THE DISTRIBUTION OF BIOMASS AND NUTRIENTS IN PRIMARY BRANCHES OF *PINUS RADIATA* D. DON

By

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DECLARATION

Except where otherwise indicated

this thesis is my own work.

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ABSTRACT

The distribution of biomass and the nutrients nitrogen, phosphorous, potassium, calcium, magnesium and manganese were examined in the primary branch of the 4th order spring whorl of 15-year old Pinus radiata D. Don trees. Branch samples from eight trees were taken from each of two treatment plots at the biology of forest growth study site in the Australian Capital Territory. Foliage, bark/phloem and xylem tissue were sampled for each growing season/internode and then biomass and nutrient gradients were examined both along and across the branch.

Biomass production showed a lagged response to treatment, with the non-fertilised trees having a greater increment in the second post-treatment growing season. Mutual shading from the upper crown may have caused this decline in the fertilised trees.

Nutrient concentration gradients along the branch showed decreasing concentrations of nitrogen, phosphorous and potassium and increasing concentrations of calcium with increasing age in all tissue types. Concentration gradients for the labile nutrients (nitrogen, phosphorous and potassium) across xylem growth rings were u-shaped, indicating a withdrawal of nutrients from middle to outer rings.

In fertilised tree branches, nitrogen levels were raised in all tissue types but there was no difference between treatments for phosphorous, potassium, calcium and magnesium. Manganese concentrations were significantly higher in unfertilised branch tissues.

In foliage, concentrations of phosphorous and potassium were at or about optimal for P. radiata in both treatments. For nitrogen, optimal levels were attained only in the fertilised treatment. Calcium concentrations were elevated in the growing season following treatment in both plots suggesting a possible response to irrigation but not fertiliser.

Season to season changes in the xylem content of phosphorous, potassium and calcium reflected biomass rather than changes in nutrient concentration. However, for nitrogen, high concentrations were found in the fertilised treatment, indicating excess uptake and accumulation. Higher concentrations in the xylem rather than the foliage, which were maintained close to optimum, suggest efficient retranslocation of the labile nutrients in these branch tissues.

A comparison of the sampling strategy used here with two others showed that one mid-point sample from eight to ten branches may be adequate for estimating primary branch nutrient content at a given whorl for P. radiata.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

1.1 General Introduction

In recent years there has been a significant increase in the number of studies focusing on biomass and nutrient distribution in forest ecosystems. The trend towards shorter tree crop rotations, intensive forest management, and whole tree utilization (WTU) has encouraged interest in estimating biomass, nutrient distribution patterns, and total nutrient content of forest stands. Continued evaluation of silvicultural treatments, such as fertilisation, irrigation and thinning practices, is necessary in order to produce tree crops efficiently while maintaining site productivity. Of particular concern to foresters is the potential impact of WTU on site nutrient depletion. WTU provides a greater biomass yield, but also removes nutrient-rich crown material that is normally left behind when conventional bole harvests are employed (Messina et al., 1983).

The assessment of silvicultural treatments and land management practices depends on description and quantification of nutrient pools and fluxes within the ecosystem. This requires individual tree and component sampling, the results of which can then be applied to the stand as a whole. Component sampling provides estimates of biomass and nutrient content of various tree parts, and ultimately, total nutrient content of the stand.

There are several tree components that have been examined in studies of tree biomass and nutrient distribution. These are: (i) roots, (ii) bolewood and bole bark (including living phloem and dead bark), (iii) branchwood and branch bark, (iv) foliage, and (v) reproductive structures. Unfortunately, studies of root production and mineral nutrient content are limited due to the labour intensity and high cost of root extraction procedures. Most researchers tend to analyse the aboveground components, particularly the merchantable bolewood and the foliage (e.g. Wells and Metz, 1963; Mead and Will, 1976; Comerford, 1981; Comerford and Leaf, 1982b; Madgwick et al., 1983; Mead et al., 1984). Foliar analysis has been used extensively to assess the nutrient status of a site and to measure the amounts of nutrients the tree is extracting from the soil. Bolewood analysis may also provide this information, but it requires destructive sampling of trees and is more time-consuming. However, where the impact of a bolewood harvest on the nutrient status of the site is of interest, destructive sampling is necessary to provide estimates of stand nutrient content. Reproductive structures may hold a significant amount of the tree's nutrients, but there has been little work in this area. Estimates of branch biomass and nutrient content have been included in some studies where the primary aim is to determine tree nutrient content with inference to the entire stand.

Branches represent a significant part of the aboveground biomass of trees. Branches are defined here as branchwood plus dead bark and living phloem (bark/phloem). In a study presently underway in a Pinus radiata D. Don forest near Canberra, Australia, branches of fifteen-year old trees are estimated to hold 20 percent of the total

aboveground tree biomass (Benson, pers. comm.). Indeed, branch weights in P. radiata stands include some of the highest values recorded for pines (Madgwick et al., 1977). In a stand of twenty-six year old P. radiata, Orman and Will (1960) found that the crown, while holding only 10 percent of the total dry matter, contained 19 percent of the calcium, 29 percent of the potassium, 36 percent of the phosphorous, and 42 percent of the nitrogen in the tree crop. Forrest and Ovington (1971) found that tree crowns contained 70 to 80 percent of the total aboveground nutrients in a P. radiata stand at crown closure. While much of this may be found in the foliage, a considerable amount would be expected to occur in branches. If this material is left on-site after a harvest, many of these nutrients will be available to the next crop. However, where such practices as burning of slash or WTU are employed, much or all of this nutrient capital may be lost through volatilization or removal. An evaluation of the biomass, nutrient distribution and content of branches can provide important information when considering forest management options. At the present time, however, there is very little of this information available.

1.2 A Review of the Literature

In investigations of tree nutrient distributions, there are commonly three parameters examined for the tree component being studied: biomass, nutrient concentration, and nutrient content. Procedures for determining these parameters in forest stands continue to be debated, both in terms of sampling methods and sample handling. Forests are extremely complex, and their morphological and structural

diversity cause sampling and statistical difficulties (Forrest, 1969). Few researchers are completely satisfied with present procedures, and work in this area is ongoing.

1.2.1 Biomass

It is impossible to describe and quantify nutrient distribution in a forest without measurements of biomass. The amount and distribution of dry matter must be taken into account, since variations in nutrient concentrations do not necessarily reflect differences in absolute nutrient content (Barker, 1973).

Forest stand biomass studies have adopted one of three possible approaches to sampling:

(i) the mean tree method, where samples consist of one or more trees that are assumed to represent the average tree size in the stand;

(ii) the unit area method, where samples are taken from all trees on a plot of known area.

(iii) the regression method, whereby samples, selected by random or stratified random sampling procedures to include trees from all size classes, are then related to the general population with regression techniques (Messina et al., 1983).

Several authors have compared the above methods (Forrest, 1969; Comerford and Leaf, 1982a; Messina et al., 1983), and there is general agreement that regression analysis not only provides greater accuracy of measurement, but is less costly than the other methods and requires the destructive sampling of fewer trees.

Where regression analysis has been used, an allometric relationship has been found to exist between bole size and the component dry weight. Hingston et al. (1981) used a regression of logarithms of the dry weights of various tree components on bole diameters to estimate aboveground biomass in a jarrah (Eucalyptus marginata Donn Ex Sm.) ecosystem in Western Australia. Grier et al. (1984) employed a similar method in a study of Douglas-fir trees (Pseudotsuga menziesii (Mirb.) Franco) in Washington, USA. Logarithmic regressions were of the form:

$$\ln Y = a + b \ln X$$

where Y is component biomass (kg), X is diameter at breast height (cm), and ln is the logarithm to the base e. This formula is commonly used for estimating biomass of many tree species, including pines (for example, Madgwick et al., 1977; Bockheim et al., 1983; Feller, 1983).

Biomass data are necessary in determining stand productivity. Stand productivity is usually measured as an annual increment (m^2 ha^{-1}). It includes the amount of organic matter which goes to increase the biomass, which is discarded from the trees as litter, which is lost through the death of individuals, and which is consumed by heterotrophs (Attiwill, 1979). Such data are useful in comparing the effects of different sites or silvicultural treatments on stand productivity. For example, Will (1971) examined the effects of nitrogen fertilisation on branch and stem diameter growth in a P. radiata stand, Jackson and Gifford (1974) studied the influences of different sites on the growth of P. radiata, and Mead et al. (1984) estimated the biomass of a seven-year old P. radiata stand in relation to thinning practices. Biomass data are also useful in comparisons of different genotypes growing in similar conditions (Forrest and Ovington, 1971; Madgwick, 1983).

Biomass data are required to estimate nutrient content of various tree components. Along with nutrient concentration data, they have been used to determine the nutrient content of P. radiata trees in mineral nutrition studies (Madgwick et al., 1977; Webber and Madgwick, 1983).

Branch productivity and mineral nutrition have been analysed with the use of branch biomass estimates. Whittaker (1965) states that "branches and roots are the two fractions responsible for uncertainty in measuring net production of forests", and therefore, accurate means of measuring these components are needed. He estimated branch production of Rhododendron maximum and Quercus alba in the southeastern USA from regressions of branch dry weight in relation to branch age, and found the analysis to be complicated by the fact that growth rates vary from branch to branch within the crown. Forrest (1969) found that branchwood biomass of P. radiata is dependent on initial stocking rates as well as on differences in site quality. In a P. radiata stand in New Zealand, Madgwick (1975) estimated gross annual wood and bark/phloem production of branches by relating the biomass of each branch whorl to tree diameter (dbh) using a logarithm regression. For one particular site, branch growth was approximately 3 t ha^{-1} a^{-1}, and mostly occurred in spring and summer.

In this investigation, branch biomass has been determined primarily to calculate the total amounts of nutrients per branch. The differences in biomass between branches growing under different fertiliser conditions will also be discussed.

1.2.2 Nutrient Concentration

Measuring nutrient concentration levels in tree components provides information about the tree's requirement for the particular element. In effect, it provides a measure of the 'activity' of the nutrient within the tree. Such information has practical application in determining the nutritional needs of a tree and in detecting deficiencies.

Many studies of nutrient levels within trees have been made, and have demonstrated the effects of several factors on concentrations in various tree components. Will (1965) and Knight et al. (1983) related site nutrient status to nutrient levels in foliage, bark/phloem, and sapwood of P. radiata. In both investigations, fertilisation resulted in increased levels of the nutrients supplied. Seasonal variations in foliar nutrient levels have been observed in both deciduous (Barker, 1973) and coniferous (Fife and Nambiar, 1982) tree species. In young P. radiata trees, Fife and Nambiar (1982) found concentrations of nitrogen, phosphorous, and potassium in the current season's foliage to decrease markedly from spring to early summer. Crown position and stocking density may also affect nutrient levels due to differences in photosynthetic efficiency in different parts of the tree. ~~However~~, ~~there is no conclusive evidence that crown position plays an important role in nutrient distributional gradients~~. Comerford (1981) found that the vertical distribution of nutrient concentrations in red pine (Pinus resinosa (Ait.)) was dependent on foliar age and not crown position. Tree age was shown to influence elemental levels in a P. radiata stand in New Zealand, where trees ranged in age from two to twenty-two years. Nutrient concentrations in bolewood and branches were seen to decrease with tree age, except calcium and manganese, which increased (Madgwick

et al., 1977). Nutrient levels have been shown to vary with age of the tree component. Variations with age in the nutrient content of branches, leaves and bolewood of non-deciduous conifers generally indicate decreasing concentrations of the labile elements and increasing concentrations of the less mobile elements (Wells and Metz, 1963; Barker, 1973; Comerford, 1981; Lang et al., 1982). Studies of P. radiata foliar nutrient levels consistently demonstrate that concentrations of labile elements, particularly nitrogen, phosphorous, and potassium, tend to decrease with needle age (Florence and Chuong, 1974; Madgwick et al., 1977; Mead and Will, 1976; Madgwick et al., 1983).

Seasonal changes in nutrient levels, particularly in tree crowns, have been attributed to the dilution effect (Barker, 1973) and to retranslocation of nutrients to different tree parts (Fife and Nambiar, 1982; 1984). For deciduous trees in early summer, rapid growth and biomass production result in decreased concentrations of nitrogen, phosphorous and potassium in foliage (Barker, 1973). This effect was also observed in P. radiata needles during the growing season (Fife and Nambiar, 1982; 1984). However, Fife and Nambiar (1982; 1984) also observed decreases in nutrient levels of one-year old needles of P. radiata and attributed this to a retranslocation of nutrients from these needles to developing shoots. This occurred regardless of irrigation and fertiliser regimes and is therefore not related to senescence and ageing of needles. Previous studies (Wells and Metz, 1963) had indicated that translocation of nutrients from foliage occurs only prior to abscission. Fife and Nambiar (1982; 1984) conclude that new shoots are primary 'sinks' for retranslocatd nutrients and one-year

old foliage acts as a 'source' of nutrients for these shoots. They postulate that there is ongoing competition between different parts of a branch for nutrients, with preference given to the youngest shoot. Indeed, the concept of 'sources' and 'sinks' within trees has been illustrated in a number of nutrient distribution studies. A general trend is seen to occur where the concentration of nutrients in leaves > branchwood > bole bark > sapwood > heartwood (Madgwick et al., 1977; Bockheim et al., 1983). Evidence suggests preference for nutrients is given to those components with the greatest metabolic activity.

Foliar analysis is widely used as a means of measuring the nutrient status of a tree, as well as estimating site nutritional status. While most investigators seem to agree that foliar nutrient levels reflect nutritional differences between stands (Madgwick et al., 1983), there is some debate as to whether site fertility can be estimated from these levels, since tissue concentrations do not always reflect the nutritional status of the soil (Comerford, 1981). Foliar analysis has also been used to determine nutrient levels which are optimum for tree growth. Several investigators have estimated these levels for various tree species as summarized by Morrison (1974). Ingestad (1959) suggested optimal levels for the major nutrients (nitrogen, phosphorous and potassium) in foliage of conifers. An increase in one element beyond the optimal level may result in deficiencies in the remaining elements. For example, Heilman and Gessel (1963) reported decreased concentrations of phosphorous and potassium in foliage of Douglas-fir (Pseudotsuga menziesii) as a result of nitrogen fertilisation.

Most studies of nutrient gradients in trees have examined gradients across age classes of foliage (e.g. Wells and Metz, 1963; Comerford and Leaf, 1982a). Orman and Will (1960) examined nutrient

concentration gradients across age classes in P. radiata bolewood by separating sample bole discs into (i) the outer five rings of sapwood, (ii) remainder of sapwood, and (iii) the heartwood. Phosphorous and potassium occurred in highest concentrations in regions of greatest metabolic activity and only in small amounts in the non-living heartwood. Nitrogen was at its highest level in the outer sapwood of the bole. Similar patterns were seen by Banks (1985, unpublished), who analysed bolewood density and nutrient gradients in a 15-year old stand of P. radiata located in the BFG experimental forest. Nitrogen, phosphorous, and potassium displayed similar concentration patterns with high concentrations in the top 20 percent of the stem and extending down the bole in the outer growth ring. Calcium, magnesium and manganese, all relatively immobile elements, had highest concentrations in oldest growth rings.

1.2.3 Nutrient Content

Tree and stand nutrient content have been measured to evaluate potential losses resulting from harvests as well as to compare various sites and fertiliser treatments in terms of the amounts of nutrients being taken up by the trees. Wells and Metz (1963) found that soils of varying nutritional status influence the nutrient content of Pinus taeda in Wisconsin, USA. Likewise, Heilman and Gessel (1963) observed that two times the nitrogen, greater quantities of potassium, and approximately equal amounts of phosphorous were contained in Douglas-fir (Pseudotsuga menziesii) needles on certain fertilised plots compared with unfertilised plots.

Stand nutrient content has been determined in a number of investigations. Bockheim et al. (1983) measured absolute nutrient amounts in a P. resinosa stand in Wisconsin, USA. Total elements in the aboveground and below ground biomass ranked N > Ca > K > Mg > S > P. Madgwick et al. (1977) and Forrest (1969) found similar patterns in P. radiata trees, where N = K > Ca > Mg = P Mn. The above studies also measured gross annual uptake (kg ha^{-1} a^{-1}) of nutrients as a means of evaluating site nutrient status.

Nutrient contents of tree components have been measured to calculate the proportional allocation of nutrients within the tree. Orman and Will (1960) found that, while needles, branches and bark represent only 20 percent of the dry matter of twenty-six year old P. radiata trees, they hold 50 percent of the nutrients. Needles, which comprise 2.5 percent of the tree biomass, contain 20 percent of the nitrogen phosphorous, and potassium. A later study by Madgwick et al. (1977) confirms these earlier findings. Figure 1 shows the relative distribution of dry matter and eight nutrients in this P. radiata stand in New Zealand.

In studies of tree nutrient distribution and movement, measurements of concentration levels alone can be misleading, since biomass production and distribution affect both concentrations and absolute levels of nutrients, as mentioned. Increases and decreases in nutrient concentration levels may result from changes in nutrient content, changes in biomass, or both. For example, Madgwick et al. (1977) found great differences in nutrient concentrations between trees in a P. radiata stand, but little variation in total nutrient content. This reflected differences in biomass among trees in the stand. Nutrient

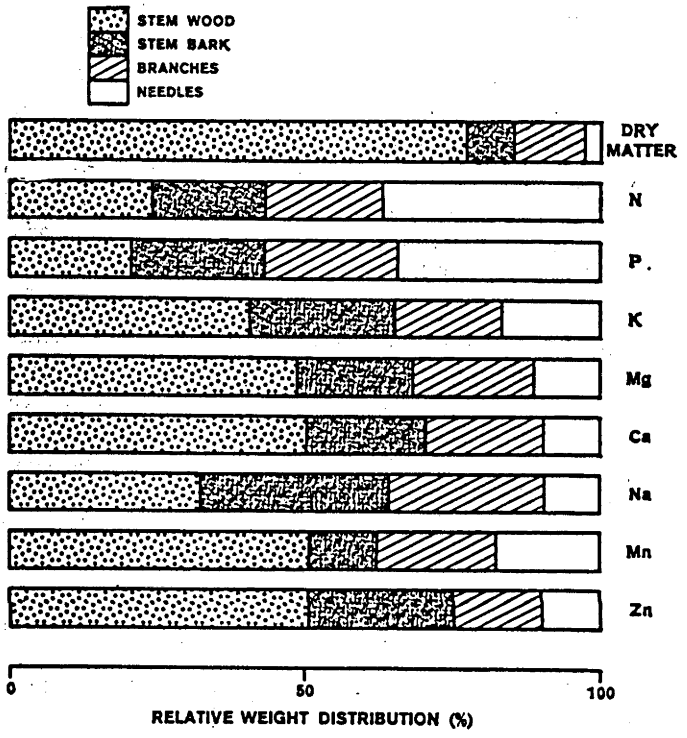


Figure 1: The relative distribution of dry matter and 8 nutrients in the main above-ground components of a 22-year-old radiata pine stand. (Madgwick et al., 1977)

levels decrease at times of high biomass production due to the dilution effect. However, if lower concentrations do not coincide with increasing biomass (i.e. if the actual nutrient content is decreasing), this may indicate a real deficiency. For this reason, nutrient content data are essential in evaluating tree and stand nutritional status.

Since foliage holds a significant amount of the tree's nutrient capital, many studies have analysed foliar nutrient content. Nutrient content of bolewood has also been calculated to determine losses from bolewood harvests. Figure 1 clearly illustrates that branches hold a considerable amount of the nutrient capital in P. radiata trees. However, few researchers have looked at the contribution of branches to the nutrient content of a tree.

1.2.4 Sampling Procedures to Evaluate Nutrient Distribution in Tree Components

Sampling strategies for estimating biomass, nutrient concentration, and nutrient content of tree components are essential for determining the roles of various tree parts in the overall distribution of nutrients. Many researchers have criticised the costly and time-consuming procedures frequently used to estimate tree component and stand nutrient content. Such procedures have involved removal of large numbers of trees from a stand for chemical analysis. It is generally recognized that sampling techniques must be improved in terms of both efficiency and accuracy. Since this investigation is concerned with the branch component of P. radiata, discussion here will be limited to methods of branch sampling.

One of the first considerations in choosing a sampling strategy is nominating an appropriate time for the sampling to take place. Rennie (1966) states that, unless one is interested in the pattern of nutrient cycling throughout the year, the best time for tree sampling is during the period of physiological dormancy. Mead and Will (1976) argue that, in order to detect nutrient deficiencies and site differences with the greatest possible sensitivity, samples should be taken when the differences between sites or treatments are greatest i.e. the middle of the growing season, when trees are most stressed. However, trees differ in their responses to stress and in their activity throughout the growing season (e.g. some trees will produce flowers while others will not). Sampling in autumn or winter reduces the amount of tree to tree variation due to metabolic activity, and most researchers have adopted this policy (Wells and Metz, 1963; Barker, 1973; Madgwick and Jackson, 1974; Messina et al., 1983).

In tree nutrient studies where two or more silvicultural treatments are being assessed, choosing the number of trees for destructive sampling is a critical stage in the sampling procedure. Valentine et al. (1984) state that the variance of an estimate of biomass or mineral content is dominated by the variance that results from this stage in the sampling. The object here is to attain sufficient precision of the estimate to allow comparison of treatments or to assess nutrient distribution. In most studies of nutrient distribution, including both deciduous and coniferous species, eight to ten trees per treatment have been chosen from a range of size classes within each treatment (e.g. Orman and Will, 1960; Forrest, 1969; Knight, 1978; Hingston et al., 1981; Comerford and Leaf, 1982a; Messina et al., 1983; Carlyle and Malcolm, 1986). In an analysis of forest sampling procedures for

nutrient uptake studies, Rennie (1966) found that, for mature red pines (P. resinosa), three to four trees provide mean data for several important attributes with confidence limits not exceeding ± 10 percent.

Estimates of branch biomass and annual production may be obtained without felling trees if regression techniques are employed. These were successfully obtained for deciduous trees by Whittaker (1965) and for P. radiata by Madgwick and Jackson (1974). However, nutrient studies require removal of branches to provide material for chemical analysis. The methods by which this is done vary considerably. Several authors (Rennie, 1966; Heilman and Gessel, 1963; Feller, 1983) have separated branch material into live and dead branches and then subsampled from these two categories. Rennie (1966) further divided the live and dead branches into four size classes and randomly selected one branch per group for analysis. Forrest (1969) selected only one branch per tree to provide estimates of leaf and branch dry weights in P. radiata. Hingston et al. (1981) separated the crown into upper, middle, and lower branches and subsampled from these categories. Branches of Pinus sp. have been separated by whorls. Comerford and Leaf (1982a) and Carlyle and Malcolm (1986) composited all branchwood of the same whorl and selected one branch at random from each whorl. Madgwick et al. (1977) separated crowns of P. radiata into whorls and then subdivided all first and second order branches by the age of needles which they bore (i.e. age classes). Subsamples from each age class were separated into needles and branches for analysis. All the methods described above are labour-consuming, involving destructive sampling of an entire tree and sorting of all branches in the crown.

Several researchers have examined ways of improving sampling techniques to arrive at a minimum number of samples that will characterise the nutrient content and distribution of a single tree. In an investigation of sampling variation of nutrient element content within and between P. resinosa trees, Young and Carpenter (1976) conclude that choosing a random branch in the mid-portion of the crown and a random mid-branch disc is adequate for estimating the nutrient content of branches. Messina and others (1983), however, found that a single branch disc subsample was unable to accurately estimate crown nutrient concentrations in six bottomland hardwood species of the southeastern US, and recommend intensive sampling of the tree crown for nutrient evaluations. Comerford and Leaf (1982a) recommend a systematic 20 percent crown sample for P. resinosa for estimating crown element content within 10 percent allowable error. Valentine et al. (1984) have developed a method of selecting disc subsamples for chemical analysis. Randomized sampling is combined with importance sampling, a technique of Monte Carlo integration which involves the selection of discs from different components of the tree. A path is selected up the tree and each bole and branch internode is represented by a disc subsample. This method may overcome some of the problems in disc selection encountered by other authors.

It may be seen from this review of the literature that branch samples have been selected arbitrarily, or at best, systematically, and the estimates and variances from such samples are known to be biased (Valentine et al., 1984). The nutrient concentration range is pronounced within a branch and among branches within a crown (Messina et al., 1983), and this range must be proportionally represented in the

subsamples chosen for chemical analysis if estimates are to be accurate. To date, no studies have been found that specifically examine nutrient concentration gradients within branches. More information is needed concerning nutrient concentration gradients across branches from apex to base as well as gradients from bark/phloem to pith across branch rings.

