

Foliar Morphology and the Acclimation
of Shade Tolerant Conifers to Varying Light Levels

by

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Master's Thesis

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Preface

This thesis has been organized into three chapters, each of which is designed to stand independently of the others. The references cited in the introduction are included in the list of references for Chapter 1, the literature review. It is my hope that each of the three chapters will eventually be published in an appropriate journal; however, following collaboration with reviewers and co-workers, certain material will undoubtedly be deleted and/or new material included.

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education.

Introduction

Shade tolerant conifers are, in general, a neglected resource that is promoted only rarely silviculturally in the Pacific Northwest region. This situation is particularly unfortunate when one considers not only the vast genetic diversity that these species contain, but also the fact that they are among some of the most productive species in the world, as has been demonstrated for both the Pacific Northwest (Fujimori 1971) and Europe (Hamilton and Christie 1971). This thesis examines two aspects of the adaptations and acclimation in foliar morphology to shade by representative Pacific Northwest species. First, it examines the flexibility of plasticity that exists within these species and how this is related to their tolerance to shade. Second, it describes some costs associated with being highly shade tolerant and how a shade tolerant species acclimates to a dramatic and sudden change in light.

The ideas for this thesis originated from two major sources of interest and direction. The first was an undergraduate thesis that I completed at Oregon State University with Dr. William Emmingham. This undergraduate thesis described the changes in leaf morphology of advance regeneration western hemlock following clear and shelterwood cutting (Tucker and Emmingham 1977). The second source of direction came through the opportunity of working on a National Science Foundation grant with Drs. Thomas Hinckley and Jerry Leverenz. The objectives of this grant were to study the influence of shoot structure on net photosynthesis, water relations, leaf area development and productivity in conifers and were based on the general hypothesis that shoot

structure is a key factor in determining the shade tolerance and productivity of conifers.

This thesis is composed of three parts. Chapter 1 is a literature review of foliar morphology as it pertains to Pacific Northwest members of the Pinaceae. This review follows a progression starting with the anatomy of the individual leaf, continuing to the structure of the collective leaves on a branch or twig (i.e., shoot structure), then to the form or architecture of a whole tree, and finally, to the structure of a stand of trees and its foliage canopy.

The second chapter is a study of the plasticity of foliar morphology in sun and shade foliage of seven study species, and of how the evolution of members of the Pinaceae is related to this plasticity and, therefore, to shade tolerance. This chapter addresses the hypothesis that the plasticity of foliar morphology dictates shade tolerance in conifers.

The third chapter is basically an example of the practical application of the knowledge of foliar morphology and how it pertains to the acclimation of advance regeneration of Pacific silver fir (Abies amabilis Forbes) following clearcutting. It is based on the aforementioned work on western hemlock (Tsuga heterophylla (Raf.) Sarg.); however, where the previous research concentrated on changes in leaf morphology of the individual leaf, this present work examines changes in foliar morphology of the collective shoot and crown.

Chapter 1: Foliar Morphology--

A Review with Special Reference to the Pinaceae

1.1 Introduction to Chapter 1

The structure and function of leaves are of greatest importance when viewed as the assimilating and converting apparatus that houses photosynthesis--the primary life supporting system on earth. This paper reviews the wealth of literature on foliage structure as it relates to species and environment and as it influences function. This review will be principally restricted to information from the pine family or Pinaceae.

The significance of the foliar morphology of conifers is not without its practical ramifications. The shade tolerance of plants is largely displayed in their leaf morphology (Boardman 1977). The morphology of the foliage in turn affects its light capturing and hence photosynthetic capabilities (Leverenz 1980). This in turn affects the role in succession as well as the reaction of a species to silvicultural treatment (Minore 1979, Tucker and Emmingham 1977).

1.11 Conifer Evolution

The Family Pinaceae is in the order Coniferales which, along with the order Cordaitales, occupies an entire Division in the plant Kingdom--the Coniferophyta (Scagel et al. 1969). The pine family contains most of the ecologically and economically important genera of temperate zone conifers such as Pinus, Pseudotsuga, Tsuga, Abies, Picea, and Larix; with minor but notable exceptions are Sequoia, Chamaecyparis, Thuja, Juniperus, and Cupressus of the Taxodiaceae and Cupressaceae.

Before discussing foliar morphology of the pine family, it is important to understand the evolution of this family and the special constraints this may or may not have placed on morphological adaptations. The evolution of conifers dates to the Carboniferous Period (Florin 1951, Scott 1974) which predates the emergence of angiosperms in the Cretaceous Period (Regal 1977) by over 145 million years. During the Mesozoic Period, conifers were the dominant form of forest vegetation throughout the world (Florin 1963, Miller 1977). Since the Cretaceous Period, angiosperms with their more sophisticated flowering systems, their larger-diameter conducting elements (vessels), and their larger foliar structures have come to dominate in tropical and subtropical areas. However, modern conifers still dominate in many areas within the temperate zone particularly in the northern hemisphere, a good example being the Pacific Northwest of North America (Waring and Franklin 1979).

Much of the reason why conifers dominate a particular area can be linked to their foliar morphology; furthermore, conifer foliage can be seen as an architectural constraint on evolution within the group. In other words it is a morphological feature that confines (or canalizes) further evolution within a lineage and in doing so, the constraint becomes more important and interesting than any given adaptation (Gould and Lewontin 1979). The foliage of the Pinaceae shows definite progression from the needle-like shapes of Pinus and Picea to the more broad planar shapes of Tsuga and Abies which, however, are still largely constricted in form (see Chapter II).

1.12 Evergreen Versus Deciduous

With the exception of the genus Larix, the family of pines is composed of species with evergreen foliage that may persist for three (e.g., Pinus sylvestris) to over 50 years (e.g., Pinus longaeva) (Ewers and Schmid 1981). Most perennial angiosperms in temperate regions are deciduous; however, several species of Quercus, Rhododendron, Ceanothus, and Prosopis have evergreen foliage that may persist from a little more than one to five years.

In general, angiosperms have higher photosynthetic rates than gymnosperms, and in both groups deciduous foliage has higher rates than evergreen foliage (Mooney and Gulmon 1982). In spite of the higher rates of photosynthesis found in deciduous foliage, from the point of view of carbon and nutrient budgets, it is more expensive to produce a completely new set of foliage each year than partially replace the existing foliage complement (Mooney 1972).

Where conifers and equally large aborescent angiosperms are found together, such as in the Eastern North America, the conifers represent the early or occasionally, the mid-seral successional component (Bazzaz 1979) and the broadleaf trees the late successional or climax. Under these circumstances, conifers are generally found on younger, nutrient-poor sites, whereas angiosperms appear on the better developed and nutrient-richer sites. The extremely shade tolerant Tsuga canadensis is an obvious exception.

Conifers have characteristically much greater longevity than angiosperms (Clark 1982). Oak trees may live to be 500 to 1000 years old whereas Douglas-fir will live to be over 1000 years old and bristlecone pine in California has been dated to be over 5000 years old.

There are also some regions such as the Pacific Northwest where massive long-lived evergreen coniferous forests exist representing both pioneer, intermediate, and climax stages of succession. Only the nitrogen fixing broadleaf, red alder, is a major member of the pioneer group of species found in this region (Waring and Franklin 1979).

There are three main reasons for the dominance of conifers in the Pacific Northwest region and they are all linked to the evergreen characteristic of their foliage (Waring and Franklin 1979). First, the abundance in this region of coarse, highly leached, nutrient-poor soils derived for example from volcanic or glacial parent material cannot support a complete yearly turnover of foliage. Second, climates with prolonged and predictable summer droughts favor xerophytic conifer foliage over mesophytic deciduous leaves. Third, mild winters allow conifers to photosynthesize year-round and thus make up for relatively low rates of maximum photosynthesis during the summer.

By being nutrient and carbon conservative, conifers can be very competitive and also very productive (Cole and Rapp 1981). For example, Tsuga heterophylla on the coast of Oregon has been found to be among the most productive species in the world (Fujimori 1971).

1.13 Morphologic Variation

Two main types of variation in foliar morphology exist: (1) variation both within and between genetically similar individuals in varying microclimates; i.e., phenotypic variation (Leverenz and Jarvis 1980), and (2) variation among individuals of relatively dissimilar genetic material which may or may not be in varying microclimates; i.e.,

genotypic variation (Lewis 1968, Mergen et al. 1966, Pallardy and Kozlowski 1979).

Although phenotypic variation in leaf morphology is well documented for conifers, genotypic variation within any given species is not. The reason is simply that clonal material is much more difficult to obtain for conifers, and hence the genetic analyses have not been done. There is good reason to believe, however, that equally as much clonal variation exists in conifers as has been observed in angiosperms (e.g. Lewis 1968). For example, several species of the Cupressaceae have been cloned horticulturally through cuttings or grafting, and clones of these species have very distinctive foliar morphologies (e.g., Chamaecypeucis pisifera varieties aurea and filifera, and Juniperus chineis varieties columnaris and pyramidalis, Wyman 1965, Krussman 1972). With the advent of practical tissue culture and genetic engineering techniques to clone conifers, genotypic variation in leaf morphology along with other traits will be much better understood and, therefore, more easily selected for by plant breeders (Bonga and Durzan 1982).

Phenotypic variation of foliar morphology changes with varying microclimate. A characteristic example of this is the case of 'sun' versus 'shade foliage.' This subject is dealt with indepth later in this review; however, suffice to say that it is the result of both changes in light environment and varying soil moisture (Penfound 1931, Richter 1974).

1.2 Leaf Morphology of the Pinaceae

1.21 Early Work on Leaf Morphology

The significance of foliar morphology and foliage distribution has been studied extensively over the last century. In 1893 Groom wrote, in the Annals of Botany, on "The Influence of External Conditions on the Form of Leaves". In this article, he documented the increased thickening of leaves in association with increasing levels of light. In 1924 the text entitled "Physiological Plant Anatomy" by Haberlandt brought together a discussion of the significance of many plant structures. By then such topics as leaf chlorophyll content, sun-shade leaves, and the physiological significance of varying leaf anatomies were firmly entrenched in the literature.

From an ecologist's or a forester's point of view, one of the conceptually most important early works was the "Structure and Life of Forest Trees" by Busgen and Munch (1924) which was translated from the original German. Among other things discussed was the fact that the foliage of suppressed, understory trees was morphologically more characteristic of shade grown foliage than that found on the lower branches of a dominant tree in the same light environment. In addition, they discussed the branch forms of trees in open grown and stand grown situations which is of continuing importance in many aspects of silviculture.

More recent reviews have been compiled regarding leaf morphology from the stand point of its evolutionary and adaptive significance (Givinish 1978, 1979), its role in energy exchange (Gates and Papian 1971, Parkhurst and Loucks 1972, Taylor 1975) and its importance in

carbon and water balance (Bazzaz 1979, Grime 1979, Larcher 1975, Lewis 1972, Mooney 1972, Mooney and Gulmon 1982). There are, however, many questions that are unanswered (Grubb 1977) and perhaps even more so for conifers, because most of work has concentrated on broadleaf species.

1.22 General Characteristics

Although the shape of the leaves of members of the Pinaceae varies drastically from that of broadleaf angiosperms, the different cell and tissue types (epidermis, mesophyll, etc.) are very similar. The features that strongly characterize pine foliage, as compared to broadleaf foliage, are probably a high concentration of phenolic compounds and a suberized endodermis (Soar 1922).

Detailed descriptive work has been done on conifer leaf anatomy both for the entire order (Napp-Zinn 1966) and also for individual species (Owens 1968, Gambles 1974). Genotypic variation of the anatomy of conifer leaves is most commonly used for identification purposes. Such features as the placement of resin canals in the genus Abies (Liu 1971, Roller 1966) and the haploid or diploid nature of the stele in the genus Pinus (Mirov 1967, Sutherland 1934) can be very characteristic of a given species or hybrid (Keng and Little 1961).

The endodermal tissue, which surrounds the stele, is typically suberized in the Pinaceae, which gives the leaves the advantage of being able to regulate water flow from the stele to the mesophyll cells much like the casparian strip found with endodermal cells of roots (Soar 1922). This undoubtedly enhances the xerophytic nature of the family.

Heteroblasty, or ontogenic changes of leaf anatomy with developmental maturation, is a characteristic which is curiously absent

in the Pinaceae (Clark 1982), although present in some members of the Cupressaceae; e.g., Thuja, Juniperus, and Chamaecyparis.

1.23 Energy Exchange by Leaves

The transfer of energy between the leaf and the environment varies greatly with the anatomical and physical features of the leaf (Gates and Pipan 1971, Gates 1980). Silver cast replicas of shoots were used by Tibbals et al. (1964) to describe the energy balance for foliage of blue spruce and white fir. As ambient temperature and wind speed were varied, the exchange of solar and thermal radiation and the foliage's temperature and the thickness of its boundary layer were measured. This work helped define the drought and temperature avoidance characteristics of conifer foliage which, due to a much thinner boundary layer and a lower absorption of radiation per unit area, will stay cooler than broadleaf foliage. Because of the cooler foliage, the evaporative gradient and, therefore, the demand on transpiration are much less in conifer foliage than in broadleaf foliage.

The reflectance, absorbance, and transmittance of visible and nonvisible solar radiation are important not only from the point of view of energy balance and carbon and water balance, but also for detecting stress affected foliage by remote sensing (Puritch 1981). However, measurements of the optical properties of conifer foliage are difficult because a single leaf does not provide enough surface area for good spectrographic analysis. Work done with groups of leaves aligned side by side has shown that in Douglas-fir, for example, reflectance of wavelengths between 0.7 and 1.3 μ m is much greater in mature leaves of than in immature leaves (Woolley 1971). In addition, similar work has

demonstrated that transmittance of radiation by conifer leaves is almost zero (Leverenz 1978), in contrast to broadleaves where the transmittance can be quite high. Consequently, the spectral character of light under a dense conifer canopy is much different than at the surface of the canopy (Morgan and Smith 1982). What little light does reach the forest floor comes from the zenith directly overhead (Norman and Jarvis 1975).

1.24 Sun and Shade Leaves

Phenotypic responses of leaf morphology to environment are most obvious with leaves that have developed under different regimes of light and moisture. The factors that characterize 'sun and shade leaves' have been well documented for both broadleaf (Isanogle 1944, Peterson et al. 1976, Pieters 1974) as well as conifer species (Aussenac 1973, Larsen 1927, and Stover 1944). Less is known about the exact biochemical properties of the photomorphogenetic response than the resultant leaf morphology, but both are clearly a developmental response on the part of the apical meristem and the leaf primordia to varying wavelengths of light (Morgan and Smith 1982).

The following features of foliar morphology separate sun from shade foliage. With decreasing light, conifer shade leaves become thinner and in most cases broader. This can be observed by an increase in the ratio of leaf width to thickness if not just in the absolute measure of leaf width (Aussenac 1973, Tucker and Emmingham 1977). In the genera Picea and Pinus, however, shade leaves are actually narrower and with a lower width to thickness ratio as compared to sun leaves (Leverenz and Jarvis 1980, see Chapter II). This is interesting because in neither of these genera is there a differentiation between palisade and spongy mesophyll

cell types which could provide an explanation for their inability to produce a flat, planar shade needle. This could also be seen as a primitive trait because both Picea and Pinus appeared in the fossil record before other genera such as Tsuga, Pseudotsuga, and Abies (Miller 1977), which do produce more planar needles. In addition, both Pinus and Picea are relatively intolerant to shade which represents corroborative support because the flat planar form appears to be a necessary adaptation/acclimation to low light levels. Further work should be done on Larix and Cedrus which have similar leaf anatomies as Picea and Pinus but for which no analysis of leaf morphology has been published so far.

