The effect of thinning and fertilizer application on the relationship between leaf area and production in established Sitka spruce (*Picea sitchensis*) stands.

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CHAPTER ONE

INTRODUCTION

Inorganic fertilisers are widely used in British forestry in the establishment of conifer plantations on infertile sites. In contrast to other countries, however, their use has been largely restricted to the period between planting and canopy closure and there are few published accounts of the effect of fertiliser application on the productivity of established stands of Sitka spruce (*Picea sitchensis* (Bong) Carr), the major species used in British forestry. Experience in other countries, notably New Zealand and North America, has shown that established stands of pine and fir species may respond significantly to fertiliser application and in view of the relatively small area of land devoted to forestry in Britain and the anticipated timber shortages of the 21st century, it would be of value to know whether the productivity of established Sitka spruce stands in this country can be similarly increased. It has often been noted that stands thinned prior to fertiliser application may show a greater response than unthinned stands and experiments comparing fertiliser response at different stand densities have confirmed that a significant interaction between thinning and fertiliser application may take place. The first objective of this study therefore was to determine the effect of fertiliser application, in the presence and absence of thinning, on the productivity of established Sitka spruce stands.

While the results of such empirical experiments are in themselves valuable, an understanding of the mechanisms involved is important if results are to be extrapolated beyond the boundaries of the experiment. The importance of the leaf biomass in determining the level of productivity has long been recognised and examination of the relationship between leaf biomass and productivity has proved to be a useful way of determining the effect of treatments on crop growth rates in both the agricultural and forest situation. The second, and main, objective of the study therefore, was to determine the effect of thinnings and fertiliser application on the leaf biomass or leaf area of stands and to investigate the effect of these treatments on the relationship between leaf area or biomass and productivity for both individual trees and stands. Of particular interest in this field, because of the difficulties involved in measuring leaf area is the recent work on the relationship between leaf area and the cross sectional area of conducting tissue (sapwood area). There are no published data for Sitka spruce, so the opportunity will be taken to examine this aspect in the present study.

The need for efficient use of fertiliser in forestry demands a method of predicting, for a given stand, the degree of response that will occur to a given fertiliser application. Determination of the nutrient concentrations in oven dried tree foliage is often used as a means of identifying nutrient deficiencies and predicting fertiliser responses, but current methods used in Sitka spruce stands are based on work done in young stands generally less than 3 to 4 m in height and involve sampling current foliage from the topmost whorl of the tree. These methods may not be the most appropriate in older stands where redistribution of nutrients within the tree crown may take place, leading to the establishment of concentration gradients with respect to crown position and age of needle. Such gradients have been noted in stands of several species and it has been suggested that they might be used to develop a sampling system having greater diagnostic capabilities than the present one. There are no published accounts of nutrient distribution in the crowns of Sitka spruce trees and the third objective of this study therefore, was to investigate the effect of needle age and crown position on the nutrient concentrations in the foliage of established Sitka spruce stands.

CHAPTER TWO

LITERATURE REVIEW

2.1 The effect of fertilizers on the productivity of established conifer stands.

The volume of literature on the response of established conifer stands to fertilizer application has increased considerably over the past 10 years. The following review is not intended to be exhaustive but provides examples from the major areas of fertilizer usage of the nature of the effects of fertilizer application on the growth of established stands.

The use of fertilizers in forestry has been reviewed on a world scale by Bengtson (1977), Atterson (1978), and Baule (1973). The principal areas associated with large scale operational usage and publication of research findings are the Pacific Northwest area of N America, the Southeastern United States, New Zealand and Scandinavia.

In the Pacific Northwest, interest centres on the application of nitrogen to 15 to 60 year old stands of Douglas fir (Pseudotsuga menziesii (Mirb) Franco) and 350,000 ha of such stands were fertilized between 1975 and 1980 (Gessel and Peterson, 1981). In research trials nitrogen has been applied at 224 and 448 kg/ha to thinned and unthinned stands and results to date were reported by Gessel (1980). The average increase of basal area after eight years over control in Douglas fir stands was 18% at 224 kg/ha and 24% at 448 kg/ha in unthinned stands and 25% and 31% in thinned stands. Significant diameter increases following nitrogen application in Douglas fir stands have also been reported by Brix and Ebell (1969), Mitchell and Kellogg (1970) and Miller and Piennar (1973) who also found that large trees responded proportionately more than small trees. In a long term study, Miller and Tarrant (1983) reported that the volume response to a single ammonium nitrate application was still evident after 15 years and fertilized trees during that period had produced 51 to 111 per cent greater volume growth than untreated trees. In the Southeastern United States fertilizer application is aimed at increasing the productivity of slash pine (Pinus elliottii var elliottii Engelm) and Loblolly pine (Pinus taeda L) stands by application of both nitrogen and phosphorus and Bengtson (1979) estimated that by 1978, some 27 000 ha were being treated annually. Fisher and Garbett (1980) reported 8 year volume responses ranging from 0 to 36 m^3/ha following application of nitrogen (0 to 220 kg/ha) and phosphorus (0 to 55 kg/ha) to both species and Shoulders and Tiarks (1980) recorded a volume increase over control of 50 m^3/ha over the 6 years following application of nitrogen (403 kg/ha) and phosphorus (95 kg/ha) to a 13 year old Slash pine stand. Responses to nitrogen application have also been reported by Van Lear (1980) in a 17 year old Loblolly pine stand and by Fisher and Pritchett (1982) in 9 to 18 year old slash pine stands.

In New Zealand each year some 7 000 ha of established Monterey pine (Pinus radiata D Don) stands were being fertilized by 1976 (Ballard and Will, 1978) with nitrogen and phosphorus and the results of fertilizer experiments in such stands have been reported by Mead and Gadgil (1978). Application of phosphate resulted in a significant increase in basal area and volume increment giving up to 368 m^3/ha additional volume over a 14 year period and application of nitrogen increased basal area increment in a thinned, 12 year old stand by 18% over 6 years. Stem analysis showed that fertilizer treatment can result in a change in the volume to basal area ratio and this was confirmed by Woollons and Will (1975) who found nitrogen responses of 7 years in duration in high productivity stands amounting to volume increases over control of up to 61 m^3/ha.

Shortage of available nitrogen is the factor which commonly limits the growth of the boreal forests of Scandinavia (Tamm, 1979) and responses to application of nitrogen are frequently reported. In Finland, some 2.6 million ha of forest had been fertilized up to 1981 (Kolari, 1982) and results from Swedish fertilizer trials have been reported by Hagberg (1966), Tamm *et al* (1962) and Tamm (1982). In slow growing stands of both Scots pine (*Pinus sylvestris* L) and Norway spruce (*Picea abies* L) application of nitrogen at rates between 150 and 200 kg/ha increased height growth for 5 to 9 years and diameter growth for 5 to 8 years. Changes in stem form following fertilizer treatment have sometimes been indicated but this is thought to be of little practical importance.

In Britain, the use of fertilizer has been confined almost exclusively to plantations in the establishment phase and application to established stands has been restricted largely to research trials (Mayhead, 1976). The first trials in established stands were laid down in 1958 and 1959 and consisted of 15 experiments in stands of Scots pine, Sitka spruce, Douglas fir and Norway spruce, all at the first thinning stage of development. All these trials were laid out as factorials of N, P, K, Ca, Mg (Anon, 1960). Initial results (Anon, 1962) indicated increased foliar uptake of the nutrients applied and very small growth responses to both N and P were observed in some experiments. Later results (Anon, 1965) suggested significant basal area responses to P in four experiments and to N in two experiments. No response to K, Ca or Mg was noted but visual observation suggested that application of Ca had greatly increased litter breakdown. Binns and Grayson (1967), reviewing the results of these experiments stated that a response to N had been found in one Norway spruce stand and four Scots pine stands and indications of a response to P were apparent in three Sitka spruce stands and one Douglas fir stand. An analysis of the length of the response period in these experiments (Anon, 1969a) suggested that the response to N was relatively short lived (six years) but that response to P appeared to last for nine years or more. Three further experiments were established in Scots pine stands between 1964 and 1967 in which treatment consisted of application of two rates of a compound NPK fertilizer (Anon, 1967). A basal area response was noted in all three experiments (Anon, 1968) paralleled by an increase in needle weight and foliar N concentration. Later assessment (Anon, 1970) suggested that the response in two of the experiments had ceased after six years. A summary of the results of these and other trials established between 1964 and 1969 (Anon, 1972) indicated a significant fertilizer response in four out of four Scots pine experiments, a single Douglas fir experiment and four out of eight Sitka spruce experiments. Further information on the effect of fertilizers on Scots pine stands was provided by Miller et al (1977). Application of nitrogen to an 80 year old stand resulted in a significant increase in ring width at both breast height and, more particularly, at a height of 7.6 m up the stem. In a comprehensive study of the effects of nitrogen application to a 36 year old Corsican pine (*Pinus nigra* var *maritima* (Ait)) stand growing on sand dunes, Miller and Cooper (1973) recorded increase in height, basal area and volume growth and changes in taper following application of ammonium sulphate at rates equivalent to 84, 168, 336 and 504 kg elemental nitrogen per ha. Height growth after treatment was greatest for middle-sized trees but basal area response tended to be proportional to tree size. Although form factor showed no change with treatment, a significant response in stem taper was noted over trees of all sizes.

2.2 The use of growth analysis techniques to determine the mechanism of response.

Studies of the basis of variations in productivity between crops and between plants are fundamental to an understanding of the effects of cultural practices on yield, and techniques for the analysis of plant growth and yield have received considerable attention in the field of agricultural science. Blackman (1919) was among the first to recognise the importance of the effect of plant size on subsequent growth rates and he introduced the term relative growth rate (RGR), defined as the dry weight accumulated per unit of plant dry weight per unit of time. Gregory (1917) recognised the value of expressing growth as a function of the quantity of photosynthetic tissue and introduced the term net assimilation rate (NAR) defined as the dry weight accumulated per unit of leaf area (or weight) per unit of time. These ideas were further developed by Briggs et al (1920) and Gregory (1926) who expressed growth rate (RGR) as a function of two particular plant attributes, ie the amount of photosynthetic tissue (expressed as the leaf area per unit of plant dry weight (leaf area ratio) or the leaf area per unit of land area (leaf area index)) and the efficiency of that tissue (NAR). Much of the subsequent work on growth analysis has been concerned with attempts to determine the relative importance of these two attributes in determining the effect of environmental variables on plant growth. Watson (1952) prepared a very useful and comprehensive review of the literature up to 1951, quoting examples from a wide range of agricultural crops. He concluded that, although examples could be found of variations in NAR with time and in response to changes in temperature, moisture or nutrient status, these were of relatively little importance compared with the effects of these variables on leaf area ratio. Increase in dry matter yield was often associated with an increase in mean leaf area but there was no obvious correlation between yield and NAR (eg Watson, 1947). Watson's conclusions that crop treatments aimed at increasing yield must function primarily through increasing leaf area was supported by Wallace et al (1972) in a later review of experiments in agricultural crops. Watson (1958) pointed out that the process of increases in yield associated with increase in leaf area index could not be expected to continue indefinitely, since at some stage mutual shading of the leaves would decrease photosynthesis by part of the foliage and so decrease NAR. He demonstrated this for kale and sugar beet, thus confirming his earlier work in potatoes (Watson, 1947). The concept of a leaf area index beyond which productivity would decrease has also been outlined by Rees (1963) using data from an experiment with oil palms.

The application of growth analysis procedures in forestry has been discussed by Wareing (1966), Ledig (1974), Zavitovski et al (1974), Ledig (1976) and Satoo and Madgwick (1982). Their general conclusion was that, as in agricultural crops the quantity of photosynthetic tissue was likely to be more important than its efficiency in determining productivity and response to changing environmental circumstances but, with the exception of Satoo and Madgwick, they quote few examples and most of these relate to tree seedlings. Direct measurements of dry matter production in tree species are rare beyond the seedling stage because of the obvious difficulties associated with handling large sized material (Ledig, 1974) and productivity is often expressed in terms of one component of the biomass (eg stem volume increment) or else total dry weight is estimated from allometric equations relating dry matter to some easily measured variable (eg stem diameter).

Further evidence of the importance of the quantity of photosynthetic tissue is found in the literature relating productivity of trees and stands to leaf biomass or area. Matthews (1963) reviewed a number of the early papers and quoted several examples of significant relationships between leaf mass and productivity in a range of conifer species. Perhaps the most useful contribution in this field is the work of T. Satoo in Japan. In a series of studies he found that above-ground production (kg/tree/year) was linearly proportional to leaf biomass (kg/tree) in individual trees among stands of Pinus densiflora (Satoo, 1968), Betula maximowicziana (Satoo, 1970), Abies sachalienensis (Satoo, 1974a), Thujopsis dolobrata (Satoo, et al 1974) and Metasequoia glyptostroboides (Satoo, 1974b). In some stands a slight correlation seemed to exist between net above ground production and leaf efficiency among suppressed trees but generally there was no indication of a relationship between productivity and leaf efficiency in any of the stands investigated. Similar studies of stand rather than individual tree, production in Betula maximowicziana (Satoo, 1970) and Larix leptolepis (Satoo, 1971) stands indicated similar results but in Cryptomeria japonica stands at varying levels of productivity Satoo (1967) found not only a significant linear relationship between stemwood production and foliage biomass but also a relationship between stemwood production and NAR. However, in the case of NAR the relationship was only strongly linear in the lower part of the graph suggesting that variations in NAR are most influential in stands of low productivity.

Albrektson et al (1977) found a significant linear relationship between dry weight production above ground and leaf area index in both Norway spruce (LAI of 1.5 to 6) and Scots pine (LAI of 0.8 to 3.2) stands for a particular year and Albrektson (1980) showed a significant relationship between stem wood production and needle biomass using data from a range of Scots pine stands. As shown in the agricultural situation by Watson (1958), leaf biomass and net assimilation rate are not independent of one another and NAR may be expected to decrease as leaf biomass/area increases. Using data from a number of conifer stands Satoo (1971) demonstrated that leaf efficiency was inversely proportional to leaf biomass and similar results were noted by Waring et al (1981). The interaction between leaf biomass and leaf efficiency and the effects of stocking density etc have been discussed by Satoo and Madgwick (1982) in relation to the concept of an optimum leaf area index at which other factors being equal, productivity is at a maximum.

There have been a number of studies of the way in which both the quantity and photosynthetic efficiency of tree foliage is affected by fertilizer application. Helms (1964) found no change in net assimilation rate of mid crown foliage in the year following nitrogen application to a 38 year old Douglas fir stand and concluded that the observed diameter response was due to an increase in the area of photosynthetic tissue. Keay et al (1968) however, in a visually poor Pinus pinaster stand with low foliar nutrient concentrations, found that fertilizer application resulted in an increase in the rate of CO_2 fixation by needles of all ages as well as an increase in needle weight. Nitrogen application increased diameter growth and needle area in a 20 year old Douglas fir stand (Brix and Ebell, 1969) but had no effect on the rate of photosynthesis. In the same stand, however, Brix (1971) reported an increase in the photosynthetic capacity of shoots produced in the same year as nitrogen was applied and a similar result was found by Brix (1972). In a later study Brix (1981a) found a significant relationship between foliar nitrogen concentration and rate of photosynthesis. Nitrogen applied to a 36 year old Corsican pine stand increased needle retention in the year of application (Miller, Cooper and Miller, 1976) and in the subsequent year, needle number and area were increased as well as net assimilation rate (Miller and Miller, 1976a). Linder and Troeng (1980) found a significant increase in both biomass and photosynthetic efficiency following application of nitrogen to a 20 year old Scots pine stand and increases in needle weight or area following fertilizer application have also been reported by Albrektson _et al_ (1977) and Turner and Olsen (1976).

2.3 The effect of thinning on fertilizer response

A number of the authors previously quoted (eg Mead and Gadgil, 1978; Gessel, 1980) have observed that the response to fertilizer application often appears to be greater in stands which have been thinned prior to treatment than in unthinned stands. Experiments set up to determine fertilizer response at different levels of thinning have, however, produced conflicting results. Instances where fertilizer response has been found to be similar in both thinned and unthinned treatments have been reported in stands of Douglas fir (Lee, 1974; Miller _et al_, 1979; Scanlin and Loewenstein, 1979), Jack pine (Morrison _et al_, 1977), Black spruce (Weetman _et al_, 1980) and Red oak (_Quercus rubra_ L) (Graney and Pope, 1978). Ryker and Pfister (1967) however, found that in a white pine (_Pinus strobus_) stand a response to fertilizer only occurred in the thinned plots and Agee and Biswell (1970) reported an interaction between thinning and fertilization in a white pine stand with a significantly larger response to fertilizer in the thinned plots than in the unthinned. Studies of the effects of thinning and fertilizer application in Loblolly pine stands (Anon, 1983) showed that the greatest net volume growth and crop tree response resulted from a combination of thinning and fertilization in most experiments and the response to the treatments combined was greater than the simple additive effects of the two treatments applied separately. Perhaps the most comprehensive study to date has been the thinning/fertilization experiment in a Douglas fir stand in British Columbia of which the results at nine years were reported by Barclay et al (1982). While the authors report a highly significant thinning/fertilization interaction in terms of the average volume increase per tree in this study, the reported gross volume increments per hectare suggest that the response to fertilizer application has been similar in both the thinned and unthinned treatments. Attempts to elucidate some of the processes involved in the interaction between thinning and fertilization have been confined largely to the work of Brix (1981b, 1983) in this British Columbian experiment. Brix (1981b) showed that 5-7 years after treatment, thinning and fertilization had separately increased needle mass per tree by 90% and when combined by 271%. This was due to an increase in needle size, needle number per shoot and number of shoots produced. Foliage distribution was affected most in the top half of the crown by fertilization and in the bottom half by thinning. Brix (1983) showed that increased productivity following thinning and fertilization was due both to increased foliage biomass and an increase in canopy efficiency (production of biomass per unit of foliage).

2.4 Measurement of leaf area

The importance of leaf weight or area determinations is evident from the preceeding paragraphs but the actual measurement has long been a problem in tree biomass studies due to the laborious nature of direct measurements. Various methods have been developed to estimate leaf biomass. Carbon et al (1979) proposed a method of visual estimation with correction of the estimates using sample tree data but most methods are based on allometric equations which predict branch, tree or stand leaf weight or (area) from readily measured variables. Loomis et al (1966) and Hepp and Brister (1982) established relationships between foliage weight and branch diameter in Shortleaf pine (Pinus echinata) and Loblolly pine respectively and used these to estimate crown biomass as did Ek (1979) who found that inclusion of a measure of the branch position in the crown improved the precision of the prediction of leaf weight in hybrid poplar (Populus tristis). The use of diameter at breast height as a predictor of foliage weight was extensively reviewed by Kittredge (1944) who concluded that in a given stand, there was a significant linear relationship between dbh and foliage weight in a range of tree species but that the value of the constants in the equation varied from site to site. Similar results were noted in stands of Cryptomeria japonica (Satoo, 1966). Thus while dbh may be a useful estimator of foliage weight or area at a given site (Baskerville, 1965; Kira and Shidei, 1967; Rothacher et al., 1954) the relationship cannot be considered as constant for a given species on different sites (Satoo, 1962; Satoo and Madgwick, 1982).

The pipe model theory of Shinozaki et al (1964a, 1964b) proposes that a given unit of leaves is serviced by a continuation of conducting tissue (sapwood) of constant cross sectional area and that a linear relationship exists between the weight of foliage and the amount of sapwood from the base of the live crown upwards. This idea has been used to estimate leaf area from measurements of sapwood area at breast height and significant linear relationships have been established in a range of tree species by Grier and Waring (1974), Waring et al (1977), Whitehead (1978), Rogers and Hinckley (1979) and Kaufman and Troendle (1981). Snell and Brown (1978) compared dbh and sapwood area at breast height as estimators of foliage weight in seven conifer species and found that while in four species the precision of sapwood area and dbh was not significantly different in three species sapwood area was a significantly better estimator than dbh. Kaufman and Troendle (1981) reported no difference in the amount of leaf area supported by a unit of sapwood area measured at various points on the stem from breast height upwards but Waring et al (1982) considered that in trees with a high proportion of clean stem between breast height and the live crown, sapwood area should ideally be measured at the base of the live crown or else a measure of the degree of sapwood taper between breast height and the base of the live crown should be included. In a review of the relationship between foliage area and area of conducting tissue Whitehead and Jarvis (1982) suggest that the slope of the sapwood area: foliage area line will not only vary between species but that within a species differences in slope may be expected in response to changes in conductivity of the sapwood, and transpiration rate (Jarvis et al, 1976). Some support for this hypothesis is provided by Whitehead (1978) who found small variations in the sapwood area: foliage area relationship between Scots pine stands in different climatic regions of Britain. Recent work by Brix and Mitchell (1983) has suggested that the sapwood area:

foliage area relationships may also be affected by thinning and fertilization treatments within a stand. Extensive use of sapwood area as a substitute for foliage area has been made by Waring who proposed that the ratio of basal area growth to sapwood basal area could be used as an index of tree vigour (Waring _et al_, 1980; Waring, 1980). This index later referred to as E (an index of growth efficiency) has been used to explain observed differences in susceptibility to attack by mountain pine beetle in Lodgepole pine (_Pinus contorta_ Dougl) stands (Mitchell _et al_, 1983) and as a measure of the effects of different thinning intensities in a Douglas fir stand (Waring _et al_, 1981).

2.5 Nutrient distribution in tree crowns

The role of foliar nutrient concentration determination in the diagnosis of the nutrient status of trees has been extensively reviewed by Van den Driessche (1974). Sampling of current year's foliage in the topmost whorl in the dormant season is the generally accepted method but increasing recognition of the pattern of nutrient translocation from old to new needles has led to an increasing number of studies of the vertical (crown position) and horizontal (age of needle) concentration gradients in tree crowns.

Van den Driessche (1974) recognised 5 different patterns of vertical distribution:

1. No significant concentration gradient.
2. Decreasing concentration towards the base of the crown.

3. Increasing concentration towards the base of the crown.
4. A mid crown maxima with decreasing concentrations towards the top and bottom of the crown.
5. A mid crown minima with increasing concentration towards the top and bottom of the crown.

He noted that the type of distribution may vary between different elements within a single tree and may vary between trees of the same species on different sites. Few comprehensive studies of vertical distribution have been made since the review of Van den Driessche although a number of workers have looked at a restricted number of crown positions. Morrison (1972) for example, on the basis of samples from upper, mid and lower crown positions, found no significant vertical gradient for N in 30 year old *Pinus banksiana* but a decrease in P and K concentrations down the crown and an increase in Ca concentration. In *Abies balsamea* however, (Morrison, 1974) he found no significant vertical trends. McLean and Robertson (1981) recorded higher N, P and K levels in the upper crown of *Picea rubens* stands than in the lower crown and Reemtsma (1979) found that current foliage in whorl seven of Norway spruce stands had consistently lower P concentration than whorl one. In a more comprehensive study, Comerford (1981) sampled each whorl of a 49 year old red pine stand and found significant vertical gradients in both current and one year old foliage for N, P and K. Nitrogen concentration decreased down the crown while K concentration increased and P concentration was lowest at the mid crown position. Foliage older than one year generally showed no significant trend. While there is clearly some variability in the patterns of vertical distribution there is considerable agreement over the pattern of horizontal gradients. A decrease in P and K concentrations with increasing needle age has been recorded for a number of tree species by Comerford (1981), Morrison (1972), Morrison (1974), Florence and Chuong (1974), Keay et al (1968), Leyton and Armson (1955) and Madgwick (1964) and a similar trend exists for nitrogen concentration except that Comerford (1981) noted that N levels were highest in one year old foliage. Calcium concentration, on the other hand, tends to increase with increasing needle age (Morrison, 1972; Morrison, 1974; Madgwick, 1964). Attempts to relate such concentration gradients to tree nutrient status have suggested that the decline in nutrient concentration with age of needle may be steeper on poorer sites where the trees are more nutrient deficient (Florence and Chuong, 1974). Measurement of foliar nutrient concentrations in fertilizer experiments in established Sitka spruce stands in Britain (Anon, 1969b) have shown that even in stands where a significant response to applied phosphate fertilizer has occurred, the foliar P concentrations in the top whorl of the control trees may be well above the levels regarded as satisfactory in younger stands (Binns et al 1980). This may reflect the fact that the foliar nutrient concentration associated with optimum growth changes with tree size (Miller et al 1981) thus necessitating a revision of the levels considered as satisfactory in older stands or it may be a true reflection of the inadequacy of the top whorl sampling position as an indicator of nutrient status.

The use of tissue other than foliage has been examined and includes phloem (Rehfuess and Baum, 1980) vegetative buds: (Arnold and Roomans, 1983), roots (Van den Driessche and Webber, 1977) and litter (Miller and Miller, 1976b; Adams, 1974; Carey and Farrell, 1978). In a review of various methods Van den Driessche (1979) suggested that analysis of litter fall may be a particularly useful alternative to foliage sampling.

2.6 Conclusions

It is clear that the productivity of established conifer stands in many parts of the world can be increased by the application of fertilizers and that nitrogen and phosphorus are the elements giving the most consistent benefits. Fertilizers normally increase both height and basal area increment and there are indications that the relationship between volume and basal area may also sometimes be affected. Similar results have been found in established pine stands in Britain but data from Sitka spruce stands is limited and suggests that about half of the stands treated have shown a significant response.

Results of experiments designed to test the interaction between thinning and fertilizer application have been conflicting with thinning having either no effect on the level of fertilizer response or, particularly it appears in pine species, causing a significant increase in the level of fertilizer response. There are no published accounts of the interaction of thinning and fertilization in Sitka spruce stands.

It is generally assumed that, as in agricultural crops, increased productivity is achieved by an increase in leaf biomas but nevertheless, there are examples of increases in leaf efficiency (net assimilation rate) following fertilizer application to tree species. There are no published accounts of the relative importance of these two factors in thinned and/or fertilized Sitka spruce stands.

Sapwood cross sectional area has proved to be a useful measure of leaf area in a number of species and the relationship appears to be more independent of site factors than that between leaf area and stem diameter. There is a need to examine this relationship in Sitka spruce stands and to see how it varies with stand treatment.

The use of foliar nutrient concentrations as a technique for diagnosing nutrient deficiences and predicting fertilizer response has proved valuable in many species but there is increasing recognition of the need to examine nutrient distribution patterns with respect to crown position rather than to rely on the conventional top whorl sampling position. There are no published accounts of the pattern of variability in Sitka spruce crowns, but the suspected inadequacy of the top whorl position in established Sitka stands suggests that this aspect must be examined.

CHAPTER THREE

METHODS

3.1 Introduction

The data used in this study were collected from two field experiments established in pole-stage Sitka spruce stands. The first experiment (Benmore 18/77) was established by the Research and Development Division of the Forestry Commission in 1977 and the second (Wauchope 14/80) was established by the author in the autumn of 1980.

3.2 Experiment sites and treatments

3.2.1 Benmore This experiment was established in 1977 in Benmore forest in the Argyll district of the Strathclyde Region (Grid ref NS 139736) in a 27 year old unthinned Sitka spruce stand planted on upturned turfs and with a stocking density in 1977 of 2900 stems/ha. The site is gently sloping at an elevation of 315 m and the average annual rainfall is 2000 mm. The underlying rock is Dalradian slate phyllite and mica-schist and the soil type is a peaty gley (Pyatt, 1970) with a mean peat depth of 31 cm. At the start of the experiment the mean basal area was 39.71 m^2/ha and top height (mean height of the 100 largest diameter trees/ha) was 10.8 m indicating a general yield class of 12 (Hamilton and Christie, 1971). In 1977 a randomised block experiment was laid out with four replicates of four treatments:-

O - Control

N - Application of 330 kg/ha urea (46% N). [151 kg N per ha.]

P - Application of 375 kg/ha ground phosphate rock (13% P). [49 Kg P per ha.]

NP - Combination of 330 kg/ha urea and 375 kg/ha rock phosphate.

Treatment plots were chosen so that differences in initial basal area were minimised and all dead and dying trees were removed. The treatment plots were square and 0.05 ha in size and contained an average of 148 trees. The fertilizers were broadcast in May 1977 and a re-application of nitrogen as 330 kg/ha urea was made to the N and NP treatments in May 1982.

3.2.2 Wauchope This experiment was established in 1980 in Wauchope forest in the Roxburgh district of Borders Region (Grid ref NY 599 058). The stand was 23 years old, unthinned and planted on spaced single furrow cultivation. Stocking density in 1980 was 3610 stems/ha. The site has a slope of 6-9°, is at an elevation of 330 m and receives an average annual rainfall of 1200 mm. The underlying rock is greywacke and shale of Silurian age and the soil is a surface water gley. Mean basal area at the start of the experiment was 45.4 m^2/ha and top height was 12.9 m, indicating a general yield class of 20. In 1980 a randomised block experiment was established with five replicates of six treatments:

O -	Control.
N -	Application of 330 kg/ha urea.
P -	Application of 375 kg/ha rock phosphate.
T -	Thinning carried out.
TN -	Thinning plus urea application.
TP -	Thinning plus phosphate application.

The thinning was carried out in the winter of 1979/80 and consisted of the removal of approximately 33% of the standing basal area in a low selective thinning. The fertilizers were broadcast over the treatment plots in May 1980. Treatment plots were 0.05 ha in extent and contained on average, 180 trees/plot in the unthinned treatments and 100 trees/plot in the thinned treatments. Dead and dying trees were removed from the unthinned treatments. During the winter of 1981/82, a heavy fall of wet snow resulted in considerable damage to plots in blocks I and II, particularly in the thinned treatment, and the number of bent, snapped and uprooted trees was so great that these plots had to be abandoned. The 1983 assessments are therefore based on blocks III, IV and V only.

3.3 Growth measurements

3.3.1 Diameter In both experiments a circular assessment plot of 0.02 ha in size was established in the centre of each treatment plot at the start of the experiment and all trees within this plot were numbered and marked with a white painted band at breast height (1.3 m). Using a graduated girthing tape calibrated to read diameter to the nearest 0.1 cm, the diameter of each tree was measured at the start of the experiment and annually thereafter, during the dormant season.

3.3.2 Height increment height measurements were determined retrospectively by measuring, to the nearest cm, internode lengths on felled sample trees.

3.3.3 Stem volume The stems of felled sample trees were divided into three metre lengths from the base upwards to the point where the diameter over bark was seven cm and the volume of each section (over-bark) was determined by Huber's formula ($\pi r^2 h$) where r is determined at the mid point of each section.

3.4 Leaf biomass/area determination

3.4.1 Introduction Samples for the determination of leaf area were collected on one occasion at Benmore and twice at Wauchope. Although the selection of sample trees and the number of whorls sampled varied in each case, the method of dealing with the sample trees was the same.

3.4.2 Field procedure After felling of the sample tree, all branches from the sample whorl were clipped off at their junction with the stem and were weighed along with any internode branches between the sample whorl and the one above. After recording of the total whorl weight, one representative branch per whorl was selected and the others discarded. The sample branch was placed in a polythene bag and transported within 24 hours to storage at -20°C.

3.4.3 Laboratory procedure After defrosting, all needle bearing twigs from each sample branch were clipped off and allocated to one of the four age classes (1 year, 2 years, 3 years, 4 years and older) according to their position on the branch. From each age class four representative shoots were chosen and 50 needles removed from each. The remaining shoots were dried for 24 hours at 105°C prior to separating the needles from the twigs. The twigs were discarded and the dry weight of the needles recorded. The 200 needle sample was weighed, then placed between two clear, acetate sheets, the needles were separated and laid flat and the sample was passed through a Li-Cor L1-3100 area meter measuring surface area to an accuracy of 0.1 mm^2. Thereafter the 200 needle sample was dried and the resulting dry weight used to establish a fresh weight: dry weight conversion factor for that age class. Similarly the area measurement was used to determine a fresh weight: area conversion factor for each age class of needle.

3.5 Sapwood cross sectional area

Sapwood area of sample trees was determined at breast height either from discs or from cores. Discs of approximately three cm in thickness were cut at breast height and stored at -20°C. After defrosting, the discs were immersed to half their depth in a 5% solution of toluidine blue inside an evacuated jar. After 15 minutes the discs were removed and sawn, first across the longest diameter and then at right angles to it, to produce cut surfaces in which penetration of the dye could be noted. Dye penetration was taken to coincide with sapwood, the width of which was measured along four radii. Cores were somtimes used to avoid felling of sample trees. Using a motorised borer, two five mm diameter cores were removed at breast height, each one penetrating to the pith. The first core was taken along the direction of the plough ridge and the second at right angles to it. Each case was held up to the light and the sapwood/heartwood boundary taken as the junction between translucent and opaque wood. Sapwood width and core radius were measured to the nearest mm.

3.6 Nutrient concentration determination

A subsample of approximately 10 g was removed from each dried needle sample and finely ground. 0.1 g of the ground material was subjected to digestion with sulphuric acid and hydrogen peroxide at 350°C for 5 hours. The digests were then transferred to 50 ml volumetric flasks and made up to volume with distilled water. Nitrogen and phosphorus concentrations were determined by standard colormetric techniques using an auto-analyser and potassium was determined by flame emission using an atomic absorption spectrometer.

3.7 Choice of sample trees

Apart from the annual diameter measurements, which were based on all trees within the assessment plots, measurements were carried out on sample trees.

3.7.1 Benmore Sampling was carried out on one occasion in November 1979, three growing seasons after treatment. A random sample of five trees per plot was selected from treatments 0 and NP and felled. Stem volume and retrospective height measurements were made on each tree and a 2.5 cm thick disc removed at breast height for sapwood area determination. A sample branch for leaf area determination was removed from every live whorl in blocks

I and III and from every second live whorl in blocks II and IV.

3.7.2 Wauchope

a. In March 1980, during the thinning operation, a random sample of four trees from each thinned plot was selected for stem volume measurement to establish the pre-treatment volume to basal area relationship.

b. In October 1981, two growing seasons after treatment a random sample of four trees was selected from each plot in block I and II. A sample branch for leaf area determination was removed from whorl one (the first whorl from the top) and from the whorls nearest to points one third and two thirds of the way down the crown on each tree and a three cm thick disc removed at breast height for sapwood area determination.

c. In June 1983, sampling was carried out in treatments O, N, T and TN in blocks III, IV and V. Three co-dominant or dominant trees per plot were selected on the basis of similar diameter at the start of the experiment. One branch for leaf area determination was removed from whorls one, four and seven on each tree but on this occasion total whorl weight was not recorded. Stem volume and retrospective height measurements were made on each tree.

d. At the end of each of the 1980, 1981 and 1982 growing seasons, a non-destructive assessment of sapwood areas was carried out on five randomly selected trees per plot in all treatments and all blocks (necessarily restricted to three blocks for the 1982 assessment). Sapwood width was determined from cores described in section 3.5. To prevent excessive damage to trees as a result of the core removal, trees chosen for sampling were excluded from subsequent sampling exercises.

3.8 Statistical analysis

All standard analyses of variance and regression analyses were carried out using Genstat packages mounted on the mainframe computer at the Edinburgh Regional Computing Centre.

CHAPTER FOUR

EFFECTS OF THE EXPERIMENTAL TREATMENTS ON PRODUCTION

4.1 Benmore experiment

4.1.1 Basal area increment The annual diameter measurements were converted to basal area (πr^2) and summed to provide plot basal area figures. Treatment comparisons were made by analysis of variance and covariance of basal area (m^2) per hectare but since the inclusion of initial basal area as a covariate did not affect the outcome (starting basal areas were very similar), the final analysis of variance was done using unadjusted increment figures. Annual and total basal area increments by treatment and the results of the analysis of variance are shown in Table 1. Application of nitrogen in 1977 resulted in a significant increase in basal area increment in that year and in each of the following three years but had no effect in 1981. Re-application of nitrogen in 1982 resulted in a significant increase in basal area increment in that year. Total basal area increment over the 6 year period was 29% higher than control in the N treatment and 43% higher in the NP treatment. Although application of phosphate fertilizer appeared to increase basal area increment at both levels of nitrogen, this effect was not significant at any time. Total increment in the P treatment was 16% higher than control. There was no significant interaction between the effects of N and P which appeared to be additive.

