CROWN DEVELOPMENT AND ARCHITECTURE

OF *FRAXINUS PENNSYLVANICA* VAR. *SUBINTEGERRIMA*

(VAHL) FERN. AT DIFFERENT STAGES OF GROWTH AND

UNDER DIFFERENT ENVIRONMENTAL CONDITIONS

by

Grant A. Bartlett

A Thesis Submitted to

the Faculty of Graduate Studies

University of Manitoba

In Partial Fulfilment of the

Requirements for the Degree

of

Master of Science

Department of Plant Science

© September 1997

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CROWN DEVELOPMENT AND ARCHITECTURE OF
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GRANT A. BARTLETT

A Thesis/Practicum submitted to the Faculty of Graduate Studies of The University

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Grant A. Bartlett   1997 (c)

ACKNOWLEDGEMENTS

I would like to thank my advisor Bill Remphrey for accepting me as his graduate student. I would like to thank him for all his help in the preparation of my thesis. I am sure his patience was pushed to the limit sometimes when he had to keep reading the same section over again and I appreciate all the time and effort he put into this thesis with me.

I would also like to thank my committee, Dr. C. Davidson, Dr. S.R. Rimmer, and Dr. M. Sumner for their suggestions, support, and encouragement. A special thanks to Mr. Davidson for his input on the collection of data in Morden.

There are several people who helped me out along the way and I would like to thank them: Suzanne Gobin who works at the Agriculture and Agri-Food Centre in Morden whose help was greatly appreciated especially in operating the high-up lift truck; Linda Pearn for her assistance in the collection of some data and in various aspects of this project; Fred Meier for his assistance in many areas; Tammy Jones-Dobbie for taking time to read drafts of some sections; and people of the Horticulture lab (past and present). I would also like to thank anyone else who helped out along the way for their encouragement and advice.

I would like to extend my biggest thanks to my parents who have provided me with this opportunity to complete this masters degree. Without their encouragement and support all of this would not have been possible.

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ABSTRACT

Bartlett, Grant A. M.Sc., Department of Plant Science, University of Manitoba. *Crown development and architecture of Fraxinus pennsylvanica var. subintegerrima (Vahl) Fern. at different stages of growth and different environmental conditions.* Major Professor: Dr. W.R. Remphrey.

The architecture of a tree does not remain static and varies in space and time through alterations in shoot development in different crown locations and as the tree ages. Shoot architecture is influenced by global environmental factors such as the climate and availability of light and also more locally by other shoots through mutual shading or competition for resources. The objectives of the thesis were to examine spatial (crown location) differences and temporal (aging) differences on various aspects of *F. pennsylvanica* crown architecture characteristics. The major characteristics examined were the number of shoot units per shoot, shoot-unit length and the fate of buds. The other objective was to examine how shoot development and architecture are affected by the light environment when the whole tree is shaded. To examine the spatiotemporal change in architecture, trees of approximately 8, 10, 20, 50, and 60-years-old were selected at the Agriculture and Agri-Food Centre in Morden, Manitoba and measurements in each of 3 crown locations were made. To examine the relationship between light and shoot architecture, 2-years-old seedlings were transplanted and subsequently covered with shade cloth of varying shade intensities (60, 80, 92, and 96 %) and a control grown in the open at the University of Manitoba. Architectural measurements along with environmental

variables (soil moisture content, air temperature, relative humidity and the red to far-red light ratio) were made in each treatment. In the mature trees spatial location of the shoot in the crown resulted in a decrease in the number of shoot units per shoot, shoot-unit length, and the number of lateral shoots and inflorescences from the top to the bottom of the crown. Aging resulted in a decrease in the number of shoot units per shoot and in lateral branching, but had little effect on shoot-unit length. Whole tree shading resulted in shorter height growth increments (HGIs), fewer lateral shoots, fewer shoot units per HGI, and shorter shoot-unit lengths. Many of the observed differences between the top and inside of the crown, such as a decrease in the number of shoot units per shoot or reduced lateral branching are similar for older trees and those trees heavily shaded. Reductions in photosynthesis were hypothesised as a major factor responsible for the differences in the developmental patterns of the shoots in both studies.

INTRODUCTION

Fraxinus pennsylvanica var. *subintegerrima* (Vahl) Fern. is a large oval to round tree reaching heights of 15 to 18m (Fig.0.1a-c). The leaves are compound and borne in a decussate arrangement. *Fraxinus pennsylvanica* is a very common tree in North America ranging from Nova Scotia to southeastern Alberta and south to the Gulf of Mexico. It is very important as a shelterbelt species on the prairies because of its strong rooting habit and vigourous seedling growth (Burns and Honkala, 1990). It has also become a very important street tree throughout North America because it is highly adaptive to different habitats. In Winnipeg, it is used extensively to replace the *Ulmus americana* population which is declining due to Dutch Elm Disease.

A more complete understanding of the growth and development of *F. pennsylvanica* is considered useful to facilitate proper maintenance of the current plantings and to assess the future potential of this species as a significant component of the landscape. The current study is an extension of previous work on this species conducted at the University of Manitoba and at the Agriculture and Agri-Food Research Centre in Morden, Manitoba. A long term objective of this program is to develop a comprehensive computer simulation model to evaluate the importance of architectural variables involved in the development of the crown. It is hoped that such a model will be useful for

Fig. 0.1. Photographs showing morphology and structure of *Fraxinus pennsylvanica*. **a)** Specimen of 'Patmore' in summer. **b)** Leafless specimen of a boulavard tree in Winnipeg, Manitioba. **c)** Compound leaf of 'Patmore'. (Photos by W.R. Remphrey)

assessing the effect of environmental variables on architectural development and the development of the crown over time.

The architecture of a tree is defined as the visible, morphological, expression of the genetic blueprint of organic growth and development (Hallé et al., 1978). The architecture is created through the repeated formation of shoots, defined as yearly increments of growth in temperate regions. Shoots are composed of shoot units which are defined as a leaf axillary bud and the subtending internode. Ultimately, crown development occurs through the repeated production of these shoot units.

Within a shoot there is variation in shoot unit numbers and their lengths. Their development is not static and their size varies both in relation to spatial location in the tree and in time as the tree ages. Variation in shoot unit size in the crown is important in giving the tree its characteristic architecture. Because of longevity and size of a tree, there is the possibility for quantitative patterns to change in response to the increasing complexity of the branching structures and alterations in the environment through time.

The effects of time and space on tree development can occur on two levels, global or local. Global factors may include whole tree aging and environmental changes due to climate. Thus the architecture of the whole tree is simultaneously impacted upon. Conversely, architecture may be defined more locally, for example, the change in architecture of a branch as it develops and

ages in the crown. In this case, the variation may be due to increasing complexity in the branch system resulting from internal physiological differences. Nevertheless, the variation may result from the effects that the developing branching structures have on localized environmental parameters such as the light climate which may in turn affect architecture.

The development of the tree through time is known as aging (Wareing, 1959). The pattern of development can be described as following a sigmoid curve (Wareing, 1970). After germination, a tree may grow quite slowly for a year or two and then begins to grow very rapidly. The period of time of rapid growth differs between trees and may be pre-programmed or determined by environmental factors. Eventually the tree reaches maturity and growth slows down. In general, as the tree ages beyond this point, certain changes occur such as a reduction in annual growth increment, a loss of apical dominance, and a reduction in geotropic responses resulting in a more rounded crown (Wareing, 1970). These changes in growth and development result in an alteration in architecture.

The local light environment within the crown of a tree is highly variable. Differences occur between the outer and inner part of the crown. Larcher (1975) found in some trees there was less than 10 % of full sun intensity in the interior of the tree. Based on this difference in the local light environment different zones seem to occur in the tree where different developmental patterns occur.

In general, the top of the tree is more vigorous and this results in greater development of shoots and in branching, where as shoots growing inside the tree grow very slowly and produce few laterals.

A tree that is completely shaded by other trees may adapt to the light situation in a different manner than localized parts of an individual tree. For localized effects, there are other areas of the crown that are not shaded and this may result in internal physiological factors becoming important. Therefore the response in the interior of the crown is probably not a response to shading alone and other physiological factors are involved. Nevertheless, there are similarities. A general response to shade is a reduction in lateral shoot production and shoot elongation resulting from changes in the quantity and quality of light. Despite the similarities, there have been no attempts to relate the patterns of development observed from local shading with patterns of development observed from global shading.

In relation to aging, shoot architecture in individual branches several years old have been examined (Remphrey and Davidson, 1992) but no studies have explored architecture in relation to whole tree aging. There have been studies on shoot unit growth rates (Remphrey and Davidson, 1994b; Prusinkiewicz *et al.* 1994) and preformation (Remphrey and Davidson, 1994a) and neoformation (Davidson and Remphrey, 1994) in relation to crown zone. One study addressed architecture at the shoot level in relation to individual

branch aging (Remphrey and Davidson, 1992). There are no studies which have examined either shoot unit size in relation to specific crown zones or the fates of individual buds, that is, whether they develop into flowers, vegetative shoots, abort or remain dormant. One of the additional benefits of information on the growth and development of *F. pennsylvanica* in relation to aging, crown location, and shading is the construction of models which can simulate growth and development through time and space.

The objectives of the present study are:

1) to determine the effects of tree aging on shoot unit architecture for both terminal and lateral shoots along with the effects on bud production and their eventual products.

2) to determine the relationship between the different crown zones and shoot unit architecture and fate of buds.

3) to determine the effects of whole tree shading on *F. pennsylvanica* seedling development and architecture. A secondary objective is to relate patterns observed in whole tree shading to those observed in older tree crowns.

LITERATURE REVIEW

DESCRIPTION OF *Fraxinus pennsylvanica*

Fraxinus pennsylvanica var. *subintegerrima* (Vahl) Fern. commonly known as green ash is considered a botanical variety of *Fraxinus pennsylvanica* (Marsh) which is typically called red ash. The botanical variety of green ash is the prevalent type in the Canadian prairies and differs from the species in that the leaf stalks, leaves, twigs, flower stalks, and fruit stalks are almost hairless (Farrar 1995). Some authors (Dirr 1990) do not recognize the botanical variety and refer to this species throughout its range as simply *Fraxinus pennsylvanica* (and usually as green ash). The material used in the present study was considered to be *Fraxinus pennsylvanica* var. *subintegerrima* (Vahl) Fern.

Fraxinus pennsylvanica is a flood-plain species and is common along stream banks and moist bottom lands and occasionally in drier uplands. *Fraxinus pennsylvanica* is usually found associated with *Acer negudo, Acer rubrum, Populus deltoides, Populus tremuloides, Salix nigra,* and *Ulmus americana. Fraxinus pennsylvanica* is large tree up to 25m with the crown usually half the height (Fig. 0.1a,b). The tree has a relatively fast growth rate of up to 1m per year in the early stages of development. It can exceed 100 years of age.

The leaves are pinnately compound, 20 to 30 cm long, with 5 to 9 leaflets (Fig. 0.1c). Twigs are stout, smooth, and light grey. The terminal bud is

vegetative, reddish-brown, hairy, and conical; lateral buds are hairy also but smaller and rounded and may be vegetative or reproductive (Fig. 0.2b). The species is dioecious with separate male and female trees. The flowers are inconspicuous, usually borne before the leaves in late April to early may, and in axillary clusters initiated the year before flowering (Remphrey 1989). It is a profuse fruit producer. The fruit is a samara and usually persists into the winter. The wood is strong and used for tool handles and bentwood (Burns and Honkala, 1990). There are several cultivars including 'Patmore' (narrow, conical) and Marshall's Seedless' (broad, round) which are seedless male clones. 'Patmore' is used ornamentally in many areas of North America.

TREE ARCHITECTURE

Development of a Tree

Introduction

The architectural construction of trees has received considerable attention in recent years, although interest in how the characteristic structure of a tree arises has been around since the beginning of the scientific study of plants (Fisher, 1984). Tree architecture is defined as the holistic and dynamic description of tree form, from the seedling to the aged, senescent individual (Hallé *et al.*, 1978). The basic architectural plan is created through the

expression of the genetic blueprint of the tree (Hallé *et al.*, 1978). However, to a large extent the interaction between environmental factors and developmental morphology that creates a characteristic architecture of a species (Bilbrough and Richards, 1991). In general the genetic program of the tree determines branching angles, internode length, which buds will develop, or remain dormant (Jones and Harper, 1987), yet all these may be modified by the environment. Analyzing crown architecture is difficult because of the often large size of the tree and the very large number of shoots present (Wilson and Kelty, 1994). The topics to be covered in the following sections include: development of a tree, specific architectural tree characteristics, and spatiotemporal effects on tree architecture.

Tree Architecture and Models

In order to examine a tree's architecture, it is necessary to understand what is a tree. According to Hallé *et al.* (1978) the definition of a tree depends on one's point of view. For example foresters and ecologists may possess different definitions. A simple definition of a tree is that it is one of the tallest free standing, perennial plants usually with a single stem at the base, is much branched above, and has well developed, long-term cambial activity (Wilson, 1970). Trees are composed of smaller pieces or units that when added together produce a highly ordered organism that varies in time and space.

Trees can be classified according to their architectural pattern through the use of qualitative models. Such models are based on the spatial arrangement or orientation of shoots around the stem, number of axes, the position of flowers, whether terminal or lateral, and the effects on branching pattern, and whether the tree is a monocotyledon or a dicotyledon (Barlow, 1989). Hallé *et al.* (1978) have attempted to classify most trees into one of twenty-three different qualitative models. The models of Hallé *et al.* (1978) do not provide quantitative details about the architectural development of a tree. Nevertheless, they are beneficial because they show that even though each species has a slightly different set of rules for growth and development, they may still follow the same basic architectural model.

Some qualitative architectural models are relatively simple, for example where the tree is monoaxial (built by a single apical meristem) and the inflorescences are terminal, (Holttum's model) (Hallé *et al.*, 1978) or whether the inflorescences are lateral, (Corner's model) (Hallé *et al.*, 1978). Other models are more complex, where the trunk is polyaxial (built by multiple apical meristems). These models require the examination of other architectural characteristics to quantitatively differentiate the models. For example, if the vegetative axes are all equivalent the tree could exhibit Tomlinson's model; if the vegetative axes are differentiated into trunk and branches it might be Rauh's model, or if the tree possesses mixed axes comprised of both a vertical

axis component and a horizontal axis component in response to gravity, it may be Mangenot's model. The *Fraxinus* species of the Oleaceae family are best described by Rauh's model. Rauh's model states that the architecture of the tree is determined by a monopodial trunk (an axis established by a single indeterminate meristem) which grows rhythmically and so develops tiers of branches which are morphogenetically identical to the trunk. The inflorescences are always lateral (axillary) with no effect on the growth of the shoot system (Hallé *et al.,* 1978). Rauh's model is very common to trees in the temperate regions.

To examine tree architecture in more detail, quantitative models have been developed. Quantitative models rely on physical measurements of the trees which might include shoot length or the number of buds on a shoot for example. The introduction of computers has allowed for an expansion of this type of modelling because of their speed and ability to do multiple calculations (Fisher, 1992). These quantitative examinations among trees of the same species may appear highly variable (Sakai, 1990), yet trees are qualitatively recognizable as being of the same species (Bell, 1979).

Many researchers are attempting to simulate the growth of a tree using computer models. According to Room *et al.* (1996) these models could have many practical uses including landscape architecture to simulate interactions between plants and buildings, in horticulture or forestry through the

identification of optimal pruning strategies, or entertainment in games, films or educational software.

Tree growth and development

Woody plant structure results from 2 processes: increment in biomass (growth) and the architectural arrangement of the biomass in space (development) (Porter, 1983). Growth and development are terms that are often confused and used to describe each other. Porter (1983) defines growth as "the irreversible increase in dry matter and maintenance of a disequilibrium between the assimilation and loss of environmental resources which are synthesized into complex chemicals within the plant". Porter (1983) describes development as being "recognizable principally as a change in the number of plant organs rather than their size". However, this definition is incomplete because development is a comprehensive process involving the organization of complex sets of tissues into organs that constitute the mature tree (Raven *et al.*, 1986). Whole tree development results from the repeated production of the basic morphological units which are integrated into larger complexes (Bell, 1979; Sakai, 1990) following the intrinsic genetic pattern of the tree (Jones and Harper, 1987; Bell, 1979).

At the cellular level, trees are composed of the same basic cell types. Shoot apical meristems produce shoot units with more meristems that become

organized into shoots (Fig. 0.2a,b) (Barlow, 1989; Wilson, 1970). A shoot unit is defined as a leaf, node, subtending internode, and associated bud (Prusinkiewicz *et al.,* 1994) and are equivalent to a metamer (Room *et al.,* 1994; Barlow, 1989). Shoot units are the product of the activity of a single meristem (Bell, 1994; Bell, 1979). The accumulation of shoot units enlarges the structure of the tree. A shoot is defined as a yearly increment of growth in temperate regions and is characterized as a single unit of growth arising from a bud and ending in a terminal bud (Remphrey and Powell, 1984). Shoot units are added together in succession each year to form a shoot. A single shoot or several years of shoot growth compose a branch. As branches accumulate the architecture of the tree is ultimately created.
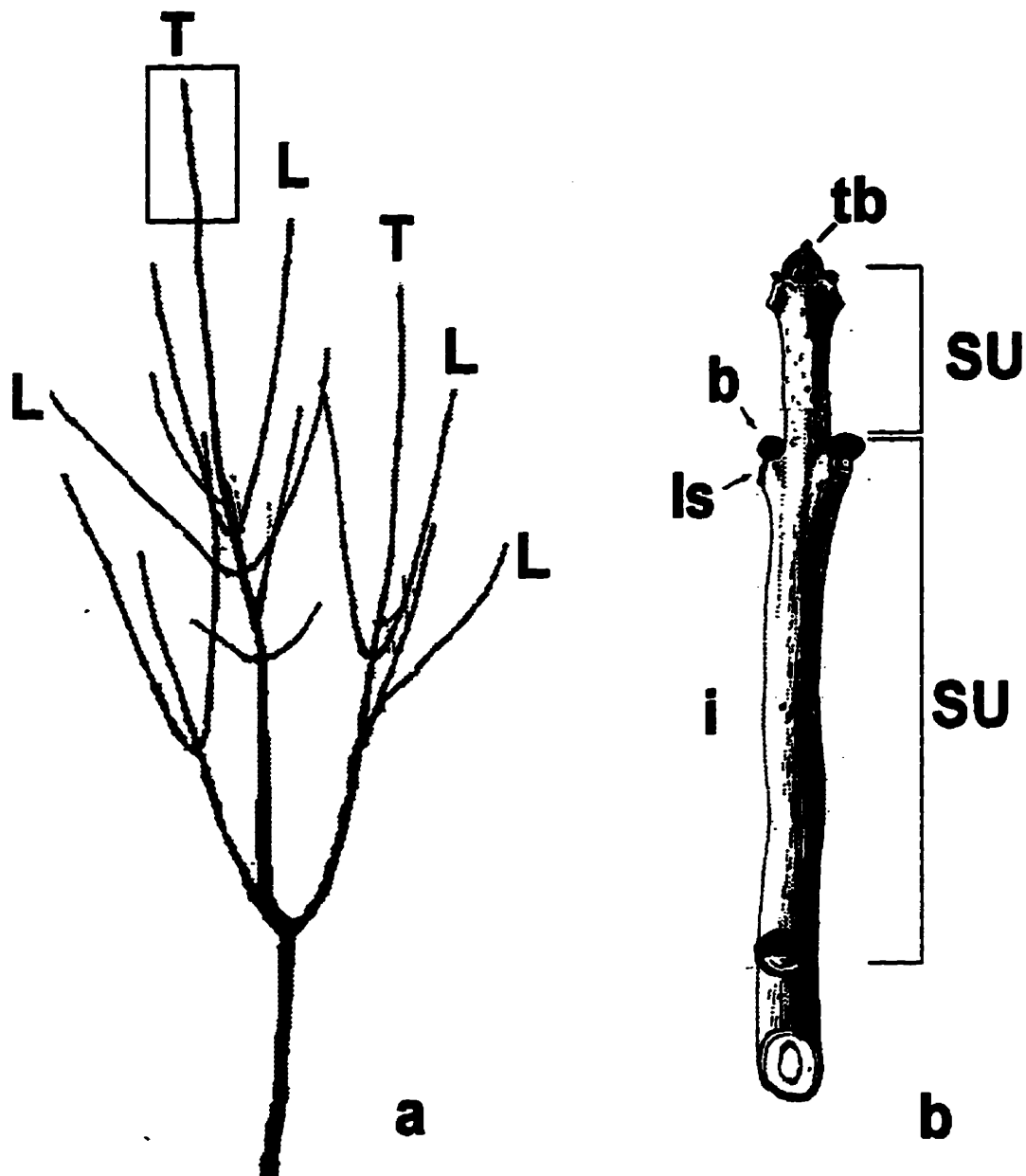
Fig. 0.2. The shoot system of *Fraxinus pennsylvanica*. a) Young sapling image scanned from actual photograph of a tree in the clonal experiment (see Chapter 1) showing terminal (T) and lateral (L) shoots involved in the expansion of the crown. Boxed in portion of the shoot corresponds to the portion shown in b. b) Upper portion of shoot showing a terminal bud (tb) and shoot units (SU). A shoot unit is composed of a leaf (ls=leaf scar), bud(s) (b), and subtending internode (i). Adapted from (Campbell and Hyland 1975).

Specific Architectural Tree Characteristics

Introduction

There are many architectural characteristics that influence the construction of a tree. Because of their obvious impact on architecture the most commonly measured characteristics are shoot length and branch angle (Borchert and Honda, 1984; Remphrey and Powell, 1984; Remphrey and Powell, 1987). Variation in characteristics including: (1) the number of shoot units per shoot, (2) the length of the shoot units for each shoot, (3) the fate of buds, and (4) the branching habit of the tree ultimately affect the architecture of a tree. One reason these parameters have received less attention is that architectural models constructed previously were much simpler. With the development of new programing languages it has become possible to include more detailed information about the shoot unit e.g (Reffye de *et al.*, 1991; Prusinkiewicz *et al.*, 1997). These variables are also important because they determine the length of shoots and the number and location of lateral shoots. Variations in these characteristics ultimately affect the architecture of a tree. The expression of these characteristics is dependent on internal and external factors. Internal factors may include the genetic make-up of the tree, the health and age of the tree, and availability of nutrient compounds especially carbohydrates. External factors include light, water, temperature, mineral supply, other plants (competition), and soil physical and chemical properties (Kozlowski, 1971).

Shoot unit production

The vast majority of plants are hierarchical in construction with smaller units added together to produce larger units (constructed in a modular way) (Porter, 1983). Organs occur at various angles and levels on the shoot framework. Shoot units are the fundamental unit of growth and development occupying the central position in this hierarchy because they produce lateral buds and more shoot units (Maillette, 1992). Each shoot unit is unique because of variation in its length and the production of lateral buds of different potentials. The combination of the number of shoot units and their respective lengths determine individual shoot lengths.

In *F. pennsylvanica* most of the shoot units that are produced in the spring are preformed (Remphrey and Davidson, 1994a; Remphrey, 1989a). Preformation occurs when the formation of a large part of the current year shoot is initiated in primordial form in the previous year's bud (Hallé *et al.*, 1978). The preformed leaf and scale primordia are produced during the growing season and normally there is a period of rest prior to expansion. Both the terminal and lateral buds are formed at this time. However, not all of the shoot units observed after growth ceases occur from preformation. In some trees syllepsis may occur, that is, the lateral apical meristems begin to expand in the same year as they are formed without a rest period and all the shoot units are neoformed (Hallé *et al.*, 1978). Neoformation occurs after the preformed

primordia that had been initiated the previous year have completed expansion and more primordia are produced which expand immediately forming leaves, buds, and intended tissue (Hallé *et al.*, 1978). In a study of neoformation in *F. pennsylvanica* (Davidson and Remphrey, 1994), it was found that neoformation is not constant and the number of neoformed shoot units per shoot varied between years and crown locations which indicated it was responsive to current year conditions. Neoformation is interpreted as being a plastic response and part of an opportunistic strategy (Davidson and Remphrey, 1994). In *F. pennsylvanica* neoformation has been found to occur only in young vigorous growing trees (Davidson and Remphrey, 1994). In mature trees, around 25-years-old no neoformation was found (Remphrey, 1989a). It is not known at what age or stage of development that neoformation ceases in *F. pennsylvanica*.

In *F. pennsylvanica*, there is some information about shoot unit production. A correlation between bud size and the number of shoot units occurs and the number of shoot units preformed in the bud is dependent on parent shoot length (Remphrey and Davidson, 1994a) but also varies between genotypes of similar aged trees growing in similar locations (Remphrey and Davidson, 1994a). In general, it was thought that in species that exhibited preformed growth, the current year conditions had no effect on the expansion of the bud (Kozlowski and Clausen, 1966). However, Remphrey (1989a) reported that in mature *F. pennsylvanica* with preformed buds, the current year

growing conditions did affect the number of shoot units per shoot because there were fewer shoot units in the expanded shoot than was estimated in the dormant bud (Remphrey, 1989a). It was hypothesized that the leaf primordia which were not highly differentiated became bud scales instead of shoot units bearing foliage leaves.

Shoot unit length

Shoot elongation occurs through the elongation, differentiation and maturation of internodal cells produced by the apical meristems (Steeves and Sussex, 1989). Elongation is the product of the number of cells present and the length of those cells (Wilson, 1970). In *Arctostaphylos uva-ursi* the number of cells present in the internode had a greater effect on shoot unit length compared to cell length (Remphrey, 1982). The number of cells present in the dormant bud is determined partially in the year of formation but the number continues to increase by cell division during shoot expansion. Cell length is determined during expansion. This makes shoot length responsive to environmental influence in the year of formation and in the year of expansion (Wilson, 1970). Internode developmental rates generally follow a sigmoid curve where internode lengths start out small and increase in size until a maximum is reached and then decrease until growth ceases (Remphrey and Davidson, 1994a; Garrison, 1973).

In *F. pennsylvanica* some information is known about shoot unit length and its relative importance to total shoot length. Internode lengths are known to vary along a shoot (Remphrey, 1989a). Internode lengths have been measured and found to be greatest in the middle of the shoot and decrease towards the base and tip (Prusinkiewicz *et al.*, 1994; Remphrey and Davidson, 1994). This pattern has been observed in other species including *Shepherdia canadensis* and *S. argentea* (Hayes *et al.*, 1989) and *Aesculus sylvatica*, *Quercus rubra*, *Liquidambar styraciflua*, *Salix nigra* and *Pinus taeda* (Brown and Sommer, 1992).

Shoot length and corresponding shoot unit length decrease with increased branch order (Remphrey and Davidson, 1992). The main stem of a tree is designated as order 0; branch axes arising directly from the main stem were order 1 and so on (Remphrey and Powell, 1984). Daughter terminal shoot length and corresponding shoot unit length are usually smaller than the parent terminal shoot length (Remphrey and Davidson, 1992). This pattern is observed in most species because of a decrease in vigour as the tree ages (Leopold, 1980).

Fate of buds

In many temperate woody plants including *F. pennsylvanica*, lateral bud development generally occurs from buds that were produced in the previous year in the axil of the leaves. These buds may be reproductive or vegetative.

Every year the fate of the bud is realized (Bell, 1994). Fate is defined as the outcome of the development of any bud based on the 'experiences' of the individual bud (Bell, 1991). The 'experiences' of a bud can be environmental or related to internal physiological factors such as hormones or nutrients. If a bud is vegetative it may form a lateral shoot, remain dormant, or abort. If a bud is reproductive it may become a inflorescence, set seed or abort. In a species with lateral flowering, the ratio of vegetative to reproductive buds has an impact on the architecture of the tree. Reproductive buds remove potential sites where a lateral shoot may form and thus reduces branching which can impact on the structure of the crown (Maillette, 1992). Reproductive buds also consume energy which is therefore unavailable to support vegetative growth (Maillette, 1992).

In theory it may be possible to determine the fate of a bud based on the inherent organization of the shoot system as a whole (Barlow, 1989). Fate may be determined by the position of the bud along or around the shoot, or by the position of the shoot within the tree. Therefore, the patterns of bud production and development within the shoot system determine the shape of the whole tree (Jones and Harper, 1987). In some species, vegetative buds may occur in specific locations along the shoot such as *Artemisia tridentata* ssp. *vaseyana* where long shoots were concentrated in the terminal and mid position, flowers were near the distal end of the shoot, and dead shoots were near the base

(Bilbrough and Richards, 1991). In *Purshia tridentata* long shoots were generally more concentrated in the distal end of the shoot (Bilbrough and Richards, 1991). In *F. pennsylvanica* vegetative buds are more localized towards the distal end of the shoot, dormant buds are located towards the base, and reproductive buds generally occupy the mid position of the shoot (Remphrey, 1989b; Remphrey and Davidson, 1992). Longer shoots have been found to produce proportionally more vegetative buds than reproductive buds when compared to shorter shoots (Remphrey, 1989b).

It has also been observed that the lateral shoots near the distal end of the shoot are longest and there is a decrease in shoot length towards the base of the parent shoot (Remphrey and Davidson, 1992). A similar pattern has been observed in *Larix* where short shoots were almost exclusively found on the lower half of the parent shoot (Remphrey and Powell, 1984). This type of lateral shoot development is termed acrotony (Champagnat, 1978). The lateral shoots are generally shorter than the leading shoot but may occasionally become longer than the leader shoot. Finally, the length of the lateral shoots are generally related to the length of the parent shoot in that longer parent shoots produce longer lateral shoots (Remphrey and Powell, 1984; Davidson and Remphrey, 1990).

Branching habit and crown form

Internal physiological control mechanisms such as apical control are important in the development of the branching structure. Apical control occurs when the terminal bud on a shoot influences the growth of lateral shoots through direct hormonal control or control of nutrient allocation (Raven *et al.*, 1986). Apical control has a significant effect on the architecture of the tree because it affects the differential elongation of buds and branches (Brown *et al.*, 1967). Apical control can be affected by environmental influences such as light (to be discussed in a later section).

Two different patterns of development may occur because of varying intensities of apical control. When the terminal bud exerts a strong apical control over lateral bud development, an excurrent pattern of development occurs (Brown *et al.*, 1967). The excurrent form is seen in many *Pinus* or *Picea* species and is characterised by a strong differentiation between the leader and lateral branches with a single main stem resulting in a pyramidal shape. Conversely, the decurrent form is seen in many hardwoods where the leader shoot is hard to identify and results in a more rounded shape. The decurrent form results from very weak apical control.

It is possible that small changes in apical control might cause a change from an excurrent to a decurrent branching pattern. Different branching patterns result in varied crown shapes. It has been observed that *Fraxinus*

pennsylvanica produces different branching patterns ranging from excurrent to decurrent and this appears to be related to the recognition of different crown shapes (Remphrey *et al.*, 1987).

Apical control may also affect lateral shoot angle of divergence and elevation which can have a profound effect on crown shape. There is some evidence that auxins control branch angles (Wareing, 1970). Increases in branch angles can lead to a very upright tree because of high branch angles above the horizontal such as *Populus tremula* cv Erecta. This is compared to very spreading trees with low branch angles above the horizontal such as *Salix alba* var. *tristis*. Using computer models (Honda, 1971) has shown that small changes in the branching angle result in very different crown shapes.

Spatiotemporal Effects on Tree Architecture

Introduction

The architecture of the tree varies in space and time. Spatial differences between locations in the crown have been observed. As the tree expands it occupies more of its space creating the potential for increased variation from one crown location to another. Trees are long-lived and age physiologically over time resulting in architectural changes. The change from the juvenile to the mature tree is an example of physiological aging.

Crown Zone

It has been observed that shoot growth patterns are different within the crown of a single tree (Sakai, 1990). In *F. pennsylvanica* neoformation was found to be reduced in the lower third of the crown (Davidson and Remphrey, 1994). Total shoot length was greatest in the upper third of the canopy and shortest in the lower third (Davidson and Remphrey, 1990; Davidson and Remphrey, 1994). The angle of elevation of the shoot decreases from the top of the crown to the bottom (Davidson and Remphrey, 1990).

The fate of buds is known to change with position in the tree and represents different investments of energy (Maillette, 1982). In other species such as *Betula pendula* (Jones and Harper, 1987; Maillette, 1982), there was a dramatic decrease in long shoots in the bottom of the crown and an increase in short shoots and dormant buds. In *F. pennsylvanica* a reduction in branching from the top of the crown towards the bottom has been observed (Davidson and Remphrey, 1990) but not studied in much detail.

Different environmental conditions exist within the crown of a tree. For example, differences in light availability have been found which create areas of high and low light intensity (Larcher, 1975; Jones and Harper, 1987). Generally the interior of a tree crown receives less light than the exterior. Light intensity varies because of mutual shading by leaves (Kozlowski *et al.*, 1991). In the interior of the crown, light intensity has been found to be less than 2% of

light intensity in full sun for some species (Larcher, 1975; Kramer and Kozlowski, 1979). The light environment in the tree crown "has been considered to be the primary determinant of crown morphology and structure" (Hashimoto, 1990; Hashimoto, 1991).

Similarities in some tree architecture characteristics have been found between the interior of the crown and small trees that are completely shaded. The observed developmental patterns in the interior of the tree are not simply caused by shading of interior shoots. These shoots are part of a larger shoot system which may include other shoots which are not shaded and could contribute to their growth. In an attempt to determine some effects of shade on tree development it may be possible to shade the whole tree and observe the response. This topic will be dealt with further in a later section.

Aging

The effects of aging on tree architecture can be observed through reduced growth rates and branch vigour (Leopold, 1980; Wilson, 1989), diminished apical control, increased propensity to flower, decreased stomatal conductance, and increased chlorophyll content and net photosynthesis (Ritchie and Keeley, 1994). Woody plants exhibit two main phases in their life cycle, a juvenile and an adult phase (Schaffalitzky de Muckadell, 1954; Robinson and Wareing, 1969). The juvenile phase may be very short (1-2 years) or very long (30-40

years) with the average around 10 years (Hackett, 1985; Robinson and Wareing, 1969). The end of the juvenile phase is marked with the onset of flowering (Robinson and Wareing, 1969). Many different factors, both internal and external, affect the length of juvenile period in woody plants (Zimmerman, 1972). Clearly the effects of aging on plant organs have been studied in some detail, but less is known about the effect on the overall architecture of the tree.

Aging often results in a loss of apical control as indicated earlier, and this causes the well marked leaders to become indistinguishable from the branches (Moorby and Wareing, 1963). When apical control is lost, lateral shoot length tends to be similar to the length of the terminal shoot which results in a change in the developmental pattern of the crown. In *Larix laricina* there was a change in the branching habit of the tree in the older trees compared to younger trees (Greenwood *et al.*, 1989). The trees also produced more reproductive buds which further affected branching.

The effects of aging on shoot development have been studied in species including *Pseudotsuga menziesii* (Ritchie and Keeley, 1994), *Pinus ponderosa* and *P. contorta* (Yoder *et al.*, 1994), and *Larix laricina* (Greenwood *et al.*, 1989). However the number of shoot units per shoot or shoot unit length was never examined. In *F. pennsylvanica* little is known about the effects of aging on tree development. It has been reported that as the tree ages there was a general decline in shoot length (Remphrey and Davidson, 1992). However this decline

is variable and shoot length may increase or decrease from one year to the next. Nevertheless, the overall pattern is more stable producing an obvious reduction in shoot length (Remphrey and Davidson, 1992). The impact of aging, as measured by reduced shoot growth from one year to the next, is also more rapid in higher order branches when compared to lower order branches (Remphrey and Davidson, 1992).

LIGHT AND ARCHITECTURE

Light Characteristics and Shade Tolerance

Introduction

Plant development is influenced by a variety of factors including changes in the environment. Light is one of the many environmental influences that can affect tree development. Light intensity, duration of exposure (photoperiod), and light quality (wavelength) must be considered for their impact on tree development (Kozlowski, 1971). Light is one component of the energy spectrum that is emitted by the sun. The visible light spectrum is between 400 and 700 nm (Kramer and Kozlowski, 1979). Portions of these wavelengths are used in photosynthesis and are referred to as photosynthetically active radiation (PAR). Wavelengths on either side of the visible spectrum, ultraviolet (less than 400 nm) and far to infra red (greater than 700 nm) are also important to biological life. Far-red light is between 700 and 775 nm and is important in plant development, although not specifically used in photosynthesis. The topics to be covered in the following sections include an introduction to light characteristics, shade tolerance in trees, and the effects of shade on shoot system architecture, leaf characteristics, and biomass production.

Light quantity and photosynthesis

The quantity of light is a measure of the total amount of energy useable in photosynthesis. Light is composed of particles called photons. The energy contained within a photon of light is inversely proportional to the wavelength, hence the longer the wavelength, the lower the energy (Raven *et al.,* 1986). Different wavelengths of the visible light spectrum contain more energy than others, with the violets (approximately 400 nm) and blues (approximately 450 nm) containing the most (Kramer and Kozlowski, 1979). These colours or wavelengths are preferentially absorbed by the leaves because of their high energy content. The other colours of light contain less energy, but are still absorbed by the leaf, with most of the green light being reflected by the leaves.

It is well known that light is important in powering photosynthesis. Photosynthesis is a process where carbon dioxide and water in the chloroplast, in the presence of light, result in the production of carbohydrates, oxygen, and water (Raven *et al.,* 1986). Light is used to split water molecules and release electrons into the photosystem, where the hydrogen atoms are used to make carbohydrates and the oxygen is released into the atmosphere (Raven *et al.,* 1986). Carbohydrates are used by the plant for development and maintenance of the tree structure. However, development is not closely correlated with the rate of photosynthesis, but is dependent to a large extent on the quantity of food

supplied by the process (Kozlowski, 1971). This means that the rate of photosynthesis can be measured in a leaf, but this will not provide an accurate measure of the amount of development that will occur.

After light has passed through the canopy of a tree, the quantity of some wavelengths decrease because most of the useable energy has been absorbed in photosynthesis. As a result, the light transmitted through the upper layer of leaves contains very little energy for photosynthesis inside the crown (Lee, 1985). Typically, 90% of the wavelengths between 400 and 700 nm are absorbed by a leaf with only 10% of the radiation between 750 and 1100 nm being absorbed (Lee, 1985). Under low light conditions, photosynthesis has been shown to be directly proportional to light intensity (Shirley, 1929). The lack of light useable in photosynthesis results in large decreases in productivity inside the crown of the tree.

Light quality

Light quality is defined as the spectral distribution of photons (Smith, 1982). Differences in spectral light quality produce various responses within the plant. For example, leaf blade expansion is prevented in darkness, is retarded in green light, is intermediate in blue, and is greatest in natural light (Kramer and Kozlowski, 1979). Spectral differences occur as a result of shading and differential absorption as light passes through the canopy (see last section).

Changes in light quality result in diverse physiological responses and alterations in growth and development, involving photoperiodism, photodormancy, and photomorphogenesis (Kozlowski *et al.*, 1991). The most often studied aspect of light quality is the ratio of red to far-red light because of its significance in the phytochrome system. The phytochrome system is important in the perception of shade and is responsible for some of the observed changes in plant development when shaded.

The phytochrome molecule, which makes up the phytochrome system is composed of the light absorbing chromophore and a large protein portion (Raven *et al.*, 1986). The chromophore absorbs light in a similar manner to chlorophyll. The phytochrome molecule can exist in two forms, an active form P_{fr} and an inactive form P_r (Kozlowski *et al.*, 1991). When red light in the wavelength of 660 nm is absorbed by P_r it is converted into the biologically active form P_{fr} (Raven *et al.*, 1986). However, when P_{fr} is subjected to far-red light, in the wavelength of 730 nm, it is converted into the biologically inactive form of P_r (Raven *et al.*, 1986).

