

## SHOOT GROWTH CHARACTERISTICS OF HETEROPHYLLOUS WOODY PLANTS

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### Abstract

Observations were made on relationships between contents of winter buds and subsequent shoot growth characteristics of *Betula papyrifera*, *B. alleghaniensis*, *Populus tremuloides*, and *P. grandidentata*. In both species of *Betula*, winter buds expected to produce long shoots contained both embryonic leaves and leaf primordia. Both early and late leaves were produced by growing shoots. In contrast, in both species of *Populus* all leaves produced on the observed shoots appeared at bud break and matured rapidly. Evidence for a variety of patterns and degrees of dependency of expanding shoot systems on reserve foods and currently produced carbohydrates is presented. Shoot elongation of species with shoots fully preformed in the winter bud utilizes large amounts of reserve carbohydrates. In growth of long shoots of heterophyllous species considerable current photosynthate appears to be used. In *Betula* the contribution of early and late leaves to shoot growth differed markedly. Covering of early leaves before mid-June inhibited shoot growth. The presence of normally growing early leaves was essential for normal shoot development and survival.

### Introduction

Two widely different patterns of shoot growth occur in Temperate Zone trees. In one group of species the shoots are fully preformed in the winter bud. Shoot formation involves differentiation in the bud during the first year and extension of the preformed parts into a shoot the second year (Sacher 1954; Kozlowski 1958, 1963, 1964a). Only one type of leaves occurs. Examples are species of *Pinus*, *Acer*, and *Fagus*. In a second group some shoots are not fully preformed in the winter bud and both early and late leaves are produced. For example, several species of *Betula* and *Populus* exhibit heterophylly or leaf dimorphism on long shoots (Critchfield 1960; Clausen and Kozlowski 1965). Leaves at the base of the shoot are typical of the species and frequently differ from distal leaves in venation, size, toothiness, thickness, stomatal development, and other characteristics. The basal, or early, leaves emerge at or shortly after bud break, and the distal or late leaves appear later in the growing season, after the first leaves are well expanded. Early leaves are also found on short shoots whose internodes fail to elongate appreciably and which lack late leaves.

Shoot growth of species with predetermined shoots in the bud generally occurs during a relatively short part of the frost-free season while, in contrast, heterophyllous shoots usually grow for a long time (Kozlowski 1964a; Wareing 1964). These variations as well as the differences in timing of growth of early and late leaves suggest that the sources of carbohydrates for shoot growth, and proportional use of reserves and currently produced carbohydrates, vary

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between predetermined and heterophyllous species. With these considerations in mind observations were made on four species of deciduous trees to evaluate relationships between contents of winter buds and subsequent shoot growth characteristics. The time and rate of elongation of leaves and internodes of shoots of paper birch (*Betula papyrifera* Marsh.), yellow birch (*Betula alleghaniensis* Britt.), trembling aspen (*Populus tremuloides* Michx.), and bigtooth aspen (*Populus grandidentata* Michx.) were recorded. Observations of bud contents were made before and after the growing season. The role of leaves contained in the winter bud and those formed later was studied with respect to use of reserves and currently produced carbohydrates in shoot expansion.

### Methods

#### *Shoot Development*

In 1964 shoots and buds were observed from naturally occurring trees growing on Crivitz loamy sand (Pence-Vilas sandy loam) on the grounds of the Kemp Biological Station of the University of Wisconsin, near the village of Lake Tomahawk in northern Wisconsin. Individual experimental trees ranged from 2 to 5 in. diameter breast height and from 6 to 35 ft in height. Twigs observed grew at heights of 5 to 15 ft.

Ten buds expected to produce terminal long shoots and 10 expected to produce lateral shoots were collected from each species late in April, about 2 weeks before bud break. During leaf fall in late September, 10 buds of the former type were collected from the two species of *Betula*. Buds expected to produce terminal long shoots were located at the tip of a long shoot which had grown vigorously in the preceding growing season. Buds expected to produce lateral shoots were located on lateral shoots of the same twigs. In *Betula* only those lateral shoot buds formed on the previous year's short shoots were selected. No such obvious short shoots were found in *Populus*.

The embryonic leaves and leaf primordia within these buds were counted and measured with a millimeter rule or ocular micrometer. Primordia were measured from tip to base, embryonic leaves from tip to point of attachment of stipule.

Before bud break, five trees of each species, except *Populus grandidentata*, of which only one tree was accessible, were chosen for study. At frequent intervals throughout the growing season measurements were made of terminal and lateral shoot growth on five twigs of each tree. Criteria for selection of these shoots were the same as for selection of buds to be dissected.

Measurements included length of each leaf from tip to point of attachment to stipules, and length of each internode. Leaves were numbered in the order of appearance, and internodes were numbered according to terminating leaf.

#### *Role of Early and Late Leaves in Shoot Growth*

To test the separate and joint contributions of early and late leaves to shoot elongation the following treatments were applied in 1965 to *Betula papyrifera* long shoots. (A) Early leaves covered, (B) late leaves covered, (C) early and late leaves covered, and (D) control, no leaves covered. As soon as leaves were 1 to 2 cm long they were covered with small aluminum foil envelopes. In treatments B and C weekly examination of shoots was necessary so new late leaves could be covered as they unfolded.