Table 1. Effect of fertilisers on basal area increment in the Benmore experiment

Treatment		Initial basal area m^2/ha	Basal area increment (m^2/ha)						Total increment m^2/ha	% over control
			1977	1978	1979	1980	1981	1982		
0		39.70	1.34	0.89	1.72	1.20	0.79	0.86	6.80	-
N		39.29	1.95	1.30	2.04	1.63	0.74	1.13	8.79	29
P		41.22	1.53	1.18	1.87	1.52	0.80	1.00	7.90	16
NP		38.63	1.99	1.74	2.38	1.77	0.75	1.11	9.74	43
<u>Analysis of variance</u>										
Net effect of N	SED		0.14	0.18	0.17	0.15	0.11	0.08	0.66	
	significance		**	*	*	*	ns	*	*	
Net effect of P	SED		0.14	0.18	0.17	0.15	0.11	0.08	0.66	
	significance		ns	ns	ns	ns	ns	ns	ns	
N x P interaction	SED		0.19	0.25	0.25	0.21	0.16	0.11	0.93	
	significance		ns	ns	ns	ns	ns	ns	ns	

*P<0.05: **P<0.01: *** P< 0.001

Table 2. Diameter increments in the Benmore experiment in relation to treatment and tree size

Size Class	Treatment	n	Initial diameter (cm)	Diameter increment	% increment
Small	O	42	10.06	0.58	5.8
	N	70	9.94	0.59	5.9
	P	67	9.92	0.70	7.1
	NP	55	10.01	0.81	8.1
	Mean		9.98	0.67	6.7
Medium	0	71	12.77	0.97	7.6
	N	83	12.68	1.25	9.8
	P	85	12.64	1.03	8.2
	NP	77	12.76	1.42	11.1
	Mean		12.71	1.17	9.2
Large	0	76	16.15	1.69	10.4
	N	75	15.90	1.96	12.3
	P	77	16.03	1.71	10.7
	NP	66	16.34	2.34	14.3
	Mean		16.11	1.93	12.0

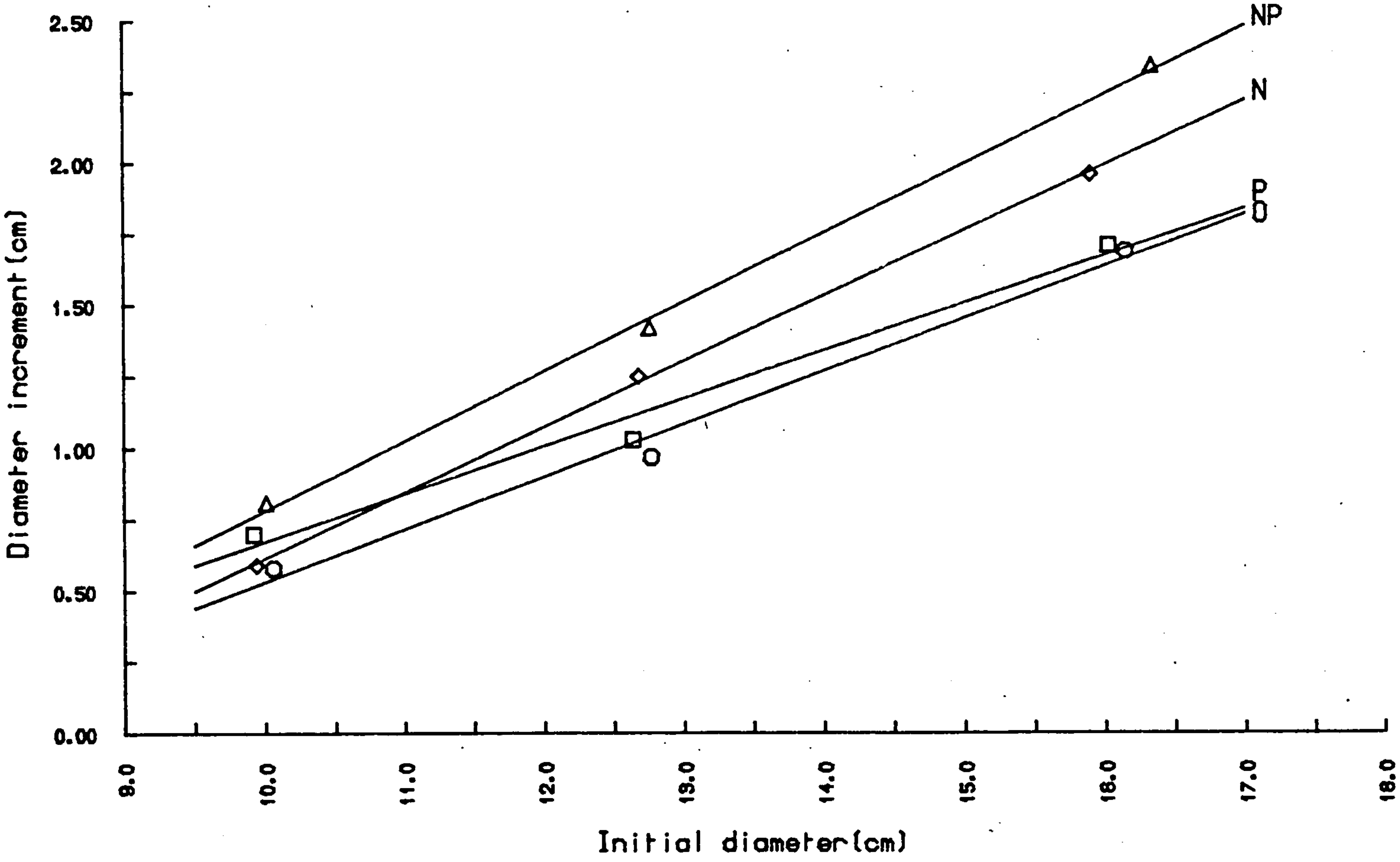
Table 3. Results of the analysis of variance of size class diameter increments in the Benmore experiment

Source	DF	SS	MS	VR	
Blocks	3	0.2555	0.0852	3.629	
Nitrogen	1	0.9688	0.9688	9.626	**
Phosphorus	1	0.3202	0.3202	3.182	
N x P	1	0.1088	0.1088	1.081	
Residual (a)	9	0.9057	0.1006	4.288	
Size	2	12.8140	6.407	273.011	
Size x N	2	0.3253	0.1627	6.931	**
Size x P	2	0.01392	0.00696	0.297	
Size x N x P	2	0.03991	0.01995	0.850	
Residual (b)	24	0.56323	0.02347		
Grand Total	47	16.31534			

Footnote

This is a split plot analysis. Here, as in all subsequent ANOVA tables residual (a) is the 'between plot' error term and residual (b) is the 'within plot' error term.

Fig. 1 Diameter increment in relation to initial diameter in the Benmore experiment



4.1.2 Diameter increment in relation to tree size In each treatment, all trees within the assessment plots were divided into three size classes on the basis of their diameter at the start of the experiment. The size classes were arbitrarily fixed to ensure approximately equal numbers of trees in each and were designated as small (up to 11.4 cm diam) medium (11.5 to 14.0 cm) and large (14.1 cm and above). Six year (1977-1982) diameter increments were then calculated for each tree and diameter increments compared by treatment and size class (Table 2). The results indicated a significant relationship between starting diameter and diameter increment in all treatments (Fig 1) and also suggested a size x treatment interaction. This was confirmed by an analysis of variance of the increments (Table 3) which showed a significant nitrogen effect and a significant size x nitrogen interaction. Mean diameter increment was significantly greater ($P = 0.01$) overall for trees fertilized with nitrogen but while trees in the medium and large classes had significantly greater diameter increment when fertilized with nitrogen ($P = 0.05$ and $P = 0.01$ respectively) there was no significant difference between diameter increments in the small trees. In the above, and in subsequent analysis, size is treated as a split-plot factor.

4.1.3 Volume to basal area relationship and volume increments

Sample tree volumes and basal areas were converted to volume (m^3) to basal area (m^2) ratios and an analysis of variance carried out. To account for the effect of tree size on the ratio, an analysis of stem volumes was carried out both with and without adjustment of the volumes by covariance analysis using basal area as a covariate. Results are shown in Table 4. There was

Table 4. Mean stem volume and volume to basal area ratios in the Benmore sample trees

Treatment	Mean volume to basal area ratio	Mean stem volume (m^3)	Adjusted mean stem volume (m^3)
O	4.46	0.056	0.057
NP	4.80	0.062	0.061
5% LSD	0.55	0.012	0.010

Table 5. Volume increment in the Benmore experiment

Treatment	Standing Volume m^3/ha		Volume increment m^3/h
	1977	1982	
0	200.2	246.1	45.9
N	195.2	254.3	59.1
P	204.7	258.0	53.0
NP	193.7	259.4	65.7

an apparent treatment effect with fertilized trees having a greater volume for a given basal area than control trees. Adjustment of the stem volumes to allow for differences in basal area reduced but did not eliminate the apparent treatment effect. There were, however, no significant differences between ratios and between volumes, either adjusted or unadjusted and accordingly a single regression equation including the data from both treatments was drawn up to relate volume to basal area:-

$$\text{Volume } (m^3) = 6.738 \text{ basal area } (m^2) - 0.024 \quad r = 0.97$$

Applying this equation to the data from the initial and final tree diameter assessments gave standing volumes and volume increments as shown in Table 5. Volume increment was 13.3 m^3/ha (29%) greater than control in treatment N, 7.5 m^3/ha (16%) greater in treatment P and 19.8 m^3/ha (43%) greater in treatment NP.

4.1.4 Height increment Results of the retrospective height measurements are shown in Table 6. Mean height increment of trees fertilized with NP was not significantly different from the control treatment in 1976 but in the year of fertilizer application (1977) and in the succeeding two years there was a significant ($P = 0.05$) increase amounting to an extra 14 cm in each year. Following division of the sample trees, on the basis of their pre-treatment height, into three size classes (small up to 8.8 m; medium 8.81 to 9.70 m; large, over 9.7 m), height increment was examined by treatment and size class (Table 7). The results suggested that trees of all size classes were affected by fertilizer application. In the control treatment, trees appeared to grow,

Table 6. Mean annual shoot lengths in the Benmore experiment

cm

Year	0	NP	Difference	5% LSD
1976	38	42	4	10
1977	37	51	14	
1978	39	53	14	
1979	31	45	14	

Table 7. Mean annual height increment in the Benmore experiment by treatment and size class

Size Class	Treatment	n	Initial height (m)	3 year increment (m)	% increment
Small	0	5	8.36	0.81	9.7
	NP	6	7.91	1.19	15.0
Medium	0	8	9.31	1.10	11.8
	NP	6	9.05	1.63	18.0
Large	0	7	10.07	1.21	12.0
	NP	8	10.17	1.63	16.0

in terms of actual and percentage height increment, in proportion to their size but in the NP treatment mean three year height increment of medium trees was equal to that of large trees and in percentage terms was higher (18% increase cf. 16%).

4.2 Wauchope experiment

4.2.1 Basal area increment Basal area increments are shown in Table 8 and the analysis of variance in Table 9. Again the inclusion of initial basal area as a covariate did not significantly alter the result and the analysis presented is for unadjusted increments. Increments for the 1982 growing season are based on three replicates only due to the snow damage to thinned treatments in blocks I and II during the 1981/82 winter. Application of nitrogen increased basal area increment in each of the three growing seasons and although the effect was not significant in any year, the cumulative effect over three growing seasons was significant ($P = 0.05$). Phosphate application had little apparent or significant effect in any year, nor was the cumulative increment significantly different from control. Thinning increased basal area increment/ha in each year and the effect was very highly significant ($P = 0.001$) in 1981. The cumulative effect was also significantly greater than control ($P = 0.05$). There was no significant or apparent interaction between the effects of the thinning and fertilizer treatments in any year or in the cumulative increments. Thinning and fertilizer effects appeared to be additive.

4.2.2 Diameter increment in relation to tree size Trees were assigned to three size classes; small (up to 11.0 cm), medium

(11.1 to 13.5 cm) and large (over 13.5 cm). The number of trees in each class was smaller for the thinned treatments, particularly in the small class which was almost absent from the thinned plots. Diameter increment by treatment and size class are shown in Table 10. The results demonstrated a clear relationship between diameter increment and initial diameter (Fig 2) and a clear separation between thinned and unthinned treatments was observed. An analysis of variance of the increments (Table 11) gave a very highly significant thinning effect ($P = 0.001$) but no size x thinning interaction was detected, suggesting that trees of all sizes had responded to the thinning. The small number of small trees present in the thinned plots however, renders the results from this size class suspect, particularly as those small trees present in the thinned plots had a higher mean initial diameter than their counterparts in the unthinned plots. Although the effect of fertilizer was not significant overall, there were significant differences among the fertilizer treatments. Mean diameter increment for treatment N (1.08) was significantly ($P = 0.05$) greater than treatment O (0.98 cm) but was not significantly different from treatment P (1.05 cm). Treatment P was not significantly different from treatment O and there was no significant size x fertilizer interaction.

4.2.3 Volume to basal area relationship and volume increment

Volume (m^3) to basal area (cm^2) ratios for the 1983 sample trees were calculated and subjected to an analysis of variance along with mean stem volume adjusted and unadjusted for basal area as previously described. Treatment means and the results of the analysis of variance are shown in Table 12. Trees in both

Table 8. Effect of thinning and fertiliser treatments on basal area increment in the Wauchope experiment

Treatment	Initial basal area m^2	Amount removed in thinning	Basal area increment m^2/ha			Total increment m^2/ha	% Increment
			1980	1981	1982		
0	43.91	-	2.16	1.87	2.16	6.19	14.1
N	47.39	-	2.32	2.22	2.60	7.14	15.1
P	44.52	-	2.15	2.11	2.23	6.49	14.6
T	47.06	15.65	2.37	2.39	2.63	7.39	15.7
TN	46.65	14.74	2.47	2.47	2.72	7.66	16.4
TP	42.97	13.75	2.29	2.25	2.70	7.24	16.8

Table 9. Results of analysis of variance of Wauchope basal area increments

Source	1980			1981			1982			Total		
	DF	MS	VR	DF	MS	VR	DF	MS	VR	DF	MS	VR
Blocks	4	0.336	6.51	4	0.152	3.45	2	0.273	2.41	4	2.06	6.74
Fertiliser	2	0.084	1.62	2	0.122	2.77	2	0.241	2.12	2	1.33	4.36*
Thinning	1	0.197	3.81	1	0.708	16.11***	1	0.442	1.96	1	1.96	6.43*
Fertiliser/thin	2	0.003	0.07	2	0.090	2.04	2	0.153	1.35	2	0.08	0.28
Residual	20	0.052	-	20	0.044	-	10	0.113	-	14	0.31	-
Total	29	0.095	-	29	0.080	-	15	0.158	-	23	-	-

Footnote

In the analysis of variance of the total increments, missing values for the thinned blocks damaged in the 1981/82 winter were estimated using a least-squares procedure.

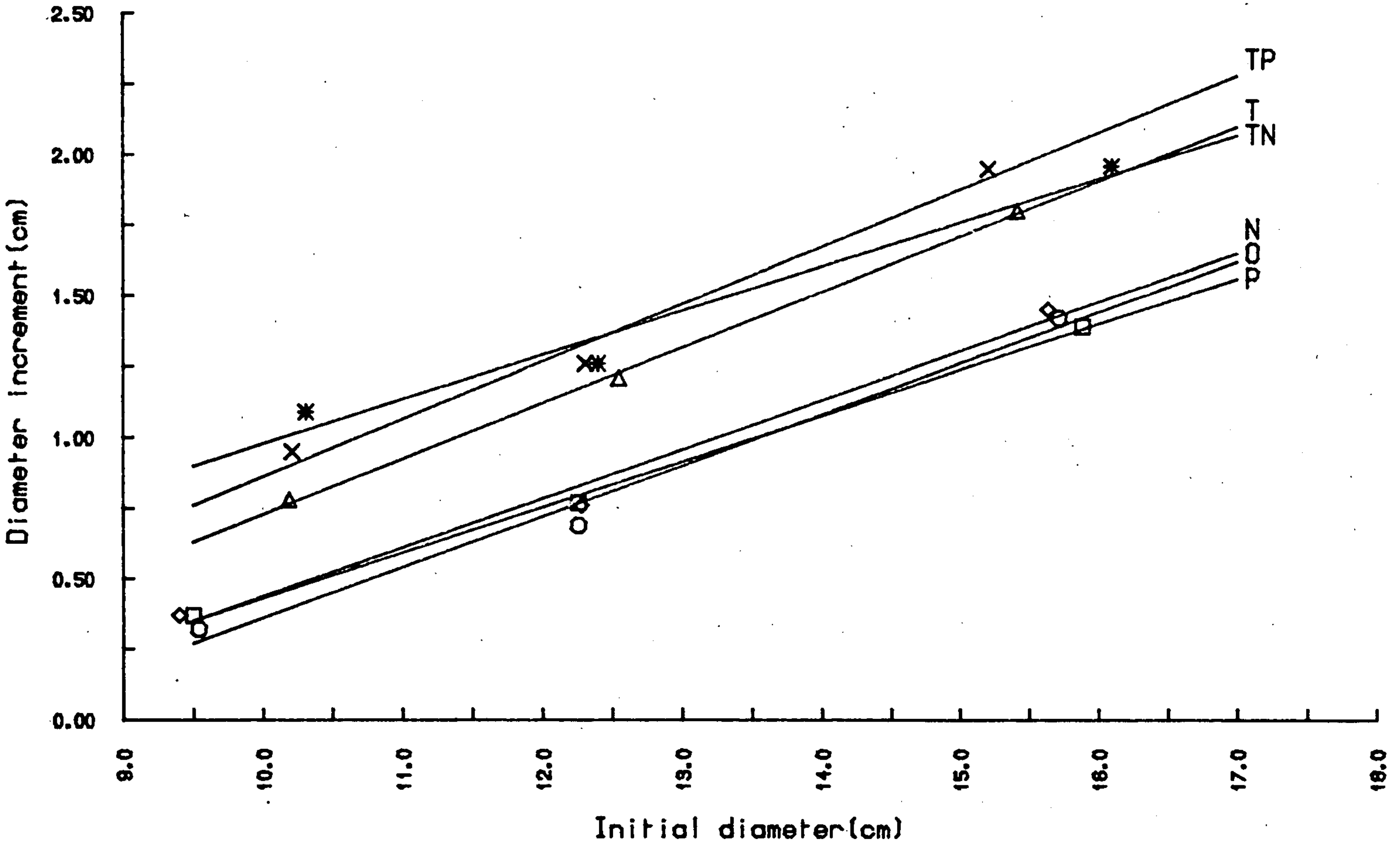
Table 10. Diameter increment in the Wauchope experiment in relation to treatment and tree size

Size Class	Treatment	N	Initial diameter (cm)	Diameter increment (cm)	% increment
Small	O	118	9.54	0.32	3.4
	P	119	9.50	0.37	3.9
	N	126	9.40	0.37	3.9
	T	12	10.19	0.78	7.7
	TP	21	10.21	0.95	9.3
	TN	8	10.31	1.09	10.6
	Mean		9.86	0.65	6.6
Medium	0	110	12.26	0.69	5.6
	P	121	12.26	0.77	6.3
	N	115	12.28	0.76	6.2
	T	45	12.55	1.21	9.6
	TP	52	12.31	1.26	10.2
	TN	42	12.40	1.26	10.2
	Mean		12.34	0.99	8.0
Large	0	108	15.72	1.42	9.0
	P	103	15.89	1.39	8.7
	N	124	15.64	1.45	9.3
	T	65	15.42	1.80	11.7
	TP	54	15.21	1.95	12.8
	TN	65	16.10	1.96	12.2
	Mean		15.66	1.66	10.6

Table 11. Results of analysis of variance of size class diameter increments in the Wauchope experiment

Source	DF	SS	MS	VR
Blocks	4	1.2584	0.3146	18.089
Fertiliser	2	0.11715	0.0586	3.354
Thin	1	3.7026	3.7026	212.03***
ThinXFertiliser	2	0.0439	0.0219	1.258
Residual (a)	14	0.2445	0.0175	1.004
Size	2	12.9853	6.4926	373.332
FertiliserXsize	4	0.0211	0.0053	0.303
ThinXsize	2	0.0308	0.0154	0.886
FertiliserXthinXsize	4	0.0510	0.0128	0.734
Residual (b)	36	0.6261	0.0174	-
Grand total	71	19.0808		

Fig.2 Diameter increment in relation to initial diameter in the Wauchope experiment



the thinned and fertilized treatments appeared to have slightly less volume for a given basal area than control trees but the differences were not significant. Similarly there was no significant difference between the adjusted stem volumes but there was still a suggestion of a lower volume for a given basal area in the fertilized treatments. Adjustment of the stem volumes did however, appear to remove the apparent thinning effect.

Since the 1983 sample trees were chosen on the basis of similar pre-treatment size (diameter), it was considered that the range of sizes was too small to allow construction of a meaningful volume to basal area relationship for comparison with the 1980 data. Accordingly the two data sets were amalgamated to form a single regression of volume on basal area. Best fit (highest correlation coefficient) was obtained using a log-log scale and the calculated equation was of the form:

$$\log \text{volume} = 1.569 \log \text{basal area} + 4.143 \quad r = 0.98$$

Application of this equation to individual tree diameters allowed calculation of plot volumes as shown in Table 13, based on three replicates only. Volume increment in the unthinned treatments was 10.4 m^3/ha (15%) higher than control in treatment N and 5.6 m^3/ha (8%) lower in treatment P. Thinning alone, increased volume increment over control by 9.1 m^3/ha (13%) and within the thinned treatments, volume increment was 9.6 m^3/ha (12%) higher than treatment T in treatment TN and 1 m^3/ha (1%) lower in treatment P. Thinning and nitrogen application together resulted in an increase over control of 18.7 m^3/ha (28%).

Table 12. Volume to basal area ratio and adjusted mean stem volume in the Wauchope experiment

Variate	Treatment mean				Analysis of variance				
	0	N	T	TN	Source	DF	SS	MS	VR
Volume to basal area ratio	7.12	6.72	6.91	6.72	Blocks	2	0.4306	0.2153	0.624
					Nitrogen	1	0.7727	0.7727	2.626
					Thin	1	0.0954	0.0954	0.324
					N x T	1	0.1031	0.1031	0.350
					Residual	6	2.7656	0.2943	0.853
					Total	11	3.1673		
Volume (m^3) adjusted for basal area	0.148	0.140	0.147	0.143	Blocks	2	0.000475	0.000238	2.16
					Nitrogen	1	0.000346	0.000346	2.589
					Thin	1	0.000025	0.000025	0.018
					N x T	1	0.0000352	0.0000352	0.263
					Covariates	1	0.000171	0.000171	1.276
					Residual	5	0.000669	0.000134	1.217
					Total	11	0.00127		

Table 13. Volume increment in the Wauchope experiment

Treatment	Standing Volume m^3/ha		Volume increment m^3/ha
	1980	1982	
0	251.4	319.4	68.0
P	249.3	311.7	62.4
N	289.6	368.0	78.4
T	191.0	268.1	77.1
TP	178.8	254.9	76.1
TN	204.0	290.7	86.7

4.2.4 Height increment Results of the retrospective height measurements made on the 1983 sample trees are shown in Table 14. Despite the fact that the sample trees had similar pre-treatment diameters, there was a considerable difference between the initial (1980) heights and the height increments were therefore adjusted by analysis of covariance. Analysis of variance and covariance (Table 15) gave no significant treatment effects but there was a suggestion that thinning particularly in combination with nitrogen application, had reduced height increment. Mean three year height increment was 16% of initial height in both 0 and N treatments but dropped to 15% and 14% in the T and TN treatments respectively.

4.3 Discussion

In both the experiments, application of nitrogen fertilizer has significantly increased basal area and volume increment and at Wauchope, the response to N was evident both in the presence and absence of thinning. In both experiments the response occurred in the year of application and this was repeated following application of a second nitrogen treatment to Benmore in 1982. The response was evident in each of the three years of the Wauchope experiment and at Benmore it persisted for four growing seasons, having completely disappeared by the fifth. Application of phosphate fertilizer appeared to increase basal area and volume growth at Benmore but the effect was not significant. At Wauchope, although there was no apparent response to P in the unthinned treatments, basal area and volume growth were slightly greater with P in the thinned treatments. In view of the size of the

Table 14. Height increment in the Wauchope experiment

Treatment	Initial height	3 year height increment (m)	Adjusted 3 year height increment
0	11.98	1.88	1.80
N	11.17	1.79	1.87
T	11.56	1.78	1.78
TN	11.57	1.57	1.57

Table 15. Results of the analysis of variance of the Wauchope height increments

Source	DF	SS	MS	VR
Blocks	2	0.2489	0.1244	0.557
Nitrogen	1	0.0197	0.0197	0.048
Thin	1	0.2272	0.2272	0.559
N x Thin	1	0.0704	0.0704	0.174
Covariates	1	0.0372	0.0372	0.091
Residual	5	2.0339	0.4068	1.82
Total	11	2.6373	0.3898	

effect in relation to the overall variability in basal area and volume growth however, there is little to suggest that this is a 'real effect', particularly since the response is contained entirely within the 1982 increments, the year in which the number of replicates was reduced to three. The response to thinning at Wauchope is an interesting one in that although 33% of the basal area was removed from the thinned plots, basal area and volume growth per hectare were still greater than in the unthinned treatments at all levels of fertilizer. In respect of fertilizer and fertilizer/thinning combinations there were no indications of interactions. At Benmore the effects of N and P appeared, when applied together, to be simply additive and this was also the case with the thinning/fertilizer effects at Wauchope.

In both experiments, individual tree diameter increments were strongly related to initial diameter with large trees having greater increment than small trees. This pattern was largely reflected in the treatment responses too, with medium and large sized trees benefiting most from fertilizer treatments. The effects of thinning appeared to be similar on all tree sizes but data for small sized trees in the thinned treatments are insufficient to allow conclusions to be drawn.

The data suggest that the ratio of volume to basal area for individual trees was increased by NP fertilizer application at Benmore and reduced by both thinning and nitrogen at Wauchope. Since the volume to basal area ratio varies with tree size anyway however, changes in the ratio do not necessarily imply a change in the relationship between volume and basal area. Analysis of variance of mean tree volume using basal area as a covariate has been used here as a means of accounting for the effect of tree size and this has generally reduced the apparent treatment effects, suggesting that at least part of the effects can be accounted for by differences in tree size.

Height increment was clearly increased by NP application at Benmore and appeared to benefit the medium sized trees most. The Wauchope results are less conclusive, with no significant treatment effects. However, there is a definite indication that thinning particularly in combination with nitrogen application, reduced height increment.

CHAPTER FIVE

EFFECTS OF THINNING AND FERTILIZER TREATMENTS ON LEAF AREA

5.1 Benmore

5.1.1 Methods Sampling was carried out at the end of the third growing season after treatment as described in section 3.7 and treatment of the sample whorls is described in section 3.4. Using the conversion factors derived from the 200 needle sample, the fresh weight of each needle age class was determined as a percentage of the total branch fresh weight. This percentage was then applied to the total whorl weight to establish the total fresh weight of each needle age class in the whole whorl; ie if one year needles accounted for 30% of the branch weight, it was assumed that 30% of the whorl weight was one year needles. Fresh weight was converted to projected needle area using the conversion factors from the 200 needle samples and in this way the total projected needle area of each whorl, by needle age class, was determined. Using the data from blocks I and III, where every whorl was sampled, total tree leaf area (TLA) was regressed on leaf area as a total of every second whorl (HLA). [ie. 1,3,5,7 etc.] A significant linear relationship was found with the equation:-

$$\text{TLA } (\text{m}^2) = 2.203 \text{ HLA } (\text{m}^2) - 0.71 \quad (r = 0.98)$$

This equation was used to determine total leaf area for the trees in blocks II and IV.

Table 16. The effect of fertiliser treatment on some crown dimensions in the Benmore experiment (Crown % is crown depth expressed as a percentage of the total tree height).

Dimension	Treatment 0	Treatment NP	sed	5% lsd
Number of live whorls	11.6	10.8	0.66	2.1
Crown depth (m)	4.67	4.88	0.14	0.43
Crown %	45.1	45.7	1.03	3.3

5.1.2 Crown depth and number of live whorls The bottom of the live crown was defined as the last whorl where at least one branch carried a significant amount of live foliage. Average crown depth, number of live whorls per tree and crown depth as a percentage of tree height are shown in Table 16. Crown depth varied from 3.65 m to 6.35 m in treatment 0 and from 2.26 to 6.53 m in treatment NP. Crown depth as a percentage of tree height varied from 37% to 55% in treatment 0 and from 25% to 58% in treatment NP and the number of live whorls varied from 10 to 14 in treatment 0 and from 6 to 15 in treatment NP. Mean crown depth was slightly (0.21 m) greater in treatment NP and number of live whorls slightly (0.8) less but the differences were not significant. Crown depth as a percentage of tree height was very similar in both treatments.

5.1.3 Mean leaf area per tree Mean total projected leaf areas per tree are shown in Table 17 where the sample trees have been divided into three size classes on the basis of diameter. Leaf area per tree ranged from 8.10 m^2 to 41.51 m^2 in treatment 0 and from 6.48 m^2 to 48.71 m^2 in treatment NP. On average, leaf area per tree was 4.05 m^2 (25%) greater in the NP treatment and this difference was reflected in trees of all size classes. An analysis of variance (Table 18) following log transformation and treating size as a split-plot factor, showed no significant difference at any size level.

5.1.4 Leaf area distribution Mean leaf area by whorl number and age of needle is shown in Table 19 and the results of an analysis of variance in Table 20. In the analysis of variance, two factors were allowed for, one being the fertilizer effect

Table 17. Mean projected leaf area per tree in the Benmore sample trees

Size Class (diameter)	Treatment	Number of trees in class	Mean leaf area (m^2)
Small	0	7	11.17
(8.9-11.5 cm)	NP	7	14.39
Medium	0	7	14.73
(11.6-13.4 cm)	NP	7	17.46
Large	0	6	24.18
(13.5-17.0 cm)	NP	6	30.73
All	0	20	16.32
	NP	20	20.37

Table 18. Results of the analysis of variance of the mean leaf area data

Source	DF	SS	MS	VR
Blocks	3	0.178	0.059	0.44
Treatments	1	0.405	0.405	3.02
Residual (a)	3	0.100	0.033	-
Size	2	3.93	1.964	14.66***
Treatment x size	2	0.01	0.004	0.03
Residual (b)	28	4.04	0.144	-
Total	39	8.663		

Table 19. Mean projected needle area by whorl and needle age class in the Benmore experiment

(Whorl 1 refers to the first whorl from the top of the tree).

cm^2

Whorl	Age	Treatment	
		0	NP
1	1	472	728
3	1	4628	9168
	2	2095	4354
	3	391	643
	Total	7114	14165
5	1	6418	10411
	2	4172	9155
	3	2980	5703
	4	1472	2213
	Total	15042	27482
7	1	5501	5939
	2	6093	8493
	3	7369	8158
	4	8593	7862
	Total	27556	30456
9	1	2452	1772
	2	2815	4425
	3	5084	4912
	4	8096	5521
	Total	19447	16630
11	1	1372	250
	2	2845	1063
	3	3148	1760
	4	5151	2897
	Total	12516	5970
13	1	101	27
	2	276	115
	3	370	196
	4	954	426
	Total	1701	764

Table 20. Results of the analysis of variance for mean total projected needle area by whorl number and age of needle (log transformation)

Source	DF	SS	MS	VR
Blocks	3	0.9673	0.3224	1.370
Fertiliser	1	0.2846	0.2846	0.176
Residual (a)	3	4.8607	1.6202	6.884
Position	19	145.7673	7.6720	32.596***
Position x Fertiliser	19	8.9482	0.4710	2.001*
Residual (b)	114	26.8314	0.2354	-
Grand Total	159	187.659	-	-

(Table 21 appears on page 67.)

Table 22. Results of the analysis of variance of mean sample branch areas in the Benmore experiment

Source	DF	SS	MS	VR
Blocks	3	1.0111	0.3370	1.683
Fertiliser	1	0.0423	0.0423	0.020
Residual (a)	3	6.4303	2.1434	10.701
Position	19	129.2642	6.8034	33.965***
Position x Fertiliser	19	6.9258	0.3645	1.820*
Residual (b)	114	22.8351	0.2003	-
Grand Total	159	166.5088	-	-

Footnote

The analysis of variance used here assumes that the design of the experiment lends itself to a split-plot type analysis. As pointed out by Dr Farrel, the use of this type of analysis assumes that the variance - covariance matrix is homogenous i.e. that the degree of dependence between all the observations is constant. It is acknowledged that this is unlikely to be the case with the data used for this analysis and that a more detailed analysis procedure of the type proposed by Gill and Hafs (1971) would have been more appropriate. The result of the use of such procedures would be that the tests of significance would become more conservative. While this would not affect the fact that 'position' emerged as a significant factor, it is likely that the 'position' X fertiliser interactions in tables 20, 22 and 25, which emerged as significant in the split plot type of analysis, would not be significant.

and the other being a measure of the effect of whorl number and age of needle (position factor). Although this meant the use of a pooled standard error for comparing treatments at any whorl/age class, it did allow more degrees of freedom than a separate analysis of variance for each whorl/age class. Following the initial analysis, a plot of fitted values against residuals demonstrated a pattern of increasing scatter with increasing fitted values and accordingly the final analysis of variance was based on a log transformation. The pattern of leaf area distribution was examined with respect to both whorl number (fig 3) and whorl height. The picture was essentially the same in both cases and subsequent analyses and discussions are based on whorl number only.

