



Unique responses of respiration, growth, and non-structural carbohydrate storage in sink tissue of conifer seedlings to an elevation gradient at timberline

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ARTICLE INFO

Article history:

Received 23 November 2009
Received in revised form 27 April 2010
Accepted 4 May 2010

Keywords:

Abies lasiocarpa
Carbon balance
Pseudotsuga menziesii
Relative growth rate
Starch
Timberline

ABSTRACT

The role of carbon balance, and particularly carbon sinks, to forest boundaries and climate responses is a major question in forest ecophysiology. At timberline, low-temperature limitations on carbon-sink processes of stem and especially root tissue have been implicated in hypotheses of the upper range limits to tree distributions. Studies on carbon sinks in root and stem tissue of trees at timberline typically report variation in only one carbon sink, such as either growth, respiration, or non-structural carbohydrates (NSCs). However, these carbon sinks may differ in their response to elevation. We asked how three carbon-sink processes in root and stem tissue (i.e. all tissue below the crown of needles) change in conifer seedlings growing from the lower (2450 m) to the upper (3000 m) edges of the timberline ecotone throughout their first growth season. We repeatedly measured respiration (mg^{-1} and individual^{-1}), growth (relative growth rates [RGR] and biomass), and NSCs in root and stem tissue of *Abies lasiocarpa* and *Pseudotsuga menziesii*.

RGR of root and stem tissue were less at the upper compared to lower elevation, but only for the first few weeks of the growing season. Total biomass of root and stem tissue was generally less at the upper site, apparently due to low early season RGR, but ultimately did not significantly differ between sites by the end of the growing season. Unlike growth, respiration rates (mg^{-1}) did not differ between elevations during any period of the growing season. Nevertheless, total respiration of CO_2 from root and stem tissue (individual^{-1}) was 22% less at the upper site, which was attributable to less biomass. NSCs of root and stem tissue, specifically starch, were overall greater at the upper site, particularly for *A. lasiocarpa* at the end of the season, which did not parallel spatiotemporal trends in growth or respiration. The differences in seasonal trends and the effects of elevation on carbon sinks indicate a degree of independence or uncoupling of growth, respiration, and NSCs of root and stem tissue, which is not commonly appreciated in hypotheses about physiological limitations for trees at timberline.

Published by Elsevier B.V.

1. Introduction

A significant portion of carbon utilization in plants occurs in roots, stems, and branch tissues that are partially belowground, are difficult to measure, and are often sampled near the soil surface (Larcher, 2003; Litton et al., 2007). Environmental effects on carbon sinks in root and stem tissues are important because limitations on carbon use in roots and stems have been pointed to as a possible constraint to successful establishment, survival, reproduction, and ultimately species distributions in cool climates (Körner, 1998). Growth, respiration, and carbon storage are primary carbon sinks

in roots and stems of plants, and are tightly coupled to one another through their roles in carbon and energy supplies and demands. However, these processes could be unique in their responses to the environment, leading to changes in their relationships under different conditions (Gill et al., 2002).

Temperature can have a large influence on rates of carbon utilization, particularly those processes that involve enzyme activity (Pregitzer et al., 2000). Relatively low soil temperatures at high elevation can slow, or completely inhibit rates of biosynthesis, respiration, and carbon storage in root and stem tissue, and some have speculated that this restricts tree distributions near alpine-treeline (Körner, 1998; Alvarez-Uria and Körner, 2007; Körner and Hoch, 2006). Even though there is considerable interest in limitations to carbon utilization in trees near treeline, no studies have compared how growth, respiration, and carbon storage of root and stem tissue respond to elevation. Newly germinating seedlings are more susceptible to the negative effects of elevation on carbon-sink

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processes compared to older age classes because of their sensitivity to environmental stress, combined with high growth requirements and low carbon resources (Luxmoore et al., 1995; Germino and Smith, 1999; Smith et al., 2003; Bansal and Germino, 2010).

Growth of root and stem tissue may be particularly sensitive to low temperatures. Chilling reduced growth of roots relative to leaves in tree seedlings under laboratory conditions (Alvarez-Uria and Körner, 2007). Respiration is also temperature-sensitive (Sowell and Spomer, 1986; Ryan, 1991; Weger and Guy, 1991), especially in young tissues (Palta and Nobel, 1989), and is inherently linked to growth. Specifically, reduced growth in cool conditions should reduce the demand for ATP and thus respiration rates (Atkin and Tjoelker, 2003). Also, less growth of root and stem tissue produces less respiratory biomass, which can reduce total respiration from root and stem tissue (individual⁻¹). Consequently, even small changes in growth of root and stem tissue can have a significant impact on the extent of CO₂ respired from root and stem tissue.

Despite the importance of respiration to tree carbon balance, data on respiration from root and stem tissue are scarce, especially *in situ* in trees growing in the timberline ecotone. The rarity of data is likely because respiration of root and stem tissue is largely below-ground and is difficult to separate from other sources of soil CO₂ efflux, such as microbial respiration. Water or nutrient limitations can also decrease respiration rates, which may interact with temperature effects on respiration (Slot et al., 2008). Root and stem tissue of first-year conifer seedlings primarily consists of roots, with a relatively small stem, and no branches. It is therefore possible to overcome the challenge of measuring the root contribution to root and stem respiration by using semi-confined pots embedded in soil to control for micro-environmental variation, and to allow complete extraction of root tissues.