Within each treatment, eight subtreatments were applied, consisting of different dates on which treatment was begun. Intervals between subtreatments were 1 week early in the season, and 2 weeks later (Table IV). Treatment began May 31, but late leaves were not available before July 23. Each treatment and subtreatment was applied once in each of 10 trees. Trees were selected for uniformity of habit, healthy appearance, and accessibility of rapidly growing shoots. All were growing in the open in the Oneida County Forest near Rhinelander, Wisconsin. Height varied from 8 to 16 ft and diameter breast height from 0.5 to 2 in. It was estimated that less than 15% of the long shoots on each tree were treated. Apparently healthy buds on previous year's long

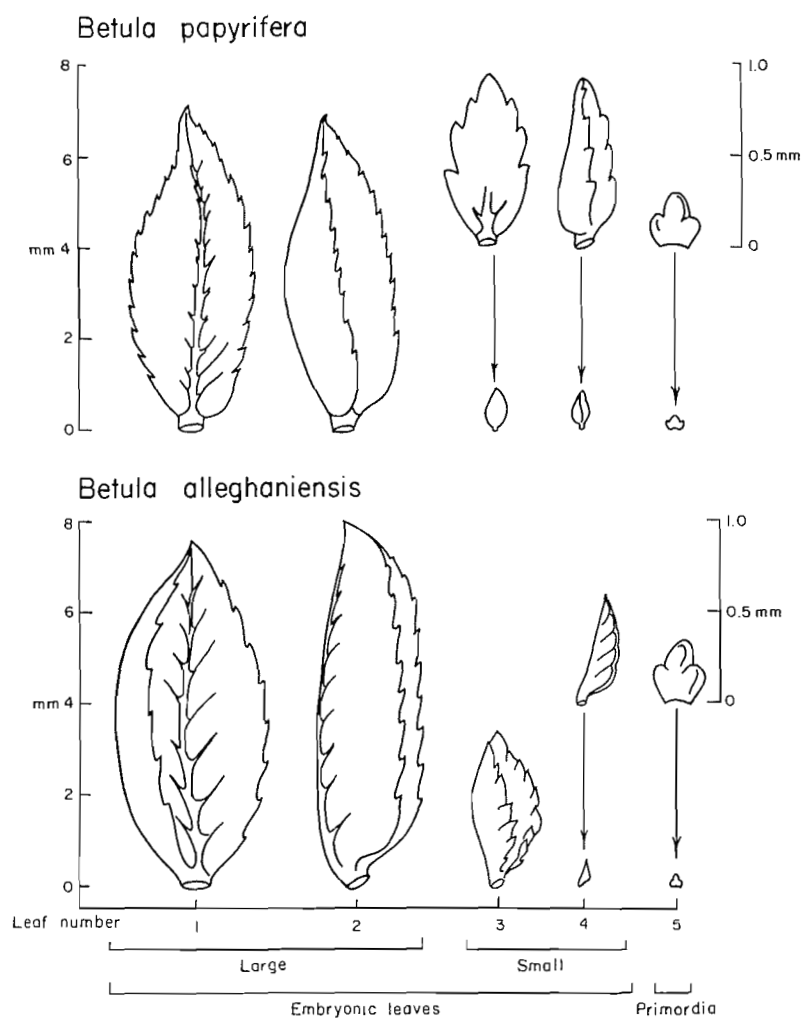


FIG. 1. Contents of long shoot buds of *Betula papyrifera* and *B. alleghaniensis* in the spring.

shoots were preselected and randomly assigned to treatment before buds opened. Shoots which died before treatment were replaced.

A cumulative record of elongation of each shoot was maintained. On September 14 all shoots were harvested and number of internodes, final shoot length, and bud and stem dry weight for the current year determined.

## Results

### Bud Contents

Numbers and sizes of components of spring and fall buds are given in Figs. 1 and 2 and Tables I and II.

#### *Betula papyrifera*

Both embryonic leaves and leaf primordia were found in the spring within each bud expected to produce a long shoot. The former were clearly leaf-like, with well-defined teeth, petiole, and veins. The latter were small lobed structures without detail. The embryonic leaves fell into two size classes separated by a break of 2 to 6 mm. The large leaves were pubescent and firm. The largest of the small leaves were pubescent, but most were glabrous, translucent, and delicate in texture. The long shoot buds collected in the fall contained fewer small leaves and shorter large leaves.

Short shoot buds contained the same type of leaves as long shoot buds, but on the average they had a somewhat greater number of large leaves, fewer small leaves, and about the same number of primordia. Mean lengths in each class were approximately the same as in the long shoot buds.

