



Responses of planted *Populus tremuloides* seedlings to grass competition during early establishment

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Abstract

Key message Root systems of aspen seedlings display limited architectural plasticity in response to below-ground competition, but seedlings compensate for restricted rooting space and reduced root system size, by optimizing water uptake.

Abstract Below-ground competition with grasses often plays a critical role during tree seedling establishment, but many underlying mechanisms are not well understood. We used a controlled field experiment to study how trembling aspen (*Populus tremuloides* Michx.) seedlings compete with smooth brome grass (*Bromus inermis* L.) for space during the first 3 years of seedling establishment and how it affected aspen seedling development. Our study showed that competition with grasses had a limited impact on architectural plasticity of aspen seedlings. Seedlings faced with competition from smooth brome were overall smaller and most architectural parameters, with the exception of shoot height, appeared simply scaled down proportionally. Shoot height changed less than other parameters, because aspen competing with grass allocated relatively more carbon to shoots than roots and adopted a slender shoot morphology to quickly overtop the competition. Aspen growing with grass competition had significantly smaller root systems. Both lateral extent and maximum rooting depth were reduced by ~50%. In response to the restricted rooting space, roots of aspen seedlings faced with grass competition had a lower specific root length. Root carbohydrate reserves were not affected by competition; however, aspen roots growing with grass competition had higher soluble sugar concentrations which may be associated with the observed three times higher water uptake efficiency per unit root biomass. Our findings suggest that aspen seedlings have limited capacity for architectural plasticity in response to root competition, but are at least temporarily able to compensate for reduced root system size and rooting space, by optimizing water uptake efficiency.

Keywords Trees · Grasses · Competition · Eco-physiology · Biological space

Introduction

One of the most pervasive competitive struggles among terrestrial plant lifeforms is that between trees and grasses which plays out wherever climatic conditions are suitable for both lifeforms to occur, particularly in the transitional regions (ecotones) between natural grasslands (prairies and savannas) and closed forests. Once established, both forests and grasslands tend to form relatively stable ecosystems with boundaries delineated by mean annual temperature and precipitation (Chapin et al. 2011); however, disturbances, both natural and anthropogenic, that remove the existing vegetation, can create conditions that lead to a renewed struggle for dominance between trees and grasses and a shift in these boundaries (e.g., Conway and Danby 2014). These forces are also often in play in afforestation and reforestation where

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planted tree seedlings typically experience intense above- and below-ground competition from fast-growing grasses during the early stages of establishment after disturbance (e.g., Franklin et al. 2012; Henkel-Johnson et al. 2016). The outcomes of these competitive interactions are often hard to predict, as they are driven by a complex interplay of site conditions, as well as the growth strategies and competitive abilities (sensu Grime 1977) associated with the respective competing species.

Shade-intolerant, early successional tree species are particularly affected by low light conditions and their survival hinges on their ability to outgrow above-ground competition (e.g., Chapman 1945). They typically achieve this through high relative growth rates of above and below-ground organs, rapid leaf area development, and by selectively placing fine roots and leaves in areas with the highest resource availability (Adams et al. 2013; Pierik et al. 2013). The ability to perceive light levels and composition, for example, allows them to optimize crown architecture and avoid shade (Pierik et al. 2013). As light is typically considered the most limiting factor in forest ecosystems, these species also allocate most of their assimilated carbon-to-shoot growth which is reflected in generally low-root mass fractions (Poorter et al. 2011).

Grasses, of course, also compete for light, especially during germination and early establishment; however, the disproportionate allocation to roots observed in many grasses suggests that most of the competition might occur below ground (Poorter et al. 2011). Several studies have shown that many perennial grasses invest in oversized, extremely dense root systems in an attempt to consolidate rooting space and pre-empt access to the resources within (Mommer et al. 2011; Ravenek et al. 2016). Some of the most competitive grasses have the ability to colonize soil aggressively through rhizomes, colonizing rooting space as a moving front in what has been called a ‘phalanx-formation’ (Doust 1981; Saiz et al. 2016). Fast-growing early successional trees, in contrast, are more likely to employ a selective root placement strategy, proliferating high root densities into resource-rich patches within the soil (Bauhus and Messier 1999; Kembel et al. 2008; Bardgett et al. 2014), while attempting to avoid root competition through spatial segregation (Messier et al. 2009). Spatial segregation, however, may not be an option when newly establishing tree seedlings are faced with intense root competition from grasses establishing at the same time. Under such circumstances, these traits are likely to result in severely restricted root system development, reducing the soil volume in which seedlings can access resources.

Competitive interactions are best understood by taking into account both the competitive effects, such as reductions in resource availability, as well as the response observed in the individual plants (Goldberg 1990). While the competitive effects are often simple, mechanistic, and relatively

easy to quantify, the responses of individuals to competition can be more complex and sometimes difficult to measure. The most frequently reported response to competition is a reduction in plant fitness (survival, growth, and reproduction) (e.g., Franklin et al. 2012). However, other responses include changes in carbon allocation to different plant organs (Craine 2006; Poorter et al. 2011), trade-offs between allocation to growth, defence, and reserves (Donaldson et al. 2006; Maguire and Kobe 2015), changes in architectural (i.e., the spatial arrangement of the shoot and root system); morphological (i.e., the properties of individual organs) (Valladares and Niinemets 2007; Hodge et al. 2009; Bardgett et al. 2014; Van de Peer et al. 2017) and physiological traits (Hodge 2004; Bardgett et al. 2014).

Competition has been studied extensively by evolutionary biologists, community ecologists, and ecophysiologicalists; however, many of the underlying mechanisms are still not fully understood, particularly as they relate to below-ground competition (Connolly et al. 2001; Trinder et al. 2013; Wilson 2014). Although a large body of literature exists that explores competitive interactions and mechanisms, only a small fraction of these studies addresses root competition, particularly under field conditions (Wilson 2014). Due to the logistical difficulties associated with studying roots in the field, one area in which knowledge is particularly lacking is how below-ground competition affects the ability of different species to occupy and consolidate rooting space (Casper et al. 2003; Wilson 2014). Fortunately, recent advances in molecular techniques now allow researchers to identify the presence of individual species in mixed root samples and thus gain new insights into spatial aspects of below-ground competition (Mommer et al. 2008; Taggart et al. 2011; Randall et al. 2014).