Different ratios of P_r:P_{fr} are used as a signal to turn on some plant reactions and to turn others off. P_r:P_{fr} ratios have been recorded by others between 1.05 and 1.35 in full sun, while in dense natural shade the ratio was around 0.20 (Lee, 1996). Plant development responses that occur because of changes to the phytochrome system include: increased leaf petiole length,

reduced leaf area, increased stem dry weight, reduced branching, changes in chlorophyll content, and changes in nitrogen reductase activity (Smith, 1982). The biggest change in growth comes in an increase in internode length commonly referred to as etiolation (Smith, 1982). Etiolation will be discussed in more detail below.

Shade tolerance

Trees vary in their ability to tolerate shade or changes in light quantity and quality. Shade tolerance is a relative term and is dependent on factors such as age, the location of a species in its natural range, and environmental conditions (Kramer and Kozlowski, 1979). It has generally been found that heavy shading reduces shoot growth of gymnosperms more than angiosperms (Kozlowski, 1971). In New Brunswick, fifty-year-old *Abies balsamea* trees that were growing in deep shade have been observed to be less than 1 m tall (W.R. Remphrey personal communication). For forestry and horticultural purposes, trees are classified according to their shade tolerance. This classification is used in silvicultural and ornamental planting recommendations (Kozlowski *et al.*, 1991). In general, shade tolerance is related to differences in the ability of the photosynthetic apparatus to adapt to shade. Species with higher levels of shade tolerance possess a greater ability to adapt (Kramer and Kozlowski, 1979).

Generally, trees show two types of responses to shading, and can be classified accordingly as shade-avoiders, which are generally shade intolerant, or shade-tolerators, which are generally classified as shade tolerant. Shade-avoiders show enhanced axis development (etiolation) in response to shading along with increased petiole extension, strong apical dominance (little branching), and limited leaf development (Hart, 1988). As their classification would indicate these trees attempt to grow out of the shade or avoid it. Shade-tolerators tend to show greater leaf development along with low respiration rates, low photosynthetic light-compensation points, low rates of leaf turnover, and are most often slow growing (Hart, 1988). Changes in light quantity seem to evoke the developmental response displayed by shade tolerating species, while changes in the ratio of R:Fr light evoke the developmental response displayed by shade avoiders (Smith, 1982).

Artificial shading studies

Studying shade often relies on measurements of trees already established in a natural setting. This greatly limits the number of species that can be studied because only trees with some degree of shade tolerance will be found. As a result it is difficult to study the effect of shade on intolerant species. Also in the natural environment very little control can be exerted over the site, which can lead to problems interpreting the data (Lee, 1985). In an attempt to combat

this problem trees maybe studied under artificial shade cloth composed of a neutral polyethylene fabric in an experimental setting.

Despite the advantages of artificial shade, problems are associated with this method as well. Difficulties arise in using shade cloth to study the effects of light quality because it does not accurately simulate natural conditions and problems occur in maintaining sufficient light intensity (Lee, 1985). The neutrality of the shade cloth does not alter the R: Fr ratio which occurs under natural shade. The problem of not accurately simulating natural shading is often overlooked in most research. New research into light quality effects in herbaceous plants is providing more information on the importance of studying light quality. With recent advances, new materials have been designed that can affect light quality without influencing light quantity, which makes it possible to study the effects together or separately (Lee, 1985). Studies of light quantity and quality can occur together or separately which can be useful in determining the exact response in the plant to them without the confounding effects of the other.

Shoot System Architecture

Introduction

As indicated in the previous section, alterations in light conditions can result in morphological and developmental changes which affect tree

architecture (Kozlowski, 1971). Light intensity is important for tree development because it influences bud formation by impacting on the expansion of previously developed shoot units and the production of future shoot units (Kramer and Kozlowski, 1979; Kozlowski, 1971). As previously defined a shoot unit consists of a leaf, axillary bud and, its subtending internode. Developmental changes caused by differences in light conditions are manifested in changes in shoot development. The number of shoot units, shoot unit length, total shoot length, and the number of lateral branches produced are all altered by differences in light conditions.

Shoot length

Shoot length has been examined on two levels, as mean shoot length or as cumulative shoot length. Shading may cause changes in mean shoot length because of reduced assimilate supplies in the shade and hence reduced growth. In a study of a *Malus* species (Jackson and Palmer, 1977) and of *Abies fraseri* (Hinesly, 1986) there were decreases in the mean shoot length in the shade when compared to trees in full sun.

Cumulative shoot length is a measure of the total shoot growth of a tree. Cumulative shoot length may be greatly affected by the availability of light. In *Castanopsis fargesii* (Cornelissen, 1993) and *Quercus velutina* (Wilson and Kelty, 1994) there was a significant decrease in total cumulative shoot length

between full sun and shade (Cornelissen, 1993). However, in one study of apple (*Malus* sp.) cumulative shoot length in full sun and in 37% shade was not different (Jackson and Palmer, 1977). Generally, there appears to be a trend towards a decrease in the amount of overall shoot growth that occurs in the shade.

Cumulative shoot length is dependent, to a certain extent, on the degree of branching because a tree with more lateral shoots, in theory, should have a greater cumulative shoot length. Although the distribution of shoot length within the whole of the tree would probably be affected by shading, there is little information in the literature.

Lateral shoot production

The production of lateral shoots in woody plants is dependent on the interaction between external and internal factors. Lateral shoot production is generally believed to be under apical control. Several theories have been postulated to explain apical control. Generally it is believed that the apical bud exerts control over assimilate transport through the use of hormones which can promote or inhibit axillary bud development. The hormone most often associated with apical control is auxin (Raven *et al.*, 1986). Apical dominance (control) is very sensitive to changes in light quantity and new evidence suggests that light quality is also important (Cline, 1991).

High light intensities generally weaken apical dominance resulting in a proliferation of lateral shoots (Cline, 1991). Conversely shade enhances apical dominance resulting in a decrease in lateral shoot production (Cline, 1991). In one study of *Lonicera maackii*, as shading was increased to 95% there was a significant decrease in the number of lateral shoots produced (Luken *et al.*, 1995). *Abies balsamea* showed the same results growing in 25% of full sun, where 3 to 5 shoots were produced while in 5% of full sun 1 or 2 shoots were produced (Parent and Messier, 1995). In *Acer rubrum*, *Quercus velutina*, and *Prunus serotina*, (Gottschalk, 1994) there was a decrease in the number of lateral shoots produced as shading increased. However in *Quercus rubra* there was on average one more lateral shoot produced in light shade levels (Gottschalk, 1994). However, over all the plants studied, there appears to be a reduction in lateral shoot production with increased shade.

As mentioned earlier, differences in light quality can affect lateral shoot production. It has been demonstrated that red light, which is most abundant in full sun, weakens apical dominance, while far-red light, which is abundant in the understory of a forest or closely planted trees, strengthens apical dominance (Cline, 1991). Clearly, both the quantity and quality of light are important in determining lateral shoot production.

Branching angle

Changing light conditions are reflected in changes in the lateral shoot angle of elevation. It has been observed that in the shade lateral shoots become oriented more horizontally (Marler *et al.*, 1994). This change is an adaptation by the tree to contend with decreased light intensities and results in decreased mutual shading and increased light interception (Marler *et al.*, 1994). In full sun, the opposite occurs and lateral shoots become more vertically oriented which may be of adaptive value to the tree (Marler *et al.*, 1994). A more vertical shoot orientation leads to decreased light interception and increased mutual shading (Marler *et al.*, 1994). In *Averrhoa carambola*, the shoot angle above the horizontal was 55° in the sun and only 17° in the shade, which was significantly different (Marler *et al.*, 1994).

Number of leaves (shoot units) per tree and shoot

The production of leaves, which has been often studied, can be used as a measure of the number of shoot units. The number of leaves, on a whole tree basis, changes with decreasing light intensities, and is variable between species. In *Quercus rubra*, there was an increase in total shoot unit numbers to 60% shade and then a decrease with further shading (Gottschalk, 1994). Conversely, in *Acer rubrum*, *Quercus velutina*, and *Prunus serotina* there were no changes in the number of leaves per tree as the shade intensity increased (Gottschalk,

1994). Also in *Lonicera maackii*, there were similar numbers of leaves per tree in 100 and 25% shade, but in 5% shade there was a significant decrease (Luken *et al.*, 1995). However, in a separate study of *Q. velutina*, the shade treatment resulted in a significant decrease in the number of leaves per tree when compared to full sun (Wilson and Kelty, 1994). Similarly in *Castanopsis fargesii*, in 18 % shade there was a significant decrease in the number of leaves per tree when compared to full sun (Cornelissen, 1993).

A decrease in the number of shoot units per tree may occur because of decreases in the number of shoot units per shoot, for both lateral and terminal shoots, or a reduction in branching as discussed previously. This latter observation alone could account for the decrease in the number of shoot units per tree. Nevertheless, in a study of *Fagus grandifolia, Acer rubrum, Quercus rubra*, and *Liriodendron tulipifera* by (Loach, 1970) there were significant reductions in shoot unit numbers per shoot with increased shading. More studies of the effect on the number of shoot units per shoot are needed.

Shoot unit length

As previously mentioned, an increase in shoot elongation can occur in the shade, a phenomenon known as etiolation which is thought to occur because of a decreased R:Fr ratio. Etiolation is inhibited by high light intensity, particularly when the R:Fr ratio is high (Kozlowski *et al.*, 1991). Etiolation

affects shoot unit extension, and is thought to be useful because an increase in HGI shoot unit length and accompanying total HGI length may help the tree improve its position in the forest canopy and increase light interception (Tinoco-Oanguren and Pearcy, 1995; Kozlowski *et al.*, 1991). This response is seen in *Averrhoa carambola* (Marler *et al.*, 1994) where shoot unit lengths showed an increase with increased shading. In *Castanopsis fargesii*, there appears to be an increase in shoot unit length based on calculations from the data presented in a table and picture (Cornelissen, 1993). Calculations were necessary because shoot unit length had not been directly measured. In recent studies of *Endospermum malaccense, Parkia javanica, Hopea wightiana, Sindora echinocalyx, Dryobalanops aromatica,* and *Shorea singkawang* the internode length decreased significantly or remained the same with increased shading (Lee, 1996) In all studies a neutral shade cloth covering was used which only altered the quantity of light entering the tents, the R:Fr ratio was not altered.

Generalizations about the response of shoot unit length to shading are difficult to make based on only a few studies. However, it would appear that shoot unit length increases in the shade, which seems contrary to the general literature on the reduction in light quantity. Generalizations about the growth response of shoot units to shade, especially because of confounding, due to the quantity and quality of light are difficult. Clearly more detailed studies of the

effects of reduced light quantity on shoot unit length in woody species are required.

Shade and Leaf Characteristics

Introduction

The architecture of the tree changes because of reduced light intensities, which are reflected in modifications in the characteristics of the leaves. Changes occur that are beneficial to the tree such as the production of shade leaves, alteration of leaf angle, or an increase in leaf area. In general these adaptations result in improved survival by the tree in the shade.

Shade leaves

There are many types of morphological and physiological responses to variations in light intensity. The production of shade leaves by a tree is an important response to limited light quantities. Shade leaves are produced from shoots that were previously shaded and continue to grow in the shade. There is some indication that the light conditions of the previous year tend to determine the morphology of the leaf in the following year (Kozlowski *et al.*, 1991). When previously shaded branches were exposed to high light levels during the next growing season, shaded buds produced either shade leaves or

leaves with characteristics that were intermediate between sun and shade leaves (Kozlowski *et al.*, 1991).

Shade leaves generally have characteristics of being thinner, broader, with larger chloroplast, fewer layers of palisade mesophyll, and shorter palisade cells (Kramer and Kozlowski, 1979; Hart, 1988; Boardman, 1977). In one study of *Fraxinus pennsylvanica*, shade leaves were found to be 16μ smaller than leaves growing in full sun (Jackson, 1967). The leaves in the shade also had a lower palisade to spongy mesophyll ratio and had one less row of palisade mesophyll cells compared to leaves grown in full sun (Jackson, 1967). In a similar species, *Fraxinus americana*, the blade thickness, which is composed of the upper epidermis, lower epidermis, palisade layer, spongy mesophyll, was reduced in the shade (Wylie, 1951). Vein spacing was greater in the shade, which might indicate a larger leaf surface area; however, leaf area was not measured. A thinner leaf in the shade allows the chlorophyll to be distributed in a thin layer in the leaf, resulting in better exposure to the light (Lewandowska and Jarvis, 1977).

Another characteristic of shade leaves is a change in chlorophyll content. In a study by Loach (1967), all five species of trees examined showed an increase in total chlorophyll (mg chlorophyll per g leaf tissue) in the shade. On a mass of chlorophyll to a unit area of leaf basis, the results were less dramatic, but there was still an increase in chlorophyll content. The richer content of

chlorophyll in the chloroplast along with thinner leaves allows for a more efficient use of light at low light intensities (Kozlowski *et al.*, 1991; Boardman, 1977). In addition, shade-grown leaves contain larger photosynthetic units, which have a higher proportion of light harvesting chlorophyll a/b-protein than sun leaves and results in greater efficiency at lower light intensities because of the decreased light saturation point (Kramer and Kozlowski, 1979). With a lower light saturation point, photosynthesis is maximized at a lower light level, meaning that photosynthesis is operating at full capacity and no energy is lost. If, however, shade leaves are exposed to full sun, more energy is available to the leaf than can be utilized and reduces the light usage efficiency.

Leaf area

Leaf area per tree

A change in total leaf area per tree in response to decreased light intensities is the result of changes in individual leaf areas. There are two responses that have been reported to occur when trees are shaded. One response is an increase in leaf area per tree and should occur in the more shade tolerant species. In a study of 5 species of trees, of different shade tolerance, 4 out of 5 of the species showed an increase in leaf area in moderate levels of shade (Loach, 1970). Only the most shade tolerant species did not show an increase. No statistical tests were preformed on this data, which makes it

difficult to determine if the differences were significant. In a study of *Quercus rubra*, there was an increase in leaf area in moderate levels of shade that was significant (Gottschalk, 1994). *Quercus rubra* is listed as having an intermediate level of shade tolerance, so it is not unexpected that the trees would show a shade-tolerator response. Similarly, in a study of *Averrhoa carambola* there were significant increases in total leaf area per tree as the percentage of shade decreased which occurred because of the high levels of shade tolerance by the tree (Marler *et al.*, 1994).

The other reported response to shade is a decrease in leaf area per tree. In a study of *Q. Velutina* (Wilson and Kelty, 1994), *Fagus grandifolia* (Loach, 1970), and *Prunus serotina*, *Acer rubrum*, and *Quercus velutina* (Gottschalk, 1994) there were significant decreases in total leaf area per tree as shading increased. *Abies fraseri*, a coniferous species, showed a decrease in total needle area as the percentage of shade increased (Hinesly, 1986). The existence of two responses may lead to the conclusion that they are related to their classification as shade avoiders or shade tolerators. However, since species of high shade tolerance (shade tolerators) and low shade tolerance (shade avoiders) both show increases and decreases in leaf area per tree. It is difficult to characterize the response of a species based on its' shade tolerance.

Individual leaf area

Light conditions can have a significant effect on leaf area. Similar to total leaf area per tree, two responses have been observed. The first one is an increase in individual leaf area. An increase in leaf area would be beneficial to the tree because more light can be intercepted by the leaf without having to increase the support structure. In a study of *Quercus rubra*, when the tree was grown in the heaviest shade, it produced the largest leaves (Gottschalk, 1994). The other option to increase leaf area and light interception is to increase the number of leaves. However this may require a support structure, which is more costly to construct when compared to increasing leaf area.

The other observed response is a decrease in individual leaf area. In a study of *Acer rubrum* and *Prunus serotina* (Gottschalk, 1994) there were initial increases in leaf area, but by 60 % shade leaf area decreased. In a study of *Quercus velutina* (Gottschalk, 1994) and of *Abies fraseri* (Hinesly, 1986) there was a weak trend towards a decrease in leaf area as the shading increased. The lack of a very strong trend is because the species studied are all intermediate in shade tolerance.

Leaf angle

The angle of the leaf in relation to the horizontal (elevation angle) is also affected by shading. In one study of *Fraxinus pennsylvanica*, the angle of

elevation in the sun was $36.8 \pm 18.9°$ above the horizontal, whereas in the shade the angle of elevation was $14.4 \pm 13.8°$ above the horizontal (Mc Millen and Mc Clendon, 1979). The conclusion from the study was that there was no response to the direction of light, only to its quantity (Mc Millen and Mc Clendon, 1979). The differences in leaf angle allow the plant to regulate solar energy interception by the leaf and reduce heat loads.

In the sun, leaves become more vertically oriented, leading to a reduced heat load through interception of less light and increased mutual shading (Marler *et al.*, 1994; Mc Millen and Mc Clendon, 1979). Light is also used more efficiently by the chlorophyll because of increased leaf elevation (Marler *et al.*, 1994; Mc Millen and Mc Clendon, 1979). In addition, because of a reduced heat load and more efficient light usage, photochemical inactivation of the photosynthetic apparatus may diminish (Marler *et al.*, 1994; Mc Millen and Mc Clendon, 1979). In the shade, heat load is not a problem, but there is a lack of light for photosynthesis, which reduces assimilate supplies. Therefore, in the shade, leaves are oriented to intercept the maximum amount of light for the least cost (Mc Millen and Mc Clendon, 1979). In *F. pennsylvanica* it would appear that approximately 14° above the horizontal is the optimum leaf angle of elevation in the shade.

Biomass Production

Changes in tree development and architecture are reflected in changes in biomass production. A reduction in biomass because of shading is a fairly consistent response across the species studied. In a study of *Quercus velutina* there was a decrease in leaf biomass (Wilson and Kelty, 1994). Similarly, *Castanopsis fargesii* (Cornelissen, 1993) and *Lonicera maackii* (Luken *et al.,* 1995) showed a decrease in total tree biomass. Also in *Abies fraseri* there was a decrease in cumulative shoot and total tree biomass (Hinesly, 1986) and in *Fagus grandifolia, Quercus rubra,* and *Populus tremuloides* there were decreases in total leaf biomass, cumulative shoot biomass, and total tree biomass.

There are a few reports of increased biomass in the shade. In *Acer rubrum* and *Liriodendron tulipifera,* there were increases reported but there was no statistical test done to determine if the differences were significant (Loach, 1970). The most probable cause for the generally reported decrease in biomass in the shade is a reduction in photosynthesis leading to a decrease in assimilate production.

Cumulative shoot and leaf biomass can be examined on a percentage or proportional basis. The proportions are calculated by dividing the mass of either the cumulative shoot biomass or the total tree leaf biomass by the total

tree biomass. The corresponding ratios are either the shoot weight ratio or the leaf weight ratio, respectively (Jackson and Palmer, 1977). Kuroiwa *et al.*, (1964) observed that shade-intolerant herbaceous species translocate less assimilate into leaf material as shading increased, whereas the opposite occurred in shade tolerant species. In a study of 5 species of woody plants, only the most shade tolerant species translocated more assimilate to leaf production (Loach, 1970). In a study of six tropical woody plants all showed an increase in the amount of dry matter allocated to the leaves with increased shading (Lee, 1996). Conversely the amount of dry matter allocated to the stems increased as shading decreased (Lee, 1996). This has the advantage of allowing the plant to maximize light capture without increasing the support structure which costly to produce.

The accumulation of biomass by the tree is also affected by reduced levels of light. In a study of one species of apple, by Maggs (1960), biomass accumulation in the spring was equal in shade and full sun initially. However, by 200 days into the growing season, the full sun treatment had accumulated 150 g of dry matter compared to only 15 g in the deepest shade.

Chapter 1

The Influence of Crown Location and Tree Age on Shoot

Architecture Parameters in *Fraxinus pennsylvanica*.

ABSTRACT

In *Fraxinus pennsylvanica* var. *subintegerrima* (Vahl) Fern. spatiotemporal variation in crown architectural patterns has been observed. The objectives of the present research were to examine the effects of crown location (spatial) and tree age (temporal) on the three main architectural traits: number of shoot units per shoot, shoot unit length, and the fate of buds. Trees were located at two different sites at the Agriculture and Agri-Food Diversification Research Center in Morden, Manitoba. One site contained trees 8-years-old and the other site contained trees 10, 20, 50, and 60-years-old. The number of shoot units per shoot, shoot unit-length, and the number of lateral shoots and inflorescences produced decreased from the top to the inside of the crown. Generally lateral shoots were concentrated near the apical end of the shoot, inflorescences in the middle, and aborted buds near the base. Neoformation was not detected in any age-class tested. Aging resulted in a decrease in the number of shoot units per shoot, and the number of lateral shoots produced. There was little difference in shoot-unit length between the different age-classes. Differences in the light environment may have been involved in the change in shoot growth and development from the top to the inside of the tree. Because the crown is composed of shoot systems, internal physiological factors such as apical control may also be involved. Reductions in photosynthesis and increasing structural complexity are thought to result in physiological aging, thus reducing shoot vigour and altering shoot development patterns.

INTRODUCTION

The architecture of a tree is the result of the interaction between its genetic blue print and the environment (Bilbrough and Richards, 1991; Hallé *et al.*, 1978) and is defined as the holistic and dynamic description of tree form (Hallé *et al.*, 1978). The architecture of a tree can be described through the use of qualitative models which rely on the visual assessment of the trees' architecture. Hallé *et al.* (1978) have classified trees into one of 23 models using architectural characteristics such as stem growth, branch development and orientation, and flowering location. *Fraxinus pennsylvanica* var. *subintegerrima* (Vahl) Fern. best fits Rauh's model which describes the tree as being determined by a monopodial trunk (an axis established by a single indeterminate meristem) which grows rhythmically and so develops tiers of branches which are morphogenetically similar to the trunk.

Trees can also be described in a quantitative manner through the direct measurement of crown components. The most common units of the tree measured are shoot length and branch angle (Borchert and Honda, 1984; Remphrey and Powell, 1984; Remphrey and Powell, 1987). For trees growing in temperate regions, a shoot is defined as a yearly increment of growth and is characterized as a single unit of growth arising from a bud and ending in a terminal bud (Remphrey and Powell, 1984). This information is used to develop

empirical models to describe the observed developmental patterns. Recently it has become of interest to measure smaller units of tree architecture, such as the shoot unit (Reffye de *et al.*, 1991; Prusinkiewicz *et al.*, 1997).

The shoot unit has been recognized as a basic building block in tree crown development (Bell, 1979; Barlow, 1989; Prusinkiewicz *et al.*, 1994). Tree development occurs in a modular way with shoot units added together to produce shoots, which are organized into branches, and finally contribute a whole tree.

The number of shoot units per shoot can be preformed in the bud and in *F. pennsylvanica* the majority of shoot units are preformed (Remphrey and Davidson, 1994a), except in young trees some may be neoformed (Davidson and Remphrey, 1994). It is not currently known when neoformation ceases. Neoformation was not observed in 25-year-old trees (Remphrey, 1989) and had declined significantly in young saplings to the point that it was minimal after 3 years of age (Davidson and Remphrey, 1994).

Each shoot unit controls development because they directly produce other shoot units and lateral buds (Maillette, 1992). In *F. pennsylvanica* the buds of each shoot unit can become vegetative and produce more shoot units, or they may become reproductive. If buds become vegetative they may produce shoots, they may remain dormant for some time or they may abort. Buds which are reproductive may form an inflorescence or they may abort. The proportion of

buds which become vegetative greatly affects tree development (Maillette, 1992). In *F. pennsylvanica* dormant buds are generally localized towards the base of the shoot and vegetative buds are near the top. This pattern of lateral branch development is known as acrotony (Champagnat, 1978).

The number and length of lateral shoots, along with lateral shoot angle of elevation and angle of divergence from the parent shoot determine the shape of the crown (Honda, 1971). These architectural characteristics can be influenced by a variety of external and internal factors resulting in zones in the crown with variations in shoot growth parameters (Sakai, 1990). Differential growth may be related to light or apical control. Light availability varies between different locations in the crown (Larcher, 1975). Zones depicting variation in light availability can be recognized in the tree. In *F. pennsylvanica* differential developmental patterns have been observed between the top, middle, and bottom of the crown (Davidson and Remphrey, 1990; Davidson and Remphrey, 1994) but not studied in much detail.

Aging also affects tree development because as the tree ages it becomes more complex. The effects on plant organs have been studied in detail (Ritchie and Keeley, 1994) but not much is known about how it affects crown development. Generally vigour decreases with age and results in fewer shoot units per shoot, shorter shoot units, or a reduction in lateral branching (Leopold, 1980; Wilson, 1989). Aging causes a reduction in apical control and often

results in the loss of a clear leader shoot (Moorby and Wareing, 1963). In *F. pennsylvanica* a decrease in shoot growth occurs as the tree ages (Remphrey and Davidson, 1992) but little is known about the effect on shoot unit development and lateral bud development.

The objectives of this study were to examine shoot architecture in relation to location of the shoot in the crown and to aging and specifically to 1) determine the effect of different crown zones on shoot unit length, shoot unit numbers per shoot, and on the fate of a bud along a shoot, 2) to determine the relative age when neoformation ceases, and 3) determine the effect of tree age and crown zone within an age class on shoot unit length, the number of shoot units per shoot, and the fate of buds along a shoot.

MATERIALS AND METHODS

Study Site Descriptions

A study to investigate various tree architectural characteristics in relation to different locations within the crown and to tree aging was located at the Agriculture and Agri-Food Diversification Research Centre, in Morden, Manitoba, Canada. Two different plantings of *Fraxinus pennsylvanica* var. *subintegerrima* (Vahl) Fern. were sampled.

Site 1 was a previously established clonal experiment (details in Davidson and Remphrey 1994). The planting contained four clones, two male and two female. Both male clone controls and one female clone were selected and used for the data collection. Only one female clone was selected because many specimens of the other female clone had died or were unhealthy. The trees in the experiment had previously undergone various pruning treatments so only the control trees were used. Several data sets were created with the information gathered from these trees over a two-year period from 1994 to 1995.

Site 2 was located in the arboretum at the Morden Research Centre. The arboretum contained trees of *Fraxinus pennsylvanica* of various ages. Four age classes of trees, approximately 10, 20, 50, and 60-years-old were identified and 5 trees per age-class were selected for the study (see Appendix A for more details). In the 10 and 20-year-old age-classes, 3 out of the 5 trees had been propagated from scions because there was an insufficient number of trees

propagated from seed to provide the necessary number of trees for sampling. However, only one copy of each tree was used.

Data Collection: Site 1

Data set 1 was collected in May 1995 to study how the ratio of bud types (Table 1.1) on a shoot change between different locations within the crown (Fig. 1.1). From the available trees, one tree of each clone was sampled in each of the three blocks in the experiment. Three trees of each clone or nine trees in total were sampled. Twenty samples from both the top and bottom zones of the tree were randomly selected and examined according to the parameters outlined in Table 1.2. From the inside zone, the shoot samples were very similar, but were fewer shoots to sample so only five samples were chosen. The following parameters were measured: shoot length, number of shoot units per shoot, and for each bud: bud scar type, position of each bud on and around the shoot, and bud type.

Table 1.1 Classification and description of the various bud type categories.

Classification	Description
1- reproductive	inflorescences
2- aborted	buds that did not grow in the spring and were not present in subsequent examinations
3- dormant	buds that did not grow out in the spring and remained alive on the shoot
4- vegetative	buds that grew to produce a new shoot
5- missing	buds that were no longer present on the tree at the time of sampling
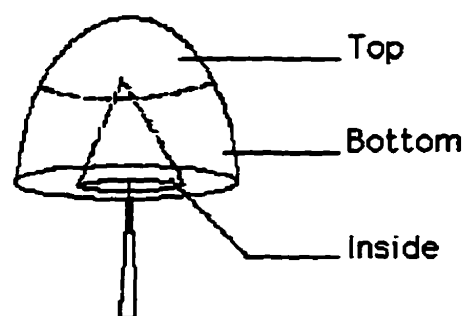
Fig 1.1 Illustration of the three crown zones identified in a tree and used for sampling (After Larcher (1975)).

Table 1.2 A description of the measurements made throughout the various data sets.

Measurement	Description
Lateral bud or shoot location along parent shoot (shoot zone)	The nodes on a shoot were numbered from the base to the tip and the position of each lateral bud or shoot was recorded according to the specific node along the shoot where it occurred. Each shoot was then divided into four zones based on the number of shoot units per shoot (Table 1.3). Approximately one-quarter of the buds occurred in each zone.
Lateral shoot length	Shoot length was measured from the point of attachment on the parent shoot to the base of the terminal bud.
Mean-shoot unit length	The total length of the shoot was divided by the number of shoot units for that shoot. Shoot unit lengths were assigned to categories, each representing a range of 5 to 10 mm length intervals. The number on the graph represents the top of the range. For example 10 on the graph is 0.1-10 mm, 20 on the graph is 10.1-20 mm and so on.
Number of shoot units per shoot	Shoot units were counted starting at the base, with buds at leaf scars and transitional leaf-scale scars considered as shoot units.
Position of bud around parent shoot	The position of each bud around a shoot was referenced in relation to a clock face in a vertical plane while looking directly down the shoot (Fig 1.2).
Shoot order	The main axis of the tree was designated as zero and any axes arising from the main axis were first order and so on.
Terminal shoot length	Shoot length was measured from the base of the terminal shoot to the base of the terminal bud.
Transitional-leaf scale scars	These scars are located less than 1 cm from the base of the current-year shoot, are narrow, and separated from other scale scars or are near the top of the shoot and are narrow.

Table 1.2 (cond.)

Measurement	Description
True scale scars	These scars are located at the base of the current-year shoot, are narrow with no separation from the base of the shoot.
True leaf scars	These scars are described as being located 1 cm from the base of the shoot and are crescent-shaped.

Table 1.3 The division of the location of a bud along the shoot into different shoot zone categories based on the total number of shoot units per shoot.

Number of shoot units per shoot	Specific shoot unit in each zone.			
	Lower (1)	Lower middle (2)	Upper middle (3)	Top (4)
3	1		2	3
4	1	2	3	4
5	1	2	3	4, 5
6	1	2	3, 4	5, 6
7	1	2, 3	4, 5	6, 7
8	1, 2	3, 4	5, 6	7, 8
9	1, 2	3, 4	5, 6	7, 8, 9
10	1, 2	3, 4	5, 6, 7	8, 9, 10
11	1, 2	3, 4, 5	6, 7, 8	9, 10, 11
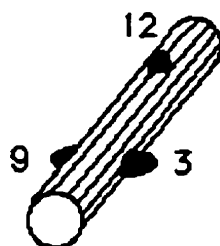
Fig 1.2 Diagram showing how the position of the bud around the shoot was determined. The viewer is positioned at the apical end of the shoot and looks down the shoot.

Data set 2 was collected (July 1994) after growth had ceased to study the influence of shoot location in the crown on the number and length of shoot units per terminal and lateral shoot, and on the number of lateral shoots produced per shoot. Four trees of each clone were sampled and three samples were obtained from each zone. Sampling consisted of examining whole shoot complexes. A shoot complex consisted of a parent shoot that grew in 1993 and the daughter terminal and laterals that grew in 1994. Shoot complexes with healthy daughter terminals and many lateral shoots present were sampled because it was necessary to have a large sample of lateral shoots. The measurements obtained included: parent and daughter terminal shoot length, daughter lateral shoot lengths, number of shoot units per shoot, and position of lateral shoots on a parent shoot (Table 1.2). The following year the lengths of the new growth

from terminals and laterals that grew in 1994 were measured and a count of the number of laterals that grew on the 1994 terminal shoot was made.

Data Collection: Site 2

The second data collection site (site 2) was located in the Morden arboretum. For sampling, the trees were divided into three crown zones: upper, middle, and lower thirds. This zonation was used because the older trees were very large, and thus there were very few live shoots toward the inside of the crown. It was also very difficult to get inside the interior crown to sample.

Data were collected in October 1994, May 1995, and July 1995. These data were collected to: (1) determine the number of primordia preformed in the terminal bud as a first step in determining if neoformation occurs in older trees, (2) to determine how the percentage of bud types on a shoot change as the tree ages, and (3) to determine the effect of tree aging on the number of shoot units per shoot and shoot-unit length of terminal and lateral shoots.

Preformation and neoformation

In order to determine if neoformation occurred it was necessary to collect the following data: the total number of primordia present in the dormant bud, the number of scales produced in the bud, the number of preformed leaf primordia (shoot units) in the bud, and the actual number of shoot units

produced on a mature expanded shoot. The number of preformed shoot units was estimated by subtracting the number of scales produced from the total number of primordia in the dormant bud. If the number of shoot units the next season per expanded shoot exceeds the number of preformed shoot units in the resting bud, then the extra shoot units are neoformed. If there is no difference, neoformation did not occur.

The total number of primordia was determined by dissecting terminal buds collected in October 1994 under a stereo microscope and counting the primordia in the bud. Three samples from each crown zone (180 shoots in total) were collected using pole pruners or a high-up lift truck and stored in a walk-in cooler for further laboratory examination. Each terminal bud was removed from the shoot and dissected under a stereo microscope.

The number of scales was determined by counting the number of true scales present (on shoots still present on the tree) when the buds expanded in May 1995. Three samples from each crown zone (180 shoots) were examined and averaged.

A count of the number of shoot units per expanded shoot was made in July 1995 after growth had ceased. Three shoots from each crown zone (180 shoot in total) were sampled and averaged.

Fate of buds

To study in detail the effect of aging on the percentage of bud types along parent shoots, two different samples were collected. In October 1994 when the shoots were removed from the tree, each sample contained at least two years of growth (180 samples in total). From the shoots used for terminal bud dissection all the lateral buds along each shoot were dissected and classified according to the categories in Table 1.1. In addition, the number and location of the previous year's lateral shoots on the sample were also recorded.

Data were also collected in July 1995 to examine the percentage of buds produced in 1994 which developed into lateral shoots. The data consisted of recording how many new lateral shoots had developed and where they occurred along the shoot. However, it was not known what the fate of the other buds that did not form lateral shoots would have been because sampling occurred in the summer after the inflorescences and aborted buds had fallen off the tree making it difficult to determine the fate of buds. Therefore bud types were recorded as either lateral shoots or unknown.

Shoot unit numbers and length

In order to study the effect of aging on shoot unit numbers and shoot-unit length, data were collected in July 1995 from shoots present on the tree. Three shoots in each crown location of the 20 trees were sampled (180 shoots in total).

Measurements included the parent terminal shoot length, daughter terminal shoot length, daughter lateral shoot length, number of shoot units per shoot and position of lateral shoots along the parent shoot. Shoot-unit length was not measured directly but was calculated by dividing total shoot length by the number of shoot units to produce a mean shoot-unit length for that shoot.

Statistical Analysis

Analysis of the data was accomplished using a chi-square goodness of fit test. The chi-square test was chosen because the data were arranged in frequency tables and categorized, which made it easier to visualize the data and to produce tables and graphs. Although means could have been used the variation in the data may have obscured some of the resulting patterns. Chi-square is useful when attempting to describe the anticipated structural patterns in the data (Mead *et al.*, 1993). The null hypothesis of this test was that the variables tested were independent from the factor being tested. An example would be that the number of shoot units produced per shoot is not dependent on the age of the tree. The use of chi-square to analyze this particular data is useful because the data is arranged in categories of age by the number of shoot units. Any test with a lesser value than 0.05 for the probability of χ^2, resulted in a rejection of the null hypothesis and a determination that the variables tested were dependent.

To examine in more detail the effect of aging on shoot unit numbers per shoot and mean shoot-unit length within a crown zone the data were analysed using analysis of variance with a split-plot design using Statistical Analysis System (SAS Institute Inc. 1989-1995). The age-class of the tree was used as the main effect, the location of the shoot in the tree was the sub-effect, and the tree number was used as replication. This model was based on the model used by Remphrey and Davidson (1994).

RESULTS

Shoot Architecture and Crown Location in 8-year-old Trees

Number of shoot units per shoot

Terminal shoots

In general the number of shoot units per terminal shoot in the experimental trees was dependent on the location of the shoot in the crown (Fig. 1.3). In all clones combined the top crown location had more shoot units per shoot compared to other crown locations and the inside location had the fewest (Fig 1.3a).

In the top crown location the three clones were similar with 8 or 9 shoot units per shoot most common (Fig. 1.3b-d). All three clones had near unimodal distribution of the number of shoot units per shoot.

In the bottom of the crown, clone 1 had a unimodal distribution and 6 shoot units per shoot was most common (Fig. 1.3b-d). Clone 2 had a more bimodal distribution of the number of shoot units per shoot and 5 or 8 shoot units per shoot was most common. Clone 3 had a unimodal distribution of the number of shoot units per shoot with 8 and 9 shoot units per shoot more common.

In the inside crown location, clones 1 and 2 did not have a unimodal distribution of the number of shoot units per shoot. In clone 1 most shoots contained 3 or 4 shoot units per shoot (Fig. 1.3b-d). In clone 2 most shoots had
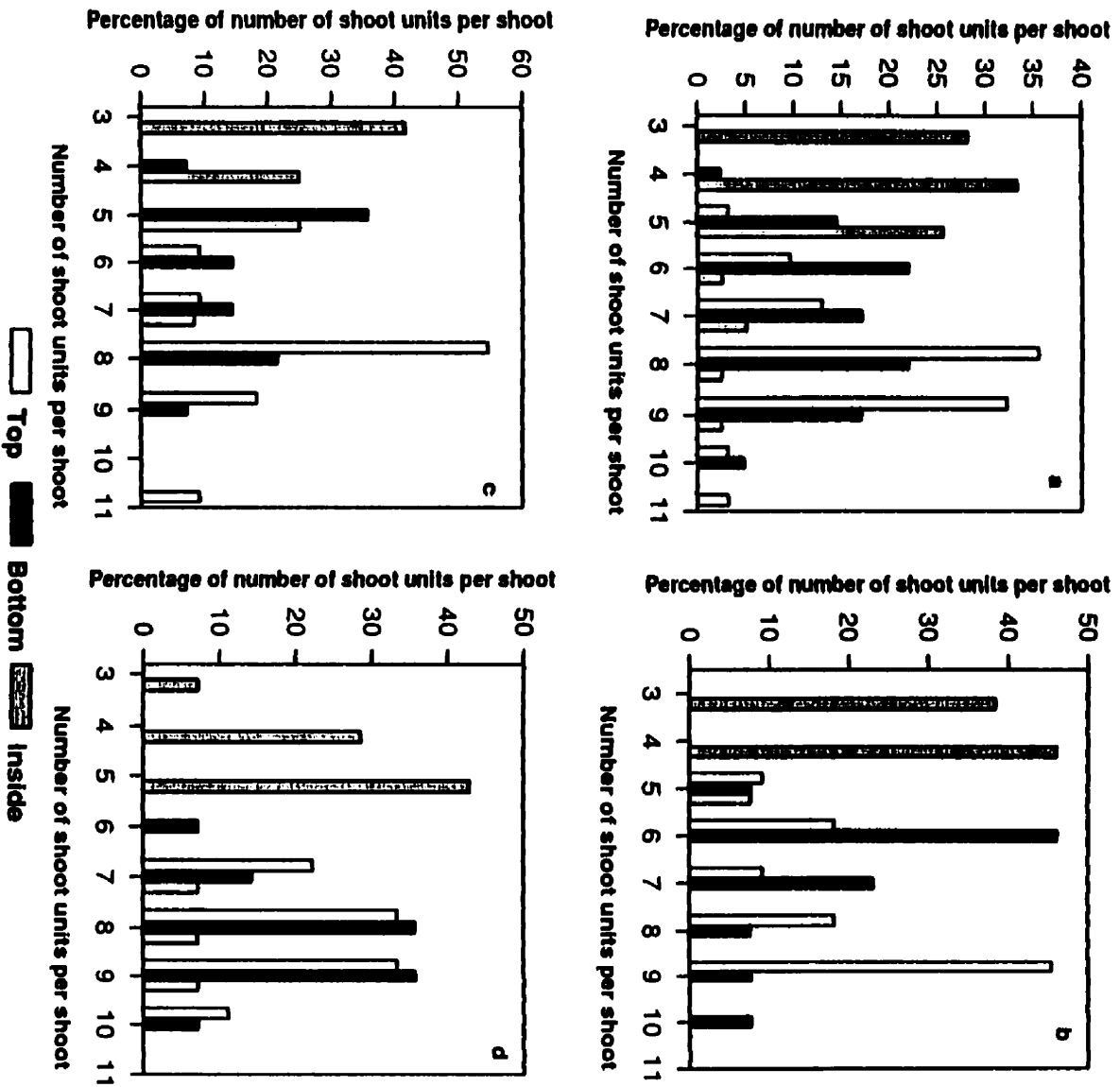
Fig 1.3. The number of shoot units per terminal shoot in the top, bottom, and inside crown locations. Chi-square tests of independence between the number of shoot units per terminal shoot and crown location. **a)** all clones combined $(\chi^2=79.61, P=0.001, n=111)$ **b)** clone 1 $(\chi^2=40.53, P=0.001, n=37)$ **c)** clone 2 $(\chi^2=31.47, P=0.001, n=37)$ **d)** clone 3. $(\chi^2=27.52, P=0.001, n=37)$

less than 5 shoot units per shoot. Clone 3 was more normal compared to the other two clones and most shoots had less than 5 shoot units per shoot.

