Forest Science, Vol. 37, No. 2, pp. 524–539

Effects of Time and Frequency of Cutting on Hardwood Root Reserves and Sprout Growth

JONATHAN S. KAYS
CHARLES D. CANHAM

ABSTRACT. We examined the effects of time and frequency of cutting during the growing season on fall root starch reserves and sprout production in saplings of four hardwood tree species—red maple, gray birch, white ash, and black cherry. For all species, there was a well-defined window of time during the growing season when cutting resulted in low levels of starch in roots at the end of the growing season, and subsequent low sprout growth rates the following year. Cutting at the very beginning or the very end of the growing season resulted in the highest levels of fall root reserves and sprout production. The duration of the window varied for each species and was closely related to the phenology of aboveground growth. The species with a determinant shoot growth pattern had the shortest window (white ash), while the two species with the most indeterminant shoot growth pattern had the longest windows (red maple, gray birch). FOR. SCI. 37(2):524–539.

ADDITIONAL KEY WORDS. *Acer rubrum, Betula populifolia, Fraxinus americana, Prunus serotina,* starch reserves, sprouting.

LEVELS OF CARBOHYDRATE RESERVES in hardwood tree roots follow predictable seasonal patterns related to the phenology of aboveground growth (Kramer and Kozlowski 1979). Root reserves decrease sharply in the spring during the initiation of shoot growth, reach a low in midsummer, increase to a maximum in the fall as new photosynthate is translocated to the roots for storage, then maintain high but gradually declining levels during the dormant season (Woods et al. 1959, Kozlowski and Keller 1966, Wargo 1971, Kramer and Kozlowski 1979, McLaughlin et al. 1980). Hardwood species rely heavily on stored root reserves to subsidize sprouting after cutting (Aldous 1929, Tew 1970, Schier and Zasada 1973). Since root reserves exhibit their largest fluctuations during the growing season, cutting of aboveground stems at different times within the growing season may result in large differences in stored root reserves available for subsequent sprout production (Wenger 1953, Woods et al. 1959).

Minimizing sprout growth following cutting of hardwood trees and saplings is of interest to vegetation managers in many situations, particularly for control of vegetation height along utility rights-of-way and to minimize competition between undesirable sprouts and more desirable regeneration following logging. It is known that season of harvest can have a significant effect on sprouting vigor, with stems cut during the dormant season sprouting more vigorously than those cut during the growing season (Brown 1930, Buell 1940, Kays et al. 1984). While numerous studies have assessed seasonal changes in root carbohydrate reserves for uncut trees (e.g., Priestley 1964, Wargo 1971, McLaughlin et al. 1980), there has been little study of the relationship between time of cutting during the growing season and levels of root reserves present at the end of the growing season (Woods et al. 1959).

The objectives of our study were to determine the effects of time and frequency of cutting within a growing season on fall root starch reserves and subsequent sprout production in saplings of four hardwood species along powerline rights-of-way in southeastern New York. Phenological measurements at the time of cutting were used to characterize the seasonal growth pattern of each species and its relationship to starch reserves and subsequent sprout production.

METHODS

Species and Site Selection

The four species chosen for study—red maple (*Acer rubrum* L.), gray birch (*Betula populifolia* Marsh.), white ash (*Fraxinus americana* L.), and black cherry (*Prunus serotina* Ehrh.)—are among the most abundant hardwood tree species found along utility rights-of-way in southeastern New York. The four species were sampled on three study sites located in Dutchess and Ulster counties (lat. 41°35′–42°58′N, long. 73°47′–74°05′W). Gray birch saplings were sampled along a 20 m wide right-of-way with thin soils over shale bedrock. The majority of the saplings originated from seed, and all saplings selected for this study were single-stemmed. White ash saplings were sampled along an 85 m wide right-of-way located on a limestone ridge with thin and rocky soils. All saplings were single-stemmed and of sprout origin. Red maple and black cherry saplings were sampled at a third site along a 85 m wide right-of-way, located on thin, rocky soils. All saplings were of sprout origin with a mixture of single and multiple stems. Saplings of all four species were dominant or codominant stems between 1.5 and 4 m tall. All saplings of sprout origin were from stumps less than 2 cm. in diameter. All stems were a minimum distance of 1 m from any other selected stem and were distributed throughout the right-of-way.

Treatment Descriptions

Fifteen saplings of each species were randomly assigned to an uncut control group and to 12 treatment groups, representing different cutting dates and frequencies of cutting (Table 1). Due to a shortage of suitable black cherry stems, treatment groups for black cherry were composed of only 12 saplings. Treatments A thru H were cut at 3-week intervals beginning May 7, 1986, while treatments I thru L consisted of two or three successive cuttings within the 1986 growing season (Table 1). All stems were cut within 5 cm of the ground. New sprouts removed in the successive cutting treatments (I–L) were clipped flush with the stump. The earliest cutting treatment (A) occurred shortly after bud break by all four species. The last cutting (treatment H, ca. October 1) occurred after stems of all four species had begun to drop leaves.

TABLE 1.

Cumulative mortality rates (% of stems with no live sprouts by the end of the third growing season) in the 12 different cutting treatments. Cutting dates listed are the middle of the 3–4 day period required for each treatment.

