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Depth of root placement, root size and carbon reserves determine reproduction success of aspen root fragments

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ABSTRACT

The vegetative recovery of species capable of resprouting is strongly driven by the disturbance type, the resprouting traits of the species, and the resource availability in the surviving tissues. Since aspen (*Populus tremuloides*) commonly regenerates from root suckers after disturbance; we can take advantage of its ability to sprout by applying salvaged surface soils containing aspen root fragments to reclaim heavily disturbed forest sites where soil surfaces have been displaced by resource extraction. In two studies we investigated the role of root size, root carbohydrate reserves, and the presence of fine roots on the ability of root fragments to initiate and grow suckers from different soil depths. Roots of different diameters were collected from natural aspen stands and buried at three different soil depths (5, 20 and 40 cm). Non-structural carbohydrate (NSC) reserves were determined initially and after the experimental period at the end of August. The initiation of suckers was not affected by soil depth, root size, and the presence of fine roots. Suckers, however, did not emerge from the soil if root fragments were buried at a depth of 40 cm. The largest suckers were found on root fragments that were 2.1–3 cm in diameter. Sucker performance and root fragment survival increased with the initial NSC reserves stored in the root fragments. Insufficient initial NSC supply for suckering resulted in the death of root fragments indicating that there might be a lower threshold of NSC root reserves. The presence of fine roots appear to be a liability, as overall sucker numbers were three times higher in root fragments that had all their fine roots removed compared to root fragments with fine roots attached.

1. Introduction

The rapid recovery of photosynthetic potential from protected buds (budbank) is a common strategy in plants living in disturbance prone environments. Species capable of resprouting have strategies that allow them to translocate resources from surviving organs to the regenerating tissues and organs. The vegetative recovery of these species after disturbance is strongly driven by the disturbance type, the resprouting traits of the species involved, and the associated resource availability in the surviving tissues (Chapin et al., 1990; Poorter et al., 2012; Clarke et al., 2013). Biomass allocation patterns and the related storage of non-structural carbohydrates (NSC) reserves fundamentally drive the resource availability for resprouting after a severe disturbance, where reserves need to be allocated to the maintenance of the surviving tissues (respiration) and the regeneration and maintenance of new stem, leaf, and root tissues (Lambers et al., 2002). These allocation patterns are known to be under the control of environmental variables such as light, temperature and moisture (Poorter et al., 2012).

Trembling aspen (*Populus tremuloides* Michx.) regenerates through suckering from its root system after disturbances such as fire or logging disturb the above-ground portion of the clone (DesRochers and Lieffers, 2001; Farmer, 1962; Frey et al., 2003). Vegetative regeneration is dense and vigorous when these disturbances create little damage to the root system (Frey et al., 2003; Renkema et al., 2009). In contrast heavy mechanical soil disturbances from trafficking of the forest floor during conventional forest harvesting (e.g. log decking areas) or after complete removal of roots during road construction or mineral resource extraction can cause severe reduction in the suckering potential from the fragmented root system (Renkema et al., 2009). In the latter case the surface soils are often salvaged and stored for several months in stockpiles and then placed back onto the disturbed area after operations have ceased (“roll back”), where the root fragments in the roll back material could be available for sprouting and aspen regeneration.

The success of sucker initiation after this roll back of soil and root fragments is likely influenced by factors such as the depth a root fragment is placed, the physiological state of the fragment, and its ability to interact with the surrounding soil. Under natural undisturbed soil conditions most suckers originate from smaller diameter roots (0.5–2.5 cm) (DesRochers and Lieffers, 2001;

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Kemperman, 1978; Schier and Campbell, 1978) and from roots that are located at depths of 4–15 cm; this is likely a result of the more favourable conditions in these upper soil layers (e.g. warm soil temperature, aeration, and high concentration of nutrients) (Brown and DeByle, 1987; Horton and Maini, 1964; Kemperman, 1978; Navratil, 1991; Schier, 1973; Schier and Campbell, 1978). There is relatively little information on the vertical distribution of aspen roots in soil (Strong and LaRoi, 1983), but aspen roots can also be found in deeper parts of the soil profile, as a result of root competition with other woody species (Mundell et al., 2007) or moisture limitation (Snedden unpublished). However there is little knowledge of the suckering ability of these deeper roots.

Available non-structural carbohydrate (NSC) reserves influence suckering performance of aspen roots (Landhäusser and Lieffers, 2002; Schier and Zasada, 1973). Although NSC concentrations appear not to influence the initiation of suckers, they are important for early sucker shoot expansion and growth (Frey et al., 2003; Landhäusser and Lieffers, 2002; Schier and Zasada, 1973). As a result root NSC concentrations might be pivotal to success of suckers when they originate from greater soil depths or are slowed by physical barriers (Landhäusser et al., 2007a, 2007b; Renkema et al., 2009). The role of the content of NSC reserves in aspen roots, however, is less clear. If present, plant NSC reserves can readily be mobilized and translocated within the plant to sinks where NSC are needed; however in root fragments the NSC reserves are limited by the size of the root fragment and as a result pool size of the fragments might play a larger role. Plant NSC reserves can be expressed as a concentration (tissue status) or content (pool size - root size and concentration) (Dirr and Heuser, 1987; Ede et al., 1997; Nguyen et al., 1990).

