Rate of Twig Elongation of Chamise

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Chamise *(Adenostoma fasciculatum)* is one of the major shrubs of the chaparral belt in California. Increasing emphasis on watershed management and the manipulation of brush covers for livestock and deer feed requires that additional information be obtained on the growth habits of the important plants. The objectives of this study were to determine the rate of twig elongation and the pattern of chamise growth. Three growth forms of chamise were studied. These were ungrazed mature plants which attain a height of 6 to 8 feet, plants that were hedged by deer browsing to heights of about 3 feet or less, and root crown sprouts which occurred after the tops had been killed by fire. The response of twigs to removal of the terminal bud was determined.

The study was conducted on three sites on the Hopland Field Station of the University of California during the 1956 growing season. The Station is approximately 110 miles north of San Francisco and 40 miles inland from the ocean. The elevation varies from 500 to 3000 feet. Precipitation averages about 35 inches per year, although in 1955-1956 it was about 40 percent above normal. Most of the area is of the oak-woodland and annual grass types with belts of chamise and other chaparral species on the upper slopes.

Previous Studies

Chamise is a native plant of California and is found exclusively in California and Lower California (U. S. Forest Service, 1937). Cooper (1922) made some of the earliest anatomical and ecological descriptions of chamise in his study of the broad-scleorphyll vegetation in California. A difference between leaves of mature plants and those of sprouts was recognized.

Watkins and de Forest (1941) found that chamise in southern California exhibited irregular growth. Twig elongation was greater on northern exposures than on southern exposures. Much of the growth on mature plants was from lateral buds because the terminal buds had developed inflorescences the previous year. Twig elongation was uneven, in that some twigs grew before others started, and showed variation in length ranging from 0.1 mm. to 20 cm. A second but shorter period of growth occurred in the fall during favorable years.

Miller (1947) found the growth rate of chamise to be highest during early April. His studies substantiated those of Bauer (1936) who found that growth was highly correlated with evaporation rate. Setchell (1925) presented evidence that temperature controlled time of flowering. Vegetative growth precedes flowering in chamise. There is a lag of 13 to 18 days in time of flowering for each rise of 1,000 feet in elevation in the Santa Ana Mountains of southern California (Pequegnot, 1951).

Chamise sprouts from the root crown following fire or other means of top removal. Sampson (1944), Biswell, *et al.* (1952), and Horton and Kraebel (1955) reported rapid increase in brush density following fire. Sprouts at the end of the first year ranged between 22 and 32 inches in height in northern California (Biswell, *et al.*, 1952) and 19.1 inches in southern California (Horton and Kraebel, 1955). Sprouts are eaten by deer and livestock and furnish nutritious forage at least for a year or two after burning (Reynolds and Sampson, 1943).

These studies indicate that chamise grows more in certain locations than others and that the response will vary from year to year. The present study was

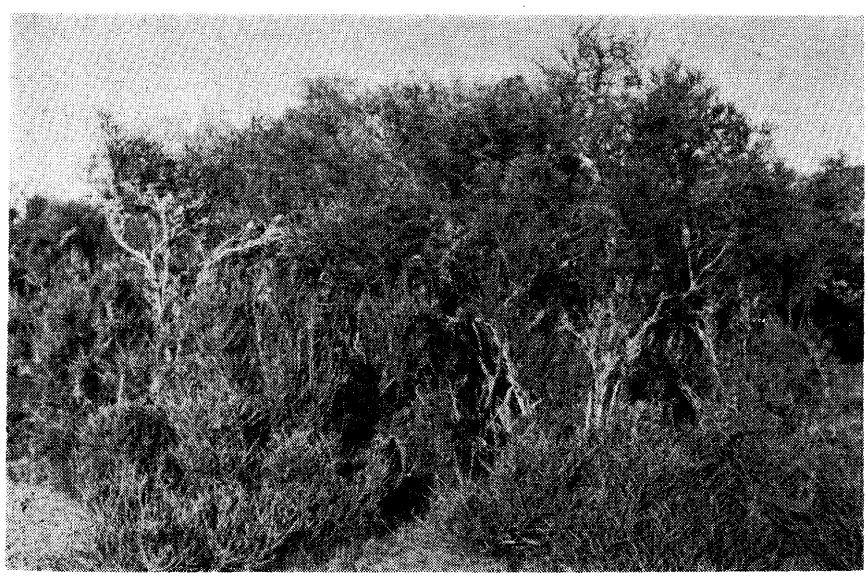

FIGURE 1. Ungrazed mature plants of chamise are shown in the background with hedged plants in the foreground. Photo taken November 7, 1956.

undertaken to determine if growth variations also occurred between different growth forms and between twigs located at different positions on a plant.