Leaf area was approximately normally distributed with respect to whorl number in both treatments with maximum leaf area occurring in the mid crown around whorl seven. Although the effect of fertilizer treatment was not significant overall, there were very highly significant (P = 0.001) differences between positions and a significant (P = 0.05) position x fertilizer interaction. Fertilizer treatment appeared to result in an increase in leaf area in the upper part of the crown and a reduction in the lower crown. At whorls one, three, five and seven treatment NP resulted in an increase of 54%, 99%, 83% and 11% respectively while at whorls nine, eleven and thirteen, leaf area was reduced by 14%, 52% and 55% respectively. Examination of the leaf area distribution with respect to age of needle (figs 4 and 5) indicated that the increased leaf area in the upper crown was largely attributable to needles in the one year and two year age classes, ie needles

Fig 3. leaf area distribution by whorl

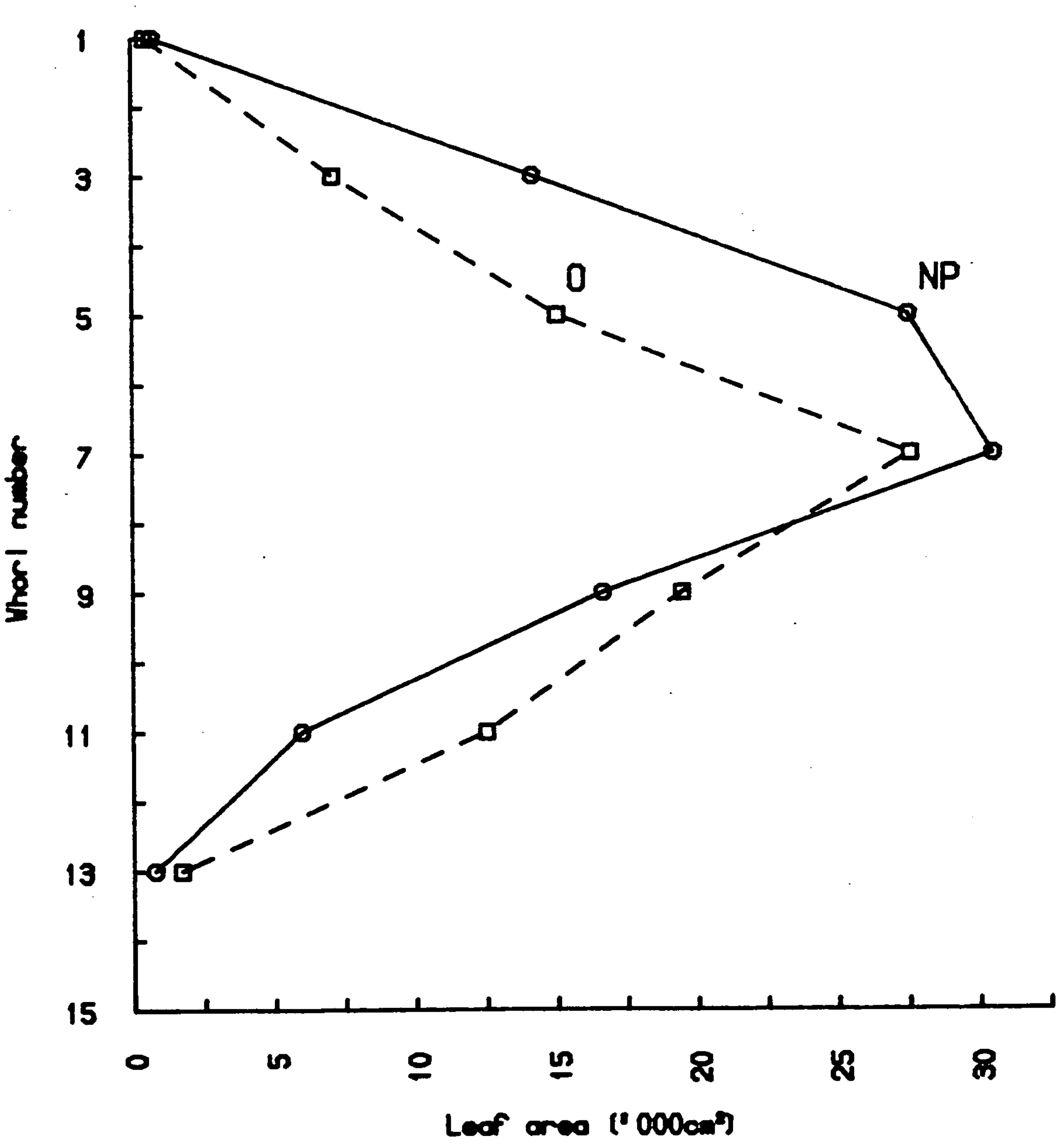


Fig.4 distribution of 1 and 2 year needles

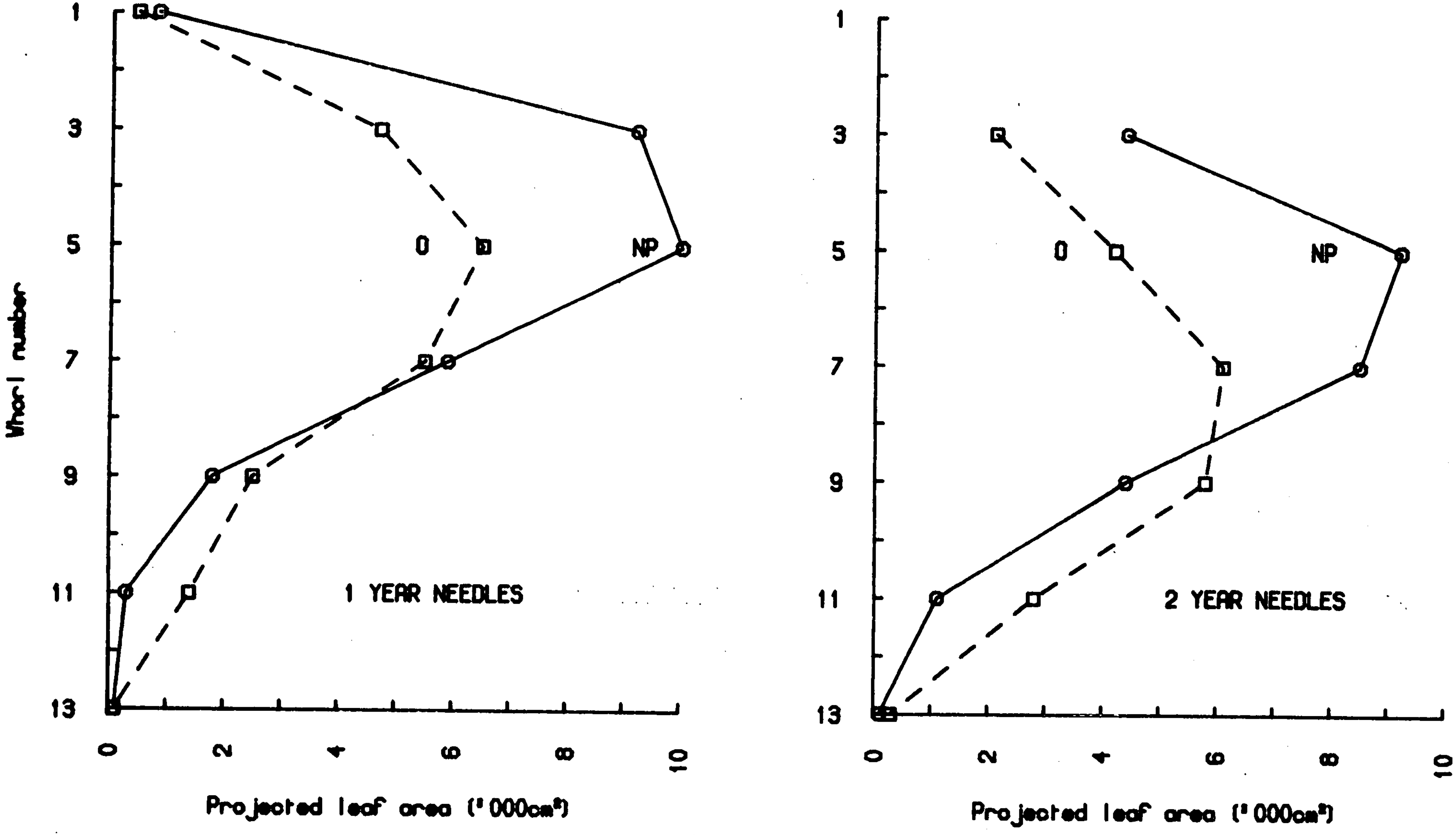
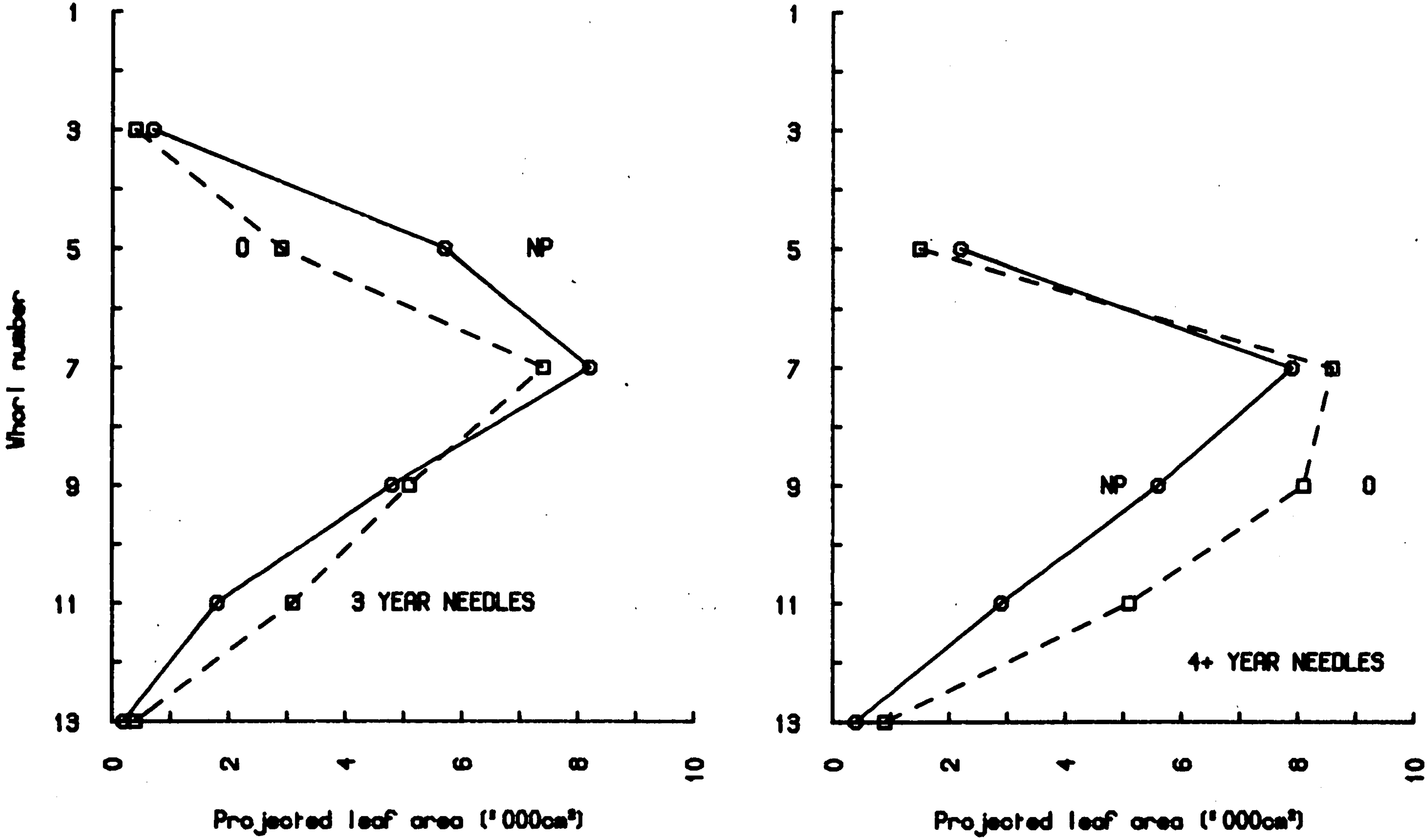


Fig.5 Distribution of 3 and 4+ year needles



formed in 1979 and 1978 respectively. Area of three year needles, ie needles formed in 1977 (the year of fertilizer application), showed a small increase in the upper crown but needles in the four years and older age class were unaffected. The reduction in leaf area in the lower crown of fertilized trees was reflected in needles of all ages but appeared to be particularly large in the case of 4 years+ needles.

5.1.5 Analysis of the components of leaf area To determine which components of the leaf area had been affected, the data from the sample branches were analysed by whorl number and age of needle to examine the effect of fertilizer treatment on leaf area, dry weight of needle, number of needles, average needle weight, average needle area and specific needle area. Due to the small number of data from whorls 13 and below, the analyses were restricted to whorls 1, 3, 5, 7, 9 and 11. Each data set was subjected to the same type of analysis of variance used for the total whorl leaf areas and in the case of leaf area, needle dry weight and number of needles, a log transformation was used.

a. Leaf area Mean leaf area per sample branch is shown in Table 21 and the results of the analysis of variance in Table 22. There was no significant effect overall but there was a significant (P = 0.001) position effect and a significant (P = 0.05) position x fertilizer interaction. Mean leaf area was consistently higher in treatment NP at whorls 1, 3, 5 and 7 but was lower than treatment 0 at whorls 9 and 11. The pattern of leaf area distribution was very similar to the pattern displayed by the total whorl leaf areas with an increase in leaf area in the 1 and 2 year needles in the upper crown of fertilized trees and a reduction in the lower crown, largely at the expense of the 4 years+ needles.

b. <u>Needle dry weight and number of needles</u> Mean total needle dry weight per sample branch is shown in Table 23, mean needle number in Table 24 and the results of the analyses of variance in Table 25. As with the whorl and sample branch leaf areas, there was a significant position effect ($P = 0.001$) and a significant position x fertilizer interaction ($P = 0.05$) but no significant overall fertilizer effect. Fertilized trees had, on average, more needles and a greater total needle dry weight than control trees and the pattern of distribution was similar to the whorl and branch leaf area distribution. Both needle weight and needle number were greater in treatment NP at whorls 1, 3, 5 and 7 and smaller than treatment 0 at whorls 9 and 11. Again the increase was reflected largely in the 1 and 2 year old needles at all needle ages, was largely at the expense of the 4 years+ needles.

c. <u>Average needle area</u> Average needle area is shown in Table 26 and the results of the analysis of variance in Table 28. The pattern of variation in average needle area with respect to crown position is portrayed in fig 6. Average needle area showed a consistent decline from the top to the bottom of the crown in both treatments and this pattern was present at all needle ages. With the exception of whorls 3 and 5 in treatment 0, where 2 year needles had smaller average needle weight than 1 year needles, there was also a consistent pattern of increasing average needle area with increasing age of needle and this was reflected at all whorls. Overall weighted mean needle area of treatment NP was 1.53 mm^2 (9%) greater than treatment 0 and this trend was present at all whorls in the 2, 3 and 4+ needle age classes. In the 1 year needles however, treatment 0 had higher average needle area at whorls 3, 7, 9 and 11. In the analysis of variance only position emerged as a significant factor there being no significant fertilizer effect and no significant position x fertilizer interaction.

d. Average needle weight Average needle weight is shown in Table 27, the results of the analysis of variance in Table 28 and a pictorial representation in fig 7. As with average needle area, average needle weight decreased from whorl 1 to whorl 11 at all needle ages and at all whorls there was a consistent pattern of increasing needle weight with increasing age of needle. Overall weighted mean needle weight was 0.35 mg (13%) higher in treatment NP but the analysis of variance showed no significant fertilizer effect or position x fertilizer interaction. Treatment differences were particularly apparent in the 2, 3 and 4+ needles where average weight was consistently higher in the fertilized trees but there was little apparent difference between fertilized and unfertilized trees in respect of 1 year needles.

e. Specific needle area Specific needle area, expressed as projected area (cm^2) per g of dry weight was calculated from the 200 needle sub-samples and mean specific needle areas by treatment, whorl number and age of needle are shown in Table 29 and the results of an analysis of variance in Table 30. At all needle ages specific needle area showed a consistent increase from whorl 1 to whorl 11 in both treatments and a consistent decrease with increasing age of needle at all whorls (fig 8). Although the effect of crown position was again significant ($P = 0.001$) there was no significant fertilizer effect and no position x fertilizer interaction. Specific needle area of 1 year needles appeared to be lower in treatment NP at whorls 1 and 3 and higher than control at whorls 9 and 11 and there was an apparent decrease in specific needle area in the 4+ needles from fertilized trees but otherwise there were no apparent treatment differences.

5.2 Wauchope

5.2.1 Methods In the 1983 sampling carried out in the Wauchope experiment, no attempt was made to establish total whorl or total tree leaf areas but treatment comparisons were made purely on the basis of one representative sample branch from each of 3 whorls (1, 4 and 7). The parameters measured on each sample branch were leaf area, needle dry weight, number of needles, average needle area, average needle weight and specific needle area, and each was measured at four needle ages. As with the Benmore results, each data set was subjected to an analysis of variance to determine treatment and position effects and log transformation of the data were included where necessary.

Table 21. Mean projected needle area per sample branch by treatment, whorl number and age class in the Benmore experiment

cm^2

Whorl	Age	Treatment	
		0	NP
1	1	472	728
3	1	786	1065
	2	350	490
	3	64	81
	Total	1200	1636
5	1	1313	1848
	2	869	1607
	3	645	962
	4	299	390
	Total	3126	4807
7	1	1009	1303
	2	1047	1845
	3	1253	1779
	4	1516	1736
	Total	4825	6663
9	1	404	290
	2	677	848
	3	1007	1019
	4	1594	1201
	Total	3682	3358
11	1	116	77
	2	319	262
	3	434	555
	4	983	618
	Total	1852	1512

Table 23. Mean total needle dry weight per sample branch in the Benmore experiment

g

Whorl	Age	Treatment	
		0	NP
1	1	9.50	14.45
3	1	13.83	20.99
	2	7.11	10.24
	3	1.66	1.85
	Total	22.60	33.08
5	1	21.60	29.50
	2	15.95	29.23
	3	12.15	18.85
	4	6.29	8.36
	Total	55.99	85.94
7	1	15.54	20.07
	2	18.14	30.09
	3	22.82	31.03
	4	29.22	33.46
	Total	85.72	114.65
9	1	6.86	4.55
	2	11.68	12.45
	3	16.64	15.05
	4	29.08	19.85
	Total	64.26	51.90
11	1	2.08	1.16
	2	5.23	4.15
	3	6.93	6.24
	4	17.20	10.42
	Total	31.44	21.97
	Grand Total	269.5	321.9

Table 24. Mean number of needles per sample branch in the Benmore experiment

g

Whorl	Age	Treatment	
		0	NP
1	1	1814	2679
3	1	3362	5068
	2	1676	2166
	3	274	330
	Total	5312	7564
5	1	7111	9480
	2	4866	8038
	3	3161	4537
	4	1422	1693
	Total	16560	23748
7	1	6843	9060
	2	6932	11152
	3	7596	9858
	4	7731	8304
	Total	29102	38374
9	1	3387	2894
	2	5572	6385
	3	7102	6295
	4	9557	6250
	Total	25618	21825
11	1	1293	911
	2	3342	2472
	3	3770	4028
	4	6942	4050
	Total	15347	11461
	Total	93753	105651

Table 25. Results of the analyses of variance for mean total needle dry weight and mean number of needles in the Benmore experiment

Source	DF	Average total needle dry weight			Average number of needles		
		SS	MS	VR	SS	MS	VR
Blocks	3	0.7938	0.2646	1.25	0.0447	0.0149	0.085
Fertiliser	1	0.0497	0.0497	0.019	0.0272	0.0272	0.030
Residual (a)	3	7.9409	2.6470	12.507	2.7482	0.9161	5.213
Position	19	135.1742	7.1144	33.616***	120.2826	6.3307	36.028***
Position x fertiliser	19	7.5984	0.3999	1.89*	6.1241	0.3223	1.834*
Residual (b)	114	24.1269	0.2116		20.0313	0.1757	
Grand total	159	166.8994			149.258		

Table 26. Average needle area by treatment, whorl and age class in the Benmore experiment

mm^2

Whorl	Age	Treatment	
		0	NP
1	1	25.30	26.46
3	1	23.39	21.01
	2	20.87	22.64
	3	23.36	24.55
	Mean	22.59	21.63
5	1	18.46	19.49
	2	17.86	19.99
	3	20.39	21.20
	4	21.05	23.02
	Mean	18.87	20.24
7	1	14.75	14.38
	2	15.10	16.54
	3	16.49	18.05
	4	19.61	20.90
	Mean	16.58	17.36
9	1	11.92	10.01
	2	12.15	13.28
	3	14.18	16.18
	4	16.68	19.21
	Mean	14.37	15.38
11	1	8.98	8.42
	2	9.56	10.58
	3	11.52	13.77
	4	14.16	15.27
	Mean	12.07	13.19
overall weighted mean		16.15	17.68

Fig.6 Average needle area in relation to crown position

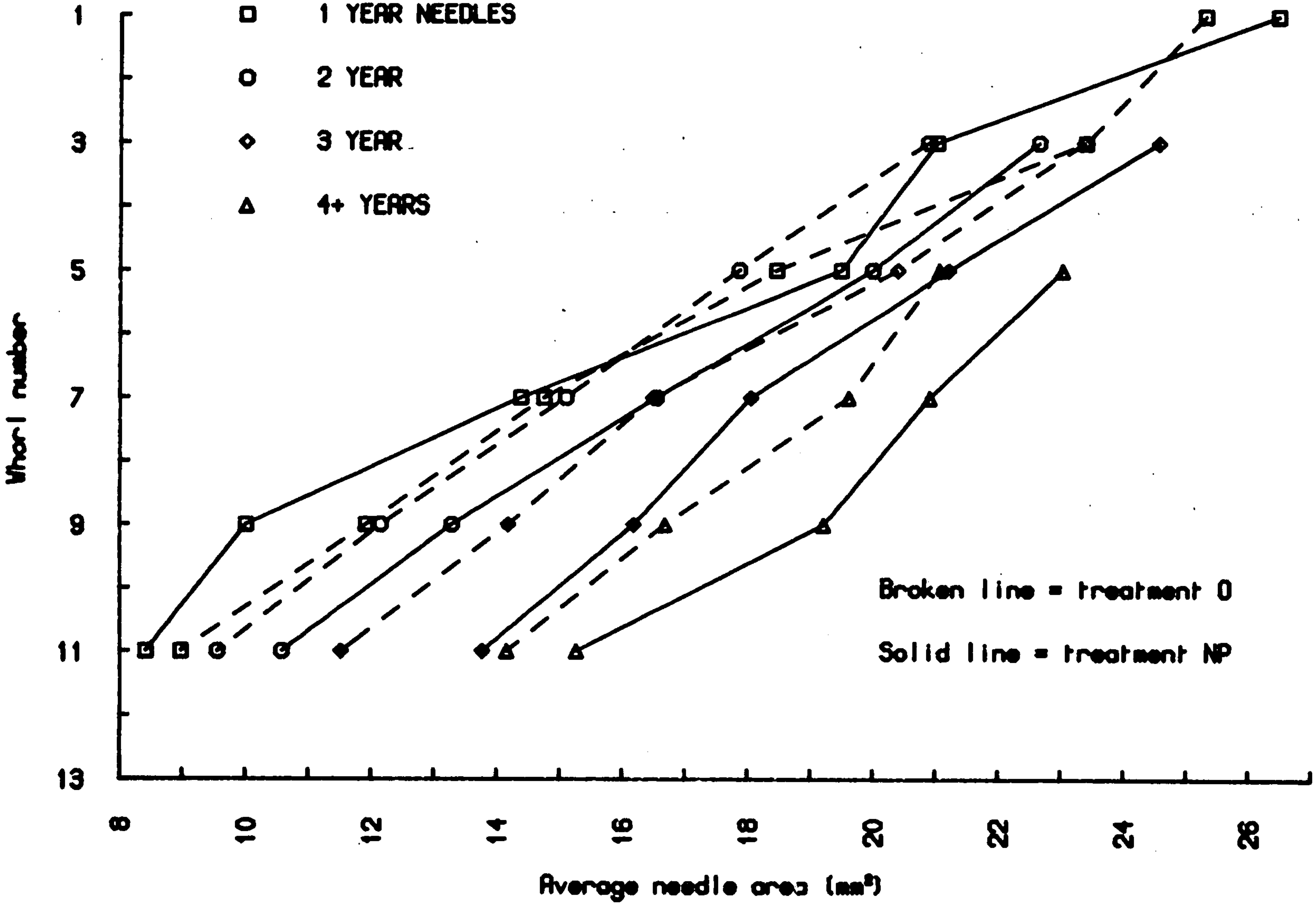


Table 27. Average needle weight (mg) by treatment, whorl number and age class in the Benmore experiment

Whorl	Age	Treatment	
		0	NP
1	1	5.06	5.52
3	1	4.09	4.06
	2	4.17	4.71
	3	5.91	6.20
	Mean	4.21	4.34
5	1	3.04	3.20
	2	3.33	3.73
	3	4.12	4.23
	4	4.51	4.94
	Mean	3.46	3.70
7	1	2.13	2.14
	2	2.55	2.81
	3	2.91	3.21
	4	3.75	4.18
	Mean	2.86	3.05
9	1	1.64	1.41
	2	1.81	1.93
	3	2.23	2.57
	4	2.91	3.57
	Mean	2.31	2.52
11	1	1.14	1.02
	2	1.32	1.46
	3	1.70	1.74
	4	2.36	2.52
	Mean	1.87	1.90
Overall weighted mean		2.77	3.12

Table 28. Results of the analyses of variance for average needle weight and average needle area in the Benmore experiment

Source		Average total needle dry weight			Average number of needles		
	DF	SS	MS	VR	SS	MS	VR
Blocks	3	0.050050	0.01668	19.823	244.5767	81.525	37.375
Fertiliser	1	0.020090	0.02009	0.749	36.6592	36.659	0.490
Residual (a)	3	0.08049	2.6470	31.882	224.4114	74.804	34.293
Position	19	2.87175	0.15115	179.607***	3526.5516	185.609	85.091**
Position x fertiliser	19	0.020164	0.00106	1.261	65.3331	3.439	1.576
Residual (b)	114	0.095939	0.00084	-	248.6683	2.181	
Grand total	159	3.13846			4346.195		

Fig.7 Average needle weight in relation to crown position

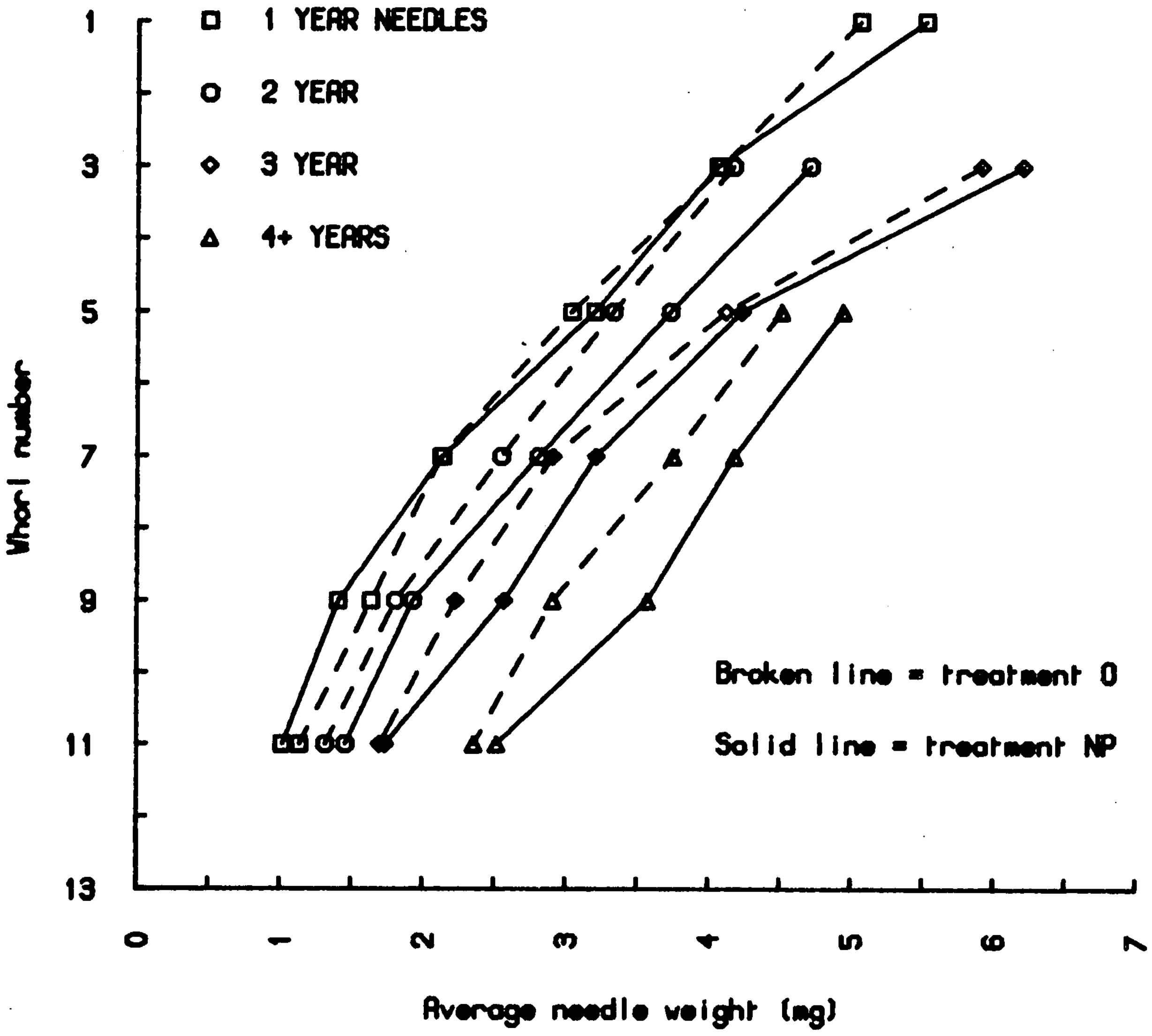


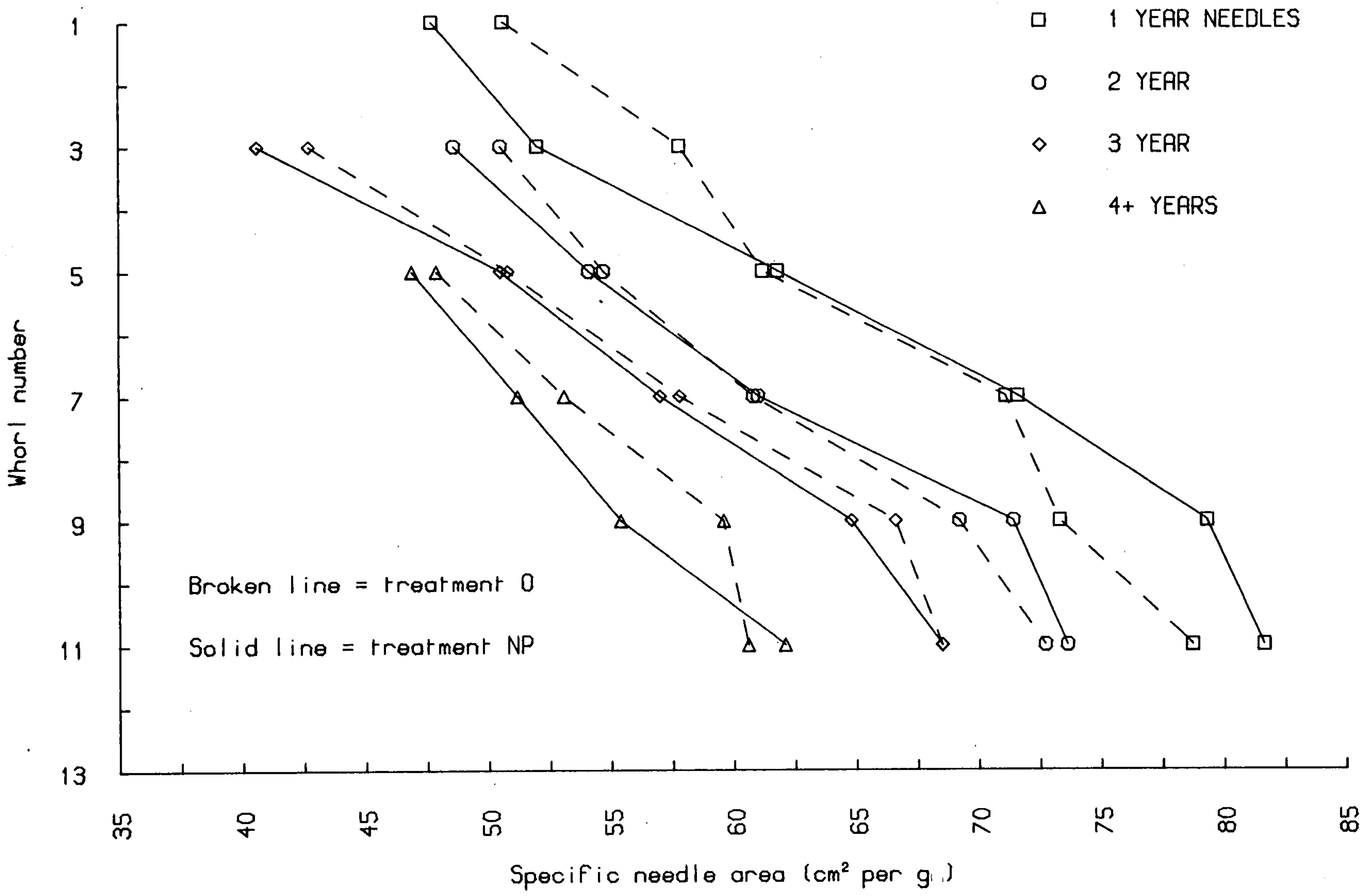
Table 29. Mean specific needle area per sample branch by whorl number and age of needle in the Benmore experiment

Whorl	Age	Treatment	
		0	NP
1	1	50.6	47.7
3	1	57.8	52.0
	2	50.5	48.6
	3	42.7	40.6
	Mean	54.72	50.53
5	1	61.2	61.8
	2	54.7	54.1
	3	50.8	50.5
	4	47.9	46.9
	Mean	56.16	55.97
7	1	71.1	71.6
	2	60.8	61.0
	3	57.8	57.0
	4	53.1	51.2
	Mean	60.39	60.35
9	1	73.3	79.3
	2	69.2	71.4
	3	66.6	64.8
	4	59.6	55.4
	Mean	65.44	65.96
11	1	78.72	81.64
	2	72.73	73.64
	3	68.54	68.51
	4	60.58	62.06
	Mean	66.71	68.38
overall weighted mean		61.55	60.37

Table 30. Results of the analysis of variance for mean specific needle areas in the Benmore experiment

Source	DF	SS	MS	VR
Blocks	3	692.22	230.74	6.356
Fertiliser	1	0.28	0.28	0.002
Residual (a)	3	384.44	128.15	3.53
Position	19	18606.35	979.28	26.975***
Position x Fertiliser	19	357.8458	18.83	0.519
Residual (b)	114	4138.5151	36.30	-
Grand Total	159	24179.64	-	-

Fig.8 Specific needle area in relation to crown position



5.2.2 Leaf area Projected leaf areas per sample branch are shown in Table 31 by treatment, whorl number and needle age class and the results of the analysis of variance, based on a log transformation, are shown in Table 32. As expected there was a significant (P = 0.001) position effect with leaf area increasing from whorl 1 (W1) to whorl 4 (W4) and from W4 to whorl 7 (W7). In addition there was a significant (P = 0.05) overall fertilizer effect, a significant (P = 0.05) overall thinning effect and a significant (P = 0.01) position x thinning interaction. Application of nitrogen resulted in a reduction in projected leaf area at all whorls and although there was no significant position x fertilizer interaction, the reduction in leaf area at whorls 1 (-13%) and 7 (-12%) appeared to be greater than at W4 (-3%). Two year needles in W4 and W7 of the fertilized trees showed a slight increase in leaf area over unfertilized trees but all other ages reflected the pattern of reduced leaf area in response to nitrogen application, particularly the 3 and 4+ needles in W4 and the 1 and 4+ needles in W7.