1.3 Rationale for this Investigation

Nutrient distribution studies are important in understanding the physiological processes of trees and have direct application in forest management decisions such as choosing appropriate fertiliser applications. Because P. radiata is an important commercial crop in Australia and several other countries, more information is needed regarding the mineral nutrition of this species. In particular, the lack of information in the literature with respect to nutrient distribution patterns in branches highlights a need to explore these patterns in order to get a clearer picture of the role of branchwood and branch bark/phloem in the overall nutrient story for this species. The aims of this project are:

(i) To examine in 15-year old P. radiata the distribution of biomass, nutrient concentration and content in branches initiated in the spring of 1982.

(ii) To compare the above parameters in two treatment plots: an irrigated plot, and an irrigated and fertilised plot.

(iii) To utilise the findings of this investigation to suggest possible considerations in sampling strategies for determining nutrient content in this species.

CHAPTER 2

METHODS AND MATERIALS

2.1 Background to the Biology of Forest Growth Project

The Biology of Forest Growth (BFG) project site was established in February 1983, by the Division of Forest Research, C.S.I.R.O., in collaboration with the A.C.T. Forests Branch D.C.T. to provide a facility for multi-disciplinary research. The research projects generally aim to study the processes of tree growth and associated soil factors in order to develop biological growth models for Pinus radiata crops. These models will be used to predict growth and development of P. radiata crops under different site and climate and conditions of management. The projects presently underway are listed below.

LIST OF PROJECTS - B.F.G.

Project	Responsible
Soil water under P. radiata stands	T. Talsma
Nutrient cycling under P. radiata stands	R.J. Raison, P.K. Khanna
Gas exchange in field grown P. radiata	S. Linder
Carbohydrate dynamics in P. radiata	A. Wheeler
Biomass and growth in P. radiata	M.L. Benson
Dynamics of mineral nutrients in P. radiata	W.J.B. Crane, J.C.G. Banks
Water relations of field grown P. radiata	B.J. Myers
Soil phosphorous and exchangeable cations under fertilized P. radiata	I.R. Willett, M.A. Bekunda
Seasonal patterns of reproductive growth in P. radiata	K.W. Cremer

2.2 Site Description

The Biology of Forest Growth (BFG) experimental forest is located 20 km west of Canberra, A.C.T., at a latitude of 35° 21' S, a longitude of 148° 56' E, and an altitude of 625 m. Climatic data has been collected since October, 1983, and include observations of rainfall, screen temperatures, screen humidity, and soil temperatures. An automatic weather station, installed in March, 1984, records rainfall events, radiation, wind speed and direction, humidity, and temperature. Evaporation is recorded both under the canopy and in the open. Table 1 shows precipitation and evaporation data for two study plots from October 1984 to October 1986.

The soil is a yellow podzolic Dy 3.61 derived from adamellite (coarse grained, calcium rich, granitic rock). External drainage is good but internal drainage is poor as evidenced by the death of most trees along the poorly drained gullies. The A horizon is up to 40 cm deep but bulk density increases quickly with depth. Water storage in the A horizon is about 50 mm; this horizon has modest permeability and rather limited water retention. The B horizon has very poor permeability and has a bulk density between 1.7 and 1.8 g cm^{-3}. Fine roots are confined to the A horizon, with a few coarse roots extending to depths of several metres.

The soil has low organic matter and hence low total nutrient reserves. Fertility is concentrated in the 0-10 cm layer. Organic carbon content decreases from 2.4% in the 0-2.5 cm layer to only 0.5% in the 10-15 cm region. pH (1:5 in water) is 5.8 in the surface and decreases to 5.5. at 40 cm depth.

The site was cleared of the original eucalypt woodland in 1934-35, broadcast burned and planted to P. radiata in winter, 1935. This tree crop was harvested in 1972, the slash was heaped and burned and replanting was carried out in June 1973 with 2-year old seedlings raised from a mix of seed from the Stromlo plantations and the Tallaganda seed orchard. Each tree was fertilised soon after planting with a Ko Kei fertiliser tablet (71 g, N 6.28%, P 4.35%, K 3.32%). The initial tree stocking was nominally 997 stems ha^{-1} but subsequent deaths reduced this to approximately 700 stems ha^{-1}.

2.2.1 Treatments

The experimental forest consists of ten 0.25 ha plots, established in February, 1983 (figure 2). The treatments which have been applied are:

- C - control (plot 6)
- I - irrigated (plot 5)
- F - fertilised - solid (plot 7)
- IF - irrigated and solid fertilised (plots 3 and 4)
- IL - irrigated and liquid fertilised (plots 1 and 2)
- S - sewage sludge (plot 10)
- D - demonstration trials of four solid fertiliser treatments (plots 8 and 9)

For the purpose of this project, branches were collected from the irrigated plot (plot 5) and ~~an~~ the irrigated and liquid fertilised plot (plot 1). These are referred to as the I and IL treatment plots. The irrigation treatment, both on its own and in conjunction with liquid fertiliser, was chosen to remove soil moisture as a factor limiting tree growth.

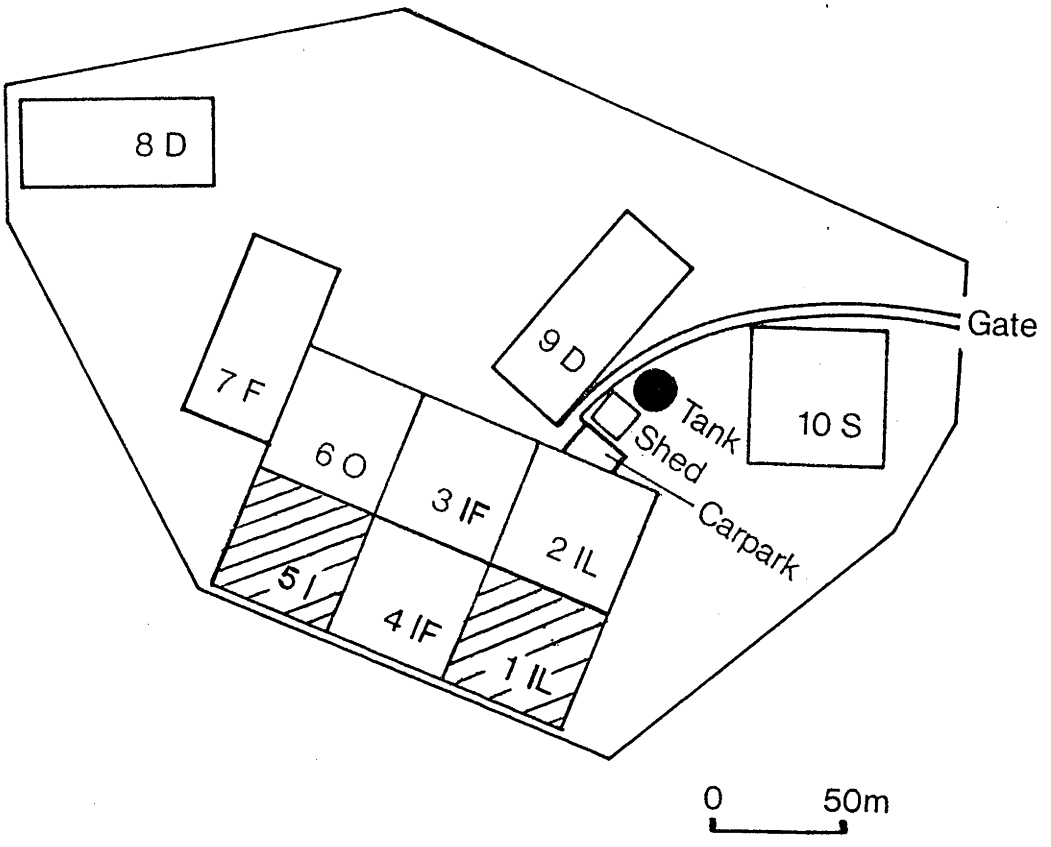


Figure 2: Lay-out of the Biology of Forest Growth radiata pine project

I-irrigated

L-liquid fertiliser

F- solid fertiliser

D-demonstration fertiliser trials

S- sewage sludge

- plots used in this study for branch sampling

In the I and IL plots, water is applied by sprinklers at a rate sufficient to maintain soil moisture at or near field capacity (approx. 50 mm). The irrigation treatment in both plots commenced in August 1984.

The liquid fertiliser treatment commenced in August/September 1984. It consists of regular applications of complete nutrient solutions delivered through the irrigation system. Major elements (N, K, P, CA, Mg, S) are applied weekly and minor elements (Fe, Mn, B, Cu, Zn, Mo) four weekly, at rates designed to provide adequate nutrients for tree growth throughout the season - mid-August to mid-May. The liquid fertiliser used is Ingestad L-65/13 liquid soluble NH_4/NO_3 ratio of 30/70. The major elements are supplied in the ratio N/K/P/CA/Mg/S = 100/65/13/7/8.4/9. Minor elements are in the ratio Fe/Mn/B/Cu/Zn/Mn = .7/.4/.2/.03/.03/.007. The equivalent of 240 kg ha^{-1} of N were added in 1984-85 with peak application rates in the spring and early summer (200 kg ha^{-1} of N by the end of January).

Different amounts of water are applied to the two plots depending - calculated using a model based on open pan evaporation on demand. The amount of water applied from commencement to October 1986 is set out in table 1, along with precipitation and evaporation data.

2.2.2 Growth Data

At the commencement of the project, trees in plots 1-7 were measured for diameter. Subsequently, measurements of diameter and height have been carried out at regular intervals.

TABLE 1: Water relations for *Pinus radiata* in two treatment plots.

PERIOD	IRRIGATION (mm)		PRECIPITATION (mm)	EVAPORATION (mm)
	I*	IL*		
10/84	90	104	79.4	92.1
11/84	87	98	37.2	137.3
12/84	135	150	23.4	163.3
01/85	145	156	2.0	195.8
02/85	154	248	6.6	141.4
03/85	107	92	210.0	122.9
04/85	21	19	25.4	49.1
05/85	44	29	66.0	31.0
06/85	0	0	32.2	15.8
07/85	15	16	48.4	24.5
08/85	0	6	151.8	33.3
09/85	10	21	79.8	48.3
10/85	48	58	70.2	82.9
11/85	71	116	79.0	106.4
12/85	115	127	35.8	131.4
01/86	171	205	52.4	195.4
02/86	221	225	2.6	157.6
03/86	221	174	0.6	121.4
04/86	110	126	70.2	106.4
05/86	10	48	78.4	27.8
06/86	10	9	10.8	13.0
07/86	0	0	156.0	13.7
08/86	14	24	65.6	42.0
09/86	43	56	45.6	60.6
10/86	59	79	117.4	69.7
TOTAL IRRIG.	1901	2186	1546.8	2183.1
RAINFALL	1546.8	1546.8		
TOTAL WATER	3447.8	3732.8		

* I Irrigated only

IL Irrigated and fertilised

Prior to any treatments being applied the stand was relatively uniform in terms of basal area. There was some variation in stocking (600 to 700 stems ha^{-1}) with a commensurate variation in mean diameter (15.3 to 13.7 cm). Heights were very consistent. Growth data for the I and IL plots are summarised in table 2.

2.3 Sampling Procedure

2.3.1 Field Procedure

On June 17-18, 1986, a total of sixteen trees were selected for branch sampling in the I and IL treatment plots, with eight trees chosen from each plot. Both trees and branches were selectively chosen to obtain branches representative of the treatment plot. Trees were selected across the range of basal areas for that plot, so that trees of all sizes would be proportionally represented. Eight trees per treatment was considered to be a reasonable sample size to account for tree to tree variability. One branch was selected and removed at the bole from each of the 16 trees. These were taken from the whorl initiated in the spring of 1982. In the IL plot, these whorls held an average of 7 branches, while the I plot carried 6 branches per whorl. The branch with a diameter closest to the whorl mean was sampled so that each tree was represented by one branch. Because only one branch was chosen for each tree, branch to branch variation within a tree cannot be accounted for here. The cardinal position of the branches was not considered in this study, since it has been found to be insignificant in determination of biomass and nutrient content in both deciduous and coniferous tree species (Young and Carpenter, 1976).

TABLE 2: Growth data for *Pinus radiata* in two treatment plots.

Treatment	I *	IL*
Stocking (ha^{-1})	703	795
Mean Diameter (cm)		
2/83	13.9	13.7
5/84	16.3	16.2
8/84	16.7	16.6
2/85	18.0	18.3
6/86	20.7	22.3
Basal Area ($m^2 ha^{-1}$)		
2/83	11.2	12.2
5/84	15.3	17.0
8/84	16.0	17.7
2/85	18.7	21.7
6/86	22.8	26.5
Basal Area Increment ($m^2 ha^{-1}$)		
2/83 - 5/84	4.1	4.8
5/84 - 8/84	0.7	0.7
8/84 - 2/85	2.7	4.0
2/85 - 6/86	4.1	4.8
Height (m)		
2/83	9.0	9.3
5/84	10.2	10.3
6/86	12.2	12.5

* I Irrigated only
IL Irrigated and fertilised

In the IL plot, seven of the eight branches held four years' growth (1982/83 - 1985/86), while this was only true for three of the eight branches in the I plot. The remaining six branches held three years' growth (1983/84 - 1985/86). Since the I and IL treatments commenced in 1984, the treatment period is represented in all branches.

The sampled branches were immediately brought to Canberra and stored at 4°C until 21 July 1986, when they were subdivided for nutrient analysis. It is assumed that storage at this low temperature over one month resulted in negligible loss in branch mass.

2.3.2 Laboratory Procedure

On 21 July 1986, foliage was removed from the branches and approximately 5 g of needles of each age class were set aside for nutrient analyses. On all branches except one in the I plot, two age classes of foliage were present, the 1985/86 current foliage ('C' foliage) and the 1984/85 foliage ('C+1' foliage). The smallest branch sampled from the I plot held only current (C) foliage. All side branches were removed and discarded, leaving only the main axis of each branch. The defoliated branch was divided into age classes, as shown in figure 3. Fresh weights were obtained for each internode of the main axis, and discs were taken from the midpoint of each internode using secateurs and a band saw. Xylem and bark/phloem were separated by age classes and fresh weights of each recorded. All sample material (foliage, bark/phloem, and xylem) was air dried at room temperature for one week and then oven dried at 85° C for 24 hours. This slow-drying method was employed to avoid any loss of nutrient rich liquid into the paper

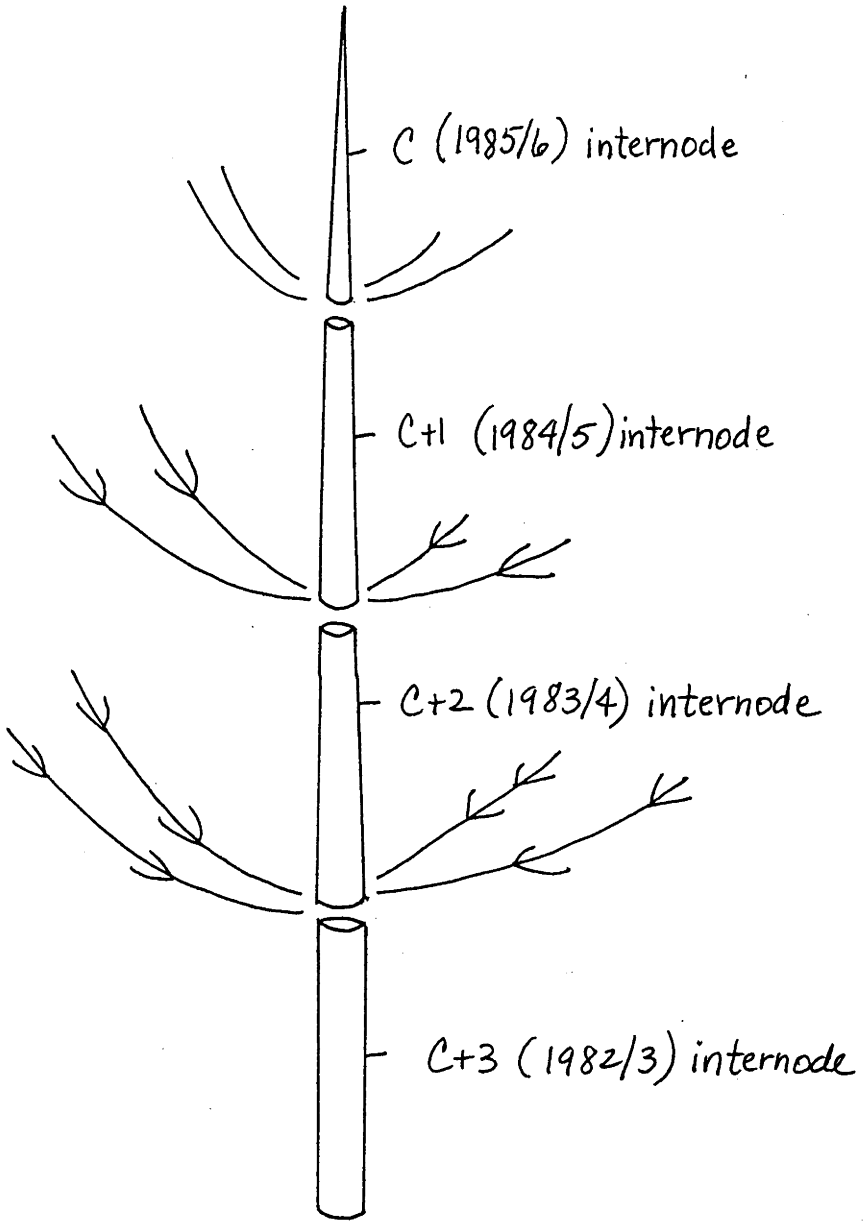


Figure 3: Subdivisions of defoliated *Pinus radiata* branch for sampling

containers which may occur when fresh plant material is oven dried at higher temperatures. Oven dry weights (ODW) were obtained for all samples.

Approximately 3 g (ODW) of each sample of foliage and bark/phloem were ground in a Braun Aromatic KSM2 coffee grinder for nutrient analyses. In order to obtain biomass and nutrient data for each age class in the xylem, rings in the xylem sample discs were identified and their areas (cm^2) recorded from diameter measures. This data was later used to determine the mass for each growth ring in each internode using the cross-sectional area ratio:

$$\text{Growth ring mass per internode} = \frac{\text{Ring area } (cm^2)}{\text{Total sample disc area } (cm^2)} \times \text{Total xylem mass of an internode}$$

Samples of each ring at each internode were required for biomass and nutrient data based on age classes of xylem. Rings in the xylem sample discs were separated using a carpenter's chisel and scalpel and cut into 1 cm "matchsticks" to provide sufficient material (approximately 3 g ODW) for nutrient analysis.

2.4 Nutrient Analysis for Nitrogen, Phosphorous, Potassium, Calcium, Magnesium and Manganese

Determination of nitrogen and phosphorous was carried out at the Division of Forest Research, CSIRO, in Canberra, and followed the Division's standard procedure for nutrient analysis. Prior to chemical analysis, each sample was redried at 85° C for 35 minutes (Heffernan, 1985). For foliage and bark/phloem samples, 0.1 g proved adequate, but for xylem material 0.2 g was required to give the correct range of

cation concentrations in the digest. The digest solution was diluted to 50 ml with distilled water and analysed for nitrogen and phosphorous concentrations by the Technicon automated spectrophotometric method (Heffernan, 1985).

Chemical analysis for potassium, calcium, magnesium and manganese was conducted in the Soil and Plant Nutrient Analytical laboratory at the Department of Forestry, ANU. Samples were digested in a 1:3 solution of hydrochloric acid (conc.) and nitric acid (conc.) on a hot plate until the volume was reduced to 1 ml. Samples were then filtered through Whatman No. 41 filter paper and diluted with distilled water. For foliage, 0.25 g of sample material was required, while 0.30 g of bark/phloem and 0.35 g of xylem were used in the digest. The digested samples were analysed on an AA5 Varian-Techtron atomic absorption spectrophotometer.

CHAPTER 3

RESULTS

The sampling matrix used to illustrate distribution patterns for biomass, nutrient concentration and content is shown in figure 4. Unfortunately, foliage biomass data were not available and therefore nutrient content of foliage could not be calculated. However, foliar nutrient concentrations were obtained from samples and are presented in section 3.2.

Although magnesium and manganese concentration levels in branch tissue were obtained, these nutrients showed no identifiable distribution patterns in the branches and are therefore discussed only briefly in section 3.2. Branch magnesium and manganese content were not calculated. Rather, the investigation focuses on the three major labile nutrients - nitrogen, phosphorous and potassium - and calcium, an immobile nutrient.

3.1 Biomass of the Sample Branches

3.1.1. Distribution of Biomass

Biomass data for the primary branches, including xylem and bark/phloem, are listed in table 3. Although branches with diameters closest to mean values for each whorl were selected, there is a high degree of variability in branch biomass within treatments. This variability negated statistical analyses of differences within treatments.

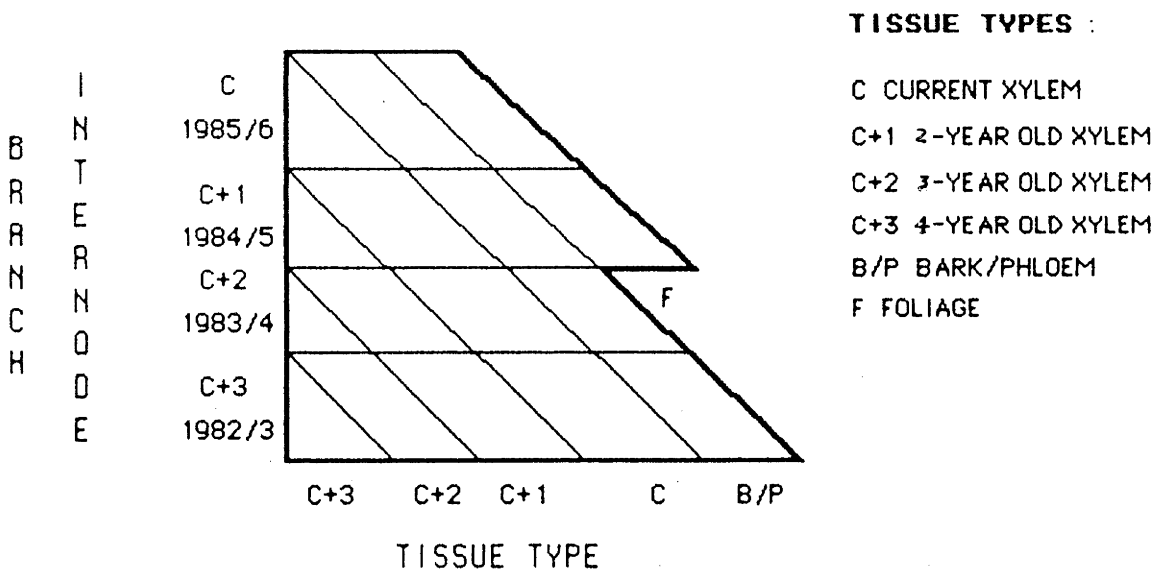


Figure 4: SAMPLING MATRIX FOR BRANCH TISSUE TYPES

Table 3: Biomass (g) of *Pinus radiata* xylem and bark/phloem in 4th order spring whorl primary branches by internode age and tissue type.