Lateral shoots

The number of shoot units per lateral shoot in all clones combined was highly variable between the three crown locations (Fig. 1.4). Generally, lateral shoots in the top crown location for all clones combined had the most shoot units per shoot while the bottom and inside appeared to be similar and had fewer shoot units per shoot (Fig. 1.4a).

In the top crown location the clones were generally similar except that clone 2 had some lateral shoots with 11 shoot units per shoot and clone 3 had no shoots with less than 7 shoot units per shoot (Fig. 1.4b-d). Also in clone 1 the distribution of the number of shoot units per shoot was skewed downward from 9 shoot units per shoot compared to the other two clones which had a more unimodal distribution of the number of shoot units per shoot.

In the bottom of the crown, clones 1 and 2 did not have a unimodal distribution of the number of shoot units per shoot (Fig. 1.4b-d). Clone 2 had a somewhat bimodal distribution of the number of shoot units per shoot with 5 and 8 shoot units per shoot most common. Clone 3 had a near unimodal distribution of the number of shoot units per shoot with 8 and 9 shoot units per shoot most common.
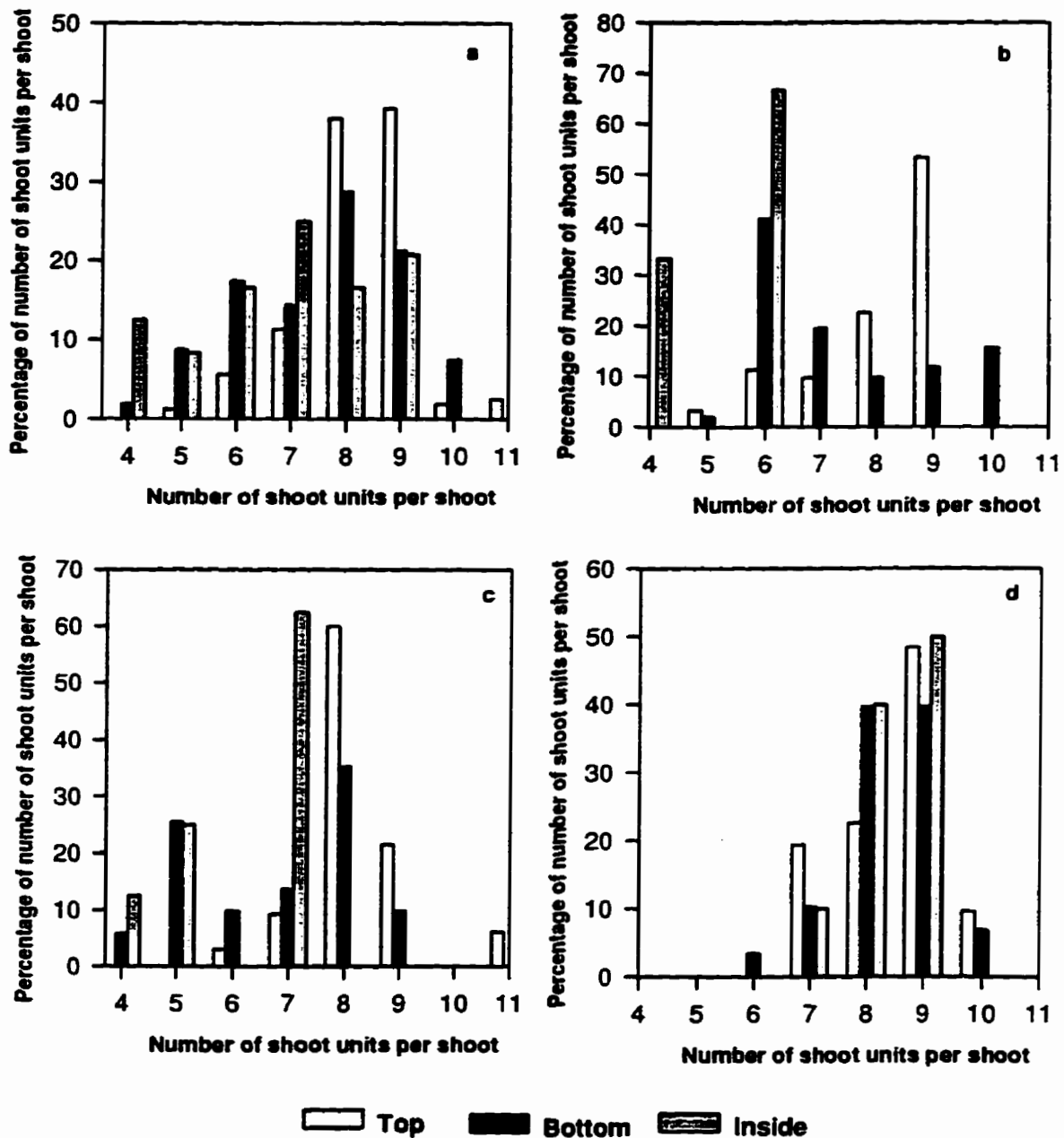
Fig. 1.4. The number of shoot units per lateral shoot in the top, bottom, and inside crown locations. Chi-square tests of independence between the number of shoot units per lateral shoot and crown location. a) all clones combined (χ^2=64.99, P=0.001, n=342) **b**) clone 1 (χ^2=85.20, P=0.001, n=119) **c**) clone 2 (χ^2=53.84, P=0.001, n=124) **d**) clone 3 (χ^2=6.04, P=0.064, n=99).

In the inside crown location, clone 1 had either 4 or 6 shoot units per shoot and clone 2 had most shoots with either 5 or 7 shoot units per shoot (Fig. 1.4b-d). In clone 3 the distribution was more unimodal than the other two clones with 8 or 9 shoot units per shoot the most common.

Shoot unit length

Terminal shoots

The length of shoot units in terminal shoots for all clones combined was dependent on the position of the parent shoot in the crown based on tests of independence (Fig. 1.5). The top crown location had a greater percentage of larger shoot-unit lengths compared to the other crown locations (Fig 1.5a). Most shoot-unit lengths in the inside crown location were less than 20 mm (Fig. 1.5b-d).

In the top crown location clone 1 had a relatively unimodal distribution in shoot-unit lengths (Fig. 1.5b-d) and clone 2 was somewhat bimodal. Clone 3 also appeared bimodal and no single shoot unit-length category was dominant.

In the bottom of the tree clone 1 had a more or less unimodal distribution in shoot-unit lengths (Fig. 1.5b-d). Clone 2 had more shoot-unit lengths concentrated in the 35-40 mm range. Clone 2 had a near unimodal distribution in terminal shoot-unit lengths but was slightly skewed towards longer shoot-unit lengths. Clone 3 was bimodal with shoot-unit lengths concentrated in the 40 and 70 mm category.
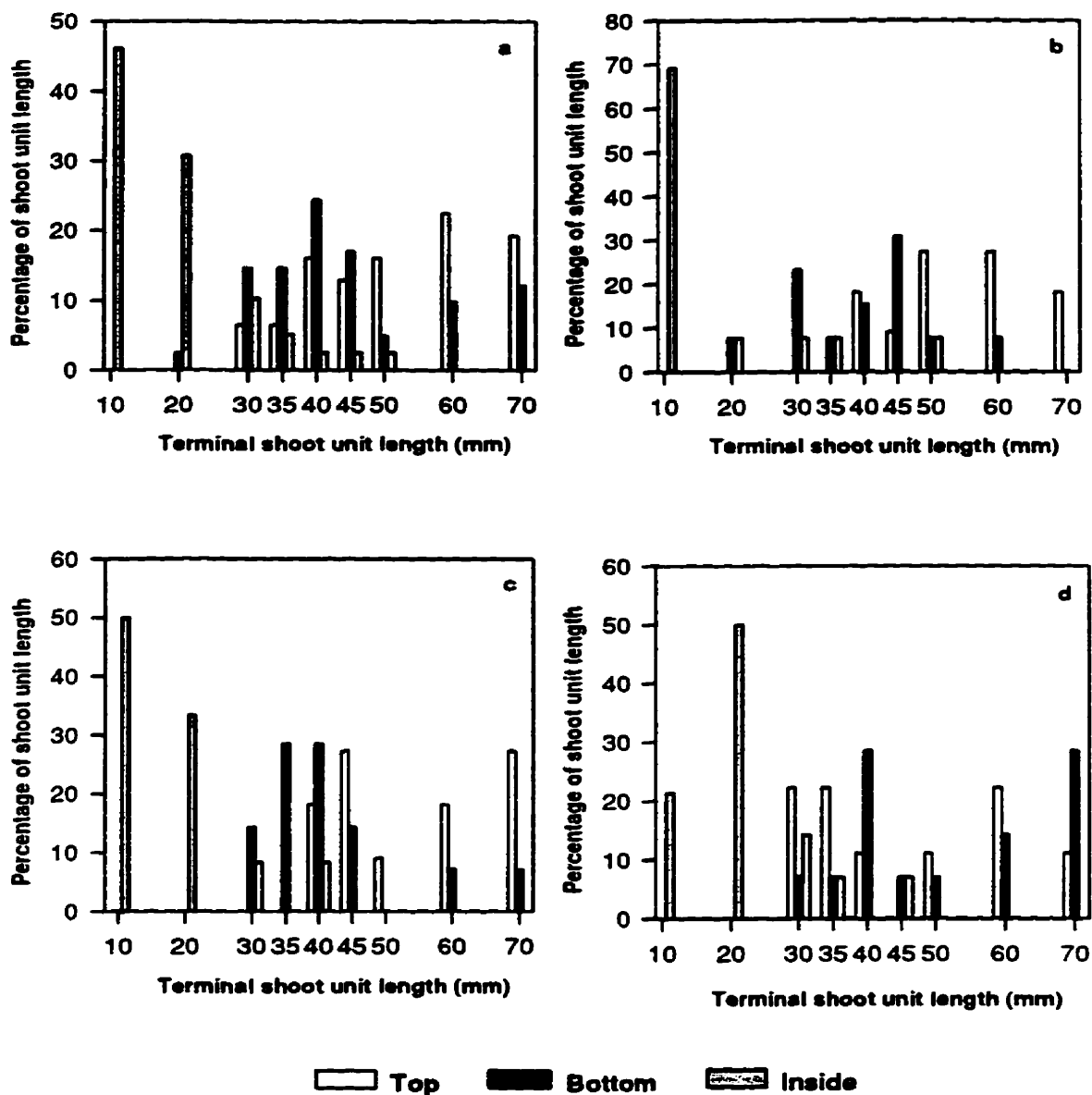
Fig. 1.5. Terminal shoot unit length categories of shoots in the top, bottom, and inside crown locations. The numbers depicting each category represent a range of shoot unit lengths; e.g., 0.1-10mm, 10.1-20mm, etc.. The number denotes the high point of the range. Chi-square tests of independence between shoot unit length category and crown location. a) all clones combined (χ^2=86.81, P=0.001, n=111) b) clone 1 (χ^2=39.61, P=0.001, n=37) c) clone 2 (χ^2=42.46, P=0.001, n=37) d) clone 3 (χ^2=32.15, P=0.01, n=37).

shoot-unit lengths were less than 20 mm. The highest concentration of shoot-

In the inside crown location shoot-unit lengths of 10 mm were most common in clone 1 (Fig. 1.5b). Clone 2 did not have a unimodal shoot-unit length distribution and most shoot-unit lengths were less than 20 mm. Similarly, in clone 3 the distribution of shoot-unit lengths was not unimodal and most unit lengths was in the 20 mm category.

Lateral shoots

Similar to terminal shoot-unit lengths the length of shoot units in lateral shoots for all clones combined was dependent on the position of the parent shoot in the crown based on tests of independence (Fig. 1.6a). The top crown location had the greatest percentage of shoots with longer shoot-unit lengths. The inside crown location had the smallest range in lateral shoot-unit lengths. The bottom of the crown had a relatively unimodal distribution compared to the top where the distribution was bimodal. Lateral shoot-unit lengths were slightly different than terminal shoot-unit lengths because there were generally fewer longer shoot-lengths compared to the terminal shoots.

In the top crown location clone 1 had the highest percentage of 70 mm shoot-unit lengths but was otherwise unimodal distribution (Fig. 1.6b-d). In clone 2 shoot-unit lengths at the top were unimodally distributed. In clone 3 all shoot-unit lengths were short or less than 35 mm.
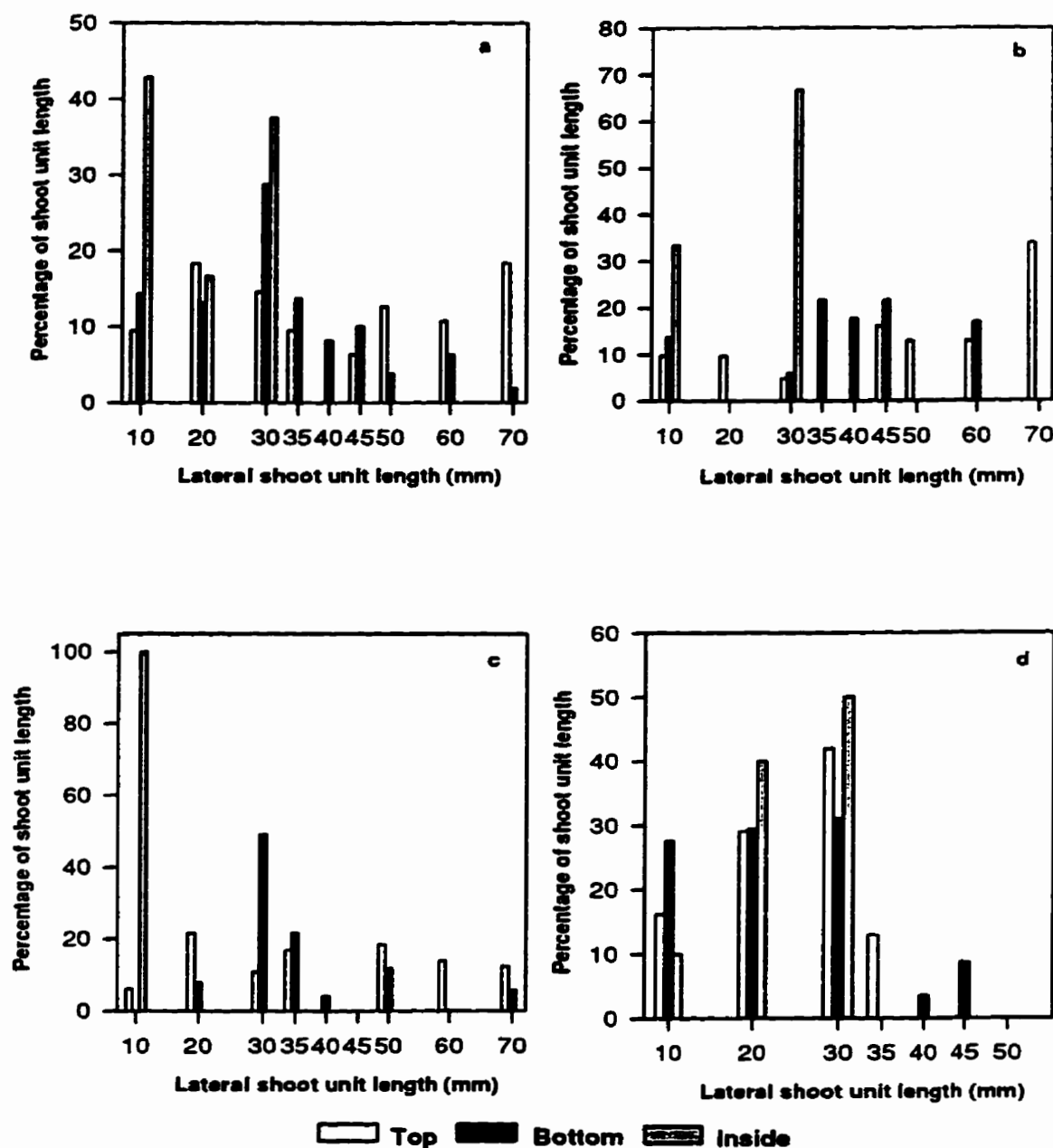
Fig. 1.6. Lateral shoot unit length categories of shoots in the top, bottom, and inside crown locations. The numbers depicting each category represent a range of shoot unit length; e.g., 0.1-10mm, 10.1-20mm, etc.. The number denotes the high point of the range. Chi-square tests of independence between shoot unit length category and crown location. **a)** all clones combined (χ^2=92.18, P=0.001, n=342) **b)** clone 1 (χ^2=90.29, P=0.001, n=119) **c)** clone 2 (χ^2=113.66, P=0.001, n=124) **d)** clone 3 (χ^2=17.24, P=0.07, n=99).

In the bottom in clone 1, shoot-unit lengths were more or less unimodal distribution between 10 and 60 mm (Fig. 1.6b-d). In clone 2 half of the shoot-unit lengths were in the 30 mm category. In clone 3 most of the shoot units were less than 30 mm.

In the inside in clone 1, shoot-unit lengths were either in the 10 or 30 mm category (Fig. 1.6b-d). In clone 2 all shoot-unit lengths were in the 10 mm category. In clone 3 the distribution was not unimodal with most shoot-unit lengths in the 20 or 30 mm category.

Fate of buds

The fate of buds was examined in relation to many factors which are described below.

Crown location

Based on tests of independence for each clone the fate of buds was generally dependent on the position of the shoot in the crown for all clones combined (Fig. 1.7a-d). The greatest proportion of lateral shoots and inflorescences was found in the top crown location and the greatest proportion of aborted buds occurred in the inside crown location (Fig. 1.7a). Relatively few buds remained dormant in any location. Clones 1 and 2 generally produced the greatest proportion of lateral shoots in all crown locations.
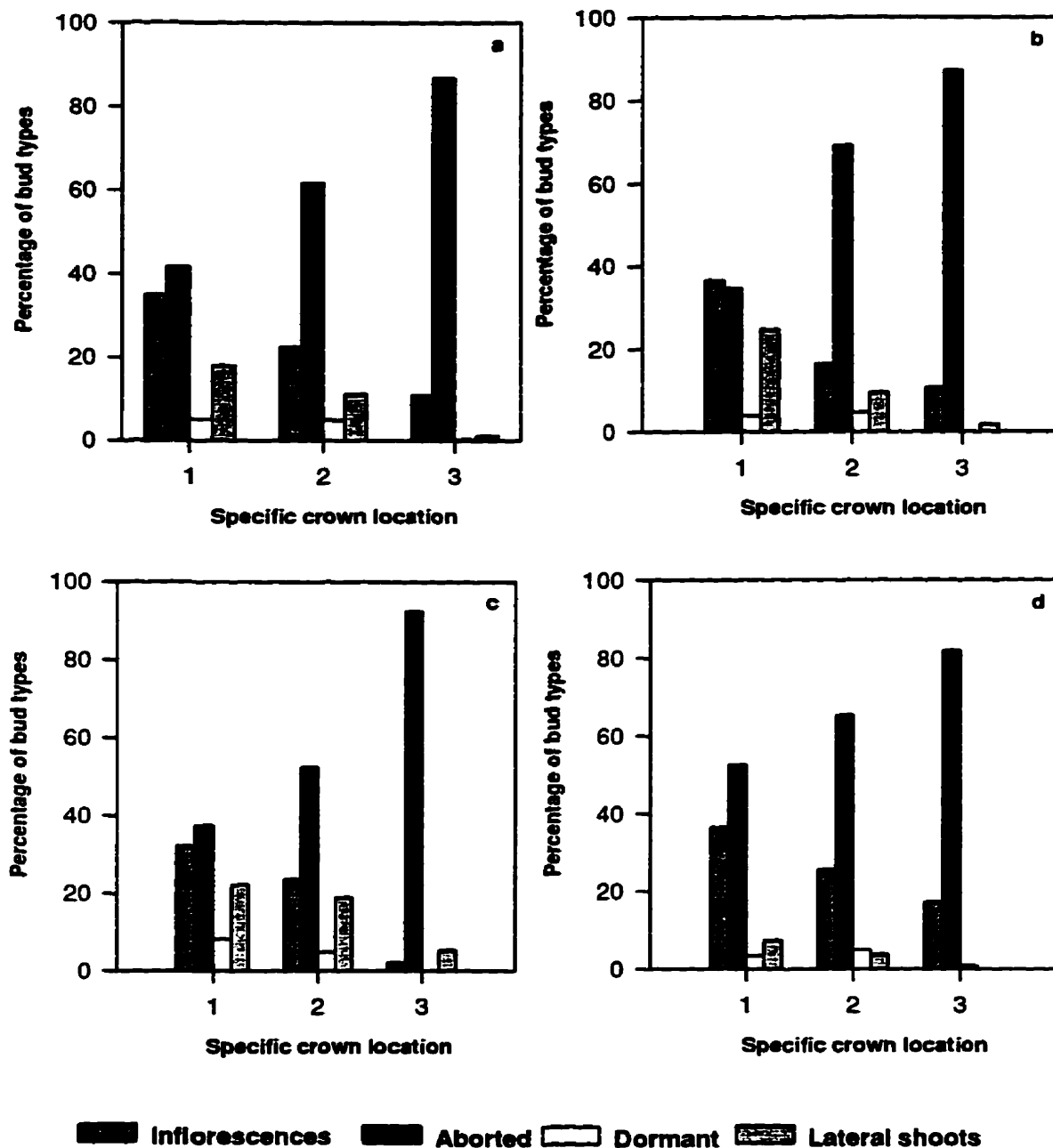
Fig. 1.7. Fate of buds on a shoot in the top, bottom, and inside crown locations. Chi-square tests of independence between the fate of buds and crown location. 1=top, 2=bottom, 3=inside. **a)** all clones combined (χ^2=328.11, P=0.001, n=4391) **b)** clone 1 (χ^2=223.27, P=0.001, n=1417) **c)** clone 2 (χ^2=111.52, P=0.001, n=1446) **d)** clone 3 (χ^2=61.03, P=0.001, n=1528). (n=number of individual buds)
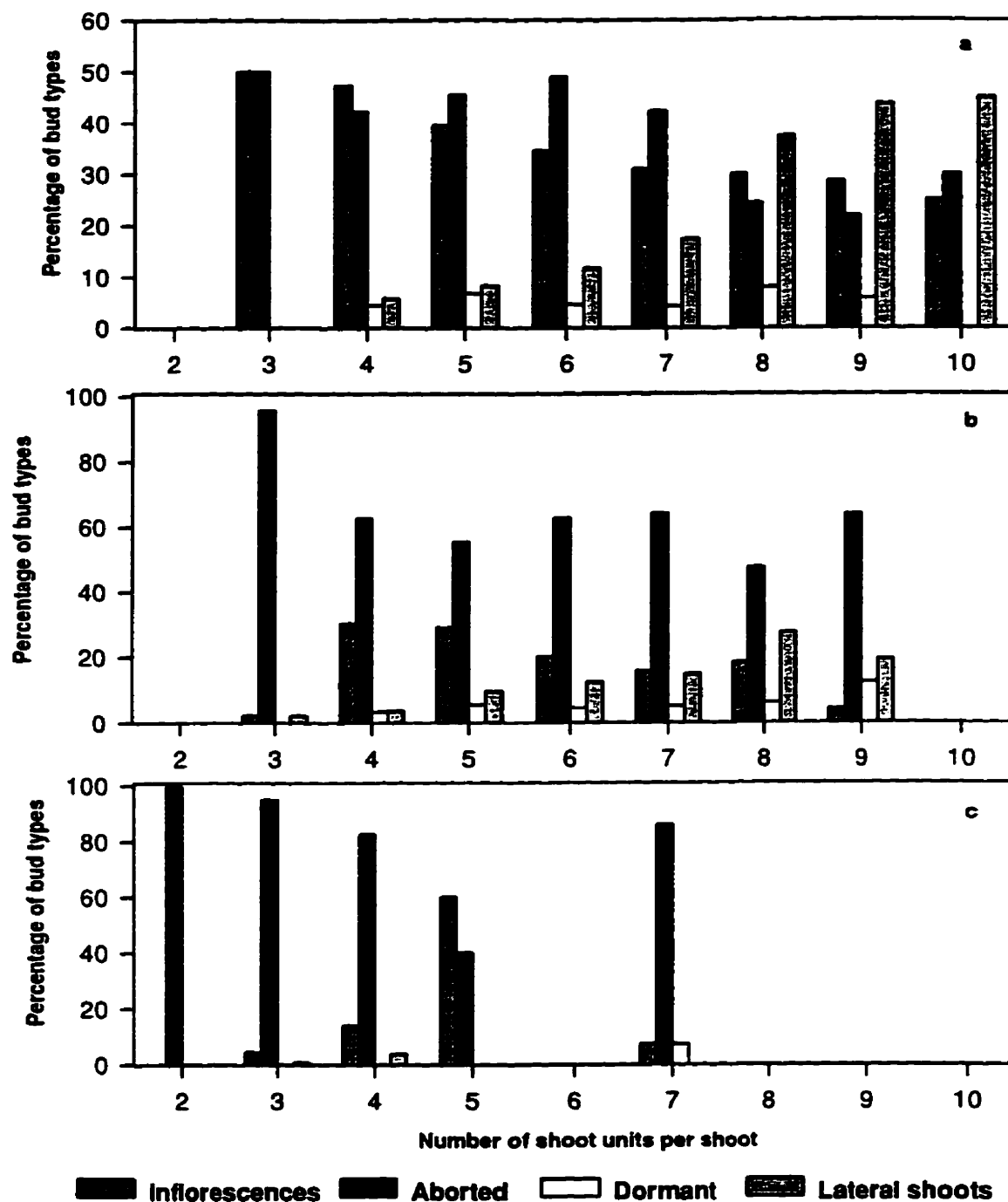
Fig. 1.8. The fate of buds on a shoot for shoots with different numbers of shoot units for all clones combined. Chi-square tests of independence between the fate of buds and the number of shoot units per shoot. **a)** top crown location (χ^2=265.55, P=0.001, n=2096) **b)** bottom crown location (χ^2=123.94, P=0.001, n=1930) **c)** inside crown location (χ^2=59.90, P=0.001, n=326)

Number of shoot units per parent shoot

In the top and bottom of the crown, as the number of shoot units per parent shoot increased, the proportion of daughter lateral shoots increased and the proportion of inflorescences and aborted buds decreased (Fig. 1.8a-c). In the inside of the crown all shoots (except shoots with 5 shoot units per shoot) a large proportion of buds aborted. For shoots with the same number of shoot units per shoot, the shoots in the top of the crown produced a greater proportion of inflorescences and buds producing lateral shoots compared to shoots in the bottom or inside of the crown.

Shoot length

Similar to the number of shoot units per parent shoot, the fate of buds on a shoot is dependent on its length (Fig. 1.9a-c). Longer shoots generally had the greatest proportion of lateral shoots. As shoot length decreased the proportion of buds producing lateral shoots declined and the proportion of buds producing inflorescences increased. Shoots less than 250 mm had the greatest proportion of buds that aborted. Comparing shoots in the 75 mm category between crown locations, the top crown location had the greatest proportion of inflorescences and the inside of the crown had the lowest proportion. For the 75 mm category, the bottom and inside of the crown contained the highest proportion of aborted buds but the inside had the greatest proportion of lateral shoots. The above
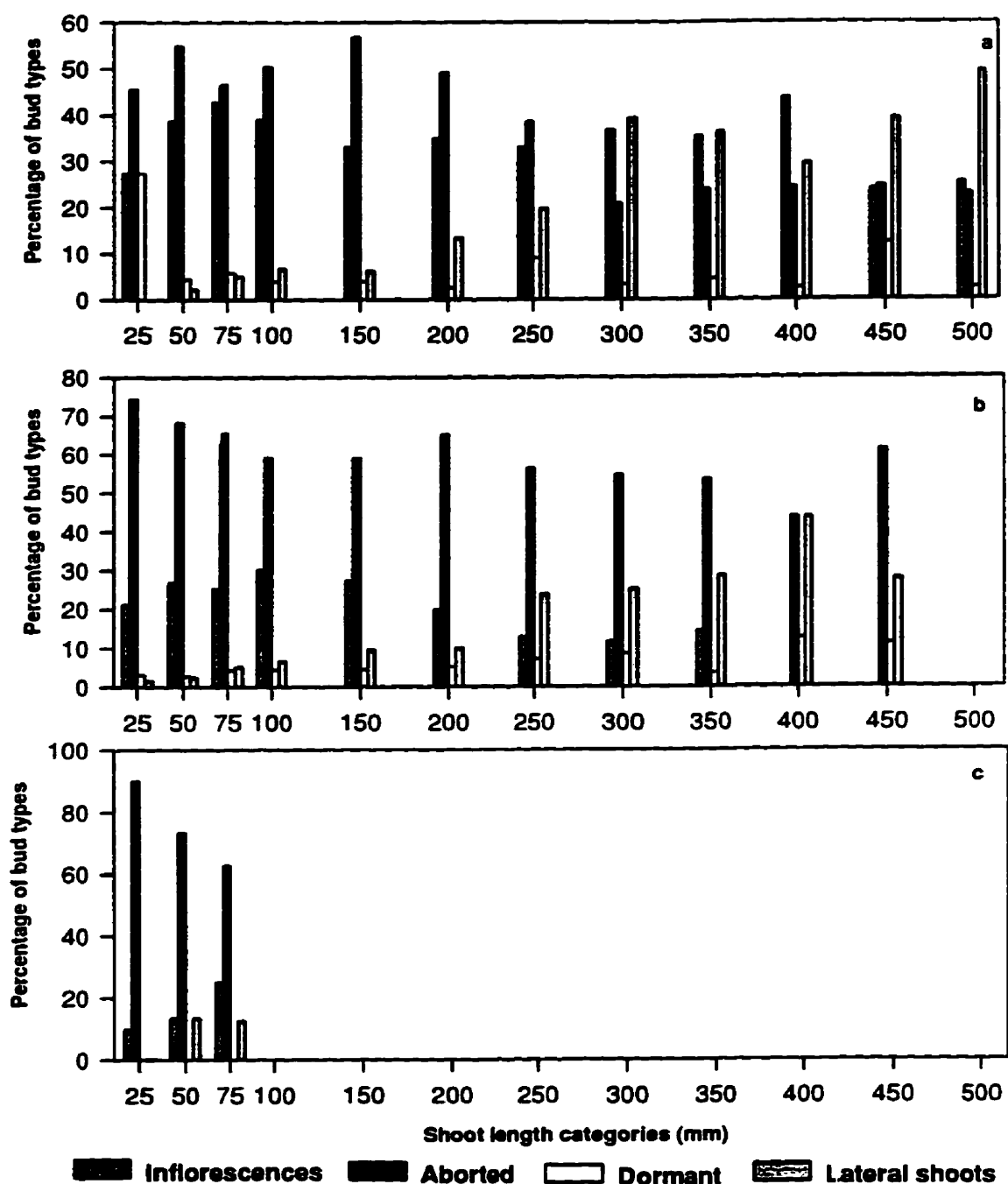
Fig. 1.9. The fate of buds on shoots in different length categories for all clones combined. Chi-square tests of independence between the fate of buds and total shoot length category. a) top crown location (χ^2=432.31, P=0.001, n=2096) b) bottom crown location (χ^2=206.37, P=0.001, n=1930) c) inside crown location (χ^2=33.47, P=0.001, n=312).

pattern was evident in each of the three clones (data not shown).

Shoot zone

For all clones combined the fate of buds was affected by shoot zone (position along shoot see materials and methods) in each crown location (Fig 1.10a-c). In all crown zones the highest proportion of buds aborted near the base of the shoot (shoot zone 1), the greatest proportion of inflorescences occurred in shoot zones 2 and 3, and the greatest proportion of lateral shoots was present near the tip in shoot zone 4. For each shoot zone, the proportion of buds that developed into inflorescences and lateral shoots decreased while the number of buds which aborted increased from the top to the inside of the crown.

Position around shoot

The position of the bud around the shoot in all clones combined and each clone separately (data not shown) did not affect its fate (Fig. 1.11). In each position around the shoot the proportion of inflorescences, aborted buds, dormant buds, and lateral shoots remained the same. When the position of the bud around the shoot was examined in each clone separately in each crown location its fate was independent of position around the shoot (data not shown).
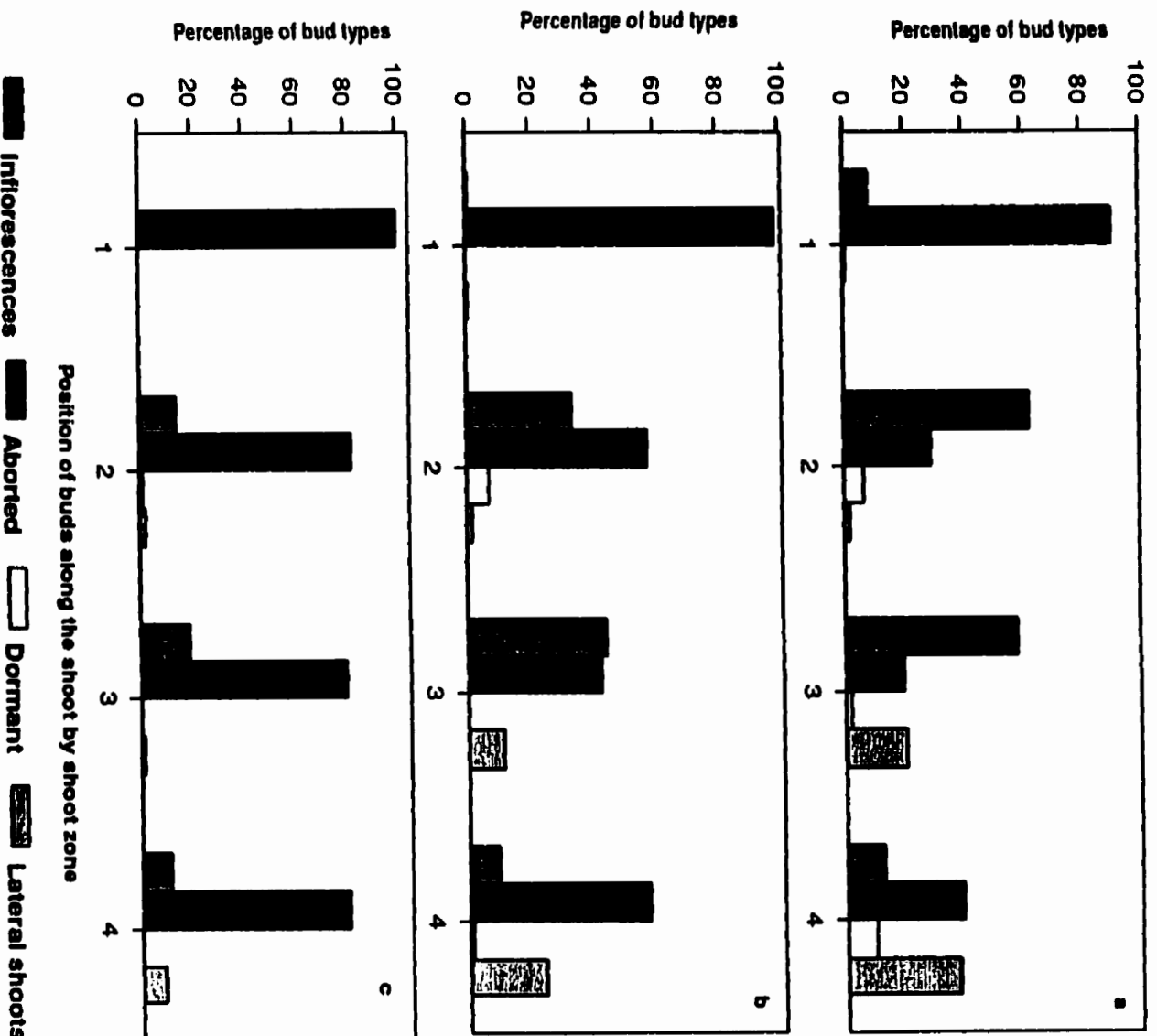
Fig. 1.10. The fate of buds along the shoot by shoot zone for all clones combined. Chi-square tests of independence between the fate of buds and the position of the bud along the shoot. 1=bottom, 2=lower middle, 3=upper middle, 4=top. **a)** top crown location (χ^2=1044.93, P=0.001, n=2115) **b)** bottom crown location (χ^2=595.47, P=0.001, n=1930) **c)** inside crown location (χ^2=34.21, P=0.001, n=326).