Forest reclamation sites offer an ideal opportunity to study below-ground competition between grasses and early successional tree species. They offer sizeable areas of bare soil with relatively uniform soil properties and known site history where tree–grass interactions can be studied under relatively controlled field conditions and over the course of several years. Reclamation sites are often rapidly colonized by highly competitive grasses that are either seeded to prevent soil erosion or naturally disperse onto the site from nearby seed sources. Among the species commonly found colonizing these sites, perennial grasses, often invasive exotic species, have been shown to have a particularly strong competitive impact on planted trees (Franklin et al. 2012; Henkel-Johnson et al. 2016; Bockstette et al. 2017). In an earlier study, we showed that grass competition with smooth brome (*Bromus inermis* L.) strongly reduced growth of trembling aspen (*Populus tremuloides* Michx.) seedlings by reducing both water and nitrogen availability (Bockstette et al. 2017). The objective of the present study was to examine more closely how aspen seedlings respond to grass

competition, with a particular focus on changes carbon allocation to roots and shoots, as well as to reserves.

Materials and methods

Site description

The research was conducted on a large reclamation area at the Genesee coal mine, approximately 80 km west of Edmonton, Alberta, Canada. The mine is situated within the transition zone between prairie and boreal forest in gently undulating aspen parkland, characterized by a mix of grasslands and patches of forests dominated by trembling aspen, a fast-growing, shade-intolerant early successional species. The local climate is continental, with warm summers and cold winters. Total annual precipitation averages 500–550 mm (1971–2000). Most precipitation (> 400 mm) occurs as rainfall during the growing season between May 1 and August 31, the remainder as snow, particularly between November and January (Alberta Government 2015a). For the 3-year period of our experiment (2012–2014), the mean annual precipitation was ~510 mm which was slightly below the long-term average of 550 mm (Alberta Government 2016). The dominant natural soil types prior to disturbance were moderately well-drained Luvisols, as well as imperfectly to moderately well-drained Solonetz soils (IUSS Working Group WRB 2014; Alberta Government 2015b). The study site was located mid-slope on a reconstructed north-facing hill (2–5% slope) in the northeastern part of the mine (53.34°N, 133.27°W), extending 25 m north–south and about 575 m east–west for a total area of about 1.5 ha. More detailed information on the reclamation site and its reconstruction can be found in Bockstette et al. (2017).

Study design

The experiment consisted of 12 blocks (25 × 36 m) which contained three treatment plots (9 × 12 m) randomly assigned to one of three vegetation covers: aspen growing alone (A), aspen growing with smooth brome (AB), and smooth brome growing alone (B). Half of the blocks had been deep tilled in 2010 for a companion study; however this deep tillage treatment had no impact on the vegetation (Bockstette et al. 2017). Deep tillage was, therefore, not considered a factor in the present study. The entire study site was surrounded by a buffer of 4–5 rows of planted aspen on all sides to minimize edge effects in treatment plots. After repeated herbicide applications (2010/11) to remove all the existing vegetation, 1-year-old container stock of trembling aspen seedlings (see below) was planted at a regular 1 × 1 m spacing (10,000 stems ha⁻¹) in (A) and (AB) plots in June 2012. In the aspen only treatment, all competition was suppressed

using a combination of hand-weeding and a non-selective herbicide [Glyphosate; 5–7% (v/v); Monsanto Canada Inc., Winnipeg, MB, Canada]. Between tree rows, herbicide was applied using a non-drift roll-on applicator (Danville DEX 30, Danville Industries, Harper, KS, USA) to avoid herbicide accidentally coming in contact with aspen seedlings. For spot applications around the bases of stems, handheld sprayers were used. Herbicide applications were repeated as often as necessary, whenever sufficient new growth had emerged.

In plots where aspen grew together with smooth brome, plugs of container-grown smooth brome (see below) were inter-planted between established tree rows at 1 × 1 m spacing a few days after tree planting. In smooth brome subplots, plugs were planted at 1 × 0.5 m to achieve the same initial plant density as plots where aspen grew together with smooth brome. Smooth brome was selected for this study, because it is a very hardy and drought-resistant cool-season grass, commonly used in reclamation and agriculture, that forms dense sods and spreads aggressively through rhizomes, tillers, and seeds (Otfinowski et al. 2007). It is known for its ability to rapidly colonize a site, displace native species, and form dense monocultures (Dillemuth et al. 2009; Fink and Wilson 2011; Salesman and Thomsen 2011).

Plant material

Aspen seedlings used in this study were commercially grown container stock from local seed source. Seeds were sown into Styroblock containers in 2011 (PSB 615A; 60 × 152 mm (336 ml); Beaver Plastics Ltd., Edmonton, AB) and grown for one growing season at Smoky Lake Forest Nursery (Smoky Lake, AB) using standard nursery protocols. Seedlings were stored frozen at –3 °C prior to planting in early June 2012. At the time of planting, seedlings had a mean height of 30 ± 3 (± SD) cm and an initial root mass fraction ($g_{\text{root}} g_{\text{total mass}}^{-1}$) of 0.77 ± 0.04.

Smooth brome was also started from seed in Styroblock containers (PSB 315A; 30 × 152 mm (80 ml); Beaver Plastics Ltd., Edmonton, AB) and grown for 6 weeks (May–June 2012) at the University of Alberta before being planted onto the site at the same time as the aspen seedlings. Plants were grown under natural light at 20 °C, watered daily, and fertilized weekly. All grass plants were clipped back regularly to a height of about 15 cm to ensure uniform growth.

Root-length density and leaf area index (plot-level measurements)

Root-length densities were assessed using soil cores collected in October 2013. Using a hydraulic direct push machine (Geoprobe® model 7730DT, Geoprobe Systems, Salina, KS, USA) equipped with a 100 × 6.35 cm core sampler, one undisturbed soil core was collected per plot,

for a total of 12 cores per treatment. Travelling along an east–west transect, the machine collected cores at random locations within each plot with the restriction that no cores would be taken closer than 2 m to neighbouring plots. Core samples were immediately separated into four depth increments (0–15, 15–30, 30–60, and 60–90 cm). These were wrapped, labelled, and subsequently stored in a freezer at $-20\text{ }^{\circ}\text{C}$ until they could be processed. Samples were taken from the freezer at random and thawed prior to processing. Using a small core sampler ($d=1.45\text{ cm}$), one subsample was collected at a random location within each 7.5 cm-depth increment for a total of two and four subsamples for 15 and 30 cm-long cores, respectively. Roots from bulk samples were extracted using running cold water and sieves with a minimum mesh size of 0.5 mm, while the smaller subsamples were first soaked in water to allow the soil break up and then washed over sieves with minimum diameter of 0.25 mm. Clean extracted roots were scanned with WinRhizo™ (Regent Instruments Inc., Québec City, QC, Canada) to determine root-length density (RLD) (cm cm^{-3}). After scanning, roots were dried at $70\text{ }^{\circ}\text{C}$ until constant weight to determine root mass. By comparing root-mass per volume of soil (g m^{-3}) from subsamples with those from bulk samples, we were able to determine that bulk sampling underestimated root mass density by approximately 30%. We, therefore, used a correction factor of 1.3 to estimate actual root mass density for bulk samples.