Internode	C 1985/6			C+1 1984/5				C+2 1983/4					C+3 1982/3						
Tissue Type	Bark/ Phloem	C	Whole Internode	Bark/ Phloem	C	C+1	Whole Internode	Bark/ Phloem	C	C+1	C+2	Whole Internode	Bark/ Phloem	C	C+1	C+2	C+3	Whole Internode	Total Branch Biomass
Irrigated 1	7.50	22.90	30.43	12.60	23.30	27.60	63.46	4.90	14.40	11.10	4.20	34.57	9.90	12.30	13.60	21.30	15.20	72.20	200.66
2	7.90	11.90	19.86	18.10	33.50	28.60	80.25	5.70	12.10	12.80	3.90	34.43							134.54
3	11.00	16.90	27.89	22.80	57.60	19.60	100.00	6.50	2.50	13.10	15.50	37.65	12.70	7.10	30.60	33.00	12.40	95.72	261.26
4	13.90	37.60	51.57	42.40	124.10	83.90	250.51	6.70	23.40	21.70	12.70	63.76							365.84
5	21.70	66.80	88.47	18.50	34.60	47.60	100.76	10.50	27.10	10.70	28.60	76.34							265.57
6	6.80	14.60	21.39	29.20	93.20	86.30	208.74	8.20	22.60	23.20	35.90	89.96							320.09
7	4.60	7.80	12.44	3.10	2.60	6.40	12.15	8.60	4.10	11.40	7.70	31.82							56.41
8	13.70	32.60	46.20	37.50	132.40	60.60	230.49	11.30	14.00	30.20	46.90	102.42	8.80	19.90	17.40	37.60	16.40	100.05	479.16
$\bar{x}$	10.90	26.40	37.28	23.00	62.70	45.10	130.80	7.80	15.00	16.80	19.40	58.87	10.50	13.10	20.50	30.60	14.70	33.50	260.44
SE																			46.99
Irrigated and 1	1.60	1.20	2.79	3.60	3.60	1.60	8.73	3.10	0.60	4.50	1.70	9.96	8.80	5.60	7.80	8.10	2.00	32.29	53.77
fertilised 2	9.90	11.30	21.19	6.60	5.00	15.40	26.97	5.10	2.50	5.90	7.50	26.04	15.10	28.10	19.90	9.20	3.30	75.59	149.79
3	7.30	16.90	24.19	22.60	77.40	21.50	121.48	8.40	36.10	21.50	4.40	70.46							216.13
4	8.80	14.30	23.09	6.10	11.20	10.40	27.73	7.40	8.10	15.20	8.70	39.31	11.80	6.90	29.80	18.30	2.90	69.66	159.79
5	7.30	12.50	19.87	7.20	13.10	9.70	29.93	18.90	19.30	43.70	10.70	92.60	41.90	43.00	83.80	56.10	10.30	235.13	377.53
6	2.90	2.80	5.73	2.20	3.20	1.60	6.92	2.20	2.30	1.60	0.50	6.60	5.50	2.80	7.80	4.20	1.10	21.43	40.68
7	1.30	0.80	2.09	2.60	2.80	2.20	7.54	2.30	1.80	2.80	1.00	7.91	4.70	3.60	3.10	1.70	4.00	17.06	34.60
8	16.70	39.70	56.43	14.80	23.30	25.10	63.28	43.40	65.50	62.80	83.70	255.38	14.40	18.20	14.60	16.30	5.90	69.41	444.50
$\bar{x}$	6.90	12.40	19.42	8.20	17.50	10.90	36.57	11.40	17.00	19.80	14.80	55.61	14.60	15.50	23.80	16.30	4.20	65.07	184.60
SE																			63.95

Figure 5 illustrates the distribution of biomass in the two treatments. Biomass of the bark/phloem at each internode is consistently less than that of the corresponding xylem. Beyond this pattern, there is no identifiable trend in biomass distribution in the branches. The highest values are seen in the C+1 internode in branches from the irrigated only (I) plot. This internode was laid down in 1984, the year treatments commenced in both plots.

3.1.2 Comparison of Biomass Between Two Treatments

The branch pattern resulting from the 1982/3 growing season varies between trees (table 4). Only 7 trees are uninodal, 5 produced an additional summer whorl, and 4 a double summer whorl. There is no statistical difference (α = .05) between treatments. The number of branches produced in the spring whorl varies from 4 to 8. Again, there is no statistical difference (α= .05) between treatments.

The primary branch biomass of the sample branches is higher in the I than in the IL treatment (table 3). A breakdown of biomass into growing seasons (table 5) indicates that the I treatment branches in 1982/3 held significantly more biomass (α= .05) than the IL branches initially. In the 1983/4 to 1984/5 growing seasons, I branches continue to carry greater biomass, but the difference between treatments is not significant at the 5 percent level. The greatest biomass increases in both plots occur in the 1983/4 growing season. This season, which had high rainfall, followed a very dry (1982/3) growing season (Benson, pers. comm.). The initiation of treatments at the end of the 1983/4 season did not result in significant differences in biomass between the two treatment plots.

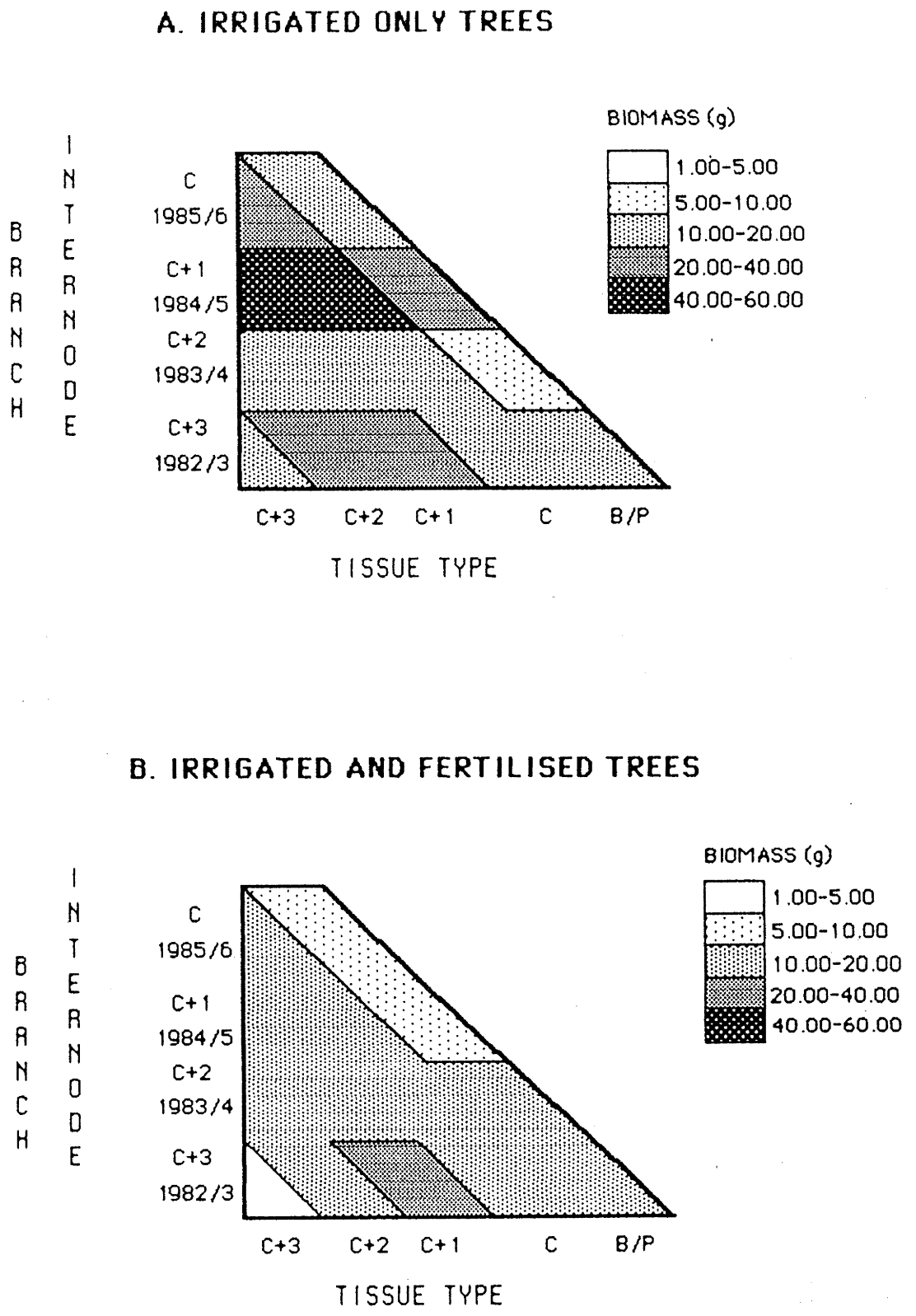


FIGURE 5: BRANCH BIOMASS PROFILES IN 4th ORDER SPRING WHORL IN 15-YEAR OLD *PINUS RADIATA*

TABLE 4: *Pinus radiata* branch growth data for the 1982/3 growing season in two treatment plots.

Treatment	Tree No.	No. of whorls produced in the1982/3 growing season	No. of branches in the sampled 1982/3 spring whorl
I - irrigated only	1	1	4
	2	2	7
	3	3	8
	4	3	7
	5	2	5
	6	1	7
	7	1	4
	8	1	6
	mean	1.75 SE = .313	5.00 SE = .655
IL - irrigated and liquid fertilised	1	2	6
	2	1	7
	3	1	7
	4	2	5
	5	1	6
	6	2	8
	7	3	7
	8	3	8
	mean	1.88 SE = .295	5.75 SE = .420

TABLE 5: Primary branch biomass production by growing seasons for irrigated (I), and irrigated and fertilised (IL) trees

Treatment	Growing Season			
	1982/3	1983/4	1984/5	1985/6
I	$\bar{x}$ 14.7	30.9	69.9	108.9
	SE 1.7	10.3	13.6	24.8
IL	$\bar{x}$ 4.2	29.0	51.3	47.9
	SE 1.2	13.9	18.0	16.7

Mean biomass in the I branches increases at a fairly consistent rate with each growing season (figure 6). In IL branches, biomass increases through the 1984/5 growing season, but levels off in the 1985/6 season.

3.2 Nutrient Concentration

3.2.1 Nutrient Concentration Patterns in Primary Branches

Nitrogen, phosphorous and potassium, the labile nutrients, have similar concentration patterns (figures 7-9). In both the I and IL trees, highest levels were found at the branch apex in all tissue types, and levels decrease towards the base of the branch. Concentrations are consistently highest in foliage followed by bark/phloem and xylem, respectively. Within the xylem, levels of all three nutrients decrease from current (C) to C+3 xylem. This occurs in both treatments, although it is not illustrated clearly in the I trees due to the narrow range of values in this treatment.

In the IL trees, high concentrations of nitrogen and potassium extend throughout the length of the outermost growth ring, i.e. the current xylem. There is an increase in nitrogen, phosphorous and potassium concentrations at the inner growth ring of each internode in the IL trees. This also occurs in the I trees, but is not clearly shown by the figures, again due to the narrow range of concentration values. A similar pattern to this was identified by Banks (1985, unpublished) in bolewood of P. radiata growing on the same site.

Calcium levels are highest in bark/phloem > foliage > xylem in both treatments (figure 10). Within each tissue type, concentrations are generally higher in older tissue.

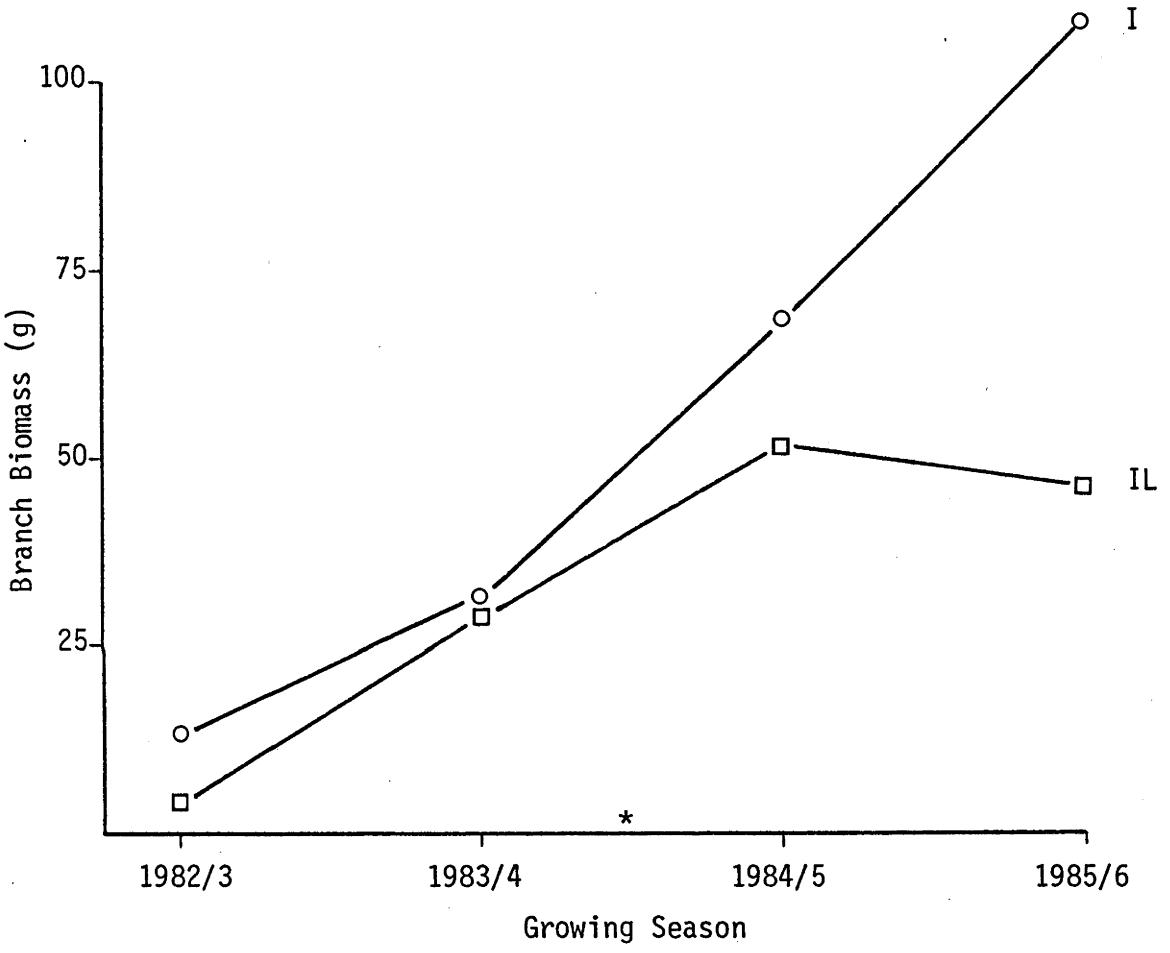
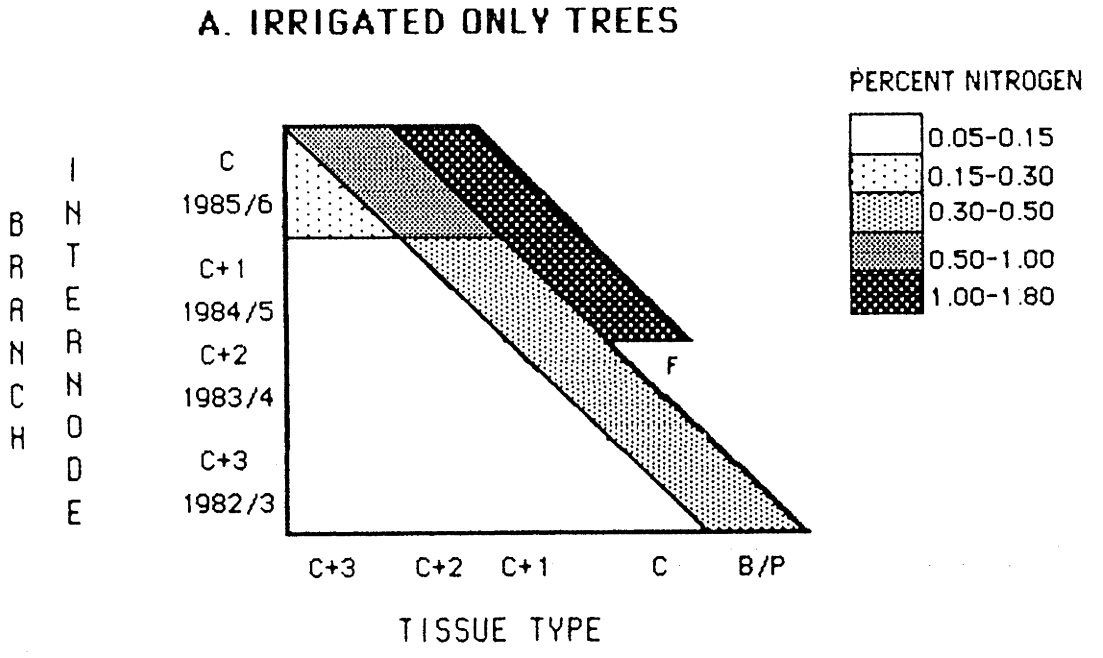


Figure 6: Mean primary branch biomass (g) in 4 growing seasons for irrigated (I) and irrigated/fertilised (IL) P.radiata branches. *treatment imposed spring 1984.



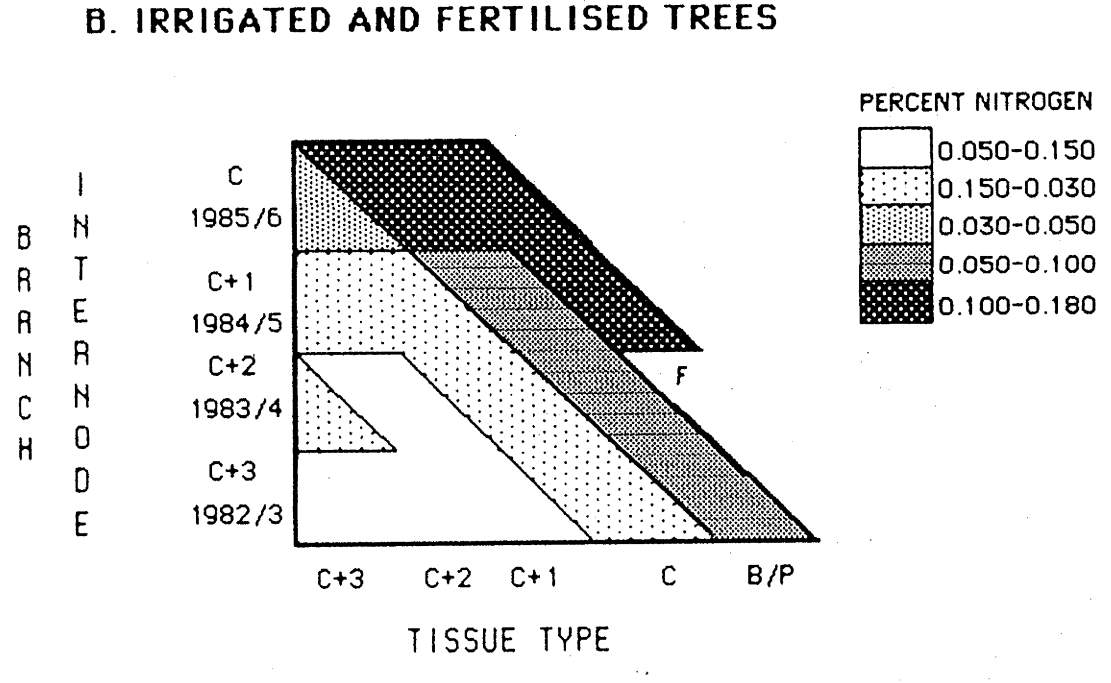


Figure 7: BRANCH NITROGEN CONCENTRATION PROFILES IN 4th ORDER SPRING WHORL IN 15-YEAR OLD *PINUS RADIATA*

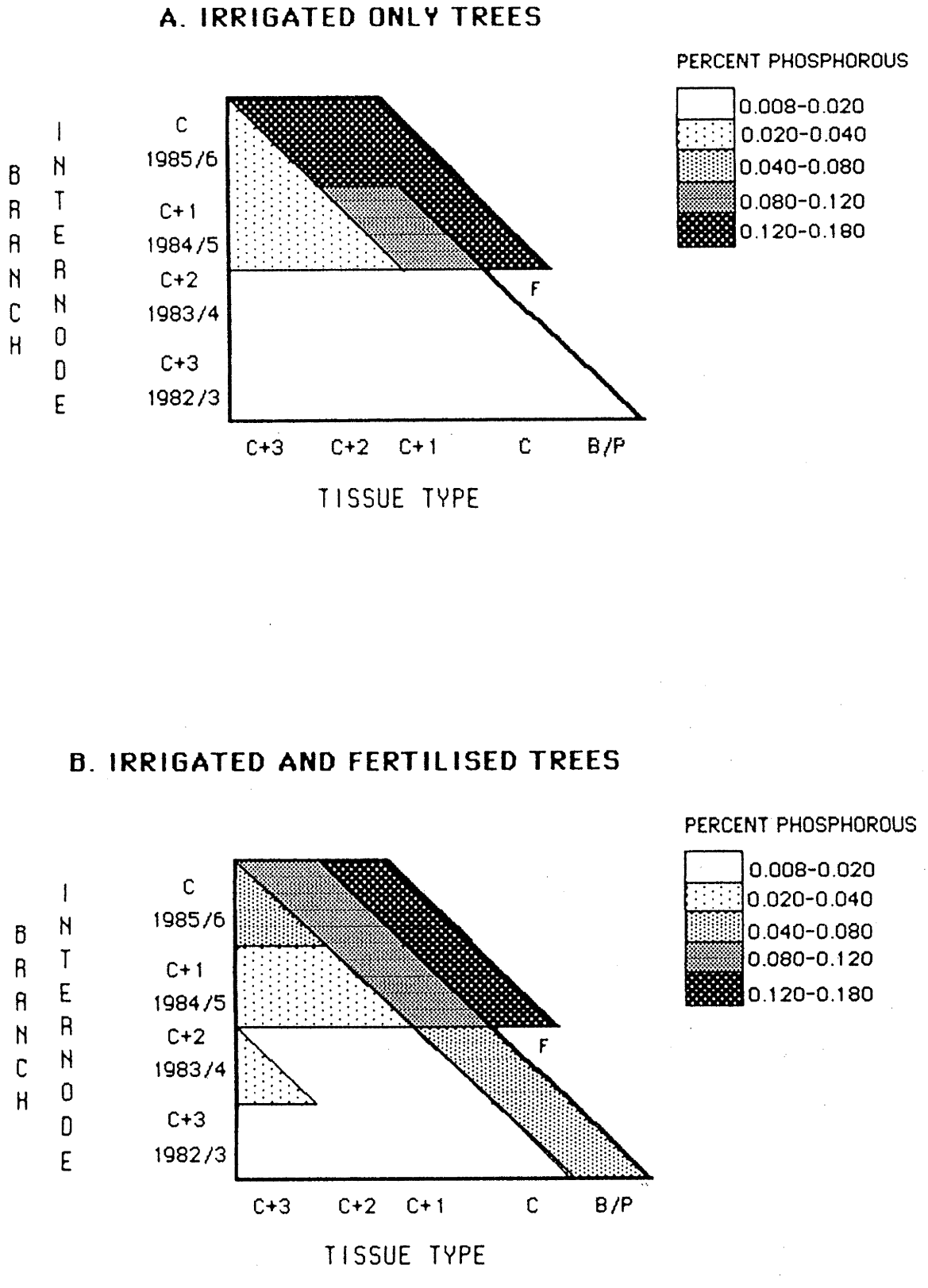
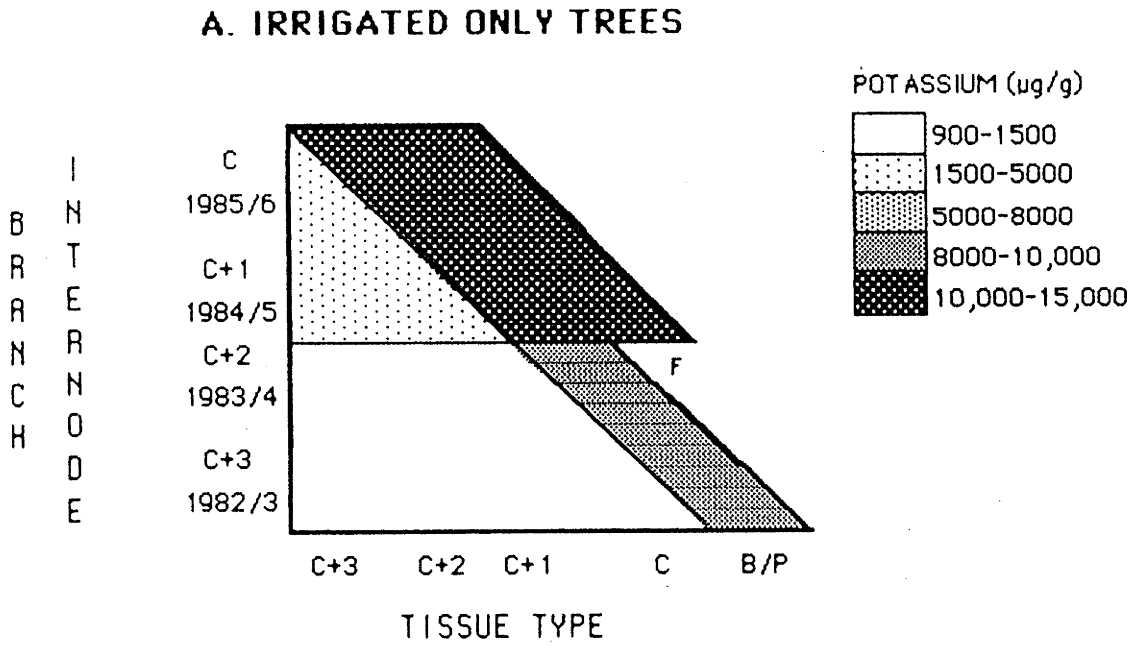


