



Variation in the concentration and age of nonstructural carbon stored in different tree tissues

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Trees store nonstructural carbon (NSC), in the form of sugars and starch, in the ray parenchyma cells of woody tissues. These reserves provide a carbon buffer when demand (growth, protection, or metabolism) exceeds supply (photosynthesis). This is particularly important in the context of resilience to stress and disturbance, such as might be associated with various global change factors. However, storage allocation processes and the availability of stored reserves remain poorly understood in woody plants.

To better understand how NSC reserves are distributed throughout the tree, and the degree to which NSC reserves mix across ring boundaries and tissue types, we destructively sampled two 30-year-old trees (one red oak, *Quercus rubra* L., and one white pine, *Pinus strobus* L.) growing at Harvard Forest, an oak-dominated temperate forest in the northeastern United States. We analyzed stemwood samples (divided into individual rings, bark, and phloem), coarse and fine branches, and coarse (separated into three depths) and fine roots for concentrations of total sugars and starch. For a subset of samples we used the radiocarbon (14C) “bomb spike” method to estimate the mean age of extracted sugars and starch.

In oak, stemwood sugar and starch concentrations were highest (50 mg/g) in the youngest (most recently-formed) rings, and dropped off rapidly (to 10 mg/g or less) across the 10 most recent rings. In oak phloem tissue, sugar concentrations were high (90 mg/g) compared to starch (10 mg/g). In pine, sugar concentrations dropped off rapidly across the three most recent rings (from 30 mg/g to 10 mg/g) whereas starch concentrations were low even for the youngest rings (10 mg/g or less). In pine, phloem concentrations of both sugar (190 mg/g) and starch (20 mg/g) were both substantially higher than in oak. Such strong radial trends must be accounted for when scaling up to whole-tree budgets, as whole increment cores cannot properly integrate (on a ring-area basis) across the depth profile.

In oak, fine root concentrations of sugar and starch were similar (40 mg/g), and coarse roots had very high concentrations of starch (140 mg/g) compared to sugar (50 mg/g). In pine, fine root concentrations of both sugar and starch (60 mg/g) were higher than in coarse roots (10 mg/g). Coarse root NSC concentrations did not vary substantially along a radial gradient into the root. Even assuming a 1:5 root:shoot ratio, these data indicate that a large portion of the whole-tree NSC budget is stored belowground.

For both sugars and starch, the 14C data indicated substantial mixing of new and older carbon across the youngest stemwood rings (up to 5 y), beyond which NSC age increased linearly with ring age. Coarse root NSC age also increased with radial depth and wood tissue age, and root NSC was consistently younger in pine than oak. The fact that NSC age is not constant with radial depth in the aboveground samples demonstrates that NSC reserves cannot be treated as a single, well-mixed pool. Rather, these results are consistent with previous observation suggesting last-in/first-out dynamics. From a modeling standpoint, these results support a simple two-pool structure where new photosynthate not used for current growth or metabolism enters a well-mixed and young “fast” pool, but over time storage in older rings is transferred to a distinct and older “slow” pool with which mixing no longer occurs.