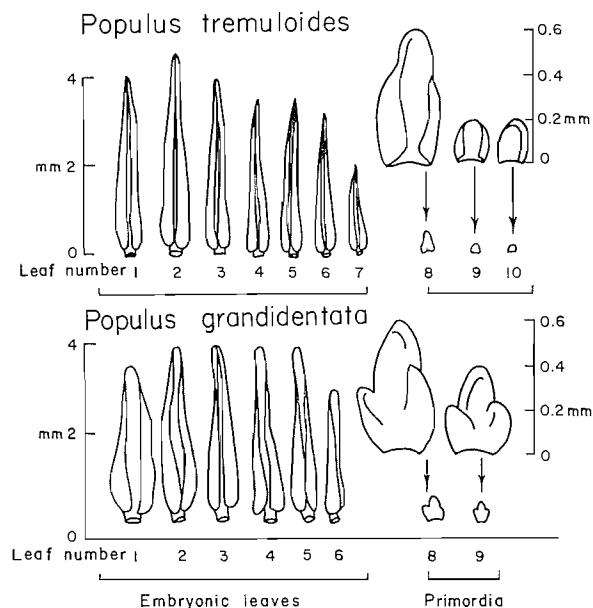


FIG. 2. Contents of terminal buds of *Populus tremuloides* and *P. grandidentata* in the spring.

TABLE I  
Mean numbers of early and late leaves produced and numbers of leaves in spring and fall buds

Species	No. leaves on summer shoot		Spring buds				Fall buds	
	Early	Late	Embryonic leaves		Primordia	Embryonic leaves	Small	Primordia
			Large	Small				
<i>Betula papyrifera</i>	2.0	3.8	2.1	2.6	Long shoot or terminal shoot	2.0	1.2	1.6
<i>Betula alleghaniensis</i>	2.0	3.3	2.1	3.2		2.1	0.6	0.9
<i>Populus tremuloides</i>	7.3	—	6.6	—		—	—	—
<i>Populus grandidentata</i>	6.4	—	5.6	—		—	—	—
<i>Betula papyrifera</i>	2.4	—	2.7	0.9	Short shoot or lateral shoot	—	—	—
<i>Betula alleghaniensis</i>	2.1	—	2.2	0.6		—	—	—
<i>Populus tremuloides</i>	5.9	—	5.9	—		—	—	—
<i>Populus grandidentata</i>	4.5	—	3.9	—	—	—	—	—

TABLE II  
Size of components of spring and fall buds (first number in each column is the mean; numbers in parentheses give the observed range)

Species	Spring buds			Fall buds		
	Length of embryonic leaves (mm)		Length of primordia (mm)	Length of embryonic leaves (mm)		Length of primordia (mm)
	Large	Small		Large	Small	
<i>Betula papyrifera</i>	6.9 (4.1-9.0)	1.2 (0.4-2.9)	Long shoot or terminal shoot 0.3 (0.2-0.3)	5.2 (4.2-7.7)	1.3 (0.7-2.0)	0.5 (0.2-0.8)
<i>Betula alleghaniensis</i>	7.5 (4.2-9.5)	2.4 (0.2-6.5)	0.3 (0.1-0.7)	5.4 (3.5-6.6)	2.8 (2.2-3.4)	0.5 (0.2-1.1)
<i>Populus tremuloides</i>	4.0 (2.0-5.5)		0.4 (0.1-1.0)			
<i>Populus grandidentata</i>	3.7 (1.2-4.7)		0.4 (0.1-0.8)			
<i>Betula papyrifera</i>	7.1 (4.3-10.1)	1.0 (0.2-2.3)	Short shoot or lateral shoot 0.2 (0.1-0.4)			
<i>Betula alleghaniensis</i>	7.7 (6.5-9.8)	1.4 (0.4-3.6)	0.4 (0.1-0.8)			
<i>Populus tremuloides</i>	3.8 (2.0-4.9)		0.3 (0.1-0.8)			
<i>Populus grandidentata</i>	3.6 (1.4-4.9)		0.3 (0.2-0.6)			

*Betula alleghaniensis*

Leaf structures in the spring buds of this species can be classified in the same way as those of paper birch. Fall long shoot buds contained fewer small and shorter large leaves. In the short shoot buds approximately the same number of large leaves and primordia per bud were found as in long shoot buds, but fewer small leaves were present.

*Populus tremuloides* and *P. grandidentata*

In these species embryonic leaves and leaf primordia also were found. Only spring buds were studied. The gradation in length of embryonic leaves was gradual and all were similar, so they were not subdivided.