Figure 8: BRANCH PHOSPHOROUS CONCENTRATION PROFILES IN 4th ORDER SPRING WHORL IN 15-YEAR OLD *PINUS RADIATA*



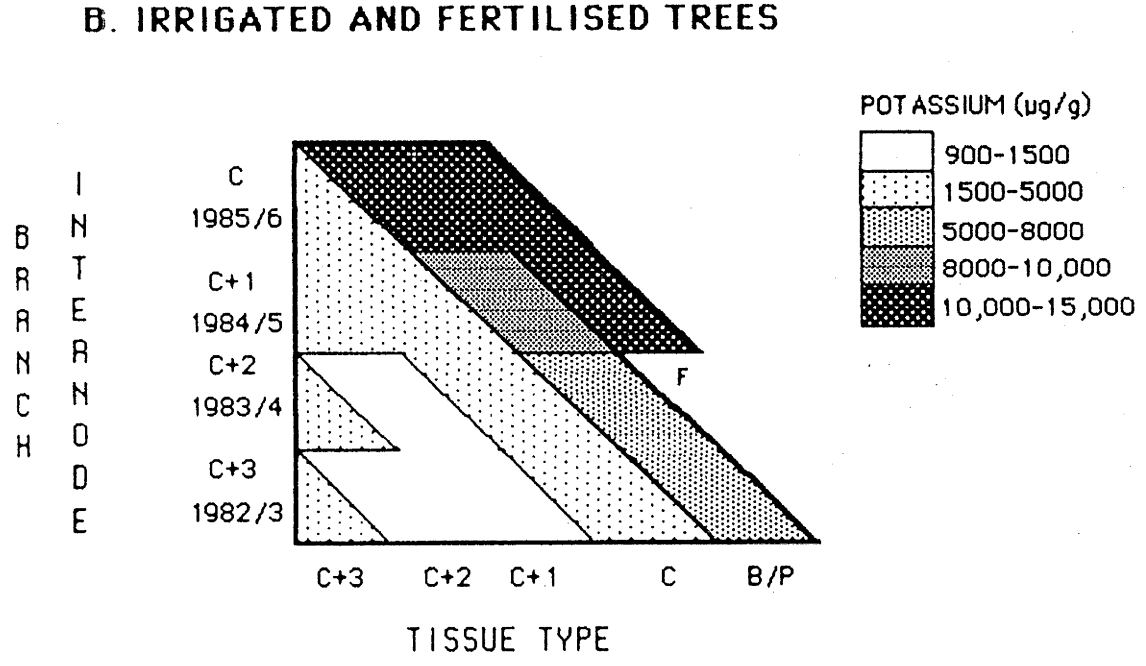


Figure 9: BRANCH POTASSIUM CONCENTRATION PROFILES IN 4th ORDER SPRING WHORL IN 15-YEAR OLD *PINUS RADIATA*

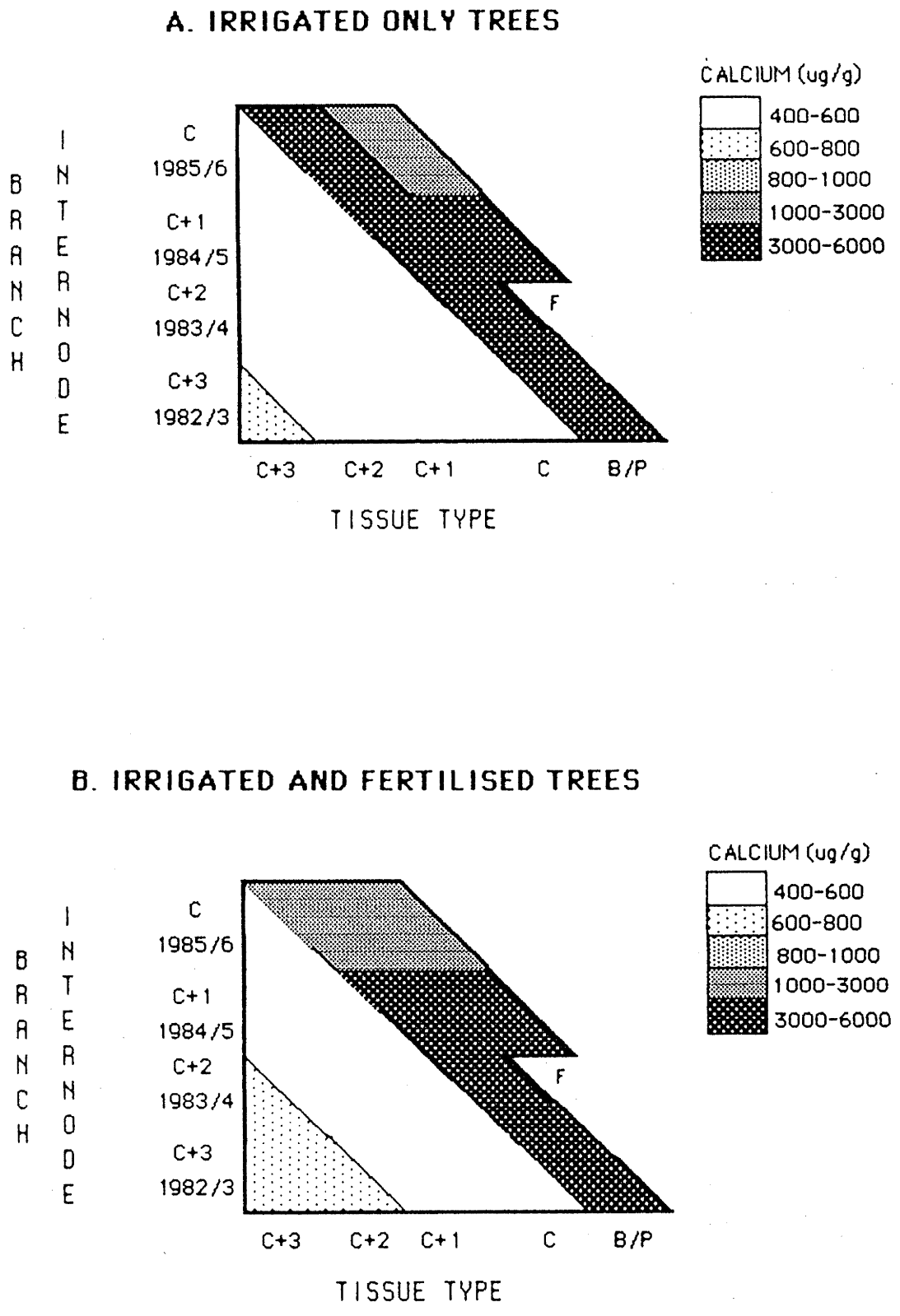


Figure 10: BRANCH CALCIUM CONCENTRATION PROFILES IN 4th ORDER SPRING WHORL IN 15-YEAR OLD *PINUS RADIATA*

Mean foliar concentrations for nitrogen are 1.2 - 1.8 percent, phosphorous 0.15 - 0.17 percent and potassium 10,000 - 11,000 ug/g (Appendix 1). This range is consistent with values reported for other P. radiata stands (Forrest, 1969). Phosphorous and potassium values vary by a factor of 1.1 while nitrogen values vary by a factor of 1.5. Nitrogen values are ten times higher than phosphorous levels, but only slightly higher than potassium concentrations. Calcium levels in foliage range from 1800 - 3000 ug/g, an increase of 1.7.

In bark/phloem, nitrogen and phosphorous show similar ranges in concentration values, varying by a factor of 3, while potassium varies by only 1.7 (Appendix 2). Again, nitrogen levels are ten times higher than phosphorous levels, but mean potassium levels are higher than those for nitrogen. Nitrogen, phosphorous and potassium ranges are 0.4 - 1.3 percent, 0.04 - 0.13 percent and 9000 - 15,000 ug/g, respectively. Calcium values range from 2400 -6000 ug/g, an increase of 2.5.

In xylem, concentration ranges for nitrogen, phosphorous and potassium are much wider, with higher values occurring in the current xylem (Appendix 3). Ranges for the three elements are 0.05 - 0.35 percent, 0.008 - 0.04 percent and 900 - 8000 ug/g, respectively. By contrast, the concentration range of calcium in xylem is relatively narrow, varying by a factor of only 1.75, from 400 - 700 ug/g. Concentrations of calcium are generally highest in older xylem and lowest in current xylem.

3.2.2 Analysis of Nutrient Concentration Gradients: Effect of Treatments

For both the I and IL treatments, nutrient concentration gradients along the primary branch were derived using analysis of variance of the natural logarithms of the concentration values. Gradients along the branch were derived for foliage, bark/phloem, and the current (C) and previous season's (C+1) xylem. In addition, gradients across the branch at the C+3 and C+2 internodes were also derived. Considerable variation between branches in each treatment was observed for each nutrient. However, mean branch values did show distinctive gradients.

(i) Foliage

Mean foliar nutrient levels for branch foliage are listed in table 6. Nitrogen and phosphorous concentrations are significantly higher (α = .05) in current foliage than in C+1 foliage in both the I and IL treatments. This is consistent with findings of several researchers looking at various coniferous species (Florence and Chuong, 1974; Comerford, 1981; Lang et al., 1982; Bockheim et al., 1983). Nitrogen levels in current foliage are significantly higher (α = .05) in the IL branches, but there is no real difference between treatments in C+1 foliage. For phosphorous, there is no difference in concentrations between the two treatments.

Potassium levels show a slight increase from C to C+1 foliage although it is not significant (α = .05). There is also no difference in concentration between treatments, although levels in I branches appear to be marginally higher.

TABLE 6: Foliar nutrient concentration in 4th order spring whorl *Pinus radiata* branches, for irrigated (I), and irrigated and fertilised (IL) plots..

Element	Treatment	Foliage Age	
		C - current	C+1 - one-year old
Nitrogen *	I	1.386 SE 0.0750	1.212 SE O.0940
	IL	1.725 SE 0.0791	1.428 SE 0.0737
Phosphorus *	I	0.168 SE 0.0160	0.151 SE 0.0140
	IL	0.168 SE 0.0100	0.150 SE 0.0120
Potassium **	I	10,662 SE 786	11,157 SE 1855
	IL	11,093 SE 380	10,253 SE 545
Calcium **	I	2312 SE 258	3116 SE 190
	IL	1815 SE 217	3146 SE 218

* concentrations expressed as percent
** concentrations expressed as μg/g

Calcium levels are significantly higher ($\alpha = .05$) in C+1 foliage in both treatments. This pattern of increasing calcium concentration with foliage age has been reported by various investigators for Pinus species (Wills and Metz, 1963; Bockheim et al., 1983). There is no difference in calcium concentration between treatments.

(ii) Bark/phloem

Within the bark/phloem, only nitrogen levels are significantly higher ($\alpha = .05$) in the IL branches at all internodes, as shown by the error bars in figure 11a. For nitrogen, phosphorous and potassium, there is a significant gradient ($\alpha = .05$) along the primary branch from apex to base in both treatments, where concentration levels decrease with increasing internode age. The greatest increases in concentration are in the current internode. There is no significant difference in phosphorous levels between treatments at any internode, but for potassium, levels are significantly higher in I branches at the current and C+1 internodes. This is also true for calcium. Calcium displays a concentration pattern quite different to the labile elements. Concentrations tend to increase from current to C+3 bark/phloem. However, an interruption in this pattern occurs at the C+1 internode, which was laid down the year both treatments commenced.

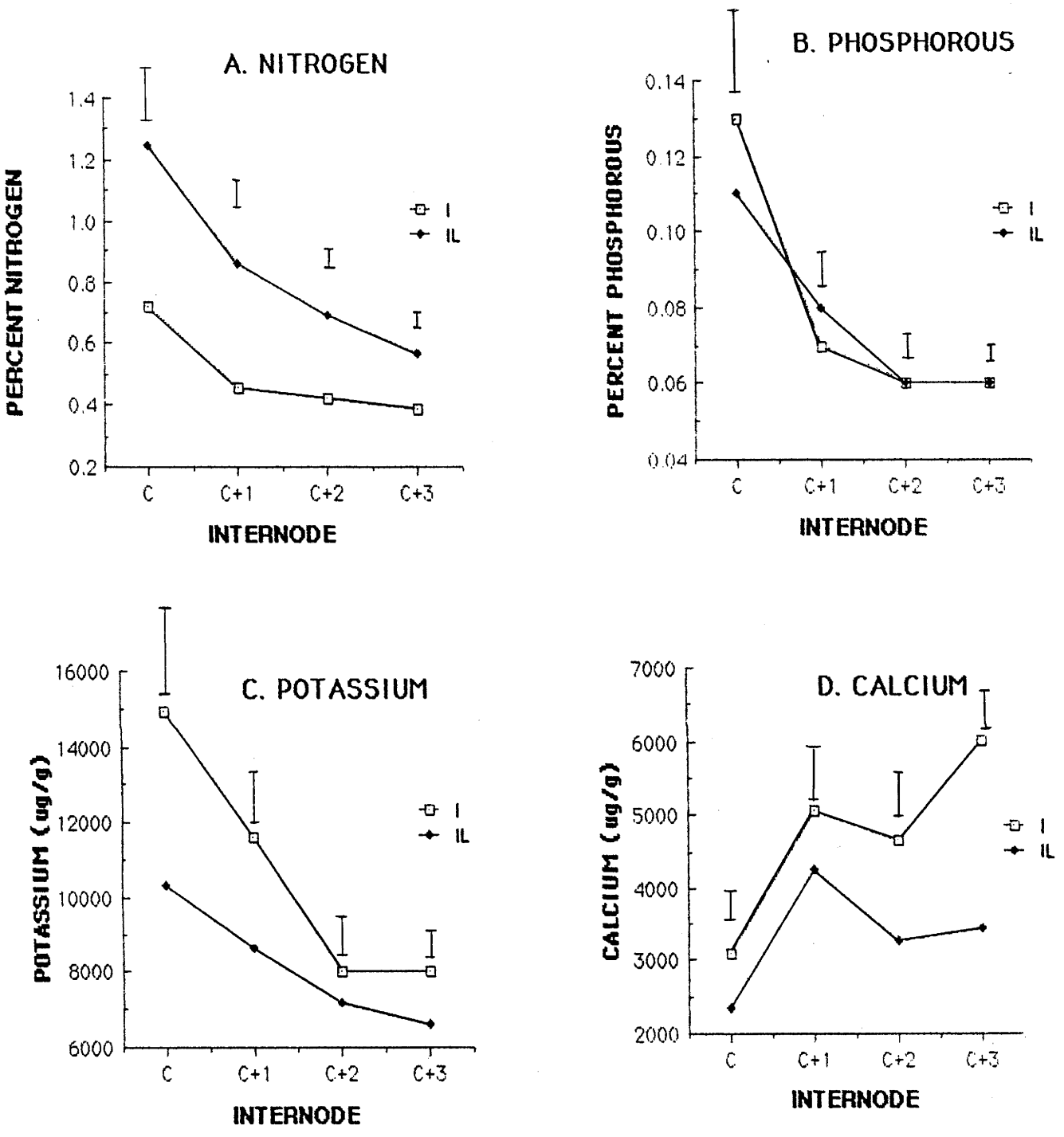


Figure 11: Bark/phloem nutrient concentrations along the length of 4-year old branches of *Pinus radiata* where I=irrigated and IL=irrigated/ fertilised trees.

(iii) Current xylem (C)

There is a significant (α = .05) increase in concentrations of nitrogen, phosphorous and potassium across the gradient from the oldest to the current internode in both treatments (figures 12a-c). Levels generally show greatest increases from C+1 to C internodes, and increase more gradually from C+3 to C+1 internodes. For all three elements, IL branches hold higher concentrations at all internodes with the exception of phosphorous levels at the C internode. However, this difference is only significant at the 5 percent level at the older internodes. For nitrogen, IL levels are significantly higher at C+1, C+2 and C+3 internodes. For phosphorous and potassium, IL levels are significantly higher at C+2 and C+3 internodes.

The calcium concentration pattern here is similar to that seen in the bark/phloem (figure 11d), with a significant increase occurring at the C+1 internode. There is no significant difference (α = .05) between treatments.

For nitrogen, phosphorous, potassium and calcium, there is no difference (α = .05) between the two treatments in terms of age response i.e. both treatments show similar gradient patterns for each nutrient (figure 12).

(iv) Previous season's xylem (C+1)

There is no significant difference (α = .05) in age response between the two treatments for nitrogen, phosphorous and potassium. Rather, similar gradient

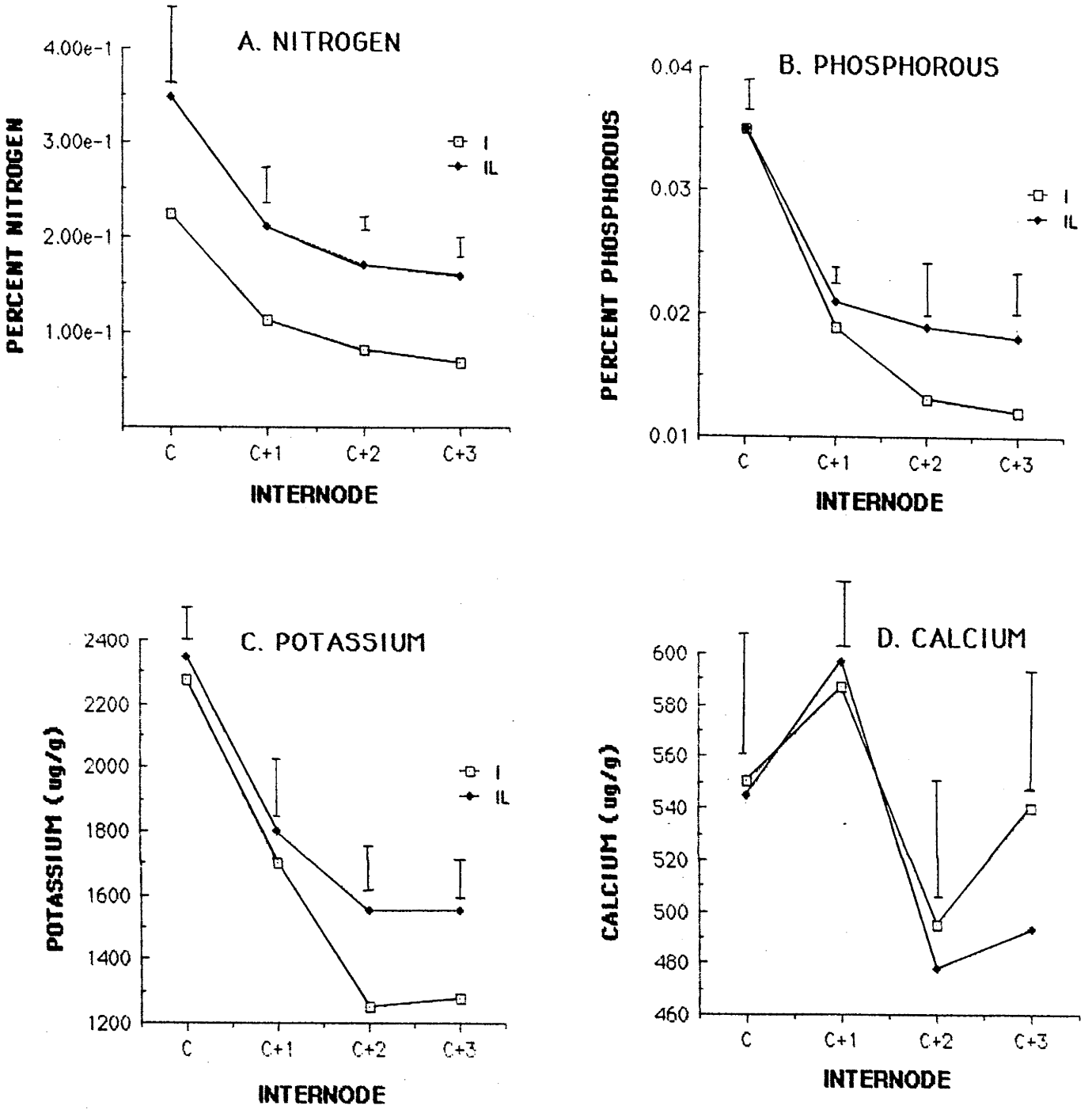


Figure 12: Current (C) xylem nutrient concentrations along the length of 4-year old branches of *Pinus radiata* where I=irrigated and IL= irrigated/fertilised trees.

patterns may be seen in both the I and IL branches (figures 13a-c). For nitrogen, there is a significant concentration gradient (α = .05) across the C+1 xylem, with highest levels occurring at the C+1 internodes (figure 13a). At all internodes, IL levels are significantly higher than I levels. Phosphorous concentrations are highest at the C+1 internode (figure 13b). Although concentrations appear to rise again at the C+3 internodes, there is no real difference between levels at the C+2 and C+3 internodes (α = .05). Potassium gradients are very similar to those seen for phosphorous (figure 13c). Concentrations at the C+1 internode are significantly higher than those at the older internodes, with the latter two not different from each other.

Calcium concentrations within C+1 xylem vary little between the internodes as seen by the narrow range of values in figure 13d. There is no significant difference in concentration, either within branches of the same treatment or between treatments.

(v) Cross-sectional gradient at the C+3 internode

Figures 14a-c illustrate similar trends in concentrations for nitrogen, phosphorous and potassium, with highest values found in the current and C+3 growth rings. For the three elements, the C and C+3 rings hold significantly higher levels (α = .05) than the middle rings in both treatments. As indicated by error bars, there is no significant difference between the I and IL branches at the

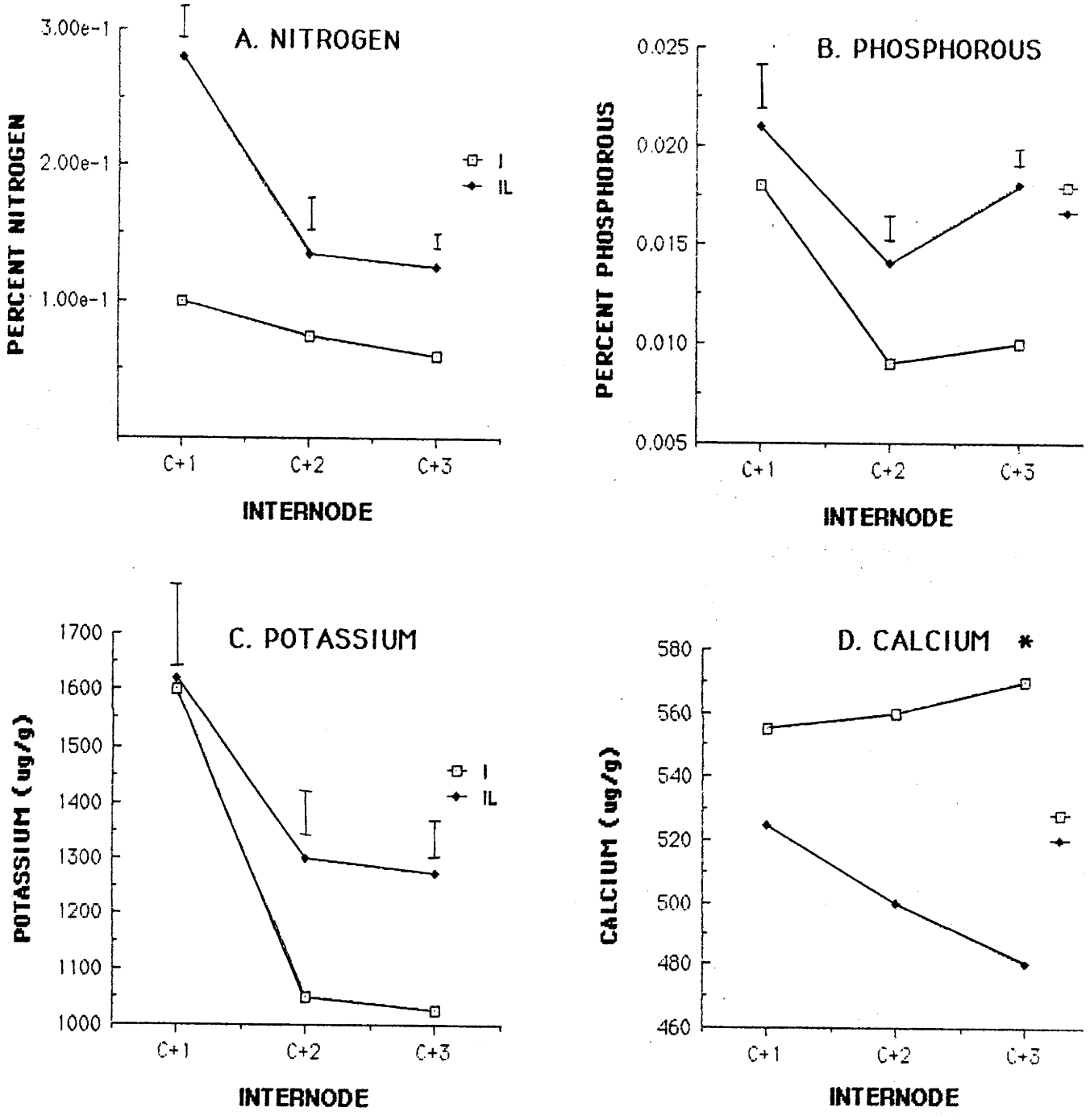


Figure 13: Previous season's (C+1) xylem nutrient concentrations along the length of 4-year old branches of *Pinus radiata* where I=irrigated and IL= irrigated/fertilised trees.