Treatment	Cutting date(s)	Gray birch	Red maple	White ash	Black cherry
A	5/7	86	11	0	0
B	5/28	40	0	0	0
C	6/18	50	20	10	13
D	7/9	50	10	0	0
E	7/30	50	33	20	0
F	8/20	40	10	22	0
G	9/10	50	13	0	0
H	10/1	23	10	14	14
I	5/7, 7/9	88	20	0	29
J	5/7, 7/9, 8/20	90	57	10	75
K	6/18, 8/20	90	30	11	13
L	6/18, 8/20, 10/1	90	50	20	0

Total sapling height (m), previous year's growth of the terminal leader (cm), and basal diameter of each stem (at 5 cm above the ground) were measured immediately prior to cutting. In order to quantify the phenology of aboveground growth, the terminal leader of the dominant stem from each stump was removed at the time of cutting and brought back to the lab for measurements of current year growth (cm), total leaf area (cm^2) (measured using a LI-COR LI 3100 Area Meter), number of leaves, the presence of developing leaves or buds, and evidence of multiple growth flushes within the current growing season.

Sprout production was measured during or after leaf fall in October of the first through third growing seasons (1986–1988). Height of the tallest sprout, basal diameter of each sprout at 15 cm above the ground, and the number of sprouts over and under 15 cm in height were recorded at the end of each growing season. For the second and third growing seasons (1987 and 1988), the individual lengths of all sprouts >15 cm tall were also measured. Evidence of browse damage was recorded each year. However, there was only minor damage in any year, and the browsed stems were not analyzed separately.

Measurement of Incident Light Levels

A photographic technique was used to calculate seasonal average light levels experienced by sprouts during the 1987 growing season for four of the single cutting treatments (treatments A, C, E, and H). For the calculations, a fish-eye photograph (using an Olympus 7 mm true fisheye lens) was taken at a 0.5 m height above the ground, centered over each stump, with all sprouts pulled back below the plane of the photograph. The photographs were then digitized with an image-analysis system (CIS-2, Olympus Corp.), and analyzed with software that calculated the percent of seasonal total photosynthetically active radiation (PAR) that penetrated through foliage of shrubs and herbs surrounding the stump (Canham 1988).

Root Sampling Procedures

A 10 cm piece of a major lateral root was collected at the end of the growing season from five individuals in each treatment (four for black cherry). These individuals were dropped from further growth measurements and analyses because of the damage associated with root sampling. The sampled individuals were randomly selected from within a limited range of total basal area to minimize differences in root biomass which might affect carbohydrate patterns and sprout response. Root samples were immediately placed in plastic bags and frozen in a cooler with dry ice to minimize respiration losses. All samples were stored in a freezer at −18°C upon returning to the laboratory.

The concentration of carbohydrate reserves in roots is heavily dependent on root diameter (Wargo 1976). Therefore, the range of diameters of roots collected for each species was limited as much as possible. The diameter ranges for each species were: (1) red maple, 8.5–9.5 mm, (2) white ash, 9–10 mm, (3) black cherry, 7–8 mm, and (4) gray birch, 6–7 mm. All root samples were collected between October 27 and November 14, 1986.

The frozen root material was removed from the freezer within 30 days, and the outside bark and fine roots were removed by scrubbing with a kitchen scour pad. The roots were then sliced into thin segments to facilitate drying and put into a drying oven for 72 hr at 70°C. After drying, the root material was ground in a Wiley mill to pass a 0.5 mm sieve screen and stored in a drying oven until it was analyzed.

Woody plants employ a diverse array of storage compounds; primarily carbohydrates, but also lipids to a lesser degree (Ziegler 1964, Nelson and Dickson 1981). Of the carbohydrates, starch concentrations are generally highest in the fall and spring, while soluble sugars and sugar alcohols predominate during the winter (Kramer and Kozlowski 1979). For our purposes, we have assumed that analysis of starch concentrations in roots at the end of the growing season provides an adequate index of variation among the cutting treatments in overall levels of stored reserves present at that time. The total quantity of root reserves obviously depends on not only their concentration but also on the total size of the root system. However, our experimental design is randomized across individual saplings, and therefore randomized across sapling size. Our goal was thus to evaluate the relative effects of time of cutting on levels of root starch reserves at the end of first growing season, and examine the relationship between the observed levels of root starch reserves and sprout growth during the subsequent growing season. We did not examine storage compounds in shoots of new sprouts produced during the first growing season by the early cutting treatments. It is likely that reserves stored aboveground in these new sprouts also contributed to shoot growth during the second growing season.

An enzyme digestion procedure was used to measure starch levels in the roots (Tecator Inc. 1987). One sample was analyzed from each individual. One-half gram of the dried root material was put in a centrifuge tube with 25 ml of acetate-buffer solution and 50 μl Termamyl 120L (Tecator Inc. 1987). It was then placed in a boiling water bath for 30 minutes to gelatinize the starch. After cooling, 0.15 ml of amyloglucosidase was added, and the samples were put in a shaking water bath at 60°C for 60 min to convert the gelanitized starch to glucose (Tecator, Inc. 1987). The samples were then centrifuged for 10 min at 1500 rpm to settle out the residual root material. One ml of the supernatant was mixed with 19 ml of distilled water so that the values of the glucose concentrations would fall within the range of a set of glucose standards. One ml of the dilute solution was mixed in a vial with 2 ml distilled water and 2 ml of glucose oxidase reagent. The vials were placed in dark incubation for 60 min at 20°C, and then absorbance was measured with a spectrophotometer at 650 nm. The concentration (g) was calculated per gram of root material, and expressed as a percentage (grams starch per gram of root material).

