Sprouting and Carbohydrate Reserves of Two Wildland Shrubs Following Partial Defoliation

E. EARL WILLARD AND CYRUS M. McKELL

Highlight: Two wildland shrubs, little rabbitbrush and snowberry, were subjected to three intensities of defoliation at each of four distinct stages in the carbohydrate reserve cycle. These treatments, comparable to browsing and other forms of natural defoliation, were designed to determine the effects on sprouting and associated carbohydrate reserve levels the following spring. Little rabbitbrush plants had reduced carbohydrate reserves, shorter sprouts, and more sprouts following most defoliation tretments. In contrast, carbohydrate reserves increased in snowberry plants with all intensities of defoliation, but there were no significant variations in their sprouting characteristics. Most dormant buds on the root crowns of little rabbitbrush and snowberry plants that were protected from defoliation were prevented from developing as basal sprouts because of apical dominance. Removal of twig tips, however, stimulated more of these buds to produce sprouts. Once a sprout began to grow, a direct relationship seemed to exist between its elongation and the amount of carbohydrate reserves available to it.

Basal sprouting of woody plants, as influenced by mortality of all aboveground plant material, has been the subject of numerous experiments. Many of these studies have related the carbohydrate reserve levels in the roots and root crowns to sprouting responses of plants with killed tops (Aldous 1929; Wenger 1953; Sterrett et al. 1968). Severe defoliation releases dormant buds on the root crown from competition with aboveground plant tissues for stored carbohydrates. Unfortunately, it also eliminates the photosynthetic material that produces these reserves. The removal of all topgrowth provides little insight into natural processes induced by insects, native and exotic herbivores, fire, and prolonged drought that effect sprouting in shrub communities.

We previously used simulated grazing systems to define the effects that large herbivores might have on sprouting of wildland shrubs (Willard and McKell 1973). In the present study, we examined the effects of partial defoliation at different controlled intensities during various stages of the carbohydrate reserve cycle. Our aim was to define resultant influences on sprouting and associated carbohydrate reserve levels the following spring. Two wildland shrubs, little rabbitbrush (*Chrysothamnus viscidiflorus*) and snowberry (*Symphoricarpos vaccinioides*), were selected as representative of the many sprouting shrub species.

At the time of study, the authors were research assistant and professor, Range Science Department, Utah State University, Logan 84322. Willard is presently assistant professor, School of Forestry, University of Montana, Missoula 59812.

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McKell (1956) observed sprouting of little rabbitbrush plants that were no more than 3 months of age after their tops had been damaged by an extreme drought. Sprouts 10 to 15 cm long were also observed as regrowth when tops were removed to clear research plots for other purposes. Stoddart and Smith (1955) reported that root sprouting is common in little rabbitbrush following a fire. Top removal of snowberry by mowing induces basal sprouting (Aldous 1929). These reports indicate the potential of these species to produce sprouts following disturbance of topgrowth.

Studies to determine the influence of defoliation by insects show a significant decrease in flower and seed production (Simmonds 1951; Cameron 1935; Jameson 1963); however, the life of the plant may be prolonged through inducing the formation of sprouts (Cameron 1935). A review of the influence of insect defoliation on trees (Kulman 1971) indicates that complete defoliation results in partial mortality of buds and new shoots.

Site Description

Plants used in the investigation were taken from exclosures that had excluded livestock grazing for more than 10 years prior to our study. The fenced areas were at approximately 2,080 meters elevation in the Cache National Forest in the Wasatch Mountains of northern Utah. In all cases, the exclosures were on the mountain-brushland type on slopes with south or southwest exposures.

Precipitation in the study area averages 75 cm, with the major portion falling in winter as snow or sleet. Snowmelt in the spring brings soil moisture close to field capacity. Rainfall is normally high from March through June, but is low in July, August, and early September. Many plants on the site complete their annual growth cycle by the onset of the dry summer period or else their growth rates are reduced. Certain species, mostly shrubs, renew growth in the fall as rainfall increases.

Soils on the brushy slopes average 75 cm in depth and consist of A, B, and B_2 horizons. Textures range from a silt loam at the surface to a clay at 75 cm, which blends into rocky subsoil.