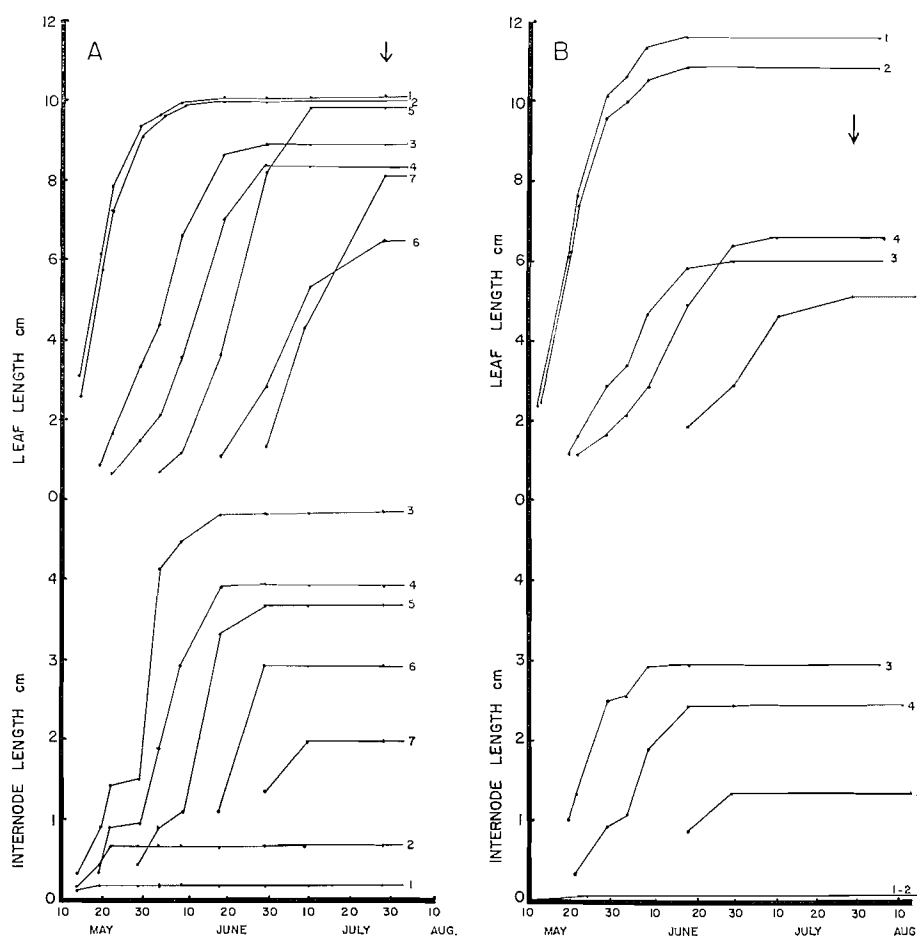


FIG. 3. Seasonal elongation of leaves and corresponding internodes of a representative long shoot of *Betula papyrifera* (A) and *Betula alleghaniensis* (B). The arrow indicates the date the tip bud formed. Numbers at right refer to leaf and internode number.

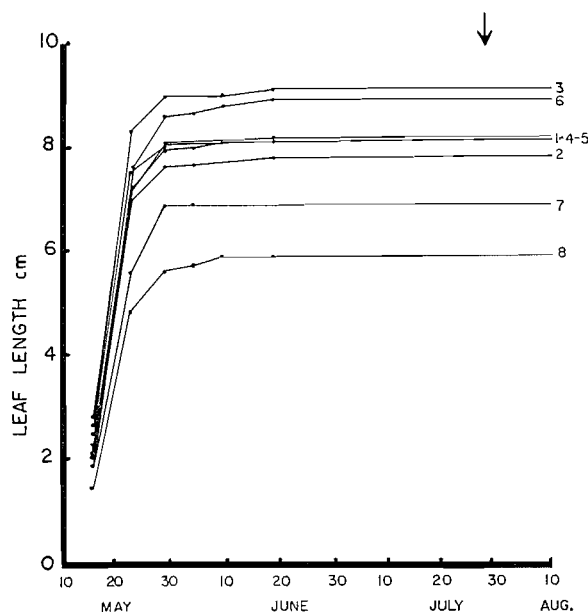


FIG. 4. Seasonal elongation of leaves of a representative terminal shoot of *Populus tremuloides*. The arrow indicates the date the terminal bud formed. Numbers at right refer to leaf number.

#### Leaf and Internode Elongation

Data on the seasonal course of expansion of leaves and internodes of representative shoots are given in Figs. 3 to 5. Lengths of leaves and internodes at the end of the growing season are summarized in Table III.

#### *Betula papyrifera*

The first pair of long shoot leaves began to unfold about May 15, and grew very rapidly in the next 2 weeks. Their growth then slowed and ceased in the third week. The third leaf became apparent when the first two were more than half grown, usually no later than May 30. Succeeding leaves appeared at intervals of approximately 5 to 10 days until a mean total of 5.8 leaves per shoot had emerged. Because of the 2-week interval between the occurrence of the first two leaves and succeeding ones, and their generally firmer texture and more apparent double toothing, leaves 1 and 2 were classified as early leaves and the remainder as late leaves. Behavior of a representative long shoot is shown in Fig. 3A.

Late leaves elongated at a rate slower than that of the early leaves, and growth usually was completed in about 3 weeks. Growth in all but one or two leaves ceased after July 29. There was a tendency for each leaf to be smaller than the one formed previously on the same shoot, and in only one case did the length of any of the late leaves exceed that of the early ones.