With increasing light intensity, foliage increases in thickness. This is largely due to an additional one or two layers of palisade mesophyll cells which have a larger concentration of chloroplasts than the thinner, shade foliage. Hence the 'sun leaf' is much better able to absorb and to utilize via, photosynthesis, the higher levels of light. Sun foliage is also a response of foliage to increased moisture stress. This response is most often exhibited in the upper crown of tall trees and in newly exposed trees that have not yet developed an extensive root system (Tucker and Emmingham 1977). It develops as a means of acclimating to increased light levels and evaporative demand. In the case of trees suddenly exposed to higher radiation levels, leaf number is not usually reduced; the number of leaf primordia are typically fixed, but dimensions of the leaf are not. These leaves are shorter and thicker with a much lower ratio of surface area to weight (Aussenac 1973). Such moisture stress effects on 'sun leaves' were well documented by Richter (1974) who partially severed xylem tissue in the

main stem of a Taxus brevifolia tree in order to produce more negative water potentials in foliage on epicormic shoots growing in shaded conditions in the lower crown. "Sun-like" foliage was produced where there had been shade foliage before severing. Clearly, both changes in light intensity/quality (Morgan and Smith 1981) and the energy load/moisture demand are responsible for the production of sun or shade features.

1.25 Leaf Mesophyll

The vast majority of the cells in any leaf is made up of a type of parenchyma cell known as mesophyll. The mesophyll tissue is normally divided into the chloroplast rich palisade mesophyll on the top and the spongy mesophyll beneath. The spongy mesophyll cells are loosely packed and, therefore, incorporate most of the exposed internal surface of the leaf which is the interface for gas exchange (Nobel 1974, Rand 1978).

One means of estimating the surface area available for gas exchange is by measuring internal surface area. Internal surface area can be measured geometrically from leaf cross-sections by assuming that mesophyll cells are cylindrical with hemispherical ends (Turrel 1936, Nobel 1976) or by using the frequency distribution of cell walls (Chabot and Chabot 1977, Weibel 1969). This latter technique is probably more accurate in accounting for irregularities of cell shape.

Nobel et al. (1975) reported for the broadleaf Plectranthus parviflorus that mesophyll internal surface area, expressed on a leaf area basis (A_{mes}/A), deviated only slightly from a linear correlation with leaf thickness. (Similar results were noted by Deans et al. (1982) for leaves of Juglans nigra.) As leaves increase in thickness, with

increasing illumination, a larger proportion of the ratio A_{mes}/A is in spongy mesophyll. Hypothetically this would benefit stand grown trees because this would reduce the mesophyll resistance to CO_2 absorption in the upper canopy where CO_2 concentration is lower. Because mesophyll resistance has no effect on the diffusion of water, transpiration would not change, but water-use efficiency would.

Nobel (1977) also reported that shade tolerant mosses, which have much lower photosynthetic rates than sun-tolerant species, also have much lower ratio of A_{mes}/A when compared to understory herbs and less tolerant shrubs. Similar work needs to be done also for forest trees of varying shade tolerances.

1.26 Leaf Surface Area

Leaf surface area is the most frequent parameter of foliar morphology measured and is being used increasingly for estimates of forest productivity on a stand on a per hectare basis (see Section 5). It poses a very special problem, however, since conifers as compared to broadleaf species have foliage is three-dimensional as compared to two-dimensional (Kvet and Marshall 1971, Drew and Running 1975). Projected leaf area becomes increasingly less representative of true leaf area as one goes from shade to sungrown leaves. This is particularly true for Pinus and Picea whose leaves lack any resemblance to a planar form even in deep shade.

There are several ways one can deal with this problem. First is to measure the leaf and then geometrically model its dimensions. For pines, this is actually quite practical and accurate since fascicle length and diameter can be measured easily (Beets 1978, Madgwick 1964).

For other conifers with more complex leaf form the problem becomes increasingly difficult (Kerner et al. 1977) and more amenable to a purely mathematical point of view. A second approach would be to coat the leaf or shoot with a substance and then measure the coating with the assumption that it is directly proportional to the surface covered (Thompson and Leyton 1971, Helbing and Kausch 1974). In the application of this technique, one assumes a complete, uniform coating. A third method, and the one most satisfactory for most conifers, is to measure the projected surface area as one would a broadleaf and then apply a correction factor based on the cross-sectional perimeter of the leaf versus its width (Barker 1968). The only drawback is that one needs an optical planimeter to measure projected surface area. They are available commercially but only at a relatively high cost. Designs for laboratory built models have been available for sometime (Davis 1966, Kramer 1937) but they are much less accurate than current commercially available models. In the future, video image analyzers, which can differentiate between healthy and chlorotic portions of leaves, will become state-of-the-art technology for measuring foliage surface area.

Leaf surface area on a dry weight basis or on a specific leaf area basis, is of interest not only for accurate biomass/leaf area estimates but also from a physiological and carbon and nutrient cycling standpoint. Most investigators have reported that conifer foliage becomes increasingly heavier per unit area with age or with increasing illumination (Tucker and Emmingham 1977, Del Rio and Berg 1979, Drew and Ferrell 1977). Such increases in dry weight could be due to:

(1) progressive deposits of cutin or epicuticular wax on the surface of the leaf or of suberin in the endoderms, (2) dry matter accumulation, or

(3) increases in photosynthetic waste products as suggested by Cole and others (1968). The trend of increasing foliage weight with age is, however, in contrast to recent work by Ford (1982) on highly productive pole-stage Picea sitchensis. He reported that needles generally lost weight as they aged.

1.27 Leaf Epidermis and Cuticle

Transpirational loss of water by leaves is controlled by leaf resistance which is composed of a stomatal and a cuticular component. Stomatal resistance is highly variable and can be regulated by the foliage (Running 1976) while cuticular resistance is generally high and only changes over long periods of time as the foliage ages or acclimates to changes in environment (Seymour 1980).

Stomatal complexity has been found to increase from cotyledons to primary leaves and then secondary leaves of Pinus radiata as the plant also becomes increasingly complex physiologically (Riding and Aitken 1982). Genotypic variation in stomatal anatomy was reported by Bo Larsen and others (1981) for Abies grandis where inland varieties had a much larger stomatal tube, that is, the stomate was much more deeply recessed in the epidermis, as compared to coastal varieties. Zobel (1973, 1975), studying variation of stomatal anatomy within the intergrading of the Abies grandis-Abies concolor complex, found that individuals on drier sites have larger numbers of adaxial stomata, a characteristic of Abies concolor, than individuals on moister sites. Populations of Abies concolor on moister high elevation sites in the Sierras have been shown to have a decreasing number of adaxial stomata which could be a result of selection favoring such individuals on these

sites (Hamrick 1976). Zobel also noted that stomata of west-side Cascade varieties of Abies grandis had a more sensitive response to decreasing relative humidity than did east-side Cascade varieties. Such findings have strong implications for the water relations and survival of these populations on drier inland sites.

Phenotypic variation in stomatal features was reported by Phillips (1967) who found that exposed sun leaves of Pseudotsuga menziesii had much more recessed stomates than shade leaves of the same tree and that the number of stomatal bands increased from shade to sun leaves. The number of stomata per unit length of leaf was found to increase from shade to sungrown leaves of understory and exposed Tsuga heterophylla (Tucker and Emmingham 1977). Such findings would suggest that in increasingly exposed environments, plants with higher numbers of stomates are favored because they are able to better regulate water loss. In addition, the greater number of stomates may enhance carbon exchange in sun as compared to shade leaves.

The cuticle is the result of the deposition of complex fatty substances known collectively as cutin and is found on the outer walls of epidermal cells (Esau 1977). As a protective sheath, cuticle is strongly impervious to water; it can be found on stems, leaves, fruits or any tissue which has an epidermis. The cuticle of the leaf usually generates great interest ecologically and physiologically because it acts as a major barrier to gas exchange, particularly water loss. In addition, it is found occluding the stomatal antichamber where it acts as a very effective antitranspirant. Jeffree and others (1971) in fact have reported that its presence in Picea sitchensis reduced transpiration by 67% and photosynthesis by 38%. Thus, the cuticle and

its associated waxy deposits have an important adaptive significance, particularly for plants faced with very xeric environments (Pallardy and Kozlowski 1980).

For conifers, which lack possibly more evolutionarily advanced mechanisms for avoiding the extreme moisture and temperature stresses of arid environments, such as pubescence (Elhringer and Bjorkman 1978), solar tracking (Elhringer and Forseth 1980), or the CAM photosynthetic pathway, the cuticle is of special importance. The very thick cuticle and sunken stomata which characterize the foliage of members of the genus Pinus act as an effective means of avoiding severe desiccation and controlling gas exchange.

Hanover and Reicosky (1971), studying six species of conifers found that the quantity and quality of surface waxes varied between and within species and within leaves of the same individual of a given species. Chronological development of surface waxes in Picea pungens has been shown to start in the stomatal antichamber and to progress from there to the more outermost epidermal surfaces. Also with time, the crystalline structure of the waxy substances degrades into a more uniform, amorphous coating on the leaf (Reicosky and Hanover 1976).

Genotypic variation in the thickness of the leaf cuticle of grand fir has been documented recently (Larsen et al. 1981). They showed that coastal provenances had significantly thinner (3.5 m) cuticles when compared to Cascade provenances (4.0-4.5 m).

In addition to acting as a major barrier to transpirational water loss, the leaf cuticle is also very effective in the reflectance of light. Glaucous foliage of Picea pungens was found to absorb far less light than non-glaucous foliage, particularly in the near UV or 350 nm

region of the spectrum (Clark and Lister 1975, Reicosky and Hanover 1978). This behavior is very similar to the effect of leaf pubescence of many desert angiosperms (Elhringer and Bjorkman 1978). When this leaf pubescence desiccates, it also effectively increases the reflectance of solar radiation.

1.28 Leaf Chlorophyll Content

Over the years, the leaf component that has received perhaps the greatest attention is chlorophyll, the pigment responsible for the absorption of solar radiation and its subsequent conversion in the photosynthetic process. Techniques have been well established for its extraction and quantification. Of particular interest has been the role that varying concentrations of this pigment play in the physiology of sun and shade plants (Gabrielsen 1948, Boardman 1977).

Recent studies have confirmed that chlorophyll content is greater, on a weight basis, in shade tolerant plants grown at low light intensities than in either shade tolerant or intolerant plants grown at high light intensities (Magnussen 1981, Armitage and Vines 1982). For example, Magnussen (1981) found 21.9 versus 7.7 mg chlorophyll/dm² in shade versus sun phenotypes of the same genotype of Abies grandis. It is interesting to note that chlorophyll content can also change in quite different ways over relatively short periods of time, as has been demonstrated with Norway spruce (Picea abies) (Hawkins et al. 1981). When seedlings of Norway spruce were subjected to a 50% decrease in light intensity, chlorophyll content decreased sharply. These rapid changes mean that foliage developed in the sun acclimates as it becomes older and mutual shading increases. These changes occur in both

deciduous (Wallace and Dunn 1980) and evergreen species (Hawkins et al. 1981), but may be of greater adaptive significance in the evergreens because any given leaf will be maintained for several years.

From a practical standpoint, leaf chlorophyll content is closely tied to soil nitrogen content and this, in turn, strongly dictates conifer site index as a measure of growth potential (Radwan and DeBell 1980). This is because nitrogen is an important element in the chlorophyll molecule and hence is often a limiting nutrient. Also the degradation of chlorophyll and associated chlorosis caused by, for example, solarization at high altitudes, can have a strong negative effect on seedling survival, growth and reoccupation of a site (Ronco 1970, 1972, and 1975).

1.3 Shoot Structure

The orientation of broadleaf branches and foliage can be generally assessed by the measurement of branch and leaf angles (e.g., Kieison 1978). These angles have been found to be of important adaptive and acclimative significance regarding both position in the canopy and tolerance to low light (Wylie 1951, Honda and Fisher 1978, McMillen and McClendon 1979).

Similarly, the structure of a conifer shoot, or the spatial arrangement of the collective group of leaves on a twig, is of major eco-physiological significance with regard to sun-shade acclimatizing and tolerance adaptations. When subject to a unidirectional source of light, the flat, planar shade shoots of Sitka spruce have higher rates

of net photosynthesis than sun shoots with their radially arranged leaves (Leverenz 1979, Leverenz and Jarvis 1980a).

The description of conifer shoot structure, however, presents a special problem because the quantification and expression of all the many leaf angles is particularly difficult. Shoot structure is an important component in a model of radiation penetration through forest canopies developed by Norman and Jarvis (1975) with Sitka spruce. Their model is very interesting because it deals with the very complex problem of how a canopy modifies incoming light. Therefore, the proper description of shoot structure is necessary in order to model accurately the light environment of a canopy. Unfortunately, the authors made the assumption that the foliar morphology of any given shoot is such that it casts a continuous and solid shadow when, in actuality, there are more often than not gaps between the needles.

Another method which has been used with conifers to quantify foliage geometry is the technique of optical diffraction analysis. Working with Pinus contorta, Kimes and others (1979) concluded that the distribution of needle angles is constant throughout the canopy and that this is a "characteristic of a large class of needle-bearing species." A major hypothesis of my study is that this is not true, not only for Pinus but for the entire Pinaceae (see Chapter 2). Had the authors worked with a more shade tolerant species with flat, planar needles of shade shoots, in contrast to the more upright needles of sun shoots, the differences in leaf angles would have been much more obvious.

An additional technique to measure the shoot structure of conifers, and one which has proven quite useful and accurate was developed by Daniels (1969) as part of a genetic analysis of the grand fir-white fir

complex. In this method, one simply views the shoot endwise and measures the upper and lower angles between foliage. With a planar shade shoot, both of these angles would approach 180° whereas with a sun shoot the lower angle would be much higher and the upper angle much lower (if not zero) due to the more upright foliage. Using this technique, the author was able to demonstrate very significant differences not only within an individual tree for sun and shade foliage, but also between different provenances of the same species.

Still another technique for measuring shoot structure was done with Norway spruce by Greis and Kellomaki (1981). Using the same endwise view of the shoot as Daniels (1969), they estimated the amount of foliage in the different quadrants or pie-shaped divisions of foliage radiating from the center of the twig. What they found were significant differences in phenotypic variation which they related to light conditions and potential photosynthesis.

The most satisfactory method for measuring shoot structure is probably the silhouette area ratio or SAR (Leverenz 1980). With this technique, the surface area of the shoot silhouette viewed from above is expressed as a function of the total leaf area of that shoot. Species with very planar shade shoots, such as grand fir, will have a SAR of 1.0 whereas lodgepole pine, with its radial arrangement of leaves will have a SAR of less than 0.5. The shade tolerance of a given conifer species will be dependent on its ability to produce planar foliage in order to intercept light from the zenith under a dense canopy. Furthermore, species that have planar foliage will carry more foliage than species which do not and, therefore, the former species will be more productive

than the latter. These two hypotheses are part of a larger project for which this study is to provide supporting data.

1.4 Tree Architecture and Canopy Form

The topic of the adaptive geometry of trees has received considerable attention particularly as it relates to angiosperms. Perhaps the most well-known model that illustrates the adaptive significance of tree geometry, at least for temperate species, is one developed by Henry Horn (1971). Like many models, Horn's makes some assumptions which are oversimplified. However, it provides an important framework to look at the problem. The model, for example, provided theoretical confirmation of the tolerance ratings of trees which until that point had been based almost completely on simple comparative observations.

A whole series of models have been developed to describe the many varied forms of tropical trees (Halle et al. 1978, Tomlinson and Zimmermann 1978). These models are not without their problems either. For example, due to plasticity of tree architecture, environmentally induced variations have been found in one of these known as Auberville's model, where three distinctly different crown shapes are described by the same architectural model (Fisher and Hibbs 1982). Like Horn's model, this model is, regardless of its problems, a useful heuristic device.

Perhaps the most widely used concept for describing branching morphology is the bifurcation ratio which was originally developed by geomorphologists for analyzing river drainages (Horton 1945). The

ratio, an index of the degree of branching, has proven useful, for example, as a component in a complex mathematical model of the mechanical design of trees (McMahon and Kronauer 1976) or simply in describing the open-grown versus the shade-grown crown structure of sugar maple (Steingraeber et al. 1979).