Growth of Mature Chamise

One branch of the previous year's growth was selected on 20 mature plants, and these branches were tagged below the new growth with an aluminum tag. Each twig to be measured was marked with colored string. The new growth was measured at two-week intervals to the nearest 1/100 foot from its point of origin to the terminal tip. Twigs from three distinct positions on the branch were measured: one nearest the end of the branch, a second near the middle, and the lowest twig on the branch. Only branches above the reach of browsing animals were selected (Figure 1.) The initial measurements were made on April 14, 1956, shortly after growth had commenced.

Two distinct twig patterns were observed at the beginning of the study. One type consisted of a single long leader without lateral branching and the other consisted of a shorter leader with lateral branches. Current growth was initiated from lateral buds of both types. Twigs on both growth patterns were measured. However, because of similarity in the growth rates the data were combined for final presentation.

On April 14 all growth was vegetative. By April 28 flower buds were emerging. On June 8 the plants were in full bloom and by June 23 the petals had begun to drop and the pollen was gone. Between June 8 and June 23 elongation ceased, and thereafter the twigs became somewhat coarse and woody.

The regression curves of accumulated growth for the terminal position twigs, middle position twigs, and lower position twigs are shown in Figure 2. The fitted curves were calculated from the recorded lengths of the twigs by the formula, $Y = a + b \log X$. "Y" is the length expressed in feet, and "X" is the number of days from inception of growth. Equations which express these data are for the terminal, middle, and lower positions, respectively:

$Y = -0.4453 + 0.4429 \log X$,
Standard error of estimate = 0.1253
$Y = -0.3039 + 0.3227 \log X$,
Standard error of estimate = 0.1053
$Y = -0.2082 + 0.2332 \log X$,
Standard error of estimate = 0.0839

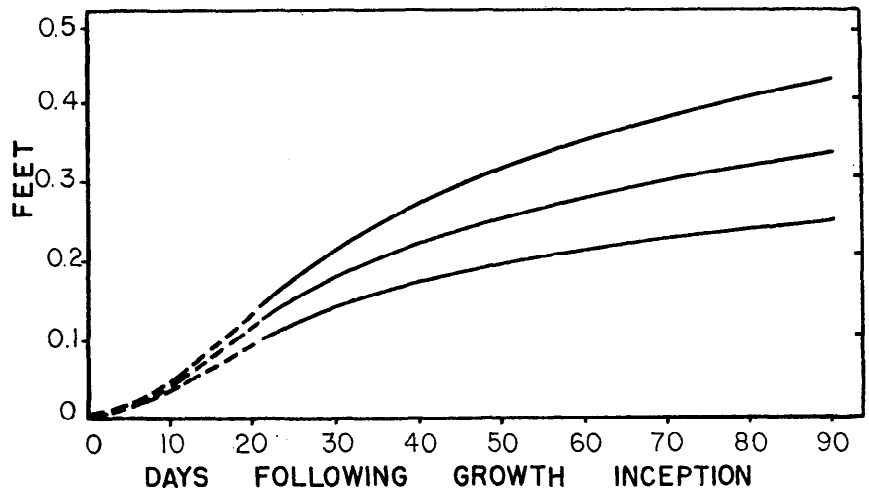

FIGURE 2. Regression curves of chamise twig elongation for current growth on various parts of the mature plant. The upper curve is for terminal position twigs, the middle curve for intermediate position twigs, and the lowest curve for twigs in the bottom position on the major branches.

Average length for the terminal twigs was 0.41 foot, for the middle twigs, 0.3 foot, and for the lower ones, 0.23 foot. The higher the twig on the plant the faster was its growth and the greater its final length.

The exact date of growth inception was not known, as growth was in progress at the time of first measurement. Average twig lengths on April 14 were 0.13 foot, 0.1 foot, and 0.08 foot for the terminal, middle, and lower twigs, respectively. However, an arbitrary inception date was needed to compute the regression. By extrapolation of the growth data a lapse of 21 days was assumed to have occurred between the start of growth and the first measurement. Computation places the growth initiation date as approximately March 24. As twig elongation ceased after June 23, a 91 day growing season was found for mature chamise in this area for the environmental conditions of 1956. Possibly twig diameters continued to increase after than date. The variations in growth between years needs to be determined.