Methods

Clipping dates were set at monthly intervals to coincide with early (June 1), mid (July 1 and August 1), and late (September 1) phases of the growing season. These phases corresponded with definite changes in the carbohydrate depletion and storage cycles of little rabbitbrush and snowberry as described by Baker (1967). Carbohydrate reserves on June 1 were at or near the low point in the depletion which occurs with the initiation of new growth. By July 1, the reserves were still low, but had begun to increase after the earlier depletion. The August 1 treatment occurred when the reserves were at the annual high for snowberry and near the annual high for little rabbitbrush. Flowering and seed production reduced or slowed the storage of carbohydrates after August 1. By September 1 the storage for the growing season was completed and plant growth had essentially ceased. Twenty-four plants of each species were assigned to each of the four defoliation dates. On each date, eight of the 24 plants were clipped at each degree of defoliation: light (30%), moderate (60%), and intense (90%). Another group of 24 plants of each species was left unclipped as a control unit. Each individual plant was identified with a numbered stake.

Preliminary practice on nontest plants before each clipping date insured a high degree of accuracy in removing the desired percentages of leaf and twig tissues. The percentage of clipped foliage was determined by ocular estimates.

Plants were clipped during the summer of 1969, and then allowed the remainder of that year to respond to the treatments applied. All clipped and control plants were carefully excavated on June 1, 1970 to obtain as much of the root system as possible. This date was assumed to equate with maximum carbohydrate depletion. The roots were carefully washed to remove all foreign matter, and then divided into two groups: 6 mm or less and greater than 6 mm in diameter. Root crowns formed a third category, and were defined as the tissue between the first root and the first branch. Samples were stored in 95% ethanol for later drying with steam-heated ovens and grinding in a micromill.

Roots and root crowns were also collected periodically from unclipped control plants of both species throughout the 1969 growing season and analyzed for total available carbohydrates (TAC) to correlate points in the carbohydrate reserve cycle with clipping treatments.

Several plants of both species were excavated during the dormant period to determine if buds were present on root crowns as a potential source of sprouts the next spring.

Sprouting responses were determined on clipped and control plants when the plants were excavated in 1970. Quantification involved counting the number of sprouts emanating from the root crown of each plant and measuring the length of each sprout.

Root and crown samples were analyzed for total available carbohydrates using laboratory techniques described by Coyne (1969). Total available carbohydrates were defined as reducing and nonreducing sugars, starches, dextrins, and fructosans by Weinmann (1946) and Smith et al. (1964). Results are reported as milligrams of available carbohydrates per gram of oven-dry material (mg/g).

Our clipping dates corresponded to four definite periods in the TAC cycle of little rabbitbrush (Fig. 1). The June and July defoliation dates occurred when reserves were at or near low points in the depletion phases of the cycle. The two latest dates occurred when reserves had been replenished.

The clipping dates also correspond to distinct periods in the carbohydrate reserve cycle of snowberry (Fig. 2). June 1 and July 1 defoliation treatments were applied when reserves were just beginning to recover from periods of rapid depletion. The August 1 defoliation coincided with the peak of the storage cycle, while the September 1 treatment occurred when seed production was complete and reserves were being restored. The effect of twig and leaf removal (whether by man, browsers, or defoliators) at these distinct points in the carbohydrate reserve cycle of little rabbitbrush and snowberry can thus be determined.

The small roots of little rabbitbrush and the root crowns of snowberry are the most important and active sites of carbohydrate reserves (Willard 1972). These tissues contain the greatest amounts of total available carbohydrates, and in the 1972 work were more responsive to clipping treatments and seasonal fluctuations than were the other tissues analyzed. These are the storage sites implied, therefore, when carbohydrate reserves are mentioned in the following discussion and figures.

Results

Little Rabbitbrush

The carbohydrate reserve cycle of little rabbitbrush during the 1969 growing season is shown in Figure 1 D. Reserves were rapidly depleted during the latter part of May as leaf buds began to swell and open. Replenishment was rapid after leaf development until early June, followed by an extended period when reserves were again depleted for flower production in late June and early July. Reserves then increased rapidly again until the first of August, after which the rate of replenishment was much reduced.

