SOME ASPECTS OF THE SEED DEVELOPMENT AND SEEDLING GROWTH OF RIMU, *DACRYDIUM CUPRESSINUM*, LAMB.

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ABSTRACT

The morphological stages of seed development in rimu were analysed by studying microtome sections and by dissections of ovules under a stereomicroscope. Development takes 18 months from the time ovules become visible and losses occur throughout this time. Many empty seed are produced and this has been shown to be due to failure of fertilisation which is usually the result of failure of pollination 12 months earlier. Of the 1,500 ovules examined 21% contained no pollen grains, 47% 1 grain, 23% 2 grains and 9% between 3 and 5 grains. High levels of pollination (mean 1.5 pollen grains per ovule) were found in Whirinaki and Ashley Forests and low levels (mean less than one grain per ovule) in Tautuku and Puketi. Pollination failure was probably caused by wet weather. The percentage of ovules surviving after fertilisation varied between localities, high percentages being found in samples from Saltwater and Ashley Forests and low percentages in samples from Otaki Forks and Pakawau. All ripe red receptacles carried sound seed.

Rimu seedlings from 5 provenances (Puketi, Waitakere, Pureora, Westland and Catlins) were used in a variety of growth experiments to examine their responses to different growing irradiances, temperature regimes, photoperiods and seasons. Growth was assessed by growth analysis and direct measurement. Gas exchange studies were made using an infra-red gas analyser and an assimilation chamber in an open circuit system.

Photosynthesis and dark respiration rates were measured in rimu and compared with Pinus radiata D.Don. Light saturated photosynthesis rate (g CO_2 absorbed per m^2 total foliage surface area per hour) of P. radiata (0.79g m^{-2} h^{-1}) was more than four times that of rimu (0.18g m^{-2} h^{-1}), but the dark respiration rates were not significantly different (P. radiata 0.12g m^{-2} h^{-1}, rimu 0.07g m^{-2} h^{-1}) ($p = 0.05$). Light compensation points of the two species were similar, rimu's being only slightly lower than that of P. radiata (P. radiata 38.8μE m^{-2} s^{-1}; rimu 30.8μE m^{-2} s^{-1}) and the quantum requirements (number of Einsteins of energy required to fix each mole of CO_2) were also not significantly different (P. radiata 45.5 E mol^{-1}; rimu 53.3 E mol^{-1}). Stomatal resistance to CO_2 of the two species did not vary greatly (P. radiata 8.05 s cm^{-1}; rimu

7.52 s cm^{-1}), but the internal leaf resistance of rimu was more than 13 times as great as that of pine (P. radiata 7.35 s cm^{-1}; rimu 100.0 s cm^{-1}).

Growth rate of rimu seedlings grown under varying irradiances showed that 2 year old seedlings could survive at 1% full sunlight, but their growth was negligible (-0.03g g^{-1} day^{-1} x 10^{-2}) whereas there was little difference between the growth rates of seedlings grown at 17% and 42% sunlight (0.26 and 0.24g g^{-1} day^{-1} x 10^{-2} respectively). On the other hand small first year seedlings had significantly greater mean relative growth rates in the later part of the growing season (February-March) when grown in higher irradiances. Growth rates were 0.93, 1.21 and 1.62g g^{-1} day^{-1} x 10^{-2} for plants grown at 28%, 60% and 73% sunlight respectively.

Chlorophyll concentrations of seedlings grown at low irradiance (140μE m^{-2} s^{-1}) were significantly higher (0.69 mg g^{-1} fresh weight) than concentrations in plants grown at 385 and 650μE m^{-2} s^{-1} (0.28 and 0.26 mg g^{-1} fresh weight respectively). However, medium irradiance plants had a somewhat higher relative growth rate (0.83g g^{-1} day^{-1} x 10^{-2}) while low and high irradiance plants grew at similar rates to each other (0.59 and 0.60g g^{-1} day^{-1} x 10^{-2} respectively). Light saturated photosynthesis rate of medium irradiance plants was lowest (0.38g m^{-2} h^{-1}) while those of low and high irradiance plants were the same (0.43g m^{-2} h^{-1}). Net photosynthesis rates of plants from the three growing irradiances all responded to increasing temperature in a similar way and the optimal temperature range for photosynthesis was between 18^{o} and $22^{o}C$.

With increasing temperature there was a trend towards increased relative growth rate in eight month old Pureora provenance seedlings: 1.52, 1.70 and 1.73g g^{-1} day^{-1} x 10^{-2} for plants grown in $17^{o}/9^{o}C$, $22^{o}/14^{o}C$ and $27^{o}/19^{o}C$ regimes respectively. The medium regime, however, gave best growth in fifteen month old Puketi provenance seedlings; 1.04 compared with 0.93 and 0.82g g^{-1} day^{-1} x 10^{-2} in the warm and cool regimes respectively. These differences were believed

to be due to ontogentic stage rather than to provenance. Seedlings of both provenances became brown in the cool regime.

$5^{o}C$ nights with $18^{o}C$ days also caused two year old seedlings to become brown. Chlorophyll a + b concentrations decreased with decreasing night temperature (0.50, 0.38, 0.32 mg g^{-1} fresh weight at 20^{o}, 12^{o} and $5^{o}C$ nights respectively). Relative growth rates increased with increasing night temperature (0.78, 0.98 and 1.08g g^{-1} day^{-1} x 10^{-2} at 5^{o}, 12^{o} and 20^{o} nights respectively) as did light saturated photosynthesis rates (0.16, 0.18 and 0.19 g m^{-2} h^{-1}). Internal leaf resistance to CO_2 increased greatly with decreasing night temperature (58.8, 100.00 and 142.9s cm^{-1} for plants grown at 20^{o}, 12^{o} and $5^{o}C$ nights respectively) and the Q_{10} of dark respiration rate increased slightly with decreasing night temperature (1.7, 1.9 and 2.0 for plants grown at 20^{o}, 12^{o} and $5^{o}C$ nights respectively). Several Puketi, but no Waitakere provenance seedlings, died after several months in $5^{o}C$ nights.

Different provenances of rimu seedlings responded to photoperiod in different ways. In Puketi plants 20 hour and 15 hour days caused significantly more total shoot growth than 10 hour days. This trend: long day $>$ medium day $>$ short day, was repeated in the Pureora provenance, but there was no obvious trend in shoot growth in the Waitakere or Westland provenances. Shoot surface areas of all four provenances, however, followed the trend: long day $>$ medium day $>$ short day, with significant differences in both the Puketi and Pureora provenances, and relative growth rate, measured only in the Waitakere provenance, followed the same trend: 1.51, 1.43 and 1.30 g g^{-1} day^{-1} x 10^{-2} for plants grown in 20 hour, 15 hour and 10 hour days respectively.

Winter dormancy in rimu seedlings is imposed by low mean temperatures and can be broken by increased temperatures without a period of chilling. Provenances from four localities grown in a nursery in Rotorua all ceased growth at the same time in winter (June) and their seasonal growth patterns were similar. Provenances from warmer climates (Puketi,

Waitakere and Westland) grew as well in Rotorua as the Pureora provenance from a colder upland climate. All seedlings became brown before growth ceased in winter and remained brown until November or December. There were some distinct morphological differences between certain of the provenances.

Results of the various growth experiments are discussed in relation to the ecology of the species.

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Note: Botanical names follow Dallimore and Jackson (1966) (Conifers) and Allan (1961) (New Zealand species)

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CHAPTER 1 : GENERAL INTRODUCTION

Rimu is a slow growing endemic conifer belonging to the family Podocarpaceae which evolved in Gondwana in the upper Cretaceous (Miller, 1977; Mildenhall, 1980). The study of fossil pollen has shown that rimu has been widespread and dominant in the New Zealand flora for about 80 million years. In post Pleistocene pollen assemblages abundant rimu pollen is used as an indicator of warmer climatic periods (e.g., Harris, 1963). In New Zealand warm climatic periods are also relatively moist and rimu forest today grows in lowland regions with damp, maritime climates (Franklin, 1968). However, the species is able to tolerate a relatively wide range of temperatures and occurs from near North Cape (latitude 34°S) to Stewart Island (latitude 47°S) and from close to sea level to altitudes of about 900 m above sea level in the north of the North Island, about 600 m in the central parts of New Zealand and about 450 m in the south of the South Island (Nicholls, 1982 in press).

Rimu is also tolerant of a wide range of soils and grows on all but the driest sites, although growth is faster on more fertile soils (Franklin, 1968).

Establishment of rimu seedlings may occur in a wide variety of sites from heavily shaded positions below a mature forest canopy, to seral scrub or fully exposed open ground. Rimu seedlings always grow relatively slower than angiosperm shrubs and trees and therefore are frequently suppressed by surrounding vegetation. However, they have the capacity to survive for many years with very little growth and then to respond to an opening in the forest canopy by increasing their growth rate. Eventually, because of their longevity and tall stature rimu trees often emerge above the main canopy layer and become dominant in a forest. Mature rimu trees are usually up to 35 m tall, with exceptional individuals reaching 60 m (Franklin, 1968). Most live for 600 to 800 years; a rare few for as long as 1200 years (e.g., Franklin, 1968; June, 1982).

Because of its original abundance throughout the country and good form, rimu has been the most important indigenous timber species in New Zealand for many years (Franklin, 1968).

Birds disperse rimu seed and thus the species is able to be distributed rapidly over relatively great distances, but much seed is also dispersed by gravity and wind and falls close to the parent tree.

As a result of its tolerance to a wide range of climates, soils and irradiances, ability to survive many years of suppression by faster growing species, longevity and the fact that the seed are dispersed by birds, rimu is the most widespread of all indigenous forest trees and is present in a great many forest types. In the North Island, for example, rimu is widely distributed and prominent in ten out of fourteen forest classes described by Nicholls (1976). In three of these classes it is a common tree in the lower canopy layers, in five it occurs usually as an emergent tree above the canopy, while in the remaining two classes rimu is frequent and often dominant (Franklin, 1968). Rimu is also present in the north, along the west coast and in the south of the South Island, and on Stewart Island, with a few other more isolated locations in the east of the South Island. The species, therefore, has a wide ecological amplitude and has been important in the forests of the New Zealand archipelago since the upper Cretaceous, particularly during warm, moist periods. On the other hand many present day northern hemisphere conifer species, particularly in the family Pinaceae, have evolved since the beginning of the Pleistocene, within the last 1.7 million years (Berggren and Van Couvering, 1979) as pioneer species on ice-cleared landscapes, under selection pressures which favoured relatively rapid growth rate in full sunlight and close adaptation to local climates and seasonal changes in photoperiod (Mirov, 1967). Much of the physiological research in conifer growth has been made on such species, many of which are well suited to plantation forestry. Rimu also acted as an early pioneer following glacial retreat, particularly in Westland and similarly following volcanic eruption in central North Island, because of its rapid means of dispersal and ability to establish in full sunlight or under low seral scrub or forest. However, unlike many northern conifers, rimu is able to survive in many different ecological situations and is not restricted to the pioneering role. Therefore one would expect its seedlings to be tolerant of many different light environments. Also, because rimu grows throughout New Zealand it is probable that the seedlings are able to acclimate to a wide range of growing temperatures, although it is possible that different provenances have developed which are adapted to local climates.

Rimu is representative of the southern conifer families, (the Podocarpaceae and Araucariaceae) which have had a separate evolutional history from the northern conifers since the Paleozoic but, in spite of this long divergence, all conifers fall into two categories in terms of their seed development. In one group development from pollination to seed fall occurs in one growing season, while in the other two seasons are required. Both categories are represented in both the northern and southern groups of conifers. Rimu seed take two seasons to develop and in Chapter 2 of this thesis the morphological and phenological stages of its seed development are described and some of the causes of empty seed production are examined.

In Chapter 3 certain aspects of rimu seedling growth are studied: a comparison of the photosynthesis and dark respiration rates of rimu and Pinus radiata seedlings is made in section 3.3; the responses of rimu seedlings of different age to growing irradiance are examined in section 3.4; the responses of rimu seedlings of different age and provenance to growing temperature and to thermoperiod (day/night temperature differential) are investigated in section 3.5; and the responses to photoperiod and the pattern of seasonal growth of four rimu provenances are described in section 3.6.

In Chapter 4 the conclusions drawn from the morphological and physiological studies are discussed in relation to the geological history and present day ecology of the species.

CHAPTER 2 : THE MORPHOLOGICAL STAGES OF SEED DEVELOPMENT IN RIMU

2.1 Introduction and Literature Review

2.1.1 Introduction

In temperate forest trees seed production is often very irregular and unpredictable. (Kramer and Kozlowski, 1979). Lack of regular seed years may be related to the difficulty of building up carbohydrates to the necessary threshhold level for flower or strobilus production which may only be achieved over a period of years. (Kozlowski, 1962) Seed production is also limited by loss of potential seed at various stages during development and this problem is particularly important in species in which seed development is slow.

Rimu produces a large seed crop periodically, but the interval between good seed years is not regular. A good seed year may be followed by a small or moderate seed crop the following year, but there is often a period of four or more years between seed crops. (Beveridge, 1964) The reproductive cycle in rimu spans two years during which time many factors contribute to the loss of potential seed. Many ovules are initiated and become visible only to die before maturity and many full-sized seeds are found to be empty.

