment and growth of regenerating individuals in the understory of Brazilian subtropical mixed rain forests.

The goal of this study was to examine the effects of plant competition (particularly at the root level) on *A. angustifolia* seedlings, a species which is involved in three different processes: grassland and exotic crop colonisation, and forest regeneration. We evaluated the growth responses and survival of *A. angustifolia* to below and aboveground competition in grasslands, as well as to belowground competition in a *Pinus* plantation and in a native *Araucaria* forest. The experimental approach we used was neighbour exclusion by trenching in the forests and total or partial removal of herbaceous plants in the grassland. Neighbour effects on soil resources were evaluated by comparing water and nutrient contents between different neighbour removal treatments. We hypothesised that: (1) root competition limits seedling growth and establishment of *A. angustifolia* in the grasslands, *Pinus* plantation and native forest; and (2) that the negative effects of root competition are more pronounced in the grassland and *Pinus* plantation than in the native forest. This second hypothesis is based on the premises that roots of tree seedlings will most likely explore the same soil layers as do grasses, and that the vigorous and aggressive growth of *Pinus elliottii* will result in more intense root competition than that in a mature *Araucaria* forest.

### Study sites

The study was conducted at the São Francisco de Paula National Forest (29°24' S and 50°22' W; 912 m above sea level) located in the city of São Francisco de Paula, Rio Grande do Sul, Brazil. The annual rainfall is around 2469 mm, and no dry

season is present (Mota 1951). The annual mean temperature is about 14.5 °C, and the means of the highest and lowest monthly temperatures are 20.3 °C and 9.9 °C, respectively. The soils in the region are cambisols, characterised by acidic pH (4.4 in water), and high levels of exchangeable Al and organic matter (Fernandes & Backes 1998).

The vegetation in the national forest is mostly comprised of plantations of *A. angustifolia*, exotic tree plantations (*Pinus taeda*, *P. elliottii* and *Eucalyptus* spp.), native forests with *A. angustifolia* and small areas of native grasslands (without management). Stands of a *Pinus* plantation and a native forest, as well as a grassland area, were chosen for this study. These three sites will be named hereafter 'Pinus', 'native forest' and 'grassland', respectively. In all three communities, recruitment of new individuals of *A. angustifolia* was taking place.

The grassland site was located about 0.3 km from the native forest site, and both were about 1 km away from the *Pinus* site. The sites strongly differed in plant composition and structure. The grassland was characterised by the presence of *Andropogon lateralis* Nees (Poaceae), *Senecio* spp., *Bacharis* spp. (Asteraceae), *Eryngium* sp. (Apiaceae), among others. Vegetation height was 0.5 to 0.8 m and was not under the influence of burning and cattle grazing. Scattered saplings of *A. angustifolia* were found there. The *Pinus* site was a 10-year-old, 15 m tall, timber-harvest plantation located in an area formerly occupied by native grassland. It was intensively colonised by young plants (height c. 20 cm) of *A. angustifolia*, *Podocarpus lambertii* Klotz. (Podocarpaceae) and species of Myrtaceae and Melastomataceae. The native forest site had not experienced major disturbance for a long time and was 20 m tall. *Araucaria angustifolia* emerged from the upper canopy, which was mostly composed of *P. lambertii* (Podocarpaceae), *Ilex* spp. (Aquifoliaceae), *Roupala brasiliensis* Klotz. (Proteaceae) and several species of Myrtaceae. In the herb layer, *Piper* spp. (Piperaceae), *Stillingia oppositifolia* Baill (Euphorbiaceae), *Mollinedia elegans* Tull. (Monimiaceae), *Myrciaria* spp. (Myrtaceae) and many tree seedlings (including *A. angustifolia*) were present.

## Methods

### *Experimental designs and plant survival*

#### *Competition in grasslands*

Field competition experiments in the grassland site lasted 9 months (August 2004 to May 2005), and seedlings of *A. angustifolia* were transplanted and tracked under three neighbourhood conditions, each one comprising 10 experimental units: no neighbours (NN), neighbour roots (NR) and neighbour shoots and roots (NSR). Three pre-germinated seeds were planted and enclosed inside a cone made with 3 cm mesh chicken-wire. These cones, which were 50 cm high and had top and bottom diameters of 30 and 10 cm, respectively, were used to protect the growing seedlings from predation and also to manipulate the shoots of the neighbouring vegetation (Belcher et al. 1995). In the NSR treatment, the surrounding vegetation was maintained intact. In the NR treatment, the aboveground parts of the surrounding vegetation (mostly tall grasses) were guided to the outside of the cone and bent down. In the NN treatment, the aboveground parts of the surrounding vegetation were fully removed (clipped) from a 1 m × 1 m area around the cone. In this case, the removed biomass was placed on top of the bare soil to reduce soil water evaporation. The experimental units were 4 m apart from each other. Due to high incidence of ant herbivory in the grassland area, all three plants in each cone were kept throughout the experimental period. A previous experiment had been conducted from September 2002 to July 2003, where only one plant was kept inside the cone. Due to the major damage inflicted by ants to this single plant (which resulted in 75% mortality), the results were discarded and the experiment repeated.

Plant survival was computed at the end of the experiment in the grassland site (9 months). Because there was no plant removal within the experimental plots, the total number of plants we surveyed for each treatment was 30.