In comparison to most angiosperms, conifers are relatively simple in their architecture with a determinant monopodial form. Variation in growth form is only really found with apparent suppression of normally strong apical dominance. This can be seen, for example, in the short terminal shoot condition of juvenile longleaf pine (Pinus palustris), better known as its "grass stage." Also trees produce a branchy "wolf tree" form when grown free of competition and, conversely, some species when strongly suppressed in the understory will restrict apical dominance and display a broad plate-like or umbrella-shaped crown, in which yearly lateral branch increment exceeds height increment (Kohyama 1980, Greis and Kellomaki 1981, see Chapter 3). All of these growth forms, that is, the "grass stage," the open-grown "wolf tree" and the umbrella- or plate-shaped crown are merely variations on the same determinant monopodial form. This lack of diversity in growth form may provide a clue to why conifers as a group, are so intolerant to shade in that the only examples of conifers, at least in the Pacific Northwest region, which have indeterminate growth form, and, therefore, have a broad branch form, are western hemlock and two members of the Cupressaceae, redcedar incense-cedar and Alaska cedar. All of these species are relatively shade tolerant. Nonetheless, like other conifers they are typically confined to the upright monopodial form which can be

regarded as the epitomy of an architectural constraint (Gould and Lewontin 1979).

1.5 Stand Structure and Leaf Area Index

The ultimate assemblage of foliage is, of course, the stand in which foliar morphology is represented by stand structure. Perhaps the most universal law of plant stand structure is the $-3/2$ power law for self-thinning. First developed by Japanese scientists working with soybeans (Kira and Shinozaki 1956), it has since been applied to broadleaf trees (White and Harper 1977) and to conifers, with some important implications for management (Tadaki and Shidei 1963, Drew and Flewelling 1977, 1979). Basically, the law states that when one plots the log of stand density versus the log of mean plant dry weight or mean stem volume, that various stands will all lie within an upper limit whose slope will always equal $-3/2$. This law is amazingly consistent and, hence, has proven to be a very powerful tool for predicting stand dynamics of many species. The relationship has furthermore been postulated to be controlled by leaf area as opposed to plant weight (Westoby 1977).

The quantity of foliage supported by an individual tree or a stand of trees can also be related to stem density of stem cross-sectional area as was originally postulated by the Pipe Model theory (Shinozaki et al. 1964, Fujimori et al. 1976). This relationship between foliage quantity and cross-sectional area was further developed by Morikawa (1970) and by Grier and Waring (1974) who correlated foliage biomass or area to sapwood cross-sectional area. Since the sapwood of conifers

acts as the principal transport path and storage source of water, this allometric relationship has functional support. Equations based on this relationship have proven useful in modeling stand leaf area as expressed by the leaf area index (LAI) (Gholz et al. 1976, 1979; Grier and Running 1977; Whitehead 1978), although best results are obtained when equations are developed for individual stands.

Leaf Area Index has in turn been correlated with stand primary productivity (Kira 1975, Emmingham 1982). This is of particular interest in the Pacific Northwest where the climax coniferous forests carry the highest leaf area indices in the world (Waring and Franklin 1979). Thus, it is no mere coincidence that the region also has some of the most productive forests in the world (Fujimori 1971). The productivity of Pacific Northwest forests rival or surpass even those of the tropics (Gordon et al. 1982).

1.6 Summary and Conclusions

Conifers in general, and the Pinaceae in particular, have been reviewed with many comparisons drawn between their foliar morphology and between them and deciduous angiosperms. In general, conifers are consistently constrained by the architecture of their leaf anatomy, their shoot structure and their canopy structure. At each level, they are confined in their capacity to produce a broad planar shade-tolerant form. However, there appears to be enough adaptive advantage in the evergreen foliage to enable them to be equally as productive as the most productive broadleaf tropical forests.

Chapter 2: Plasticity of Foliar Morphology and the Evolution of Shade Tolerance in the Pinaceae

2.1 Introduction to Chapter 2

Forest ecologists have endeavored for many years to obtain a better understanding of the concept of shade tolerance, particularly as it relates to forest trees. Shade tolerance is generally accepted as the capacity of a plant to develop and grow in the shade of other trees (Shirley 1943) in a more or less competitive manner (S.A.F. 1944). The topic has been discussed widely and researched since at least the early 1900's (Zon 1907, Smith 1908) and there have even been attempts to quantify the degree to which any species is a "sun" or "shade" plant (Burns 1923, Ashe 1915, Graham 1954). To date, however, the best method of differentiating species is simply based on field observations which rank associated species in a relative listing (Minore 1979) onto which different shade tolerant levels can be arbitrarily scored as very tolerant, tolerant, intolerant, etc. (Baker 1950).

Obviously a more accurate and precise system needs to be developed, but even controlled environment studies are fraught with inconsistencies as compared to field observations. For example, Krueger and Ruth (1969) described the relationships between net photosynthesis and light in four Pacific Northwest species; using the compensation point to rank species, red alder was found to be more tolerant than western hemlock. The main difficulty is that many other factors in addition to light may be affecting the plant's response to the understory environment (e.g. soil moisture, nutrients, and temperature). As an example, plants undergoing moisture stress have a lower tolerance to shade than plants that are

not. If one factor is not limiting, than surely another will be (Blackman 1905). In addition, to studies of the relative response of plants under optimal conditions are not always helpful when the concept is applied to field situations.

The intent of this study is to examine foliar morphology and its evolution in the Pinaceae in the hope of better defining the concept of shade tolerance in this family of plants. The basic hypothesis is that plasticity of foliar morphology, or the degree of difference between sun and shade foliage, reflects shade tolerance in conifers. This hypothesis is based on the assumption that the capacity of a conifer to tolerate shade lies in its ability to produce flat, planar foliage in the understory in order to intercept light from its most common source, the zenith (Norman & Jarvis 1975). Stated differently, for a conifer to be shade tolerant, it is not enough for it to be efficient at utilizing the multi-directional and high radiation on the top of the canopy, it must also have the capacity to utilize low light levels in the understory. Hence, conifers that exhibit the greatest plasticity will also be the most tolerant. If so plasticity of foliar morphology could be used as a measure of the shade tolerance of conifers.

This idea regarding plasticity is contrary to what has been found for broadleaf deciduous trees. This contrast is not necessarily contradictory given the differences in the evolution and the ecology of angiosperms in comparison to gymnosperms. Jackson (1965, 1967a, 1967b) found that, in terms of leaf thickness of angiosperm trees, the greatest plasticity was found between sun and shade leaves of intolerant species with sun leaves being much thicker than shade. This difference apparently is related to the environments from which these two groups

evolved. Conifers are evolutionarily much older than angiosperms (Scott 1974). The oldest member of the pine family was in the genus Pinus and probably appeared during the Jurassic some 150 million years before present (see Figure 1). Conifers with greater foliar plasticity, such as Pseudotsuga, Tsuga and Abies, evolved after the genus Pinus. It was these later groups that occupied more mesic sites and successionaly became more competitive with climax types. Angiosperms, on the other hand, emerged during the Cretaceous approximately 50 million years after the genus Pinus had emerged. The appearance of angiosperms revolutionized terrestrial ecosystems, many of which until that time had been dominated by conifers (Regal 1977). Flowering plants possibly made their early inroads in the tropical lowlands (Daubenmire 1978, Hickey and Doyle 1977, Rettallock and Dilcher 1981) and displaced the conifers, ultimately to upland sites at higher latitudes where their evergreen foliage gave them a competitive advantage on droughty, nutrient-poor sites (Waring and Franklin 1979). The rise in the dominance of angiosperms is attributed largely to flowers and fruits which predisposed flowering plants to interaction and coevolution with insects, birds and mammals who were diversifying during the same period and became resources as pollinators and seed and seed dispersers for many species (Regal 1977). An important additional reason for the angiosperms rise to dominance may have been their broad planar leaves which are adapted to intercepting light in the moist shady tropical environment. Hickey and Doyle (1977) postulated that early (not necessarily the earliest) angiosperms may have been streamside herbs in lowland, possibly estuarine, settings. These then moved into the forest

Figure 1. The Fossil Record for Five Genera of the Pine Family
 (from Miller 1977 and Florin 1963)

(Angiosperms)

Millions of Years	B.P.	Era	Period	Epoch	Pinus	Picea	Abies	Tsuga	Pseudo-Tsuga
	1 to 2		Quaternary						
	13			Pliocene					
	25	Cenozoic		Miocene					
	36		Tertiary	Oligocene					
	58			Eocene					
	63			Paleocene					
	135		Cretaceous						
	180	Mesozoic	Jurassic						

as understory shrubs. The authors claim to have fossil evidence to support this. Young (1981), in a rather controversial article, suggested that early angiosperms had vessels. If this is correct, it may have further promoted their competitive advantage over conifers.

Primitive conifers, unlike early angiosperms, did not have broad leaves. The vegetative organs of the Upper Carboniferous and Lower Permian conifers were scalelike and very similar to the modern Araucaria (Florin 1951). The leaves from fossils of the earliest members of the pine family are from the genus Pinus and are very much like those of modern members of the genus. Because they were now more elongated, they could, therefore, by drooping, assume a more horizontal shade tolerant form than their predecessors. Other members of the pine family that followed, e.g. Tsuga and Abies, became increasingly shade tolerant in leaf form. Thus shade tolerance seems to have appeared in conifers, or at least the Pineaceae, as a modification in a basic intolerant architectural plan in a group that never achieved great species diversity. In contrast, angiosperms appear to have had broad leaf foliage from the time of their origin which may have allowed a greater variety of ecological diversification, including the evolution of both intolerant seral and tolerant late successional forms. Each group of plants is contrasted by the inherent plasticity of leaf morphology which will direct, in part, the kinds of leaf architecture that can occur in new species. In many ways, and in a somewhat simplified sense, conifers and angiosperms can be viewed as coming from opposite ends of the tolerance spectrum. Conifers evolved new species that were more shade tolerant, whereas angiosperms may have evolved more intolerant species.

To test this hypothesis regarding plasticity in foliar morphology, differences in foliar morphology were examined between sun and shade foliage of codominant, stand grown trees of seven different species of the Pinaceae indigenous to the Pacific Northwest. The objective was to describe (1) intraspecific positional variations of foliar morphology within a canopy composed of similar trees of a given species, and (2) the interspecific genotypic variation of foliar plasticity between these seven species.

To achieve this, the shoot structure of seven species was measured by the Silhouette Area Ratio technique (Leverenz 1980) and measurements were taken of the gross leaf morphology. These morphological parameters were then compared to an existing tolerance rating (Minore 1979) and the conifer fossil record (Miller 1977, Florin 1963).

2.2 Materials and Methods

The species examined in this study are listed in Table 1 and were chosen to represent a broad range of shade tolerant taxa in the Pinaceae of the Pacific Northwest. Trees of each species (except Sitka spruce) were sampled at plots west of the Cascade crest where above ground biomass and leaf area index were also being examined. Therefore, leaf and shoot samples were taken in conjunction with the destructive biomass sampling process.

Each plot was a pure stand of the given species, and was of a relatively high site quality; that is, it represented a productive soil and micro-climate. Finding a pure, vigorously growing stand of all the

Table 1. Study Species and Site Locations. LAI is leaf area index, site quality I is the highest, V the lowest.

Species *	Location	Elevation	Age	LAI	Site Quality
<u>Abies grandis</u> (Dougl.) Forbes grand fir	On gentle west-facing slope of Devil's Pk., 5 km NW of Conway, WA	300 m	-	-	II -
<u>Abies amabilis</u> (Dougl.) Forbes Pacific silver fir	On south slope of Boulder Ridge, along southern boundary of Cedar River Watershed	1200 m	60-90	14	III
<u>Abies lasiocarpa</u> (Hook.) Nutt. subalpine fir	On Maiden Pk. Ridge approx. 5 km west of Deer Park Ranger Station	1650 m	85-120	6.6	IV +
<u>Abies procera</u> Rehder noble fir	On SE slope of Larch Pk. in the Capital Peak area, SW of Olympia, WA	800 m	14 ± 2	12.2	III -
<u>Pseudotsuga menziesii</u> (Mirb.) Franco Douglas-fir	On gentle west-facing slope of Devil's Pk., 5 km NW of Conway, WA	300 m	9 ± 1	9.8	II -
<u>Picea sitchensis</u> (Bong.) Carr.	On Quinault Indian Reservation approx. 9 km SW of Lake Quinault, WA	25 m	30-35	-	II
<u>Pinus contorta</u> Dougl. lodgepole pine	On Maiden Pk. Ridge approx. 4 km west of Deer Park Ranger Station	165 m	50 ± 5	6.6	IV

*Species citation according to Hitchcock and Cronquist (1973)

species on the same site was impossible. As site quality improved, other, more tolerant species became a component of the stand. It was felt that each site represented the highest quality where the particular study species would remain pure and free of competition from other species. All stands were young (less than 100 years) and had undergone canopy closure so that the lowest two to six whorls of branches were dead.

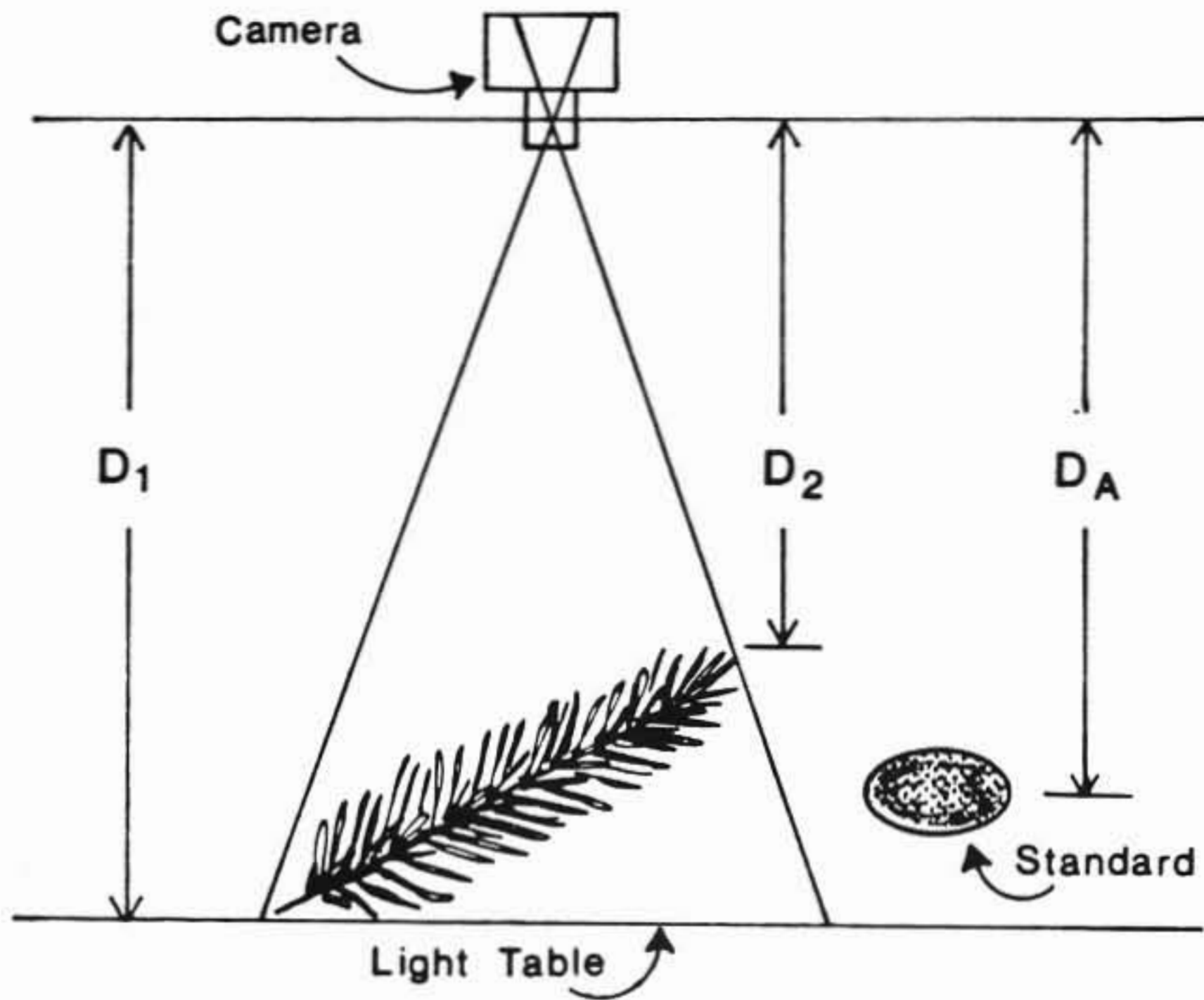
In each stand 3 or 4, 0.05 to 1 hectare plots were mapped with a 50 m tape, a hand compass and a clinometer. Diameter at breast height (1.37 m from ground surface) was measured on all trees within each plot, and five trees were selected to represent the range of diameters sampled. These trees were then harvested, the bole divided into 2 m intervals, the live and dead branches and the bole were separated, weighed and then subsampled, the subsample weighed and these subsamples returned to the laboratory for measurements of bole, twig and foliage biomass and specific leaf area to calculate the leaf area index of the stand. Foliage biomass and specific leaf area were determined for the current, 1, 2 and 3 plus age classes.