The irregularity of good seed crops in rimu trees will continue to be a management problem because fresh seed cannot be collected every year, but an understanding of the morphological stages of seed development and of the major causes of empty seed production should allow planning of seed collections when good crops of sound seed are forecast.

The study recorded in this section of the thesis was undertaken to examine the factors influencing the production of empty seed. The morphological stages of seed development were investigated from the time the ovule is distinguishable until seed maturity, and an attempt was made to determine the major causes of empty seed production. Ovules were collected to photograph and section for the description of normal development and larger samples of ovules in their second year of development were collected and dissected. The relationship between

locality and successful seed development was examined by studying ovules from sites throughout New Zealand and ovules were collected before and after the time of fertilisation to discover whether (1) unpollinated ovules developed until the time of fertilisation; and (2) failure of fertilisation was a major cause of empty seed production. Because only healthy ovules in their first year were examined nothing quantitative can be concluded about the loss of potential seed during this time.

2.1.2 Literature Review

2.1.2.1 Female reproductive structure

Rimu is dioecious and in the female tree the fertile branch terminates in a few spirally arranged scales, the uppermost, the carpidium, bearing a single ovule. There are occasionally two fertile scales or megasporophylls and the transition from linear foliar leaves to lanceolate fertile scales is gradual. (Stiles, 1912) The ovule is carried on the upper surface of the epimatium which arches over the young ovule like a hood. The ovule consists of a nucellus which is conical at first and is surrounded by, though free from a four-layered integument. (Stiles, 1912) It is inserted on the sclerenchymatous epimatium a short way above the junction of the epimatium and the carpidium.

The most complete description of gametophyte development and embryogeny of rimu was made by Sinnott (1913) who described a reproductive cycle extending over two seasons. In January or February minute ovules, recently pollinated, occur on the same branches as ovules of the previous year which have almost reached their full size, and in which fertilisation and embryo development is taking place. Within the nucellus of the young ovule the development of "spongy tissue" is less conspicuous than in the genus Podocarpus, L'Herit. ex Pers. but the growth of the megaspore mother cell and its meiosis to produce a linear tetrad of megaspores occur in a similar manner.

The megaspore at the end opposite the micropyle develops into the gametophyte while the other three degenerate. The functional megaspore undergoes free nucelar division as it expands in size, and

(according to Sinnottt, who gives no date), is early filled by the centipetal growth of endosperm tissue which occurs before the gametophyte has reached half its final size.

Development of the functional megaspore is similar to that in other conifers. The nucleus divides many times and the resulting nuclei come to lie against the spore wall while the central region is occupied by a large vacuole. The first cell walls are laid down anticlinally to produce radiating tubular structures called "alveoli" which are at first open towards the centre. Each alveolus is later divided into a row of cells usually after centripetal expansion has ceased. This results in a body of thin-walled uninucleate cells arranged in rows radiating from the centre. This gametophyte tissue is haploid and becomes the endosperm.

In rimu all the gametophyte cells are uninucleate at first, but a cone of multiinucleate and more densely protoplasmic cells soon appears below the archegonial region. By the time fertilisation occurs all endosperm cells are multiinucleate. The female gametophyte is surrounded by a strongly thickened megaspore membrane. (Quinn, 1966b) Three archegonia develop near the apex of the gametophyte while it is still very small. (Sinnott, 1913) Each arises from a superficial cell and is separated from the others by sterile tissue. The initial archegonial cell divides into primary neck and primary central cells and the former divides anticlinally to give a neck of one tier of cells, while the central cell elongates greatly and becomes filled with thin vacuolate contents. The central cell is later surrounded by a single row of uninucleate jacket cells and its nucleus divides to produce a ventral canal nucleus and an egg nucleus. The former breaks down, but the latter drops a little into the cytoplasm and enlarges almost filling the upper part of the archegonium. The archegonia of D. cupressinum are similar in shape to those of D. bidwillii Hook f. ex Kirk, longer and narrower than those of Podocarpus nivalis Hook. , but less so than those of D. laxifolium Hook.f. (Quinn, 1966b).

Fertilisation was not observed by Sinnott (1913), but he described the male nuclei as being like those of Podocarpus, one naked, and the other functional one surrounded by a mass of protoplasm.

Sinnott (1913) reported that the development of the proembryo in rimu was similar to that in the Section Eupodocarpus of the genus Podocarpus. However, Buchholz (1933) stated that "the proembryo (of rimu) is unknown" and his drawings and description of early stages of embryo development after suspensor elongation has commenced are different from his and Sinnott's descriptions of the equivalent stage in Eupodocarpus. It is believed that the fusion nucleus undergoes one mitosis in situ, followed by three more mitoses when the two daughter nuclei have descended to the base of the archegonium. Thus sixteen nuclei are produced before walls are formed. From the known, slightly later stages, it is assumed that the first walls divide the nuclei into an upper tier of 7-11 cells which are open to the archegonium above, and a group of 5-7 (occasionally 9) primary embryo cells below. An internal divison then produces an upper tier of 7-11 ephemeral cells open to the archegonium, above a tier of 7-11 suspensor cells which soon begin to elongate, and below these a group of 5-7 (or 9) binucleate embryo cells. In almost all podocarps the internal division of nuclei in the primary embryo cells is not followed immediately by wall formation. Hence the embryo cells are at first binucleate. The embryo cells are arranged in two tiers with usually only one cell in the lower tier. The mature proembryo therefore consists of the upper tier, suspensor tier and group of embryo cells. The embryo cells enter a resting stage while the suspensor cells elongate, and then undergo a double division resulting in the formation of a group of four cells (an embryo tetrad) from each binucleate embryo cell. This is typical of the family Podocarpaceae.

Cleavage polyembryony occurs when the group of embryo cells in the proembryo cleaves or divides and each cell develops independently to form an embryo. This occurs in Pinus L, Cedrus, Link. and Tsuga Carr. of the family Pinaceae, the families Cupressaceae and Taxodiaceae (Doyle, 1963), and in certain species in the family Podocarpaceae including Podocarpus usambarensis Pilger (an advanced member of the Section Stachycarpus) (Buchholz, 1936), P. nagi (Thunberg) Makino (Section Nageia) (Tahara, 1941), Section Eupodocarpus (Boyle and Doyle 1954; Brownlie, 1953), Dacrydium bidwillii (Section C of Dacrydium), (Florin 1931; Quinn, 1966b),

Microstrobos niphophilus Garden and Johnson (Elliott, 1948) and in rimu, Dacrydium cupressinium (Buchholz, 1933). In Microstrobus and rimu determinate cleavage polyembryony occurs. In the normal or indeterminate type of cleavage polyembryony there are no indications from the appearance of the proembryo that any of the embryonic units will have a distinct advantage during embryonic competition. In determinate cleavage polyembryony however, one embryonic unit, usually the terminal one, is more favourably situated than the others and this is the dominant embryo from the start. Any other of the cleavage embryos can become functional only if the terminal embryo aborts for some reason. Rimu, like most other conifers, also has simple or polyzygotic polyembryony which occurs when more than one of the three archegonial egg cells are fertilised following multiple pollination. In all cases it is usual for only one embryo to survive in each seed. Polyzygotic polyembryony allows genetic selection as the fastest growing embryo is the most likely to survive.

While most of the developmental stages of the ovule in rimu have been well documented, it is still not known when the ovule is initiated, what stage the female gametophyte has reached when growth ceases over the winter months (if in fact it does), nor when the archegonia are produced. Pollination and fertilisation have not been observed and the early proembryo is unknown. Unfortunately this study has not succeeded in answering these questions. However, the visible stages and phenology of normal ovule development are described and illustrated and the causes of empty seed production are examined.

2.1.2.2 Causes of loss of potential seed in other conifer species

1. Weather

Unseasonal frosts and storms may kill developing ovules and this may lead to conelets falling. Mechanical damage due to strong winds may also break conelets off the tree. (Sarvas, 1962)

2. Insects

Certain insects damage the vascular supply to conelets or eat the developing endosperm. (Wright, 1953, seen in Sarvas, 1962)

3. Lack of Pollination

   a. In some species unpollinated ovules wither soon after the time pollination should have occurred and if a sufficient proportion of ovules in a conelet are unpollinated the conelet drops, e.g., Pinus sylvestris L. and Juniperus communis L. (Sarvas, 1962) The dropping of first year conelets on poor sites may cause the loss of more than 80% of potential seed in P. sylvestris. Sarvas (1962) concluded that lack of pollination was much the greatest cause of ovule abortion in P. sylvestris.

   b. In other species unpollinated ovules develop until the time fertilisation should occur, after which they die. This produces nearly full-sized seed which appear to be empty or hollow, although their shrivelled contents are always visible on close inspection. Certain Pinus species with a two year cycle fall into this category, e.g. P. cembra L. (Sarvas, 1962), P. resinosa Ait., P. taeda L. and P. nigra Arn. var. austriaca Endl. (Lyons, 1956). Other species producing hollow seed from unpollinated ovules include Abies alba Mill., Larix laricina (Du Roi) K.Koch (Lyons, 1956), Picea Link and Pseudotsuga Carr. (Sarvas, 1962).

4. Self-fertilisation

   In monoecious species self-pollination leads to self-fertilisation and this often results in the production of empty seed because of the union of lethally defective genes. (Sarvas, 1962)

5. Other causes of empty seed

   a. Seeds develop normally until the stage of archegonia production when chance failure or damage by unseasonal frosts or storms may prevent the archegonia being formed.

   b. The pollen grain may germinate, but the pollen tube may not develop normally or the male gamete may fail to fertilise the egg.

   c. Fertilisation may occur, but the zygote fails to develop beyond a certain stage probably due to the union of recessive lethally defective genes. This is thought to be a very common cause of seed loss in monoecious conifers and may occur following sib- as well as self-fertilisation. (Sarvas, 1962)

d. Pollination by a closely related species may allow normal development to proceed until the time of fertilisation, after which the ovule dies.

This study attempted to discover the relationship between lack of pollination, failure of fertilisation and the production of empty seed in rimu. Injurious agents such as frosts, storms and insects were not included in the study.

2.2 Methods

Collections were made of ovule-bearing rimu foliage from five different trees at each location from sites throughout the country. Usually two collections were made from each location, one before and one after January, the month when fertilisation is thought to occur in most parts of the country. Collections were made either by hand picking from the ground or by shotgun. Table 2.1 lists the collection localities and dates. Table 2.2 describes the localities. The Coulter climate classification is from Coulter (1975), the forest classification from Nicholls (1976 and pers. comm) and soils classification from DSIR Soil Bureau Bulletins (n.s.) 5 (1954) and 27 (1968) and Leamy (1974).

Ten ovules per tree were examined using an American Optical Company, Model 570 dissecting microscope. Up to five less mature ovules per tree were also examined if present.

Ovules were supported in Plasticene and dissected using mounted pins. The stage of ovule development and number and position of pollen grains were recorded as well as the mortality or otherwise of the ovule.

Additional ovules collected at different stages of development were fixed in FAA and later dehydrated in a TBA series, embedded in Poly-Ester wax, microtome sectioned and stained in Safranin and Fast Green. Slides of developmental stages were photographed using a photomicrographic Remica III camera attached to a Reichert Zetopan Research Microscope with Kodak Tri-X black and white film. Drawings were made of the ovule throughout the eighteen months of its visible development.

Colour transparencies were taken of developmental stages using a Wild Photoautomat MKa5 camera attached to a Wild M5 Stereomiscroscope with Agfachrome 50L Professional. One black and white photograph was made using the same camera and microscope with Ilford FP4 film. Collection localities and dates are included in the captions of figures of these ovules.

Two way and three way analyses of variance were used, together with Students Newman Kuel's multiple range tests (SNK). Means are tabulated and results sharing the same letter, a, b, etc., do not differ significantly. ($p = 0.05$)

Table 2.1: The localities and dates of the collections of ovule-bearing rimu foliage

Locality	Island	Date First Collection	Date Second Collection
Puketi Forest	North	11.12.77	1.2.78
Hunua Range	North	16.2.78	5.4.78
Whirinaki Forest	North	3.2.78	1.4.78
Otaki Forks	North	28.11.77	31.1.78
Pakawau	South	23.11.77	25.1.78
Ashley Forest	South	29.11.77	9.2.78
Saltwater Forest	South	24.12.77	3.2.78
Rowallan Forest	South	-	3.4.78
Tautuku	South	-	6.4.78
Hinahina	South	-	6.4.78

2.3 Results

2.3.1 Morphological Stages of Seed Development

2.3.1.1 Ovule before pollination

In November in the central North Island, New Zealand, certain shoot tips of female rimu trees turn upward through an angle of 90° (Fig. 2.1, 1). The upper and innermost of the spirally arranged scale-like leaves of such an upturned tip bears a swelling apparently on its adaxial surface (Fig. 2.1, 1). This leaf is the carpidium and the swelling consists of the developing ovule enclosed in the epimatium. The ovule is composed of a conical nucellus growing from the base of a three layered integument. The entire structure is

TABLE 2.2 : DESCRIPTION OF THE OVULE COLLECTION LOCALITIES

Name	Latitude S	Longitude E	Altitude m a.s.l.	Months with no Screen Frosts	Mean Annual Temp °C	Mean Annual Rain-fall mm	Coulter Climate Classi-fication	Closest Meteoro-logical Station	Forest Type	Soils Classification
Puketi Forest	35°15'	173°45'	340	12	15.6	1406	A2	Waitangi Forest	B2	122b Te Ranga clay loam and stony loam
Hunua Range	37°04'	175°11'	462	6	14.0	1346	A	Ardmore Auckland	A,B,C. Kauri-Podocarp-Hardwood	122b
Whirinaki Forest	38°37'	176°42'	-	2	11.2	1542	B-M	Minginui	L1, L2, M2	125a Urewera sandy silt and sand
Otaki Forks	40°52'	175°15'	300	8	12.8	1095	D	Levin	D13 Residual Rimu Hardwood	78a Kopua stony loam or 124 Ruahine stony silt loam
Pakawau	40°34'	172°41'	30	10	13.7	1266	E	Farewell Spit	Podocarp, Hard beech, rata, kamahi	62b H Pakawau Hill soils mostly sandy loams.

