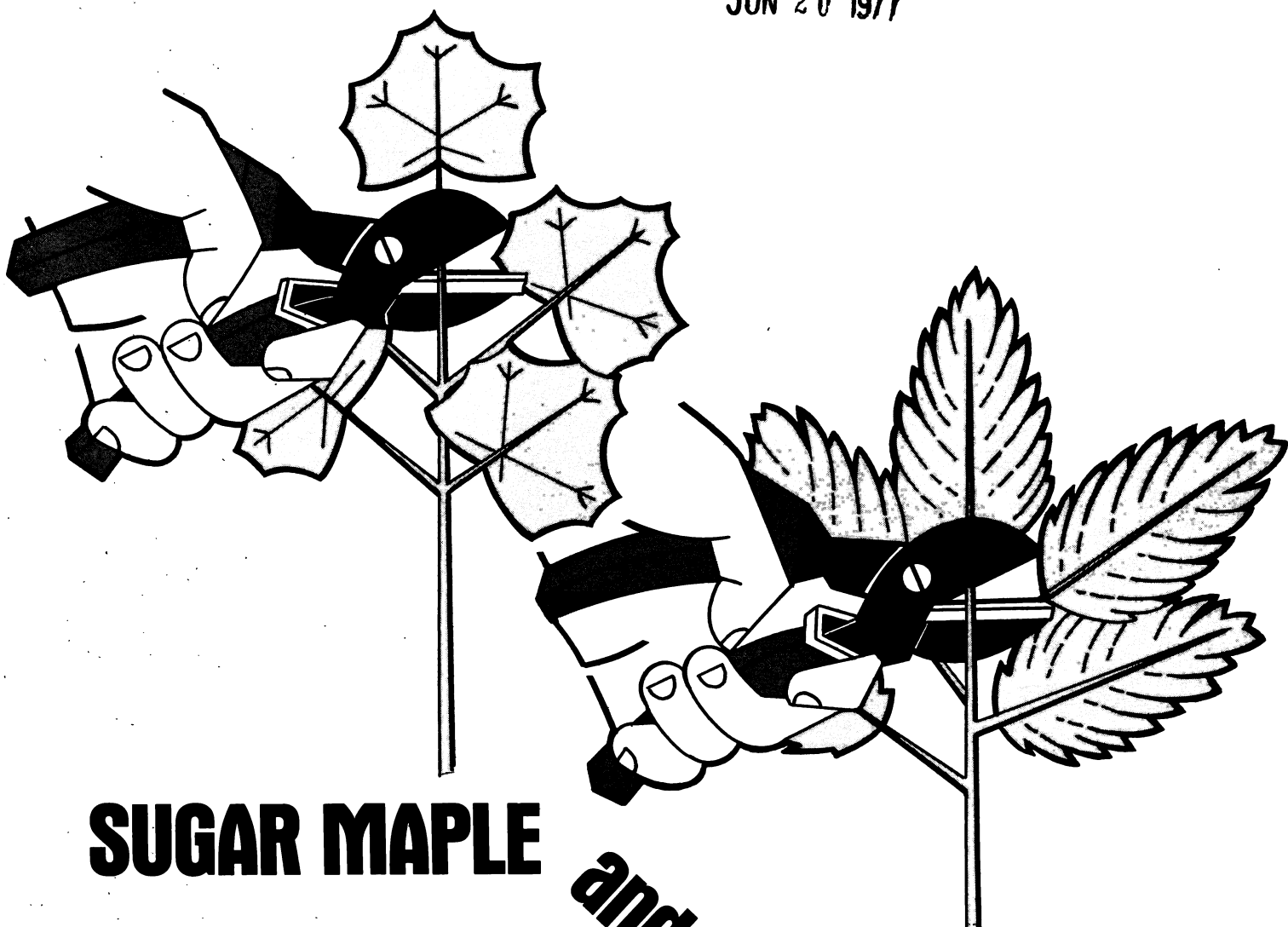


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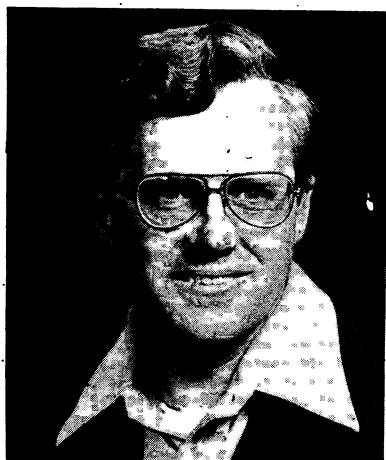
SUGAR MAPLE and YELLOW BIRCH SEEDLING GROWTH after SIMULATED BROWSING