#### *Belowground competition in forests*

Competition experiments in the two forest sites lasted 34 months (from planting in July–August

2002 to harvest in May–June 2005). Soil trenching was used to alleviate root competition with newly planted *A. angustifolia* seedlings. Ten pairs of 1 m × 1 m plots, approximately 5 m apart from each other, were systematically placed in the native forest and *Pinus* sites. In the native forest, we maintained a minimum distance of 3 m between each plot and the nearest mature neighbour tree. In the *Pinus* site, plots were established in the centre of the square defined by four mature planted pine trees. Visual soil topography and leaf area index (LAI) above the plots were as similar as possible within each pair (see section ‘Estimates of leaf area index’ for description of LAI measurements). One plot of each pair was maintained intact (untrenched, UT), and the other was trenched (T) along the sides. Trenches (20 cm wide and 30 cm deep) were dug with a pickaxe and a shovel. Vegetation within the trenched plots was removed by clipping the aboveground parts or pulling the whole plant when possible. During the experiment, trenches were maintained with a shovel every 2 months. Pre-germinated seeds of *A. angustifolia* were planted in groups of four in each plot, with one plant at each corner of a central 50 cm × 50 cm square within the 1 m × 1 m plot. The four growing seedlings of each plot were protected from predation with a cage (50 cm × 50 cm × 70 cm) made of 3 cm mesh chicken-wire. By the end of the first year (September–October 2003), the three smallest of the four planted seedlings were removed from all plots, in both forest sites.

In the *Pinus* and native forest sites, the number of plants surviving 11 months after the beginning of the experiment was computed. This happened just before plant thinning. In this case, the number of plants surveyed for each site and treatment was 40. Six (native forest) and one (*Pinus*) additional deaths occurred after the survival evaluation period, but these deaths were not computed in the survival data.

#### *Seed and seedling sources*

The *A. angustifolia* seeds were obtained from local gatherers in São Francisco de Paula, Rio Grande do Sul. Seeds with 7–8 g of fresh mass were selected, disinfected with a 2.5% solution of sodium hypochlorite (NaClO) for 20 min, and then

thoroughly rinsed in distilled water. The upper third (radicle-protruding region) of the seed had its external integuments removed to speed germination (Áquila & Ferreira 1984), which took place in plastic trays with wet vermiculite, under laboratory conditions. Pre-germinated seeds (radicles 1.5–3.0 cm long) were transplanted to the native forest and *Pinus* sites in July and August 2002, and to the grassland site in August 2004. Only the radicle was buried in the soil, while the seed remained at the soil surface.

### *Plant measurements*

On a monthly or bimonthly basis, total shoot length (height + length of lateral branches) was recorded. At the end of the experiments, plants were harvested for additional measurements: leaf mass per area (LMA), shoot and root masses, and chlorophyll content. Plants were harvested by cutting and removing a soil block (50 cm × 50 cm × 40 cm) from around the plant (s). With the aid of running water and tweezers, roots were carefully extracted from the soil block. About 10 internode lengths were measured along the main shoot region, right below the first whorl of branches. Lateral root and main root lengths were obtained through root images from four selected plants in each treatment. The root system was separated into lateral and main roots and then spread in blue paper for better contrast, with a L scale of 30 × 30 cm, graduated every 1 cm. Root images were captured with a digital, 5.1 mega pixels-resolution camera (DSC-P100; Sony Corp. Tokyo, SKD, Japan). Root lengths were measured with SigmaScan<sup>®</sup> Pro 5.0 (SPSS Inc., Chicago, IL, USA). Roots were oven-dried at 75 °C, weighed, and the specific root length (SRL) was computed. Ten mature leaves were taken from the first whorl of branches for measurements of LMA. Leaf digital images were captured with a digital, 5.1 mega pixels-resolution camera, and a L scale (5.5 cm × 5.5 cm), graduated every 0.5 cm, was added to the images. Leaf area was then calculated with SigmaScan<sup>®</sup> Pro 5.0. Leaves were oven-dried at 75 °C, weighed and LMA was computed. Ten additional young, fully expanded leaves, collected from the upper branches, had their area measured as previously described and were then

immersed in black vials containing 100% ethanol for chlorophyll extraction. Prior to immersion, leaves were softly sandpapered to facilitate ethanol penetration through the cuticular layer. Extraction took place at room temperature during a 1-month period (Knudson et al. 1977). Chlorophylls were spectrophotometrically quantified (Brastectro, SP—220), with absorbance readings at 649 and 665 nm wave lengths, and chlorophyll contents ( $\mu\text{g mL}^{-1}$  of solution) calculated according to Wintermans & DeMots (1965). Leaf chlorophyll concentrations were then expressed on an area basis. All major plant parts (shoot, main root and lateral roots) had their oven-dried (75 °C) masses evaluated, and these were used to compute the mass ratio between root and shoot.

### *Soil and foliar measurements*

#### *Soil chemistry and moisture*

At the end of each field experiment, 2 cm diameter soil cores were collected between 0 and 20 cm depth (litter layer excluded), 50–60 cm away from the *A. angustifolia* plants, for chemical analyses. These were conducted in the Analyses Laboratory of the Soil Department of the Federal University of Rio Grande do Sul, and included pH, organic matter (OM), cation exchange capacity (CEC), base and Al saturation of CEC, and P, K, Ca, Mg and Al concentrations. Acidity (pH) was measured in water solution (1:1, v/v); determinations of P and K were based on the Mehlich I method; OM was obtained by sulfocromic solution oxidation with external heat; exchangeable Al was extracted with KCl 1 mol L<sup>-1</sup>, and S–SO<sub>4</sub> with CaHPO<sub>4</sub> 500 mg L<sup>-1</sup> of P (Tedesco et al. 1995). Additional soil samples were also collected every 3 months, as previously described, for measurements of gravimetric water content (GWC). Average values of GWC across all months within each of two seasons (fall/winter and spring/summer), and for each treatment and site, are reported.