Table 2.2 (continued)

Name	Latitude S	Longitude E	Altitude m a.s.l.	Months with no Screen Frosts	Mean Annual Temp °C	Mean Annual Rain-fall mm	Coulter Climate Classi-fication	Closest Meteoro-logical Station	Forest Type	Soils Classification
Ashley Forest	43°11'	172°34'	480	5	11.2	820	F2	Ashley Forest	I2 Mountain beech, rimu	41a Hurunui Steep-land soils mostly stony silt loams.
Saltwater Forest	43°9'	170°28'	50	5	10.8	3936	E	Harihari	P4 Rimu Hill Forest	87a Kini soils. peats and peaty loams 60a Kumara soils. peaty to sandy loams.
Hinahina	46°31'	169°38'	137	5	10.1	831	G2	Nugget Point	F2	61 Tautuku soils. Mostly silty loams
Tautuku	46°31'	169°12'	46	5	10.1	831	G2	Nugget Point	F2	61
Rowallan	46°11'	167°30'	100	1	9.7	1068	G2	Otautau	B2	44a Lillburn Hill soils. Silt loams and clay loams.

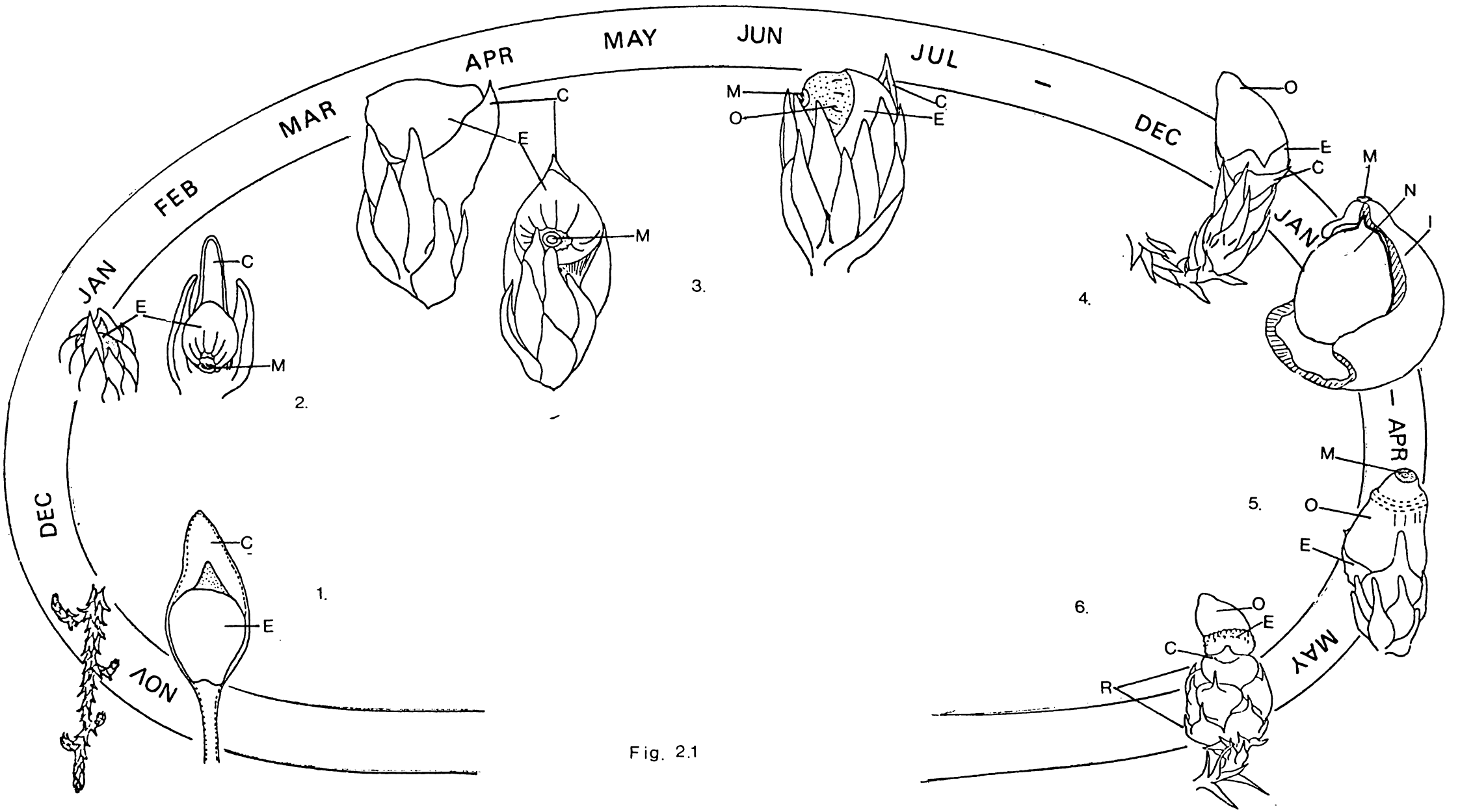


Fig. 2.1

Fig. 2.1 The stages of seed development in Rimu.

1. Shoot tips turn up and the ovule becomes visible.
2. Pollination and female meiosis occur.
3. The ovule grows and begins to turn upwards, emerging gradually from the epimatium.
4. Fertilisation occurs.
5. The receptacle leaves swell and begin to turn orange.
6. The mature seed on a ripe red receptacle.

Key:

C - carpidium

E - epimatium

M - micropyle

O - ovule

N - nucellus

I - integument

R - receptacle

green at this stage (Fig. 2.2). The carpidium is considered to be a bract and the epimatium, which develops in the axil of the bract, is equivalent to the ovuliferous scale of other conifers, the ovule developing on its adaxial surface. Fig. 2.3 is a section through an ovule collected in January in Tihoi Forest, West Taupo, close to the time of pollination. The carpidium at the top of the figure subtends the axillary epimatium which bears the ovule and arches around to enclose it partially. The micropyle is visible and is composed of unequal extensions of the middle layer of the integument. The nucellus is not visible.

The epimatium at this stage can be seen from above with the naked eye as a glaucous bulge at the tip of the upturned shoot (Fig. 2.1, 2). The micropyle is a cup-like structure, directed downwards and protruding beyond the epimatium. (Figs. 2.1, 2, 2.2 and 2.3.)

2.3.1.2 Pollination

Pollination takes place in January in the central North Island. Pollen grains which land on the upturned shoot tip must travel down a passage formed by the inner surface of the tip of the carpidium (which extends beyond the ovule), and the epimatium, on the one hand, and the inner surface of the leaf opposite the carpidium, on the other. All these surfaces are glaucous. (Fig. 2.1, 2.) On reaching the base of this passage the grains must be transported upwards, against gravity, through the micropylar canal to reach the projecting tip of the conical nucellus.

The pollination mechanism has not been demonstrated in rimu, but Doyle (1945) suggested that a pollination drop is involved. Pollination drops have been described in several conifers (e.g., Sarvas, 1962; Lill, 1974). They are produced when the humidity is high, usually at night, and flow from the nucellus out through the micropyle. Any pollen grains are picked up by the drop and may float upwards through it as in Pinus radiata D. Don. (Lill, 1974) or the drop may be resorbed, carrying the grains into the ovule and on to the nucellus tip (Sarvas, 1962). The two bladders on rimu pollen grains are very small and heavily sculptured and may not act as floatation bladders as do the bladders on P. radiata pollen grains.

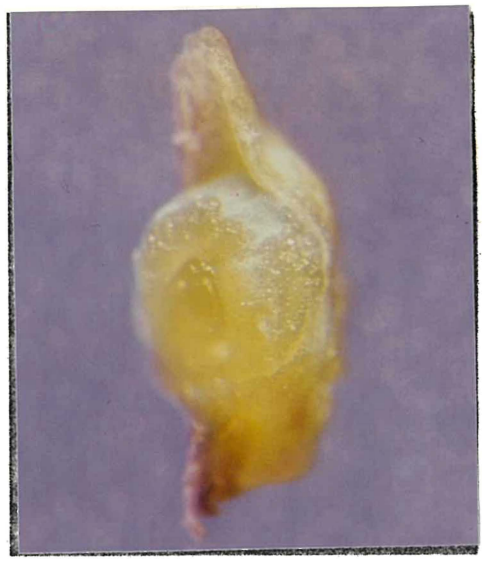


Fig. 2 .2

A young ovule removed from the surrounding leaves (Length 1mm.). The green carpidium partially surrounds the axillary epimatium, also green, which arches around the ovule. The micropyle can be seen on the left. Collected Mamaku Plateau in mid December about a month before pollination.

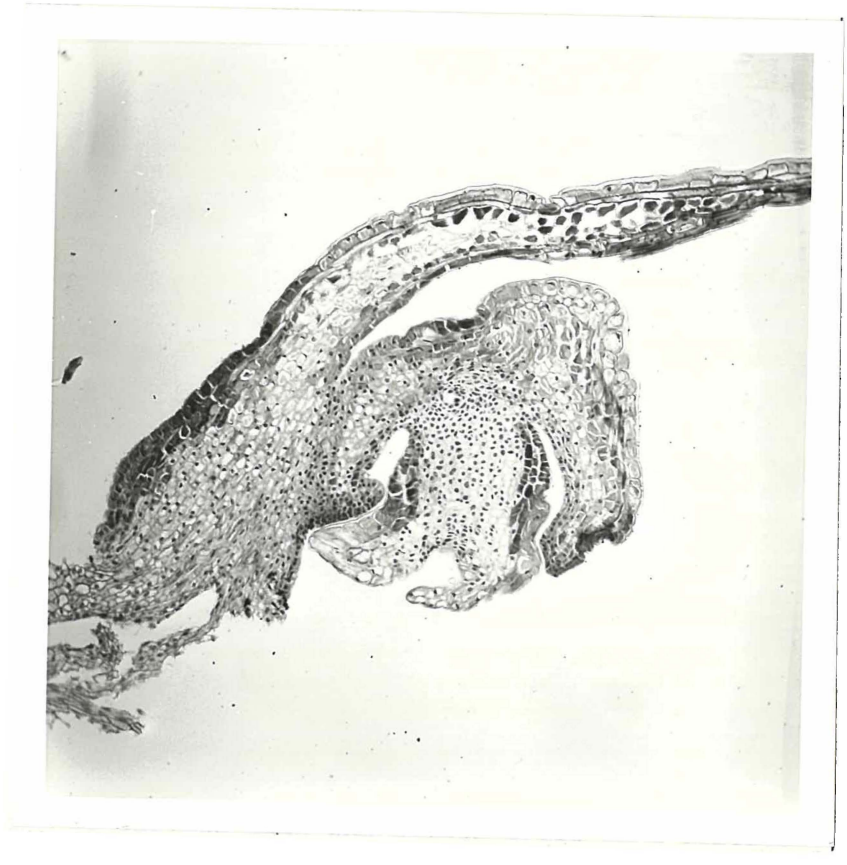


Fig. 2 .3

L.S. through a young ovule close to pollination. The micropyle can be seen at the bottom. Collected Tihoi Forest, in January. (x63).

Figs. 2.4 and 2.5 show a pollen grain on the nucellus tip of an ovule collected in February in the Hunua Range, South Auckland. The epimatium has arched around the ovule to enclose it more fully and the whole structure has grown relative to the carpidium which can be seen at the top of Fig. 2.4. The micropylar canal is almost closed. Of the 1500 ovules dissected in the course of this study very few were seen with pollen grains in any position other than on the nucellus tip. The majority of pollinated ovules contained only one grain, although ovules with two and three grains were also encountered. When four or five (maximum) grains were present only two or three of them were on the nucellus tip, the remainder being below these in the micropylar chamber. Occasionally pollen grains were seen adhering to the wall of this chamber. Only rimu pollen was found within the micropyle of the ovules examined. Very few healthy ovules had dust particles or anything other than rimu pollen within the micropyle. Table 2.3 shows the percentage of ovules with 0-5 pollen grains.