FREDERICK T. METZGER

North Central Forest Experiment Station
John H. Ohman, Director
Forest Service - U.S. Department of Agriculture
Folwell Avenue
St. Paul, Minnesota 55108

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THE AUTHOR

Frederick T. Metzger has been working on the ecology and regeneration of the Great Lakes northern hardwood forests at the Station's Northern Hardwoods Laboratory since 1966. Before that he served as a forester on the Black Hills National Forest in South Dakota and the Roosevelt and Rio Grande National Forests in Colorado. He received both his bachelor's and master's degrees in forestry from the University of Minnesota.

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Many shoots and buds of northern hardwood reproduction are damaged by insects (Knight 1968) and browsing animals (Stearns 1968). Such damage to the terminal shoot has long been considered detrimental to height growth, stem form, and vigor.

Jacobs (1969) found deer browsing does not always hamper sugar maple seedling development. His results prompted a study of how growth of damaged seedlings is influenced by seedling characteristics and leader injury during the dormant season.

Sugar maple (*Acer saccharum* Marsh) and yellow birch (*Betula alleghaniensis* Britton) seedlings were used and represent two broad groups of trees that differ in shoot organization. Sugar maple's winter buds contain preformed shoots; they have true terminal buds and the lateral buds are opposite. Shoots in the winter buds of yellow birch are not fully preformed (Kozlowski and Clausen 1966) and apical buds may abort; lateral buds are alternate.

METHODS

The study was conducted in two stands of sugar maple-beech-yellow birch (SAF type 25) on the Upper Peninsula Experimental Forest near Marquette, Michigan. The sugar maple seedlings were under a shelterwood overstory cut to 97 ft² of basal area per acre (22 m²/ha) and treated with herbicides in 1960 and recut to 80 ft² (18 m²/ha) in 1966. The yellow birch seedlings grew in a clearcut area 2 chains (40 m) by 8 chains (160 m) cut and treated with herbicides in 1960. Both stands were originally mature to overmature. No natural animal injury to leaders occurred during the study.

Under natural conditions the number and size of buds on leaders and the length of leaders vary greatly. A bud position index was devised to account for these differences and permit standardizing treatments. Values were derived by dividing the number of lateral bud positions on a leader

into the number of buds or bud pairs located above a selected bud (fig. 1). Buds with a given index value bear a relatively constant relation to the lengths of the other buds on the leader.