Before branches had been removed from the study trees, two co-dominant trees were selected and the lowest live branch and a branch from the upper crown were selected for separate samples of leaf and shoot morphology. This gave a representative sample of the extremes of sun and shade foliage throughout the crown. In addition, branch angles could be measured. Except for noble fir, only current foliage was sampled. In some cases with nobel fir, the current cohort was represented by shade leaves that were extremely suppressed with obviously stunted growth.

Leaf samples were immediately placed in formalin fixing solution (Johansen 1940) to preserve their form. Transverse, hand-sections were made at the mid-point of each of 5 leaflets, from one sun and one shade branch for each of two trees; that is, there were 10 sun and 10 shade leaves from each species. Microscopic measurements of leaf width and thickness were taken on each sample.

Shoot structure was sampled on sun and shade shoots taken from each of the five harvested trees (i.e., 5 samples from each type of shoot from each species). Occasionally, samples were also taken from nearby suppressed individuals if the five study trees did not contain a representative of this crown class. Shoot structure was measured by means of the silhouette area ratio (SAR) method (Leverenz 1980). This is the area of the shoot silhouette as viewed from above, divided by the area of all the leaves detached from the shoot, and is a measure of how the leaves on the shoot are oriented and, because of this orientation, how much overlap occurs. For example, a shoot with very horizontal leaves such as those of a shade shoot of grand fir, may have a SAR approaching 1.0 (i.e., no overlap, planar structure) whereas a sun shoot with much more upright leaves, may have a SAR of less than 0.5.

The procedure for measuring silhouette area ratio was as follows: (1) branch angle was recorded in the field with a clinometer for each shoot, (2) samples were then clipped, (3) suspended vertically in boxes with partitions to prevent crushing, (4) wrapped in plastic to prevent desiccation, (5) transported to the University of Washington and (6) stored at -10°C . Normally within two weeks of harvest, samples were positioned at their original branch angle on a light table that provided a single unidirectional source of light (Figure 2). With the aid of a



$$D_A = \left(\frac{2}{\frac{1}{D_2^2} + \frac{1}{D_1^2}} \right)^{1/2}$$

Figure 2. Photographic technique for determination of silhouette area ratio

copy stand, they were photographed from directly overhead onto 35 mm Kodak 2415 technical pan film with a 50 mm lens. Also in each photograph, a standard of known area was positioned in such a way that errors in silhouette area at opposite ends of a shoot and, therefore, at different distances from the lens, could be accounted for and eliminated (see equation in Figure 2).

The negatives were developed to high contrast and printed onto Kodalith type 3 ortho film with the aid of a standard photographic enlarger and developed with Kodalith Super RT developer. The resultant transparencies of foliage silhouettes and their respective standards were then measured with a LiCor Model 6000 surface area meter. Shoots had been stripped of foliage in order to measure their projected surface area with the leaf area meter. The silhouette areas were corrected to their true area by means of the standard. In addition, the area of the naked stem that was visible on the shoot was recorded and subtracted from the silhouette area.

2.3 Results and Discussion

Measurements of foliar morphology for sun and shade foliage have been summarized in Table 2, which lists species in order of decreasing shade tolerance. Shade leaves are in all cases thinner and narrower than sun leaves for any given species and all species except subalpine fir have shorter shade leaves. There is, however, no clear trend involving these parameters with regard to shade tolerance as has been observed for leaf thickness of deciduous trees by Jackson (1967). The ratio of leaf width to thickness (W/T) in most cases increases from sun

Table 2. Sun and shade, leaf and shoot morphology for seven Northwest species of the Pinaceae. Measurements of leaf length, width and thickness are in millimeters, W/T ratio is the ratio of leaf width to thickness, SAR is the silhouette area ratio. All Measurements are followed by the standard error of the mean.

Species *	Type	Leaf Length	Leaf Width	Leaf Thickness	W/T Ratio	Shoot SAR
<u>Abies amabilis</u>	Sun	32 ± 1.3	2.33 ± .029	0.88 ± .02	2.6 ± .06	0.45 ± .02
(Pacific silver fir)	Shade	18 ± 1.2	1.49 ± .023	0.52 ± .01	2.9 ± .07	0.84 ± .06
<u>Abies lasiocarpa</u>	Sun	16 ± .69	2.09 ± .09	1.08 ± .04	1.9 ± .03	0.29 ± .03
(Subalpine fir)	Shade	18 ± 1.3	1.54 ± .02	0.62 ± .01	2.5 ± .06	0.68 ± .04
<u>Abies grandis</u>	Sun	46 ± 2.5	2.49 ± .01	0.94 ± .02	2.7 ± .07	0.38 ± .00
(Grand fir)	Shade	33 ± 1.2	2.10 ± .02	0.64 ± .01	3.3 ± .06	1.00 ± .07
<u>Picea sitchensis</u>	Sun	19 ± .87	1.60 ± .05	0.95 ± .02	1.7 ± .03	0.44 ± .04
(Sitka spruce)	Shade	18 ± 1.4	0.96 ± .02	0.73 ± .02	1.3 ± .03	0.88 ± .05
<u>Pseudotsuga menziesii</u>	Sun	22 ± .75	1.28 ± .02	0.63 ± .01	2.0 ± .05	0.51 ± .04
(Douglas-fir)	Shade	20 ± .84	1.02 ± .04	0.40 ± .01	2.6 ± .13	0.84 ± .04
<u>Abies procera</u>	Sun	29 ± 2.1	2.20 ± .02	0.93 ± .04	2.4 ± .14	0.34 ± .02
(Noble fir)	Shade	13 ± .39	1.16 ± .03	0.52 ± .02	2.2 ± .10	0.72 ± .02
<u>Pinus contorta</u>	Sun	56 ± 2.2	1.66 ± .03	0.94 ± .02	1.8 ± .03	0.15 ± .02
(Lodgepole pine)	Shade	25 ± .73	1.14 ± .03	0.66 ± .02	1.7 ± .04	0.29 ± .04

* Species listed in order of decreasing shade tolerance (Minore 1979).

to shade leaves, which indicates a relatively broader shade leaf that should be more efficient at absorbing light in the understory. This is similar to what has been found for leaf width in absolute terms (i.e., not as a ratio) for suppressed understory Tsuga heterophylla saplings (Tucker and Emmingham 1977).

However, in this study, there are three cases where the width to thickness ratio actually decreases from sun to shade. Two of these species, Picea sitchensis and Pinus contorta lack a differentiation between palisade and spongy mesophyll in the leaf lamina and, therefore, may be unable to produce a broad shade leaf. Indeed, all broad-leaf angiosperms and all other genera of the Pinaceae, except Larix and Cedrus, produce distinctly different palisade mesophyll in sun and shade foliage. The palisade cells are important in allowing development of broad laminar leaf form; the ability to produce palisade mesophyll could be viewed as an evolutionarily advanced (or derived) trait in the Pinaceae since Picea and Pinus, both lacking in palisade mesophyll, are the geologically oldest genera of the Pinaceae (see Figure 1.). Others of the Pinaceae, including Abies, Tsuga, and Pseudotsuga, appear after Pinus and Picea in the fossil record. In addition, Abies, Tsuga and Pseudotsuga all produce palisade mesophyll in relatively broad shade leaf lamina.

In contrast to Pinus contorta and most Pinus spp., Picea sitchensis is ranked as moderately tolerant to tolerant to shade; however it also lacks palisade mesophyll. This ability to grow in moderately shaded environments may be due to the fact that the range of Picea sitchensis is principally limited to the immediate coastline of the Pacific Northwest, known as the fog-belt, where the prevalent light is diffuse

and may not favor a conifer with broad shade leaves. In spite of its inability to produce a laminar leaf structure, Picea sitchensis is capable of producing a shade shoot structure (0.85 SAR) and this shoot has a very efficient quantum yield (Leverenz and Jarvis 1980).

Abies procera also showed a decrease in the width to thickness ratio from sun to shade foliage. In contrast to Picea sitchensis, this was thought to be an artifact in that this is the only species in which highly suppressed and stunted shade foliage was sampled.

The characteristic which showed the greatest difference between sun and shade foliage and, hence the greatest plasticity within the tolerant species, was the silhouette area ratio. Grand fir was the species which showed the greatest plasticity of foliage SAR ($\Delta = 0.62$) and the highest absolute SAR which was very nearly 1.00 or completely planar in orientation. Clearly, a shoot of this form is well adapted to intercepting understory light. Three species exhibited the second highest plasticity of SAR ($\Delta = \sim .40$). These were Abies amabilis, A. lasiocarpa and Picea sitchensis, all of which are ranked tolerant to very tolerant (Baker 1950). Pseudotsuga menziesii and Abies procera were next ($\Delta = \sim .35$) and these species are ranked intermediate and intolerant, respectively. Last was lodgepole pine ($\Delta = .15$) which is ranked as very intolerant.

Additional plasticity in the silhouette area ratios can be observed in these species if suppressed understory trees or foliage from the upper crown of large trees is included. For example, understory saplings of Abies procera and Abies lasiocarpa had foliage SAR's of 0.90 and 0.80, respectively while Picea sitchensis had SAR's of 0.90 and 0.30 for shade foliage of an understory sapling and for sun foliage from the

upper crown of a mature, dominant tree, respectively. Such observations suggest that plasticity within a single codominant individual is not as great as the maximum plasticity within the species where individuals may be found as saplings in a dense understory or as dominants, in very exposed environments. In addition, considerable genotypic plasticity may exist. Neither the genotypic or the maximum phenotypic expression of foliar and shoot structure plasticity were assessed in this study. This study was originally aimed at only describing these forms of plasticity within codominant individuals from one, pure stand. If one compares the SAR's found for shade foliage with the leaf area indices found for these species (Table 1 vs. Table 2), a strong positive relationship can be seen.

2.4 Conclusions

Through comparison of the fossil record, shade tolerance ratings and the leaf morphology of the Pinaceae, it appears that shade tolerance probably did not develop in this family of conifers until after the early Eocene. This is 50 to 60 million years before present and at least 5 million years after the emergence of Angiosperms which already had a broad planar leaf and hence, an inherent possibly pre- or exadapted (Gould and Urba 1982) advantage in tolerating shade. The presence of palisade mesophyll in the Pinaceae appears to be crucial in promoting shade tolerance. This is a variation on the needle-like foliage in conifers, which appears to have exerted a strong canalizing influence on the kinds of ecosystems conifers could occupy. Such architectural constraints (S. J. Gould and R. C. Lewontin 1979) clearly

are important in the evolution of this family of plants and in the conifers in general.

The silhouette area ratio is the parameter of foliage morphology most useful for measuring plasticity and its relation to shade tolerance in the Pinaceae. Abies grandis, which shows the greatest foliar plasticity and highest silhouette area ratio, should be the most shade tolerant. It is, however, ranked only 'tolerant' as opposed to the ranking of 'very tolerant' for Abies amabilis and A. lasiocarpa. New indications of relative shade tolerance in Abies grandis may be forthcoming when a maximum leaf area index is determined for this species. Leaf area index, a measure of the quantity of foliage carried, may in itself be the best indication of shade tolerance.

In conclusion, it should be noted that while this study dealt with only one aspect of intraspecific phenotypic variation in foliar morphology, intraspecific variation of differing genotypes would be of interest for future studies, particularly because this variation may provide a measure of the ability of a given clone to produce planar foliage, a high leaf area index, and hence a highly productive tree/stand.

Chapter 3. Adjustments of Foliar Morphology in the Acclimation of Pacific Silver Fir Advance Regeneration Following Clearcutting

3.1 Introduction to Chapter 3

Shade tolerant conifers are, by definition, capable of regenerating in the understory of mature stands. The potential of these understory trees as advance regeneration and their response when released with overstory removal has been recognized for quite some time (Hatcher 1964, Bellon and Kowalski 1968). Recently much attention has been given to the silvicultural implications of these post-logging residual trees, particularly on higher elevation sites in western North America. Ferguson and Adams (1980) pointed out that in northern Idaho, advance regeneration grand fir (Abies grandis (Dougl.) Forbes) on many sites can shorten the rotation and eliminate the necessity for site preparation and/or planting. Other investigators working in the Pacific Northwest (Halverson and Emmingham 1982) and the Intermountain Region (McCaughey and Schmidt 1982) with Pacific silver fir (Abies amabilis (Dougl. Forbes) and the combination of Engleman spruce (Picea englemanni Parry) and subalpine fir (Abies lasiocarpa (Hook.) Nutt.), respectively, have found on harsh sites that the surest and least expensive method to establish a new stand is by promoting advance regeneration.

Silvicultural manipulation is most successful when it takes advantage of the ecology of the species in question. Seidel (1977) working with Shasta red fir (Abies magnifica A. Murr.) and grand fir in central Oregon, observed that these species maintained relatively full

crowns even when heavily suppressed in the understory. This observation was attributed to their shade tolerance. Pre-logging stocking surveys of Pacific silver fir in coastal British Columbia have proven accurate in predicting the response of residual trees following release (Herring and Etheridge 1976). The use of this technique has been quite successful and advance regeneration Pacific silver fir is commonly used for regeneration at high elevation sites in this region. Rapid response to release has been reported for white fir (Abies concolor (Gord. and Glend.) Lindl.) and Shasta red fir trees having been suppressed for 40 years in the understory (Gordon 1973). Results will vary with different species/sites, but where they are present at sufficient stocking levels, the potential of advance regeneration should by no means be ignored.

In the management of advance regeneration, post-logging natural regeneration can often complement or compete with the residual trees. On a favorable site in western Washington, post-logging natural regeneration of Pacific silver fir outgrew and dominated vigorous residual trees (Wagner 1980). The combination of a successful population of advance regeneration trees and the large number of post-logging natural regeneration on this site resulted in an extreme stand density of 100,000 trees per hectare. In such a case, density control must be included in order to maintain tree growth.

In contrast, in the boreal forest of Canada, the growth of advance regeneration Englemann spruce and subalpine fir was so superior to post-logging natural regeneration that authors predicted that they would be merchantable decades before the natural regeneration (Herring and McMinn 1980). On the other hand, on drier sites in the Pacific Northwest, a shelterwood cut may be preferable to a complete clearcut in

order to promote advance regeneration of western hemlock (Tsuga heterophylla (Raf.) Sarg.) (Haddock 1976). Therefore, in some cases additional measures such as pre-commercial thinning or shelterwood cutting may be necessary to enhance the ecology of the species and the establishment of a new stand.

The management to promote advance regeneration is nothing more than inducing what is commonly known in hardwood ecology as gap phase succession (Bray 1956, Ehrenfeld 1980). Shade tolerant trees which have developed in a gap in the canopy can then, by silvicultural manipulation, be promoted to a position of stand dominance. The ecophysiological acclimation of these trees to their newly exposed environment is achieved by an increase in transfer conductance (stomatal and mesophyll conductances) which is ultimately due to adjustments in leaf anatomy (Wallace and Dunn 1980). The same type of gap phase response has been observed in shelterwood releases of advanced regeneration of western hemlock (Tucker and Emmingham 1977). The anatomical differences of sun and shade foliage representing an acclimation by the plant to differing light environments are well documented for conifers (Larsen 1927, Stover 1944, Aussenac 1973).