Statistical Analyses

Cutting treatment effects were analyzed by analysis of variance and covariance (SAS 1987). Analysis of covariance (ANCOVA) revealed that the basal area of the stump at the time of cutting had a significant effect on almost all aspects of subsequent sprout growth. Thus, when there were significant covariates with homogeneous slopes across all treatments, adjusted least squares means were computed for each treatment to correct for random variation among treatments in the average size of stumps at the time of cutting (SAS 1987). Unless otherwise noted, sprout growth patterns summarized below are calculated using only the stumps in each treatment for which at least one sprout survived to the end of the third growing season (1988).

RESULTS

Fall Root Starch Reserves

Fall root starch reserves of the uncut control saplings equalled or exceeded the highest starch concentrations produced by any of the cutting treatments (Figure 1). Variation in the time of cutting produced a similar pattern of variation in starch concentrations for all four species. The highest starch concentrations occurred in saplings cut at either the very beginning or the end of the growing season, with an intervening window of treatments that produced significantly lower fall root reserves. The duration of the window varied from 9 weeks for white ash to 18 weeks for red maple (Figure 1). For all species, the window of low starch concentrations began with treatment B (May 28); thus, differences among species in the duration of the window were due to differences in the effects of cutting later in the growing season.

Phenology of Shoot Growth

The four species exhibited a range of seasonal patterns of shoot growth (Figure 2). The species with the most indeterminate growth pattern (gray birch) continued producing new shoot material until leaf fall. This contrasts with the determinate growth pattern demonstrated by white ash saplings that formed all of their new leaves and shoots within a short period at the beginning of the growing season (Figure 2) (Marks 1975). The timing of shoot growth in red maple and black cherry was intermediate between gray birch and white ash. The two most indeterminate species (gray birch and red maple) had the longest windows of low

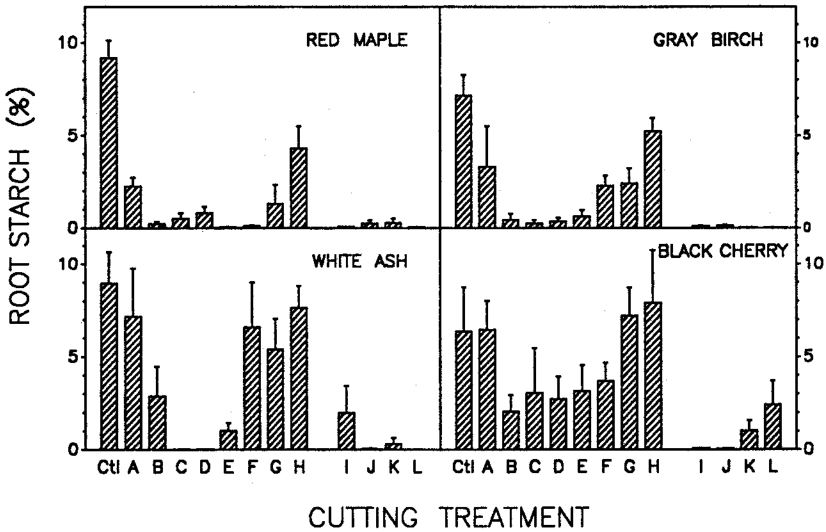

FIGURE 1. Mean and standard errors of root starch concentrations (% by weight) at end of the first growing season for each cutting treatment and the uncut controls, by species. One-way ANOVA F-statistics for effects of cutting treatment on TNC were significant for all four species at $P < 0.05$.

root reserves, while the most determinate species (white ash) had the shortest window (Figure 1).

Stump Mortality Following Cutting

Individual stumps were considered dead if there were no live sprouts produced by the end of the third growing season (1988). Gray birth was the only species to

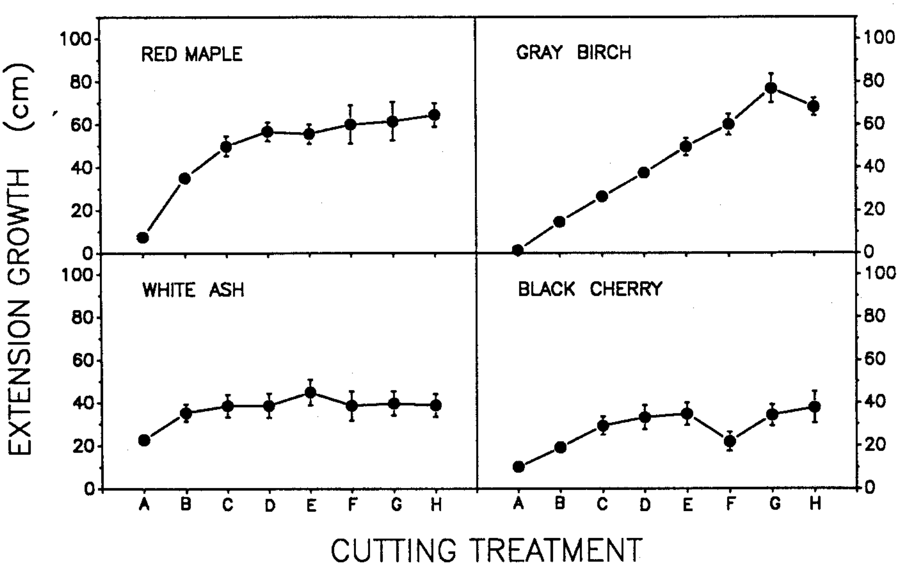

FIGURE 2. Extension growth of the terminal leader at the time of cutting for each of the single cutting treatments, by species. Vertical bars around the mean represent one standard error.

show significant mortality of stumps as a result of the single cutting treatments (Table 1). We cannot rule out that the higher overall mortality rates observed in gray birch might have been due, in part, to the fact that the gray birch saplings originated primarily from seed, rather than as sprouts from cutting during previous management (in contrast to the other species, which were all of sprout origin). The particularly high mortality rate for gray birch stems cut on May 7 (Treatment A) may be due, in part to the low average light levels experienced by those stems (see results on effects of shading, below). The multiple cutting treatments were particularly lethal to gray birch (88–90% mortality), but also produced significant mortality in red maple and black cherry. Most of the mortality occurred in individuals that did not produce any new sprouts following the last of the cutting treatments.