In Figure 2 the lower portion of each regression curve is shown by a dashed line. This assumes that the early growth follows an "s" curve (Meyer and Anderson, 1952). These curves cannot be used beyond the 91st day of growth because twig elongation had ceased by that time.

On all tagged twigs, growth for the 1956 growing season was terminal with lateral branching absent; however, lateral branching occurred on other twigs. After approximately 35 days of growth flower buds appeared near the ends of most of the twigs. Maximum daily temperature was in the high 60's at that time, and according to Setchell (1925) and Pequegnot (1951) flowering of chamise is correlated with rise in air temperatures above 59° F.

The average percentage by length of the vegetative part of the twigs remaining after flower maturity was 49.4, 41.5, and 48.1,

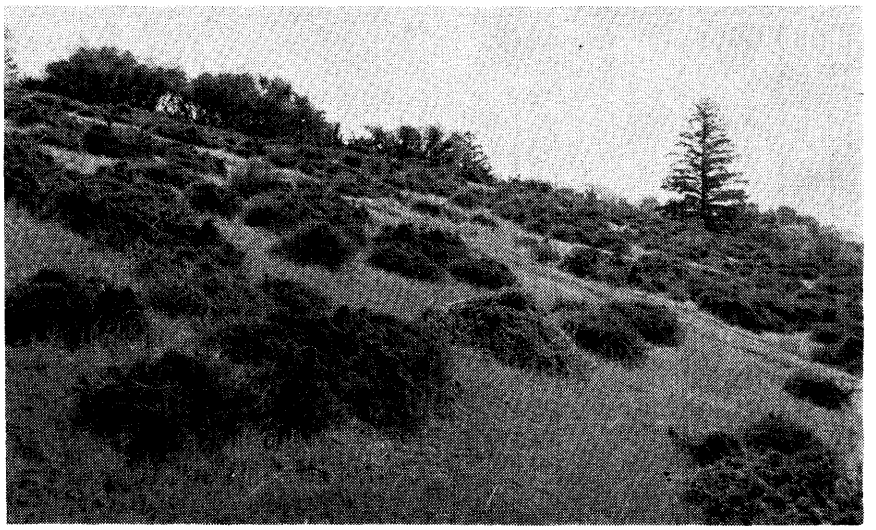

FIGURE 3. These hedged chamise plants are low-growing and have dense foliage. Photo taken April 2, 1957.

for twigs in the three positions. On all twigs an average of 46 percent remained alive after the flowers had died.

Hedged Mature Plants

After fire many root crown sprouts and seedlings of chamise appear. Browsing by animals restricts the plants from attaining their full normal height, and a hedged growth form develops as the plants mature.

The size and shape of the hedged plants varied greatly. Most were very low-growing, relatively wide across, and had dense foliage. This shape is the result of removal of all new twig growth each year on the tops of the plants and partial removal on the sides (Figure 3).

In this study 18 hedged plants were caged on April 14. Typical, uniform plants were selected. Two twigs on the tops and two twigs on the side of each plant were selected and marked with aluminum tags. The tag on each twig was attached at the point where new growth began; in that way it served as a reference point for each measurement. Twig lengths were measured in the same manner as with mature plants.

Twig growth at the first of the growing season was typified by an increase in length; the terminal growing point elongated and no lateral branching occurred. Flower buds appeared on the side branches of some plants by May 11. Usually these were only on the upslope side. Deer graze mostly on the downslope side of the plants and consequently that side of the plant was more severely hedged. Apparently, pressure of browsing by deer on the tops of plants inhibits or restricts the plant from forming reproductive growth on these branches. However, twigs on the tops of the plants had more vigorous vegetative growth than the side twigs. There appeared to be a direct relationship between the degree of flowering and the degree of hedging. By July 9 the petals were dropping, and the inflorescences had become dry and brown. This is approximately two weeks later for hedged than for ungrazed plants in the same area.

Figure 4 presents the regression curves of accumulated length of the top and side branches, respectively. In a similar manner as described with mature chamise the date of growth inception was approximated to be 18 days prior to April 14. Elongation of twigs had ceased by July 24, thus giving a 119-day growing season.