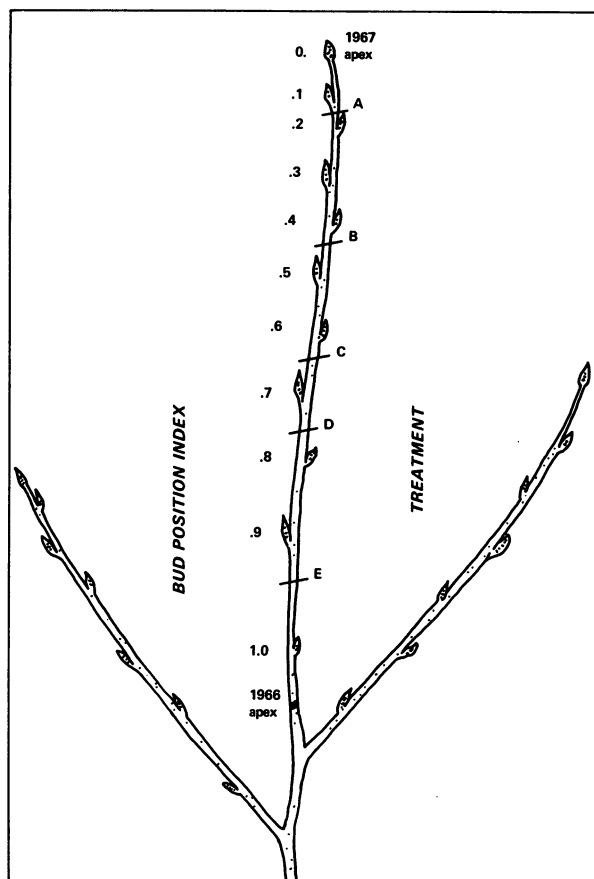


Figure 1.--Shoot of yellow birch illustrating treatment locations and bud position indices for an 11-bud leader.

Treatments simulated natural damage by removing portions of the current-year leader above specific bud position indices (fig. 1). Bud position and size, and the amount of leader removed by treatment is given in table 1. The 6 treatments were replicated 10 times, using a total of 60 seedlings of each species.

Table 1.--Summary of treatments: mean bud lengths, positions, and percent of leader and buds removed

YELLOW BIRCH						
Treatment	: Control :	A :	B :	C :	D :	E :
Bud length (mm)	5.4	² 6.4	7.6	² 6.3	5.8	2.2
Bud position ¹	0	0.15	0.41	0.66	0.84	0.95
Buds removed (percent)	0	14	37	61	77	87
Leader removed (percent)	0	13	35	63	85	97
SUGAR MAPLE						
Bud length (mm)	² 6.8	3.5	² 6.3	² 6.0	4.8	0.9
Bud position ¹	0	0.18	0.46	0.64	0.82	1.00
Buds removed (percent)	0	15	39	54	70	85
Leader removed (percent)	0	1	30	63	84	98

¹See text for definition.

²Bud length means that do not differ significantly at 0.05 level, Duncan's new multiple range test. All other bud length means differ from others within a species.

Elongation of all shoots developing in 1968 that originated from buds on the 1967 leader was measured weekly during the period of rapid growth and less often later in the season. The dominant shoot was determined at the last measurement in October.

The relation of a bud's length to its position on the leader was determined from measurements on 100 undisturbed seedlings of each species.

Treatments were arranged in a randomized block design. T-test, analysis of variance, and Duncan's new multiple range test with a 0.05 level of significance were used. Stepwise multiple regression procedures (UCLA-BMD02R programs) were used to screen tree characteristics related to shoot elongation. Final equations consisted of variables whose contribution to reducing the residual variance was significant at the 0.05 level.

RESULTS

Yellow Birch

Bud length as related to leader position on undamaged seedlings is described by a quadratic equation that accounts for 54 percent of the variation in length (fig. 2). Maximum lengths occur between bud position indices 0.33 to 0.50. The shortest buds are at the base of the leader. Eighty percent of all lateral buds are longer than the terminal.