Sprout Production

All four of the species produced sprouts soon after the early cutting treatments. Red maple was the only species to show effects of the single cutting treatments on the number of sprouts per stump ($F = 2.55$, $P < 0.05$, for the cutting treatment effect on number of sprouts at the end of the second growing season in an ANCOVA model with basal area at the time of cutting as a covariate). The number of sprouts per stump at the end of the second and third growing seasons was quite variable in all four species (Table 2). Sprout numbers were significantly correlated with stump basal area in all four species. However, the correlation coefficients were all quite low (<0.51). By the end of the third growing season, mortality of individual sprouts in the denser clumps produced relatively uniform densities of sprouts among the eight single cutting treatments (Table 2).

Sprout Growth

By the end of the first growing season (1986), the average height of the tallest sprout from each stump cut on the first date (treatment A) ranged from 0.63 m in gray birch to 1.23 m in black cherry. Sprout heights at the end of the first growing season declined steadily for the later cutting dates, with no immediate sprout production from the last of the single cutting treatments (treatment H) (data not presented). The greatest height growth rates during the second growing

TABLE 2.

Numbers of sprouts per stump averaged across all eight of the single cutting treatments (A–H) at the end of the second and third growing seasons (1987–1988).

Year		Red maple	Gray birch	White ash	Black cherry
1987	Mean	9.1	9.2	6.1	5.9
	CV (%)	64	70	51	58
	Range	1–27	1–31	1–12	1–18
1988	Mean	6.2	5.2	5.2	4.3
	CV (%)	72	80	55	66
	Range	1–19	1–20	1–12	1–14

season were in the late-summer single cutting treatments (Treatments F–H, data not presented). These treatments produced either no sprouts or very small sprouts immediately following cutting the previous year, but had high levels of root reserves (Figure 1). However the early cutting treatments had the tallest overall sprouts by the end of the second growing season because lower height growth rates during the second season were augmented by sprout growth during the first growing season (Table 3).

There were no treatment effects on height growth rates during the third growing season (1988) for any of the four species. 1988 height growth rates averaged across all 12 treatments were 11.1 cm/yr for gray birch, 15.3 cm/yr for red maple, 24.2 cm/yr for white ash, and 25.5 cm/yr for black cherry. However, because of variation in height growth during the first two growing seasons, maximum sprout heights among the single cutting treatments were still significantly different at the end of the third growing season for red maple, black cherry, and white ash (Table 4 and Figure 3). Maximum sprout heights during the third growing season for gray birch were not significantly different among the single cutting treatments (Table 4), however, differences in average sprout heights were marginally significant (Table 5), and maximum sprout heights in the four treatments used in the analysis of effects of shading (see below) did show significant cutting treatment effects (Table 6).

Basal area growth of sprouts during the second growing season (1987, the first full growing season for all treatments) closely mirrored the patterns of root starch reserves measured the previous fall (Figure 4). Our results thus confirm the general relationship between fall root starch reserves and sprout growth during the following year in these 4 species.

The effects of time of cutting on basal area growth in the third growing season

TABLE 3.

Height (cm) of the tallest sprout in each clump at the end of the second growing season. Values are least-squares means computed from analysis of covariance to remove effects of variation among treatments in the basal area of stems (except for treatments A, I, J, K and L in gray birch where only one stump in each treatment still had live sprouts at the end of 1987 and the measurement on that clump is reported).

Treatment	Gray birch	Red maple	White ash	Black cherry
A	136.0	182.9	146.4	164.1
B	132.8	137.6	108.2	147.7
C	111.4	94.7	80.7	109.9
D	100.2	72.7	80.9	106.9
E	82.9	89.5	65.3	115.8
F	76.0	91.4	96.0	118.9
G	103.2	82.4	121.2	110.3
H	108.5	100.3	132.4	131.8
I	103.0	90.3	89.7	73.4
J	69.2	62.2	65.6	78.1
K	0.0	43.7	85.4	132.3
L	63.0	62.5	79.2	88.3

TABLE 4.

ANCOVA results for the effects of the eight single cutting treatments (TRT) on basal area growth in the second and third growing seasons (1987–1988), total sprout basal area at the end of the third growing season (1988), and maximum sprout height at the end of the third growing season (1988), with the basal area (BA) of the stem at the time of cutting as the covariate.