The regression equations which express the growth for the top and side branches respectively are:

$Y = -0.859 + 0.81 \text{ Log } X$

Standard error of estimate = 0.3137

$Y = -0.4966 + 0.5376 \text{ Log } X$

Standard error of estimate = 0.2427

With progression of the season two growth patterns appeared.

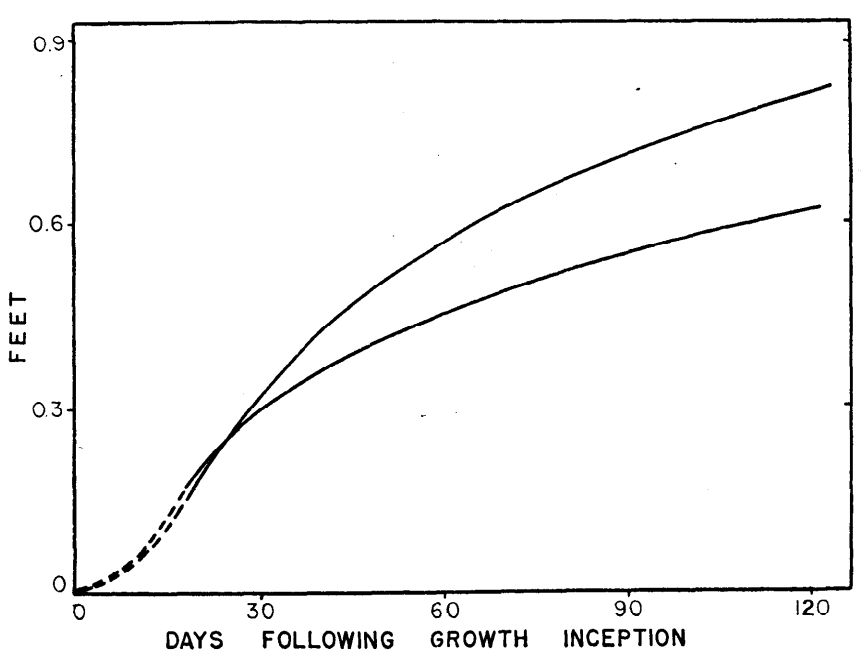

FIGURE 4. The top regression curve shows the elongation of top branches on hedged chamise plants, and the lower curve is for side branches.

Some twigs of the larger, more vigorous plants initiated lateral branching from the basal portion upward toward the twig tip. Lateral branches were at 45 to 60 degree angles from the main axis of the twig. Larger size and greater plant vigor seemed to be factors correlated with degree of branching. However, the majority of all twigs continued terminal growth without branching. The unbranched twigs were more leafy and succulent, while the branched twigs had fewer leaves in proportion to twig size and became more woody. Both patterns were observed on the same individual plant.

Root Crown Sprouts

The crown sprouts appeared approximately April 14, one month after a controlled spot burn. Sprouting occurred first from the periphery of the root crowns and later from the basal portion of the charred stems.

Twenty charred root crowns were selected on April 28. Exclosures to exclude deer, sheep, and rabbits were erected about each crown (Figure 5). Three sprouts per crown were selected, and their total lengths measured at approximately two-week intervals until cessation of growth, December 12, after 235 days.

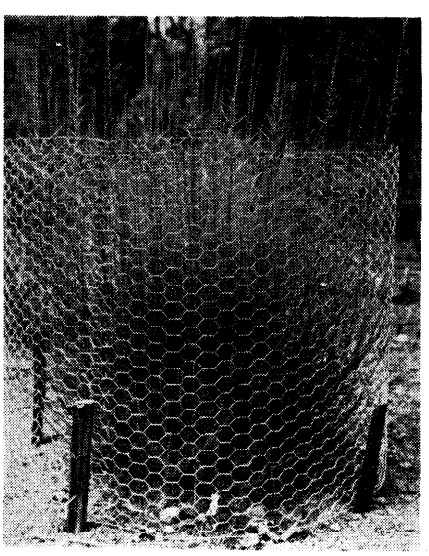

FIGURE 5. Chamise sprouts protected from grazing and showing growth after 203 days. Growth continued for approximately one month after photo was taken. Maximum height was 4.67 feet. Uncaged sprouts in the vicinity were grazed and did not attain a height of more than one inch.

Sprouts from root crowns differ markedly from the new growth on mature and hedged plants. The rate of shoot elongation is extremely rapid from the start of growth through the hot, dry, summer months and into the fall (Figure 6). This curve was computed in the same manner as those shown earlier. The regression formula for accumulative sprout growth is:

$$Y = -2.23 + 1.925 \log X$$

Standard error of estimate = 0.62

Extrapolation of the growth data gave an arbitrary growth inception date 10 days prior to the first measurement.