There was no significant thinning x fertilizer interaction and none was apparent at whorls 1 and 7 but at W4 nitrogen application appeared to result in an increase in leaf area in the absence of thinning and a reduction in leaf area when accompanied by thinning. The net effect of thinning (meaned over T and TN) was an overall increase in leaf area, an increase which was due almost entirely to the effects on W7 foliage. At W1 there was an apparent reduction in leaf area in the thinned treatments when compared to the unthinned (mean of O and N) and there was

Table 31. Projected leaf area of the Wauchope sample branches

cm^2

Whorl	Age of needle	Treatment 0	N	T	TN
1	1	146	131	129	109
4	1	2424	2657	2629	2253
	2	1480	1676	1706	1564
	3	516	432	523	423
	4	134	102	124	99
	Total	4554	4867	4982	4348
7	1	1477	817	1861	2050
	2	1480	1223	2213	2655
	3	1156	852	1324	1398
	4	2529	2000	3464	2565
	Total	6642	4892	8862	8668

Table 32. Results of the analysis of variance of the sample branch leaf areas (log transformation)

Source	DF	SS	MS	VR
Blocks	2	0.00843	0.00421	0.067
Fertiliser	1	0.40825	0.40825	6.551*
Thin	1	0.80797	0.80797	12.965**
Fertiliser x thin	1	0.11248	0.11248	1.805
Residual (a)	6	0.37392	0.06232	0.994
Position	8	139.8198	17.4775	278.690***
Position x fertiliser	8	0.28476	0.03560	0.568
Position x thin	8	1.82105	0.22763	3.630**
Position x fertiliser x thin	8	0.70061	0.08758	1.395
Residual (b)	64	4.01362	0.06271	
Total	107	148.35085		

no apparent difference at W4 but at W7 the area of 1 year needles was increased by 70% (P = 0.001), 2 year needles by 80% (P = 0.01), 3 year needles by 36% (P = 0.05) and 4 years+ needles by 33% (P = 0.05). Total leaf area of thinned treatments was 20 cm (17%) less at W1, 46 cm^2 (1%) less at W4 but 2998 cm^2 (52%) greater at W7. The reduction at W1 was apparent in both the presence and absence of N as was the increase at W7 but at W4, thinning appeared to increase leaf area in the absence of N and to reduce it when accompanied by N.

5.2.2 Needle dry weight Average total needle dry weight per sample branch is shown in Table 33 and the results of the analysis of variance in Table 34. Total dry weight of needles was significantly (P = 0.001) greater at W7 than at W4 which had significantly (P = 0.001) greater dry weight than W1 and this pattern was reflected in all treatments except treatment N where needle weight at W7 was slightly (11%) less than at W4. Application of N significantly (P = 0.05) reduced needle weight while thinning resulted in a significant (P = 0.05) increase and there was a significant (P = 0.001) position x thinning interaction. The reduction in total needle weight due to N application was evident at all whorls and needle ages except 2 year needles in W4 where there was a slight (3%) increase in the fertilized treatments. Although there was no significant position x fertilizer interaction the reduction appeared to be proportionately greater at whorls, (-13%) and 7(-11%) than at W4 (-4%). At W1 total needle weight was reduced by N application both in the presence and absence of thinning while at W4 the reduction occurred only in the thinned plots and at W1 occurred only in the unthinned plots. Thinning increased total needle weight at W7 but there was no significant effect at W1 where thinning appeared to reduce the needle weight or at W4 where there was little apparent difference. At W7 total needle dry weight of 1 year needles was increased by 77% (P = 0.001), 2 year needles by 85% (P = 0.001), 3 year needles by 36% (P = 0.05) and 4 years+ needles by 31% (ns). Total needle weight at W7 was 76.5 g (52%) greater in the thinned treatments. Thinning resulted in a slight reduction in total needle weight both in the presence and absence of N at W1 and an increase at both levels of N at W7 but there was an apparent, though not significant, interaction at W4. In the presence of N, thinning appeared to reduce total needle weight but increased it in the unfertilized plots.

5.2.3 Number of needles Average number of needles per sample branch is shown in Table 35 by treatment, whorl number and age of needle and the results of the analysis of variance in Table 36. As with needle area and dry weight there was a significant position effect with more needles held at W7 than at W4 and more at W4 than at W1, a pattern repeated in all treatments. Fertilizer application had no significant or apparent effect on needle number which was slightly higher in fertilized trees at whorls 1 (+2%) and 4 (+6%) but slightly (-5%) lower at W7. This pattern was not consistent at both levels of thinning and although there was no significant interaction, it appeared that (at W1 + W4) nitrogen application had increased needle number in the unthinned plots but decreased it in the thinned plots while at W7 needle number was decreased by N application in the absence of thinning but increased when combined with thinning. The overall effect of thinning was significant (P = 0.01) and there was a significant (P = 0.001) position x thinning interaction. At W1 and W4 thinning resulted in a small and non significant reduction in needle number but at W7 the number of needles was 14064 (50%) higher in thinned treatments and this difference was apparent at all needle ages. One year needles were increased by 61% (P = 0.001), 2 year needles by 71% (P = 0.001), 3 year needles by 34 % (P = 0.05) and 4 years+ needles by 32% (P = 0.05). Overall there was a tendency for thinning to lead to lower needle numbers in W1 in both the presence and absence of nitrogen while at W4 thinning tended to increase needle numbers in the absence of nitrogen while decreasing number of needles when combined with nitrogen. At W7, the thinning effect was similar at both levels of nitrogen.

5.2.4 Average needle area Average needle areas are shown in Table 37 and the results of the analysis of variance in Table 38. The only significant effect to emerge was position. Average needle area decreased from W1 to W4 and from W4 to W7, a pattern which was present in all treatments. At W7 there was a consistent increase in average needle area with increasing age of needle in all treatments but this pattern was less obvious at W4. Application of nitrogen appeared to have resulted in a reduction in average needle area at all whorls and at both levels of thinning, an effect which is also present at almost every needle age. Overall, the effect of thinning was to slightly increase average needle area, particularly in the presence of nitrogen but there was no persistent trend.

5.2.5 Average needle weight Average needle weights are shown in Table 39 and the results of the analysis of variance in Table 40. Again there were significant position differences with a consistent pattern of decreasing average needle weight with increasing whorl number which was evident in all treatments. There was also a consistent pattern, at each whorl in all treatments, of increasing average needle weight with increasing age of needle. The overall effect of nitrogen was also significant (P = 0.05) and resulted in a decrease in average needle weight in fertilized trees, a pattern which was particularly evident in the unthinned treatment where all needle ages in all whorls of the fertilized trees had smaller average needle weight than from unfertilized trees. In the presence of thinning, this pattern was present at W1 and W4 but at W7 there was no consistent effect. Thinning had no significant effect on average needle weight, nor was there any position x thinning interaction. Generally thinning appeared to result in smaller average needle weight in the absence of nitrogen and larger average needle weight in the presence of nitrogen but the differences were not large and overall average needle weight in thinned treatments (6.66 mg) was very similar to that of unthinned treatments (6.69 mg).

5.2.6 <u>Specific needle area</u> Average specific needle areas are shown in Table 41 and the results of the analysis of variance in Table 42. The only two significant effects were position and an interaction between thinning and fertilizer application. Specific needle area increased with increasing whorl number in all treatments and at W4 and W7 there was a consistent pattern of decreasing specific needle area with increasing age of needle in all treatments. Nitrogen application appeared to increase

Table 33. Total needle dry weight of the Wauchope sample branches

g

Whorl	Age of needle	Treatment			
		0	N	T	TN
1	1	4.50	3.98	4.12	3.50
4	1	69.06	70.67	69.90	60.64
	2	42.52	49.35	47.22	43.34
	3	14.98	12.94	15.44	12.67
	4	4.55	3.25	3.99	3.29
	Total	131.11	136.21	136.55	119.94
7	1	31.82	16.91	37.68	48.42
	2	37.79	29.02	55.09	68.51
	3	30.60	21.22	33.25	37.12
	4	74.59	53.73	92.67	75.94
	Total	174.8	120.88	218.69	229.99

Table 34. Results of the analysis of variance of the sample branch needle dry weight (log transformation)

Source	DF	SS	MS	VR
Blocks	2	0.01410	0.00705	0.111
Fertiliser	1	0.48861	0.48861	7.402*
Thin	1	0.83635	0.83635	12.671*
Fertiliser x thin	1	0.22131	0.22131	3.353
Residual (a)	6	0.39605	0.06601	1.038
Position	8	122.1752	15.27190	240.143***
Position x fertiliser	8	0.25128	0.03141	0.494
Position x thin	8	2.03385	0.25423	3.998***
Position x fertiliser x thin	8	0.80099	0.10012	1.574
Residual (b)	64	4.07009	0.06360	
Total	107	131.28785		

Table 35. Number of needles on the Wauchope sample branches

Whorl	Age of needle	Treatment			
		0	N	T	TN
1	1	484	581	457	441
4	1	10079	11582	10713	9909
	2	5230	7145	6162	6156
	3	1850	1734	1865	1708
	4	462	405	406	424
	Total	17621	20866	19146	18197
7	1	8850	5298	10734	12054
	2	7333	7224	11341	13550
	3	5325	4426	5792	7289
	4	10079	8000	13137	10766
	Total	31587	24948	41004	43659

Table 36. Results of the analysis of variance of needle number (log transformation)

Source	DF	SS	MS	VR
Blocks	2	0.00073	0.00037	0.008
Fertiliser	1	0.01663	0.01663	0.381
Thin	1	0.67552	0.67552	15.51***
Fertiliser X thin	1	0.0527	0.0527	1.21
Residual (a)	6	0.20567	0.03428	0.772
Position	8	164.0864	20.51079	470.92***
Position x fertiliser	8	0.3659	0.04574	1.05
Position x thin	8	1.48920	0.18615	4.27***
Position x fertiliser x thin	8	0.53783	0.06723	1.54
Residual (b)	64	2.84316	0.04442	
Total	107	170.27373		

Table 37. Average needle areas on the Wauchope sample branches

mm^2

Whorl	Age of needle	Treatment 0	N	T	TN
1	1	29.86	25.21	29.15	25.26
4	1	25.31	23.15	24.80	23.52
	2	27.79	24.25	27.64	25.57
	3	26.39	25.26	27.59	25.18
	4	24.37	25.31	30.42	24.79
	Weighted mean	26.13	23.74	26.10	24.40
7	1	15.55	14.82	14.90	16.43
	2	19.71	16.92	20.27	19.28
	3	21.55	19.00	22.29	18.97
	4	25.53	24.50	25.66	24.83
	Weighted mean	20.71	19.27	20.88	19.81

Table 38. Results of the analysis of variance of average needle areas

Source	DF	SS	MS	VR
Blocks	2	10.922	5.461	0.938
Fertiliser	1	111.369	111.369	4.898
Thin	1	12.095	12.095	0.532
FertiliserXthin	1	0.127	0.127	0.006
Residual (a)	6	136.434	22.739	3.907
Position	8	1612.653	201.502	34.637***
Position x fertiliser	8	41.547	5.193	0.892
Position x thin	8	20.728	2.591	0.445
Position x fertiliser x thin	8	42.970	5.371	0.923
Residual (b)	64	372.470	5.820	-
Total	107	2361.314	21.775	-

Table 39. Average needle weight for the Wauchope sample branches

mg

Whorl	Age of needle	Treatment			
		0	N	T	TN
1	1	9.32	7.66	9.01	8.18
4	1	6.91	6.13	6.57	6.28
	2	8.23	7.05	7.75	7.20
	3	8.75	7.53	8.29	7.44
	4	9.95	8.16	9.88	8.18
	Weighted mean	7.51	6.60	7.19	6.74
7	1	3.59	2.97	3.37	3.89
	2	5.10	4.00	4.67	4.97
	3	5.69	4.91	5.57	5.02
	4	7.63	6.88	7.03	7.10
	Weighted mean	5.58	4.87	5.21	5.21

Table 40. Results of the analysis of variance of average needle weight

Source	DF	SS	MS	VR
Blocks	2	0.01584	0.01584	1.326
Fertiliser	1	0.14466	0.14466	10.111*
Thin	1	0.00024	0.00024	0.017
FertiliserXthin	1	0.02427	0.02427	1.696
Residual (a)	6	0.08584	0.01431	2.394
Position	8	3.33122	0.41640	69.674***
Position x fertiliser	8	0.06240	0.00780	1.305
Position x thin	8	0.00803	0.0010	0.168
Position x fertiliser x thin	8	0.01610	0.00201	0.337
Residual (b)	64	0.38249	0.00598	-
Total	107	4.07109		

Table 41. Specific needle areas in the Wauchope sample branch data

cm^2/g

Whorl	Age of needle	Treatment 0	 N	 T	 TN
1	1	37.96	33.00	32.48	30.92
4	1	36.75	37.75	37.75	37.56
	2	33.89	34.56	35.82	35.61
	3	32.49	33.73	33.79	33.89
	4	25.49	31.27	21.01	30.51
	Weighted mean	35.16	36.20	36.60	36.39
7	1	43.83	52.69	44.62	43.19
	2	39.17	43.49	46.02	39.80
	3	38.26	39.24	41.60	38.07
	4	33.48	35.62	36.39	35.00
	Weighted mean	38.51	42.17	41.94	39.26

Table 42. Results of the analysis of variance of specific needle areas

Source	DF	SS	MS	VR
Blocks	2	2.397	1.199	0.164
Fertiliser	1	10.266	10.266	1.51
Thin	1	4.514	4.514	0.66
FertiliserXthin	1	139.640	139.640	20.48**
Residual (a)	6	9.179	1.530	0.209
Position	8	2551.492	318.936	46.78***
Position x fertiliser	8	62.280	7.785	1.14
Position x thin	8	94.867	11.858	1.74
Position x thin x fertiliser	8	84.889	10.611	1.56
Residual (b)	64	468.023	7.313	
Total	170	3427.547		

specific needle area in the unthinned plots and to decrease it in the presence of thinning, a pattern evident at almost all whorls and at most needle ages and this interaction was significant (P = 0.01). Thinning, alone, had no significant effect but at most crown positions there was a tendency for trees in thinned treatments to have higher specific needle area than in the unthinned treatments.

5.3 Discussion

Although there were no significant treatment effects in the Benmore experiment there is clear evidence that application of fertilizer has resulted in an increase in the leaf area of treated trees. This increase has occurred entirely in the upper crown (Whorls 1 to 7) and is due to an increase in the area of needles formed following fertilizer application. The area of needles formed prior to the application (4+ needles) has not been affected, there was a small increase in the area of needles formed in the year of application (3 year needles) and the greatest increase occurred in the needles formed in the succeeding 2 years (1 and 2 year needles). This increase in area in the upper crown was accompanied by a small reduction in the leaf area of fertilized trees relative to control trees in the lower crown where production of 1, 2 and 3 year needles has been reduced or else retention period has been shortened and where retention of 4+ needles has been reduced. Distribution, by whorl, of leaf area and the various factors contributing to it is shown in fig 9 where the treatment NP values have been expressed as a percentage of the control values. The picture clearly shows that changes in leaf area in the treated trees are closely associated with changes in total needle dry weight and needle number. Average needle area and average needle weight are generally consistently higher in fertilized trees but their contribution, along with that of specific needle area, to the observed leaf area differences is relatively small.

Although a number of significant treatment effects have emerged in the analysis of the Wauchope data, the pattern of treatment effects is less easily discernible than in the Benmore experiment. Distribution by whorl, of leaf area and the factors contributing to it are shown in fig 10a and 10b where the treatment N, T and TN values are expressed as a percentage of the control values. Generally, leaf area appeared to be smaller in all thinned and fertilized plots at W1, appeared to be relatively little affected at W4 and at W7 leaf area was smaller in the N treatment but substantially increased in the T and TN treatments. Both the observed reduction in the N treatment at W7 and the increase in the T and TN treatments were reflected at all needle ages. The pattern of leaf area distribution is closely mirrored by that of leaf dry weight, and is very similar to that of needle number. Generally leaf area and leaf weight are closely related as are average needle area and average needle weight and this is reflected in the specific needle area values which show little treatment effects. Application of nitrogen appears to have resulted in a reduced needle area at W1 as a result of smaller average needle area, needle number being slightly greater than control. Thinning alone did not have a big effect but the observed drop in leaf area appears to have been a consequence of both fewer needles and a smaller average needle area and in the TN treatment the reduction in leaf area relative to control appeared to also be a result of both fewer needles and smaller average needle area. At W4 although leaf area was not significantly affected, there was a tendency for trees in all treatments to have more needles than control trees but smaller average needle area. At W7, the drop in needle area in the N treatment is largely due to a smaller number of needles and average needle area has been relatively little affected and this also applies to the observed increase in area in the T and TN treatments.

The sample trees on which the data are based were chosen on the basis of similar pre-treatment diameter in order to reduce variability. However, examination of the mean diameter increments of the sample trees over the 3 years of the experiment shows a pattern which is not consistent with the overall results. Mean diameter increment in the T (2.16 cm) and TN (2.33 cm) treatments relative to control (1.71 cm) reflects the pattern observed in the plot basal area increment data but diameter increment in the N treatment sample trees (1.32 cm) does not. This suggests that some caution should be exercised over the leaf area results from treatment N. The observed reduction in leaf area in the N treatment may be a real result or it may reflect the non-representativeness of the N sample trees, a fact which seems more likely since this reduction in leaf area due to N application did not occur in the thinned treatment. A genuine, interaction cannot however be ruled out, particulary since average needle area was apparently smaller with N application at both levels of thinning.

The general picture emerging from the Wauchope experiment therefore, is one of a suggestion of smaller leaf area at W1 in all treatments, due largely to both fewer needles and smaller average needle area, little effect at W4, a suggestion of smaller leaf area in treatment N at W7 due to fewer needles and a clear indication that needle area at W7 has been increased by thinning, at both levels of N, as a result of more needles. Since this result is reflected at all needle ages it appears that the increase in needle number has been due to both increased needle production and increased needle retention since the number of 4 year+ needles (formed prior to treatment) can clearly only be increased by greater retention while the number of needles in the post-treatment needle ages can be increased both by greater production and by greater retention.

Fig.9 Relative leaf area of fertilized trees at Benmore

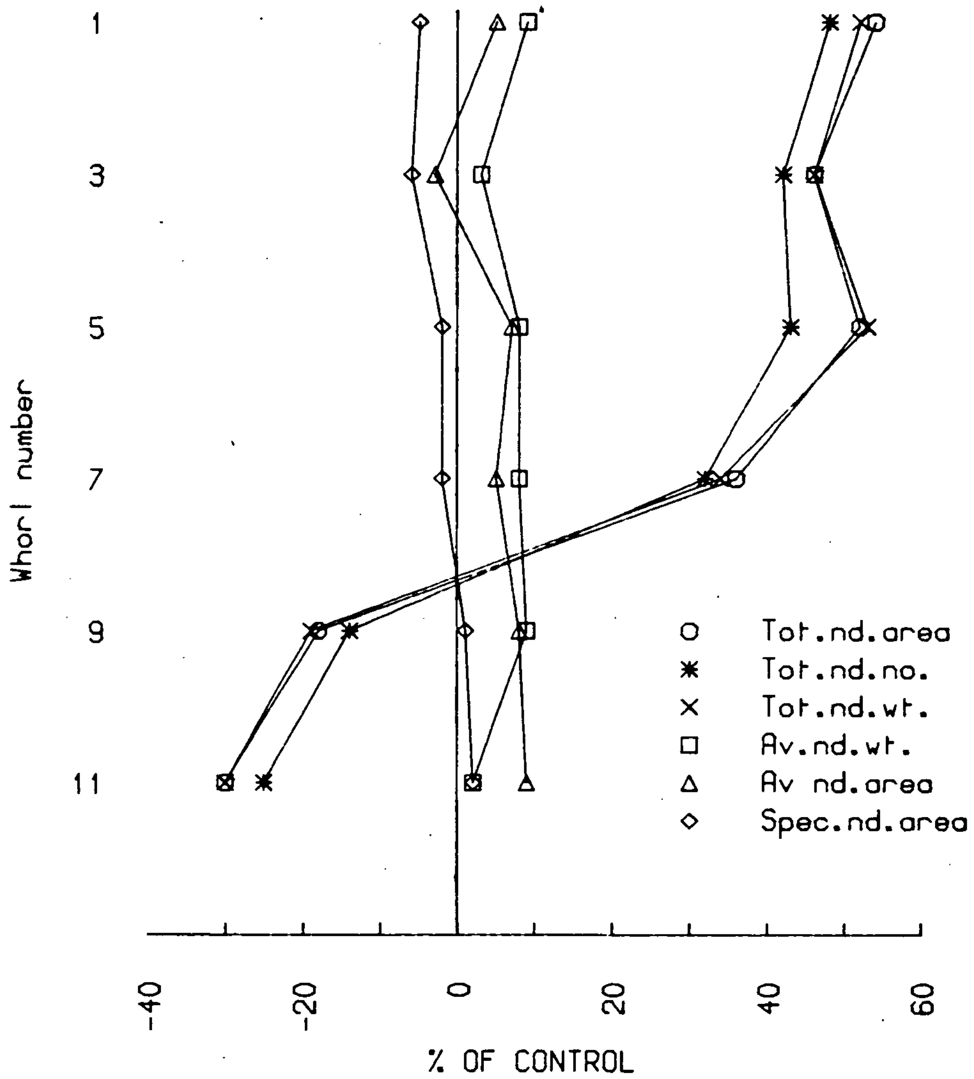


Fig 10a. Relative leaf area of thinned and fertilized trees at Wauchope (total leaf area, total needle weight, needle number)

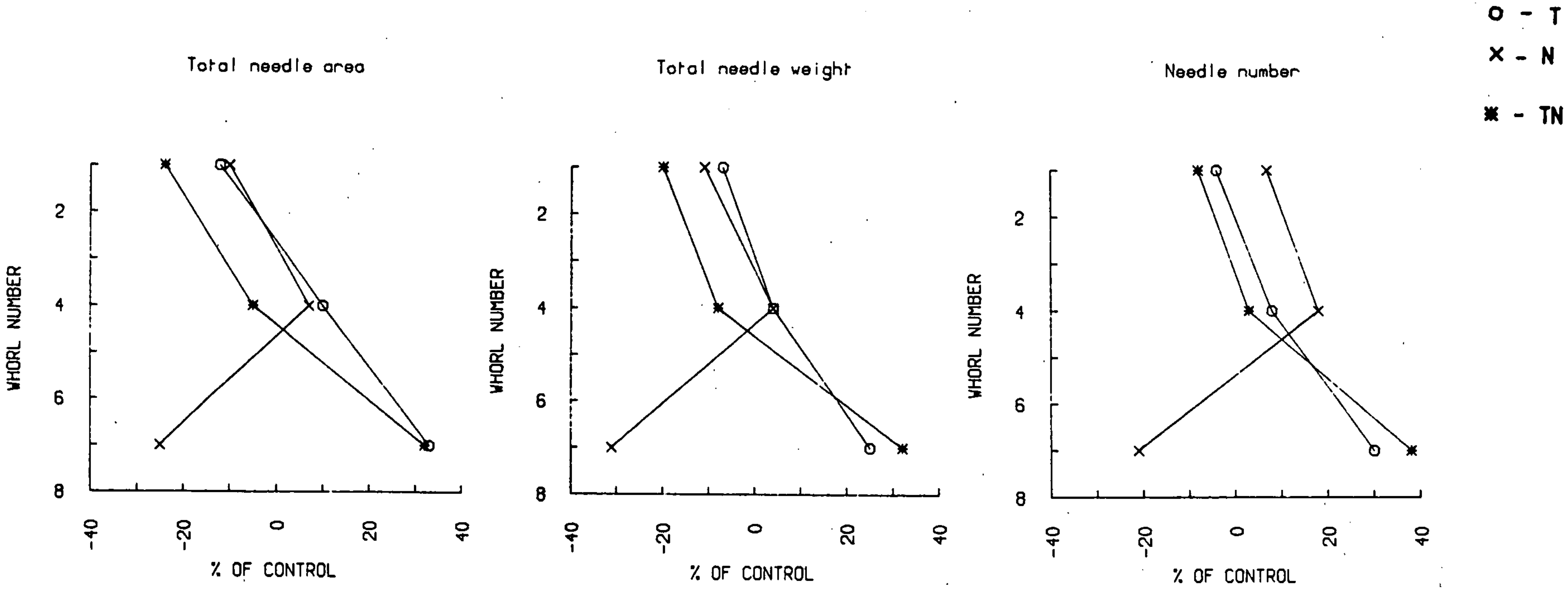
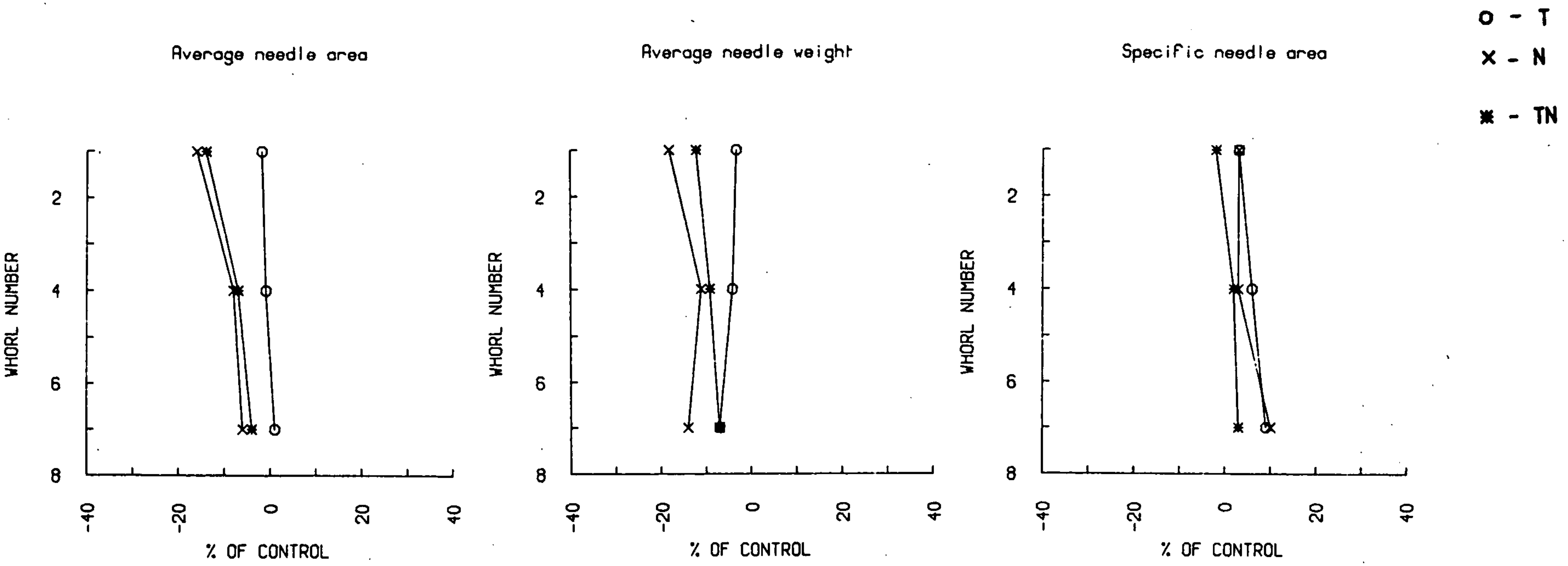


Fig 10b. Relative leaf area of thinned and fertilized trees at Wauchope (av. needle area, av. needle weight, specific needle area)



CHAPTER SIX

FOLIAGE AREA IN RELATION TO DIAMETER AND SAPWOOD AREA

6.1 Benmore

6.1.1 Sapwood areas Discs taken from breast height on the sapwood trees were treated as per section 3.4. Dye penetration normally occurred to a depth of around 5 mm and, in the main, the boundary between sapwood and heartwood was clear. On some discs, the sapwood was visibly wet in comparison with the heartwood and this was used as a further check on the validity of the dye penetration. Eight equally spaced radii were inscribed on the disc prior to sectioning and cross sectional areas of both the disc and the sapwood were calculated from the mean radius (πr^2).

Mean sapwood areas are shown in table 43. In treatment 0, sapwood area ranged from 34.1 cm^2 to 127.9 cm^2 with a mean of 65.8 cm^2 while in treatment NP, sapwood area ranged from 35.4 cm^2 to 122.4 cm^2 with a mean of 71.7 cm^2. Sapwood area expressed as a percentage of the total cross sectional area of the disc (under bark) amounted to, on average, 62% in treatment 0 and 66% in treatment NP. Although mean sapwood area was 5.9 cm^2 (9%) greater in treatment NP, an analysis of variance showed no significant difference.

6.1.2 Sapwood area related to foliage area Sample tree projected leaf areas were plotted against sapwood areas and regression analysis was carried out on the data and on a logarithmic transformation. The log transformation did not improve the correlation coefficients and only the untransformed data are presented here. There was a significant linear relationship between foliage area and sapwood area in both treatments (Fig 11) and little apparent difference between the slopes of the fitted lines. Mean leaf area per cm^2 of sapwood was 0.25 m^2 in treatment 0 and 0.27 m^2 in treatment NP. In a regression analysis carried out on the data, a single line, two parallel lines and two separate lines were fitted and an analysis of variance carried out (Table 44). The overall regression of leaf area on sapwood area was highly significant but there was no significant difference between the slopes and intercepts of the various fitted lines indicating that a single line fit was most appropriate. The regression equations were as follows:-

Treatment 0 - Leaf area(m^2) = 0.314 sapwood area(cm^2)-4.32 ($r = 0.78$)
Treatment NP - Leaf area(m^2) = 0.393 sapwood area(cm^2)-7.79 ($r = 0.84$)
Combined - Leaf area(m^2) = 0.364 sapwood area(cm^2)-6.70 ($r = 0.80$)

6.1.3 Diameter related to foliage area Diameter was linearly related to foliage area (Fig 12) in both treatments and the relationship was not improved by logarithmic transformation. Mean unit of leaf area per cm of diameter was 1.32 m^2 in treatment 0 and 1.63 m^2 in treatment NP. Regression analysis as for sapwood area against foliage area showed a highly significant overall regression (table 45) but no significant difference between the slopes and intercepts of the fitted lines. The regression equations were:-

Treatment 0 - Leaf area(m^2) = 3.58 diameter(cm)-28.09 ($r = 0.75$)

Table 43. Mean sapwood areas in the Benmore sample trees

Treatment	Mean sapwood area (cm^2)	Mean sapwood area as a % of mean basal area
0	65.75	62
NP	71.70	66
5% lsd	10.50	-

Fig. 11 Sapwood area in relation to foliage area (Benmore)

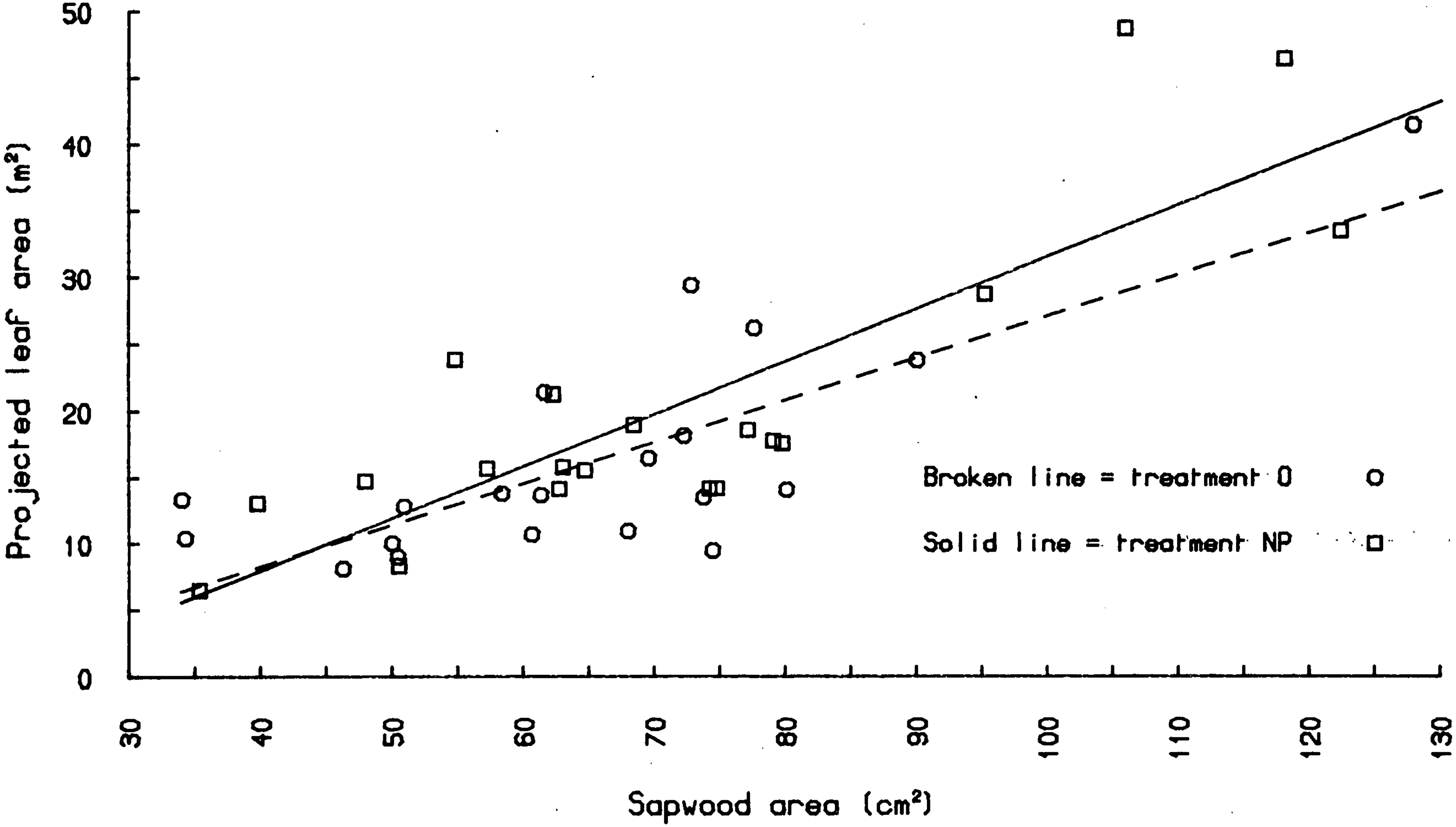


Fig.12 Diameter in relation to foliage area (Benmore)

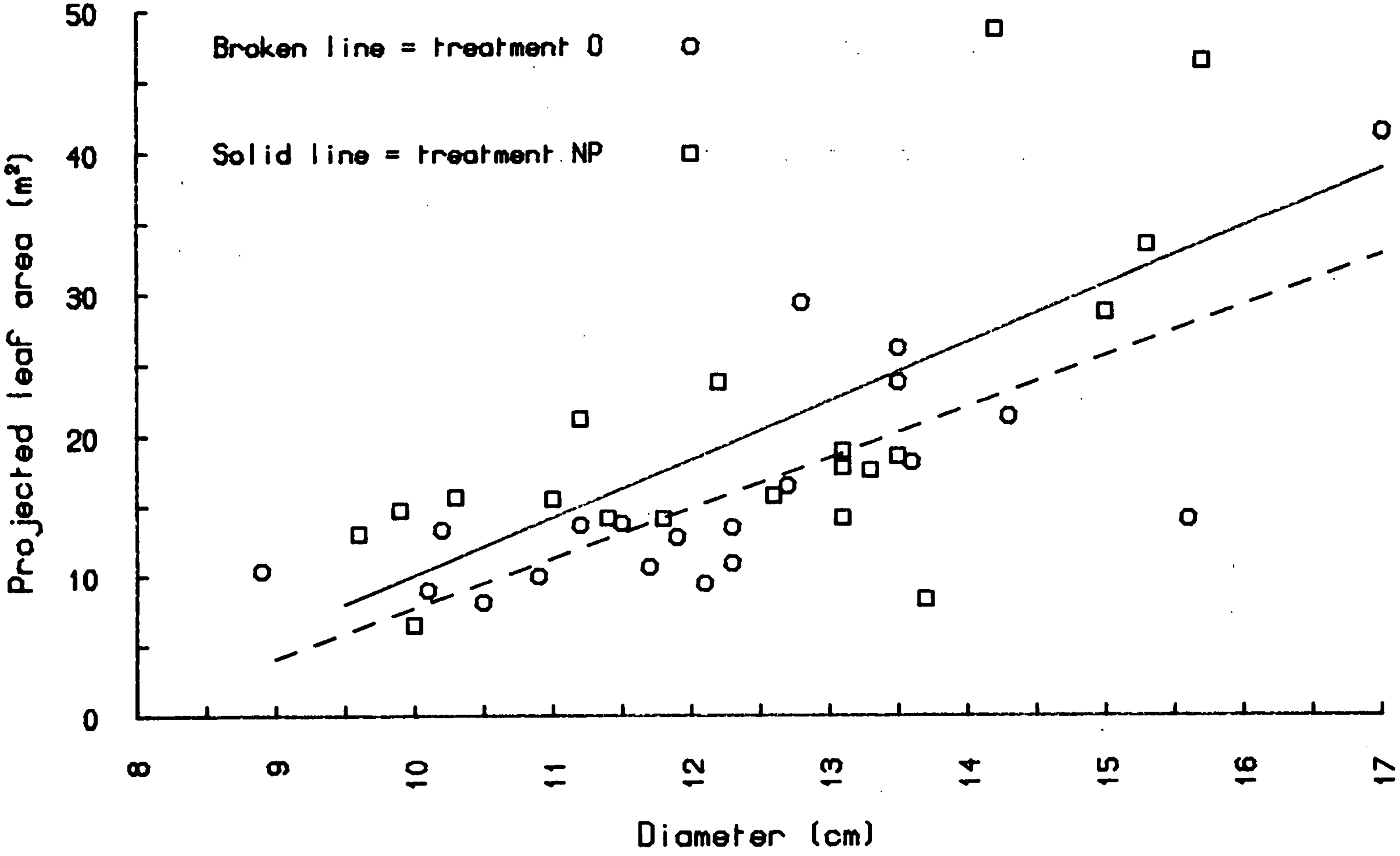


Table 44. Results of the analysis of variance of the leaf area on sapwood area regressions (Benmore)

Source	DF	SS	MS	F
Overall regression	1	25087024	25087024	69.899***
Intercepts	1	399844	399844	1.114
Slopes	1	311424	411424	0.868
Residual	36	12922497	358958	1.000
Total	39	38720800		

Table 45. Results of the analysis of variance of the leaf area on diameter regressions (Benmore)

Source	DF	SS	MS	F
Overall regression	1	19322688	19322688	39.062***
Intercepts	1	1208944	1208944	2.444
Slopes	1	381424	381424	0.771
Residual	36	17807728	494659	1.000
Total	39	38720800		

Treatment NP - Leaf area(m^2) = 4.13 diameter(cm)-31.26 ($r = 0.68$)

Combined - Leaf area(m^2) = 3.86 diameter(cm)-29.74 ($r = 0.69$)

6.2 Wauchope

6.2.1. Foliage areas In the 1981 sampling exercise based on four randomly selected trees per plot in blocks I and II, a sample branch was removed from whorl 1 of each tree and from the whorls nearest to points one third and two thirds of the way down the crown. This normally corresponded to whorls 4 and 7. Total foliage area for each sample whorl was calculated as previously described and the area of the three whorls summed to provide a total leaf area (hereafter called the sample leaf area) for each tree. Using the data from blocks I and III of the Benmore experiment, the relationship between total tree leaf area and sample leaf area was examined. A significant linear relationship was found which was best described by the equation:-

$$\text{log total leaf area} = \frac{\text{log sample leaf area} + 1.2892}{0.9351} \quad (r = 0.89)$$

This equation was applied to the Wauchope sample leaf areas to establish a total leaf area for each tree. Mean leaf areas per tree are shown in table 46.