In the initial acclimation of the crown to the exposed environment, soil moisture is a limiting factor, hence it takes at least one full year for a growth response. This is commonly attributed to a reduced root/shoot ratio of understory trees (Herring and Etheridge 1976, Kotar 1972) and recent controlled environment studies on European silver fir (Abies alba Mill.) and grand fir confirm this (Magnussen 1980, Magnussen and Peschl 1981). In these studies the investigators found that photosynthetic rates and transpiration rates were much higher in

seedlings grown at high light intensity but that this was only achieved at the cost of a relatively larger root system or greater allocation to belowground biomass.

The objective of this study was to investigate features of the collective foliar morphology of the shoot or crown as an ecophysiological and growth response mechanism by which advance regeneration Pacific silver fir and other shade tolerant conifers acclimate to overstory removal. Three principal hypotheses were examined:

- (1) The combination of a shade shoot/shade needle morphology and a poor root to shoot ratio would result in growth losses and foliar abscission the first year of exposure.
- (2) Shoot structure is not a fixed feature, whereas the number of needle primordia are; therefore, sun foliage will appear if the tree is exposed prior to bud burst.
- (3) Successful acclimation of advanced regeneration trees will be in major part due to their ability to produce sun foliage.

To achieve this I examined foliage phenology, shoot structure, component biomass, specific leaf area and crown structure as induced by clearcut harvest and the subsequent exposure of advance regeneration of Pacific silver fir.

3.2 METHODS AND MATERIALS

3.21 Site Description

The study site was a newly clearcut area and an adjacent old-growth stand at approximately 1,200 meters elevation on the southwest slopes of Mt. Gardner in the Cedar River Watershed approximately 50 km east of

Seattle, Washington (Figure 3). The community type of the area was Abies amabilis/Tsuga mertensiana (del Moral and Long 1977), and a sample of 13 overstory trees indicated an average stand age of 252 ± 4.2 years. The old growth stand was dominated by mountain hemlock (Tsuga mertensiana (Boug.) Carr.) and Pacific silver fir, while Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco.), western hemlock, western white pine (Pinus monticola Dougl.), noble fir (Abies procera Rehder) and western red cedar (Thuja plicata Donn.) were also present.

Clearcut harvesting of the area took place in 1981, with felling in February of that year and high lead yarding during the following spring and summer. Subsequently, the site was left unburned with little or no site preparation. The overstory removal exposed abundant advance regeneration trees which were almost entirely composed of Pacific silver fir. Understory trees in the adjacent uncut stand were undisturbed and were used as a control.

3.22 Sampling Transect

A transect was established perpendicular to the east-west line which formed the southern boundary of the clearcut (Figure 3). The transect ran from 25 meters within the uncut stand to a point approximately 65 meters into the clearcut area for a total distance of approximately 90 meters. Four plots were established along the transect and represented four basic environments: Plot A was located 25 m within the old growth stand, plots B and C at the edge of the clearcut, were located within 10 m into the stand and within 40 m into the clearcut, respectively, and plot D was 65 m in the clearcut. Plot C was hypothesized to be influenced by the residual stand.

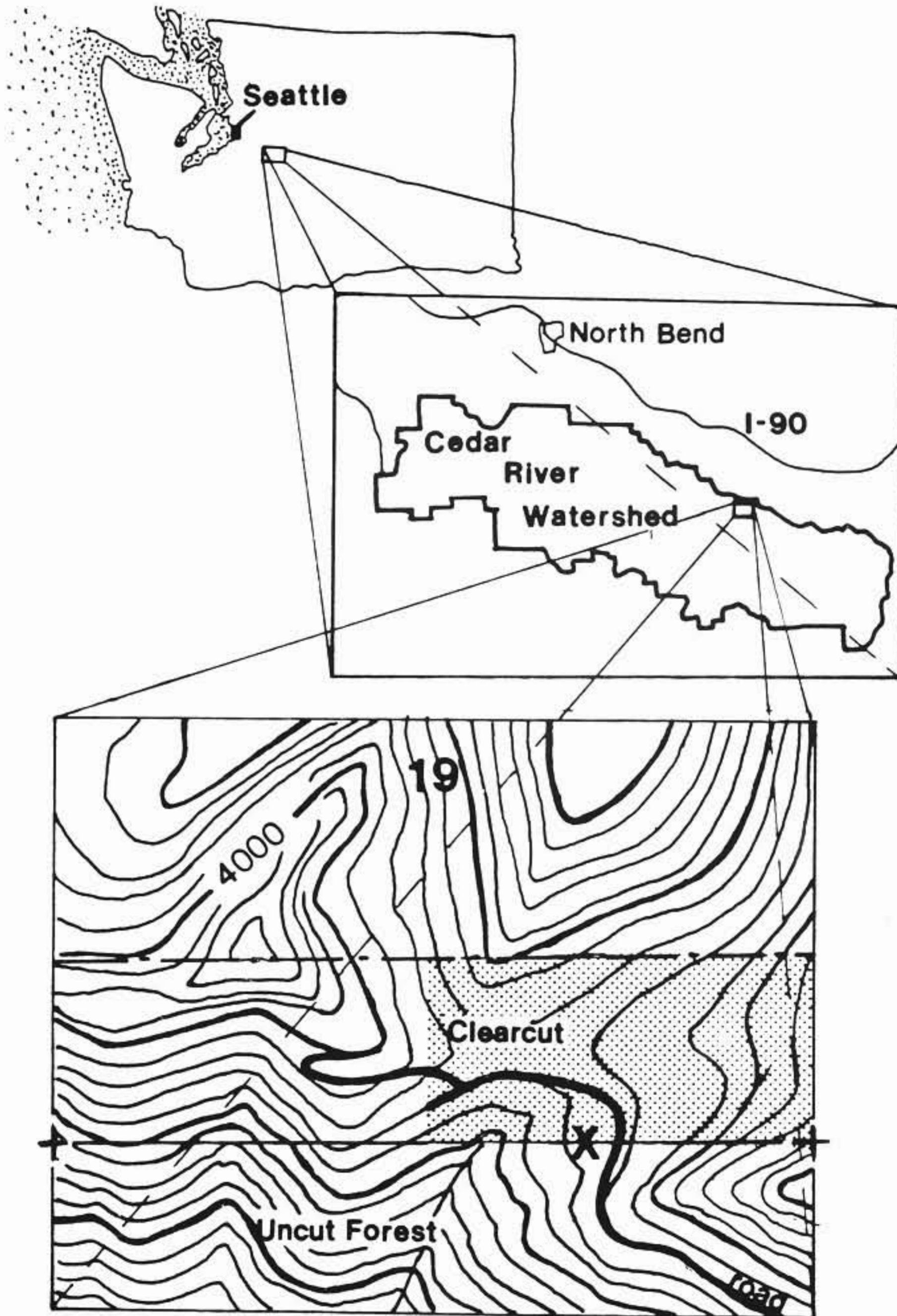


Figure 3. Location of study site in western Washington (figure design from Wagner 1980). Transect location indicated by "X", contour interval 80 ft.

3.23 Microclimate

To characterize the light environment along the transect, hemispherical photographs (Anderson 1964, Pope and Lloyd 1975) were taken at 1.5 meters above the ground at each site. The camera was leveled, true north was indicated, and a picture was taken with Kodak Tri-x 35mm film, using a Nikkor fisheye lens (1:2, f=8mm). Solar tracks were calculated for the 21st day of each month at 47 degrees 30 minutes north latitude and were then superimposed on the print (Evans and Coombe 1959).

Modified piche evaporimeters (Gholz 1982, Muelder et al. 1963) were monitored throughout the summer of 1982 to estimate differences in evaporative demand at each site. At each site, two replicate instruments were suspended so that their bases were 1.0 m from the ground. Each evaporimeter consisted of a 2.5 cm diameter (i.d.), 50 cm long acrylic tube with a circular, 0.6 cm thick section of ponderosa pine (Pinus ponderosa) sapwood sealed in the bottom end, with the entire unit shielded by 10 cm diameter PVC tubing. The evaporimeter was suspended in the shield so that it was flush with the bottom of the shield. Ten evaporimeters were constructed in early June and were calibrated over a two week period. The best eight were left in the field from July 7 until October 11, 1982. Readings were taken every 3 to 5 weeks and the evaporimeter was refilled so there was exactly 30 cm of water above the wooden plug.

3.24 Foliar Morphology and Growth

Phenological measurements of vegetative growth were taken on 21 trees along the transect at approximately two to three week intervals throughout the 1981 growing season. There were at least three trees at each of the four study sites. In addition to the four distinct plots, the transect was more finely subdivided and additional trees between the plots were examined. On each tree, the terminal and three branches were chosen and the main terminal on each branch was tagged. At each sample period, the size of the bud (before bud burst) whether the bud had burst or not, the amount of elongation and the condition of the current (1981) and noncurrent (1980, 1979, 1978) foliage should be measured. Foliar condition was based on a six stop color code ranking where 0 was green and 5 was brown.

Shoot structure was estimated with the silhouette area ratio (Leverenz 1980) by means of a photographic technique (see Chapter 2). The silhouette area ratio is the surface area of the shoot silhouette as viewed from above divided by the surface area of the detached leaves. It is a measure of the planar orientation of the shoot, hence a flat shade shoot would be almost 1.0 and a more upright sunshoot could be less than 0.5. When samples were taken in October 1981, five replicates of foliage were sampled from representative trees in each plot for 1981 and 1980 foliage and in the fall of 1982 for 1982, 1981 and 1980 foliage. For the sample set taken in 1982, following analysis for silhouette area ratio, the foliage was then oven dried and weighed to obtain a surface area to dry weight ratio. This sample was also different from the previous year in that for both calculations of silhouette area ratio and surface area to dry weight ratio, a

cross-sectional correction factor was used to account for the three-dimensional nature of the leaves. The correction factor was calculated by dividing one-half of the cross-sectional perimeter of the leaf by leaf width (Barker 1968) and was determined for each year at each plot (Tucker and Emmingham 1977).

Measurements of total leaf dry weight and fresh diameter at the soil surface were taken for 17 advance regeneration trees along the transect. These trees were destructively sampled in the fall of 1981. The foliage was removed from each tree, oven dried for 48 hours at 70°C, removed from the twig and weighed.

The proportion of foliage in different age classes was measured for two trees from each of the four plots in the fall of 1982. From each tree, three branches were removed, one each from the top, middle, and lower portions of the crown. For each branch the 1980, 1981 and 1982 length increments were measured on 2 to 4 major twigs. Foliage was then clipped by age class (1982, 1981 and remainder), pooled by plot, oven dried, separated from twigs and weighed.

Foliage distribution and crown structure were examined as an indication of growth form for control trees and exposed advance regeneration from the study plots and for acclimated trees from a nearby clearcut harvested in 1972. At each of these three sites, two trees were harvested in the fall of 1982 and a Duff and Nolan (1953) crown analysis was performed. Each internode along the main stem was marked and the length measured. The length of each branch increment was also measured for a maximum of four live branches selected from each whorl along the main stem.

3.3 RESULTS AND DISCUSSION

Advanced regeneration of Pacific silver fir was examined for a 15 month period along a transect extending from within a 250 year old forest into a newly harvested clearcut. Observations on gross and fine tree morphology, growth and phenology were made and linked with measures of microclimate. Wagner (1980) had noted that 0.5 to 1.5 m tall advance regeneration Pacific silver fir showed no distinct advantage over trees originating from post-logging natural regeneration. In fact, by 25 years following clearcutting, the post-logging trees had generally assumed dominance. Previous work (Tucker and Emmingham 1977) had demonstrated that advanced regeneration trees underwent appreciable adjustments and that these adjustments might delay the growth response of these trees. This study documents in detail the adjustments made in advanced regeneration Pacific silver fir.

Understory Pacific silver fir appears well adapted to its shady environment. Prior to overstory removal, the sapling foliage is displayed in a characteristic umbrella-shaped crown (Plate 1 and Figure 4). The form of these trees results from a yearly branch increment that is actually greater than height increment, hence crown width is frequently over 150% of stem height for trees between 25 and 50 years old. Similar results have been found for heavily shaded deciduous trees (Tamai and Shidel 1973, Steingraeber et al. 1979) and for other conifers (Kohyama 1980, Greis and Kellomaki 1981). Because leaf and branch angles are almost completely horizontal, the tree has an optimum arrangement of foliage for the interception of the characteristically uni-directional, low intensity light from above. In addition to



Plate 1. Understory Abies amabilis sapling with characteristic umbrella-shaped crown.

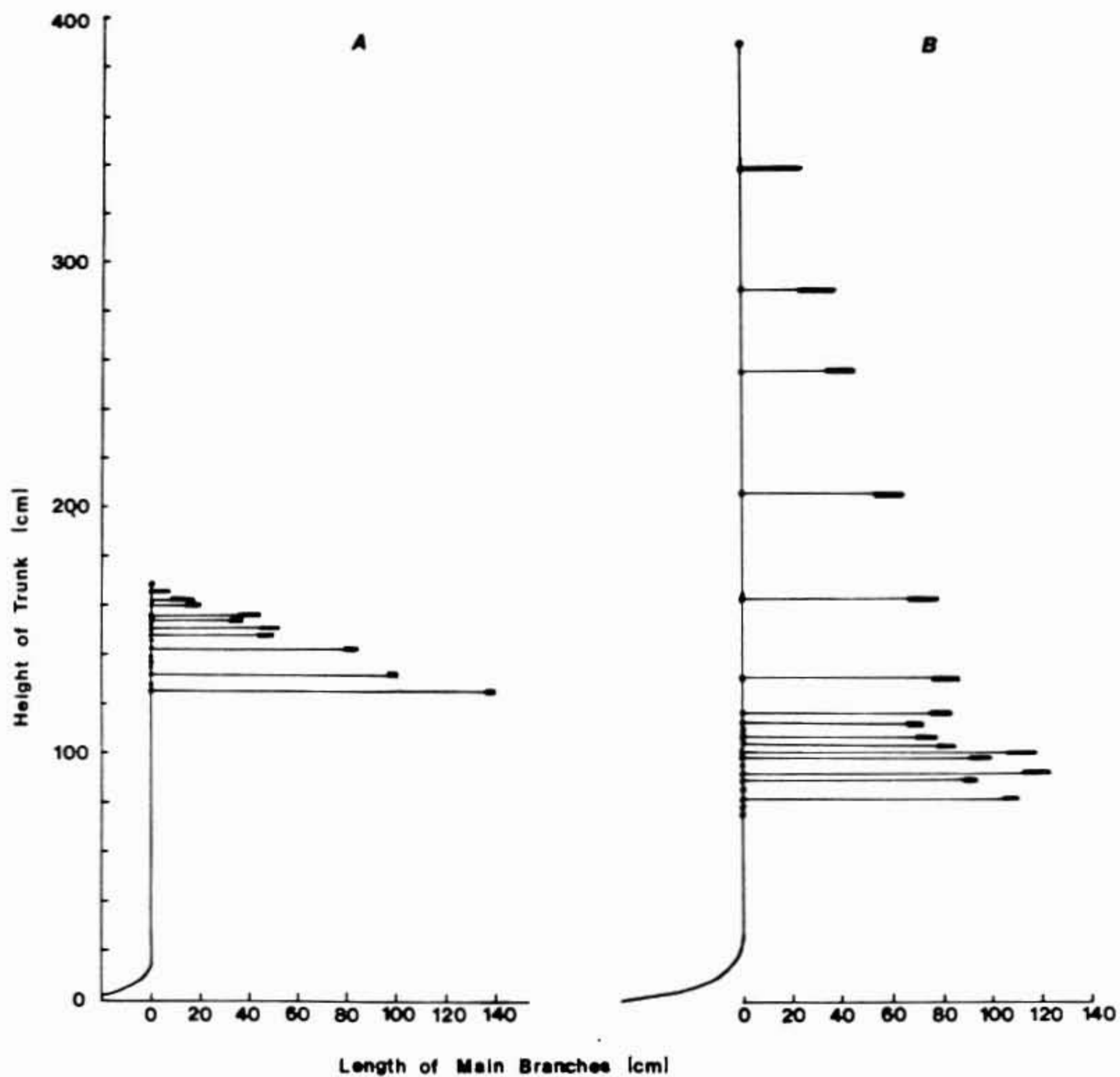


Figure 4. Growth form of advance regeneration before (A) and after (B) release with removal of overstory canopy (removed in 1972).

plasticity of foliar morphology (see Chapter 2), Pacific silver fir has the capacity to suppress apical extension as an acclimation to shade.