*** Error bars were too large to display here. There is no significant difference (α=.05) between treatments at all internodes**

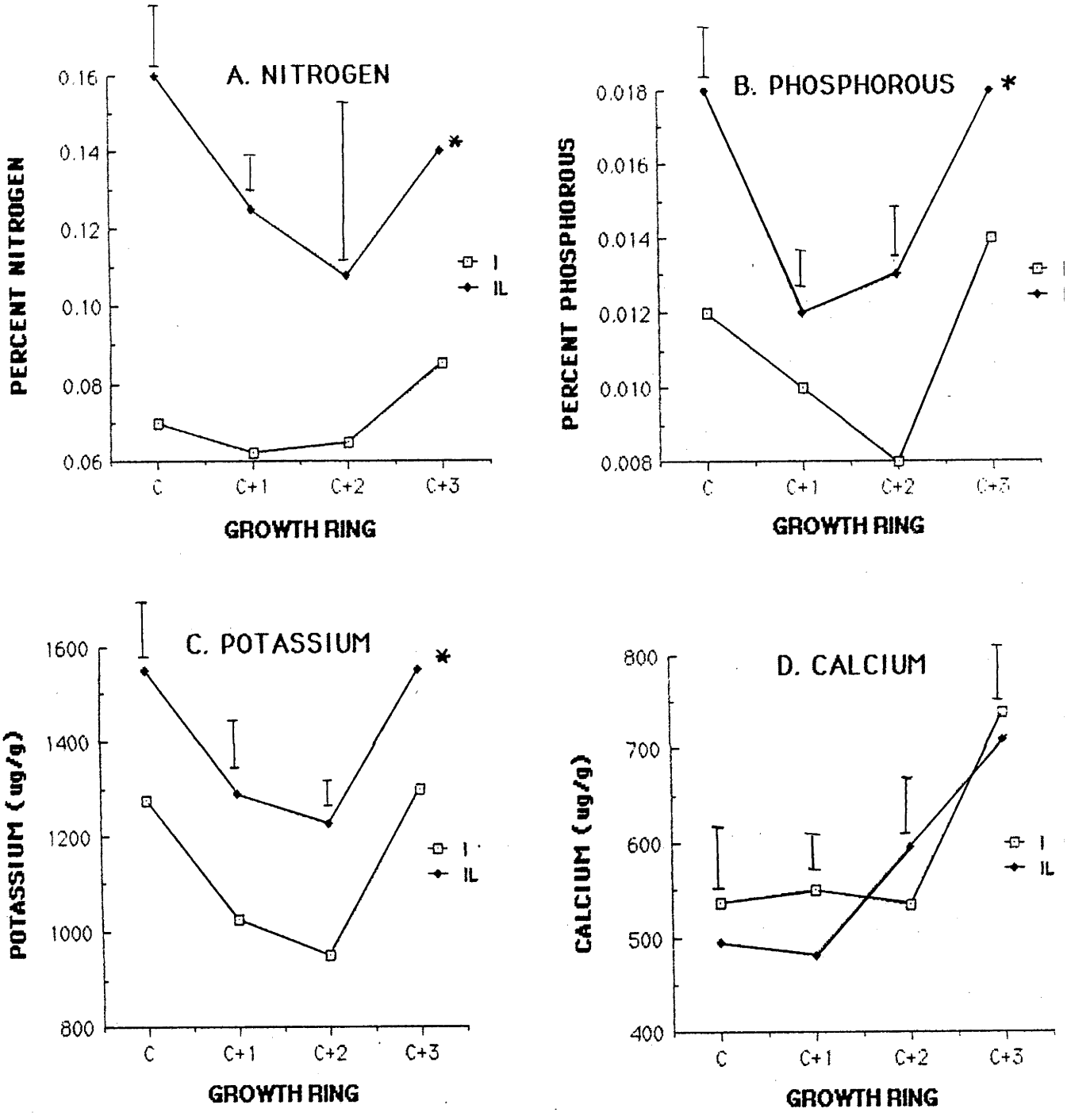


Figure 14: Cross-sectional nutrient concentration gradients at 4-year old (C+3) internodes of 4-year old *Pinus radiata* branches where I=irrigated and IL=irrigated/fertilised trees.
*** Error bars were too large to display here. There is no significant difference (α=.05) between treatments.**

C+3 growth ring for all three labile elements, although concentrations in IL branches are significantly higher in the current and C+1 growth rings.

For calcium, there is no significant difference between I and IL branch levels, but in both treatments there is a significant trend of increasing concentrations in older growth rings, with highest levels in the C+3 ring (figure 14d).

(vi) Cross-sectional gradient at the C+2 internode

Nitrogen and phosphorous show similar concentration patterns (figures 15a and b), with C+1 levels lower than C and C+2 levels. Current and C+2 levels are not different from each other ($\alpha = .05$). For the two elements, IL branch concentrations are significantly higher than I branches at this internode.

For potassium, the age response is different ($\alpha = .05$) for each treatment (figure 15c). In I branches, potassium levels in the C+2 ring are higher than in the current ring, while the opposite is true in the IL branches, with highest levels occurring in the current ring. Concentrations are significantly higher in IL branches in the current (C) and C+1 growth rings, but there is no difference between treatments in C+2 rings.

At this internode, calcium displays similar patterns to those seen at the C+3 internode (figure 15d). However, as with the C+3 internode, there is no difference ($\alpha = .05$) in growth ring concentration here, either within branches of the same treatment or between treatments.

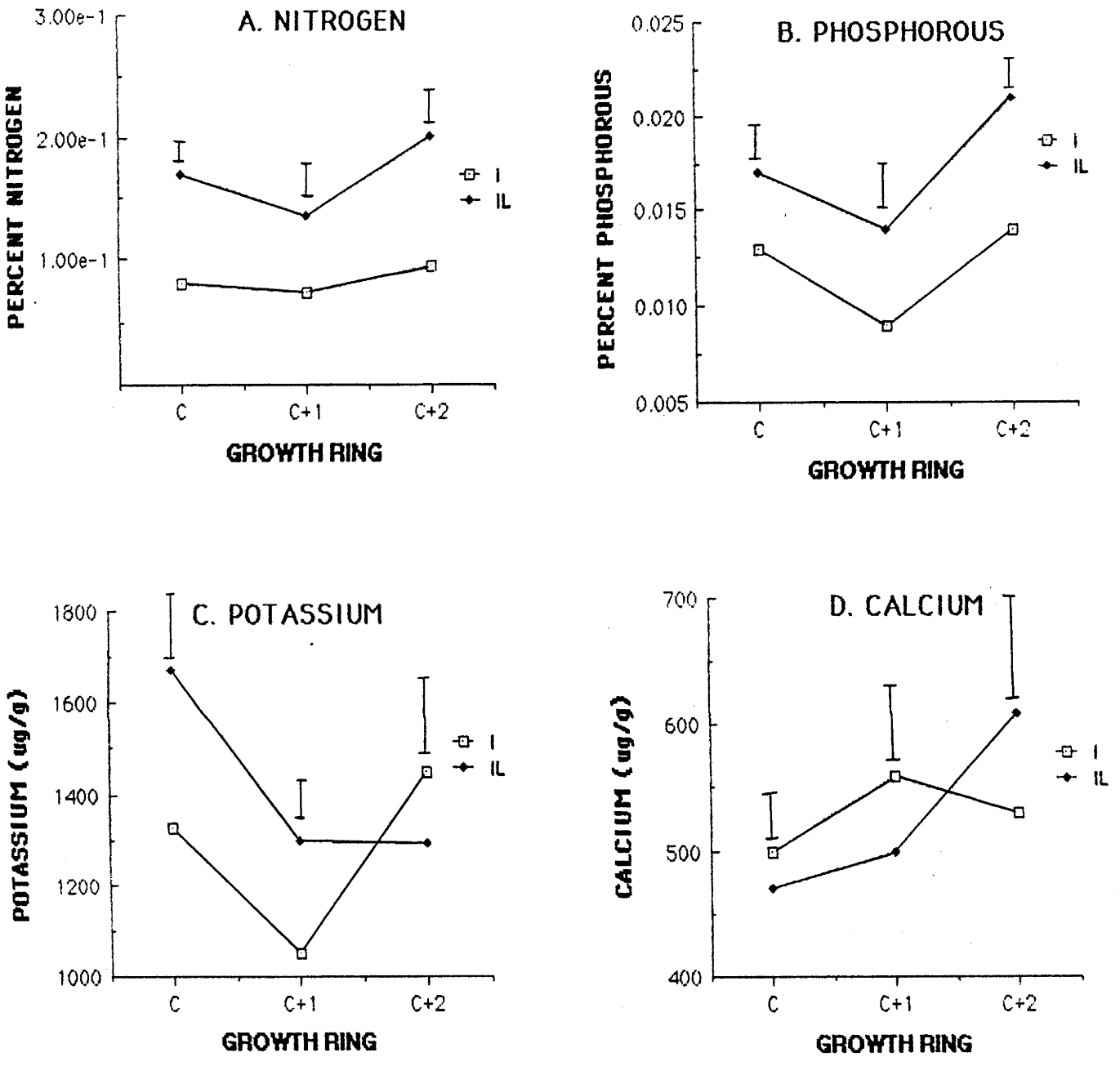


Figure 15: Cross-sectional nutrient concentration gradients at 3-year old (C+2) internodes of 4-year old *Pinus radiata* branches where I=irrigated and IL= irrigated/fertilised trees.

(vii) Magnesium and manganese

Magnesium concentrations range from 800 - 1200 ug/g in foliage, 1050 - 1450 ug/g in bark/phloem, and 180 - 350 ug/g in xylem. Manganese levels range from 200 - 400 ug/g in foliage, 70 - 170 ug/g in bark/phloem, and 20 - 60 ug/g in xylem. Both nutrients display irregular concentration patterns, possibly due to the wide variation between branches for these elements. This inconsistency suggests that factors other than irrigation and fertilisation may be responsible for deposition patterns.

For magnesium, there is no significant difference ($\alpha = .05$) in concentration between treatments, while for manganese, levels are consistently higher in I branches at all branch samples taken.

3.3 Branch Nutrient Content

3.3.1 Nutrient Distribution

The total content of nitrogen, phosphorous, potassium and calcium were derived for each of the 16 primary branches (table 7). Nutrient content data for each internode and tissue type are given in Appendix 4 and 5. Foliage content is not included as the data were unavailable. For all four elements, total content per branch reflects branch biomass (see table 3). Lowest content is found in the smallest branches and highest content in the largest branches in both the I and IL treatments. A high variability in branch biomass results in similar variability in nutrient content both within and between branches.

TABLE 7: Total nutrient content (g) of xylem and bark/phloem in primary branches of *Pinus radiata* in two treatment plots

Treatment	Tree No.	Nutrients			
		Nitrogen	Phosphorus	Potassium	Calcium
I*	1	0.3822	0.0637	0.5310	0.2570
	2	0.2769	0.0397	0.4735	0.2140
	3	0.6439	0.1032	0.9457	0.4912
	4	0.6612	0.1333	1.2104	0.5032
	5	0.4075	0.0650	0.9276	0.3043
	6	0.5065	0.0755	1.2034	0.2666
	7	0.0968	0.0069	0.1593	0.0771
	8	0.7019	0.1358	1.7252	0.5300
	mean	0.4596	0.0779	0.8970	0.3304
	se	0.0743	0.0157	0.1762	0.0572
IL*	1	0.1569	0.0175	0.1438	0.0853
	2	0.6365	0.0542	0.5104	0.1890
	3	0.7878	0.0757	0.8058	0.1948
	4	0.5080	0.0495	0.4305	0.2030
	5	1.0260	0.0894	1.0230	0.3866
	6	0.1270	0.0133	0.1570	0.0479
	7	0.1410	0.0114	0.1050	0.0589
	8	0.9480	0.1161	1.2580	0.4415
	mean	0.5414	0.0534	0.5542	0.2009
	se	0.1303	0.0136	0.1537	0.0516

* I Irrigated only
IL Irrigated and fertilised

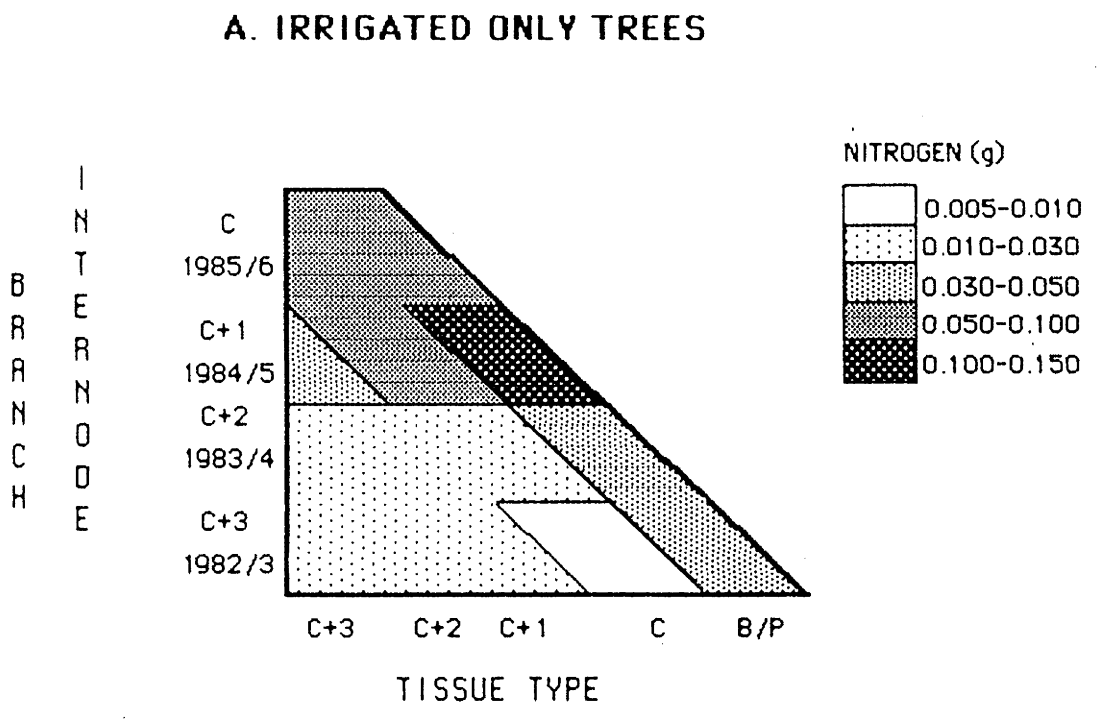
Nutrient content in the branches in decreasing order of magnitude is K > N > Ca > P in both treatments (table 7). This is similar to patterns seen in total aboveground nutrient content of P. radiata trees by Magwick et al. (1977) and Forrest (1969), although both studies found total content of nitrogen and potassium to be equal.

Nutrient content was calculated for each internode and tissue type (see figures 16-19). Nitrogen content ranges from 0.30 - 0.14 g in bark/phloem and 0.005 - 0.064 g in xylem. Phosphorous ranges from 0.009 - 0.092 g and from 0.002 - 0.012 g in bark/phloem and xylem, respectively. Potassium ranges from 0.055 - 0.293 g in bark/phloem and 0.011 - 0.111 g in xylem, and calcium ranges from 0.016 - 0.065 g in bark/phloem and 0.003 - 0.036 g in xylem (Appendix 4 and 5).

3.3.2 Comparison of Nutrient Content Between Two Treatments

Mean values for total branch nutrient content show that nitrogen content is higher in IL branches although the difference between treatments is not significant at the 5 percent level (table 7). Phosphorous content is lower in the IL treatment but the difference between treatments is not significant ($\alpha = .05$). Potassium and calcium contents are significantly higher in I treatment branches.

A breakdown of nutrient content into growing seasons indicates that branches in the I plot hold significantly higher amounts of all four nutrients ($\alpha = .05$) than IL branches in 1982/3 xylem and bark/phloem (table 8). This corresponds to higher biomass in the I treatment in this season (table 5). In the 1983/4 to 1984/5 growing seasons, there is no difference between treatments in nutrient content and again, this coincides with comparable biomass production in both treatments. The imposition of treatments at the end of the 1983/4 season did not affect



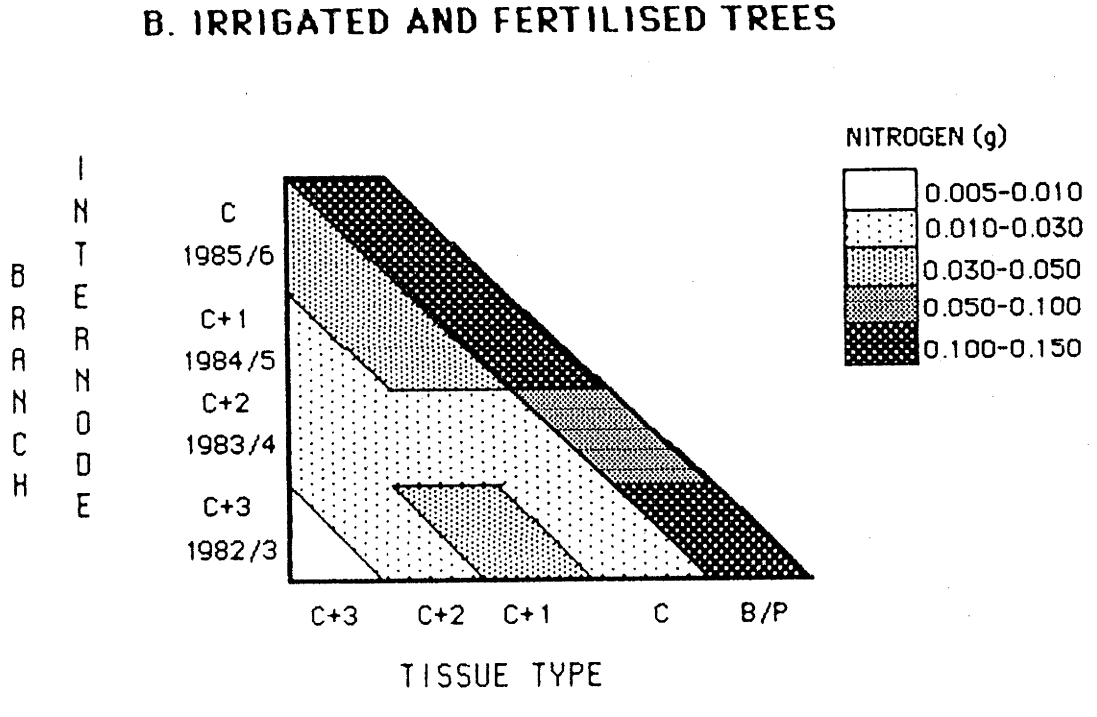
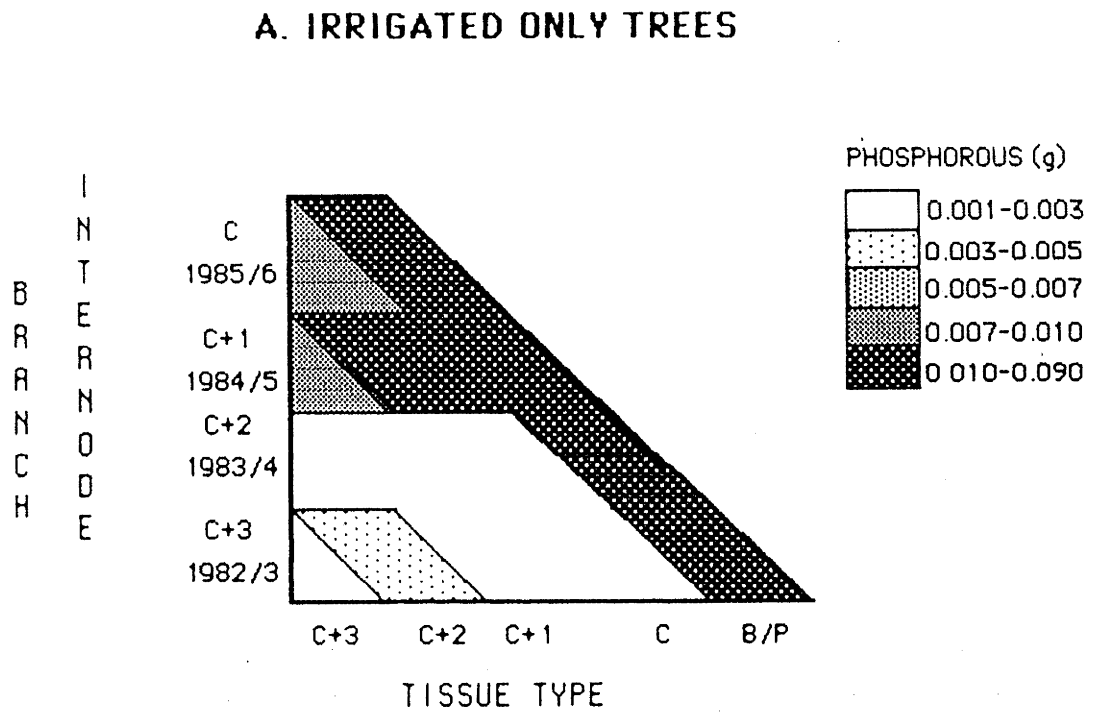


Figure 16: BRANCH NITROGEN CONTENT PROFILES IN 4th ORDER SPRING WHORL IN 15-YEAR OLD *PINUS RADIATA*



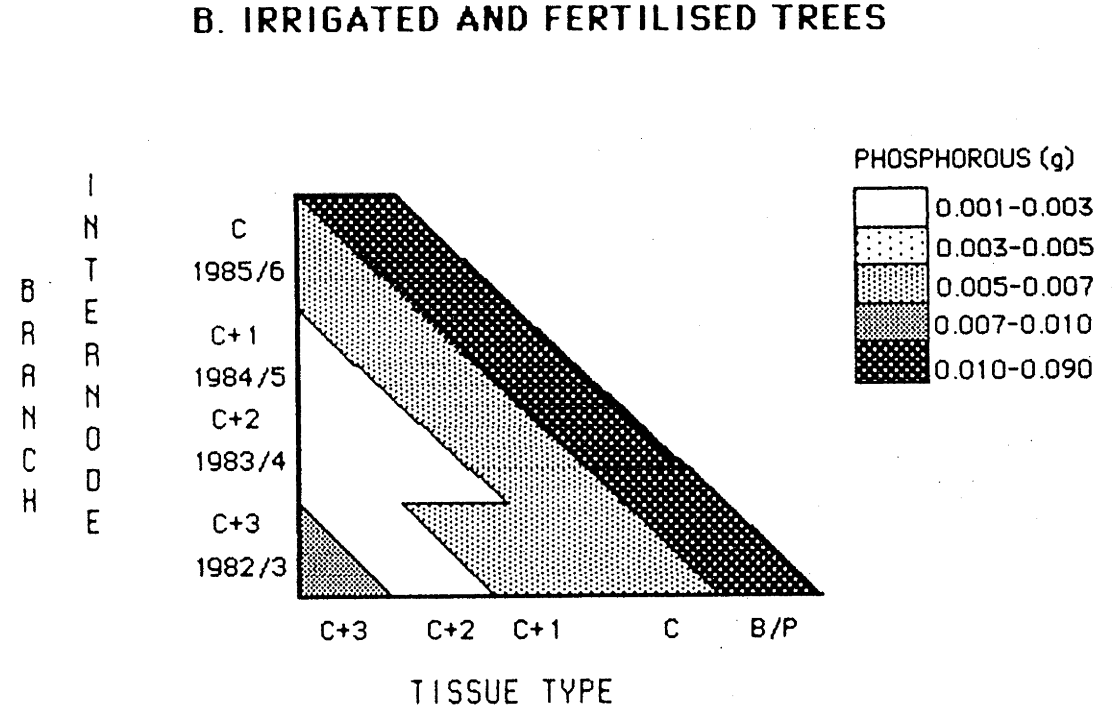
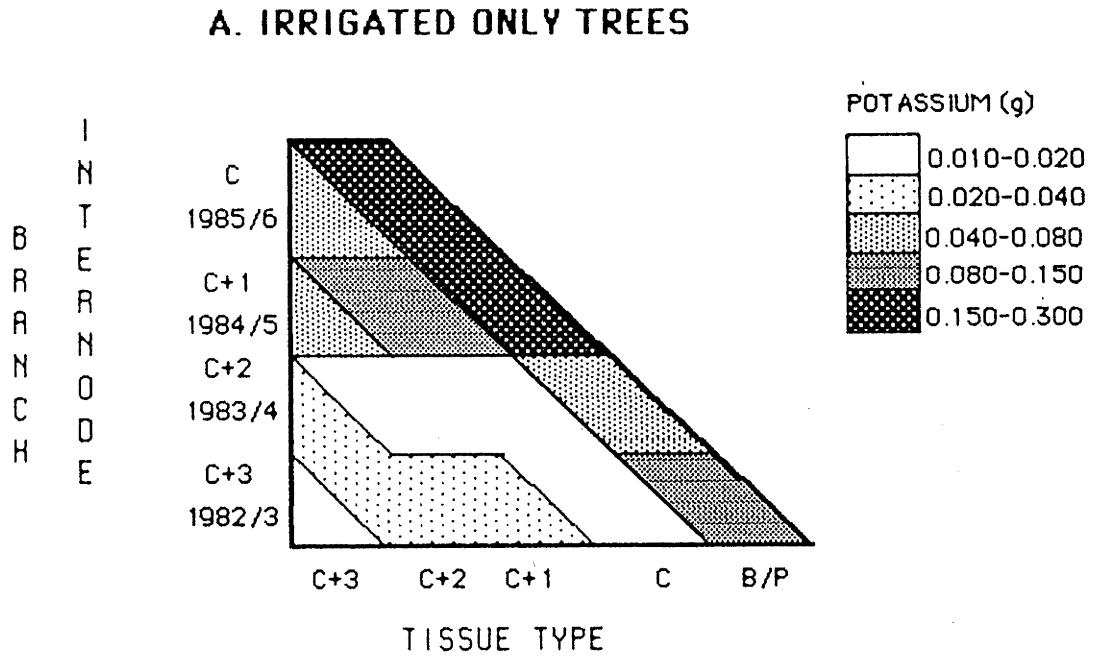