In July 2014, plot-level leaf area index (LAI, $\text{m}^2\text{ m}^{-2}$) was measured using the LAI 2220C Plant Canopy Analyzer in combination with the FV2200 software (LI-COR Biosciences, Lincoln, NE, USA). Measurements were taken under uniform clear sky conditions using one wand. In plots where brome either grew alone or together with aspen, we took one above- and four below-canopy readings following a diagonal transect from NE–SW. In plots where aspen was growing alone, we followed the suggested procedure for small tree plots and took one above- and one below-canopy reading looking into the plot from each of its four corners. All measurements were taken using a 90° view-cap. Sky readings were taken at regular time intervals, following the suggested 4A sequence, to allow for scatter correction when calculating actual LAI. Above-ground biomass for smooth brome was determined by harvesting all standing leaf mass in two randomly located ($0.5\times 0.5\text{ m}$) clip plots per plot, around the same time.

Root identification using species-specific primers

To determine the presence of both aspen and smooth brome roots at different soil depths, a second round of soil cores was collected in September 2014. Because the trees were now too tall to operate a vehicle in the plots, we instead used a percussion drill set consisting of a jackhammer and a

1 m-long coring tool ($d=5\text{ cm}$) equipped with a plastic liner inside the tool (Eijkelkamp Soil and Water, Giesbeek, NL) to collect two undisturbed core samples per plot. Plastic liners were immediately sealed, labelled, and stored in a freezer ($-20\text{ }^{\circ}\text{C}$) the same day. Samples were taken from the freezer in random order and allowed to thaw for about 1 h at room temperature. The 1 m-long cores were cut into 10 cm-long samples. Roots were extracted under running water using a 0.25 mm sieve. Extracted roots were carefully cleaned under running de-ionized water to remove any adhering soil particles and subsequently placed on paper towels to remove excess moisture before being stored in labelled aluminum pouches for freeze drying. Freeze-dried root samples were first pooled by plot ($n=12$) and depth increment and then ground using a TissueLyser II ball mill (Qiagen Inc., Missisauga, ON, Canada) to extract DNA. Total genomic DNA was extracted from ground root samples using a commercial PowerSoil® DNA Isolation Kit (MoBio Laboratories Inc., Carlsbad, CA, USA) with slight modifications to improve yield and quality. The extracted DNA was further purified by ethanol precipitation. Using species-specific primers for aspen and smooth brome designed for this study, fragments of the DNA at a non-coding chloroplast region were amplified by PCR and visualized by gel electrophoresis. The presence of the unique bands corresponding to either of the two species signified their presence in the root materials at the respective depth in the soil. Average maximum rooting depth (2014), as determined by DNA analysis, was combined with mean lateral root system radius of excavated seedlings (see below) to calculate potential rooting space using a simple cylinder as a spatial representation of the soil volume in which any individual seedling could potentially have roots. We introduce potential rooting space as an architectural measure to establish a direct link between the size of individual root systems, i.e., vertical and horizontal extents of all roots belonging to one individual, and the soil volume in which they can forage for resources. A cylinder was deemed an adequate spatial model for young aspen due to their rooting pattern consisting of long, shallow lateral roots from which vertical sinker roots emerge at roughly regular intervals.

Aspen seedling measurements

Aspen heights and basal diameters were recorded each fall after leaf abscission. Measurements were taken on all trees in every second tree row (i.e., four out of nine rows), representing 45% of the total population in each treatment plot. Seedling mortality during the first three growing seasons was overall low ($\sim 13\%$) irrespective of treatments. After three growing seasons (2014), height and basal diameter data were used to calculate height-to-diameter (h/d) ratios for individual seedlings. Specific stem length (SSL, cm g^{-1})

was calculated as stem height divided by stem dry mass (Poorter et al. 2011). Both h/d ratio and SSL are morphological parameters used to describe shoot growth form (slenderness) and the relative investment in height growth versus diameter growth, which has been used as an indication of light competition in trees (Erickson et al. 2009; Zhang et al. 2015).

To explore the impact of grass competition on tree water use, aspen sap flow was measured between May and September 2014 using the heat balance method described by Baker and Bavel (1987). In six of the 12 blocks, two representative aspen seedlings ($N=24$) were randomly selected in treatment plots containing trees and equipped with Dynagage[®] sap flow sensors (Dynamax Inc., TX, USA). Three sizes of sensor were used to accommodate variations in caliper among seedlings [$9\times$ SGA5 (5–7 mm), $1\times$ SGA10 (9.5–13 mm) and $14\times$ SGA13 (12–16 mm)]. All sensors were installed below the first branch to ensure that sap flow measurements represented the entire leaf area. Sensors were mounted at least 20 cm off the ground and wrapped in weather shielding (Dynamax Inc. 2005). Water uptake efficiency (UE), defined as sap flow per root mass (Leitner et al. 2016), was calculated using growing season average total daily sap flux (g day^{-1}) of individual seedlings divided by their respective total root dry mass (g) (see below). At the end of the measuring period, all leaves of the equipped trees were collected and scanned to determine individual seedling leaf area using a LI-3100C Leaf Area Meter (LI-COR Biosciences, Lincoln, NE, USA). Leaf area data from aspen growing with smooth brome ($n=12$) were then used to estimate the relative contribution of aspen leaf area to total leaf area in plots where aspen grew together with smooth brome.

In April 2015, prior to leaf flush, two representative seedlings were randomly selected in each treatment plot and destructively sampled ($N=48$). Seedlings were carefully excavated to include as much of the root system as possible following roots until they were less than 1 mm in diameter. Excavated seedlings were labelled and bagged in the field and subsequently stored in a freezer at $-20\text{ }^{\circ}\text{C}$. Once thawed, each seedling was separated into root and stem. Both roots and stems were thoroughly cleaned under running cold water to remove all soil before being dried at $70\text{ }^{\circ}\text{C}$ until constant weight to determine root, stem, and total woody mass. The length of the three longest lateral roots of each seedling was averaged as a measure of maximum root system radius. To quantify structural allocation to above- or below-ground parts of the tree, root, and stem mass fraction (RMF, SMF, g g^{-1}) were calculated for all 48 excavated seedlings by dividing root and stem dry mass by the total woody mass (root + stem).