Internodes 1 and 2 of long shoots were very short, seldom exceeding 1 mm final length. The period of rapid elongation of any subsequent internode lay within that of the leaf which terminated it, but was completed a few days



TABLE III  
Final size of shoot components (first number in each column is the mean; numbers in parentheses give the observed range)

Species	Leaf length (cm)		Final internode length (mm)			Total shoot length (mm)	Leaves per shoot
	Early leaves	Late leaves	All internodes	First 2 internodes	Internodes 3 and beyond		
<i>Betula papyrifera</i>	8.9 (6.9-11.7)	<sup>a</sup>	14.9 (1-48)	5.4 (1.5-14)	21.4 (4-48)	85.5 (31-181)	5.8 (4-9)
<i>Betula alleghaniensis</i>	10.6 (9.7-11.6)	5.9 (2.9-7.1)	14.4 (0.5-33)	0.7 (0.5-1.0)	22.7 (13-33)	77 (61.5-102.5)	5.3 (5-6)
<i>Populus tremuloides</i>	7.8 (3.7-10.4)		2.7 (0.5-9.0)			19.8 (5-41)	7.3 (6-9)
<i>Populus grandidentata</i>	13.1 (8.1-15.4)		4.8 (2-14)			30.4 (16-46)	6.4 (5-7)
<i>Betula papyrifera</i>	10.2 (6.2-13.2)		1.0	Long shoot or terminal shoot			
<i>Betula alleghaniensis</i>	9.4 (6.7-12.4)		1.0	Short shoot or lateral shoot			
<i>Populus tremuloides</i>	6.8 (4.1-9.6)		1.4 (0.5-7)				
<i>Populus grandidentata</i>	11.1 (8.6-13.5)		2.2 (1-5)				

<sup>a</sup>Not determined because of considerable insect injury to late leaves.

sooner. Elongation of the final internode was usually complete by the time the first late leaf had ceased growth. Final length decreased in succeeding internodes after internode 3. Length of internodes 1 and 2 was only 6.3% of total final shoot length.

Of the 25 lateral shoot buds selected, one produced a long shoot and was discarded. Most of the remaining buds produced two leaves, but a few produced three or four. Leaves 3 and 4 appeared at the same time as 1 and 2 and were of the same type. Internodes did not exceed 1 mm in length on short shoots, and leaves were slightly longer than early leaves on long shoots.

*Betula alleghaniensis*

The first pair of leaves appeared slightly before May 13, and their elongation was completed by June 18. Only 3 of the 25 buds expected to produce long shoots did so. The rest were discarded. Elongation of a representative long shoot is shown in Fig. 3B. Leaves 3 and 4 of the long shoots available emerged within a few days of the appearance of early leaves, and completed their expansion by June 30 or shortly thereafter. Leaves 5 and 6 appeared 20 to 30 days later and completed expansion by July 10 or shortly thereafter. Although the time interval was greatest between appearance of leaves 4 and 5, the morphological difference was greatest between the first two and the succeeding leaves. Leaves 1 and 2 were 3 to 4 cm longer than leaves 3 and 4, and were of firmer texture. Differences in size and texture between leaves 3 and 4 and succeeding leaves were not pronounced. Thus, leaves 1 and 2 were classified as early leaves and succeeding leaves as late leaves. Inferences are limited because of lack of material.

Late leaves decreased in size toward the shoot tip. Only 0.9% of total final shoot length was due to internodes 1 and 2. Elongation of each internode ended at the same time or slightly before elongation of the terminating leaf was completed. Only 2 of the 25 short shoots produced a third leaf, and it, like the first two, resembled the early leaves of the long shoots. Internodes on the short shoots remained about 1 mm long.

*Populus tremuloides*

All leaves produced by terminal shoots appeared at bud break, approximately May 15. Rapid growth for the next 10 days was followed by a period of slower growth. Very slight increase in length occurred after June 8, and only 2 leaves of the 182 measured increased in length after June 19. Figure 4 shows leaf elongation in a typical terminal shoot. The mean number of leaves produced per terminal shoot was 7.3. All of these appeared at the same time and resembled each other so that heterophyly was not observed. Mean final length of the longest leaf, usually located near the center of the shoot, was 8.9 cm.

Internodes elongated only slightly, elongation being completed by late May or early June before leaf growth ceased. The longest internodes usually were near the tip of the shoot.

Leaves and internodes of lateral shoots began and ended growth concurrently with terminal shoots. All leaves produced on the shoot appeared at bud break. The longest leaves, usually near the center of the shoot, had a mean length of 7.9 cm.

*Populus grandidentata*

All leaves on observed twigs unfolded at the same time and no subsequent leaves appeared. The longest leaf, mean length 14.1 cm, was usually located near the center of the shoot. Elongation was completed by June 30. Internode elongation in terminal shoots was completed by June 3, somewhat before leaf elongation ceased. Mean length of the longest leaf of lateral shoots was 12.4 cm.

*Contribution of Early and Late Leaves to Shoot Growth*

Most leaves abscised within a week or two after they were covered with aluminum foil. However, some leaves were detached by windstorms. Abscission usually was related to leaf mortality since the separation took place in the normal abscission zone at the base of the petiole. The few covered leaves that did not abscise were discolored.

No differences were noted among treatments and subtreatments in phenology of late leaf production. Two early and two to six (usually two to four) late leaves were produced on shoots that lived. Leaf growth ceased during mid-July.

Treatments B and D (late leaves covered and control) produced low shoot mortality subsequent to treatment. In contrast, treatments A and C (early leaves covered or all leaves covered) were followed by high shoot mortality especially in early subtreatments (Table IV). Death of shoots often occurred shortly after leaves were covered and was followed by shrivelling and loss of the distal portion of the shoot.