#### *Foliar nutrients*

To reduce costs, the experimental units were grouped into three compound samples for the following

chemical analyses of the plant shoots: C, N, P and K tissue concentrations. All analyses were performed by the Analyses Laboratory of the Soil Department of the Federal University of Rio Grande do Sul, following techniques described in Tedesco et al. (1995). Nitrogen was determined by semi-micro-Kjeldahl analysis; P was determined spectrophotometrically, and K by flame spectrophotometry. Carbon was determined by oxidation with dichromate in acid medium, followed by titration of the excessive  $\text{Cr}^{6+}$ .

### *Estimates of leaf area index*

Leaf area index above the experimental plants was estimated with a plant canopy analyser (LI-2000; Li-Cor Inc., Lincoln, NE, USA), horizontally placed at seedling level. Measurements were taken in four directions (north, south, east and west) with the 90° view cap, which helped to hide the operator and to restrict the sensor's field of view. For each below-canopy reading, an above-canopy reading was made in an open field area. Readings were taken in the winter, spring, summer and fall of 2003.

### *Statistical analyses*

Due to the high plant mortality, the blocks initially planned for analysing the data in the native forest site were abandoned and data from all sites ended up being analysed according to a completely randomised design. One-way analysis of variance (ANOVA) within each site was used to determine the competition effects on plant and soil parameters and to compare LAI among treatments within each season. Two-way ANOVAs were used to compare soil GWC between treatments and seasons within each site. In all cases, Tukey's test was used for mean comparisons and the experimental units were the group of plants in each plot. In the forest sites, only one plant made up the experimental unit after plant thinning occurred. The above analyses were performed by SigmaStat 3.5. Binary survival data were analysed through ANOVA with randomisation test (Pillar & Orlóci 1996), using the statistical program MultivMinor v.2.3.17 (Pillar 2004). Because a dissimilarity matrix is needed for computing the ANOVA, the Euclidean distance was

used. Plant survival in the grassland was compared among treatments through one-way ANOVA and orthogonal contrasts. A two-way ANOVA, followed by mean comparisons through orthogonal contrasts, was used to test for site and treatment effects on plant survival in the *Pinus* and native forest. Survival in the grassland site was not compared to the other two sites because of important differences in the overall design between this site and the other two. A 5% level of significance was used in all analyses, but differences associated with levels of significance which approached this value (< 10%) were reported as trends.

## **Results**

### *Treatment effects on soil and canopy environments*

#### *Competition in grasslands*

In the grassland experiment, total neighbour removal (NN) was associated with soils with higher saturation of Al ( $F_{2,6} = 11,84$ ,  $P = 0.007$ ) and lower saturation of bases ( $F_{2,6} = 8.45$ ,  $P = 0.015$ ) of the CEC than soils in the NSR treatment (Table 1). The GWC of the soil was not affected by season (fall/winter vs. spring/summer), but was significantly reduced in the NN ( $0.56 \pm 0.018$  in fall/winter and  $0.54 \pm 0.009$  in spring/summer) treatment compared to NSR ( $0.64 \pm 0.013$  in fall/winter and  $0.70 \pm 0.012$  in spring/summer) and NR ( $0.66 \pm 0.011$  in fall/summer and  $0.69 \pm 0.009$  in spring/summer;  $F_{2,308} = 68.15$ ,  $P < 0.001$ ). As expected, the LAI above the experimental plants was significantly higher in the NSR in all seasons (winter,  $3.84 \pm 0.31$ ,  $F_{2,28} = 32.36$ ,  $P < 0.001$ ; spring,  $4.14 \pm 0.18$ ,  $F_{2,28} = 280.60$ ,  $P < 0.001$ ; summer,  $5.07 \pm 0.26$ ,  $F_{2,28} = 235.78$ ,  $P < 0.001$  and fall,  $6.09 \pm 0.19$ ,  $F_{2,28} = 237.20$ ,  $P < 0.001$ ) than in NR (winter,  $0.50 \pm 0.25$ ; spring,  $0.42 \pm 0.06$ ; summer,  $0.70 \pm 0.12$ ; and fall,  $0.28 \pm 0.04$ ) and NN (winter,  $0.98 \pm 0.32$ ; spring,  $0.15 \pm 0.01$ ; summer,  $0.31 \pm 0.06$ ; and fall,  $0.18 \pm 0.02$ ) treatments.

#### *Belowground competition in forests*

Trenching and season (fall/winter vs. spring/summer) did not affect soil GWC in the forest sites, with

**Table 1** Soil chemistry and shoot nutritional analyses for the different sites and competition treatments. Experiments lasted 5 months in the grassland and 34 months in the forest sites.