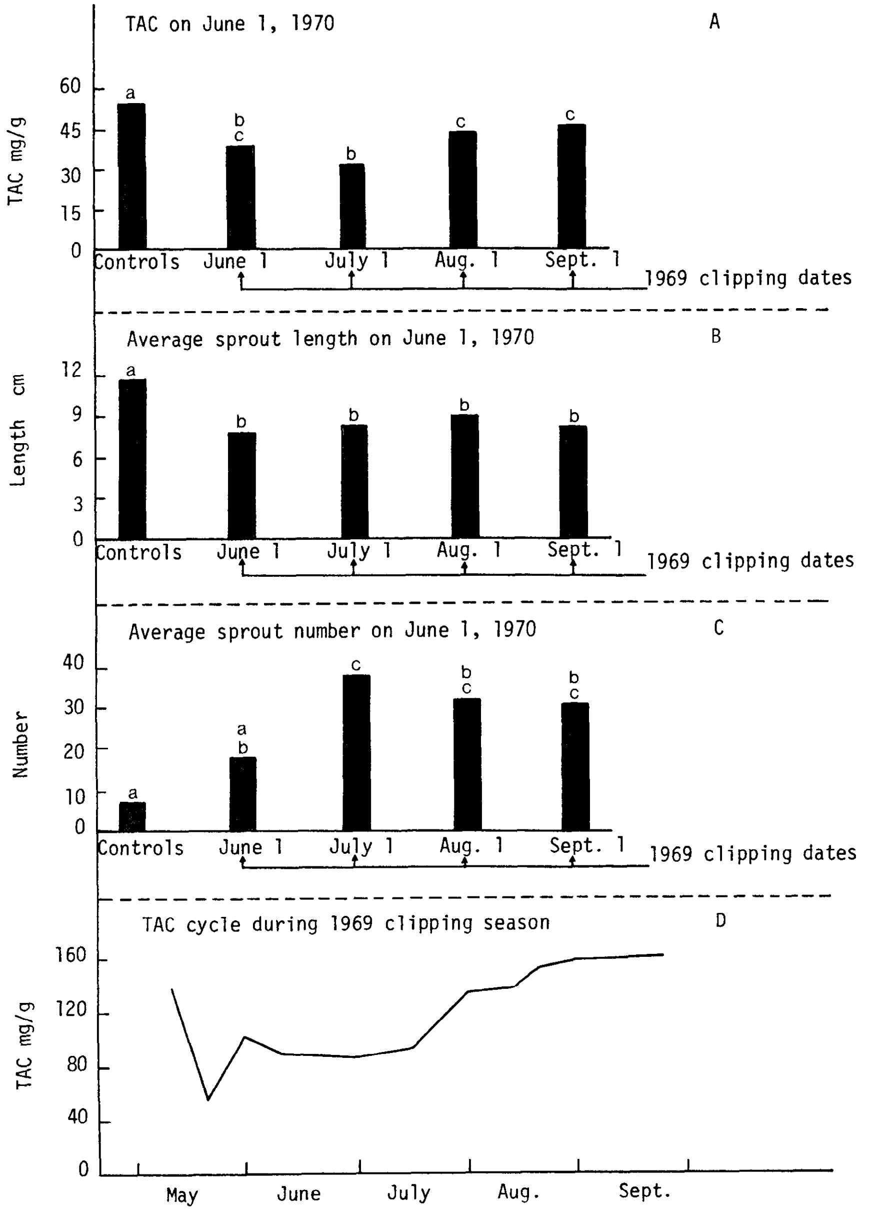

Fig. 1. *Total available carbohydrates (A) and sprouting responses (B, C) of little rabbitbrush on June 1, 1970, after partial defoliation at different dates in 1969 as related to carbohydrate reserves of unclipped plants (D) at the time of defoliation. Bars labeled with the same letter are not significantly different at the .05 level.*