	Red maple			Gray birch			White ash			Black cherry		
Source	df	F	p	df	F	p	df	F	p	df	F	p
(A) 1987 Basal area growth (cm^2/yr)												
Overall	15	3.13	0.001	14	3.19	0.006	15	10.19	<0.001	15	6.11	<0.001
TRT	7	3.98	0.002	7	3.03	0.019	7	11.17	<0.001	7	2.97	0.013
BA	1	15.67	<0.001	1	18.55	<0.001	1	63.70	<0.001	1	64.65	<0.001
TRT * BA	7	0.48	0.842	6	0.82	0.562	7	1.56	0.167	7	0.88	0.528
Error	49			25			53			42		
(B) 1988 Basal area growth (cm^2/yr)												
Overall	15	1.32	0.228	14	1.12	0.390	15	7.88	<0.001	15	4.18	<0.001
TRT	7	0.77	0.613	7	1.01	0.448	7	4.91	<0.001	7	3.90	0.002
BA	1	4.96	0.031	1	4.71	0.040	1	71.49	<0.001	1	19.69	<0.001
TRT * BA	7	1.35	0.228	6	0.65	0.693	7	1.77	0.113	7	2.24	0.049
Error	49			25			53			42		
(C) 1988 Total sprout basal area (cm^2)												
Overall	15	2.36	0.012	14	1.86	0.077	15	12.84	<0.001	15	5.90	<0.001
TRT	7	2.19	0.052	7	1.30	0.285	7	9.36	<0.001	7	3.44	0.005
BA	1	12.44	<0.001	1	14.16	0.001	1	114.51	<0.001	1	57.02	<0.001
TRT * BA	7	1.09	0.381	6	0.46	0.829	7	1.80	0.103	7	1.06	0.403
Error	49			43			61			43		
(D) 1988 Maximum sprout height (m)												
Overall	15	2.63	0.006	14	2.12	0.042	15	4.04	<0.001	15	4.96	<0.001
TRT	7	3.91	0.002	7	1.27	0.301	7	3.31	0.005	7	5.03	<0.001
BA	1	8.13	0.006	1	14.03	0.001	1	33.71	<0.001	1	31.78	<0.001
TRT * BA	7	0.56	0.785	6	1.13	0.368	7	0.55	0.796	7	1.07	0.398
Error	49			29			61			43		

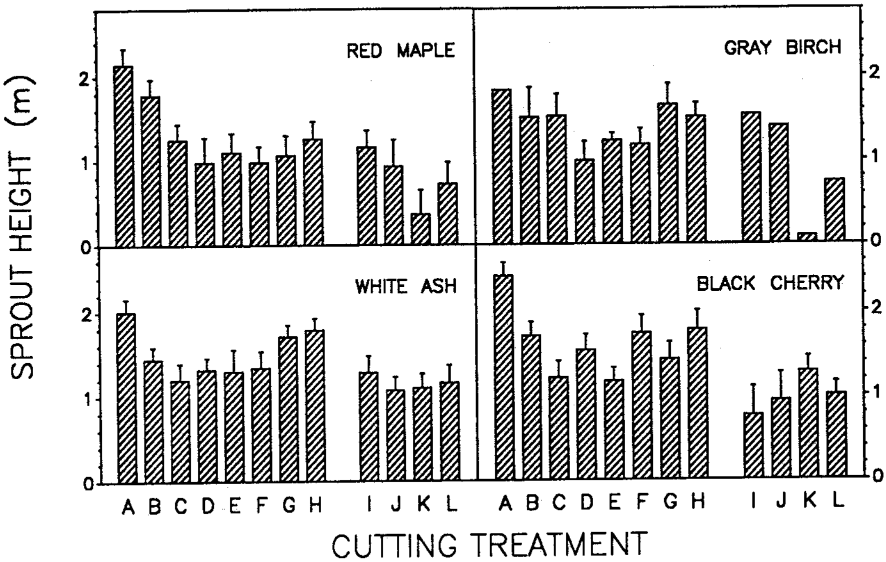

FIGURE 3. Height of the tallest sprout (m) in each clump at the end of the third growing season (1988) following cutting. Error bars represent one standard error.

were significant in only white ash and black cherry (Table 4). However, there were also marginally significant differences in total sprout basal area at the end of the third growing season among the single cutting treatments for red maple because of variation in growth during the preceding two years (Table 4).

While the multiple cutting treatments induced high mortality rates in a number of the species-treatment combinations, the sprout growth rates of surviving individuals were not generally lower than the lowest growth rates produced by single cutting treatments (Figures 3 and 4). For many stumps there were no new sprouts to remove after the first or second cutting.

EFFECTS OF SHADING ON SPROUT GROWTH AND MORTALITY

Analysis of covariance revealed a significant effect of shading on both sprout biomass (measured as basal area growth during the second growing season and total sprout basal area at the end of the third growing season) and the height of

TABLE 5.

ANCOVA results for variation in average sprout height at the end of the third growing season (1988) in gray birch for the eight single cutting treatments (TRT), with basal area (BA) at the time of cutting as a covariate.

Source	df	F	p
Overall	14	2.19	0.036
TRT	7	2.27	0.057
BA	1	7.48	0.011
TRT * BA	6	1.23	0.320
Error	29		

TABLE 6.

ANCOVA results for effects of four different time of cutting treatments (TRT) on (A) basal area growth during the second growing season (1987), (B) total sprout basal area at the end of the third growing season (1988), (C) maximum sprout height (per clump) at the end of the second growing season (1987), and (D) maximum sprout height at the end of the third growing season (1988). Both the basal area (BA) of the stem at the time of cutting and average seasonal light level (LIGHT) (% of full sun) during 1987 were used as covariates. Results for white ash and black cherry were omitted because there were no significant main effects of light levels on sprout growth in those two species.