6.2.2 Sapwood areas Sapwood area was calculated from measurements of 3 cm thick discs cut at breast height from the 1981 sample trees and treated as previously described. Sapwood areas (table 46) ranged from 23.1 cm^2 to 185.5 cm^2 in the unthinned treatments with a mean of 78.4 cm^2 and from 51.4 cm^2 to 176.9 cm^2 with a mean of 111.8 cm^2 in the thinned treatments.

6.2.3 Sapwood area related to foliage area Both sample and total leaf areas were plotted against sapwood area for each tree (Fig 13) and in both cases a significant linear relationship was found. There was a suggestion of curvature, particularly in the total leaf area data but, while this apparent curvature was removed by plotting leaf area against log sapwood area, this exercise did not affect the correlation coefficient. The regression equations for the untransformed data are:-

Total leaf area(m^2) = 0.291 Sapwood area (cm^2)-0.129 (r = 0.86)
Sample leaf area(m^2) = 0.0609 Sapwood area (cm^2)+0.257 (r = 0.86)

To test for differences in the sapwood area: total leaf area relationship between treatments, regression analysis was carried out on the data as previously described with a single line, parallel lines and separate lines fitted. Analysis of variance of the slopes and intercepts (table 47) showed a highly significant overall relationship between foliage area and sapwood area but no significant treatment differences.

6.2.4 Diameter related to foliage area Diameter at breast height of each sample tree was plotted against the corresponding total leaf area (Fig 14) and regression analysis was carried out as previously described with an analysis of variance of slopes and intercepts (table 48). There was a significant linear relationship between foliage area and diameter which can be described by the equation:-

Table 46. Mean foliage and sapwood areas in the 1981 Wauchope sample trees (± 1 SE)

Treatment	Mean foliage area (cm^2)	Mean sapwood area (cm^2)	Foliage area per unit of sapwood	Sapwood area as a percentage of basal area
O	15.85 ± 5.07	59.31 ± 11.58	0.27	64
P	21.91 ± 4.69	77.99 ± 15.40	0.28	56
N	30.34 ± 8.50	95.08 ± 20.66	0.32	61
T	34.83 ± 4.48	139.36 ± 10.76	0.25	64
TP	28.44 ± 3.98	87.83 ± 13.69	0.32	63
TN	33.13 ± 3.83	112.20 ± 10.38	0.29	60

Fig. 13 Sapwood area in relation to foliage area (Wauchope)

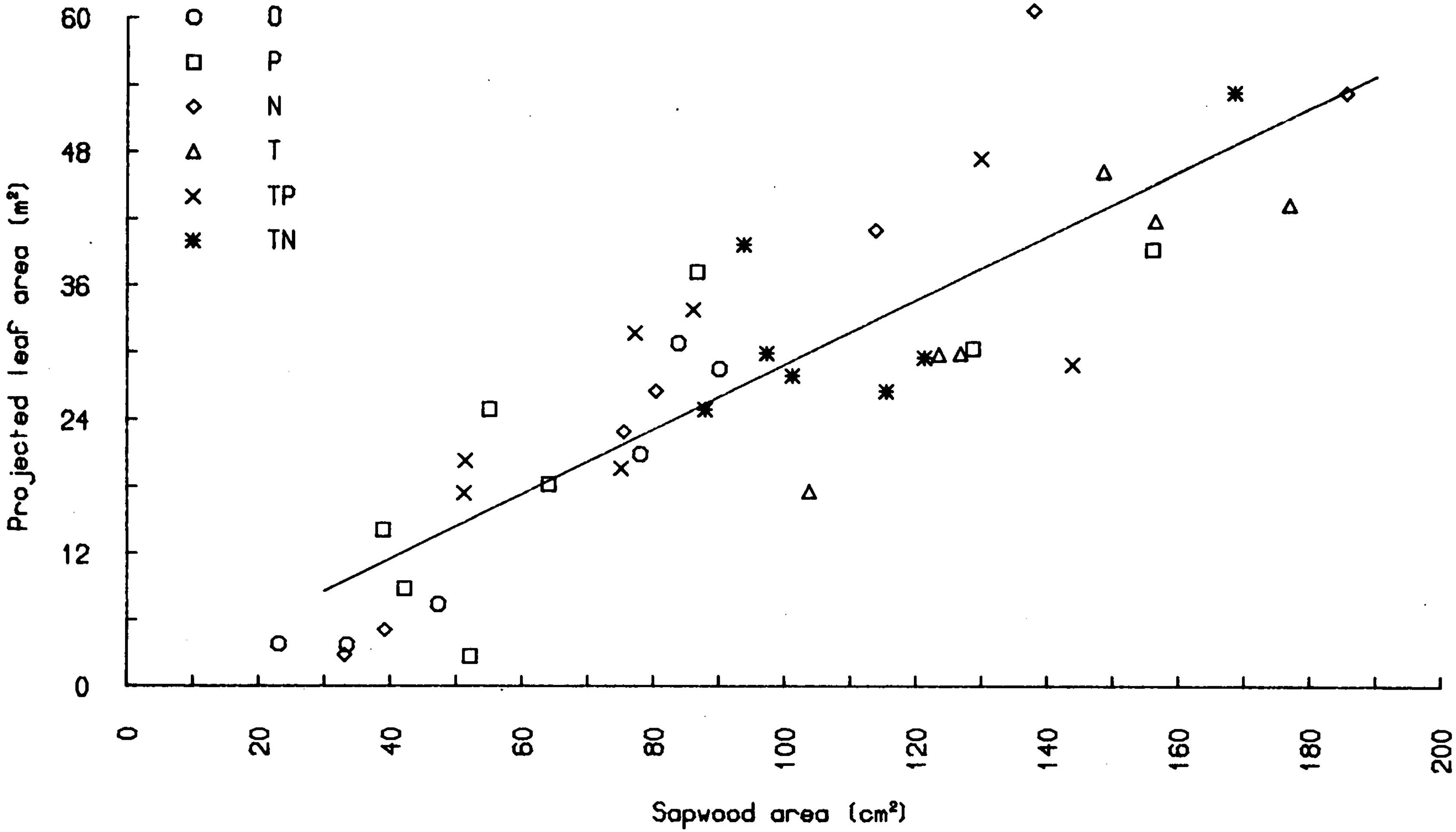


Fig. 14 Diameter in relation to foliage area (Wauchope)

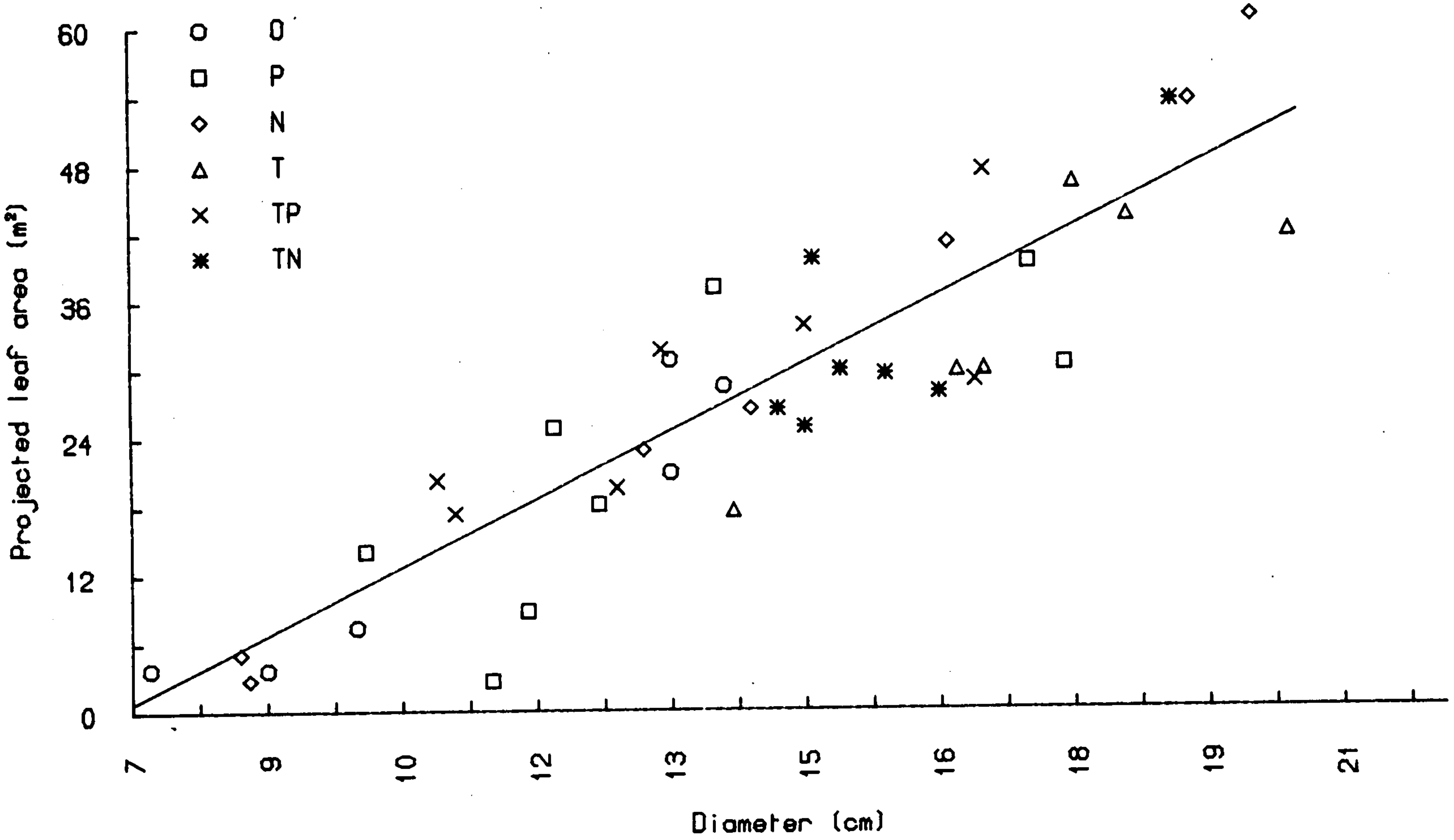


Table 47. Results of the analysis of variance of the leaf area on sapwood area regressions (Wauchope)

Source	DF	SS	MS	F
Overall regression	1	6330.043	6330.043	115.153***
Intercepts	1	349.179	69.836	1.270
Slopes	5	316.172	63.234	1.150
Residual	29	1594.150	54.971	1.000
Total	40	8589.563		

Table 48. Results of the analysis of variance of the leaf area on diameter regressions (Wauchope)

Source	DF	SS	MS	F
Overall regression	1	6910.238	6910.238	167.840***
Intercepts	5	325.790	165.158	1.583
Slopes	5	159.543	31.909	0.775
Residual	29	1193.975	41.171	1.000
Total	39	8589.563		

Leaf area (m^2) = 3.963 Diameter (cm)-26.92 (r = 0.90)

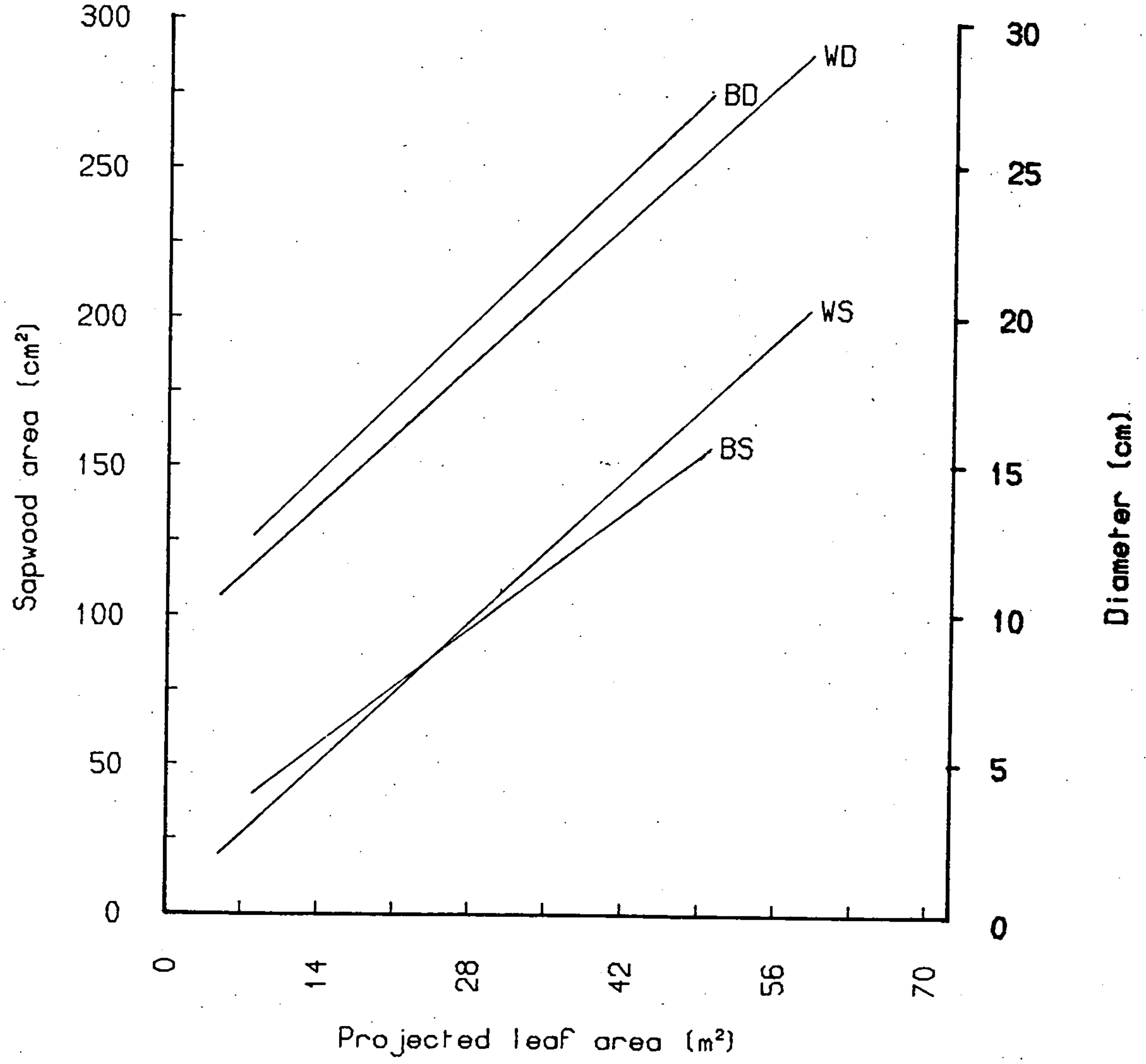
but again there were no significant or apparent treatment differences.

6.3 Discussion

Cross sectional area of sapwood is of the same order of magnitude in both experiments, although the thinned treatments at Wauchope, with a larger average tree size clearly also will have a greater average sapwood area. Mean sapwood area in the Benmore stand was 68.73 cm^2 compared with a mean of 77.46 cm^2 in the unthinned treatments at Wauchope and 113.13 cm^2 in the thinned treatments and in both experiments sapwood accounts for over 60% of the total cross sectional area (66% at Benmore, 61% at Wauchope).

At both sites leaf area of individual trees was linearly related to both sapwood area and diameter at breast height. In the Benmore experiment sapwood area (r = 0.80) was a better estimator of foliage area than diameter (r = 0.69) but at Wauchope, diameter (r = 0.90) was slightly better than sapwood area (r = 0.86). Comparison of the sapwood area: foliage area and diameter:foliage area relationships across the two site (Fig 15) suggested that the relationships were essentially the same in both stands. Fertilizer and thinning treatments did not appear to have affected the relationship between foliage area and sapwood and foliage area and diameter. Three growing seasons after treatment there was no apparent or significant difference between the fitted lines for fertilized and unfertilized trees at Benmore and similarly at Wauchope there were no apparent or significant differences two growing seasons after application of thinning and fertilizer treatments.

Fig. 15 Leaf area related to diameter (D) and sapwood area (S) at Wauchope (W) and Benmore (B)



CHAPTER SEVEN

THE RELATIONSHIP BETWEEN LEAF AREA AND PRODUCTION

7.1 Benmore

7.1.1 Leaf area related to basal area increment for individual trees Leaf area of the 1979 sample trees was plotted against their basal area increment during the 1979 growing season and regression analyses carried out as previously described with an analysis of variance of slopes and intercepts of the fitted lines to test for the effect of fertilizer treatment on the relationship between leaf area and basal area increment. Basal area increment was linearly related to leaf area (fig 16) in both treatments and there was an apparent difference in slope between the fitted lines. The regression equations were:-

Treatment 0 - Basal area increment (mm^2) = 19.71 leaf area (m^2)-4.18 ($r = 0.84$)

Treatment NP - Basal area increment (mm^2) = 28.01 leaf area (m^2) ($r = 0.83$)

Mean basal area increment per unit of leaf area (m^2) was 20.0 mm^2 in treatment 0 and 24.8 mm^2 in treatment NP. The analysis of variance however (Table 49) confirmed that the overall relationship between leaf area and basal area increment was highly significant but showed no significant difference between the slopes of the fitted lines for the two treatments.

Fig. 16 Basal area increment related to leaf area (Benmore)

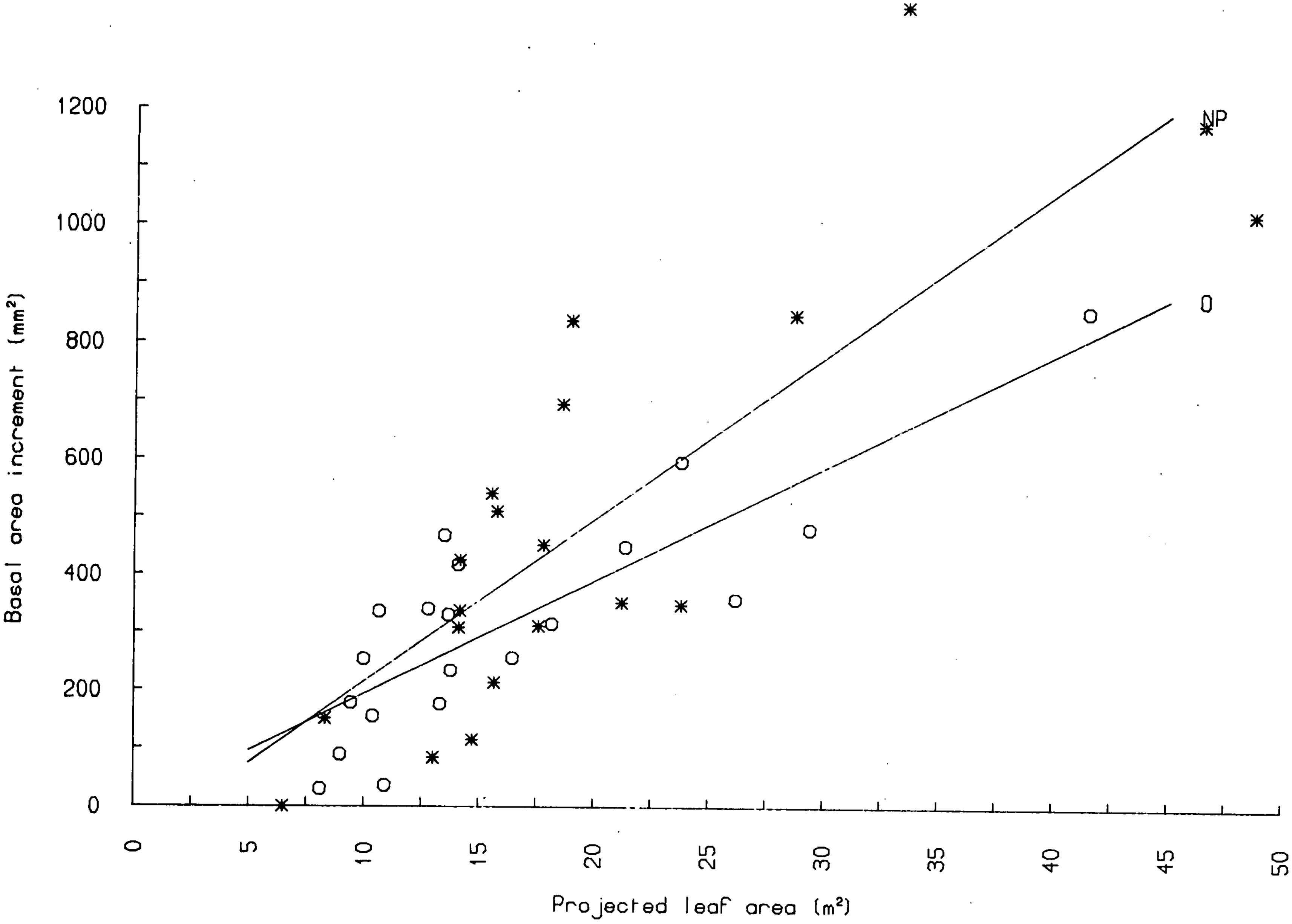


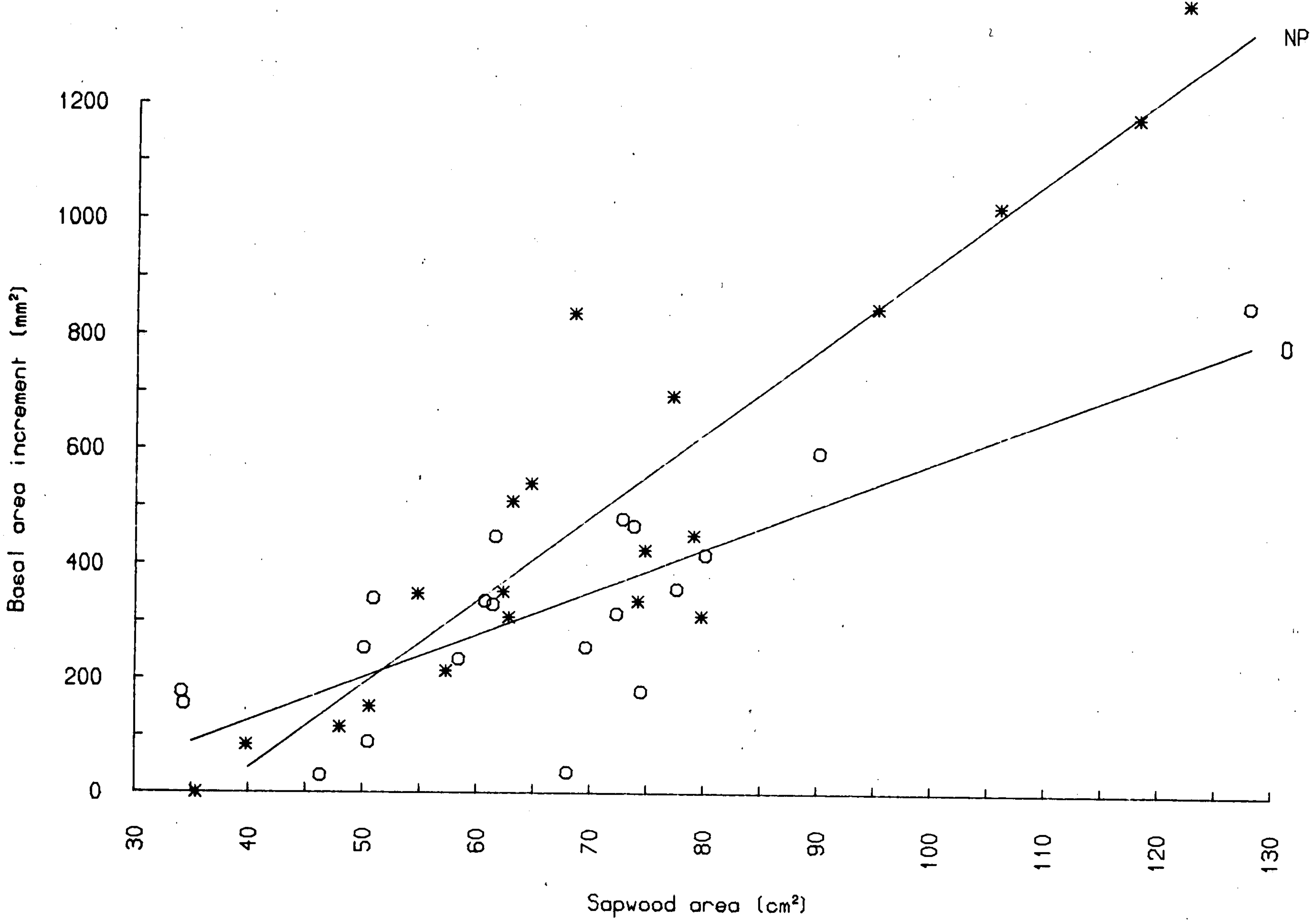
Table 49. Results of the analysis of variance of the leaf area : basal area increment regressions (Benmore)

Source	DF	SS	MS	F
Overall regression	1	2599866	2599886	87.97**
Intercepts	1	713434	713434	2.41
Slopes	1	59000	59000	1.99
Residual	36	1063906	29553	1.00
Total	39	3794136		

Table 50. Results of the analysis of variance of the sapwood area : basal area increment regressions (Benmore)

Source	DF	SS	MS	F
Overall regression	1	2690715	2690715	137.52***
Intercepts	1	146225	146225	7.47**
Slopes	1	252829	252829	12.92**
Residual	36	704366	19566	1.00
Total	39	3794136		

Fig. 17 Basal area increment related to sapwood area (Benmore)



7.1.2 Sapwood area related to basal area increment for individual trees Sapwood area of the 1979 sample trees was plotted against the 1979 basal area increment and regression analyses carried out as for the leaf area data. As expected from the relationship between leaf area and sapwood area, sapwood area also showed a linear relationship with basal area increment (fig 17) in both treatments and again there was an apparent treatment effect. The regression equations were:-

Treatment 0 - Basal area incr (mm^2) = 7.51 sapwood area (cm^2)-175.91 ($r = 0.77$)

Treatment NP - Basal area incr (mm^2) = 14.99 sapwood area (cm^2)-564.28 ($r = 0.91$)

Mean basal area increment per cm^2 of sapwood was 4.96 mm^2 in treatment 0 and 7.04 mm^2 in treatment NP. The analysis of variance (table 50) on this occasion showed not only a highly significant overall relationship between sapwood area and basal area increment but also significant differences between the slopes and intercepts of the fitted lines indicating a significant effect of fertilizer treatment on the sapwood area to basal area increment relationship.

7.1.3 Basal area increment related to leaf efficiency Using the 1979 sample tree data a measure of leaf efficiency (basal area increment per unit of leaf area) was calculated for each tree and, as a further comparison between leaf area and sapwood area, efficiency was also calculated as basal area increment per unit of sapwood area (sapwood efficiency). Each of these measures of efficiency was plotted, for individual trees, against their 1979 basal area increment (Fig 18). Basal area increment appeared to be related to both leaf efficiency and sapwood efficiency. Basal area increment generally increased with increasing leaf efficiency but the relationship was strongest at the lower levels of basal area increment. At higher levels of both basal area increment and leaf efficiency, normally represented by trees from treatment NP, the relationship was not as clear. Sapwood efficiency on the other hand, was closely related to basal area increment at all levels and the relationship was clearly curvilinear.

7.1.4 Efficiency related to leaf area

To determine the effect of leaf area of individual trees on efficiency, leaf area and sapwood area were plotted against leaf efficiency and sapwood efficiency respectively (Fig 19). In both cases there was a suggestion of increasing efficiency in response to increasing leaf area or sapwood area. The correlation coefficient was higher in the case of sapwood efficiency ($r = 0.59$) than in the leaf area to leaf efficiency relationship ($r = 0.24$) though in neither case was the relationship particularly clear.

7.1.5 Stand productivity related to leaf area and leaf efficiency

To determine the relationship between basal area increment, leaf area and leaf efficiency on a stand, rather than individual tree, basis it was necessary to determine the leaf area index (m^2 leaf area per m^2 of ground surface) of each plot. Since the diameter of all trees in the assessment plots was known and since a significant relationship between diameter and leaf area had been established (section 6.1.3), this relationship was used to compute a leaf area for all trees within the assessment plots and leaf area index (LAI) was determined from the total plot leaf area divided by the plot area (200 m^2). Estimated LAI at the end of 1979, plot basal area increments during 1979, and basal area increment per unit of LAI are shown in table 51. LAI varied from 5.39 to 7.56 with a mean of 6.24 in treatment 0 plots and from 6.42 to 8.73 with a mean of 7.74 in treatment NP plots. LAI appeared to be linearly related to stand basal area increment (Fig 20) and the fitted line was best described by the equation:-

Basal area inc (m^2/ha) = 0.309 LAI -0.10 (r = 0.75)

The data were insufficient to attempt regression analyses to test for treatment differences but, on the basis of the ratio of basal area increment to LAI, there was an apparent treatment effect. Basal area increment per unit of LAI (stand leaf efficiency) varied from 0.25 to 0.33 with a mean of 0.28 in treatment 0 and from 0.24 to 0.38 with a mean of 0.31 in treatment NP. Stand efficiency appeared to be linearly related to stand basal area increment but there was little suggestion of a relationship between LAI and stand efficiency (Fig 20).