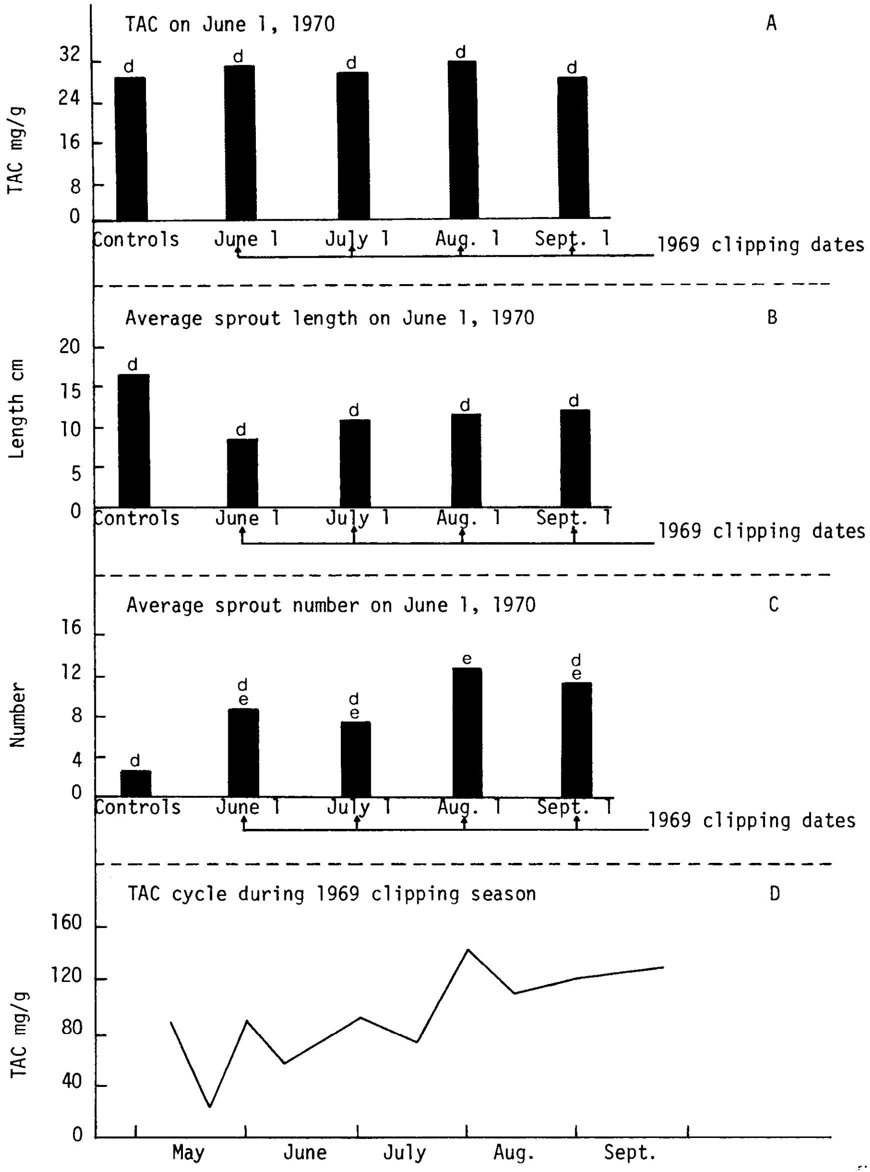

Fig. 2. *Total available carbohydrates (A) and sprouting responses (B, C) of snowberry on June 1, 1970, after partial defoliation at different dates in 1969 as related to carbohydrate reserves of unclipped plants (D) at time of defoliation. Bars labeled with the same letter are not significantly different at the .05 level.*

Partial defoliation of little rabbitbrush at any of the four points in the TAC cycle reduced reserves the following spring (Fig. 1 A). Reserves were reduced more by clipping on July 1 during flower formation than by clipping later in the summer. However, carbohydrate reserves in plants clipped during the initial spring depletion (June 1) period did not sgnificantly differ from those in plants clipped during flowering depletion (July 1) (Fig. 1 A).

All clipping intensities imposed during 1969 reduced stored carbohydrates in little rabbitbrush the following spring (Fig. 3 A). The light intensity treatment reduced TAC reserves more than did the moderate intensity. No other differences in reserves were detected among clipping intensities (Fig. 3).

The number of subsequent new sprouts was significantly increased by clipping during flower formation (July 1) or later in the summer (Fig. 1 C). Sprouts were shorter on clipped plats regardless of defoliation dates, however, than on unclipped plants. All clipped plants had sprouts of essentially the same length (Fig. 1 B).