80
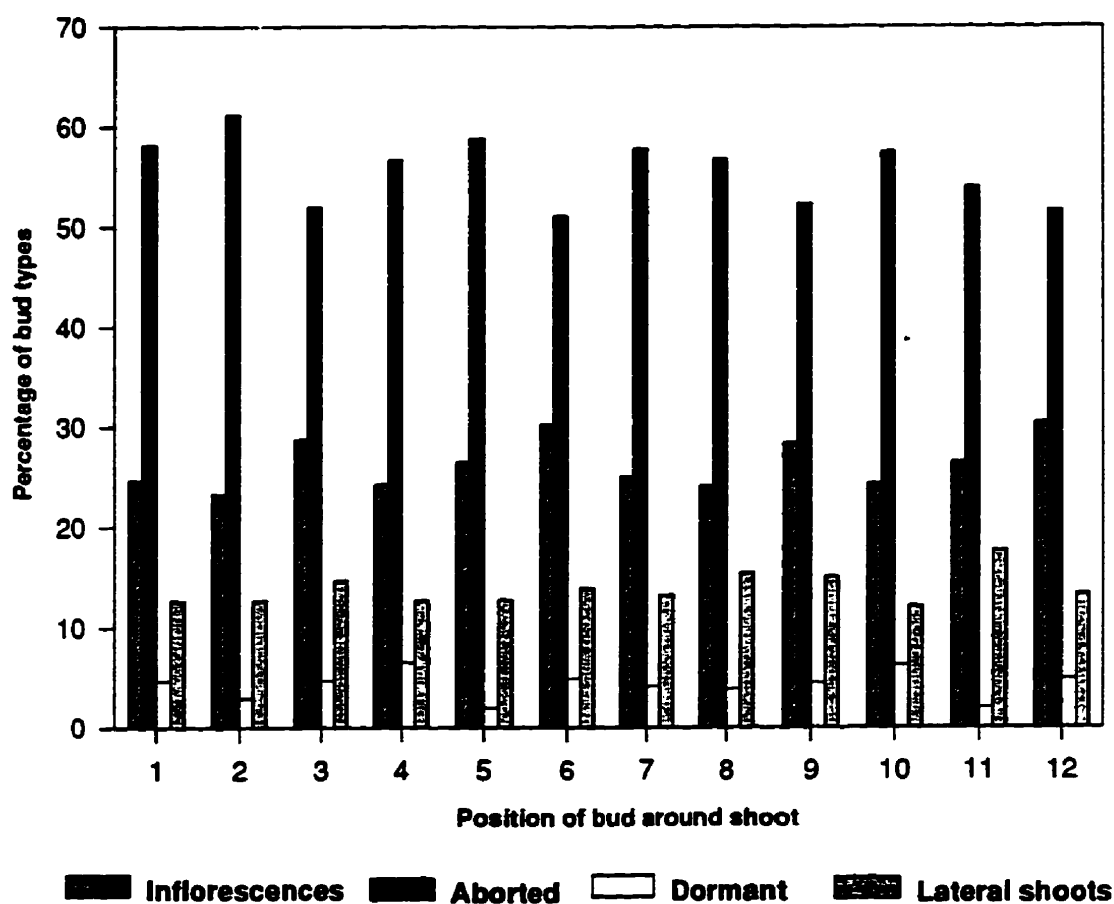
Fig. 1.11 The fate of buds around a shoot for all clones and crown locations combined. Chi-square tests of independence between the fate of buds and position of bud around the shoot. (χ^2=28.75, P=0.68, n=4399).

Shoot Architecture and Aging

Number of shoot units

Terminal shoots

Based on tests of independence, it was determined that the number of shoot units per shoot was dependent on the age class of the tree (Fig. 1.12). Similarly, analysis of variance revealed a significant difference (P=0.0096) in the mean number of shoot units per shoot indicating that tree age affected the number of shoot units produced. The 10-year-old trees had the greatest variation in range of the number of shoot units per shoot. The other 3 age-classes had a large percentage concentrated in the 5 shoot unit length category (Fig. 1.12).

Comparing crown zones within each age-class, the pattern in the 10 and 20-year-old trees was similar to the pattern described earlier in the clonal experiment where the top had a greater number of shoots with more shoot units per shoot compared to the bottom (Fig. 1.3 and Fig. 1.13a-d). In the 50 and 60-year-old trees the above pattern was not as apparent because there was less variation in the number of shoot units per shoot between the crown zones. In the 50 and 60-year-old trees the number of shoot units per terminal shoot was not dependent on the position of the shoots in the crown based on tests of independence (Fig. 1.13c,d).
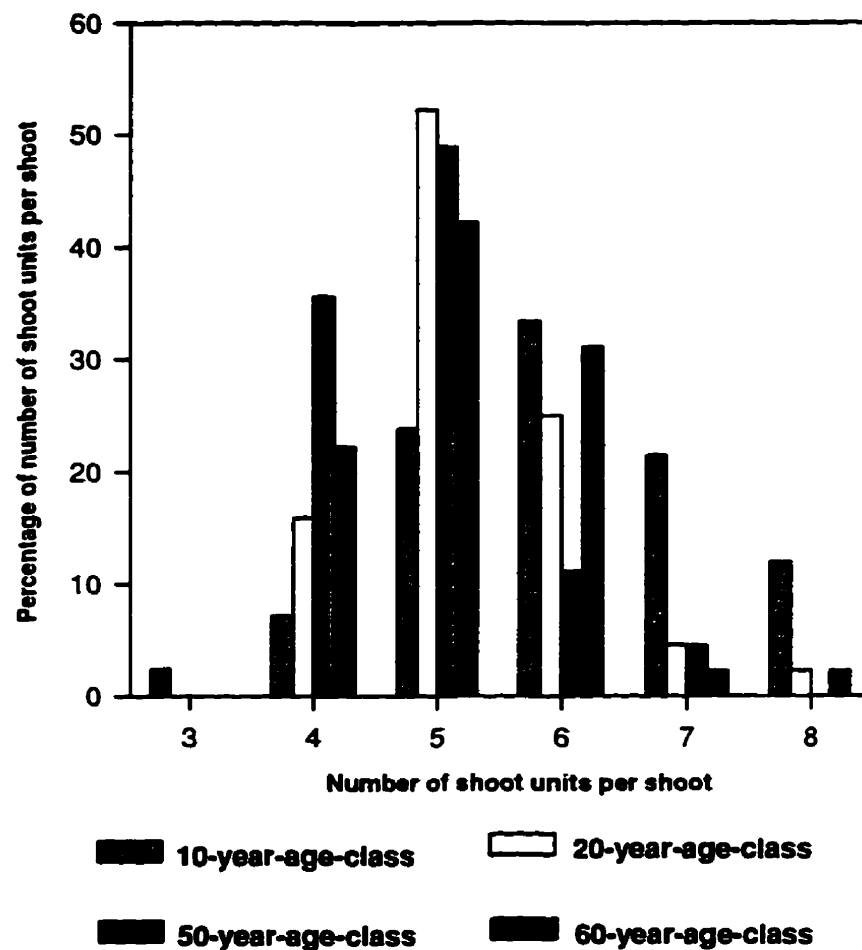
Fig.1.12. The number of shoot units per terminal shoot in the different age-classes for all crown locations combined. Chi-square tests of independence between the number of shoot units per terminal shoot and age-class. (χ^2=44.47, P=0.001, n=176)
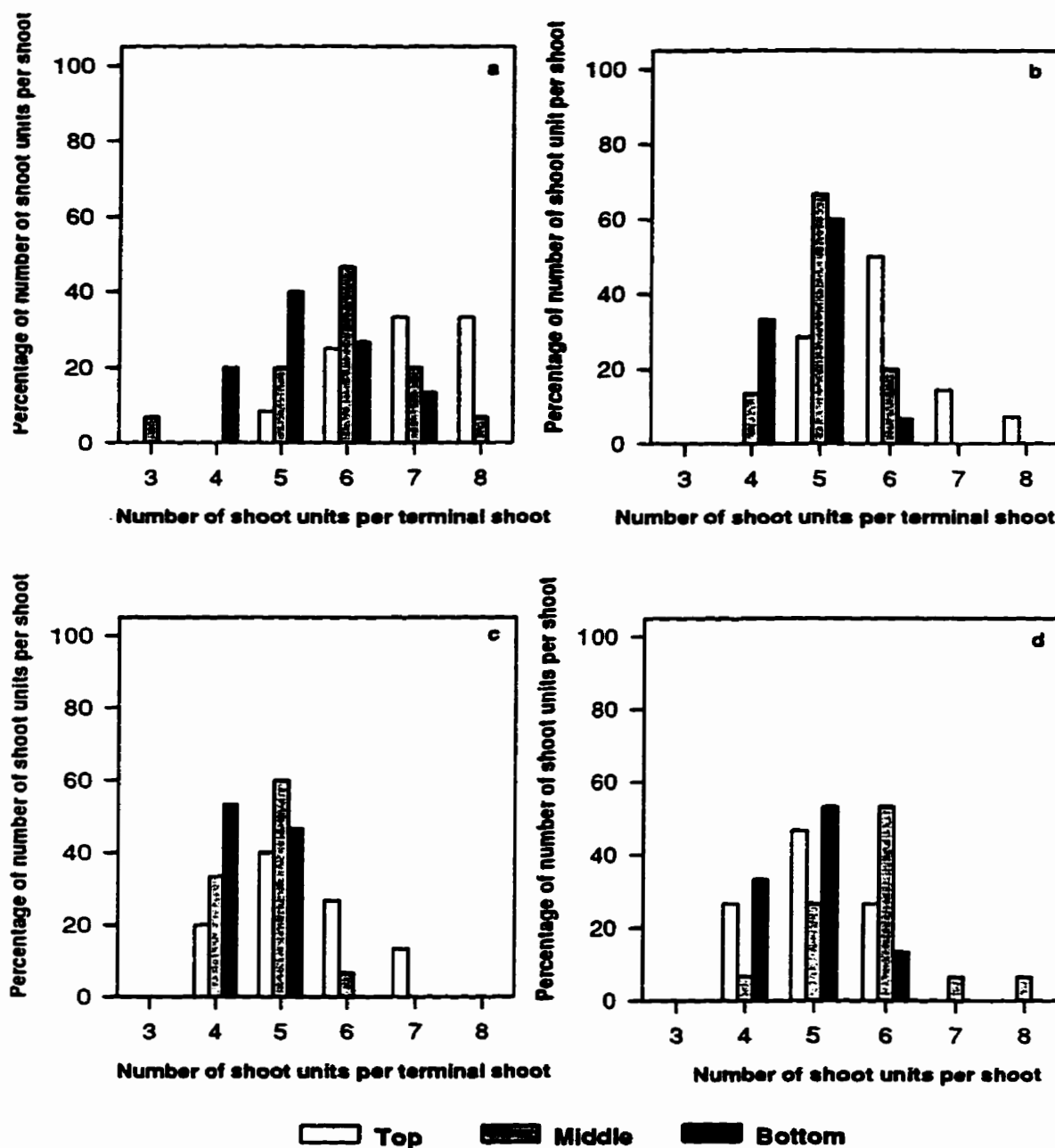
Fig. 1.13. The number of shoot units per terminal shoot in the top, middle, and bottom crown locations. Chi-square tests of independence between the number of shoot units per terminal shoot and crown location. **a)** 10-year-old trees (χ^2=19.42, P=0.035, n=42) **b)** 20-year-old trees (χ^2=19.52, P=0.012, n=44) **c)** 50-year-old trees (χ^2=12.21, P=0.057, n=45) **d)** 60-year-old trees (χ^2=11.97, P=0.15, n=45).

The number of shoot units per shoot in the top and middle of the crown was dependent on the age-class of the tree based on tests of independence (P=0.006 and P=0.01, respectively). In the top of the crown the 10-year-old trees had a larger percentage of shoots with 7 or 8 shoot units per shoot compared to the other age-classes and the 60-year-old trees had none (Fig. 1.13). In the middle of the crown only the 60-year-old trees had shoots with 7 or 8 shoot units per shoot. In the bottom of the crown the tests of independence were not significant (P=0.119) and the number of shoot units per shoot was not dependent on the age of the tree.

In all four age classes tested there was no evidence that neoformation occurred. A comparison of the mean number of shoot units per shoot between the crown locations in each age-class indicated that there was no difference between the estimated number of preformed shoot units and the actual number of shoot units formed (Table 1.4). In a few cases the number of estimated preformed primordia was slightly greater than the actual number of shoot units produced. The number of preformed primordia and the variation (as measured by the standard deviation) in the bud decreased from the top to the bottom of the crown.

Table 1.4 The estimated and actual number of shoot units per terminal shoots determined during the dissection of terminal buds and the number produced the following year.

Age-class	Specific crown location	Estimated number of preformed shoot units	Standard deviation	Actual number of preformed shoot units	Standard deviation
10	top	7.27	1.28	6.92	1.00
10	middle	5.17	0.72	5.93	1.16
10	bottom	4.57	0.64	5.33	0.98
20	top	5.47	0.99	6.00	0.88
20	middle	4.67	0.62	5.07	0.59
20	bottom	4.13	0.35	4.73	0.59
50	top	5.00	1.31	5.33	0.98
50	middle	4.20	0.77	4.73	0.59
50	bottom	4.27	0.59	4.47	0.51
60	top	5.47	0.92	5.00	0.75
60	middle	5.00	0.78	5.80	0.94
60	bottom	4.53	0.74	4.80	0.67

Note: ANOVA indicated a significant (P=0.0005) effect of age-class X crown zone on shoot unit length.

Lateral shoots

Similar to terminal shoots, the number of shoot units per lateral shoots was dependent on the age-class of the tree based on tests of independence (χ^2=37.16, P=0.005). ANOVA revealed a significant (P=0.019) difference in the

mean number of shoot units per lateral shoot indicating that tree age affected the number of shoot units produced. The youngest trees had a greater percentage of shoots with an increased number of shoot units per lateral shoot (data not shown).

The tests of independence between crown zones within an age-class were not significant indicating that the number of shoot units per lateral shoot was not dependent on crown location (Fig. 1.14a-d). Similarly, an ANOVA test of the mean number of shoot units per lateral shoot in relation to crown location was not significant (P=0.29)

Comparing crown locations among the age-classes, the number of shoot units per lateral shoot in the top crown location was dependent on the age-class (χ^2=31.654, P=0.024). In this location, the number of shoot units per lateral shoot decreased as the tree aged (data not shown). In the middle and bottom of the crown the number of shoot units per lateral shoot was independent of the age-class of the tree (χ^2=23.215, P=0.08 and χ^2=17.389, P=0.136, respectively).

Shoot unit length

Terminal shoots

ANOVA revealed that age-class significantly (P=0.0004) affected terminal shoot-unit length. However, tests of independence indicated that terminal shoot unit-lengths were dependent on the age-class when all crown locations were
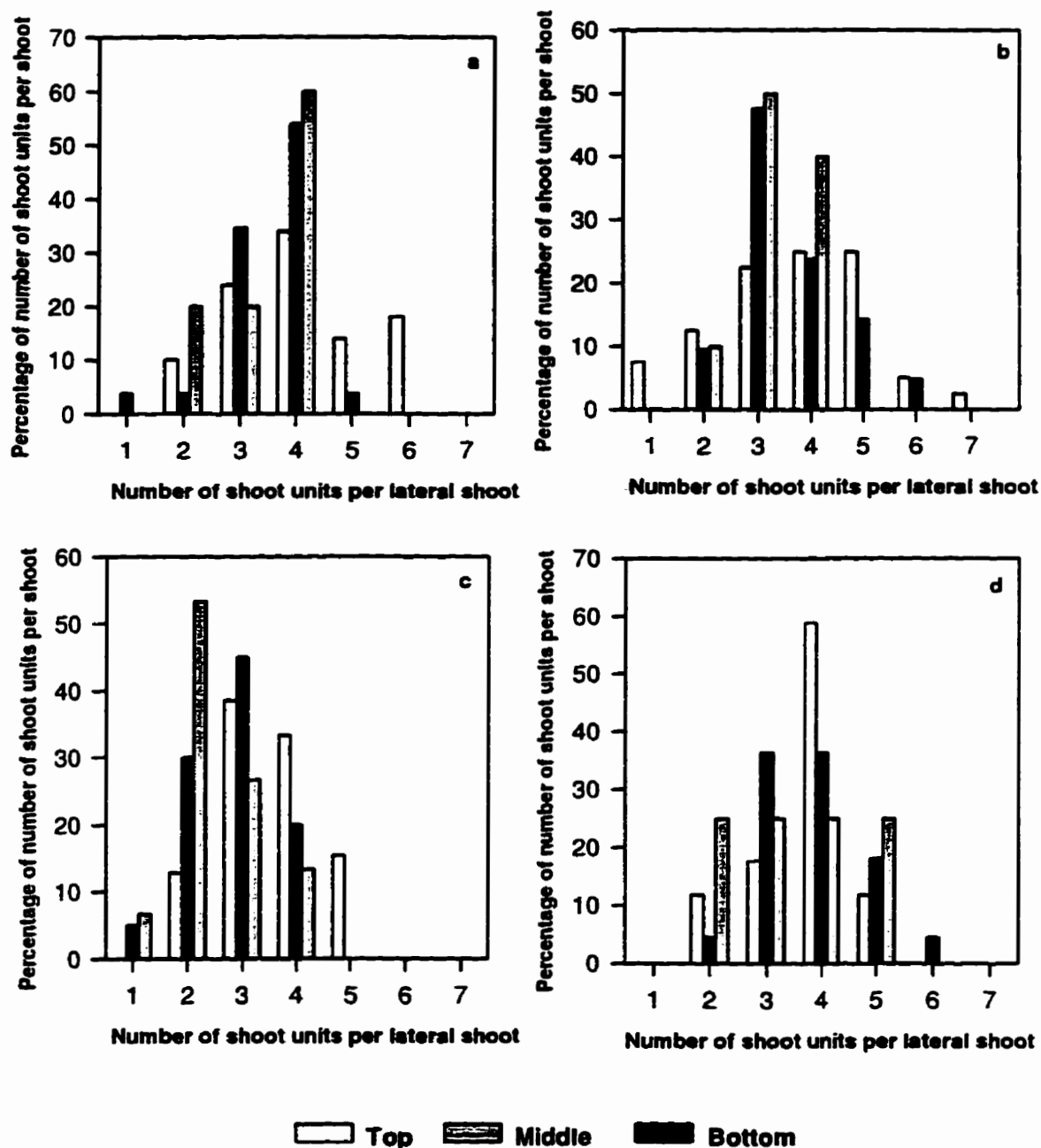
Fig. 1.14. The number of shoot units per lateral shoot in the top, middle, and bottom of the crown. Chi-square tests of independence between the number of shoot units per lateral shoot and crown location. **a)** 10-year-old-trees (χ^2=14.38, P=0.16, n=81 **b)** 20-year-old-trees (χ^2=10.59, P=0.55, n=71) **c)** 50-year-old-trees (χ^2=5.79, P=0.67, n=74) **d)** 60-year-old-trees (χ^2=17.62, P=0.24, n=43).
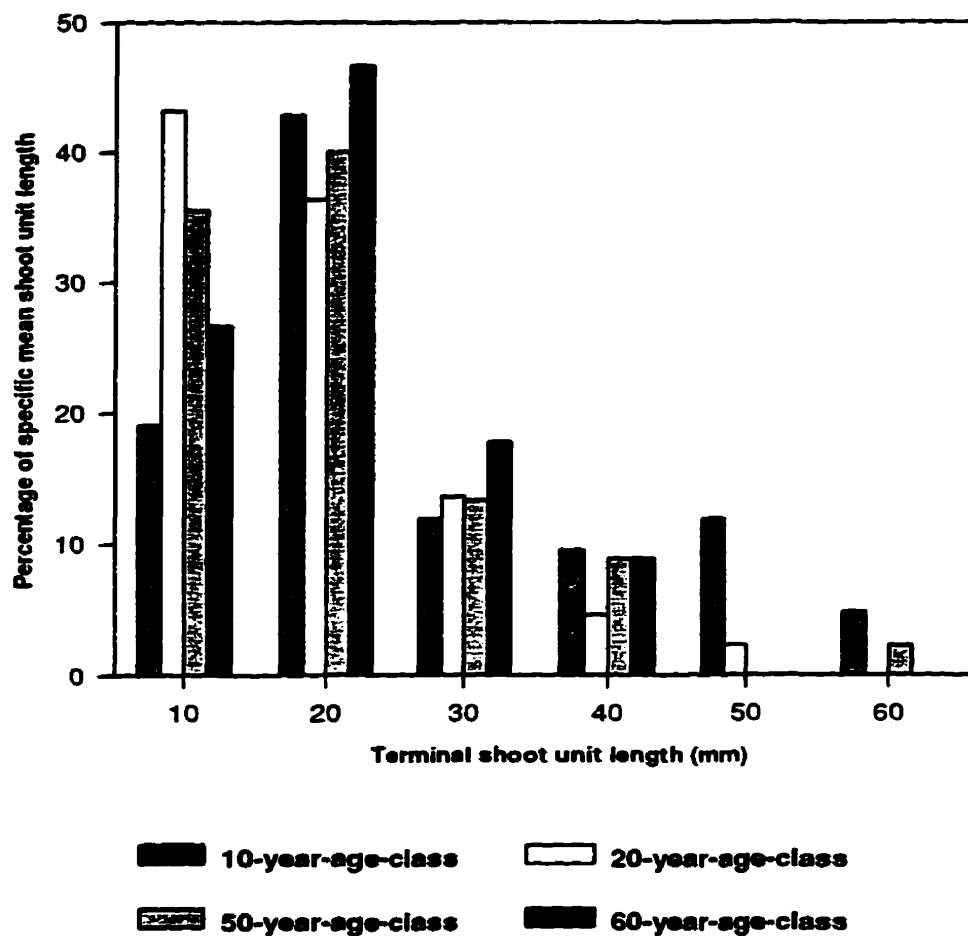
Fig. 1.15 Terminal shoot-unit length of shoots in the various age-classes of trees for all crown zones combined. The numbers depicting each category represents a range of shoot-unit lengths; e.g., 0.1-10mm, 10.1-20mm, etc.. The number denotes the high point of the range. Because of the small number of samples in the 50 and 60 mm category they were combined for chi-square tests of independence between terminal shoot unit length and age-class at the 5 % level of significance (χ^2=21.348, P=0.046, n=176).

combined (Fig. 1.15). The 10-year-old trees had the greatest percentages of longer shoot units. The 60-year-old trees had the smallest range in shoot-unit lengths.

Terminal shoot-unit lengths in the 10, 20, and 50-year-old trees were dependent on the position of the shoot in the crown based on tests of independence (Fig.1.16a-c). Generally the top of the crown in these three age-classes had a greater percentages of longer shoot-unit lengths compared to the middle and bottom. The range of shoot-unit lengths was smaller in the middle and bottom of the crown. In the 60-year-old trees shoot-unit length was not dependent on the position of the shoot in the crown (Fig. 1.16d). In these trees shoot-unit length was greatest in the middle of the crown compared to the other crown locations. The means of shoot-unit length are shown in Table 1.5.

When crown locations were analysed separately, it was found that the terminal shoot-unit length was dependent on the age-class of the tree in the top crown location (χ^2=32.352, P=0.006). In the middle and bottom of the crown shoot-unit length was not dependent on the age-class of the tree (χ^2=12.976, P=0.164 and χ^2=14.724, P=0.099, respectively).

Lateral shoots

Shoot unit lengths appeared similar across the age-classes (Fig. 1.17). Based on tests of independence lateral shoot-unit length was not dependent on
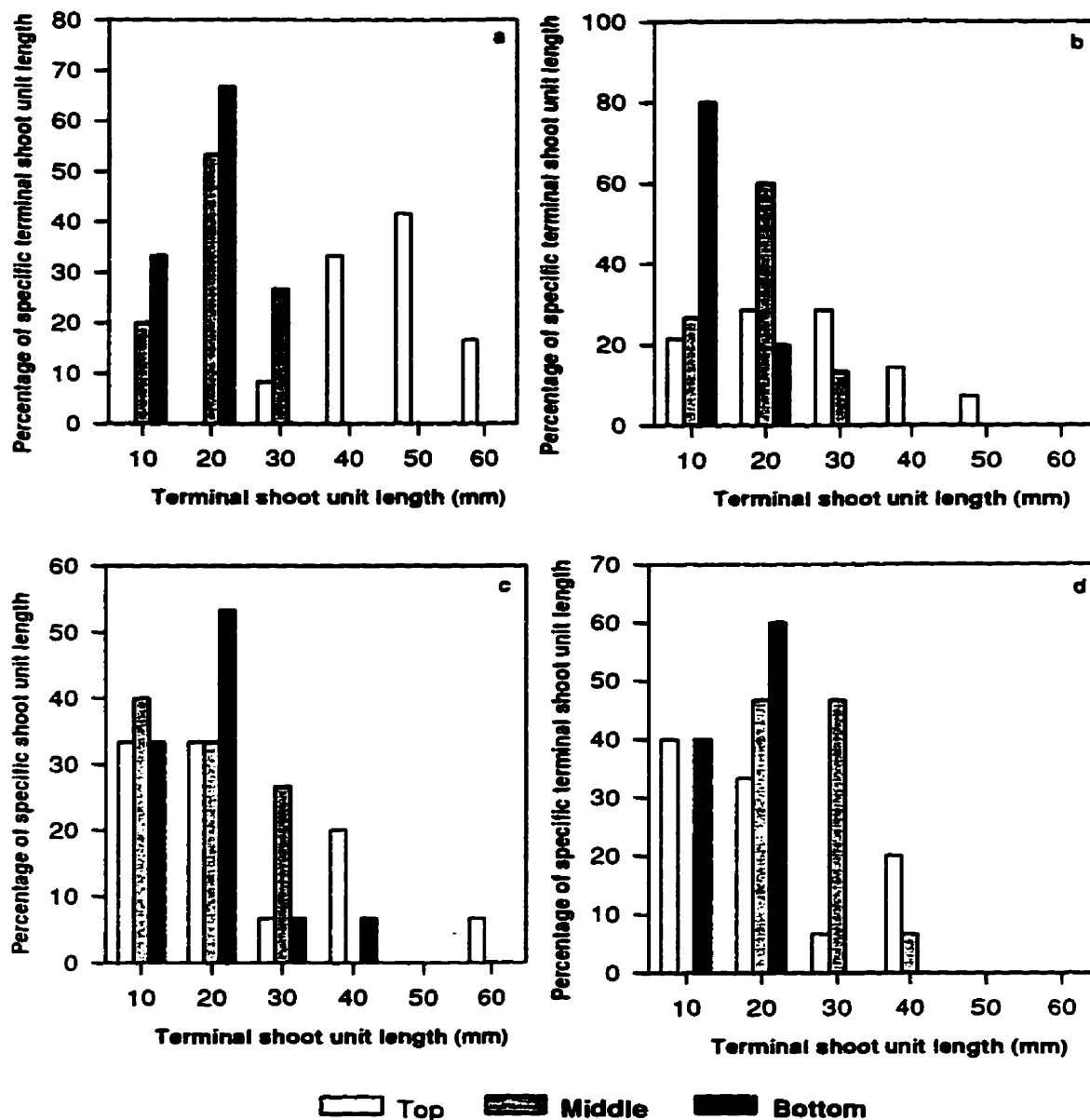
Fig. 1.16. Terminal shoot-unit length of shoots in the top, middle, and bottom of the crown. The numbers depicting each category represent a range of shoot-unit length; e.g., 0.1-10mm, 10.1-20mm, etc.. The number denotes the high point of the range. Chi-square tests of independence between terminal shoot-unit length and crown location. **a)** 10-year-old-trees (χ^2=43.57, P=0.001, n=42) **b)** 20-year-old-trees (χ^2=21.60, P=0.006, n=44) **c)** 50-year-old-trees (χ^2=21.39, P=0.002, n=45) **d)** 60-year-old-trees χ^2=9.62, P=0.292, n=45).

Table 1.5 The effects of aging on mean terminal shoot-unit length in each crown location.

Age-class	Crown location	Mean shoot-unit length (mm)	Standard deviation
10	top	41.83	7.92
10	middle	17.81	6.92
10	bottom	11.44	1.04
20	top	20.24	10.53
20	middle	13.21	4.95
20	bottom	7.78	3.35
50	top	19.45	14.19
50	middle	12.61	5.70
50	bottom	13.10	8.12
60	top	16.24	10.70
60	middle	20.92	6.33
60	bottom	10.26	3.53

Note: ANOVA indicated a significant ($P=0.001$) effect of age-class X crown zone on shoot-unit length.
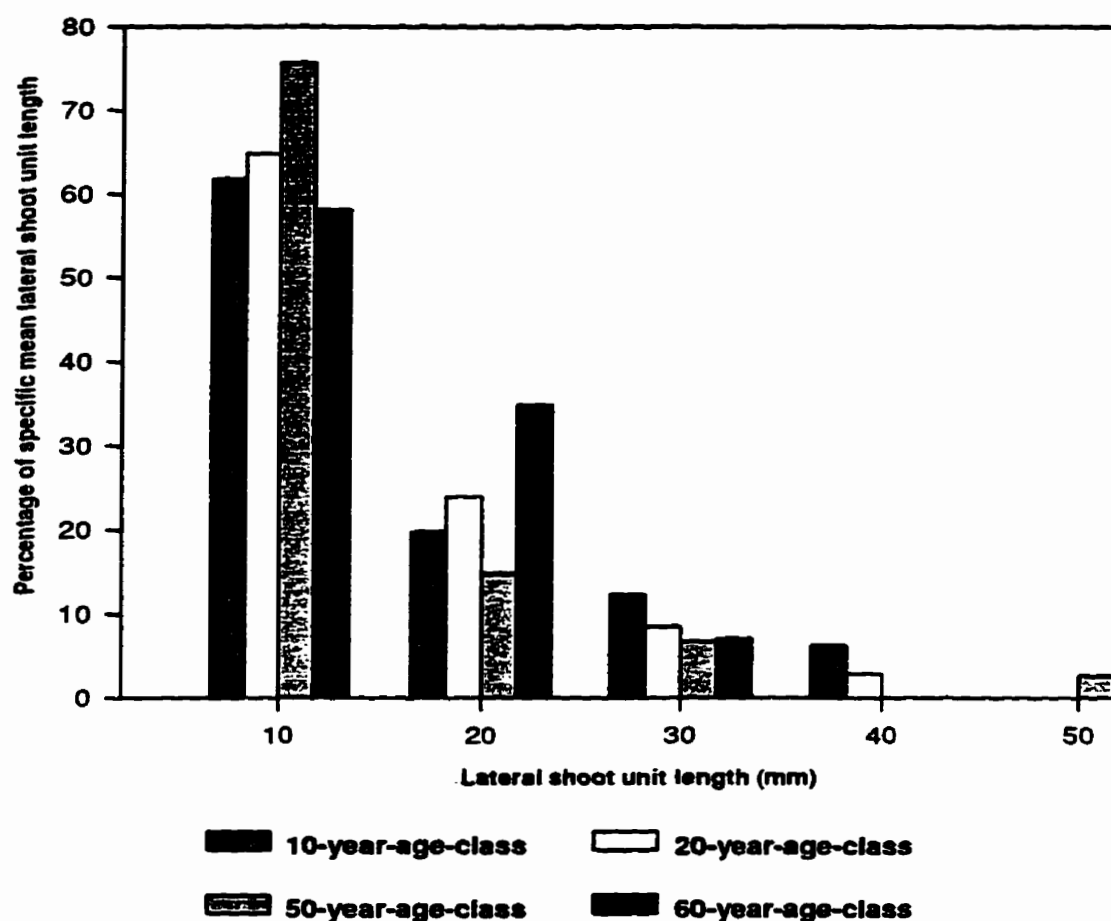
Fig. 1.17. Distribution of lateral shoot-unit length of shoots throughout the crown for the four age-classes. The numbers depicting each category represents a range of shoot-unit lengths; e.g., 0.1-10mm, 10.1-20mm, etc.. The number denotes the high point of the range. Because of the small number of samples in the 40 and 50 mm category they were combined in the 30 mm category for chi-square tests of independence between lateral shoot-unit length and age-class at the 5 % level of significance (χ^2=12.153, P=0.205).

the age-class of the tree (P=0.205) (Fig. 1.17). The ANOVA was highly not significant (P=0.9077) indicating that lateral shoot-unit length was not affected by the age-class of the tree. The range of lateral shoot-unit lengths was smaller than in the terminal shoots. Although the 10-year-old trees did not have the longest shoot-unit lengths (i.e., 50 mm category), they had the highest percentage in the 30 and 40 mm categories. In all four-age-classes, the 10 mm shoot-unit length category was the most frequent. The 60-year-old trees had the least variation in range of lateral shoot-unit lengths.

The means of lateral shoot-unit length are shown in Table 1.6. Similar to the terminal shoots, in the middle of the 60-year-old crowns, lateral shoot-unit length was greater than in the other two crown locations.

Table 1.6. Mean lateral shoot-unit length in each crown location.

Age-class	Crown location	Mean shoot-unit length (mm)	Standard deviation
10	top	13.19	9.39
10	middle	6.01	3.72
10	bottom	4.65	2.56
20	top	11.76	8.84
20	middle	9.55	4.75
20	bottom	6.46	2.51
50	top	10.32	8.28
50	middle	6.10	2.48
50	bottom	8.58	9.54
60	top	8.27	5.20
60	middle	10.58	6.12
60	bottom	7.19	6.07

Note: ANOVA, Age X crown location (P=0.0046)

Similar to terminal shoot-unit length, when crown locations were analyzed separately, it was found that lateral shoot-unit length was dependent on the age-class of the tree in the top crown location (χ^2=35.673, P=0.002). However, in the middle and bottom of the crown, lateral shoot-unit length was not dependent on the age-class of the tree (χ^2=11.638, P=0.234 and χ^2=15.693, P=0.74, respectively).

Fate of buds

The fate of buds on a shoot is dependent on the age-class of the tree (Fig 1.18). To utilize the maximum range of ages, measurements of lateral shoot production in the 3-year-old trees growing at the University of Manitoba were included in the sample (Table 1.7). In general there is a decrease in the number of lateral shoots as the tree ages. The trees growing at the University of Manitoba produced the greatest number of lateral shoots per parent shoot and the 60-year-old trees produced the fewest.

The potential of the tree to produce lateral shoots and the actual number which is produced are very dissimilar. In all four age-classes when lateral buds were dissected, a large percentage of the buds were vegetative (e.g., 60 % in 50-year-old trees) and had the potential to form lateral shoots (Fig. 1.18a). However, when actual measurements of the fate of buds were made on shoots in the crown after growth had ceased, there were considerably fewer lateral shoots present (e.g., less than 20 % in all age classes) (Fig. 1.18b).

The high proportion of buds in the unknown category (Fig. 1.18a) were missing or severely damaged by ash plant bug eggs (*Tropidosteptes amoenus* Reuter) which made it difficult to determine their potential fate. The high proportion of buds in the unknown category after shoots had grown out (Fig. 1.18b) occurred because only lateral shoots were scored; all others including inflorescences were not classified.
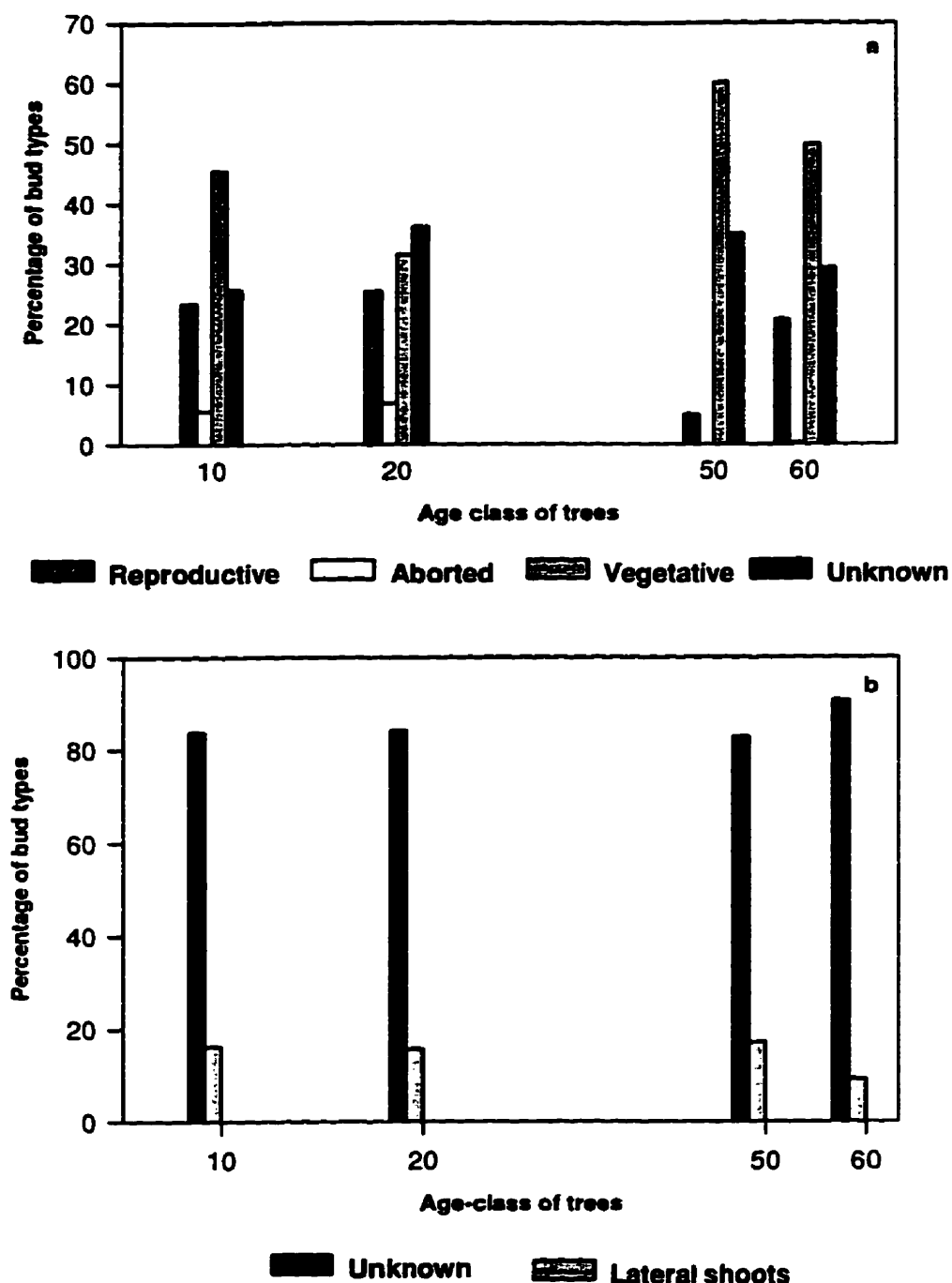
Fig. 1.18. The fate of buds on a shoot in the four age-classes of trees. Chi-square tests of independence between the fate of buds and the age-class. a) determined through dissections of lateral buds in 1994 (χ^2=155.7, P=0.001, n=1794) b) the actual fate of buds measured on shoots still present in the tree crown (χ^2=14.71, P=0.002, n=1876)

Table 1.7. The effect of aging on the number of buds which produced lateral shoots.

Age-class (years-old)	Percentage of buds producing lateral shoots (%)
3[a]	36
8[b]	18
10	16
20	16
50	17
60	9

[a] These values were obtained from trees growing at the University of Manitoba.
[b] These values were obtained from trees growing in experimental plot at Morden.