Table 2.3 : The Percentage of Rimu Ovules found with different numbers of pollen grains (n = 1500)

Number of pollen grains	% of Ovules
0	21.07
1	46.70
2	23.27
3	7.39
4	1.10
5	0.47

There was a significant difference between certain collection localities in the number of pollen grains found in each ovule. (See Table 2.4) However, there was also a highly significant difference ($p = 0.01$) in this value between different sample trees within a locality. This is probably due to the different spatial relationships of various male and female trees in a forest. Pollen being wind dispersed, ovules located closer to male cone-bearing trees would be likely to receive more pollen than more distant ovules.

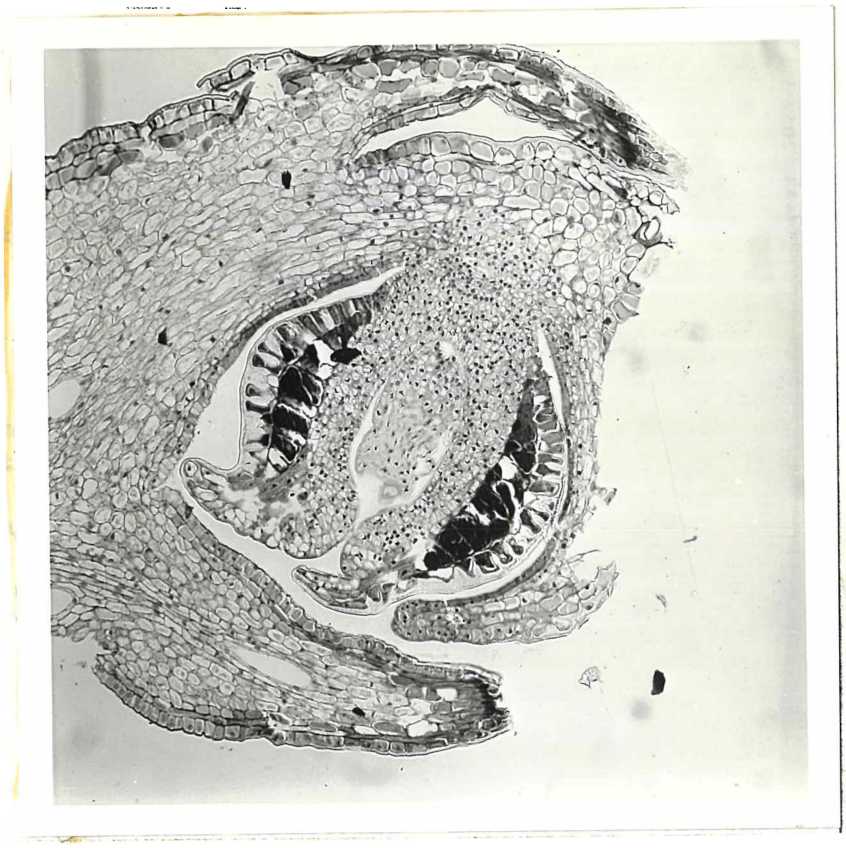


Fig.2.4

L.S. through a pollinated ovule. A single pollen grain can be seen on the nucellus tip. Collected Hunua Range, in mid February. (x63).

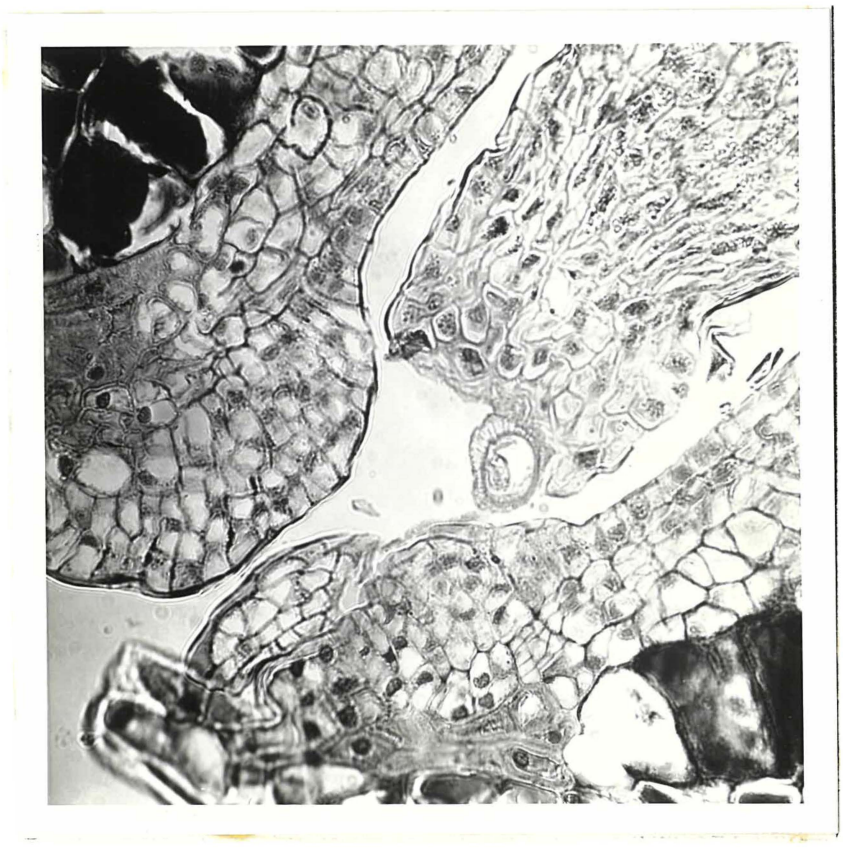


Fig.2.5

Enlargement to show the size of the pollen grain relative to the micropylar chamber. The reduced and heavily sculptured bladders are visible. (x 252)

Table 2.4 : The mean number of pollen grains per ovule for rimu ovules from various localities (10 ovules/tree: 5 trees/locality)

Locality	Whirinaki Forest	Ashley Forest	Hinahina +Rowallan	Otaki Forks	Pakawau	Saltwater Forest	Tautuku Forest	Puketi Forest
Mean No. pollen grains per ovule	1.58a	1.54a	1.44a b	1.14a b	1.08a b	1.04a b	0.99 b	0.94 b

Whirinaki and Ashley Forests had a significantly higher number of pollen grains per ovule than Tautuku (low altitude, Southland) and Puketi Forest (Northland). There was no significant difference between any of the other localities. Multiple pollinations do occur in rimu, but the reason why any one forest has a higher frequency of multiple pollinations than any other forest may be due more to weather conditions at the time of pollination rather than to differences in forest type. For example, both Whirinaki Forest with high or medium density podocarps (mostly rimu) and Ashley Forest where indigenous forest is restricted to a few steep valleys, had high levels of pollination.

2.3.1.3 Ovule after pollination

Soon after pollination the micropyle becomes closed by a thickening of the integument (Figs. 2.4 and 2.5). The waxy coating on the outside of the integument becomes very thick over the micropylar end of the ovule. The ovule continues to grow during the summer and autumn months. Fig. 2.6 shows an ovule collected in late March, 10-11 weeks after pollination, on the Mamaku Plateau. The ovule has grown until it is visible above the tip of the carpidium (upper left) and the other surrounding leaves. During this period of growth the ovule becomes reoriented so that the closed micropyle is directed outwards from the carpidium at an angle between 45^{o} and 90^{o}. The reorientation is caused by unequal growth at the base of the ovule where it is joined to the epimatium. Fig. 2.1, 3 shows the ovule enlarging to protrude from the carpidium and later from the epimatium which eventually consists of a small skirt around the base of the ovule (Fig. 2.1, 4 and 5, and Figs. 2.12 and 2.15).

Fig. 2.6

Side view of an ovule collected in late March on the Mamaku Plateau. The ovule has grown until it is visible above the tip of the carpidium and other surrounding leaves. (Length 4mm.).

Fig. 2 .7

An ovule collected in Auckland in late September, 9 - 10 months after pollination.

The closed micropyle faces the camera and $\frac{1}{4}$ of the ovule has emerged from the epimatium. (Length 4mm.).

Fig. 2 .6

Fig. 2 .7

Ovules grow at different rates even on the same tree and by June, when growth has ceased for the winter (central North Island), ovules can be found with their micropyles oriented at several different angles. In some cases the epimatium is still completely enclosing the ovule, apart from the protruding micropyle (as in Fig. 2.1, 3 on the left), but in other cases the ovule has begun to grow out of the epimatium (as in Fig. 2.1, 3 on the right). Ovules can be described as being 1/4, 1/2 or 3/4 emerged from the epimatium. Fig. 2.6 is a side view of an ovule collected in late March on the Mamaku Plateau. The epimatium is still enclosing the dark ovule except for the closed micropyle, but the ovule has grown so that it is visible above the carpidium and other surrounding leaves. Fig. 2.7 shows an ovule collected after the winter in late September in Auckland. The micropyle faces the camera and 1/4 of the dark ovule has emerged from the epimatium. The carpidium is not visible, but all except the lowest 4 or 5 leaves in the photograph will become the receptacle. Most unpollinated ovules continue to develop normally until the time fertilisation should occur.

2.3.1.4 Meiosis and gametophyte development

The timing of the meiotic division of the megaspore mother cell is not accurately known, but is thought to occur soon after pollination in January or February in the central North Island. Fig. 2.8 is a longitudinal section through the nucellus and integument of an ovule collected in the Hunua Range in mid February. The large elongated cell in the centre of the nucellus is thought to be the megaspore mother cell. Figs. 2.9 and 2.10 are sections through an ovule collected in mid March on the Mamaku Plateau. The linear tetrad of megaspores is visible in the centre of the nucellus with the one furthest from the micropyle enlarging to become the functional megaspore. The megaspore closest to the micropyle seems to have begun to degenerate. In Fig. 2.11 a similar stage is shown in an ovule collected in the Hunua Range in mid February.

No "spongy tissue" was found surrounding the megaspore mother cell or megaspore. It is believed that free nuclear division occurs in the enlarging megaspore before development ceases, probably in June, for several months during winter (Sinnott, 1913). The female gametophyte becomes cellular when development of the ovule recommences in

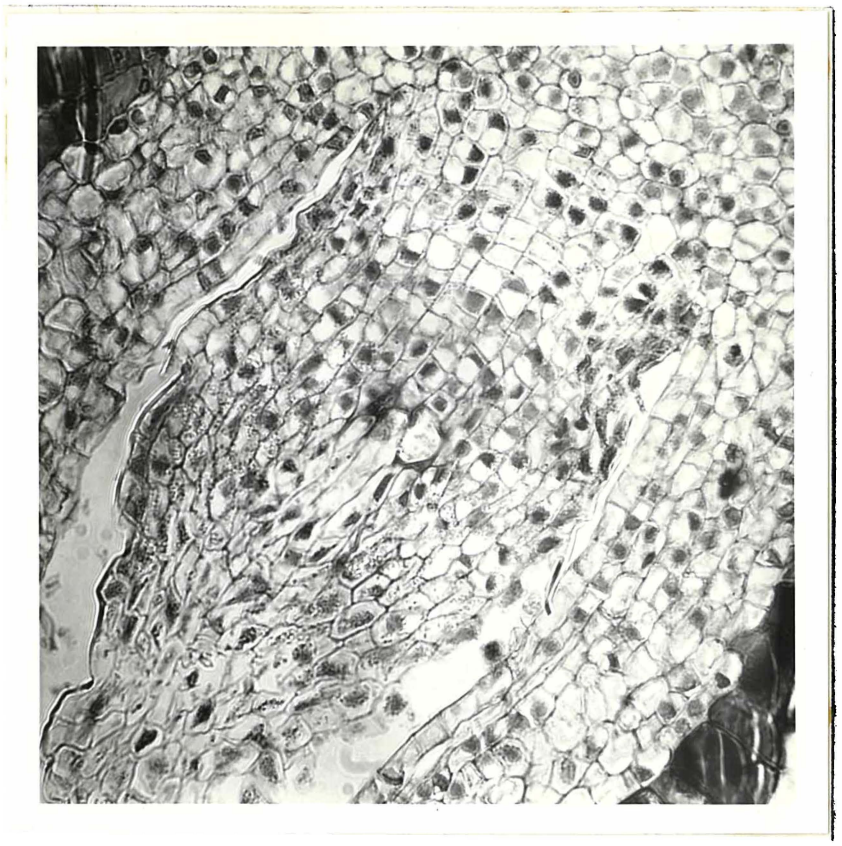


Fig. 2 .8

L.S. through the nucellus and integument of an ovule collected in the Hunua Range in mid February. The large elongated cell in the middle of the nucellus may be the megaspore mother cell. (x 252)

