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Aspects of comparative growth, morphology and anatomy of long and short shoots of Betula papyrifera Marsh

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ASPECTS OF COMPARATIVE GROWTH, MORPHOLOGY AND ANATOMY OF LONG AND SHORT SHOOTS OF *Betula Papyrifera* MARSH.

by

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A thesis submitted in partial fulfillment
of the requirements for the degree of
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"The twigs of the birch imprint the December sky
Like branching veins upon a thin old hand . . . . "

THOMAS HARDY, December 1912

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To my mother and relatives especially Mr. Adinortey Puplampu who made it possible for me to come to Lakehead

University, I say thank you so much, I shall never fail you.

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TABLE OF CONTENTS

TABLE OF CONTENTS (Cont'd.)

TABLE OF CONTENTS (Cont'd.)

CHAPTER 5

CHAPTER 6

Comparative anatomy of long and short shoots: A Quantitative Analysis with Emphasis on Aspects of Stem Anatomy

CHAPTER 7

LIST OF FIGURES

LIST OF FIGURES (Cont'd.)

LIST OF FIGURES (Cont'd)

LIST OF FIGURES (Cont'd.)

LIST OF FIGURES (Cont'd.)

LIST OF FIGURES (Cont'd.)

LIST OF FIGURES (Cont'd)

LIST OF FIGURES (Cont'd.)

LIST OF TABLES

CHAPTER 1

"O Lord, I beg upon my knees
That all my various syntheses
May not turn out to be inferior
To those conducted by bacteria."

Anon., discovered by K.V. Thimann.

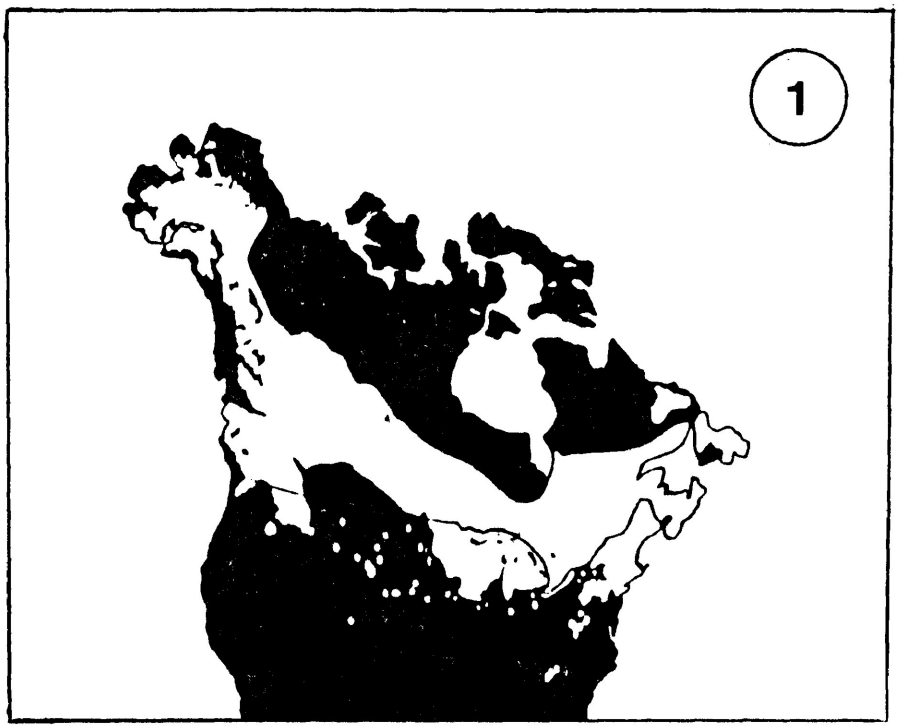
CHAPTER 1

GENERAL INTRODUCTION AND LITERATURE REVIEW

Deciduous monoecious trees and shrubs of the genus Betula, family Betulaceae (Sargent 1922; Rehder 1940; Lawrence 1951; Dugle 1966) are widespread in North America (Nuttall 1842; Sargent 1896, 1905, 1922; Wells and Rue 1927; Halliday and Brown 1943), Europe (Regel 1865; Gunnarson 1925; Helms and Jorgensen 1927; Jentys-Szaferowa 1937; Lindberg 1939; Jenssen 1940) and Asia (Tkachenko 1941; Jung 1960; Wang 1961). Approximately 52 species are currently recognized (Clausen 1973). The geographical range of paper birch (Betula papyrifera Marsh) in North America is transcontinental (Quigley and Babcock 1969) (see Fig. 1). According to Quigley and Babcock (1969) paper birch is a "characteristic species of the Boreal forest region of Canada and Alaska, becoming shrublike as it approaches the northern limits of its range."

Paper, or white birch (Brittain and Grant 1965), is of immense economic importance in the pulp, paper, veneer, sawn products and furniture industries (Wells and Rue 1927; Davis 1953; Carpenter 1969; McDonald 1969; Quigley and Babcock 1969: Saunders 1969). Most of the

FIG. 1. Distribution of paper birch in North America. (Quigley and Babcock 1969).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other members of the genus Betula are economically valuable tree species (Bügsen and Münch 1929; Lehonkoski 1940; Jenssen 1940; Hyvarinen 1968). Hence extensive silvicultural studies have been documented (e.g. Klaehn and Runquist 1952; Hutnik 1954; Clausen 1965; Marquis 1966; Hyvarinen 1968; Bjorkbom 1969, 1971).

A wide range of studies on Betulaceae spanning various disciplines have been documented. The earliest study on birch I have encountered is that of Leeuwenhöek (1695), who in the course of his anatomical investigations on certain plant cells, examined birch wood. Since then most of the work on the Betulaceae have been taxonomic, palaeobotanical, physiological, morphological, etc. (Table 1-1). Only about 20 to 25 per cent of these studies involved Betula papyrifera. It is apparent that most of the work reported indicates the economic importance of these tree species to foresters in particular.

The occurrence of long ahd short shoots in plants has been documented for over a century. Areschoug (1877) is the first person to observe the occurrence and growth habits of the two shoot types in the literature. Since then a number of studies has been reported (Table 1-2). However, different approaches have been taken to understand the occurrence of these shoot types. The most comprehensive are those combining anatomy with physiology

TABLE 1-1. A survey of representative literature on studies of Betulaceae.

Discipline	Authors
Anatomy	Leeuwenhöek 1695; Hanstein 1868; Boubier 1896; Plaut 1910, 1918; Hoar 1916; Bügsen and Münch 1929; Cousins 1933; Abbe 1935, 1938; Rafalski and Wardyn 1939; Tkachenko 1941; Thunnel 1942; Kujala 1946; Garrison 1949; Hall 1952; Gardiner 1958; Clausen 1963; Bhat and Kärkkäinen 1981; Zimmermann and Jeje 1981; Bhat 1982.
Ecology and/or phytogeography	Raup 1936; Hesselman 1937; Acatay 1951; Kåsa 1952; Malmström 1954; Kitamura 1964; Tabata 1964; Dansereau and Pageau 1966; Maillette 1982a, 1982b; Oldemeyer 1982; Smith and Tumey 1982.
Embryology	Nawaschin 1894; Wolpert 1910; Hagman 1963; Davis 1966; Maini and Wang 1967.

TABLE 1-1 (cont'd.)

Evolution	Berry 1923; Hall 1952; Tabata 1964; Wolfe and Leopold 1967; Wolfe et al. 1966; Kikuzawa 1982.
Floral anatomy and/or morphology	Spach 1841; Payer 1858; Wolpert 1910; Streicher 1918; Zimmermann 1922; Bügsen and Münch 1929; Abbe 1935, 1938; Macdonald 1971.
General Morphology	Lubbock 1899; Kŏstal 1903; Moore 1909; Gunnarsson 1925; Foster 1928; Bügsen and Münch 1929; Ruostalo 1954; Magomedmirzaev 1970; Macdonald and Mothersill 1983; Macdonald et al. 1983.
Genetics and Cytogenetics	Jack 1895; Woodworth 1929, 1930, 1931; Anderson and Abbe 1934; Johnsson 1941, 1944, 1945, 1949; Smith and Nikols 1941; Schreider 1949; Clausen 1962a,1963, 1969, 1973; Tucovic and Javanovic 1969; Dancik and Barnes 1972.

TABLE 1-1 (Cont'd.)

Palaeobotany	Berry 1923; Flint 1947; Lindquist 1949; Braun 1950; Wolfe et al. 1966.
Palynology	Dyakowska 1937; Pohl 1937; Jentys-Szaferowa 1938; Kujala 1946; Sarvas 1952; Clausen 1962b.
Phytopathology	Simpson 1932; Balch and Prebble 1940; Hawbolt 1947; Barter and Balch 1950; Greenidge 1953; Redmond 1951, 1955, 1957; Conklin 1969; Shigo 1969.
General Phenology	Moberg 1857, 1894; Kihlman 1900; Kujala 1924; Kaikko 1940; Kienholz 1941; Burton and Leslie 1952; Sarvas 1952; Kozlowski and Ward 1957; Clausen and Kozlowski 1967; Clausen and Garrett 1969; Sharik 1970; Danilov 1971; Kozlowski 1971; Dancik and Barnes 1972; Gross 1972; Kikuzawa 1978; Clausen 1980;

TABLE 1-1 (Cont'd.)

General Phenology	Kuivinen and Lawson 1982; Maillette 1982a; Schultz et al. 1982.
Physiology and Ecophysiology	Gibbs 1939, 1940; Björkman 1941, 1949; Dimbleby 1952; Tranquillini 1952; Wareing 1954; Ingestad 1957; Vaartaja 1957, 1959; Longman and Wareing 1959; Kawase 1961a, 1961b; Yelenosky 1961; Kozlowski 1963; Eagles and Wareing 1964; Logan 1965; Tubbs 1965; Kozlowski and Keller 1966; Domanski and Kozlowski 1968; Hoyle and Bjorkbom 1969; Gee and Federer 1972; Takahashi 1972, 1973, 1975; Harrison and Saunders 1975; Federer 1976, 1977, 1980; Federer and Gee 1976; Dathe et al. 1978; Downs and Bevington 1981; Tang and Kozlowski 1982; Öquist et al. 1982a, 1982b; Tuomi et al. 1982.
Phytogeology	Flint 1947.

TABLE 1-1 (Cont'd.)

Silviculture	Klaehn and Runquist 1952; Hutnik 1954; Marquis 1966; Bjorkbom 1969, 1971, 1972; Leak et al. 1969; Marquis et al. 1969, etc.
Taxonomy and Cytotaxonomy	De Candolle 1827; Hooker 1838; Nuttall 1842; Regel 1861, 1865; Prantl 1894; Sargent 1896, 1922; Fernald 1902, 1945; Rosendahl 1916, 1928; Schneider 1916; Winkler 1930; Hultén 1944; Kujala 1946; De Pouques 1949; Lawrence 1951; Krüssmann 1962; Brittain and Grant 1965, 1966, 1967, 1968; Dugle 1966.

TABLE 1-2. A chronology of selected studies on long and short shoots, 1877 to date.

YEAR	WORKER	ASPECT OF STUDY	PLANT MATERIAL(S)
1877	Areschoug	General observations	A number of species
1886	Dickson	Bifoliar short shoots	Pinus sylvestris
1916	Herrmann	Frequency of xylem vessels	Berberis Ginkgo Pomaceae Acer Fagus
1929	Bügsen and Münch	General observations and various aspects	A number of species
1929	Schüepp	Heterophylly	Acer
1935	Doak	Dwarf shoots; shoot apex	Pinus
1938	Foster	Shoot apex	Ginkgo
1946	Gunckel & Wetmore	Anatomy, vascular ontogeny, general observations.	Ginkgo
1947	Müller	General observations	Fagus
1949	Gunckel & Coworkers	Shoot expression; auxin relations (physiological)	Ginkgo
1949	Swamy and Bailey	General observations; short shoot anatomy	Cercidiphyllum
1954 1955	Sacher	Shoot apex	Pinus spp.

TABLE 1-2 (Cont'd.)

YEAR	WORKER	ASPECT OF STUDY	PLANT MATERIAL(S)
1955	Titman and Wetmore	Shoot expression auxin relations; anatomy	Cercidiphyllum
1956	Wetmore	Anatomy	Ginkgo
1960	Dasanayake	Morphogenesis	Pteridium aquilinum
	Critchfield	Heterophylly; shoot growth	Populus trichocarpa
	Frampton	Developmental anatomy	Larix decidua
1961	Gottlieb	Morphogenesis	Pteridium
1964	Ginzburg and Reinhold	Physiology of short shoot buds	Pinus halepensis
1965	Clausen and Kozlowski	Heterophylly	Betula papyrifera
1966	Kozlowski and Clausen	Shoot growth	Betula papyrifera
1967	Clausen and Kozlowski	Seasonal growth features	Larix laricina
	Hanawa	Growth and development of dwarf shoots	Pinus densiflora
	Smith	Leaf dimorphism	Liquidambar styraciflua
1970	Critchfield	Heterophylly; shoot growth	Parthenocissus Ginkgo
	Sokolova and Ghosh	Anatomy	Malus domestica
1971	Critchfield	Heterophylly; shoot growth	Acer
1973	Ghosh	Long shoot-short shoot photosynthesis	Malus domestica
1974	Hoddinott & van Zinderen Bakker	Photosynthesis; short shoot-long shoot leaf anatomy	Ginkgo
1979	Owens and Molder	Bud growth, anatomy	Larix
1980	Gregory	Heterophylly; shoot expression and growth; Terminal bud anatomy	Acer saccharum

TABLE 1-2 (Cont'd.)

YEAR	WORKER	ASPECT OF STUDY	PLANT MATERIAL(S)
1982	Isebrands & Nelson	Branch morphology	*Populus* clone
	Maillette	Bud growth and branch morphology	*Betula pendula*
	Nelson & Michael	Photosynthesis	*Populus*
	Powell & coworkers	Heterophylly; general observations	*Acer*
	Steingraeber	Heterophylly; general observations	*Acer*
	Tuomi & coworkers	Reproductive cost	*Betula pendula*
1983	Macdonald & Mothersill	Organogenesis of short shoots	*Betula papyrifera*
	Caesar & Macdonald	Reproductive Cost in short shoots; growth analysis	*Betula papyrifera*
	Macdonald & coworkers	Long shoot organogenesis	*Betula papyrifera*

as in Ginkgo (Gunckel and Thimann 1949; Gunckel et al. 1949) and Cercidiphyllum (Titman and Wetmore 1955) with emphasis on auxin relations. In the light of recent understanding of hormonal control of plant growth it seems unlikely that auxins alone are the determining factors in regulating long shoot-short shoot growth. Other hormones e.g. gibberellins and cytokinins, as well as nutrients and water availability, may be involved. Factors which inhibit stem elongation also may be implicated in the short shoot habit (Sachs 1965).

Comparative anatomical studies of long and short shoots have received little attention, and, in general, they lack the details reported here. Most previous studies, especially on gymnosperms, emphasized shoot apical comparisons (Gunckel and Wetmore 1946a, 1946b; Titman and Wetmore 1955; Cutter 1965; Zimmermann and Brown 1971; Owens and Molder 1979) in which differences in pith rib meristematic activity were reported. Hoddinott and van Zinderen Bakker (1974) and Ghosh (1976) have compared leaf anatomy qualitatively for Ginkgo and quantitively for Malus, respectively. A few studies have been reported for ferns (Webster and Steeves 1958; Gottlieb 1961, 1962). In addition to differences in rib meristematic activity, Owens and Molder (1979) have recently pointed out differences in apical dome size and vigour in Larix occidentalis

prior to dormancy. However, Cutter (1965) in her review, has remarked that the apices of long and short shoots are "anatomically the same". In the case of Cercidiphyllum (Titman and Wetmore 1955), she contends that the apices are "histologically alike". Betula species have not been described. Organogenic studies (Macdonald and Mothersill, 1983; Macdonald et al. 1983) have revealed that the potential for a bud developing as a long shoot is predetermined the year before flushing, as early as mid-July, when a slight extension of internode 4 and internode 5 may be evident in long shoot axillary buds.

Developmental anatomical studies and the anatomical basis for development of long and short shoots of Betula papyrifera Marsh are unknown. Garrison's work (1949) did not compare the anatomy of long and short shoot buds. Her studies involved the successive developmental phases of axillary buds of B. papyrifera and Euptelea polyandra with respect to the sequence of procambium, phloem and xylem differentiation during bud formation. She made no distinction between potential long shoot axillary and potential short shoot axillary buds, although it is clear that she used axillary buds on a long shoot. Since potential short shoot axillary buds do not carry secondary axillary buds (bud primordia in the axils of leaf primordia within a primary bud), as revealed by organogenic studies (Macdonald and Mothersill 1983; Macdonald et al. 1983),

it seems probable that Garrison (1949) examined pseudoterminal, i.e., long shoot buds.

Growth analysis techniques are used in this study to compare long and short shoot growth, as well as vegetative and reproductive shoot growth in order to correlate morphological and anatomical differences. The development of plant growth analysis stems mainly from Gregory (1918) and Blackman (1919) as well as studies by Briggs and co-workers (Briggs et al. 1920a, 1920b). The primary concepts as defined by West et al. (1920) still remain the basis of growth analysis (Radford 1967; Evans 1972; Hunt 1978). The concept has largely been employed by horticulturists and foresters. Most of the earlier studies employed destructive sampling procedures, involving whole plants and trees (all leaves, stems and roots). As noted by Ledig (1974), classical growth analysis was not applied to forest species until recently, "because of the obvious difficulties in harvesting and weighing large trees". Thus, such applications have been restricted to seedling stages (e.g. Rutter 1957; Sweet and Wareing 1968a, 1968b; Ledig and Perry 1969; Madgwick 1971). It is my belief that growth analysis of twigs utilizing appropriate sampling and modelling techniques could yield useful data, without destroying the trees. This study is an evaluation of shoot growth utilizing some of these techniques as a basis

for correlating and/or explaining morphological and anatomical differences between long and short shoots of paper birch. A comparison of vegetative and reproductive growth is also made. Growth analysis of long and short shoots using classical growth indices has not been reported.

Objectives

The primary objectives of this research were:

1) To compare long and short shoot growth utilizing growth analysis techniques.
2) To describe the general morphology of long and short shoots and to compare them using morphometric analysis.
3) To compare vegetative and reproductive shoot growth and to assess the cost of reproduction.
4) To study the inception and apical organization of potential long and short shoot buds at selected stages of development and ascertain any differences.
5) To compare the anatomy of long and short shoots, with emphasis on stem anatomy.
6) To correlate these data in order to develop an understanding of how long and short shoot

growth in paper birch relates to other studies of long and short shoots.

The results/observations and discussion, with appropriate introductory paragraphs pertaining to specific portions of this study are presented as separate chapters. A general summary chapter will collate and discuss the pertinent findings. This format is adopted to enhance convenience of presentation and readability since some of the chapters have been submitted for publication.

CHAPTER 2

CHAPTER 2

MATERIALS AND METHODS

Twigs (i.e., developing branches and their buds) were collected twice a week in April - August, 1981 and 1982 from open-grown 40 year-old paper birch (Betula papyrifera Marsh.) trees situated in the Aboretum of Lakehead University. During September collections were made once a week in both years. These trees, together with others of comparable age in Fort William and Port Arthur locations, were examined for branching patterns and flushing sequences during the same period. In all 11 trees comprising 3 juvenile (20-year-old) and 8 older trees (40 years-old or more) were studied. Samples were collected from the Aboretum trees from branches maximally exposed to sunlight, from the mid-crown region. It is assumed that leaves were mostly sun-leaves, since leaf thickness is affected by shading (Jackson 1967). Both one-year-old long and short shoots growing on the previous year's long shoots are more exposed to light than older short shoots, due to position within the crown.

Determination of leaf shape

Leaf shape was determined according to the classification of Radford et al. (1974).

Determination of leaf area

An Apple II plus microcomputer equipped with a

digitizer was used to determine leaf areas from photocopies of fully expanded leaves (Caesar and Macdonald 1983), by tracing outlines on to a graphics tablet. Freshly collected samples and material fixed in formalin-acetic acid-alcohol were used for the various quantitative analyses. To supplement data in the case of plastochron determination in long shoots, five pseudoterminal buds were tagged during winter 1982 and leaf measurements were recorded daily in a non-destructive manner after leaf emergence. These data complemented those of fixed material. Preliminary investigations indicated that dry weight of material was not significantly affected by fixation. Leaf size was not affected either. Shrinkage of fixed leaves was 1.70 ± 0.75% of fresh leaf size and it depended on leaf size. To alleviate any unwarranted problem of further shrinkage during the recording of measurements, leaves of fixed material were placed between two large microscope slides and photocopied immediately. Leaves which were too small, as at the time of dissection, were outlined by means of a camera lucida attached to a Zeiss microscope before area was determined by the computer technique.

Determination of dry weight

Dry weight of buds, leaves and stems were obtained by drying

to constant weight in an oven at 70°C. For developmental analyses, 15 - 28 randomly selected buds were used for dry weight determinations for each collection date from April 21 to June 15 in 1982. Comparable data for 1981 was restricted to May 15 to May 29, the period most sensitive to annual variations, if any. For each collection the buds were partially dissected to determine whether they were reproductive or vegetative. Sample size of leaves was more than twice the sample size of buds (i.e. $n > 30$), in short shoots, since a number of short shoot buds (25%) possess 3, or even 4, preformed foliage leaves (early leaves). In long shoots minimum sample size was 30 since they usually possess two early leaves. Long shoots which were transformed from short shoots usually (approximately 20% cases) may possess, 3 or 4 early leaves. This is possibly due to prior short shoot determination before transformation into long shoot was induced. All of these long shoots, however, were not included in short shoot/long shoot comparisons.

Growth analysis

The following growth indices were used as a basis for comparing long and short shoots and vegetative and reproductive short shoots: relative growth rate of buds (Bud-RGR); relative leaf growth rate (Leaf-RGR); Stem:leaf ratio (SLR); Stem weight ratio (SWR); relative growth rate

of stem (Stem-RGR); stem dry weight increment (SDWI); leaf area ratio (LAR); leaf weight ratio (LWR); Specific leaf area (SLA); Specific leaf weight (SLW);Unit leaf rate (ULR) or net assimilation rate (NAR). In addition, leaf, petiole and internode lengths were determined during expansion for long and short shoot comparisons. Leaf-RGR (based on leaf dry weight or leaf area), SLA, SLW, LAR, and LWR were derived from standard formulae of Evans (1972) and Hunt (1978). Based on RGR derivations of Evans and Hunt, Bud-RGR and Stem-RGR were formulated using dry weights of buds and stems, respectively.

The following formulae were used:

1. $$\text{Bud-RGR} = \frac{1}{Wb} \cdot \frac{dWb}{dT} = \frac{\log_e Wb_2 - \log_e Wb_1}{T_2 - T_1}$$

Wb - bud dry weight; T - time in days.

2. $$\text{Stem-RGR} = \frac{1}{Ws} \cdot \frac{dWs}{dT} = \frac{\log_e Ws_2 - \log_e Ws_1}{T_2 - T_1}$$

Ws - stem dry weight; T - time in days.

3. (a) $$\text{Leaf-RGR} = \frac{1}{WL} \cdot \frac{dWL}{dT} = \frac{\log_e WL_2 - \log_e WL_1}{T_2 - T_1}$$

WL = leaf dry weight; T - time in days.

(b) $$\text{Leaf-RGR}^* = \frac{1}{LA} \cdot \frac{dL}{dT} = \frac{\log_e LA_2 - \log_e LA_1}{T_2 - T_1}$$

LA - leaf area; T - time in days.

4. $SLR = \frac{Ws}{WL}$

5. $SWR = \frac{Ws}{W_{SL}}$ where W_{SL} is stem + leaf dry weight

6. $LAR = \frac{LA}{W_{SL}}$

7. $LWR = \frac{WL}{W_{SL}}$

8. $SLA = \frac{LA}{W_L}$

9. $SLW = \frac{WL}{LA}$ or $SLW = \frac{1}{SLA}$

10. $ULR^1 = \frac{\text{Leaf-RGR}}{LAR}$

The complete list of growth analysis abbreviations and definitions are summarized in Table 2-1.

In determinations of SLR and SWR of each bud, bud scales were not included in dry weights.

Allometry

Allometry, as defined by Hunt (1978), is "the study of the growth and development of one part of an organism in relation to another". Allometric growth, otherwise termed heterogonic growth (Hammond 1941), is based on Huxley's (1932) formula $y = bx^k$, the main developments being

[1] Although I am aware of the limitations and inherent errors in this instantaneous derivation of ULR (Evans 1972; Hunt 1978) I have used it only to provide a rough estimate of what I would term "Bud-ULR".

TABLE 2-1. List of growth analysis abbreviations.

SYMBOL	DEFINITION	EVANS (1972) AND HUNT (1978) CONNOTATION	UNITS
Bud-RGR	Mean relative growth rate of a bud		day^{-1}
Stem-RGR	Mean relative growth rate of a stem		day^{-1}
Leaf-RGR	Mean relative growth rate of a leaf based on leaf weight	$\bar{R}$	day^{-1}
Leaf-RGR*	Mean relative growth rate of a leaf based on leaf area	$(\bar{R}A)$	day^{-1}
SLR	Ratio of stem dry weight to leaf dry weight		dimensionless
LAR	Leaf area per shoot dry weight	LAR (=F)	$cm^2 \cdot g^{-1}$
SWR	Stem to shoot dry weight ratio	SWR	dimensionless
SLA	Specific leaf area; leaf area per unit leaf dry weight	SLA	$cm^2 \cdot g^{-1}$
SLW	Specific leaf weight; leaf weight per unit leaf area; reciprocal of SLA	SLW	$g \cdot cm^{-2}$
LWR	Leaf weight ratio; the ratio of leaf weight to shoot weight	LWR	dimensionless
ULR(=NAR)	Unit leaf rate otherwise termed net assimilation rate; ratio of leaf-RGR to LAR; an approximate measure of the efficiency of leaves as producers of new photosynthetic material	E	$g \cdot cm^{-2} \cdot day^{-1}$

due to Pearsall (1927, cited by Hunt 1978) and Troughton (1955, cited by Hunt 1978). In the formula x and y are the two dimensions of the organ (e.g. leaf length and leaf width, or leaf weight and stem weight), k is the constant ratio between their growth rates, and b is a constant representing an initial relation between the dimensions.

Striking differences between lamina length to width ratios of long and short shoot early leaves as well as late leaves of long shoots influenced my applying the allometric formula. Consequently, it was useful to analyse the growth relations between stem and leaf, petiole length and lamina length, leaf area and leaf weight, and shoot dry weight and total early leaf area in the manner used by Whitehead and Myerscough (1962).

The following formulae and their logarithmic transformations were used:

1) $LW = bLL^k$

$\log LW = \log b + K \log LL$ where LW and LL are lamina width and length, respectively.

2) $SDW = bLDW^k$

$\log SDW = \log b + K \log LDW$ where SDW and LDW are stem and leaf dry weight respectively.

3) $PL = bLL^k$

$\log PL = \log b + K \log LL$ where PL is petiole length, and LL as in equation 1.

4) $LA = bLDW^k$

$\log LA = \log b = K \log LDW$ where LA is leaf area and LDW is leaf dry weight as in equation 2.

This concept was also used to evaluate the anatomical relationship between wood and bark formation in one-year-old long and short shoots, using the formula:

$$X_R = bB_R^k$$

$\log X_R = \log b + K \log B_R$ where X_R and B_R are xylem and bark radii, respectively.

The K values were obtained using regression analysis of log transformations and were compared for statistical differences based on regression (Sokal and Rohlf 1981).

Leaf and internode extension

Buds collected from April to August were used. Prior to flushing, buds were dissected in 70% alcohol, and

the leaf lengths and subjacent internodes were measured using a dissecting microscope calibrated to the nearest 0.1 mm. After leaves and internodes had attained lengths of 1 cm they were measured by means of a ruler to the nearest 0.5 mm. In all, a minimum of 16 and a maximum of 22 buds were measured for each collection date in 1981 and 1982, except for the April collections in which sample size averaged 10 buds (8 - 13 buds). To complement these measurements, ten each of long shoots and short shoots were tagged on a younger tree (about 25 years old) and the leaf lengths and internodes were measured every two days. Data from both methods were found to be similar.

Morphometric measurements and analyses

Fully mature organs were used in all morphometric measurements. The following were measured:

1) leaf area (early and late leaves)
2) lamina length to width ratio
3) number of side nerve pairs
4) number of serrations per unit length of leaf margin
5) petiole length
6) petiole dry weight
7) internode length
8) bud dry weight per node

9) specific leaf area

10) total early leaf area per node of n + 2 year old long shoots

11) lamina length to petiole length ratio.

Histological methods

Material fixed in FAA was washed in 70% ethanol prior to dehydration in tertiary butyl alcohol (TBA) series (Johansen 1940). After dehydration material was infiltrated with Paraplast (MP. 58 - 61°C) at 60°C in an oven for 2 - 3 days. Material was subsequently embedded in disposable Tissue-Tek embedding rings on a Tissue-Tek II thermoelectric embedding centre (Fisher Scientific Co., Ltd), and kept in a refrigerator at 4°C until ready for sectioning.

Transverse and longitudinal sections (4 - 10 μm) were made with an American Optical 820 rotary microtome. Sections were floated on to Corning micro-slides (thickness 0.96 - 1.06 mm) in 3% Formalin. Slides were precleaned in 100% entanol and then pretreated with Haupt's adhesive (Johansen 1940; Jensen 1962) to hold sections on to slides. These were then placed on a Precision Scientific Company slide warmer at 35° to 40°C. Slides were stored in slide boxes until ready for staining.

The following histological stains of BDG and Fisher Scientific Company grades were used:

a) Safranin

b) Fast Green

c) Orange G

d) Toluidine blue O

e) Tannic acid

Safranin-Fast green combination of the composition given by Johansen (1940) and Sharman's (1943) tannic acid-iron alum with Safranin and orange G were used. For rapid staining,the polychromatic toluidine blue O stain was used (Sakai 1973). A combination of Sharman's (1943) technique counterstained for 5 seconds in Fast green, was also found to give excellent contrast. Original staining schedules (Johansen 1940; Sharman 1943) were modified to obtain desirable results. Stained sections were routinely mounted in permount.

Photomicrography

A Zeiss microscope fitted with a camera mount was used. Kodak technical pan film 2415 with different stain-filter combinations depending on type of stain was employed. Films were developed to maximum contrast using Kodak HC-110 developer, dilution D, for 6 minutes. Silhouette drawings of bud composition were obtained with the aid of a Zeiss camera lucida. In the case of mature leaves, as in Fig. 4-3a draw-

ings were made directly from photocopies.

Comparative anatomical analysis

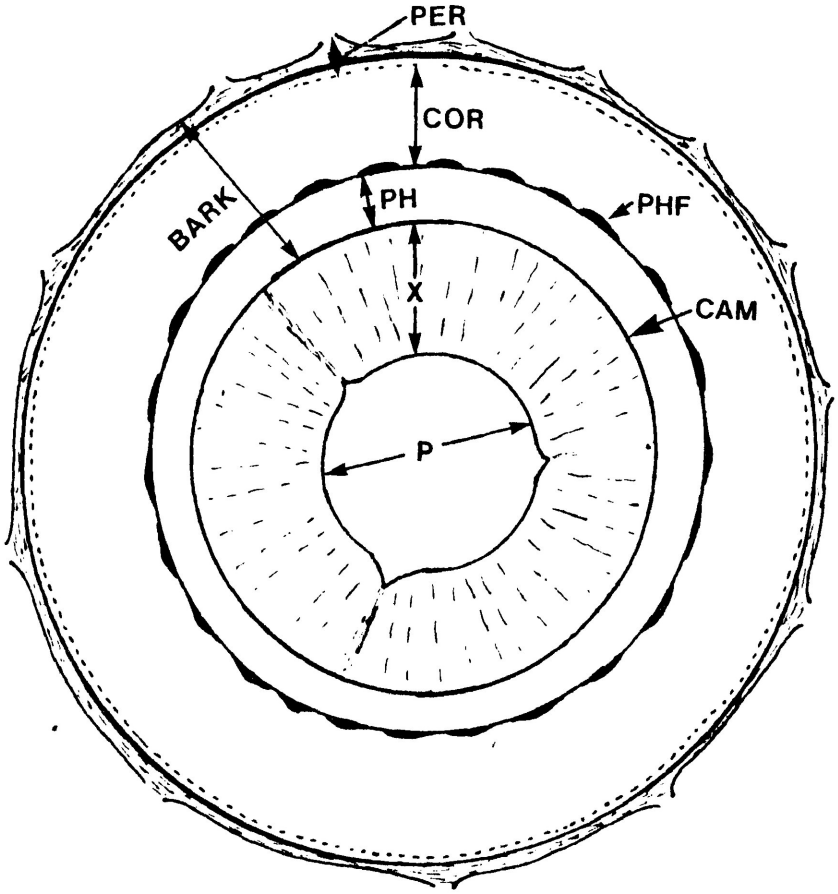
To compare shoot apical organization transverse and longitudinal sections of potential long and short shoot buds (n+1 year-old) were used in addition to terminal short shoot buds (n+2 to n+5 years). Both shoots had a 2/5 phyllotaxy. It was also noted that the rudimentary leaves of the current season's growth occurred on the same orthostichies as previous year's rudimentaries in older short shoots.

The following anatomical characters were observed qualitatively or quantitatively to compare internode 2 of n+2 year old long and short shoots and internode 4 of older short shoots, after the internodes have ceased to elongate:

1) wood to bark ratio (wood radius divided by bark radius)
2) radial diameter of xylem vessels
3) secondary xylem radial width
4) secondary phloem radial width
5) diameter of pith
6) mean diameter of pith parenchyma cells
7) radial width of cortex
8) periderm width

See Fig. 2-1 for locations of measurements.

FIG. 2-1. Locations of various anatomical features measured.



ABBREVIATIONS:

PER	:	PERIDERM	
COR	:	CORTEX	
PH	:	PHLOEM	SECONDARY TISSUE
X	:	XYLEM	
CAM	:	CAMBIUM	
PHF	:	PHLOEM CAP FIBRES	
P	:	PITH	

Statistical analysis

Standard parametric statistical techniques were used as described by Snedecor and Cochran (1980), Parker (1973) and Sokal and Rohlf (1981). To compare the various growth characteristics, morphometric and anatomical data, Student's t-test ($p = 0.05; 0.01; 0.001$) and analysis of variance were calculated for each data set. Where F-ratios indicated that the homogeneity of variance did not hold, a conservative t-test (Snedecor and Cochran 1980) was used. In the case of allometric relationships, transformation of data to natural logarithms (Hunt 1978; Sokal and Rohlf 1981) was desirable in order to obtain linear relationships between variables in addition to stabilizing residual variance between respective growth and morphometric measurements.

Linear regressions were run comparing various attributes e.g. lamina length : width, bud weight : node number etc. of long and short shoots as well as vegetative and reproductive shoots. Significant linear regressions were determined using Student's t-test and analysis of variance ($p = 0.05; 0.01; 0.001$). Slope of the regression different from zero was tested using analysis of variance at $p = 0.01$.

CHAPTER 3

CHAPTER 3

COMPARISONS BETWEEN MORPHOLOGY, GROWTH CHARACTERISTICS AND EXPRESSION OF VEGETATIVE LONG AND SHORT SHOOTS.[1]

Introduction

Paper birch, Betula papyrifera Marsh., is one of a number of temperate woody species which bear two distinctly different shoot types broadly classified as long and short shoots (Clausen and Kozlowski 1965; Kozlowski and Clausen 1966). Either may be vegetative or reproductive. Long shoots tend to be predominant in the upper crown (Kozlowski 1971; Maillette 1982a) and short shoots are more common in the lower crown. Furthermore, juvenile trees bear more vigorous long shoots than older trees. The proportion of the long shoots decreases with tree age, which has also been clearly demonstrated for Ginkgo (Gunckel and Wetmore 1949) and Fagus (Müller 1947). In the latter, the percentage of leaves borne on short shoots increased with age from 55% in 24-year-old trees to 92% in an 83-year-old tree.

[1]Most of the growth data in this chapter have been submitted for publication in the Canadian Journal of Botany as:

a) Macdonald, A. D., D. H. Mothersill and J. C. Caesar. Shoot development in Betula papyrifera III. Long shoot organogenesis; and,

b) Caesar, J. C. and A. D. Macdonald. IV. Comparisons between growth characteristics and expression of vegetative long and short shoots.

What, then, determines the long and short shoot habit and when during bud development can the distinction be seen? Is determination of a bud a pre- or post-dormancy phenomenon? Finally, how can bud growth be related to the differences in shoot types?

Studies on long and short shoots are comparatively few. The majority of them relate to anatomy (e.g., Foster 1938; Gunckel and Wetmore 1946a, 1946b; Rouffa and Gunckel 1951; Titman and Wetmore 1955; Zimmermann and Brown 1971; Owens and Molder 1979) as well as shoot expression in Ginkgo (Gunckel et al. 1949; Critchfield 1970a), Cercidiphyllum (Swamy and Bailey 1949; Titman and Wetmore 1955), Fagus (Müller 1947, 1954), Larix (Frampton 1960; Clausen and Kozlowski 1967, 1970; Owens and Molder 1979), Acer (Schüepp 1929; Critchfield 1971; Fischer 1977; Metzger 1977; Gregory 1980; Powell et al. 1982), Betula (Clausen and Kozlowski 1965; Kozlowski and Clausen 1966; Metzger 1977; Maillette 1982a), Pinus (Dickson 1886; Doak 1935; Sacher 1955; Hanawa 1967; Kozlowski 1971; Zimmermann and Brown 1971), Populus (Critchfield 1960; Kozlowski and Clausen 1966; Maini 1966a, 1966b; Isebrands and Nelson 1982), Parthenocissus (Millington 1963; Critchfield 1970b; Moore 1975), Liquidambar (Smith 1967; Zimmermann and Brown 1971; Lam III and Brown 1974), Magnolia (Postek and Tucker 1982), and Malus (Felber 1948; Pratt et al. 1959).

In addition to these, Bügsen and Münch (1929) have discussed aspects of the two shoot types in some of the above species as well as in Quercus, Fraxinus, Ulmus, Berberis, Prunus and Rhamnus carthatica L. Some of these studies concentrated on aspects of heterophylly (e.g., Critchfield 1960, 1970b, 1971; Kozlowski and Clausen 1966; Kozlowski 1971; Curtis and Lersten 1978; Gregory 1980; Powell et al. 1982; Steingraeber 1982). Although in many of these studies growth of leaves and internodal extension are described, none of them evaluates growth indices such as relative growth rate, specific leaf area, leaf area ratio, leaf weight ratio, etc., from a developmental perspective. Nelson and Michael (1982) recently reported studies on specific leaf weight (SLW) in mature leaves only, with respect to photosynthetic rate and leaf conductance in long and short shoots of a Populus hybrid clone. Similar variations in leaf size and specific leaf weight between long and short shoots of Populus has recently been reported (Isebrands and Nelson 1982).

This study reports general observations on shoot morphology, bud organography and shoot expression utilizing 1) growth analysis procedures, and 2) morphometric measurements to establish differences between the two shoot types in paper birch.

Observations and Discussion

Gross morphology

Morphologically, paper birch, B. papyrifera Marsh., possesses two distinctly different shoot types, broadly classified as long and short shoots. Long shoots (Fig. 3-1a) have extended internodes (0.5 to about 5.0 cm) and short shoots (Fig. 3-1b), which fail to elongate more than a few millimetres, rarely exceed 4 cm in length after 10 years. Only one-year-old long shoots and short shoots of all ages bear leaves directly on their axes. Long shoots bear two sets of foliage leaves, "early" leaves and "late" leaves; and short shoots form only "early" leaves. Consequently, long shoots are termed heterophyllous shoots (Clausen and Kozlowski 1965). In contrast to Magomedmirzaev (1970) who describes 4 types of shoots, 6 subcategories of long and short shoots may be identified in B. papyrifera. These are: 1) vegetative long shoots with late shoot tip abortion (shoot tip abortion occurring from August till the end of the growing season) (Fig. 3-2a); 2) long shoots which exhibit early shoot tip abortion i.e., in late June - early July (Fig. 3-2b, d); 3) reproductive long shoots in which the terminal vegetative apex is transformed into the male inflorescence apex

FIG. 3-1a. Long shoot showing early leaves, late leaves, and extended internodes.

FIG. 3-1b. Vegetative (b_1) and reproductive (b_2) short shoots. Note larger and widely ovate leaves associated with vegetative shoots. Reproductive shoots have smaller and elliptical leaves. A branched short shoot system is shown.

3-1a

3-1b

FIG. 3-2. x0.5. Drawings of various categories of long shoots with leaves removed.

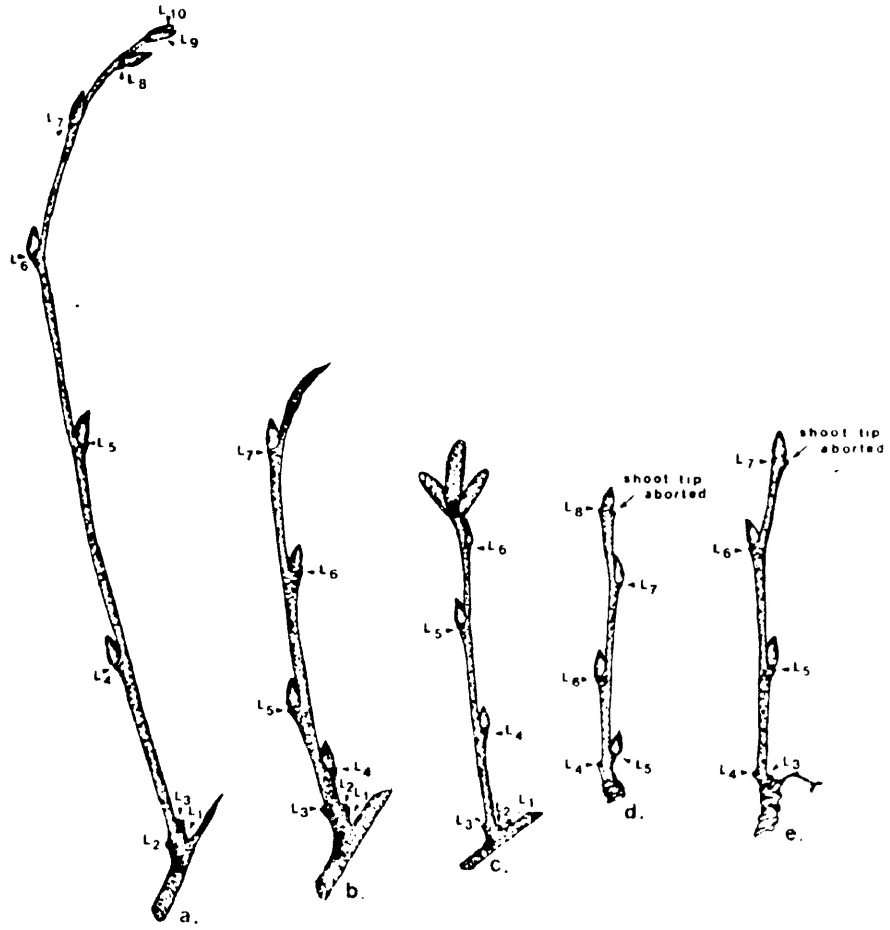
a. vigorous long shoot with terminal cluster of small unexpanded late leaves.

b. long shoot with aborted shoot tip due to insect damage (see Fig. 3-7).

c. male reproductive long shoot.

d. long shoot formed terminally on a previous year's short shoot.

e. long shoot which developed from an axillary bud on a previous year's reproductive short shoot.


L10
L9
L8
L7
L6
L5
L4
L3
L2
L1
a.
L7
L6
L5
L4
L3
L2
L1
b.
L6
L5
L4
L3
L2
L1
c.
shoot tip aborted
L8
L7
L6
L5
L4
d.
shoot tip aborted
L7
L6
L5
L4
L3
e.

