Target Root Starch Concentrations Before Storage: Testing the Model¹

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Abstract.--Because carbohydrate reserves decline with long-term storage, it is important to know whether this depletion will affect subsequent survival and growth after planting. Sufficient target starch concentrations which enable the seedling to buffer itself against reserve depletion during storage, have not been defined. We found little evidence to support the model of a target (pre-storage) root starch concentration. No seedling target can be viewed alone. If the seedling is not preconditioned to grow but reserves are plentiful, a poor correlation between carbohydrate reserves and survival or growth is to be expected.

INTRODUCTION

Carbohydrate reserves have essential functions in trees. Reserves are utilized for maintaining living tissue (maintenance respiration) as well as providing substrates for growth (growth respiration). During certain periods of the year, trees may rely heavily on stored reserves for growth or for buffering against environmental stress and injury (Waring and Schlesinger 1985).

Roots generally contain the largest concentration of nonstructural carbohydrates and are often considered the primary storage organ (Loescher et al. 1990). However, the mechanisms responsible for causing root reserves to be mobilized and how they are trans located are not well understood; additionally, specific relationships between reserve carbohydrates and tree survival or growth have not been clearly established (Duryea and McClain 1984, Loescher et al. 1990).

Carbohydrate reserves occur primarily in the form of starch and sugars, with starch generally being the most abundant form of carbohydrate reserve in tree species (Little 1970, Glerum 1980). Accumulated root starch

2Graduate research assistant and Assistant Professor, Department of Forest Science, Oregon State University, Corvallis, Oregon. reserves may supplement spring root growth (Wargo 1979). At the time of initiation, starch concentration in fine roots determines how long the fine roots survive (Marshall and Waring 1985).

The notion of achieving or maintaining a target or optimum amount of stored carbohydrates in nursery seedlings comes from the concept that cultural practices which reduce reserves may ultimately decrease field survival, root growth, and shoot growth (Duryea and McClain 1984, Marshall 1985). Nursery practices that could deplete reserves are those which influence photosynthesis and respiration. These include: a) growing seedlings at high seedbed densities (reducing light), b) inducing dormancy by decreasing irrigation (reducing available soil moisture and increasing leaf temperature), and c) altering fertilizer regime (increasing available nutrients causing large respiratory costs) (Marshall 1985, McNabb 1985).

The potential for depletion of carbohydrate reserves is especially high with long-term cold storage in the dark (McCracken 1979, Ritchie 1982). The fixation of carbon is halted, but respiration continues even at storage temperatures slightly below freezing. Additionally, the photosynthetic machinery may be damaged in storage (McCracken 1978), necessitating recovery and repair of photosynthetic mechanisms after planting. With the popularity of fall lifting and long-term freezer storage in the Northwest (Hee 1986), we ask the question: should seedlings be cultured to achieve target reserve concentrations prior to storage?

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THE MODEL

Marshall (1985) presented a <u>hypothetical</u> situation comparing the carbohydrate reserve concentration of two seedlings at lifting, during storage, and after planting (fig. 1). Both seedlings decline in carbohydrate concentration with storage, but the seedling that survives and grows is the one with sufficient pre-storage reserves (upper line). These reserves provide an adequate buffer for losses due to: maintenance respiration (during storage), re-organization of the photosynthetic apparatus (after planting), and using reserves in preparation for shoot elongation (prior to starch accumulation).

The appropriateness of this model can be examined by determining if there is a relationship between carbohydrate reserves and outplanting growth or survival with and without storage. If different storage treatments create classes of seedlings with different reserve concentrations, we would expect seedlings with very low reserves to die or grow poorly.

TEST OF THE MODEL

Methods

In an ongoing investigation into the effects of fall lifting and long-term storage on seedling physiology (Omi and Schuch 1987), ponderosa pine (<u>Pinus ponderosa</u>) seedlings were lifted 3 times in the fall (Sept., Oct., and Nov., 1987), stored overwinter at -1.5 °C, and compared with seedlings lifted and handled conventionally (Mar., 1988, cold storage, 2-4 °C for 2 weeks). Seed for the bareroot seedlings were sown in 1986 and grown with standard cultural regimes used at the USDA Forest Service Bend Pine Nursery in central Oregon (44° 5' N, 121° 16' W, 1100 m elevation).



Figure 1.--Hypothetical carbohydrate reserve concentration (% dry weight) of two seedlings at lifting, through storage, and after planting. One seedling (top) survives; the other (bottom), with inadequate reserves, dies (Adapted from Marshall 1985).

Root starch concentration (% dry weight) was determined at lifting and after storage using an enzymatic (α - amylase and amyloglucosidase) digestion method (Rose et al. 1990).

Seedlings were outplanted on a vacant field at the nursery in March 1988. We measured several responses at the end of the growing season, including survival (%), height (cm), growth (cm, final height - initial height), and fascicle length (mm). We also planted seedlings at a forest site in April 1988; however, the ranking of treatments was similar so only the Bend data is included in this paper. Coincident with outplanting, a 30-day root growth potential test was initiated in a greenhouse. We measured the percent of seedlings that initiated new roots, and the dry weight (mg) of new roots.

Data analysis is not complete, so the means and significance of the differences among means should be considered preliminary. To determine the relationship between initial root starch and subsequent field performance, field response variables were regressed against initial root starch.

Results

Root starch concentration declined in storage so that at the time of planting (after storage), there was a significant difference in starch among the treatments (table 1). However, there appeared to be little relationship between initial root starch and subsequent root initiation or field survival and growth. September-lifted seedlings had low root starch, the lowest root initiation and dry weight of new roots, and the poorest field performance. This would be consistent with the model.