With removal of the overstory canopy by clearcutting in 1981, the most obvious microclimatic change was increased light levels. This fact is very evident from the hemispherical photographs (Figure 5). Plot D, in the middle of the clearcut, receives continuous direct sunlight February through October. The remaining mature forest shades the residual trees in plot D only between November and January, and these trees would be covered by snow during this period. This is in strong contrast to plot A in the understory which receives direct sunlight only intermittently at any time of the year. The photographs also show a distinct edge-effect on Plot C caused by moderate shading of 5 of the 7 solar tracks by the adjacent stand. This would be particularly crucial in late August and September when plot C receives only intermittent direct sunlight in contrast to plot D which, on a clear day, would receive light continuously. To quantify this, a series of hourly readings of photosynthetically active radiation (PAR) and leaf temperature (T_1) between 0900 and 1900 hours were made on August 22, 1982, at the four plots. Measurements of PAR for plots A, B, C, and D averaged 240, 122, 358, and 1244 $\mu\text{moles}/\text{m}^2/\text{s}$, respectively (where 1800 to 2000 $\mu\text{moles}/\text{m}^2/\text{s}$ is a solar noon reading), while T_1 for the same plots was and 18.9, 19.8, 21.3 and 23.5°C, respectively. Within the stand, T_1 never exceeded 22.1°C, while at plots C and D it reached 23.4 and 27.4°C, respectively. Clearly, plot D had the highest potential transpiration on this day.

The modified piche evaporimeters (Gholz 1982) provided a long-term estimate of evaporative demand along this transect in comparison to the

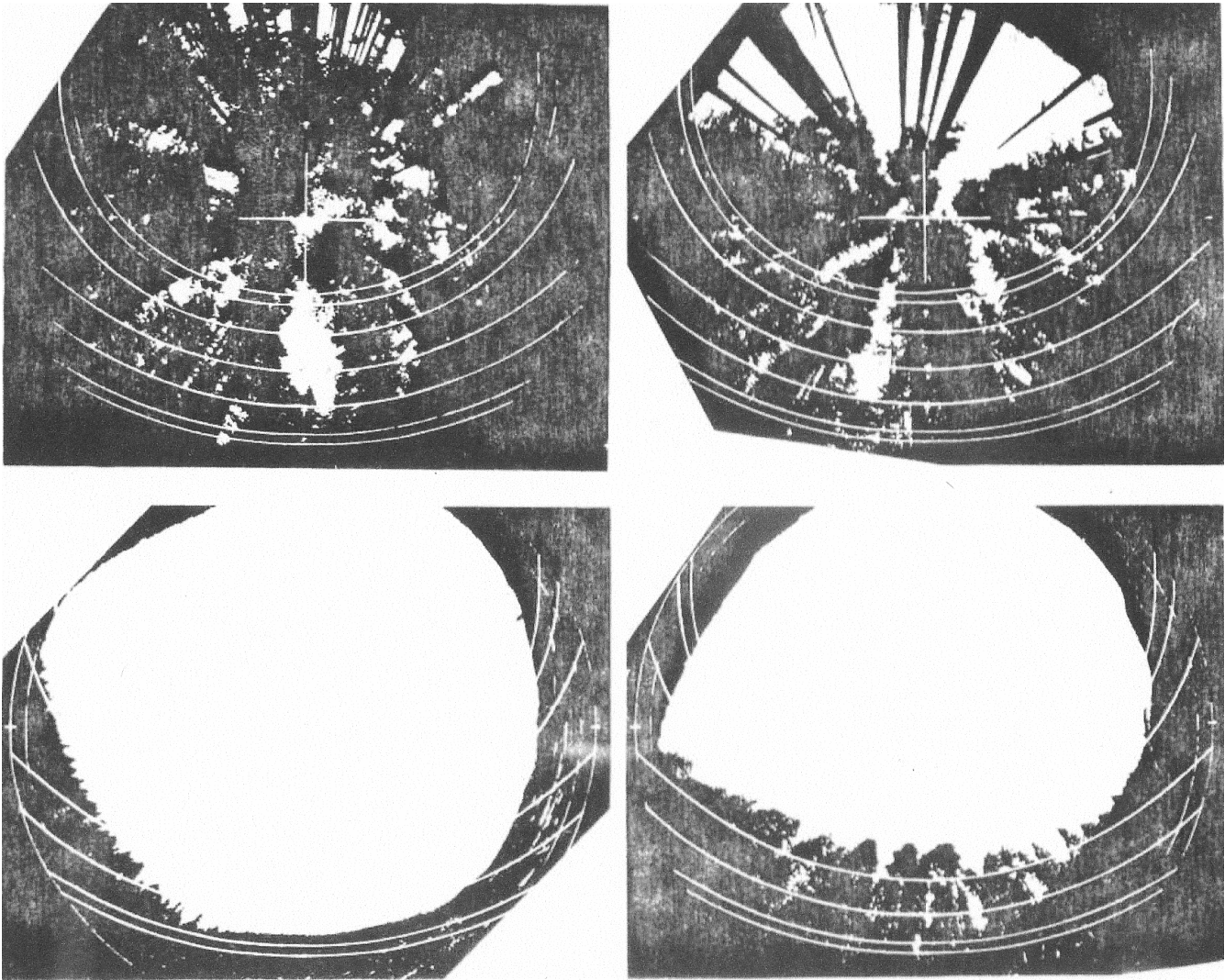


Figure 5. Hemispherical photographs taken along sampling transect with superimposed solar tracks for the 21st of each month (the highest and lowest tracks on each photo are for June and December respectively, the other ten tracks overlap two each). Clockwise from the upper left the photos are from the control stand (plot A) the stand edge (plot B) the clearcut edge (plot C) and the exposed section of the clearcut (plot D).

one day sample provided on August 22 (Figure 6). However, the evaporimeter at Plot A provided different estimates of evapotranspiration at the site. If data from one of these instruments are not considered in the calculations, a consistent trend of increasing evaporative demand is demonstrated from the control stand to the exposed portion of the clearcut. Evaporation in the transition from the mature stand to the clearcut (plots) showed distinct affinities with the understory control (plot A), illustrating the edge-effect of the mature forest. Evaporation of the clearcut edge (plot C) was only approximately 5% greater than that of the understory control (plot A), whereas in the exposed portion of the clearcut (plot D), the evaporation was 25% greater than the control (plot A).

In conjunction with the August 22, 1982 readings of PAR and T_1 , values of stem water potential (ψ) and leaf conductance (g_{wv}) were also measured to allow further assessment of the levels of stress resulting from exposure. The averages of ψ for plots A, B, C, and D were 0.93, 0.98, 1.08 and 1.27 mPa and of g_{wv} were 0.12, 0.10, 0.16 and 0.17 cm/s, respectively. In spite of these differences which corresponded to the gradients in light, temperature and evaporative demand, values of neither ψ nor g_{wv} indicated significant levels of tree moisture deficits (Teskey 1982). In fact, the most negative value of ψ , -1.57 mPa, was observed at plot C and not D. However, these values were taken approximately 14 months after release of these advanced regeneration trees. Trees at plots C and D may have had sufficient time to acclimate.

The initial physiological response of the newly exposed advance regeneration can be inferred from the phenological measurements taken

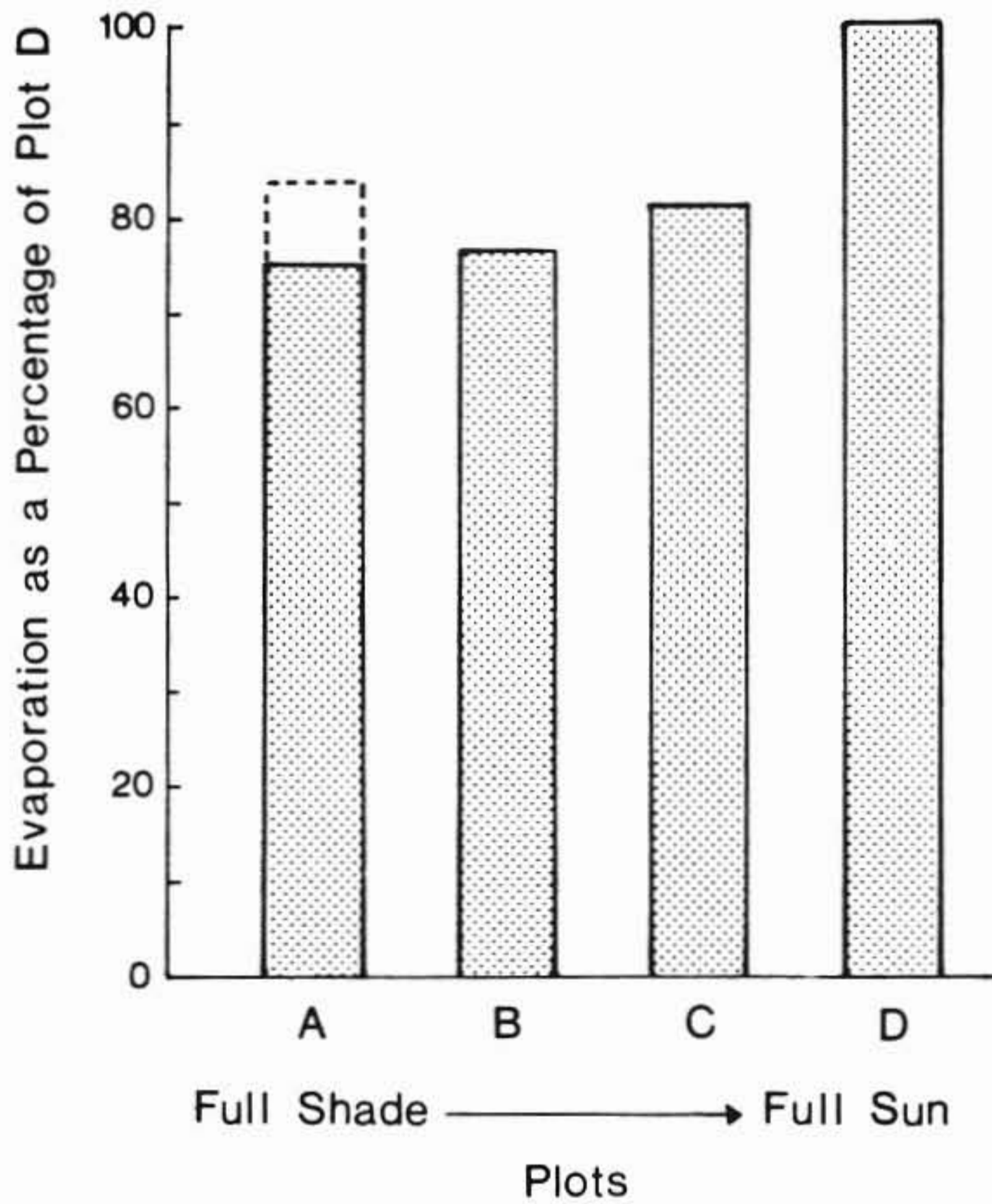


Figure 6. Evaporative demand as measured by modified Piche evaporimeters. Dotted line includes data from an inconsistent instrument at plot A.

Table 3. Phenological observations made in 1981 on 21 advance regeneration Pacific silver fir trees along a transect. Foliage color index (0 = green, 5 = brown) is an average of observations from three to five trees.

Site	Bud Swell	Bud Burst	Expansion Complete	Foliage Color Index		
				6/5/81	9/9/81	10/10/81
A	<6/5	<6/16	~8/5	0.00	0.00±0.00	0.00±0.00
B	<6/5	<6/16	~8/5	0.00	0.03±0.03	0.67±0.33
C	<6/5	<6/16	~8/5	~0	0.50±0.20	1.25±0.29
D	<6/5	<6/16	~8/5	~0	3.75±0.43	3.12±0.13

during the 1981 growing season (see Table 3). While the timing of both terminal and branch bud burst was relatively similar along the transect (the first two weeks of June at all plots), the subsequent branch increment was very different, showing approximately a 50% reduction at the exposed end of the transect (plot D) as opposed to the control stand. Branch increment in 1981 averaged 6.5 cm in the upper branches of trees from plot A, while it averaged 3.4 cm on plot D. Since 1980's branch increment was not significantly different between plots A and D, why did exposure lead to this reduction in growth?

There were several costs related to the acclimation of residual trees to their new environment. One of the most obvious of these was the loss of chlorophyll and the subsequent discoloring (Plate 2 and Table 3) and abscission of older leaves. Chlorophyll degradation, as measured by the color code ranking, was quite evident at site D such that by the end of the first growing season, noncurrent foliage was graded 3.0 and 3.5 on the 0 to 5 ranking (0=green, 5=brown), whereas the control trees (site A) were 0, indicating no apparent chlorosis. It was hypothesized that the broad, thin form and reduced mesophyll thickness of these shade formed leaves were unable to tolerate the increased radiation and evaporative demand by regulating transfer conductances. But the previously discussed data on ψ and g_{wv} suggested that water stress was not a critical factor, at least one year after partial acclimation. It is unlikely that foliar temperatures per se caused the chlorosis (Seymour et al. 1982, Teskey 1982); however, photo-oxidation may have occurred.

Chlorosis to the extent observed at plot D, can have strong effects not only on photosynthetic rates but also on stomatal control. Davies



Plate 2. Latest branch increment of foliage on newly exposed trees is greatly reduced and has a shoot structure much more like sun-foliage in comparison to older shade-foliage, which is chlorotic and undergoing leaf abscission.

and Kozlowski (1974) have shown greatly reduced stomatal control in angiosperms with the loss of chlorophyll due to extreme light intensities. The extensive chlorosis must affect the growth and survivability of such newly exposed trees; however, established advance regeneration apparently have a distinct advantage over newly planted, nursery grown seedlings which often encounter problems of solarization at such high elevation sites (Ronco 1970, 1972, 1975). In many ways, nursery grown seedlings, especially those grown in dense seedbeds, have foliar and shoot morphologies similar to shade grown trees. However, these newly planted seedlings would probably not have the reserves of the established trees.