Total non-structural carbohydrate (NSC) concentrations, a physiological measure used to quantify the carbohydrate reserve status, were calculated as the sum of starch and total

soluble sugars concentrations found both in coarse and fine roots. Coarse and fine roots were analyzed separately as they play different functional roles (i.e., absorption versus storage). To gain further insight into potential differences in carbohydrate dynamics created by the treatments, we calculated the starch and sugar fractions of total NSC. Each root system was, therefore, separated into coarse and fine roots using a threshold diameter of 2 mm. These samples were then ground to 40 meshes using a Wiley mill. Ground samples were extracted three times with 80% hot ethanol at $95\text{ }^{\circ}\text{C}$. Extracts obtained in this fashion were analyzed for total soluble sugar concentration using phenol–sulphuric acid. Post-extraction residues were digested using an α -amylase-amyloglucosidase enzyme mixture to determine starch concentration, followed by colorimetric measurement of the glucose hydrolysate using peroxidase-glucose oxidase-*o*-dianisidine reagent (Chow and Landhäusser 2004).

Data analysis

With the exception of root-length density and specific root length, all response variables were analyzed using one-way analysis of variance (ANOVA) with vegetation cover as the fixed factor. Individual seedlings were considered independent measures as they were far enough apart that neither their crowns nor roots overlapped. Differences in root-length densities and specific root length were assessed as a two-way ANOVA using vegetation cover and depth as the two fixed factors. Assumptions for ANOVA were tested prior to the analyses and transformations were applied when necessary. Data for seedling root and shoot mass, specific stem length (SSL), leaf area index (LAI), soil water potential, and uptake efficiencies were all log-transformed for the analysis; shown are the untransformed means. Post-hoc comparisons of significant main effects or interactions were conducted using a Sidak correction to control the type I error rate. All analyses were executed using SPSS 20.0 (IBM Corp., 2011). Differences between means were considered significant at $\alpha=0.05$.

Results

After three growing seasons, aspen without grass competition had a mean leaf area index (LAI) of 1.2 ± 0.5 ($\text{m}^2\text{ m}^{-2}$, \pm SD) which was much lower than that of smooth brome without aspen (4.6 ± 1.3) ($p<0.001$). Aspen and smooth brome growing together had a combined mean LAI of 4.7 ± 1.0 , which was almost identical to that of smooth brome growing alone ($p=0.983$). Aspen growing with smooth brome had a mean leaf area of 0.12 ± 0.1 m^2 per seedling. Given the planting density of 1 seedling m^{-2} , aspen leaf area thus constituted only about 2.6% of total LAI when

growing together with smooth brome. Above-ground biomass for smooth brome, a proxy for leaf area, did not differ between smooth brome growing alone ($5.7 \pm 1.5 \text{ Mg ha}^{-1}$) or together with aspen ($5.9 \pm 2.5 \text{ Mg ha}^{-1}$) ($p = 0.642$).

Roots extracted from soil cores collected in 2013 revealed that aspen growing alone had lower root-length densities (RLD) than smooth brome growing alone at the 0–15 and 15–30 cm soil-depth range, while RLD was similar for both species below 30 cm (vegetation \times depth, $p < 0.001$). In addition, RLD did not change with depth for aspen growing alone, whereas it decreased rapidly between 0 and 60 cm depth for smooth brome. The combined RLD of aspen

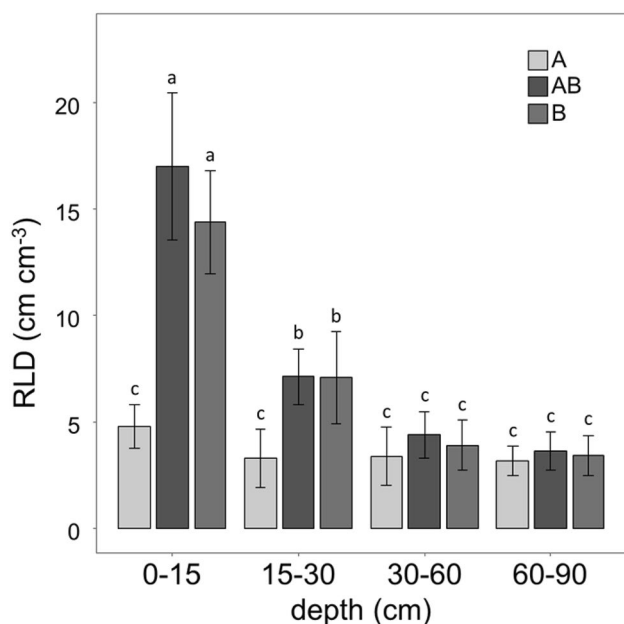


Fig. 1 Root-length density (RLD) by depth for aspen growing alone (A), aspen growing with smooth brome (AB) and smooth brome growing alone (B). Letters indicate significant differences between means. Error bars represent 95% CI ($n = 12$)

growing with smooth brome was statistically identical to that of smooth brome growing alone at all depths (Fig. 1). When growing alone, both aspen and smooth brome had similar mean specific root lengths (SRL, cm g^{-1}), with means of 104 ± 40 and 102 ± 39 , respectively. However, aspen and smooth brome growing together had a 15% lower combined mean SRL (88 ± 30) than either species growing alone (vegetation, $p = 0.015$). Specific root length was the lowest at the 0–15 cm soil depth, while remaining similar below 15 cm (depth, $p < 0.001$).

DNA analysis of root samples revealed that aspen growing alone reached an average maximum rooting depth of $0.8 \pm 0.1 \text{ m}$, while aspen growing with smooth brome only reached a maximum rooting depth of $0.4 \pm 0.3 \text{ m}$ ($p < 0.001$) (Table 1). However, variability in maximum rooting depth was greater for aspen growing with smooth brome (CV 75%) than for aspen growing alone (CV 12.5%). Maximum rooting depth of smooth brome was not affected by the presence of aspen, ($p = 0.701$) as roots were consistently found at the maximum sampling depth of 1 m in all soil cores.

Aspen growing with smooth brome was on average shorter, which had a smaller root collar diameter, lower stem dry mass, and less leaf area per individual seedling than aspen growing alone ($p < 0.001$ for all) (Table 1). Aspen growing with smooth brome also had more slender stems than aspen growing alone ($p < 0.001$) with mean height-to-diameter ratios (cm cm^{-1}), of 99 ± 10 and 80 ± 3 , respectively. Likewise, specific stem length, i.e., height per unit shoot dry mass (cm g^{-1}), was three times greater for aspen growing with smooth brome (2.7 ± 0.6) than for aspen growing alone (0.8 ± 0.2) ($p < 0.001$).