3-2

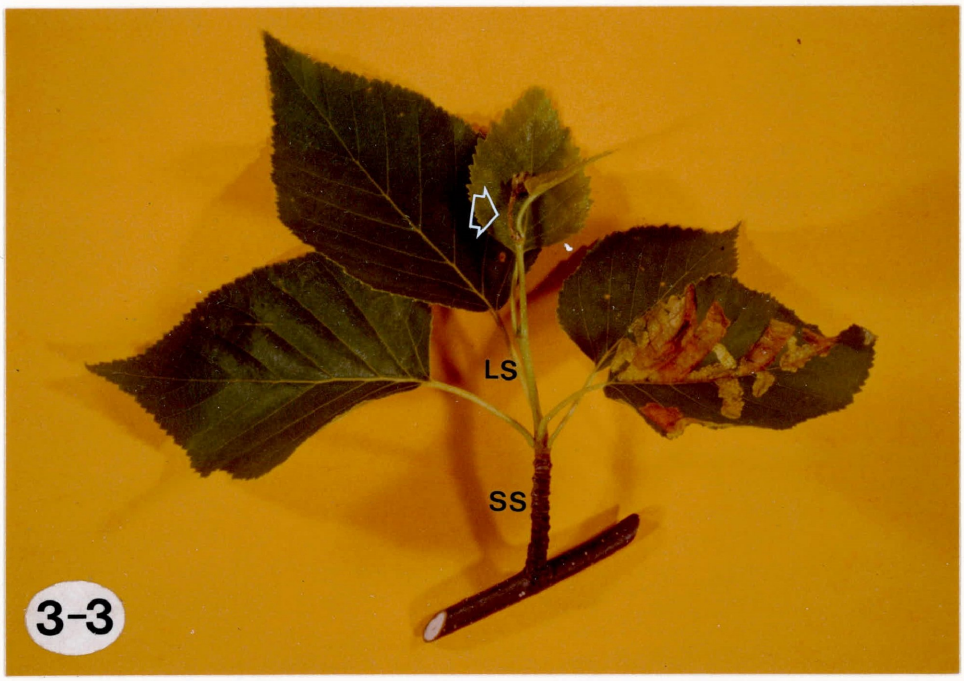
(Fig. 3-2c); 4) vegetative short shoots (Fig. 3-1b$_1$); 5) reproductive short shoots with terminal female inflorescence (Fig. 3-1b$_2$), and 6) short shoots which metamorphose into long shoots (Figs. 3-2d and 3-3).

Only long shoots bear more than one bud, which are all axillary; there is no true terminal bud because shoot tip abortion occurs. Thus, the last formed axillary bud becomes the presumptive terminal, hence it is referred to as the pseudoterminal. Reproductive long shoots have one terminal male inflorescence and 1 - 3 distal, axillary inflorescences. Short shoots on the other hand develop a single terminal bud as a rule. However, axillary buds develop only when the terminal apex is transformed into a female inflorescence apex. Such short shoots have a greater internodal extension between early leaves than comparable vegetative shoots. What triggers the slight internodal extension is not known. Two axillary buds may occur in female short shoots in the axils of each early leaf.

Bud organography

In B. papyrifera axillary buds are borne in all leaf axils of long shoots except leaves 1 (a rudimentary leaf) and usually 2 and 3 (early leaves). Leaf position on an axis is described in acropetal sequence as L_1, L_2, L_3... etc. Occasionally, the early leaves may bear small

FIG. 3-3. Long shoot developed from terminal vegetative bud of an eight-year-old short shoot - note the cluster of four early leaves at the base. Also note browning of distal internode (arrow), onset of shoot tip abortion.

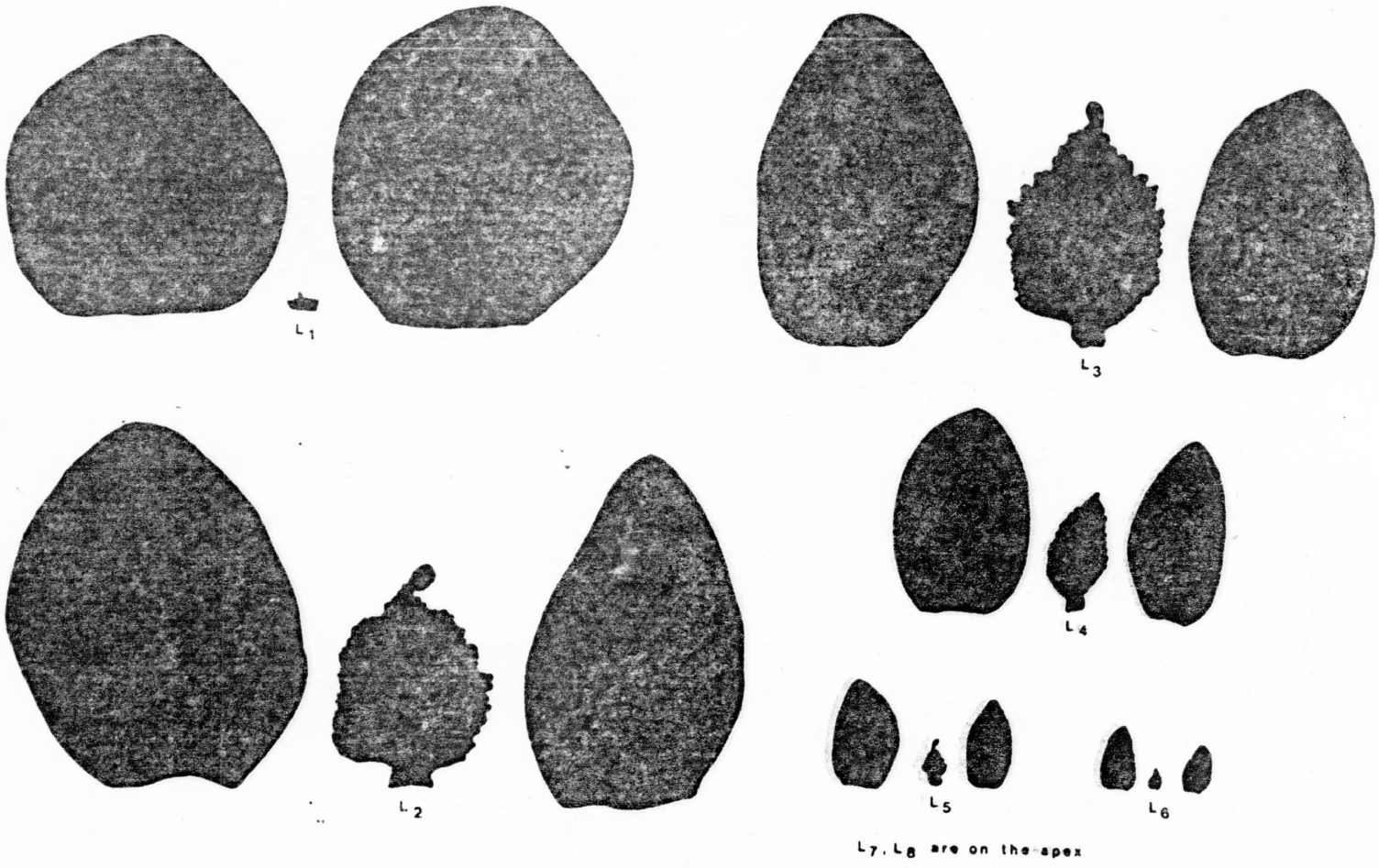

LS
SS
3-3

abortive buds in their axils. In a centripetal order, that is, in acropetal sequence, axillary buds on a long shoot have the following characteristics: 1 stipulate rudimentary leaf, 2 large embryonic foliage leaves with stipular bud scales, 1 small embryonic leaf with stipules, three progressively smaller leaf primordia with attached stipules and a leaf buttress (Fig. 3-4). On a long shoot distal buds usually develop into long shoots and proximal buds flush as short shoots. Therefore, based on position these buds are termed potential long shoots and potential short shoots, respectively. Both bud types have the same bud composition except a fewer number of leaf primordia in potential short shoot buds. Before the end of the growing season, however, potential long shoot buds exhibit a slight expansion of the internodes between L_3 - L_4 and L_5 - L_6, the presumptive late leaves (Fig. 3-5). This is first noticeable upon dissection in mid-July (Macdonald and Mothersill 1983; Macdonald et al. 1983). A slight internodal expansion has similarly been observed prior to the end of the growing season in long shoots of Larix (Owens and Molder 1979). Thus for buds of comparable age, potential long and short shoot buds (n + 1 year-old) have similar bud composition and characteristics and differ only in that long shoot buds exhibit 2 - 3 slightly expanded internodes and 1 - approximately 3 additional leaf primordia.

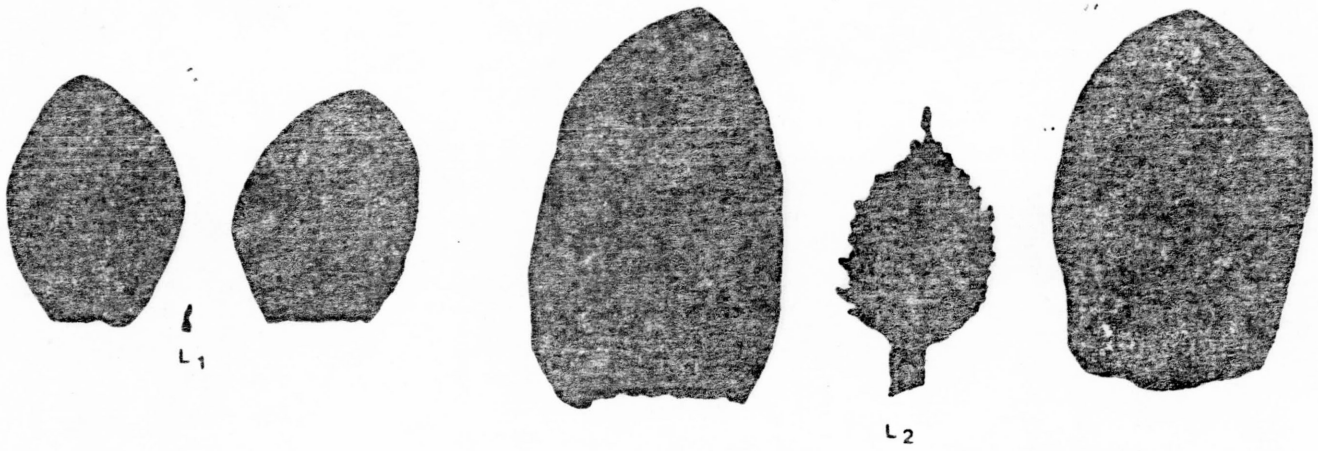
FIG. 3-4. X 9. Bud compositions of axillary long shoot buds.

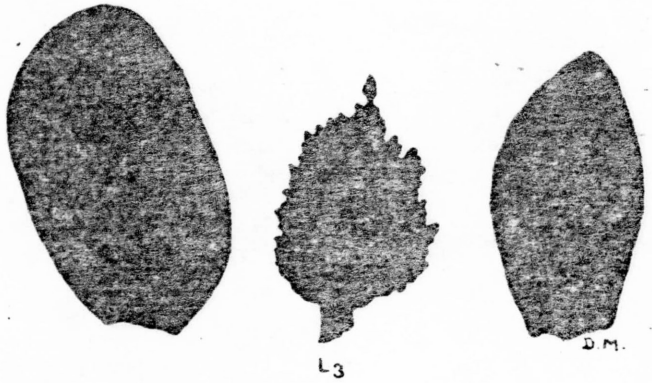
a. Composition of a vegetative bud situated distally on a long shoot i.e., potential long shoot bud. L_1, rudimentary leaf; L_2, L_3, embryonic foliage leaves; L_4, smaller embryonic foliage leaf; L_5, L_6, L_7, L_8, primordial foliage leaves.

b. Bud composition and aestivation of appendages of a proximally situated bud on a long shoot i.e., potential short shoot bud. L_1, rudimentary leaf; L_2, L_3, embryonic foliage leaves; L_4, L_5, L_6, primordial rudimentary leaves.



3-4A

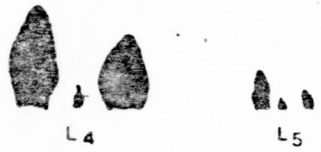




LEGEND

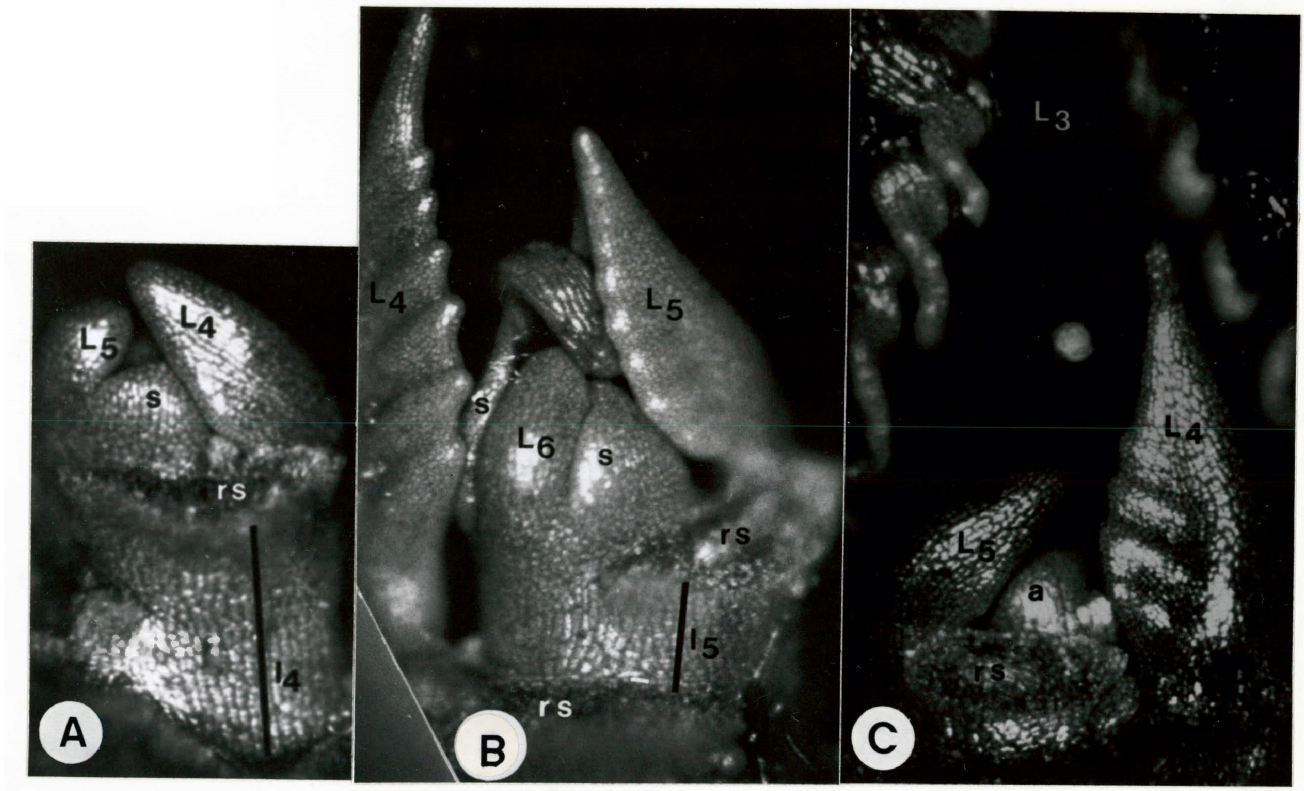
axis leaf stipule

3-4B



L_6 is on the apex

FIG. 3-5. Dissected buds of potential long and short shoots of 14 July 1981 collection showing relative internodal distances (from Macdonald et al. 1983).

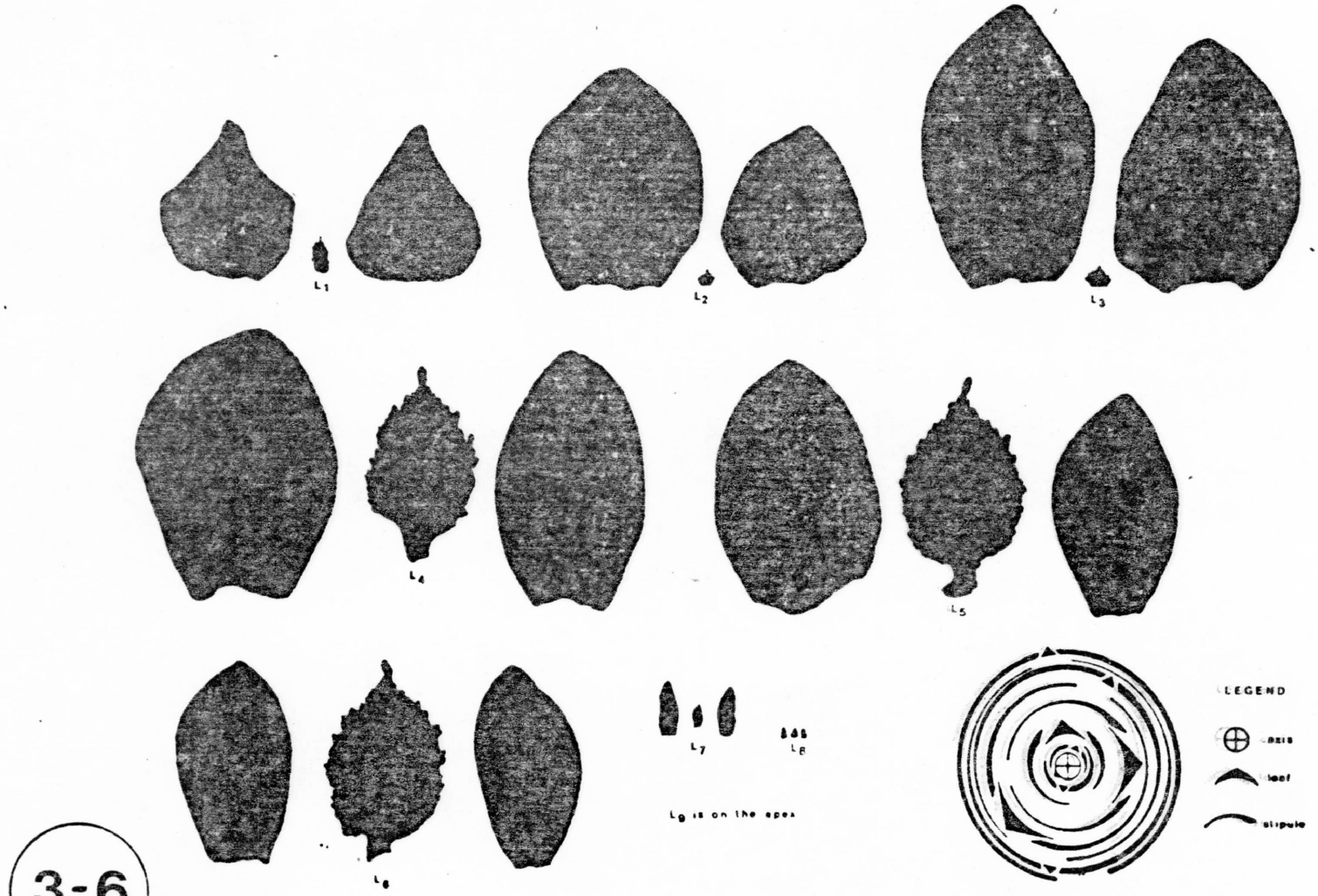

L5
L4
s
rs
l4
A
L4
L5
s
L6
s
rs
l5
rs
B
L3
L4
L5
a
rs
C

However, the terminal bud of older vegetative short shoots is different from potential long and short shoot buds, in that it has 3 rudimentary leaves with prominent stipular bud scales (instead of 1), 2 - 3 (rarely four) embryonic foliage leaves with stipules and three very small leaf primordia with stipules. These last primordia suffer lamina abortion and become the three rudimentary leaves of a subsequent year. Fig. 3-6 illustrates the aestivation. For a seven-node long shoot i.e., so-called "determinate" long shoots, bud size, as defined by the number of leaf primordia contained in the bud, increases acropetally. This may not be related to bud length as in Populus (Maini 1966a) and Acer (Metzger 1977). It is possible that in extremely long, long shoots, the most distal axillary buds i.e., at nodes 11, 12, 13 in a thirteen-node long shoot may have fewer primordia than other more developed potential long shoot buds immediately proximal to them. Does this relate to flushing sequence on a long shoot?

Shoot expression

Long shoots develop from distal axillary buds of a previous year's long shoot; short shoots form from proximal axillary buds of the previous year's long shoot, short shoot terminal and short shoot axillary buds

Fig. 3-6. X 6. Composition and aestivation of appendages of vegetative short shoot terminal buds. L_1, L_2, L_3, rudimentary leaves; L_4, L_5, L_6, embryonic foliage leaves; L_7, L_8, L_9, primordial rudimentary leaves.


L1
L2
L3
L4
L5
L6
L7
L8
L9 is on the apex
LEGEND
axis
leaf
stipule

3-6

(Macdonald et al 1983). Long shoots may also develop from terminal short shoot buds (long shoot metamorphosis) or axillary buds of reproductive short shoots.

In spring, it is the potential long shoot buds which flush first on previous year's long shoots, but this may be related to age and developmental stage of the buds. In extremely long long shoots flushing begins in the middle portion of the shoot, progressing first acropetally and then basipetally. The potential long shoots in the middle portion are definitely older and perhaps more developed than the most distal ones. The extent of branching subsequently depends on the vigour/length of the long shoot. The number of current-year long shoots on a previous year's long shoot is highly correlated with previous year's long shoot length or node number. For a sample of 115 vegetative long shoots the relation between the number of buds (X) on a previous year's long shoot and the number of current year long shoots (Y) which develop from them is:

$$Y = 0.48X + 0.87, \quad (r = 0.857;\ p < 0.001).$$

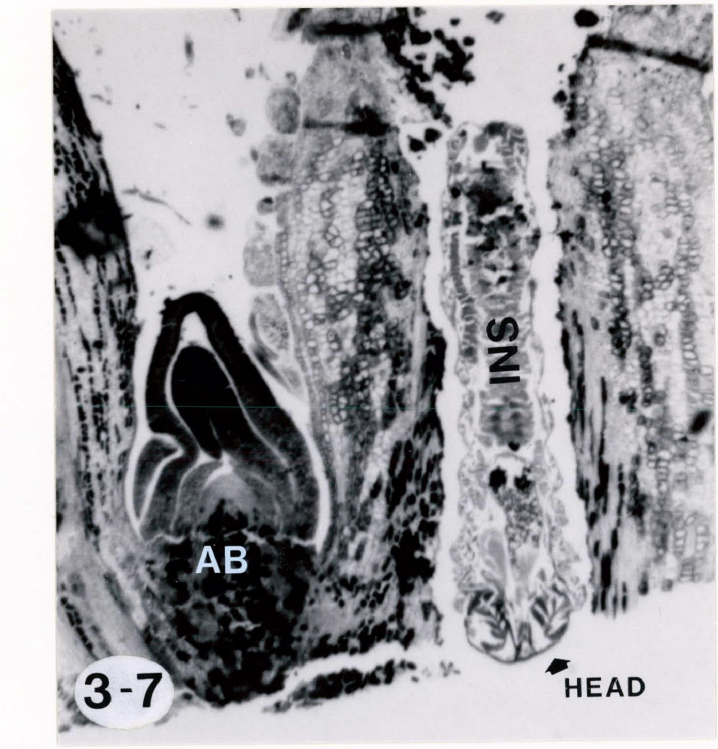
Mean number of buds on previous year's shoots was 8.8 ± 3.3 and mean number of buds which develop into long shoots was 5.1 ± 2.7. This implies that 44 to 64% of the buds have long shoot growth potential depending on the length of the parent long shoot.

In mature B. papyrifera trees used in this study, buds of both long and short shoots do not flush during the same season in which they are formed, that is, "sylleptic" branches (Hallé et al 1978) or "lammas" shoots (Kramer and Kozlowski 1960; Kozlowski 1971) do not occur. Thus axillary buds on mature paper birch trees produce only proleptic branches. Nevertheless, I have observed the induction, by pruning, of syllepsis in 40-year-old trees. Syllepsis has been observed in Populus species (Nelson et al 1979), silver birch (Maillette 1982a) and young paper birch (Caesar, unpublished observation). The same phenomenon which Champagnat (1965) terms "rameau anticipees" has been observed in very vigorous long, long shoots of juvenile trees. The vigour and branching potential of long shoots will determine crown expansion of individual trees and this presumably relates to photosynthetic potential (Macdonald et al 1983) and/or efficiency. Short shoots, as a rule, do not branch. However, when the short shoot terminal apex is transformed into an inflorescence apex, axillary buds are formed. Usually two axillary buds are formed in the axils of the early leaves but the one subtended by the first early leaf is smaller and aborts. Depending on the size and vigour of both axillary short shoot buds, both may flush as short shoots in the following year and result in a

branched short shoot (Fig. 3-1b). Müller (1947) did not, however, observe branched short shoots in beech.

Although long shoots determine crown size which may be related to photosynthetic turnover, on the other hand, shoot tip abortion and male inflorescence induction curtail long shoot vigour, reduce branching potential and therefore limit photosynthetic capacity (i.e., fewer late leaves occur on less vigorous long shoots hence smaller photosynthesizing area). Long shoots of birch frequently suffer shoot tip abortion (Millington 1963; Romberger 1963; Millington and Chaney 1973) as is typical of most indeterminate species (Kozlowski 1971) including paper birch (Marks 1975). The causes are probably chiefly insect damage (Fig. 3-7) and also water stress and/or other less understood physiological phenomena which Kozlowski (1971) refers to as "a natural characteristic of a wide variety of temperate zone woody plants". However, it is clear that the incidence of shoot tip abortion during the growing season is bimodal, with two peaks, one in late June-early July, and one in August. Perhaps the latter may be related more to water stress, an area which must be examined. The size or length of a long shoot is determined when shoot tip abortion occurs, or when the vegetative long shoot terminal apex is transformed into a male inflorescence apex. Invariably, reproductive long

FIG. 3-7. x 56. Insect damage of long shoot tip i.e., shoot tip abortion. Note insect larva (INS) with head in basipetal direction, lying in pith of main axis which has been eaten away. Axillary bud (AB) next to larva could be affected if damage is further basipetal. Cell contents of axillary bud stain intensely, and may indicate onset of bud destruction. (Section was stained with 0.25% Azure A and counterstained with 1% Rose Bengal).



3-7

shoots are shorter than vegetative types (Fig. 3-8), but they may be comparable (i.e., in length) to long shoots which suffer early shoot tip abortion. An extreme example is in Parthenocissus in which Millington (1963) has implicated shoot tip abortion as the cause of the short shoot habit. Although the physiological basis of shoot tip abortion is not understood, recent studies on the cessation of apical growth and concommitant shoot tip abortion in Salix (Juntilla 1976) indicate some hormonal correlations. In kinetin-treated control plants, 100 per cent occurrence of the abscission zone was observed in July, whereas in gibberellin-treated plants, abscission peaked in September (ie., end of the growing season). It is not known if Juntilla's results may have any bearing on the control mechanism of early and late shoot tip abortion in B. papyrifera.

Growth analysis

Growth of axillary buds on a long shoot before and after flushing differs from one node to the other. Most distally positioned axillary buds accumulate dry matter at a faster rate than buds proximal to them. Consequently, they have the highest Bud-relative growth rate (Bud-RGR) (Fig. 3-9). The axillary bud immediately proximal to the pseudoterminal bud grows faster than all

FIG. 3-8. Frequency distribution of lengths of various categories of mature shoots of paper birch.

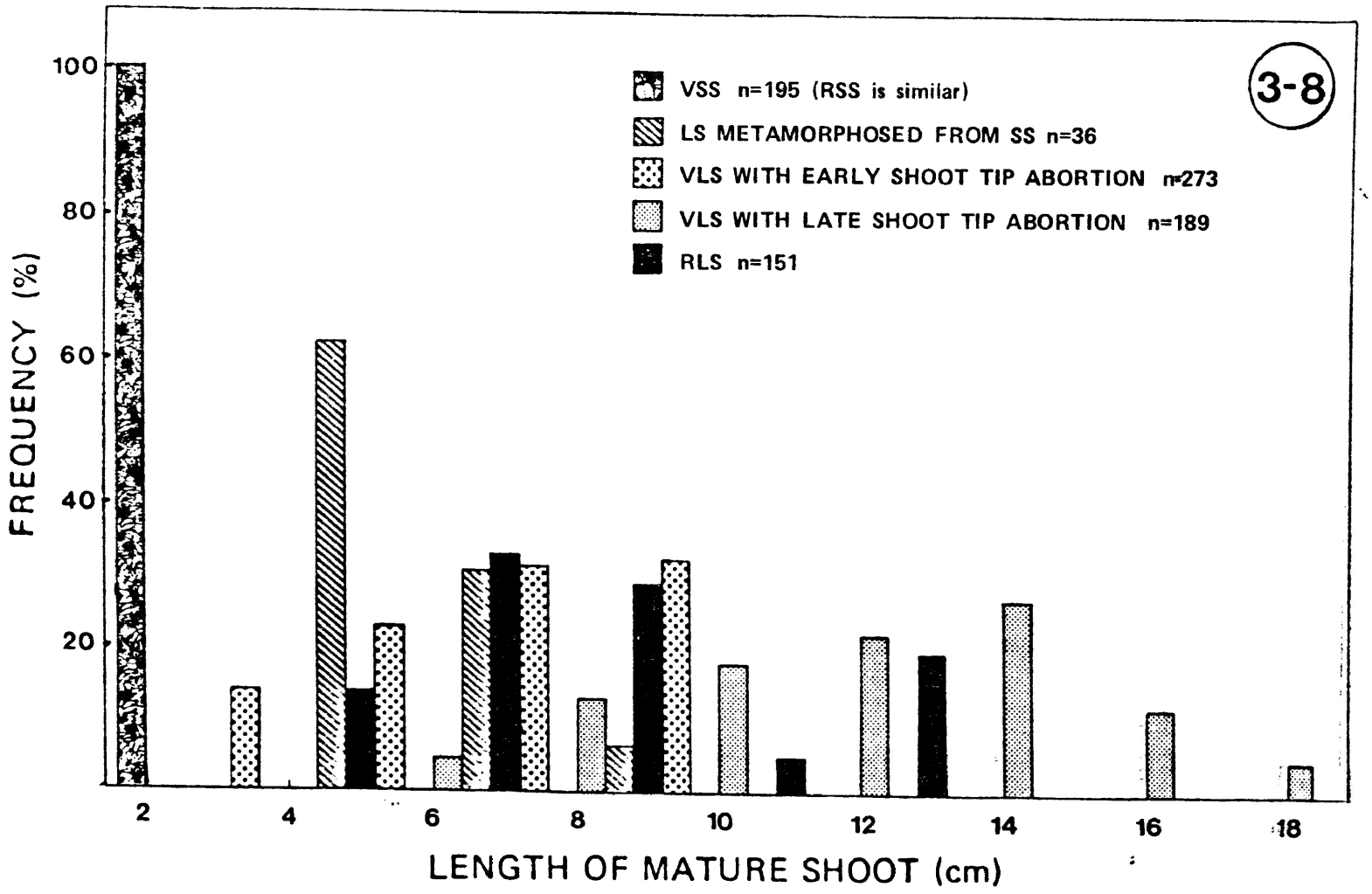
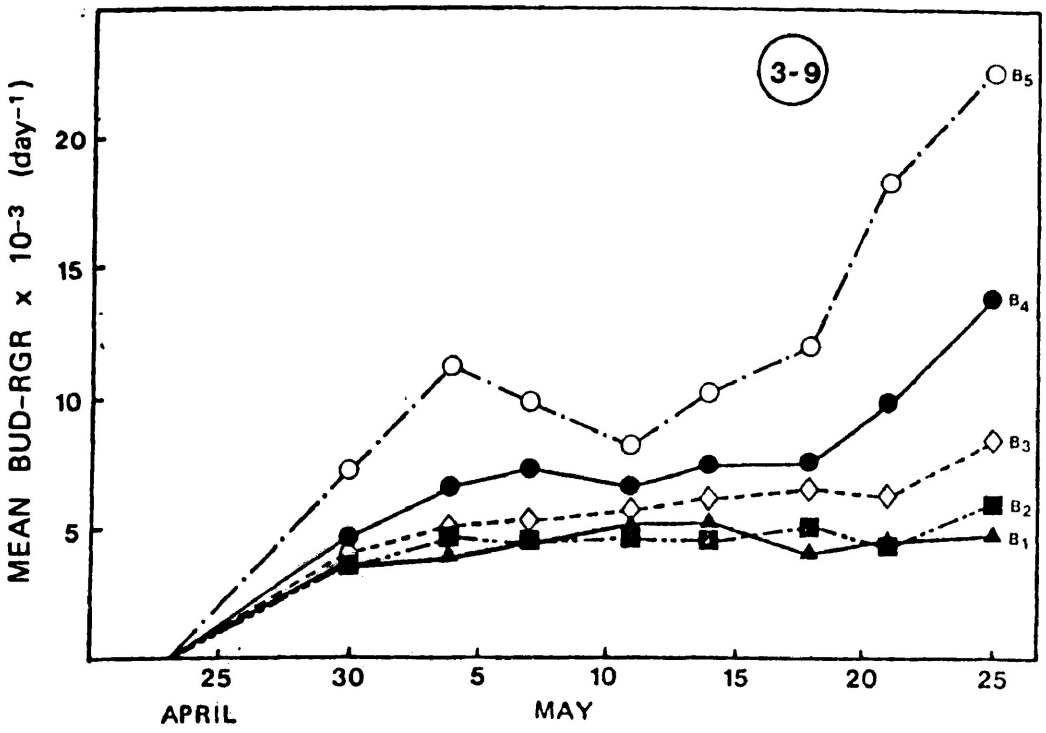

3-8
VSS n=195 (RSS is similar)
LS METAMORPHOSED FROM SS n=36
VLS WITH EARLY SHOOT TIP ABORTION n=273
VLS WITH LATE SHOOT TIP ABORTION n=189
RLS n=151
FREQUENCY (%)
100
80
60
40
20
2
4
6
8
10
12
14
16
18
LENGTH OF MATURE SHOOT (cm)

FIG. 3-9. Mean relative growth rate of axillary buds on a previous season's long shoot. B_1 to B_5 indicate acropetal sequence of axillary buds normally subtended by late leaves on a long shoot. Differences between B_1 to B_4 are not significant until May 25 when B_4 has higher Bud-RGR (p 0.01). B_5 has a higher average growth rate ($p < 0.001$). N = 30 for each point.


3-9
MEAN BUD-RGR x 10-3 (day-1)
20
15
10
5
B5
B4
B3
B2
B1
25
30
5
10
15
20
25
APRIL
MAY

buds proximal to it. The differences in Bud-RGR between all axillary buds except the most distal or pseudoterminal bud is not statistically significant ($p < 0.05$) until after May 18, a few days after flushing. The Bud-RGR's of the more proximal buds seem to overlap at various points before and after flushing (Fig. 3-9). Thus the only bud which behaves distinctly differently on a long shoot with seven nodes or less is the pseudo-terminal which is, incidentally, the potential long shoot. It has been observed that in extremely long, long shoots (with more than 7 nodes) this may not necessarily be the case, since the axillary buds of the median nodes may be bigger than the pseudoterminal. This is possibly related to bud length as in yellow birch (Metzger 1977). One must be cautious about any conclusions pertaining to bud dry weight as it relates to shoot length, unless the number of nodes of the particular long shoots are specified. It is however, clear from this study that the growth rate of the potential long shoot bud (i.e., pseudoterminal bud) is considerably greater than other axillary buds before and after flushing. Although in Populus (Maini 1966b), Pinus (Kozlowski et al. 1973) and Abies (Powell 1977a) bud length has been correlated with the length of the shoot which develops from it, this does not seem to be the general case in paper birch. In

Populus, Pinus and Abies the most distal buds are usually the longest buds. However, in yellow birch Metzger (1977) found that the longest buds are located in the middle portion of a long shoot (i.e., of juvenile trees). His data do not include bud dry weight therefore, the results presented here cannot be compared. A few days after flushing distal buds of long shoots with seven nodes or less have higher bud dry weights than the proximal ones. In all cases, including extremely long, long shoots, the bud at node 4, i.e., the one subtended by L_4, the first late leaf, has the lowest bud dry weight (Fig. 3-10) irrespective of whether the long shoot is reproductive or vegetative (see Chapter 5). Bud dry weight can be more accurately correlated with node number only when a long shoot has at most seven nodes (ie., 4 axillary buds). For these long shoots the relationship of bud dry weight (Y) to node number (X), a week after flushing (Fig. 3-10) is:

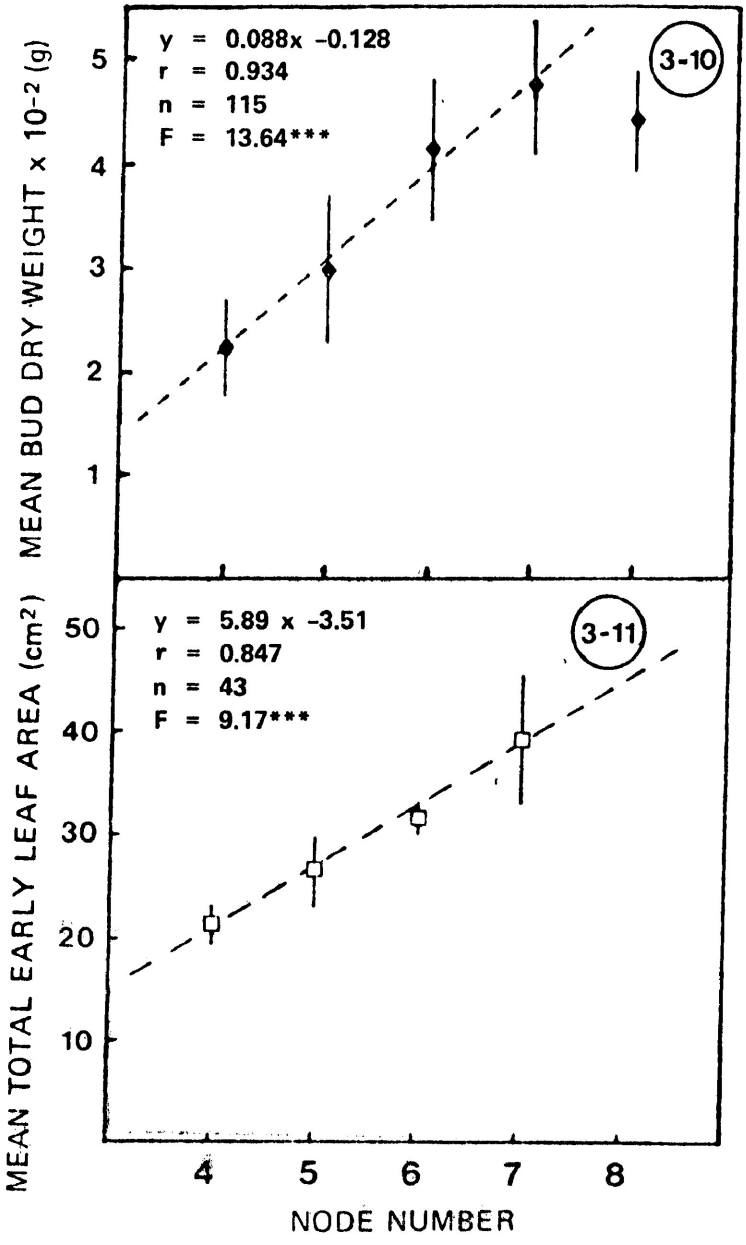
$$Y = 0.088X - 0.128, \ (r = 0.934, \ p < 0.001).$$

Consequently, mean early leaf size is related to node number (i.e., bud position) on a seven-node long shoot (Fig. 3-11). The relationship between node number (X) and leaf size of mature early leaves (Y), three weeks after flushing is:

$$Y = 5.89X - 3.51, \ (r = 0.847, \ p < 0.001).$$

FIG. 3-10. Mean bud dry weight of two-year-old vegetative long shoots (seven-node type) as a function of node number one week after flushing. N = 115. Value at node 8 was added to show how relationships derived between bud dry weight and node number in text can be altered when long shoots with more than seven nodes are considered.

FIG. 3-11. Mean total early leaf area of two-year-old vegetative long shoots (seven-node type) as a function of node number three weeks after flushing. N = 43.


y = 0.088x -0.128
r = 0.934
n = 115
F = 13.64***
3-10
y = 5.89 x -3.51
r = 0.847
n = 43
F = 9.17***
3-11
MEAN BUD DRY WEIGHT x 10-2 (g)
MEAN TOTAL EARLY LEAF AREA (cm2)
NODE NUMBER
1
2
3
4
5
10
20
30
40
50
4
5
6
7
8

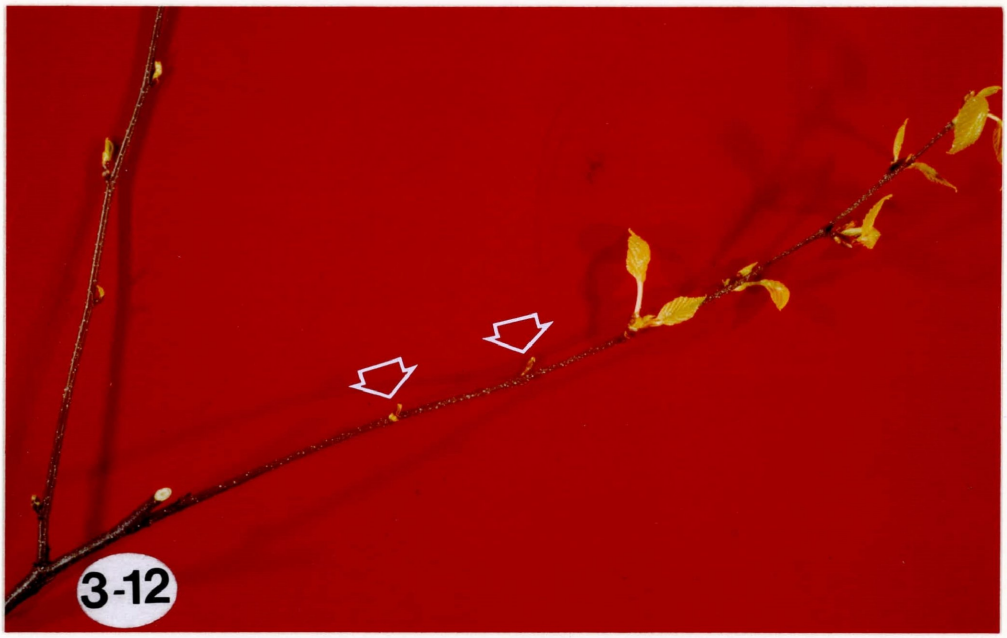
This reinforces the notion that at least in the reference long shoot (i.e., seven-node type) node number is important in determining bud vigour. Zieslin et al. (1976) have, however, presented data on rose plants (Rosa hybrida "Baccara") in which bud position is correlated to bud weight. From the present study it may be concluded that axillary buds with higher Bud-RGR's are the potential long shoots and those with lower Bud-RGR's are the potential short shoots This reflects the vigour of potential long shoot buds, and is consistent with evidence from dissected buds, namely, that potential long shoot buds have more leaf primordia in addition to slight internodal extension before bud burst. These conclusions are based on long shoots with seven internodes or less. With increase in node number variations alter the above conclusions. However, correlation between node number and Bud-RGR is even greater in shoots with six nodes (i.e., 3 axillary buds). Consequently, the inhibitory influence of the distal bud becomes more pronounced with decreasing long shoot length and/or number of nodes. Probably, in long shoots with early shoot tip abortion, the pseudoterminal bud obtains a greater share of nutrients as it becomes the major "sink". As a rule, the pseudoterminal always flushes as a long shoot. Its subtending

leaf, which is also the youngest of the late leaves, may be importing from mature leaves, since younger leaves are net importers of assimilates from mature leaves (Larson et al. 1980). A major source would be mature leaves on the same orthostichy (Milthorpe and Moorby 1969).

The question is, what factors influence the distal-most bud to exhibit the inhibitory characteristics associated with apical dominance/control. Clearly a positional effect exists, but in addition, temporal factors must also be considered. For example, the pseudo-terminal bud is morphogenetically determined prior to winter dormancy; it forms more primordia and shows inter-nodal extension. These features are not found in the proximal buds, the potential short shoot buds. Further-more, determination is correlated, in time, with shoot tip abortion or induction of male inflorescences. Leaves subtending the pseudoterminal bud are also the last to abscise at the end of the growing season. Other than these it is not clear what physiological factors are involved in regulating the differences in the bud types. This subject will be discussed at the end of this chapter.

The pseudoterminal bud invariably has a higher long shoot growth potential than all buds proximal to it. Accordingly flushing sequence is strictly basipetal (Fig. 3-12). This feature may be correlated with higher Bud-RGR of

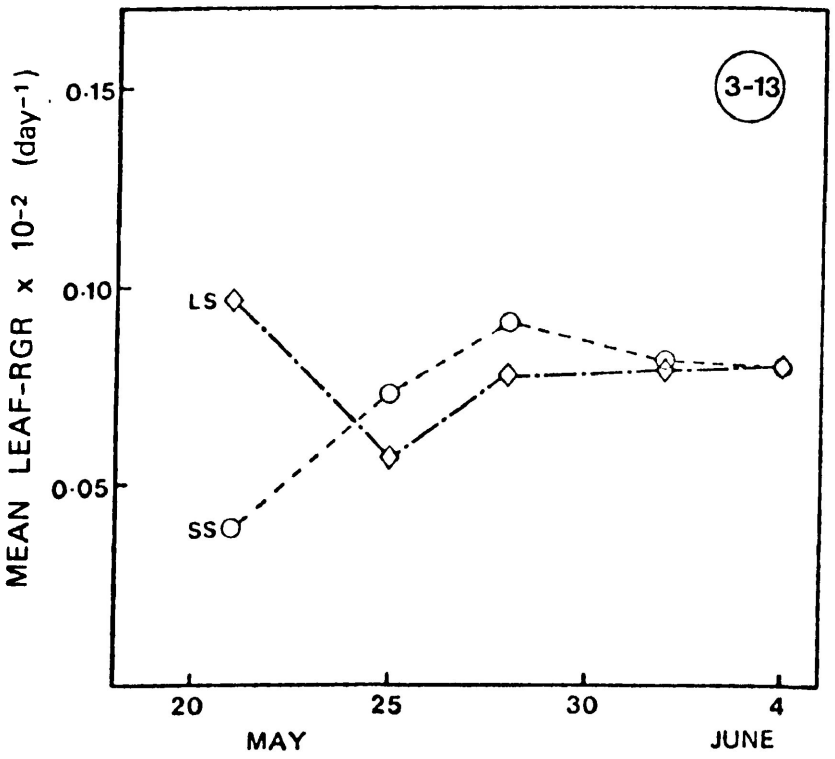
FIG. 3-12. Flushing sequence in a vegetative long shoot. Note distal half of buds have flushed. Median buds were first to flush. Proximal buds (arrows) have expanded and are just about to flush.