	Grassland			<i>Pinus</i>		Native forest	
	NSR	NR	NN	UT	T	UT	T
<i>Soil chemistry (n = 10)</i>							
pH (H <sub>2</sub> O)	4.53 ± 0.12 <sup>a</sup>	4.43 ± 0.09 <sup>a</sup>	4.37 ± 0.03 <sup>a</sup>	4.37 ± 0.03 <sup>a</sup>	4.33 ± 0.07 <sup>a</sup>	4.45 ± 0.05 <sup>a</sup>	4.38 ± 0.05 <sup>a</sup>
Organic matter (%)	>10	>10	>10	9.70 ± 0.25 <sup>a</sup>	9.43 ± 0.42 <sup>a</sup>	9.88 ± 0.13 <sup>a</sup>	9.33 ± 0.29 <sup>a</sup>
Al+H mequiv/100g	28.50 ± 1.10 <sup>b</sup>	33.17 ± 1.23 <sup>a</sup>	33.17 ± 1.23 <sup>a</sup>	35.80 ± 1.40 <sup>a</sup>	35.80 ± 1.40 <sup>a</sup>	34.53 ± 1.61 <sup>a</sup>	36.75 ± 2.72 <sup>a</sup>
CEC mequiv/100g	32.30 ± 1.06 <sup>a</sup>	36.60 ± 1.11 <sup>a</sup>	35.53 ± 1.22 <sup>a</sup>	37.03 ± 1.36 <sup>a</sup>	37.53 ± 1.10 <sup>a</sup>	38.95 ± 1.41 <sup>a</sup>	39.45 ± 2.23 <sup>a</sup>
% Base saturation	11.33 ± 1.33 <sup>a</sup>	9.00 ± 0.58 <sup>ab</sup>	6.33 ± 0.33 <sup>b</sup>	3.00 ± 0.58 <sup>a</sup>	4.33 ± 0.88 <sup>a</sup>	11.00 ± 1.23 <sup>a</sup>	6.75 ± 2.25 <sup>a</sup>
% Al saturation	61.45 ± 2.89 <sup>b</sup>	68.43 ± 2.66 <sup>ab</sup>	77.33 ± 0.77 <sup>a</sup>	87.50 ± 2.43 <sup>a</sup>	83.07 ± 3.70 <sup>a</sup>	58.25 ± 4.20 <sup>a</sup>	75.15 ± 6.49 <sup>a</sup>
Al (mg dm <sup>-3</sup> )	7.93 ± 0.18 <sup>a</sup>	7.43 ± 0.46 <sup>a</sup>	6.07 ± 0.20 <sup>b</sup>	8.30 ± 0.27 <sup>a</sup>	8.40 ± 0.40 <sup>a</sup>	6.18 ± 0.50 <sup>a</sup>	8.08 ± 0.66 <sup>a</sup>
P (mg dm <sup>-3</sup> )	7.73 ± 0.61 <sup>a</sup>	7.33 ± 0.54 <sup>a</sup>	5.73 ± 0.37 <sup>a</sup>	9.33 ± 2.51 <sup>a</sup>	5.57 ± 0.23 <sup>a</sup>	13.20 ± 2.99 <sup>a</sup>	8.38 ± 0.90 <sup>a</sup>
K (mg dm <sup>-3</sup> )	217.33 ± 32.73 <sup>a</sup>	171.68 ± 25.47 <sup>a</sup>	145.33 ± 20.28 <sup>a</sup>	80.33 ± 13.5 <sup>a</sup>	62.67 ± 8.41 <sup>a</sup>	141.50 ± 15.80 <sup>a</sup>	110.25 ± 14.26 <sup>a</sup>
<i>Shoot nutrients (n = 3)</i>							
C (%)	44.67 ± 0.67 <sup>ns</sup>	45.67 ± 0.33	46.00 ± 0.58	–	–	–	–
N (%)	1.20 ± 0.06 <sup>a</sup>	0.68 ± 0.05 <sup>c</sup>	0.87 ± 0.05 <sup>b</sup>	0.48 ± 0.03 <sup>b</sup>	0.62 ± 0.03 <sup>a</sup>	1.33 ± 0.12 <sup>a</sup>	1.40 ± 0.15 <sup>a</sup>
C:N	37.35 ± 1.38 <sup>c</sup>	67.78 ± 4.53 <sup>a</sup>	53.18 ± 2.50 <sup>b</sup>	–	–	–	–
P (%)	0.32 ± 0.02 <sup>a</sup>	0.15 ± 0.01 <sup>b</sup>	0.10 ± 0.01 <sup>b</sup>	0.13 ± 0.01 <sup>a</sup>	0.16 ± 0.01 <sup>a</sup>	0.27 ± 0.05 <sup>a</sup>	0.28 ± 0.06 <sup>a</sup>
K (%)	1.77 ± 0.03 <sup>a</sup>	0.77 ± 0.03 <sup>b</sup>	0.86 ± 0.13 <sup>b</sup>	0.62 ± 0.05 <sup>b</sup>	0.77 ± 0.02 <sup>a</sup>	1.50 ± 0.17 <sup>a</sup>	1.60 ± 0.17 <sup>a</sup>

Means (± SED) with different letters within each site are significantly different ( $P \leq 0.05$ ).

NSR, neighbour shoots and roots; NR, neighbour roots; NN, no neighbours; UT, untrenched; T, trenched.



values ranging from 0.52 to 0.55 in the *Pinus* site and from 0.62 to 0.66 in the native forest. Overall, LAIs above seedlings were very similar in trenched and untrenched plots in both sites and in all four seasons. As expected, there were seasonal variations in LAI in the *Pinus* site: values of LAI ranged from 3.35 in the winter to 4.55 in the summer, while in the native forest this range was from 2.35 to 4.50.