Total root dry mass was significantly lower for aspen growing with smooth brome ($p < 0.001$) (Table 1). Aspen growing with smooth brome also had a lower mean root mass fraction (RMF, g g^{-1}) and higher stem mass fraction (SMF, g g^{-1}) than aspen growing alone ($p < 0.001$) (Fig. 2). Root systems of aspen seedlings growing together with

Table 1 Root and shoot characteristics (mean, \pm SD) for 3-year-old individual aspen seedlings growing with and without competition from smooth brome ($n = 24$)

Parameter	Aspen alone	Aspen with brome	Competition response
Shoot			
Height (cm)	$205^a \pm 11$	$152^b \pm 17$	–26%
Basal diameter (mm)	$26^a \pm 2$	$15^b \pm 1$	–42%
Stem dry mass (g)	$312^a \pm 70$	$59^b \pm 16$	–81%
Leaf area (m^2)	$0.77^a \pm 0.4$	$0.12^b \pm 0.1$	–84%
Root			
Root system radius (m)	$2.1^a \pm 0.8$	$1.0^b \pm 0.5$	–52%
Maximum rooting depth (m)	$0.8^a \pm 0.1$	$0.4^b \pm 0.3$	–50%
Root dry mass (g)	$214^a \pm 59$	$28^b \pm 10$	–87%

Competitive response shows the net change in each parameter due to competition. Letters indicate significant differences

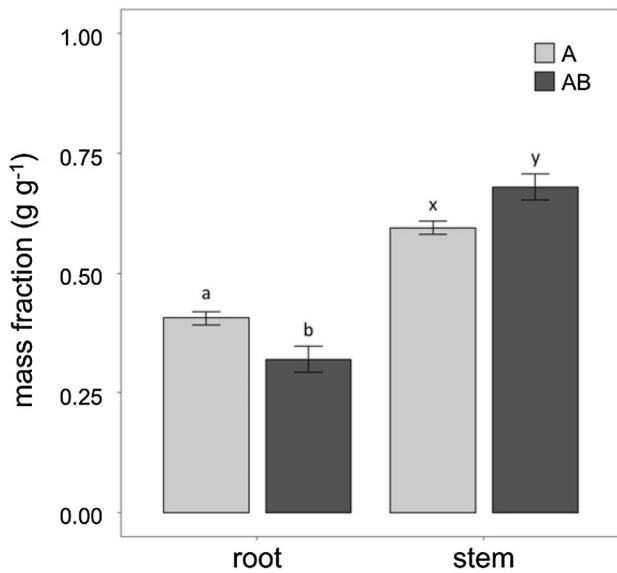


Fig. 2 Root and stem mass fractions for aspen growing alone (A) and together with smooth brome (AB) ($n=24$). Letters indicate significant differences. Error bars represent 95% CI

smooth brome had an average radius of 1.0 ± 0.5 m, compared to 2.1 ± 0.8 m for aspen growing alone ($p < 0.001$). In combination with maximum rooting depth (see above), this resulted in a potential rooting space of 11.1 m^3 for aspen growing alone, compared to 1.3 m^3 for aspen growing with smooth brome (Fig. 3).

Total non-structural carbohydrate (NSC, soluble sugars plus starch) concentrations in roots of aspen growing alone did not differ from those found in aspen growing together

with smooth brome ($p=0.224$), but fine roots ($d < 2$ mm) generally had significantly higher NSC concentrations than coarse roots ($p < 0.001$) Aspen growing together with smooth brome showed a significantly lower starch fraction and higher sugar fraction (% NSC) than aspen growing alone ($p < 0.001$) (Table 2). Root water uptake efficiency, i.e., the mean daily total sap flow rate (g day^{-1}) per unit root mass (g), was about four times greater in aspen growing with smooth brome (11.99 ± 9.5) than in aspen growing alone (2.99 ± 1.2) ($p < 0.001$).

Discussion

We used a controlled field experiment to study how planted aspen seedlings compete with smooth brome grass for growing space during the first 3 years of seedling establishment and how this interaction affects aspen seedling root and shoot architecture, morphology, and physiology. Our study showed that competition with grasses had a minimal impact on architectural plasticity of aspen seedlings. Seedlings faced with competition from smooth brome were overall smaller, but all architectural parameters, with the exception of height and root collar diameter, appeared to be simply scaled down proportionally. Aspen growing with grass competition had significantly smaller root systems; however, both lateral extent and maximum rooting depth were each reduced by $\sim 50\%$ in response to competition, and thus, the overall spatial proportions of the root system did not change. Maximum rooting depth was about 40% of root system radius both for aspen growing alone and together with smooth brome, suggesting a fixed coarse architectural pattern rather than architectural

Fig. 3 Root system architecture and potentially accessible rooting space for aspen seedlings growing with and without smooth brome

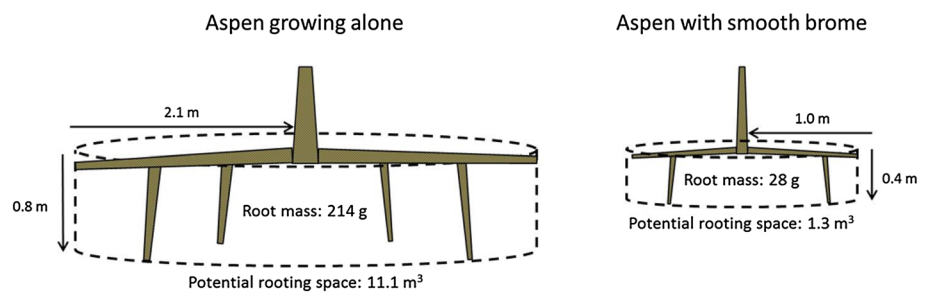


Table 2 Total non-structural carbohydrate (NSC) reserves (mean, \pm SD), starch and sugar fractions in coarse ($d > 2$ mm), and fine root ($d < 2$ mm) tissues of aspen seedlings excavated in April 2015 ($n=24$)

Parameter	Tissue	Aspen alone	Aspen with brome
Total NSC (% dry weight)	Coarse roots	9.7 ± 3.0^b	9.0 ± 1.7^b
	Fine roots	12.5 ± 2.8^a	12.0 ± 2.1^a
Starch fraction (% NSC)	Coarse roots	16.6 ± 11.2^a	4.6 ± 3.9^b
	Fine roots	17.7 ± 11.3^a	8.3 ± 6.2^b
Sugar fraction (% NSC)	Coarse roots	83.4 ± 11.2^b	95.4 ± 3.9^a
	Fine roots	8.23 ± 11.3^b	92.7 ± 6.2^a

plasticity in response to root competition, at least during this early stage of seedling growth. It should be noted that our findings pertain to planted aspen seedlings growing in a simultaneously establishing grass cover. The responses might be different when looking at below-ground interactions in natural ecotonal grassland-forest ecosystems. Kallikoski et al. (2008) presented radial extent and maximum rooting depth for three boreal tree species (*Betula pendula*, *Picea abies*, and *Pinus sylvestris*) at three developmental stages (sapling—pole—mature). Using their data to calculate the relationship between radial extent and maximum rooting depth revealed that *B. pendula* and *P. abies* maintained a fixed pattern throughout all three stages, while, in *P. sylvestris*, maximum rooting depth increased more rapidly than radial extent. To our knowledge, no study has explored this relationship for planted aspen seedlings.