Figure 17: BRANCH PHOSPHOROUS CONTENT PROFILES IN 4th ORDER SPRING WHORL IN 15-YEAR OLD *PINUS RADIATA*



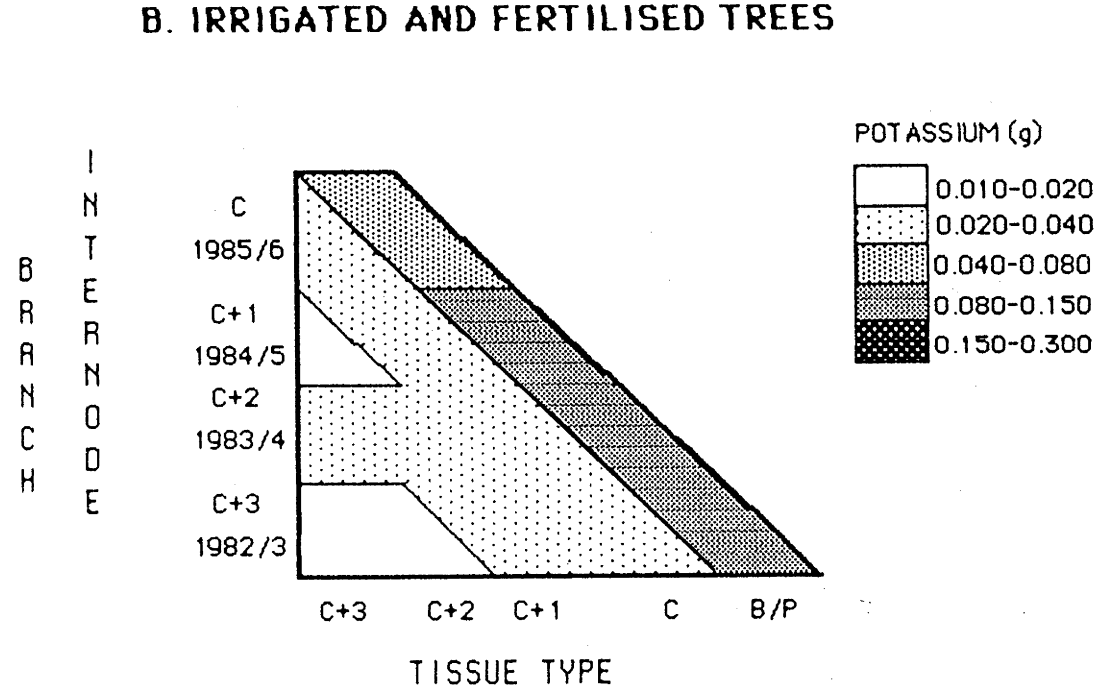


Figure 18: BRANCH POTASSIUM CONTENT PROFILES IN 4th ORDER SPRING WHORL IN 15-YEAR OLD *PINUS RADIATA*

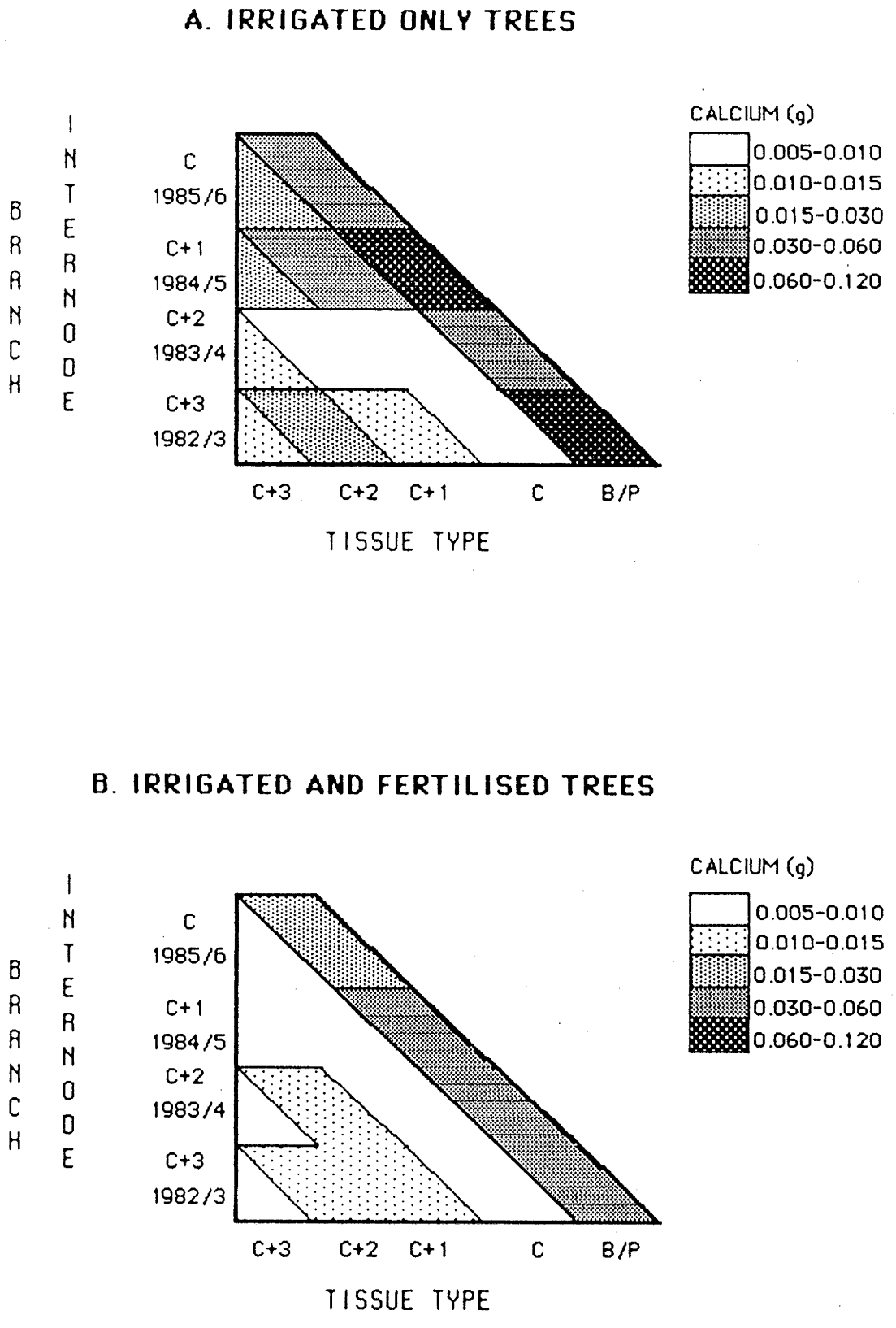


Figure 19: BRANCH CALCIUM CONTENT PROFILES IN 4th ORDER SPRING WHORL IN 15-YEAR OLD *PINUS RADIATA*

Table 8: Mean primary branch nutrient content by growing seasons for irrigated (I) and irrigated/fertilised (IL) *P.radiata* trees

Nutrient	Treatment	Growing Season			
		1982/3	1983/4	1984/5	1985/6
Nitrogen	I	$\bar{X}$ 0.0127	0.0242	0.0622	0.1309
		SE 0.0006	0.0060	0.0118	0.0235
	IL	$\bar{X}$ 0.0056	0.0334	0.0724	0.1262
		SE 0.0011	0.0118	0.0214	0.0374
Phosphorous	I	$\bar{X}$ 0.0020	0.0033	0.0107	0.0235
		SE 0.0001	0.0008	0.0022	0.0051
	IL	$\bar{X}$ 0.0006	0.0038	0.0074	0.0121
		SE 0.0001	0.0014	0.0023	0.0041
Potassium	I	$\bar{X}$ 0.0187	0.0382	0.1048	0.1911
		SE 0.0011	0.0108	0.0219	0.0416
	IL	$\bar{X}$ 0.0066	0.0391	0.0719	0.1098
		SE 0.0012	0.0167	0.0234	0.0346
Calcium	I	$\bar{X}$ 0.0109	0.0173	0.0380	0.0608
		SE 0.0010	0.0048	0.0066	0.0133
	IL	$\bar{X}$ 0.0028	0.0172	0.0264	0.0306
		SE 0.0006	0.0076	0.0095	0.0097

nutrient content in IL branches. In the 1985/6 season, significantly higher amounts (α = .05) of phosphorous, potassium and calcium are found in I treatment branches which also held more biomass, but there is no difference in nitrogen content between the treatments.

Figures 20-23 illustrate nutrient content trends across four growing seasons. Phosphorous, potassium and calcium content reflect biomass production (figure 6). However, a different trend is apparent for nitrogen which continues to increase in IL branches despite a levelling off of biomass production in this treatment.

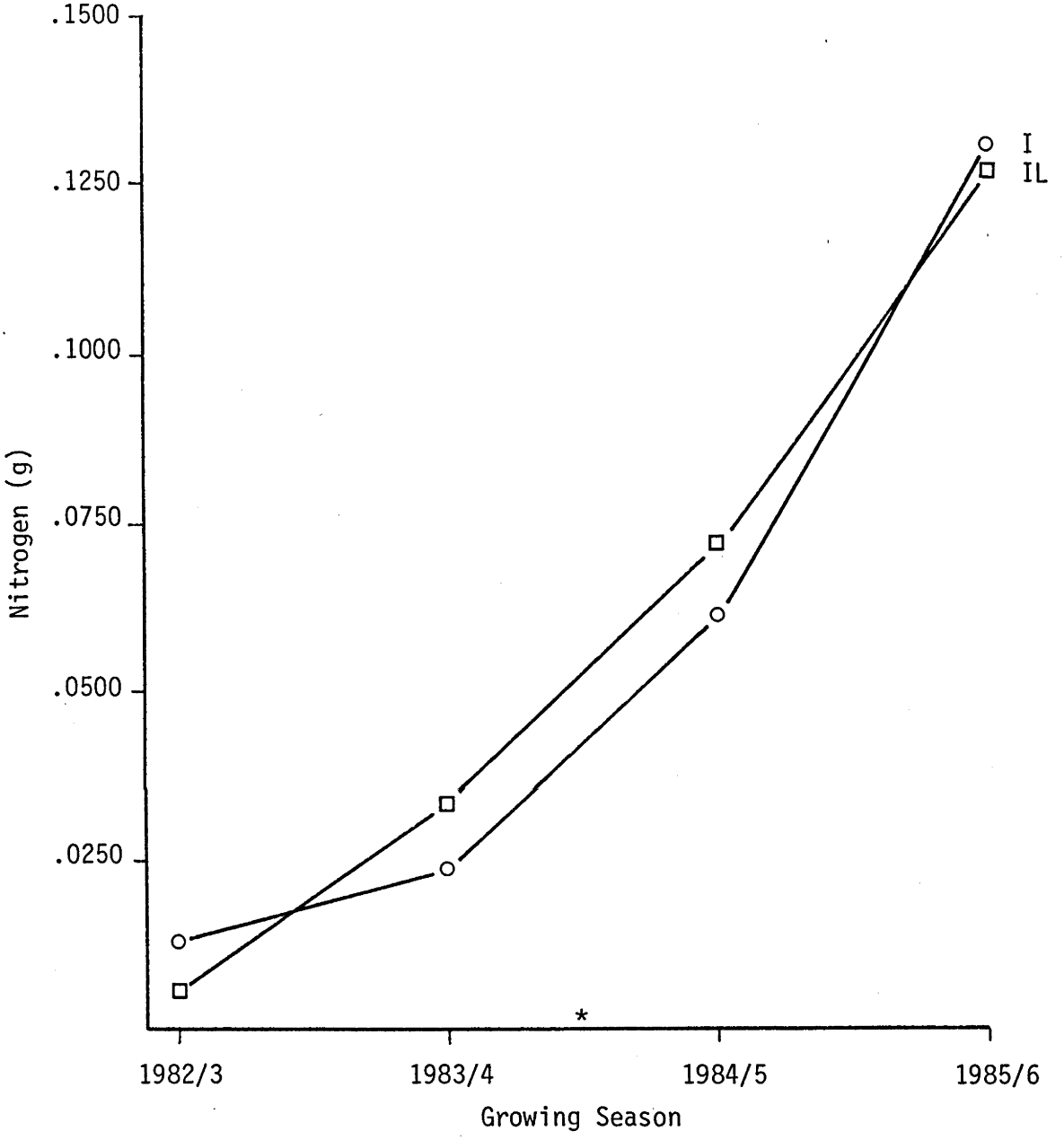


Figure 20: Mean primary branch nitrogen content (g) in 4 growing seasons for irrigated (I) and irrigated/fertilised (IL) P.radiata trees. *treatment imposed spring 1984.

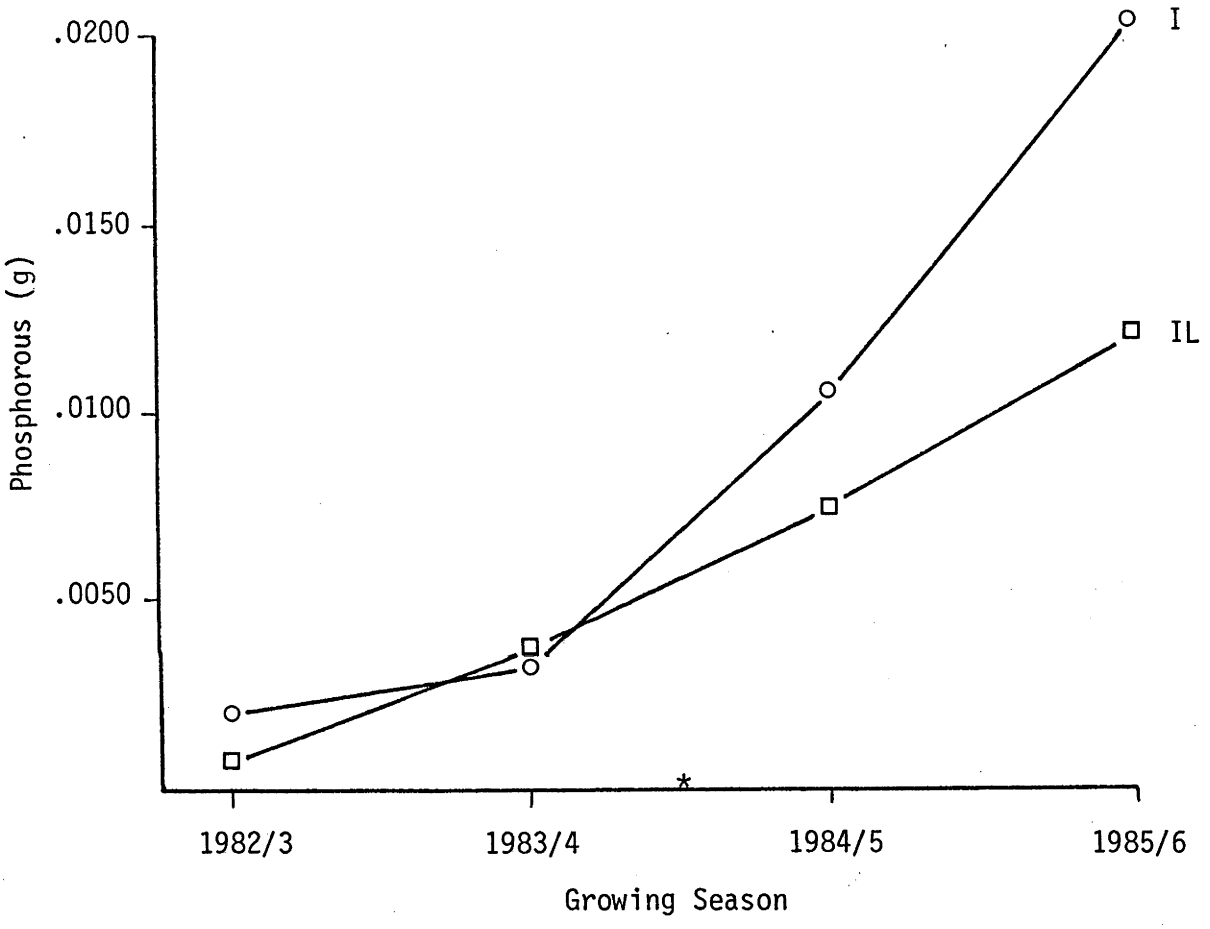


Figure 21: Mean primary branch phosphorous content (g) in 4 growing seasons for irrigated (I) and irrigated/fertilised (IL) P.radiata trees. *treatment imposed spring 1984.

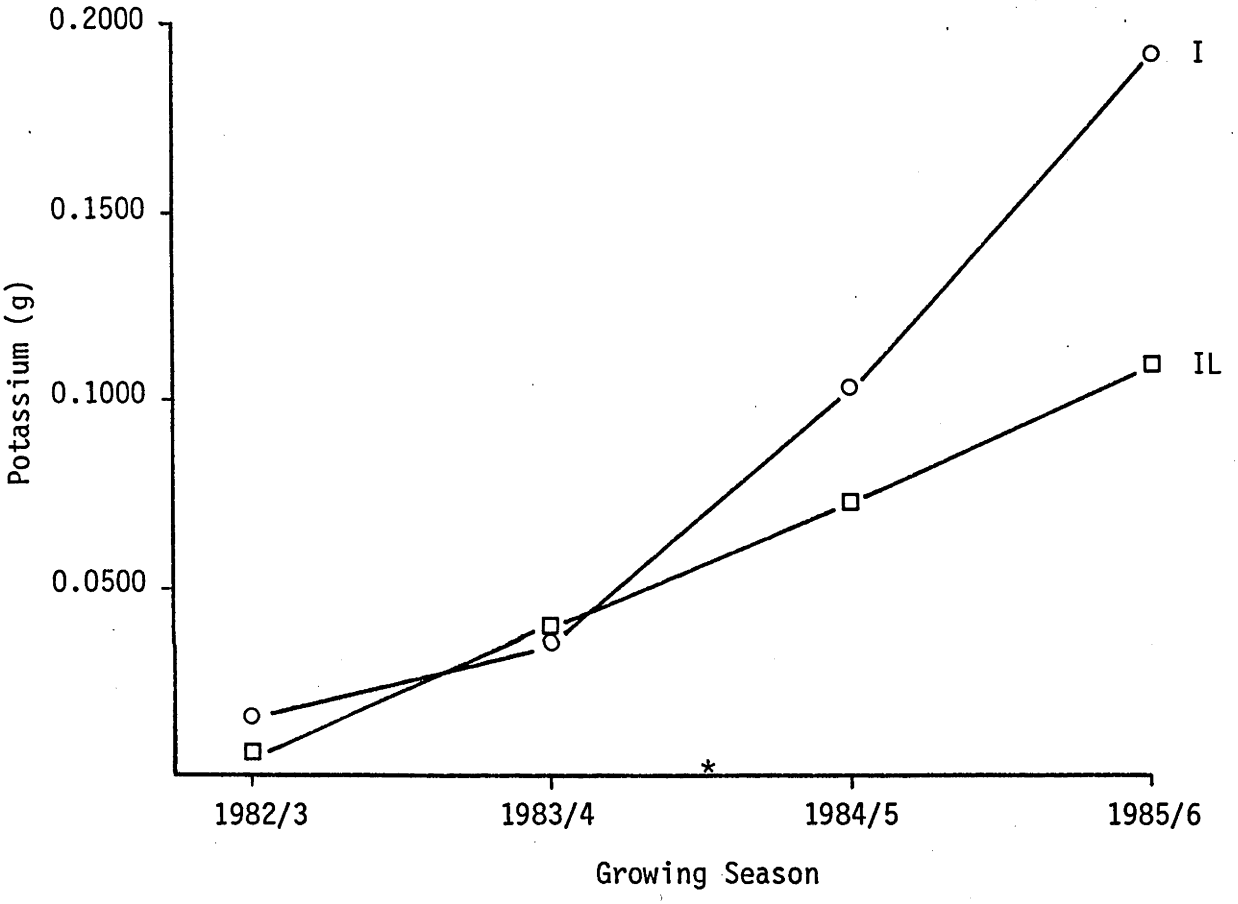


Figure 22: Mean primary branch potassium content (g) in 4 growing seasons for irrigated (I) and irrigated/fertilised (IL) P.radiata trees. *treatment imposed spring 1984.

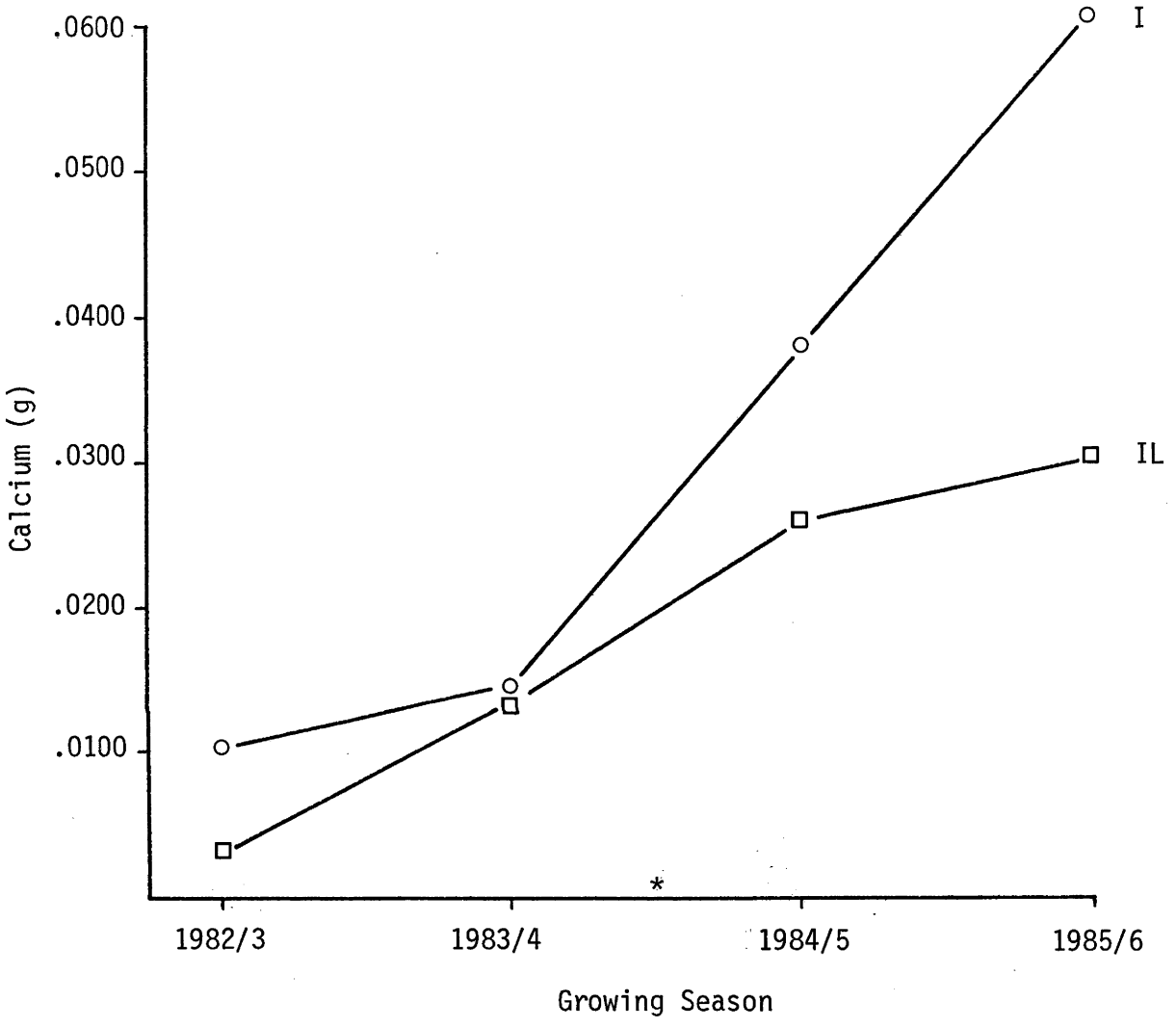


Figure 23: Mean primary branch calcium content (g) in 4 growing seasons for irrigated (I) and irrigated/fertilised (IL) P.radiata trees. *treatment imposed spring 1984.