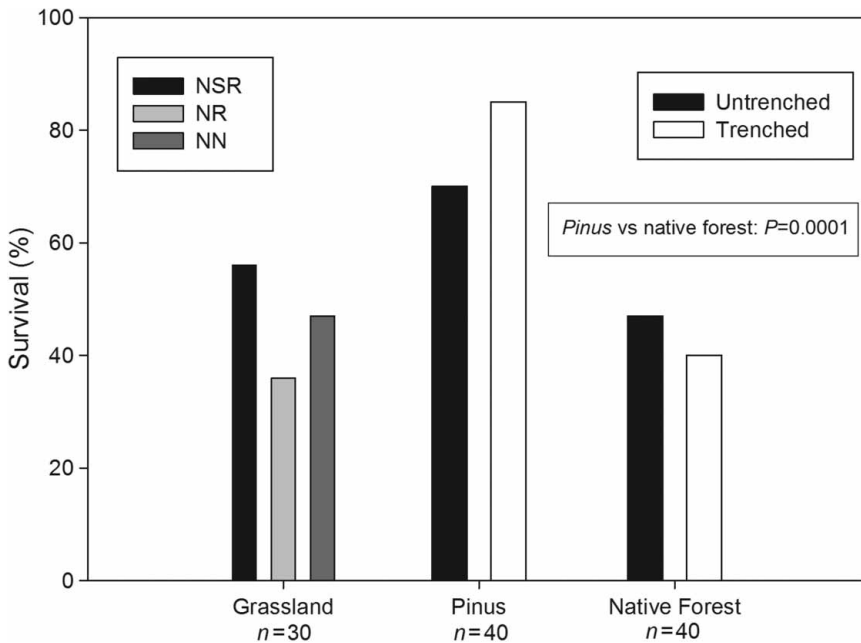
### Plant survival and growth

#### Competition in grasslands

No significant differences in plant survival among treatments were present in the grassland site (Fig. 1). At the end of the experiments, the number of plants remaining was five, four and six for NN, NR and NSR, respectively. The high mortality in the grassland was due to ant herbivory, caused by *Acromyrmex crassispinus* and *Atta* sp.

Total shoot length (TSL) was significantly greater in the NSR than in the NR and NN plants, throughout most of the experimental period (Fig. 2A; fifth measurement had  $F_{2,24} = 12.11$ ,  $P = 0.0002$ ). However, by the end of the experimental period, when plants were about 25 cm tall, no significant differences were detected, despite a visible trend towards a greater shoot growth of the NN plants.

Dry mass accumulation by different plant parts was generally greater in plants growing under full neighbour removal (NN) than in those surrounded by shoots and roots of neighbouring plants (NSR). Plant growing under the impact of neighbour roots (NR) accumulated mass in a similar way to the NN plants, and had greater root mass than the NSR plants (Table 2; total mass,  $F_{2,14} = 11.35$ ,  $P = 0.002$ ; shoot mass,  $F_{2,14} = 8.69$ ,  $P = 0.005$ ; root mass,  $F_{2,14} = 14.97$ ,  $P < 0.001$ ). As the degree of vegetation removal increased in the grassland site



**Figure 1** Plant survival under different treatments and in different sites. Experiments lasted 5 months in the grassland and 34 months in the forest sites.

There were no significant differences between treatments at any given site. Only the two forest sites (*Pinus* and native forest) were statistically compared ( $P$  value is indicated in the graph).

NSR, neighbour shoots and roots; NR, neighbour roots; NN, no neighbours; UT, untrenched; T, trenched.

(NSR→NR→NN), so did the investment in lateral root ( $F_{2,9} = 5.34$ ,  $P = 0.03$ ). Plants in the NR treatment showed a trend towards a greater root:shoot ratio (Table 2) than those in the other two treatments ( $F_{2,11} = 3.68$ ,  $P = 0.06$ ). Vegetation removal in the grassland site led to increases in LMA (only in NN plants;  $F_{2,12} = 28.42$ ,  $P < 0.001$ ).

#### Belowground competition in forests

In the *Pinus* site (Fig. 2B), the trenched plants had a greater TSL (eighth measurement had  $F_{1,60} = 101.62$ ,  $P = 0.002$ ) than the untrenched ones, although differences were only statistically significant between 119 and 287 days after planting. The mass accumulated by the two groups of plants was very similar, except for a trend towards a greater mass of lateral roots in the untrenched than in the trenched plants (Table 2;  $F_{1,12} = 4.35$ ,  $P = 0.059$ ). Soil trenching only resulted in a lower root:shoot ratio in the *Pinus* site ( $F_{1,12} = 23.41$ ,  $P < 0.001$ ). In the native forest (Fig. 2C), the untrenched plants started to exhibit a trend towards a greater TSL 916 days after planting ( $F_{1,5} = 4.27$ ,  $P = 0.09$ ). Trenched and untrenched plants showed a marginally significant difference in shoot mass (Table 2;  $F_{1,5} = 6.15$ ,  $P = 0.056$ ), in a way which was consistent with the TSL data (tendency for more mass accumulation in the untrenched plants).