On unclipped yellow birch, shoot elongation from terminal and lateral buds on

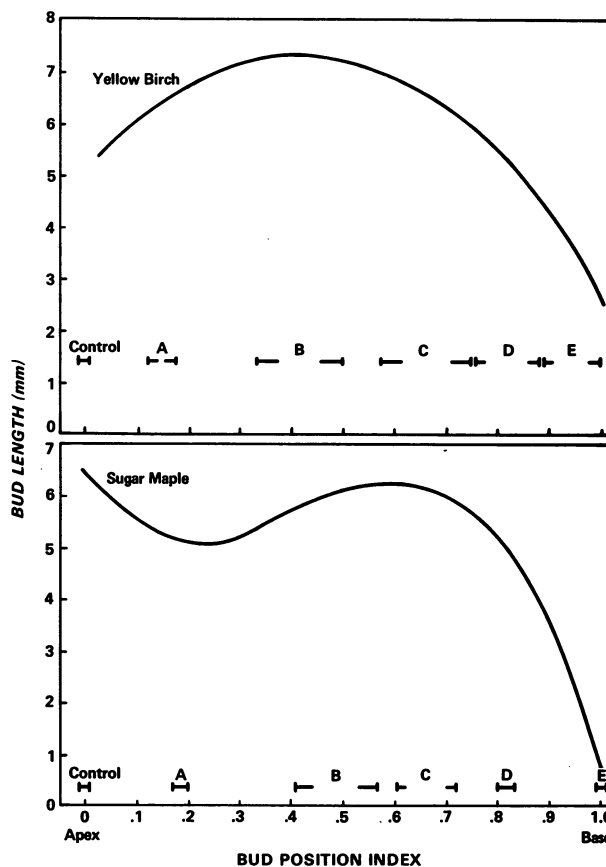


Figure 2.--Relation between bud length and position on 1967 leaders and range of positions included in clipping treatments. Regression equation for the relations are: yellow birch-- $BL = 5.12 + 11.01 BPI - 13.25 BPI^2$; Sugar maple-- $BL = 6.64 - 15.91 BPI + 48.86 BPI^2 - 38.83 BPI^3$; where BL is bud length and BPI is bud position index.

the leaders was related to bud length. The longest shoots originated from the longest buds; they were 60 percent longer than the leaders (fig. 3). After the 1968 growing season, these lateral shoots also projected above the leaders on 40 percent of the seedlings. Below a bud position index of 0.50, bud length became unimportant, as only short-shoots (less than 0.02 ft) developed. Short-shoots developed rapidly, ceasing elongation by late May. Long-shoot laterals and the leader continued elongation into August.

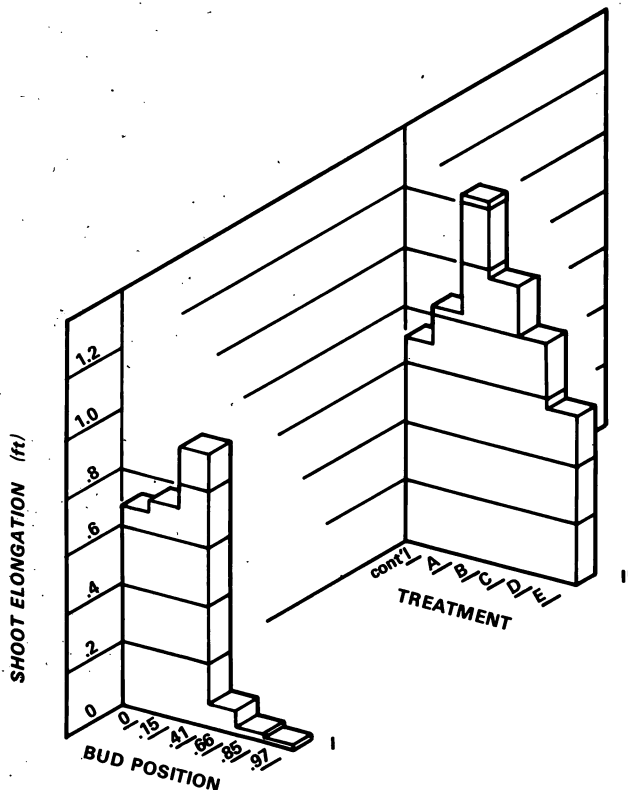


Figure 3.--Shoot elongation of yellow birch in relation to bud position and degree of clipping. (I) Normal pattern on unclipped seedlings for terminal and lateral buds in positions comparable to those in treatments. (II) Pattern for buds left uppermost on clipped seedlings and the leader of the control.

Clipping did not adversely affect elongation of replacement leaders (fig. 3). In all treatments, the replacements elongated as much as normal leaders on unclipped seedlings. Comparing shoots from buds at the same position on clipped and unclipped seedlings showed no differences in lengths for treatments A and B. However, clipping

stimulated elongation in treatments C, D, and E. Buds that normally would have been short-shoots on unclipped seedlings elongated as much as normal leaders.

One season after clipping the heights of treatment A and B seedlings were comparable to the controls (0.05 level, table 2). The growth of replacement leaders in treatments C, D, and E was not stimulated enough to offset the loss of the old leader and their heights declined significantly.

The period of most rapid elongation was delayed in proportion to the severity of treatment. In seedlings with the severest clipping, peak growth rate was delayed 20 days.