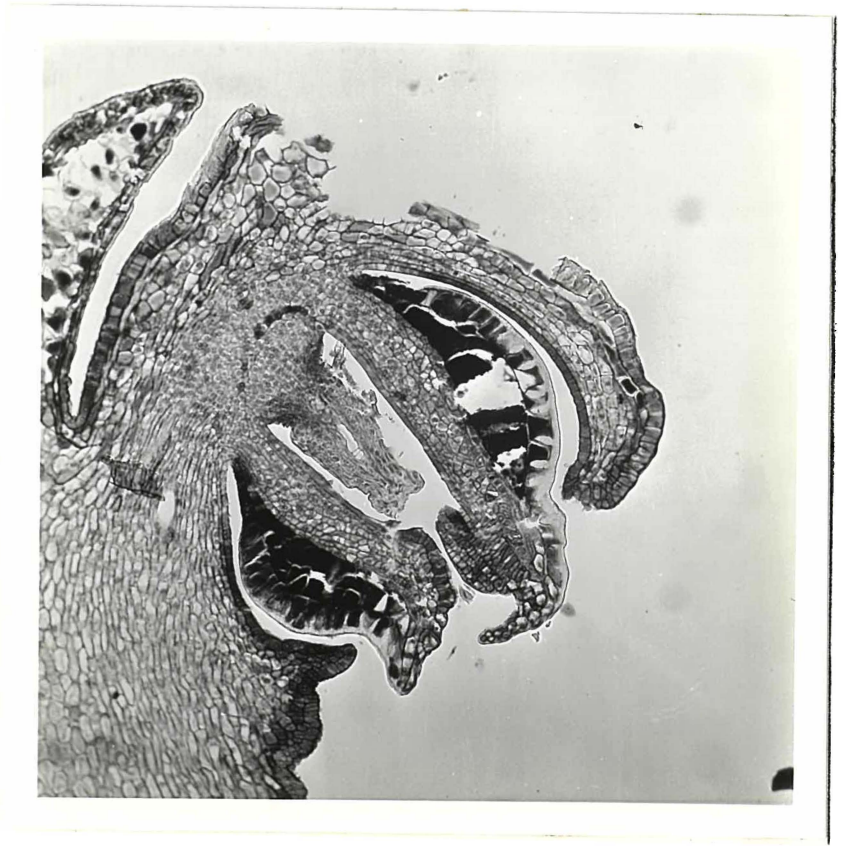


Fig. 2 .9

L.S. through an ovule collected on the Mamaku Plateau in mid March. The linear tetrad of megaspores is visible in the nucellus. (x 63)

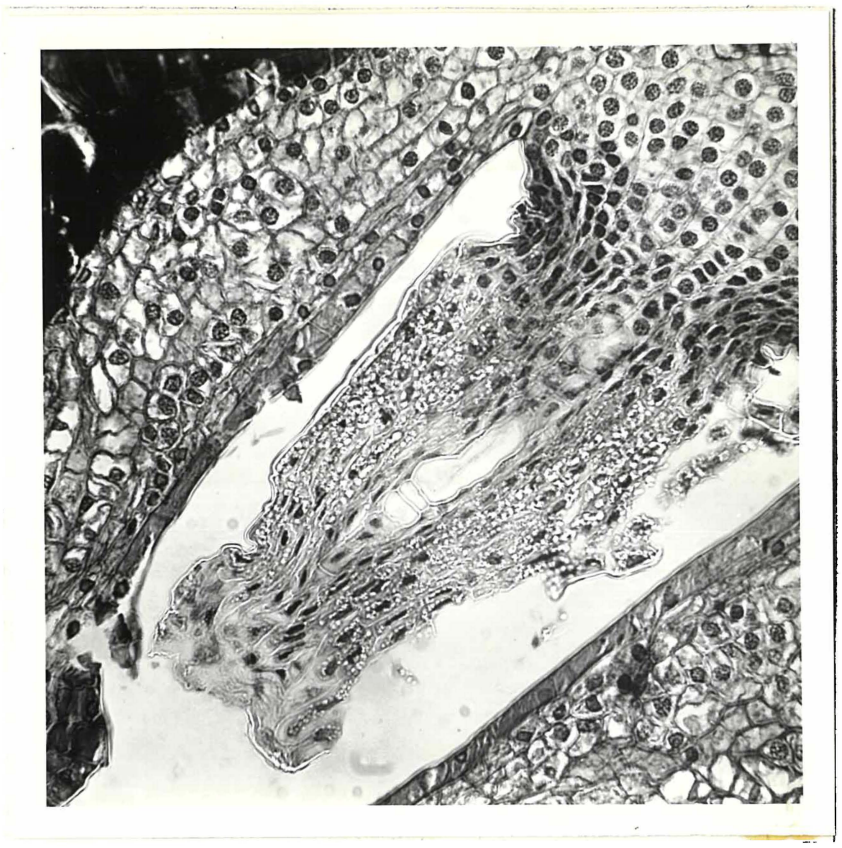


Fig. 2.10

Enlargement of Fig. 2.9. This ovule was not pollinated. (x 252).

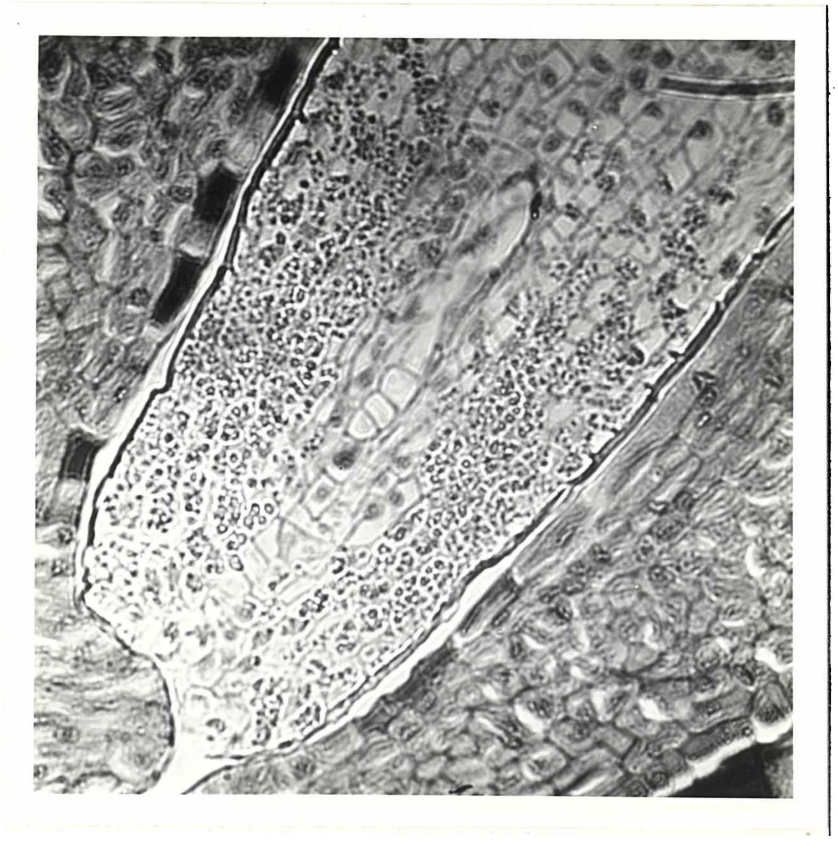


Fig. 2.11

L.S. of an ovule collected in the Hunua Ramge in mid February. The tetrad of megaspores is visible with the functional one enlarging. (x 252).

September or October and by November it can be dissected from the nucellus under a dissecting microscope as it is protected by a thick megaspore membrane (Quinn, 1966b).

Difficulty was encountered in sectioning ovules between March following pollination and January or February of the next year. The ovule develops a thick waxy coating on the integument which prevents penetration of the fixative and makes infiltration of the embedding wax difficult. However, dissections showed that between October (in the second spring) and January the gametophyte, a white oval structure, grows at the expense of the nucellar tissue. The shape of the nucellus changes from conical during its first summer, to flask-shaped as the gametophyte begins to swell from October to December, and finally to its mature ovoid form with a distinctive pointed tip (Fig. 2.1, 4) (January until seed fall in April or May.) Eventually the nucellus tip and its surmounting pollen grains are pushed up into the closed micropylar canal.

Fig. 2.12 shows an ovule collected on the Mamaku Plateau in early November. The ovule is 3/4 emerged from the cup-like epimatium and the receptacle leaves have begun to swell a little although they remain green. Figs. 2.13 a and b show an ovule which has been opened by removal of part of the integument. It was collected on the Mamaku Plateau in mid December and was removed from the epimatium to which it was attached only at the base and which surrounded only its lower 1/4. The flask shaped nucellus is visible with one pollen grain on its tip, directly below the micropylar canal. The nucellus is torn and the large whitish female gametophyte is bulging out of it. The nucellus is joined to the integument only at the base.

By late November the gametophyte occupies nearly the entire space inside the nucellus. Three archegonia are formed near the micropylar end of the gametophyte (Sinnott, 1913) and in sections of an ovule collected in late November from Pakawau, Farewell Spit, two of the archegonia were distinguished (not illustrated).

During January and February in a fertilised ovule a gradual change occurs in the gametophyte tissue which is converted to endosperm. The gametophyte earlier appears translucent and watery (Fig. 2.13 a),

Fig. 2 .12

An ovule on its receptacle collected on the Mamaku Plateau in early November. The ovule is $\frac{3}{4}$ emerged from the epimatium which forms a small green cup at its base. The micropyle is on the right and the tip of the carpidium is just visible on the left, touching the epimatium. (Length 8mm.).

Fig. 2 .13 a.

An ovule opened by removal of part of the integument. Collected on the Mamaku Plateau in mid December. (Length 4mm.).
The parts of the ovule are identified in Fig. 2 .13 b, below.

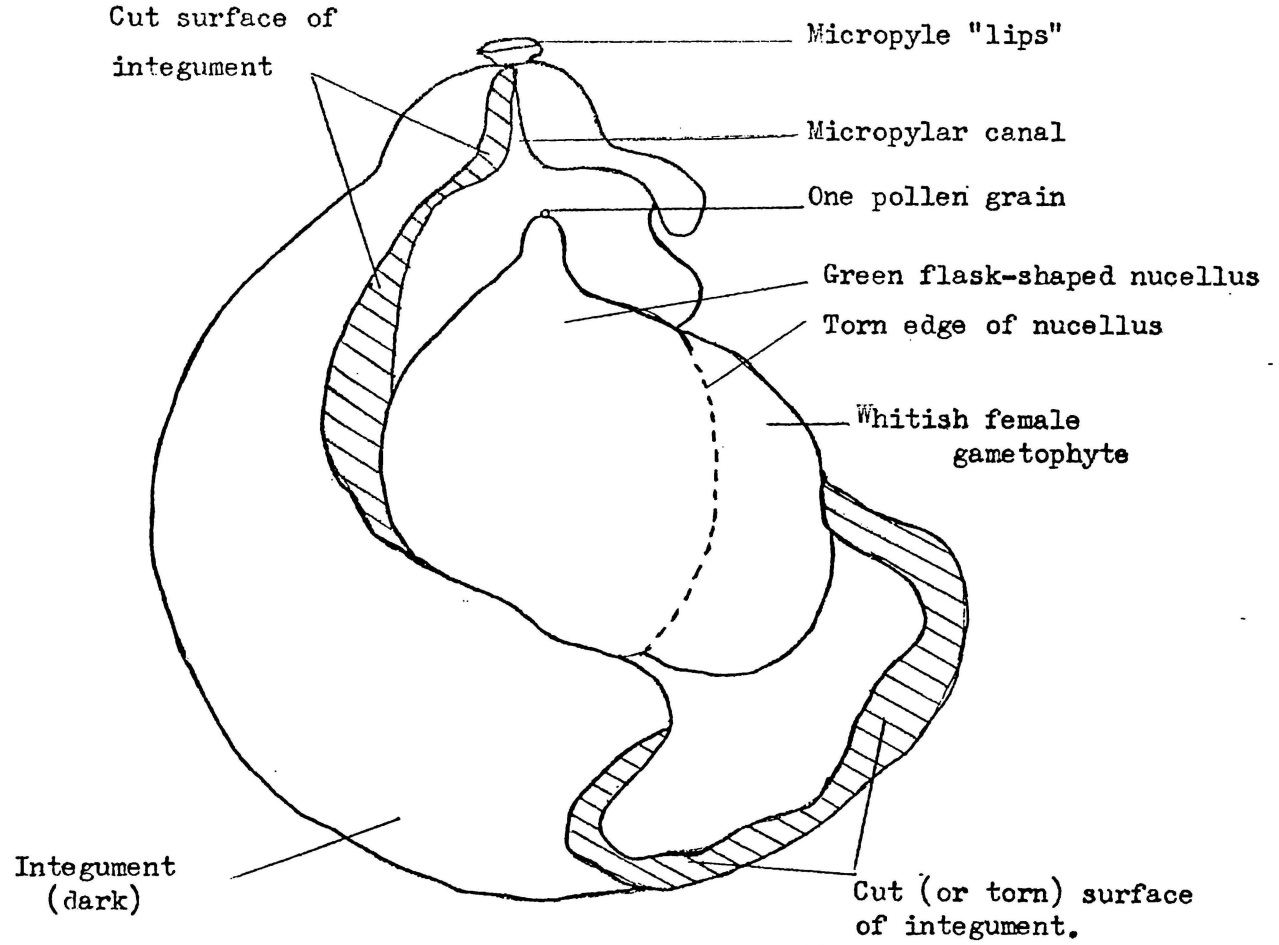


Fig. 2 .13 b.

but it is gradually changed to endosperm which appears white and either granular or oily. By March or April the nucellus has been reduced to a thin papery layer adjacent to the inner layer of the integument. This latter has also become thin and papery while the middle layer of the integument has become hardened, especially at the micropyle end. The outer layer of the integument remains fleshy and pigmented though relatively thinner than in the young ovule. The integument has now become the seed coat or testa and is covered with a coating of wax which is thickest at the micropyle end.