Non-structural carbohydrates (NSCs) can account for up to 20% root and stem tissue biomass (Kozłowski, 1992). NSCs in root and stem tissue are intrinsically linked to many physiological processes in plants, and may fluctuate considerably in response to variations in growth or respiration (Pregitzer et al., 2000). Many studies on trees at treeline have reported increases in NSCs concentrations in root and stem tissue with increasing elevation (e.g., Körner, 1998; Hoch et al., 2002; Hoch and Körner, 2003), which is assumed to occur in part from reductions in biosynthesis or respiration, or may also result from active accumulation of carbon stores for coping with long periods of sub-zero temperatures (Ögren et al., 1997; Janusz et al., 2001; Tolsma et al., 2007).

Even though carbon-sink processes in root and stem tissue are physiologically linked to each other, they may differ in their response to elevation. Studies on carbon sinks in root and stem tissue of trees at treeline typically report variation in only one carbon sink, such as either growth, respiration, or NSCs (e.g., Alvarez-Uria and Körner, 2007; Wieser and Bahn, 2004; Hoch et al., 2002), but we found no studies comparing all three variables together. Thus, the comparative sensitivity of each sink to high elevation conditions is not well known. In this study, we present new data on the effects of elevation on respiration of root and stem tissue (i.e. all tissue below the crown of needles) in conifer seedlings of *Abies lasiocarpa* and *Pseudotsuga menziesii*, and analyze how the effects of elevation on respiration compare to growth and NSCs of the same tissue.

2. Materials and methods

2.1. Study site and species

The study area was located on the west slope of Fred's Mountain in the Teton Range of the Rocky Mountains, USA (43°47.26'N; 110°57.52'W). In 2006, we established sites at the lower and upper

edges of the timberline ecotone (2450 and 3000 m, respectively). At each site, we grew seedlings of *P. menziesii* (Mirb.) Franco and *A. lasiocarpa* (Hook.) Nutt., which are co-dominant species of the sub-alpine forests in the Rocky Mountains. *Abies lasiocarpa* has a natural range that occurs up to alpine-treeline, near 3100 m, whereas *P. menziesii* typically does not occur above 2700 m (300 m below our upper site).

2.2. Seed source and propagation of seedlings

Seeds of *P. menziesii* were obtained from U.S. Forest Service collections made at 2125 and 2425 m in the same genetic and geographic seed zone as the study area. Seeds of *A. lasiocarpa* were collected at approximately 3000 m from San Isabel National Forest, about 3° latitude south in the Rocky Mountains (Dean Swift Seed Co., Jaroso, CO, USA). Seed sources of both species were from approximately 500 m below treeline elevation at their respective origins. Provenance studies with conifers indicate that the effects from altitude and latitude of seed source would be minimal for our response variables (based on data from Oleksyn et al., 1998, 2000; Teskey and Will, 1999). Seed masses were similar between the two species (70–80 seeds/g).

Seeds were germinated under greenhouse conditions at the University of Idaho Forest Research Nursery, Moscow, ID, USA (46°43.57'N; 116°59.01'W) in plastic "conetainers" (Ray Leach Cells™, 3.8 cm diameter, 21 cm depth, Eugene, OR, USA) in a commercial conifer potting mix (Pro-mix, Wilbur Ellis, San Francisco, CA, USA) that was mycorrhizae-free, sterilized, and had peat moss, bark, dolomite limestone, and other small quantities of organic and mineral conditioners. We transported the newly emerging seedlings to the study site within 1 week of germination (4th week of June). Holes were pre-drilled at the field sites to fit the conetainers, and the seedlings were outplanted into the holes so their soil surface was level with the surrounding soil, and they remained rooted in their containers to facilitate recovery of entire root system. Seedlings were watered to promote survival following outplanting.

2.3. Plot layout, microclimate measurements, and sampling schedule

We established 10 plots with four seedlings of each species at each of the sites. Plots were approximately 1 m × 2 m, and positioned at random distances along five 30-m transects (2 plots/transect) within a 0.5 ha area having relatively flat topography and representative herb cover and soils. Mean (±1 SE) canopy openness across all plots was not significantly different between the 2450 and 3000 m elevation sites (64.5 ± 6.1% and 61.7 ± 10.9% openness, respectively).

We placed three HOBO temperature data loggers (Model Pro 8, Onset Corp., Bourne, MA, USA) at each site. The console with an internal sensor was buried 5 cm below the soil surface. Instantaneous temperature readings were logged every 30 min. These data were used to calculate daily mean, maximum, and minimum temperatures in soil from the time of outplanting to harvest.

Sampling events started 10 days after outplanting, and were repeated about every 3rd week during the growing season, giving a total of four sampling events. During each sampling event, we randomly selected four to six of the 10 plots at each elevation, and then one seedling per species per plot was randomly selected for measurements of respiration, growth, and NSCs of root and stem tissue, giving a total of 72 seedlings throughout the growing season. There was low replication for the *A. lasiocarpa* respiration measurement on the third sampling date due to time limitations from other measurements.

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