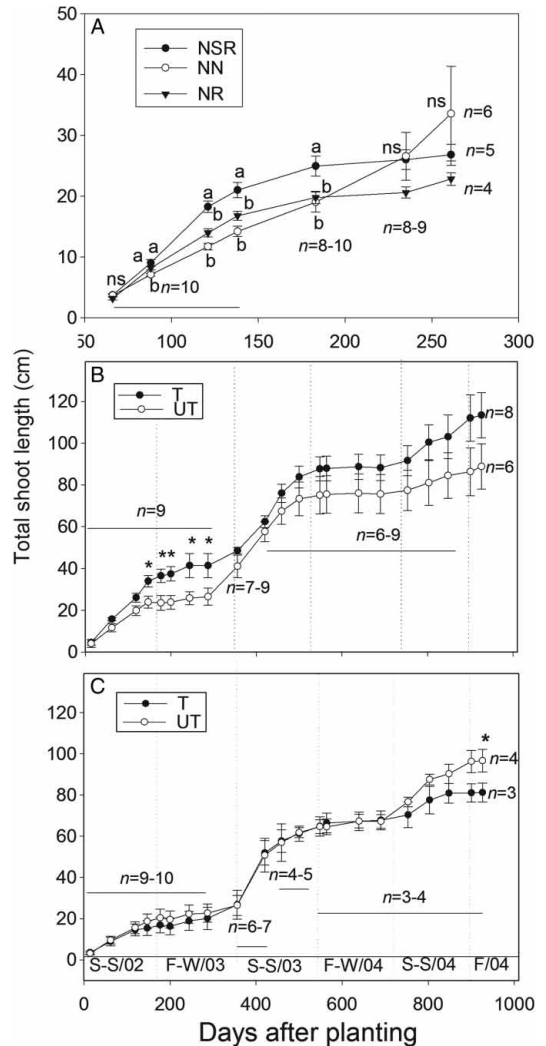
#### Leaf chlorophyll concentration

##### Competition in grasslands

Plants fully surrounded by vegetation (NSR) had similar concentration of chlorophylls in their leaves as those alleviated from shoot (NR) or shoot + root (NN) competition (Table 2).

#### Belowground competition in forests

Both trenched and untrenched plants in the native forest had similar chlorophyll concentrations, but trenching resulted in higher concentrations of total chlorophyll in the *Pinus* site (Table 2,  $F_{1,12} = 4.96$ ,  $P = 0.046$ ).



**Figure 2** Increases in total shoot length (mean  $\pm$  SED) of *A. angustifolia* subjected to different treatments. **A**, Grassland; **B**, *Pinus*; **C**, native forest. Experiments lasted 5 months in the grassland and 34 months in the forest sites.

In the grassland, means followed by different letters were significantly different ( $P \leq 0.05$ ); ns, not significant. In the *Pinus* and native forest, \* indicates a significant difference between the two means ( $P \leq 0.05$ , except for the native forest, where  $P \leq 0.09$ ).

NSR, neighbour shoots and roots; NR, neighbour roots; NN, no neighbours; UT, untrenched; T, trenched; S-S, spring and summer; F-W, fall and winter; 02, year 2002; 03, year 2003; 04, year 2004.

**Table 2** Root and shoot parameters of *A. angustifolia* plants growing under different treatments and sites. Experiments lasted 5 months in the grassland and 34 months in the forest sites.

Site and treatment	Total plant mass (g)	Shoot mass (g)	Total root mass (g)	Lateral root mass (g)	Root: shoot ratio (g g <sup>-1</sup> )	LMA (g m <sup>-2</sup> )	Chlorophyll concentration (mg m <sup>-2</sup> )
<i>Grassland</i>							
NSR ( <i>n</i> = 5)	1.12 ± 0.18 <sup>b</sup>	0.85 ± 0.14 <sup>b</sup>	0.26 ± 0.03 <sup>b</sup>	0.05 ± 0.007 <sup>b</sup>	0.33 ± 0.05 <sup>b*</sup>	68.70 ± 3.20 <sup>b</sup>	232 ± 23.54 <sup>a</sup>
NR ( <i>n</i> = 4)	2.34 ± 0.23 <sup>a</sup>	1.62 ± 0.20 <sup>ab</sup>	0.72 ± 0.03 <sup>a</sup>	0.18 ± 0.03 <sup>ab</sup>	0.47 ± 0.04 <sup>a*</sup>	99.70 ± 4.20 <sup>ab</sup>	148 ± 13.33 <sup>a</sup>
NN ( <i>n</i> = 6)	2.84 ± 0.43 <sup>a</sup>	2.34 ± 0.43 <sup>a</sup>	0.55 ± 0.09 <sup>a</sup>	0.31 ± 0.06 <sup>a</sup>	0.24 ± 0.06 <sup>b*</sup>	112.19 ± 5.00 <sup>a</sup>	185 ± 25.00 <sup>a</sup>
<i>Pinus</i>							
UT ( <i>n</i> = 6)	5.89 ± 1.07 <sup>a</sup>	4.43 ± 0.85 <sup>a</sup>	1.45 ± 0.22 <sup>a</sup>	0.31 ± 0.07 <sup>a*</sup>	0.34 ± 0.02 <sup>a</sup>	76.60 ± 2.90 <sup>a</sup>	217 ± 16.22 <sup>b</sup>
T ( <i>n</i> = 8)	6.43 ± 0.61 <sup>a</sup>	5.25 ± 0.51 <sup>a</sup>	1.18 ± 0.12 <sup>a</sup>	0.16 ± 0.02 <sup>b*</sup>	0.23 ± 0.01 <sup>b</sup>	71.60 ± 2.60 <sup>a</sup>	288 ± 31.78 <sup>a</sup>
<i>Native forest</i>							
UT ( <i>n</i> = 4)	3.54 ± 0.19 <sup>a</sup>	3.06 ± 0.15 <sup>a*</sup>	0.47 ± 0.04 <sup>a</sup>	0.08 ± 0.01 <sup>a</sup>	0.15 ± 0.01 <sup>a</sup>	68.20 ± 1.50 <sup>a</sup>	258 ± 21.93 <sup>a</sup>
T ( <i>n</i> = 3)	2.78 ± 0.26 <sup>b</sup>	2.35 ± 0.26 <sup>b*</sup>	0.42 ± 0.003 <sup>a</sup>	0.06 ± 0.005 <sup>a</sup>	0.18 ± 0.02 <sup>a</sup>	65.50 ± 6.20 <sup>a</sup>	237 ± 35.67 <sup>a</sup>

Means (± SED) with different letters within each site are significantly different ( $P \leq 0.05$ ).