All intensities of clipping similarly increased the numbers of new sprouts (Fig. 3 A) and in all cases, these sprouts were shorter than ones of unclipped plants (Fig. 4 A).

Snowberry

The carbohydrate reserve cycle of snowberry during the 1969 growing season is shown in Figure 2 D. Trends in reserves were similar to those of little rabbitbrush. The most obvious difference was that the reserves in snowberry were depleted to a much lower level than those of little rabbitbrush during initiation of spring growth. TAC reserves were rapidly replenished in late May and early June when plants were in full foliage, with another reduction during flowering from mid-June to mid-July. A gradual increase then occurred until early August, when reserves were utilized for seed production. Net storage was slight after mid-August.

Total available carbohydrate reserves and sprout lengths of plants partially defoliated at any of the four points in the TAC reserve cycle did not vary significantly from those of unclipped plants the following year (Fig. 2). Clipping on August 1, however, when reserves were at their high point for the growing season, increased the number of new sprouts produced the following spring (Fig. 2). These data suggest that snowberry is not as much influenced by the timing of partial defoliation as is little rabbitbrush.

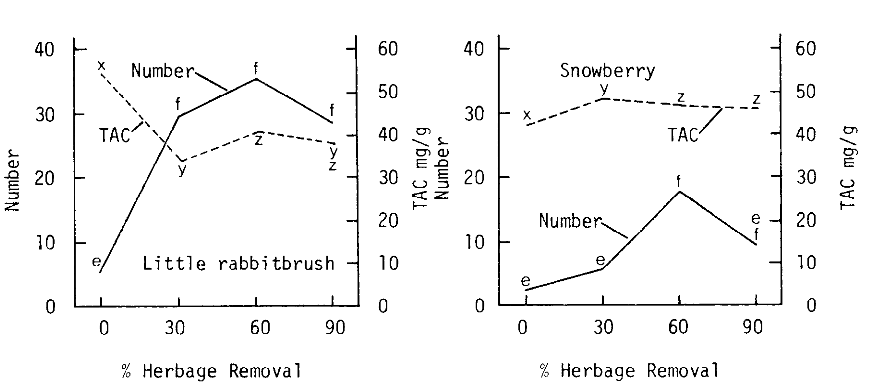

Fig. 3. *Numbers of new sprouts and TAC reserves of little rabbitbrush (A) and snowberry plants (B) in the spring following partial defoliation at different intensities the previous year. Points on curves labeled with the same letter are not significantly different at the .05 level.*

By contrast, the degree of defoliation appears relatively influential on the TAC reserves and sprouting of snowberry. All intensities of defoliation produced an increase in carbohydrate reserves the following spring. Plants clipped lightly had greater reserves than did those more severely defoliated (Fig. 3 B).

The intensity of defoliation did not influence the length of new sprouts the following spring (Fig. 4 B). However, the moderate clipping treatment significantly increased the number of new sprouts over those of unclipped or lightly clipped plants (Fig. 3 B).

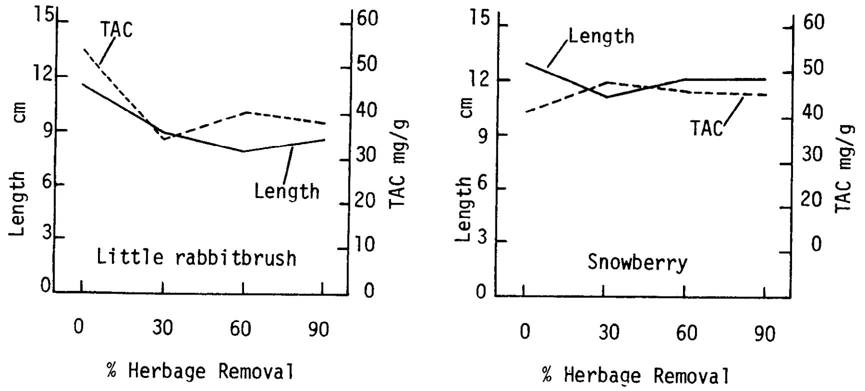

Fig. 4. *Lengths of new sprouts and TAC reserves of little rabbitbrush (A) and snowberry plants (B) in the spring following partial defoliation at different intensities the previous year. Points on curves labeled with the same letter are not significantly different at the .05 level.*

Discussion

Unclipped plants of snowberry and little rabbitbrush that were excavated during the winter had numerous buds on their root crowns. These were apparently the source of new root crown sprouts the following spring. The number of new sprouts varied on clipped plants depending upon the clipping treatment of the previous year. We were unable to detect if adventitious buds developed following the clipping treatments. It is apparent, however, that both plant species have a sprouting potential that does not require defoliation as an activator. Also, varying numbers of buds were observed on the root crowns of both clipped and unclipped plants at the same time that sprouts were well developed. Why some of the buds remained dormant is unknown.