	Red maple			Gray birch		
Source	df	F	p	df	F	p
(A) 1987 Basal area growth (cm^2/yr)						
Overall	11	6.68	0.001	11	11.38	<0.001
TRT	3	11.04	<0.001	3	14.46	<0.001
BA	1	1.87	0.191	1	37.54	<0.001
Light	1	20.44	<0.001	1	26.70	<0.001
TRT * BA	3	3.71	0.035	3	2.63	0.074
TRT * Light	3	2.32	0.117	3	3.22	0.041
Error	15			23		
(B) 1988 Total sprout basal area (cm^2)						
Overall	11	4.33	0.004	11	8.86	<0.001
TRT	3	4.64	0.016	3	7.18	0.001
BA	1	3.00	0.102	1	25.33	<0.001
Light	1	18.68	0.001	1	31.91	<0.001
TRT * BA	3	2.39	0.106	3	0.74	0.539
TRT * Light	3	1.60	0.229	3	5.48	0.005
Error	16			26		
(C) 1987 Maximum sprout height (m)						
Overall	11	3.34	0.016	11	3.72	0.004
TRT	3	4.22	0.024	3	2.88	0.058
BA	1	1.34	0.265	1	14.00	0.001
Light	1	6.14	0.026	1	5.92	0.023
TRT * BA	3	4.88	0.015	3	1.12	0.360
TRT * Light	3	0.64	0.603	3	2.99	0.052
Error	15			23		
(D) 1988 Maximum sprout height (m)						
Overall	11	2.29	0.064	11	2.94	0.012
TRT	3	4.33	0.021	3	3.16	0.042
BA	1	0.12	0.734	1	10.05	0.004
Light	1	5.18	0.037	1	8.00	0.009
TRT * BA	3	2.01	0.153	3	0.15	0.927
TRT * Light	3	0.31	0.820	3	1.45	0.251
Error	16			26		

the tallest sprout (in the second and third growing seasons) for both red maple and gray birch (Table 6). However, there were no significant effects of shading on any aspect of sprout growth in white ash and black cherry. The slopes of the responses of 1987 basal area growth versus light level varied for the different treatments in gray birch, with the late season cutting (treatment H) showing the

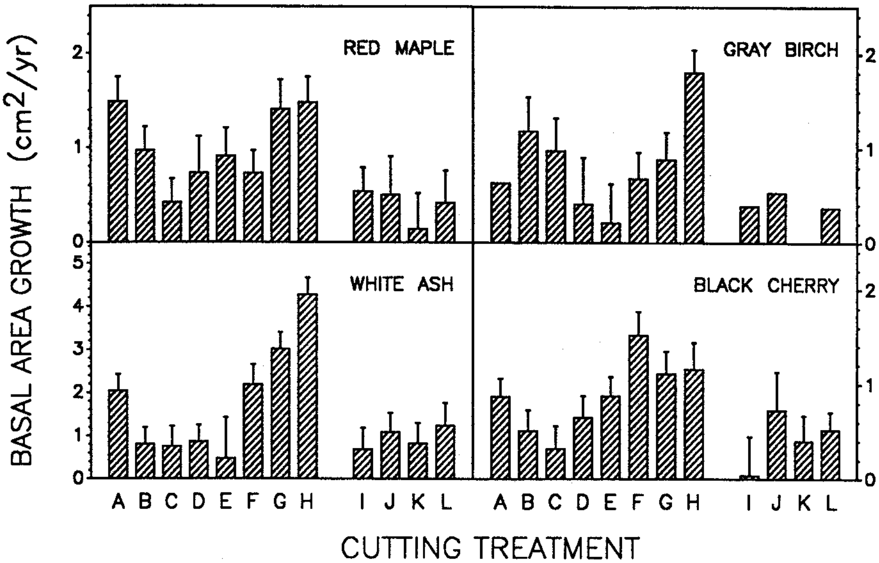

FIGURE 4. Sprout basal area growth (cm^2/yr) during the second growing season (1987) following cutting. Error bars represent one standard error of the mean.

steepest increase in growth with increasing light, while the midsummer cutting (treatment E) showed the weakest response to light (Figure 5). Red maple is generally considered the most shade-tolerant of the four species; however, it showed the strongest overall response to shading of any of the four species (Figure 5).

By chance, gray birch saplings in treatment A had very low average light levels (mean = 11.8% of full sun), while treatment H experienced relatively high average light levels (mean = 39.6% full sun *versus* 15.8% and 21.3% for treatments C and E, respectively). These average light levels were inversely correlated with the mortality rates observed in the 4 treatments (Table 1). When averaged across all four of the gray birch treatment groups, the mean light level for the 18 dead stumps (8.25% full sun, S.E. = 1.61) was significantly lower than the light levels received by the 20 surviving stumps (35.0% full sun, S.E. = 5.64) ($t = -4.34$, $df = 36$, $P < 0.0001$). Our results therefore suggest that heavy shading can cause not only significant reductions in early sprout growth, but also failure to successfully sprout in at least this tree species.