3-12

potential long shoot buds (Fig. 3-9), node versus bud dry weight (Fig. 3-10) and node versus total early leaf area (Fig. 3-11). Buds with higher Bud-RGR i.e., potential long shoot buds flush before potential short shoot buds. Although Felber (1948) did not evaluate Bud-RGR he observed that in apple the terminal bud flushes first and then the wave of flushing moves basipetally. Probably potential long shoot buds have a head-start in initiating the events of bud burst i.e., internodal extension and leaf expansion (Bügsen and Münch 1929; Felber 1948; Romberger 1963; Kozlowski 1971; Powell 1982). This will be substantiated later when leaf and internode extension trends are discussed.

Relative leaf growth rate (Leaf-RGR) based on both leaf area and leaf dry weight is higher in long shoots than in short shoots a week after flushing, i.e., on May 21. Thereafter it falls for long shoots, then increases, but to a level lower than that of May 21 (Fig. 3-13). In contrast, Leaf-RGR of short shoots increases almost linearly till May 28 and then falls only slightly. Growth rate is higher in short shoots than long shoots between May 25 and 31, becoming almost equal on June 4, three weeks after flushing (Fig. 3-13). This trend may be explained by the fact that during the same period short shoot early leaves do not contribute to internodal extension while in long shoots they do. Such a contribution of

FIG. 3-13. Mean relative leaf growth rate of long (LS) and short shoot (SS) early leaves. N = 40 at each point.


3-13
MEAN LEAF-RGR x 10-2 (day-1)
0·15
0·10
0·05
LS
SS
20
25
30
4
MAY
JUNE

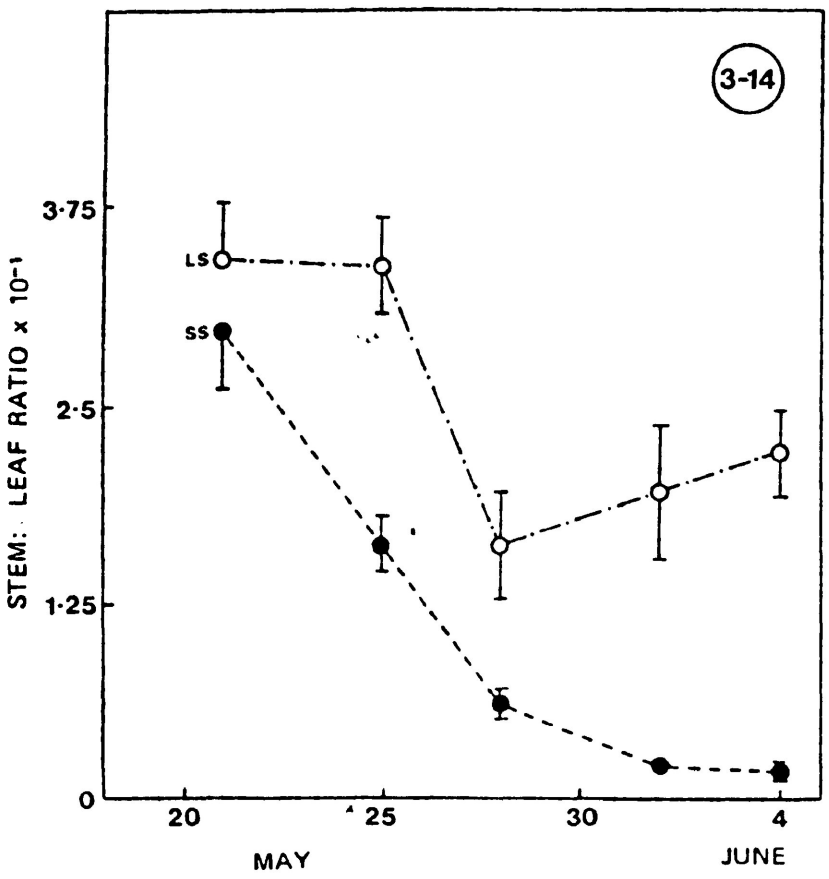
assimilate is probably due to internodes 3 and 4 (see Fig. 3-22) and cambial activity. This is supported by the very high allometric K value of 3.41 (Table 3-1) in the growth relationship between stem and leaf, on the basis of dry matter production during the same period. Subsequently, stem growth is greater in long shoots than in short shoots, to the detriment of "early" leaf growth. It is also possible that the elongating internode above the early leaves (I_4) of long shoots as well as the developing late leaves (see Fig. 3-22) and cambial activity in lower internodes may be acting as competing "sinks" which depend on the importation of assimilates from early leaves. At the same time, developing axillary buds in the axils of late leaves may be importing from the fast growing early leaves. In addition to this, they may be competing with late leaves which subtend them. This may explain why extension growth of late leaves is more gradual than that of early leaves (see Fig. 3-22). This is substantiated by the work of Kozlowski and Clausen (1966) for the same species growing in Massachusetts. A similar trend occurs in Populus (Critchfield 1960). Competition for nutrients between late leaves and their axillary buds probably occurs, since in birch the bud trace is an offshoot of the central leaf trace (Garrison 1949), as in Populus deltoides (Larson and Pizzolato 1977; Richards and Larson 1981). Is this the pathway of sink

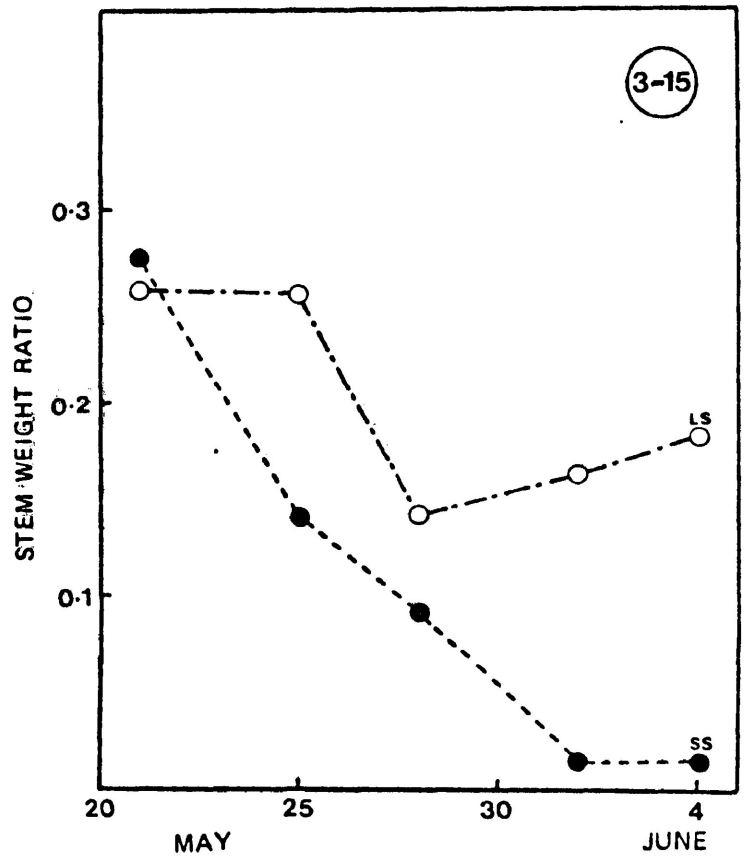
competition?

Stem to leaf ratio (SLR), the ratio of stem dry weight to leaf dry weight, decreases with time for short shoots until it approaches zero, i.e., assymptotes close to zero (Fig. 3-14). In long shoots, however, the trend is different. There is a sharp decline between May 25 and 28 and it increases thereafter. Stem weight ratios (SWR) of the two shoot types follow the same trend (Fig. 3-15). In long shoots the decline in May is due to increased extension of the fourth internode (I_4). This may explain the fall in long shoot leaf-RGR (Fig. 3-13) between May 21 and 25. These SLR and SWR trends indicate that in short shoots, early leaves grow at the expense of stem elongation and the subsequent development and expansion of later formed leaves. Late leaves do not, however, occur in short shoots because the comparable late leaf primordia suffer lamina abortion before bud break in a manner probably similar to the case in Populus (Goffinet and Larson 1982). Such leaves have been termed rudimentary leaves (Macdonald and Mothersill 1983; Macdonald et al. 1983). In potential short shoots (i.e., year n + 1 long shoot proximal axillary buds), L_1 is a rudimentary leaf as in potential long shoot buds. In sequentially formed short shoots (i.e., years n + 2, n + 3, n + 4, ... etc.) three rudimentary leaves L_1, L_2, and L_3 occur (Macdonald and Mothersill 1983). What role does

FIG. 3-14. Mean stem: leaf ratios of LS and SS indicating preferential allocation of dry matter to stem in LS ($p < 0.01$). Each point represents a sample of 20 for Fig. 4 to 11.

FIG. 3-15. Ratio of stem dry weight to shoot dry weight indicates higher stem dry weight allocation in LS ($p < 0.01$).


3-14
STEM: LEAF RATIO x 10⁻¹
3·75
2·5
1·25
0
LS
SS
20
25
30
4
MAY
JUNE


3-15
STEM WEIGHT RATIO
0·3
0·2
0·1
LS
SS
20
25
30
4
MAY
JUNE

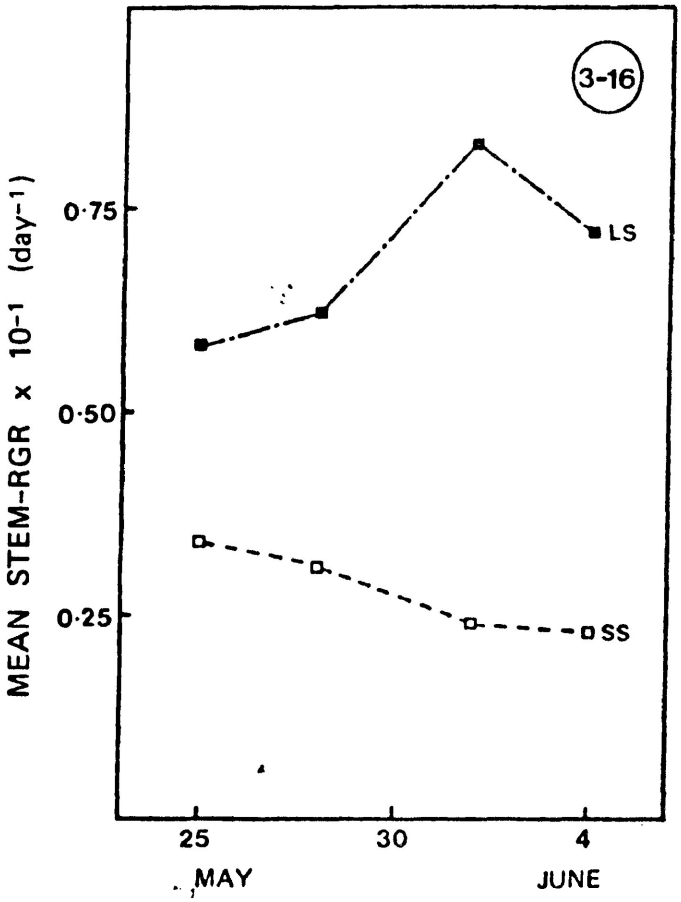
the aborting, i.e., rudimentary, leaves play in the formation of the primary vascular pattern and subsequently secondary vascular differentiation of the short shoot axis? Answers to this may be directly or indirectly related to the trends in SLR and SWR. The fall in SLR in late May (Fig. 3-14) coincides with the period of rapid early leaf growth (see Fig. 3-22).

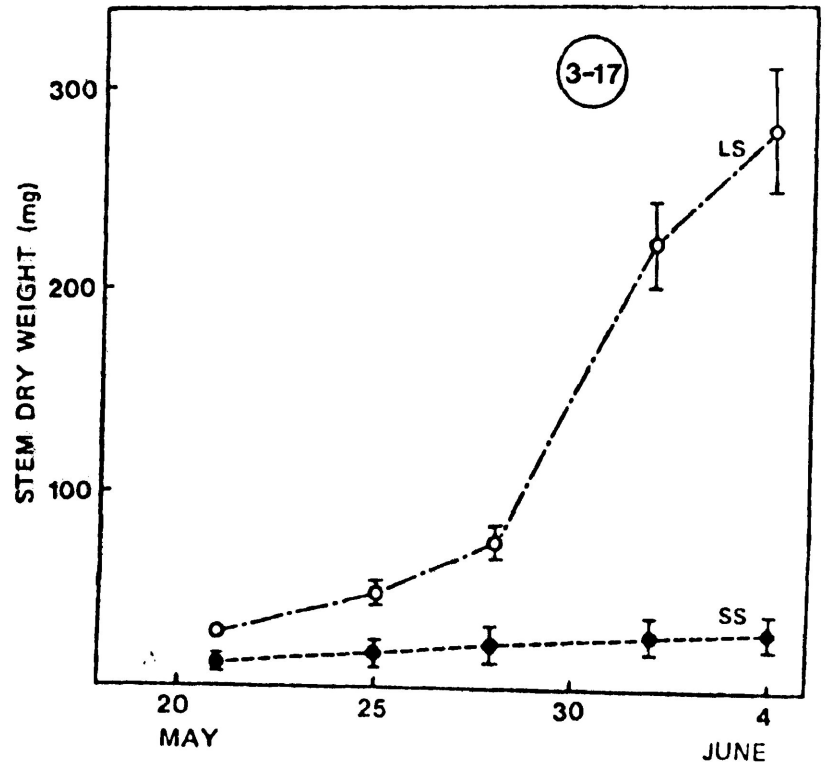
Stem-RGR is significantly higher in long shoots ($p < 0.01$) a few days after flushing (Fig. 3-16) and it remains consistently higher due to subsequent stem elongation and cambial activity. There is a consistent gradual decrease in Stem-RGR of short shoots, but this is not so in long shoots. A fairly rapid increment in stem weight of long shoots occurs between May 28 and June 1 (Fig. 3-17). This coincides with the logarithmic phase of I_4 extension (see Fig. 3-22). Afterwards Stem-RGR falls slightly (Fig. 3-16), possibly due to competition for assimilates by the expanding L_4, the first late leaf, and the concommitant increase in "leafiness".

Leaf area ratio (LAR), an "index of leafiness" (Hunt 1978), increases with time immediately after flushing (Fig. 3-18) indicating that early leaves expand at a rapid rate while stem or internode extension, if any, lags. LAR is higher in short shoots and lower in long shoots. This becomes statistically significant ($p < 0.01$)

FIG. 3-16. Mean relative growth rate of LS and SS stems. ($p < 0.001$)

FIG. 3-17. Increment in stem dry weight of LS and SS after flushing. $p < 0.001$ after May 30.


3-16
MEAN STEM-RGR x 10⁻¹ (day⁻¹)
0·75
0·50
0·25
LS
SS
25
30
4
MAY
JUNE


3-17
STEM DRY WEIGHT (mg)
300
200
100
LS
SS
20
25
30
4
MAY
JUNE

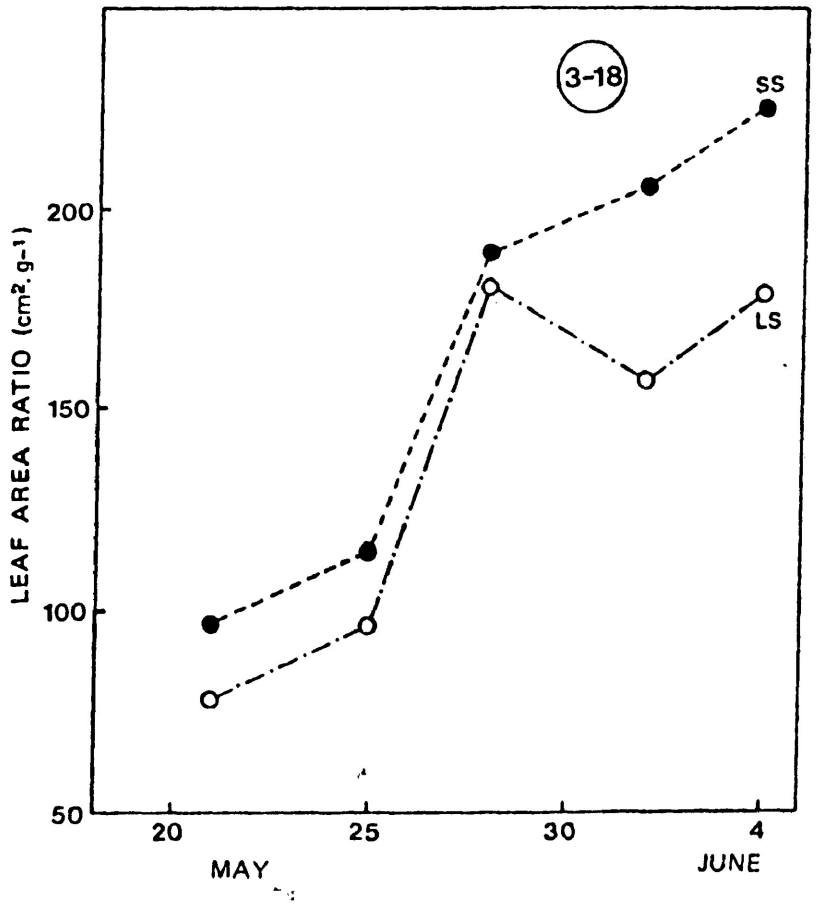
by the end of May. The lower LAR of long shoots is explained by higher stem dry weight increment (Fig. 3-17) and rapid stem growth (Fig. 3-16) in long shoots, since LAR is an expression of the ratio of leaf area to entire shoot weight. Some changes in LAR may be due to changes in SLA, as has been reported in Impatiens (Hughes 1965). Subsequent increase in LAR of long shoots is due entirely to the expansion of late leaves.

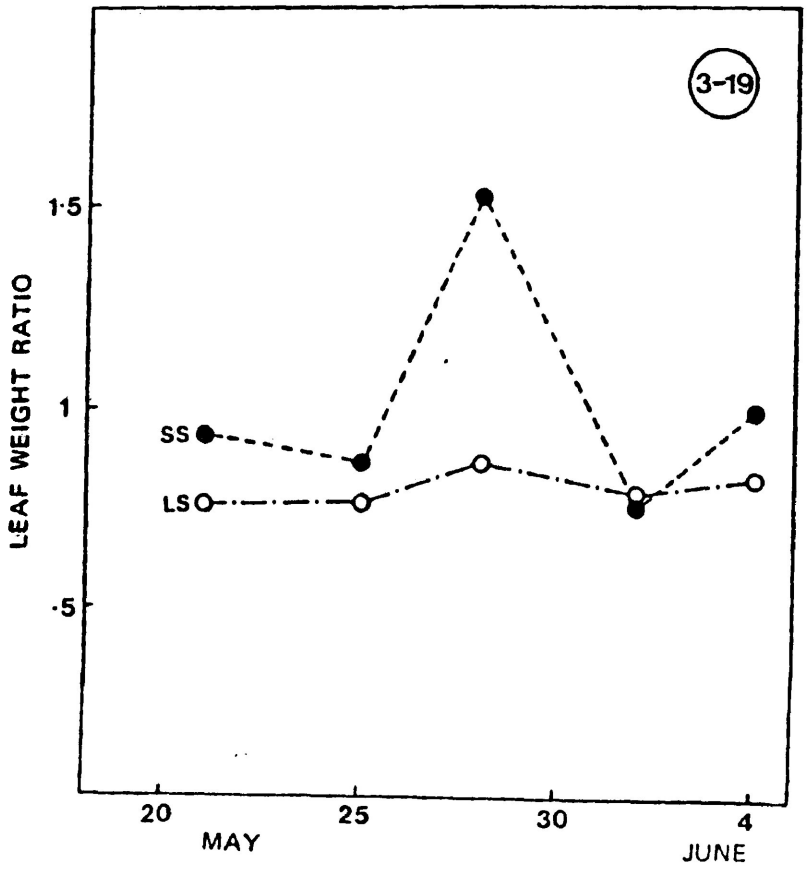
Leaf weight ratio (LWR), the ratio of leaf dry weight to shoot dry weight, fluctuates for short shoots but remains almost constant for long shoots (Fig. 3-19). The high value of LWR on May 28 coincides with the logarithmic phase of early leaf expansion and growth immediately after flushing. The increase in short shoot LWR needs supplementary explanation. It may indicate that new material (assimilates) remain stored in the expanding early leaves of short shoots. The stable trend in long shoot LWR, on the contrary, may suggest that their early leaves are involved in the supply of photosynthates for shoot extension. The small fluctuation in LWR for long shoots is possibly because of an "equilibrium" between assimilate allocation to the stem, and retention within leaves for growth and expansion, since both LAR and LWR represent the ratio of photosynthesizing to respiring material.

Assimilate distribution in the growing shoots seems

FIG. 3-18. Changes in leaf area ratio of LS and SS with time, after flushing, $p < 0.01$ only after May 30.

FIG. 3-19. Post-flush changes in leaf weight ratio of LS and SS with time. Differences between values are not significant except between May 25 and May 31 and at maturity ($p < 0.05$).

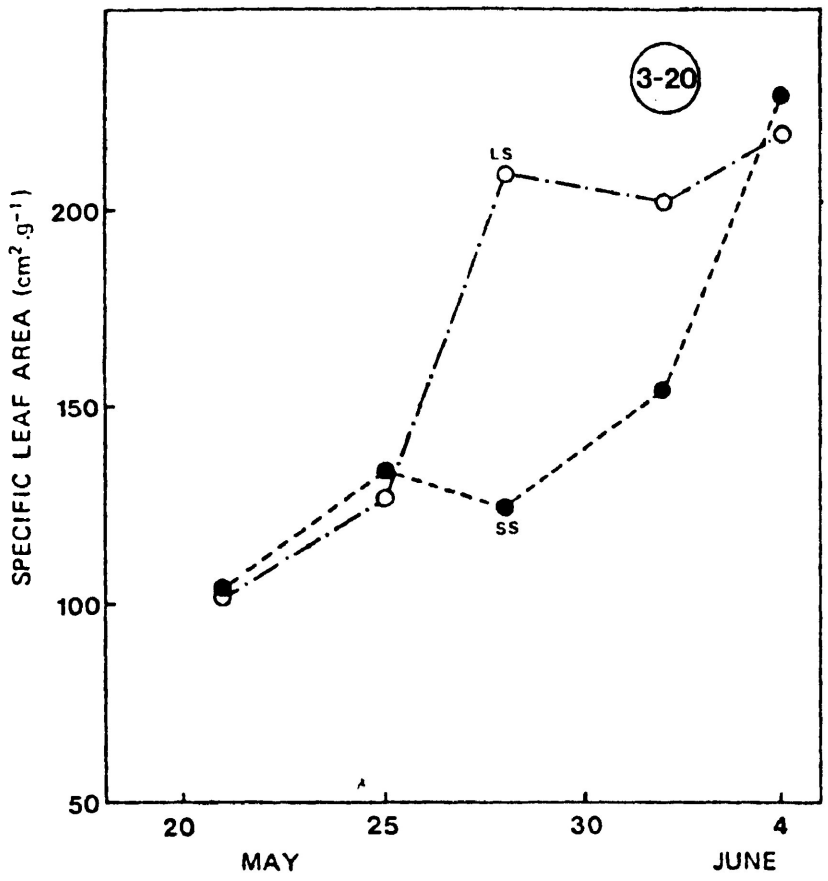

3-18
SS
LS
LEAF AREA RATIO (cm².g⁻¹)
200
150
100
50
20
25
30
4
MAY
JUNE

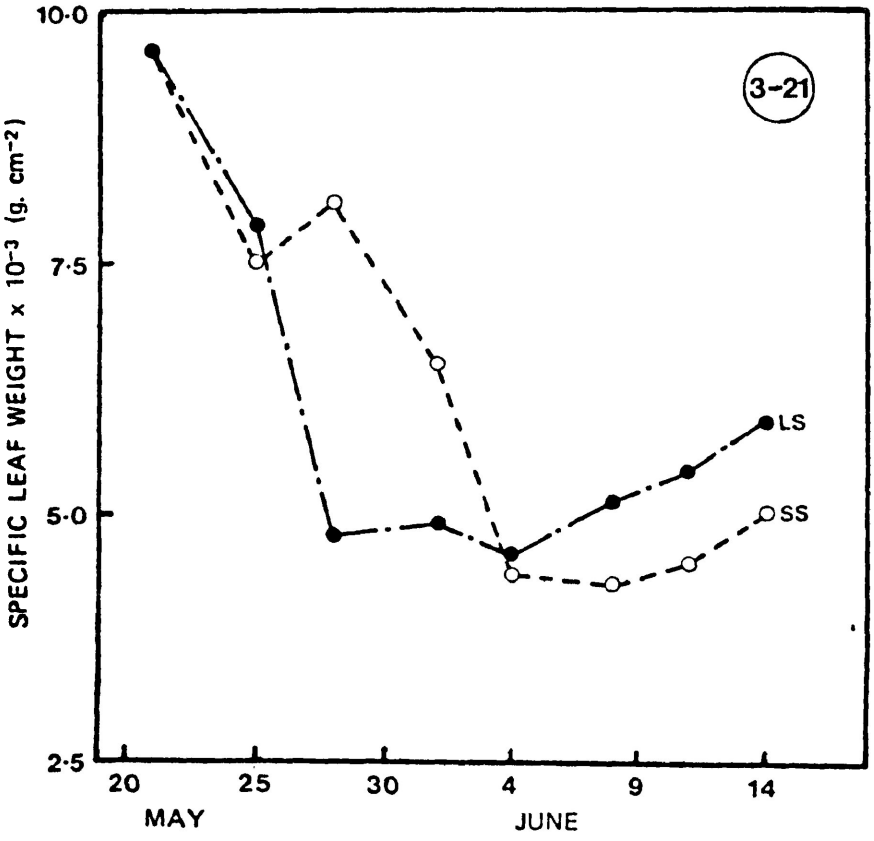

3-19
LEAF WEIGHT RATIO
1·5
1
·5
SS
LS
20
25
30
4
MAY
JUNE

to reflect differences in specific leaf area (SLA) and specific leaf weight (SLW). This is shown in Fig. 3-20 and 3-21, respectively. SLA, the ratio of leaf area to leaf weight, is slightly lower in long shoot early leaves than in comparable short shoot leaves, but becomes significantly higher in long shoots than short shoots ($p < 0.05$) after which the converse situation persists (Fig. 3-20). This indicates that although early leaves of long shoots accumulate less dry matter per leaf area than short shoots between May 25 and June 3 especially, they possibly retain more dry matter at maturity. Also, it has been suggested that increase in SLA is a consequence of the greater expansion of the same amount of leaf dry material and, more precisely, the greater expansion of possibly the same number of cells (Evans and Hughes 1961; Hughes 1965). Probably during the same period (May 25 - June 3), expanding long shoot early leaves actively export assimilates to the stem for internode extension and to the developing late leaves, their expanding internodes and associated axillary buds. This may further explain trends in LWR. The important contribution of long shoot early leaves to subsequent shoot elongation has long been suggested (Kozlowski and Clausen 1966). This demand on early leaves is a possible cause of higher SLA in long shoots a few days after flushing. However, 4 - 6 weeks after flushing and before the end of the growing season,

FIG. 3-20. Post-flushing changes in specific leaf area of LS and SS as a function of time. Differences between values are significant between May 28 and June 1, and at maturity ($p < 0.01$).

FIG. 3-21. Changes in mean specific leaf weight after flushing. $p < 0.01$ between May 28 and June 1.


3-20
SPECIFIC LEAF AREA (cm^2.g^{-1})
200
150
100
50
LS
SS
20
25
30
4
MAY
JUNE


3-21
SPECIFIC LEAF WEIGHT x 10^{-3} (g. cm^{-2})
10·0
7·5
5·0
2·5
LS
SS
20
25
30
4
9
14
MAY
JUNE

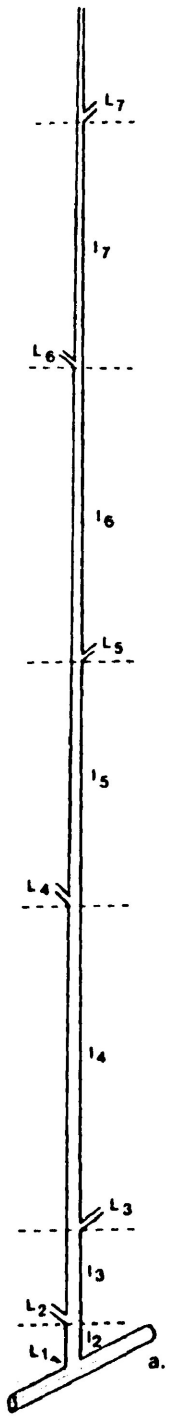
when most late leaves on long shoots have expanded, the early leaves either fail to export to mature and less "dependent" late leaves, import assimilate from the latter, or retain assimilates. This means the expanding young late leaves become "photosynthetically independent". As a result, long shoot early leaves at maturity have lower SLA and hence are thicker than short shoot early leaves (Fig. 3-33). There is a possibility that the relative positions of long shoots and short shoots on an axis within the crown results in less shaded long shoot early leaves, hence higher leaf dry weight in long shoots. The most typical shade leaves in beech are short shoot leaves (Müller 1954). To minimize such problems only long and short shoots on the same axis were used in all analyses. SLW which is actually the reciprocal of SLA shows a trend (Fig. 3-21) consistent with the above concept. Accumulation of more dry matter per unit leaf area in long shoots than comparable short shoot early leaves is suggestive, and possibly reflects leaf thickness in long shoots. The fall in SLW values between May 21 and June 4 (Fig. 3-21) may be due to the net demand on long shoot early leaves to export assimilates to the extending internodes and the developing late leaves. SLW for long shoots begins to increase only at a time when resource demand seems to be reduced. The fall in

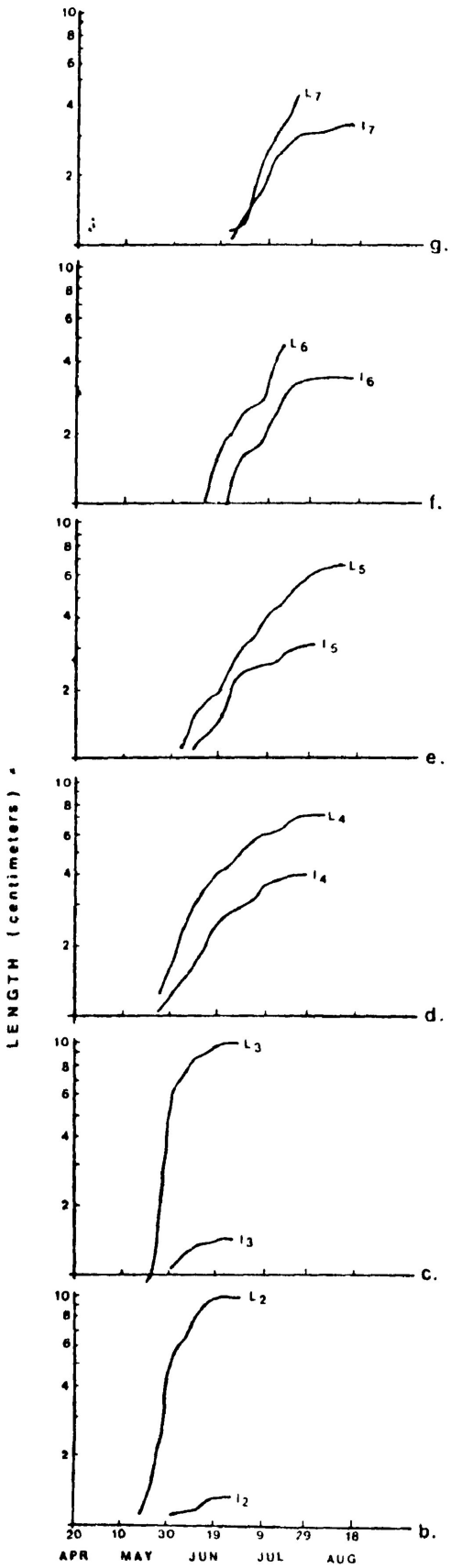
SLW for both shoot types between May 20 and June 4 (Fig. 3-21) is possibly caused by the rapid expansion of early leaves during the same period. In long shoots, the rapidly expanding L_4 (first late leaf) (see Fig. 3-22) probably maximizes its photosynthetic efficiency with concurrent expansion and development. Younger, fully expanded leaves are known to be photosynthetically more efficient (Larson and Gordon 1969; Dickmann 1971). Higher photosynthetic rate in long shoots than short shoots of Populus have been attributed to the younger average age of leaves due to the formation of late leaves (Nelson and Michael 1982). Few reports based on mature early leaves (Isebrands and Nelson 1982; Nelson and Michael 1982) indicate that long shoot early leaves have higher SLW than short shoots. Although they did not evaluate SLA, it is clear that short shoots have higher SLA than long shoots since SLA is the reciprocal of SLW. Nelson and Michael (1982) did not find any statistical difference in photosynthetic rates between long shoot and short shoot early leaves. These data indicate that, on a developmental basis, SLW is not at all times higher in long shoot early leaves than short shoot early leaves. Such differences manifest themselves only when the leaves are approaching maturity and retain the distinction till they abscise at the end of the growing season.

Leaf and internode extension in long shoots

Leaf and internode extension measurements revealed interesting correlations. For example, it was found that internode elongation ceases before petiole elongation; the elongation of the lamina is the last to cease. A similar trend was recently reported in Populus (Pieters 1983) while this thesis was in preparation. Leaf and internode elongation for L_2 to L_7 and subjacent internodes I_2 to I_7, respectively, are presented in Fig. 3-22 for a hypothetical long shoot with mean values taken from actual measurements. Early leaves elongate very rapidly and attain final length 18 - 21 days after flushing. Rapid early leaf elongation has similarly been observed in Populus trichocarpa (Critchfield 1960), Acer (Critchfield 1971; Wilson and Fischer 1977; Gregory 1980), P. balsamifera (Macdonald et al., unpublished data) and in the same species in another location (Kozlowski and Clausen 1966). In most cases L_3 attains a slightly greater length than L_2, although they may both be about the same length immediately after flushing. The growth of L_3 exceeds that of L_2 during the second week after flushing. In 1982, they attained the same length between May 26 and 27, in long shoots. The comparable state in one-year-old short shoots lags behind that of long shoots by 5 to 6 days i.e., it occurred between June 2 and 3 in 1982, and May 30 and 31 in

FIG. 3-22. A hypothetical 7-node long shoot of paper birch with internode distances drawn to scale and showing the rate and duration of expansion in length of leaves, L_2 - L_7, and their subjacent internodes, I_2 - I_7.


L7
l7
L6
l6
L5
l5
L4
l4
L3
l3
L2
l2
L1
a.


LENGTH (centimeters)
10
8
6
4
2
L7
l7
g.
L6
l6
f.
L5
l5
e.
L4
l4
d.
L3
l3
c.
L2
l2
b.
20 10 30 19 9 29 18
APR MAY JUN JUL AUG

1981. Flushing occurred on May 12 and 14 in 1981 and 1982, respectively. In 1983 unusually low temperatures in spring, delayed flushing till May 27. For both shoot types, however, L_3 is longer than L_2 at maturity. Kozlowski and Clausen's (1966) data (i.e., see Fig. 3) for the same species indicate that L_2 (i.e., L_1 in theirs) is slightly longer than L_3 (i.e., L_2 in theirs) at maturity. This disparity cannot be readily explained. The plastochron between L_2 and L_3 for long shoots was determined according to Erickson and Michelini's (1957) method as 1.5 ± 0.5 days; that for short shoot early leaves was 2.25 ± 0.25 days. As determined from inception times, it averages 7 days. The plastochron between late leaves averaged 7 - 10 days, while that between L_3 and L_4 (i.e. first late leaf) averaged 13 - 20 days. This is possibly a consequence of the organogenic pause between L_3 and L_4 inception times (Macdonald et al. 1983).

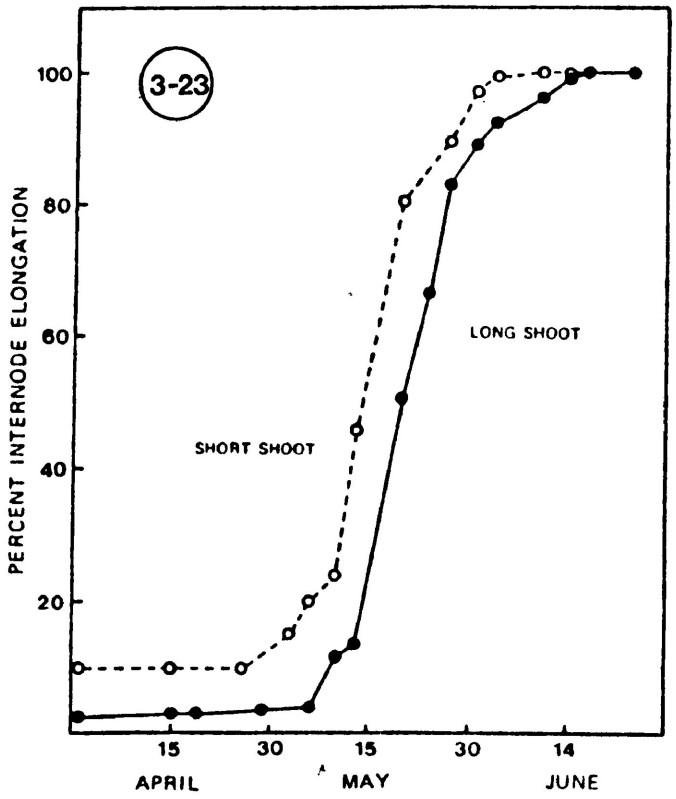
Subjacent internodes of early leaves attain finite lengths rapidly. Growth of I_4, the internode subjacent to L_4 elongates more gradually than other late leaf internodes; it takes 21 - 30 days to mature. Usually it is the longest internode. Dissections of April 16 collections indicated that there was already appreciable difference between internodes of long and short shoot buds, complementing the observation that a slight internodal extension occurs in potential long

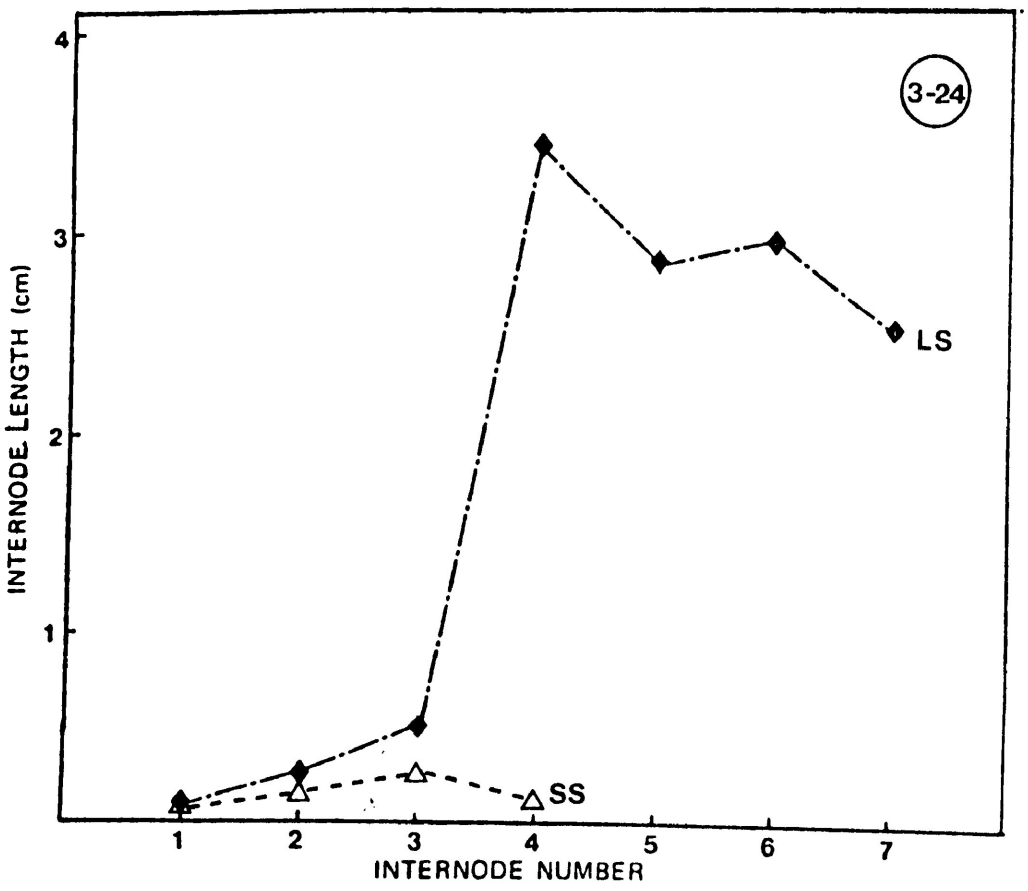
shoot buds prior to dormancy. Between April 16 and May 21 there was a gradual increase in I_3 (internode between early leaves) of long shoots, thereafter a sudden jump and more rapid growth occurs (Fig. 3-23). There is virtually no extension growth in short shoots until two days before flushing i.e., May 11, when a fairly rapid extensional growth begins and ceases about 7 - 10 days before that of the long shoot. The gradual but early increase in I_3 of potential long shoots prior to flushing may substantiate the earlier suggestions relating Bud-RGR to the observation that potential long shoot buds flush first. What factors induce the precocious extension of the potential long shoot buds are not, unfortunately, known. Nevertheless, for both shoot types, the onset of the logarithmic phase of I_3 extension seems to coincide with the time of flushing. Perhaps data on stipule elongation may also be meaningful, but they are not available. Early mobilization of stored carbohydrate prior to bud burst in potential long shoot buds may also explain the precocious extension of internode. As indicated by Maini (1966b), stem extension may be determined by environment as well as growth substances and by photosynthate produced. Progressively increased kinetin-like activity (implicated in bud burst) prior to bud burst has been reported in the same species (Domanski and Kozlowski 1967). Unfortunately, they did not distinguish

between one-year-old potential long and short shoot buds, hence I cannot relate these observations to the activity of growth substances. This is an area to be explored. Notwithstanding the inability to relate these observations to hormonal activity, one may presume that the greater number of leaves and primordia in potential long shoot buds contributes towards the greater extension of long shoot internodes. Thus there possibly exists a reciprocal contribution to total shoot length by leaf growth and internode extension (Esau 1954; Allsopp 1964; R. M. Sachs 1965; Roberts 1969; Halperin 1978; T. Sachs 1981). Does this mean that lamina abortion of short shoot bud primordia may causally be related to the absence of internodal elongation? Or is this related to the state and timing of cambial activity in short shoots? Crucial studies on the timing of cambial activity, for example, are possible clues for further research. From studies relating stem/internode extension to morphometric anatomy (e.g., Bindloss 1942; Holmsen 1960; Garrison 1973; Lam III and Brown 1974) there is a clear indication that cell division (intercalary activity) and consequently cell number accompanied by cell elongation (perhaps hormonally mediated) result in internode elongation. Cell elongation alone is not the important factor per se. Mature internode length of over 200 each of one-year-old long and short shoots are presented in Fig. 3-24. Internodes of the

FIG. 3-23. Comparison of the % increment in length of the internode 3 (I_3) i.e., internode between early leaves of potential long and short shoots. N = 37 and 33 for long and short shoots, respectively.

FIG. 3-24. Mean internode lengths of long shoots and short shoots in late August-early September when most internodal extension has ceased. $N \geq 217$ for each internode. Internodes 1, 2 and 3 are significantly shorter than 4, 5, 6 and 7 ($p < 0.001$) in long shoots.


3-23
PERCENT INTERNODE ELONGATION
100
80
60
40
20
SHORT SHOOT
LONG SHOOT
15
30
15
30
14
APRIL
MAY
JUNE


3-24
INTERNODE LENGTH (cm)
4
3
2
1
LS
SS
1
2
3
4
5
6
7
INTERNODE NUMBER

middle portion of the shoots are longest, decreasing at the proximal and distal ends.