Data on development of shoot components under various treatments are given in Table V, and shoots from a representative tree appear in Fig. 5. One bud was produced per late leaf node in all treatments. Mean number of live buds per shoot on shoots apparently whole at harvest ranged from two to almost four in treatments A, B, and D. In treatment C the number was irregular and sometimes lower, but showed no pattern according to subtreatment. Mean dry weight per bud varied from 5.4 to 14.5 mg.

There were no significant differences among treatments for shoot weights exclusive of buds. However, differences among subtreatments were significant (Table VI). Mean dry weights per centimeter of shoot did not vary significantly.

TABLE IV  
Number of shoots (out of 10) dead at time of harvest

Subtreatment dates	A Early leaves covered	B Late leaves covered	C Early and late leaves covered	D Control
(1) May 30	9	0	9	2
(2) June 7	8	1	10	1
(3) June 15	5	2	6	0
(4) June 23	2 <sup>a</sup>	0	6	1
(5) July 8	0	0	7	1
(6) July 22	0 <sup>a</sup>	1	6 <sup>a</sup>	0 <sup>a</sup>
(7) August 5	0	0	2	0
(8) August 23	0	0	0	0

<sup>a</sup>Only 9 of the original 10 shoots remained on the tree at the end of the experiment.

TABLE V  
Effect of covering early and late leaves alone or in combination on growth of long shoots of *Betula papyrifera*

Subtreatment	No. <sup>a</sup> live buds	Dry wt. (mg)			Shoot wt. <sup>a</sup> per cm	Number <sup>a</sup> internodes	Mean length <sup>a</sup> per internode (mm)	Maximum <sup>c</sup> shoot length (mm)
		Per bud <sup>a</sup>	Shoot <sup>b</sup> minus buds	Total <sup>b</sup> shoot				
Treatment A: early leaves covered								
1	2.0	6.8	11.9	13.3	20.3	6.0	9.6	18.4
2	2.0	8.3	30.6	35.6	12.0	4.2	11.3	33.1
3	2.5	10.9	56.4	71.9	12.9	5.0	13.0	49.0
4	2.7	9.5	88.3	106.8	13.9	5.0	13.7	64.6
5	2.6	10.1	78.9	105.7	11.3	5.2	16.8	69.4
6	2.2	9.3	68.2	87.8	11.0	4.7	13.4	70.3
7	3.3	9.6	130.3	162.4	14.0	5.6	15.2	89.4
8	3.1	9.5	106.9	135.4	13.0	5.3	15.0	80.6
Treatment B: late leaves covered								
1	2.3	7.6	74.7	93.6	10.8	4.8	13.7	68.8
2	1.9	9.1	69.7	86.5	10.7	5.0	12.6	63.8
3	3.2	10.0	102.7	127.8	12.1	5.9	12.8	87.8
4	2.5	10.2	96.8	121.9	12.2	5.0	14.5	78.6
5	2.3	7.3	65.7	82.5	10.6	4.8	12.8	62.2
6	2.1	8.7	88.0	107.2	10.6	5.0	15.1	73.7
7	2.9	8.5	111.6	136.2	12.2	5.3	16.4	87.9
8	3.7	12.7	197.0	244.4	15.0	5.9	17.7	111.1
Treatment C: early and late leaves covered								
1	2.0	5.4	17.4	19.6	13.5	5.0	5.4	35.3
2	—	—	42.7	42.7	31.6	5.0	21.1	21.1
3	3.2	6.9	48.8	59.8	11.5	5.3	11.5	50.1
4	1.6	7.6	74.0	87.1	9.1	5.1	12.3	69.0
5	0.8	8.6	76.7	83.6	8.3	5.0	13.7	79.3
6	1.6	6.8	106.4	116.3	10.9	5.5	15.6	86.3
7	2.8	7.8	173.8	195.9	14.2	6.6	16.8	115.1
8	3.0	8.7	99.2	125.3	12.9	5.2	13.1	70.9
Treatment D (control): no leaves covered								
1	2.4	10.4	100.9	133.4	24.9	5.1	16.0	71.8
2	2.4	10.0	83.5	108.2	12.7	4.8	14.7	67.8
3	3.0	10.7	106.2	136.5	12.2	5.1	15.5	77.7
4	2.3	9.5	82.0	104.2	13.0	4.9	13.2	61.2
5	2.5	14.5	166.8	196.1	17.2	5.2	15.0	81.9
6	2.7	9.6	111.6	137.4	13.0	5.2	14.5	77.4
7	3.4	9.3	142.8	176.0	13.4	5.6	15.7	93.2
8	3.5	10.4	152.1	186.2	15.9	5.5	15.5	89.9

<sup>a</sup>Obviously fragmentary shoots omitted from calculations.  
<sup>b</sup>Based on all shoots in harvest condition.  
<sup>c</sup>Based on all shoots in harvest condition.

