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ScienceDirect
Forest Ecology and Management 246 (2007) 222–231
Forest Ecology and Management
www.elsevier.com/locate/foreco

Root allocation and water uptake patterns in riparian tree saplings: Responses to irrigation and defoliation

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Received 21 November 2006; received in revised form 30 March 2007; accepted 4 April 2007

Abstract

The genus *Populus* relies on shallow groundwater for successful recruitment and is often the focus of riparian restoration efforts. Under some circumstances mature trees take up a substantial proportion of their water from unsaturated soil water derived from growing season rainfall, but it is unknown how *Populus* saplings may alter root allocation patterns and water use in response to water availability and carbon limitations. Although it has been inferred that root allocation differs with changes in water uptake patterns as determined with stable isotope studies, this notion has rarely been tested. We conducted a glasshouse experiment with *Populus fremontii* (Frémont cottonwood) saplings to determine how allocation to fine and coarse roots, leaf gas exchange, root respiration and water uptake from hydrologically isolated upper and lower soil compartments would be altered by above- and belowground resource limitations. Aboveground carbon limitations were imposed with defoliation. Belowground resource limitations were imposed by maintaining high or low soil water availability in lower soil compartment. Isotopically labeled water was supplied in pulses to upper soil compartments to determine the proportion of transpiration water derived from each compartment. Above- and belowground resource limitations differentially altered use of surface water pulses and affected patterns of fine root allocation. Proportional use of water sources was plastic and changed in response to water availability and defoliation. Changes in fine root biomass allocation were associated with changes in water-source use for water-stressed plants. Defoliated plants in both watering treatments used proportionally less of the surface pulse than undefoliated plants. In contrast, plants that were water limited, but not carbon limited had a higher ratio of shallow fine roots to deep fine roots and took up proportionally more water from the surface pulse. These data suggest that carbon limited saplings take up less water with shallow roots. Thus, *P. fremontii* exhibited belowground allocation tradeoffs in response to spatial heterogeneity of soil water and carbon limitations. Furthermore, our data suggest that successful recruitment events may be influenced by the occurrence of summer rainfall, and by factors affecting canopy carbon gain.
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Keywords: *Populus fremontii*; Root respiration; Stable hydrogen isotope ratios; Water-source use; Rhizopods

1. Introduction

There has been considerable research focused on the genus *Populus* and its reliance on groundwater. Several studies have examined the effects of different rates of groundwater decline on the survival and growth of cottonwood using experimental pots ('rhizopods'), which simulate groundwater decline (Mahoney and Rood, 1991; Amlin and Rood, 2002). In general, shoot growth is reduced with increasing rates of water table decline, from 1 to 10 cm day^{-1}, and this results in an increased root:shoot ratio (Mahoney and Rood, 1991, 1992; Kranjcec et al., 1998; Amlin and Rood, 2002). Root elongation rates are generally greatest with moderate (2–4 cm day^{-1}) water table declines (Mahoney and Rood, 1992; Kranjcec et al., 1998; Amlin and Rood, 2002), however in some cases severe drawdown (10 cm day^{-1}) promoted the greatest rates of root elongation (Mahoney and Rood, 1992; Kranjcec et al., 1998; Amlin and Rood, 2002). The highest rates of seedling survival have been found for moderate drawdown rates (Mahoney and Rood, 1991; Segelquist et al., 1993), which varied from 2 to <1 cm day^{-1} for hybrid *Populus* in Canada and *Populus deltoides* in Colorado, respectively. Optimal rates of drawdown for root elongation and seedling survival are likely to vary with climate, species and soil substrate (Kranjcec et al., 1998).

Few studies have examined whether plants may be able to substitute shallow soil water for groundwater in these

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0378-1127/$ – see front matter. Published by Elsevier B.V.
doi:10.1016/j.foreco.2007.04.032

controlled experiments. In many riparian systems summer monsoon rains during the height of the growing season could provide alternative sources of water to promote successful recruitment events. The recruitment box model (Mahoney and Rood, 1998) integrates rates of stream hydrograph decline with cottonwood seed viability and root elongation rates to predict successful recruitment events, which is useful for restoration. For example, a 2.5 cm day^{-1} groundwater decline facilitates successful recruitment of cottonwood along the Truckee River in Nevada. Yet other sources of water may be available to both native and non-native species, which may impact recruitment events and the applicability of the recruitment-box model if species are able to substitute precipitation for groundwater. Understanding what abiotic and biotic conditions promote use of shallow and deep water sources by woody plants and characterizing responses by species and populations is critical for establishing predictive relationships under future climate change scenarios or changing groundwater levels.