Regression analyses showed that the extent of shoot elongation was dependent upon both bud and other seedling properties. Sixty-three percent of variation in shoot elongation was accounted for by height growth two seasons before clipping and the interaction terms of position of the bud originating the shoot and its length, total seedling height, and height growth during the second season before clipping. These variables were about equally important on the basis of standard partial correlation coefficients. Similar analyses of the change in height caused by clipping and regrowth gave a slightly more precise equation with fewer variables. Seedling height and bud length and position accounted for 66 percent of the variation in the change. Bud position and percent of stem removed could be interchanged in the equation without affecting its precision.

Sugar Maple

Bud-size patterns in sugar maple differed from yellow birch. Terminal buds were the longest bud on 69 percent of the leaders. When they weren't, only one pair of lateral buds usually exceeded them in length. The longest lateral buds occurred between positions 0.4 and 0.6. Buds immediately below the terminal bud were the shortest lateral buds in leaf axils. Buds at the base of the leader were even shorter (usually <0.5 mm) but these were associated with the bud scale scars of the prior year's terminal bud (Church and Godman 1966). Seventy-eight percent of the variation in bud length was accounted for by a cubic expression of bud position (fig. 2).

Table 2.--Net height increment¹ following clipping
(In feet)

Species	Control	Treatment				
		A	B	C	D	E
Yellow birch	0.99 _a	0.96 _a	0.75 _a	0.33 _b	-0.34 _c	-0.56 _c
Sugar maple	.80 _a	.51 _b	.44 _b	.37 _b	.00 _c	-.42 _d

¹Net height increment = height one season after clipping - height before clipping.

²Common suffix indicates species means that do not differ significantly at the 0.05 level of rejection.

In contrast to yellow birch, leaders on unclipped sugar maple elongated twice as much as any lateral shoot (fig. 4). Most of the lateral shoots originated from the larger lateral buds at positions 0.3 to 0.5. On the balance of the leader, only one-third of the buds in leaf axils and none of the basal buds at position 1.0 broke dormancy. Leaders attained 90 percent of their elongation by mid-June. Lateral shoots did so more rapidly, reaching this level by early June.

Clipping promoted elongation of the replacement leaders in treatments B, C, and D; they equalled normal leader growth on unclipped seedlings (fig. 4). The new leaders in treatments A and E were less than one-fourth the length of leaders of unclipped seedlings. Thus heights of all clipped seedlings were significantly less than unclipped maple at the end of season (table 2).

Damage to the terminal bud often results in forking, a serious defect in older trees. Consequently, lengths of bud pairs left uppermost after clipping and their shoot growth were compared. Fork members on clipped seedlings were comparable in length (± 10 percent) on 26 percent of the seedlings. Length of the bud pairs had to differ by more than 0.5 mm before the larger bud would consistently originate the dominant shoot, this difference only occurred in 28 percent of all bud pairs.

Seventy-five percent of the variation in shoot elongation was accounted for by the position of the bud from which the shoot originated and interaction terms of position, bud length, and leader growth in each of the two preceding seasons. The most useful variable in the equations was bud position. Similar analyses of the change in seedling height after clipping showed 70 percent of its variation was due to bud length, bud position, and leader growth the year prior to clipping. Here again, bud position and percent of stem removed could be interchanged without affecting precision of the equation.