PLATE I

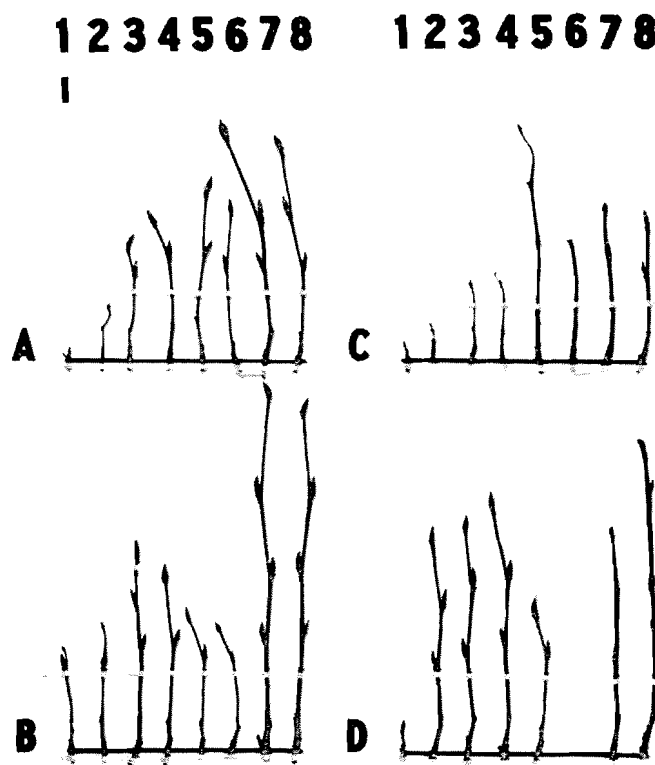


FIG. 5. Effect of covering early and late leaves alone and in combination on shoot development of *Betula papyrifera* long shoots. (A) Early leaves covered; (B) late leaves covered; (C) early and late leaves covered; (D) control, no leaves covered. Numbers refer to subtreatments. Vertical bar in upper left corner indicates 1 cm.

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TABLE VI  
Summary of variance analyses

Characteristics	Treatments A, B, C, D		Treatments A, C, D	
	Among treatments	Among subtreatments	Among treatments	Among subtreatments
Shoot weight, minus buds	NS	*	NS	NS
Total shoot weight	NS	*	*	NS
Maximum shoot length	NS	**	**	**

\*Significant at 5% level.  
\*\*Significant at 1% level.

While variance analyses of total shoot weight showed no significant differences among treatments they did show significant differences between subtreatments. If treatment B, whose results most closely resembled those of D, was omitted, significant differences were found among treatments but not among subtreatments (Table VI).

Mean length per internode on shoots apparently whole at harvest ranged from 5.4 to 17.7 mm. Except for subtreatment 1 in treatment A and C, for which very few acceptable twigs survived, internode length showed no pattern in relation to treatment.

Many shoots were shorter at the time of harvest than earlier because of death of shoots, breakage, and insect damage, and because *Betula papyrifera* twig tips usually die back to the youngest lateral bud. Variance analyses of maximum shoot length recorded during the growing season showed no significant differences among treatments, but differences among subtreatments were significant. When treatment B, whose results most resembled those from treatment D was omitted, differences among treatments and subtreatments were significant (Table VI). Examination of data of cumulative shoot elongation showed that subtreatments 5 through 8, which were applied after early June, did not affect shoot length as elongation was nearly completed by that time.

### Discussion

Terminal shoots produced longer early leaves than lateral shoots in all species except *Betula papyrifera*, and they produced longer internodes in all species. In Table I the bud contents are compared with summer leaf production. Approximately two large, firm-textured embryonic leaves were found in both spring and fall buds of both species of *Betula*. Their position and number corresponded to that of the early leaves expanded during the growing season.

The number of late leaves produced in *Betula alleghaniensis* corresponded well with the number of small embryonic leaves found in the spring long shoot bud. In *Betula papyrifera* the number of leaves produced during the summer was greater than the number of small embryonic leaves in the spring bud. Late leaves probably develop from the small embryonic leaves and also from primordia present in the spring. The number of primordia which develop into late leaves undoubtedly is influenced by shoot vigor. Short shoot buds contained a few small embryonic leaves and primordia in excess of leaves produced

on short shoots in the summer. Presumably development of such structures is suppressed.

The number of small embryonic leaves found in fall buds was much smaller than in spring buds but the number of primordia was similar. Possibly growth processes slow toward the end of the growing season, the rate of primordium formation decreases, and only leaves which reach a critical point continue development to the embryonic leaf stage. Further development may occur in spring before bud break.

In the two species of *Populus* studied, the number of leaves expanded during the summer exceeded somewhat the number of embryonic leaves found in the buds. This probably resulted from sampling variation, since all leaves produced during the current summer appeared immediately at bud break. Possibly some primordia are capable of developing into late leaves under favorable growing conditions or after defoliation and otherwise are suppressed. These results resemble those of Critchfield (1960) for *Populus trichocarpa*.

Experiments on covering early and late leaves, alone and in combination, emphasized that the contributions of the two types of leaves on *Betula* long shoots to current shoot growth differed markedly. Covering or removal of early leaves before mid-June caused a decrease in mean shoot length traceable primarily to death of shoots before the end of the lengthening period. This effect was achieved by covering early leaves alone or in combination with late leaves, but not by covering late leaves alone. The last internode often had completed expansion before even the first late leaf was finished elongating and frequently did so in spite of serious injury in late leaves. Hence, the presence of normally growing early leaves was essential for normal shoot development and survival.