7.2 Wauchope

7.2.1 Sapwood area related to basal area increment for individual trees Sapwood area was calculated from the core readings for every tree sampled in 1980, 1981 and 1982 and basal area increment for each tree was derived from the annual diameter measurements. Mean sapwood areas by treatment are shown in table 52 along with

Fig. 18. Basal area increment in relation to leaf efficiency and sapwood efficiency (Benmore)

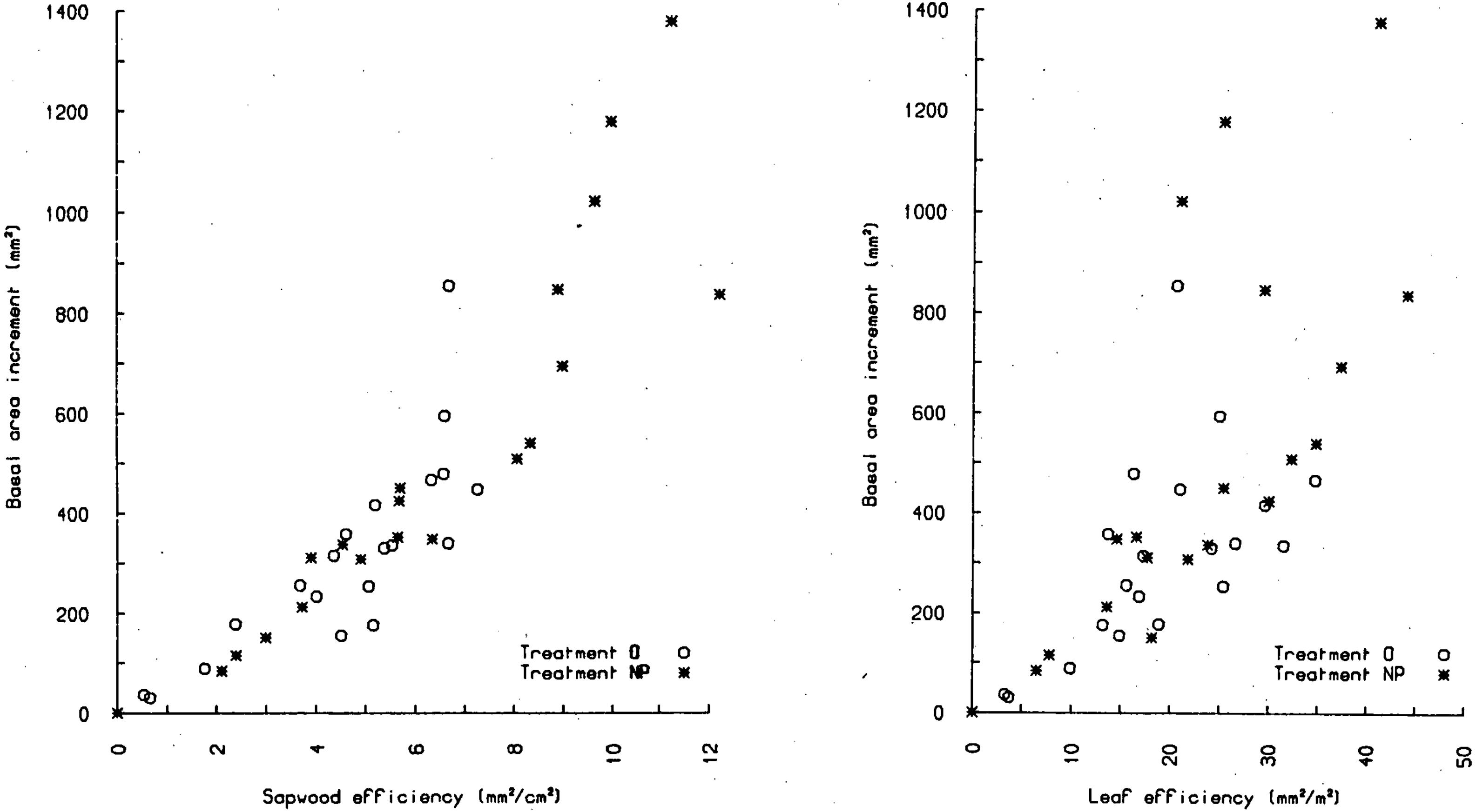


Fig. 19. Sapwood efficiency in relation to sapwood area and leaf area in relation to leaf efficiency (Benmore)

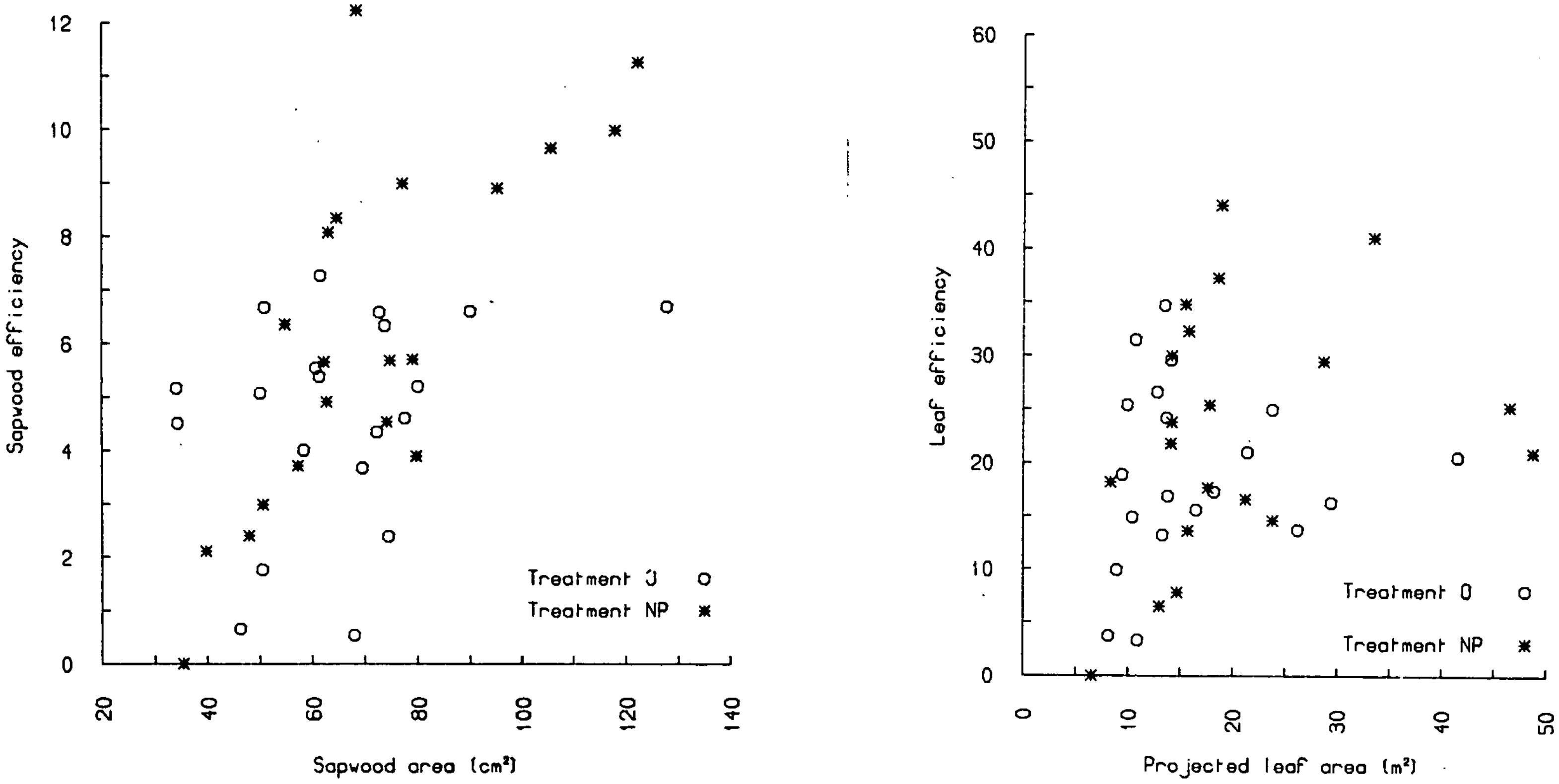


Table 51. Leaf area index (LAI), plot basal area increment (BAI) and stand leaf efficiency (SLE) in the Benmore experiment

Treatment	Block	LAI	BAI m^2/ha	SLE
0	I	7.56	1.99	0.26
	II	6.22	1.68	0.27
	III	5.80	1.91	0.33
	IV	5.39	1.35	0.25
	Mean	6.24	1.73	0.28
NP	I	8.73	2.68	0.31
	II	8.19	1.99	0.24
	III	7.62	2.87	0.38
	IV	6.42	1.99	0.31
	Mean	7.74	2.38	0.31

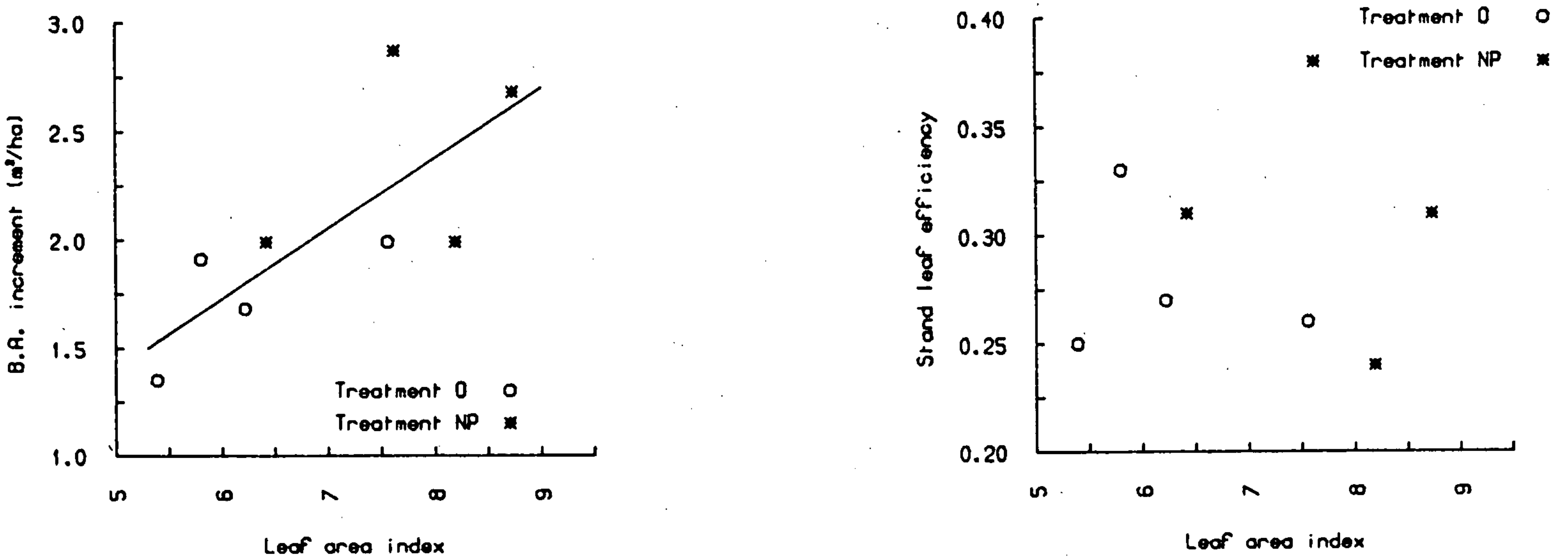


Fig. 20. Stand basal area increment and stand leaf efficiency in relation to leaf area index (Benmore)

mean basal area increments and mean sapwood efficiency (basal area increment per unit of sapwood). The results of an analysis of variance carried out on this data are shown in table 53. Mean basal area increment per tree of treatments within the thinned areas was significantly greater than that of unthinned treatments in 1980 (P = 0.001), 1981 (P = 0.001) and 1982 (P = 0.05). Taken over the whole three year period, mean basal area increment per tree was 93% greater in the thinned treatments. Fertilizer treatment had no significant effect on basal area increment per tree in any year but some trends were apparent. In 1980, the year of application of the thinning and fertilizer treatments, basal area increment per tree was lower for fertilized trees than for unfertilized and this was apparent in both the presence and absence of thinning. In 1981 and 1982 however, basal area increment in trees in the N and P treatments was higher than in treatment O. Measured over the three year period, basal area increment was 15% higher than control in treatment P and 12% higher in treatment N. In the thinned treatments however this trend was only apparent in treatment TN where mean basal area increment over the three years was 7% greater than treatment T. In treatment TP basal area increment was lower than treatment T in each of the three years.

Mean sapwood area showed a similar pattern to basal area increment. Trees from thinned treatments had larger mean sapwood area than from unthinned treatments in 1980 (P = 0.01), 1981 (P = 0.001) and 1982 (not significant). Fertilizer treatment did not significantly affect mean sapwood area in any year but again the pattern in the unthinned treatments was one of lower mean sapwood area than control (O) in both the fertilizer treatments (N and P) in 1980 and higher mean sapwood area in the fertilized treatments in both 1981 and 1982. In the thinned treatments this pattern was repeated for treatment TN but in treatment TP, mean sapwood area was lower than in treatment T in all three years.

Mean sapwood efficiency was consistently higher in trees from thinned treatments (mean sapwood efficiency over the three years - 11.84) than in trees from unthinned treatments (7.98) and this difference was apparent in every year. For treatment N and P mean sapwood efficiency was lower than treatment O in 1980 and 1981 but higher in 1982. Mean sapwood efficiency for treatment TP was lower than for treatment T in 1980, higher in 1981 and lower in 1982 while in treatment TN, mean sapwood efficiency was higher than in treatment T in all three years.

The above results show a distinct effect of thinning on mean basal area increment, mean sapwood area and mean sapwood efficiency but the effects of the fertilizer treatments are less clear. As a test for the treatment effects on the relationship between sapwood area and basal area increment, regression analyses were carried out separately for each years data, and analyses of variance carried out to test for differences in the slopes of the fitted lines. The results (Table 54) indicated significant differences in slope between the fitted lines in all three years. In 1980 there was a distinct and significant difference between thinned and unthinned treatments (Fig 21) but no apparent or significant fertilizer effect. In the 1981 data, there was again a significant thinning effect and an indication (non significant) that the slope coefficient for treatments where nitrogen was applied were greater than the other treatments at both levels of thinning (Fig 22). In the 1982 data the only significant difference to emerge was that treatment N had a greater slope coefficient than all other treatments (Fig 23).

7.2.2 Basal area increment related to sapwood area and sapwood efficiency Using the mean (over three years) value for each treatment, basal area increment per tree was plotted against both mean sapwood area and mean sapwood efficiency (Fig 24). Mean basal area increment was clearly related to both mean sapwood area and mean sapwood efficiency and tended to increase with increasing levels of both these factors. There was an apparent slope difference between thinned and unthinned treatments which was particularly apparent in the case of sapwood efficiency. The rate of increase in basal area increment with increasing sapwood area and sapwood efficiency was apparently greater in the unthinned than in the thinned treatments.

Sapwood efficiency appeared to be linearly related to sapwood area (Fig 25) and showed no sign of levelling off even at the highest levels of mean sapwood area recorded.

7.2.3 Stand productivity related to leaf area and leaf efficiency Leaf area index for individual treatment plots at the end of 1981 was calculated as previously, using the relationship between diameter and foliage area for individual trees calculated from the 1981 sampling exercise (see section 6.2.4). Mean leaf area indices per treatment are shown in table 55 along with mean basal area increments per ha and mean stand leaf efficiency (Basal area increment (m^2/ha) per unit of LAI.) LAI varied from 8.61 to 9.32 in the unthinned treatments and from 6.07 to 6.60 in the thinned treatments and at both levels of thinning, LAI was highest where nitrogen fertilizer had been applied. Stand basal area increment appeared to increase with increasing LAI when treatments were compared within a level of thinning but there was a clear difference between levels of thinning. Stand basal area increment for a given LAI was considerably higher in thinned treatments. Stand leaf efficiency varied from 0.22 to 0.24 in the unthinned treatments and from 0.37 to 0.38 in the thinned treatments. Although there was a distinct difference between thinning levels, stand leaf efficiency did not vary much between fertilizer treatments but at both levels of thinning the nitrogen treatment had stand leaf efficiency which was as high as or higher than the other treatments. Stand basal area increment tended to increase with increasing stand leaf efficiency but the relationship was not strong (Fig 26) in either the thinned or unthinned treatments; nor was there any clear relationship within a thinning treatment, between LAI and stand leaf efficiency, although stand leaf efficiency was clearly lower at the higher leaf area indices encountered in the unthinned treatments.

7.3 Discussion

In the Benmore experiment there are clear indications that the productivity (basal area increment) of individual trees is closely related to both leaf area and leaf efficiency. The effects of fertilizer treatment on leaf area have been discussed in chapter 5 and the data presented in this current chapter suggest that the relationship between leaf area and basal area increment (leaf efficiency) has also been affected by fertilizer treatment. Looked at either in terms of mean ratio of basal area increment to leaf area or in terms of regression analyses using individual tree data, it appears that trees fertilized with NP produced greater basal area increment for a given leaf area than unfertilized trees, implying a greater leaf efficiency. Substituting sapwood area for leaf area gave a very similar picture but whereas there was an apparent but not significant difference between the leaf area: basal area increment regressions for fertilized and unfertilized trees, in the case of sapwood area: basal area increment the effect of fertilizer treatment was significant. This may imply that sapwood area is not a true reflection of leaf area or more likely, that the difference reflects the greater accuracy possible when measuring sapwood area compared with leaf area. This was also the case in the regression of leaf efficiency on both leaf area and sapwood area where the relationship between sapwood area and leaf efficiency was much clearer than that based on leaf area. The results indicate that further increases in both leaf area and leaf efficiency in trees in the Benmore stand would lead to further increases in productivity since in both cases the relationships between basal area increment and both leaf efficiency and leaf area are generally linear and show no tendency towards levelling out. Similarly the relationship between leaf area and leaf efficiency does not suggest that leaf efficiency is becoming limited by increasing leaf area. The relationship between leaf area and leaf efficiency is very weak though better when based on sapwood area rather than leaf area, but does still suggest, within the range of the data, a pattern of increasing leaf efficiency with increasing leaf area. The pattern of stand productivity in relation to stand leaf area and leaf efficiency presents a similar picture to that for individual trees. Stand productivity was closely related to both leaf area index and stand leaf efficiency, and both of these parameters appear to have been increased by fertilizer application. Again the relationship between stand basal area increment and both LAI and stand leaf efficiency are linear over the range of the data suggesting that further increases in productivity are possible. There is no clear indication of any effect of LAI on stand leaf efficiency.

In the Wauchope experiment, judgements of the effect of leaf area and leaf efficiency on productivity (basal area increment) are based on measurements of sapwood area and sapwood efficiency respectively and in both of these parameters significant effects due to thinning treatment have clearly emerged. As expected, because of the larger average tree size in the population of trees from the thinned treatments, mean basal area increment per tree and mean sapwood area per tree were both significantly greater in trees from thinned treatments in each of the three years investigated. More significantly, however, sapwood efficiency was higher in trees from thinned treatments when judged either on the basis of mean basal area increment: sapwood area ratios or more appropriately, by regression analyses and comparison of slopes using individual tree data. These analyses have shown a clear separation between thinned and unthinned treatments, a difference which cannot be accounted for purely by the fact of higher average tree size in the thinned treatments. Thus over the three year period productivity (basal area increment) of individual trees has been shown to be related to both sapwood (leaf) area and sapwood (leaf) efficiency and thinning has considerably increased mean sapwood (leaf) efficiency. (Thinning effects on leaf area discussed in chapter 5.) On a stand basis the LAI of thinned plots was considered less than that of unthinned plots at the end of the second year of the experiment, yet stand basal area increment was higher. Clearly then, the increase in leaf efficiency of individual trees in thinned plots was more than enough to compensate for the reduction in LAI. Possible fertilizer effects on leaf area and leaf efficiency at either the stand or individual tree level are harder to identify from the data. No significant differences in leaf or sapwood quantity have emerged but there are indications of a nitrogen effect. Measured over the three year period mean sapwood area was higher than treatment T or TP in treatment TN and higher than treatment O in treatment N (though not higher than treatment P) and LAI at the end of the second growing season was greater, at each level of thinning, in trees receiving nitrogen fertilizer. Similarly stand leaf efficiency was slightly higher at the end of the second growing season in the N and NT treatments and at the individual tree level, sapwood efficiency, judged from the regression analyses, appeared to be highest, in both the presence and absence of thinning, in the treatments receiving nitrogen. In the third growing season sapwood efficiency was significantly higher in treatment N than in any other treatment. Taken together, these observations suggest that, in the second and third growing season at least, application of nitrogen had improved sapwood (leaf) efficiency at both the stand and individual tree level. As with the Benmore data the indications are that basal area increment, leaf area and leaf efficiency at both the stand and individual tree level have scope for further increase in this stand for the relationships between these factors are linear over the range of the data presented. Similarly there is no indication of a reduction in sapwood (leaf) efficiency at the highest levels of sapwood (leaf) area either at the stand or individual tree level, suggesting that optimum leaf area index has not yet been reached.

Table 52. Mean sapwood area, basal area increment and sapwood efficiency in the Wauchope sample trees

(data presented are on a per tree basis)

Parameter	Treatment	Year			Mean
		1980	1981	1982	
Mean sapwood area (cm^2	0	81.9	73.7	74.9	76.8
	P	61.8	89.9	100.1	83.9
	N	75.7	80.8	79.5	78.7
	T	99.0	108.7	108.4	105.4
	TP	96.9	103.7	101.5	100.7
	TN	87.2	114.2	122.3	107.9
Mean basal area increment (mm^2)	0	617	607	543	589
	P	407	719	908	678
	N	564	647	769	660
	T	1295	1153	1346	1265
	TP	1184	1117	967	1089
	TN	1180	1362	1526	1356
Mean sapwood efficiency	0	7.53	8.24	7.25	7.67
	P	6.59	8.00	9.07	7.89
	N	7.45	8.01	9.67	8.38
	T	13.08	10.61	12.42	12.04
	TP	12.22	10.77	9.53	10.84
	TN	13.53	11.93	12.48	12.65

Table 53. Results of the analyses of variance of mean sapwood area and mean basal area increment in the Wauchope sample trees

Parameter	Source	1980			1981			1982		
		DF	SS	VR	DF	SS	VR	DF	SS	VR
Mean basal area increment	Blocks	4	53333264	4.62	4	4634682	2.30	2	1253623	0.92
	Thin	1	17869600	45.91***	1	11472252	20.21***	1	6552359	9.73*
	Fertiliser	2	643216	0.83	2	407465	0.36	2	854927	0.64
	T x F	2	164982	0.21	2	624469	0.55	2	2609942	1.94
	Residual	20	7785230	1.35	20	11353034	1.12	10	6732982	0.99
	Trees	120	34614128	-	120	60593424	-	72	49012064	-
	Total	149	66410400	-	149	89085312	-	89	67015888	-
Mean sapwood area	Blocks	4	7979	1.57	4	15675	1.94	2	2778	0.49
	Thin	1	16903	11.35**	1	28214	15.06***	1	15132	4.16
	Fertiliser	2	3502	1.18	2	1199	0.32	2	1687	0.23
	T x F	2	3828	1.29	2	3509	0.94	2	7066	0.97
	Residual	20	29790	1.17	20	37469	0.93	10	36368	1.27
	Trees	120	152396	-	120	242118	-	72	206268	-
	Total	149	21439	-	149	328184	-	89	269299	-

Fig. 21 wauchope basal area increment in relation to sapwood area (1980)

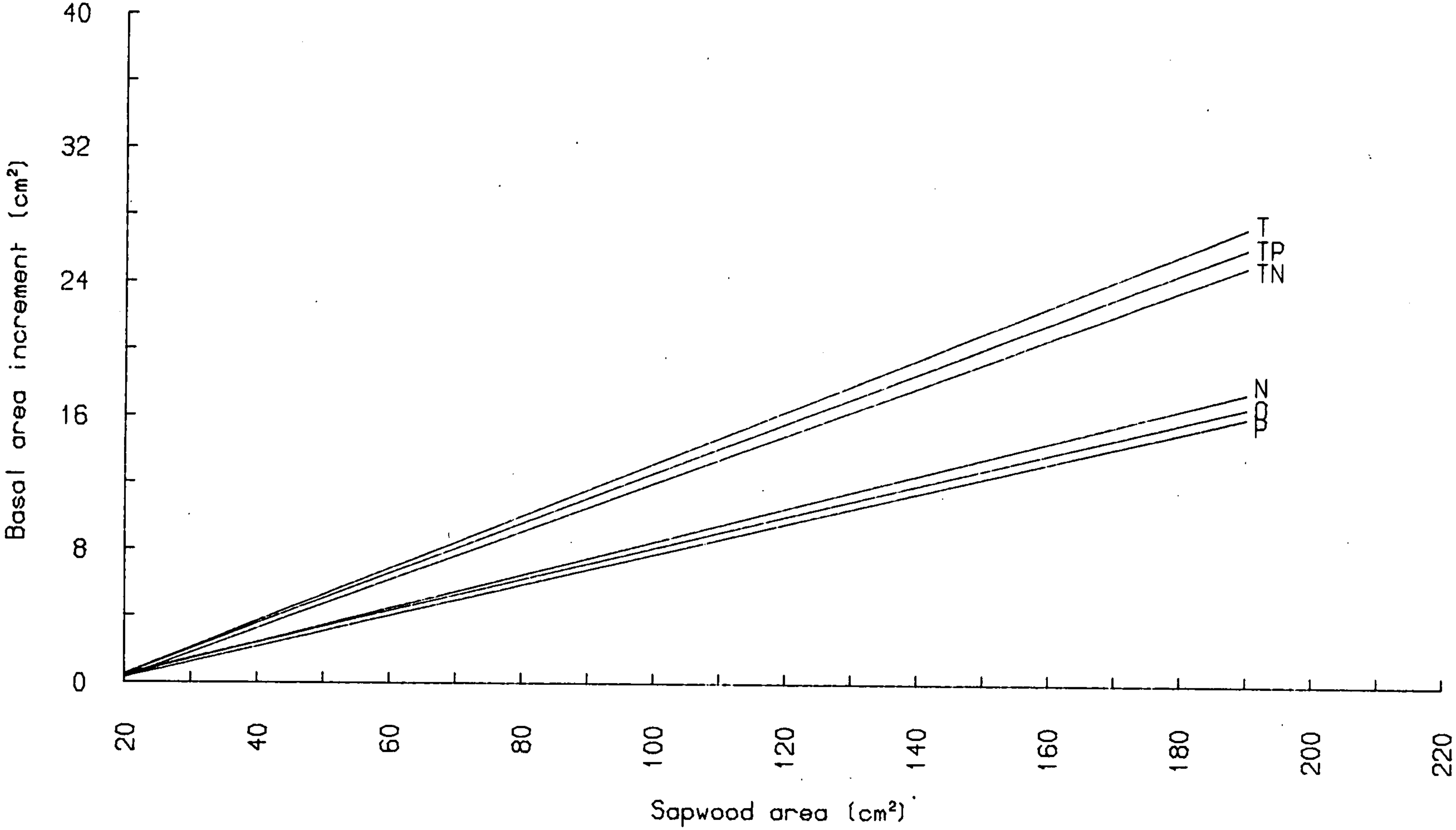


Fig. 22 wauchope basal area increment in relation to sapwood area (1981)

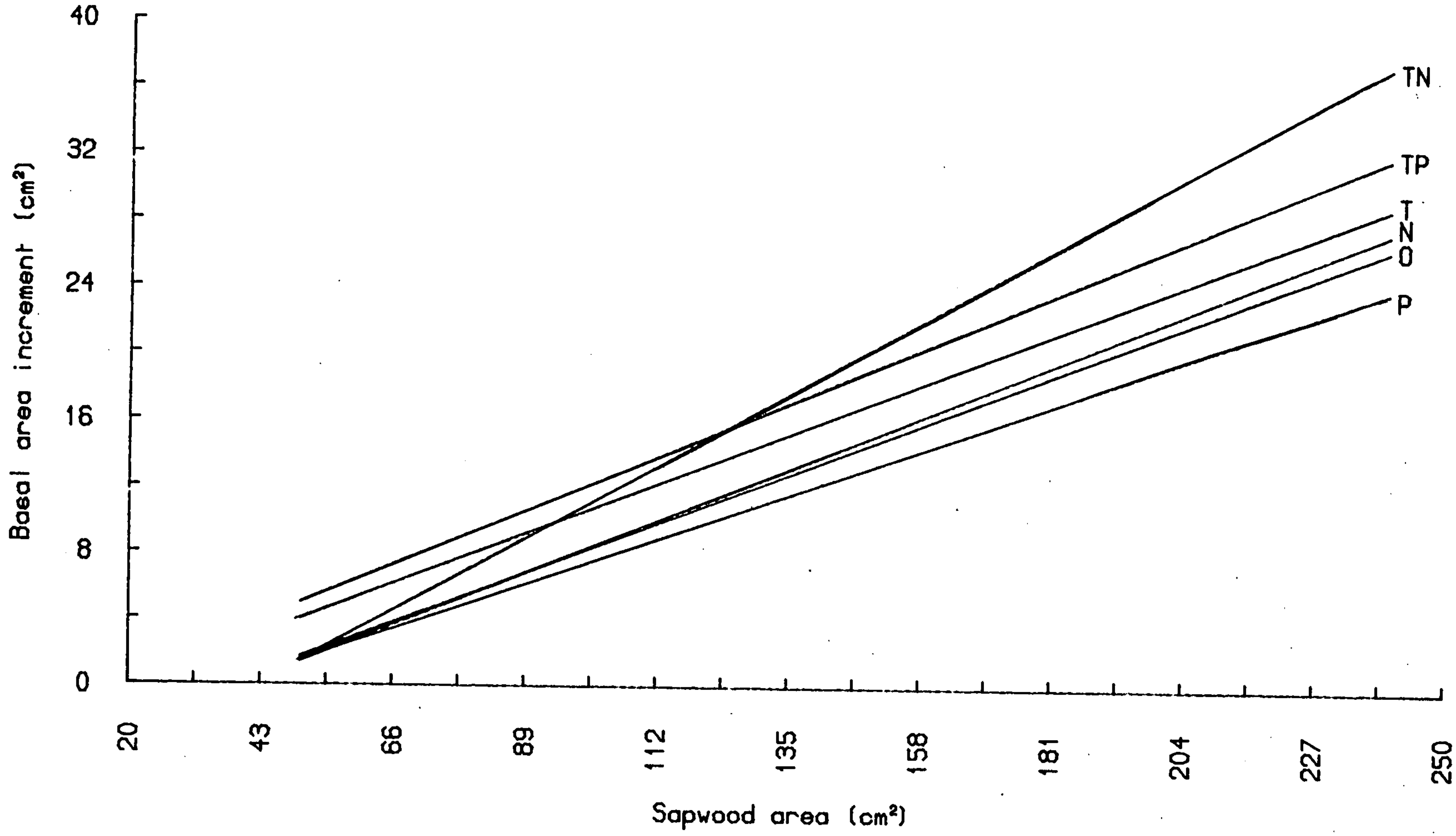


Fig. 23 wauchope basal area increment in relation to sapwood area (1982)

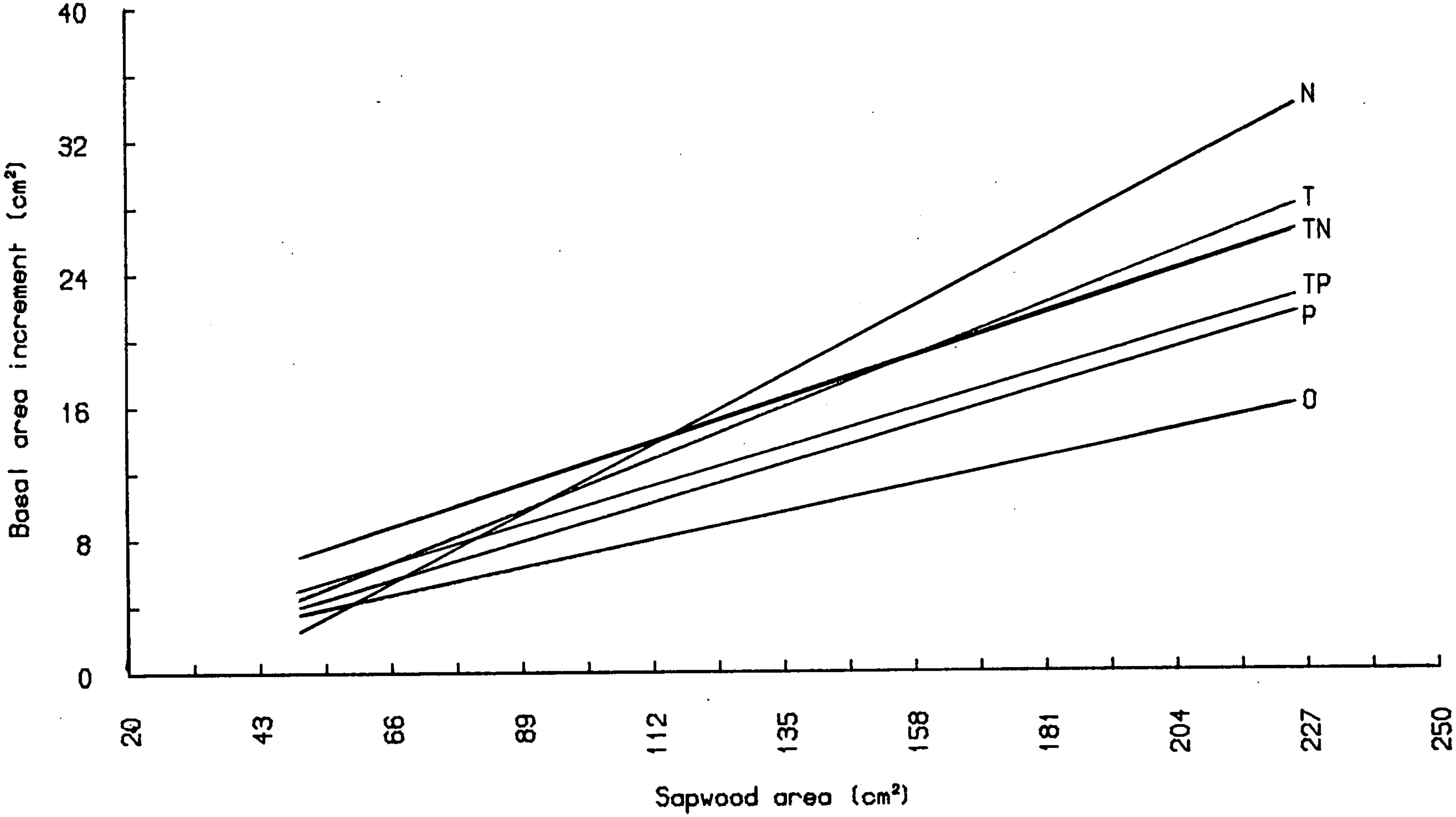
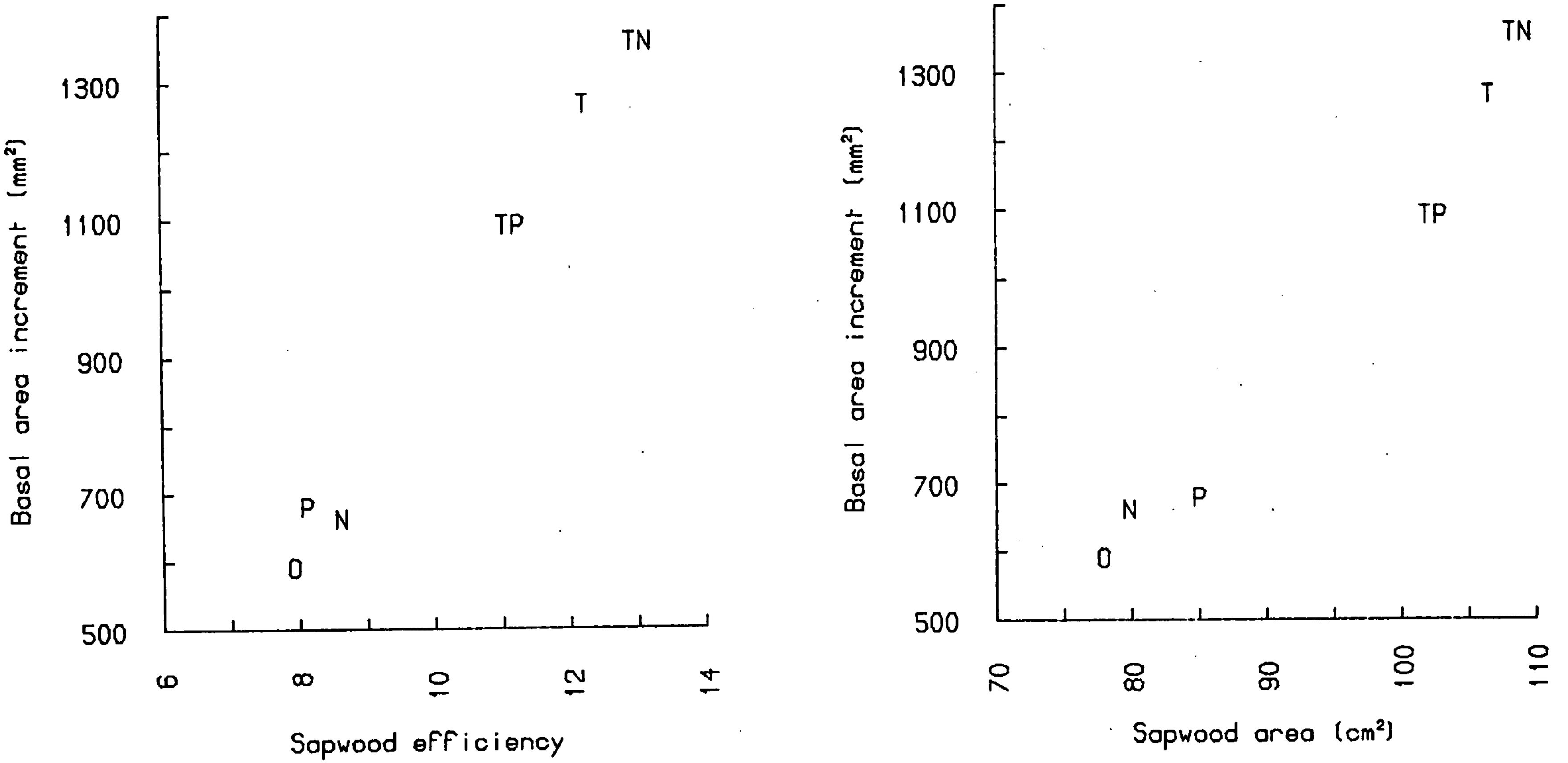


Table 54. Results of the analyses of variance of the basal area increment : sapwood area regressions for the Wauchope sample trees

Year	Source	DF	SS	F
	Overall regression	1	42595296	370.79***
	Intercepts	5	6433056	11.20
1980	Slopes	5	1529280	2.66*
	Residual	138	15852792	1.00
	Total	149	66410480	
	Overall regression	1	67366336	508.70***
	Intercepts	5	1448960	2.18
1981	Slopes	5	1994864	3.01*
	Residual	138	18275168	1.00
	Total	149	89085392	
	Overall regression	1	46163184	244.87***
	Intercept	5	2057840	2.18
1982	Slopes	5	4090128	4.34**
	Residual	78	14704695	1.00
	Total	89	67015936	

Fig 24. Wauchope basal area increment in relation to sapwood area and sapwood efficiency. (Data points are means, over three years, of the sample tree values.)