CHAPTER 4

DISCUSSION

4.1 Biomass

Even in a relatively uniform plantation stand, individual tree growth is influenced by micro-site conditions. In this study, the variability of branch biomass within treatments reflects such micro-site differences. In particular, depth in the crown of the sampled whorl and shading by surrounding trees are likely to affect branch biomass production at any given crown position. For this reason, it is difficult to identify clear and consistent biomass distribution patterns within treatments.

In comparing biomass production between treatments, it is important to note that the sample branches were initiated two years prior to the application of treatments to the plots i.e. in the 1982/3 low rainfall year. As illustrated in table 5 and figure 6, the irrigated only (I) branches were significantly higher in biomass in 1982/3 than the irrigated and fertilised (IL) branches. By the end of the following season (1983/4) this difference had disappeared, presumably in response to the growing conditions of that season. By the time treatments were imposed in the early spring of 1984 the sample branches, while varying greatly within treatments, nevertheless were comparable between treatments. Following the imposition of treatments, the biomass in both treatments responded with an average 100 percent increase in the

1984/5 growing season, i.e. with no treatment effect apparent. This suggests that site factors other than treatment were dominant. In the following season (1985/6) the I branches once again held significantly more biomass than IL branches. This suggests that response to fertiliser is lagged and/or masked by other site and tree growth factors, i.e. at this whorl, development in the crown above may be influencing branch development. In particular, increased shading by the upper crown may be responsible for the levelling off of biomass production after the 1984/5 growing season in IL branches (figure 6).

4.2 Nutrient Concentration

4.2.1 Nutrient Concentration Patterns

Studies of nutrient distribution in conifers have revealed a general trend of decreasing concentrations of labile nutrients and increasing levels of less mobile nutrients with tissue age, as mentioned (Wells and Metz, 1963; Comerford, 1981; Lang et al., 1982). This study supports these findings for primary branches of P. radiata. Highest concentrations of the labile nutrients (nitrogen, phosphorous and potassium) occur in current growth in all tissue types and decrease in older tissue. Concentrations of these elements decrease in the order foliage > bark/phloem > xylem. This supports results of other investigators that show labile elements to be most concentrated in areas of greatest metabolic activity (Madgwick et al., 1977; Bockheim et al., 1983).

Calcium, a relatively immobile element, increases with tissue age, as expected. Concentrations follow patterns seen in other conifers where levels of bark/phloem > foliage > xylem (Lang et al., 1982).

Magnesium and manganese do not follow these generalized trends. For both nutrients, there is no distinguishable pattern within tissue types. Magnesium concentrations decrease in the order bark/phloem > foliage > xylem while manganese is highest in foliage > bark/phloem > xylem.

4.2.2 Nutrient Concentration Gradients: Effect of Treatments

(i) Nutrient concentration gradients in foliage

Foliar nutrient concentration levels are relatively stable between treatments. In the current foliage, differences in nutrient concentrations between treatments are seen only for nitrogen, where the IL branches contain significantly higher levels than the I branches. Fertiliser application has raised nitrogen levels but has not affected those of phosphorous, potassium or calcium (table 6). These concentrations coincide with optimal levels for P. radiata (Morrison, 1974), e.g. 1.6 percent for nitrogen, 0.1 percent for phosphorous and 1.1 percent for potassium. In this study, these levels have been maintained for phosphorous and potassium in the I and IL plots. The addition of fertiliser in the IL plot has raised nitrogen to optimal levels. This result suggests that once optimal concentrations have been attained, the availability of additional nutrients has little or no effect on foliar concentrations. Either the additional nutrients are 'diluted' by greater biomass, or foliar concentrations are maintained at or close to optimal by efficient internal cycling.

(ii) Nutrient concentration gradients along the primary branch in the bark/phloem, current (C) xylem and previous season's (C+1) xylem

Concentration gradients for nitrogen, phosphorous and potassium exist along the branch in the bark/phloem, current xylem and C+1 (one-year old) xylem (figures 11-13). These gradients display a decline in concentrations from youngest to oldest internodes, with a sharp decline occurring between the youngest internode and the adjacent older internodes in all three tissues. This suggests that higher levels of the labile elements occur in the terminal internode where metabolic activity is greatest. Added fertiliser (IL treatment) has not affected these gradients.

Calcium concentrations display the reverse pattern, with increasing concentrations from younger to older internodes (figures 11d and 12d). However, this pattern is interrupted in both treatments (I and IL) between the C+1 (1983/4) and C+2 (1984/5) internodes. This is interpreted as an effect of irrigation which was initiated in the interval between these two growing seasons. Thus in both treatments calcium concentrations have been raised in response to the altered soil water regime, which has apparently allowed the tree root system greater access to available calcium. In C+1 xylem (figure 13d), calcium concentration values fall within a very narrow range (485 - 575 ug/g) and no trends with tissue age are evident.

As with the foliage, the addition of fertiliser (IL treatment) has had a limited effect on nutrient concentration levels. It raised nitrogen levels in bark/phloem, current xylem and C+1 xylem at all internodes. The one exception to this is in current xylem at the current internode (figure 12a) where the raised values for the IL treatment fall just within the 95 percent confidence interval. There is no treatment effect on phosphorous concentrations in the youngest (C and C+1) internodes, but concentrations in the IL treatment are significantly higher at older (C+2 and C+3) internodes. This indicates that in the I treatment, movement of phosphorous between older and younger internodes is occurring. Retranslocation may be towards or away from the branch apex to maintain concentrations at or close to optimal levels. Alternatively, phosphorous may be present in excess in the IL treatment as evidenced by 'back filling' i.e. retranslocation into the older tissues. This pattern is also seen for potassium in xylem but not in the bark/phloem.

Calcium concentrations are not affected by additional fertiliser (IL treatment), but rather by irrigation applied in both treatments. This effect is seen only in the first post-treatment growing season indicating that the effect of irrigation was short-lived. Irrigation may also have influenced the availability of nitrogen, phosphorous and potassium but their mobility has masked any short term effect.

(iii) Cross-sectional gradients

The effect of xylem age on nutrient concentrations across growth rings is most clearly seen at the C+3 (1982/3) internode (figure 14), although it is also evident at the C+2 (1983/4) internode (figure 15). For nitrogen, phosphorous and potassium, highest values occur in the outer- and innermost growth rings, with lower levels occurring in the middle rings. This u-shaped pattern has also been observed by Banks (1985, unpublished) in the upper bolewood of P. radiata on the same site, and may be caused by the retranslocation of nutrients adjacent to the outer ring. This withdrawal may be part of an internal mechanism to maintain optimal levels close to centres of active growth. The effect of the IL treatment has been to magnify the trend. Fertiliser application raised concentrations of the labile nutrients in the younger xylem i.e. C and C+1 growth rings.

For calcium, the concentration gradient across the growth rings displays an increase with increasing tissue age (figures 14d and 15d). This agrees with the pattern found along the branch in bark/phloem and current xylem. Treatments have no significant effect on the gradient, suggesting that any additional uptake was compensated for by changes in biomass.

4.3 Branch Nutrient Content

4.3.1 Nutrient Distribution

Nutrient content of a tissue is the product of its concentration and biomass. In this study, the bark/phloem was found to contain more of the nutrients nitrogen, phosphorous, potassium and calcium than the xylem (figures 16-19). This reflects high concentrations in this tissue rather than its biomass, which is lower than that of xylem (figure 5). Within the bark/phloem, content of the labile elements decreases with tissue age while calcium content increases, strongly reflecting the concentration patterns (figures 7-10). In the xylem, nutrient content is related more to biomass than to nutrient concentration, which is relatively low in this tissue. For example in the I branches, relatively high amounts of all nutrients are found at the C+1 internode, corresponding to high biomass at this internode.

4.3.2 Comparison of Nutrient Content Between Two Treatments

Mean values for total nutrient content in primary branch xylem and bark/phloem show significantly higher amounts of potassium and calcium in the I treatment branches (table 7). Since there is no significant difference between treatments in total branch biomass (table 3), it would appear that factors other than biomass must be responsible for higher content of these two nutrients. However, a breakdown of nutrient content into growing seasons (table 8 and figures 21-23) shows that potassium and calcium, along with phosphorous, reflect biomass production in every season i.e. the three nutrients occur in significantly higher amounts in I branches only when biomass is

significantly higher. For these three nutrients, seasonal change in content is a direct result of change in biomass (figure 6). The imposition of treatments early in the 1984/5 growing season has had no effect on contents of these nutrients, rather, content continues to increase as biomass increases.

In general, treatment has had no effect on nitrogen content, which increases as biomass increases. The exception is in the youngest (1985/6) xylem where nitrogen content of the IL branches reflects increasing nitrogen concentrations. This suggests that while nitrogen concentrations in foliage have remained at optimal levels (Morrison, 1974), the addition of fertiliser has caused an accumulation of nitrogen in the xylem. The xylem may therefore be acting as a temporary internal nutrient pool.

4.4 A Comparison of Sampling Strategies for Estimating Primary Branch Nutrient Content

Several methods for estimating branch nutrient content have been employed, but there is general dissatisfaction with current procedures. The basic problem lies in the distribution of nutrients both within and between branches. The present study has focused on the former.

In order to accommodate changes in nutrient concentration from apex to base, Young and Carpenter (1976) suggested taking a single branch mid-point sample to represent the whole branch. Alternatively, Valentine et al. (1984) used randomized sampling to select a path along the tree branch, and at each internode along the path removed one or more sample discs. In both studies, no account was taken of

cross-section nutrient gradients. In the present study, sampling was also done at each internode but only one mid-internode disc was removed. Compared with Young and Carpenter's (1976) mid-point method, sampling at each internode involves considerably more time and produces greater numbers of samples for chemical analysis. The important question here is: what sampling strategy best accommodates nutrient variation along the branch using a minimum of samples?

In this study, nutrient concentration is neither similar in all internodes nor in the form of a linear gradient i.e. highest concentrations occur in the youngest internodes. The Young and Carpenter (1976) approach of one sample per branch may therefore seriously underestimate nutrient content by failing to account for high concentrations in the terminal internode, particularly if there are numerous terminal branchlets. On the other hand, the sampling of each internode may be unnecessary given the relative uniformity of the older internodes. An alternative approach is to treat the terminal internodes separately, taking one sample from these and another from the mid-point of the remainder. In this way, higher concentrations in the terminal internode are represented by samples. These three sampling methods were compared using branch data from this investigation and the results are presented in table 9. The latter two methods were compared to 'best estimates' provided by this study for determining nutrient content in primary branches of P. radiata in the 4th order spring whorl.

There was no significant difference ($\alpha = .05$) in mean nutrient content values between the three methods. The mid-point method (method 2) did not consistently underestimate nutrient content as was

Table 9: Estimates of primary branch nutrient content of P.radiata using 3 sampling methods for I = irrigated; IL = irrigated/ fertilised trees

Nutrient	Treatment	Branch Sampling Method	Mean	SE	Percent Difference	Mean Percent Difference
Nitrogen	I	1	0.2216	0.0393	-	-
		2	0.2870	0.0488	+42 to -9	+15
		3	0.2446	0.0499	+41 to -3*	-11
	IL	1	0.2393	0.0603	-	-
		2	0.2865	0.0794	+40 to -42	+10
		3	0.2432	0.0609	+29 to -8	+3
Phosphorous	I	1	0.0404	0.0082	-	-
		2	0.0423	0.0090	+62 to -30	+5
		3	0.0444	0.0098	+41 to -12	+10
	IL	1	0.0244	0.0070	-	-
		2	0.0296	0.0089	+37 to -26	+19
		3	0.0243	0.0066	+23 to -16	+4
Potassium	I	1	0.3457	0.0735	-	-
		2	0.3850	0.0876	+40 to -6	+15
		3	0.3880	0.0883	+40 to -2	+11
	IL	1	0.2264	0.0664	-	-
		2	0.2470	0.0721	+17 to -25	+7
		3	0.2267	0.0657	+16 to -9	+2
Calcium	I	1	0.1201	0.0226	-	-
		2	0.1199	0.0240	+7 to -16	+1
		3	0.1202	0.0239	+16 to -9	-1
	IL	1	0.0767	0.0245	-	-
		2	0.0791	0.0274	+30 to -24	+5
		3	0.0718	0.0223	+9 to -11	-4

* One branch overestimated nitrogen content by +345 percent due to high concentrations in the sample disc.

1 - internode
2 - midpoint
3 - current internode + midpoint

expected. This may be due in part to branch mid-points occurring in current (C) and one-year old (C+1) internodes which are high in nutrients i.e. in small upper crown branches, internode length can influence the mid-point position. In individual branches, however, nutrient content was over- and under-estimated by as much as 40%. This was also seen in method 3 and indicates that if only one branch were selected to represent the whorl, as Young and Carpenter (1976) have suggested, serious over- or under-estimations may result. The simplest mid-point method is comparable to the 'best estimate' (method 1) if a sufficiently large sample is taken i.e. 8 branches.

For estimating crown nutrient content, the problem of how many branches should be sampled is complex. Each branch is essentially unique in its total biomass and the distribution of that biomass between its internodes. Branch development is determined by position in the crown and spatial arrangements, and the latter is influenced by the number of branch initiates and female coning. In the present study, the sample whorl was constant so that branch age and crown position was uniform between samples. Also, the sample branch was chosen as the one closest in size to the whorl mean branch. Even so the variability between branches i.e. trees was considerable in both branch biomass and nutrient content, although nutrient concentration gradients were similar. In spite of the narrow selection criteria used, at least 8 branches were needed to obtain a reasonable error of estimate for nitrogen, phosphorous, potassium and calcium but not for magnesium and manganese. The number of branches needed to adequately represent the tree crown of a stand was not addressed in this study but from the results it would seem that the suggestion of 8-10 (Orman and

Will, 1960; Knight, 1978; Messina et al., 1983; Carlyle and Malcolm, 1986) may be sufficient provided that these represent all branch whorl categories e.g. upper and lower crown.

CHAPTER 5

SUMMARY

5.1 Biomass

- Given the selection criteria the variability of individual branches within the treatments is considerable.
- Treatment effects are not found in the whole primary branch. However, when the biomass is examined by growing seasons significant differences are evident but these are found only in the second growing season of treatment. The effect was unexpected in that the fertilised (IL) plot had a smaller increment, suggesting dense new growth in the crown above was shading the study whorl zone compared with the unfertilised (I) plot.

5.2 Nutrient Concentration

- For the labile elements (nitrogen, phosphorous and potassium) concentrations decrease in the order foliage > bark/phloem > xylem.
- For calcium and magnesium concentrations decrease in the order bark/phloem > foliage > xylem while for manganese, concentrations are similar to the labile nutrients with foliage > bark/phloem > xylem.

- In all branch tissue types (foliage, bark/phloem and xylem) concentration gradients from branch apex to base show that concentrations of the labile elements decrease with age while calcium concentrations increase.
- Cross-sectional concentration gradients for nitrogen, phosphorous and potassium in xylem are u-shaped, indicating a withdrawal of nutrients from middle to outer rings. This trend is best expressed in the ferilised (IL) treatment. Calcium concentrations increase with xylem age across growth rings.
- The fertilised (IL) treatment has consistently raised nitrogen concentrations in all branch tissue types but has not affected concentrations of phosphorous, potassium and calcium.
- In foliage, optimal levels of phosphorous and potassium occur in both treatments and fertiliser has not increased concentrations. However, for nitrogen, fertiliser has raised levels from below optimal to optimal.

5.3 Nutrient Content

- The content of phosphorous, potassium and calcium reflects the biomass of each growing season.
- In the current xylem, nitrogen content is not significantly different between treatments, however, this results from a significantly lower biomass and higher concentrations in the IL treatment. This high concentration may represent accumulation in the xylem as the foliar concentrations have been raised to optimal levels but no higher.

5.4 Sampling

One mid-point sample from 8-10 branches may be adequate for estimating primary branch nutrient content at a given whorl for P. radiata.

Appendix 1: Nutrient concentration in foliage of *Pinus radiata* branches.

Treatment/ Tree No.		Tissue Age*	Nitrogen %	Phosphorus %	Potassium µg/g	Calcium µg/g
I	1	C	1.572	0.173	10443.739	2872.731
		C+1	1.343	0.173	8405.980	4042.568
	2	C	1.493	0.196	11713.275	2548.904
		C+1	1.253	0.163	10858.186	3257.189
	3	C	1.466	0.233	13064.242	1076.758
		C+1	1.243	0.188	9925.548	3484.670
	4	C	1.493	0.189	9392.745	2096.799
		C+1	1.304	0.154	9742.683	3108.708
	5	C	1.054	0.117	8156.223	3579.328
		C+1	0.761	0.091	7942.831	2629.507
	6	C	1.607	0.202	14388.494	1923.921
		C+1	1.245	0.174	22066.001	2793.760
	7	C	1.101	0.129	9720.541	2285.841
		C+1				
	8	C	1.294	0.103	8423.395	2112.167
		C+1	1.333	0.109	9162.303	2496.202
IL	1	C	1.792	0.163	11627.266	1423.508
		C+1	1.613	0.140	9581.543	3257.029
	2	C	1.992	0.184	12699.470	2517.695
		C+1	1.503	0.157	11176.084	2831.794
	3	C	1.981	0.229	11626.945	1966.631
		C+1	1.577	0.129	9535.363	2198.114
	4	C	1.863	0.153	11031.723	1490.703
		C+1	1.410	0.118	10231.946	2849.424
	5	C	1.609	0.141	11851.038	1487.413
		C+1	1.630	0.145	9609.492	3503.927
	6	C	1.643	0.149	10007.936	1628.366
		C+1	1.314	0.132	10189.969	3562.821
	7	C	1.573	0.143	9419.924	1094.181
		C+1	1.376	0.149	8260.484	2762.018
	8	C	1.339	0.181	10486.235	2914.908
		C+1	0.997	0.228	13441.542	4204.485

* C=1985/6, C+1=1984/5 Foliage

Appendix 2: Nutrient concentration in bark/phloem of *Pinus radiata* branches.

Treatment/ Tree No.	Tissue Age*	Nitrogen %	Phosphorus %	Potassium µg/g	Calcium µg/g
1 1	C	0.651	0.159	13580.416	2380.825
	C+1	0.449	0.106	9737.482	5328.966
	C+2	0.431	0.064	6234.013	3880.415
	C+3	0.373	0.052	6604.436	4882.917
2	C	0.749	0.077	10629.016	2237.855
	C+1	0.523	0.059	10196.855	6150.565
	C+2	0.457	0.054	6091.707	4922.525
	C+3				
3	C	1.431	0.146	15265.468	3481.156
	C+1	0.621	0.077	12785.404	8089.482
	C+2	0.444	0.057	9192.269	7137.214
	C+3	0.413	0.057	8476.936	7931.337
4	C	0.750	0.189	14090.473	3862.290
	C+1	0.488	0.088	11455.296	5316.683
	C+2	0.465	0.086	7280.386	7133.856
	C+3				
5	C	0.415	0.076	13348.564	3431.205
	C+1	0.410	0.055	11225.774	3508.712
	C+2	0.362	0.047	9564.666	3601.409
	C+3				
6	C	0.658	0.167	26554.731	2939.573
	C+1	0.452	0.062	14723.023	3011.704
	C+2	0.493	0.071	10610.048	3471.422
	C+3				
7	C	0.371	0.054	8401.677	3185.027
	C+1	0.363	0.046	6824.759	4587.915
	C+2	0.324	0.037	5335.364	3290.018
	C+3				
8	C	0.764	0.167	17575.294	3381.378
	C+1	0.392	0.074	15894.566	4470.404
	C+2	0.388	0.063	10062.333	4012.521
	C+3	0.382	0.057	8947.961	5226.629

* C=1985/6, C+1=1984/5, C+2=1983/4, C+3=1982/3 Bark/Phloem

Appendix 2: Nutrient concentration in bark/phloem of *Pinus radiata* branches (cont.)

Treatment/ Tree No.	Tissue Age*	Nitrogen %	Phosphorus %	Potassium µg/g	Calcium µg/g
IL 1	C	1.129	0.109	10118.150	2791.136
	C+1	0.751	0.085	8060.694	4295.133
	C+2	0.536	0.058	4316.625	3472.882
	C+3	0.461	0.054	4125.993	3860.129
2	C	1.828	0.153	11434.771	3130.052
	C+1	1.106	0.097	9163.286	4998.294
	C+2	0.899	0.081	7350.238	3051.430
	C+3	0.710	0.074	7084.785	3622.826
3	C	1.329	0.177	14823.332	2151.153
	C+1	1.107	0.082	12196.123	3208.630
	C+2	0.817	0.066	9393.531	3162.154
	C+3				
4	C	0.919	0.092	8555.364	1983.759
	C+1	0.773	0.075	8429.559	4584.584
	C+2	0.579	0.058	5461.407	4247.385
	C+3	0.591	0.057	6847.435	4987.059
5	C	1.350	0.087	10805.549	1561.282
	C+1	1.011	0.075	9479.837	4396.208
	C+2	0.783	0.063	7559.944	3478.689
	C+3	0.609	0.054	7159.445	2704.798
6	C	1.176	0.094	11032.780	1631.722
	C+1	0.644	0.069	8496.153	3421.845
	C+2	0.632	0.069	8451.334	2713.243
	C+3	0.539	0.060	7386.297	2680.722
7	C	1.605	0.102	7857.483	3494.914
	C+1	0.877	0.071	5813.181	5007.548
	C+2	0.692	0.059	6067.518	3454.331
	C+3	0.537	0.052	5590.148	4148.323
8	C	0.686	0.086	7808.762	2346.677
	C+1	0.569	0.070	7691.800	4129.723
	C+2	0.551	0.060	8626.759	2526.608
	C+3	0.542	0.068	8107.850	2357.088

Appendix 3: Nutrient concentration in xylem of *Pinus radiata* branches.

Treatment/ Tree No.	Internode Age/ Tissue*	Nitrogen %	Phosphorus %	Potassium µg/g	Calcium µg/g
1/1	1985/6 C	0.144	0.026	1732.093	616.230
	1984/5 C	0.210	0.028	1997.551	600.217
	C+1	0.092	0.023	1606.795	708.091
	1983/4 C	0.068	0.013	1004.293	557.084
	C+1	0.079	0.013	1002.133	692.364
	C+2	0.093	0.017	1322.125	586.144
	1982/3 C	0.062	0.011	941.611	574.576
	C+1	0.053	0.009	833.752	603.621
	C+2	0.060	0.009	921.864	579.213
	C+3	0.079	0.013	1093.023	752.298
1/2	1985/6 C	0.263	0.039	2723.662	636.342
	1984/5 C	0.875	0.017	1541.269	654.959
	C+1	0.093	0.017	1823.331	449.108
	1983/4 C	0.075	0.015	1136.368	490.598
	C+1	0.088	0.012	1080.597	509.609
	C+2	0.112	0.020	1685.890	657.547
1/3	1985/6 C	0.476	0.079	3145.859	589.874
	1984/5 C	0.116	0.021	1683.191	432.010
	C+1	0.119	0.016	707.522	651.435
	1983/4 C	0.079	0.012	1553.908	330.936
	C+1	0.084	0.010	1317.196	557.084
	C+2	0.109	0.017	1969.511	816.687
	1982/3 C	0.074	0.127	1438.631	416.893
	C+1	0.070	0.011	1240.240	588.692
	C+2	0.073	0.008	1071.475	687.843
	C+3	0.096	0.014	1564.330	719.024
1/4	1985/6 C	0.171	0.033	1856.573	458.754
	1984/5 C	0.100	0.018	1574.296	589.661
	C+1	0.097	0.023	1789.836	615.352
	1983/4 C	0.085	0.014	1138.551	543.190
	C+1	0.068	0.009	972.561	695.908
	C+2	0.098	0.018	1362.627	528.156

* C=1985/6, C+1=1984/5, C+2=1983/4, C+3=1982/3 Xylem

Appendix 3: Nutrient concentration in xylem of *Pinus radiata* branches (cont.)