Another factor possibly influencing the suckering ability of root fragments in rolled back materials could be related to the ability of the root fragments to connect with the surrounding soil and its ability to take up water and nutrients. Nutrient and water uptake occurs largely through fine roots and it is not clear if fine roots associated with fragments are a net benefit to the suckering ability of root fragments.

In two controlled field studies we explored the regeneration potential of aspen from root fragments in relation to (i) soil depth (e.g. depth of root burial), (ii) root tissue non-structural carbohydrate reserve concentration and content, and (iii) the importance of attached fine roots on root fragments for sucker initiation, emergence, and growth performance. We hypothesized that root fragment buried at a deeper soil depth will require more reserves to reach the soil surface and might face greater reserve exhaustion. We further hypothesized that root fragments with attached fine roots will have improve soil contact, allowing the regenerating root suckers to access water and nutrient resources more easily.

2. Methods

2.1. Research site

The experimental site was located at the Crop Diversification Centre North near Edmonton, Alberta (53°38′N, 113°21′W; 668 m a.s.l.). A level agricultural field was used for the experiment. The soil texture of the soil was a silty loam which was deep and well drained. Precipitation during the study between May 1 and August 30, 2010 amounted to 174.1 mm and no extended drought periods were observed. Mean air temperature over the four months was 14 °C (Environment Canada, 2010) and average soil temperatures were 16.9 °C at 5 cm soil depth, 16.1 °C at 20 cm, and 15.3 °C at 40 cm.

2.2. Plant material

The root material used in this study was collected in February 2010 near Genesee, Alberta (53°19′N, 114°18′W) from an aspen stand (4 ha) that had been cut and naturally regenerated 9 years earlier. Trees were up to 7 m tall and stem density was 13,000 stems/ha. The roots and soil materials were collected using large scale operational methods where the above-ground portion of the aspen stand was sheared off close to the soil surface under frozen conditions (>20 cm soil depth) using a straight blade mounted on a large bulldozer. Then the top 20 cm of the frozen forest floor and mineral soil containing the aspen roots were pushed into large windrows. On the same day, thirty root fragments (>65 cm in length) were chosen for each of three diameter size classes (Class 1: 1–2 cm, Class 2: 2.1–3 cm; Class 3: 3.1–4 cm) for a total of 90 roots. All selected fragments were straight, had no major lateral roots, and were visibly undamaged. To test the influence of the presence of fine roots attached to fragments an additional 20 undamaged root fragments (0.6–1.5 cm in diameter, 18–60 cm long) were collected. All of those selected fragments had fine roots (>1 mm diameter) still attached and were collected at the same time. All collected roots were wrapped in plastic, and stored at −5 °C until the end of April 2010.

2.3. Treatments

In late April, fragments were slowly thawed over two days and both ends were re-cut to remove potential pathogens that may have attached during storage. A sample of each root fragment (1 cm in length) was also taken to determine root non-structural carbohydrate (NSC) reserve concentrations (see below) prior to planting. To explore the impact of fragment size and burial depth, all root fragments were trimmed to a total length of 50 cm. To estimate root fragment volume, root diameter was measured at both ends of each fragment. Root fragments were planted (buried) horizontally at 3 different soil depths (5, 20 and 40 cm) at the research site. The experiment was designed as a complete block design with 10 blocks (2 × 3 m), each consisting of three plots (1 × 1 m), which were randomly assigned to one of the three soil depths and each containing one root fragment of each of the three different diameter size classes (class 1: 1–2 cm; class 2: 2.1–3 cm; class 3: 3.1–4 cm). HOBO soil temperature data loggers (Onset Computer Corporation, Bourne, Mass.) were also placed at the three soil depths ($n = 3$ at each depth) to record soil temperatures over the four summer months.

To test the impact of the presence of fine roots, collected root fragments were slowly thawed under moist conditions. The experiment was a paired design with 10 pairs of root fragments of similar diameter and length, as well as similar in the number and length of attached fine roots. Among the pairs, the number of attached fine roots per root fragment ranged from 8 to 19 fine roots. One of the root fragments in each pair had all fine roots removed prior to planting and a sample of each root fragment (1 cm) was taken to determine initial NSC reserves of each of the 20 root fragments. Each pair was buried horizontally at a depth of 10 cm. A soil temperature data logger was also placed at the same location.

Over the course of the growing season (May 1, 2010 to August 24, 2010) the plots were visited several times in order to remove weeds and to monitor sucker emergence.

2.4. Measurements

At the end of August, root fragments (and their suckers) were then carefully excavated and the entire clone was kept on ice until brought back to the lab. In the lab all roots and suckers were carefully washed and then separated into dead and live root fragments.