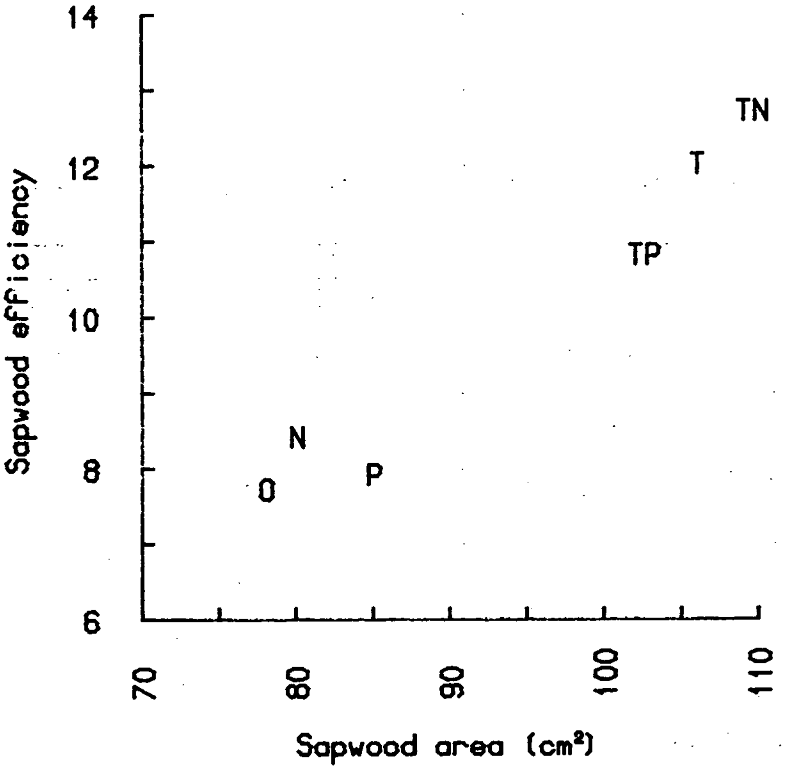


Fig 25. Wauchope sapwood efficiency in relation to sapwood area for individual treatments. (Data points are means, over three years, of the sample tree values.)

Table 55. Mean leaf area index (LAI), plot basal area increment (BAI) and and stand leaf efficiency (SLE) by treatment in the Wauchope experiment at the end of 1981

Treatment	LAI	BAI m^2/ha	SLE
O	8.61	1.88	0.22
P	8.75	2.11	0.24
N	9.32	2.21	0.24
T	6.49	2.39	0.37
TP	6.07	2.25	0.37
TN	6.60	2.48	0.38

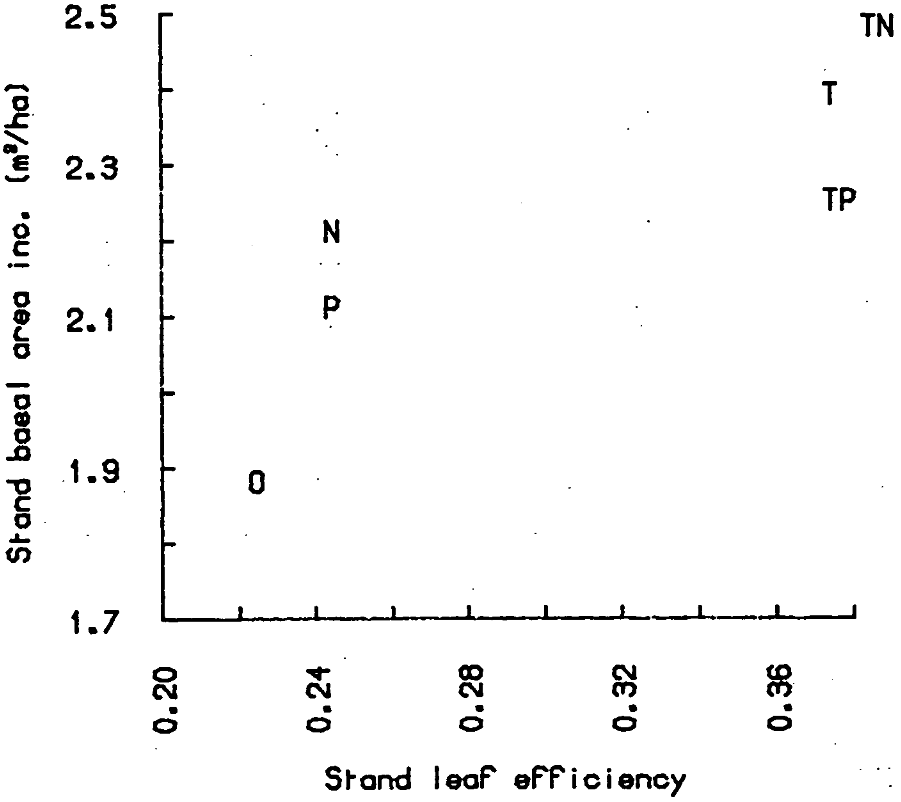


Fig 26. Wauchope stand basal area increment over 1980 and 1981 in relation to stand leaf efficiency over the same period.

CHAPTER EIGHT

FOLIAR NUTRIENT CONCENTRATION STUDIES

8.1 Methods

In the Benmore experiment where fertilizer was applied in 1977 the intention was to carry out foliar nutrient concentration determination on a sub-sample of dried needles from each needle age class of each of the whorls sampled in 1979. Following the destruction of a large number of samples (due to circumstances outwith the author's control) prior to their being analysed, a more limited investigation was necessary which concentrated on all needle age classes at whorls 1, 3, 5, 7 and 9 only, giving a total of 16 possible data values per tree for each of the nutrient elements examined (N, P, K). It was possible to use the data from 13 trees in treatment NP with 15 missing values out of a total of 208 and in treatment 0, 14 trees were used with 60 missing values out of a total of 224. In order to produce a table of treatment means, missing values were estimated using a least-squares procedure as provided by the 'Genstat' analysis of variance package.

The data from four trees per treatment, chosen randomly from those trees with no missing values, were used to calculate nutrient quantities in relation to foliage area, as grams of nutrient per square metre of fresh foliage.

In the Wauchope experiment, which had been fertilized in 1980, foliage was sampled according to normal procedures, ie five dominant trees per plot were randomly selected and marked and in each October of 1980 to 1982 inclusive one lateral shoot from whorl 1 was removed from each tree and foliar nutrient concentration determination carried out on the bulked five-shoot sample as described in section 3.6.

8.2 Benmore results

Mean foliar nitrogen (N), phosphorus (P), and potassium (K) concentrations by treatment, whorl number and age of needle are shown in Table 56 and weighted mean concentrations with respect to whorl number (vertical distribution) and age of needle (horizontal distribution) are shown in Figs 27 and 28.

8.2.1 Vertical distribution

There was a tendency for the concentrations of all three nutrients to decline from the top of the crown to the bottom, a decline which was most noticeable in the case of potassium and least marked in the case of nitrogen. Mean foliar N concentration at whorl 9 was 93% of the whorl 1 concentration in treatment 0 and 80% in treatment NP, while the corresponding figures for foliar K concentrations were 53% and 56%. Decline in foliar P concentrations was intermediate with whorl 9 concentrations at 69% and 12% of the whorl 1 concentrations in treatments 0 and NP respectively. The rate of decrease in concentration was most marked in the top half (W1 to W5) of the crown and was confined largely to the 1 and 2 year old foliage. In the 1 and 2 year old needles in the lower crown and in the 3 and 4+ needles at all whorls, nutrient concentrations were relatively constant except that there was a rise in foliar K concentrations between whorl 7 and whorl 9, a trend evident at all ages of needles.

Foliar K concentration was slightly (8%) higher at W1 in the fertilized trees but otherwise there was little difference in foliar K concentration between fertilized and control trees at any whorl. Foliar N and P concentrations, however, were consistently higher at every whorl in the fertilized trees and the concentration differences appeared to be highest at W1, were progressively reduced at whorls 3 and 5, and remained relatively constant at whorls 7 and 9. Thus mean foliar N concentration was 29% higher in fertilized trees at W1 and 10% higher at W9 and the corresponding figures for foliar P concentration were 29% and 15%.

8.2.2 Horizontal distribution Foliar P and K concentrations declined consistently with increasing age of needle, a pattern evident at all whorls and in both treatments. Foliar P concentrations of 4+ needles were 73% and 64% of the W1 concentrations in treatments 0 and NP respectively, and the corresponding figures for K concentrations were 53% and 48%. Foliar N concentrations however, generally increased between 1 and 2 year foliage and thereafter decreased with increasing needle age. N concentration of 4+ foliage therefore, was 93% of 1 year foliage in treatment 0 and 88% in treatment NP. Differences in foliar N and P concentrations between fertilized and unfertilized trees were evident at all needle ages but the largest differences were in the 1 year foliage. Foliar N concentration of fertilized trees was 17% higher in 1 year needles and 10% higher in 4+ needles and the corresponding figures for foliar P concentrations were 23% and 8%. Foliar K concentration was slightly (10%) higher in 1 year needles from fertilized trees but otherwise there was no treatment effect.

8.2.3 Nutrient content per unit of leaf area The expression of nutrient content as a function of the leaf area gave values of between 1.47 and 3.34 g/m^2 for nitrogen, 0.20 to 0.52 g/m^2 for phosphorus, and 0.57 to 1.86 g/m^2 for potassium. The pattern of variation was however, very similar to that of the nutrient concentrations (Table 57),

Table 56. Mean foliar nutrient concentrations from the Benmore experiment

Nutrient	Age of needles	Whorl Number									
		1		3		5		7		9	
		0	NP	O	NP	O	NP	O	NP	O	NP
% N	1	1.22	1.62	1.24	1.51	1.15	1.29	1.15	1.32	1.01	1.34
	2	-	-	1.30	1.37	1.26	1.47	1.24	1.33	1.19	1.34
	3	-	-	1.14	1.44	1.19	1.35	1.18	1.26	1.19	1.28
	4+	-	-	-	-	1.08	1.27	1.11	1.22	1.09	1.21
% P	1	0.185	0.238	0.163	0.202	0.158	0.185	0.159	0.195	0.157	0.192
	2	-	-	0.155	0.176	0.136	0.160	0.137	0.158	0.141	0.166
	3	-	-	0.139	0.156	0.124	0.134	0.130	0.130	0.126	0.145
	4+	-	0	-	-	0.111	0.128	0.123	0.127	0.118	0.129
% K	1	0.78	0.84	0.57	0.58	0.56	0.59	0.56	0.68	0.64	0.76
	2	-	-	0.48	0.44	0.40	0.40	0.43	0.43	0.49	0.56
	3	-	-	0.44	0.43	0.34	0.33	0.35	0.33	0.40	0.47
	4+	-	-	-	-	0.32	0.32	0.31	0.30	0.34	0.36

% oven dry weight

Fig.27 Nutrient concentrations in relation to whorl number (Benmore)

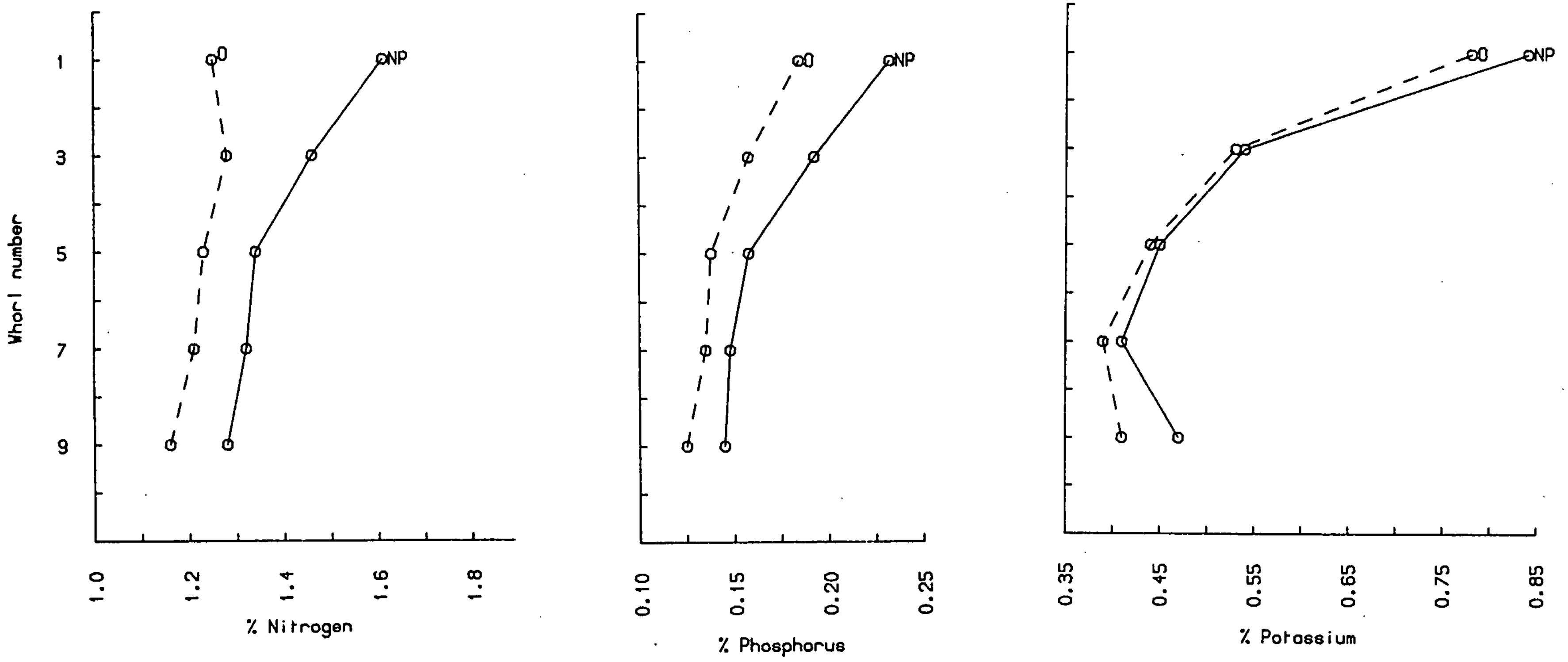


Fig.28. nutrient concentration in relation to needle age

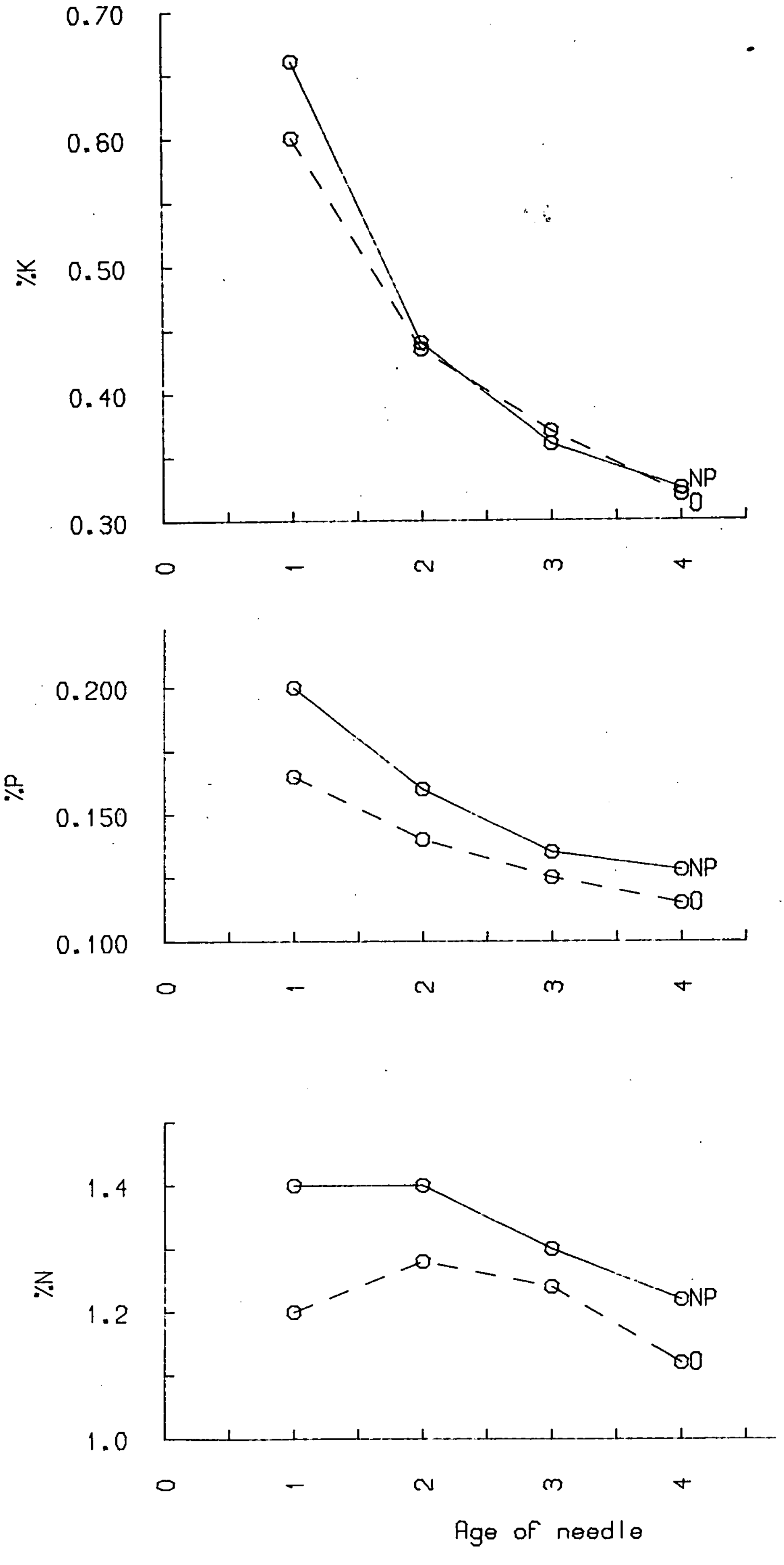


Table 57. Mean foliar nutrient concentrations (a) and mean foliar nutrient quantities (b) by whorl number and age of needle (Benmore)

Treatment			Whorl Number					Age of Needle			
			1	3	5	7	9	1	2	3	4+
N	0	a	1.22	1.23	1.17	1.17	1.12	1.15	1.25	1.18	1.09
		b	2.41	2.38	2.16	1.90	1.77	1.88	2.15	2.19	2.04
	NP	a	1.62	1.44	1.35	1.28	1.29	1.42	1.38	1.33	1.23
		b	3.34	3.07	2.60	2.26	2.06	2.58	2.50	2.56	2.04
P	0	a	0.199	0.154	0.130	0.131	0.136	0.169	0.142	0.127	0.109
		b	0.39	0.30	0.24	0.23	0.22	0.28	0.25	0.24	0.23
	NP	a	0.251	0.196	0.163	0.155	0.167	0.216	0.175	0.147	0.135
		b	0.52	0.42	0.32	0.27	0.27	0.40	0.32	0.28	0.26
K	0	a	0.86	0.52	0.41	0.43	0.47	0.66	0.47	0.39	0.32
		b	1.67	1.00	0.74	0.68	0.74	1.07	0.81	0.73	0.60
	NP	a	0.91	0.55	0.49	0.48	0.68	0.77	0.51	0.47	0.44
		b	1.86	1.18	0.94	0.81	1.01	1.40	0.92	0.89	0.74

concentrations expressed as % oven dry weight
quantities expressed as g/m^2

with quantities generally decreasing in response to increasing age of needle and increasing whorl number. Expression of the data in terms of nutrient quantity (g/cm^2) gave a very similar picture of the relative differences between fertilised and control trees as that obtained using nutrient concentrations. consequently the relationship between concentration (% oven dry wt) and content (g/m^2) was examined separately for each nutrient in a series of linear regression analyses and the resulting correlation coefficients for N, P and K were 0.80, 0.85 and 0.88 respectively.

8.3 Wauchope results

Top whorl foliar nutrient concentrations for the years 1980 to 1982 inclusive are shown in Table 58 and the results of analysis of variance in Table 59. Foliar N concentrations ranged from 1.65 to 2.13% and there were no significant differences between fertilizer treatments in any year. In 1980 foliar N concentrations were highest in trees from nitrogen fertilized plots (nearly significant at 5% level), but in 1981 and 1982 there were no apparent fertilizer effects. Thinning resulted in a significant ($p = 0.05$) reduction in foliar N concentrations in 1981, from a mean of 2.02% in unthinned plots to 1.93% in thinned treatments and this reduction was evident in all fertilizer treatments. In 1981 and 1982 however, there were no significant or apparent thinning effects.

Foliar phosphorus concentrations ranged from 0.22% to 0.31% and no significant or apparent treatment effects were detected in any year. Similarly, foliar potassium concentrations which ranged from 1.04% to 1.30% showed no significant treatment effects although there was a tendency for trees in fertilized plots (both P and N) to have slightly (1 to 8%) higher foliar K concentrations in each year.

8.4 Discussion

Foliar nutrient concentration results from the Benmore experiment are affected by the extent to which missing values, particularly in treatment 0, have had to be estimated and for this reason no statistical analysis of this data was attempted. Nevertheless the results indicate consistent trends with regard to the effect of crown position on needle nutrient concentrations. Foliar N, P and K concentrations show a sharp decrease over the first 5 whorls and a reduced rate of decline between whorls 5 and 9. Foliar K concentrations show signs of recovery at W9 and both P and K concentrations decline progressively with increasing age of needle. The pattern appears to be slightly different in the case of N where there is a suggestion of an increase in concentration from age 1 to age 2 needles, particularly in the control treatment, followed by a progressive reduction in the 3 and 4+ needles. W1 nutrient concentrations in the Wauchope experiment are considerably and consistently higher than those at Benmore but the effect of fertilizer application is more clearly demonstrated at Benmore where foliar N and P concentrations were consistently higher in fertilized trees at all whorl positions. At Wauchope N concentration appeared to be increased in the first year following nitrogen application but otherwise there were no apparent fertilizer effects. One year needles, particularly those in the top whorl, appeared to show the greatest differentiation between fertilized and unfertilized trees at Benmore and, on the basis of a limited sample, it appears that expression of nutrient levels as a function of leaf area gives a very similar result to the use of concentrations. Thinning appeared to reduce foliar N concentrations in the first year of the Wauchope experiment but otherwise had no apparent effect on foliar nutrient concentrations.

Table 58. Foliar nutrient concentration results from the Wauchope experiment

Element	Treatment	Year		
		1980	1981	1982
N	0	1.98	1.73	1.86
	P	1.96	1.65	1.81
	N	2.13	1.82	1.85
	T	1.88	1.81	1.85
	TP	1.94	1.85	1.91
	TN	1.95	1.78	1.82
P	0	0.27	0.22	0.25
	P	0.28	0.24	0.28
	N	0.31	0.25	0.28
	T	0.29	0.25	0.27
	TP	0.30	0.27	0.31
	TN	0.29	0.24	0.26
K	0	1.16	1.04	1.19
	P	1.24	1.12	1.25
	N	1.24	1.18	1.23
	T	1.18	1.12	1.20
	TP	1.30	1.11	1.15
	TN	1.23	1.07	1.20

% oven dry weight

Table 59. Results of the analyses of variance of the Wauchope foliar nutrient concentration results

Element	Source	DF	1980		1981		1982	
			SS	VR	SS	VR	SS	VR
N	Blocks	4	0.2810	4.45	0.1299	2.84	0.1806	5.82
	Fertiliser	2	0.0740	2.34	0.0121	0.49	0.0027	0.17
	Thin	1	0.0691	4.37*	0.4646	3.76	0.0026	0.34
	T x F	2	0.0336	1.06	0.0685	2.78	0.0219	1.41
	Residual	20	0.3160	-	0.2466	-	0.1550	-
	Total	29	0.7739	-	0.5036	-	0.3628	-
P	Blocks	4	0.0101	4.37	0.0054	3.09	0.0058	1.47
	Fertiliser	2	0.0014	1.25	0.0015	1.75	0.0051	2.56
	Thin	1	0.0001	0.28	0.0011	2.47	0.0005	0.48
	T x F	2	0.0019	1.66	0.0026	2.95	0.0045	2.24
	Residual	20	0.0116	-	0.0087	-	0.0199	-
	Total	29	0.0252	-	0.0193	-	0.0357	-
K	Blocks	4	0.1767	4.95	0.0699	2.27	0.2821	8.53
	Fertiliser	2	0.0504	2.82	0.0088	0.57	0.0025	0.15
	Thin	1	0.0041	0.46	0.0009	0.13	0.0101	1.22
	T x F	2	0.0076	0.43	0.0443	2.87	0.0180	1.09
	Residual	20	0.1787	-	0.1541	-	0.1654	-
	Total	29	0.4175	-	0.2781	-	0.4781	-

CHAPTER NINE

DISCUSSION AND CONCLUSIONS

9.1 Productivity Mean annual volume increment over the period of this study was 8 m^3/ha in the Benmore experiment and 23 m^3/ha at Wauchope and estimated general yield classes (average annual volume increment over the life of the stand) were 12 and 20 respectively. These stands therefore fall into the category of 'average' and 'highly productive' when compared to the 'normal' range of yield class (6 to 24) encountered in Britain (Hamilton and Christie, 1971). Both stands however responded significantly to the application of nitrogen fertiliser. In the Benmore experiment the average annual increase in volume increment due to the application of nitrogen was estimated to be 2.2 m^3/ha (29%) while at Wauchope the increase amounted to 3.4 m^3/ha (15%) in the absence of thinning and 3.2 m^3/ha (12%) in the thinned plots. These values are well below the increases of 4.5 to 19.4 m^3/ha/year recorded in some Radiata pine stands in New Zealand (Mead and Gadgil, 1978) and are less than the 3.78 to 7.49 m^3/h/year increases recorded in Douglas fir stands in the Pacific Northwest (Miller *et al*, 1979). They compare favourably however, with the values of 0.6 to 3.4 m^3/ha/year recorded following nitrogen application to spruce stands on mineral soils in Sweden (Tamm, 1982). Miller (1981) has suggested that fertiliser responses are less likely in conifer stands once the crown is fully formed and attributes this to the effects of canopy closure on nutrient immobilisation in the tissues (reduced), recycling of nutrients (increased) and capture of atmospheric inputs (increased). The rate of uptake by the stand at this stage may be matched by the inputs from recycling, atmospheric inputs and internal redistribution of nutrients and the tree becomes less dependent on the soil and less likely to respond to the addition of fertilisers. As Tamm (1982) points out however, nitrogen immobilisation in an accumulating litter layer is a feature of most northern coniferous forests and where high rates of immobilisation coincide with sites of low total nitrogen capital, nitrogen deficiency is the likely result, as described by Miller et al (1973) in their work on the response of Corsican pine on sand dunes to nitrogen application. The Benmore experiment is located on a relatively infertile site with a relatively deep organic layer in which nitrogen mineralisation rates might be expected to be very low, coupled with wet, cool conditions favouring the net accumulation of litter. Under these conditions it is perhaps not surprising that there was a degree of nitrogen deficiency but it is interesting to note the response at Wauchope where the stand is of high productivity and a site type normally regarded as one of the most fertile (Pyatt, 1970).

Basal area increment in these experiments generally has mirrored the volume responses, indicating a relatively stable relationship between volume and basal area. In other studies however, (eg Woollons and Will, 1975), fertiliser application has been found to have significant effects on the ratio of volume to basal area, with estimates based on basal area alone generally resulting in an underestimate of the volume response. Similar changes in tree shape following fertiliser application have been recorded by Miller and Cooper (1973) Mitchell and Kellogg (1972) and Meng (1980). A point overlooked by some authors is that increases in volume increment will normally result in a change in stem form due to the effects of tree size on stem form and a distinction should be made between this effect and the effect of fertilisers per se. In this study the ratio of volume to basal area was compared across treatments both before and after adjustment of the stem volumes by covariance analysis in an attempt to account for the effects of tree size (basal area). No significant fertiliser effects were found but in the Benmore experiment application of fertiliser appeared to increase the ratio of volume to basal area, an increase which was partly but not entirely reduced by adjustment of the stem volumes. There is a suggestion therefore that fertiliser application per se affected the volume to basal area ratio but no firm conclusions can be drawn. The measurements of volume and basal area were made only 3 years after fertiliser application and the volume response was relatively small so it is not perhaps surprising that no significant effects have emerged. In a study of the effect of fertiliser treatment on tree shape on a 31 year old Sitka spruce stand which had shown a marked response to fertiliser applied 9 years previously; Arabatzoglou (1983) found a significant increase in form factor due to fertiliser application and Snowdon et al (1981) found significant differences in the average taper of fertilised and unfertilised trees which could not be accounted for simply by the differences in tree size.

Height increment in the Benmore experiment was significantly increased by fertiliser (NP) application along with basal area and volume but in the Wauchope stand, although nitrogen application increased volume and basal area increment no height response was recorded. This may reflect the non-representativeness of the 1983 Wauchope sample trees in treatment N, to which reference has already been made (Section 5.3), or it may be a true result since a similar result has been recorded by Woollons and Will (1975) who found no height increment response in a high productivity Radiata pine stand following fertiliser application even though a significant volume response was recorded.

As regards the effect of tree size on fertiliser response it appears that basal area response of trees was in direct proportion to their size and this agrees with the conclusion of Miller and Cooper (1973) that fertiliser response can generally be described by using the simple analogy of an accelerated time scale.

The effect of the thinning treatment on the growth of the remaining trees in the Wauchope experiment was to significantly increase basal area and volume increment. This is the typical result obtained after thinning when opening of the canopy and provision of greater growing space leads to an increase in the diameter increment of the remaining trees. The interesting feature of the Wauchope experiment is that despite the removal of one third of the basal area (44% of the tree stems), basal area increment per hectare was significantly increased by thinning, implying that the increase in basal area growth of the remaining trees was more than enough to compensate for the reduction in tree numbers. Similar results have been noted by Bradley (1963) and Assmann (1970). Assmann considered that this situation was likely to occur in young stands which have not yet reached the peak of their current annual volume increment (CAI). Thinning at this stage may result in accelerated growth of the remaining trees so that they reach the culmination of their CAI earlier than unthinned trees. This implies that the time of reduction in CAI will also be reached earlier so that the net increase in volume increment per hectare may eventually be cancelled out, resulting eventually, in similar volume production from thinned and unthinned stands. Hamilton and Christie (1971) suggest that the maximum CAI of a yield class 20 stand is reached around age 30. Thinning was applied in the Wauchope experiment at age 23 which puts it into the category where response to thinning might be of the type outlined. There are no indications in this study of any thinning effects on the volume to basal relationship of individual trees. Thinning is generally considered to result in a shift of increment down the stem in response to increased exposure and crown size (Reukema, 1961) and may lead to a decrease in the cylindricity of the stem (Larson, 1963). In this study the period of measurement was perhaps too short, and the methods of measurement, too coarse, to show up any significant effects. The negative effect of thinning on height increment in the Wauchope experiment is a commonly reported phenomenon sometimes referred to as 'thinning shock' (Miller and Reukema, 1977; Crown _et al_, 1977). Harrington and Reukema (1983) have suggested that the severity of 'thinning shock' is related to thinning intensity, site quality and tree species, vigour and age and that it is normally only a short term (2-3 year) effect.

The results of the Wauchope experiment suggest that in this case the effects of thinning and fertiliser, when applied in combination, are simply additive and no interaction is apparent. Additional estimated volume increment over control was 10.4 m^3/ha attributable to N, 9.1 m^3/ha attributable to the effects of thinning and 18.7 m^3/ha when both treatments were combined. This result is similar to those obtained in Douglas fir stands by Barclay _et al_ (1982), Lee (1974) and Miller _et al_, (1979) but differs from results in pine stands (Ryker and Pfister, 1967; Agee and Biswell, 1970).

9.2 _Mechanisms of response_ This study set out to examine the effects of thinning and fertiliser treatments on the relationship between productivity and two principal contributors to the level of productivity, ie the quantity of photosynthetic tissue and the efficiency of that tissue. The results suggest that both of these variables have been affected. In the Benmore experiment fertiliser application increased both leaf area and leaf efficiency and in the Wauchope experiment leaf area and leaf efficiency appeared to be affected by thinning and possibly by fertiliser application.

9.2.1 Leaf area Three years after fertiliser treatment in the Benmore experiment, fertilised trees carried greater leaf area than control trees. Mean leaf area per tree was 25% greater in fertilised trees and leaf area index was 24% greater. The increase in leaf area was largely attributable to an increase in the area of needles formed in the upper crown in the second and third years following fertiliser application and was associated with a slight reduction in the area of all needle ages in the lower crown. Examination of the components of the leaf area indicated that an increase in needle number was the main factor responsible and only small, non-significant effects on average needle size were indicated. In the Wauchope experiment the results were less clear. Nitrogen application appeared to result in an estimated 8% increase in LAI in the absence of thinning and a 2% increase in LAI in the thinned plots based on the regressions of 1981 leaf area on diameter. On the basis of the sample trees felled 3 years after fertiliser treatment however, nitrogen application appeared to have reduced leaf area at the whorl 1 and whorl 7 positions. The reduction in needle area at W1 appeared to be as a result of smaller average needle size while at W7 the reduction appeared to be due to fewer needles and needle size was relatively unaffected. The results of these two exercises are at variance and need some discussion. The 1981 estimate of leaf area index is based on the leaf area : diameter regressions. In view of the error inherent in the use of these regressions (diameter accounted for 81% of the variability in leaf area) and the within treatment variability in LAI, the small differences in LAI recorded, which are not statistically significant, cannot be considered to be 'real'. Similarly, the lower leaf area recorded in the N treatment in the 1982 sample trees at Wauchope may possibly be explained by the non-representativeness of the N treatment sample trees as previously discussed. In view of the above factors it is not possible to draw any definite conclusions about the effects of fertiliser application on leaf area in the Wauchope experiment but it is clear that any changes which occurred must have been relatively small since the methods used should have identified any significant effects.

In contrast, the effect of thinning on leaf area in the Wauchope experiment is clearly demonstrated and resulted in an apparent, but non-significant, reduction in leaf area relative to control at W1, no apparent effects at W4 and a highly significant increase at W7. Similarly LAI of thinned plots was clearly much lower (28%) than that of unthinned treatments. The lower leaf area recorded at W1 is consistent with the height increment reduction already discussed since a smaller terminal shoot is likely to also have smaller leaf area. Similar effects have been recorded by Maguire (1983) who found that thinning resulted in increased bud production but lower terminal and lateral shoot growth in Douglas fir stands and by Brix (1981b) who demonstrated that Douglas fir trees subjected to thinning produced, in the first 2-3 years at least, lower leader length and needle production. The increase in needle area at W7 is consistent with the results of Brix (1981b) who found that thinning effects on needle mass were most noticeable in the lower crown and this is to be expected since the improved light conditions following thinning are clearly likely to be of greatest benefit in the lower crown. Greater leaf area at W7 in trees in thinned plots was due to greater leaf dry weight through an increase in the number of needles of all ages and average needle area and average needle dry weight were not significantly affected. The increase in the number of 4+ needles (laid down prior to the treatments being applied) is likely to be due to increased needle retention but the increased needle number in 1, 2 and 3 year age classes could be due to an increase in needle production following thinning. Determination of the way in which changes in needle number were brought about is outwith the scope of this study but Brix (1981b) attributed such increases partly to an increase in the number of shoots produced and partly to an increase in the number of needles per shoot. As with the productivity data, no interactions between thinning and fertiliser effects on leaf area were evident in the data from the Wauchope experiment.