The average length of sprouts at the final measurement, December 12, was 2.24 feet, the tallest tagged sprout measured 3.75 feet and the shortest, 0.66 feet. Longer and shorter sprouts were present. Considerable variation in lengths of twigs occurred at any one time of measurement. The shorter twigs elongated at a slower rate after 60 days, while the longer twigs continued at a fast rate.

The number of sprouts varied according to the size of the root crown. Sprouting occurred very rapidly, and in a short time after the first appeared there were as many as 500 sprouts on a single large crown. A peak number was counted on May 25, and many sprouts died before July 24. Thereafter, numbers decreased at a much slower rate. Great density of sprouts and their competition for light may be one reason for the sharp decrease in the numbers of sprouts. As the growing season progressed the larger sprouts gained greater dominance. By December not more than half of the sprouts remained alive on the larger crown. The mortality was not as great on small crowns. An occasional new sprout appeared throughout the season.

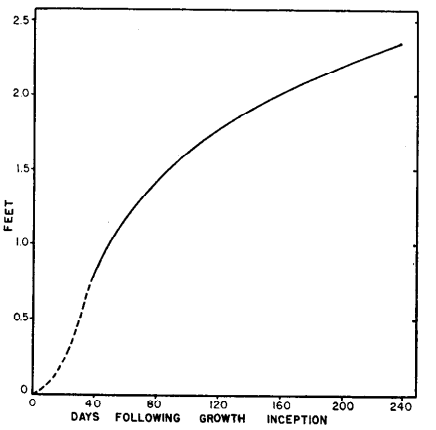

FIGURE 6. The regression curve shows elongation of root crown sprouts in relation to time in days. Note that the scale is different from that in Figures 2 and 4.

Growth of new sprouts was without branching at first but by July 10 branches were present. As the growing season progressed the sprout stems and branches became woody. Some of them attained a half-inch diameter at the base.

Effects of Terminal Bud Removal on Twigs of Mature Plants

This study was concerned with the growth of axillary branches in response to removal of the terminal bud. On many species of plants axillary buds are stimulated to grow when the terminal bud is removed. This is known as apical dominance (Meyer and Anderson, 1952). It expresses the inhibiting effect of a terminal bud upon lateral bud development. Chamise exhibits apical dominance, but no previous data were found for this species.

The removal of the terminal portion containing six leaf fascicles was made to simulate grazing at different dates throughout the growing season. The plants studied were in an exclosure, and the study was initiated on May 12 shortly after active growth began.

A sample of twenty plants was used. On nineteen plants of the sample one twig was treated every two weeks from May 12 to

August 6. On one plant five twigs were treated every two weeks to observe whether the same growth responses that occurred between plants existed within a single plant. Only actively growing twigs were selected. Some twigs had an inflorescence and some did not. Each twig tipped was marked with an aluminum tag.

The twigs exhibited four different responses to tipping: no noticeable growth response, reproductive axillary growth; vegetative axillary growth, and enlargement of leaves (Figure 7). When part of an inflorescence was removed the remaining pedicels lengthened laterally and gave the flower cluster a spread-out or opened appearance. Lateral vegetative branches developed on part of the tipped twigs. In some cases the tipped twig neither flowered nor grew lateral branches, but the leaves were larger and more succulent. The responses to tipping that occurred within a single plant were the same as those between individual plants. More than one type of response occurred on twigs of the same plant for the majority of tipping dates.

The results indicate the extent of different responses in relation to time. At the time of initiation of the study some of the twigs were already setting flower buds. These buds opened approximately June 1, and by the first week in July blooming had ceased and petals were falling. This is substantiated by the fact that no new axillary branching of the flower clusters occurred following the June 23 treatment. The greatest amount of flower branching on tipped inflorescenses occurred with the May 25 treatment, which was in a period of rapid growth. Slightly more branching occurred with the June 23 treatment than with the June 7 treatment. In all cases this response was complete by July 23.

Vegetative axillary branching occurred only in twigs tipped on May 12, May 25, and June 7.