2.3.1.5 The loss of ovules before fertilisation

The study made no quantitative examination of ovules in their first year of development from the time they become visible in November until the following November. Therefore no estimate of the loss of ovules during this time can be made. Ovules collected for study before the time of fertilisation, in November and December of their second summer, were all normal looking superficially. Ovules with dead contents had either died recently, in which case the nucellus and gametophyte were not entirely dry, or they had died one year earlier and had remained on the tree. (In the latter case the integument usually appeared dry and brownish.)

Ovules at two stages of development may be found on rimu branches during the summer; small ovules in their first (pollination) season, and larger ovules in their second (fertilisation) season. However, many of the specimens examined also carried a few ovules which did not fit into either of these categories. These abnormal ovules were intermediate in size and development between the first and second year ovules. They fell into three groups, although superficially all looked alike:

1. When all the abnormal ovules on a specimen were dead it was presumed that they had died at an earlier stage of development. If numerous healthy normal ovules were present on the same specimen it seemed likely that the dead ovules belonged to the previous seed crop in which case they had remained dead on the tree for more than 12 months.

2. Abnormal ovules which had recently died were concluded to belong to the present crop, but to have ceased development for some unknown reason. (Many of these and the other abnormal ovules were pollinated.)

3. Abnormal ovules which were apparently perfectly healthy seemed to be undergoing delayed development. It is not known whether these ovules continue to develop and mature several months later than the main seed crop (possibly in the following spring) or whether they ultimately die.

From these observations and others of minute dead ovules at approximately the stage of pollination, it is assumed that many potential ovules die during their first year of development. The causes of ovule loss during their first year are unknown, but it is likely that severe weather conditions and possibly competition with other organs for metabolites are involved. Lack of pollination does not seem to cause the death of young ovules as many of the healthy, normally developing ovules in their second summer were not pollinated.

For all collections of superficially normal looking ovules made before the time of fertilisation the mean percentage of those with living contents was 77.5%. Details for different localities are given in Table 2.5, section 2.3.1.8.

2.3.1.6 Fertilisation and embryo development

Fertilisation has not been observed, but is believed to occur approximately twelve months after pollination (Fig. 2.1, 4). Minute embryos were found in dissected ovules collected in January. Sections of ovules collected in mid January showed embryos past the proembryo stage (not illustrated) and in several ovules collected in February and March, two embryos were found in dissections. It was not possible to tell whether these resulted from polyzygotic or cleavage polyembryony, although the determinate nature of the cleavage in rimu makes it seem likely that two eggs were involved. By the time embryos are large enough to be found in dissections, the endosperm has enlarged to occupy the entire space within the integument and the

nucellus tip with the pollen grains has been forced up into the micropylar canal from which it is difficult to dissect out intact to count the grains.

Fig. 2.14 shows a developing embryo with two cotyledons in the endosperm of an ovule collected in February in the Mamaku Range. The embryo grows as the suspensor system pushes it further into the endosperm and it follows a crack down the middle of the endosperm which results from the way the female gametophyte develops from the megaspore. When the alveoli become divided into rows of cells radiating from the centre, two cell walls come to lie adjacent to one another and these are later easily separated by the passage of the embryo.

Rimu seed vary a little in size and shape from tree to tree and even on one tree. The dimensions of a typical seed are 3.34 mm long x 2.62 mm broad x 2.24 mm deep (G.W. Hedderwick pers.comm.). Embryos dissected from mature seed varied a little in size and position in the endosperm. They were approximately 1/10 the length of the seed or smaller. Germination trials showed that rimu seed from ripe red receptacles germinates over many months. The first seed to germinate in a germinator at 20°C did so after 21 days. Most germination occurred by about 80 days, but a few seed continued to germinate after seven months in the germinator. Slow embryo development may be responsible for this delay in germination.

2.3.1.7 The receptacle

From the time of fertilisation, or sometimes earlier, the twelve or so leaves above the distinctive right angle bend in the ovule-bearing shoot begin to swell (Figs. 2.12, 2.1, 4, 5 and 6). The swelling occurs first in the base of the leaves, which remain green (Fig. 2.12). As the embryo grows inside the seed these receptacle leaves continue to swell and coalesce and, from March to May, they change colour, ripening like a tomato from green through yellow to orange and finally to red. (Fig. 2.1, 5 and 6, Fig. 2.15.) Colour changes also occur in the seed coat which turns from green to a dark greenish brown and then becomes either a very dark glossy brown or a rich glossy red. Anthocyanins are responsible for these colour changes (Lowry, 1972). Commonly only one seed is carried on each receptacle, but occasionally twin seeds are found.

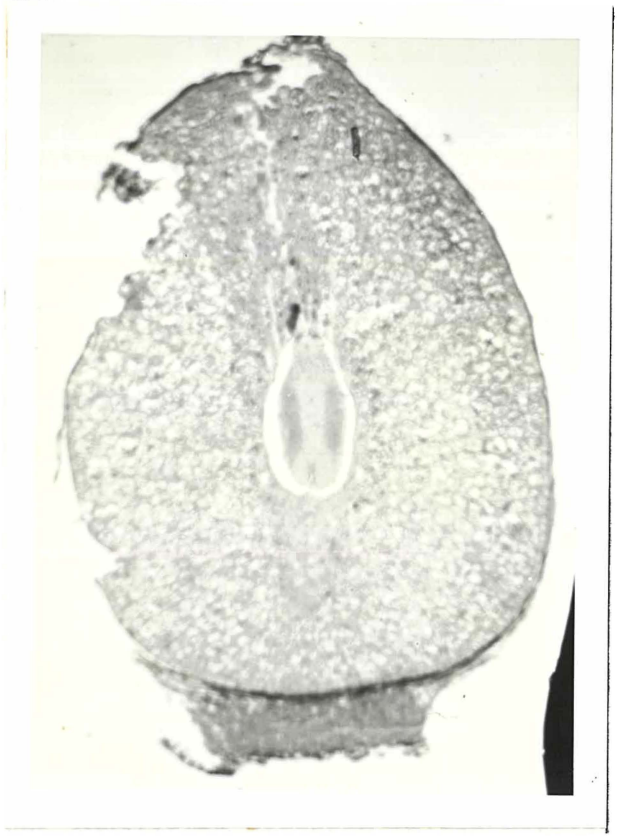


Fig. 2 .14

L.S. through the endosperm of an ovule collected in the Hunua Range in February. An embryo with two cotyledons is visible and the crack the suspensor system has forced through the endosperm can also be seen. (x 25.2)

Fig. 2 .15

A ripe rimu fruit collected on the Mamaku Plateau in late March. The seed is a glossy dark brown, the receptacle and epimatium red and fleshy. (Length 8mm.).

2.3.1.8 Ovule survival after fertilisation

Unpollinated ovules continue to develop normally until the time fertilisation should occur, after which they die. This implies that failure of fertilisation due to lack of pollination is a major cause of empty seed production in rimu. The percentage of living ovules in all collections made before and after the time of fertilisation were compared by t-test. The mean percentage after fertilisation (63.6%) was significantly lower than that before fertilisation (77.5%). These figures, however, include all ovules, pollinated and unpollinated, and show that failure of fertilisation for whatever reason, is a significant factor in the production of empty seed.

To discover whether localities differed in the percentage ovule survival before and after fertilistion, data from different localities was examined by a factorial analysis of variance. Because of the binomial distribution of survival data an arcsine transformation was performed. The analysis of variance of the transformed data was very similar to that of the untransformed data so the latter was used. t-tests were used to compare collections before and after fertilisation from each locality. For Puketi and Otaki Forks in the North Island there were highly significant differences in the percentage of living ovules between the two collections indicating that failure of fertilisation caused a large proportion of the loss of potential seed in these two localities. However, there was no significant difference between collections from Pakawau, Ashley or Saltwater Forests in the South Island (Table 2.5).

Differences in the percentage of living ovules between localities were analysed by the SNK Multiple Range Test. The overall difference (for both collections combined) showed Pakawau to have significantly lower survival ($p = 0.01$) than the other localities, which did not differ significantly from each other ($p = 0.05$).

When differences between localities in percentage of living ovules before fertilisation were compared, it was found that Pakawau and Saltwater Forest had significantly lower survival than the other three localities (Table 2.5).

After fertilisation time there was a significantly lower percentage of living ovules in collections from Pakawau and Otaki Forks than from Ashley Forest ($p = 0.05$), but collections from Saltwater and Puketi Forests did not differ significantly from Ashley Forest on the one hand or Otaki Forks on the other (Table 2.5).

It can be seen in Table 2.5 that there was a higher percentage of living ovules in the collection after fertilisation time than in the one before in both Saltwater Forest and Pakawau. In these forests failure of fertilisation was not a major cause of ovule death.

It is believed that most ovules which are successfully fertilised develop into sound seed, but a small proportion may fail to develop due to death of the embryo, perhaps for genetic reasons. Other seed losses following fertilisation are due to storms, insects and birds. When a large seed crop is maturing in a forest there may be a build up of populations of insects which feed on developing seeds (e.g., Tortricid caterpillars) and these may cause significant seed losses. Similarly seed eating birds such as introduced finches may be attracted in large flocks to rimu trees on which many seeds are maturing in early autumn (A.E. Beveridge, pers. comm.).

Table 2.5 : Comparison of the percentage of ovules with living contents between five localities and two collections, before and after fertilisation time. (10 ovules per tree; 5 trees per locality at each collection)

Locality	Mean Overall % of living ovules	Mean % of living ovules before fertilisation	Mean % of living ovules after fertilisation	Significance of difference between the two collections
Puketi Forest	80.00 a	98.00 a	62.00 abc	$p = 0.01$
Otaki Forks	72.00 a	98.00 a	46.00 bc	$p = 0.001$
Pakawau	37.00 b	34.00 b	40. 00 c	N.S.
Ashley Forest	90.34 a	96.68 a	84.00 a	N.S.
Saltwater Forest	65.00 a	52.00 b	78.00 ab	N.S.

2.4 Discussion

Conifer reproductive cycles fall into two general types; those in which pollination and fertilisation take place within the same growing season (short cycle); and those in which fertilisation occurs approximately one year after pollination (long cycle). Amongst New Zealand tree podocarps Podocarpus totara G. Benn. ex D.Don., P. hallii Kirk, P. dacrydioides A. Rich. and Phyllocladus trichomanoides D. Don. belong to the former category with seed development occurring in one year, while in Podocarpus spicatus R. Br. ex Mirbel, P. ferrugineus G. Benn, ex D. Don and rimu the reproductive cycle takes two years to complete.

Many potential conifer seeds are lost due to death of ovules and abscission of strobili, particularly in trees with long reproductive cycles (Sweet, 1973). It is not possible to estimate the total loss of potential seed in rimu from the present study as there is no easy way of calculating the number of ovules which were initiated, but failed to develop and no quantitative study was made of the loss of ovules during their first year of growth. Estimates of such losses are always difficult. Sweet (1973) reported that between one and thirty percent of the total dry weight of litter on a forest floor may be made up of reproductive parts, but what proportion of these were wasted through premature abscission is not known. Only between 30% and 80% of control-pollinated cones of several Pinus species developed to maturity and similar numbers of wind-pollinated strobili are also lost. This type of conelet drop in which there is no evidence of physical injury is termed physiological drop. Numerous losses of potential seed are also caused by physical damage due to frost, wind, draught, high temperatures and insect and fungal attack. In Pinus radiata and P. echinata Mill. it is estimated that probably three to five percent of female strobili abort before anthesis and cessation of development at this early stage has also been reported for Chamaecyparis obtusa (Sieb. & Zucc.) Endl. (Sweet, 1973).

The largest loss of developing cones in most forest trees occurs in the time between pollination and fertilisation particularly in species with a long reproductive cycle. In one study of Pinus radiata more than 90% of cones were shed during this time, but the amount of drop varies between species, genotypes, sites and position in individual tree crowns. (Sweet, 1973) The present study did not allow for any estimates of seed

losses during this period of development as only foliage carrying normal looking ovules was collected for examination. Also it was not possible to determine precisely when dead ovules had died as such ovules apparently remain on the tree for many months. However, it is concluded that the biggest single factor causing the production of empty seed in rimu is lack of pollination leading to lack of fertilisation the following year. This appears to have occurred in Puketi Forest and Otaki Forks (Table 2.5) and the former locality was one in which insufficient pollination was recorded in Table 2.4.

Rimu differs from certain Pinus species including P. radiata or P. sylvestris in that unpollinated ovules usually continue to develop normally for a whole year until soon after fertilisation should have occurred, when the gametophyte gradually shrivels leaving the near empty integument. Empty seed caused by failure of fertilisation following lack of pollination are also found in Podocarpus totara in New Zealand as well as in certain northern hemisphere conifers with a short reproductive cycle such as Pseudotsuga menziesii (Mirb.) Franco (Allen and Owens, 1972) and Picea A. Dietr., and also in some with a long reproductive cycle (see section 2.1.2.2).