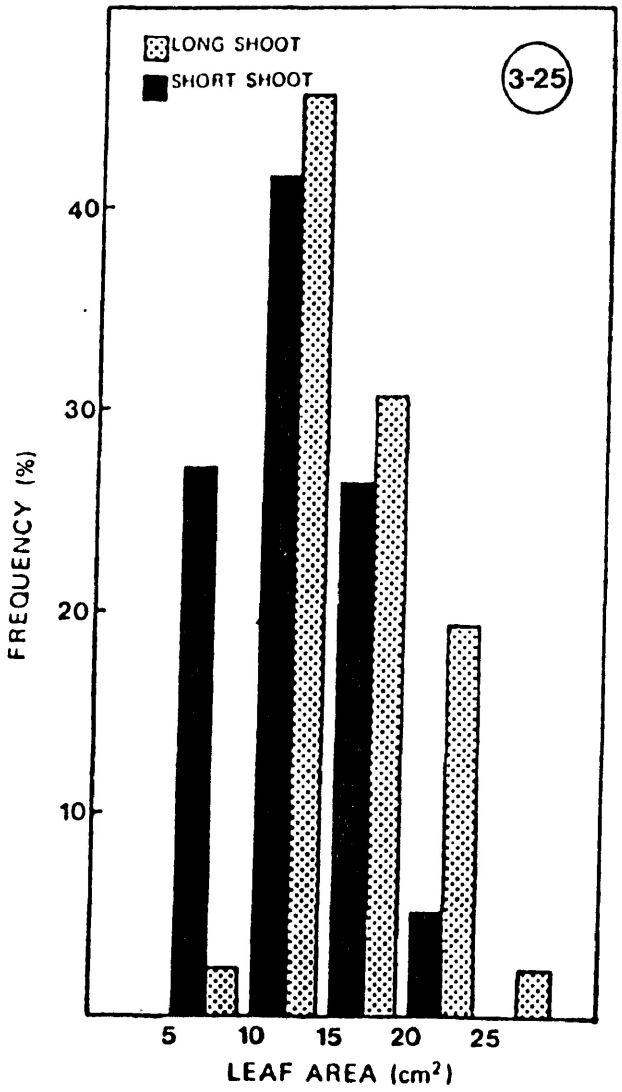
Morphometric measurements

Measurements based on fully mature leaves and subjacent internodes are reported. Only early leaves of long and short shoots are considered in this section. Relations between leaves on the same shoot e.g., early and late leaves of long shoots i.e., heterophyllous shoots, are discussed in Chapter 5.

Leaf size:

Long shoots have larger early leaves than short shoots of comparable age (Fig. 3-25). Mean values are compared in Table 3-2. It is possible that overall shoot vigour of long shoots influences leaf size. This may be related to bud position versus dry weight (Fig. 3-10) and bud position versus mean total early leaf area (Fig. 3-11). Shoots of comparable age (i.e., n + 2 year old) show this difference. In contrast, older short shoots, which are further removed from long shoots have larger leaves than n + 2 year-old short shoots (i.e., short shoots on a previous year's long shoot) possibly because of greater autonomy of older short shoots. The role of apical dominance/control (Brown et al. 1967; Little 1970; Phillips 1969, 1975) in shoot expression is a plausible explanation. This feature will be discussed further at

FIG. 3-25. Frequency distribution of early leaf size in LS and SS. Mean values are significantly different ($p < 0.01$).


LONG SHOOT
SHORT SHOOT
3-25
40
30
20
10
FREQUENCY (%)
5
10
15
20
25
LEAF AREA (cm²)

the end of this chapter.

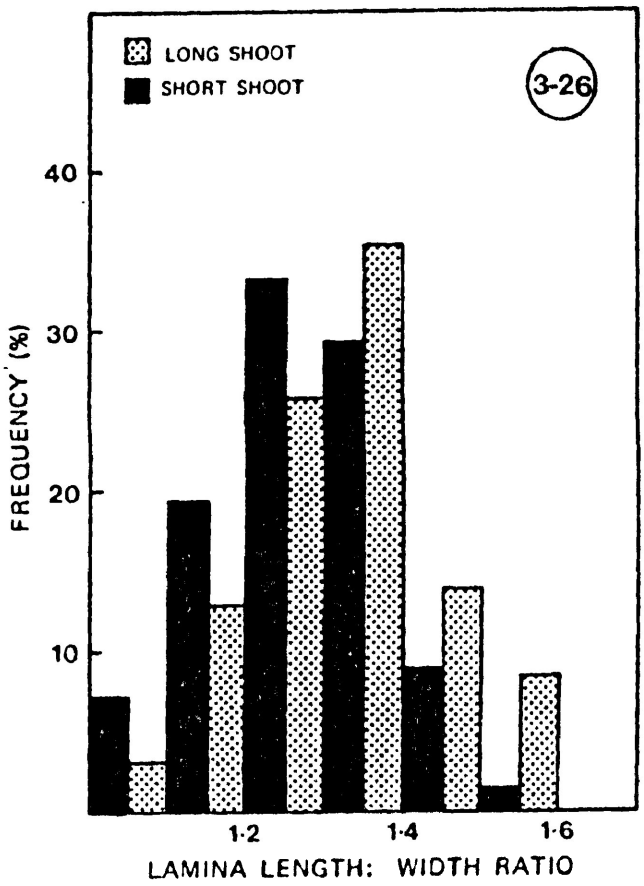
The higher Bud-, Stem- and Leaf-RGR's and the presence of developing secondary axillary buds in the pseudoterminal bud may all contribute in its establishment as a large metabolic sink drawing nourishment away from the proximal buds. Perhaps this may be analogous to the strong terminal (metabolic) sinks reported by Ragneker and Forward (1973) and Powell (1977a).

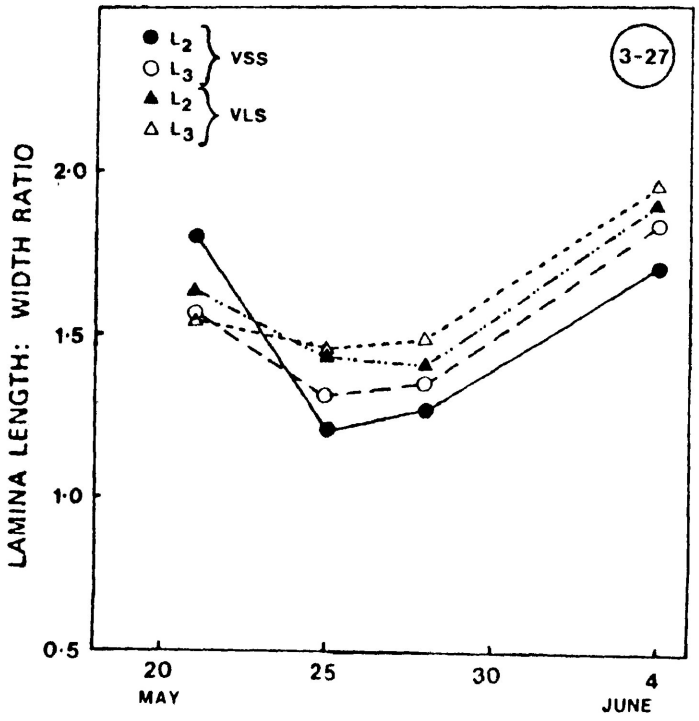
The ratio of lamina length to width:

Early leaves of long shoots grow more in length than in width than do leaves of short shoots (Fig. 3-26). Mean values are compared in Table 3-2. Changes in the ratios of lamina length to width occur immediately after flushing and thereafter become constant till maturity (Fig. 3-27). The first embryonic early leaf (L_2) of short shoots usually has the highest ratio, but falls rapidly to become the lowest at maturity relative to the second early leaf (L_3). A similar trend occurs in long shoots. Comparative "lengthiness" of long shoot early leaf laminae than those of short shoots is presumably due to a number of factors, for example, higher Bud-RGR and Leaf-RGR, greater intercalary growth or lamina expansion in the spring, and better secondary vascular tissue development.

FIG. 3-26. Frequency distribution of lamina length to width ratios in LS and SS early leaves. Mean values are significantly different. ($p < 0.05$).

FIG. 3-27. Changes in lamina length, width ratios of early leaves after flushing.


LONG SHOOT
SHORT SHOOT
3-26
40
30
20
10
FREQUENCY (%)
1·2
1·4
1·6
LAMINA LENGTH: WIDTH RATIO


L2
L3
VSS
L2
L3
VLS
3-27
2·0
1·5
1·0
0·5
LAMINA LENGTH: WIDTH RATIO
20
MAY
25
30
4
JUNE

Side nerve pairs:

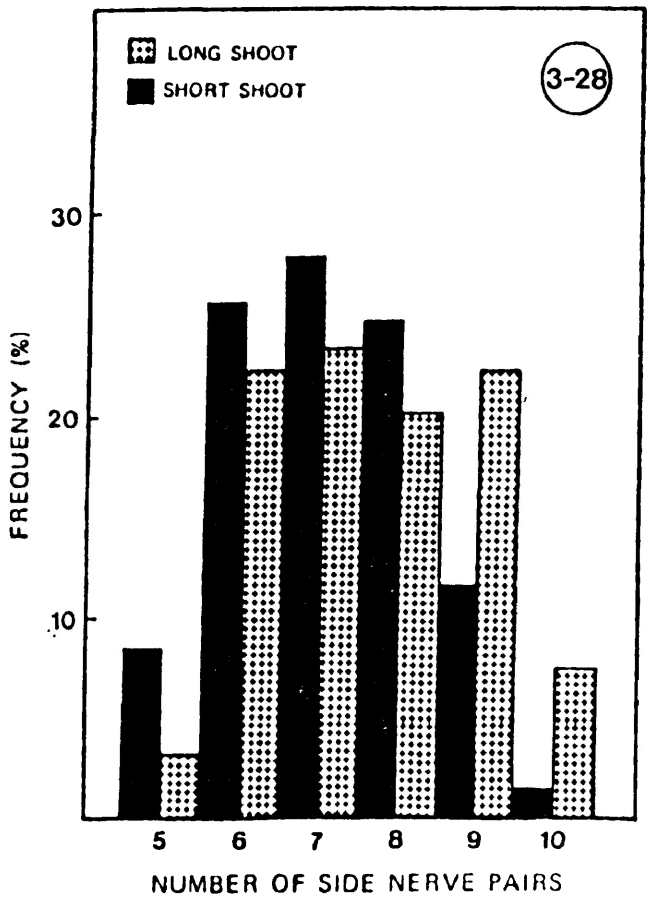
The number of side nerve pairs is greater in long shoot early leaves than in short shoot early leaves (Fig. 3-28; Table 3-2). Is this related to lamina length? Or is it a consequence of poorer vascularization of short shoot leaf laminae? Can this be related to shoot vigour? Further research is needed. However, it is possible that this results in a difference in translocation efficiency.

Petiole length and dry weight:

Petioles of long shoot early leaves grow longer than those of comparable short shoots (i.e., one-year-old). Similarly, dry weights of petioles are higher in long shoots (Figs. 3-29 and 3-30; Table 3-2). These observations, i.e., petiole lengths, are consistent with those of Jentys-Szaferowa (1937) for other Betula species. However, petioles of older (2 - 10 year-old) short shoot leaves are longer than petioles of both long shoot and one-year-old short shoot early leaves (Fig. 3-31). This survey was conducted to confirm the observations of Kozlowski and Clausen (1966) who reported longer short shoot petioles than long shoot petioles in paper birch. The results shown here do not agree with their finding. Realising that older short shoot early leaves seem to be larger, it was decided to evaluate the data on a

FIG. 3-28. Frequency distribution of number of side nerve pairs of LS and SS early leaves. Mean values for the two shoot types are significantly different for shoots of the same age ($p < 0.05$).

FIG. 3-29. Frequency distribution of lengths of 1 year old LS and SS early leaf petioles. LS early leaves have longer petioles than SS early leaves ($p < 0.01$).


LONG SHOOT
SHORT SHOOT
3-28
30
20
10
FREQUENCY (%)
5
6
7
8
9
10
NUMBER OF SIDE NERVE PAIRS

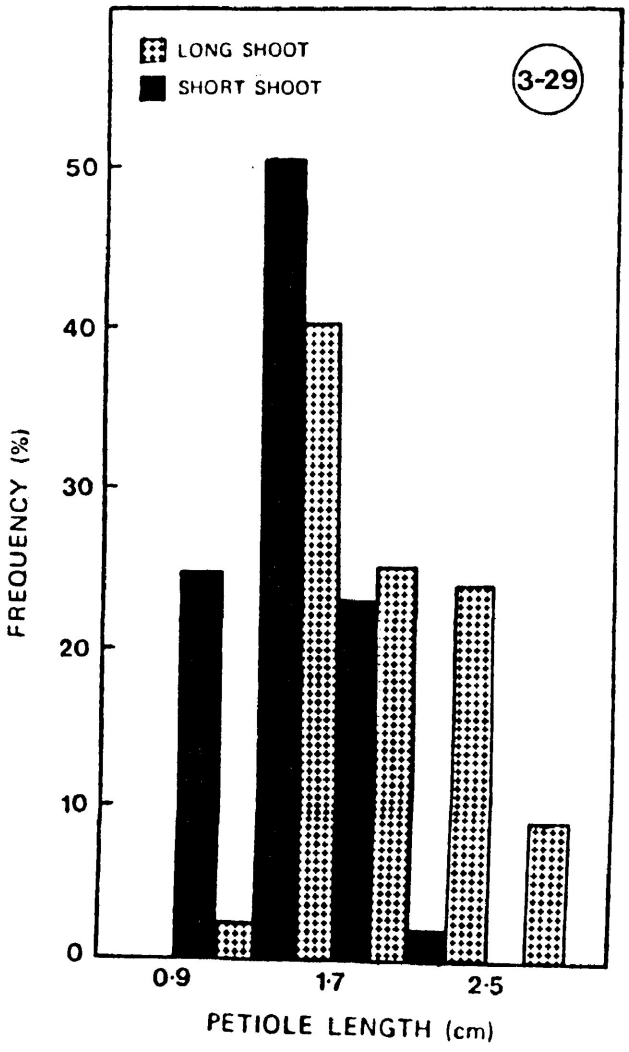
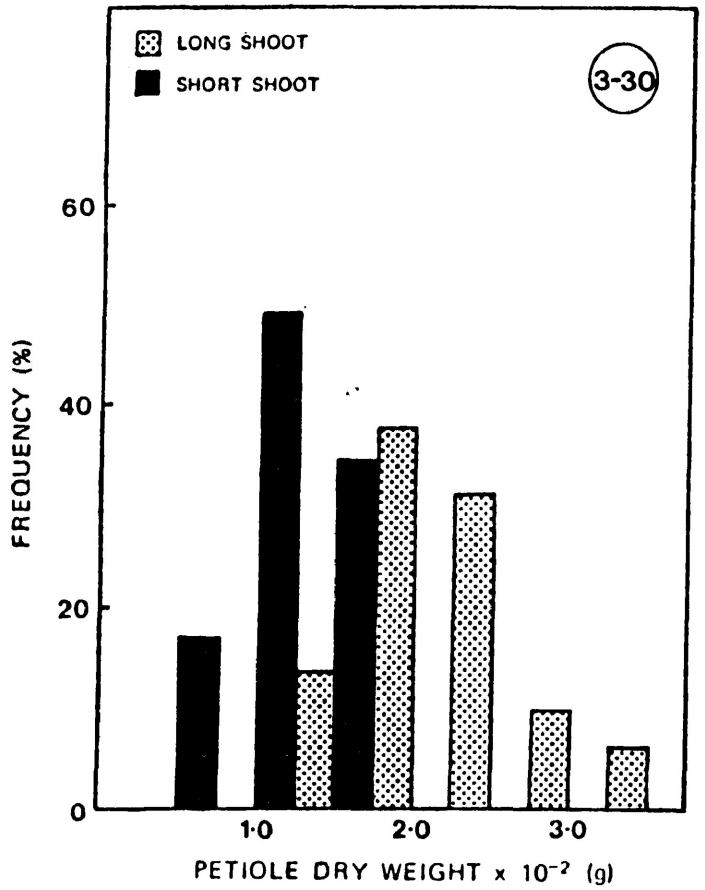
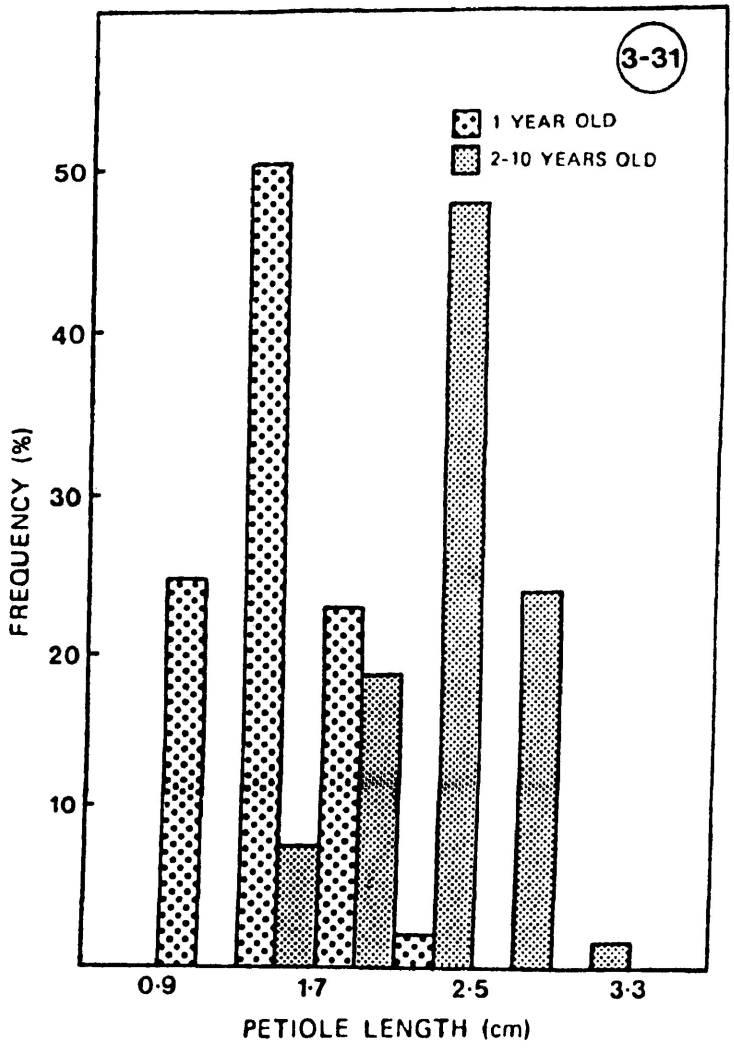

LONG SHOOT
SHORT SHOOT
3-29
50
40
30
20
10
0
FREQUENCY (%)
0·9
1·7
2·5
PETIOLE LENGTH (cm)

FIG. 3-30. Frequency distribution of early leaf petiole dry weight of 1 year old LS and SS. Difference between mean values is highly significant ($p < 0.001$).

FIG. 3-31. Frequency distribution of petiole lengths in 1 year old and 2 - 10 year old SS. Leaves from short shoots which are more than 1 year old have longer petioles ($p < 0.001$). Sample size for 2 - 10 years old SS leaves is 185.


LONG SHOOT
SHORT SHOOT
3-30
60
40
20
0
FREQUENCY (%)
1·0
2·0
3·0
PETIOLE DRY WEIGHT x 10^{-2} (g)


3-31
1 YEAR OLD
2-10 YEARS OLD
50
40
30
20
10
FREQUENCY (%)
0·9
1·7
2·5
3·3
PETIOLE LENGTH (cm)

shoot-age basis. It can be concluded that for comparable shoots of the same age, long shoots have longer petioles than short shoots. No data comparing petiole dry weights is available for any other species, so comparisons cannot be made with other studies. Perhaps in successively older short shoots, petioles attain a greater length because of 1) autonomy from the possible inhibitory influence of the pseudoterminal bud and/or 2) the location of older short shoots in the crown which, in turn, relates to light intensity. Similar findings, i.e., short shoot leaves as predominantly shade leaves, have been reported for Fagus (Müller 1947, 1954). In shoots of comparable age, a more developed petiole may be correlated with the growth of lamina length and width, and probably also to the number of side nerve pairs. Although the allometric relationship between lamina length and petiole length for long shoot early leaves differ significantly ($p < 0.01$) from that of short shoot early leaves (Table 3-1), the ratio of lamina length to petiole length for mature early leaves of long shoots did not differ significantly ($p > 0.05$) from that of short shoots (Table 3-2). This may be explained by the fact that in mature early leaves there is a high correlation between the final lamina length and petiole length in both shoot types. Growth of the lamina and petiole may, indeed by closely related (Humphries and Wheeler 1963). Petiole dry weight is probably related

TABLE 3-1. Comparisons of allometric constants between various growth parameters of long and short shoots. Correlation coefficients (r) for each shoot type are stated in parentheses.

GROWTH CHARACTERISTICS	ALLOMETRIC CONSTANT, K		ANOVA F-RATIO
	SHORT SHOOT	LONG SHOOT	
1. Lamina length versus lamina width	1.06 (0.772)	1.32 (0.745)	8.94 **
2. Lamina length versus petiole length	0.69 (0.675)	0.42 (0.459)	11.32 **
3. Stem dry weight versus leaf dry weight	3.41 (0.955)	1.04 (0.946)	22.47 ***
4. Leaf dry weight versus leaf area	1.21 (0.981)	0.48 (0.302)	17.63 ***

**, $P < 0.01$;

***, $P < 0.001$.

TABLE 3-2. Mean values of various morphometric measurements of vegetative long and short shoots.

CHARACTERISTIC	MEAN ± STANDARD DEVIATION		ANOVA
	SHORT SHOOT	LONG SHOOT	F-RATIO
1. Early leaf area (cm^2)	13.2 ± 3.3	20.4 ± 2.9	7.31**
2. Lamina length (mm)	55.1 ± 7.5	69.8 ± 4.9	9.76**
3. Lamina width (mm)	40.9 ± 9.2	45.5 ± 4.3	4.19*
4. Lamina length:width ratio	1.35 ± 0.16	1.53 ± 0.05	4.83*
5. Lamina length: petiole length ratio	3.92 ± 0.10	3.97 ± 0.13	2.26^{NS}
6. Petiole length (mm)	14.1 ± 2.1	17.6 ± 1.6	5.33**
7. Petiole dry weight (mg)	12.9 ± 3.5	19.8 ± 4.9	11.41**
8. Number of side nerves	7.1 ± 1.2	7.6 ± 0.9	3.91*
9. Number of serrations per unit margin length (cm^{-1})	3.47 ± 0.15	3.39 ± 0.21	1.94^{NS}
10. SLA ($cm^3.g^{-1}$)	104.2 ± 5.7	92.6 ± 3.3	7.78**

*, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$; NS, not significantly different.

to the extent of petiolar xylem development. Does this make long shoot early leaves better importers and exporters of assimilate? Would this relate to localized water stress and attendant reduction of photosynthetic efficiency? Studies correlating water content with anatomical and physiological attributes of the leaves are needed. It is not known whether assimilation potential of leaves is influenced by differences in leaf morphology in long and short shoots of paper birch. However, work on Ginkgo by Hoddinott and van Zinderen Bakker (1974) indicates that, at least in Ginkgo, there is no difference in net assimilation between long and short shoots. There is an indication in apple, Malus domestica Borkh., that higher light-absorbing potential of long shoot leaves is due to greater thickness (lower SLA) and better development of palisade tissues (Ghosh 1973).

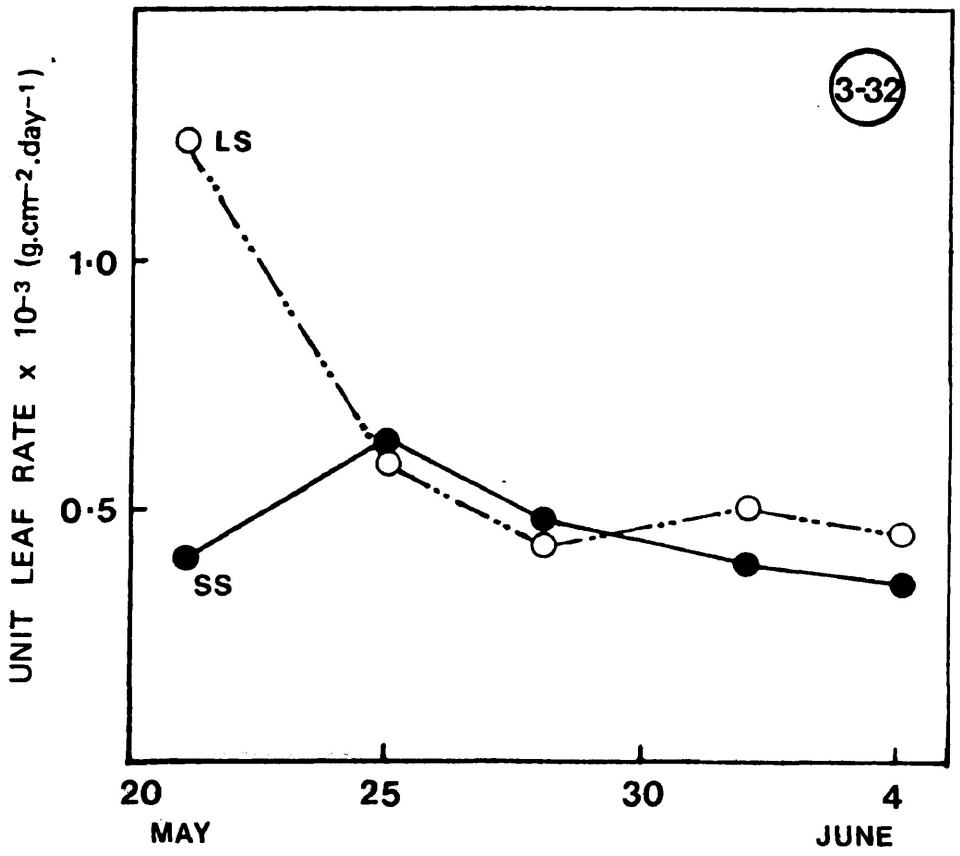
Work on Populus has revealed that photosynthetic rates are higher in long shoots than in short shoots when all leaves, both early and late, are considered (Nelson and Michael 1982). These authors did not find the difference between comparable early leaves of the two shoot types to be significant. Petiole development may, however, be related to the number of water-conducting vessels in the stem of the particular shoot. To ascertain any differences in photosynthetic efficiency between long and short shoot early leaves, ULR (=NAR, net assimilation rate) was derived

by obtaining ratios of Leaf-RGR to LAR. Fig. 3-32 shows trends in ULR. Long shoot early leaves have higher ULR immediately after flushing possibly because they flush first and their leaves are subsequently exposed earlier. In fact, it has been observed in B. papyrifera (long and short shoots were not distinguished) that early leaves have a low diffusive resistance even when they are small. A feature which was viewed as "an advantage in quickly developing photosynthetic capability in spring" (Federer 1976). Although differences in net assimilation rate (i.e., ULR) between long and short shoot leaves of Ginkgo were not statistically significant, long shoot leaves have a lower diffusive resistance and a slightly higher net assimilation rate than short shoot leaves (Hoddinott and van Zinderen Bakker 1974, i.e., Table 1). It must be noted that the ULR of long shoot early leaves in paper birch are slightly higher than short shoot early leaves about two weeks after flushing although the difference is not statistically significant (Fig. 3-32).

Bud dry weight and total early leaf area per node:

In a two-year-old long shoot bearing one-year-old long shoots distally and same-age short shoots proximally, total early leaf area increases acropetally especially for seven-node long shoots. The correlations between post-flush bud dry weight and leaf area have been discussed and need not be repeated (see page 52).

FIG. 3-32. Post-flush derived values of Unit Leaf Rate (ULR). Initial difference between LS and SS is significant ($P < 0.01$).


3-32
LS
SS
1·0
0·5
UNIT LEAF RATE x 10-3 (g.cm-2.day-1)
20
MAY
25
30
4
JUNE

Number of serrations:

Early leaves are double-serrate. Differences in leaf sizes and lamina lengths as well as number of side nerve pairs prompted this investigation. However, the differences between long and short shoots are not significant (Table 3-2). These may, however, relate to the development of laminae.

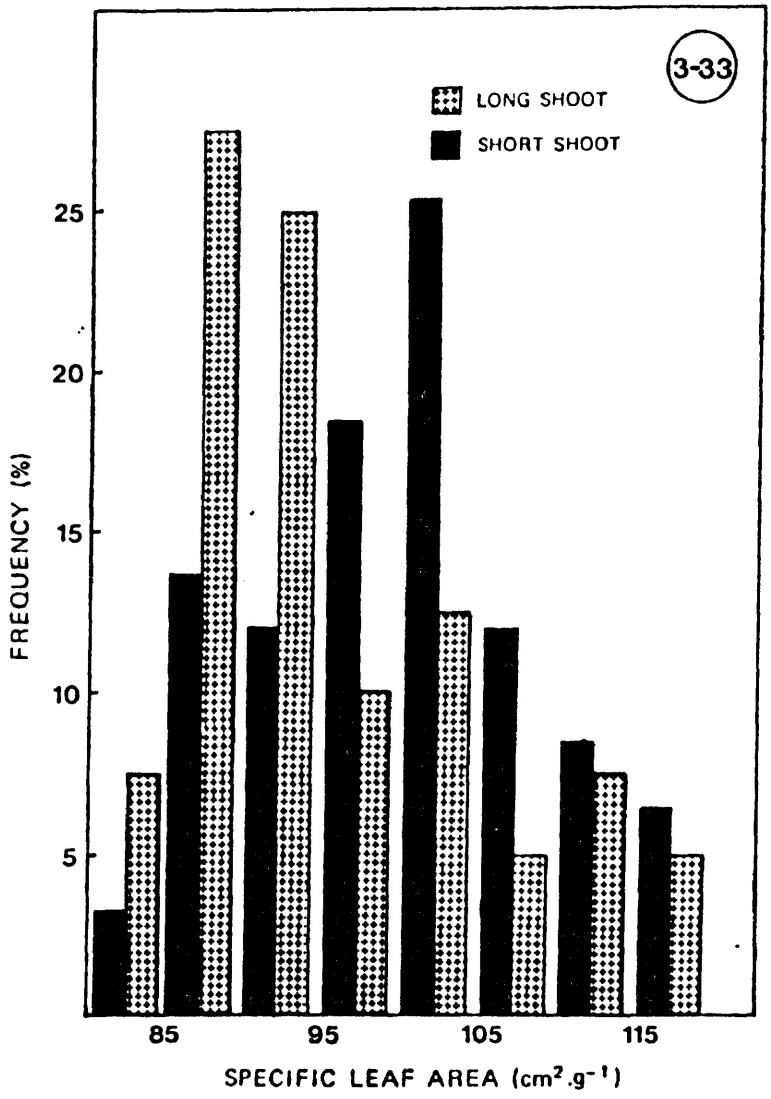
Specific leaf area:

At maturity SLA of long shoot early leaves are lower than those of short shoots (Fig. 3-33). These may be the consequence of leaf thickness or the capacity of the long shoot leaves to retain more dry matter. It is also possible that in long shoots early leaves import assimilates from younger and photosynthetically more efficient late leaves (Nelson and Michael 1982). Storage of assimilates long before senescence may lead to lower SLA. Changes in SLA of Betula platyphylla have been reported (Araki 1972). Autumn leaves contained more dry matter per unit area than spring leaves, although no distinction between long and short shoots was drawn. The capacity for birch leaves to store dry matter during the growing season is implicated.

An hypothesis to explain shoot expression:

The inhibition of axillary buds has been reviewed by Champagnat (1965), Phillips (1969, 1975), Rubinstein

FIG. 3-33. Frequency distribution of specific leaf area of mature LS and SS early leaves at the end of August. LS sample size = 148; SS sample size = 173. Sample sizes are the same for Figs. 12 - 16. Mean values are significantly different ($p < 0.01$).


3-33
LONG SHOOT
SHORT SHOOT
FREQUENCY (%)
25
20
15
10
5
85
95
105
115
SPECIFIC LEAF AREA (cm².g⁻¹)

and Nagao (1976) and McIntyre (1977). The phenomenon is almost always attributed to apical dominance, which Brown et al. (1967) re-examined and suggested the term "apical control". The mechanism of whole-plant morphogenesis has also been attributed to this phenomenon (Zajączkowski et al. 1983), and involves hormonal, nutritional and water factors. The apparent inhibitory influence of the pseudoterminal long shoot bud over axillary buds proximal to it may not be a simple case of apical dominance within one growing season alone. An hypothesis has been suggested for it in birch on the basis of organogenic studies (Macdonald et al. 1983). During the year of secondary bud inception, the parent, or primary bud shoot tip may strongly influence or regulate secondary bud development and bud determination. The response of the secondary bud may depend on its stage of development relative to the activity of the primary bud shoot tip. It can be hypothesized that, initially, the proximal, first-formed secondary buds are affected by strong apical control or dominance, thus promoting short shoot determination. As the primary bud shoot tip grows, forming late leaves, control of dominance weakens due to senescence (short tip abortion), or due to the transformation into a male inflorescence apex. Consequently, the more distal secondary buds, being less

influenced by the primary bud shoot tip, develop as long shoot buds. Therefore, as axillary buds are formed sequentially, in time and space, they are affected differently because of the changing growth activities of the shoot tip. It was also suggested that at least the qualitative nature of apical control or dominance changes with time (Macdonald et al. 1983) and possibly organogenic events within the primary bud. These affect the secondary axillary buds in some way, depending on the stage of development of the axillary bud and likely, also, its axillant leaf and subjacent internode and possibly supradjacent internode, the position of the branch within the crown, the age of the tree, etc. It can be hypothesized that short shoot vegetative terminal buds do not form secondary buds because of a high degree of apical control. Only in the event that the short shoot apex is transformed into a female inflorescence apex, is the control reduced and thus secondary axillary buds are formed (Macdonald et al. 1983). This occurs in late June - early July, at which time the single secondary bud forms rapidly in the axil of the second early leaf. Two secondary axillary buds may also be formed in the axils of both early leaves. Such reproductive short shoots have greater internodal extension between their early leaves. There is evidence for a stimulation of stem

elongation concommitant with anthesis induction (Thomas 1963). An extreme case is that of bolting in rosette plants in which rapid stem elongation and the onset of anthesis are closely correlated. Such instances have been shown to be the consequence of the stimulation of cell division by gibberellic acid (Sachs et al. 1959). Perhaps internodal extension of reproductive short shoots is yet another example of anthesis-induced internode elongation. Thus, it can be suggested, inflorescence induction results in the partial loss or diminution of apical dominance or control. Experimental, anatomical and physiological experiments (e.g, gibberellin and/or other hormonal activities during inflorescence induction) are called for. It is possible that at the onset of inflorescence induction in short shoots there is some sort of "hormonal imbalance" which activates internodal cell division and elongation as well as the inception of secondary axillary bud apices. Exactly what these relations are can only be speculative at the moment. Nevertheless, an hypothesis has been suggested for testing.

CHAPTER 4

CHAPTER 4

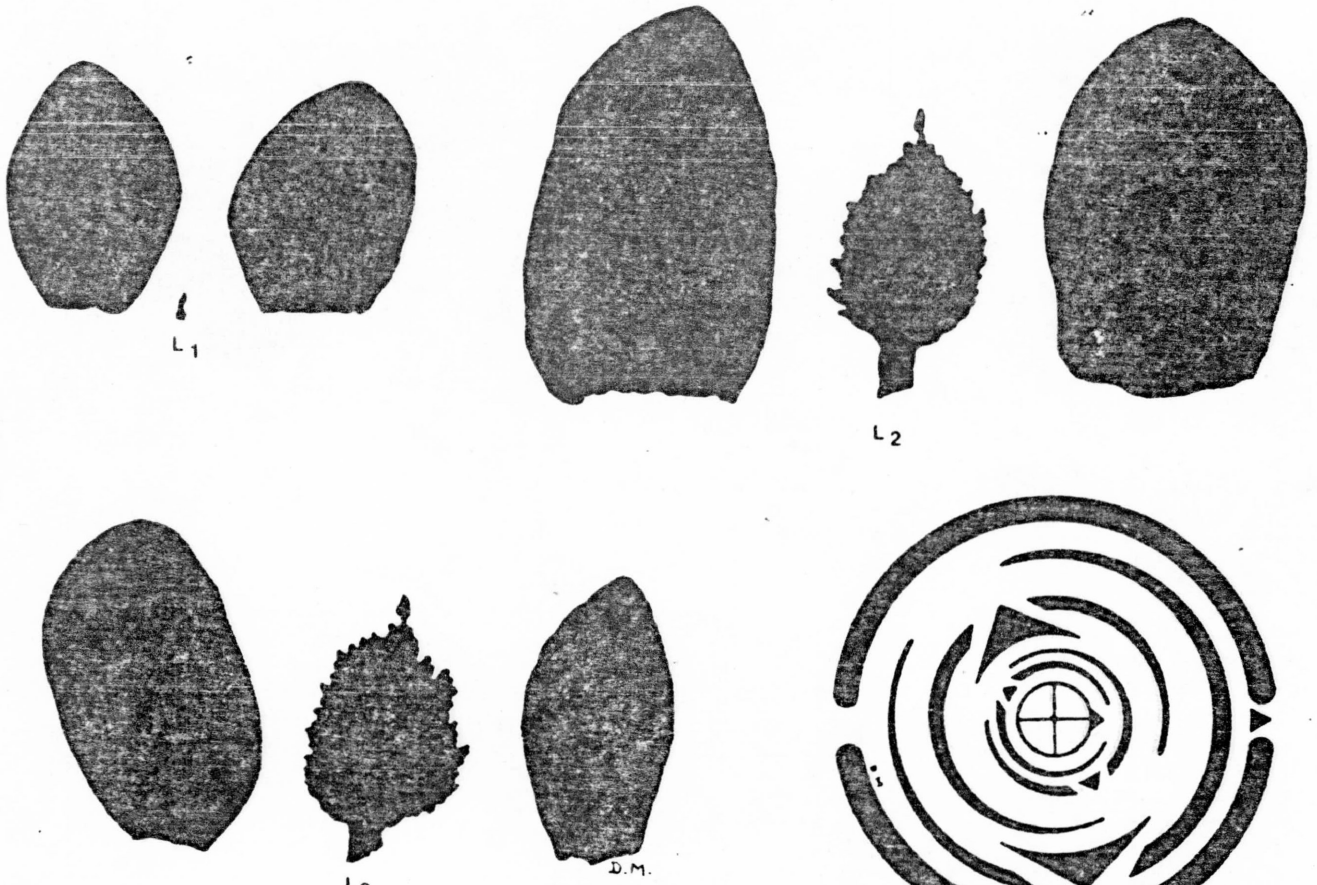
COMPARISON OF VEGETATIVE AND REPRODUCTIVE SHORT SHOOT GROWTH[1]

Introduction

Recent studies on shoot morphogenesis in Betula papyrifera Marsh indicate variations in the time of inception and early development of appendages of vegetative and reproductive short shoot buds (Macdonald and Mothersill 1983). That study shows the difference in the composition and development of buds of reproductive and vegetative short shoots. As stated earlier, short shoots develop from the proximal axillary buds on long shoots and from short shoot terminal buds. Either may carry an embryonic female inflorescence. Long shoots, on the other hand, develop from pseudoterminal long shoot buds, or the most distally positioned axillary buds on a long shoot. Axillary short shoot buds are comprised of an outer rudimentary leaf, 2 - 3 embryonic foliage leaves, and 3 rudimentary leaf primordia (Fig. 4-1). The stipules of the outer leaves form the bud scales. A terminal bud, which forms from an axillary bud apex when the bud flushes, is composed of 3 outer rudimentary leaves and stipular bud scales, 2 - 3

[1]This chapter has been submitted for publication in the Canadian Journal of Botany as: Caesar, J. C. and A. D. Macdonald. Shoot development in Betula papyrifera II - Comparison of vegetative and reproductive short shoot growth; and has since been accepted for publication.

FIG. 4-1. Bud composition and aestivation of appendages of a proximally situated bud on a long shoot i.e., potential short shoot bud. L_1, rudimentary leaf; L_2, L_3, embryonic foliage leaves; L_4, L_5, L_6, primordial rudimentary leaves.



4-1

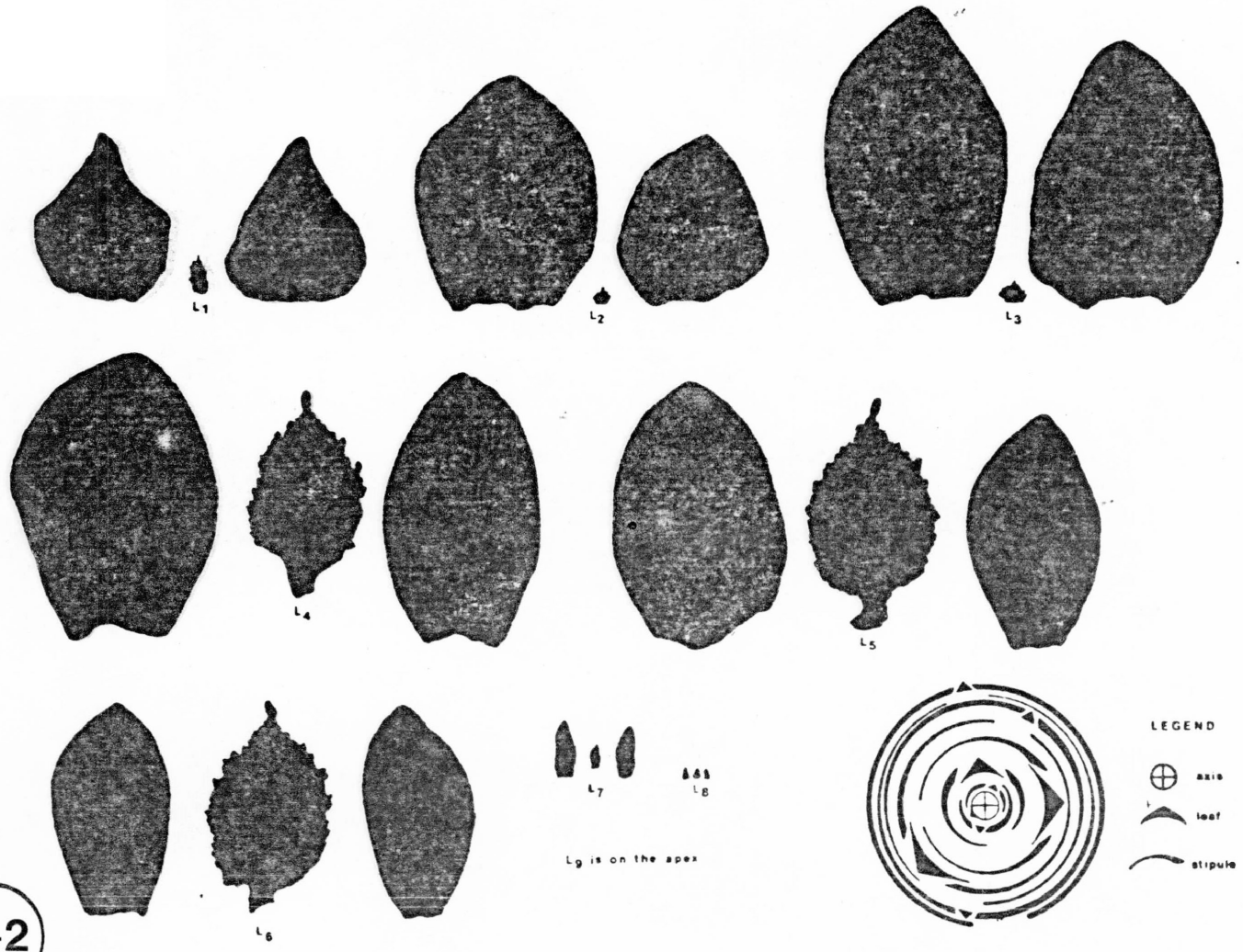
embryonic foliage leaves and finally, 3 rudimentary leaf primordia (Fig. 4-2). If floral induction occurs at the end of June, the last formed 3 rudimentary leaf primordia in both bud types do not form. Instead, at the time of induction, 2 transitional leaves arise in sequence, and the apex continues to broaden, forming inflorescence bracts (Macdonald and Mothersill 1983).

Preliminary observations show differences in the rate of growth of foliage leaves in these buds during and after bud break. Foliage leaves of the reproductive shoot seem to develop more in length than width, in contrast to the vegetative shoot. Reproductive short shoot foliage leaves at maturity are unequal in size, whereas vegetative short shoot foliage leaves attain almost the same size at maturity (see Figs. 4-6, 4-14 and 3-1b$_1$). Foliage leaves of the reproductive shoot seem to have fewer serrations per unit length of leaf margin than other foliage leaves (Fig. 4-3). This study illustrates the quantitative differences in leaf growth of the vegetative and reproductive short shoots.

