Nonstructural Carbohydrate Depletion in Snowberry (*Symphoricarpus oreophilus*)

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Highlight: Nonstructural carbohydrate (NC) concentrations in defoliated snowberry (*Symphoricarpus oreophilus*) plants were compared over two seasons with trends of NC concentrations in untreated plants. Nonstructural carbohydrate concentrations in small roots and stems of defoliated plants decreased slowly from the time of initial defoliation. The NC concentrations in large roots and root crowns remained stable until prolonged, intense defoliation caused a significant decrease in NC concentrations in these plant parts. NC concentrations in stems, large roots, and root crowns decreased significantly before plant death. The decrease in NC concentrations in large roots and root crowns coincided with an increase in NC concentrations of stems prior to leaf production. Defoliated plants did not produce new stems after defoliation began and stem mortality during dormancy was great. NC concentrations apparently were inadequate to support the entire plant through dormancy. Nonstructural carbohydrates remaining in dead plant parts constitute an unused portion of the carbohydrate reserves.

Changes in carbohydrate reserves in response to various intensities, seasons, and durations of defoliation have been studied in several plants (Cook 1966; Donart and Cook 1970; Trlica and Cook 1971; Menke 1973; Willard and McKell 1973). Defoliation during periods of normal reserve depletion often induces more serious reserve depletion. In general, defoliation that is too heavy or too frequent results in decreased nonstructural carbohydrates (NC). Most defoliation and clipping treatments on snowberry (*Symphoricarpus oreophilus*) failed to reduce NC concentrations below that measured during leaf production. Frequent, intense defoliation would be expected to cause NC to decrease to concentrations lower than those measured during leaf production in untreated plants. Defoliation treatments by Donart and Cook (1970) and Willard and McKell (1973) apparently were not sufficiently intense to accomplish a permanent reduction in NC concentration. In these studies, partial to total replenishment of reserves was achieved after the treatments were imposed, but before dormancy began. Recovery from defoliation implies that snowberry's carbohydrate pool may be greater than the amount of NC used during the normal annual cycle. An estimate of the size of the carbohydrate reserve pool might be obtained by determining how much of the extractable NC can be depleted during continuous defoliation. In 1973 and 1974 a depletion study of NC in snowberry was conducted in Logan Canyon, Utah, to determine the trend and ultimate level of NC concentration present in defoliated and untreated shrubs.

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Methods and Materials

Fifty-six snowberry plants of similar size were selected for the study. Twenty-eight of these plants were defoliated by hand picking all of the leaves. After the initial leaf removal on June 1, 1973, leaf regrowth was removed every 2 weeks on June 15, June 29, and July 13. Leaves were not replaced in 1973 after the fourth defoliation. The defoliated plants produced leaves the following spring and defoliation was resumed on May 15, 1974, followed by defoliations on May 30 and June 15.

Four plants were sampled on May 26, 1973, before defoliation began. After defoliation, four defoliated plants and four untreated plants were sampled on June 7, June 17, and August 3, 1973; and May 1, June 8, and July 15, 1974. Stem production by defoliated plants was observed as an indicator of plant vigor. Stem mortality was determined by ocular estimate.

Defoliated and untreated plants were excavated to a depth of 61 cm and representative sub-samples of stems, small roots (less than 6 mm in diameter), large roots (greater than 6 mm in diameter), and root crowns were collected. On each collection date, plant material was frozen in dry ice and taken to the laboratory where it was stored in a freezer until it was freeze-dried. The freeze-dried plant samples were ground in a Wiley Mill through a 40-mesh screen and stored in desiccators.

The NC was extracted from the ground plant samples using 0.2 N sulfuric acid as described by Smith et al. (1964). This method hydrolyzed NC to reducing sugars, which were analyzed using the dinitrosalicylic acid method (Luchsinger and Cornesky 1962). Glucose was used as a standard. The product of this procedure has conventionally been called total available carbohydrates but this term is a misnomer, according to Stoddart et al. (1975) and George (1976).

Data were subjected to analysis of variance and Duncan's new multiple range test (Duncan 1955) was used to separate means where a significant difference occurred ($p < 0.05$).