In all age-classes the fate of buds on a shoot were dependent on the position of the shoot in the crown (Fig. 1.19a-d). In all age-classes except the 60-year-old trees the proportion of lateral shoots per shoot was greatest in the top of the crown and decreased linearly towards the bottom of the crown. In the 60-year-old trees the proportion of lateral shoots in the top and middle of the crown was very similar.
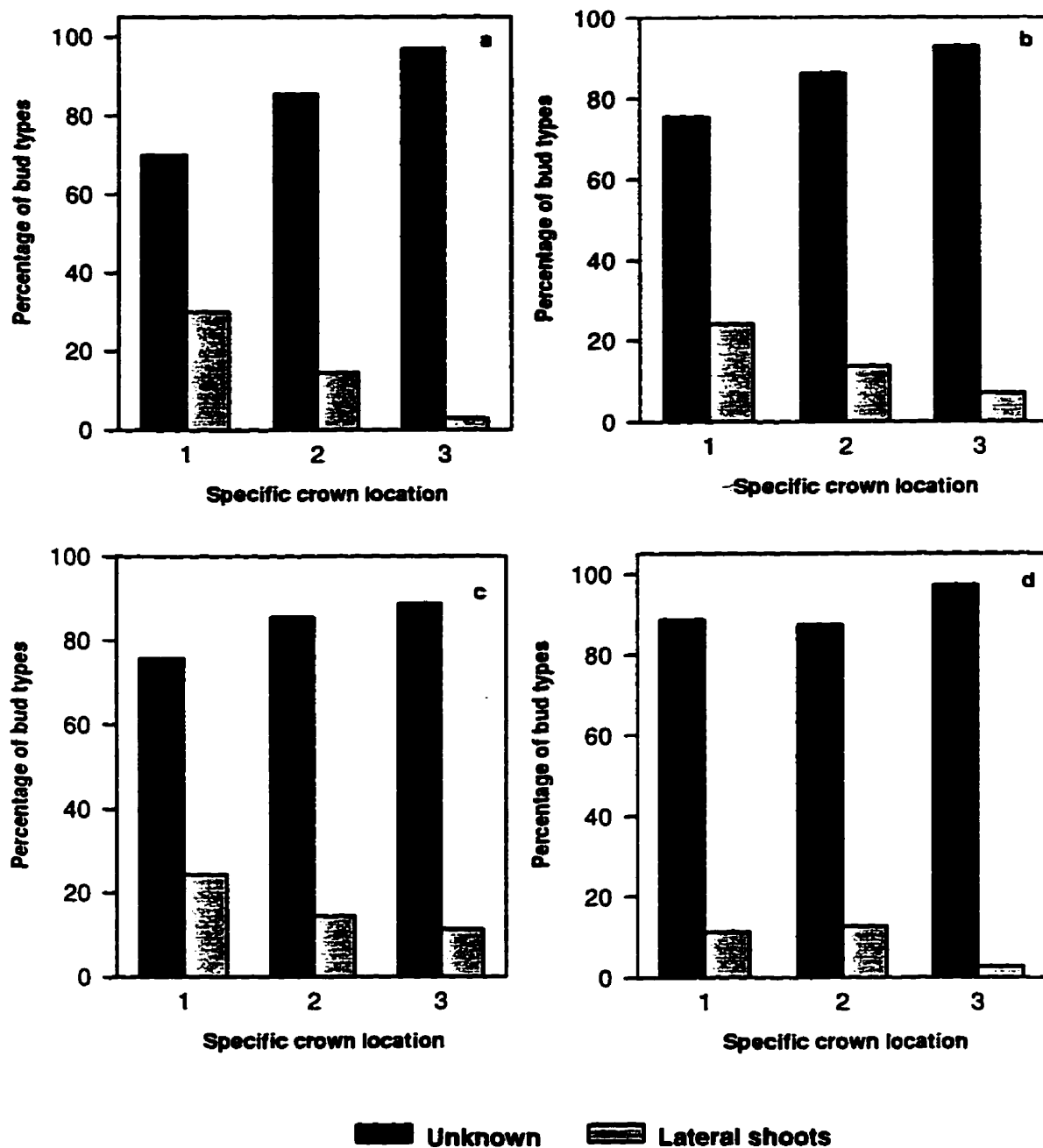
Fig. 1.19. The fate of buds on shoots in the top, middle, and bottom of the crown. Unknown buds could be inflorescences or aborted. 1=top, 2=middle, 3=bottom. **a)** 10-year-old-trees (χ^2=43.94, P=0.001, n=502) **b)** 20-year-old-trees (χ^2=18.26, P=0.001, n=466) **c)** 50-year-old-trees (χ^2=9.78, P=0.008, n=431) **d)** 60-year-old-trees (χ^2=10.41, P=0.005, n=468).

DISCUSSION

Shoot length is composed of two morphological characteristics, the number of shoot units and shoot-unit length. Differences in the number of shoot units per shoot were found between the different crown locations in *Fraxinus pennsylvanica*. For both the terminal and lateral shoots, the shoots in the top of the tree were more vigourous compared to shoots in the bottom or inside of the crown. This resulted in more shoot units per shoot. Previously it had been reported that shoot length decreased from the top to the bottom of the crown (Davidson and Remphrey, 1994). One explanation for the decrease in shoot length is that the number of shoot units per shoot decreased because of changes in PAR (light quantity) or the energy spectrum (light quality) which affects growth and morphogenesis (Kramer and Kozlowski, 1979).

Light is necessary for photosynthesis because it provides the energy for growth. Photosynthesis is affected the most when light is extremely limiting (Kramer and Kozlowski, 1979). In *Quercus acuta* and *Q. gilva* light intensities less than 30 and 10 % of full light, respectively could not sustain a shoot population (Koike, 1989). Shade intolerance was considered to be the cause of the limitations. Reductions in light intensity occur because of mutual shading. This results in zones of differing light intensity. Measurements of light intensity throughout the crown have been made in several species including peach (Baraldi *et al.* 1994), olive, apple, and cypress (Larcher, 1975), and

citrus (Kramer and Kozlowski, 1979). Measurements of light in the crown of *F. pennsylvanica* were made (Appendix B) revealing that light quantity decreased from the outside to the inside of the crown where the centre of the tree had the lowest light intensities. Light quantity was not equal throughout the crown and areas of high light intensity were surrounded by areas of low light intensity. Hashimoto (1990, 1991) has concluded that the light environment was the primary determinant factor of crown morphology and structure.

Internal physiological control mechanisms may affect the number of shoot units per shoot. For example, apical control may be an important factor. The trees at Morden in the experimental site #1 were only 8-years-old and the crowns were not very large. As a result the terminal buds in the top of the crown may still be able to exert control over shoot development in the inside of the crown. Also the inside of the crown is heavily shaded which strengthens apical control (Baraldi *et al.* 1994; Cline, 1991).

The number of shoot units per terminal shoot was not consistent for all age-classes between the top and bottom of the crown. Previously in *F. pennsylvanica* it was reported that shoot length decreased for 25-year-old trees from the top to the bottom of the crown (Davidson and Remphrey, 1990). Similarly in the 20-year-old age-class in the present study, the number of shoot units per shoot decreased from the top to the bottom. For terminal shoots the pattern weakens as the tree ages so that in the 60-year-old trees there were no

differences. Moreover, in the 60-year-old trees the number of shoot units per shoot was slightly greater in the middle of the crown compared to the top or bottom. Although not specifically studied, this increase in vigour may suggest reiteration (Hallé *et al.* 1978) or partial reiteration (Bell, 1994). Reiteration is the development of shoots outside the normal expression of the architectural model ultimately producing a replica of the original architectural model (Hallé *et al.* 1978). Partial reiteration only replaces part of the original model and involves the development of other axis rather than the main stem (Bell, 1994).

Physiological processes may change with age and affect the allocation of photosynthates or nutrients within the tree (Kramer and Kozlowski 1979). For example, it has been observed that apical control decreases with aging, resulting in less shoot growth because of greater competition for resources (Moorby and Wareing, 1963; Leopold, 1980; Wilson, 1989; Ritchie and Keeley, 1994). Increased stress in the top of the crown could be responsible for reduced apical control. Increased stress may occur because of the increased competition for nutrients between apices (Wareing, 1970). Also the distance of the shoot system to roots might affect the transport of photosynthates to the roots and root growth and inturn may affect shoot growth (Wareing, 1970). The combination of reduced apical control from the top of the crown on the middle of the crown combined with potentially more favourable conditions may lead to greater numbers of shoot units per shoot.

As the tree ages physiologically it has been determined that shoot vigour decreases (Ritchie and Keeley, 1994). In *Larix* (Ward and Stephens, 1994) and *F. pennsylvanica* (Remphrey and Davidson, 1992) measurements of decreased shoot length have been recorded. Fewer shoot units per shoot are produced in much older trees compared to young trees and may be the result of lost vigour. One possible explanation is that the nutritional or photosynthate level in the tree decreases (Yoder *et al.* 1994). In *Pinus contota* and *P. ponderosa* nitrogen in the leaves decreased as the tree aged and photosynthesis was reduced by 14 to 19% and 27 to 30% respectively from the young to the old trees (Yoder *et al.* 1994). The reduced rates of photosynthesis would result in less photosynthate available in the tree. Unfortunately Yoder *et al.* (1994) cautioned about the interpretation of the data stating that "these results do not provide a definite answer but instead fail to disprove the hypothesis that photosynthetic reductions are an important cause of growth decline with age". Alternately another possible explanation for aging is an increase in respiration rates, resulting in less efficient utilization (Hallé *et al.* 1978; Little, 1970; Yoda *et al.* 1965; Whittaker and Woodwell, 1967). However, their hypothesis did not completely explain the measured decreases in growth (Yoder *et al.* 1994). Nevertheless, decreasing photosynthate supplies result in less energy for shoot growth and development.

Neoformation has previously been identified in *F. pennsylvanica* in young trees up to 3-years-old (Davidson and Remphrey, 1994). Neoformation was not detected in any age-class of tree in the present study. This is consistent with findings by Remphrey (1989) where trees 25-year-old had completely preformed shoots. Therefore neoformation appears to cease after 3-years of age and before 10-years of age. Neoformation has been interpreted as a plastic trait which enables the tree to respond to current year conditions (Remphrey and Powell, 1984). Other factors such as location or environment, genetics, and the position of the bud in the crown can affect the amount of neoformation (Davidson and Remphrey, 1994). In the 3-year-old trees, there was less neoformation in the bottom compared to the top of the crown (Davidson and Remphrey, 1994). The decline in neoformation was suggested to be related to increasing structural complexity and increased nutrient competition.

The second morphological characteristic influencing shoot elongation is shoot-unit length. A decrease in shoot-unit length was observed in the clonal experiment from the top to the bottom of the crown for both terminal and lateral shoots. Shoot-unit length might be expected to decrease because of less photosynthate available in the interior of the crown leading to a reduction in shoot vigour (as indicated by the reduction in the number of shoot units per shoot). Shoot-unit length ultimately relies on the number and length of the cells present in the internode (Brown and Sommer, 1992). If photosynthate is

limiting, such as occurs in the interior of the crown (Kramer and Kozlowski 1979), then there may be fewer cells present in the internode and the length of the cells would be affected. This would result in a reduction in shoot-unit length. However in peach, shoot-unit length (internode length) increased significantly from the top to the bottom of the crown increasing from 1.7 to 2 cm, respectively (Baraldi *et al.* 1994). The suggested explanation for the results was that light quality in the interior was reduced causing etiolation (Baraldi *et al.* 1994). Etiolation is an increase in shoot-unit length under reduced light conditions usually under reduced R:Fr ratios (Smith, 1982). In previous studies of peach, shoot-unit length was found to decrease with reduced light intensities (Kappel and Flore, 1983). Therefore it was hypothesised that the increase in shoot-unit length in the inside of the crown was caused by etiolation from the reduced R:Fr ratios (Baraldi *et al.* 1994). In *F. pennsylvanica* shoot-unit length did not increase in the inside of the crown suggesting that other factors rather than just light quality affect shoot-unit length such as light quantity or apical control.

Unlike the number of shoot units per shoot, shoot-unit length throughout the crown was affected weakly by the age-class of the tree. Shoot-unit lengths were similar in the 20, 50, and 60-year-old trees. Therefore, the reduction in shoot length as the tree ages is more influenced by the decrease in the number of shoot units per shoot than the decrease in shoot-unit length. Shoot-unit

length decreases from the 10 to the 20-year-old trees but remains consistent after that.

Similar to the 8-year-old trees at site #1, in the 10, 20, and 50-year-old trees shoot unit-length decreased from the top to the bottom of the tree. In the 60-year-old trees shoot-unit lengths in the middle of the tree were longer than in the other two crown locations, corresponding to the increase in the number of shoot units in this location. Conditions may be more favourable for growth in the middle of the crown compared to the other two crown locations or there may be other reasons.

The fate of buds in an important aspect of tree development. The ratio of vegetative to reproductive buds determines the rate of development of the crown (Jones and Harper, 1987; Maillette, 1992). In *F. pennsylvanica* the distribution of buds along a shoot is similar for all shoots with the greatest concentration of lateral shoots near the tip, inflorescences in the middle, dormant buds usually located in the middle or tip of the shoot, and aborted buds near the base. This pattern of lateral bud development is called acrotony (Champagnat, 1978). The proportions of inflorescences, lateral shoots, and aborted buds along a parent shoot changes in relation to the position of the shoot in the crown, the number of shoot units per shoot, and shoot length. However it is not known what affect the sex of the tree may have on these relationships.

The number of shoot units per shoot and overall shoot length are correlated and, as would be expected, had a similar effect on the fate of buds. As the number of shoot units per shoot or shoot length increases the number of lateral shoots increases and the number of inflorescences decreases. The fate of buds also changes between different locations in the crown. Generally the percentage of lateral shoots and inflorescences decreases and the number of aborted buds increases from the top to the inside of the crown. Similarly in peach there were half as many flowers per m^2 and 50% fewer lateral shoots in the bottom compared to the top of the crown (Baraldi *et al.* 1994). The suggested explanation for the decrease was that decreased R:Fr ratios affected the phytochrome system affecting the fate of buds (Baraldi *et al.* 1994). In apple it has been shown that different R:Fr ratios "played a major role in determining the number of flowers and vegetative buds" (Rossi *et al.* 1997). This would imply that reduced photosynthetic rates does not alter the fate of buds. This would be consistent with others who have confirmed that low rates of photosynthesis due to low light availability do not regulate bud differentiation (Marini and Sowers, 1990; Baraldi *et al.* 1994). Although light quality was not measured in the present study, based on the observations from other species it is probable that in *F. pennsylvanica* there is a reduction in R:Fr ratios in the centre parts of the crown and this may alter the proportion of buds developing into inflorescences, lateral shoots, and aborted buds, and warrants further

study.

Aging also affects the fate of buds, often resulting in a decrease in the number of lateral shoots produced (Remphrey and Powell, 1987; Greenwood *et al.* 1989). In *F. pennsylvanica* as the tree ages there was a dramatic decrease in the number of buds that produce lateral shoots. Only about one-third of the buds produce lateral shoots in older trees compared to two-thirds in very young trees. Older trees have been found to have an increased propensity to flower (Zimmerman *et al.* 1985; Greenwood, 1984). In lateral flowering species such as *F. pennsylvanica*, this removes potential sites where lateral shoots will form and reduces branching. Buds dissected from 50 and 60-year-old trees had the greatest proportion of buds with the potential to form lateral shoots; however, a higher proportion of the buds aborted compared to the younger trees. The overall reduction in lateral branching may be related to decreased vigour and fewer shoot units per shoot. In the 8-year-old clones, fewer shoot units per shoot and shorter shoots were found to produce fewer lateral shoots. Therefore as the tree ages and shoot vigour is lost, fewer shoot units per shoot are produced (shorter shoots) leading to a reduction in lateral shoot production.

In older trees the reduction in lateral shoot production is still evident from the top to the bottom of the crown. In the 60-year-old trees the top and middle produced similar numbers of lateral shoots but the bottom had the fewest lateral shoots. This may suggest a trend towards reiteration in the

middle of the crown in the older trees.

In the clonal experiment the position of the bud around the shoot had no effect on the fate of buds. In *F. pennsylvanica* lateral buds are opposite and occur in pairs (Remphrey, 1989) and both buds usually had the same fate. From field measurements and bud dissection, each pair of buds were the same type. However when lateral shoots are produced they often differ in shoot length even though both shoots arise at the same node. In *F. pennsylvanica* lateral shoot length has been found to be dependent on the position of the bud around the shoot (C. Davidson personal communication).

In general the position of the shoot in the crown affects its architecture. Similarly, as the tree ages shoot architecture is altered. Much of the alterations in shoot architecture seem to be attributable to the effects of the amount of photosynthates available to for tree for physiological processes controlling growth and development. Variations in shoot development influences the development of crown architecture.

Chapter 2

The Effect of Reduced Quantities of Photosynthetically Active Radiation on

Fraxinus pennsylvanica Growth and Architecture

ABSTRACT

The quantity and quality of light have significant effects on tree growth and architecture that can be highly variable depending on the shade tolerance of the species. A study was conducted to determine the effect of decreased intensities of photosynthetically active radiation (PAR) on the growth and architecture of green ash (*Fraxinus pennsylvanica* var. *subintegerrima* (Vahl) Fern.), a moderately shade tolerant species, with a view to incorporating such information into a simulation model. Twenty-four seedlings were planted in each of the 5 shade treatments (0, 60, 80, 92, and 96 % shade, respectively). Measurements made over a two-year period revealed that with increasing shade there was generally a reduction in leaf thickness, leaf biomass, leaf numbers, internode length, shoot growth, branching frequency, lateral shoot growth, stem diameters, and above ground total tree biomass with increasing shade. However, in the moderate shade levels, there were increases in leaf numbers, overall shoot length, and branch numbers. The overall effect of heavy shading was to produce a tree with little height growth and a very poorly developed crown.

INTRODUCTION

Many aspects of tree growth and development are influenced by the exposure of trees or parts of trees to sunlight (Jackson and Palmer, 1977). Factors such as light quantity (intensity), light quality (wavelength), and duration of exposure (photoperiod) must be considered for their effect on tree growth and development (Kozlowski, 1971). Natural light is the visible part of the energy spectrum that is emitted by the sun and is composed of wavelengths of light between 400 and 700 nm (Kramer and Kozlowski, 1979). These wavelengths are important to the plant because this energy is used in photosynthesis. Light quantity is a measure of the total amount of energy useable in photosynthesis, contained within a photon of light (Kramer and Kozlowski, 1979). Changes in light quantity affect rates of photosynthesis, especially under reduced light intensities. Under low light conditions photosynthesis has been shown to be directly proportional to light intensity (Shirley, 1929).

Photosynthesis is a process where carbon dioxide and water, in the presence of light, results in the production of carbohydrates, oxygen, and water in the chloroplast (Raven *et al.* 1986). Carbohydrates are important because they are used for plant development and maintenance of tree structure. After light has passed through the canopy of a tree there is a reduction in the amount

of energy useable in photosynthesis and an alteration in light quality. Typically, 90 % of the wavelengths between 400 and 700 nm are absorbed by a leaf (Lee, 1985). The remaining 10 % of the light is transmitted through the leaf and becomes enriched with red light.

Differences in light quality result in morphogenic changes in the tree's architecture. Differences in the red to far-red $(P_{fr}:P_r)$ ratio are most often associated with inducing morphogenic changes in shaded trees (Smith, 1982). Reductions in the R:Fr in woody plants may in general result in increased shoot unit length (etiolation), increased leaf petiole length, reduced leaf area, increased stem dry weight, reduced branching, changes in chlorophyll content, and nitrogen reductase activity (Smith, 1982).

One of the difficulties in studying the effects of shade has been to separate the effects caused by changes in light quantity and light quality. In general, a shade cloth that can limit light quantity or quality has been used (Lee, 1985). These studies have focused on the effects of reduced light intensity on tree architecture. The following general observations have been reported: leaves become thinner, broader, and oriented more horizontally (Mc Millen and Mc Clendon, 1979; Gottschalk, 1994; Luken *et al.* 1995), decreased lateral branching (Jackson and Palmer, 1977; Steingraeber, 1982; Gottschalk, 1994), general reductions in above ground biomass (Mc Millen and Mc Clendon, 1979; Gottschalk, 1994; Luken *et al.* 1995), decreased shoot unit length (Marler *et al.*

1994), decreased number of shoot units per tree (Loach, 1970; Cornelissen, 1993; Gottschalk, 1994; Luken *et al.* 1995), and an increase to a decrease in shoot length (Jackson and Palmer, 1977; Wilson and Kelty, 1994). These studies generally provided good information, but few attempted to integrate them into the overall architecture of the tree. For example, although shoot unit length was measured in *Carambola* (Marler *et al.* 1994) it is difficult to extrapolate its effects to the overall architecture of the tree. Currently little information is known about the effect of shade on the architecture of *Fraxinus pennsylvanica* var. *subintegerrima* (Vahl) Fern. There have been studies of leaf thickness (Wylie, 1951) and leaf angle (Mc Millen and Mc Clendon, 1979) but there is no information on shoot and other leaf characteristics and on tree biomass production. Hence, the objective was of the present study was to determine the effects of reduced levels of PAR, through the use of shade cloth with various shade ratings, on the growth and architecture of *F. pennsylvanica* seedlings grown in the field.

MATERIALS AND METHODS

Experimental Design

An experiment to evaluate the effects of artificial shading was established on block 25 at the Department of Plant Science Experimental Site on the grounds of the University of Manitoba. Three-hundred (300) 2-year-old green ash *Fraxinus pennsylvanica* var. *subintegerrima* seedlings were obtained bare root from the PFRA Shelterbelt Center in Indian Head, Saskatchewan. The trees were visually graded on the basis of stem caliper and the number of stems. The largest and smallest caliper trees, along with multi-stemmed trees were culled and used as guards (Pearce, 1976). The remaining trees were used as the experimental trees.

The plot was laid out in a randomized design with 5 levels of shading. In total, 24 trees were used in each level of shade. The trees were grown in 5 different light regimes, using shade cloth applied over metal frames to create a tent 3 m wide X 4.8 m long X 2.4 m high (Fig 2.1). The shade cloth was rated at 60, 80, 92, and, 96 % shade. These values were chosen based on previous work by Kramer and Decker (1944) that showed the greatest effects of shade on photosynthesis and growth occurred when the leaves were heavily shaded. Trees were also grown in full sun as controls. The 60 % shade cloth was green and composed of a different material than was used in the other treatments.

Fig. 2.1. The tents housing experimental trees under various levels of shade located on block 25 at the University of Manitoba. From back to front 60, 92, 96, and 80 % shade. Control treatment is not shown. The trees visible outside the tents are guard trees. July 1995, W.R. Remphrey.

The shade cloth for 80, 92 and 96 % shade was called Sudden Shade™ and was manufactured by the Dewitt Company in Winnipeg, Manitoba. The material was sewn together by Winkler Canvas in Winkler, Manitoba. To achieve the desired level of shading two layers of shade cloth had to be sewn together. The exact composition used to achieve the desired level of shading for the three highest shade levels is shown in Table 2.1.

Table 2.1 Different strengths of shade cloth used to create the desired level of shading.

Percent shade	Strength of shade cloth used	Colour
80	1/2 80 % and 1/2 60 + 60 %	black and green
92	60 % + 80 %	black
96	80 % + 80 %	black

The shade cloth was applied in the spring before bud break and removed in the fall after growth ceased. A series of measurements was taken inside the tents to confirm that the shade cloth was producing the calculated amount of shade and to determine if light quality was affected.

Planting and cultural maintenance

The soil type where the trees were planted was a heavy clay which was roto-tilled before planting. Spatial limitations resulted in the experimental trees being located inside of the tents with guard trees around the outside. Guards were also planted around the control trees. Guard trees were planted around each plot in order to prevent edge effects from occurring. Edge effects occur because trees on the edge of the plot experience less competition and have access to more nutrients and water, which could result in better tree growth. In the control plot, 24 trees were planted in a 2 by 12 grid at 75 cm spacing. Trees in the other four light regimes were planted in a 4 by 6 grid at 75 cm spacing.

After planting in 1994 all lateral buds were removed except for one which was allowed to become the height growth increment (HGI) because the terminal bud had been removed from all but three trees. Any other lateral buds that began to grow throughout the growing season were subsequently removed in the first year in order to keep the trees to one HGI with no lateral shoot growth. In 1995 the trees were not disbudded which allowed the lateral shoots to develop. All trees were watered at the time of planting in 1994 with no further watering necessary because the summer rainfall was above average. In 1995, all trees were watered once because very little rainfall had occurred through all of July and most of August.

There is a possibility that shade cloth may alter the microclimate within the tents. Therefore, measurements were made of temperature, humidity, and soil moisture in order to fully characterize conditions within the tents. No attempts were made to control conditions inside the tent because responses in this experiment to shade are actually responses to all environmental factors altered through shading. The plots were kept weed free through cultivation.

Insect problems occurred in both years and were treated as necessary. Ash flower gall mites (*Ercophyes fraxiniflora* Felt) infected some trees with one tree severely damaged and subsequently removed from analysis. In 1995 the ash plant bug (*Tropidosteptes amoenus* Reuter) caused some damage and was controlled using an insecticide (Seven™). The damage to leaves was not severe.

In 1994, 20 of the 24 control trees were browsed by deer. This resulted in the loss of the apical meristem of these trees. Nevertheless, newly formed lateral buds burst and the most distal lateral was allowed to form the height growth increment. As a precaution against any further deer damage a permanent fence was installed prior to the 1995 growing season.

A series of measurements was made in both 1994 and 1995 (Fig. 2.2 and Table 2.2). Because the trees were established in 1994, only a limited number of measurements were made in that year. Measurements of HGI growth were made weekly while the tree was actively growing. All other measurements were made after growth had ceased.
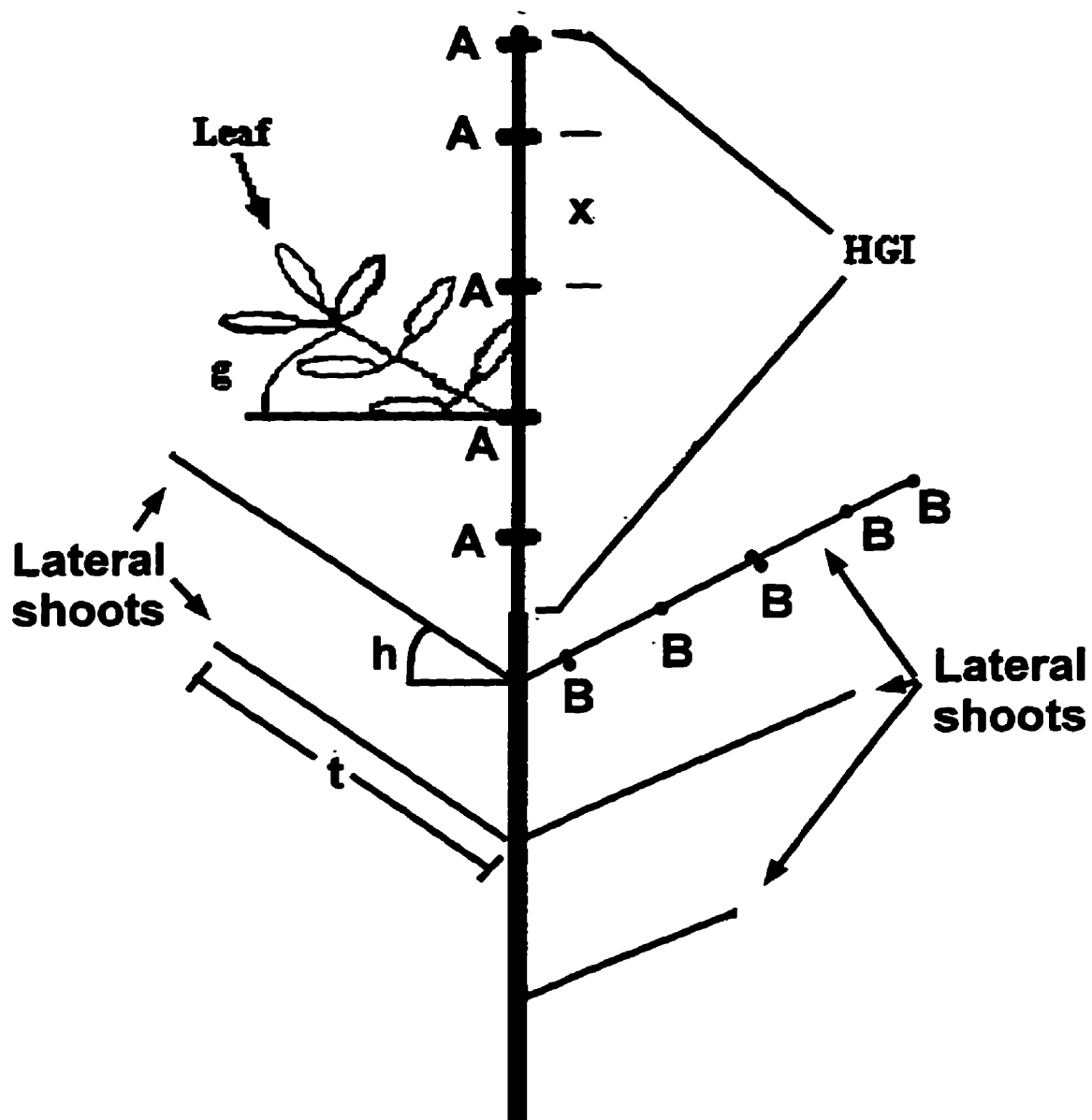
Fig. 2.2. Diagram shows the various measurements made on each tree in 1994 and 1995. A=1 pair of shoot units, all A's added together are the total number of shoot units per shoot. B= shoot unit length. C= 1 lateral shoot unit, all C's added together are the total number of lateral shoot units. D= total lateral shoot length. E= lateral shoot angle of elevation. F= leaf angle of elevation. G= 1 lateral shoot, all G's added together are the number of lateral shoots per tree.

Table 2.2 Specific measurements made and the year when the measurements were made.

Measurements made	1994	1995
Leaf thickness		✓
Total leaf area per tree	✓	✓
Leaf shape and number of leaflets	✓	✓
Number of leaves per tree	✓	✓
Number and length of shoot units per HGI	✓	✓
Number of shoot units per lateral shoot		✓
Total length of HGI	✓	✓
Lateral shoot length		✓
Leaf angle of elevation		✓
Total cumulative shoot length	✓	✓
Number of lateral shoots		✓
Lateral shoot angle of elevation		✓
Basal caliper	✓	✓
HGI caliper and 1995 caliper increment		✓
Total tree, shoot, and leaf biomass		✓
Soil water content		✓
Light quantity	✓	✓
Light quality		✓
Temperature in each light regime		✓
Relative humidity in each light regime		✓

<u>Description of Each Tree Characteristic Measured</u>

Shoot characteristics

The length of the HGI to the nearest millimeter was measured in 1994 and 1995 for each experimental tree (Fig. 2.2). The length of all lateral shoots was measured from the point of attachment to the main stem to the base of the terminal bud in 1995 and recorded to the nearest millimeter (Fig. 2.2). Total tree height was measured from soil level to the base of the terminal bud on the HGI and was recorded to the nearest millimeter in 1995. Weekly measurements were made of HGI growth and recorded to the nearest millimeter

The number of shoot units was recorded for the HGI in 1994 and 1995 and for the lateral shoots in 1995. The length of each shoot unit to the nearest millimeter was recorded for the HGI but not for the lateral shoots (Fig. 2.2). The mean shoot unit length of the lateral shoots had to be calculated by using the length of the lateral shoot divided by the number of shoot units for that shoot.

The number and position of the 1995 lateral shoots on the HGI were recorded (Fig. 2.2). The position of the lateral along the HGI corresponds to the specific shoot unit number in the sequence where the lateral shoot arose. The elevation angle of each lateral on the main stem was measured for every tree and recorded to the nearest degree. The angle of elevation was measured from the horizontal to the lateral shoot and recorded whether it was above or below the horizontal. Measurements of the angle were obtained with a carpenters' tool for calculating angles and roof pitch with respect to gravity.

The caliper (or diameter) of the HGI in 1995 was measured using electronic calipers 1 cm above the base of the shoot. Caliper measurements were also made at the base of the tree at a spot marked at the time the trees were planted. Measurements were made when the trees were planted and each September after that. The caliper increment from year to year was calculated by subtracting the previous years caliper measurement from the current year caliper.

Leaf characteristics

Ten leaflets from the HGI were randomly chosen from trees in each light regime to determine lamina thickness. Three different methods were used to measure lamina thickness in order to determine if each test would produce the same results and could be used to measure lamina thickness. Sections of 1 cm^2 were removed from each leaflet and the thickness measured to the nearest hundredth millimeter using a pair of electronic calipers, being careful not to crush the leaf. The leaf sections were dried and the thickness measured again using calipers to determine whether the results were similar to those of the fresh measurements. The leaf sections were also weighed to determine if this method would produce similar results and was a valid test of lamina thickness. All three tests produced the same results making it possible to measure lamina thickness with any of the previous methods. The measurements of fresh lamina thickness were used for analysis.

For detailed measurements of leaf characteristics and biomass, 6 trees in each light regime were randomly chosen from alternating trees and rows

because the removal of these plants would increase space between trees. The trees were removed in September 1995. Leaf angle of elevation was measured for all the leaves on the HGI in each light regime. The angle of elevation for each leaf on the HGI was measured in the same way as for lateral branches.

The total number of leaves per tree was measured by counting all the leaves on the 6 trees removed from the plot. From each tree all the leaves were removed and pressed. Total leaf area per tree was measured to the nearest cm^2 using a Li-cor 3100 area meter.

Biomass measurements

The trees used to measure total leaf area per tree were also used for biomass measurements. Leaf biomass was determined by measuring the mass of the dry leaves that were used to determine total tree leaf area. Trees were cut off at ground level and transported to the lab. The roots were left in the ground while the above ground part of the tree was allowed to dry for several months and then weighed. The mass of the leaves and the mass of the tree shoot structure were summed to produce a measure of the total above ground tree biomass. The mass of the leaves was divided by the total tree biomass to provide the leaf-weight ratio (Jackson and Palmer, 1977; Loach, 1970) and the shoot-weight ratio was calculated by dividing the cumulative shoot biomass by total tree biomass. These values were calculated in order to determine how the distribution of assimilates within the tree changes in different light conditions.

Environmental Measurements

Light intensity readings were obtained in each tent after the initiation of the experiment to verify the shade cloth ratings. A Li-Cor quantum light sensor model Li-185B was used for all measurements. In late July of 1994, one measurement was made above each tree. In total 24 measurements were obtained, averaged and used to determine the variability within the tent at solar noon. Measurements were also made of light intensity over the course of a day to determine if the angle of the sun in the sky affected the amount of shading that was occurring in the tents. Measurements were obtained in early July starting at 8 A.M. and every hour after that until 4 P.M. with one measurement in each light regime. The measurements were compared to readings in full sun to ensure the accuracy of the shade material.

Spectral quality of light was measured in each tent using a spectroradiometer in the visible light range in order to fully characterize the light conditions inside the tent and to determine if the different shade materials affected light quality. Measurements were made between 11 A.M. and noon on several different days and repeated twice in each light regime in early August 1996. Measurements of the light spectrum were started at 400nm and made every 12.5nm after that until 750nm. The red to far red ratio was calculated using readings at 660nm and 730nm. These values were compared to readings in full sun to determine the effects of the shade material on light quality.

Temperature and relative humidity measurements were made on an average August day in 1995 under clear skies. One measurement was made in each light regime and was made each hour starting at 8 A.M. until 4 P.M. A

sling psychronometer was used to measure humidity. The reading from the dry thermometer was used as a measure of the temperature in each light regime.

It was hypothesized that there may be differences in moisture supply between the tents and control plot. The hypothesis was based on observations that the trees inside the tent probably received less water than the control plot because the tents prevented rain water from reaching the trees. It was also noticed that the soil remained wet longer in the tents compared to the control plot. Therefore it was necessary to determine if the reduced evaporation in the tents could compensate for the reduced rainfall. If the reduced evaporation compensated for reduced rainfall similar moisture levels would be found in each light regime.

Two soil samples were collected in the plot of each light regime. Samples were taken between trees in the middle of the plot and beside the tree in the number 17 spot in the grid of each plot in order to characterize the mean water content of the plot. In mid August, a soil core sampler was used to collect samples at depths of 0, 10, 20, 40, 60, 80, and 100 cm, respectively. More measurements were concentrated in the upper 20 cm of the soil because this is where most of the roots were located in these young trees. Sampling to a depth of 100 cm was necessary to fully characterize the moisture profile within each plot. After collection, the samples were bagged and weighed immediately to determine the mass of the wet soil. The samples were then dried in an oven for 24 hours at 106° according to standard practices, weighed again and the dry soil mass subtracted from the wet soil mass to obtain a measure of the weight of the water. The mass of water in the soil divided by the mass of the oven dry sample

of soil multiplied by 100 provided a measure of the gravimetric water content of the soil.

Statistical Analysis

Analysis of the data was accomplished using regression with Statistical Analysis Systems (SAS Institute Inc. 1996). Both linear and quadratic regressions were used and the regression which best fit the data was selected. The independant variable was the rated level of shading for each light regime and the dependant variable was the morpohmetric characteristic being examined. A mean value of each morphometric characteristic was calculated for each light regime and used in the regression calculation.

RESULTS

<u>Environmental measurements</u>

Light intensity and spectral quality

In general the shade cloth produced the amount of shade claimed by the manufacturers (Table 2.4). Nevertheless, some variation existed within the tents between the calculated and actual amount of shade. The mean of the readings in the 60% shade tent was the closest to the expected but the readings were somewhat variable. The means in 92 and 80% shade tents were not as close to their expected ratings as in the 60 and 96% rated shade tents. The larger deviation in 80% shade might have occurred because several different pieces of shade cloth, of varying strength were used in its construction.

The shade cloth did not affect light quality. Although the curves appear different the slope of the line at 660 and 730nm is similar (Fig. 2.3). The R:Fr ratio was not significantly different in the shade tents compared to open grown trees (P=0.45) (Table 2.3). Light quality was reduced by the shade cloth equivalently across the spectrum (Appendix C- G).

Soil moisture

The differences in soil water content between the shade levels were significant (P = 0.02). There was a trend towards an increase in soil moisture content as shade increased (Table 2.4).

Table 2.3 Mean percentage of shade (± standard deviation) and the ratio of R:FR in each light regime.

Shade cloth	Percentage of shade[1] (%)	R:FR ratio[2]
0	0	$1.572 \pm 0.15a$[3]
60	59.46 ± 3.15	$1.575 \pm 7.07 \times 10^{-3}a$
80	83.50 ± 5.32	$1.452 \pm 0.12a$
92	95.92 ± 2.04	$1.64 \pm 0.16a$
96	97.38 ± 2.02	$1.68 \pm 0.32a$

[1] Measured in 1995. Based on relative light intensity measurements of light inside the tent compared to light outside the tent. n=24 readings per plot.
[2] Measured in 1996. Based on light quality measurements at 660 and 730 nm (after Smith, 1982). n=2 readings per plot.
[3] Means with the same letters are not significantly different (LSD, P=0.05).

Table 2.4 Mean gravimetric water (± standard deviation) present in the soil in each light regime.