Treatment/ Tree No.	Internode Age/ Tissue*		Nitrogen %	Phosphorus %	Potassium µg/g	Calcium µg/g
I/ 5	1985/6	C	0.118	0.019	1742.728	585.533
	1984/5	C	0.090	0.013	1523.035	695.709
		C+1	0.086	0.015	1692.878	626.219
	1983/4	C	0.072	0.013	1244.762	448.726
		C+1	0.061	0.008	961.835	580.152
		C+2	0.087	0.012	1246.232	540.131
I /6	1985/6	C	0.306	0.038	3117.886	411.206
	1984/5	C	0.092	0.013	1784.331	471.800
		C+1	0.102	0.014	1665.228	402.898
	1983/4	C	0.080	0.012	1295.557	466.654
		C+1	0.068	0.007	990.371	538.123
		C+2	0.101	0.013	1490.033	624.007
I/ 7	1985/6	C	0.139	0.021	1868.663	563.778
	1984/5	C	0.112	0.016	1442.267	615.761
		C+1	0.099	0.013	1186.474	499.972
	1983/4	C	0.108	0.016	1583.424	554.795
		C+1	0.075	0.008	1050.717	408.087
		C+2	0.100	0.010	1175.512	491.358
I/8	1985/6	C	0.195	0.036	2027.691	544.456
	1984/5	C	0.093	0.024	2092.041	630.836
		C+1	0.116	0.019	2343.665	501.747
	1983/4	C	0.074	0.040	1576.396	568.858
		C+1	0.060	0.008	984.551	488.164
		C+2	0.060	0.008	1308.114	544.145
	1982/3	C	0.070	0.012	1443.116	626.435
		C+1	0.057	0.008	991.786	477.756
		C+2	0.058	0.007	863.178	319.672
		C+3	0.086	0.013	1246.132	747.849

Appendix 3: Nutrient concentration in xylem of *Pinus radiata* branches (cont.)

Treatment/ Tree No.	Internode Age/ Tissue*	Nitrogen %	Phosphorus %	Potassium µg/g	Calcium µg/g
IL /1	1985/6 C	0.074	0.013	993.566	441.185
	1984/5 C	0.067	0.009	900.168	558.371
	C+1	0.135	0.021	1258.680	655.213
	1983/4 C	0.215	0.025	1629.950	590.445
	C+1	0.184	0.017	1389.950	533.176
	C+2	0.224	0.024	1715.779	616.942
	1982/3 C	0.172	0.020	1593.443	696.692
	C+1	0.147	0.013	1224.112	482.481
	C+2	0.140	0.016	1294.080	536.110
	C+3	0.173	0.022	1871.704	670.508
IL /2	1985/6 C	0.526	0.058	3958.542	485.251
	1984/5 C	0.210	0.019	2149.104	533.470
	C+1	0.227	0.020	1936.473	558.739
	1983/4 C	0.165	0.014	1380.084	391.958
	C+1	0.150	0.010	1161.091	517.083
	C+2	0.215	0.019	1894.953	380.173
	1982/3 C	0.157	0.018	1384.656	453.611
	C+1	0.125	0.010	1106.662	431.410
	C+2	0.122	0.011	1240.499	574.573
	C+3	0.188	0.020	1914.649	820.397
IL /3	1985/6 C	0.413	0.041	2361.602	575.155
	1984/5 C	0.237	0.023	2100.237	487.665
	C+1	0.192	0.018	1900.760	274.269
	1983/4 C	0.130	0.015	1718.516	354.804
	C+1	0.108	0.012	1358.954	515.551
	C+2	0.163	0.022	1898.269	578.825
IL/ 4	1985/6 C	0.491	0.048	2482.359	561.904
	1984/5 C	0.274	0.029	1828.072	558.261
	C+1	0.268	0.021	1540.194	465.439
	1983/4 C	0.175	0.015	1127.620	567.435
	C+1	0.163	0.011	1064.783	406.037
	C+2	0.177	0.015	1404.559	637.662
	1982/3 C	0.159	0.017	1309.511	533.470
	C+1	0.120	0.011	1118.092	420.128
	C+2	0.131	0.016	1317.963	704.258
	C+3	0.163	0.026	2207.140	952.039

Appendix 3: Nutrient concentration in xylem of *Pinus radiata* branches (cont.)

Treatment/ Tree No.	Internode Age/ Tissue*	Nitrogen %	Phosphorus %	Potassium µg/g	Calcium µg/g
IL/5	1985/6 C	0.337	0.030	2701.918	484.697
	1984/5 C	0.207	0.017	1489.234	316.059
	C+1	0.208	0.020	1767.908	548.967
	1983/4 C	0.177	0.015	1466.144	383.407
	C+1	0.133	0.010	1101.018	525.623
	C+2	0.194	0.022	1863.681	647.388
	1982/3 C	0.141	0.013	1396.268	523.224
	C+1	0.142	0.015	1570.984	621.886
	C+2	0.111	0.010	1055.201	561.406
	C+3	0.097	0.010	1162.531	549.899
IL /6	1985/6 C	0.128	0.016	1821.396	782.259
	1984/5 C	0.174	0.022	2179.519	621.764
	C+1	0.200	0.025	1796.032	491.518
	1983/4 C	0.165	0.020	2072.568	546.064
	C+1	0.156	0.016	1615.998	527.265
	C+2	0.206	0.023	2329.441	771.655
	1982/3 C	0.133	0.016	1715.161	279.972
	C+1	0.101	0.010	1271.273	431.986
	C+2	0.100	0.009	1257.725	580.478
	C+3	0.129	0.012	1593.492	670.904
IL /7	1985/6 C	0.611	0.043	2589.009	347.581
	1984/5 C	0.369	0.028	2036.917	925.333
	C+1	0.307	0.021	1475.802	584.246
	1983/4 C	0.201	0.013	1548.833	610.102
	C+1	0.220	0.015	1361.097	514.177
	C+2	0.336	0.026	2194.648	677.468
	1982/3 C	0.235	0.022	1776.084	503.827
	C+1	0.131	0.009	1195.099	432.355
	C+2	0.136	0.012	1230.982	521.886
	C+3	0.190	0.017	1915.792	665.394
IL /8	1985/6 C	0.202	0.023	1650.858	720.696
	1984/5 C	0.160	0.021	1712.319	761.641
	C+1	0.131	0.020	1425.657	638.891
	1983/4 C	0.138	0.016	1536.331	374.578
	C+1	0.101	0.014	1383.464	474.040
	C+2	0.088	0.011	1414.013	596.259
	1982/3 C	0.122	0.015	1720.550	460.839
	C+1	0.096	0.014	1493.173	543.559
	C+2	0.075	0.011	1198.645	658.169
	C+3	0.107	0.014	1297.036	652.030

Appendix 4: Total nutrient content (g) in bark/phloem of *Pinus radiata* branches.

Treatment/ Tree No.	Tissue Age*	Dry Weight (g)	Total Nitrogen (g)	Total Phosphorus (g)	Total Potassium (g)	Total Calcium (g)
I 1	C	7.50	0.0488	0.0120	0.1019	0.0179
	C+1	12.57	0.0564	0.0134	0.1224	0.0670
	C+2	4.94	0.0212	0.0032	0.0308	0.0192
	C+3	9.89	0.0366	0.0052	0.0653	0.0483
		34.90	0.2118	0.0338	0.3204	0.1524
I 2	C	7.92	0.0466	0.0061	0.0842	0.0177
	C+1	18.08	0.0940	0.0108	0.1844	0.1112
	C+2	5.65	0.0260	0.0031	0.0344	0.0278
		31.65	0.1646	0.0200	0.3030	0.1567
I 3	C	10.98	0.1570	0.0161	0.1676	0.0382
	C+1	22.84	0.1416	0.0176	0.2920	0.1848
	C+2	6.50	0.0286	0.0038	0.0597	0.0464
	C+3	12.72	0.0522	0.0073	0.1078	0.1009
		53.04	0.3794	0.0448	0.6271	0.3703
I 4	C	13.92	0.1044	0.0263	0.1961	0.0538
	C+1	42.43	0.2079	0.0376	0.4860	0.2256
	C+2	6.67	0.0313	0.0057	0.0486	0.0476
		63.02	0.3436	0.0696	0.7307	0.3270
I 5	C	21.66	0.0910	0.0165	0.2891	0.0743
	C+1	18.54	0.0760	0.0101	0.2081	0.0651
	C+2	10.63	0.0383	0.0050	0.1017	0.0383
		50.83	0.2053	0.0316	0.5989	0.1777
I 6	C	6.75	0.0446	0.0113	0.1792	0.0198
	C+1	29.21	0.1314	0.0181	0.4300	0.0880
	C+2	8.22	0.0403	0.0059	0.0872	0.0285
		44.18	0.2163	0.0353	0.6964	0.1363
I 7	C	4.60	0.0170	0.0025	0.0386	0.0147
	C+1	3.10	0.0112	0.0014	0.0212	0.0142
	C+2	8.61	0.0276	0.0032	0.0459	0.0283
		16.31	0.0558	0.0071	0.1057	0.0572
I 8	C	13.65	0.1037	0.0229	0.2399	0.0462
	C+1	37.50	0.1463	0.0281	0.5960	0.1676
	C+2	11.32	0.0441	0.0072	0.1139	0.0454
	C+3	8.76	0.0333	0.0049	0.0784	0.0458
		71.23	0.3274	0.0631	1.0282	0.3050

* c=1985/6 c+1=1984/5 c+2=1983/4 c+3=1982/3

Appendix 4: Total nutient content (g) in bark/phloem of *Pinus radiata* branches (cont.)

Treatment/ Tree No.	Tissue Age*	Dry Weight (g)	Total Nitrogen (g)	Total Phosphorus (g)	Total Potassium (g)	Total Calcium (g)
IL 1	C	1.60	0.0181	0.0017	0.0162	0.0045
	C+1	3.55	0.0266	0.0030	0.0286	0.0152
	C+2	3.13	0.0169	0.0018	0.0135	0.0109
	C+3	8.77	0.0403	0.0048	0.0362	0.0339
		17.05	0.1019	0.0113	0.0945	0.0645
IL 2	C	9.85	0.1802	0.0151	0.1126	0.0308
	C+1	6.60	0.0733	0.0064	0.0605	0.0392
	C+2	5.12	0.0461	0.0042	0.0376	0.0156
	C+3	15.14	0.1075	0.0113	0.1073	0.0549
		36.71	0.4071	0.0370	0.3180	0.1342
IL 3	C	7.30	0.0971	0.0131	0.1082	0.0157
	C+1	22.58	0.2484	0.0186	0.2754	0.0725
	C+2	8.44	0.0692	0.0056	0.0793	0.0267
		38.32	0.4147	0.0373	0.4629	0.1149
IL 4	C	8.83	0.0812	0.0082	0.0755	0.0175
	C+1	6.12	0.0473	0.0046	0.0516	0.0281
	C+2	7.37	0.0427	0.0043	0.0403	0.0313
	C+3	11.80	0.0696	0.0068	0.0808	0.0588
		34.12	0.2408	0.0239	0.2482	0.1357
IL 5	C	7.33	0.0990	0.0064	0.0790	0.0114
	C+1	7.16	0.0720	0.0054	0.0680	0.0315
	C+2	18.94	0.1480	0.0121	0.1410	0.0659
	C+3	41.91	0.2560	0.0226	0.3020	0.1134
		75.34	0.5750	0.0465	0.5900	0.2222
IL 6	C	2.89	0.0340	0.0027	0.0320	0.0047
	C+1	2.19	0.0140	0.0015	0.0190	0.0075
	C+2	2.18	0.0140	0.0015	0.0190	0.0059
	C+3	5.52	0.0300	0.0033	0.0410	0.0148
		12.78	0.0780	0.0090	0.1110	0.0329
IL 7	C	1.27	0.0200	0.0013	0.0100	0.0044
	C+1	2.55	0.0220	0.0018	0.0150	0.0128
	C+2	2.33	0.0160	0.0014	0.0140	0.0080
	C+3	4.69	0.0250	0.0024	0.0260	0.0195
		10.84	0.0830	0.0069	0.0650	0.0447
IL8	C	16.70	0.1150	0.0145	0.1300	0.0392
	C+1	14.82	0.0840	0.0104	0.1140	0.0612
	C+2	43.43	0.2390	0.0256	0.3730	0.1097
	C+3	14.37	0.0780	0.0098	0.1160	0.0339
		89.32	0.5160	0.0603	0.7330	0.2440

Appendix 5: Total nutrient content (g) in xylem of *Pinus radiata* branches.

Treatment/ Tree No.	Internode Age /Tissue		Dry Weight (g)	Total Nitrogen (g)	Total Phosphorus (g)	Total Potassium (g)	Total Calcium (g)
1/1	1985/6	C	22.93	0.0332	0.0060	0.0397	0.0141
	1984/5	C	23.30	0.0491	0.0066	0.0465	0.0139
		C+1	27.59	0.0255	0.0066	0.0443	0.0195
	1983/4	C	14.38	0.0098	0.0019	0.0144	0.0080
		C+1	11.09	0.0088	0.0015	0.0111	0.0077
		C+2	4.16	0.0039	0.0007	0.0055	0.0024
	1982/3	C	12.27	0.0077	0.0013	0.0116	0.0071
		C+1	13.56	0.0073	0.0013	0.0113	0.0082
		C+2	21.31	0.0130	0.0020	0.0196	0.0123
		C+3	15.17	0.0121	0.0020	0.0166	0.0114
			165.76	0.1704	0.0299	0.2106	0.1046
1/2	1985/6	C	11.94	0.0315	0.0047	0.0325	0.0076
	1984/5	C	33.56	0.0294	0.0057	0.0517	0.0219
		C+1	28.61	0.0266	0.0051	0.0522	0.0128
	1983/4	C	12.08	0.0091	0.0018	0.0137	0.0059
		C+1	12.82	0.0113	0.0016	0.0139	0.0065
		C+2	3.88	0.0044	0.0008	0.0065	0.0026
			102.89	0.1123	0.0197	0.1705	0.0573
1/3	1985/6	C	16.91	0.0806	0.0134	0.0532	0.0099
	1984/5	C	57.56	0.0673	0.0121	0.0969	0.0249
		C+1	19.60	0.0234	0.0033	0.0139	0.0128
	1983/4	C	2.53	0.0020	0.0003	0.0040	0.0008
		C+1	13.12	0.0110	0.0014	0.0173	0.0073
		C+2	15.50	0.0170	0.0027	0.0305	0.0127
	1982/3	C	7.06	0.0053	0.0009	0.0102	0.0029
		C+1	30.61	0.0216	0.0035	0.0380	0.0180
		C+2	32.96	0.0243	0.0028	0.0353	0.0227
		C+3	12.36	0.0120	0.0018	0.0193	0.0089
			208.21	0.2645	0.0584	0.3186	0.1209
1/4	1985/6	C	37.65	0.0644	0.0127	0.0699	0.0173
	1984/5	C	124.13	0.1244	0.0240	0.1954	0.0732
		C+1	83.95	0.0822	0.0196	0.1502	0.0516
	1983/4	C	23.41	0.0200	0.0032	0.0267	0.0127
		C+1	21.67	0.0148	0.0021	0.0211	0.0151
		C+2	12.01	0.0118	0.0021	0.0164	0.0063
			302.82	0.3176	0.0637	0.4797	0.1762

Appendix 5: Total nutrient content (g) in xylem of *Pinus radiata* branches (cont.)

Treatment/ Tree No.	Internode Age /Tissue	Dry Weight (g)	Total Nitrogen (g)	Total Phosphorus (g)	Total Potassium (g)	Total Calcium (g)
I/ 5	1985/6 C	66.81	0.0790	0.0132	0.1164	0.0392
	1984/5 C	34.58	0.0312	0.0048	0.0527	0.0241
	C+1	47.64	0.0412	0.0075	0.0806	0.0298
	1983/4 C	27.11	0.0197	0.0036	0.0337	0.0122
	C+1	9.98	0.0061	0.0008	0.0096	0.0058
	C+2	28.62	0.0250	0.0035	0.0357	0.0155
		214.74	0.2022	0.0334	0.3287	0.1266
I /6	1985/6 C	14.64	0.0449	0.0056	0.0456	0.0060
	1984/5 C	93.24	0.0865	0.0129	0.1663	0.0440
	C+1	86.29	0.0884	0.0125	0.1437	0.0348
	1983/4 C	22.60	0.0182	0.0026	0.0293	0.0106
	C+1	23.23	0.0158	0.0018	0.0230	0.0125
	C+2	35.91	0.0364	0.0048	0.0535	0.0224
		275.91	0.2902	0.0402	0.5070	0.1303
I/ 7	1985/6 C	7.84	0.0109	0.0017	0.0147	0.0044
	1984/5 C	2.61	0.0029	0.0004	0.0038	0.0016
	C+1	6.44	0.0064	0.0008	0.0076	0.0032
	1983/4 C	4.05	0.0044	0.0006	0.0064	0.0022
	C+1	11.42	0.0087	0.0009	0.0120	0.0047
	C+2	7.74	0.0077	0.0008	0.0091	0.0038
		40.10	0.0410	0.0052	0.0536	0.0199
I/8	1985/6 C	32.55	0.0635	0.0118	0.0660	0.0177
	1984/5 C	132.42	0.1233	0.0319	0.2770	0.0836
	C+1	60.57	0.0707	0.0119	0.1420	0.0304
	1983/4 C	13.99	0.0105	0.0019	0.0221	0.0080
	C+1	30.18	0.0180	0.0025	0.0297	0.0147
	C+2	46.92	0.0284	0.0039	0.0614	0.0255
	1982/3 C	19.92	0.0140	0.0025	0.0287	0.0125
	C+1	17.40	0.0100	0.0014	0.0173	0.0083
	C+2	37.58	0.0220	0.0027	0.0324	0.0120
	C+3	16.39	0.0141	0.0022	0.0204	0.0123
		407.92	0.3745	0.0727	0.6970	0.2250

Appendix 5: Total nutrient content (g) in xylem of *Pinus radiata* branches (cont.)

Treatment/ Tree No.	Internode Age /Tissue	Dry Weight (g)	Total Nitrogen (g)	Total Phosphorus (g)	Total Potassium (g)	Total Calcium (g)
IL /1	1985/6 C	1.15	0.0009	0.0002	0.0011	0.0005
	1984/5 C	3.63	0.0024	0.0003	0.0033	0.0020
	C+1	1.55	0.0021	0.0003	0.0020	0.0010
	1983/4 C	0.64	0.0014	0.0002	0.0010	0.0004
	C+1	4.45	0.0082	0.0008	0.0062	0.0024
	C+2	1.74	0.0039	0.0004	0.0029	0.0011
	1982/3 C	5.61	0.0097	0.0011	0.0090	0.0039
	C+1	7.79	0.0115	0.0011	0.0095	0.0038
	C+2	8.10	0.0114	0.0013	0.0105	0.0043
	C+3	2.02	0.0035	0.0005	0.0038	0.0014
		36.68	0.0550	0.0062	0.0493	0.0208
IL /2	1985/6 C	11.34	0.0597	0.0007	0.0499	0.0055
	1984/5 C	4.95	0.0104	0.0010	0.0106	0.0026
	C+1	15.42	0.0351	0.0031	0.0268	0.0086
	1983/4 C	7.50	0.0124	0.0011	0.0104	0.0029
	C+1	5.93	0.0089	0.0006	0.0069	0.0031
	C+2	7.49	0.0162	0.0015	0.0142	0.0028
	1982/3 C	28.08	0.0443	0.0053	0.0389	0.0127
	C+1	19.91	0.0250	0.0021	0.0220	0.0086
	C+2	9.19	0.0112	0.0011	0.0114	0.0053
	C+3	3.27	0.0062	0.0007	0.0063	0.0027
		113.08	0.2294	0.0172	0.1924	0.0548
IL /3	1985/6 C	16.89	0.0699	0.0070	0.0399	0.0097
	1984/5 C	77.43	0.1839	0.0184	0.1626	0.0378
	C+1	21.47	0.0413	0.0040	0.0408	0.0059
	1983/4 C	36.10	0.0473	0.0054	0.0620	0.0128
	C+1	21.49	0.0234	0.0026	0.0292	0.0111
	C+2	4.43	0.0073	0.0010	0.0084	0.0026
		177.81	0.3731	0.0384	0.3429	0.0799
IL/ 4	1985/6 C	14.26	0.0700	0.0070	0.0354	0.0080
	1984/5 C	11.17	0.0306	0.0033	0.0204	0.0062
	C+1	10.44	0.0280	0.0022	0.0161	0.0049
	1983/4 C	8.12	0.0143	0.0013	0.0092	0.0046
	C+1	15.16	0.0248	0.0018	0.0161	0.0062
	C+2	8.66	0.0154	0.0014	0.0122	0.0055
	1982/3 C	6.87	0.0193	0.0012	0.0090	0.0037
	C+1	29.75	0.0359	0.0035	0.0333	0.0125
	C+2	18.31	0.0241	0.0031	0.0241	0.0129
	C+3	2.93	0.0048	0.0008	0.0065	0.0028
		125.67	0.2672	0.0256	0.1823	0.0673

Appendix 5: Total nutrient content (g) in xylem of *Pinus radiata* branches (cont.)

Treatment/ Tree No.	Internode Age /Tissue	Dry Weight (g)	Total Nitrogen (g)	Total Phosphorus (g)	Total Potassium (g)	Total Calcium (g)
IL/5	1985/6 C	12.54	0.0430	0.0039	0.0340	0.0061
	1984/5 C	13.05	0.0270	0.0022	0.0200	0.0041
	C+1	9.72	0.0200	0.0019	0.0170	0.0053
	1983/4 C	19.27	0.0350	0.0029	0.0280	0.0074
	C+1	43.68	0.0570	0.0044	0.0480	0.0229
	C+2	10.71	0.0200	0.0024	0.0200	0.0069
	1982/3 C	42.99	0.0600	0.0060	0.0600	0.0225
	C+1	83.82	0.1170	0.0126	0.1320	0.0521
	C+2	56.06	0.0620	0.0056	0.0620	0.0314
	C+3	10.34	0.0100	0.0010	0.0120	0.0057
		302.18	0.4510	0.0429	0.4330	0.1644
IL /6	1985/6 C	2.84	0.0040	0.0005	0.0050	0.0022
	1984/5 C	3.15	0.0050	0.0007	0.0070	0.0020
	C+1	1.58	0.0030	0.0004	0.0030	0.0008
	1983/4 C	2.29	0.0040	0.0005	0.0050	0.0013
	C+1	1.64	0.0030	0.0003	0.0030	0.0009
	C+2	0.49	0.0010	0.0001	0.0010	0.0004
	1982/3 C	2.78	0.0040	0.0005	0.0050	0.0008
	C+1	7.84	0.0080	0.0008	0.0100	0.0034
	C+2	4.15	0.0040	0.0004	0.0050	0.0024
	C+3	1.14	0.0010	0.0001	0.0020	0.0008
		25.90	0.0490	0.0043	0.0460	0.0150
IL /7	1985/6 C	0.82	0.0050	0.0003	0.0020	0.0003
	1984/5 C	2.79	0.0100	0.0008	0.0060	0.0026
	C+1	2.20	0.0070	0.0005	0.0030	0.0013
	1983/4 C	1.75	0.0040	0.0002	0.0030	0.0011
	C+1	2.83	0.0060	0.0004	0.0040	0.0015
	C+2	1.00	0.0030	0.0003	0.0020	0.0007
	1982/3 C	3.57	0.0090	0.0008	0.0060	0.0018
	C+1	3.09	0.0040	0.0003	0.0040	0.0013
	C+2	1.67	0.0020	0.0002	0.0020	0.0009
	C+3	4.04	0.0080	0.0007	0.0080	0.0027
		23.76	0.0580	0.0045	0.0400	0.0142
IL /8	1985/6 C	39.73	0.0790	0.0091	0.0660	0.0286
	1984/5 C	23.34	0.0370	0.0049	0.0400	0.0178
	C+1	25.12	0.0330	0.0050	0.0350	0.0161
	1983/4 C	65.46	0.0920	0.0105	0.0980	0.0245
	C+1	62.78	0.0630	0.0087	0.0880	0.0298
	C+2	83.71	0.0740	0.0100	0.1170	0.0499
	1982/3 C	18.25	0.0220	0.0029	0.0310	0.0084
	C+1	14.64	0.0140	0.0020	0.0220	0.0079
	C+2	16.26	0.0120	0.0018	0.0200	0.0107
	C+3	5.89	0.0060	0.0009	0.0080	0.0038
		355.18	0.4320	0.0558	0.5250	0.1975

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