Investigations into causes of bud dormancy have been numerous and it was not our purpose to investigate this subject. Thimann (1937, 1948) and Romberger (1963) have reviewed the subject extensively, and they reported that lateral buds commonly begin growth following decapitation of the stem apex, which releases apical dominance. Apical dominance may contribute to the dormancy of buds on the root crowns of snowberry and little rabbitbrush, although the sprouts on unclipped plants illustrated that this dominance is not complete.

Partial apical dominance, rather than an "all-or-nothing," mechanism, seems to be regulating the number of sprouts appearing on snowberry and little rabbitbrush following partial defoliation. Plants clipped lightly had intact shoot apices left on several twigs, while those clipped moderately had fewer and heavily-clipped plants had no intact twig apices. This might explain why moderately clipped plants had greater absolute numbers of sprouts than plants under other clipping intensities or control plants. (Although not statistically significant in all instances, our data indicate a similar trend in both species.) Plants clipped moderately had fewer twig apices left to exert apical dominance than those clipped lightly or left unclipped. Thus, lowered apical dominance allowed more sprouts to grow. Those plants clipped intensely, although having no twig apices remaining, had lower TAC reserve levels than those clipped moderately. This probably explains the greater number of sprouts on moderately defoliated plants. It appears, then, that partial defoliation lessens apical dominance and mobilizes available carbohydrate reserves, which regulate the number of sprouts produced.

Once sprouts begin to grow, their vigor is related to carbohydrate reserves. Yocum (1945) reported that bud growth depends upon food reserves. Tew (1970) also reported that root sections of *Populus tremuloides* maintained in the greenhouse initially produced rapid sprout growth that ceased rather abruptly, indicating a depletion of carbohydrate reserves. Our data illustrate that in addition to affecting carbohydrate reserves, clipping also increases the number of sprouts that draw upon these reserves. Each sprout on a clipped plant has a smaller amount of carbohydrates available to it for growth than does a sprout on unclipped plants. Conversely, unclipped plants generally have longer sprouts since few sprouts are drawing upon stored carbohydrate reserves.

Differences betwen snowberry and little rabbitbrush in their depletions of TAC reserves following an initial defoliation treatment are probably related to differences in vigor between the two species when they are protected from defoliation. Snowberry has a markedly low level of vigor; it tends to produce fewer young shoots and has a shorter period of growth. Clipping stimulated growth of numerous new shoots and more leaves remained on the plant for several weeks longer in the fall. Seed production, a physiological drain on carbohydrate reserves, was quite noticeably greater in nonclipped than on clipped plants. The combination of these factors probably provides for greater net production of photosynthate for storage in the sinks of previously defoliated snowberry plants.

Little rabbitbrush plants protected from defoliation produce vigorous shoots annually on older stems. Clipping of this species simply stimulates a larger number of new sprouts, which draw upon carbohydrate reserves for initial growth. Thus, these new sprouts as a group apparently require more carbohydrates than they can replace during the year of defoliation, resulting in a net reduction in the various stoage sites.

Various degrees of defoliation of wildland shrubs by insects, drought, wild herbivores, livestock, wildfires, or other factors commonly occur in most plant communities. Our data suggest that changes in carbohydrate reserve levels and in sprouting following a partial defoliation may change the competitive ability of certain shrub species in the community. Partial defoliation may enhance the vigor and perhaps the competitive ability of shrubs such as snowberry by affecting an increase in carbohydrate reserves, sprouting, and overall plant vigor.

Other species may react differently. The significantly lower carbohydrate reserve levels and reduced sprout growth of clipped plants of little rabbitbrush suggest that the vigor of certain species may be reduced following partial defoliation.

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