Leaf abscission was considerable on exposed advance regeneration trees (e.g. plot D) (Figure 7A). Interestingly, the relationship between foliage biomass and diameter was not significantly different among plots A, B and C whereas the relationship varied considerably and generally indicated less foliage (i.e. higher abscission) for trees from plot D. Work by Magnussen (1980), and Bo Larsen (1980) et al. (1981) indicated that shade grown tolerant species such as grand fir, have a low root to shoot ratio as compared to sun grown trees. A comparison of the foliage to diameter relationship for plots A, B and C trees versus acclimated residual and post-logging natural regeneration trees grown on a similar site (Figure 7B, Keyes 1982) suggested no significant differences. Therefore, leaf abscission would help to bring into line evaporative demand from leaf surfaces with the unfavorable root to shoot ratio of newly exposed trees. Residual trees in the middle of the clearcut (plot D) showed considerable loss of foliage through abscission (Figure 7A), whereas trees on the edge of the clearcut (plot C) were

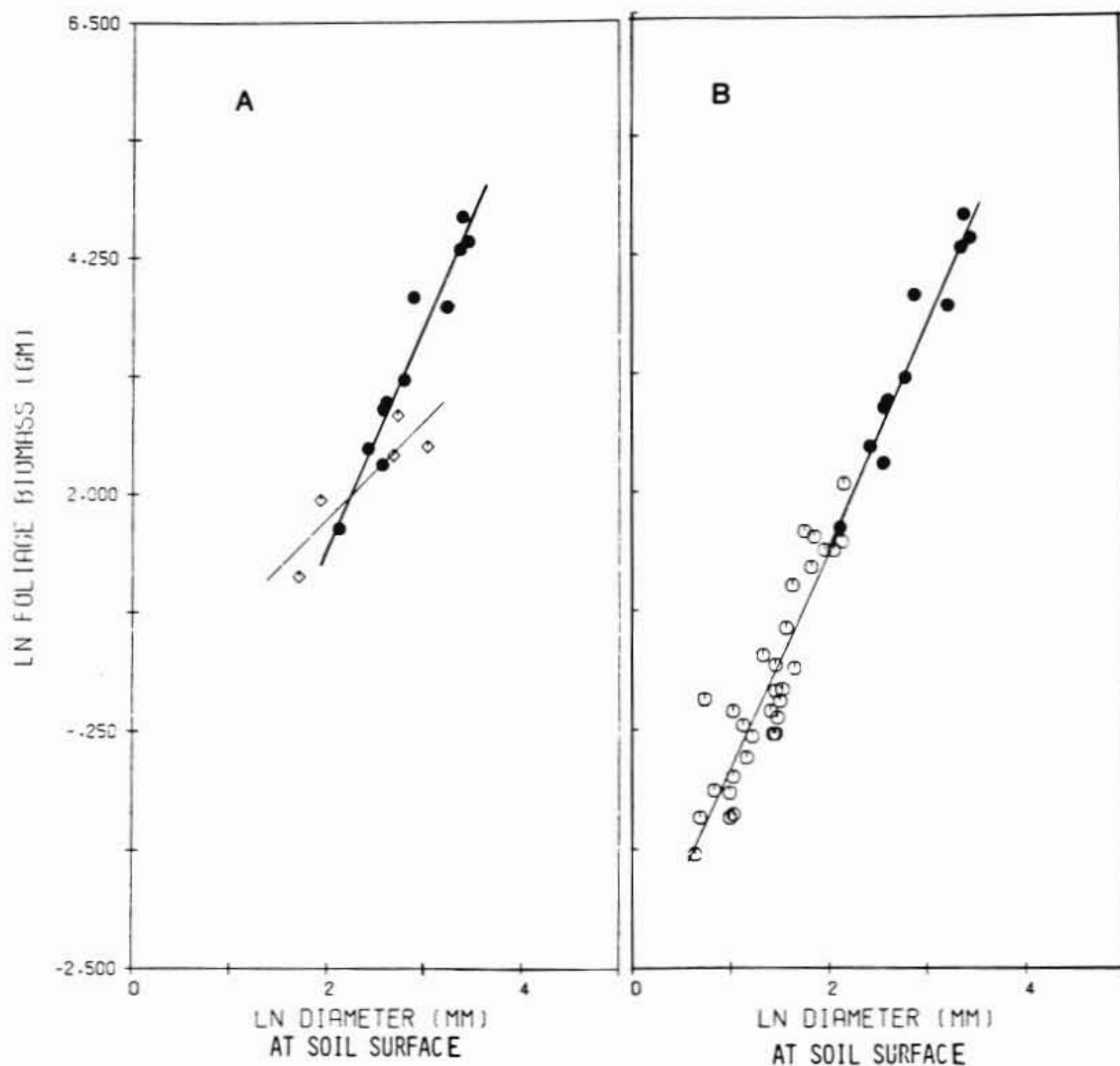


Figure 7. *Abies amabilis* foliage biomass regressions. Graph A compares understory and clearcut edge trees (\bullet) in plots A, B, and C ($R^2 = .935$) with exposed residual trees (\diamond) in plot D, which have undergone leaf abscission ($R^2 = .78$). Graph B compares the same understory and clearcut edge trees as in graph A to new post-logging natural regeneration and residual trees (\circ) in a nearby 10-year-old clearcut; ($R^2 = .81$, data courtesy of M. Keyes).

exposed to much lower evaporative demands (Figure 7) and, hence, appeared more like unexposed understory trees. Although there was considerable leaf abscission by Pacific silver fir in the most exposed plot in this study, it was comparatively less than that for newly exposed western hemlock trees from western Oregon studied by Tucker and Emmingham (1977).

One of the most dramatic changes in the acclimation process was that of the shoot structure of the 1981 foliage on trees in the exposed plots (Plate 2, Figure 8). Immediately prior to logging, the number of leaf primordia had been predetermined when the trees set bud in the late summer and early fall of 1980. Hence, when the shoots elongated in the summer of 1981 in the exposed environment, a similar number of leaves was produced as in previous years; however, their form and leaf angle were vastly different. This fact is evident in foliage silhouettes (Figure 8) and in the calculation of silhouette area ratios or shoot structure (Figure 9). The dramatic change in silhouette area ratios is not only a light response on the part of the foliage to higher light intensity originating from multidirections, but is also due to increased moisture stress in exposed foliage (Richter 1974).

Figure 9 shows first that the silhouette area ratio (SAR) increased with foliage age in the control stand and, second, that it was different in exposed as compared to unexposed trees. The change with foliage age may be due to a long term developmental response on the part of the plant or simply to winter snow loading causing increasingly horizontal leaves. It is interesting to note that SAR's from the stand edge (plot B) and the clearcut edge (plot C) were both very similar in their shoot structures. Apparently the increased light intensities associated with

Foliage Silhouettes

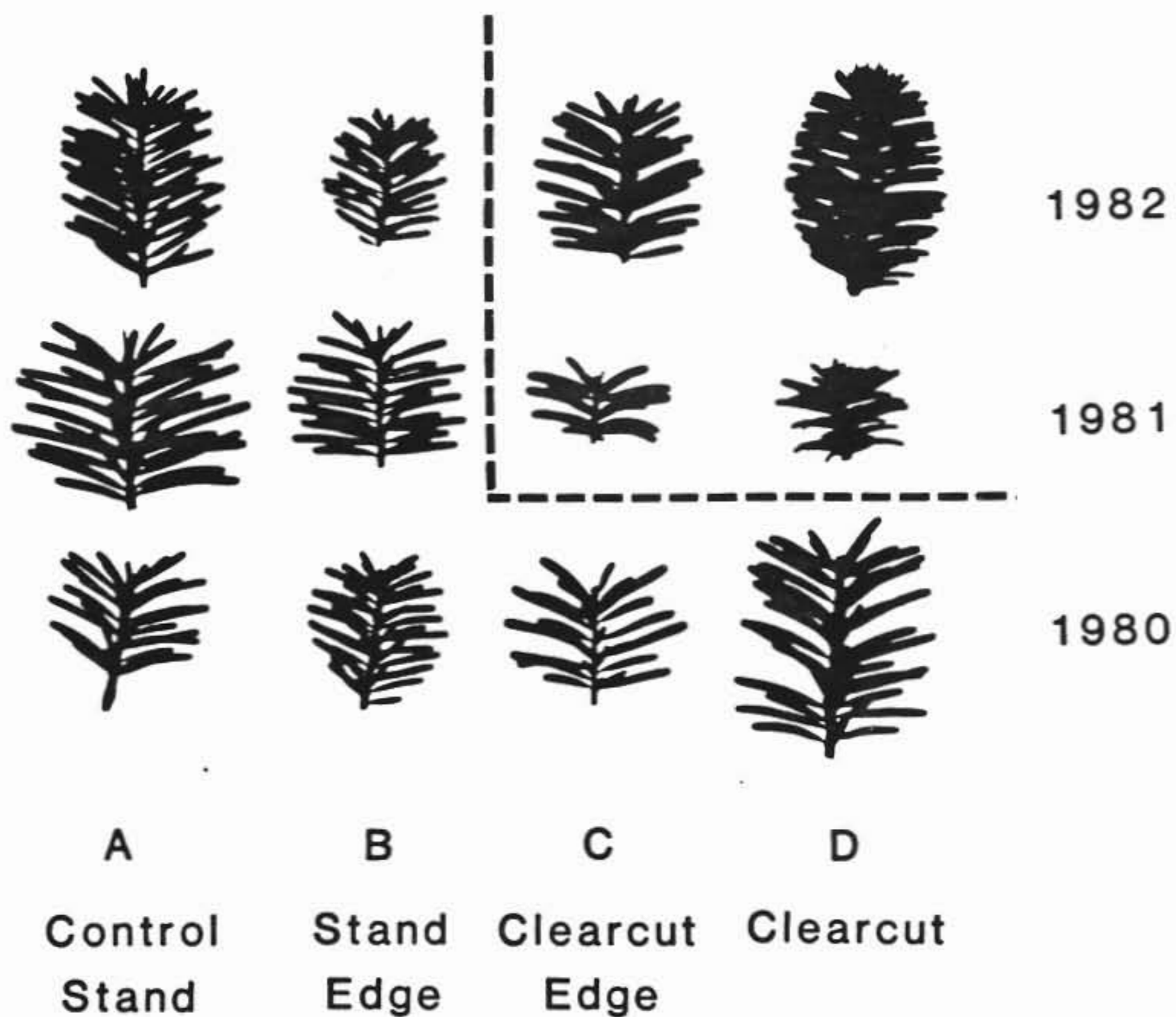


Figure 8. Representative foliage used for determination of silhouette area ratio and surface area to weight ratio. Foliage above and to the right of the dotted line elongated following exposure by clearcutting.

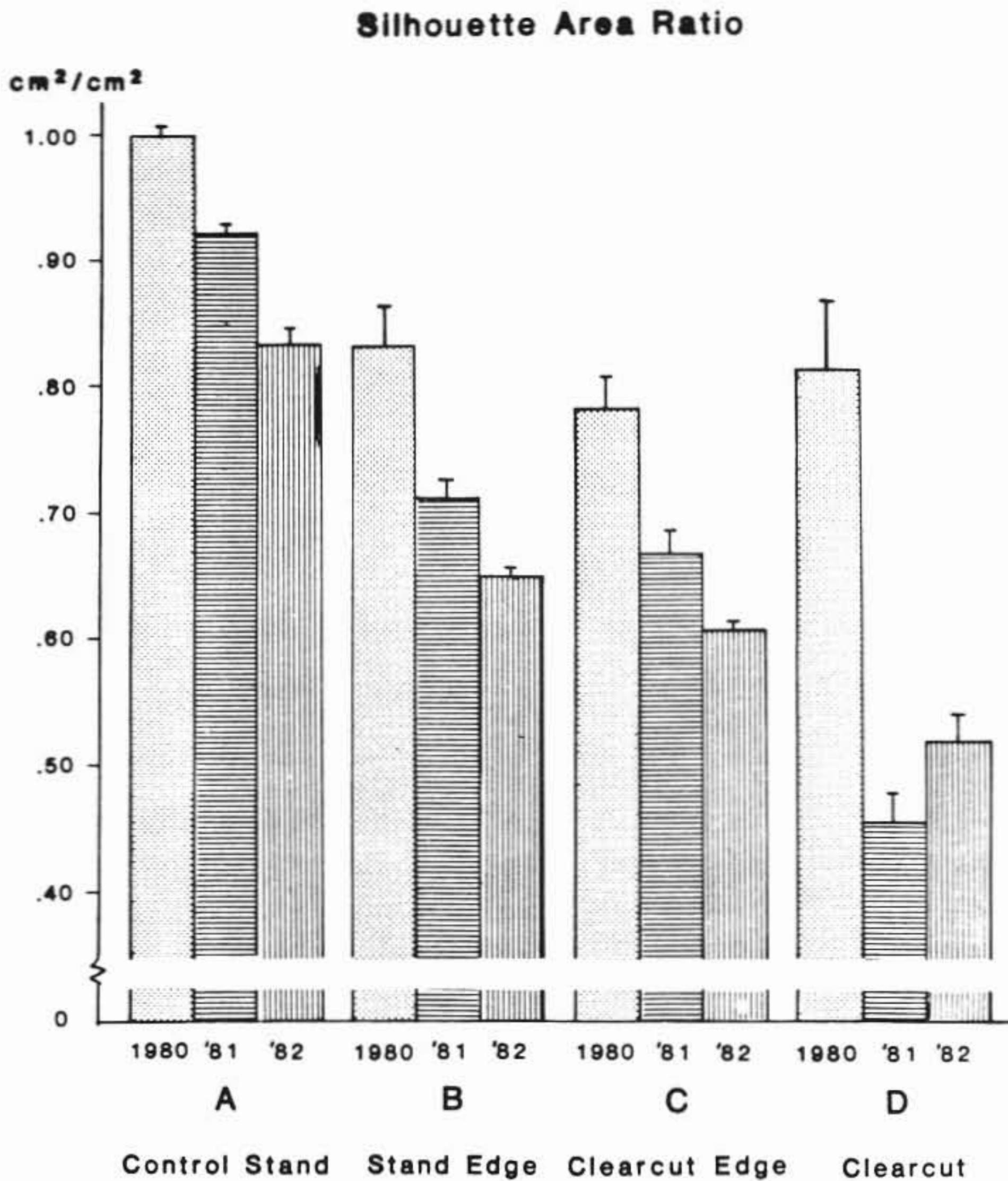


Figure 9. Silhouette area ratio for foliage in different plots (A, B, C and D) by age. Clearcutting took place just before 1981 foliage elongation.

the edge resulted in a more sun like shoot structure. This was in contrast to the ratio of surface area to weight (or specific leaf area, Figure 10); as foliage from the clearcut edge (plot C) was most similar to the foliage of the most exposed plot (D), whereas foliage from the stand edge (plot B) was very similar to that of the control (plot A). Foliage from the control showed a steady decrease in leaf specific area (i.e. increasing dry weight accumulation) with age. Foliage of 1980 had similar specific leaf area ratios on all four plots (between 132 and 146 cm/gm) whereas the foliage produced in 1981 on plots C and D was significantly less than that of plots B and A. A comparison of specific leaf area ratios of foliage produced in 1982 and 1981 on plots C and D suggested the same trend as found for plots A and B for these same years. The major difference was that foliage produced in the open had lower leaf specific area ratios than that produced in the shade.

Growth measurements taken in 1982 showed an appreciable increase in branch elongation of trees from plots C and D in comparison to either 1981 or trees from plots A and B (Tables 4 and 5). Clearly, branch growth was beginning to respond positively to exposure only one year following release; however, there was no response by the terminal at that time.

In order to examine the long-term response of advance regeneration trees, trees from a ten-year-old clearcut were removed and dissected (Figure 5B). The response of the terminal bud, inferred by increased height growth, lagged behind the response of branch increment by approximately 2 years (Figure 11). This lag may be due to the time required for physiological adjustment by the apical bud and the subsequent restoration of hormonal control and apical dominance. Within

Ratio Surface Area to Weight

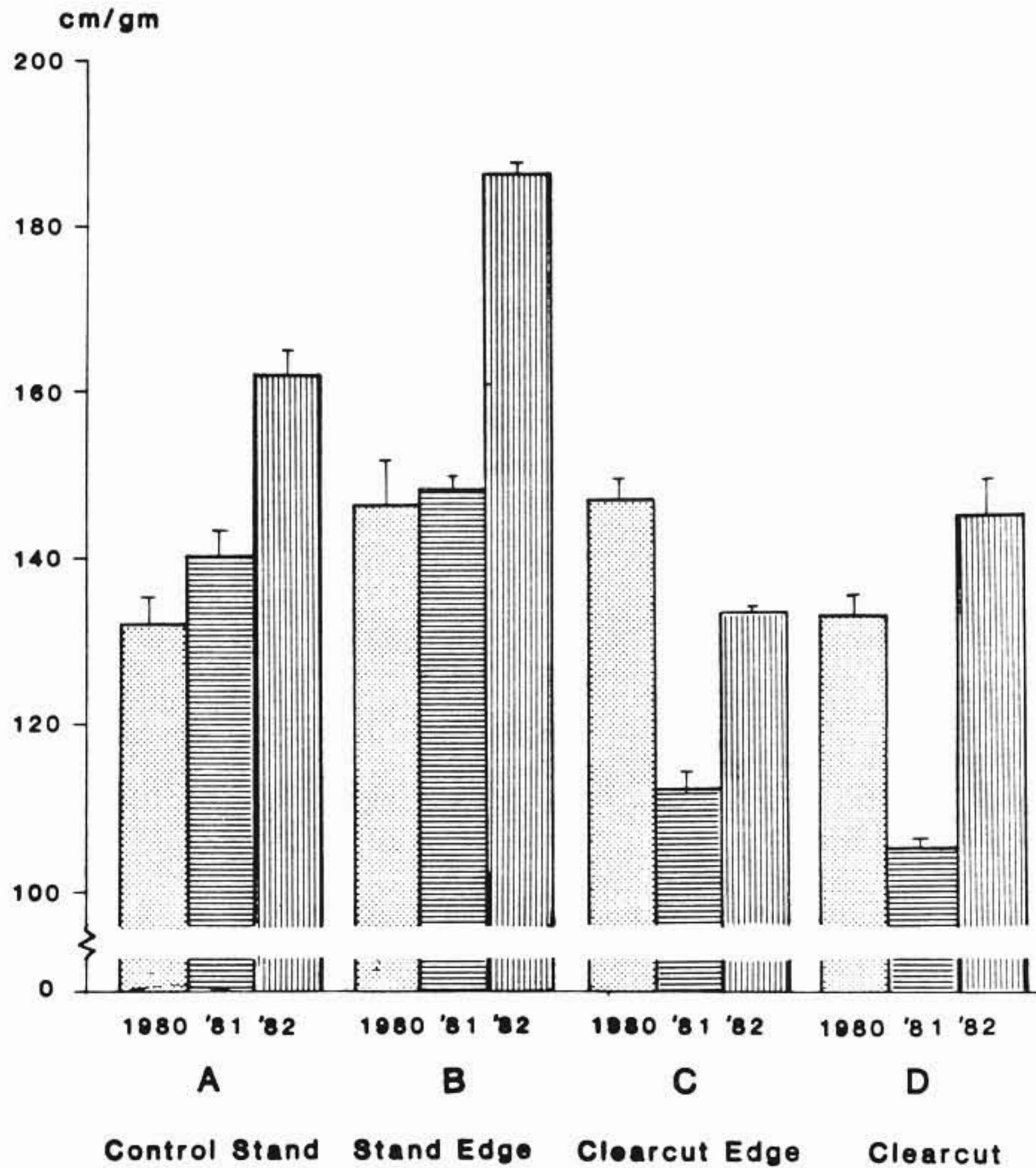


Figure 10. Foliage specific leaf area or surface area to weight ratio by age for the different plots (A, B, C and D). Clearcutting took place just before 1981 foliage elongation.