Aspen is thought to employ a selective root placement strategy, preferring to proliferate roots into resource-rich patches with a little direct competition (Bauhus and Messier 1999). A *Populus* hybrid (*P. deltoides* × *balsamifera*) has also been shown to have low tolerance for root competition. In a split-pot study, the hybrid suffered reduced fine root mass and altered root morphology (lower specific root-length, SRL) in the presence of competing grass roots (Messier et al. 2009). In our study, we also found that specific root length (SRL) was lower when aspen and smooth brome grew together. Furthermore, we observed lower SRL near the soil surface where root competition was likely most intense. Moreover, in a previous study, we demonstrated that smooth brome led to a significant reduction in water and nitrate availability in the topsoil (Bockstette et al. 2017). Nitrate is highly mobile in the soil solution and becomes less available at shallow depths as soils become increasingly dry (Lynch 2013; White et al. 2013). Faced with high root densities and resource depletion near the soil surface, vertical stratification through deep root placement is often thought to be one of the main mechanisms allowing trees to successfully compete with herbaceous vegetation (Casper and Jackson 1997; Schroth 1998; Balandier 2005). Based on their findings, it would have been plausible to expect aspen seedlings to invest in deeper roots, potentially at the expense of reduced lateral spread, to minimize direct root competition and increase nitrate and water uptake (Lynch 2013; White et al. 2013); however, this is not what we observed in our experiment. It is, however, important to note that while the average maximum rooting depth was reduced in response to root competition, there was greater variability in maximum rooting depth for aspen growing with smooth brome. This likely indicates that individual seedlings experienced different levels of root restriction when competing with smooth brome. Based on the observed root system radius and maximum rooting depth, potential rooting space for aspen was reduced by 88% in response to grass competition.

This reduction in rooting space was closely reflected in an 87% reduction in total root mass as well as an 81% lower stem mass and an 84% lower leaf area.

Aspen is considered a very shade-intolerant species (Burns and Honkala 1990; Kobe and Coates 1997; Reich et al. 1998a), and while most tree species can tolerate more shade when they are small, becoming less shade-tolerant with increasing size, this trend was not found for aspen (Kneeshaw et al. 2006). Landhäusser and Lieffers (2001) observed 100% mortality of aspen seedlings transplanted into understory light conditions (~25% light transmission) after one growing season. Competition for light is considered size-asymmetric, meaning that larger individuals have a disproportionate advantage over smaller individuals, because of their ability to intercept incoming light (e.g., Craine and Dybzinski 2013). Accordingly, aspen in our study showed greater plasticity in shoot traits in response to above-ground competition for light. Lower root mass fractions (RMF) and increased stem mass fractions (SMF) in aspen growing with grass competition indicated preferential allocation to shoot growth. In combination with altered shoot morphology (lower h/d ratios and higher SSL), this allowed aspen seedlings to maximize height growth in an attempt to outgrow smooth brome (Poorter et al. 2011; Van de Peer et al. 2017; Setiawan et al. 2017). After three growing seasons, aspen seedlings growing with grass competition were thus only 23% shorter than those without; however, it took seedlings 3 years to outgrow the shade created by smooth brome's dense canopy (Bockstette et al. 2017). Our findings agree with those of Reich et al. (1998b) who found that nine boreal tree species, ranging from shade-intolerant aspen to shade-tolerant white cedar (*Thuja occidentalis*), all increased allocation to shoot over root, had higher specific leaf area, but lower specific root length in response to low light.

Reduced light availability and drought stress have been shown to lead to a depletion in non-structural carbohydrate (NSC) reserves in roots of aspen (Galvez et al. 2011, 2013; Maguire and Kobe 2015). Despite the above- and below-ground competition from smooth brome, no depletion in root NSC reserves was observed in our study. However, we found higher sugar fractions in roots of aspen growing together with smooth brome. We attributed this shift in NSC towards soluble sugars to a potential osmotic adjustment, in response to reduced water and nitrogen availability in the presence of smooth brome (Kozłowski and Pallardy 2002; Sanders and Arndt 2012). Osmotic adjustment has been shown to play a role in maintaining cell turgor at low water potentials in aspen and other *Populus* species and allows for water uptake at lower soil water potentials (Galvez et al. 2013; Gebre et al. 1998, 1994). Therefore, it is probable that this osmotic adjustment also contributed to the higher root water uptake efficiency observed in aspen when growing with smooth brome.

In summary, our findings suggest that trembling aspen seedlings exposed to intense competition with smooth brome grass showed very little architectural plasticity, especially with regard to root architecture. Preferential allocation to shoot growth and altered stem morphology allowed aspen seedlings to maximize height growth and overtop smooth brome within 3 years; however, growth rates were still much lower compared to aspen growing without grass. Aspen seedlings were able to maintain similar concentrations of root NSC reserves with or without competition, but shifted the form of NSC to sugars rather than starch when faced with competition. It appears that aspen growing with grass competition were able to partly compensate for reduced root system size and rooting space, through higher water uptake efficiency.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