DISCUSSION

EFFECTS OF TIME CUTTING ON FALL ROOT RESERVES

Differences among the four species in the duration of the window of low root reserves (Figure 1) appear to be closely related to the phenology of shoot growth prior to cutting (Figure 2). An estimate of the approximate timing of storage of starch in roots can be obtained by comparing the root reserves of late season cutting treatments with the root reserves of the uncut controls. For example, white ash saplings must have completed much of their seasonal accumulation of

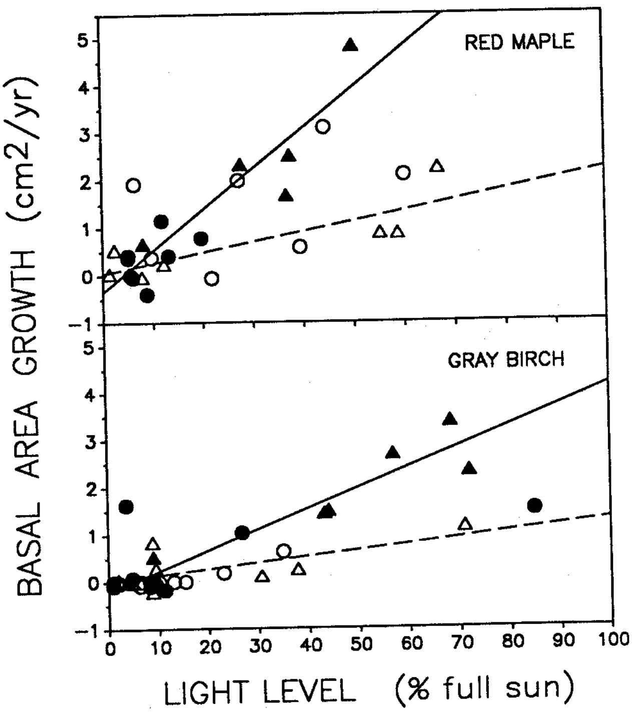

FIGURE 5. Effects of shading on basal area growth during the second (1987) growing season in gray birch and red maple for 4 of the single cutting treatments. Symbols for the treatments are: A = open circle, C = filled circle, E = open triangle and dashed line, and H = filled triangle and solid line. The lines are a least squares regression through the points for treatments E and H.

starch in the roots by August 20, since saplings cut after that date had starch levels that were not significantly lower than the uncut controls. Thus, the narrow window of effective cutting treatments for white ash appears to be a function of the early completion of both shoot growth and the translocation of current year carbohydrates from shoots to roots. This compares with dates of September 9 for black cherry and October 1 for gray birch before saplings had apparently completed significant translocation of reserves (with correspondingly longer windows of time during which cutting results in very low levels of fall root reserves). Root starch reserves of the uncut red maple saplings were significantly higher than even the last cutting treatment (October 1). It appears that even by this late date red maple had not completed storing carbohydrates produced during the current year. This may occur because indeterminate species such as red maple utilize current year's photosynthates to produce new shoot growth late into the growing season, long after determinate species have completed their shoot growth (Kozlowski 1963). This is consistent with field observations of the timing of leaf fall: while the other three species in this study had lost many of their leaves by October 1, most leaves on the red maple saplings were still firmly attached and green.

Early cutting dates appear to have affected starch concentrations in roots in several different ways. The striking difference between the amount of root reserves resulting from treatments A and those immediately afterwards suggests that the difference was not due simply to a longer time during which sprouts in treatment A could replenish root reserves. If stems are cut after root reserves have been depleted past a certain threshold level, new sprouts produced during that growing season apparently contribute little carbohydrate to fall root reserves, at least in the form of starch, regardless of the length of the growing season available to the new sprouts. Given the clear relationships between the phenology of aboveground growth, time of cutting, and starch reserves in the four species studied here, it seems likely that knowledge of the phenology of shoot growth (Marks 1975) will be essential in predicting sprout growth following cutting in other species.

Implications for the Use of Time of Cutting in Vegetation Management

This study clearly indicates that timing of cutting can have a significant effect on sprout growth during the first 1–2 years following cutting. If minimal sprout growth is desired, our results indicate that cutting should be done well after the initiation of shoot growth in the spring, but before the cessation of aboveground growth later in the summer. Cutting within this window of time will result in minimum sprout growth. Our results also suggest that the period of time for effective cutting will be shortest for species with strongly determinate growth patterns and longer for species such as red maple and gray birch that have indeterminate growth patterns.

The direct relationship between levels of fall starch reserves in roots and sprout growth the following year suggests that hormonal effects on sprouting vigor were minimal. However, the effects of the time of cutting were short-lived and only extended through 1–2 growing seasons in this study. This agrees with other studies in which the effects of season of cutting on sprout height growth lasted only several years (Roth and Hepting 1943, Kays 1985).

The lack of any effect of shading on sprout height in white ash and black cherry in our study agrees with results from other studies of sprout growth in forests under various levels of residual basal area (Little 1938, Clark and Liming 1953, Solomon and Blum 1967). The lack of a shading effect on height growth in these two species is probably related to the dependence of early growth on root reserves rather than photosynthates produced by new sprouts. Although shading after several years can be expected to reduce sprout height growth (Solomon and Blum 1967), fast-growing sprouts may have already outgrown neighboring vegetation and reached full sunlight. This is especially true for this study on rights-of-way, as well as for forest clearings, where much of the shade is cast by low-growing shrubs and herbaceous species. However, the failure of many of the most heavily shaded gray birch stumps to sprout suggests that, for some species at least, environmental controls of sprout formation may have more significant management implications than time of cutting per se.