\*Indicates a trend towards significance ( $P < 0.10$ ).

LMA, leaf mass per area; NSR, neighbour shoots and roots; NR, neighbour roots; NN, no neighbours; UT, untrenched; T, trenched.

### **Plant nutritional status**

#### **Competition in grasslands**

In the grassland, the highest and lowest N concentrations of plant shoots were measured in the NSR and NR treatments, respectively ( $F_{2,6} = 24.82$ ,  $P = 0.001$ ). Since shoot C concentration was not significantly affected by treatments, the C:N ratio varied in the opposite way (Table 1;  $F_{2,6} = 24.24$ ,  $P = 0.001$ ). Maintenance of the surrounding vegetation (NSR) in the grassland caused a greater shoot concentration of K ( $F_{2,6} = 46.52$ ,  $P < 0.001$ ) and P ( $F_{2,6} = 54.77$ ,  $P < 0.001$ ).

#### **Belowground competition in forests**

Soil trenching had no effect on shoot concentration of any of the measured elements in the native forest. In the *Pinus* site, however, it resulted in greater shoot N ( $F_{1,5} = 10.62$ ,  $P = 0.02$ ) and K ( $F_{1,5} = 11.05$ ,  $P = 0.02$ ) (Table 1).

## **Discussion**

### **Competition in grasslands**

Competition between trees and grasses has been well documented in different environments (e.g. Picon-Cochard et al. 2006; Gunaratne et al. 2014; Macias et al. 2014). Here, we demonstrate that shoot competition with grasses is also an important factor determining the successful growth of *A. angustifolia* seedlings in the invasion of undisturbed grasslands. The fast initial shoot vertical elongation observed in young trees under full interaction with grasses (NSR plants) has also been observed in seedlings growing under artificial shade (Franco & Dillenburg 2007). The fact that this response is also expressed under natural shading strongly suggests a strategy of seedlings to escape from light competition. This can be successful under conditions where shading is not imposed by tall structures such as neighbour trees. Of particular significance in such behaviour is the fact that the large seeds of this species (average of 7 g in Ferreira 1981) can support seedling growth for a quite long period (about 3–4 months), allowing for a successful vertical escape from layers of soil litter and herbaceous vegetation.

Our results have shown that when shoot competition was artificially reduced, there was a growth promotion (revealed by mass accumulation) of young plants of *A. angustifolia*. Areas which are disturbed by grazing and fire (a practice commonly used in many areas where forests with *A. angustifolia* intermingle with grasslands) will result in reduced shoot competition of the grassy vegetation with the invading trees, which may help in their establishment. Although forest encroachment in these ecosystems depends on such disturbances (Pillar 2003), fire and grazing can kill seedlings, hindering forest expansion (Hoffmann & Andersen 2003; Oliveira & Pillar 2004; Peterson & Reich 2008). However, young individuals of *A. angustifolia* can not only tolerate physical damage due to its sprouting ability after loss of shoot tissue (Alabarce & Dillenburg 2012), but also find protection from fires by commonly establishing themselves close to rocks, which are important safe sites for tree seedlings in the process of forest expansion (Carlucci et al. 2010).

In terms of plant growth, the relief from both shoot and root interactions (NN plants) did not lead to a significant growth promotion relative to plants that were only relieved from shoot interactions (NR plants). This suggests that root competition with grasses was not a major negative factor for the performance of *A. angustifolia* seedlings and/or that any competition relief was counterbalanced by reduction of possible facilitation effects. Facilitation effects of the early successional herbaceous vegetation over the establishment of trees, including *A. angustifolia*, were characterised in a highly disturbed forest edge area (Zanini et al. 2006).

Indeed, overall soil fertility (evaluated by saturation of CEC with bases) and water content were reduced under conditions of full removal of the surrounding vegetation. However, at the same time, this last condition led to greater accumulation of N and a lower C:N ratio in the shoot tissues of the target plants compared to plants that interacted with grasses at the root level, suggesting a possible competition for N in this tree–grass interaction. Carbon/nitrogen imbalances, expressed as high C:N ratios and scleromorphism of plant tissues (e.g. high LMA) are found in plants that invade grasslands under grazing pressure (Tilman 1988; Wilson

& Tilman 1993). Such characteristics were mostly expressed by plants growing under high light (NN plants) and by those interacting underground with grasses (NR plants). These last plants accumulated less N and more C in their shoot tissues than the other two groups of plants and also had the greatest root:shoot mass ratio, a typical response aimed to reduce such C:N imbalances and provide greater stability of nutrient content in the tissues and better cellular functioning (Chapin 1980; Tilman 1988). The maintenance of aboveground competition probably reduced belowground competition to levels which were lower than when only belowground tree–grass interactions were present. A reflection of this was the trend towards a lower root:shoot mass ratio and the lower investment in lateral roots of the NSR plants compared to the NR ones. The relative mass investments between shoot and root of the NSR plant did not differ from the NN plants, suggesting that, for these two groups of plants, the ratio between major aboveground (light) and belowground (N) resources was similar.