Results and Discussion

Nonstructural carbohydrate concentrations in small roots and stems of defoliated plants were depressed initially and were reduced significantly in all plant organs by the time of plant death (Fig. 1). Nonstructural carbohydrate in stems from untreated plants increased from a minimum of 5.6% on May 26 to a maximum near 12% in August. Stems from defoliated plants had only about 5% NC in August; whereas a maximum of 7.5% was found on May 1, 1974. This was followed by a decrease to 3.3% on June 8, 1974. The NC on this date was significantly lower than the NC measured on May 26, 1973, just before defoliation began, thus illus-

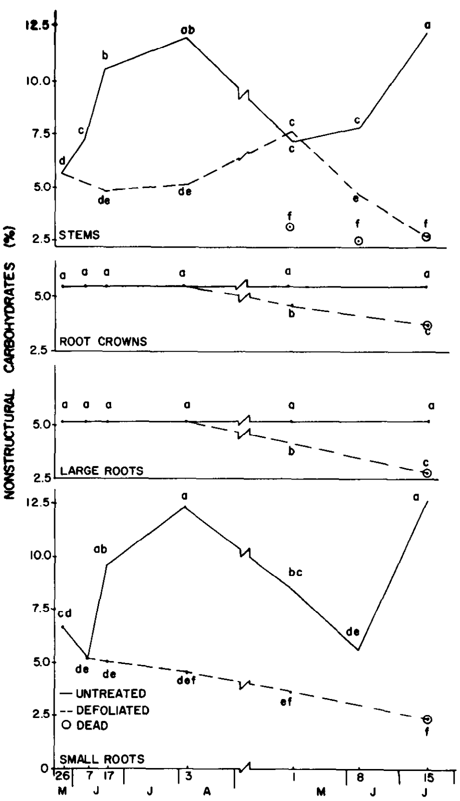

Fig. 1. *Mean NC concentration for four plant parts from defoliated and untreated snowberry plants in 1973 and 1974. Means with the same letters are not significantly different at the 5% level of probability.*

trating that NC in stems can be significantly decreased below the usual NC minimum reached in untreated plants during leaf production. During this study there was no stem production by the defoliated plants, but stem production did occur in the untreated plants.

The NC in large roots and root crowns from untreated plants maintained stable concentrations between 5 and 5.5% throughout the defoliation study in 1973 (Fig. 1). However, the NC in the large roots and root crowns from defoliated plants deviated from these normal concentrations on May 1, 1974, when NC dropped significantly to 4.1% for large roots and 4.4% for root crowns.

Small roots from untreated plants had a minimum NC concentration of 5.2% on June 7, 1973, and increased to a maximum near 12.5% in August (Fig. 1). The NC concentration in small roots from defoliated plants decreased from the beginning of defoliation until plant death occurred over a year later. However, the NC concentration within small roots did not decrease significantly from the NC minimum measured on June 7, 1973, until plant death occurred.

Nonstructural carbohydrates in stems, root crowns, large roots, and small roots collected in the second season on July 15 when the plants were dead were significantly lower than the lowest concentrations measured near the time defoliation was begun. The NC for stems, root crowns, large roots, and small roots from dead plants was 2.6, 3.4, 2.6, and 2.3%, respectively (Fig. 1). An estimated 60 to 75% of the defoliated stems died during winter dormancy. The NC in these dead stems on May 1 was 3.3%. More stems were dead on June 8 and the NC at this time was 2.5%.

Several important results were measured or observed while monitoring NC concentration in untreated and defoliated snowberry plants. The NC concentrations in stems and small roots fluctuated more and sooner than the NC concentrations in large roots and root crowns. Nonstructural carbohydrates in defoliated plants can be decreased below the depressed concentrations measured during leaf production in untreated plants. Of particular importance is the fact that NC was not replenished in severely defoliated plants, so they entered dormancy with depressed reserves. Finally, the observed lack of stem production after several defoliations and the high stem mortality during winter dormancy were important indicators of the effect of defoliations.

The fluctuation of NC concentrations in small roots and stems indicates the probable use or translocation of enough of the reserve carbohydrate pool in each of these plant parts to cause a change in concentration. This is probably because of the close proximity of these plant parts to the major sites of use. Stoddart et al. (1975) suggested that reserves nearest the place of use would be most readily available. Other researchers have shown marked depletion of carbohydrate reserves in tissue adjacent to expanding buds and shoots (Siminovitch et al. 1953; Woods et al. 1959; Priestly 1960). Coyne (1969) and Trlica and Cook (1971) showed that NC concentration in small roots was more responsive to change than NC concentration in crowns of big sagebrush and black sagebrush. The NC concentration in large roots and root crowns was relatively stable, indicating that the net use of the reserve carbohydrate pool was not gr enough to change the NC conce tration. If this reserve pool is gr enough, its contribution to metaboli may be quite important without signi cantly decreasing the NC conce tration. NC in large roots and r crowns could act as a "margin safety" to excessive carbohydrate u in the plant.