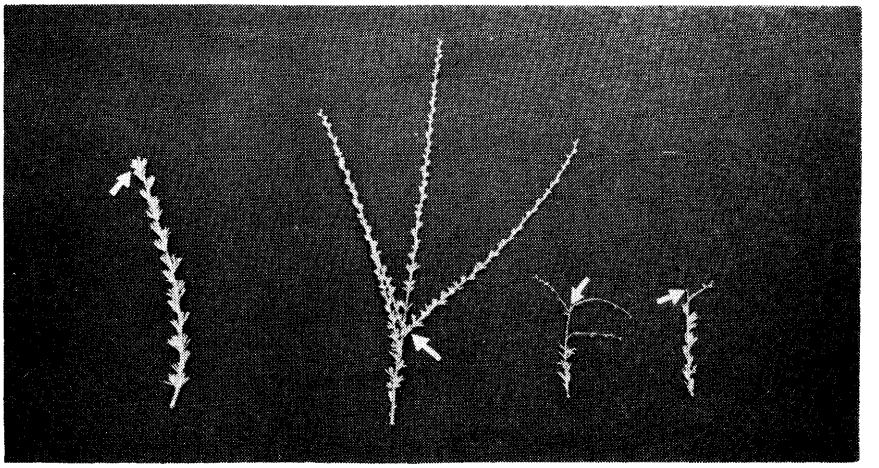

FIGURE 7. The growth responses to terminal bud removal on mature plants were, left to right: leaf enlargement, vegetative axillary growth, and the last two, reproductive axillary growth. The arrows indicate where the buds were removed.

Leaf enlargement occurred to some extent with each date of treatment and increased in all cases from July 23 to September 4. Following the July 9 treatment, all growth response was leaf enlargement with the largest amount, 68 percent, occurring with the date of treatment.

Discussion

Growth began at approximately the same time for the mature and hedged plants. However, the hedged plants grew for a longer period. In fact the sprouts grew all summer and fall. It should be noted that for the hedged plants twig elongation continued for about two weeks after the petals dropped, whereas there was little growth after this time for the mature plants.

Time of growth cessation has been mentioned as a possible guide to the time to measure production of browse species where the grazing is yearlong. The data presented indicate that shortly after flower maturity would be the ideal time for chamise. However, with sprouts there seems to be no clearcut indication of time because they grow during the entire summer and fall seasons. If new sprouts are continually removed by grazing, additional buds germinate but the extent to which this happens is not known. If the sprouts continue to grow without grazing during the first year, the basal portions become woody and cannot be classed as forage. Thus determination and measurement of browse on chamise sprouts needs additional study.

Measurement of production and use of browse on game ranges is an important tool in game management. This study indicates that, at least for chamise, the new growth may be different on different parts of the plant. Top or terminal branches grew longer than side branches. Probably grazing is more severe on the terminal branches. This is indicated when a plant develops a hedged appearance. If the ungrazed twigs are mostly side branches, which are naturally shorter than the terminals, then to use them for standards of ungrazed lengths leads to an underestimate of the amount of browse used. These data indicate that sampling of browse must take into account the position of the sample on the brush plant.

The data on effects of removing the terminal portion of chamise twigs indicates that grazing during the season of fast growth leads to branching and probably additional production of browse.

Perhaps there is also additional feed produced by the enlarged leaves through the summer and fall.

Summary

The rate of twig elongation and pattern of growth in the 1956 growing season were determined on three growth forms of chamise. These were mature plants, hedged plants, and root crown sprouts.

Crown sprouts grew faster and over a longer period than new twigs on either hedged or ungrazed mature plants. Top twigs on hedged plants were generally longer than side twigs. The higher the position of new twigs on mature plants the longer they became.

The lengths of the growth periods were different with each growth form. Initiation of twig elongation occurred on approximately March 24 for the mature and hedged plants and slightly later for the crown sprouts.

Elongation ceased by June 23 on mature plants, July 24 on hedged plants, and not until late autumn with the crown sprouts.

Patterns of twig branching between growth forms were not markedly different except for the magnitude of branching. With the hedged and mature plants the majority of the twigs did not branch. Amount of vigor was assumed to be a factor in the amount of twig branching.

Three growth responses occurred following removal of the terminal bud of twigs of mature plants: reproductive axillary growth, vegetative axillary growth, and enlargement of leaves. Some twigs showed no response. The greatest amount of vegetative lateral branching occurred in the spring period of good growing conditions and rapid plant activity. The greatest growth response over the entire growing season was leaf enlargement. This would indicate that additional plant material would be produced if twigs were grazed during the growing season.

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