### ***Belowground competition in forests***

Soil resource competition was found to be significant in the *Pinus* forest, but not in the native forest. The *Pinus* site was the one offering the less favourable conditions in terms of water and nutrient availabilities, particularly compared to the native forest site. A previous study conducted in the exact same sites (Garbin et al. 2006), but focusing on the availability of inorganic N, showed that the *Pinus* soil had almost half the concentration of total inorganic N when compared to the native forest site. These facts may explain why root competition was more intense there than in the native forest, despite the offer by both of a low irradiance environment. This depletion in soil fertility in the exotic plantation of the fast-growing species *P. elliottii* is not surprising, and was also reported for another *Pinus* plantation in southern Brazil (Tosin 1976).

The promoting effects of trenching on the growth of *A. angustifolia* seedlings in the *Pinus* site were not long-lasting, probably because of the reduction in sample size after plant thinning.

However, the initial growth response was maintained until the end of the experimental period, leading us to suggest that root competition with the exotic conifer *P. elliottii* limits the initial growth of *A. angustifolia*. Despite the lack of statistical significance in the effect of trenching on plant mass accumulation at the end of the experiment, the observed reduction of the root:shoot mass ratio in response to trenching is a strong indication that soil resources became more available. Further support is given by the reduced investment of the root system into lateral roots in plants growing in trenched plots of these plantation forests. Although soil data did not reveal differences in nutrient availability between trenched and untrenched plots, the nutritional status of shoots and the accumulation of chlorophylls (N-dependent) were consistently favoured by soil trenching.

Many other studies have shown growth-promoting effects of soil trenching on trees growing on nutrient-poor soils in tropical and subtropical forest understories (Coomes & Grubb 1998; Lewis & Tanner 2000). An experiment with another Araucariaceae tree species, *Agathis australis*, reported an increase in both leaf N content and plant growth of seedlings growing inside trenched plots (Verkaik et al. 2007). These positive effects were generally associated with an increase in availability of soil nutrients in response to trenching. However, in the more fertile soils of a Costa Rican rain forest, trenching did not have the same strong effects as those reported in the above-mentioned studies (Denslow et al. 1991).

Soil trenching in the native forest did not promote the growth of *A. angustifolia* seedlings. Instead, shoot mass and length tended to be reduced under trenched conditions. Although the small final sample size calls for caution in interpreting plant responses in the native forest, the better performance of plants in untrenched than in trenched plots suggests that, if any positive effect of trenching was present, it was counterbalanced by trenching negative effects on plant growth. Trenching could change several biotic and abiotic factors that could have, to some extent, direct or indirect negative effects. *Araucaria angustifolia* is highly dependent on mycorrhiza (Moreira-Souza & Cardoso 2001;

Zandavalli et al. 2004). Vegetation removal inside the trenches as well as trenching itself may have resulted in reduced availability of mycorrhizal propagules and/or breakage of connections to the forest mycorrhizal network, which has been shown to be of major importance for tree establishment (Teste & Simard 2008).

The major *A. angustifolia* seedling mortality observed in the native forest points to a very important and limiting factor to the establishment of *A. angustifolia* seedlings: negative interactions with pathogens. The existence of a favourable environment to pathogens is an important factor shaping plant communities in tropical forests (Janzen 1970; Gilbert 2002; Spear et al. 2015). The high seedling survival in the *Pinus* site compared to the native forest could be related to an unfavourable environment for plant pathogens caused by its lower soil water content and/or by allelochemical substances such as terpenes, which are known to be emitted by *P. elliottii* (Tingey et al. 1980). These conditions would then facilitate the establishment of *A. angustifolia* seedlings, although growth of the established ones would be reduced by root competition.

## Conclusions

We were able to demonstrate the effects of competition on the initial growth of seedlings of *A. angustifolia* in a grassland area (shoot competition) and in a tree plantation of *P. elliottii* (root competition). In a mature native forest, however, root competition did not appear as a limiting factor to the growth of seedlings. Our study suggests that soil resource competition is more intense in forests where both soil fertility and pathogen effects on plant performance are lower (*Pinus* plantation). The fact that root competition was more important in a tree plantation than in a native forest also suggests a complementarity effect, where the growth of seedlings of *A. angustifolia* would be favoured in the community with greater diversity and complementary resource use (Ratcliffe et al. 2015); in this case, the native forest.

Although this study was designed to evaluate the role of competition (particularly at the root level)

on the regeneration and colonisation abilities of *A. angustifolia*, other interactions, namely facilitation, plant–animal and plant–pathogen interactions appeared also as factors affecting the above-mentioned processes. Altogether, the results of the present study have important implications for forest management and conservation. Shoot competition with grassland species, as well as ant herbivory, are important factors to be considered in any management programme aiming to improve the process of *Araucaria* forest encroachment into grasslands. Likewise, root competition must be taken into account in mixed tree plantations (*P. elliottii* and *A. angustifolia*) or when trying to improve the growth of *A. angustifolia* seedlings that commonly colonise the plantations with the exotic pine species. Finally, management procedures for promoting the regeneration of *A. angustifolia* seedlings in the native forest understory must strongly focus on the negative effects of plant pathogens as well as on the facilitation effects of neighbour plants.

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## Disclosure statement

No potential conflict of interest was reported by the authors.

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