Table 4. Branch growth in the top, middle and bottom crown sections of four advance regeneration Pacific silver fir as a percentage of 1980's growth (see Appendix D for data).

Site	Top	Middle	Bottom
A	94.6	94.0	104.6
B	89.6	89.6	96.9
C	30.0	27.2	27.5
D	40.8	31.8	40.5

Table 5. Branch growth in the top, middle and bottom crown sections of eight advance regeneration Pacific silver fir (2 from each plot) in 1982 as a percentage of 1981's growth (see Appendix for 1982, 1981 and 1980 data)

Site	Top	Middle	Bottom
A	88.6	88.1	102.4
B	85.8	100.0	96.1
C	170.7	159.5	196.1
D	193.7	258.8	284.6

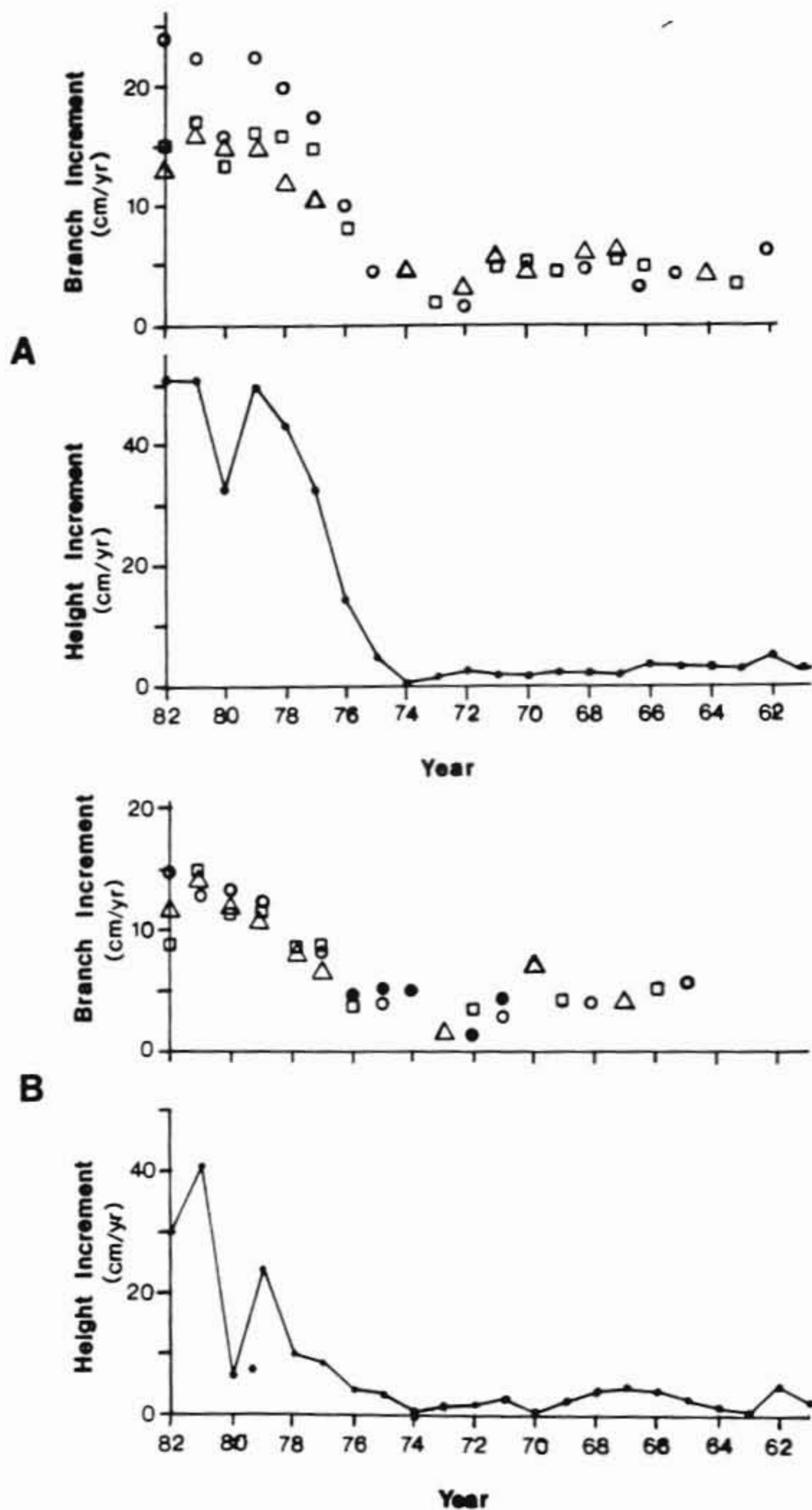


Figure 11. Type III branch increment sequences for two acclimated advance regeneration (A, B) from a 1972 clearcut. \circ = branch coliant immediately adjacent to the main stem. \square = second branch coliant from main stem. \triangle = third branch coliant from main stem. Each value is the mean of two to four values. Damage to terminal indicated by asterisk.

2 to 5 years of release, advance trees were fully acclimated, resulting in greater branch and especially leader elongation than characteristic of these trees before release.

3.4 CONCLUSIONS

Advance regeneration in this study responded to full exposure with adjustments in foliar morphology but chlorosis and leaf abscission of the older foliage were also noted and were probably due to the initially poor root to shoot ratios and shade foliage morphology of these released trees. Response of branch growth was within one year of overstory removal, however, the response of height growth lagged behind by approximately 2 years. In all cases, trees in the clearcut edge appeared to acclimate rapidly to exposure from clearcutting. These trees, in contrast to the fully exposed trees, retained their older foliage while the new foliage was sun-like in morphology. The hemispherical photographs provided a good and complete indication of the light environment for all plots. Hence such photographs could possibly be used in the future as a technique to model edge effect for its maximization in clearcut design and layout.

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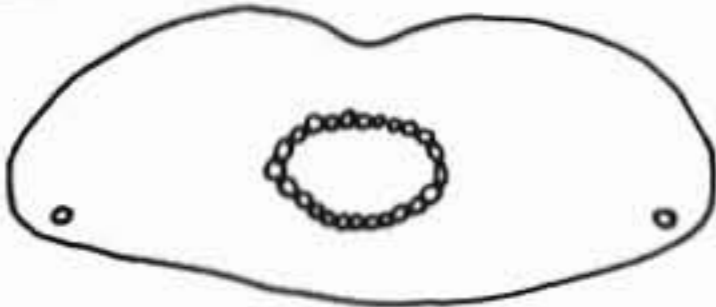


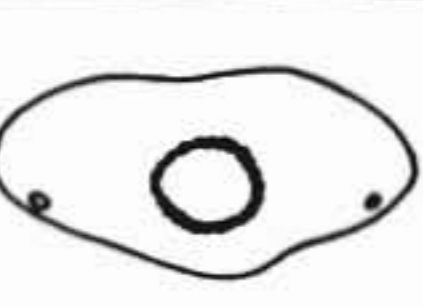






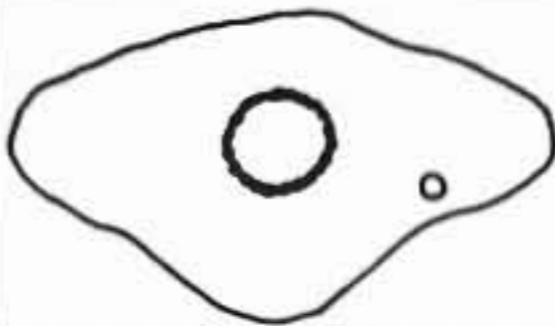


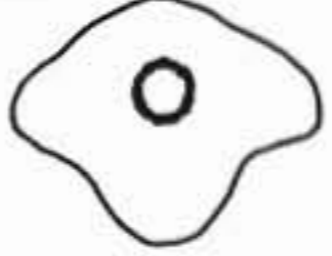

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Appendix A: Leaf Cross Sections

Table A.1 Leaf cross-sections for stand growth and suppressed trees

	<u>Abies grandis</u>	<u>Pinus contorta</u>	<u>Abies amabilis</u>	<u>Pseudotsuga menziesii</u>
Sun				
Shade				
	<u>Abies lasiocarpa</u>	<u>Picea sitchensis</u>	<u>Abies amabilis</u>	Scale:  0 1.0mm
Sun				Released Advance Regeneration
Shade				Suppressed Understory Sapling

Appendix B: 1982 Additional Silhouette Area Ratios

Table B.1 1982 silhouette area ratio measurements of large and suppressed trees in addition to biomass plots.

Species	Site	Crown Class	Crown Position	SAR \pm SE	n
Pisi	II	Suppressed	Lower	0.89 \pm 0.01	3
Pisi	II	Dominant	Upper	0.28 \pm 0.01	4
Abam	III	Codominant	Upper	0.45 \pm 0.01	4
Abam	IV	Dominant	Upper	0.24 \pm 0.01	3
Psme	V	Codominant	Upper	0.49 \pm 0.03	7

Appendix C: 1981 Additional Silhouette Area Ratios

Table C.1 1981 silhouette area ratio measurements on transect trees of foliage cohorts, as indicated by arrows.

Plot	Foliage Cohort			
	1981	1980	1979	1978
A	←←←←←←←	0.78	→→→→→→→	
B	←←←←←←←	0.79	→→→→→→→	
C	0.53	←←←←←←←	0.93	→→→→→→→
D	0.59	←←←←←←←	0.92	→→→→→→→

Appendix D: Transect Crown Measurements

Table D.1 Branch growth for 1981 and 1980 for four Pacific silver fir trees, one each from plots A, B, C and D. Three branches from top, middle and bottom of the crown of each tree were averaged. Trees sampled on October 10, 1981.

SITE	TOP		MIDDLE		BOTTOM	
	81	80	81	80	81	80
A	7.03±0.72 ^a	7.43±0.88	5.20±0.67	5.53±0.66	3.63±0.64	3.47±0.68
B	3.43±0.15	3.83±0.60	3.70±0.55	4.13±0.32	3.15±0.65	3.25±0.25
C	1.30±0.26	4.33±0.77	1.07±0.09	3.93±0.54	1.1 ^b	4.0 ^b
D	1.93±0.24	4.73±0.32	1.47±0.09	4.63±0.32	1.70±0.40	4.20±0.53

a. ± SE

b. Only one branch

Table D.2 Branch growth for 1982, 1981 and 1980 for eight Pacific fir trees, two each from plots A, B, C and D. Two branches from each tree, from each crown section were sampled. All branches from a plot were pooled and foliage biomass was measured on 1982, 1981 and remainder. Total foliage biomass for branches from plots A, B, C and D were 48.13, 55, 68, 32.05 and 40.91 grams, respectively.

SITE	YEAR	TOP	MIDDLE	BOTTOM	FOLIAGE BIOMASS	
					82 as % 81's	as % Total
A	82	2.33±0.13 ^a	2.97±0.03	3.00±0.15	83.9	11.7
	81	2.63±0.24	3.37±0.09	2.93±0.48	--	14.7
	80	3.20±0.26	3.97±0.12	2.70±0.45	--	--
B	82	3.20±0.40	2.40±0.60	3.23±0.18	85.4	13.6
	81	3.73±0.12	2.40±0.50	3.36±0.20	--	15.8
	80	5.03±0.13	3.80±0.10	5.63±0.23	--	--
C	82	3.50±0.10	3.35±0.18	3.00±0.08	317.4	32.3
	81	2.05±0.10	2.10±0.10	1.53±0.17	--	7.7
	80	5.20±0.10	4.85±0.54	2.87±0.94	--	--
D	82	6.10 1.70	4.40 0.84	3.50 0.50	316.4	41.3
	81	3.15 0.65	1.70 0.00	1.23 0.17	--	11.7
	80	5.30 1.00	3.40 0.62	2.77 0.44	--	--

A. ± SE

Appendix E: Transect Biomass Measurements

Table E.1 Diameter, height and biomass for harvested trees.

Plot	Fresh Diameter (cm)			Age (yrs)	Height (cm)	Below Ground Biomass (gm)			Above Ground Biomass (gm)		
	at soil	at 15 cm	at 30 cm			Root Collar	Adventitious Roots	"Rhizome"	Main Stem	Branches	Leaves
A	0.8	0.9	0.7	73	44	2.57	1.10	7.33	---21.69---		5.32
	1.3	1.2	1.2	85	52	4.76	7.96	22.05	---55.82---		9.83
	1.8	1.7	1.7	120	107	14.65	5.55	54.48	--153.11---		22.00
	2.9	2.6	2.3	130	120	46.84	20.59	113.28	318.40	82.31	75.48
B	3.0	2.7	2.4	140	85	5.48	56.08	131.68	288.31	132.96	102.55
	1.1	1.0	0.4	62	32	10.55	1.34	13.29	---32.61---		18.19
	1.8	1.8	1.6	135	98	5.10	10.47	34.89	--180.58---		48.20
	2.6	2.3	2.0	118	75	17.14	31.72	113.72	195.10	81.81	43.81
C	3.2	2.6	2.3	~105	85	6.70	37.89	83.93	259.62	153.41	82.02
	1.3	1.2	1.0	~50	59	2.47	3.92	18.23	---58.92---		16.54
	0.8	0.8	0.5	~21	33	3.07	0.13	2.91	---19.18---		---
	1.4	1.1	1.0	~55	53	5.25	4.49	11.42	---46.22---		17.81
D	1.5	1.5	1.4	~50	85	12.21	1.82	13.47	---12.91---		15.75
	2.1	1.9	1.9	~90	90	16.43	10.85	43.34	148.88	53.31	11.62
	1.5	1.2	1.2	~60	75	4.88	7.95	12.10	67.33	19.22	10.80
	0.7	0.6	--	~25	25	-----10.39-----			---9.64---		6.99
	0.6	0.4	--	~25	19	-----4.94-----			---4.74---		3.39
D*	4.1	3.5	3.2	--	160	--	--	--	--	--	117.64
	4.6	4.1	3.8	--	172	--	--	--	--	--	102.76
	4.4	3.8	3.8	--	149	--	--	--	--	--	148.04
D**	10.0	8.6	8.6	--	472	--	--	--	--	--	--
	7.8	7.5	7.2	--	324	--	--	--	--	--	--
	8.2	6.7	6.2	--	234	--	--	--	--	--	--

* & ** represent additional data collected in 10/82 and 7/82, respectively.