Observations and Discussion

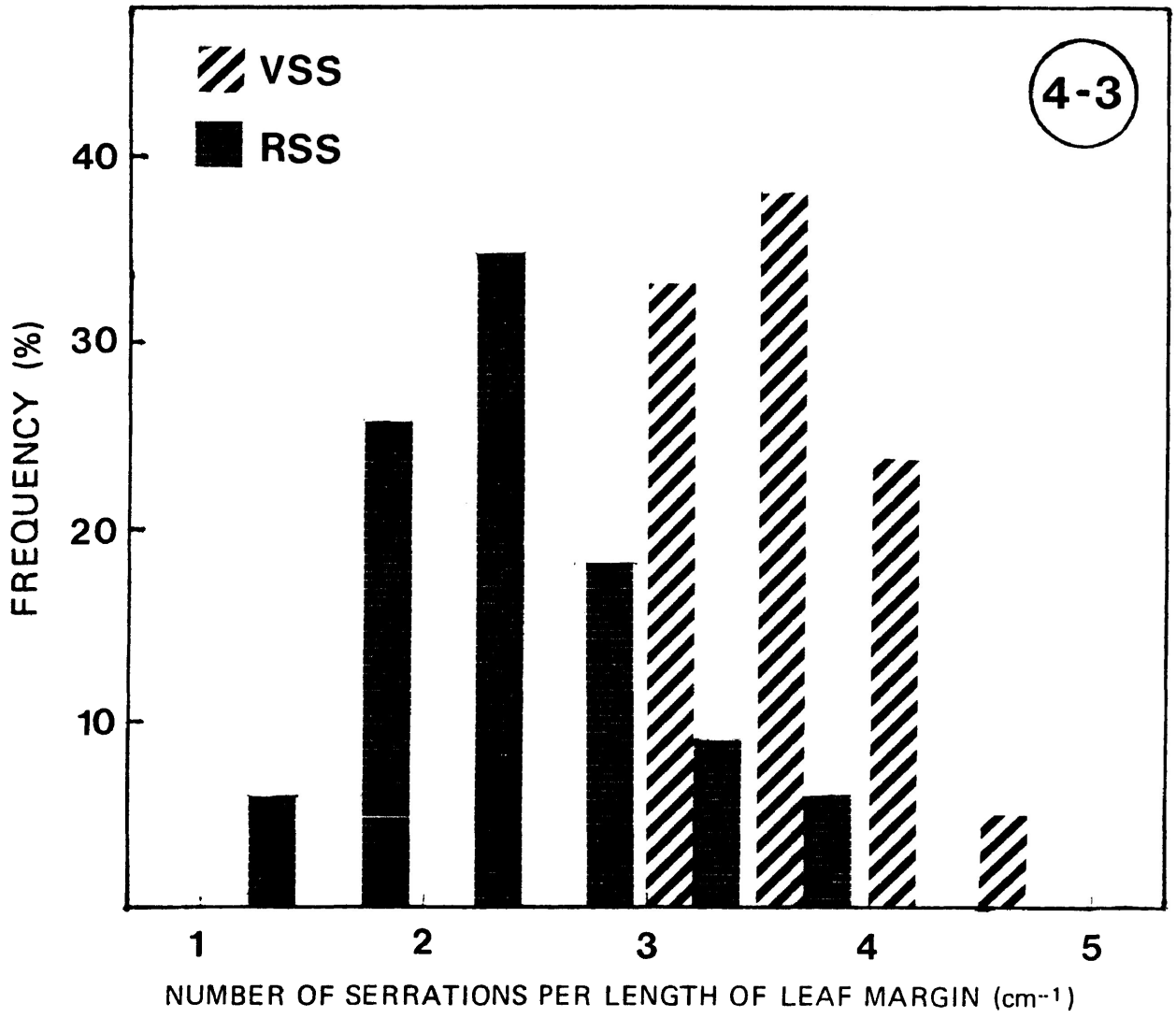
Short shoot buds have been grouped in the following age classes: 1. one-year-old buds which are the proximal axillary buds on long shoots; 2. 2-4-year-old short shoot

FIG. 4-2. Composition and aestivation of appendages of vegetative short shoot terminal buds. L_1, L_2, L_3, rudimentary leaves; L_4, L_5, L_6, embryonic foliage leaves; L_7, L_8, L_9, primordial rudimentary leaves.


L1
L2
L3
L4
L5
L6
L7
L8
L9 is on the apex
LEGEND
axis
leaf
stipule

4-2

FIG. 4-3. Frequency distribution of the number of serrations per unit length (cm) leaf margin of vegetative and reproductive short shoots.


VSS
RSS
4-3
40
30
20
10
FREQUENCY (%)
1
2
3
4
5
NUMBER OF SERRATIONS PER LENGTH OF LEAF MARGIN (cm⁻¹)

terminal buds and 3. 5-10-year-old short shoot terminal buds. Short shoot buds of different age classes differ in their mean relative growth rates (RGR's) per day (Fig. 4-4). RGR's of short shoot buds are lower than the RGR's of pseudoterminal buds. Pseudoterminal buds on the previous season's long shoots give rise to long shoots. One-year-old short shoot buds exhibit lower RGR's than 2-4 year old short shoot terminal buds until May 18. The RGR of 5-10 year old short shoot terminal buds is higher than than of younger short shoot buds. One possible explanation is that growth of the pseudoterminal bud which forms the new long shoot, exhibits an inhibitory influence on the more proximal buds. Pruning experiments in young yellow birch, Betula alleghaniensis Britton, by Metzger (1977) clearly demonstrate this apparent dominance of distal buds. Older short shoot terminal buds are further removed from expanding long shoots and consequently possess a greater degree of autonomy. This notion is reinforced by my observations of flushing sequences, i.e., distally situated buds which will grow into long shoots flush before proximally situated incipient short shoot buds. Furthermore, short shoot terminal buds flush before axillary short shoot buds. Seasonal height growth of a number of deciduous trees, including paper birch (Kozlowski and Ward 1957) and seedlings (Kozlowski and Ward 1961), begins rapidly in May in Massachusetts.

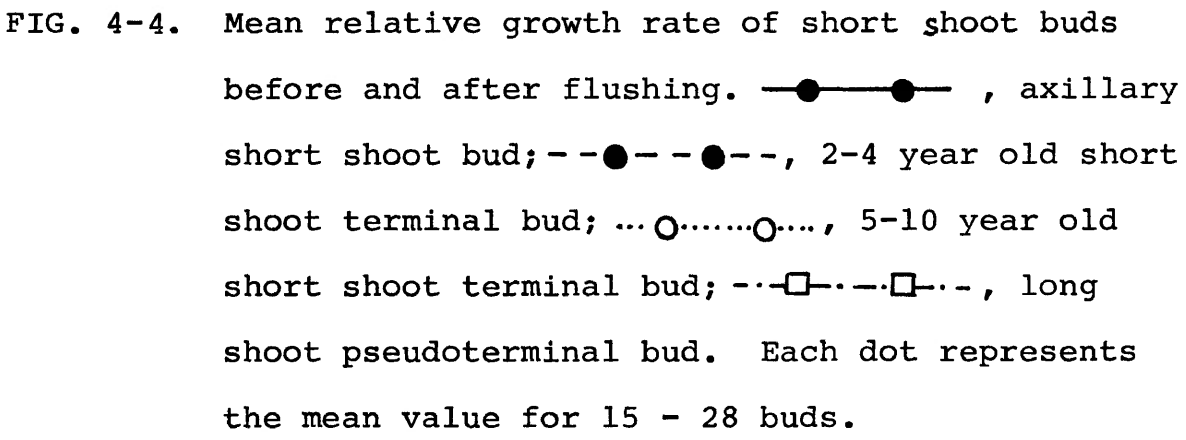
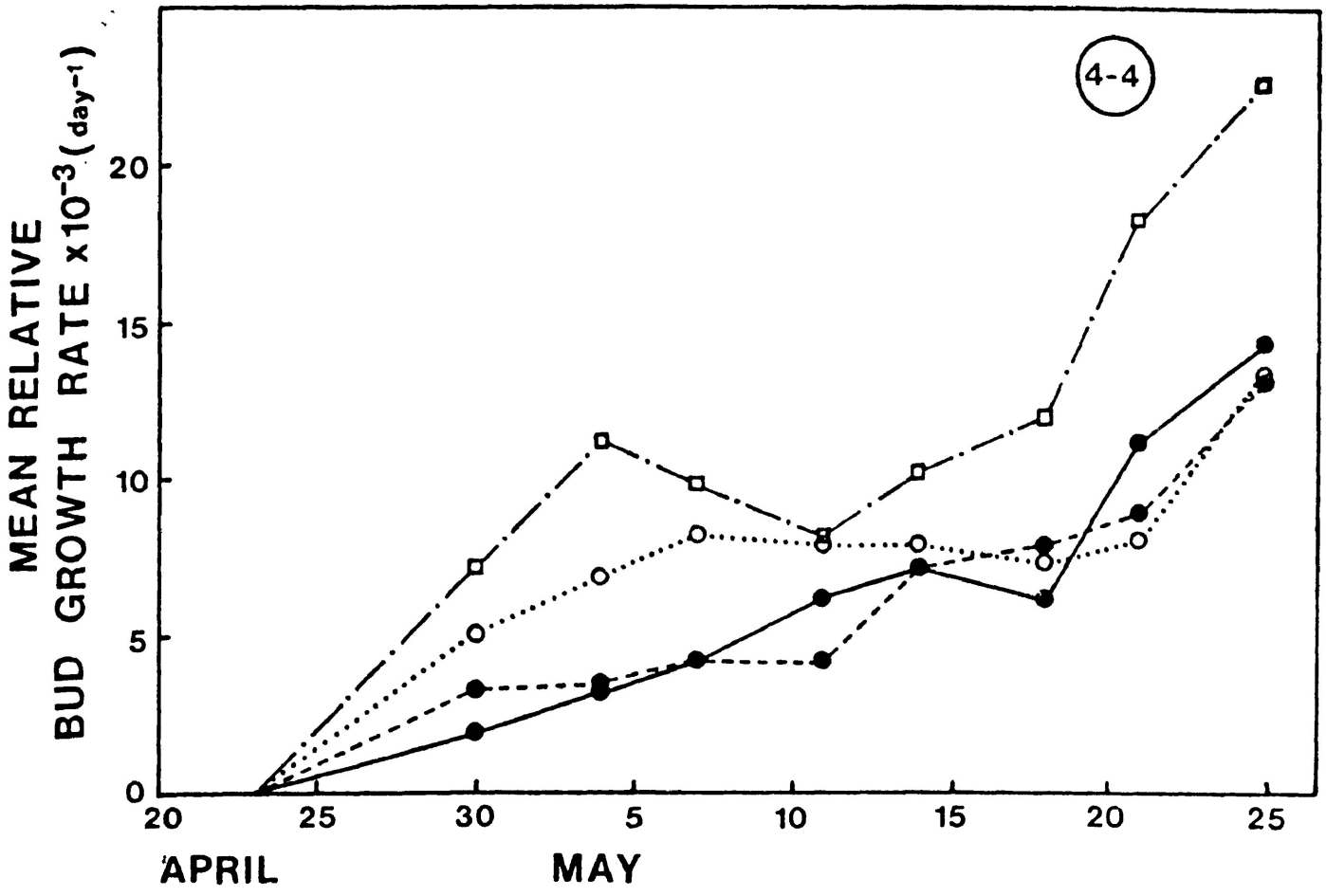


FIG. 4-4. Mean relative growth rate of short shoot buds before and after flushing. —●——●— , axillary short shoot bud; - -●- -●- -, 2-4 year old short shoot terminal bud; ...o.....o...., 5-10 year old short shoot terminal bud; -··-□-·—·□-··-, long shoot pseudoterminal bud. Each dot represents the mean value for 15 - 28 buds.


4-4
MEAN RELATIVE BUD GROWTH RATE x10^{-3}(day^{-1})
0
5
10
15
20
20
25
30
5
10
15
20
25
APRIL
MAY

The rise in RGR of buds (Fig. 4-4), which occurs toward the end of May, may be explained by the rapid increase in dry weight after bud burst brought about by the rapidly expanding foliage leaves (Fig. 4-5). Leaf elongation and expansion are very rapid in May immediately after bud burst (Fig. 4- 6). Rapid leaf growth rate of early leaves has also been documented for species of Populus and Betula by other authors (i.e., Critchfield 1960; Kozlowski 1971; Kozlowski and Clausen 1966). Mobilization of soluble sugars and increase in water content in April-May was recorded for twigs of B. populifolia (Gibbs 1940). A similar situation presumably occurs in paper birch as indicated earlier. There is an increase in RGR of leaves of both vegetative and reproductive short shoots. The RGR of leaves of the latter is significantly lower, particularly after flushing, than that of vegetative short shoot leaves (Fig. 4-5). This is likely a consequence of developing female inflorescences and foliage leaves of the same shoot competing for nutrients which must enter the shoot along a common translocation pathway. The developing inflorescence presumably is a preferred "sink" (Kozlowski and Keller 1966; Hansen 1967; Cockshull and Hughes 1968; Kriedmann 1968, 1969; Dickman and Kozlowski 1970; Ryle and Powell 1972; Davis and Sparks 1974; Tse et al. 1974; Powell 1977a, 1977b; Sachs 1977, 1979; Ramina et al. 1979;

FIG. 4-5. Relative foliage leaf growth rate of vegetative (vss) and reproductive short shoots (rss) before and after flushing. Each dot represents the mean for 30 - 45 leaves. Values are significantly different after flushing ($p < 0.01$).

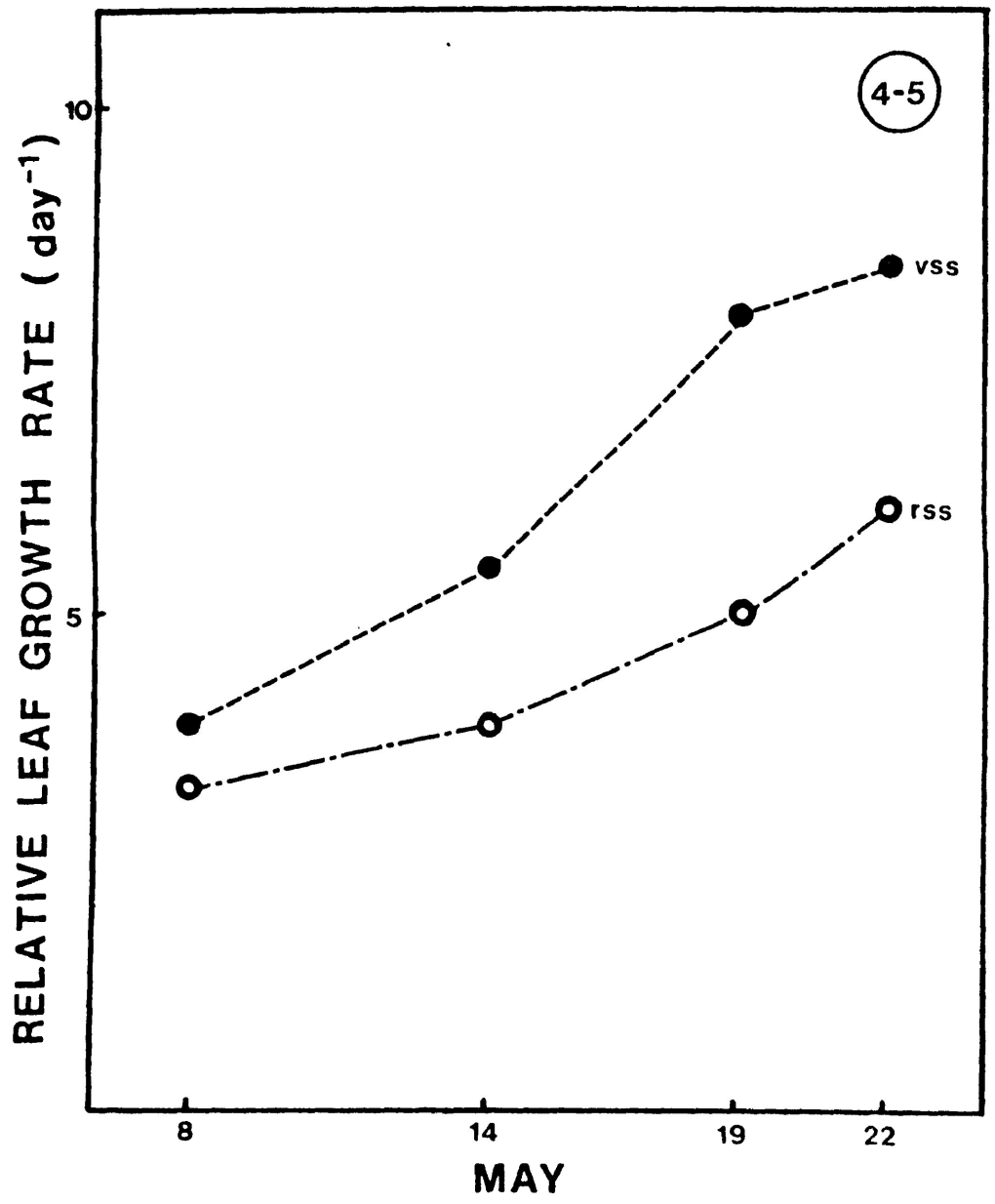
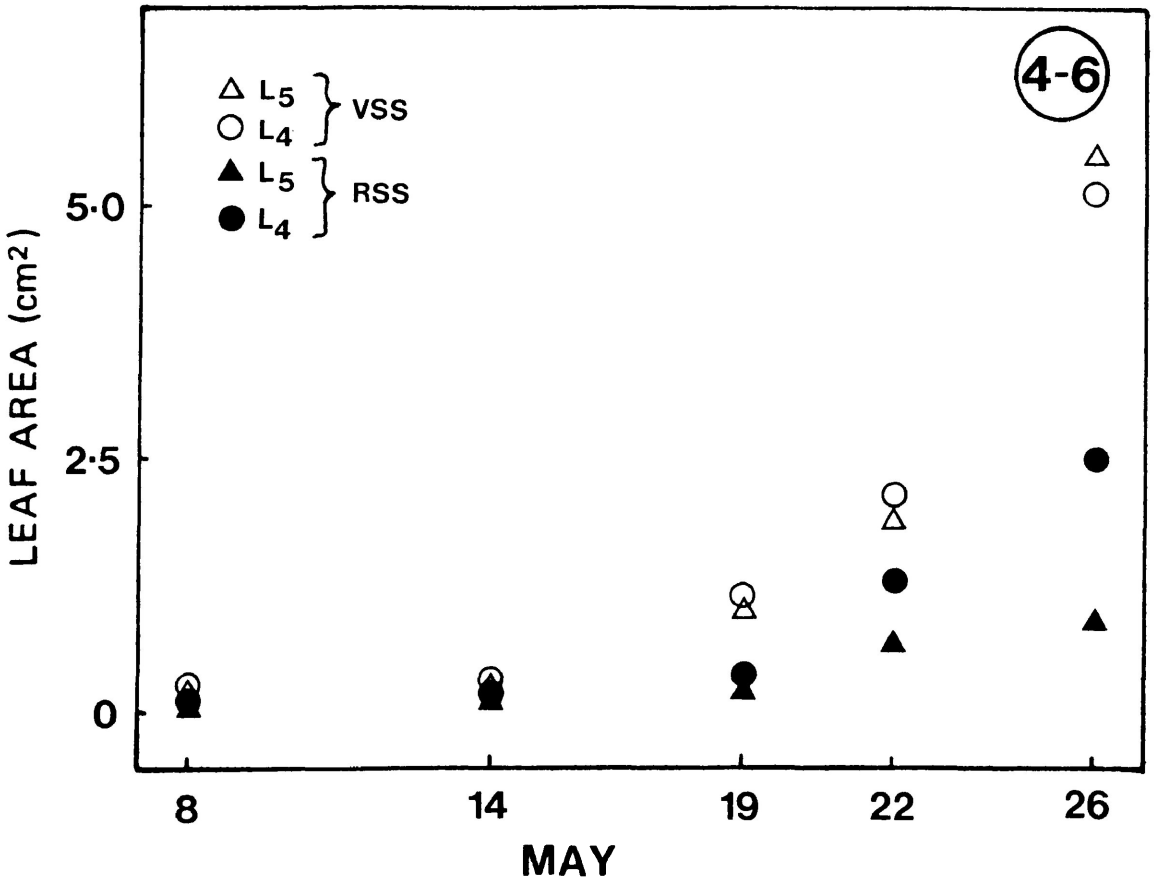

4-5
RELATIVE LEAF GROWTH RATE (day^{-1})
10
5
vss
rss
8
14
19
22
MAY

FIG. 4-6. Early leaf expansion of vegetative and reproductive short shoot leaves showing slower expansion in reproductive short shoots. Note that in vegetative shoots L_3 expansion exceeds that of L_2 in May but this is not so in reproductive shoots.


4-6
△ L5
○ L4
VSS
▲ L5
● L4
RSS
5·0
2·5
0
LEAF AREA (cm²)
8
14
19
22
26
MAY

Crawford et al. 1982; Malstrom and McMeans 1982; Tuomi et al. 1982). Reproductive short shoots also produce axillary buds which are not found on vegetative short shoots; although it is not common, these axillary buds may flush during the next growing season as long shoots (see Fig. 3-1e). Nevertheless, these developing buds may also compete for assimilates. In addition, high seed production also decreases annual wood increment in trees (Antevs 1917; Hustich 1956; Eis et al. 1965), indicating that the inflorescence also competes for assimilates which could have been exported to the cambial "sink". Both inflorescence and axillary bud development may have a correlative influence in suppressing leaf growth.

Competition for nutrients exists the summer before bud burst, probably as early as the time of transformation of the apex from the vegetative to the inflorescence state. At the time of transformation growth at the apex is very rapid (Macdonald and Mothersill 1983). This has been recorded for other species (i.e. Bernier 1971; Lyndon 1977). Increased RNA synthesis (Gifford and Tepper 1962; Bronchart et al. 1970; Jacqmard et al. 1972; Usciati et al. 1972; Lyndon 1977) and mitotic activity (Thomas 1961; Bernier 1964; King 1972; Bodson 1975; Lyndon 1977) in shoot apices have been reported during the transition to anthesis - induction and/or development. Carbohydrate mobilization

toward a reproductive apex has been reported by Bodson 1977) for Sinapis. It is possible that in birch early leaf development may be disadvantaged during this period of rapid early inflorescence development. Thus considerable competition between developing embryonic leaves and the inflorescence precedes the onset of dormancy. The potential for rapid growth in the spring of reproductive short shoot leaves, therefore would be lower.

Specific leaf area, the ratio of leaf area to dry weight, increases more rapidly for developing reproductive short shoot leaves (Fig. 4-7), especially after flushing. Consequently, mature leaves of reproductive short shoots are thinner than leaves of vegetative short shoot leaves (Fig. 4-8). Ryle and Powell (1972) found that in Lolium net allocation of resources to expanding leaves is reduced during inflorescence development and, at the same time, expanded leaves on reproductive shoots export more assimilate than comparable leaves on vegetative shoots. The significance of thinner leaves in this study is not clear. In birch, it is possible that during their early development, leaves on reproductive shoots may not be receiving optimal levels of assimilates. On the other hand, leaves of reproductive shoots may be exporting more assimilates than leaves of vegetative shoots. Either situation or a combination of both might explain the higher SLA values for reproductive short shoot leaves.

FIG. 4-7. Specific leaf area of vegetative (vss) and reproductive short shoots (rss) as a function of time: pre- and post-flushing. Sample size is the same as in Fig. 4-8. Differences on the day of flushing, May 14, and after, are significant ($p < 0.05$).

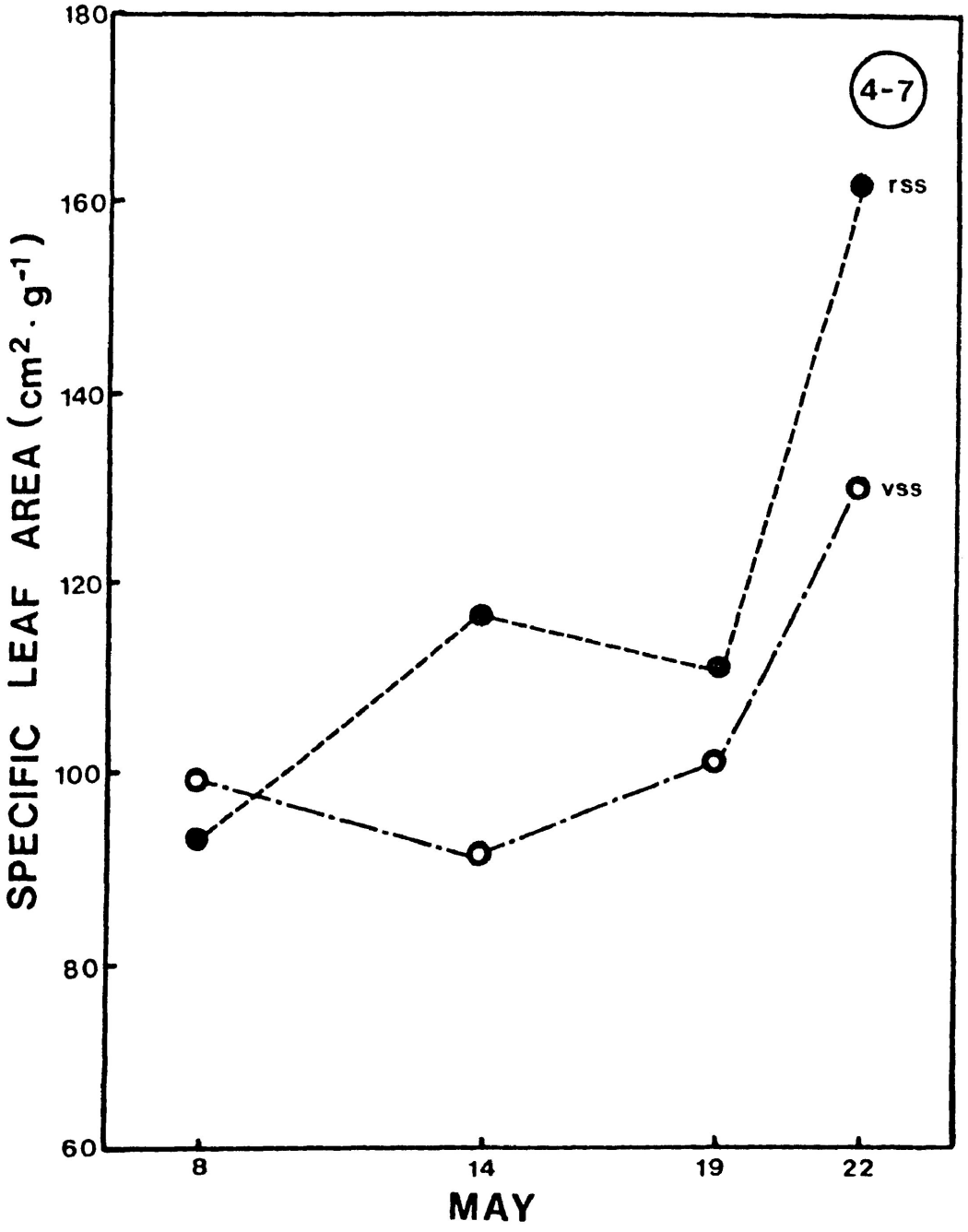
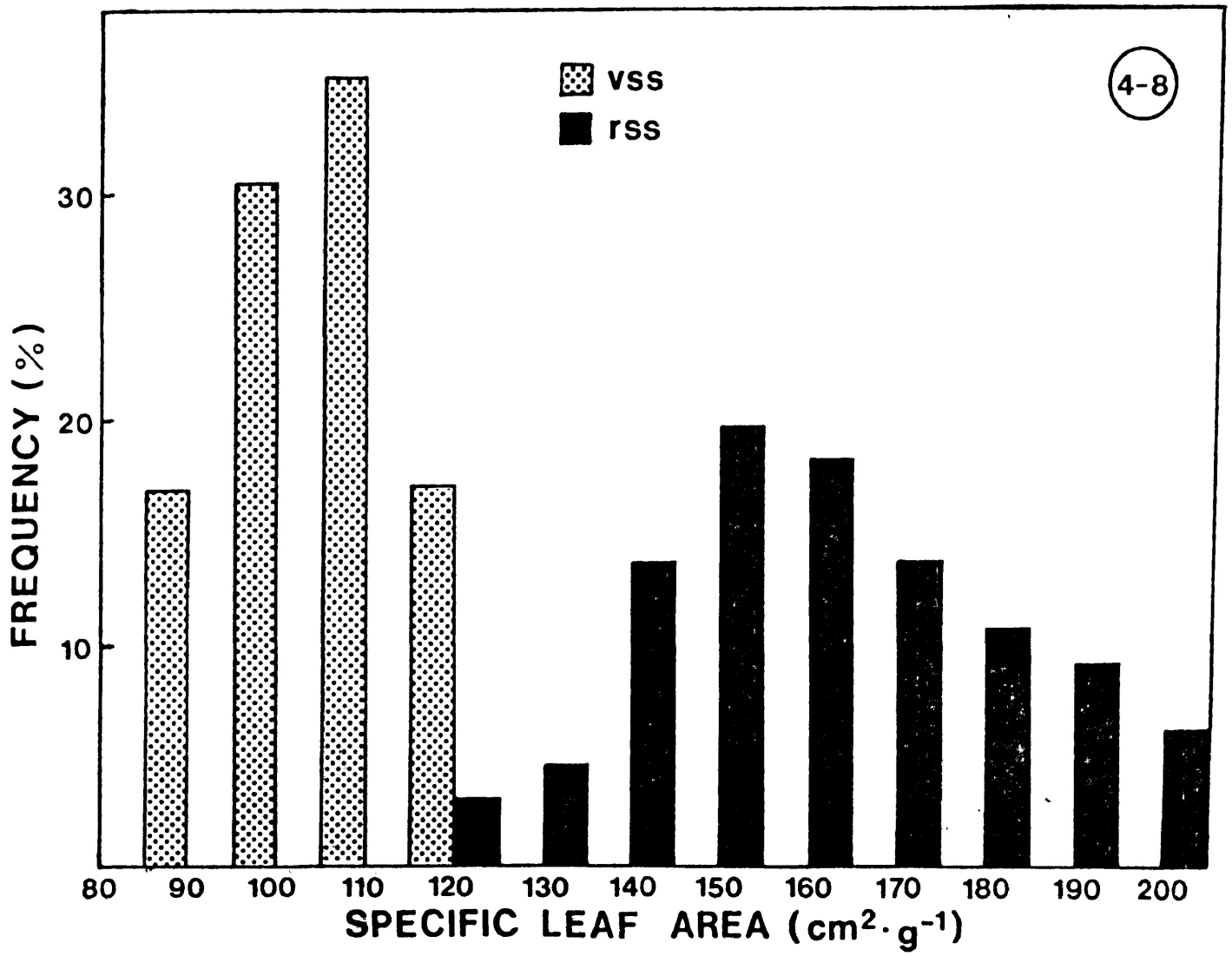

4-7
rss
vss
SPECIFIC LEAF AREA ($cm^2 \cdot g^{-1}$)
180
160
140
120
100
80
60
8
14
19
22
MAY

FIG. 4-8. Frequency distribution of specific leaf area values for vegetative and reproductive short shoot mature leaves, based on a minimum of 113 and 91 randomly selected leaves, respectively. Mean values are significantly different ($p < 0.001$).


vss
rss
4-8
FREQUENCY (%)
30
20
10
80
90
100
110
120
130
140
150
160
170
180
190
200
SPECIFIC LEAF AREA (cm2·g-1)

Leaf area ratio, the ratio of leaf area to shoot dry weight, is lower in expanding leaves of reproductive shoots than in expanding leaves of vegetative shoots (Fig. 4-9). Reproductive shoots have a lower leaf area per unit shoot weight, hence less "leafiness", according to Hunt (1978) who defines LAR as "an index of leafiness". Export of assimilates from expanding leaves to the developing inflorescence, may be the cause of lower LAR in reproductive shoots. Leaf area as affected by reproduction has been noted in some Gramineae (Borill 1959) and apple (Maggs 1963; Heim et al. 1979). In Populus tremuloides total annual leaf production was reduced due to spring production of catkins (Ovington 1963). Reproductive short shoot leaves are smaller than vegetative short shoot leaves (Fig. 4-10); this is another example of reproductive cost (Calow 1979; Tuomi et al. 1982). It is well documented that fruiting has a marked effect on vegetative growth (Mattirolo 1899, cited by Loomis 1953; Roberts 1920; Chandler and Heinicke 1925; Murneek 1926, 1932; Chandler 1934; Cameron and Borst 1938; Morris 1951; Loomis 1953; Mochizuki 1962; Maggs 1963; Rogers and Booth 1964; Kozlowski and Keller 1966; Harper and Ogden 1970; Gross 1972; Lindoo and Noodén 1976; Powell 1977a, 1977b; Calow 1979; Heim et al. 1979; Lovett Doust 1980; Malstrom and McMeans 1982; Lovett Doust and Lovett Doust 1983; Weiland et al. 1982). This

FIG. 4-9. Leaf area ratio of vegetative (vss) and reproductive short shoots (rss) as a function of time: pre- and post-flushing. Each dot represents a mean for 20 buds. Differences between values are highly significant ($p < 0.001$).

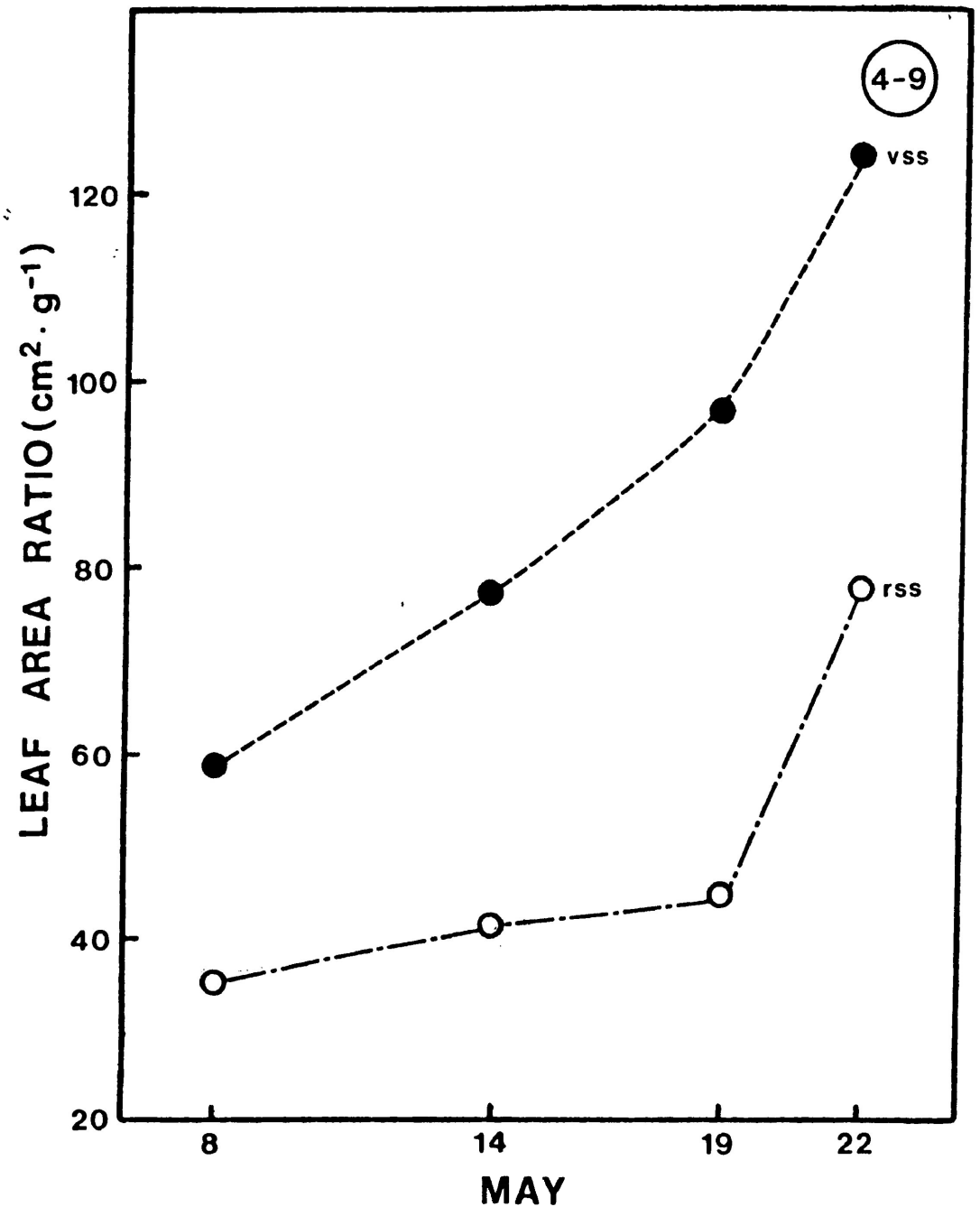
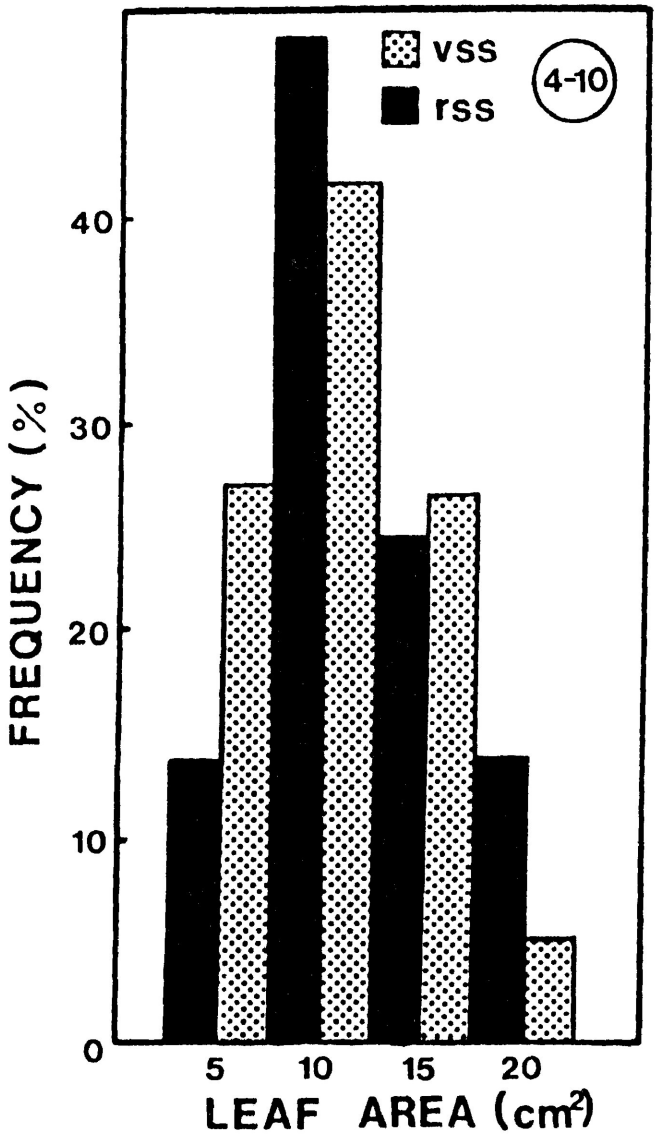

4-9
vss
rss
LEAF AREA RATIO(cm^2·g^{-1})
120
100
80
60
40
20
8
14
19
22
MAY

FIG. 4-10. Frequency distribution of leaf area: vegetative and reproductive short shoot mature leaves. Sample sizes for vss and rss are 137 and 107, respectively. Mean values of all leaves for each shoot type differ ($p < 0.05$).


vss
rss
4-10
FREQUENCY (%)
0
10
20
30
40
5
10
15
20
LEAF AREA (cm²)

effect, I believe, is manifested as a slower rate of leaf growth from the time of floral induction.

Ratios of lamina length to width (Fig. 4-11) suggest that the reproductive short shoot leaves expand in length more than in width when compared to leaves of vegetative short shoots. This results in elliptical leaves (Figs. 3-1b; 4-12; 4-13b,c, d, e). Leaves on vegetative short shoots are widely ovate (Figs. 3-1b; 4-14a; 4-13a). A regression analysis of lamina length on width for leaves from the two shoot types (Fig. 4-15) confirms the tendency toward comparative "lengthiness" of lamina at the expense of width in reproductive short shoot leaves. This feature has been documented in five other Betula species (Jentys-Szaferowa 1937). In both cases there is a high correlation between length and width of the leaf blade; r = +0.912 and +0.944 for reproductive and vegetative short shoot leaves, respectively.

The cause of the differences in leaf length : width ratios in birch is not known, however, this aspect should be examined. Borrill (1961) shows that differences in leaf blade width in Lolium is due largely to variations in cell number and that differences in blade length result from differences in cell length. In birch, if lamina width is due to the number of cells formed during embryonic leaf development the summer before flushing, the time of rapid

FIG. 4-11. Frequency distribution of leaf lamina length to width ratios in vegetative (vss) and reproductive short shoots (rss). Sample size is the same as in Fig. 4-12. Mean value for vss differs significantly from rss value ($p < 0.01$).

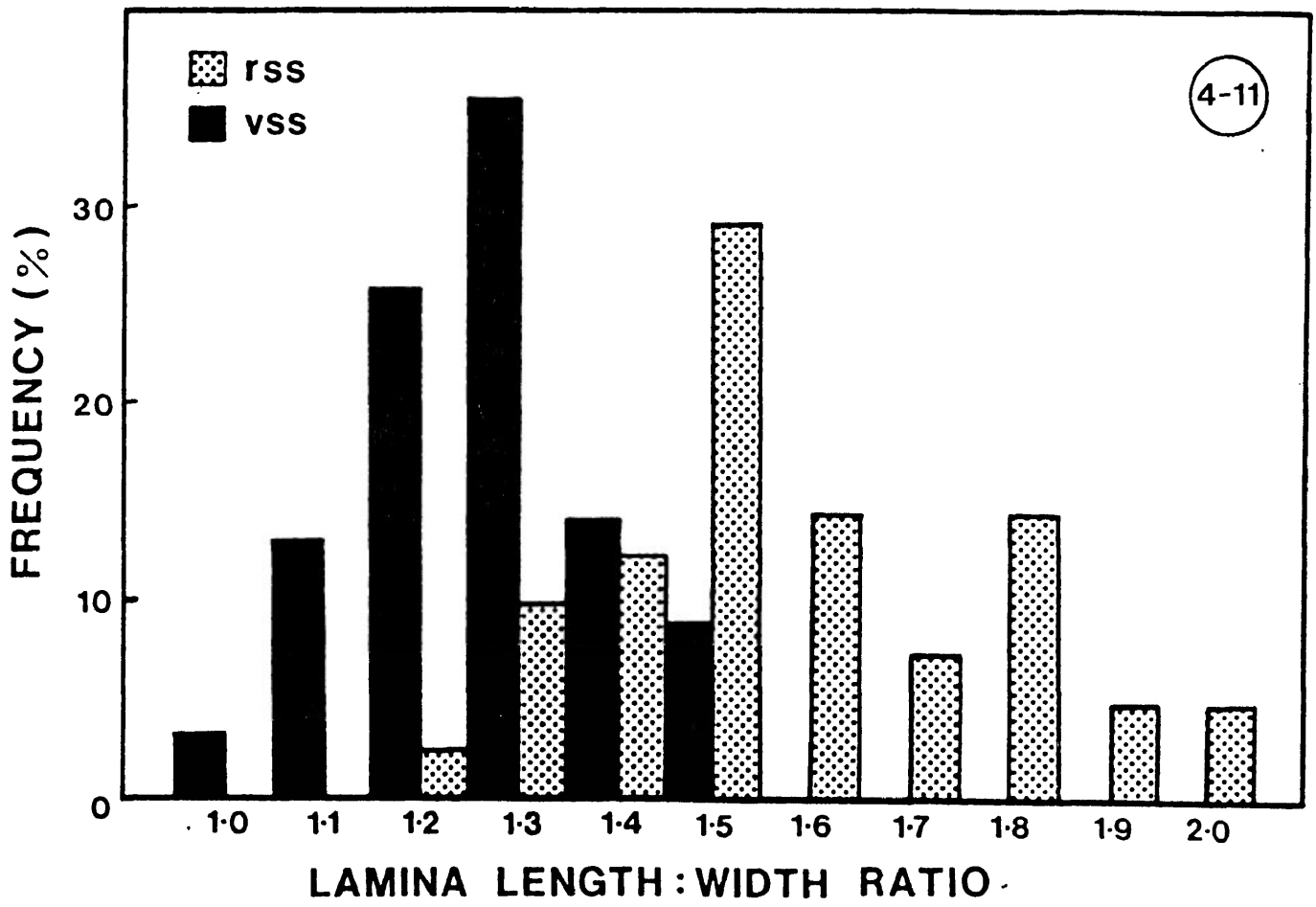

rss
vss
4-11
FREQUENCY (%)
0
10
20
30
1·0
1·1
1·2
1·3
1·4
1·5
1·6
1·7
1·8
1·9
2·0
LAMINA LENGTH : WIDTH RATIO

FIG. 4-12. x 0.70. Reproductive short shoot with elliptical leaves and female inflorescences (catkins).