- Adams TS, McCormack ML, Eissenstat DM (2013) Foraging strategies in trees of different root morphology: the role of root lifespan. *Tree Physiol* 33:940–948. <https://doi.org/10.1093/treephys/tpt067>
- Alberta Government (2015a) Agroclimatic atlas of Alberta. [http://www1.agric.gov.ab.ca/\\$department/deptdocs.nsf/all/sag6278](http://www1.agric.gov.ab.ca/$department/deptdocs.nsf/all/sag6278). Accessed 18 Feb 2016
- Alberta Government (2015b) Alberta soil information viewer. <http://www4.agric.gov.ab.ca/agrasidviewer/>. Accessed 18 Feb 2016
- Alberta Government (2016) Current and historical Alberta weather station data viewer. In: AgroClimatic Inf. Serv. <http://agriculture.alberta.ca/acis/alberta-weather-data-viewer.jsp>. Accessed 17 May 2016
- Baker JM, van Bavel CHM (1987) Measurement of mass flow of water in the stems of herbaceous plants. *Plant Cell Environ* 10:777–782. <https://doi.org/10.1111/1365-3040.ep11604765>
- Balandier P (2005) Designing forest vegetation management strategies based on the mechanisms and dynamics of crop tree competition by neighbouring vegetation. *Forestry* 79:3–27. <https://doi.org/10.1093/forestry/cpi056>
- Bardgett RD, Mommer L, De Vries FT (2014) Going underground: root traits as drivers of ecosystem processes. *Trends Ecol Evol* 29:692–699. <https://doi.org/10.1016/j.tree.2014.10.006>
- Bauhus J, Messier C (1999) Soil exploitation strategies of fine roots in different tree species of the southern boreal forest of eastern Canada. *Can J For Res* 29:260–273. <https://doi.org/10.1139/x98-206>
- Bockstette SW, Pinno BD, Dyck MF, Landhäusser SM (2017) Root competition, not soil compaction, restricts access to soil resources for aspen on a reclaimed mine soil. *Botany* 95:685–695. <https://doi.org/10.1139/cjb-2016-0301>
- Burns RM, Honkala BH, [Technical coordinators] (1990) Silvics of North America: Volume 2. Hardwoods. United States Dep. Agric. (USDA), For. Serv. Agric. Handb. 654
- Casper BB, Jackson RB (1997) Plant competition underground. *Annu Rev Ecol Syst* 28:545–570. <https://doi.org/10.1146/annurev.ecolsys.28.1.545>
- Casper BB, Schenk HJ, Jackson RB (2003) Defining a plant's below-ground zone of influence. *Ecology* 84:2313–2321. <https://doi.org/10.1890/02-0287>
- Chapin FS, Matson PA, Vitousek PM (2011) Temporal dynamics. In: Principles of terrestrial ecosystem ecology. Springer, New York, pp 339–367
- Chapman HH (1945) The effect of overhead shade on the survival of loblolly pine seedlings. *Ecology* 26:274–282. <https://doi.org/10.2307/1932406>
- Chow PS, Landhäusser SM (2004) A method for routine measurements of total sugar and starch content in woody plant tissues. *Tree Physiol* 24:1129–1136. <https://doi.org/10.1093/treephys/24.10.1129>
- Connolly J, Wayne P, Bazzaz FA (2001) Interspecific competition in plants: how well do current methods answer fundamental questions? *Am Nat* 157:107–125. <https://doi.org/10.1086/318631>
- Conway AJ, Danby RK (2014) Recent advance of forest–grassland ecotones in southwestern Yukon. *Can J For Res* 44:509–520. <https://doi.org/10.1139/cjfr-2013-0429>
- Craine JM (2006) Competition for nutrients and optimal root allocation. *Plant Soil* 285:171–185. <https://doi.org/10.1007/s11104-006-9002-x>
- Craine JM, Dybzinski R (2013) Mechanisms of plant competition for nutrients, water and light. *Funct Ecol* 27:833–840. <https://doi.org/10.1111/1365-2435.12081>
- Dillemuth FP, Rietschier EA, Cronin JT (2009) Patch dynamics of a native grass in relation to the spread of invasive smooth brome (*Bromus inermis*). *Biol Invasions* 11:1381–1391. <https://doi.org/10.1007/s10530-008-9346-7>
- Donaldson JR, Kruger EL, Lindroth RL (2006) Competition- and resource-mediated tradeoffs between growth and defensive chemistry in trembling aspen (*Populus tremuloides*). *New Phytol* 169:561–570. <https://doi.org/10.1111/j.1469-8137.2005.01613.x>
- Doust LL (1981) Population dynamics and local specialization in a clonal perennial (*Ranunculus repens*): I. The dynamics of ramets in contrasting habitats. *J Ecol* 69:743. <https://doi.org/10.2307/2259633>
- Dynamax Inc (2005) Dynagage manual. Manual, pp 1–107
- Erickson H, Harrington C, Marshall D (2009) Tree growth at stand and individual scales in two dual-species mixture experiments in southern Washington State, USA. *Can J For Res* 39:1119–1132. <https://doi.org/10.1139/X09-040>
- Fink KA, Wilson SD (2011) *Bromus inermis* invasion of a native grassland: diversity and resource reduction. *Botany* 89:157–164. <https://doi.org/10.1139/B11-004>
- Franklin JA, Zipper CE, Burger JA et al (2012) Influence of herbaceous ground cover on forest restoration of eastern US coal