On the other hand, November-lifted seedlings had low root starch, high root initiation, and the highest survival and growth (table 1). This result conflicted with the model.

All correlations between initial root starch and field response variable were nonsignificant (P>0.05) with the exception of survival. However, initial root starch accounted for only 21 percent of the variation in first-year survival (fig. 2). Field survival and growth appeared to be more closely related to the capacity of seedlings to grow new roots and not initial starch concentration (table 1).

DISCUSSION

In terms of field performance, our ability to create a precise model failed. Carbohydrate reserve status has been qualitatively associated with tree survival or growth (Hellmers 1962, Winjum 1963, Puttonen 1980), but strong quantitative relationships have not been

Table 1.--Root starch concentration (% dry weight) before and after storage, new root initiation (% of seedlings with new roots after 30 days, mg dry weight of new roots), first-year field survival (%), and first-year growth (cm) of ponderosa pine seedlings after four lifting and storage treatments. Means are averaged over 2 seed sources and 4 replications per seed source. Means down a column with different letters are significantly different (p<0.05).</pre>

Lift date	Root starch (%) after:		Root initiation after 30 days ¹		First-year:	
	lifting ²	storage	% with new roots	mg new root weight	Survival (%)	Growth (cm)
Sept.	2.3a	0.04b	15 c	2 a	24 c	2 c
Oct.	1.8b	0.06b	47 b	7 a	66 b	4 b
Nov.	0.9c	0.05b	78 a	9 a	84 a	5 a
Mar.		1.70a	80 a	8 a	80 ab	4b

 $^1\mathrm{Root}$ initiation in a 30-day greenhouse test, coincident with outplanting.

 2 After lifting - before storage.

reported (Ronco 1913, Little 1974, Ritchie 1982). Factors such as storage condition, site condition at planting, method of carbohydrate analysis, and reserve carbohydrate quantified (e.g., starch, sugar, or total) probably influence the range of results reported in the literature (Marshall 1985).

Furthermore, carbohydrate reserves and new root growth are generally poorly related (van den Driessche 1978, Ritchie and Dunlap 1980, Ritchie 1982, Rose and Whiles 1984, McNabb 1985, Reid 1986). Current photosynthates or other shoot factors may control new root growth in



Figure 2.--Relationship between first-year field survival (%) and initial root starch concentration (log % dry weight).

conifers (Shiroya et al. 1966, Gordon and Larson 1970, Marshall and Waring 1985, van den Driessche 1987), although there are likely to be differences in species response (Philipson 1988).

Other factors which could influence root growth include auxin or other plant growth regulators. Auxin stimulates root primordia in tree roots (Coutts 1987). In ponderosa pine, exogenous applications of auxin to seedlings positively affected new root growth, but not the elongation of old roots (Zaerr 1967); however, Lavender and Hermann (1970) could find no positive effect on root growth from external application of growth regulatory compounds. They concluded that a translocatable substance from foliage was necessary for root growth. Zaerr and Lavender (1974) concluded that the substance controlling root growth was not carbohydrate alone.

Therefore, if carbohydrate reserves are available, but the root or shoot is not preconditioned to grow (e.g., having the right balance of growth regulators), then a poor correlation between reserves and growth is to be expected. Douglas-fir (<u>Pseudotsuga menziesii</u>) seedling roots are highly sensitive to exposure in the fall (Hermann 1967); therefore, if any root damage occurs with fall lifting, it will likely alter future performance, irrespective of carbohydrate status. Similarly, if the plant is ready to grow and environmental conditions allow a positive carbon balance, new root growth may be more reliant on current photosynthate (van den Driessche 1987), resulting once again with a poor correlation. Stored reserves are more important if photosynthesis cannot keep up with respiratory demands (e.g., poor site conditions, van den Driessche 1987).

We only measured starch concentration; yet, sugars can make up a large fraction of the total nonstructural carbohydrate pool (McCracken 1979, Ritchie 1982). Interconversion among carbohydrates is rapid and much more needs to be learned about function and allocation of carbohydrates before we categorize them as metabolically active versus storage (McCracken 1979).

In a current study, we found that seedlings with new roots consistently had less moisture stress and higher root starch content relative to seedlings that do not initiate new roots. Thus, root starch may indicate overall seedling vitality (functioning root system and high water use efficiency) even though its predictive value was questionable in this study. Bigg (1990), however, has preliminary evidence that suggests the doubling of winter root starch concentration in Douglas-fir coincides with the lifting window and the end of dormancy.

CONCLUSIONS

No seedling target can be viewed alone. Plentiful starch reserves are insignificant if the seedling is not ready to grow, or has been damaged. A stressed seedling may accumulate starch if growth is slowed more than photosynthesis (Marshall 1985). Target starch concentrations, in combination with other factors (e.g., nutrients and root volume) will affect performance depending on site conditions. On a favorable site, seedlings with low starch may do as well as seedlings with high reserves. Using starch as a predictor, therefore, has the same problems as using root growth potential alone (Landis and Skakel 1988).

In the study discussed in this paper, there was little evidence to support the model of a target root starch concentration to enhance survival and growth after planting. However, this does not diminish the importance of maintaining reserves. Cultural practices that cause stress could reduce photosynthetic capacity or increase respiratory losses. Inadequate reserves could create nitrogen deficiency because of insufficient carbon substrates for root growth (Loescher et al. 1990). The mobilization of sugars is important for maintaining favorable water relations (Levitt 1980) and may be related to frost hardiness (Sakai and Yoshida 1968, Levitt 1978). Future research for using starch as a target should account for other biochemical or physiological conditions of the seedling, as well as site conditions.

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