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Partitioning of carbon allocation to reserves or growth determines future performance of aspen seedlings

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A B S T R A C T

Increasingly, trembling aspen (*Populus tremuloides* Michx.) is being planted in stressful situations such as forest land reclamation, afforestation and forest restoration in North America. This is due to its fast potential for growth and high resiliency, but its indeterminate growth strategy provides a special challenge in creating suitable planting stock for these sites. Clues from naturally established aspen seedlings suggest that root total non-structural carbohydrate (TNC) reserves and root:shoot ratio could be strongly related to subsequent seedling establishment and growth. Carbon allocation in plants is generally partitioned between reserve accumulation and growth and development. Under conditions in controlled nurseries, the allocation of carbohydrates to reserves could be manipulated in order to produce seedlings designed for specific environmental conditions. To manipulate seedling characteristics we attempted to induce premature bud set during nursery culture while allowing continued photosynthesis. Treatments included applying different fertilizer regimes, light intensities, reducing photoperiod and use of a shoot growth inhibitor. The shoot growth inhibitor was the most reliable treatment and resulted in complete bud set, while blackout was successful only when seedlings were grown outside. Low nutrient treatments also resulted in early bud set; however, leaves were abscised much earlier. There was a distinct trade-off between growth and reserve accumulation with the late bud set. A longer period of height growth reduced root and total TNC reserves, while early bud set allowed for continued photosynthesis and produced the highest levels of root and total TNC reserves in seedlings. Increased TNC reserves of aspen planting stock was positively related to height growth after outplanting, with root TNC reserves as high as 33% of dry weight and root:shoot ratios greater than 2 associated with the best growth.

1. Introduction

There is increasing interest in the planting of trembling aspen (*Populus tremuloides* Michx.) seedlings for the restoration of degraded aspen stands, afforestation of heavily disturbed areas such as in mining reclamation and short-rotation plantations in the boreal forest zone. However, the quality of aspen planting stock and early plant performance has traditionally been questionable and inconsistent (Van den Driessche et al., 2003). Currently there are no morphological or physiological characteristics of aspen seedlings identified that correlate well with subsequent outplanting performance. In other tree species morphological characteristics such as root volume, seedling height or total mass have been shown to be good predictors of future growth (Davis and Jacobs, 2005; Jacobs et al., 2005). These variables are currently being used for aspen and appear to be poor predictors for the quality of aspen planting stock. Stored carbohydrates reserves are important for the establishment and growth of seedlings, particularly in deciduous species that need to rely on the stored reserves to initiate leaf area and new root growth without current photosynthesis (Loescher et al., 1990; Turgeon, 1989; Chapin et al., 1990; Kozlowski, 1992; Kozlowski and Pallardy, 2002; Sprugel, 2002; Landhäusser, 2011).

The size of planting stock is often positively correlated with growth and this response is often associated with greater nutrient and carbohydrate reserve content, but this has rarely been quantified or confirmed particularly for species with indeterminate growth habits such as aspen. Naturally established aspen seedlings which were very short in stature after the first growing season had high growth rates in the second growing season, which were associated with high concentrations of carbohydrate reserve and high root:shoot ratios (Martens et al., 2007). Since carbohydrate reserves are not easily determined, we are not aware of any studies that have explored the linkage between carbohydrate reserve concentration and content, nursery growing conditions, and/or morphological features of aspen seedlings and how those affect subsequent outplanting performance.

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Trembling aspen, like most early successional and shade intolerant species in the Salicaceae, has an indeterminate growth strategy that allows it to grow significantly in height during favorable growing conditions. Under less favorable conditions, such as drought, low nutrient availability or low soil temperatures, however, aspen reduces photosynthesis and terminates height growth and the production of new leaf area, i.e. terminal bud set (Hogg and Hurdle, 1995; Landhäusser and Lieffers, 1998; Landhäusser et al., 2001; Galvez et al., 2011). Although photosynthesis is reduced in aspen under stress conditions, some carbon continues to be assimilated and is used to build carbohydrate reserves rather than structural growth (Martens et al., 2007; Galvez et al., 2011). Under these stress conditions an asynchrony between carbon supply and the immediate carbon demand for growth develops as a result of the termination of height growth (Chapin et al., 1990), allowing the plant to divert photosynthates to reserves instead of growth (Körner, 1991; Galvez et al., 2011). This change in allocation towards reserves could be useful in manipulating the reserve accumulation and status in aspen seedling planting stock as higher concentrations or content of reserves appear to positively influence the outplanting performance of the aspen planting stock (Martens et al., 2007).

In this study we investigate whether early termination of shoot growth, as a result of abiotic stresses can be used to control the amount of carbohydrate reserves in aspen seedlings. To induce bud set we limited nutrients and N, used a chemical shoot growth inhibitor or reduced the photoperiod by using blackout and grew these seedlings either under greenhouse or outside conditions. In addition, we explored how carbohydrate reserves affect subsequent initial growth performance and whether more easily-measured characteristics such as root:shoot ratio can be useful predictors for reserve status and growth performance after outplanting. We hypothesize that applying the above stresses will induce bud set in the seedlings and that bud set will increase carbohydrate reserves and root:shoot ratio in seedlings and improve outplanting performance. We further hypothesize that seedlings established under outside conditions will accumulate more carbohydrate reserves than seedlings growing under greenhouse conditions.