There were similar numbers of pollinated and unpollinated dead ovules in the collections made before the time of fertilisation. Lack of pollination did not appear to affect the survival rate of ovules before the time of fertilisation. However, of dead ovules collected after fertilisation time significantly more were unpollinated than pollinated ($p = 0.001$). Death of both unpollinated and pollinated ovules prior to fertilisation time occurred at varying stages of development and for no apparent reason. Possibly competition for available carbohydrates or severe weather conditions caused the death of developing ovules during the year between pollination and fertilisation in rimu. In Pinus radiata in Australia and New Zealand competition for carbohydrates and possibly also mineral nutrients are implicated in the loss of conelets during this development stage and water stress may be involved in certain seasons (Sweet, 1973). In comparison the major cause of conelet drop in P. sylvestris in Finland is inadequate pollination (Sarvas, 1962). In rimu it appears that many dead ovules remain on the tree for some months whereas the death of a certain proportion of ovules in a conelet in Pinus species usually leads to the abscission of the conelet.

In collections made following the time of fertilisation almost all unpollinated ovules were found to be dead or dying, although there were a small number of unpollinated ovules which were alive and healthy two months after fertilisation was expected to have occurred. No embryo was found in these ovules and it is believed that they would have died ultimately.

A small proportion of pollinated ovules collected after the time of fertilisation were found to be dead. It is possible that some or all of these may have died before fertilisation time, but in others fertilisation may have failed for some reason. In Pinus radiata fertilisation sometimes fails even after artificial pollination and this may be caused by the pollen tube failing to renew growth after the winter dormant period (Sweet, 1973). Parthenogenetic development does not occur in conifers and, with rare exceptions, unfertilised ovules abort and produce empty seeds.

In the present study severe weather conditions probably accounted for the low survival of ovules both before and after fertilisation time in the collections from Pakawau. (Table 2.5)

In rimu pollination occurs very late in the season compared with most conifers. In central North Island rimu pollen is shed in early January whereas in Podocarpus dacrydioides, P. totara, P. hallii, P. ferrugineus, P. spicatus and Phyllodadus trichomanoides pollination takes place in October or November in the same locality. The majority of rimu ovules examined (46.7%) contained a single pollen grain, but multiple pollination occurs frequently. The maximum number of pollen grains found in any ovule was 5 (Table 2.3). Multiple pollination is also common in other conifers including Pseudotsuga menziesii (Allen and Owens, 1972) and Pinus sylvestris (Sarvas, 1962). Sarvas (1962) occasionally found ovules containing 21 pollen grains, although the average number for different trees varied from three to eight.

Evidence of multiple fertilisation was found in several immature rimu seeds which contained two small embryos on separate suspensors, but it is believed that only one embryo survives in each seed.

The success or failure of pollination in conifers depends to a large extent on weather conditions at the time. Little is known about the distance rimu pollen can travel in sufficient quantities to ensure successful pollination, but it is assumed that forest structure may be more important in a dioecious species than site per se. There must be sufficient male trees within suitable distance and direction of the female trees.

In Pinus sylvestris rain was found to destroy all pollen grains on the surface of strobili whereas grains which had entered the ovules were unharmed (Sarvas, 1962). The number of pollen grains per ovule in P. sylvestris was found to vary from year to year depending on the quantity of male flowering and the weather conditions. Such variations probably also affect pollination success in rimu. The vast majority of pollen in P. sylvestris was spread in a more or less horizontal direction and the pollen catch was much greater on the windward than on the leeward side of the tree. Obstacles such as trunks and crowns of other trees were shown to hinder the free flight of pollen.

In this study no glossy brown or reddish rimu seed on fully developed ripe red receptacles (Fig. 3.15) were found to be empty or to contain dying contents except where insect larvae were present. The collections were made during the summer preceding an exceptionally good rimu seed crop in most parts of the country. In other examinations rimu seed on ripe coloured receptacles has been found to contain dead or dying contents. (A.E. Beveridge, pers. comm.) No unpollinated ovules were found to contain embryos, but a small number of unpollinated ovules survived up to six weeks after the time fertilisation should have occurred. Possibly the receptacle of such a surviving unpollinated ovule would develop and ripen in the normal way. The delayed death of the contents of such an ovule might produce an empty seed on a ripe receptacle.

Detailed information is still lacking on certain crucial stages in rimu seed development. The time of ovule (and male cone) initiation is unknown and would be very difficult to discover owing to the indeterminate nature of rimu growth. The pollination mechanism, fertilisation and proembryo development have yet to be described.

In summary, the reproductive cycle in rimu extends over two years from the probable time of ovule initiation in late summer or autumn, to anthesis in the following January (central North Island), to fertilisation approximately twelve months later and seed maturity in autumn. The principal cause of empty seed production is believed to be failure of pollination, although fertilisation occasionally fails in pollinated ovules also. Studies in pollen dispersal are recommended to determine how far rimu pollen travels in sufficient quantity to ensure adequate pollination.

CHAPTER 3 : SOME ASPECTS OF THE PHYSIOLOGY OF GROWTH OF RIMU SEEDLINGS

3.1 Introduction and literature review

Rimu is a widespread and extremely successful tree in lowland forests throughout New Zealand where it is often a dominant member of the plant community (Nicholls, 1976). Throughout its long life rimu is slow growing compared with most angiosperm trees and many other conifers (ecological observation). At the seedling and sapling stages it has the ability to tolerate low irradiances for very long periods and then to respond to increased irradiance when the forest canopy is opened up, either gradually, by the senescence and death of trees overhead, or suddenly by windfall of mature trees during storms (Beveridge, 1973). On the other hand rimu seedlings may also tolerate high irradiances and establish early in the recolonisation of burnt slopes (June, 1982) or around the edges of bogs (Holloway, 1954). In any event growth of rimu seedlings is slow relative to the herbs, shrubs and angiosperm trees in the same localities and in order to persist they must be able to survive shading and depletion of soil moisture and nutrients by these faster growing species. New Zealand has a relatively mild maritime climate and does not suffer the extremes of summer heat and winter cold experienced by large continents in northern temperate latitudes and today the forests in which rimu is found are warm temperate rainforests containing a sub-tropical element, including lianes and epiphytes. However, during the Pleistocene the New Zealand climate was much colder and rimu must have been able to tolerate these lower temperatures to have survived the glaciations in refugia. Some of this cold tolerance may have been retained as the species recolonised areas devastated by ice and periglacial outwash deposits. Similarly in the volcanic plateau of the central North Island rimu has spread into large areas blanketed in ash and pumice by the Taupo eruption 1800 years ago. Dispersal of seed over long distances by birds enables rimu to spread more rapidly than species with wind dispersed seed such as beech (Nothofagus spp). This, together with the seedlings' ability to establish in a wide range of sites has enabled rimu to become the most widespread dominant tree in New Zealand today.

Shade tolerant tree seedlings often have low relative growth rates even when grown in high light intensities and their slow growth is believed to be genetically determined (Grime, 1979). The ability to sustain slow

growth under limiting conditions for comparatively long periods, combined with the longevity of the larger tree stages, enables rimu eventually to overtop the forest canopy and become dominant. Grime (1979) describes species with this type of life history as "stress tolerant dominants". In Chile, a country with many biogeographic similarities to New Zealand, Araucaria araucana (Molina) K. Koch is a species with this type of regeneration and life history (Veblen, 1982). The seeds of A. araucana germinate rapidly and the seedlings are extremely shade tolerant and capable of growing on poorer sites than the faster growing Nothofagus species which occur in the same forests. In this way the slow growing conifer is able to persist until a canopy gap is created by death or windthrow when the added light allows some increase in growth rate. Like rimu it is the combination of the seedlings' extreme tolerance to shade, combined with the longevity of the older stages, which allows A. araucana eventually to become dominant in these Chilean forests. Certain northern hemisphere conifers such as Tsuga canadensis L. Carr. (hemlock) and to a less extent Picea abies L. Karst (Norway spruce) also survive to become dominant by their extreme tolerance to shade as seedlings, tenacity for life and longevity (Marshall, 1927; Sernander, 1936). Like rimu, which often establishes under a canopy of angiosperm trees such as Leptospermum spp J.R. et G. Forst. or Weinmannia racemosa Linn.f., hemlock is often associated with faster growing angiosperm trees such as beech (Fagus sp) and maple (Acer sp) (Hough, 1936). After several hundred years of slow growth these two unrelated conifers may overtop the angiosperm canopy and appear as scattered emergents creating a comparable forest type in the American northwest and in New Zealand.

These characters which have evolved to enable the species to survive can be traced to physiological functions. It was the objective of this part of the thesis to explore some of these. There have been few other physiological studies made of seedlings of slow growing New Zealand indigenous conifers. However, kauri (Agathis australis Salisb.) seedlings in a Leptospermum community were found to have optimal establishment rates between 4% and 12% of full sunlight with no establishment below 1.5%, while tanekaha (Phyllocladus trichomanoides D. Don) seedlings in the same locality established in greatest numbers at 4.2% full sunlight and did not occur below 1.8% (Bieleski 1959a). In kauri seedlings grown in semi-controlled environments, there was a decrease in root:shoot ratio with decreasing growing light intensity

which is a common occurrence in tree seedlings (Spurr and Barnes, 1973) . Similarly leaf assimilation rate and relative growth rate decreased with decreasing growing light intensity. In tanekaha seedlings growth increased with increasing growing irradiance between 1.7% and 33% full sunlight and it was concluded that higher growth rates would have occurred at higher irradiances than those used in the experiment (Pook, 1960). At the minimum irradiance tested, (1.7% full sunlight), tanekaha seedlings were able to grow, although only at a very low rate.

When kauri seedlings were grown at different temperatures in semi-controlled environments, increasing temperature caused a decrease in the root:shoot ratio and an increase in the assimilation rate. The optimum temperature for growth, (23^{o}-26^{o}C) was controlled by the disproportionate increase in respiration losses rather than by high temperatures limiting photosynthesis. Kauri growth was limited below 17^{o}C and seedling bud dormancy was broken more rapidly at higher temperatures (Bieleski, 1959c). Although kauri seed germinated between 10.5^{o} and 36^{o}C, initial growth was only adequate for seedling establishment between 19.5^{o} and 27.5^{o}C and the optimal temperature for germination and initial growth was close to 25^{o}C (Barton, 1978). In tanekaha the optimum temperature for seedling growth was found to be close to 26.5^{o}C and at this temperature they grew faster than kauri seedlings (Pook, 1960). However, tanekaha seedling mortality increased significantly with increasing temperature between 15.5^{o} and 35^{o}C.

The most important features of the environments of these shade tolerant forest tree seedlings are irradiance and temperature as the former is essential for photosyntheses and the latter affects the rates of the many physiological reactions involved in growth. For such plants to grow irradiance must be above light compensation point for a minimum period of time each day and the temperature must remain within a limited range below which metabolism is very slow and above which dark respiration rate increases rapidly and less metabolites are available for growth. Because growth is so dependent on these two features of the plant environment, it was decided to examine the growth of rimu seedlings under various conditions of irradiance and temperature.

3.1.1 The influence of irradiance

Rimu seedlings often become established and grow in heavily shaded sites. However, as has been described above, when such seedlings are exposed to higher irradiance whether by natural changes in the forest canopy or by releasing as a silvicultural practice, the seedlings respond by increasing their growth rate to some extent. Unlike many shade tolerant plants rimu seedlings can also tolerate high irradiances providing adequate shelter from wind and sufficient water are available (Beveridge, 1962).