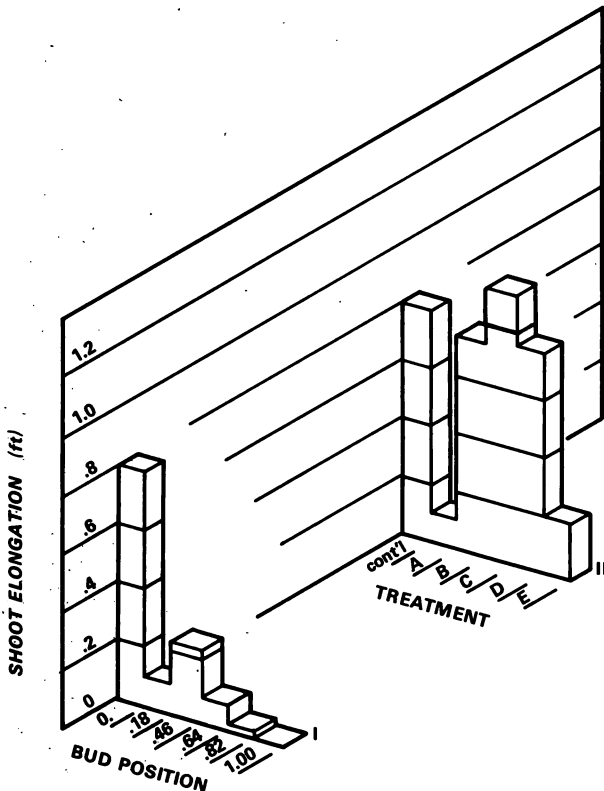


Figure 4.--Shoot elongation of sugar maple in relation to bud position and degree of clipping. (I) Normal pattern on unclipped seedlings for terminal and lateral buds in positions comparable to those in treatments. (II) Pattern for buds left uppermost on clipped seedlings and the leader of the control.

DISCUSSION

This study demonstrates that the ability of sugar maple and yellow birch seedlings to recover from dormant season damage is more related to factors that determine growth rate than to the gross extent of damage. This helps explain the

less detailed observations of others; Tubbs (1969) and Godman and Krefting (1960) found yellow birch seedlings damaged by frost often grew better than undamaged seedlings. Jacobs (1969) found growth on repeatedly browsed sugar maple seedlings equalled protected seedling growth.

Several factors help minimize the effects of leader damage on growth of sugar maple and yellow birch. Lateral buds, which can replace a damaged or lost terminal bud, are well distributed along the leader. Their growth potential is determined by conditions occurring in the growing season prior to damage and is not seriously altered by damage. The critical period occurs while the embryonic shoot is developing in the bud in the first growing season. However, damage does alter the competitive position of the buds.

Species having preformed shoots within their buds illustrate how shoot elongation potential is determined during bud development. Owston (1969) found the embryonic shoot in white pine possessed primordia for all the leaves and internodes. Critchfield (1971) suggests that elongation of preformed leaders occurs by expansion of existing rather than by formation of new tissue at the time of elongation. In such species, elongation is completed early in the growing season; it depends on stored carbohydrates produced in the season preceding elongation (Olofinboba and Kozlowski 1973, Gordon and Larson 1970). Little (1970) indicates hormone synthesis is predetermined in the bud, is related to bud size, and regulates the flow of nutrients to the elongating shoot by mediating the production of auxin during elongation. Leader elongation, terminal bud length, and climate during bud development are all correlated, whereas the two growth parameters are not as well correlated to climate during shoot elongation (Kozlowski 1964, Hellum 1967, Clements 1970).

These previous studies involved leader elongation on undisturbed trees. The seedlings' response to clipping in this study suggests that the development of a replacement leader is also influenced by events of the prior season. A considerable proportion of the variation in growth was explained by seedling characteristics determined prior to damage. This was especially evident in sugar maple, which has preformed shoots in its buds (Critchfield 1971) and rapid early shoot elongation (Jacobs 1965).

Kozlowski and Clausen (1966) reported that yellow birch has heterophyllous shoots within its buds that elongate throughout the season; thus new tissue is added and currently produced photosynthates are used. Shoot elongation in yellow birch also is dependent upon factors occurring before damage but to a lesser degree than in sugar maple. In yellow birch this dependence may be due to a relation of bud parameters to the level of development of the embryonic shoot and its two large embryonic leaves. The size of these leaves when expanded appeared related to bud length and position. These leaves are essential to the survival and elongation of the shoots (Kozlowski and Clausen 1966).

Seedling environments in this study favored vigorous development. Less favorable environments would likely reduce the seedlings' ability to respond to damage. Sugar maple seedlings having short leaders also have shorter lateral buds in relation to the terminal. Thus under conditions unfavorable to growth, the seedlings would have fewer and less-developed lateral buds.

Growth characteristics of different plant species need to be understood before appraisals of damage or browse and timber production are accurate. Even the moderate degrees of clipping used in this study showed that growth response depended on bud characteristics, vigor, size, and species of the tree. Environmental factors such as moisture, light, and competition are also important to growth and influence the analysis of seedling injury.

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