Percentage of shade	Gravimetric water content (%)
0	$24.93 \pm 4.77c$[1]
60	$27.13 \pm 3.22bc$
80	$27.70 \pm 6.05abc$
92	$31.46 \pm 7.79a$
96	$30.85 \pm 6.93ab$

[1] Means followed by the same letter are not significantly different (LSD, P=0.05). n=2 samples per plot at 0, 10, 20, 40, 60, 80, and 100cm depth.
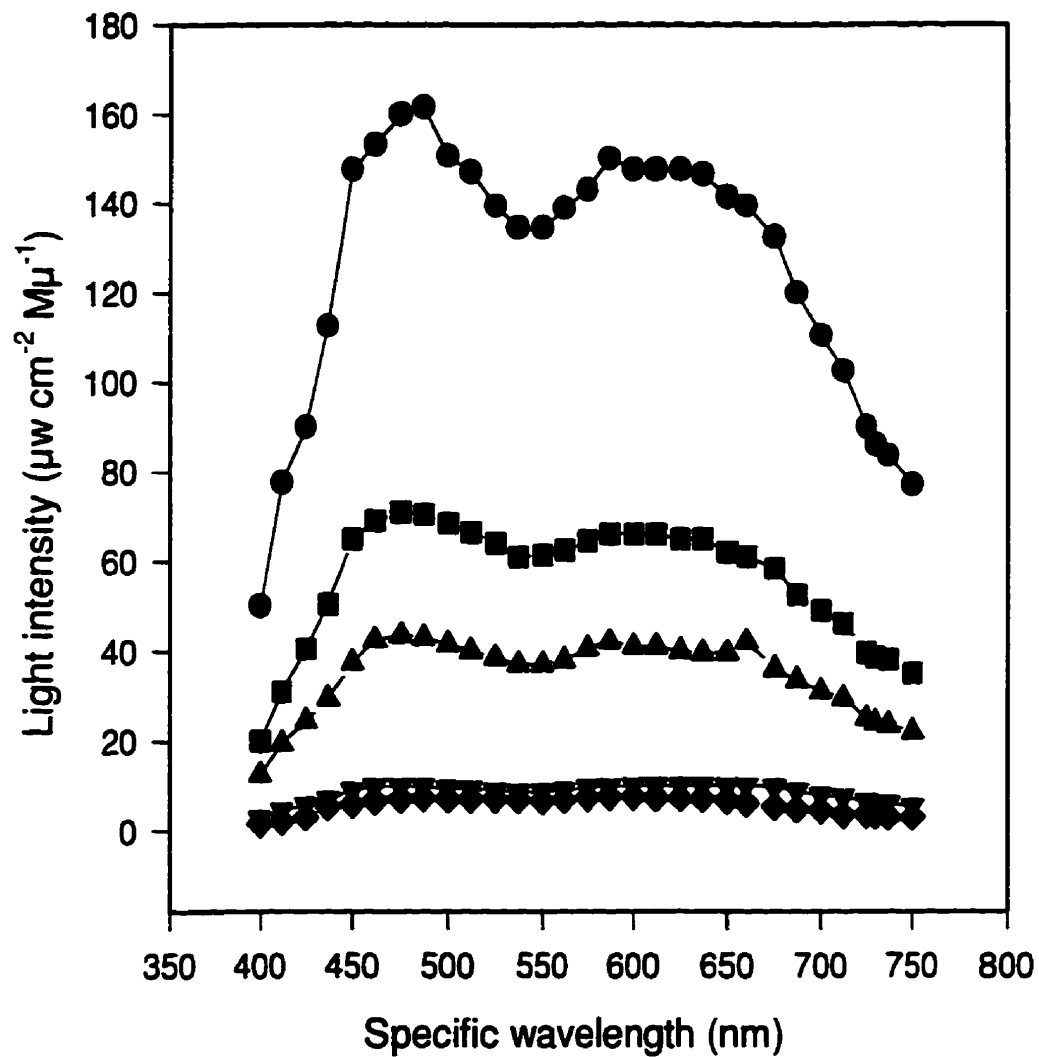
Fig. 2.3 Alteration of the spectral distribution of light inside each light regime.
●=0% shade, ■=60% shade, ▲=80% shade, ▼=92% shade, and ◆=96% shade.

Temperature and relative humidity

In general, the differences in temperature between the shade levels were not very great at any time of day (Table 2.5). The differences in relative humidity were larger, with the shade cloth leading to an increase in humidity (Table 2.5).

Table 2.5 Air temperature (°C) and relative humidity in each light regime measured over an 8 hour period in August 1995.

Time		Shade				
		0 %	60 %	80 %	92 %	96 %
0800	Temp. °C	22	23	23	23	22
	RH	86	87	87	87	91
1000	Temp. °C	25	28	27	26	26
	RH	72	73	76	80	80
1200	Temp. °C	33	31	30	30	30
	RH	62	64	70	68	64
1400	Temp. °C	33	32	31	32	31
	RH	59	62	65	65	68
1600	Temp. °C	33	32	31	32	32
	RH	62	65	65	68	68

General HGI Characteristics

Leaf characteristics

There were differences in mean leaf thickness between the different levels of shade. Leaves grown in full sun were thicker than shaded leaves and there was a strong non-linear quadratic relationship between shading and leaf thickness (Fig. 2.4).

There were also differences in the mean leaf angle of elevation between shade levels (Fig 2.5). The control leaves were oriented at a greater angle above the horizontal than leaves in 60, 80, 92, and 96% shade which became progressively more horizontal. The most heavily shaded trees had leaves oriented very close to horizontal.

Total length

The results for 1994 and 1995 were very different. In 1994 the control trees had the longest HGIs while the heaviest shaded trees were the shortest. Mean HGI length decreased as the percentage of shade increased and the relationship was strongly quadratic (Fig. 2.6a). In 1995 the relationship was also non-linear and was reasonably well represented by a quadratic regression. However, in this cases the trees in 60 and 80% had relatively longer HGIs compared to the other shade levels including the controls (Fig. 2.6b). Moreover, the HGIs of trees grown in 92 and 96% shade were considerably shorter than the other shade levelss.
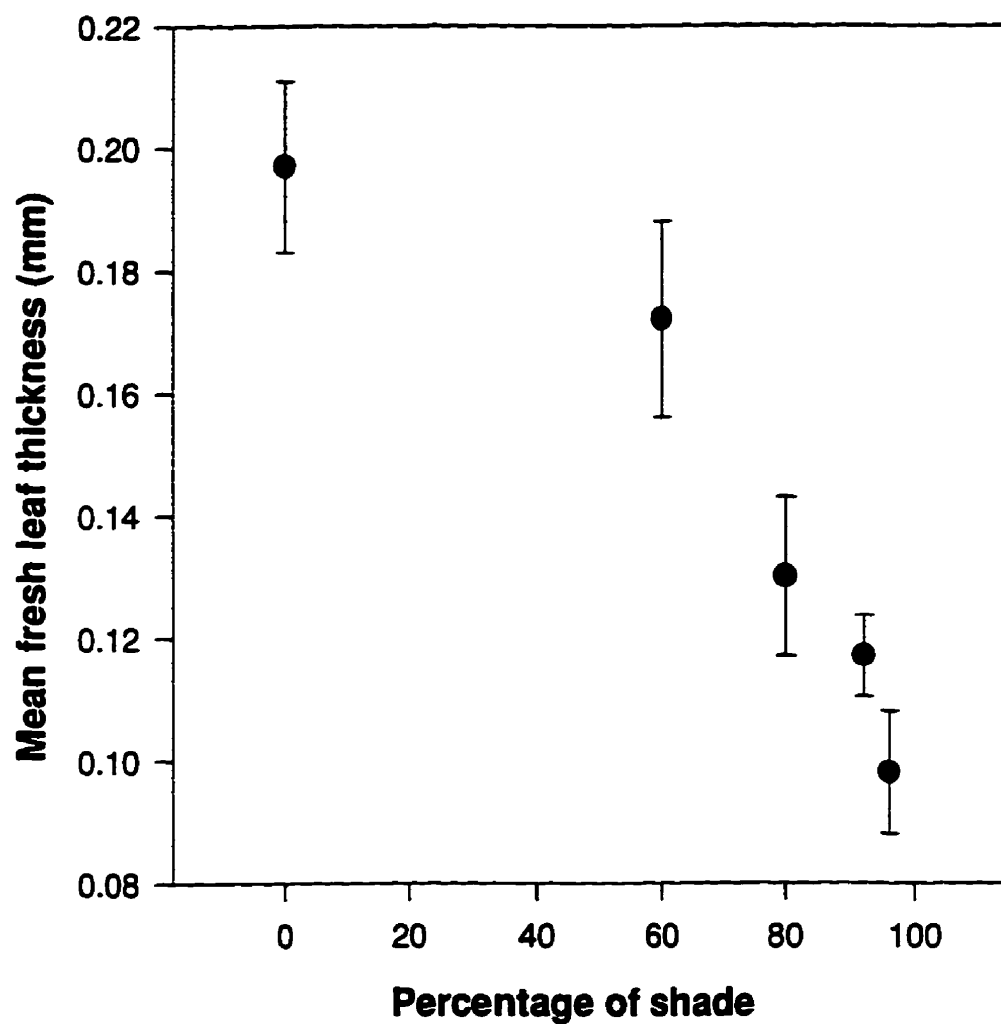
Fig. 2.4. The effect of shade (X) on mean leaf thickness (Y) in 1995. Vertical bars show standard deviation; n=20 leaves for all treatments. Y=0.1967 + 0.000464X - 0.000015X^2 (P=0.015, r^2=0.97).
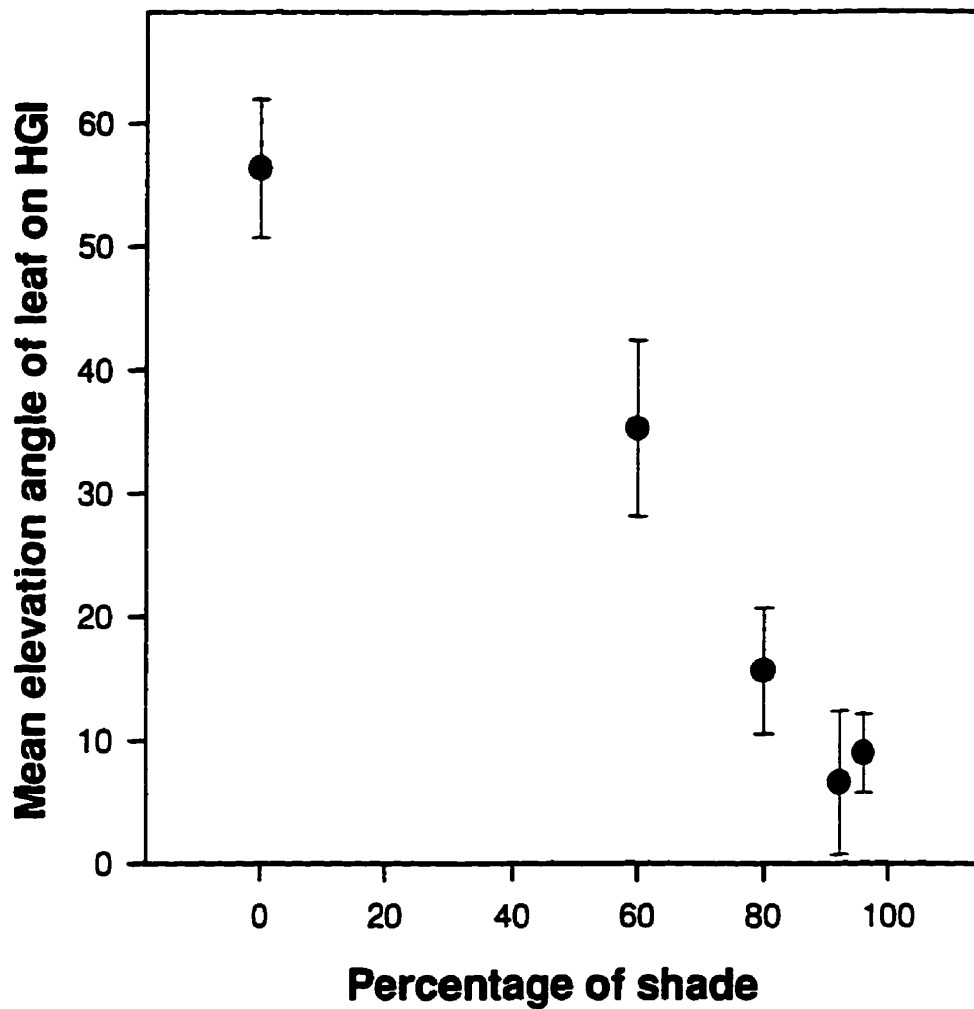
Fig. 2.5. The effect of shade (X) on the mean angle of elevation of leaves (Y) on the HGI in 1995. Vertical bars show standard deviation; n=6 trees per light regime. $Y = 56.513 - 0.158X - 0.00395X^2$ ($P=0.023$, $r^2=0.95$).
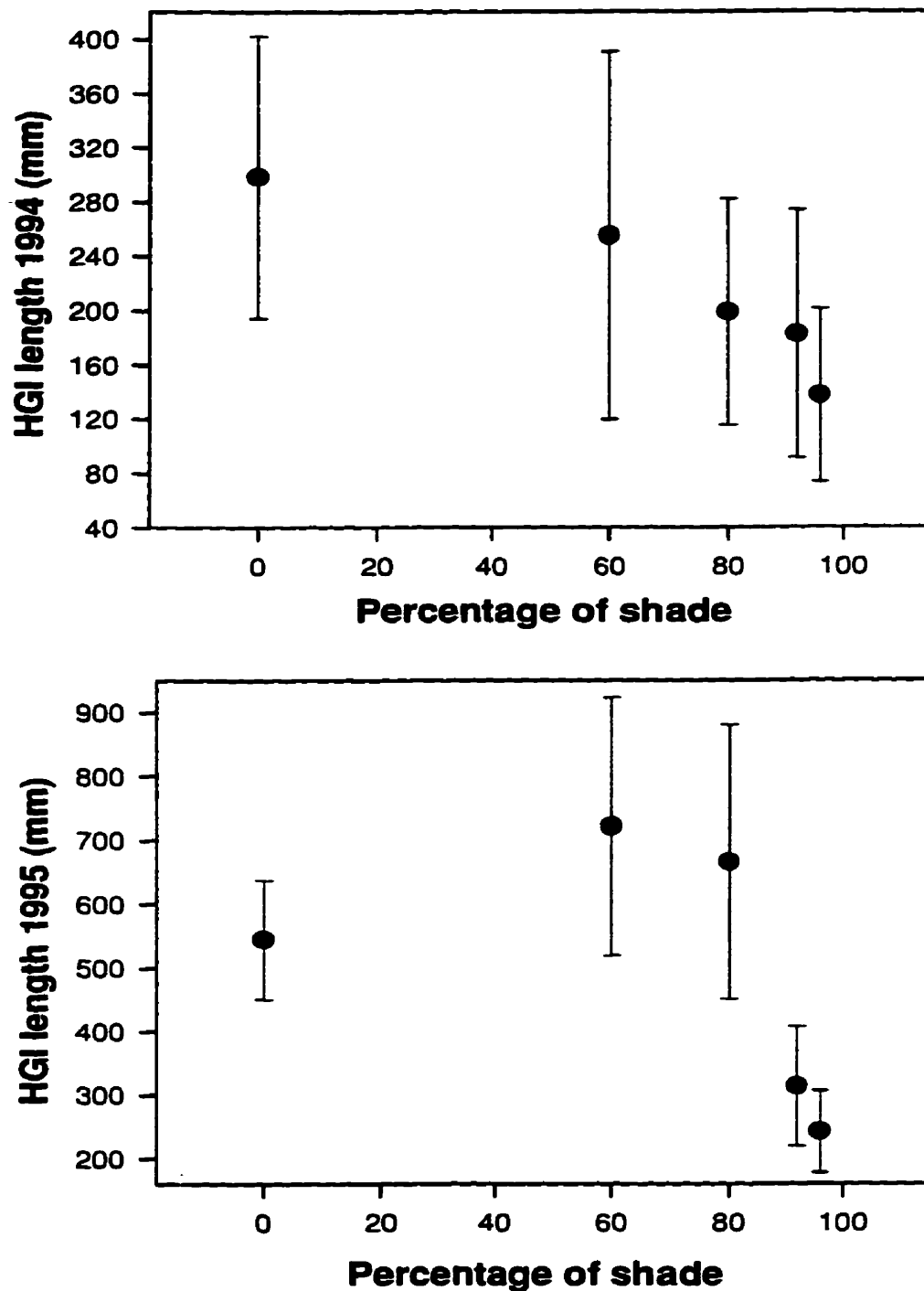
Fig. 2.6 The effect of shade (X) on mean HGI length (Y) **a.** 1994, Y=297.976 + 0.655X - 0.229X^2 (P=0.0325, r^2=0.935). **b.** 1995, Y=538.500 + 15.52X - 0.192X^2 (P=0.096, r^2=0.81). Vertical bars show standard deviation. In 1994, n=24 trees in each treatment. In 1995, n=22 trees for 0% shade, n=24 trees for 60, 92, and 96% shade, and n=21 trees for 80% shade.

Differences in mean growth rates between trees, levels of shade, and years were observed. In 1994, trees in 92% shade initially had the faster growth rate but after four weeks of growth, trees in full sun were growing much faster (Fig. 2.7a). After five weeks of growth, trees in 80, 92, and 96% shade had very little growth while trees in full sun and 60% shade continued to grow. The result is that trees in full sun produced longer HGIs. In 1995 the results were very different from 1994 (Fig. 2.7b). The control trees had the fastest growth for the first six weeks of growth, after which 60% shade had the fastest growth rate followed by 80% shade, until week ten when growth ceased. As a result 60% shade produced the most growth.

Number of shoot units

In both 1994 and 1995 the different levels of shade had an effect on the mean number of shoot units produced. The results in 1994 (Fig. 2.8a) were different from those in 1995 (Fig. 2.8b). In 1994 the control trees produced relatively more shoot units per HGI compared to the other levels of shade with a trend towards a decrease with increased shading. However in 1995, the relationship was distinctly non-linear in that trees in 60 and 80% shade produced more shoot units per HGI than either the control or the trees in the heaviest shade. However, it should be pointed out the quadratic regression did not describe the relationship particularly well.
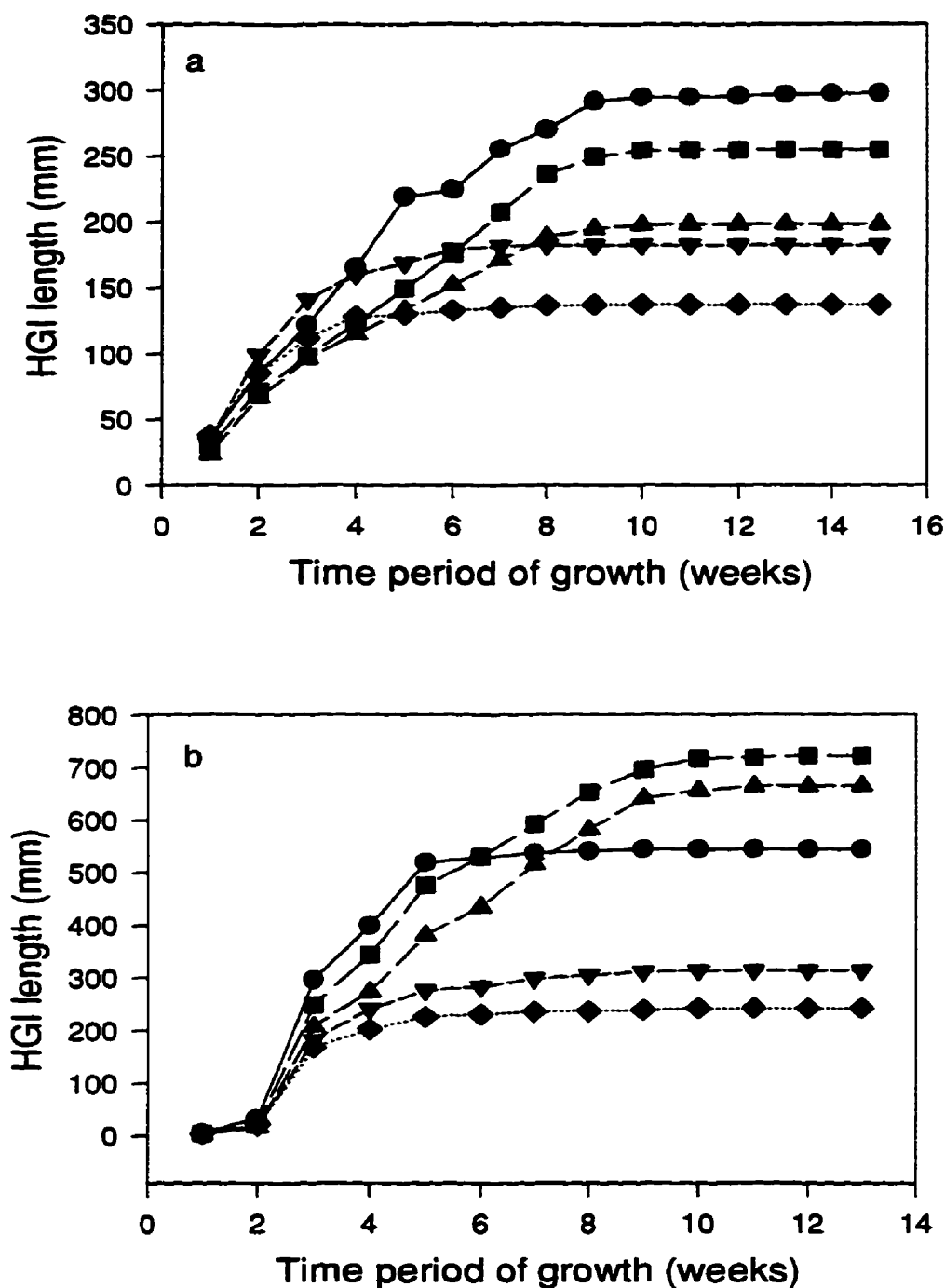
Fig. 2.7. Mean weekly growth of HGIs. **a.** 1994 and **b.** 1995. ●=0%, ■=60%, ▲=80%, ▼=92%, and ◆=96%. In 1994 n=24 trees for all shade levels. In 1995 n=22 trees for 0% shade, n=24 trees for 60, 92, and 96% shade, and n=21 trees for 80% shade.
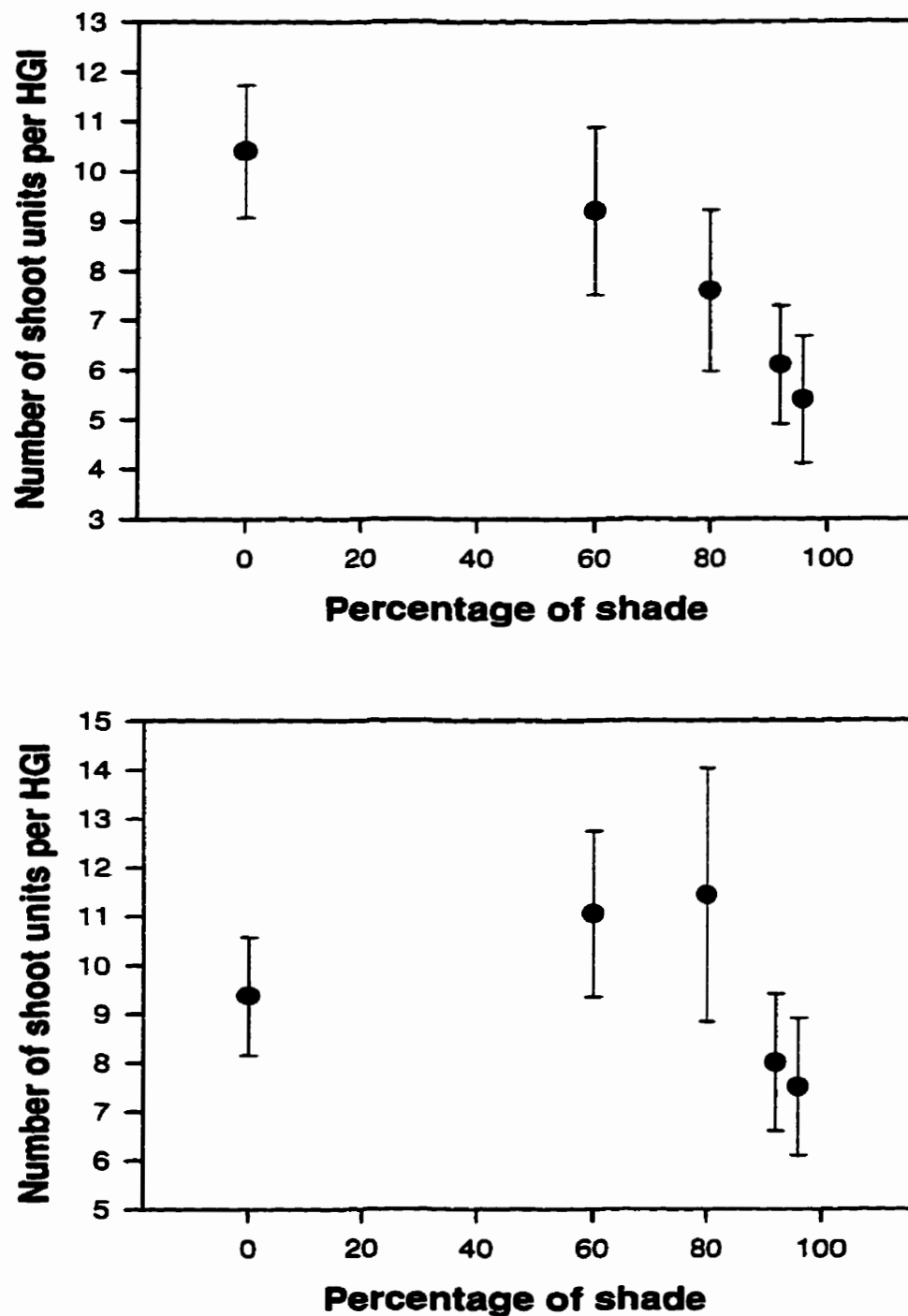
Fig. 2.8. The effect of shade (X) on the mean number of shoot units (Y) per HGI.
a. 1994, $Y=10.44 + 0.0347X - 0.000119X^2$ (P=0.0057, r^2=0.99) and **b.** 1995,
$Y=9.297 + 0.137X - 0.00159X^2$ (P=0.21, r^2=0.57). Vertical bars show standard
deviation. In 1994 n=24 trees. In 1995 n= 22 trees for 0% shade, n=24 trees for
60, 92, and 96% shade, and n=21 trees for 80% shade.

Shoot-unit length

In 1995, different levels of shade had an effect on mean shoot-unit length (Fig 2.9). Mean shoot-unit length was generally similar for 0, 60, and 80% shade and was relatively shorter in the 92 and 96 % shade. The quadratic regression described this relationship reasonably well.

In *F. pennsylvanica* it is known that internode (shoot unit) lengths start out small at the base and increase in size towards the middle of the shoot until a maximum is reached and then internode length declines (Remphrey and Davidson 1994). This pattern was exhibited by the control, 92 and 96% shade trees. However, in 60 and 80% shade a similar pattern was observed to the point where the internodes begin to decline after the maximum internode length is reached and then there was a change in the pattern. Instead of internode length continuing to decline, lengths began getting larger again with 2 more peaks before the final decline (Fig. 2.10).

Caliper

The different levels of shade had an effect on the mean caliper of the HGI and the relationship was strongly quadratic. Means for the caliper of the 1995 HGI for the control trees and 60% shade were similar, but were greater than 80, 92, and 96% shade (Fig. 2.11). Trees in 92 and 96% shade had the smallest mean HGI caliper.
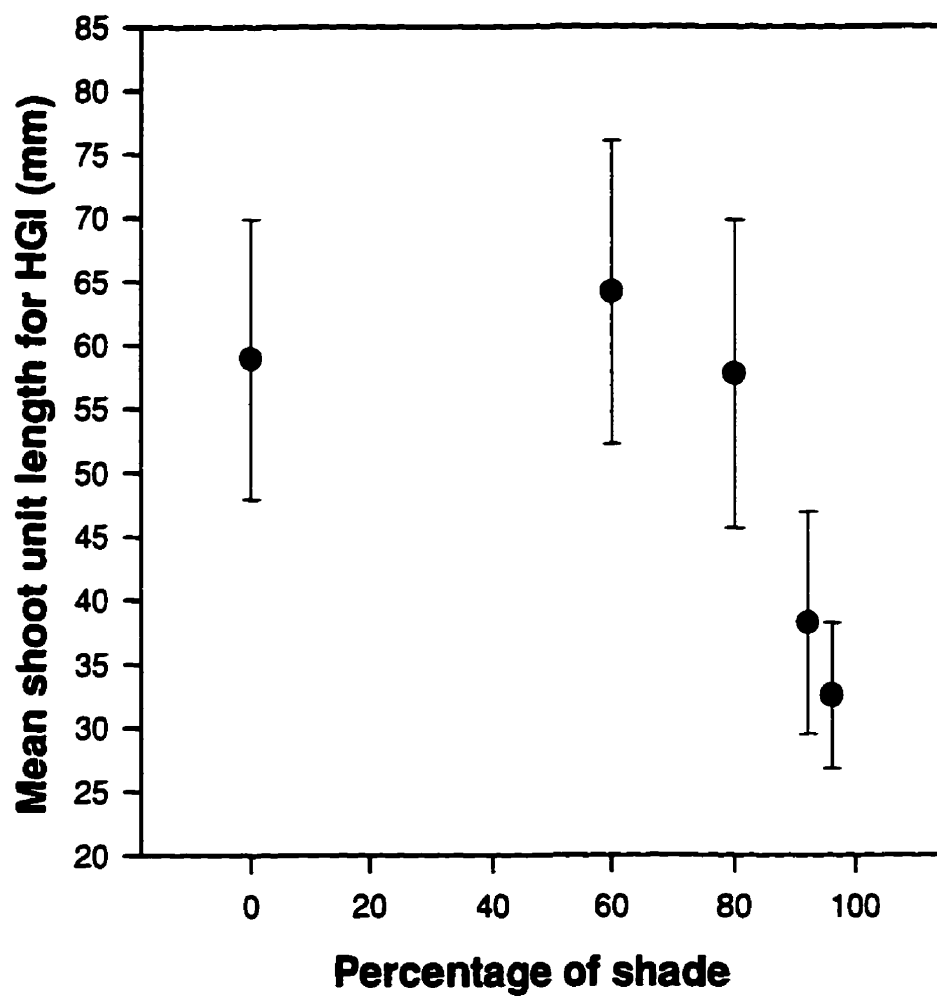
Fig. 2.9. The effect of shading (X) on the mean shoot unit length (Y) of the HGI in 1995. Vertical bars show standard deviation; n=22 trees for 0% shade, n=24 trees for 60, 92, and 96 % shade, and n=21 for 80% shade. Y=58.048 + 0.844X - 0.0113X^2 (P=0.054, r^2=0.89).
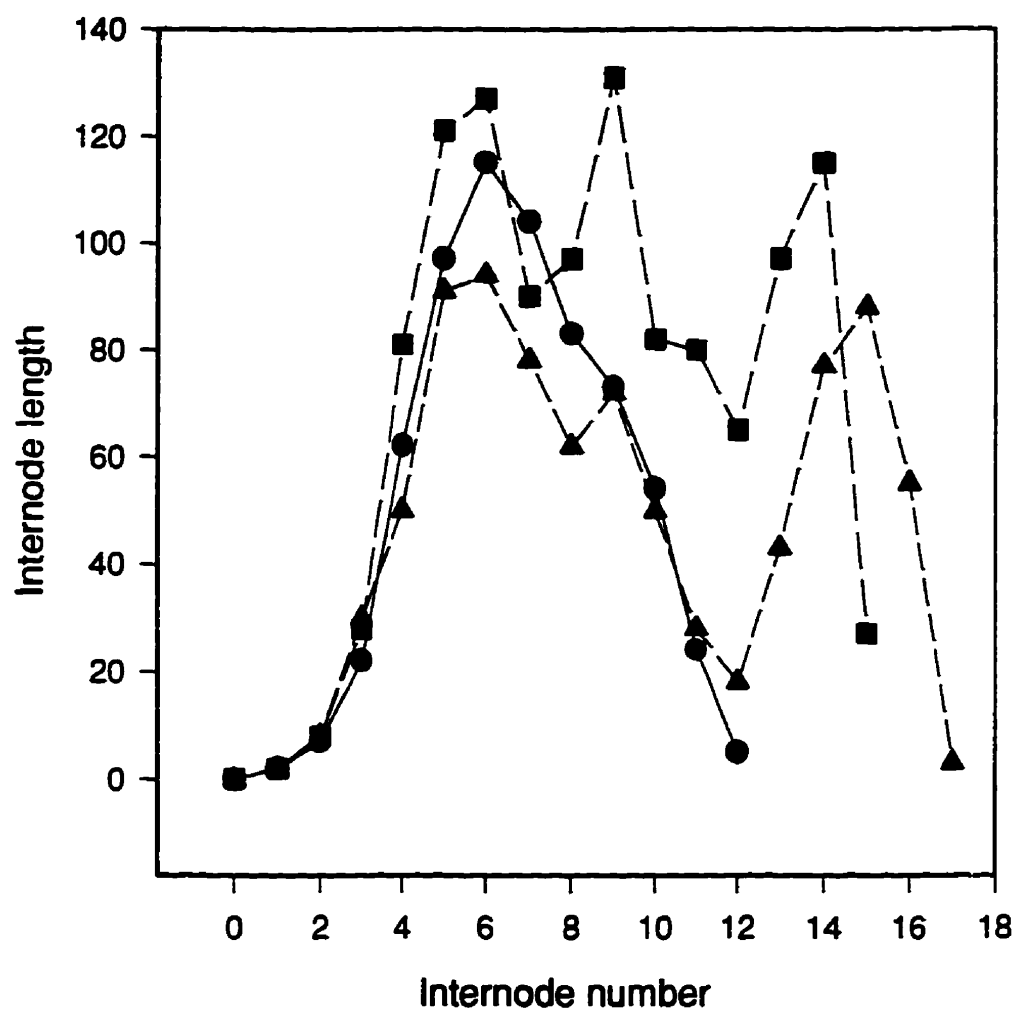
Fig. 2.10. Internode lengths along one shoot showing the normal expansion in full sun and the irregular pattern of development in 60 and 80% shade in 1995. ●=0% shade, ■=60% shade, and ▲=80% shade.
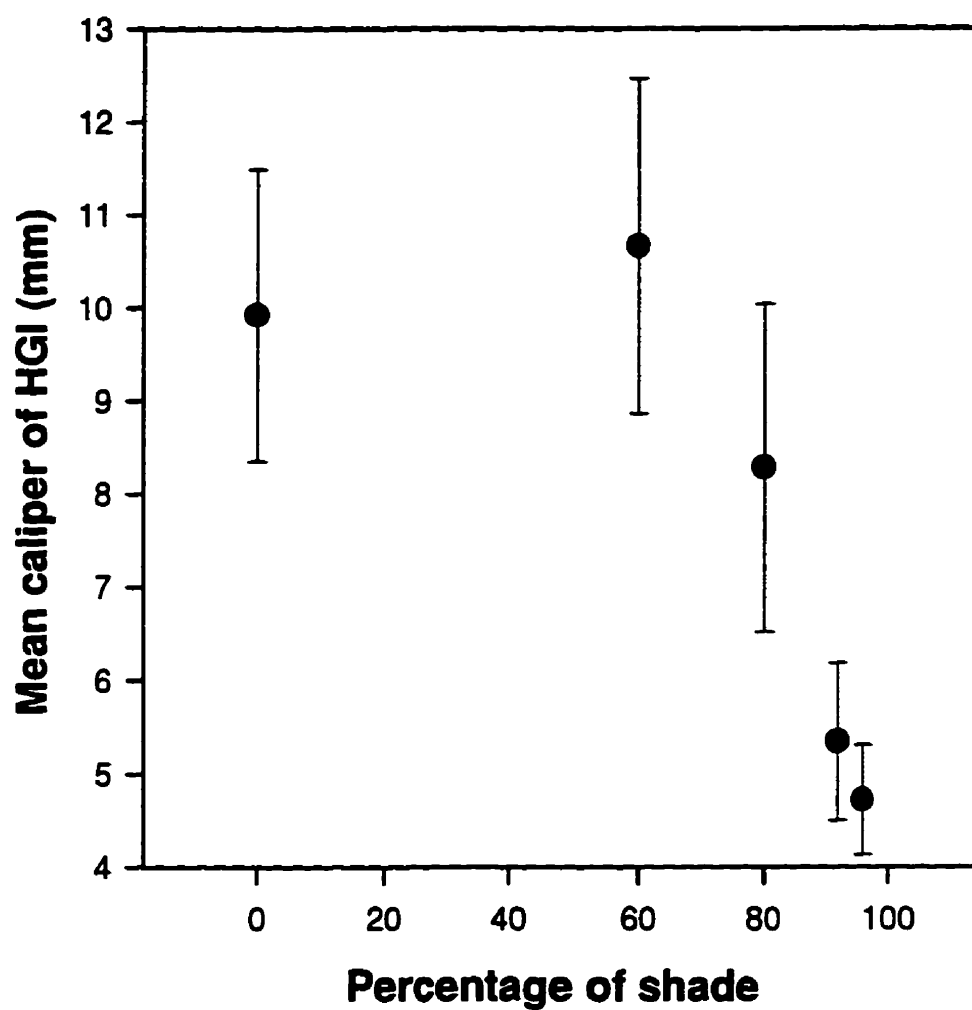
Fig. 2.11. The effect of shade (X) on the mean caliper (Y) of 1995 HGIs. Vertical bars show standard deviation; n=22 trees for 0% shade, n=24 trees for 60, 92, and 96 % shade, and n=21 trees for 80% shade. Y=9.908 + 0.131X - 0.006X^2 (P=0.0055, r^2=0.99).

Lateral shoots

Number of lateral shoots

The different levels of shade had an effect on the mean number of lateral shoots produced and the relationship was strongly quadratic (Fig. 2.12). Trees in 92 and 96% shade produced considerably fewer lateral shoots compared to the other light regimes.

Lateral shoot angle of elevation

Shading had a small effect on the mean angle of elevation of lateral shoots which was generally greater in full sun (Fig. 2.13). The relationship was not described well by either linear of quadratic regression. Nevertheless, the mean angle of elevation was lowest in the highest shade levels.

Lateral shoot length

Mean lateral shoot lengths were different among shade levels and the relationship was strongly quadratic. There was a general decline in lateral shoot length with increasing shade (Fig. 2.14).