As in other studies in which sapling sized stems were cut (Sander 1971, Mroz et al. 1985), our results show a clear, positive relationship between sprout growth and the size of the stem at the time of cutting. Studies with larger stems found a decline in sprout production with increasing stump diameter (Solomon and Blum 1967, Johnson 1977); however, the decline may be due to increasing tree age, which has a significant negative effect on sprout growth (Roth and Hepting 1943, Blake and Raitanen 1981). Our results suggest that for relatively young stems (all of the stems cut in this study were less than 12 years old), the benefits of an increase in the size of the root system over time outweigh any reduction in sprouting vigor due to age. The strong positive relationship between sapling size and subsequent sprout growth suggests that decisions about rotation periods between successive cutting along rights-of-way should take into account the consequences of stretching out the rotation period and allowing saplings to get so large that subsequent rates of regrowth might require a much shorter rotation in the following cycle.

While the multiple cutting treatments induced high mortality rates in at least some cases, the growth rates of surviving individuals were not generally lower than the lowest growth rates produced by single cutting treatments. Our results suggest that multiple cutting within a single growing season is only likely to be cost-effective in limited cases where a site is dominated by a species such as gray birch that responds to multiple cutting with very high mortality rates. While our study was not designed to test the effects of cutting in successive growing seasons, it is worth considering whether cutting at the optimal time (i.e., midsummer) during two successive growing seasons could sufficiently increase mortality rates and reduce sprout growth rates to be cost-effective.

LITERATURE CITED

ALDOUS, A.E. 1929. The eradication of brush and weeds from pasture lands. J. Am. Soc. Agron. 21:660–666.

BUELL, J.H. 1940. Effect of season of cutting on sprouting of dogwood. J. For. 38:649–650.

BROWN, B.A. 1930. Effect of time of cutting on the elimination of bushes in pastures. J. Am. Soc. Agron. 22:603–605.

CANHAM, C.D. 1988. An index for understory light levels in and around canopy gaps. Ecology 69:1634–1638.

KAYS, J.S., D.W. SMITH, and S.M. ZEDAKER. 1984. Season of harvest and site quality effects on hardwood regeneration in the Virginia Piedmont. Proc. 3rd Bienn. South. Silvic. Res. Conf.

KOZLOWSKI, T.T., and T. KELLER. 1966. Food relations of woody plants. Bot. Rev. 32:293–382.

KRAMER, P.J. and T.T. KOZLOWSKI. 1979. Physiology of woody plants. Acedemic Press, New York.

MARKS, P.L. 1975. On the relation between growth and successional status of deciduous trees of the northeastern United States. Bull. Torr. Bot. Club 102:172–177.

MCLAUGHLIN, S.B., ET AL. 1980. Seasonal changes in energy allocation by white oak (*Quercus alba*). Can. J. For. Res. 10:379–388.

NELSON, E.A., and R.E. DICKSON. 1981. Accumulation of food reserves in cottonwood stems during dormancy induction. Can. J. For. Res. 11:145–154.

PRIESTLEY, C. 1964. Carbohydrate storage and utilization. P. 113–126 *in* Physiology of tree crops, L. Luckwill, L., and C. Cutting (eds.).

SAS INSTITUTE, INC. 1987. SAS/STAT Guide for Personal Computers, Version 6 Ed. SAS Institute, Inc., Cary, NC. 1028 p.

SCHIER, G.A., and J.C. ZASADA. 1973. Role of carbohydrate reserves in the development of root suckers in Populus tremuloides. Can. J. For. Res. 3:243–250.

TECATOR, INC. 1987. Rapid convenient method for starch determination of cereals using Fibertec E prior to spectrophotometric detection. Draft paper.

TEW, R.K. 1970. Root carbohydrate reserves in vegetative reproduction of aspen. For. Sci. 16:318–320.

WARGO, P.M. 1971. Seasonal changes in carbohydrate levels in roots of sugar maple. USDA For. Serv. Res. Pap. NE-213.

WARGO, P.M. 1976. Variation of starch content among and within roots of red and white oak trees. For. Sci. 22:468–471.

WENGER, K.F. 1953. The sprouting of sweetgum in relation to season of cutting and carbohydrate content. Plant Physiol. 28:35–49.

WOODS, F.W., H.C. HARRIS, and R.E. CALDWELL. 1959. Monthly variation of carbohydrates and nitrogen in roots of sandhill oaks in wire grass. Ecology 40:292–295.

ZIEGLER, H. 1964. Storage, mobilization and distribution of reserve material in trees. P. 303–320 *in* The formation of wood in trees, M.H. Zimmermann (ed.). Academic Press, New York.

Manuscript received November 17, 1989.

AUTHORS AND ACKNOWLEDGMENTS

Jonathan S. Kays is a Natural Resources Specialist with the University of Maryland Cooperative Extension Service, 18330 Keedysville Rd., Keedysville, MD 21756. Charles D. Canham is an Assistant Scientist with the Institute of Ecosystem Studies, The New York Botanical Garden, Mary Flagler Cary Arboretum, Box AB, Millbrook, NY 12545. The authors gratefully acknowledge Karen Kays, Harold Fraleigh, Martin Burd, Everett Marshal, Geoff Lloyd, Kerry Bauman, Loren Parmalee, Jim Hill, Joyce Russell, Brian Gorsira, and Michelle Beucler-Gorsira for their able assistance with field sampling and laboratory analyses, and Dr. Philip Wargo for his comments on the manuscript. This research was supported by a grant from the Central Hudson Gas and Electric Corporation, Poughkeepsie, NY, and by the Empire State Electric Energy Research Corporation. Requests for reprints should be addressed to the second author. This study is a contribution to the program of the Institute of Ecosystem Studies, New York Botanical Garden.