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Above- and below-ground biomass partitioning and fine root morphology in juvenile Sitka spruce clones in monoclonal and polyclonal mixtures

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ABSTRACT

Six juvenile Sitka spruce (*Picea sitchensis* (Bong.) Carr) clones were grown in monoclonal (pure) and polyclonal mixtures (mixed) in a field experiment to assess effects of clonal diversity on above- and below-ground growth, biomass partitioning and fine root morphology. Shoot height and root collar diameter were measured twice annually and after the second year 48 clones were destructively harvested. Fine roots were divided into 10 diameter classes, for each of which morphological characteristics were calculated from digitized images. Competitive interactions arising from deployment type were found to significantly increase fine root surface area in mixed plots and fine root length in pure plots for two fine root diameter classes for some clones. Competitive interactions were also found to significantly alter relationships between above- and below-ground variables and reduce the strength and significance of relationships among root traits in mixed plots. Significant inter-clonal variation for many above- and below-ground parameters was also observed. The two most productive clones, in terms of height and diameter growth, differed significantly in biomass partitioning suggesting that a high degree of variation occurs among Sitka spruce clones, which may affect stand productivity and uniformity.

1. Introduction

Trees are able to sense competition from neighbours through changes in the ratio of red to far red (R: FR) wavelengths, and adjust their biomass partitioning to maximise growth before shading occurs (Aphalo and Ballaré, 1995). Although a wide variety of changes have been observed above-ground, little is known about associated changes in below-ground structures. The majority of studies which assessed below-ground responses to competition typically used trees grown from seed, making it difficult to determine genetic effects from environmental effects (Brassard et al., 2011; Domisch et al., 2015; Forrester et al., 2006; Litton et al., 2003). Using clonal material, rather than seedlings, enables the effects of genetic variability to be distinguished more readily from phenotypic plasticity (Aspelmeier and Leuschner, 2006).

Related neighbours occupy similar niches and root systems may demonstrate high degrees of plasticity by increasing root density, length or depth to avoid intra-genotypic competitive interactions (Elferjani et al., 2014; Forrester et al., 2006; Jagodzinski et al., 2016). Morphological and physiological differences have been found among clones. For example, Pregitzer et al. (1990) observed clonal variation in fine root development as well as root carbohydrate and nitrogen dynamics in *Populus*. Additionally, Nguyen et al. (1990) recorded clonal differences in non-structural carbohydrates of roots of two *Populus* clones, which corresponded to phenological differences.

Variation in tree density can also affect growth and biomass partitioning (Jagodzinski and Oleksyn, 2009b; Litton et al., 2003). Hyatt et al. (1998) found that increased density resulted in higher ratios of stem to leaf biomass in *Abutilon theophrasti*. Changes to below-ground biomass partitioning in juvenile coniferous forests have also been observed and are strongly influenced by stand density with increases in root biomass corresponding to increases in stand density (Litton et al., 2003). Additionally, above- and below-ground traits may be correlated. Hyatt et al. (1998) observed that total root biomass and shoot biomass were highly correlated in *A. theophrasti*. However, fine root length was only related with above-ground biomass in small sub-canopy plants in crowded populations and these plants did not alter their

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partitioning strategy in response to above-ground competition. In contrast, Al Afas et al. (2008) did not observe significant correlations between fine root traits and above-ground biomass in *Populus* clones but found significant differences among clones for fine root biomass.

Roots play an essential role in tree growth, however as most root study methods are crude and labour-intensive, roots are the least studied area of terrestrial ecosystems (Domisch et al., 2015). Fine roots are vital for resource acquisition and carbon dynamics, so determining competition-induced morphological changes is important since it may affect a tree's ability to compete effectively with its neighbours. Additionally, fine root length and surface area provides detailed information on how roots acquire resources and occupy soil area (Fitter, 2002). Although information on fine root distribution, growth and seasonal dynamics (Bonicel et al., 1987; Nguyen et al., 1990; Zadworny et al., 2015) is available for some tree species, to the authors' knowledge no studies have been conducted that specifically examined fine root morphology resulting from inter- and intra-clonal competitive interactions in tree clones. Furthermore, information on fine roots are not only lacking for the *Picea* genus, but for conifers as a whole.

The objectives of this study were to determine if intra- and inter-clonal competition: (1) altered the relationships between above- and below-ground variables, (2) influenced fine root morphology, biomass partitioning and stem growth within and between clones.