Number of shoot units per lateral shoot

Shading had an effect on the mean number of shoot units per lateral shoot (Fig. 2.15). The relationship was non-linear and reasonably represented
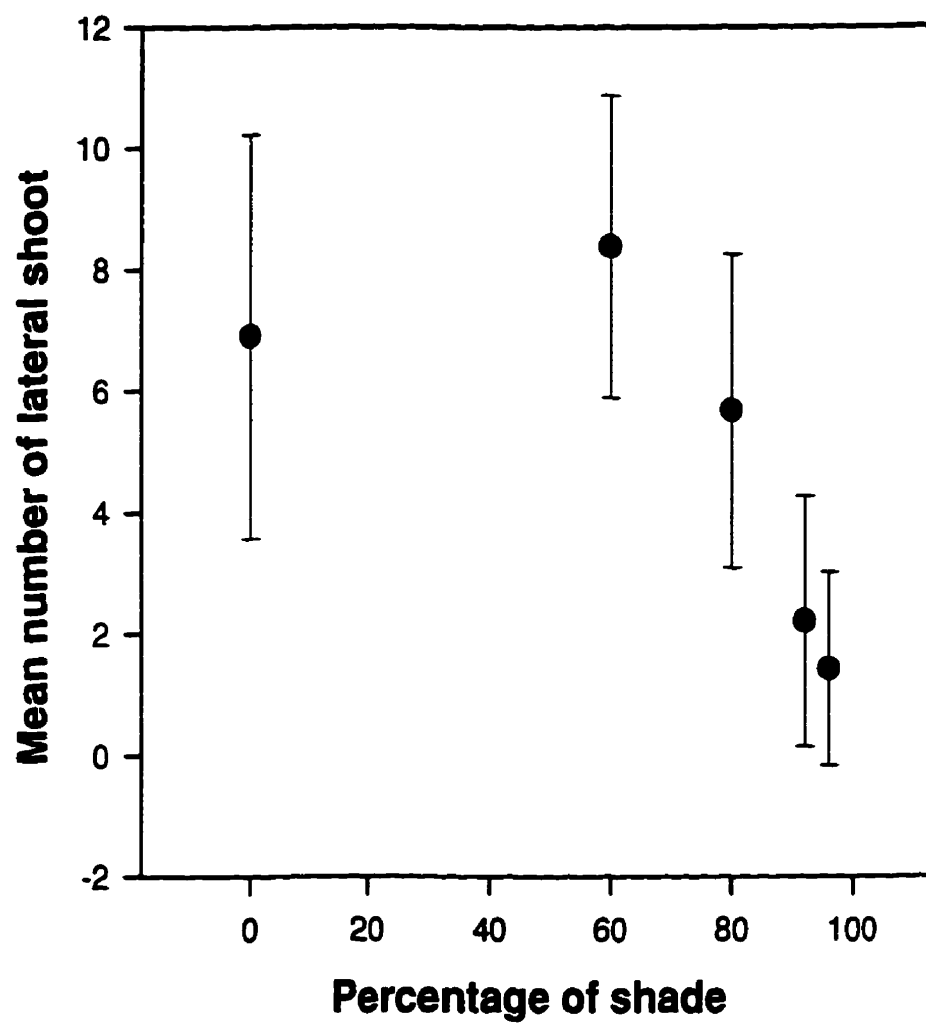
Fig. 2.12. The effect of shade (X) on the mean number of lateral shoots (Y) per tree in 1995. Vertical bars show standard deviation; n=22 trees for 0% shade, n=24 trees for 60, 92, and 96 % shade, and n=21 trees for 80% shade. Y=7.483 + 0.154X - 0.00227X^2 (P= 0.007, r^2=0.98).
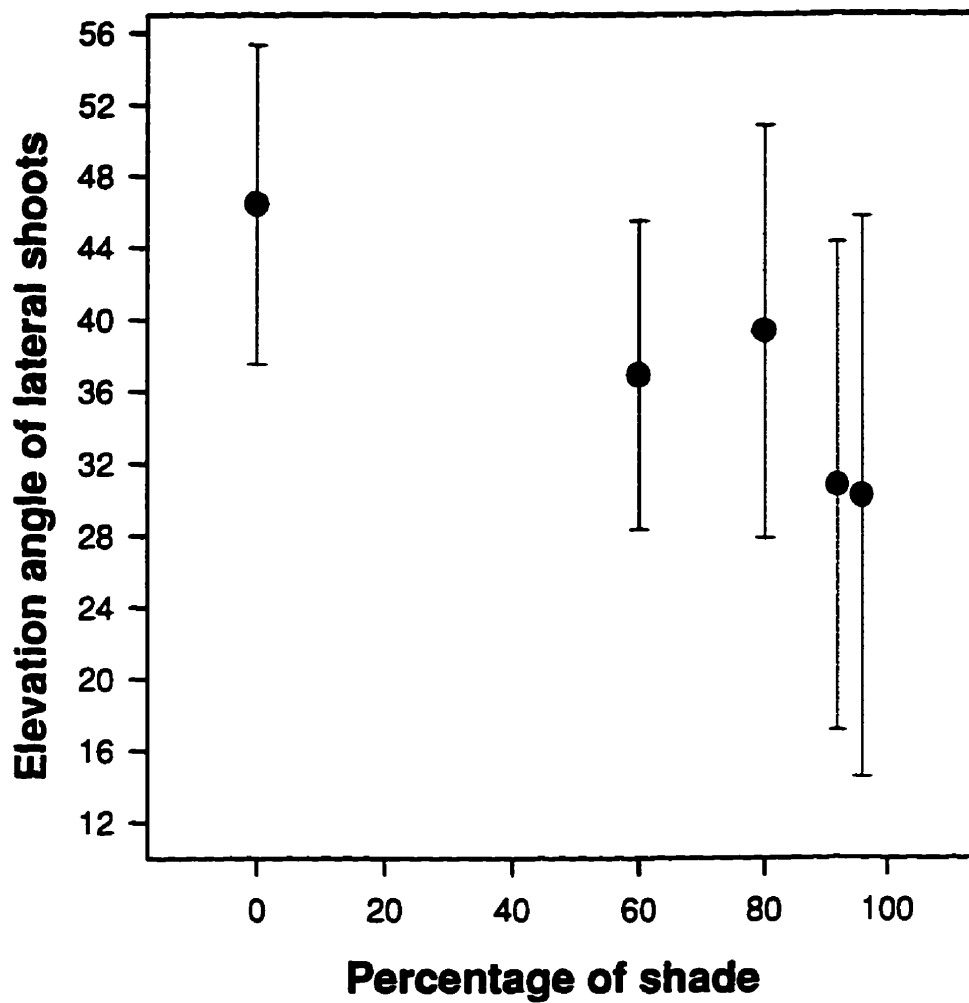
Fig. 2.13. The effect of shade (X) on mean angle of elevation of the lateral shoots (Y) off the parent shoot. Vertical bars show standard deviation; n=22 trees for 0% shade, n=24 trees for 60, 92, and 96 % shade, and n=21 trees for 80% shade. Y=45.376 - 0.127X + 0.000193X^2 (P= 0.31, r^2=0.37).
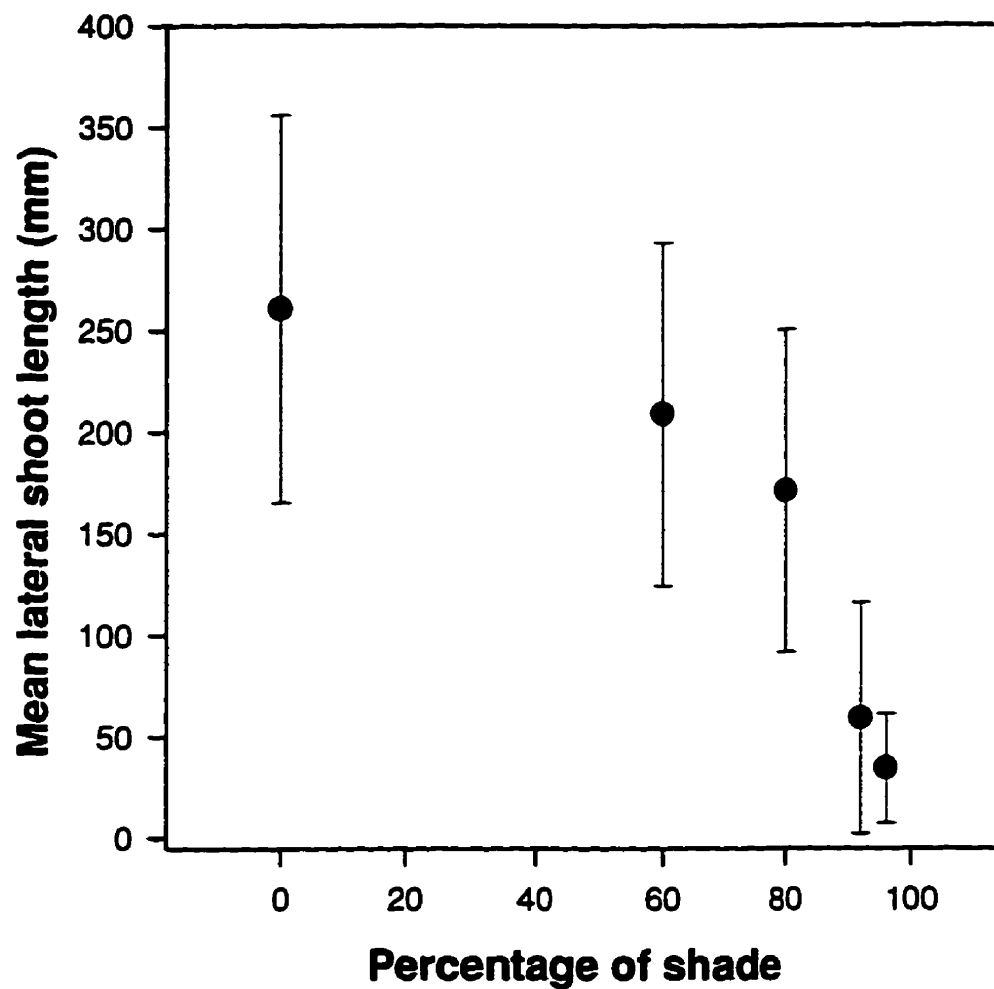
Fig. 2.14. The effect of shade (X) on the mean lateral shoot length (Y) in 1995. Vertical bars show standard deviation; n=22 trees for 0% shade, n=24 trees for 60, 92, and 96 % shade, and n=21 trees for 80% shade. Y=240.463 + 2.586X - 0.048X^2 (P=0.047, r^2=0.90).
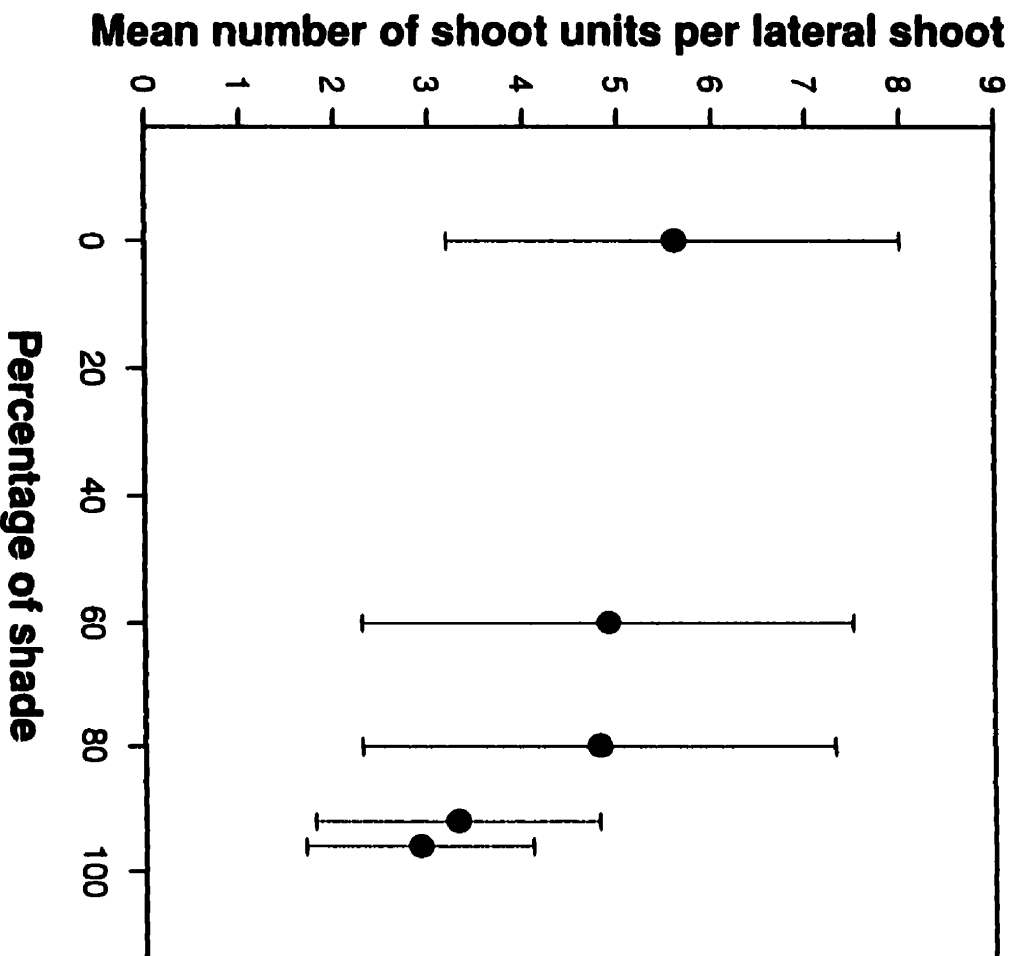
Fig. 2.15. The effect of shade (X) on the mean number of shoot units per lateral (Y) in 1995. Vertical bars show standard deviation; n=22 trees for 0% shade, n=24 trees for 60, 92, and 96% shade, and n=21 trees for 80% shade. Y=5.423 + 0.0302 - 0.000568X² (P=0.078, r²=0.84).

by the quadratic regression. The highest shade levels produced the fewest shoot units per lateral shoot compared to the other levels of shade.

<u>Global response of tree characteristics to shading</u>

In 1995 the patterns for the total mean number of leaves per tree (Fig. 2.16), total mean cumulative shoot length (Fig. 2.17), total mean above ground biomass (Fig. 2.18), cumulative mean shoot biomass per tree (Fig. 2.19), and mean leaf biomass (Fig. 2.20) were similar. In general, there was quadratic relationship between shading and total mean number of leaves per, total mean cumulative shoot length, total mean above ground biomass, cumulative mean shoot biomass per tree, and mean leaf biomass. The control and 60% shade trees were the greatest, 92 and 96% shade trees were the lowest, and 80% shade trees were intermediate.

The shoot weight ratio, which is a measure of the cumulative shoot biomass compared to whole above ground tree biomass, exhibited a general trend towards decreasing as the percentage of shade increased (Table 2.6). Trees in 96% however did not follow the general trend and showed a decrease. The leaf weight ratio, a measure of the total leaf biomass per tree compared to whole tree biomass, exhibited a trend towards increasing as the percentage of shade increased (Table 2.6).
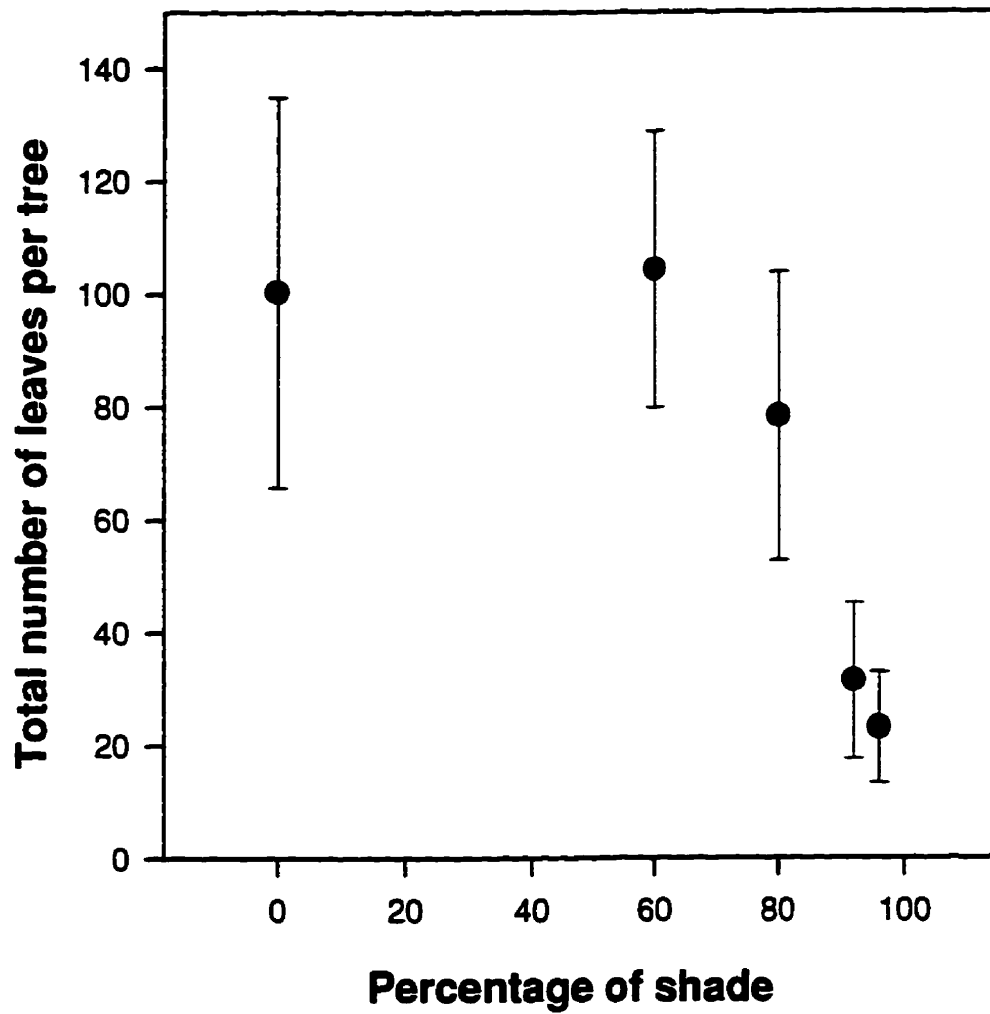
Fig. 2.16. The effect of shade (X) on the mean number of leaves per tree (Y) in 1995. Vertical bars show standard deviation; n=22 trees for 0% shade, n=24 trees for 60, 92, and 96% shade, and n=21 for 80% shade. Y=99.905 + 1.725X - 0.0263X^2 (P=0.020, r^2=0.96).
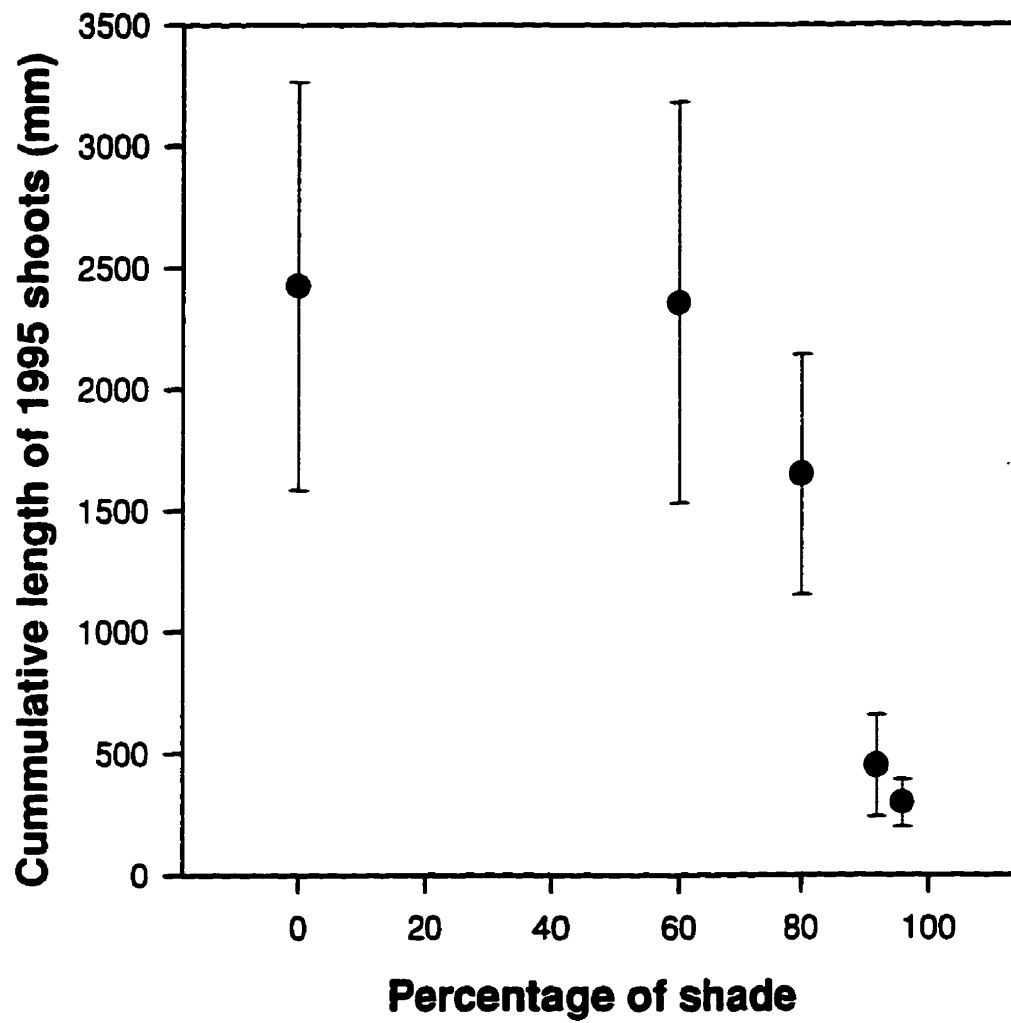
Fig. 2.17. The effect of shade (X) on the mean cumulative shoot length (Y) in 1995. Error bars show standard deviation; n=6 trees for each treatment. $Y=3148.425 + 40.762X - 0.704X^2$ (P=0.012, r^2=0.98).
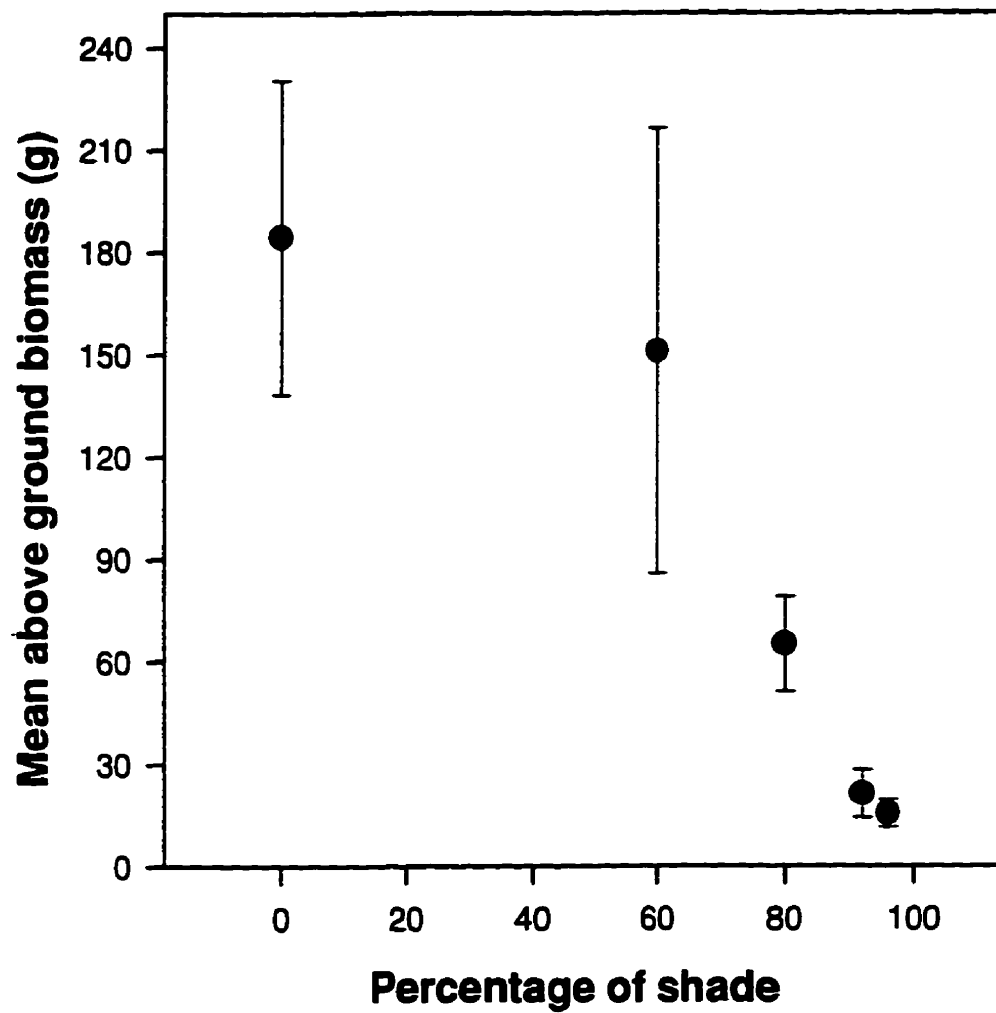
Fig. 2.18. The effect of shade (X) on the mean above ground tree biomass (Y). Vertical bars show standard deviation; n=6 trees for each treatment. Y=128.747 + 0.812X - 0.0221X^2 (P=0.015, r^2=0.97).
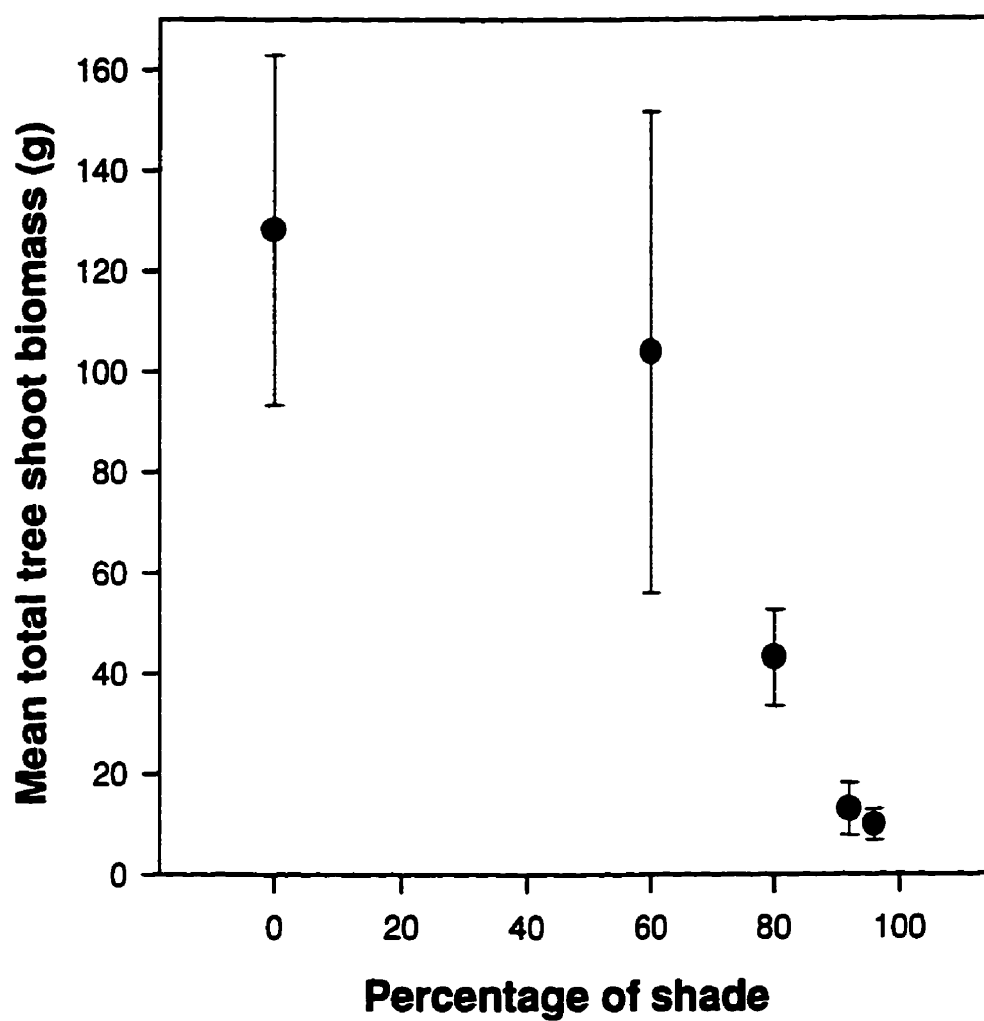
Fig. 2.19. The effect of shade (X) on the mean total cumulative shoot biomass (Y) in 1995. Vertical bars show standard deviation; n=6 trees for each treatment. Y=185.025 + 1.238X - 0.0323X^2 (P=0.014, r^2=0.97).
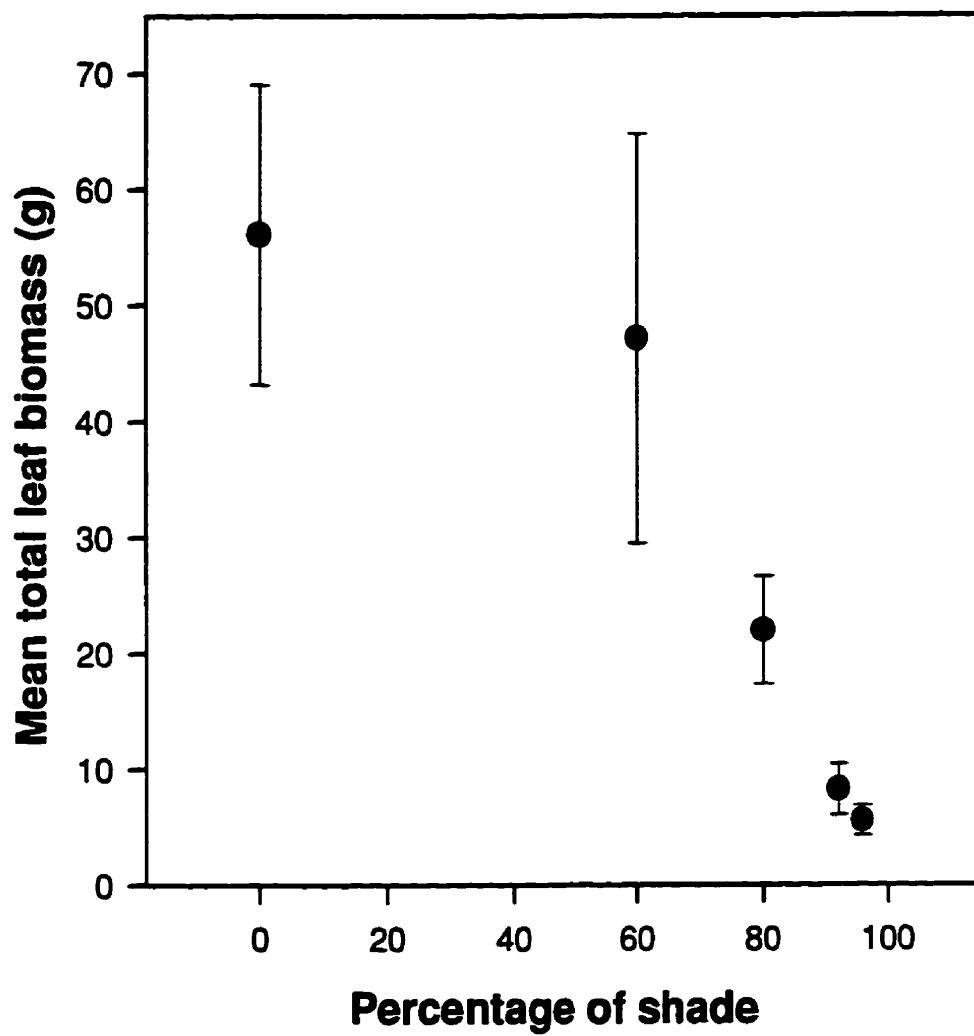
Fig. 2.20. The effect of shade (X) on the mean total leaf biomass (Y) in 1995. Vertical bars show standard deviation; n=6 trees for each treatment. Y=56.278 + 0.424X - 0.0102X^2 (P=0.0095, r^2=0.0095).

Table 2.6 Shoot and leaf weight ratio in 1995.

Percent shade	Shoot weight ratio[1] (%)	Leaf weight ratio[2] (%)
0	69.56	31.41
60	68.79	31.21
80	66.19	33.81
92	61.03	38.97
96	64.25	35.73

[1] Shoot weight ratio is the weight of the shoot biomass over the total tree biomass as a percentage.
[2] Leaf weight ratio is the weight of leaf biomass over total tree biomass as a percentage.

Total leaf area

There were differences in total leaf area among shade levels and there was a strong quadratic relationship (Fig. 2.21). Trees in 60 % shade had the greatest mean leaf area per tree, but also the most variation between trees as indicated by the standard deviation for that shade level.

Basal caliper and basal caliper increase

The different levels of shade had an effect in both 1994 and 1995 on the caliper measured at the base of the trees. In 1994 (data not presented) and in 1995 (Fig. 2.22), the basal caliper generally decreased with increased shading. However, there was not much difference between the control and 60% shade.
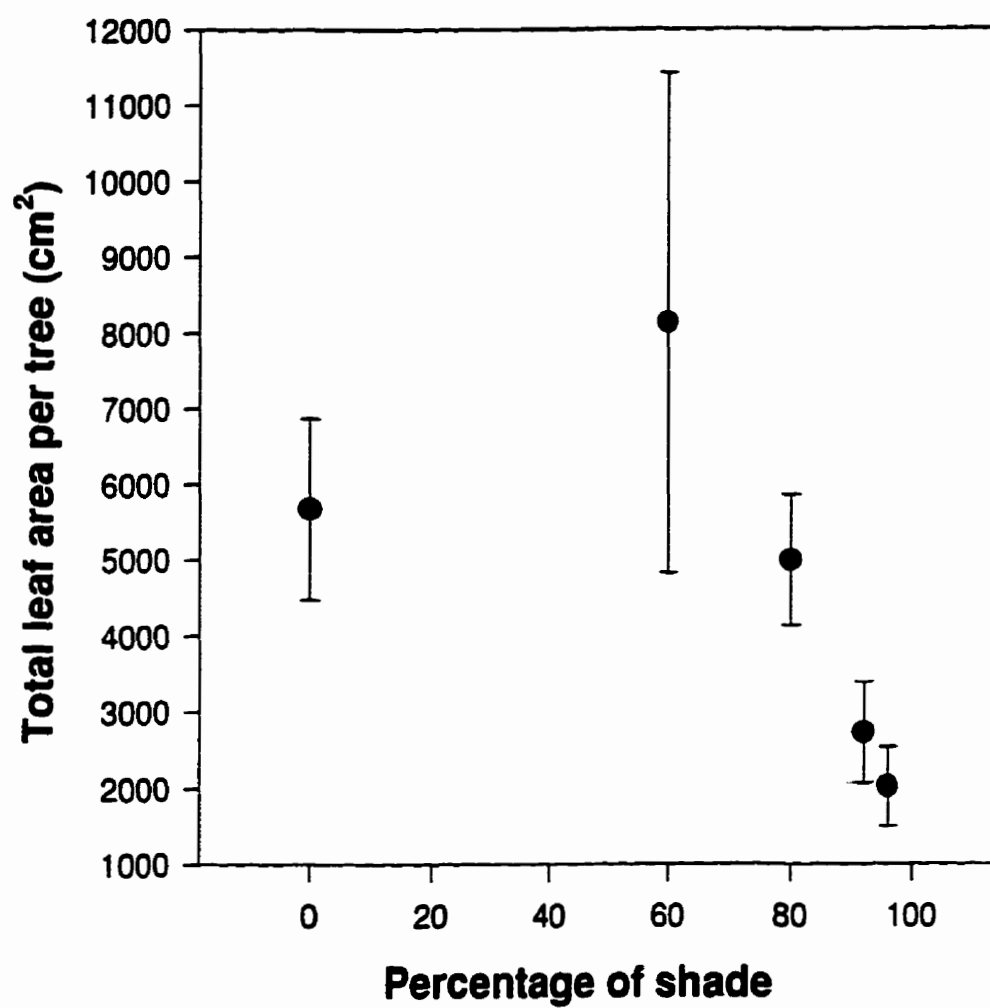
Fig. 2.21. The effect of shade (X) on the total leaf area (cm^2) per tree (Y) in 1995. Vertical bars show standard deviation; n=6 trees for each treatment. Y=5686.366 + 167.669X - 2.164X^2 (P=0.0056, r^2=0.99).
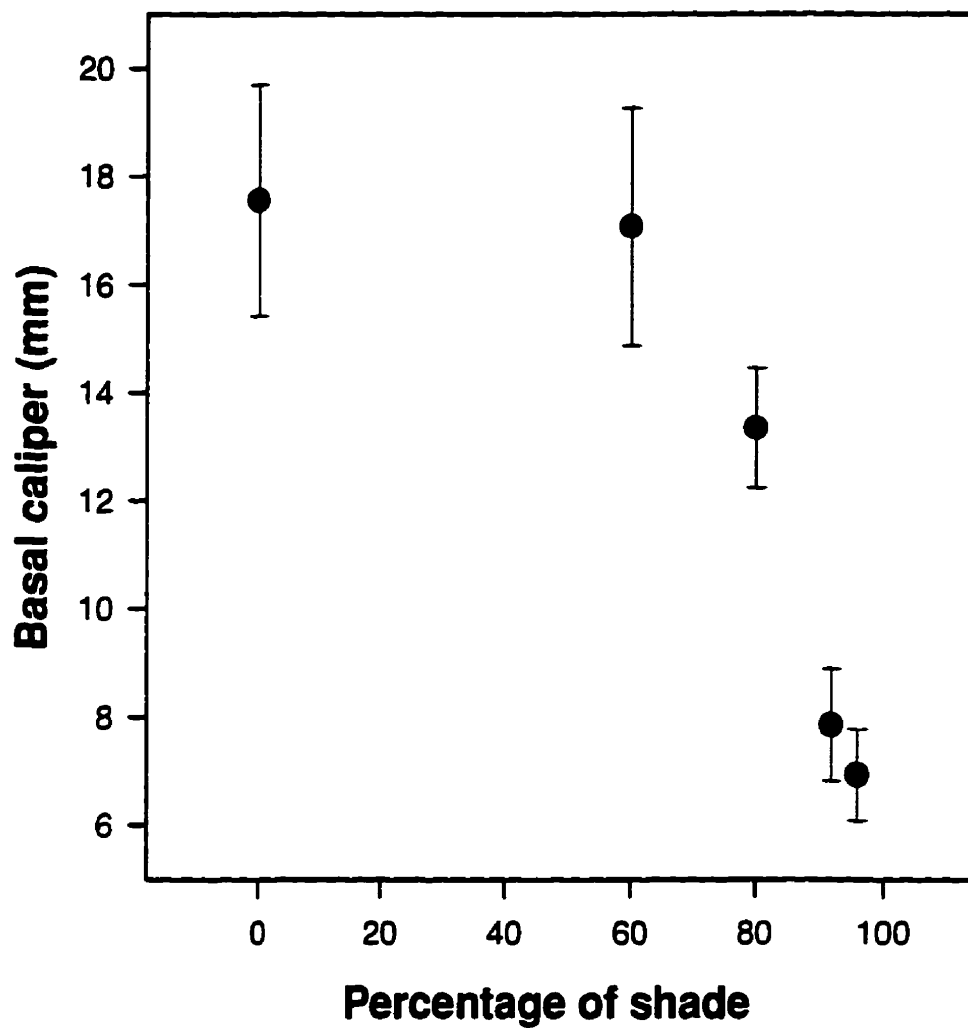
Fig. 2.22. The effect of shade (X) on mean basal caliper (Y) in 1995. Vertical bars show standard deviation; n=6 trees for each treatment. Y=17.528 + 0.182X - 0.00306X^2 (P=0.011, r^2=0.98).

There was also little difference between the 92 and 96% shade levels. The 80% shade treatment was intermediate between the other two groups. The overall relationship was strongly quadratic.