4-12

FIG. 4-13 x 0.675. Early leaves of vegetative shoot (a) and reproductive shoots (b - f), showing various gradations in size. Leaf f is a transition leaf, associated with reproductive short shoots.

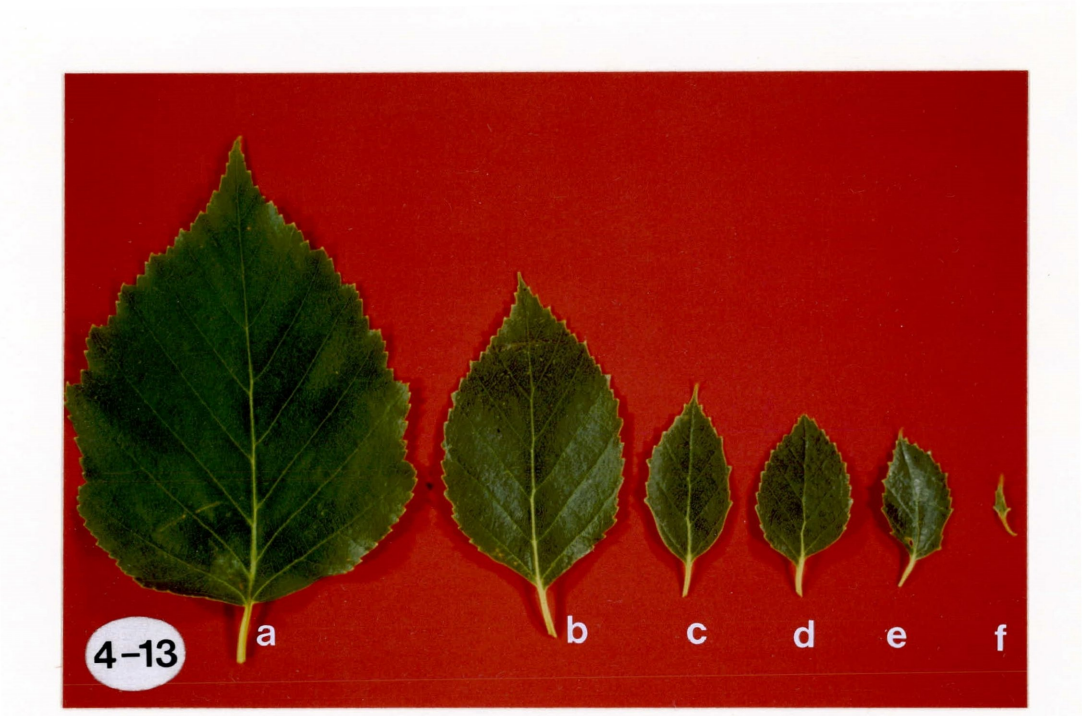
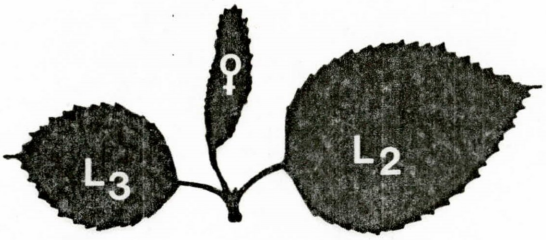
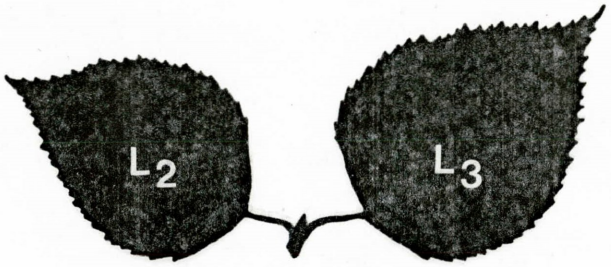

4–13
a
b
c
d
e
f

FIG. 4-14 x 0.675. Silhouette drawings of reproductive and vegetative short shoots showing size variations between shoot types and leaves L_2 and L_3. In reproductive shoots L_3 the second foliage leaf is smaller than L_2; this is not so in vegetative shoots.



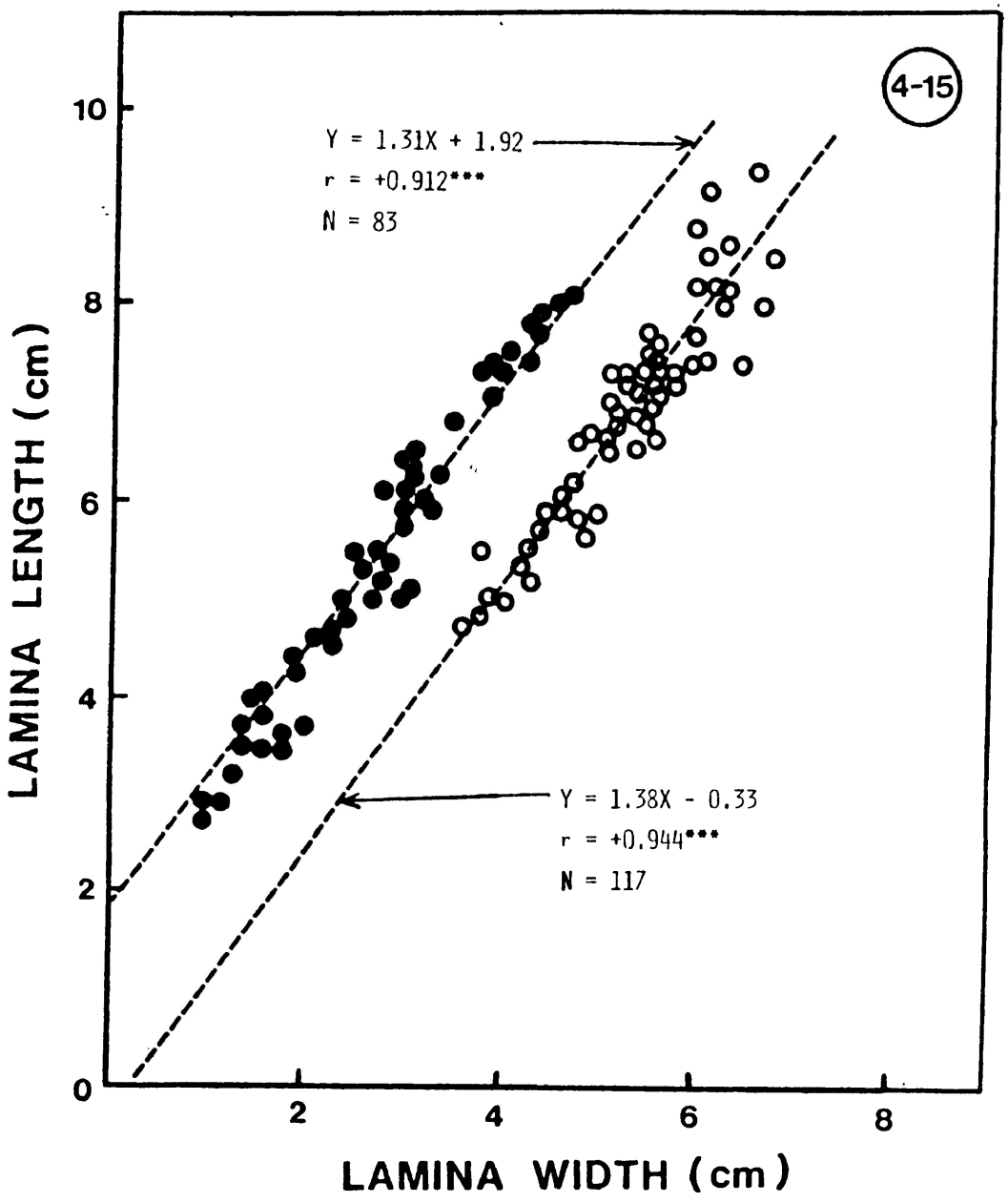
rss



vss

4-14

FIG. 4-15. Relationship between leaf lamina length and width of vegetative and reproductive short shoot leaves. Solid dots represent values for reproductive short shoots and open dots for vegetative short shoot leaves.

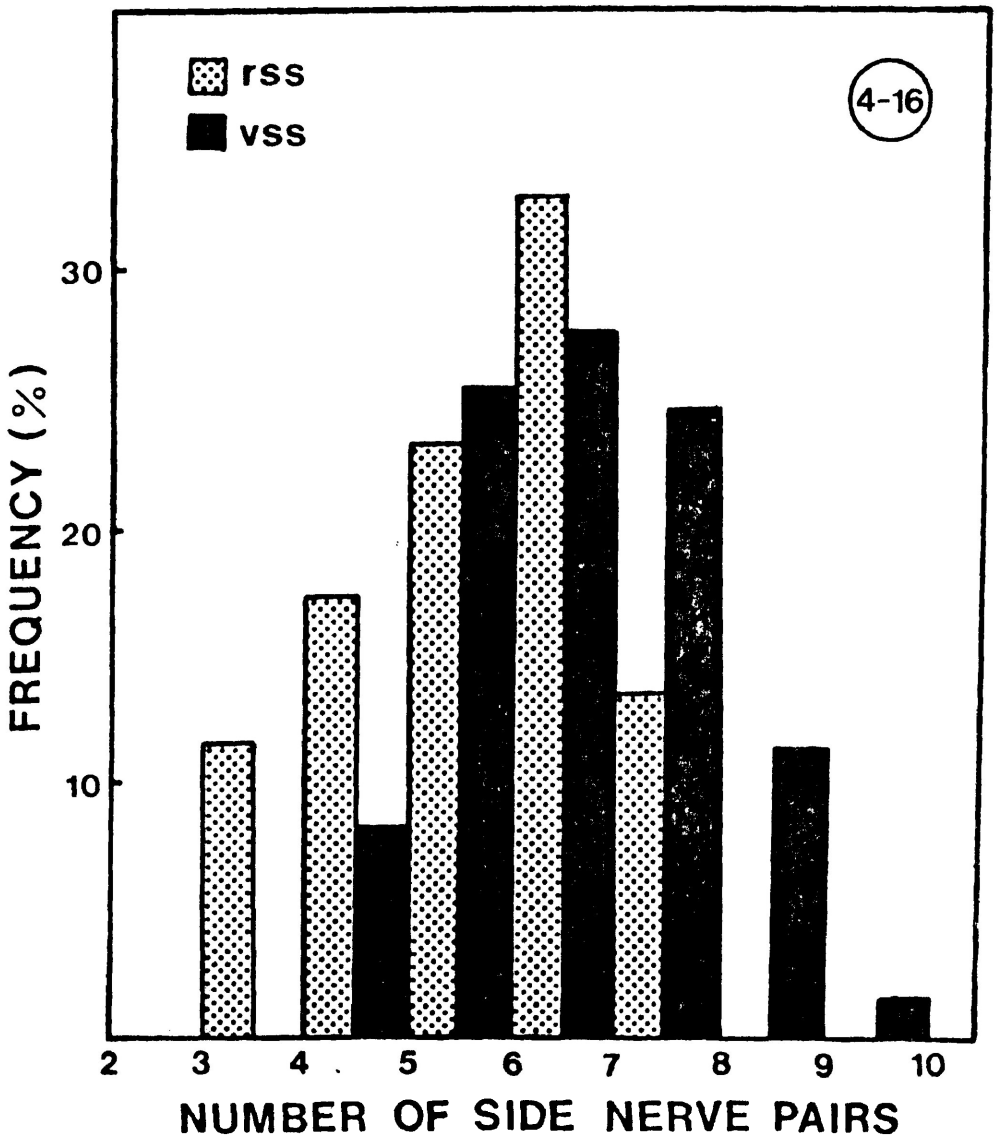

4-15
Y = 1.31X + 1.92
r = +0.912***
N = 83
Y = 1.38X - 0.33
r = +0.944***
N = 117
LAMINA LENGTH (cm)
LAMINA WIDTH (cm)
0
2
4
6
8
10

early inflorescence development would correspond to the period of leaf lamina formation and this might result in suppressed mitotic activity in these leaves. Thus, it is possible that embryonic leaves of reproductive short shoots have a reduced potential for growth in the spring. Another intriguing morphological difference between leaves of the two shoot types is the occurrence of fewer pairs of side nerves in reproductive short shoot leaves (Fig. 4-16). Does this imply that these leaves are less efficient exporters? It is possible that the occurrence of fewer nerve-pairs is associated with less accumulation of dry matter in reproductive short shoot leaves. The result of reproductive cost seems to be reflected in the differences in leaf morphology.

These findings - smaller leaf area, thinner leaves, slower leaf growth rate, higher lamina length to width ratios, fewer number of side nerve-pairs and serrations per length all reflect the cost of reproduction in short shoots of B. papyrifera.

FIG. 4-16. Frequency distribution of number of pairs of side nerves of vegetative and reproductive short shoot leaves. Sample size is the same as in Fig. 4-12. Mean number of side nerve pairs are significantly different for the two shoot types ($p < 0.01$).

CHAPTER 5


rss
vss
4-16
30
20
10
FREQUENCY (%)
2
3
4
5
6
7
8
9
10
NUMBER OF SIDE NERVE PAIRS

CHAPTER 5

EFFECT OF MALE REPRODUCTION ON LONG SHOOTS AND THEIR SUBSEQUENT DEVELOPMENT

Introduction

Reproductive short shoots have been observed to have smaller leaf sizes and other morphometric distinctions from comparable-aged vegetative short shoots (Caesar and Macdonald, 1983, in press). However, the short shoot is not the only reproductive unit. Male inflorescences are borne terminally only on long shoots but not on each long shoot. A description or evaluation of male reproductive cost in birch has not been previously reported. Previous studies have emphasized the effect of seed production on subsequent year's growth of paper birch (Gross 1972) and the cost of female reproduction on short shoots (Jentys-Szaferowa 1937; Tuomi et al. 1982). In Populus the effect of female catkin production has been similarly reported (Ovington 1963) in addition to the effects of female strobili on vegetative growth in conifers (Powell 1977a, 1977b).

Compared to a non-flowering long shoot, fewer long shoots flush on a previous season's flowering long shoot and, in extreme cases, only short shoots may flush on a reproductive long shoot. Thus branch vigour decreases when male inflorescences are formed. Since long shoots provide the framework of the developing tree crown (Macdonald

et al. 1983), the analysis of the effect of reproduction on trees, based on female reproductive units alone, is not sufficient unless the cost of male reproduction is also quantified. It could be argued that since long shoots appear to be more vigorous than short shoots that reproductive cost may be considered negligible. Is it only female catkin production and subsequent seed set, therefore, which affects the vegetative growth of paper birch?

This paper presents data on the cost of male reproduction on long shoots, their axillary buds and growth potential in the subsequent year. Some aspects are compared with female reproductive cost. Correlations between previous year's shoot vigour and current season's shoot vigour/bud growth are discussed. The effect of terminal male inflorescence development on proximal female buds is also examined.

In assessing the cost of male reproduction on a node-to-node basis, further distinctions between early and late leaves of the heterophyllous long shoots are reported, in addition to those of Clausen and Kozlowski (1965) and Kozlowski and Clausen (1966).

Observations and Discussion

To evaluate data on male reproductive cost long shoots have been grouped into two age classes: 1) current year long shoots i.e., n + 2 year-old shoots, otherwise termed one-year-old shoots; 2) one-year-old (i.e., n + 2 year-old) long shoots which have overwintered and hence are n + 3 year-old. The year of bud apex inception is year n; bud development occurs in year n + 1; and bud burst in year n + 2.

Male inflorescence induction commonly occurs at the beginning of the growing season of year n + 2 (Macdonald et al. 1983). However, based on the length attained by some comparatively shorter long shoots it is possible that in male-bearing long shoots male induction possibly occurs before the end of the previous growing season. Development of the male catkin occurs in one year and pollen is released the following spring. The catkin, when mature, is compact, but prior to pollen release it undergoes enormous elongation. This occurs at the same time as the buds flush. What, therefore, is the effect on the expansion of leaves and internodes of the axis carrying the developing inflorescences (year n + 2)? Also, is there an effect the following year (n + 3) due to flowering on the flushing of the axillary buds carried on the flowering long shoot?

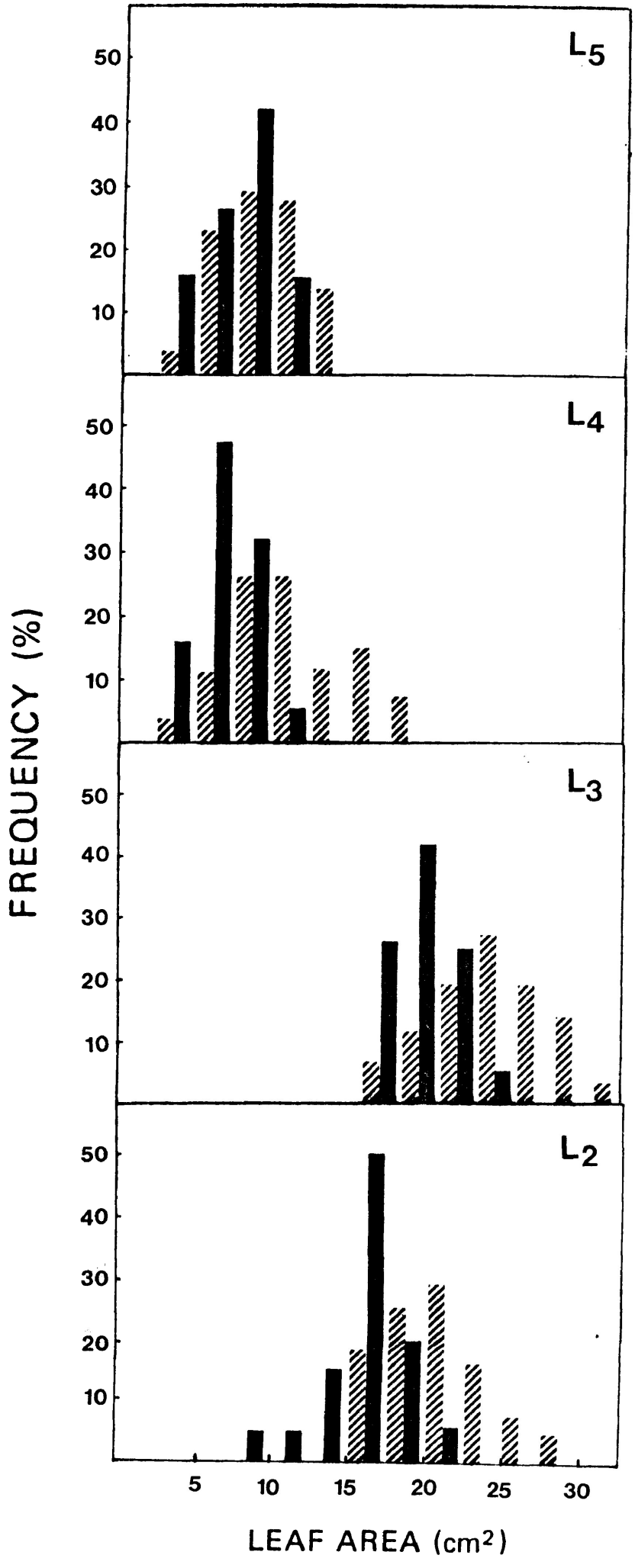
The heterophyllous shoot: vegetative versus reproductive

As noted in Chapter 3 long shoots are heterophyllous i.e., they possess early leaves and late leaves. Early leaves form from the two large embryonic foliage leaves contained within the bud, and late leaves develop from the more distal primordial leaves in the bud. Although Critchfield (1960) defined late leaves as primordia which are initiated and which expand as leaves in the same season, in contrast, two sets of late leaves have been identified in birch: 1) late leaves which develop from leaf primorida formed before the end of the previous growing season and 2) "true" late leaves as Critchfield defines them. Thus it is only long, long shoots with more than eight internodes which bear "true" late leaves. Shoots bearing male inflorescences cannot produce true late leaves, simply because the shoot apex is transformed into a male inflorescence at the beginning of the growing season (Macdonald et al. 1983).

Differences between early and late leaves have been reported in paper birch (Clausen and Kozlowski 1965) and these have been confirmed by this study. However, among others, differences in SLA are reported here. Early leaves, L_2 and L_3, and late leaves L_4 and L_5, differ in leaf area (Fig. 5-1) in both vegetative and reproductive shoots, as tested by Duncan's Multiple range test ($p = 0.01$). Vegetative shoots

FIG. 5-1. Frequency distribution of leaf area for L_2 - L_5 of vegetative and reproductive one-year-old long shoots. Based on 53 and 47 vegetative and reproductive long shoots, respectively. Solid bars represent reproductive long shoots and bars with slashes represent vegetative long shoots.

5-1



develop larger leaf laminae than reproductive shoots (Table 5-1). Reproductive cost, defined as the reduction in leaf area, calculated according to the method of Tuomi et al. (1982) is 16.1%, 16.3%, 25.3% and 21.4% for L_2, L_3, L_4 and L_5, respectively. The cost to early leaves is significantly ($P < 0.01$) lower than that for late leaves. Interestingly, the cost of reproduction is higher in L_4 than in L_5. The reason why L_4 should be more affected by male inflorescence development than L_5 which is proximally closer to the inflorescences is not clear. Invariably in all long shoots L_4 may attain a size distinctly smaller than L_5 although this relationship depends on the ratio of the supradjacent internode length (I_5) to the subjacent internode length (I_4). Data, based on over fifty long shoots, indicate that when the ratio of the supradjacent internode length (I_5) to subjacent internode length (I_4) is less than 1, the ratio of L_5 leaf area to L_4 leaf area is greater than 1, and vice versa. Consequently, leaf-internode relations are important here. The significance of these relationships is not clear, however, these correlations are more pronounced in reproductive shoots than in vegetative ones.

Clausen and Kozlowski (1965) reported that early leaves of paper birch were of a firmer texture than late leaves. However, such a difference has not been quantified.

TABLE 5-1. Comparisons between leaf areas of vegetative and reproductive heterophyllous (long) shoots.

Leaf number	Type	Mean Leaf Area (cm^2)		Difference
		Vegetative	Reproductive	
L_2	Early	18.6±2.6	15.6±2.2	3.0**
L_3	Early	22.1±3.3	18.5±2.0	3.6***
L_4	Late	9.1±3.5	6.8±1.4	2.3**
L_5	Late	9.8±2.5	7.7±2.2	2.1**

** Difference is statistically significant at the 1% level.

*** Difference is statistically significant at the 0.1% level.

SLA, the ratio of leaf area to leaf dry weight was, therefore, determined for L_2 to L_5. In both vegetative and reproductive long shoots, SLA's of early and late leaves were statistically different using Duncan's Multiple Range Test, $p = 0.01$; and so were the differences between vegetative and reproductive leaves (Table 5-2). Late leaves have higher values for leaf area per unit dry weight, and hence are thinner. SLW, which is the reciprocal of SLA, indicates that late leaves have smaller values for leaf dry weight per unit leaf area. A difference between early and late leaves based on SLA has not previously been reported. The fact that differences exist in SLA between the two sets of leaves, regardless of whether they are borne on vegetative or reproductive long shoot axes, is noteworthy. Early leaves may indeed be firmer in texture (Clausen and Kozlowski 1965) because they are thicker i.e., have lower SLA than late leaves. How these features relate to photosynthate production and contribution to shoot growth has yet to be investigated. Nevertheless in Populus the higher photosynthetic efficiency of long shoots is invariably due to late leaves (Nelson and Michael 1982).

Reproductive cost on leaf area is statistically different from that of SLA. While the effect of reproductive cost is lower in early leaves than in late leaves when calculated as a function of leaf area, the converse is true

TABLE 5-2. Comparisons between specific leaf area of vegetative and reproductive long shoots on a node-to-node basis.

Leaf number	Type	Mean SLA ($cm^2.g^{-1}$)		Difference
		Vegetative	Reproductive	
L_2	Early	130.6±11.2	158.5±15.9	27.9***
L_3	Early	136.9±13.2	154.8±13.4	17.9**
L_4	Late	156.9±22.4	167.5±23.4	10.6**
L_5	Late	172.7±11.6	177.0±16.50	4.3*

*, **, ***, Significantly different at 5% (*), 1% (**) or 0.1% (***) level.

when calculated as a function of SLA (Table 5-3). This discrepancy requires an explanation. The effect of reproduction on leaf area may reflect how reproduction affects some aspect of leaf development and expansion. SLA differences on the other hand suggest that not only leaf lamina thickness, but the assimilate retention capacity of leaves and/or export-import relations are altered in leaves of reproductive shoots. Higher reproductive cost for early leaves based on SLA would indicate that in reproductive long shoots the capacity to retain/import assimilates is diminished and/or the tendency to export is increased. It is indeed likely that, compared to vegetative shoots, early leaves of reproductive long shoots may be exporting more assimilates distally, i.e., to the inflorescence apex and the developing late leaves. A further explanation is that, in reproductive long shoots, the importation of assimilates from late leaves by early leaves would be minimized due to stronger sink effect of the developing inflorescences.

Late leaves subtending male inflorescences have higher SLA but smaller leaf areas than comparable leaves subtending the pseudoterminal bud in the event of shoot tip abortion (Figs. 5-2 and 5-3). In this case, the effect of proximity to developing male inflorescences on leaf expansion, even within the bud just prior to bud burst, is pronounced. Such late leaves also have fewer side nerve

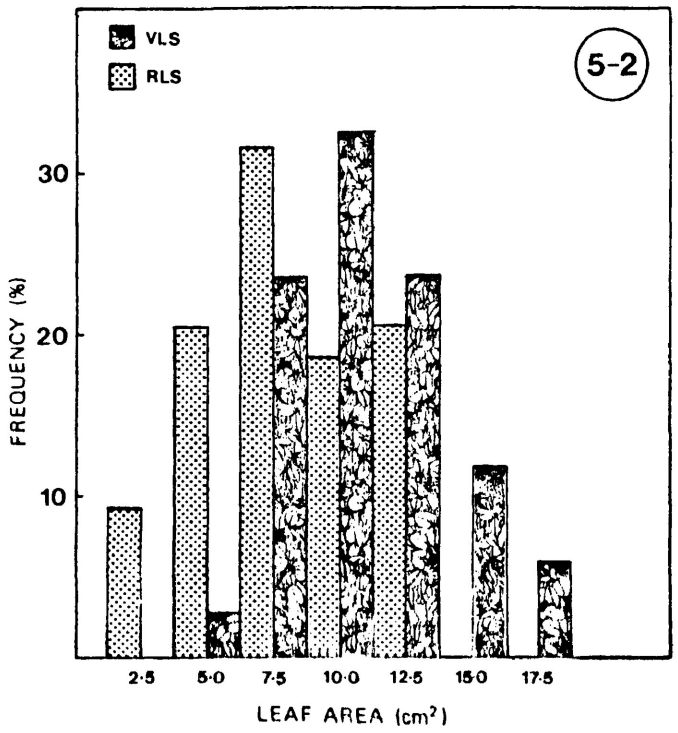
TABLE 5-3. Relative cost of male reproduction between leaves on a long shoot on i) area and ii) SLA basis.

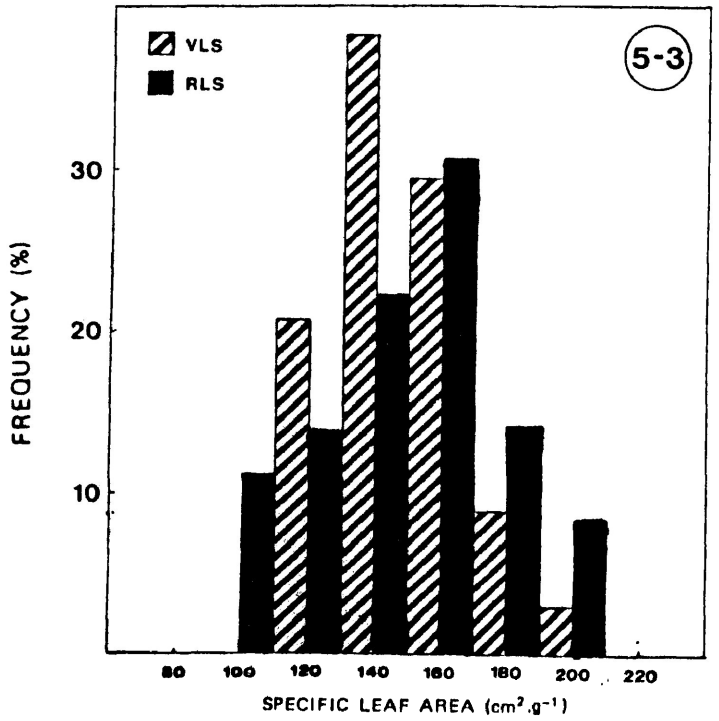
Leaf number	Reproductive Cost %		Difference
	Area	SLA	
L_2	16.1%	21.3%	5.2**
L_3	16.3%	13.1%	3.2*
L_4	25.3%	6.8%	18.5***
L_5	21.4%	2.5%	18.9***

*, **, ***, Significantly different at 5% (*), 1% (**) or 0.1% (***) level.

FIG. 5 - 2. Leaf size variations between male inflorescence subtending late leaves (N = 68) and late leaves subtending pseudoterminal buds (N = 72) of shoots of comparable length and internode number.

FIG. 5 - 3. Frequency distribution of SLA of the same leaves as in FIG. 5-2.


VLS
RLS
5-2
30
20
10
FREQUENCY (%)
2·5
5·0
7·5
10·0
12·5
15·0
17·5
LEAF AREA (cm²)


VLS
RLS
5-3
30
20
10
FREQUENCY (%)
80
100
120
140
160
180
200
220
SPECIFIC LEAF AREA (cm².g⁻¹)

pairs, fewer numbers of serrations per unit length of leaf margin, and higher lamina length to width ratios (Figs. 5-4, 5-5, 5-6). These differences, which reflect the cost of male reproduction on leaf morphology, are similar to those in reproductive short shoots (Chapter 4). Because late leaves are very close to the male inflorescences during development, explanations advanced for female reproductive cost will apply here, and they need not be reiterated.

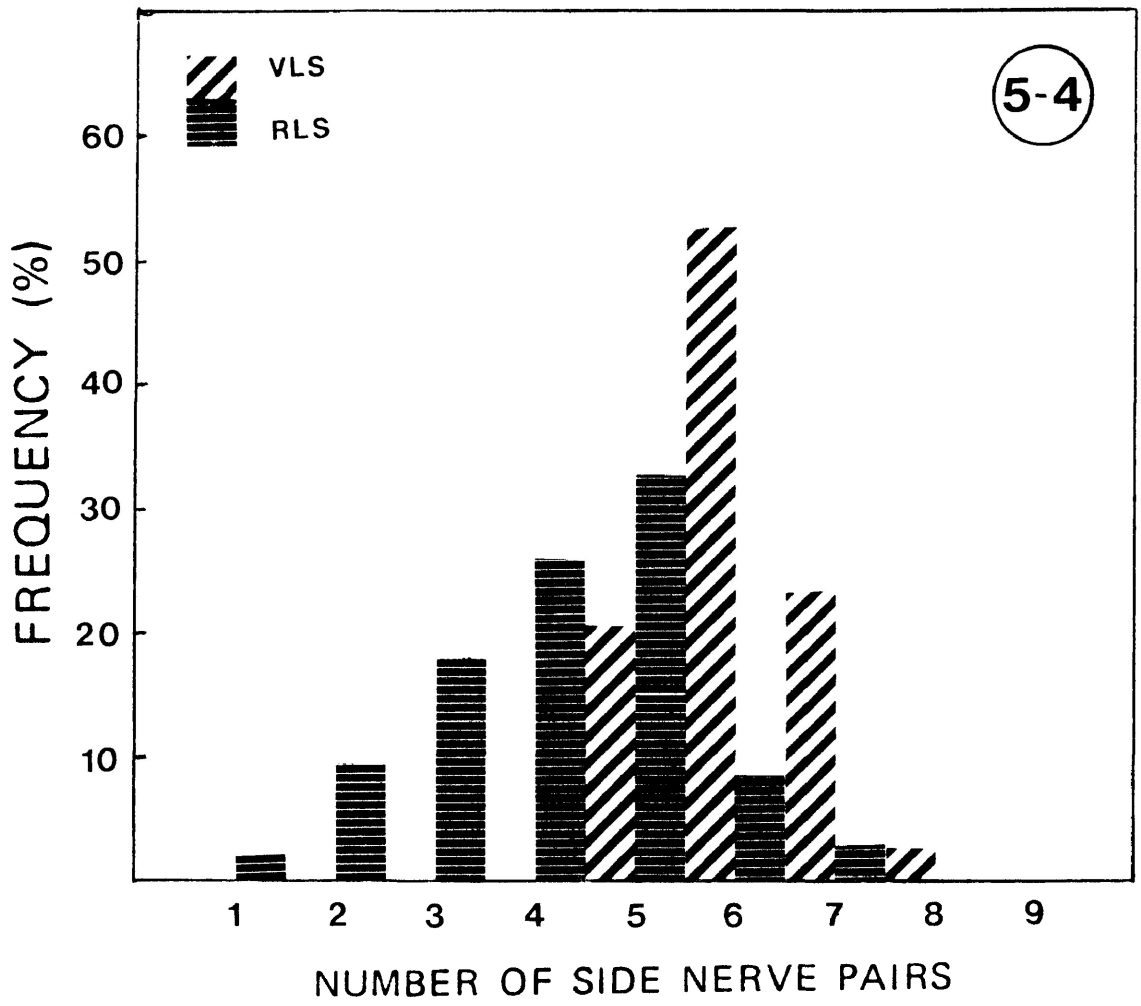
The ratio of lamina length to width for successive early and late leaves, L_2 - L_5, show slight variations (Table 5-4). In vegetative shoots L_3 has a higher ratio (i.e., grows more in length than width) than L_2. However, in reproductive long shoots the difference is not significant. This could mean two things: 1) in vegetative shoots L_3 grows more in length than L_2, while in reproductive shoots there is no difference, or 2) reproductive cost reduces lamina width expansion of L_2. It is not possible to test these hypotheses without carrying out more detailed studies of leaf growth (e.g., morphometric growth anatomy of leaf development). However, since male reproduction affects both early and late leaves, what then, is the effect on the axillary buds?

Effect of male inflorescences on axillary buds

A few days after bud burst observations indicated

FIG. 5-4. Frequency distribution of the number of side nerve pairs of the same leaves as in FIG. 5-2.

FIG. 5-5. Frequency distribution of the number of serrations per unit length (cm) of leaf margin of the same leaves as in FIG. 5-2.


VLS
RLS
5-4
FREQUENCY (%)
60
50
40
30
20
10
1
2
3
4
5
6
7
8
9
NUMBER OF SIDE NERVE PAIRS

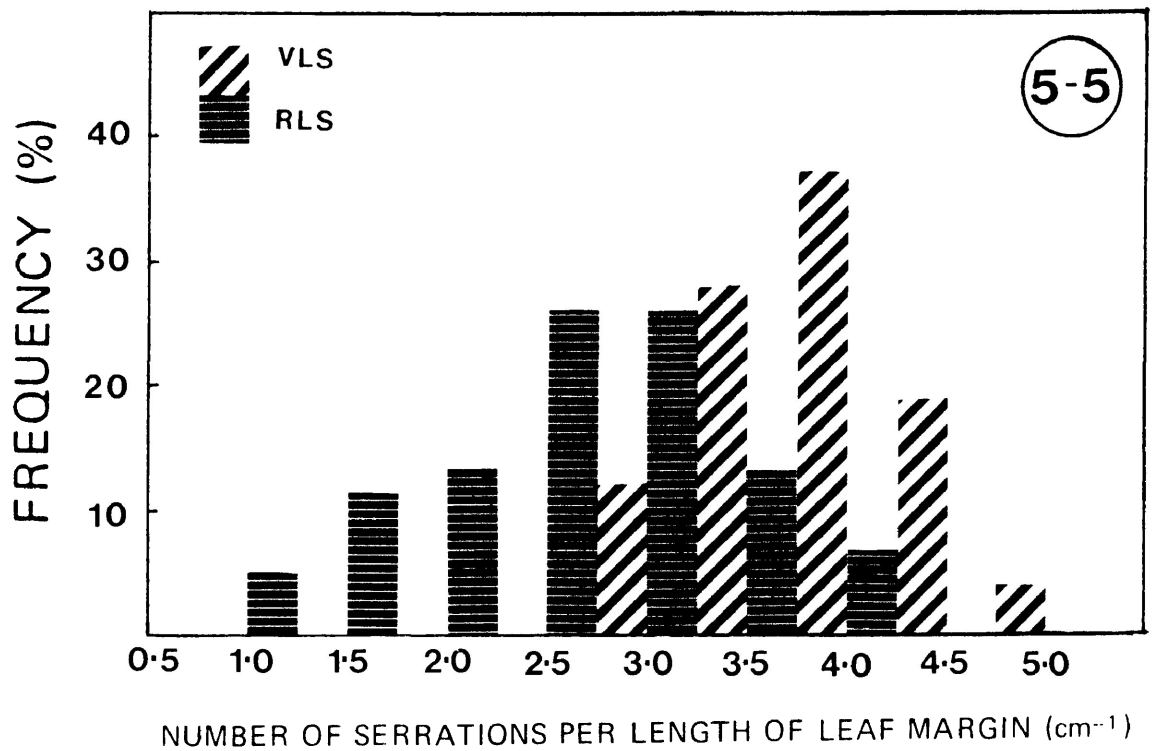

VLS
RLS
5-5
FREQUENCY (%)
40
30
20
10
0·5
1·0
1·5
2·0
2·5
3·0
3·5
4·0
4·5
5·0
NUMBER OF SERRATIONS PER LENGTH OF LEAF MARGIN (cm⁻¹)

FIG. 5-6. Frequency distribution of lamina length to width ratios of the same leaves as in FIG. 5-2.

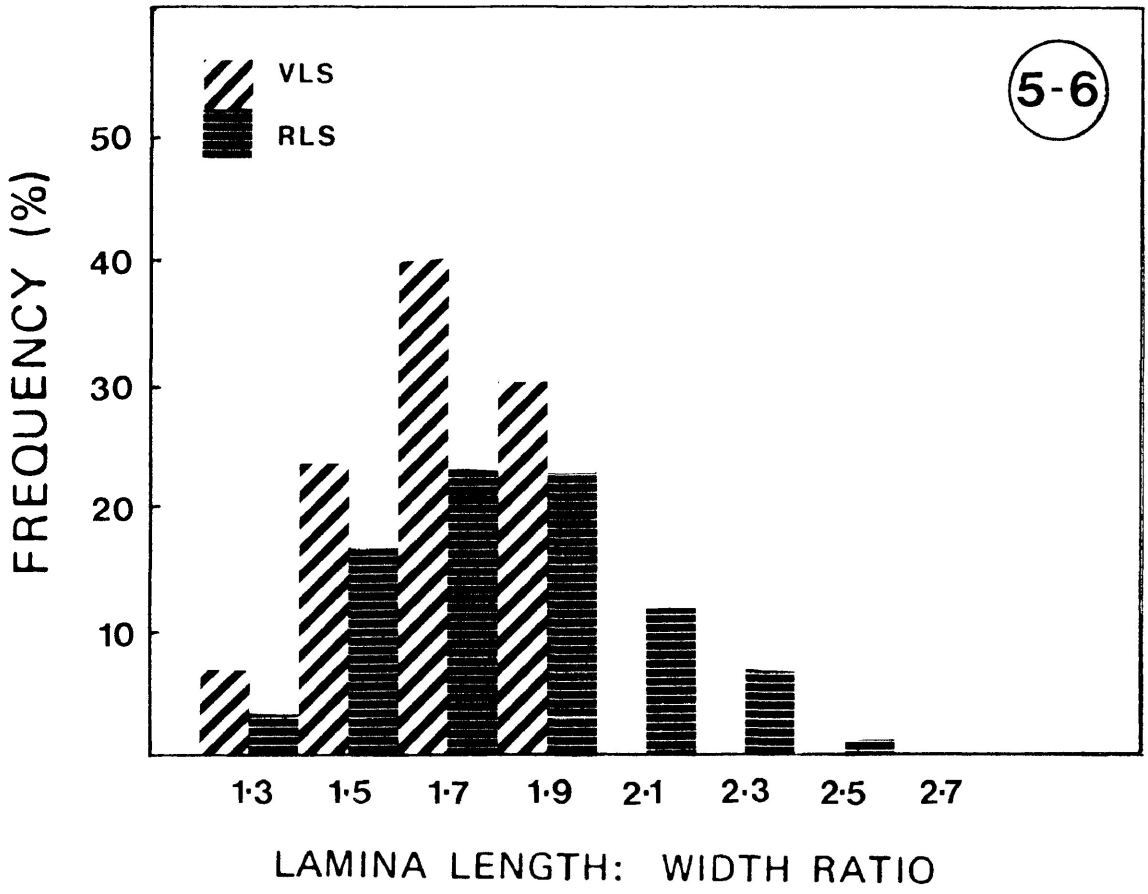

VLS
RLS
5-6
FREQUENCY (%)
50
40
30
20
10
1·3
1·5
1·7
1·9
2·1
2·3
2·5
2·7
LAMINA LENGTH: WIDTH RATIO

TABLE 5-4. Differences in ratios of lamina length to width ratios of early and late leaves of vegetative and reproductive heterophyllous shoots.

LEAF NUMBER	TYPE	MEAN LAMINA LENGTH TO WIDTH RATIO +		DIFFERENCE
		VEGETATIVE	REPRODUCTIVE	
L_2	Early	1.51 ± 0.10	1.56 ± 0.09	0.05 NS
L_3	Early	1.56 ± 0.18	1.57 ± 0.08	0.01 NS
L_4	Late	1.65 ± 0.12	1.68 ± 0.13	0.03 NS
L_5	Late	1.64 ± 0.12	1.79 ± 0.20	0.15 *

* , significantly different at 5% (*) level.

NS, not statistically significant.

+, Values not vertically side-scored by the same line are significantly different ($P < 0.05$).

that two-year-old vegetative long shoots (i.e., n + 3 year-old) appeared to be more leafy than shoots with flushing inflorescences (Figs. 5-7 to 5-10). The reduction in "leafiness" seemed to be more pronounced if the proximal axillary buds flushed as reproductive short shoots (Fig. 5-10). To test the hypothesis that male development affects the development of subjacent axillary buds, dry weights were obtained one week after flushing of buds on four categories of two-year-old long shoots. The four categories of long shoots were: 1) vegetative shoots with axillary buds expanding only as vegetative short shoots and long shoots (Fig. 5-7); 2) vegetative shoots with proximal axillary buds flushing as reproductive short shoots (Fig. 5-8); 3) reproductive long shoots with terminal male inflorescence and vegetative axillary buds (Fig. 5-9); and 4) reproductive long shoots with proximal axillary buds developing as reproductive short shoots (Fig. 5-10). In all, 242 long shoots were analyzed, representing 66, 38, 80 and 58 shoots of the categories listed above, respectively. Although vegetative long shoots with one or two proximal reproductive short shoots had slightly lower mean bud dry weight and almost identical distribution of mean bud dry weight as comparable vegetative long shoots without any proximal reproductive short shoots, the difference was not statistically significant. Hence, only three of the categories were compared.

FIG. 5-7 x 0.34. Two-year-old vegetative long shoots with flushed proximal and distal vegetative short and long shoots respectively.

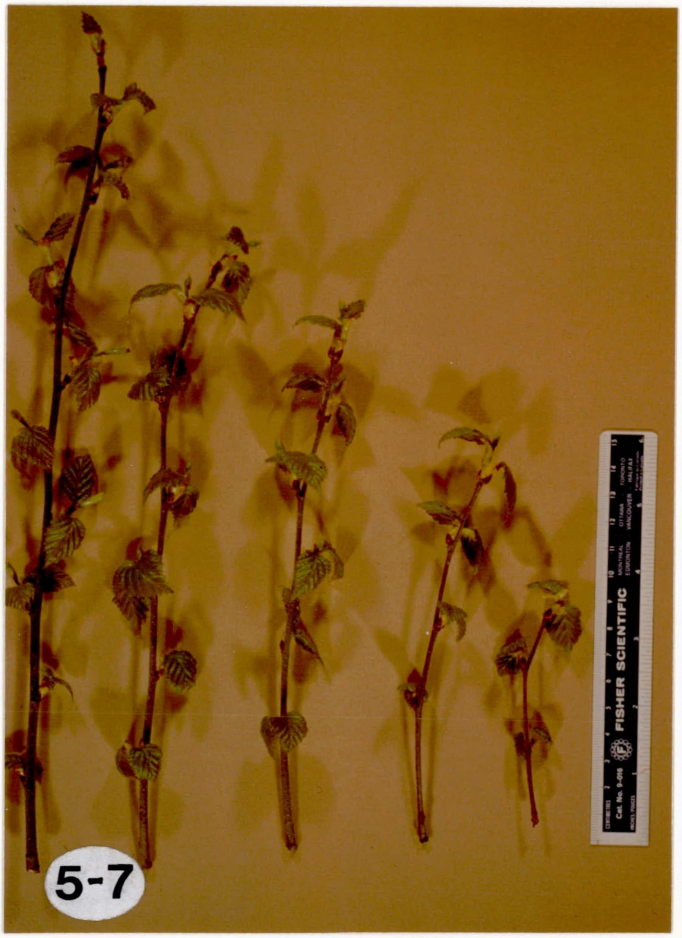

5-7
FISHER SCIENTIFIC

FIG. 5-8 x 0.41. Two-year-old vegetative long shoots with distal flushed vegetative long shoots and proximal vegetative and reproductive short shoots. Note: in all buds at node 4 have flushed as reproductive short shoots but this is not so at node 5.