2. Materials and methods

2.1. Seedling planting stock production

In the late spring of 2007, aspen seedlings were grown at the University of Alberta from seed in styroblock containers (5–12, Superblock, Beaver Plastics Ltd., Edmonton, Alberta, Canada) with cavities 5 cm in diameter and 12 cm deep for a soil volume of 220 ml. Seed was collected from a wide range of open pollinated aspen clones of the boreal mixedwood region of west central Alberta, Canada. Before seeding, styroblocks were cut into strips containing six cavities each, for a total of 120 strips. Each strip was considered to be an experimental unit that contained six cavities (sub-samples). Six strips each were combined and placed in twenty wooden racks (blocks). All cavities were filled with Pro-mix (Sunshine, SunGro Horticulture Canada Ltd., Seba Beach, Alberta, Canada) containing 55–65% sphagnum peat moss, perlite, dolomitic limestone, gypsum and a wetting agent.

Cells were hand-seeded with three to five aspen seeds per cavity in the second week of May and allowed to establish for seven weeks in a greenhouse. In the greenhouse photoperiod was ca. 17 h, with an air temperature ranging between 20 and 24 °C. Soil moisture was checked daily and the blocks were watered if necessary. All blocks were fertilized once at the beginning of week 4 (at the beginning of June) with a 10% strength of the standard fertilizer concentrations (see below for description) to provide the seedlings with some initial nutrients until treatments were implemented after week 7. In weeks 5 and 6, cells were thinned to one seedling each where the tallest seedling was left and empty cells were filled with transplanting some of the healthy thinned seedlings.

After the seven-week establishment period, each of the six strips in each block was treated randomly with one of six shoot termination treatments. To prematurely terminate shoot growth, selected seedling strips were exposed to a reduced nutrient regime, reduced photoperiod (blackout), a shoot growth inhibitor or a combination of reduced nutrients and reduced photoperiod (Table 1). Ten of the 20 blocks were randomly chosen and moved to a location outside for the remainder of the growing season, while the remaining 10 blocks were left growing inside the greenhouse resulting in a total of 12 differently treated seedling types (Table 1).

2.2. Fertilizer, photoperiod, and growth inhibitor treatments

All fertilizer treatments were applied twice a week. To achieve even fertilization, the seedlings strips common to a fertilization treatment were bundled together from all the racks and the root systems were submerged in the fertilizer solution until saturation. After fertilization, strips were placed back into their respective racks. Fertilization continued for the next 7 weeks until the end of week 14. The fertilizer solutions were prepared from a commercially used fertilizer blend that is considered standard for the production of aspen planting stock. The commercial blend contains 54 mg L^{-1} nitrogen (N), 57 mg L^{-1} phosphorous (P), 71 mg L^{-1} potassium (K), 66 mg L^{-1} calcium (Ca) and micronutrients consisting of boron, copper, iron, magnesium, manganese, molybdenum, sodium, sulfur and zinc. Seedlings treated with a low nutrient regime were subjected to a nutrient concentration at 10% the standard rate for either N (including N and Ca) or all nutrients (including N, P, K and Ca).

Blackout treated seedlings were exposed twice to short days (8 h of light) for six consecutive days during week 10 and 14 of the growing season, which corresponded to the third week of July and the third week of August. Over these six days, seedling strips assigned for blackout treatment were moved daily to a dark room for 16 h. The seedling strips assigned to the shoot growth inhibitor treatment were treated once in week 10, with 20 mg L^{-1} paclobutrazol (Bonzi®, Syngenta, Wilmington, DE, USA) by adding 5 ml Bonzi per liter to the fertilizer solution in which the root systems were submerged during the fertilization treatment.

Starting from week 15 (fourth week of August), all seedlings were fertilized twice weekly with standard fertilization rates until

Table 1
Range of treatments used to produce seedling with different levels of carbohydrate reserves and root:shoot ratios. Fertilization solutions were prepared from a commercial blend with 100 representing the standard nutrient supply and 10 representing one-tenth of the standard nutrient concentrations.

Treatment		Fertilization			
Location	Shoot termination	N	P	K	Micro
Outside	None	100	100	100	100
Outside	Blackout	100	100	100	100
Outside	Bonzi	100	100	100	100
Outside	Low N	10	100	100	100
Outside	Low N, blackout	10	100	100	100
Outside	Low N, low fertility	10	10	10	100
Inside	None	100	100	100	100
Inside	Blackout	100	100	100	100
Inside	Bonzi	100	100	100	100
Inside	Low N	10	100	100	100
Inside	Low N, blackout	10	100	100	100
Inside	Low N, low fertility	10	10	10	100