The increase in basal caliper, which is the increase in mean stem caliper from the fall of 1994 to the fall of 1995 was different between shade levels (Fig. 2.23) and exhibited the same pattern as the 1995 caliper measurement. Again the relationship was strongly quadratic.
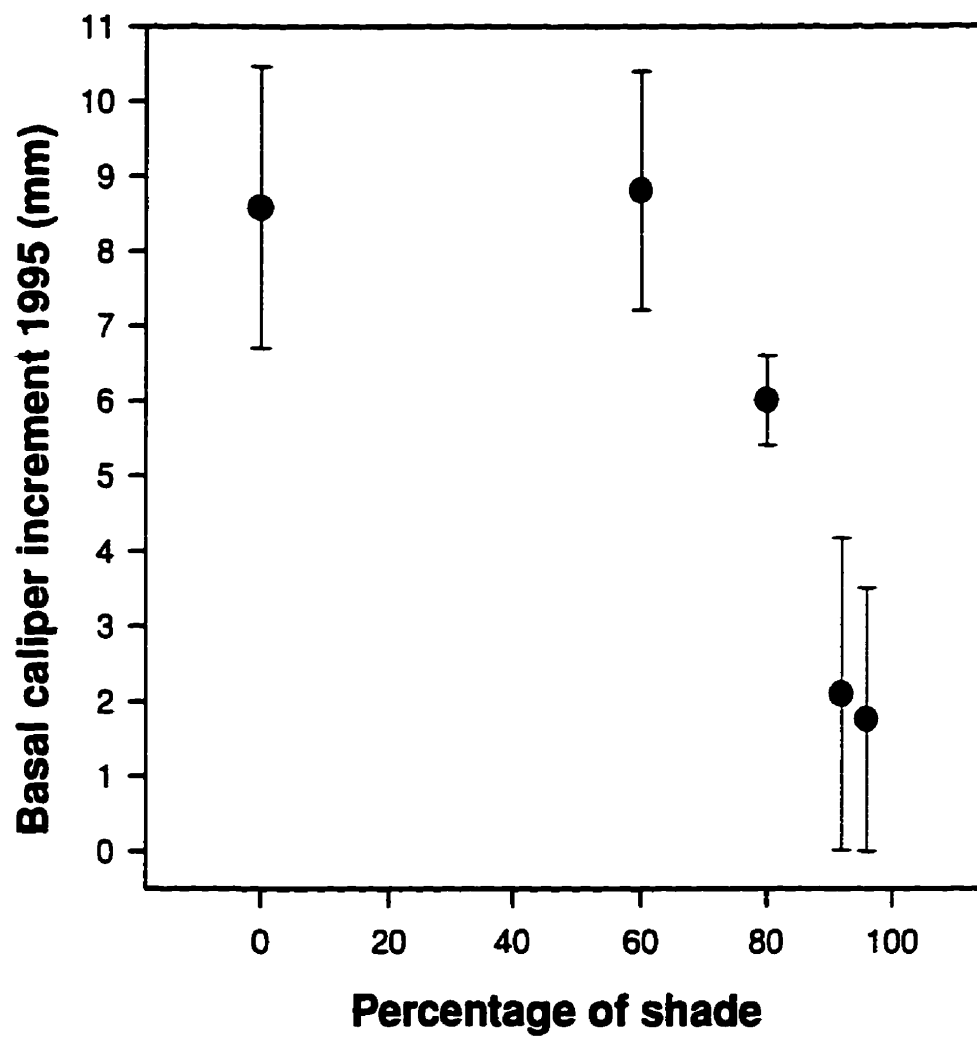
Fig. 2.23. The effect of shade (X) on the mean basal caliper increment (Y) in 1995. Vertical bars show standard deviation; n=6 trees for each treatment. Y=8.571 + 00.0279X - 0.00224X^2 (P=0.013, r^2=0.97)

DISCUSSION

In the present study, the effects of artificial shading on *Fraxinus pennsylvanica* var. *subintegerrima* seedlings followed the observed patterns reported for other woody plants. In general there was variation in most tree morphological characteristics measured with changing light intensities. Total above ground biomass (total leaf biomass and cumulative shoot biomass), total number of leaves per tree, total leaf area per tree, basal caliper, HGI caliper, and cumulative shoot length decreased in heavy shade. Such quantitative reductions in development appear to occur because decreased light intensities reduce the amount of assimilates produced in photosynthesis, which results in less energy available to the tree (Kramer and Kozlowski, 1979; Smith, 1982).

Despite their reduced assimilate production, trees have the ability to adapt to, or compensate for, reduced light intensities, thus reducing the impact on assimilate production. Reported morphological modifications to *F. pennsylvanica* include a decrease in leaf thickness (Jackson, 1967) and a decrease in the angle of elevation of the leaves (Mc Millen and Mc Clendon, 1979) in the shade. Leaf thickness in the sun was measured to be 0.20 mm which was the same as measurements reported in a study by Bostrack, (1993). However, in another study, leaf thickness was reported to be 0.12 mm in the sun (Jackson, 1967). In 96% shade leaf thickness was measured to be 0.10 mm

which was comparable to Jackson's (1967) reported measurement of 0.10 mm. The variation in leaf thicknesses in the sun between the two studies could be caused by genetic differences or attributed to locational environmental differences, such as light intensity, temperature, or moisture supply.

The mean leaf angle of elevation in the present study was 55° above the horizontal in the sun and 15° in 80% shade. McMillen and McClendon (1979) reported that the leaf angle was 37° above the horizontal in the sun and 14° in 83% shade. The standard deviation in mean leaf angles, around 6° in sun and shade in the present study, was less compared to, 19° and 14° in sun and shade respectively in the study by McMillen and McClendon (1979). When the high amount of variability is considered in the study by McMillen and McClendon (1979) the differences between the two studies for leaf angles in the sun are not as significant. The cause of the variation between the studies may be from latitudinal differences which affects light intensity and the angle of incidence of the sunlight. McMillen and McClendon (1979) did determine that there was no response to the direction of the light only to its quantity. The overall effect of shading was to decrease leaf angles closer to the horizontal which presumably results in maximum light interception.

Lateral shoot angle of elevation above the horizontal is also decreased with increased shading. The variation in the angle of elevation between sun and shade was not as great as that found with leaf angles. Similar to other

species, decreases in lateral shoot angle of elevation in the shade have been interpreted as adaptations to maximize light interception while reducing mutual shading (Marler *et al.*, 1994). In the lower latitudes, especially the tropics, leaves and branches are oriented more horizontally (Marler *et al.*, 1994) which may be related to the sun being always directly overhead. Therefore the closer an experiment is conducted to the equator the less variation in the angle of the light received from the sun. Overall these morphological changes are beneficial to the tree because they help prevent a disruption in assimilate supply in the shade.

Decreased light intensities affect the relative allocation of biomass to leaf and stem material. In full sun, 70% of the assimilates used to produce above ground biomass were allocated to shoot material and, 30% to leaf material (Table 2.6). In heavy shade relatively less assimilate, about 60 to 65%, was allocated to shoot material. The cause of the reduction in material allocated to leaf material in 96% shade is unknown, although it may be related to the heavy shading and light intensity levels being decreased beyond some threshold where the allocation of more assimilate to leaf biomass is of no advantage. Other species have been found to allocate more assimilate to leaf biomass in the shade (Loach, 1970; Lee, 1996) which has been determined to be an adaptive response, generally found in shade tolerant species (Kuroiwa *et al.*, 1964). The increase in allocation is beneficial because although it costs energy to produce, leaf

material can photosynthesize and produce more assimilate. Conversely, stem material costs energy to produce but does not directly return assimilate to the tree.

One distinctive morphological change under increasing levels of shade in the present study was an overall reduction in height growth. In 1994, HGI length was shortest in the heaviest shade and greatest in full sun. In contrast, 1995 HGI length was greatest in moderate shade but remained the shortest in heavy shading. The observed decrease in HGI length is similar to some other studies. HGI length appears to be variable and species dependent which may be related to shade tolerance. Some shade intolerant species have been found to show an increase in HGI length or show no change when heavily shaded while the shade tolerant species did not (Groniger *et al.*, 1996; Lee, 1996). Some species do not show an increase in HGI length with decreased light intensities (Groniger *et al.*, 1996; Lee, 1996). *F. pennsylvanica* is an intermediate shade tolerant species and responded to shading with a decrease in HGI length in heavy shade.

A possible explanation for the increase in HGI length in moderate shade is that variation in certain environmental conditions within the tents may have had an impact on growth. Temperatures were found to be lower, the humidity greater, and soil water content higher within the tents compared to conditions outside the tents. However, more information about soil moisture levels at

different times of the year is required in order to accurately characterize the water content of the soil in the different light regimes. These conditions may have combined to produce better growing conditions for the trees, which was manifested in greater development, especially in moderate shade. Light conditions within the heaviest shaded tents may have been too limiting to allow for increased development.

The HGI was examined in greater detail through an analysis of the two variables that determine its length: number of shoot units per HGI and the length of each shoot unit. In 1994, the HGI of trees in full sun had the greatest number of shoot units which decreased with increased shading. In contrast, in 1995, trees in moderate levels of shade had the greatest number of shoot units per HGI. HGI length (Fig. 2.6b) appeared to correspond more with the number of shoot units per HGI (Fig. 2.8b). The pattern of HGI length followed the pattern for the number of shoot units per HGI from full sun to heavy shade better than the pattern for HGI shoot unit length (Fig. 2.9).

The variation observed in the number of shoot units produced between the trees in full sun and heavy shade may have resulted from neoformation. The trees in this experiment came from a single source where they experienced similar environmental conditions in the nursery. This should result in all trees having the same number of preformed shoot units in their bud. In mature *Fraxinus pennsylvanica* it has been determined that shoots are preformed the

previous year and expand the following year (Remphrey, 1989). However, in juvenile trees when conditions are favourable, neoformation may occur (Remphrey and Davidson, 1994a). In *F. pennsylvanica* neoformation has been found to occur and was greatest within the first three years after planting (Davidson and Remphrey, 1994). In the heaviest shade it is likely that neoformation would not occur because Davidson and Remphrey (1994) observed there was little neoformation in the lower crown region of the tree because of mutual shading and competition for light energy. Therefore, variation in the total number of shoot units per HGI in 1994 would probably be the result of neoformation.

Further evidence to support the hypothesis that neoformation occurred is the irregular growth pattern exhibited in 1994 by a few trees, and in 1995 in most trees in moderate shade and a few control trees. Internode lengths increased near the distal ends of the shoots after the usual decline (Prusinkiewicz *et al.*, 1994). This irregular growth pattern suggests that it is connected to neoformation because it did not occur in the heaviest shade.

The other component determining HGI length is shoot unit length. In 1994 shading did not have much of an effect on shoot unit length. This may have occurred because 1994 was the establishment year and this may have obscured any effect of reduced light intensities. In 1995, shading had an effect on shoot unit length. The controls and moderately shaded trees had similar

shoot unit lengths and these were longer than those in the heavily shaded trees. At high levels of natural shade, etiolation, that is an increase in shoot unit length or internode length, is usually reported (Cornelissen, 1993; Marler *et al.* 1994; Lee, 1996). This increase results in an increase in HGI length which appears to be a phytochrome mediated response resulting from a decrease in the R:Fr ratio.

The shade tents used in this experiment had a shade cloth covering which had no measurable effect on the R:Fr ratio. Measurements in the tents of the R:Fr ratio ranged from 1.45 to 1.68 which was similar to others' measurements in full sun (Lee, 1996). The absence of a change in the R:Fr ratio would typically prevent etiolation from occurring because there would be no signal to the phytochrome system. Thus, the present study suggests that decreasing assimilate levels may play a role in the control of internode lengths at low light levels in *Fraxinus pennsylvanica*. However, in nature the expression of this development is often masked by the phytochrome response which eventually forces internode elongation. The responses to decreased light intensity or changes in the R:Fr ratio are highly variable and in some species changes in both light intensity and R:Fr ratio evoke changes in shoot unit length while some species only respond to changes in the R:Fr ratio (Lee, 1996).

High light intensities generally reduce apical control (Cline, 1991). Such conditions, found in full sun and moderate shade, were reflected in the

proliferation of lateral shoots produced and increased lateral shoot length in this study. Trees in the understory of a forest often have very few lateral shoots. Low light intensities strengthen apical control (Cline, 1991) which results in decreased lateral shoot production and lateral shoot length in the heaviest shade. These results are consistent with other species where decreased light intensities reduced lateral shoot production and length (Gottschalk, 1994; O'Connell and Kelty, 1994; Luken *et al.* 1995; Parent and Messier, 1995). There was a reduction in both the number of shoot units per lateral shoot and lateral shoot unit length. The reduction in lateral branch production and length through increased apical control allows a redistribution of assimilates to other areas of the tree and enhances shade tolerance of a species (O'Connell and Kelty, 1994). The assimilates that would have been used in lateral shoot biomass production can now be used to produce leaf material or height growth. However, because the phytochrome system is not activated, this response of increased height growth was not observed in the present study. From this study it is clear that light intensity is very important to apical control and lateral shoot development.

In conclusion, when all the characteristics measured are considered together, differences in architecture between the unshaded and heavily shaded trees are readily apparent. The crown size and growth rate of the trees in the shade was altered when compared to the trees in full sun. The changes in

architecture are caused by reduced light quantities. Trees in the heaviest shade have a very poorly developed crown because of few branches, which are very short and little height growth. The trees in moderate shade and full sun had very vigorous growth when compared to trees in heavy shade. These changes relate to the strategy of the plant in adapting to conditions in the sun where light energy is abundant or in the shade where light energy is greatly reduced.

GENERAL DISCUSSION

The quantitative examination of the architecture of *Fraxinus pennsylvanica* requires the measurement of several architectural characteristics. Although there is published information measured at the shoot level (e.g., Remphrey, 1989; Davidson and Remphrey, 1990; Remphrey and Davidson, 1992; Davidson and Remphrey, 1994a; Remphrey and Davidson, 1994) little information was previously known about finer architectural detail, specifically the number of shoot units per shoot, shoot unit length, and the fate of buds in relation to crown location, and tree age.

The number of shoot units per shoot was found to decrease from the top to the inside of the crown, as the tree aged, and from high to low light intensity. Shoot-unit length was found to decrease from the top to the inside of the crown and from high to low light intensities. However, as the tree aged the shoot-unit length was relatively constant. The number of lateral shoots produced decreased from the top to the inside of the crown, as the tree aged, and from high to low light intensities. The number of inflorescences decreased and the number of aborted buds increased from the top to the inside of the crown.

The variation in shoot architecture from the top to the inside of the crown and from shading is related to a decrease in the amount of light available for photosynthesis. Light is often limited because of mutual shading or shading by other trees (Kozlowski *et al.* 1991). Light intensity variation in the crown of *F.*

pennsylvanica had not been measured previously and inside the crown was greatly reduced compared to the outside of the crown (Appendix A). This results in less energy for photosynthesis and a reduction in the production of photosynthate and may account for the results observed in the completely shaded trees.

Few attempts have been made to try and correlate the developmental patterns observed in completely shaded trees and specific shaded areas within individual tree crowns. In the present study, similar developmental patterns occurred, such as fewer shoot units per shoot, shorter shoot units, and fewer lateral branches. Light quantity was similar for trees that were completely shaded and the inside of individual tree crowns (Appendix B). However, light quality was not the same as it remained unchanged in completely shaded trees but would be expected to be altered inside the crowns of individual trees. There are other factors that may confound making comparisons between the two types of shading. One factor is that within the crown, apical control can be exerted from shoots higher up in the crown. A second factor might be that other shoots in the crown are not shaded and could export food to the shaded areas. Finally, the trees used to study crown architecture are larger and more complex.

The many similarities between the inside of the crown and the heavily shaded trees would seem to indicate that light intensity is a major factor influencing the development of shoots in the inside of the crown. However, light

intensity would not be the only factor involved. Other factors might include nutrient status or light quality. More investigation into why shoots are different inside of the crown is needed. One area of particular interest would be to examine light quality, which is known to affect morphogenesis, by producing a map showing the spectral distribution of light in the crown. A study into biomass allocation between the different crown zones could also be useful in examining how photosynthate is distributed in the tree.

Another area that needs more exploration is the effect of light quality on the architecture of completely shaded trees. Questions still remain about what effect light quality has on the number of shoot units per shoot, shoot unit length and the fate of buds. This area has not been adequately explored, although some recent studies indicate that light quality is more important to the architectural development than first thought. Also of interest would be to determine if neoformation occurs in the shade under reduced light intensity and quality.

Whole tree shading affects the development and architecture of the tree. Trees do possess the ability to adapt to their environment and have developed strategies to increase or reduce light interception depending on the conditions. Trees in the heaviest shade have poorly developed crowns because of reduced lateral shoot production and lateral shoot and HGI length are reduced. This architecture is created because of a reduction in assimilate supply and a

reduction in energy available for growth and development. Lateral shoots and leaf blades are oriented very close to the horizontal in order to increase light interception. In contrast, trees in moderate shade and full sun have well developed crowns with many long lateral shoots and a long HGIs. The elevation angle of lateral shoots and leaf blades is oriented away from the horizontal in order to reduce light interception and decrease heat load.

The trees in moderate shade produced more vigourous development compared to the control trees. It was not possible to determine with certainty if improved tree development in these treatments was related to the shading treatment or the environmental influences. It may be of interest to observe if trees would grow as well in moderate shade if the environmental conditions had been the same as the control trees.

The fate of buds was affected by the position of the shoot in the crown resulting in a decrease in the number of lateral shoots and inflorescences and an increase in aborted buds from the top to the inside of the crown. The number of shoot units per parent shoot and the position of the bud along the shoot also impacted on its fate. The position of the bud around the shoot had no effect on its fate. However, there is evidence that the position of the lateral shoot around the parent shoot might affect lateral shoot length. It would if interest to determine how the number of shoot units per lateral shoot or lateral shoot-unit length are affected.

Aging also affects the fate of buds resulting in fewer lateral shoots. This may occur because of less energy for development or because there are fewer shoot units per shoot and there are fewer sites where lateral buds could be produced. However, from dissected buds there appears to be a large potential to form lateral shoots but the buds failed to develop especially in the oldest trees. In the older trees in the present study the middle of the crown is more vigourous compared to the rest of the crown. It is not known if this phenomenon can be generalized to other *F. pennsylvanica* of the same age.

The data collected here will ultimately increase our understanding of the development and architecture of *F. pennsylvanica*. A next step is to use the data to construct a computer simulation model of *F. pennsylvanica*. Following this step the validity of the model can be verified with the data to see whether it conforms to the actual measurements of the architecture of the tree.

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APPENDICES

Appendix A. Descriptive information of trees from planting #2 at the Agriculture and Agri-Food Research Centre in Morden.

Acc. number	Species	Location (area/row/tree)	Quantity used	Plant type	Year planted	Plant source
76-3335	*F. pennsylvanica*	2/26/5	2	seed	1979	Hecla Island, MB
71-2595	*F. pennsylvanica*	2/27/14	1	plant	1971	Kelowna,BC
60-0289	*F. pennsylvanica*	2/28/1	2	seed	1932	C.E.F.
60-0287	*F. pennsylvanica*	2/28/2	3	seed	1932	P.F.R.A[1]
65-0456	*F. pennsylvanica*	2/28/6	1	seed	1970	Pineland,MB
60-0288	*F. pennsylvanica*	7/105/1	5	plant	1944	Sutherland, SK
79-3740	*F. pennsylvanica #28*	2/27/11	1	scion	1982	Bottineau,ND
79-3742	*F. pennsylvanica #58*	2/27/10	1	scion	1982	Bottineau,ND
79-3741	*F. pennsylvanica #68*	2/27/8	1	scion	1982	Bottineau,ND
68-1638	*F. pennsylvanica #6902*	2/29/3	1	scion	1973	Winnipeg,MB
70-2186	*F. pennsylvanica #7009*	2/30/3	1	scion	1973	Yorkton, SK
70-2228	*F. pennsylvanica var. austinii*	2/30/1	1	scion	1972	Miami/W.R., MB

[1] Prairie Farm Rehabilitation Administration

S   N   Distance above Ground (cm)

																Distance above Ground (cm)
																340
30	26	17	18	17	13	8	60	20	24	24	40	72	80			270
	20	18	16	13	13	11	11	19	11	20	26	37	39	47		220
27	52	24	16	16	13	13	17	17	19	26	27	27				170
80	20	30	14	15	36	9	15	54	65	13	20	17	39	39		120
	66	14	12	8	6	7	10	30	40	19	17	18				70

W   E

																		340
		45	33	11	11	19	24	17	25	10	12	27	22	26				270
	81	20	94	90	28	90	16	41	29	25	73	35	12	35				220
	67	24	11	21	24	20	14	62	76	82	59	29	34	25	74			170
94	29	38	28	19	16	19	13	15	65	15	15	15	18	24	30	77		120
24	20	21	25	17	24	14	13	9	54	31	31	12	12	15	12	54	69	70

| 120 | 105 | 90 | 75 | 60 | 45 | 30 | 15 | 0 | 0 | 15 | 30 | 45 | 60 | 75 | 90 | 105 | 120 |

Distance from center of tree (cm)

Fig. B.1. The distribution of light (as a percentage of full sun) within the crown. Vertical line is the center of the crown.

S   N   Distance above Ground (cm)

																	Distance above Ground (cm)
		81	6	9	9	18		13	17	22	35	43	43	48			340
91	45	27	60	41	14	45		10	24	24	29	29	38	52			270
	95	84	49	42	33	58		31	36	24	20	60	31	31	80		220
74	56	43	37	25	80	28		15	57	30	27	54	66	67			170
	81	51	74	43	85	30		22	23	18	15	69	65	32	46	92	120
71	86	74	69	71	75	75		51	31	24	51	40	29	51	43		70

W   E

																	cm
		72	28	12	12	10			17	22	26	35	70				340
	80	16	16	16	8	12			10	11	17	22	61				270
86	58	58	51	44	40	58	35		31	37	20	61	69	92			220
45	17	29	26	27	24	31	20		15	18	57	71	31	26	36		170
	23	21	34	26	20	7	12		34	85	55	22	89	92			120
	38	23	23	22	20	17	8		90	67	72	72	72	83			70

105   90   75   60   45   30   15   0   0   15   30   45   60   75   90   105   120

Distance from center of tree (cm)

Fig. B.2. The distribution of light (as a percentage of full sun) within the crown. Vertical line is the center of the crown.

S								N								Distance above Ground (cm)
		31	29	29	100	24	5									270
	18	9	6	6	6	12	4	12	79	3	9					220
88	10	6	4	4	77	53	70	77	6	11	8	21				170
6	82	71	6	6	11	6	6	91	14	9	18	27	10			120
	97	8	8	6	6	7	7	15	5	5	6	7	8	10	59	70

W								E								
			59	100	6	9	100	6								270
	29	11	15	15	6	9	24	67	6	5						220
7	7	7	7	8	6	10	99	92	7	8	92	11	85	81	92	170
6	4	5	4	4	5	7	3	15	28	28	5	3	3	5	92	120
10	14	27	7	5	86	92	4	10	9	8	90					70

| 105 | 90 | 75 | 60 | 45 | 30 | 15 | 0 | 0 | 15 | 30 | 45 | 60 | 75 | 90 | 105 | 120 |

Distance from center of tree (cm)

Fig. B.3. The distribution of light (as a percentage of full sun) within the crown. Vertical line is the center of the crown.

Distance above Ground (cm)

S   N

						16	19	24	38	43			270
	28	10	9	7	11	12	22	29	33	29	52		220
2	1	12	76	76	9	24	5	12	14	29	78	11	19	170
	14	9	6	5	5	4	9	9	19	14	19	29	120
	81	9	9	6	5	2	4	5	25	9	14	18	70

W   E

						19	76	67	19	29				270
			19	14	10	76	20	100	29	12	5			220
	29	19	17	8	10	9	10	10	11	79	21	26		170
	14	5	7	4	5	10	53	7	4	14	19	48		120
6	13	8	10	3	5	4	4	4	5	6	9	3	20	29	70

90 75 60 45 30 15 0 0 15 30 45 60 75 90 105 120

Distance from center of tree (cm)

Fig. B.4. The distribution of light (as a percentage of full sun) within the crown. Vertical line is the center of the crown.

188

S
N

Distance above
Ground (cm)

				17	46	21	75						270
		35	26	17	12	25	27	17	25	33			220
26	15	13	10	13	9	13	14	17	18	21	29		170
78	78	78	13	13	4	8	12	14	15	7	13	29	120
79	70	25	9	57	4	6	8	8	7	9	15	26	70

W
E

			26	16	30	83							270
			30	20	17	17	29	52	21	26	43		220
70	48	78	18	17	15	13	11	15	15	13	20	35	170
	13	13	83	10	9	9	9	46	14	20	25		120
30	17	10	9	9	61	30	4	2	8	25	11	21	25	43	70

90 75 60 45 30 15 0 0 15 30 45 60 75 90 105 120

Distance from center of tree (cm)

Fig. B.5. The distribution of light (as a percentage of full sun) within the crown. Vertical line is the center of the crown.

Fig. B.6. The distribution of light (as a percentage of full sun) within the crown. Vertical line is the center of the crown.

S   9am   N   Distance above
                                                                         the ground (cm)
79	68	2	2	2	2	2	12	2	2	52	3	5	7		2.3m
72	73	11	57	2	2	1	1	2	29	3	3	4	5	10	1.5m
5	9	19	4	19	2	2	7	5	6	5	7	33	10	13	1.0m

W   9am   E
4	3	3	3	3	2	2	4	2	2	3	4	31	96	100	2.3m
4	3	3	2	2	2	2	13	20	95	2	1	4	10	90	1.5m
5	19	4	19	2	2	1	10	2	2	4	100	13	13		1.0m

S   11am   N   2.3m
100	12	3	2	2	2	1	2	2	2	2	1	10	3	4	1.5m
100	100	8	12	2	2	1	29	1	1	1	21	3	19	8	1.0m
4	4	4	3	3	2	2	1	1	1	1	2	2	4	4	

W   11am   E
5	5	3	2	2	2	1	1	2	2	2	2	2	3	62	100	2.3m
5	16	3	3	2	2	2	1	3	2	37	1	4	8	8	100	1.5m
25	2	1	75	9	2	1	1	2	2	3	16	4	6	100	1.0m

S   1pm   N
100	100	100	2	2	2	1	3	1	1	1	1	1	2	2	3	2.3m
66	56	94	100	2	2	2	1	3	5	19	3	2	2	3	3	1.5m
2	3	25	3	2	2	2	41	1	1	1	1	2	2	1	3	1.0m

W   1pm   E
2	90	7	1	91	2	20	1	1	1	1	2	2	2	5	2.3m
38	3	2	1	3	1	2	42	1	1	1	1	1	3	6	1.5m
100	13	4	3	2	1	1	1	1	1	25	2	2	3	3	98	1.0m

S   3pm   N
97	97	14	62	3	2	14	1	1	1	2	1	7	1	1	3	2.3m
97	97	97	97	2	2	3	1	1	8	1	2	2	2	3	3	1.5m
27	93	33	3	3	4	30	1	1	13	3	1	1	1	1	1	1.0m

W   3pm   E
97	97	97	3	2	2	69	1	6	5	2	3	3	1	1	3	2.3m
97	97	97	12	2	2	1	1	1	52	1	1	1	1	1	3	1.5m
100	2	2	1	7	13	3	1	1	1	1	4	3	4	3	1.0m

140 120 100 80 60 40 20 0   0 20 40 60 80 100 120 140
Distance from the center of the the tree (cm)

Fig. B.7. The distribution of light (as a percentage of full sun) within the crown for one tree at four different times. Vertical line is the center of the crown.

Distance above
the ground (cm)

S 9am .... **N**

100	11	13	13	11	15	10	3	3	5	6	32		2.3m
100	11	7	6	77	4	2	3	2	30	6	6	11	10	1.5m
	88	74	2	3	3	3	1	2	2	2	2	4	4	1.0m

W 9am .... **E**

	20	11	8	6	5	10	6	7	5	5	100	26		2.3m
5	3	3	2	3	3	13	2	2	82	5	6	6	19	12	1.5m
	6	5	13	2	2	5	2	3	3	4	7	5	7	1.0m

S 11am .... **N**

	26	14	29	29	14	14	8	8	11	8	31		2.3m
11	6	9	13	6	4	5	5	9	10	13	22	31		1.5m
100	4	10	100	3	2	2	2	1	1	1	2	2	3	4	1.0m

W 11am .... **E**

	33	23	19	18	7	6	10	17	8	12	18		2.3m
9	4	7	7	4	3	3	5	29	24	48	6	56		1.5m
	5	2	1	2	2	7	1	2	4	4	67	3	3	1.0m

S 1pm .... **N**

	9	9	86	29	23	20	2	11	4	6	9		2.3m
	67	61	81	83	2	2	1	2	2	3	3	3		1.5m
25	6	5	3	2	2	50	1	1	1	2	1	2	2	1.0m

W 1pm .... **E**

	100	46	4	3	2	3	3	6	5	6	100		2.3m
3	3	2	1	80	4	1	1	2	2	81	92	19	4	33	1.5m
6	6	2	2	2	1	1	1	1	1	3	4	3		1.0m

S 3pm .... **N**

	57	7	93	5	4	2	2	3	3	3	7		2.3m
	13	6	6	5	2	1	1	2	3	3	5	7		1.5m
3	3	1	1	90	2	3	1	1	1	16	3	11		1.0m

W 3pm .... **E**

	100	7	5	3	2	3	1	2	3	9	100		2.3m
77	3	5	3	1	1	1	2	10	2	7	4	3		1.5m
	1	28	66	2	2	2	2	1	1	3	2	7		1.0m

140 120 100 80 60 40 20 0 0 20 40 60 80 100 120 140

Distance from the center of the the tree (cm)

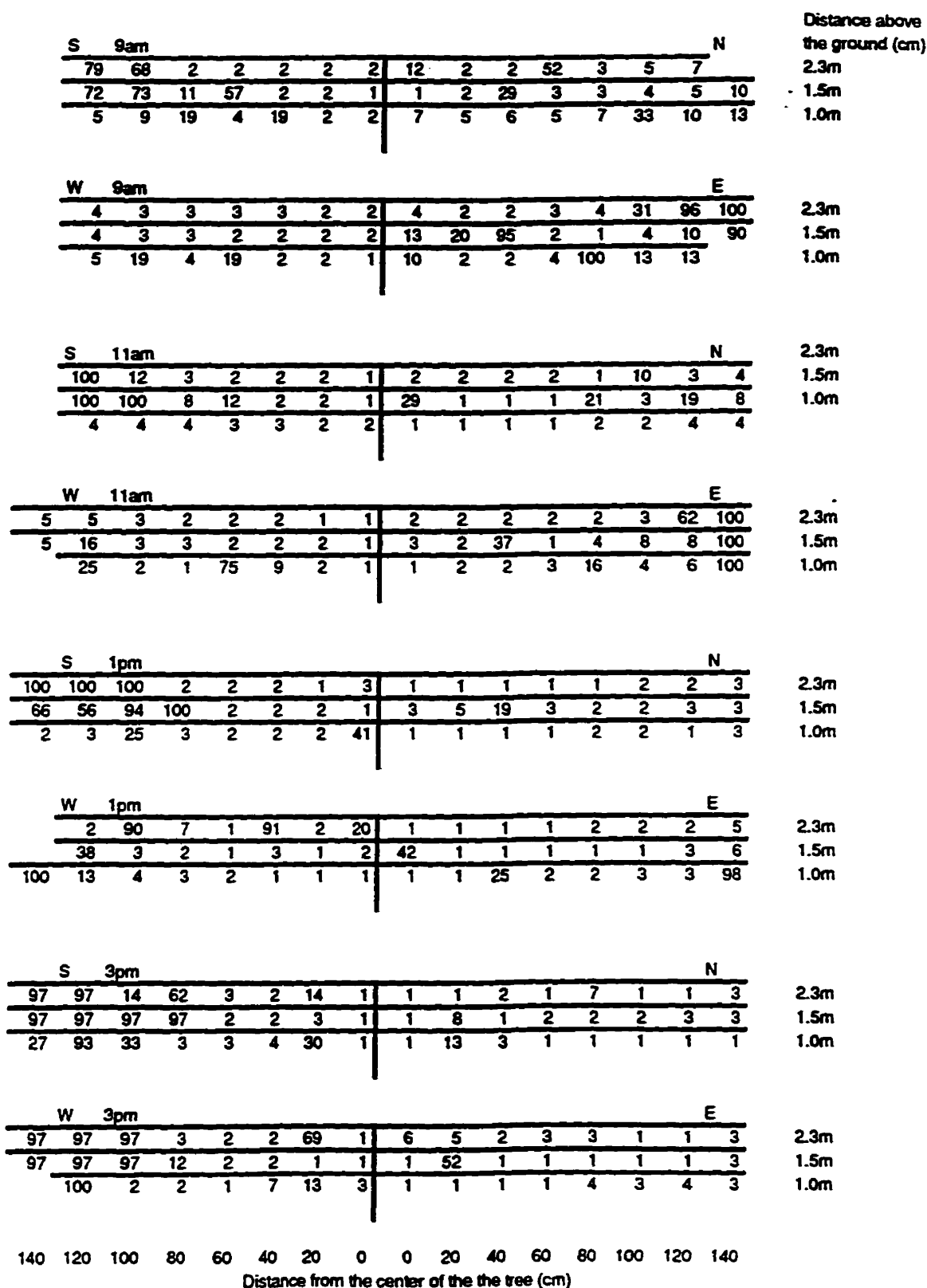**Fig. B.8.** The distribution of light (as a percentage of full sun) within the crown for one tree at four different times. Vertical line is the center of the crown.
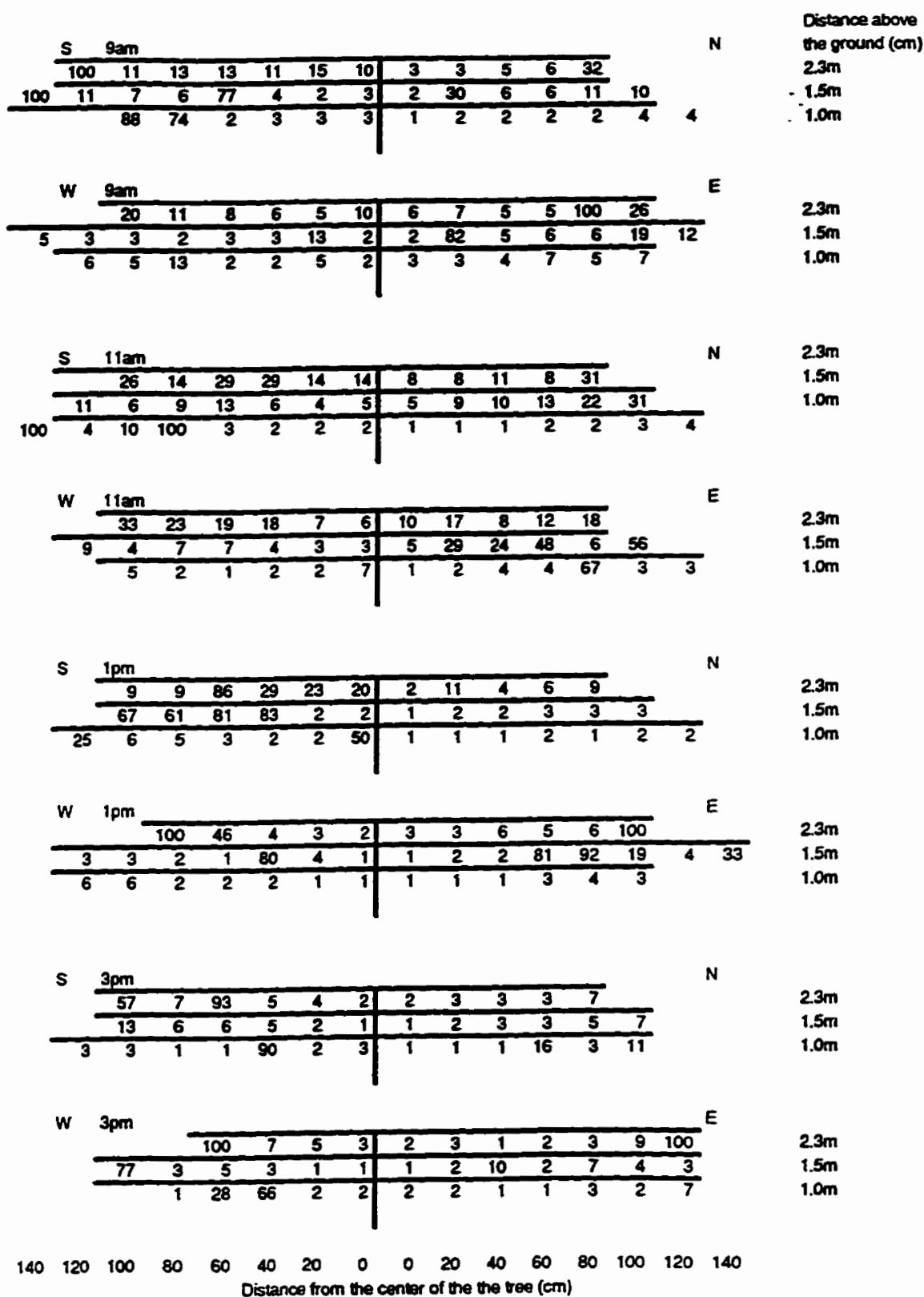
APPENDIX C. Spectral distribution in full sun.

Wavelength (nm)	Intensity (μw $cm^{-2}\ M\mu^{-1}$)	Wavelength (nm)	Intensity (μw $cm^{-2}\ M\mu^{-1}$)
400	50	587	150
412	77.5	600	147.5
425	90	612	147.5
437	112.5	625	147.5
450	147.5	637	146.5
462	153	650	141.5
475	160	660	139.5
487	161.5	675	132.5
500	150.5	687	120
512	147	700	110.5
525	139.5	712	102.5
537	134.5	725	90
550	134.5	730	86
562	139	737	83.5
575	143	750	77

APPENDIX D. Spectral distribution in 60 % shade.

Wavelength (nm)	Intensity (μw cm^{-2} Mμ^{-1})	Wavelength (nm)	Intensity (μw cm^{-2} Mμ^{-1})
400	20	587	66
412	31	600	66
425	40.5	612	66
437	50.5	625	65
450	65	637	65
462	69	650	62
475	71	660	61
487	70.5	675	58.5
500	68.5	687	52.5
512	66.5	700	49
525	64	712	46
537	61	725	39.5
550	61.5	730	38.5
562	62.5	737	38
575	64.5	750	35

APPENDIX E. Spectral distribution in 80 % shade.

Wavelength (nm)	Intensity (μw cm^{-2} $M\mu^{-1}$)	Wavelength (nm)	Intensity (μw cm^{-2} $M\mu^{-1}$)
400	12.5	587	42
412	19.5	600	41
425	24.5	612	41
437	29.5	625	40
450	37.5	637	39.5
462	42.5	650	39.5
475	43.5	660	42
487	43	675	36
500	41.5	687	33.5
512	40	700	31
525	38.5	712	29.5
537	37	725	25
550	37	730	24
562	38	737	23.5
575	40.5	750	22

APPENDIX F. Spectral distribution in 92 % shade.

Wavelength (nm)	Intensity (μw cm^{-2} Mμ^{-1})	Wavelength (nm)	Intensity (μw cm^{-2} Mμ^{-1})
400	2.7	587	9.75
412	4.35	600	9.9
425	5.75	612	10.05
437	7.0	625	10.1
450	9	637	10.1
462	9.9	650	9.9
475	9.9	660	10
487	9.9	675	9.7
500	9.45	687	8.85
512	9.35	700	7.85
525	8.95	712	7.4
537	8.6	725	6.4
550	8.7	730	6.1
562	9.0	737	5.95
575	9.5	750	5.4

APPENDIX G. Spectral distribution in 96 % shade.

Wavelength (nm)	Intensity (µw cm^{-2} Mµ^{-1})	Wavelength (nm)	Intensity (µw cm^{-2} Mµ^{-1})
400	1.6	587	7.5
412	2.1	600	7.5
425	3.0	612	7.3
437	5.3	625	7.2
450	5.8	637	7.1
462	6.6	650	6.7
475	7.0	660	6.0
487	7.3	675	5.3
500	7.0	687	4.8
512	7.0	700	4.5
525	7.0	712	3.5
537	6.9	725	3.5
550	6.6	730	3.3
562	6.9	737	3.0
575	7.3	750	3.0