FIG. 5-9 x 0.41. Reproductive long shoots (two-year-old) with proximal and distal buds flushed as vegetative short shoots and long shoots, respectively.

FIG. 5-10 x 0.47. Reproductive long shoots (two-year-old) with proximal buds flushed as reproductive short shoots. Note small leaves associated with reproductive short shoots.

5-8
FISHER SCIENTIFIC

5-9
FISHER SCIENTIFIC

5-10
FISHER SCIENTIFIC

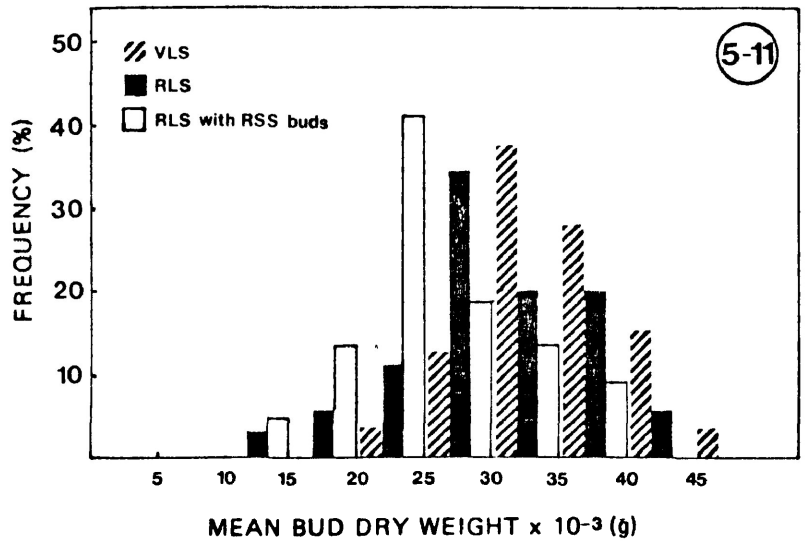
Mean bud dry weight is lower in reproductive long shoots which bear proximal developing reproductive short shoots than in vegetative long shoots (Fig. 5-11). Mean bud dry weight of reproductive long shoots with reproductive short shoots is lower than that of reproductive long shoots without reproductive short shoots. This indicates that the growth potential of axillary buds is indeed lowered by the presence of the terminal male inflorescence. To further substantiate this, bud dry weight was evaluated and compared on a node-to-node basis for over 130 long shoots of comparable length, and node number. The results indicate that in all cases the presence of proximal reproductive short shoots lowers the mean bud dry weight significantly (Fig. 5-12). The difference between vegetative long shoots and reproductive long shoots without reproductive short shoot axillary buds is not significant ($p > 0.05$) at nodes 4 and 5, but it is significant at node 6 ($p < 0.01$) and it is highly significant ($p < 0.001$) at node 7. It must be noted that the distal nodes (i.e., nodes 6 and 7) usually bear developing long shoots. It may, therefore, be concluded that the distal, potential long shoot buds are more affected by the terminal male inflorescence than the proximal potential short shoot buds. In fact, the intensity of this effect is what possibly influences all reproductive long shoot axillary buds to flush as short shoots only (see Gross 1972).

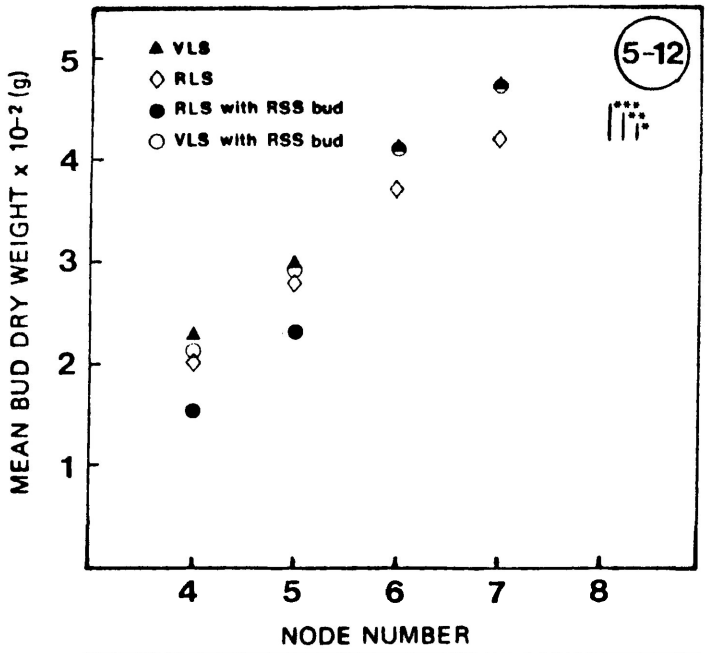
Three weeks after flushing, a sample of over 180 long shoots was collected and grouped into the same four classes to determine mean total early leaf area on a node-to-node basis. A trend similar to that for bud dry weight was obtained (Fig. 5-13). In reproductive long shoots with proximal reproductive short shoots, total leaf area at nodes 4 and 5 is greatly affected by the local competition between developing female inflorescence apices and the early leaves, thus further lowering the leaf area significantly ($p < 0.001$). Although at node 4 differences in bud dry weight between vegetative and reproductive long shoots with reproductive short shoot axillary buds were not significant ($p > 0.05$), a significant difference ($p < 0.05$) was obtained on the basis of total early leaf area (Fig. 5-13). The expanding long shoot proximal to the flushing pseudo-terminal bud i.e., at node 6, does not seem to be as affected by the presence of a terminal male inflorescence as the flushing pseudoterminal bud (Fig. 5-13). It is common to find that the long shoot closest to the male inflorescence develops far more slowly than its subjacent long shoot. The effect is that the most distal long shoot bears smaller early leaves (Fig. 5-14). Consequently, the presence of a terminal male inflorescence alters the relationship between node number and total early leaf area (Chapter 3). Compared to the usual situation of two proximal buds and distal buds

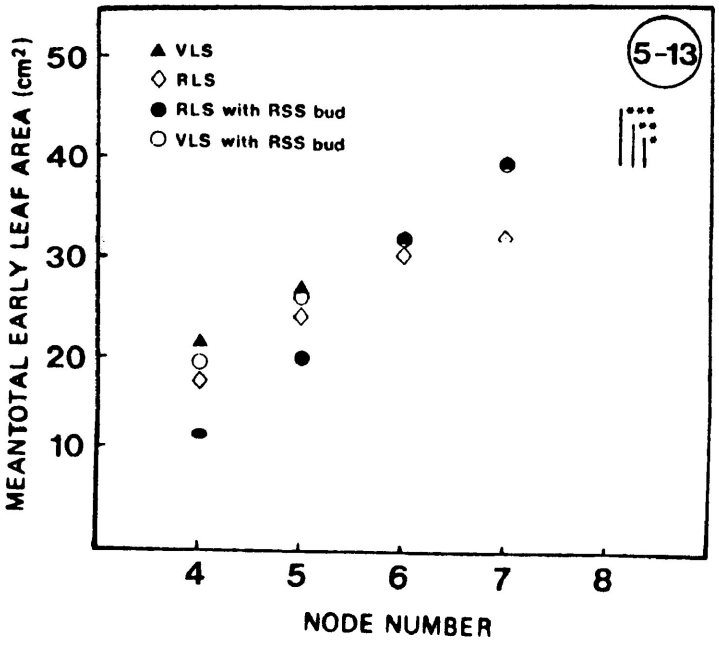
FIG. 5-11. Frequency distribution of mean bud dry weight per shoot of three categories of two-year-old long shoots. Distribution of vegetative long shoots and vegetative long shoots with proximal reproductive short shoots are identical, hence the latter is not shown.

FIG. 5-12. Relationship between node number and mean bud dry weight for different categories of two-year-old long shoots. Vertical bars represent the magnitude of significant differences.

FIG. 5-13. Relationship between node number and mean total early leaf area three weeks after flushing for different categories of two-year-old long shoots. Vertical bars represent the magnitude of significant differences.


5-11
VLS
RLS
RLS with RSS buds
FREQUENCY (%)
50
40
30
20
10
5
10
15
20
25
30
35
40
45
MEAN BUD DRY WEIGHT x 10-3 (g)

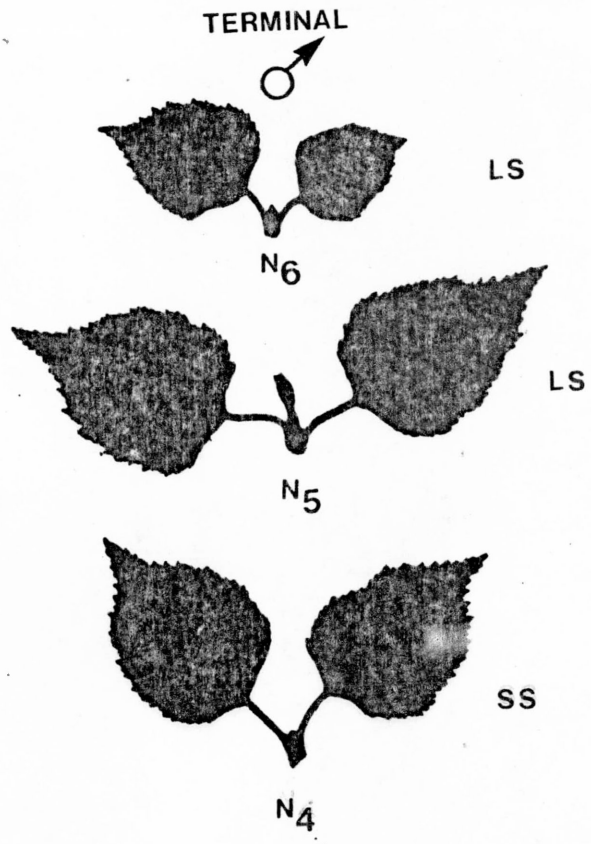

5-12
VLS
RLS
RLS with RSS bud
VLS with RSS bud
MEAN BUD DRY WEIGHT x 10-2 (g)
5
4
3
2
1
4
5
6
7
8
NODE NUMBER


5-13
VLS
RLS
RLS with RSS bud
VLS with RSS bud
MEANTOTAL EARLY LEAF AREA (cm2)
50
40
30
20
10
4
5
6
7
8
NODE NUMBER

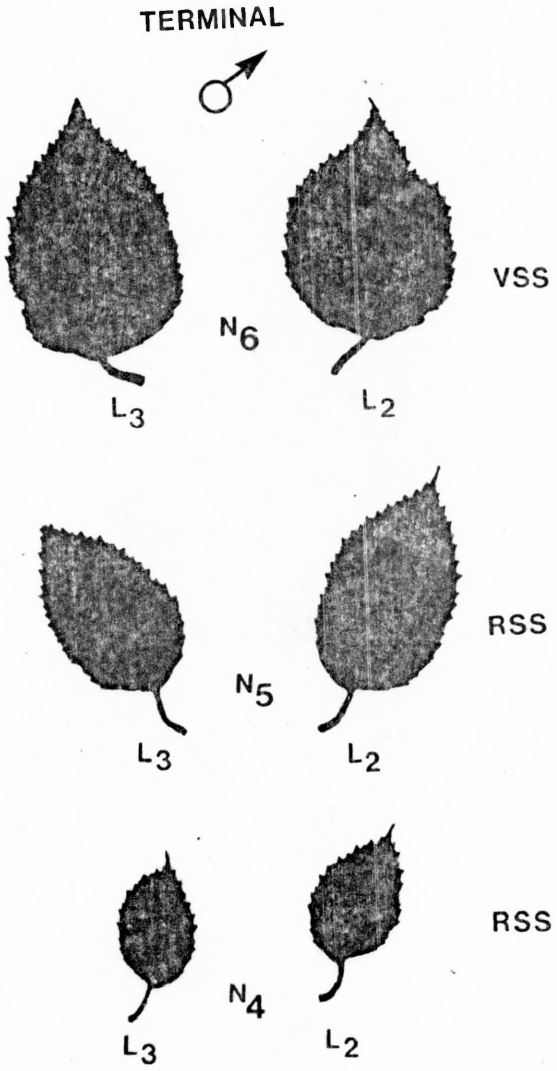
flushing as vegetative/reproductive short shoots, and long shoots, respectively, all axillary buds, proximal and distal buds close to the male inflorescence may flush as short shoots. In such instances there is a similar basipetal reduction in leaf size at specific nodes (Fig. 5-15). The short shoot at node 4 exhibits the extreme synergistic effect of terminal male inflorescence and "local" female inflorescence on total early leaf area (cf. Figs. 5-16 and 5-17). Male reproduction indeed lowers the vigour and growth potential of axillary buds and hence reduces extension of the canopy the subsequent year (Macdonald et al. 1983). An extreme case is reported in "moneymaker" pecan, Carya illinoensis, in which previous years fruiting long shoots had a markedly decreased flower and nut production the following year (Malstrom and McMeans 1982).

FIG. 5-14 x 0.675. Silhouette drawings of early leaves of one-year-old shoots from a two-year-old reproductive long shoot. Note that the most distal long shoot which is closer to the inflorescence has considerably smaller early leaves.

FIG. 5-15 x 0.675. Silhouette drawings of early leaves of one-year-old short shoots from a two-year-old reproductive long shoot with no distal long shoot. Note the extremely small size of node 4 reproductive short shoot. Synergistic effect of male and "local" female reproduction on leaf size.


TERMINAL
LS
N6
LS
N5
SS
N4

5-14


TERMINAL
VSS
N6
L3
L2
RSS
N5
L3
L2
RSS
N4
L3
L2

5-15

FIG. 5-16 x 0.72. Two-year-old vegetative long shoot with axillary buds flushed as one distal long shoot, median short shoot and most proximal reproductive short shoot. Note smaller size of node 4 early leaves (i.e., associated with female inflorescence).

FIG. 5-17 x 0.72. Two-year-old reproductive long shoot with most distal axillary bud flushed as long shoot. Two proximal buds flushed as reproductive short shoots. Compare with Fig. 5-16 and note smaller size of early leaves at node 4 and also smaller leaves of the distal long shoot when male inflorescence is present.

5-16
5-17
CENTIMETRES
Cat. No. 9-016
FISHER SCIENTIFIC
MONTREAL - OTTAWA - TORONTO
EDMONTON - VANCOUVER - HALIFAX
INCHES/POUCES
Fabriqué au Canada
Printed in Canada

CHAPTER 6

CHAPTER 6

COMPARATIVE ANATOMY OF LONG AND SHORT SHOOTS: A QUANTITATIVE ANALYSIS WITH EMPHASIS ON ASPECTS OF STEM ANATOMY.

Introduction

Comparative anatomy has long been recognized as an important tool especially in phytogenetic (Bailey and Sinnott 1914; Hoar 1916; Bailey and Tupper 1918; Tippo 1946; Moseley 1948; Hall 1952), systematic (e.g. Boubier 1896; Solereder 1908; Tippo 1948; Metcalfe and Chalk 1950) and taxonomic studies (e.g. Sinnott 1914; Cousins 1933; Heimsch and Wetmore 1939; Metcalfe and Chalk 1950; Hall 1952). Comparative anatomy is helpful in clonal studies evaluating wood quality (Isebrands 1969) and in studying within-crown variations.

Observations on cells of birch wood were first reported by Leeuwenhöek (1695). Since then the earliest generalized but brief descriptions of the wood structure of Betulaceae were made by Hartig (1859) and Sanio (1863). Subsequently, Moeller (1876) studied the systematic anatomy of the family with emphasis on Corylus, Carpinus, Betula and Alnus. During the twentieth century Solereder's account of systematic anatomy was the first in which the Betulaceae was comprehensively covered (Solereder 1908, cited by Hall 1952). Other studies were subsequently reported

(E.g., Bailey and Sinnott 1914; Hoar 1916; Hall 1952).

Comparative anatomy of long and short shoots are very few. The earliest study was reported by Herrmann (1916, cited by Bügsen and Münch 1929) who compared long and short shoots of Fagus, Acer, Pomaceae, Ginkgo and Berberis. He observed "greater narrowness" of the vessels and a greater proportion of "starch storing cells" (i.e., cortical and pith parenchyma) in dwarf shoots and concluded that the occurrence of fewer strengthening tissues (i.e., xylem) but more starch storing cells may favour the formation of flowers - usually borne on dwarf shoots. Since then the only report of this nature on angiosperms is that of the unigeneric Japanese species Cercidiphyllum japonicum (Titman and Wetmore 1955). Invariably much of the work involving long and short shoot comparisons with emphasis on shoot apical ontogeny have been on gymnosperms (e.g., Gunckel and Wetmore 1946a, 1946b; Sacher 1954, 1955; Frampton 1960; Hanawa 1967; Curtis and Popham 1972; Gabilo and Mogensen 1973; Owens and Molder 1979). Perhaps Doak (1935) was the first to notice such apical differences but erroneously labelled the dwarf shoot apex as an abortive leaf primordium (Gabilo and Mogensen 1973).

So far the single-distinct feature differentiating the two shoot apices in species other than birch has been differences in the pith rib meristem (Gunckel and Wetmore

1946a; Titman and Wetmore 1955; Romberger 1963; Cutter 1965; Sachs 1965). More recently, apical vigour and internodal extension prior to winter dormancy in long shoots of larch have been reported (Owens and Molder 1979). Differences in stem anatomy of long and short shoots of Ginkgo (Wetmore 1956) and Cercidiphyllum (Titman and Wetmore 1955), and leaf anatomy of Ginkgo (Bertrand 1874; Seward and Gowan 1900; Chamberlain 1935; Kanis and Karstens 1963) and Malus (Ghosh 1973) have been described. Most of the descriptions, except that of Malus, were qualitative. The differences in leaf anatomy reported for Ginkgo have fairly recently been questioned (Hoddinott and van Zinderen Bakker 1974). No anatomical comparisons have been reported for long and short shoots of paper birch.

It is not the purpose of this study to compare the apical dynamics of long and short shoots. Rather, this analysis of the mature stem anatomy concentrates on comparing wood to bark ratio, widths of secondary xylem, secondary phloem, cortex and periderm as well as the radial diameter of vessels and diameters of pith and pith parenchyma cells, in order to infer possible differences in the developmental pathways of the two shoot types. This, therefore, possibly forms the basis for further studies.

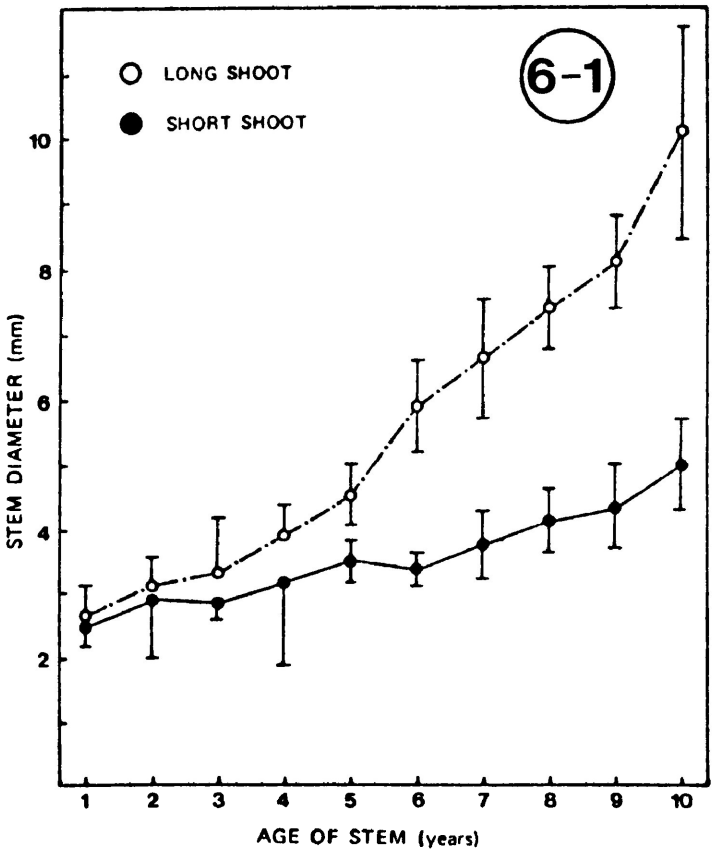
To correlate growth, morphological and morphometric

differences between long and short shoots with anatomical features, the stem anatomy of internode 2 of one-year-old long and short shoots was compared quantitatively. Since these tissues arise as a result of shoot apical activity, a quantitative study of a mature portion of the stem should depict differences which might not be discernible in the shoot apex itself.

Results and Discussion

Not only do short shoots lack significant internodal extension, but diameter increment is also affected. Long and short shoots were grouped into age-classes 1 - 10 years, and their basal diameters were measured with a micrometer gauge. For age-classes 1 - 6 years a minimum of 45 each of long and short shoots were measured; and for age-classes 7 - 10 years a minimum of 22 of each shoot type were measured. Age versus diameter increment relationships are shown in Fig. 6-1. Differences in diameter increment were not significant until after the third year. A regression analysis of diameter increment on stem-age indicated that the slope of the long shoot curve was statistically different ($p < 0.001$) from that of the short shoot. Normally, incremental differences are associated

FIG. 6-1. Relationship between stem-age and diameter increment of long and short shoots.

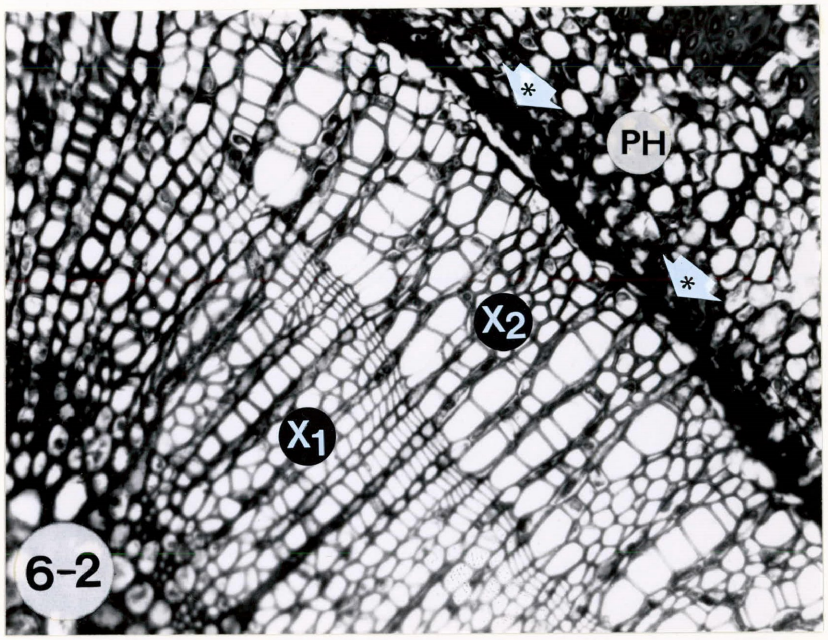

6-1
LONG SHOOT
SHORT SHOOT
STEM DIAMETER (mm)
2
4
6
8
10
1
2
3
4
5
6
7
8
9
10
AGE OF STEM (years)

with cambial activity, primarily xylem production. Therefore an analysis was made of xylem differences in long and short shoots of different age classes. In short shoots cambial activity diminishes or ceases in the second year (Fig. 6-2) and definitely is not evident after the third year (Fig. 6-3). On the other hand, cambial activity in the long shoot is normal (Fig. 6-4). The two situations have been termed manoxylic and pycnoxylic, respectively (Titman and Wetmore 1955). The similarity in diameter increment during the first three years (Fig. 6-1) needs explanation. Upon examination of sections it was observed that, compared to long shoots, short shoots have greater phellogen activity resulting in comparatively more periderm (Fig. 6-5). The enhanced phellogen activity together with the minimal vascular cambial activity results in stem diameter increments in the first 3 years which are equivalent to diameter increments of long shoots.

To ascertain the relationship between wood and bark production, the ratio of wood radius to bark radius was evaluated for one-year-old long and short shoots only. Bark is defined here as that portion of the stem tissue from the vascular cambium to the external surface (Esau 1977) of the stem. The ratio was higher in long shoots than in short shoots (Table 6-1). This indicates that even

FIG. 6-2 X 217. Transverse section of an eight-year-old short shoot stem showing an inactive cambium and secondary vascular tissue formation in internode 2. Note the dense material in the zone of "dead" cambium which has ceased activity during the second year. First-year xylem (X_1) has smaller vessels than second-year xylem (X_2). Phloem (PH) is less crushed.

FIG. 6-3 X 135. Transverse section of a ten-year-old short shoot stem showing the end of cambial activity immediately after the commencement of third-year growth (arrows). Note that first-year xylem (X_1) vessels are typically smaller than subsequent years.


*
PH
*
X2
X1
6-2

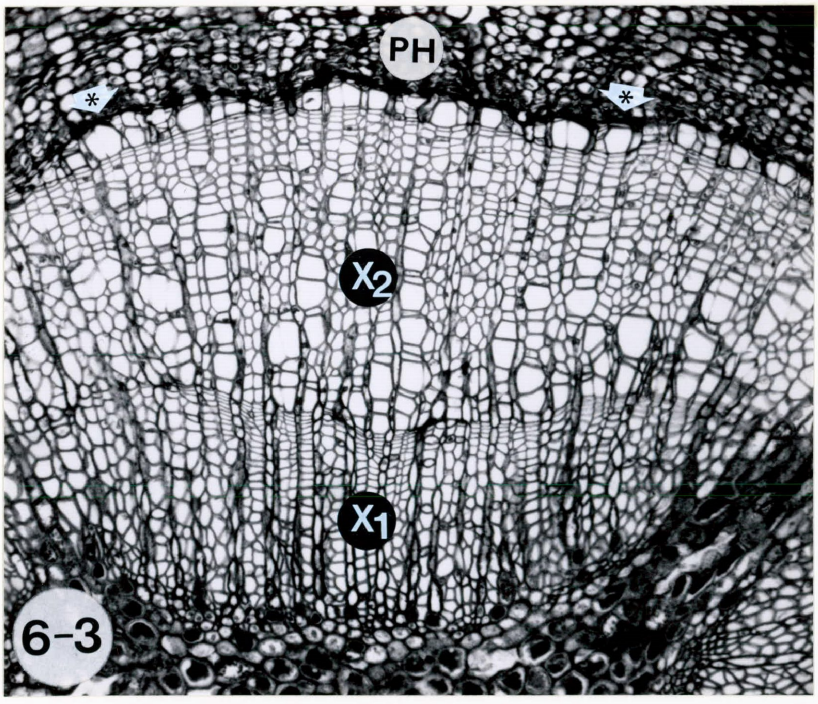
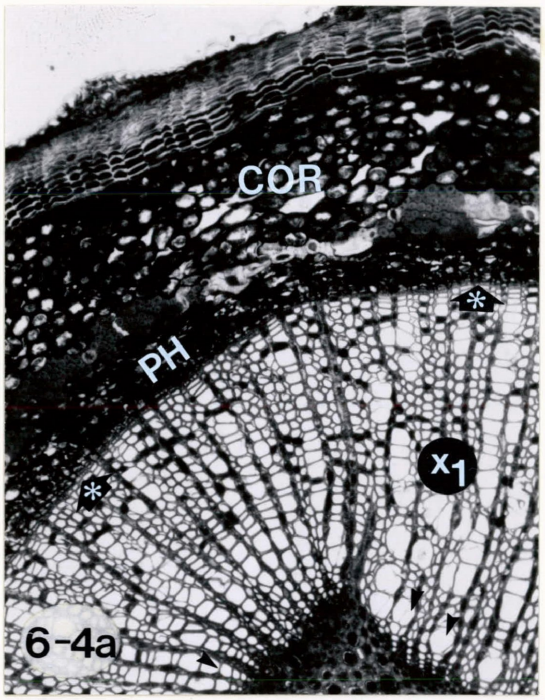
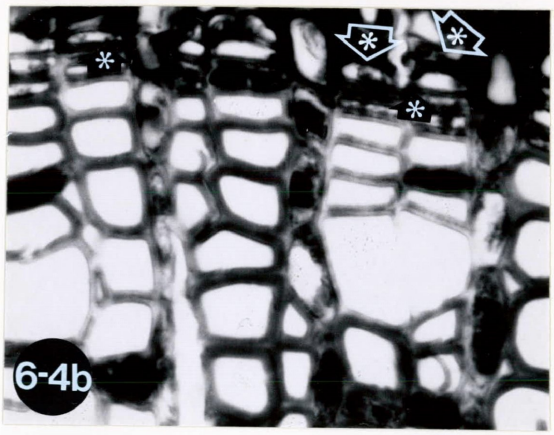

PH
*
*
X2
X1
6-3

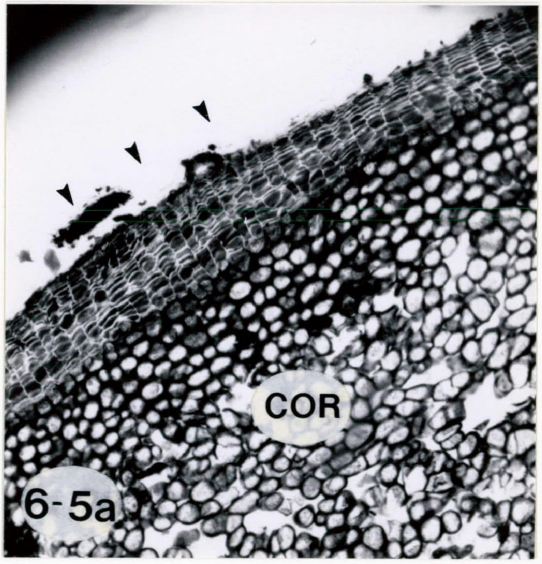
FIG. 6-4a x 123. Transverse section of internode 2 of a one-year-old long shoot showing normal cambial activity and extensive development of secondary xylem in the first year alone. Compare the radial width of first-year secondary xylem (X_1) with the corresponding one of short shoots i.e. X_1 of Figs. 6-2 and 6-3. Note the occurrence of larger vessels in the long shoot immediately after the onset of secondary growth (arrow). Also, higher frequency of large vessels in X_1 of long shoots. Cortex (COR) is more crushed in the long shoot.

FIG. 6-4b x 857. A higher magnification of a portion of the long shoot TS in Fig. 6-4a showing active cambium (arrows) without the dense (orange G or Safranin staining) material associated with the short shoot "dead" cambium (c.f. Fig. 6-2 and 6-3).

FIG. 6-5a x 92. Transverse section of a portion of a two-year-old short shoot stem showing a wider, less crushed cortex (COR) and more vigorous phellogen activity producing more phellem,part of which has sluffed off (arrows)


COR
PH
x1
6-4a


6-4b


COR
6-5a

within the first year of growth the activity of the short shoot vascular cambium lags behind that of the long shoot. Consequently, more xylem is produced in the long shoot than in the short shoot (c.f. Figs. 6-2 and 6-4). Whatever curtails short shoot cambial activity is effective during the first year. Also, vigorous xylem differentiation in the long shoot may have resulted in the crushing of secondary phloem and primary cortex, resulting in a smaller bark radius (c.f. Figs. 6-4 and 6-5a).

The radial widths of long and short shoot secondary xylem were compared. Measurements were taken on the opposite side from leaf trace divergencies since larger dimensions are sometimes associated with the side of the leaf trace divergence. Secondary xylem width is greater in internode 2 of long shoot stems than in the comparable internode of short shoots (Fig. 6-6; Table 6-1). Flushing long shoot buds have higher Bud-, Stem- and Leaf-RGR, extended internodes and produce late leaves with secondary axillary bud apices in their axils. Flushing short shoot buds, on the other hand, have lower Bud-, Stem- and Leaf-RGR, no extended internodes and produce no late leaves but form, instead, rudimentary leaves with aborting laminae and no secondary axillary buds (Chapter 3). The features exhibited by potential long shoot buds may possibly regulate earlier cambial reactivation prior to bud burst in long

TABLE 6-1. Comparisons between measurements of various anatomical features of internode 2 of one-year-old long and short shoot stems.

ANATOMICAL PARAMETER	MEAN ± S. D.		DIFFERENCE
	LONG SHOOT	SHORT SHOOT	
Wood:Bark ratio[1]	0.998±0.191	0.443±0.142	0.555***
Periderm width (μm)	62.6±18.0	92.7±30.2	30.1 ***
Secondary xylem width (μm)	1284.6±311.9	629.3±268.1	655.3***
Secondary phloem width (μm)	110.81±23.85	88.02±24.42	22.79**
Vessel diameter (radial) (μm)	23.89±9.33	17.47±6.26	6.42***
Radial file vessel number	12.4±3.8	7.35±4.50	5.05***
Ray frequency (mm^{-1})	34.10±7.20	20.96±13.35	13.14**
Pith diameter (μm)	445.5±106.8	360.9±92.1	84.6***
Pith parenchyma diameter (μm)	27.9±7.3	21.7±5.8	6.2***
Cortex width (μm)	377.8±72.8	419.1±105.9	41.3***

** , *** , Significant at 1% and 0.1% level, respectively.

[1] Allometric K values are 1.93 and 1.09 for short shoots and long shoots, respectively. Short shoots produce more bark than wood.

FIG. 6-5b. Frequency distribution of periderm width in internode 2 of one-year-old long and short shoots.

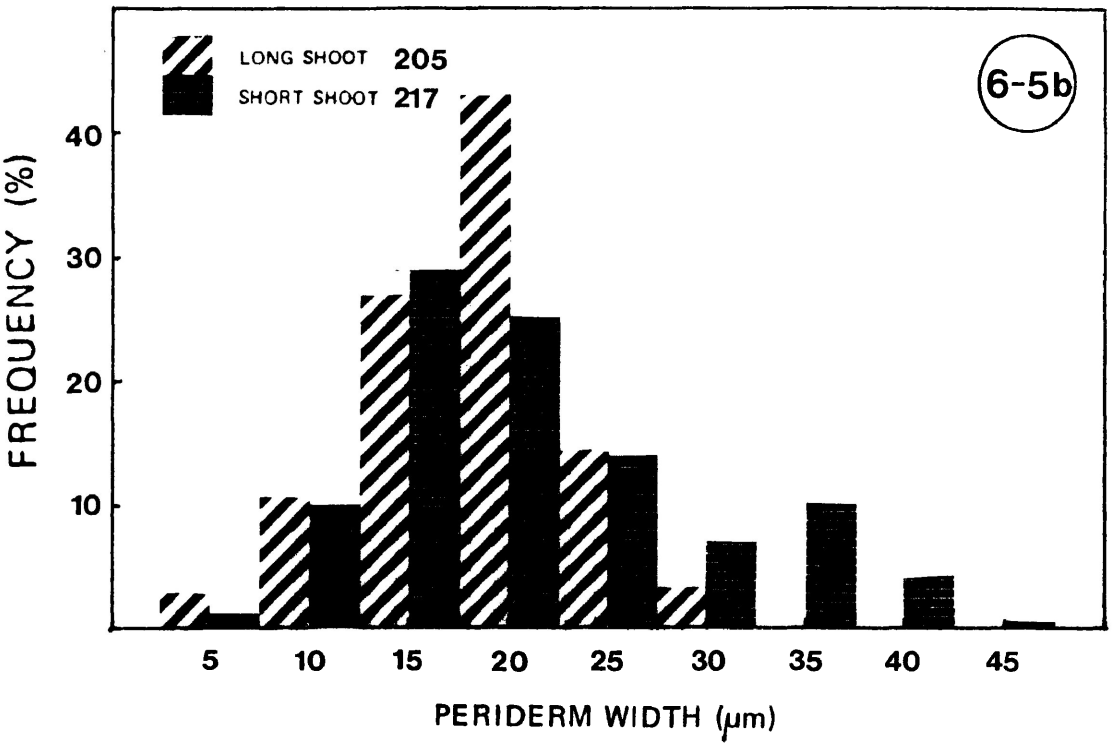
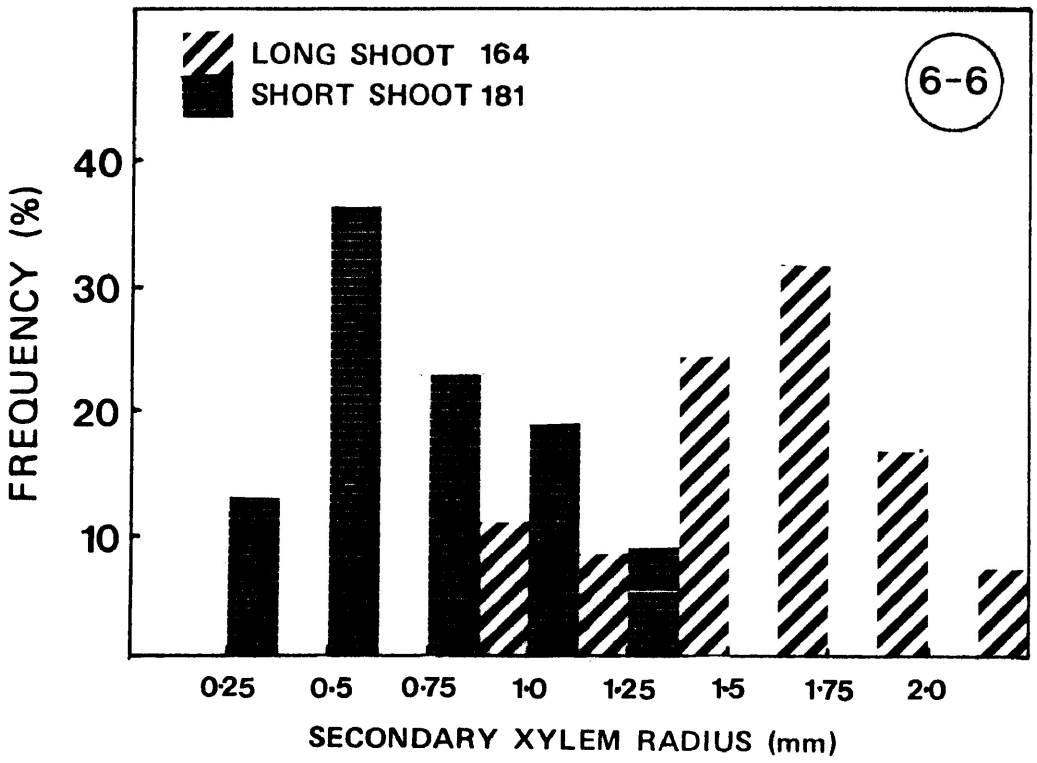

LONG SHOOT 205
SHORT SHOOT 217
6-5b
FREQUENCY (%)
40
30
20
10
5
10
15
20
25
30
35
40
45
PERIDERM WIDTH (μm)

FIG. 6-6. Frequency distribution of the radial widths of first-year secondary xylem (X_1) in long and short shoot stems, of the same age and internode as in Fig. 6-5b.


LONG SHOOT 164
SHORT SHOOT 181
6-6
FREQUENCY (%)
40
30
20
10
0·25
0·5
0·75
1·0
1·25
1·5
1·75
2·0
SECONDARY XYLEM RADIUS (mm)

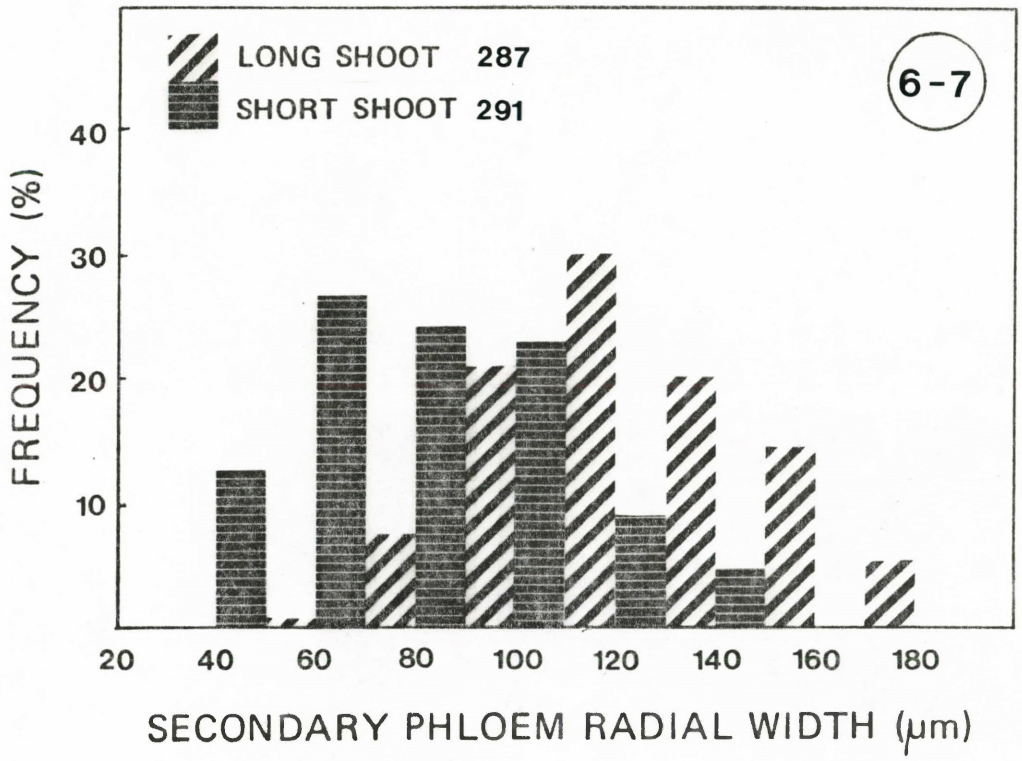
shoots than in short shoots. Consequently, in short shoot buds, the effect of lack of late leaf primordia development and the development of associated secondary axillary bud primordia, is the suppression of cambial activity. It is well known that flushing buds and young growing leaves strongly promote cambial reactivation in the spring, in temperate woody plants (Romberger 1963; Reinders-Gouwentak 1965; Zimmermann and Brown 1971).

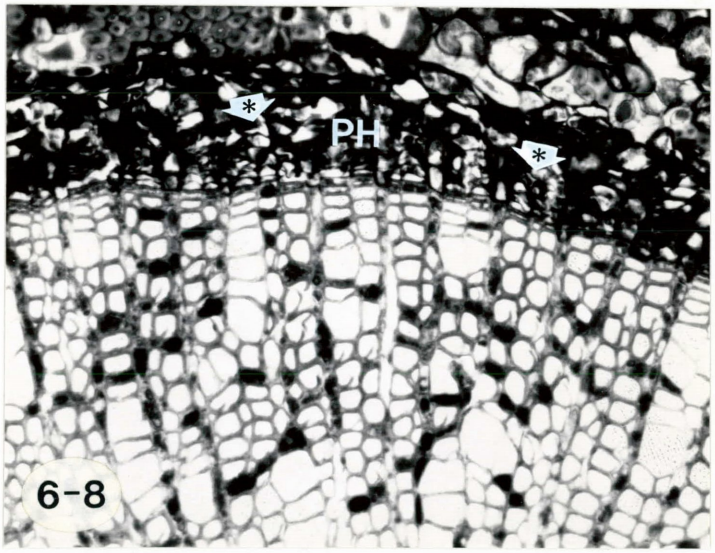
Radial width of secondary phloem is greater in long shoots than in short shoots (Fig. 6-7) although in long shoots the phloem seems to be somewhat crushed (Fig. 6-8). It is obvious that a relatively inactive cambium in short shoots would produce less secondary vascular tissue. The obvious necessity of maintaining a nutrient flow to the single short shoot terminal bud which produces foliage leaves yearly and which may form female inflorescences, suggests that there is continued phloem production. However, the fact that short shoots eventually die usually after 10 - 12 years suggests that, with age, continued phloem production may also be suppressed.

In long shoots the production of late leaves increases the foliage percentage and consequently its effect on vascular tissue formation is considerable. In trees there is evidence that the amount of foliage or canopy size is closely related to the amount of wood formed in the

FIG. 6-7. Frequency distribution of the radial widths of secondary phloem in long and short shoots of comparable age as in Fig. 6-5b.

FIG. 6-8 X A portion of the transverse section of a one-year-old long shoot stem showing a somewhat crushed phloem (PH) with dense contents (arrow).


LONG SHOOT 287
SHORT SHOOT 291
6-7
FREQUENCY (%)
40
30
20
10
20
40
60
80
100
120
140
160
180
SECONDARY PHLOEM RADIAL WIDTH (μm)


*
PH
*
6-8

stem (Larson and Isebrands 1971; Grier and Waring 1974; Cheng 1976; Rogers and Hinckley 1979; Waring et al. 1980). It is clear that extra foliage would imply more contribution of leaf traces to the sympodium, which, in turn, should result in an increase in stem diameter. Invariably more wood production would result in more conduction of water and other substances translocated in the xylem to promote an increase in foliage. The radial diameter of secondary xylem is highly correlated with the number of vessels in the radial file (r=0.792 and 0.886 for long and short shoots, respectively) (Fig. 6-9). Consequently, the number of vessels is greater in larger secondary xylem increments/annual ring. Does vigorous secondary xylem production influence the development and dimensions of vessels?