The primary objective of this study was to determine how root allocation patterns and use of shallow and deep water varied with drought and defoliation of *Populus fremontii* (Frémont cottonwood). Above- and belowground limitations were imposed by reducing carbon assimilation through defoliation and by changing belowground water availability.

Many woody plants in semi-arid and arid ecosystems have a dimorphic root system with shallow lateral roots and deep sinker or taproots. It is generally thought that plants proliferate roots in resource rich patches to optimize carbon allocation (see review by Fitter, 1994). In regions where water is often the most limiting resource to plant growth, proliferation of roots into moist patches carries a cost to the plant. In addition root growth into one patch comes as a tradeoff to growth into another moist patch. As a result if the moist patch is short lived, the cost of growing and maintaining the new root may not be repaid (Nobel et al., 1992; Fitter, 1994). Furthermore, as a plant becomes increasingly carbon-limited, there may be additional tradeoffs in resource allocation.

Traditional studies of roots using belowground harvesting have equated root proliferation with resource use from a particular patch (Fitter, 1994). However, these studies did not measure water or nutrient use directly. Recent studies of the stable isotopic composition of xylem sap have been used to directly determine water-source use from different soil depths (Brunel et al., 1995). These studies indicate that woody plants may redirect limited carbon resources in response to the relative availability of water resources (Dawson and Ehleringer, 1998; Kolb et al., 1997; Snyder and Williams, 2000). Changes in the isotopic composition of xylem sap have been used to ‘‘imply’’ that there are changes in rooting distribution or functional root area profiles. However, few studies to date have investigated whether changes in root biomass or distribution are associated with changes in water-source use (but see Dawson and Pate, 1996).

The objective of the current study was to determine if changes in root biomass distributions were associated with different water-use patterns within a controlled glasshouse environment and what abiotic and biotic conditions may promote use of shallow soil water. Additionally, we were interested in establishing some baseline data on *in situ* respiration of suberized and unsuberized roots of *P. fremontii*. We used *P. fremontii*, a woody phreatophyte, as a model plant because field studies have shown that this species can use different amounts of shallow soil water at sites with different depths to groundwater (Snyder and Williams, 2000) and because of the widespread interest in restoring cottonwood forests in the western United States. We asked the following questions: (1) does the presence of a stable deep water-source affect a plant's ability to use pulses of shallow soil water; (2) do plants exhibit plastic responses to changes in water availability belowground and are these changes manifested in root biomass patterns and water-source use; (3) does defoliation affect patterns of biomass allocation and pulse use; (4) what are the respiration rates of suberized and unsuberized roots? We predicted that plants with access to a stable deep-water source would optimally allocate to roots in wetter soil layers, and that this allocation would come as a tradeoff to root allocation in drier soil layers. Plants without a stable deep-water source were predicted to exhibit increased use of shallow soil water. As plants became increasingly carbon-limited we predicted they should exhibit more efficient foraging for water due to potentially greater respiratory costs of highly absorptive unsuberized roots.

2. Methods

2.1. Experimental design and pot construction

We constructed pots (i.e. rhizopods) to create different water availability in upper and lower compartments. The objective was to create similar soil moisture conditions in the upper compartments and different conditions in the lower compartment. Pots were constructed from polyvinyl chloride tubes 0.48 m in diameter and 1.1 m deep (Fig. 1). Pots were split in half to separate upper and lower portions of the soil column and

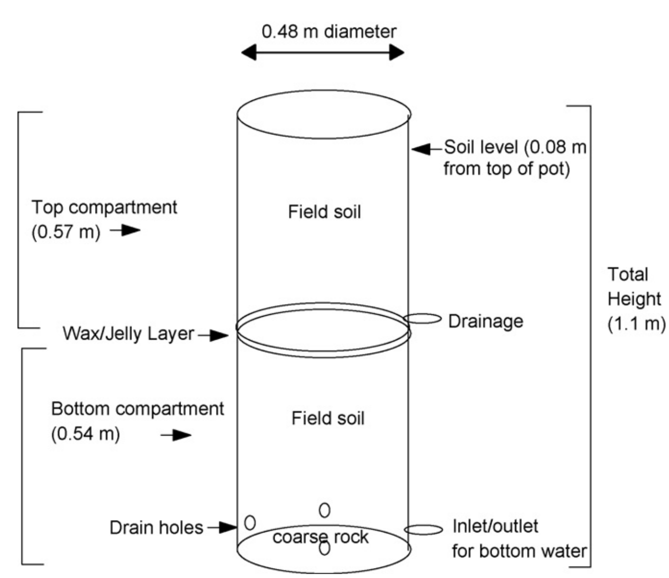

Fig. 1. A schematic of the pot design used in the glasshouse experiment.