Since some shoot elongation occurred while early leaves were small, shoot growth at that time must be dependent on food reserves. Early leaves probably contribute current photosynthate and growth regulators for subsequent shoot growth. Late leaves which have not completed growth probably do not export assimilates but continue to receive them from the nearest mature leaves. Hence their covering or removal does not seriously affect the shoot. Once late leaves mature, however, it may be expected that export of photosynthates predominates (Leopold 1964). Kursanov (1961) could not induce flow of assimilates into mature leaves even by prolonged darkening. In the untreated shoot, photosynthate from late leaves may be used primarily in bud formation since functional buds occur at the bases of late leaves but not of early leaves. Lack of evidence for this conjecture in the present study may be due to compensatory mechanisms.

There is considerable emphasis in the literature on the dependency of woody plants on prior-year photosynthate for shoot growth (Kozłowski 1964a; Kozłowski and Winget 1964). It should be recognized, however, that there is a variety of patterns and degrees of dependency of expanding shoot systems on reserve foods and currently produced carbohydrates. Root suckers, stump sprouts, and internode expansion of species with shoots fully predetermined in the winter bud apparently depend to a large extent on carbohydrate reserves. Species with shoots preformed in the winter bud usually show a single growth flush of short duration. Such shoots consume reserves in elongation and



respiration early in the season before the danger of frost is over and often before photosynthesis is productive enough to provide much food for the new shoots (Kozlowski 1964a; Kozlowski and Gentile 1958). Internode expansion in such species often is completed before the leaves are fully grown (Kozlowski 1955, 1958, 1962, 1963; Kozlowski and Ward 1957a, 1957b, 1961). Additional evidence for importance of reserves for shoot growth of species with predetermined shoots comes from studies which show closer correlation with weather of the year of bud formation than with the year of expansion of the bud into a shoot (Motley 1949; Friesner and Jones 1952; Kozlowski 1964a, 1964b). But even in predetermined species, some current photosynthate may be used. Larson (1964) showed that in the latter part of the season, currently produced carbohydrates appeared to be used in growth of the new needles of *Pinus resinosa*.

In contrast to species with predetermined shoots, those with heterophyllous shoots use considerable current photosynthate for shoot growth. The present study showed that early leaves of *Betula papyrifera* were fully grown within a few weeks and were essential for subsequent normal growth of the shoot. That current photosynthate is important for shoot growth of heterophyllous species is reinforced by Broekhuizen's (1962) observation that total shoot length in young *Populus* trees was better correlated with current-year than prior-year weather. In heterophyllous species there undoubtedly are wide variations among shoots on the same tree in their proportional use of reserve and current carbohydrates. The differences in timing of leaf development on heterophyllous and non-heterophyllous shoots in *Populus trichocarpa* (Critchfield 1960) indicate variable degrees of utilization of currently synthesized carbohydrates. The use of reserves also varies with tree age. In *P. trichocarpa* heterophyllous long shoots outnumber short shoots only in very young trees. In old trees most of the leaves are early leaves on short shoots which probably utilize large amounts of reserves for expansion (Critchfield 1960).

Distinct heterophylly was not observed in *Populus tremuloides* or *P. grandidentata* in the present study. Internode elongation in observed shoots of both species was completed before leaf elongation and it is unlikely that the new leaves contributed much carbohydrate to shoot growth. However, observation of terminal shoots and buds from the upper crowns of these trees after leaf fall showed that topmost shoots were as much as 10 to 25 times as long as those measured lower on the tree, and had borne 2 to 3 times as many leaves. Their buds, on the other hand, contained approximately the same number of embryonic leaves and leaf primordia as those from lower twigs. Presumably growth is more vigorous and of longer duration higher in the tree. Leaves in excess of the complement found in the winter bud may be late leaves. This difference in behavior of shoots on different parts of the tree may explain the discrepancy between the short elongation time of *P. tremuloides* shoots here and the long duration of growth observed in New York State by Cook (1941).

Several other woody species use considerable current photosynthate for apical growth. For example, the recurrently flushing southern pines (*Pinus taeda*, *P. echinata*, and *P. palustris*) consume large amounts of currently produced carbohydrates in shoot growth (Allen 1964). Similarly many tropical species use large amounts of currently produced carbohydrates as shown by

depletion of starch with each growth flush (Humphries 1947; Kramer and Kozlowski 1960). Even species which have preformed shoots in the bud but which also produce lammas or proleptic shoots use variable amounts of current photosynthate in shoot growth (Kozlowski 1964a; Kozlowski and Clausen 1965). Many orchard trees use both reserves and currently produced carbohydrates in shoot expansion (Mochizuki and Hanada 1957; Priestley 1962). The duration of shoot growth of orchard trees can be markedly altered by cultural practices (Merrill and Kilby 1952; Mochizuki and Hanada 1958) hence altering the proportion of currently produced carbohydrates used by expanding shoots. There also are variations among leaves of the same plant in the amount of food which they contribute to growing shoots. In young apple plants, for example,  $^{14}\text{C}$  moved from the upper leaves to the stem apex and to young leaves. In contrast, photosynthetic products from the lower leaves moved to the roots, while from an intermediate region they were translocated both to the stem tip and to the roots (Quinlan 1964).

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