Radial diameter of vessels was measured to evaluate the relationship between xylem increment and vessel diameter. In all, over 1500 vessels each of long and short shoots were measured. Vessel diameter was greater in long shoots than in short shoots (Fig. 6-10). Also the frequency of comparatively large vessels was higher in first year wood of long shoots (c.f. Figs. 6-2 and 6-4). This aspect is considered to be important because vessle dimensions are "parameters that determine the efficiency and safety of water conduction" (Zimmermann 1982). Vessel diameter was chosen because of its positive

FIG. 6-9. Relationship between secondary xylem radial width (x-axis) and the number of vessels in radial file (y-axis) for first-year wood (X_1) of long and short shoots (internode 2).

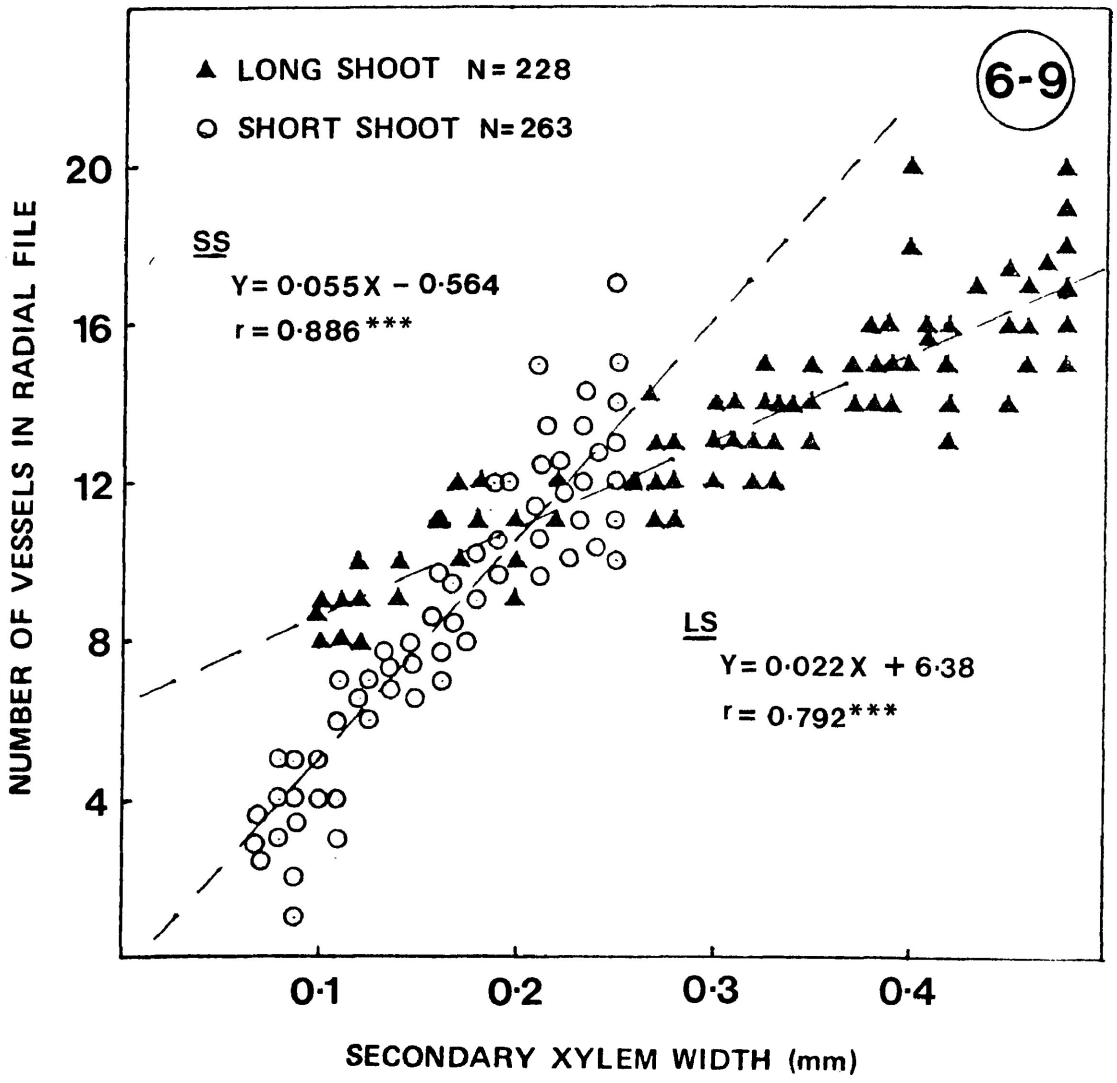
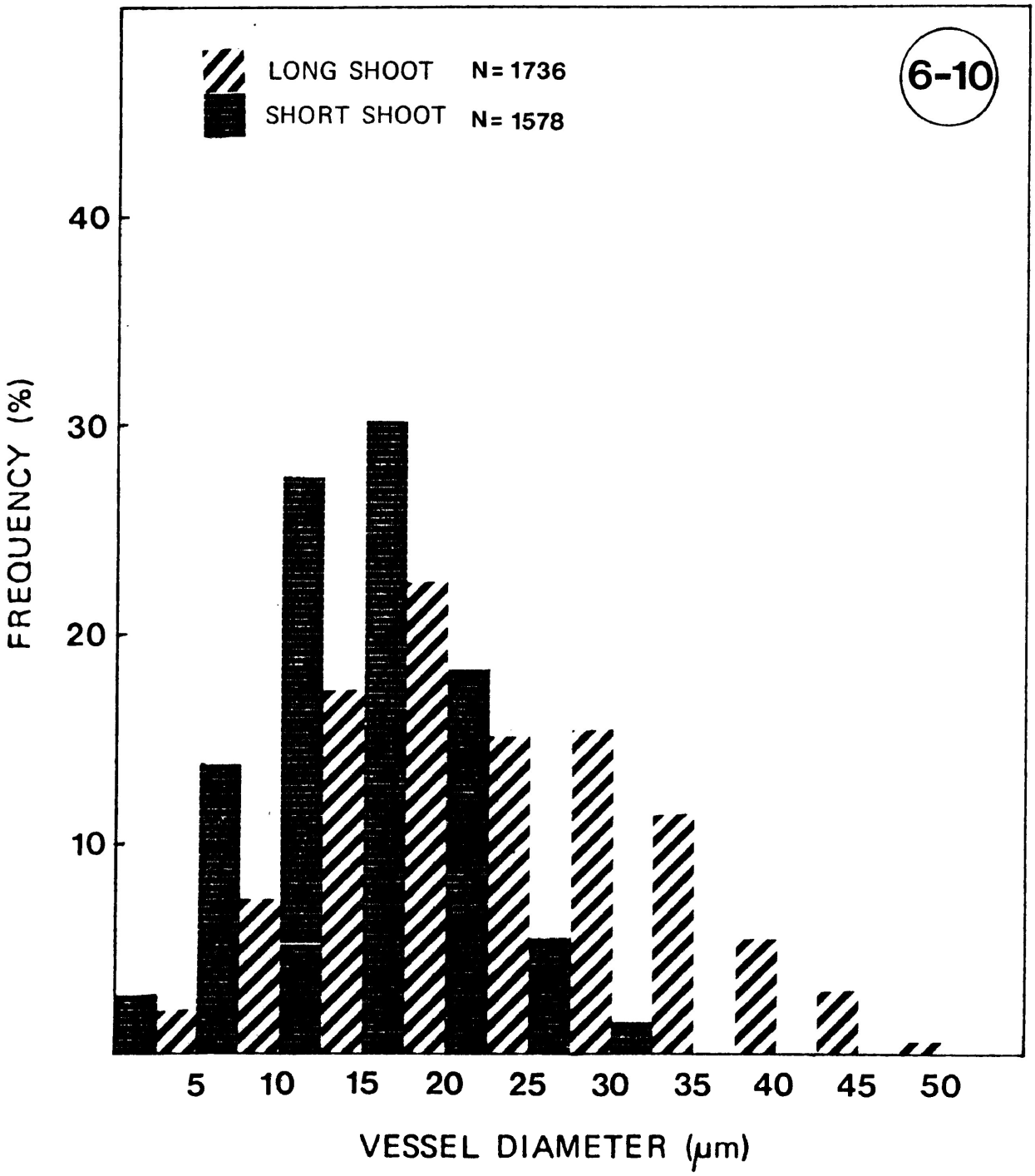

▲ LONG SHOOT N= 228
○ SHORT SHOOT N= 263
6-9
SS
Y= 0·055X − 0·564
r = 0·886***
LS
Y= 0·022X + 6·38
r = 0·792***
NUMBER OF VESSELS IN RADIAL FILE
20
16
12
8
4
0·1
0·2
0·3
0·4
SECONDARY XYLEM WIDTH (mm)

FIG. 6-10. Frequency distribution of vessel diameter (radial) in first-year wood (X_1) of long and short shoots.


LONG SHOOT N= 1736
SHORT SHOOT N= 1578
6-10
40
30
20
10
FREQUENCY (%)
5
10
15
20
25
30
35
40
45
50
VESSEL DIAMETER (μm)

correlation with length (Zimmermann and Potter 1982), the latter being more difficult to accurately measure. Furthermore, because of wide variations in vessel diameter in different species its effect on conductivity, according to Zimmermann (1982) is far greater than that of vessel length. Larger vessels conduct more water than small ones. Although conductivity measurements have not been determined *per se*, one can visualize greater bulk translocation in stems with larger vessels. Similar differences between long and short shoots have been reported in *Fagus*, *Acer*, Pomaceae, *Ginkgo* and *Berberis* (Herrmann 1916) and *Malus* (Sokolova and Ghosh 1970) on the basis of vessel frequency. The differences in water relations between long and short shoots may be significant here. In apple Simons (1956) observed that increased water supply resulted in thicker leaves and larger dimensions of palisade cells. This may explain why there is "better" leaf development in long shoots in birch, i.e., larger leaves, longer petioles, heavier petioles (i.e., more xylem) and lower SLA/higher SLW. Presumably, this is the consequence of water conduction efficiency due to the presence of more and larger vessels in long shoots, i.e., stem-node-leaf continuum. In a previous study (White 1954) there was a high correlation and an allometric relationship between petiolar xylem area and lamina size in the runner-bean, *Phaseolus multiflorous*

Willd. Water stress and its attendant limitations on various physiological processes including photosynthesis (Hsiao 1973) may directly or indirectly by implicated. Studies on the evaluation of water potential in long and short shoot buds prior to and after flushing are needed.

Frequency of rays was determined since it relates to the degree of cambial activity (Gregory 1977). Ray number was determined by counting the rays along a 100 µm line perpendicular to the rays on transverse sections. It was not surprising that long shoots had a larger number of rays per millimeter, tangentially (Fig. 6-11). If ray cells and pith parenchyma are associated with pre-dormancy storage of photosynthate, does this imply that long shoots store more and therefore have a ready supply of stored food at the beginning of the growing season?

From bud organogenic studies it was observed that the occurrence of a slight internodal extension in potential long shoot buds occurs in mid-July (Macdonald et al. 1983). Buds of that collection were, therefore, sectioned longitudinally, for general observations relating to internodal extension. As shown in Fig.6-12, there is more internodal extension in potential long shoots than in potential short shoots (Fig.6-13) The typical effect of pith rib meristematic activity associated with the long shoot habit is evident (c.f. Fig. 6-12 and 6-13). The arrest of pith rib meristematic activity in the terminal bud apices of older short shoots (year n+2 or more) is well marked especially by presence of ergastic substances and some degree of cell wall thickening immediately below the corpus (Fig. 6-14). These features are further illustrated in Fig.6-15 and occur very early in the growing season, by late May. Pith rib meristematic

FIG. 6-11. Frequency distribution of ray frequency (rays per millimetre (tangential)) obtained from transverse sections of the same internode and shoots of Fig. 6-5b.

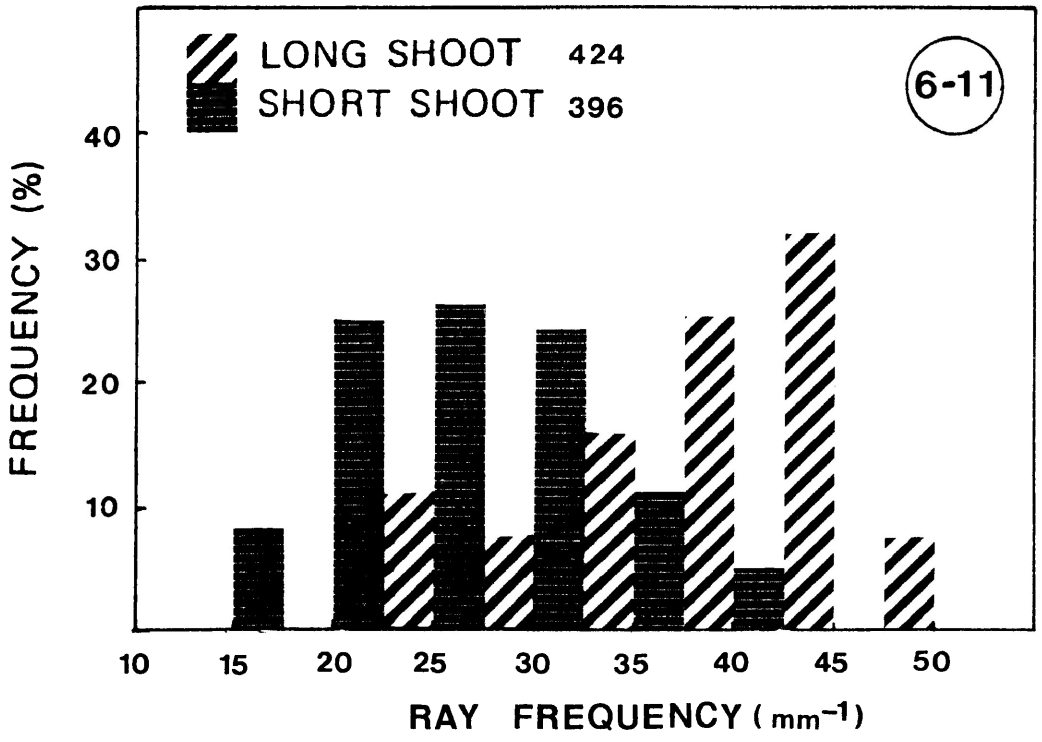

LONG SHOOT 424
SHORT SHOOT 396
6-11
FREQUENCY (%)
40
30
20
10
10
15
20
25
30
35
40
45
50
RAY FREQUENCY (mm⁻¹)

FIG. 6-12 x 105. Longitudinal section of a potential long shoot bud (pseudoterminal bud) collected on 14 July 1981 showing more internodal extension and generally more densely staining apical and subjacent tissues. Note the width of maturing subjacent internodes.

FIG. 6-13 x 97. Longitudinal section of a potential short shoot bud collected on 14 July 1981 showing slightly less internodal extension and less densely staining subjacent tissues, a sign of early maturation of tissues beneath the apex. Note that the width of the maturing subjacent internodes is smaller than in Fig. 6-12 i.e., potential long shoots despite slightly different magnifications.

FIG. 6-14 x 96. Longitudinal section of the terminal bud of a four-year-old short shoot showing virtually no internodal extension. This bud was collected on 25 May 1982. Note that after the formation of L_5 primordium (i.e. second early leaf; L_1 - L_3 are rudimentaries) there appears to be no activity at the rather broadened apex. This feature may be analogous to the stage of an organogenic pause. Less pith rib meristematic activity (RM) is evident. A concentration of ergastic substances in subjacent cells begins immediately below the apex - a possible sign of inactivity (dormancy) and maturation of tissues.

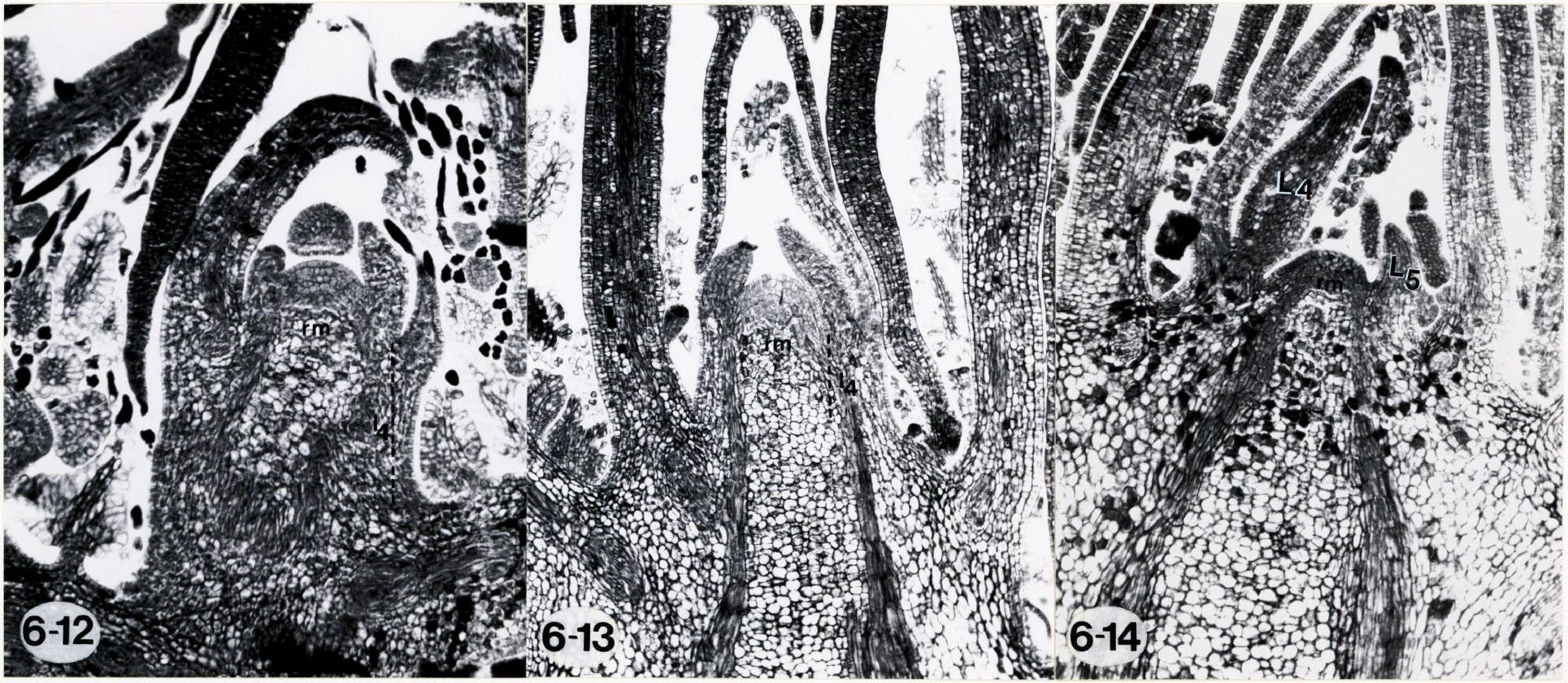
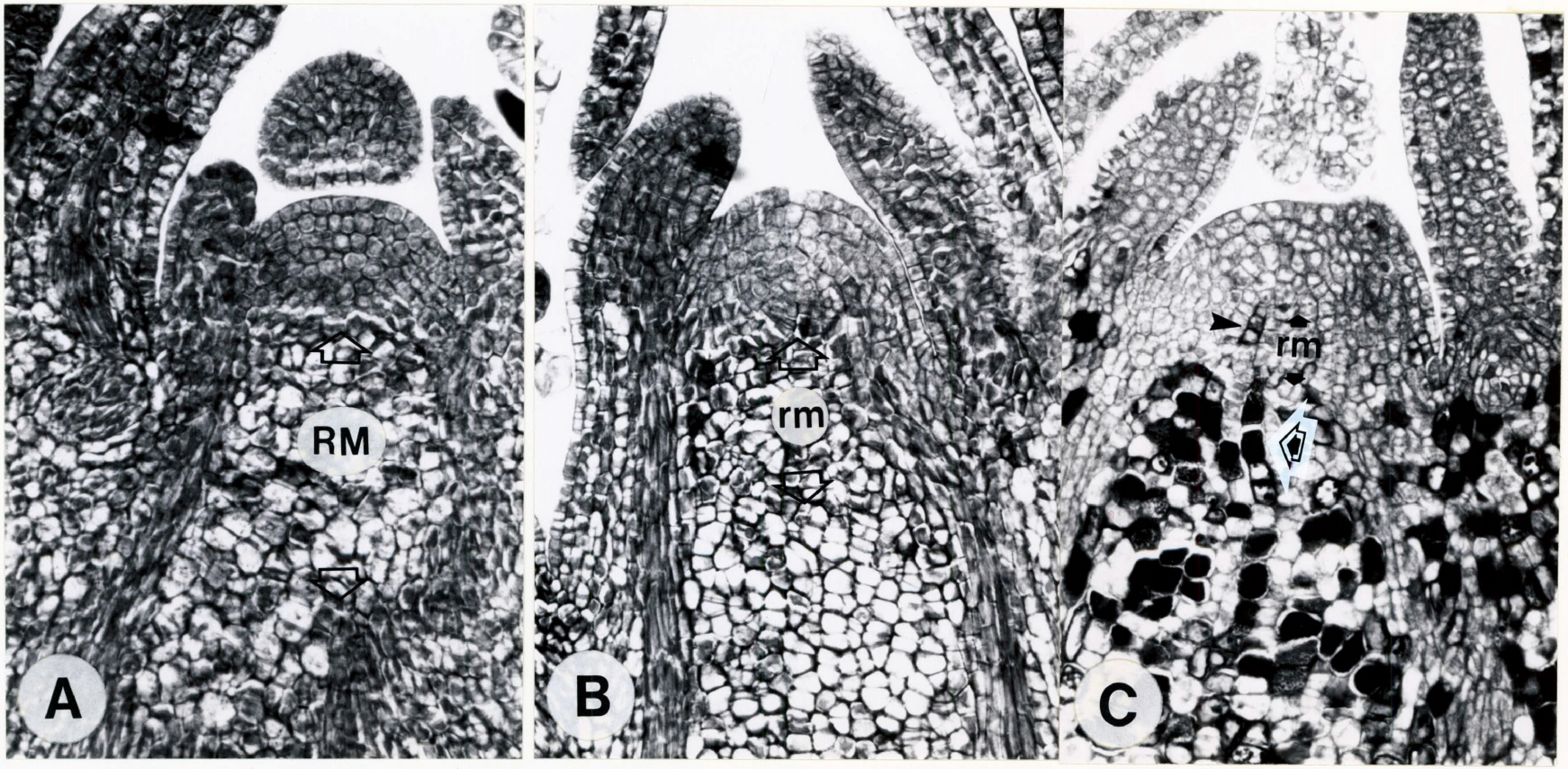

6-12
rm
L4
6-13
rm
L4
6-14
L4
L5
rm

FIG. 6-15. Enlarged long-sections of apices in Figs. 6-12, 6-13, and a terminal short shoot bud.

a. x 235. Apex of a potential long shoot bud showing extensive pith rib meristematic activity (RM) and a rather low, more active apical dome, with intensely staining nuclei.

b. x 243. Apex of a potential short shoot bud showing less pith rib meristematic activity (RM), early maturation of subjacent tissues, and typically less active, high apical dome.

c. x 250. Apex of the terminal bud of a four-year-old short shoot collected on 25 May 1982. Note less pith rib meristematic activity (RM), early maturation of subjacent tissues (arrows) and a preponderance of ergastic substances immediately below the apex.

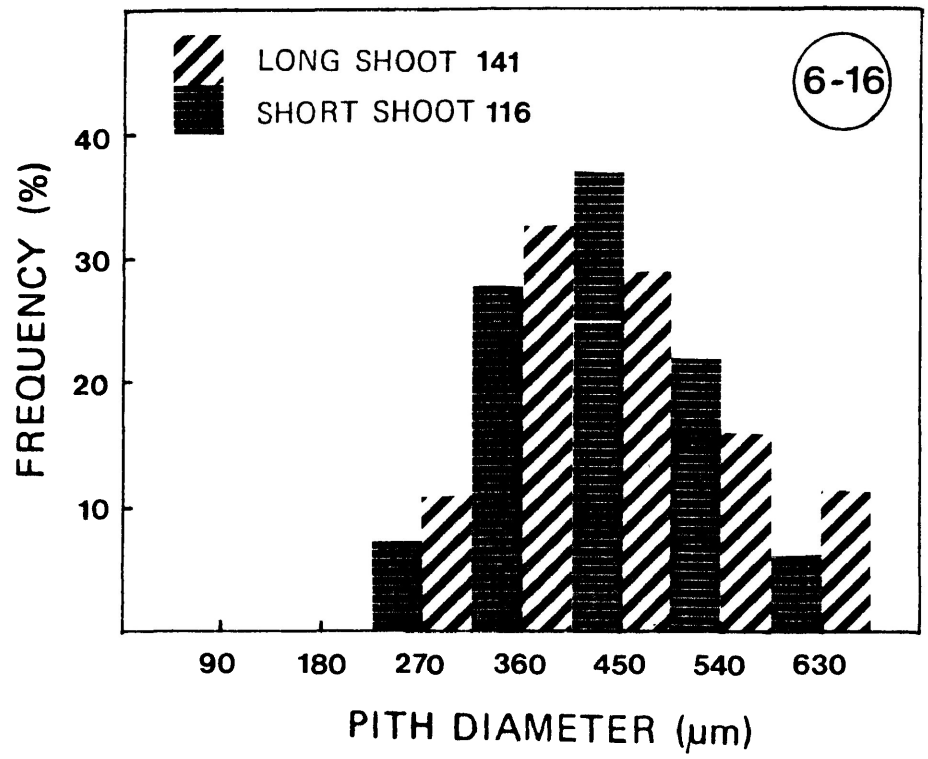

RM
rm
rm
A
B
C

activity is well known to be the possible cause of the long and short shoot habit. However, apart from qualitative descriptions of cell size in the pith rib meristem as in Pinus (Zimmermann and Brown 1971), no quantitative data is available. This meristem is the progenitor of the pith, hence the final dimensions of the mature pith parenchyma would relate to the activity of the meristem. Subsequently, pith and pith parenchyma diameters were measured. The results are shown in Figs. 6-16 and 6-17, respectively. Mean values are compared in Table 6-1. Cortical width is greater in short shoots than in long shoots (Fig. 6-18), the differences may also reflect the activity of the flank meristem of short shoots. In addition to this, vigorous secondary xylem differentiation in long shoots may facilitate the radial crushing of the cortex.

Transverse sections indicate that the phyllotaxy for potential long and short shoots (n + 1 buds) is 2/5. Interestingly, in older short shoots the rudimentary leaves of the previous and current year growth occur on the same orthostichy. Thus L_1 of the previous year is on the same orthostichy as the L_6 of that year. Thus L_6, that is, the first-formed rudimentary leaf primordium, becomes L_1 of current year. These phyllotactic observations may relate to the sequential production of 3 rudimentary leaves on older vegetative short shoot apices (Macdonald and Mothersill 1983). However, in axillary

FIG. 6-16. Frequency distribution of pith diameter in internode 2 of one-year-old long and short shoots.

FIG. 6-17. Frequency distribution of pith parenchyma size (diameter) of long and short shoots from the same sections as in Fig. 6-16.


LONG SHOOT 141
SHORT SHOOT 116
6-16
FREQUENCY (%)
40
30
20
10
90
180
270
360
450
540
630
PITH DIAMETER (μm)

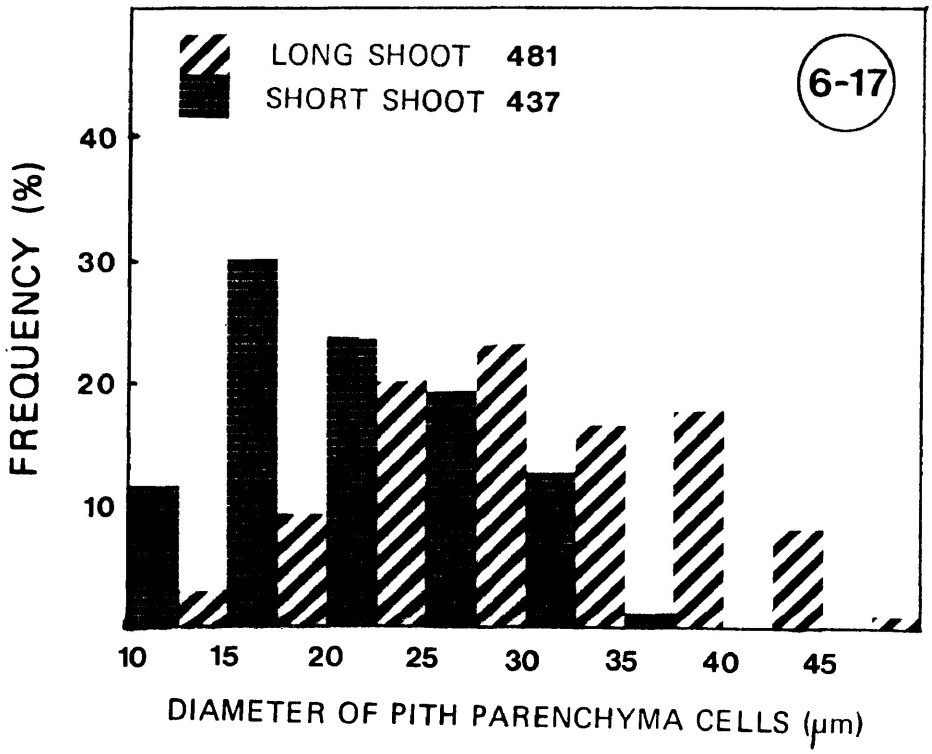
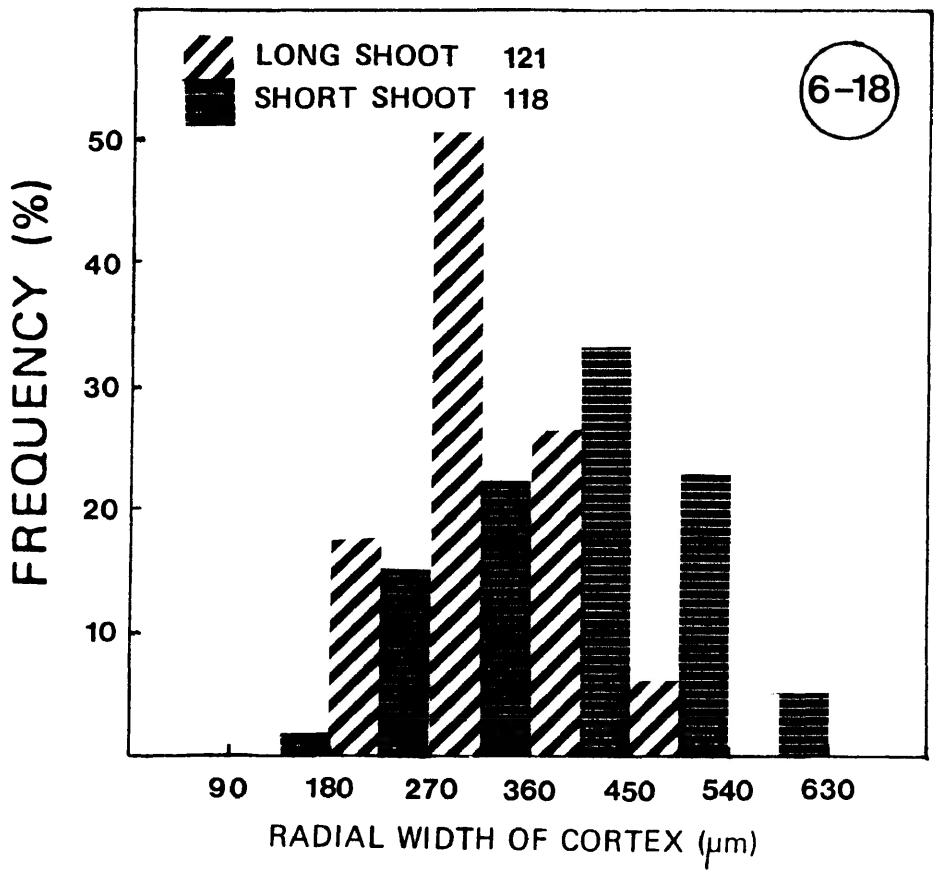

LONG SHOOT 481
SHORT SHOOT 437
6-17
FREQUENCY (%)
40
30
20
10
10
15
20
25
30
35
40
45
DIAMETER OF PITH PARENCHYMA CELLS (μm)

FIG. 6-18. Frequency distribution of cortical widths in long and short shoots from the same sections as Fig. 6-16.


LONG SHOOT 121
SHORT SHOOT 118
6-18
FREQUENCY (%)
50
40
30
20
10
90
180
270
360
450
540
630
RADIAL WIDTH OF CORTEX (μm)

potential short shoot buds there is only one rudimentary leaf, but in subsequent years 3 rudimentary leaves are formed. The cause of this transition is not understood. Specific details of how rudimentary leaf formation relates to primary vascularization has not been studied. Nevertheless, it has been observed that leaf-traces of rudimentary leaves are very small and the central leaf-trace, in particular, dissipates and becomes obscure as it enters the sympodium of the main shoot axis (Fig. 6-19). This indicates that rudimentary leaf traces do not contribute significantly to primary vasculature and hence to the development of secondary tissue. There is a more detailed evidence that in Populus xylem differentiation in the main axis is arrested in the traces of leaves with aborted laminae (Goffinet and Larson 1982) or scale-leaves (Richards and Larson 1982). Thus it could be inferred that since actively growing foliage promotes xylem differentiation (Young 1954; Wangermann 1967; Richards and Larson 1982), then, the insignificant contribution of the rudimentary leaf-traces to the axis would result in less xylem differentiation in short shoots than in long shoots because short shoots possess more rudimentary leaves than long shoots. Long shoots develop late leaves, short shoots do not. Perhaps because of there being fewer leaves, vital "physio-

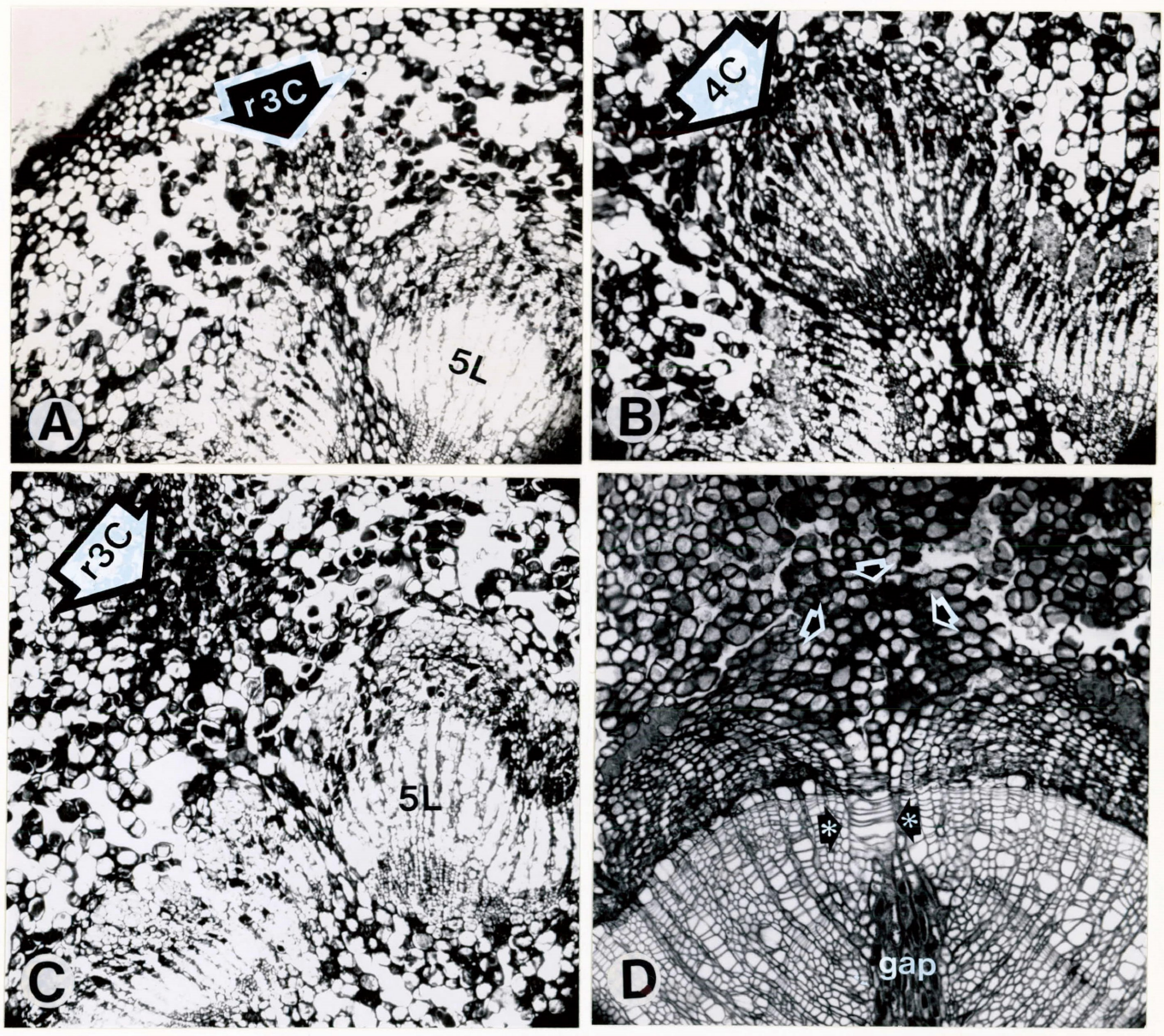
FIG.6-19. Relative contributions of rudimentary and foliage leaf-traces to the short shoot sympodium in a four-year-old shoot.

a. x 100 Transverse section of internode 4 (i.e. below the first early leaf) of a short shoot showing the central trace (r3C) of the third rudimentary leaf, L_3, "fizzling out" or dissipating prior to entering the sympodium. The right lateral trace of L_5, 5L, is shown in comparison with r3C.

b. x 103 The central trace of the first early leaf (L_4), 4C, of almost the same magnification as Fig. 6-19a is shown entering the sympodium. Its sympodial contribution is far greater.

c. x 100 Transverse section of internode 4 of another, a six-year-old short shoot showing the same situation as in Fig. 6-19a. The central trace of L_3 (r3C) is "fizzling out" long before it enters the sympodium (arrows). 5L is shown in comparison.

d. x 97 Transverse section of short shoot stem several microns below that of Fig. 6-19a showing remnants of dissipated r3C and peculiar reorganization of xylem vessels (arrow) in its gap, during secondary growth.


r3C
5L
A
4C
B
r3C
5L
C
gap
D

logical factors" contributed by active foliage leaves for xylem differentiation is reduced in short shoots. Although I have no direct evidence such factors could be hormonal (Larson 1964; Roberts 1969; Zimmermann and Brown 1971), they have not been identified in potential long and short shoot leaves of paper birch. However, young leaves are known to be a source of naturally occurring growth regulators (Jacobs 1952; Jones and Phillips 1966; Critchfield 1971; Shininger 1979). In addition, gibberellin-stimulated cambial activity in spur shoots of apricot has been reported (Bradley and Crane 1957). It is not known if short shoots produce less gibberellins or other growth regulators than long shoots in birch. Trends implicating auxin concentrations in long shoot extension in Ginkgo and Cercidiphyllum have, however, been reported (Gunckel et al. 1949; Titman and Wetmore 1955). Higher Stem-RGR in potential long shoot buds than short shoot buds may relate to the insignificant contribution of rudimentary leaf-traces to the sympodium, the inactive cambium and consequently less secondary xylem formation in potential short shoots. In addition, pith rib meristematic activity in potential long shoots would also facilitate internodal extension which is lacking in short shoots. Since defoliation strongly inhibits stem elongation (Sachs 1965) one could assume that lamina abortion in short shoots may be analogous to defoliation.

Vital physiological and biochemical studies are needed to complement these observations.

CHAPTER 7

CHAPTER 7

GENERAL DISCUSSION AND SUMMARY

The purpose of this chapter is to collate the results/observations and discussions of Chapters 3 to 6 in order to provide a better understanding of the long and short shoot habit in B. papyrifera. The previous chapters provide the foundation/framework for the correlations between observations and these correlations have been discussed. Growth analysis, morphometric measurements and various other observations have been used to establish differences between long and short shoot expression. These data have been related to organogenic studies (Macdonald and Mothersill 1983; Macdonald et al. 1983).

Based on the results/observations of this study, a descriptive model can be advanced to explain shoot expression in paper birch. Take, for example, a hypothetical seven-node long shoot. At the end of the growing season it has four buds subtended by late leaves. The distal one or two buds will flush as long shoots the next growing season, and the proximal buds as short shoots. The long shoot potential is morphogenetically determined prior to the end of the growing season. Post-dormancy Bud-, Stem- and Leaf-RGR is higher in potential long shoot buds than

potential short shoot buds. Bud-, Stem- and Leaf-RGR seem to correlate with flushing sequences. Since potential long shoot buds flush first, the branch will exhibit a basipetal flushing sequence. The potential long shoot bud(s) seem to exhibit apical dominance/control over the potential short shoot buds proximal to them. It has been hypothesized that such a dominance or control may be traced to the various morphogenetic events operating in time and space during secondary bud inception. Hormonal, nutritional and probably other physiological phenomena may be involved. But these are not known. Potential long shoots may possess a stronger metabolic sink which makes them compete more successfully for nutrients than the proximal short shoots. The two early leaves of the long shoots, after flushing, have greater surface area, lower SLA/higher SLW and longer laminae than those of the short shoots. Early leaves of long shoots contribute assimilates for the development and expansion of late leaves, their subjacent internodes, as well as for the growth and development of axillary buds. Fully developed late leaves increase the photosynthetic surface area and possibly also the photosynthetic turnover of the long shoot. Short shoots lack internodal extension and late leaves. Consequently, they do not contribute to canopy expansion and may only be acting primarily as photosynthetic units exporting assimilates for cambial activity in other (e.g. long shoot

portions) units of the canopy and root growth. Long shoot extension is terminated by shoot tip abortion or by male inflorescence formation.

If the hypothetical seven-node long shoot develops terminal male inflorescences, not only is shoot extension limited, but strong sink effect caused by both inflorescence formation and flowering, results in a suppression of long shoot development. Consequently, leaves of reproductive long shoots have smaller leaf sizes and higher SLA/lower SLW than comparative vegetative long shoots. Reproductive cost is manifested, not only in the leaves of the current long shoot, but it is also realized the following year, during flowering; the growth/developmental potential of the axillary buds proximal to the male inflorescences is markedly reduced. As a result, the reproductive cost is reflected in lower post-flush bud dry weights and total early leaf areas. The potential of the distal buds to flush as long shoots is also reduced. In extreme cases all buds may flush only as short shoots. In the event that the apices of proximal short shoot buds are transformed into female inflorescence apices, the reproductive cost is compounded. Such synergistic effect of both male and female reproduction is reflected in smaller early leaves of reproductive short shoots developing proximally to terminal male inflorescences. Thus the production of inflorescences decidedly reduces shoot vigour for at least two years.

The higher growth potential, and the occurrence of late leaves and associated axillary buds in long shoots contributes to greater cambial activity and consequently the production of more secondary xylem, larger vessels and more rays. A compounding effect due to the production of more leaves and associated axillary buds leads to greater cambial activity and better developed vascular system with larger vessels in long shoots, in a complementary manner. Short shoots on the other hand, have only early leaves since the laminae of the distal leaves, that is, those that are comparable to the late leaves of long shoots, abort. Consequently, rudimentary leaves do not contribute to the development of sympodial traces because their leaf-traces are suppressed. The differences in the secondary vascular development between long and short shoots is pronounced, and these differences, which may reflect the morphological differences may be related to differences in growth characteristics. For example, the presence of many leaf primordia and, also, secondary axillary bud apices in potential long shoot buds may be related to higher Bud- and Stem-RGR early flushing and greater cambial activity. Hormonal relations, although not known, are obviously involved. However, greater cambial activity in long shoot buds results in more secondary tissue production and larger vessel diameter. The larger vessel diameter in long shoots presumably, in turn, provides a more efficient conduit (translocation pathway) for water and other

nutrients. Larger early leaves of long shoots may be the direct result of the conduction of more water vital to expansion of cells and consequently to the expansion of leaf laminae.

Answers to some of the questions posed in this thesis have not been provided or perhaps adequately substantiated due to limitations imposed by this type of study and also to a lack of specific physiological information. One thing is obvious, there is a dire need for morphologists, anatomists, physiologists and biochemists to collaborate in order to better understand the problems associated with tree growth.

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