The defoliation in this study w frequent and intensive as a means depleting carbohydrate reserves in t subject plants. Snowberry has be clipped in other studies with little lor term effect on NC concentratio Donart and Cook (1970) found th plants clipped once during leaf pr duction at 90% would replenish part their small root reserves by late Ju Willard and McKell (1973) monitor NC concentrations in small roots, lar roots, and root crowns when th simulated several grazing systems varying the time of clipping. The on clipping regime that significantly duced NC concentrations in large ro from snowberry was clipping on Ju 15 for five consecutive years.

In this study, NC concentration large roots and root crowns of untreat plants remained relatively stal throughout the year. The NC conce tration in large roots and root crowns defoliated plants did not decrea significantly unless defoliation pressu was prolonged. This would indic that NC was used in respiration in t large roots and root crowns or that N was transported to support NC requi ments in small roots and stems. The N concentrations in stems and small ro did not decrease significantly i mediately after defoliation began. T large roots and root crowns, with larger reserve pool, may have helped maintain the NC concentrations small roots and stems. Initially th could be accomplished without measu ably lowering NC concentrations large roots and root crowns, but t carbohydrate demands of dorman and mobilization of reserves to supp spring production might eventua cause a significant reduction in N concentrations in larger roots and r crowns. Although stem NC concentr tion is maintained in live stems, li stem biomass decreased as stems di during the 1974 season. Ogden a Loomis (1972) found a similar situati in *Agropyron intermedium*. They fou equal concentrations of water-solub carbohydrates in roots from clipped and unclipped plants, but less water-soluble carbohydrate quantities in roots of clipped plants. This suggests that root biomass may decrease because of clipping, while carbohydrate concentrations remained stable.

Carbohydrate depletion may be responsible for the lack of stem production in defoliated plants, but other explanations should also be considered. Stem production would not occur if the buds were injured or killed by defoliation. Although new stems were not produced following defoliation, the terminal and lateral buds functioned in leaf replacement within 3 weeks after each defoliation until dormancy in 1973 and plant death in July, 1974. Although the objective of defoliation was to deplete carbohydrate reserves, plant morphology cannot be ignored when interpreting the effects of defoliation.

Continuous defoliation eventually results in plant death. From the beginning of defoliation, NC concentrations followed a decreasing trend in two storage organs until a plant part died. The decrease in NC to the range of critical concentrations can be a contributing cause of death. However, death could have occurred because of other reasons brought about by defoliation.

The NC concentration measured in dead plant material is difficult to interpret in terms of plant functions. Whether some of this reserve material could have been used under normal circumstances is not known, but it does represent a considerable loss to the plant. The isolation of carbohydrate reserves from the food transport system of shrubs deserves further study.

Summary and Conclusions

In continuously defoliated snowberry plants, NC concentrations in small roots and stems decreased slowly from the time of initial defoliation. The NC concentrations in large roots and root crowns remained stable until prolonged, intense defoliation eventually caused a significant decrease in NC concentrations in these plant parts. NC concentrations in stems, large roots, and root crowns decreased significantly before plant death. The decrease in NC concentration in large roots and root crowns coincided with an increase in NC concentration in stems just prior to leaf production. This indirect evidence seems to indicate that mobilization of carbohydrates in the stems is supported by NC in the large roots and root crowns. However, other carbon sources in the stems may have supported the increase in NC in the stems. The defoliation treatments also depressed plant vigor, as indicated by the lack of stem production after defoliation began and the high stem mortality suffered during dormancy. The depressed NC concentrations in stems and small roots at the beginning of dormancy appeared to be a good indicator of lowered plant welfare.

Nonstructural carbohydrate concentrations in dead plant parts represent an unused portion of the carbohydrate reserves. Although the carbohydrates in dead plant parts may be extractable using routine laboratory procedures, they appeared to be unavailable for plant use. In shrubs where stem dieback is common, such isolation may represent a great loss to the general vigor of plants and ecosystem productivity.

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