- surface mines. *New For* 43:905–924. <https://doi.org/10.1007/s11056-012-9342-8>
- Galvez DA, Landhäusser SM, Tyree MT (2011) Root carbon reserve dynamics in aspen seedlings: does simulated drought induce reserve limitation? *Tree Physiol* 31:250–257. <https://doi.org/10.1093/treephys/tpr012>
- Galvez DA, Landhäusser SM, Tyree MT (2013) Low root reserve accumulation during drought may lead to winter mortality in poplar seedlings. *New Phytol* 198:139–148. <https://doi.org/10.1111/nph.12129>
- Gebre GM, Kuhns MR, Brandle JR (1994) Organic solute accumulation and dehydration tolerance in three water-stressed *Populus deltoides* clones. *Tree Physiol* 14:575–587. <https://doi.org/10.1093/treephys/14.6.575>
- Gebre GM, Tschaplinski TJ, Tuskan G, Todd DE (1998) Clonal and seasonal differences in leaf osmotic potential and organic solutes of five hybrid poplar clones grown under field conditions. *Tree Physiol* 18:645–652. <https://doi.org/10.1093/treephys/18.10.645>
- Goldberg DE (1990) Components of resource competition in plant communities. Perspectives on plant competition. Academic Press, Cambridge, pp 27–49
- Grime JP (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am Nat* 111:1169–1194. <https://doi.org/10.1086/283244>
- Henkel-Johnson D, Macdonald SE, Bork EW, Thomas BR (2016) Influence of weed composition, abundance, and spatial proximity on growth in young hybrid poplar plantations. *For Ecol Manag* 362:55–68. <https://doi.org/10.1016/j.foreco.2015.11.010>
- Hodge A (2004) The plastic plant: root responses to heterogeneous supplies of nutrients. *New Phytol* 162:9–24. <https://doi.org/10.1111/j.1469-8137.2004.01015.x>
- Hodge A, Berta G, Doussan C et al (2009) Plant root growth, architecture and function. *Plant Soil* 321:153–187. <https://doi.org/10.1007/s11104-009-9929-9>
- IBM Corp (2011) IBM SPSS statistics for Windows, version 20.0. Armonk, NY
- IUSS Working Group WRB (2015) World reference base for soil resources 2014, update 2015. International soil classification system for naming soils and creating legends for soil maps. World Soil Resources Report 106, FAO, Rome
- Kalliokoski T, Nygren P, Sievänen R (2008) Coarse root architecture of three boreal tree species growing in mixed stands. *Silva Fenn* 42:189–210
- Kembel SW, De Kroon H, Cahill JF, Mommer L (2008) Improving the scale and precision of hypotheses to explain root foraging ability. *Ann Bot* 101:1295–1301. <https://doi.org/10.1093/aob/mcn044>
- Kneeshaw DD, Kobe RK, Coates KD, Messier C (2006) Sapling size influences shade tolerance ranking among southern boreal tree species. *J Ecol* 94:471–480. <https://doi.org/10.1111/j.1365-2745.2005.01070.x>
- Kobe RK, Coates KD (1997) Models of sapling mortality as a function of growth to characterize interspecific variation in shade tolerance of eight tree species of northwestern British Columbia. *Can J For Res* 27:227–236. <https://doi.org/10.1139/x96-182>
- Kozlowski TT, Pallardy SG (2002) Acclimation and adaptive responses of woody plants to environmental stresses. *Bot Rev* 68:270–334. [https://doi.org/10.1663/0006-8101\(2002\)068\[0270:AAAROW\]2.0.CO;2](https://doi.org/10.1663/0006-8101(2002)068[0270:AAAROW]2.0.CO;2)
- Landhäusser SM, Lieffers VJ (2001) Photosynthesis and carbon allocation of six boreal tree species grown in understory and open conditions. *Tree Physiol* 21:243–250. <https://doi.org/10.1093/treephys/21.4.243>
- Leitner D, Tron S, Schröder N et al (2016) Modelling water uptake efficiency of root systems. In: EGU general assembly conference abstracts. <https://meetingorganizer.copernicus.org/EGU2016/EGU2016-17652-1.pdf>
- Lynch JP (2013) Steep, cheap and deep: an ideotype to optimize water and N acquisition by maize root systems. *Ann Bot* 112:347–357. <https://doi.org/10.1093/aob/mcs293>
- Maguire AJ, Kobe RK (2015) Drought and shade deplete nonstructural carbohydrate reserves in seedlings of five temperate tree species. *Ecol Evol* 5:5711–5721. <https://doi.org/10.1002/ece3.1819>
- Messier C, Coll L, Poitras-Larivière A et al (2009) Resource and non-resource root competition effects of grasses on early- versus late-successional trees. *J Ecol* 97:548–554. <https://doi.org/10.1111/j.1365-2745.2009.01500.x>
- Mommer L, Wagemaker CAM, De Kroon H, Ouborg NJ (2008) Unravelling below-ground plant distributions: a real-time polymerase chain reaction method for quantifying species proportions in mixed root samples. *Mol Ecol Resour* 8:947–953. <https://doi.org/10.1111/j.1755-0998.2008.02130.x>
- Mommer L, Visser EJW, van Ruijven J et al (2011) Contrasting root behaviour in two grass species: a test of functionality in dynamic heterogeneous conditions. *Plant Soil* 344:347–360. <https://doi.org/10.1007/s11104-011-0752-8>
- Otfinowski R, Kenkel NC, Catling PM (2007) The biology of Canadian weeds. 134. *Bromus inermis* Leyss. *Can J Plant Sci* 87:183–198. <https://doi.org/10.4141/P06-071> doi
- Pierik R, Mommer L, Voesenek LA (2013) Molecular mechanisms of plant competition: neighbour detection and response strategies. *Funct Ecol* 27:841–853. <https://doi.org/10.1111/1365-2435.12010>
- Poorter H, Niklas KJ, Reich PB et al (2011) Biomass allocation to leaves, stems and roots: meta-analysis of interspecific variation and environmental control. *New Phytol* 193:30–50. <https://doi.org/10.1111/j.1469-8137.2011.03952.x>
- Randall MJ, Karst J, Pec GJ et al (2014) A molecular identification protocol for roots of boreal forest tree species. *Appl Plant Sci* 2:1400069. <https://doi.org/10.3732/apps.1400069>
- Ravenek JM, Mommer L, Visser EJW et al (2016) Linking root traits and competitive success in grassland species. *Plant Soil* 407:39–53. <https://doi.org/10.1007/s11104-016-2843-z>
- Reich PB, Reich PB, Walters MB et al (1998a) Photosynthesis and respiration rates depend on leaf and root morphology and nitrogen concentration in nine boreal tree species differing in relative growth rate. *Funct Ecol* 12:395–405. <https://doi.org/10.1046/j.1365-2435.1998.00209.x>
- Reich PB, Tjoelker MG, Walters MB et al (1998b) Close association of RGR, leaf and root morphology, seed mass and shade tolerance in seedlings of nine boreal tree species grown in high and low light. *Funct Ecol* 12:327–338. <https://doi.org/10.1046/j.1365-2435.1998.00208.x>
- Saiz H, Bittebiere A-K, Benot M-L et al (2016) Understanding clonal plant competition for space over time: a fine-scale spatial approach based on experimental communities. *J Veg Sci* 27:759–770. <https://doi.org/10.1111/jvs.12392>
- Salesman JB, Thomsen M (2011) Smooth brome (*Bromus inermis*) in tallgrass prairies: a review of control methods and future research directions. *Ecol Restor* 29:374–381. <https://doi.org/10.3368/er.29.4.374>
- Sanders GJ, Arndt SK (2012) Osmotic adjustment under drought conditions. In: Aroca R (ed) Plant responses to drought stress. Springer, Berlin, pp 199–229
- Schroth G (1998) A review of belowground interactions in agroforestry, focussing on mechanisms and management options. *Agrofor Syst* 43:5–34. <https://doi.org/10.1023/A:1026443018920>
- Setiawan NN, Vanhellemont M, Baeten L et al (2017) Local neighbourhood effects on sapling growth in a young experimental forest. *For Ecol Manag* 384:424–443. <https://doi.org/10.1016/j.foreco.2016.10.012>
- Taggart JM, Cahill JF, McNickle GG, Hall JC (2011) Molecular identification of roots from a grassland community using size differences in fluorescently labelled PCR amplicons of three cpDNA

- regions. *Mol Ecol Resour* 11:185–195. <https://doi.org/10.1111/j.1755-0998.2010.02893.x>
- Trinder CJ, Brooker RW, Robinson D (2013) Plant ecology's guilty little secret: understanding the dynamics of plant competition. *Funct Ecol* 27:918–929. <https://doi.org/10.1111/1365-2435.12078>
- Valladares F, Niinemets Ü (2007) The architecture of plant crowns. In: *Functional plant ecology*, 2nd edn. CRC Press, New York
- Van de Peer T, Verheyen K, Kint V et al (2017) Plasticity of tree architecture through interspecific and intraspecific competition in a young experimental plantation. *For Ecol Manag* 385:1–9. <https://doi.org/10.1016/j.foreco.2016.11.015>
- White PJ, George TS, Gregory PJ et al (2013) Matching roots to their environment. *Ann Bot* 112:207–222. <https://doi.org/10.1093/aob/mct123>
- Wilson SD (2014) Below-ground opportunities in vegetation science. *J Veg Sci* 25:1117–1125. <https://doi.org/10.1111/jvs.12168>
- Zhang Z, Pan X, Zhang Z et al (2015) Specialist insect herbivore and light availability do not interact in the evolution of an invasive plant. *PLoS One* 10:e0139234. <https://doi.org/10.1371/journal.pone.0139234>