The thinning and fertiliser effects on leaf area recorded in the Benmore and Wauchope experiments appear to be due to changes in total needle dry weight and needle number. Increases in needle area following thinning and fertiliser have therefore been by an increase in the number of needles and significant changes in average needle weight and area are not implicated. This result disagrees with the findings of Miller _et al_ (1976), Brix and Ebell (1969), Keay _et al_ (1968), Turner and Olson (1976) and Albrektson _et al_ (1977), all of whom recorded increases in needle size as well as needle number following fertiliser application and is at variance with the work of Brix (1981b) who found that thinning increased average needle weight in the lower crown as well as the number of needles. Small increases in both average needle weight (2 to 9% depending on whorl number) and average needle area (5 to 9%) in fertilised trees were in fact recorded in the Benmore experiment and although the differences were not significant they are of the same order as the increases noted by Brix (1981b) and may well represent a 'real' effect.

The relationship between needle area and needle weight (specific needle area) did not appear to be significantly affected by either fertiliser or thinning treatments but there was a clear trend towards increasing specific needle area (SNA) with increasing whorl number and decreasing SNA with increasing age of needle. Both the absolute levels of SNA and the variations with crown position are similar to those recorded in Sitka spruce stands by Lewandowska and Jarvis (1977) and by Ford (1982) and similar variations with crown position have been recorded for other species by Del Rio and Berg (1979) and Benecke (1979). Variations in SNA are considered to reflect differences in the degree of shade with 'shade' leaves having higher SNA than 'sun' leaves (Lewandowska and Jarvis, 1977). SNA might therefore be expected to be affected by treatments which affect the level of shade within the canopy. Data from the Benmore and Wauchope experiments do show such a trend. At Benmore SNA of lower whorl needles was slightly (though not significantly) greater in fertilised trees and this is probably a response to the increased shade present in the lower canopy as a result of the increase in leaf area in the upper canopy due to fertiliser application. Similarly at Wauchope, SNA was higher at W7 in the unthinned treatments but not in the presence of thinning.

9.2.2 Leaf efficiency Three years after fertiliser treatment the level of basal area increment per unit of leaf area (leaf efficiency) in the Benmore experiment was higher in fertilised trees. Mean basal area increment per unit of leaf area was 24% higher in fertilised trees and at the stand level, basal area increment per unit of LAI (stand leaf efficiency) was 11% greater in the fertilised treatments. In the Wauchope experiment the effects of fertiliser on leaf efficiency (judged from measurements of sapwood efficiency) are less clear. In 1980 no apparent or significant effects emerged, in 1981 there was a non-significant indication of higher efficiency in trees fertilised with N and in 1982 treatment N had significantly greater efficiency than all other treatments. Stand leaf efficiency at the end of 1981 was 9% higher in treatment N than treatment 0 and 3% higher in treatment TN than treatment T. Only in the 1982 data therefore, was there any significant increase in efficiency due to nitrogen application. Nitrogen fertilisation has been shown to influence the rate of net photosythesis in Douglas fir (Brix, 1971; 1981a) and was responsible for an increase in the net assimilation rate of Corsican pine (Miller and Miller, 1976). Brix (1983) found an increase in stem production per unit of foliage in fertilised Douglas fir in the first 2-3 years after treatment and Keay _et al_ (1968) recorded an increase in the photosynthetic capacity of white pine needles following nitrogen and phosphorus applications. At least two possible mechanisms may be postulated to explain the observed effects of fertiliser treatment on leaf efficiency. It is well known that the photosynthetic capacity of shoots generally declines with age (Linder and Troeng, 1980). In the Benmore experiment fertiliser treatment resulted in a higher proportion of 'young' shoots, especially in the upper crown. In whorls 1, 3, 5 and 7, the total area of 1 and 2 year shoots per tree was 64% greater in treatment NP and these shoots accounted for 66% of the total leaf area in those whorls as opposed to 58% in treatment 0. In addition the concentrations of nitrogen and phosphorus were consistently higher in the needles of fertilised trees at all crown positions; but especially in the 1 year shoots. Brix (1981a) found a linear relationship between foliar N concentration and rate of net photosynthesis in the foliage of Douglas fir trees and suggested that the optimum foliar N concentrations was 1.74%. Mean foliar N concentration in the foliage of unfertilised trees at Benmore were well below this figure at all whorl positions, suggesting that these mechanisms may have been involved in the observed efficiency increases.

The effects of thinning on tree and stand efficiency were clearly demonstrated at Wauchope. Mean basal area increment per unit of sapwood (leaf area) was significantly greater in trees in thinned treatments in 1980 (80% increase) and 1981 (37%) and was greater (31%), but not significantly so, in 1982. This agrees with the work of Brix (1983) who found that efficiency was increased for a 3 year period following thinning but thereafter returned to the level of unthinned treatments. He attributed increased efficiency in trees released by thinning to the greatly improved light regime, particularly in the lower crown. The effect on stand efficiency at Wauchope at the end of 1981 was similar, with an increase of 61% in thinned plots.

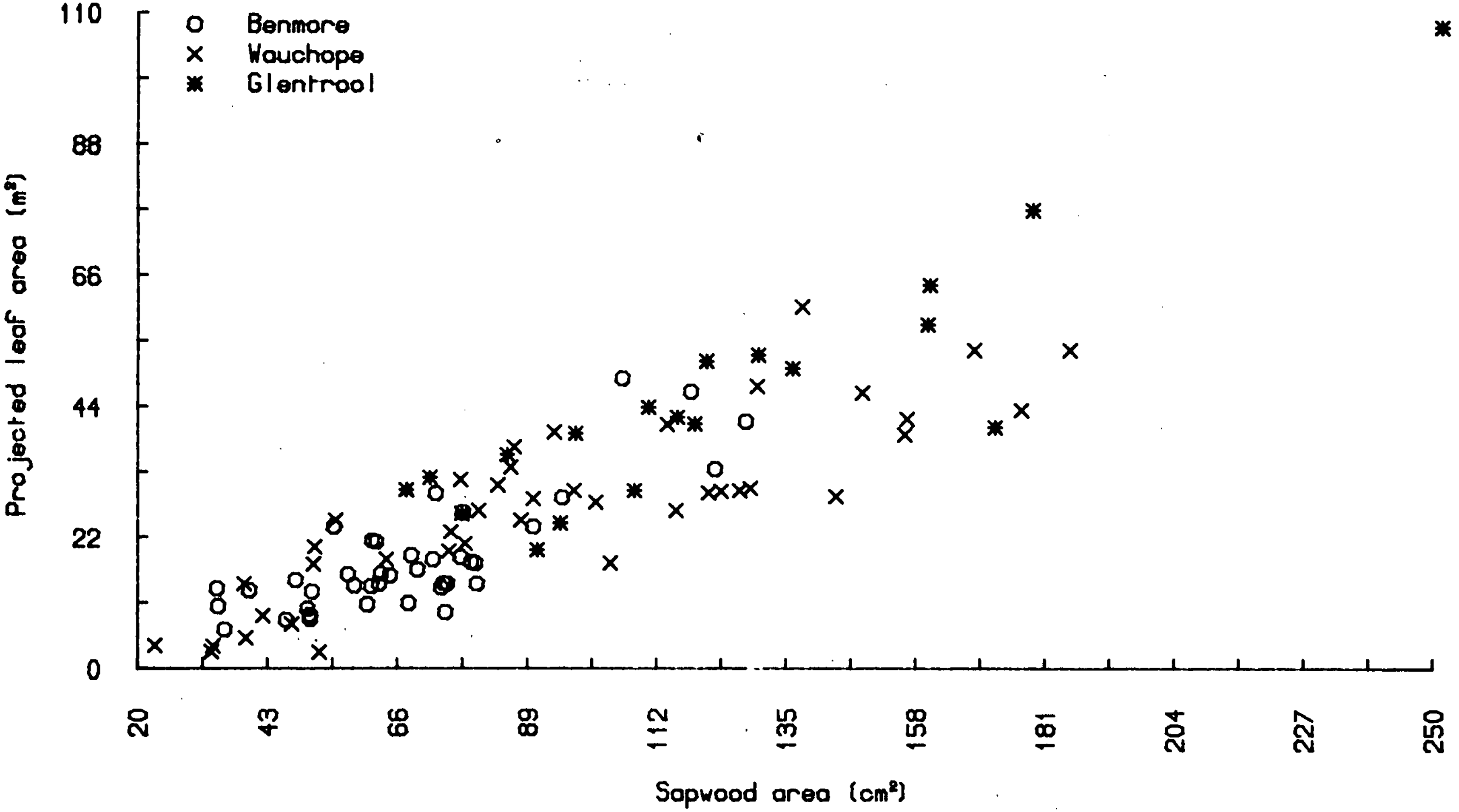
9.2.3 Leaf area : leaf efficiency : productivity relationship The concept of an optimum critical leaf area index above which the linear relationship between foliage quantity and production can be expected to break down has long been recognised in agricultural crops (Watson, 1958) but data from the forest situation are more limited. Albrektson et al (1977) demonstrated a linear relationship between LAI and above ground dry weight production in stands of spruce and pine at relatively low levels of LAI (1 to 6) and a similar result was obtained by Madgwick and Olson (1974) in thinned stands of Liriodendron tulipifera.

Waring et al (1981) however, in a Douglas fir thinning experiment, found that net stand volume growth reached a peak at LAI of 6 and further increases in LAI were not accompanied by significant increases in yield. This effect is attributed largely to the adverse effect of increasing canopy density on the efficiency of trees in the stand and a negative linear relationship between leaf biomass or LAI and leaf efficiency has been demonstrated by Waring et al (1981) and Satoo (1971). Application of fertiliser in the Benmore experiment resulted, 3 years after application, in a LAI of 7.7 compared with 6.2 in the control and mean leaf area per tree was 25% higher in fertilised plots. The relationships between leaf area and basal area increment at both the stand and individual tree level however, remained linear with increasing basal area increment in response to increasing leaf area. Similarly, in the Wauchope experiment, basal area increment tended to increase linearly with increasing leaf area and in neither experiment was there any clear indication of a reduction in leaf efficiency with increasing leaf area. At Benmore, leaf efficiency tended to increase with increasing leaf area while stand leaf efficiency showed no obvious relationship with LAI. At Wauchope sapwood (leaf) efficiency appeared to increase with increasing leaf area while there was no clear relationship between stand leaf efficiency and LAI except that all unthinned treatments had higher LAI and lower stand leaf efficiency than thinned treatments. These results suggest that neither of these stands had reached its optimum leaf area and that further increases in LAI through further fertiliser treatment, improved moisture regimes etc could lead to further increases in production.

The concept of an optimum leaf area provides a possible explanation for the appearance of fertiliser/thinning interactions in some stands but not others and also a reason for the reduction in basal area increment sometimes encountered following nitrogen application. Applications of fertiliser to a stand which is already at the optimum LAI are likely to result in increased leaf area leading to a reduction in leaf efficiency with the net result being no increase, or even a decrease in net productivity per hectare. The addition of a thinning treatment in this situation reduces LAI to below the optimum and allows the fertiliser effects to operate fully without adverse effects on leaf efficiency. These observations also suggest a mechanism for the observed fall off in increased leaf efficiency in thinned treatments in this study and the study by Brix (1983). The effect of thinning is to improve light conditions and therefore leaf efficiency in the lower crown but since this is also accompanied by an increase in foliage production in the lower crown, a progressive return to shaded conditions takes place with a concurrent reduction in leaf efficiency. Thus the effects of thinning on individual tree growth are likely to be brought about by changes in leaf efficiency in the first few years but thereafter by changes in foliage biomass, with the relative contribution of each depending on existing light conditions and the degree of thinning. Such a result has in fact been recorded by Brix (1983).

9.3 <u>The use of sapwood area as a measure of leaf area</u> At both Wauchope and Benmore, a significant linear relationship was found between the projected leaf area of a tree and the cross sectional area of conducting tissue (sapwood) at breast height (1.3 m). The mean ratio of leaf area : sapwood area (m^2/cm^2) was 0.26 at Benmore and 0.29 at Wauchope. Waring <u>et al</u> (1982), in a summary of all published accounts at that time, quoted ratios of 0.14 to 0.75 for a range of conifer species including a figure of 0.45 for Sitka spruce derived from unpublished data of Whitehead. The tendency for authors to quote these ratios makes comparisons between sites difficult. Unless the relationship between leaf area and conducting tissue is such that it passes through the origin, and few appear to do so, then the ratio will change with tree size without necessarily implying a change in the relationship. Thus the larger ratio found by Whitehead may simply be due to a larger tree size in his sample area. It was possible to obtain this data, collected in a 30 year old Sitka spruce stand in Glentrool forest, and Fig 29 shows the data from Wauchope, Benmore and Glentrool plotted together. No clear separation between the data sets is evident and it appears that the foliage area : sapwood area relationship is essentially the same at each site. This is in agreement with Waring _et al_ (1982) who considered that the relationship is relatively constant within a species but that differences in the slope of the relationship occur in different species with larger slope coefficients associated with shade tolerant species in mild, moist climates. Whitehead and Jarvis (1982) however, considered that such differences may also occur within a species in response to differences in transpiration rate and climatological conductance and there is limited support for this in the work of Whitehead (1978) who found some variation in the slope coefficients of data from Scots pine stands from different climatic regions within Britain. Average annual rainfall at the Benmore, Wauchope and Glentrool sites is 2000 mm, 1200 mm and 1500 mm respectively and under the bioclimatic classification of Birse (1971) the sites respectively fall into subregions 01, PB1, 02, H_2B^2 and 0_2H_2T1. The range of climatic conditions covered is therefore not great and further work is required to determine the

Fig.29 Comparison of sapwood area : foliage area relationships



effects of climate in the foliage area : sapwood area relationship.

The pipe model theory of Shinozaki et al (1964) suggests that cross sectional area of conducting tissue at the base of the live crown, rather than at breast height should ideally be used. Kaufmann and Troendle (1981) found no differences in the amount of leaf area supported by a unit of conducting tissue from breast height upwards but Waring et al 1982 found significant differences between the 2 sampling positions in a range of conifer species and suggested that this was largely a function of tree size with the crown base position giving a better relationship with leaf area in large trees with a high proportion of clean bole between the base of the crown and breast height. The Wauchope and Benmore trees (height range 7 to 13 m) were considerably smaller than the 18-24 m trees encountered by Waring et al (1982) and it seems unlikely that the use of the crown base position would have significantly improved the relationship in these stands. It would appear prudent, however, to take account of the degree of taper in sapwood area when larger trees are being sampled.

There is no evidence from the present study that the relationship between foliage area and sapwood area is affected by thinning and fertiliser treatments. The slope coefficient was higher in fertilised trees at Benmore but the difference was small and non-significant and, at Wauchope, no treatment effect was either apparent or detectable in the analyses. The time interval between treatment and sampling was short however, and the responses relatively small. Brix and Mitchell (1983) examined the sapwood area : foliage area relationship in a Douglas fir thinning/fertiliser interaction experiment 9 years after treatment and found significantly higher regression slopes for treated trees than for control trees and Granier (1981) found that 6 years after thinning, trees in thinned plots of Douglas fir had greater foliage area per unit of sapwood than unthinned plots. As pointed out by Whitehead and Jarvis (1982) any external influence (climate or cultural treatment) which affects either the rate of transpiration or the sapwood conductivity may influence the relationship between sapwood area and foliage area. Brix (1972) for example found that nitrogen fertilisation resulted in a decrease in the percentage of latewood in Douglas fir and since latewood does not conduct water in Douglas fir (Harris, 1961) the result may be an increase in sapwood conductivity.

Total cross sectional area at breast height (basal area) has proved to be as good an indicator of foliage area as sapwood area in this study. It seems likely that this is related to the proportion of sapwood; thus at Wauchope and Benmore where sapwood accounted for 61 and 66% respectively of the basal area, both sapwood area and basal area show a good relationship with foliage area. As stands age however, the difference between sapwood area and basal area increases with increasing average tree size (Long and Smith, 1983) and while the sapwood area : foliage area relationship appears to be largely independent of tree size, the relationship between basal area (diameter) and foliage weight has been shown to vary greatly with tree size (Baskerville, 1983).

In conclusion therefore it would appear that as a measure of leaf area at a given time in a relatively undisturbed stand, sapwood basal area can be used to provide a relatively good estimate of leaf area and it is justifiable to use a single regression equation over relatively wide stand conditions. More work is required however, to establish whether it can justifiably be used to compare leaf areas between stands subjected to different cultural treatments or in widely different climatic regions.

9.4 Foliage nutrient concentrations

Foliage nitrogen and phosphorus concentrations associated with the onset of deficiency in establishment-phase Sitka spruce stands have been set at 1.2% and 0.14% respectively and optimum concentrations are considered to be 1.5% and 0.18% respectively (Everard, 1973; Binns et al, 1980). As demonstrated by Miller et al (1981) however, optimum foliar nutrient concentrations change with increasing tree age (size) and while there are no published figures for optimum concentrations in established Sitka spruce stands by analogy with the situation in Corsican pine (Miller and Cooper, 1973), Norway spruce (Tamm, 1982), Radiata pine (Mead and Gadgill, 1978) and Douglas fir (Brix, 1981a) optimum foliar N concentration is probably around 1.8%, measured in top whorl foliage. At mean foliar N concentrations of 1.25% and 1.61% in the top whorl foliage of treatments 0 and NP respectively, the trees at Benmore appear to be in a nitrogen deficient situation. These figures, based on the mean of a random sample of trees, may be lower than would be encountered by 'normal' sampling methods based on dominant trees only but nevertheless the highest top whorl N concentration recorded in a dominant tree in the control treatment was 1.50% suggesting that N deficiency was occurring. This accords well with the growth response which took place following nitrogen application but in the Wauchope experiment top whorl foliage N concentration in the control plots varied from 1.73% to 1.98%, yet a significant growth response was recorded. Similarly at Benmore, although mean foliar P concentration in the control plots in 1979 was 0.185%, there was an indication of a growth response to phosphate application. These results agree with those from unpublished Forestry Commission fertiliser experiments in established Sitka spruce stands, recently summarised by McIntosh (in press), where there was some indication of a relationship between foliar N concentrations and response to nitrogen although responses were recorded in stands with more than 2% foliar N, and where no relationship was found between foliar P concentration and subsequent phosphate response.

The vertical and horizontal concentration gradients found at Benmore agree well with the trends generally observed by McLean and Robertson (1981), Comerford (1981), Morrison (1974), Florence and Chuong (1974) and Madgwick (1964) who all found a tendency for N, P and K concentrations to decrease with increasing depth in the crown and increasing needle age. Only Comerford (1981) however appears to have noted the situation found in the control trees at Benmore where 2 year old needles had higher N concentration than 1 year needles. These gradients are generally ascribed to the retranslocation of nutrients from ageing needles and the importance of this source of nutrients has been discussed by Switzer and Nelson (1972) and Miller (1979). Miller et al (1979) proposed that mobilisation of these 'second order' reserves of nutrients, accumulated in excess of the requirements for growth (Miller et al, 1976), would occur when recent root and foliar uptake ('first order' reserves) was insufficient to satisfy demand. This suggests that withdrawal of nutrients from older tissue including needles, might be greater on deficient sites and evidence for this is provided by Florence and Chuong (1974) who found that while site type did not appear to affect foliar N and P concentrations of current needles of Pinus radiata the vertical concentration gradients were affected with greatest concentration gradient between 1 and 4 year needles associated with the least fertile sites. Similarly Lamb (1975) found that correlations between litter nitrogen mineralisation (an index of site quality) and foliar N and P concentrations progressively improved with increasing needle age in Pinus radiata stands. These studies were both however, carried out during the growing season when concentration gradients with needle age are likely to be best developed and this may explain the difference between these results and the Benmore results. At Benmore there was little suggestion of differences in concentration gradients between the treatments, in fact the 1 year needles showed the greatest differentiation between treatments. These results suggest that while standard methods of foliage sampling using top whorl needles collected in the dormant season may provide the best indication of relative nutrient status at least in deficient trees, the absolute levels may not provide a reliable guide to the degree of fertiliser response to be expected. It appears that examination of concentration gradients during the growing season may be worthwhile as well as examination of other diagnostic techniques such as analysis of litter (Miller and Miller, 1976b or the mineralisation potential of forest soils (Shumway and Atkinson, 1978).

Smith *et al* (1981) have suggested that since major changes in tissue dry weight may occur due to fluctuations in stored carbohydrates, the expression of nutrient composition as a percentage of dry weight may lead to difficulties in interpretation and they suggested that expression of results in terms of nutrient content per unit of leaf area is superior. Similar suggestions have also been made by Stachurski and Zimka (1975) and Gholz (1978). In the Benmore study both methods of expressing the results gave similar patterns and there was a good correlation berween foliar concentration (% oven dry weight) and foliar content (g./m^2) at all crown positions indicating that nutrient concentration and nutrient content vary in proportion to one another.

This is perhaps not surprising since no effect of fertiliser treatment on average needle weight or specific needle area was found.

9.5 Conclusion In relation to the 3 original objectives of this study the conclusions are:-

1. Application of nitrogen fertiliser resulted in a significant increase in stand basal area and volume increment in both experiments. There was an indication (non-significant) of a response to phosphate application in the Benmore experiment but no apparent or significant effect at Wauchope. Height increment was also increased by fertiliser treatment at Benmore but was not affected at Wauchope. Thinning (Wauchope only) resulted in a significant increase in the basal area and volume increment of the remaining trees and also a significant increase in the level of stand basal area and volume increment. Height increment tended to be reduced by thinning. The effects of thinning and fertilisation at Wauchope were additive and no interaction was indicated. In both experiments the effect of the treatments on volume increment was closely related to the effects on basal area increment and no significant treatment effect on the relationship between volume and basal area was indicated especially after the effect of tree size on the volume : basal area relationship was taken into account.

2. a. Increased productivity following fertiliser treatment at Benmore was associated both with an increase in leaf area at the stand and individual tree level and with an increase in the level of basal area increment per unit of leaf area

(leaf efficiency). The increase in leaf area was due almost entirely to an increase in the number of needles produced following fertilisation and increases in leaf efficiency are thought to be due to an increase in needle nitrogen concentration and an increase in the proportion of 'young' shoots in fertilised trees. In the Wauchope experiment the results are less clear but it appears that fertiliser treatment resulted in an increase in leaf efficiency and may have also increased leaf area. Thinning resulted in a clear increase in leaf efficiency of individual trees, an increase which became progressively less in each of the 3 years of measurement and also resulted in an increase in leaf area in the lower crown, attributable again largely to an increase in needle number, but resulted in a slightly reduced leaf area at whorl one. The relationship between leaf area and productivity appeared to be relatively linear at the stand and individual tree level as there was no indication of a reduction in either productivity or leaf efficiency at the highest levels of leaf area and leaf area index encountered.

b. Sapwood area at breast height was linearly related to leaf area and the relationship was similar at both sites. The same was true of the foliage area : diameter at breast height relationship and neither relationship was significantly affected by thinning or fertiliser treatments.

3. Foliar nutrient concentrations at Benmore showed a progressive decline with increasing depth in the crown and increasing age of needle. Fertiliser treatment increased foliar N and P

concentrations at all crown positions and one year foliage appeared to show the greatest differentiation between the treatments. Expression of the nutrient status in terms of the quantity of nutrients per unit of leaf area gave a very similar picture to the use of nutrient concentrations. At Wauchope, where only top whorl foliage was sampled, nitrogen concentration was slightly increased following nitrogen fertiliser application but otherwise there were no apparent fertiliser or thinning effects apart from a slight reduction in the nitrogen concentrations in thinned treatments in 1980.

9.6 Implications for Management and Suggestions for Future Research

The results of this study indicate that the potential for increasing the productivity of established Sitka spruce stands by the application of fertilisers is perhaps greater than has hitherto been imagined. The response of the Benmore stand was perhaps predictable in view of the relatively infertile site and relatively low level of stand productivity but it is interesting to note that highly productive stands on relatively fertile sites, as was the case at Wauchope, may also respond to fertiliser application. Results of Forestry Commission experiments (McIntosh; in press) support the finding that responses may occur in a wide range of stand conditions but show no clear pattern of response in relation to site type, stand age, level of productivity etc. It is clearly of importance to forest managers to know that fertiliser responses are possible in established Sitka spruce stands but, in a situation where response is not clearly related to site type etc, it is essential that a system is developed which will provide a reasonably accurate forecast of the degree of response to be expected following application of fertilisers to a particular stand. This is clearly a research priority if the optimum return on investment capital is to achieved. Analysis of foliar nutrient concentrations, as presently practiced, is undoubtedly a useful tool in this respect in younger stands and may be satisfactory in established pine stands (McIntosh; in press) but there is some doubt as to the reliability of such methods in predicting fertiliser responses in established spruce stands. It was hoped that the investigations into nutrient gradients would have revealed a more sensitive sampling system/position capable of providing a better relationship between foliar nutrient levels, plant nutrient status and response to fertiliser treatment but the results of this rather limited study have been disappointing in that respect. Nevertheless it is considered that further research should be carried out into nutrient distribution with respect to age and position of needle and that this should be combined with a study of through the year variation in nutrient concentration.

The present studies of leaf area/production relationships have no direct bearing on management practices but further studies are likely to be rewarding in terms of increasing our understanding of the processes by which silvicultural treatments influence production and hence increasing our ability to predict the results of such treatments. It is suggested that further study should be made of the relationships between leaf area, leaf efficiency and production over a range of site conditions with a view to increasing our understanding of what constitutes the optimum leaf area of a stand under different conditions. Clearly if a stand can be established to be carrying the optimum leaf area then treatments like fertiliser application which are aimed at increasing leaf area, may well result in a drop in production through the relationship between stand leaf area and stand leaf efficiency.

If measurement of leaf area or leaf efficiency is to form an integral part of stand management techniques then a reliable and quick method of estimating leaf area must be found. The results of this study suggest that the use of sapwood area has some place in this but there is sufficient doubt about the ability of the sapwood area : leaf area relationship to hold steady for a species, given a range of site conditions and silvicultural treatments and it is suggested that further studies should be carried out. In particular it would seem to be worth investigating sapwood conductivity and the effects thereon of variations in site/stand conditions.

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APPENDIX I

BASAL AREA INCREMENTS BY PLOT

BENMORE BASAL AREA INCREMENTS

		Year					
Treatment	Block.	1977	1978	1979	1980	1981	1982
O	I	1·47	1·01	1·99	1·27	0·69	0·84
	II	1·15	0·85	1·68	1·03	0·96	0·82
	III	1·27	0·86	1·91	1·41	0·96	0·91
	IV	1·49	0·80	1·35	1·11	0·56	0·89
	mean	1·34	0·89	1·72	1·20	0·79	0·86
N	I	2·26	1·61	2·40	1·81	0·68	1·11
	II	1·82	1·34	2·25	1·53	0·78	1·24
	III	1·90	1·24	1·92	1·79	0·97	1·29
	IV	1·81	1·05	1·58	1·38	0·55	0·88
	mean	1·95	1·30	2·04	1·63	0·74	1·13
P	I	1·87	1·84	2·62	2·00	1·30	1·17
	II	1·84	1·41	2·24	1·84	0·62	1·20
	III	1·11	0·52	1·31	0·93	0·59	0·84
	IV	1·27	0·94	1·35	1·32	0·71	0·81
	mean	1·52	1·18	1·87	1·52	0·80	1·00
NP	I	2·09	1·97	2·68	1·88	1·01	0·97
	II	2·32	1·58	1·99	1·61	0·70	1·17
	III	2·12	2·29	2·87	2·04	0·81	1·13
	IV	1·45	1·10	1·99	1·57	0·47	1·18
	mean	1·99	1·74	2·38	1·77	0·75	1·11

WAUCHOPE BASAL AREA INCREMENTS

		Year		
Treatment	Block	1980	1981	1982
O	I	1·67	1·51	2·02
	II	2·08	1·69	2·10
	III	2·0	2·14	2·27
	IV	2·29	2·05	2·07
	V	2·76	1·99	2·30
	Mean			
N	I	1·83	1·84	2·33
	II	2·26	2·16	2·42
	III	2·44	2·69	3·57
	IV	2·26	2·26	1·99
	V	2·83	2·10	2·73
	Mean	2·32	2·21	2·61
P	I	1·77	1·77	2·24
	II	2·39	2·37	2·67
	III	2·08	2·10	2·15
	IV	2·06	2·37	1·89
	V	2·46	1·93	2·22
	Mean	2·14	2·11	2·23

WAUCHOPE BASAL AREA INCREMENTS, (continued)

		Year		
Treatment	Block	1980	1981	1982
T	I	2·14	2·15	—
	II	2·80	2·62	—
	III	2·36	2·50	2·71
	IV	2·01	2·22	2·30
	V	2·51	2·46	2·90
	mean	2·36	2·39	2·64
TN	I	2·40	2·59	—
	II	2·15	2·16	—
	III	2·52	2·74	2·45
	IV	2·47	2·53	2·55
	V	2·80	2·36	2·95
	mean	2·47	2·48	2·65
TP	I	2·28	2·11	—
	II	1·90	1·96	—
	III	2·31	2·38	2·70
	IV	2·30	2·31	2·79
	V	2·66	2·49	2·66
	mean	2·29	2·25	2·72

APPENDIX II

SAMPLE TREE DETAILS

BENMORE SAMPLE TREES

TREATMENT O

Block	Tree	Height (m)	Diam. (cm)	Sapwood area (cm²)	Leaf area (m²)	canopy class
I	1	10·62	14·3	61·6	21·4	CD
	2	10·55	11·9	51·0	12·8	CD
	3	9·75	12·3	68·0	10·9	CD
	4	11·60	11·5	58·4	13·8	CD
	5	10·70	12·7	69·6	16·5	D
II	1	11·55	17·0	127·9	41·5	D
	2	11·25	13·5	90·1	23·8	D
	3	10·22	11·2	61·4	13·7	CD
	4	9·61	12·1	74·5	9·4	CD
	5	8·75	10·5	46·3	8·1	SD
III	1	9·93	13·5	77·6	26·2	CD
	2	11·25	15·6	80·1	14·1	CD
	3	10·65	11·7	60·7	10·7	SD
	4	8·73	10·1	50·5	9·0	SD
	5	11·50	13·6	72·3	18·2	CD
IV	1	9·45	8·9	34·3	10·4	CD
	2	10·61	12·3	73·8	13·5	D
	3	11·22	10·2	34·1	13·3	CD
	4	10·80	12·8	72·8	29·4	D
	5	8·98	10·9	50·1	9·9	SD

BENMORE SAMPLE TREES (continued)

TREATMENT NP

Block	Tree	Height (m)	Diam. (cm)	Sapwood area (cm²)	Leaf area (m²)	Canopy class
I	1	12·05	15·3	122·4	33·5	D
	2	10·35	11·4	74·2	14·2	CD
	3	12·55	15·7	118·1	46·5	D
	4	8·96	10·0	35·4	6·5	SD
	5	12·1	13·7	50·6	8·3	CD
II	1	10·8	12·2	54·8	23·8	CD
	2	11·65	13·5	77·2	18·6	CD
	3	12·10	15·0	95·2	28·7	D
	4	11·45	11·8	62·8	14·1	CD
	5	11·50	13·1	74·8	14·2	D
III	1	10·8	14·2	105·9	48·7	D
	2	10·55	12·6	63·1	15·8	CD
	3	10·70	13·1	68·5	18·9	D
	4	9·53	10·3	57·3	15·7	CD
	5	10·24	13·1	79·1	17·8	CD
IV	1	9·10	11·2	62·3	21·2	CD
	2	10·87	13·3	79·8	17·6	D
	3	11·50	11·0	64·7	15·5	CD
	4	8·47	9·6	39·8	13·0	SD
	5	8·30	9·9	48·0	14·7	CD

WAUCHOPE 1981 SAMPLE TREES

Treatment	Tree	Diam (cm)	Estimated leaf area (m^2)	Sapwood area (cm^2)
O	1	13·4	28·5	90·1
	2	9·7	7·4	47·3
	3	6·9	3·8	23·1
	4	12·7	30·8	83·8
	5	8·2	3·7	33·4
	6	12·7	20·9	78·0
N	1	8·1	2·8	33·1
	2	13·8	26·5	80·4
	3	15·9	41·0	113·9
	4	18·4	53·4	185·5
	5	8·2	5·1	39·2
	6	12·7	22·9	75·5
	7	19·5	60·7	137·9
P	1	10·8	2·7	52·2
	2	11·4	24·9	55·1
	3	11·9	18·2	64·1
	4	11·3	8·9	42·2
	5	9·6	14·1	38·9
	6	13·5	37·2	86·7
	7	17·0	39·3	156·1
	8	17·4	30·3	128·7

WAUCHOPE 1981 SAMPLE TREES (continued)

Treatment	Tree	Diam (cm)	Estimated leaf area (m^2)	Sapwood area (cm^2)
T	1	17·3	46·3	148·6
	2	15·8	29·9	126·8
	3	18·1	43·4	176·9
	4	13·2	17·6	103·8
	5	16·0	29·8	123·5
	6	19·9	41·9	156·5
TN	1	15·5	19·6	75·1
	2	14·6	47·4	129·9
	3	18·6	33·8	86·1
	4	14·5	20·3	57·4
	5	14·2	17·4	51·2
	6	14·6	31·7	77·2
	7	15·4	28·9	143·9
TP	1	12·2	27·9	101·2
	2	16·4	29·9	97·3
	3	14·2	53·4	168·5
	4	10·1	24·9	87·9
	5	10·1	26·5	115·5
	6	12·6	39·7	93·8
	7	16·3	29·5	121·3

WAUCHOPE 1982 SAMPLE TREES (Continued)

Treatment	Block	Tree	Height(m)	Diam(cm)	Volume (m^3)
T	III	1	11·4	16·1	0·137
		2	11·3	16·6	0·140
		3	12·5	17·0	0·182
	IV	1	11·9	16·9	0·163
		2	11·3	16·6	0·147
		3	11·3	17·1	0·156
	V	1	12·4	17·2	0·158
		2	10·0	16·1	0·116
		3	11·9	17·0	0·172
TN	III	1	11·9	18·3	0·173
		2	11·5	15·6	0·113
		3	11·6	17·1	0·153
	IV	1	12·3	16·8	0·163
		2	11·5	16·1	0·142
		3	11·8	16·5	0·142
	V	1	11·7	17·0	0·154
		2	10·5	16·0	0·137
		3	11·3	17·1	0·153

WAUCHOPE 1982 SAMPLE TREES

Treatment	Block	Tree	Height (m)	Diam (cm)	Volume (m³)
O	III	1	14·8	16·6	0·173
		2	13·6	16·1	0·145
		3	13·2	15·6	0·130
	IV	1	13·7	15·3	0·122
		2	14·7	16·6	0·165
		3	14·2	15·9	0·136
	V	1	12·7	15·7	0·138
		2	14·5	15·9	0·143
		3	13·3	16·8	0·148
N	III	1	14·0	16·6	0·154
		2	13·2	16·0	0·146
		3	12·8	16·0	0·147
	IV	1	12·1	15·4	0·101
		2	11·8	15·2	0·114
		3	14·2	16·8	0·169
	V	1	13·0	15·7	0·133
		2	12·9	15·7	0·126
		3	12·6	15·3	0·111