

## Dying piece by piece: carbohydrate dynamics in aspen seedlings under severe carbon stress and starvation

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Carbon stress and starvation remain poorly understood in trees, despite their potential role in mortality from a variety of agents. To explore the effects of carbon stress on nonstructural carbohydrate (NSC) dynamics and recovery potential and to examine the process of starvation, we grew aspen seedlings under one of three levels of shade: 40% (light shade), 8% (medium shade), and 4% (dark shade) of full sunlight. We then exposed seedlings to 24 hours darkness at either 20° or 28° C until trees had died. Periodically, seedlings were harvested for NSC analysis and to measure stem and root respiration. In addition, some seedlings were moved back into the light to determine if recovery was possible at certain points during starvation. Specifically, we sought to address the following questions: 1) Do NSC concentrations or mass influence tree survival under carbon stress? 2) At what carbohydrate levels do trees fail to recover and starve? 3) Does temperature affect the NSC level at which trees starve?

Increasing shade reduced growth, but surprisingly did not reduce NSC levels, except in a portion of deep shade seedlings that experienced dieback. Once in darkness, leaves died first, with final NSC levels ranging from  $\sim 4\%$  (Medium shade, 28 degrees) to 7.5% (Light shade). Stem death generally occurred gradually down the stem. Stem tissues retained  $\sim 1-2\%$  NSC when dead. Recovery was still possible when only the upper half of the stem had died; at this point, seedlings had relatively high root NSC levels in their remaining roots (7-10%), with 1-3% starch. No trees recovered after the whole stem had died, at which point, some trees root systems were completely dead. However, most retained substantial amounts of live roots, averaging 5-6% NSC, with 0.25-1.5% starch.

Despite the initially similar NSC concentrations, light shade seedlings took longer to reach half stem and whole stem death than seedlings from medium and dark shade. Longer survival times were associated with greater initial NSC pool sizes and lower mass-specific respiration rates. Higher temperatures reduced the time until tissue death and also tended to reduce NSC levels at death in some tissues.

Survival time during starvation appeared to be controlled not only by the size of initial reserves, but by the rate of respiration. Relatively high leaf NSC levels of dead leaves observed during drought and during fall leaf abscission are within the range of leaf NSC levels of starved leaves seen here. Patterns of nonzero tissue NSC and the piecewise progression of mortality often observed in mature trees are not inconsistent with the process of carbon starvation, which may contribute to tree death by many causes.