2. Materials and methods

2.1. Plant material

An experiment with six genetically improved one-year old Sitka spruce (*Picea sitchensis* (Bong.) Carr.) clones was established at the National Tree Improvement Centre, Kilmacurra, Co. Wicklow, Ireland (52° 93′ N, 6° 14′ E, 133 m a.s.l.) in April 2013. According to 30 year average meteorological observations from the on-site weather station (Met Éireann) the mean annual temperature is 9.9 °C with a mean annual precipitation of 1178 mm.

Trees used in this experiment displayed superior height growth and were produced from full-sibling crosses from the Irish tree improvement programme (Table 1) and were propagated using somatic embryogenesis (Thompson, 2013). Several weeks after the early-stage somatic embryo structures were evident, plants were transferred into individual plugs with a peat pearlite (2:1) mixture containing 250 g L^{-1} fertilizer (Osmocote®, Everris International B.V.) and 5 g L^{-1} insecticide (suSCon Green, Crop Care Australasia Proprietary Ltd.). The plants were transferred to a high humidity greenhouse to acclimatise for approximately a month and were then moved to poly-tunnels prior to being planted.

2.2. Experimental design

The experiment was established in spring 2013. The soil was uniform throughout and was classified as a sandy loam with approximately 7.3% clay, 14.1% silt, 78.6% sand and 9.2% organic matter. Prior to establishment, the site was ploughed to a depth of approximately 13 cm and treated with glyphosate (Roundup, Monsanto) at a rate of 5 L ha^{-1}. The experiment was designed with two factors, deployment type and clone, replicated in four blocks. There were two deployment types, single-tree monoclonal plots (pure) and multi-clone mixtures (mixed), with six clones per plot. Each block contained seven plots: one mixed plot contained all clones and one pure plot of each of the six clones. In mixed plots, a random assortment of clones was planted around the perimeter of each plot to reduce any edge effects, while in each monoclonal plot, the same clone as the measurement clone was used to create a buffer. Pure plots contained 20 ramets, while mixed plots contained 40 ramets. All data collected in this study were derived from the central ramets of each plot. All ramets were hand planted at a distance of 0.3 m between rows and within rows.

Table 1
Clones planted in the experiment and the crosses they were derived from.

Clone number	Cross
1	230 × 519
2	377 × 574
3	583 × 519
4	574 × 519
5	27 × 306
6	377 × 519

3. Observations and measurements

3.1. Above-ground parameters

Shoot height and root collar diameter were measured twice annually in both 2013 and 2014. Interception of photosynthetically active radiation (PAR) was calculated by measuring PAR above the crown and at ground level using a Line Quantum Sensor (model LI-191 Li-Cor, Lincoln, NE, USA). Measurements were made in the centre row of each plot at the end of each growing season (October). Percentage PAR interception was calculated by dividing PAR levels at ground level by the corresponding PAR level above the canopy.

In November 2014, after two growing seasons, one ramet per treatment was selected for destructive sampling. If the selected ramet was defective (e.g. multiple leaders), or had been replaced due to mortality, the nearest defect-free ramet was selected instead. Specific leaf area (SLA, cm^2 g^{-1}) was assessed by removing needles from a 5 cm mid-section of a north-orientated branch from the topmost whorl and needle area was measured with a portable leaf area meter (LI-3000, Li-Cor, Lincoln, NE, USA). Ramets were then cut at the base and separated into foliage, branches and stem. Each component was dried at 80 °C for at least 48 h to a constant weight (PW 124, Adam Equipment, South Africa).

3.2. Below-ground parameters

A soil monolith measuring 0.30 × 0.30 × 0.25 m^3 was excavated from the base of each ramet and processed immediately. Soil monoliths were placed in individual plastic bags containing water for 24 h to loosen soil particles, after which they were carefully hand washed to remove moss, soil and stone particles. The roots were kept moist in plastic bags, stored at 1–2 °C, and then dispatched to the Institute of Dendrology, Polish Academy of Sciences, Kórnik, Poland.

Individual root samples were separated into fine (⩽2 mm) and coarse roots (>2 mm) and further dissected to facilitate scanning. Fine roots were then placed on transparent Perspex plates and digitized at 300 dpi and measured using image analysis software (WinRHIZO Pro 2013d, Régent Instruments Inc., Quebec, Canada) in conjunction with a professional flatbed scanner (Epson Expression XL 1000, Epson, Suwa, NGN, Japan) to determine total fine root length (m), surface area (SA, m^2), projected area (PA, m^2) and number of root tips per diameter class for 10 root diameter classes ranging from 0 to ⩽2 mm in 0.2 mm increments (0–0.2, 0.2–0.4, ..., 1.8–2 mm). Coarse roots (>2 mm) were excluded from any morphological analysis but were included in total root weight calculation and derived root ratio equations.