Certain plant species are adapted always to grow in low light (shade plants), while others are adapted to grow in fully exposed positions (sun plants). In the case of certain forest trees such as rimu, the seedlings usually grow in shaded sites, but the crown of the mature tree is exposed to full sunlight above the forest canopy. Much has been written about the response of plants to different growing irradiances. In general, plants from shaded habitats perform efficiently at low irradiances, but are incapable of high phtosynthesis and growth rates even when grown at high irradiances. On the other hand, plants which normally grow in high light intensities have a high light saturated rate of photosynthesis, but when grown at low irradiances may have lower photosynthesis rates than shade plants in the same conditions (Boardman, 1977). Some of the better known differences between the leaves of plants grown in shade and in sun are shown in Table 3.1. As well as the differences in individual leaves grown at low and high irradiances, plants grown in the shade usually invest a greater proportion of their photosynthate in the creation and maintenance of foliage than plants grown in the sun (Boardman, 1977). On the other hand, plants grown in higher irradiances develop better root systems than shade grown plants. Rimu seedlings are capable of growing in low light intensities, and have very low growth rates, even when grown in open positions, whereas certain other conifers such as Pinus radiata are known to grow vigorously in full light. For example, many five year old rimu seedlings in Pureora Forest (central North Island) were found to be less than 1000 mm tall (Beveridge, 1973) whereas Pinus radiata seedlings in a Rotorua nursery often reach 500 mm in 9 months from seed (van Dorsser, 1981). As photosynthesis is a fundamental growth process it was decided to compare the photosynthesis and dark

TABLE 3.1 : DIFFERENCES BETWEEN LEAVES GROWN IN LOW IRRADIANCES (shade leaves) AND HIGH IRRADIANCES (sun leaves)

Feature	Shade leaves or plants	Sun leaves or plants	Reference
Growth rate	Lower	Higher	
Light saturated rate of photosynthesis	Lower ($0.2-0.5 gCO_2\ m^{-2}\ h^{-1}$)	Higher ($1.6-2.0 gCO_2\ m^{-2}\ h^{-1}$)	Bohning and Burnside 1956
Dark respiration rate	Lower	Higher	McCree & Troughton 1966 Bjorkman etal. 1972b
Light compensation point	Lower	Higher	Bjorkman 1968
Quantum requirement	Lower	Higher	Bjorkman and Holmgren 1963 Bjorkman and Holmgren 1966 Burnside and Bohning 1957 Bjorkman et al. 1972a
Stomatal resistance (in some species only)	Higher	Lower More stomata/unit area	Holmgren et al. 1965 Bjorkman et al. 1972b
Mesophyll resistance (in some species only)	Higher	Lower	Bjorkman et al. 1972b
Leaf morphology	Thinner	Thicker Strongly developed palisade and spongy mesophyll layers	Goodchild et al. 1972
Chlorophyll concentration	More/unit weight or volume but may be less/unit area	Less/unit weight or volume	Goodchild et al. 1972
Chlorophyll a:b	Lower	Higher	Goodchild et al. 1972 Leopold and Kriedemann 1975
Carboxylation enzymes content	Lower	Higher	Bjorkman et al. 1972b

respiration rates of seedlings of these two contrasting conifer species and try to answer various questions:

Does rimu grow slowly because its light saturated rates of photosynthesis are very low compared with those of P. radiata? If so, are the rates low because rimu is less efficient at fixing CO_2 than P. radiata and therefore has a higher quantum requirement? Or does rimu have much greater stomatal resistance to CO_2 diffusion, or greater internal leaf resistance than P. radiata? Alternatively, the rates of photosynthesis of the two species might be similar, but if rimu had a much greater rate of dark respiration than P. radiata assimilate available for growth would be limited. In an attempt to answer these questions the responses of net photosynthesis rate to changing irradiance, and of dark respiration rate to increasing temperature in rimu and P. radiata seedlings grown together, are examined in section 3.3.

With the knowledge that rimu seedlings occur in a wide range of light intensities in nature, it was of interest to discover whether some or all of the differences between sun and shade plants shown in Table 3.1 occurred in rimu seedlings when they were grown in different light intensities.

In section 3.4 three experiments examining the effect of growing irradiance are described. In the first rimu seedlings were grown for seven months at three contrasting light intensities and their relative growth rates and other growth parameters measured. An extreme shade treatment of 1% full sunlight was used to approximate the lowest light intensity likely to be encountered on the floor of dense closed canopy forest; an intermediate treatment of 17% represented light conditions which might occur in many of the communities in which rimu establishes, e.g., seral Leptospermum forest (Cameron, 1960); and a high light treatment of 42% resembled conditions when the canopy is opened up by windfall or roading, etc. This experiment was designed to test the hypothesis that rimu seedlings are tolerant of extreme shade and that their growth rate is increased by increased irradiance. In a second similar experiment small seedlings growing in a nursery bed were covered with three

different levels of shade giving somewhat higher irradiances; 28%, 60% and 73% full sunlight. After six months of summer and autumn the growth of these seedlings was compared and this experiment further examined the hypothesis that growth rate is increased by higher growing irradiance. In the final experiment in section 3.4, potted seedlings were grown in three irradiances in controlled environment cabinets. This experiment was designed to show the responses to growing irradiance of various growth and photosynthesis parameters. The maximum irradiance attainable at plant level was 650μE m^{-2} s^{-1} which is well above the light saturation level measured for rimu in a trial. (Full sunlight at noon in summer is approximately 2000μE m^{-2} s^{-1}.) An intermediate irradiance of 385μE m^{-2} s^{-1} was chosen (close to saturation level) and a low one of 140μE m^{-2} s^{-1}, well below light saturation level, but above the estimated light compensation point for rimu seedlings. (It was necessary to allow some growth to occur during the experiment.) The hypothesis was that relative growth rates and unit leaf rates, light saturated photosynthesis rates and light compensation points would all be increased by higher growing irradiances and that leaf weight ratios would increase with decreasing irradiance. The results were expected to show whether rimu seedlings responded to growing irradiance in the usual way as shown in Table 3.1

3.1.2 The influence of temperature

Rimu seedlings establish naturally throughout New Zealand in lowland areas and experience a variety of temperature climates in different parts of this wide latitudinal range (34°S to 47°S). The climate of lowland New Zealand today is, however, even and mild in comparison with that of large continents in similar latitudes and the mean annual temperature at sea level only varies from a little over 15°C from Auckland northwards, to between 5° and 10°C in Southland. Summer mean daily maximum temperatures range from 25°C in parts of Hawkes Bay, Bay of Plenty and Northland to 17.5°C in Southland, while summer minimum temperatures range from 15°C to 7.5°C. Winters are cooler, although not extreme with mean daily maximum temperatures ranging from 15°C in the far north to 7.5°C in Southland and Otago and minimum temperatures from 7.5°C in Northland to -2.5°C in inland Southland and Otago (Coulter, 1975).

It is known that rimu seedlings do not occur in frost hollows in the central North Island (A.E. Beveridge, pers.comm), and it is probable that the upper altitudinal limit of rimu is controlled by low temperatures. Rimu seed falls or is dispersed by birds in late summer in Northland and in autumn further south. Germination may occur in autumn in Northland, but in most parts of the country it does not usually occur until the following spring or summer (A.E. Beveridge, pers.comm). Work examining the effect of temperature on the growth of kauri and tanekaha seedlings has been mentioned in section 3.1., but these two conifers have much more limited present day distributions than rimu and are restricted to milder localities.

Plants generally have optimum temperatures for growth and for net photosynthesis rate. When plants are grown at low temperatures their dark respiration rate at any given temperature is usually higher than that of plants grown at higher temperatures (Sorensen and Ferrell, 1973). Low night time temperatures may cause an increase in growth rate by reducing the rate of dark respiration (Hellmers and Rook, 1973). In Pinus radiata seedlings between three and six months old plants grown at $5^{o}C$ night temperatures had higher relative growth rates than those grown at warmer night temperatures and the effect of day temperature was small compared with the effect of the low night temperature, except at the extremes of the day temperature range used (17^{o} and $32^{o}C$). The seedlings grown at low night temperatures also had higher root:shoot ratios than those grown at warmer nights. The optimum temperatures for both growth and net photosynthesis rates may, however, be altered by the temperature regime in which the plant is grown (Rook, 1969). Plants which have been grown at higher temperatures tend to have higher optimum temperatures for growth and photosynthesis than plants grown at lower temperatures, but when plants are transferred from one temperature regime to another, their net photosynthesis and dark repiration rates acclimate to the new conditions within a few days (Rook, 1969; Slatyer, 1977a and b; Sorensen and Ferrell, 1973).

In Douglas fir (Pseudotsuga menziessii), seedlings originating from a lower altitude (warmer) provenance had higher net photosynthesis rates than those from a higher altitude (cooler) provenance and seedlings grown at higher temperatures had higher net photosynthesis rates than those grown at lower temperatures. However, in this

experiment growth rates of the low temperature grown plants were higher because they had higher leaf weight ratios (Sorensen and Ferrell, 1973). Growth rates are often not directly correlated with photosynthesis rates.

The way in which temperature affects plant growth, therefore, is very complicated and often difficult to predict as each plant function responds differently to changes in temperature. As well as the daily heat sum (number of degree-hours) influencing growth through its effect on the various physical and chemical reactions within the plant, growth in many species is also influenced by the difference in temperature between the day and the night (the thermoperiod). In certain plants, such as Pinus radiata, night temperature is more important in controlling growth than day temperature, but in others day temperature is the dominant influence. A few species grow best at constant temperature. The way in which a species responds to temperature, and perhaps more especially, to thermoperiod, is usually influenced to some extent by the climate in which the species has evolved (Spurr and Barnes, 1973).

Two experiments examining the influence of growing temperature on rimu seedlings are described in section 3.5. In the first seedlings from two provenances were grown in controlled environments at three temperature regimes and their growth examined by growth analysis. The regimes chosen had daytime temperatures ranging from 17° to $27^{\circ}C$ and an $8^{\circ}C$ day/night differential to approximate natural New Zealand conditions. The aim of this experiment was to discover whether growth rate in rimu seedlings increased with growing temperature. In the other experiment seedlings were grown in controlled environments at a constant day temperature and at three contrasting night temperatures: $5^{\circ}C$ (cold night conditions), $12^{\circ}C$ (representing an average summer night for much of New Zealand) and $20^{\circ}C$ (warm night conditions, the nights warmer than the days, a situation seldom found in nature). $18^{\circ}C$ was used for the day temperature because a trial had shown optimum net photosynthesis rates at $18^{\circ}C$ for seedlings grown at $22^{\circ}C$ day/$13^{\circ}C$ night. This experiment was designed to examine the effect of day/night temperature differential (thermoperiod) on the growth of rimu seedlings.

3.1.3 The influence of season

The way in which plants respond to changes in temperature and also to differences in day length, determines their seasonal pattern of growth. As mentioned in section 3.1.2, the seasonal changes of climate in New Zealand are not as distinct or severe as those found in continental areas in similar northern latitudes. The lack of deciduousness in most angiosperm trees, for example, is thought to result from the relatively mild climate and the absence of extremes of cold in winter and of drought in summer. However, the country does extend over approximately 1600 km and rimu occurs throughout the length of New Zealand from latitude 34°29'S in the far north to 47°05'S on Stewart Island. In this latitudinal range there are large differences in the way in which day length changes with season; for example, there is much less difference between the lengths of summer and winter days in Northland than there is in Southland. There has been little work done on the seasonal patterns of growth in response to changing potoperiod and temperature in southern hemisphere conifers, although the growth of kauri seedlings in controlled environments was shown to be unaffected by photoperiod (Cameron pers.comm. seen in Ecroyd, 1982). However, a great deal is known about northern hemisphere conifers in this respect and northern angiosperm trees have been shown to respond in a similar manner to conifers (Vaartaja, 1959). In most trees of the northern temperate zone decreasing photoperiod is the trigger which prepares the tree to become dormant (Weiser, 1970; Salisbury and Ross, 1978). Shortening days (lengthening nights) of late summer cause stem elongation to cease, resistance to frost damage to increase and buds to become dormant in preparation for the first frost of autumn or winter. In severe continental climates where growing shoots would be killed by early winter frosts decreasing photoperiod is a much more reliable early warning of the approach of winter than decreasing temperature. The other way in which photoperiod has been shown to influence the growth of trees (both angiosperm and conifer) in the northern hemisphere is by controlling shoot extension growth. For example, in Pinus sylvestris seedlings after the first year, long photoperiods caused an increase in internode extension (Wareing, 1950b). The longer the photoperiod in which seedlings are grown the greater the shoot extension growth and the further north the seed source the greater the response. Photoperiodic ecotypes have evolved in many

tree species so that maximum shoot extension growth occurs with increasing daylengths of spring and early summer, but the plant is always dormant and frost resistant before the first autumn frosts (Vaartaja, 1959). For example, Eastern Hemlock (Tsuga canadensis) seedlings showed a distinct clinal variation in response to photoperiod. Under all tested photoperiod regimes provenances from regions with long frost-free growing seasons formed buds and ceased elongation later than those from regions with short growing seasons (Nienstaedt and Olson, 1961).

As many northern hemisphere angiosperm trees respond to photoperiod in a similar way to conifers (Vaartaja, 1959), it is interesting to note the response of certain southern hemisphere angiosperms which have been examined. Bussell (1968a and b) studied three of the small number of deciduous New Zealand tree species, Hoheria glabrata Sprague et Summerhayes, Fuchsia excorticata (J.R. et G.Forst.) Linn.f. and Aristotelia serrata (J.R. et G.Forst.) W.R.B. Oliver, and three evergreen southern beech species, Nothofagus menziesii (Hook,f.) Oerst., N. fusca (Hook.f.) Oerst. and N.solandri var cliffortioides (Hook.f.) Poole. He compared them with the northern hemisphere deciduous Acer pseudoplatanus L. and found that whereas Acer rapidly become dormant in short days even when temperatures were warm, the New Zealand species continued to grow, regardless of photoperiod until temperatures began to decline in autumn. Temperature rather than photoperiod was also the predominant environmental control of leaf fall in the three New Zealand deciduous species. However, although short days did not cause dormancy in any of the New Zealand trees, long days did lead to longer growing seasons and it was concluded that growing season was partly determined by photoperiod in these species (Bussell 1968b). In a range of species of Eucalyptus Paton (1978) found certain temperature dependent photoperiodic growth responses, but they were much smaller than those of many trees which survive the harsh winters of northern high latitude continental regions. It was concluded that photoperiodic induction of winter dormancy had not evolved as an adaptive character in Eucalyptus species.

Similarly Vaartaja (1963) showed that many trees from warm climates of latitudes less than 36° do not respond to photoperiod in the way typical of trees of northern temperate regions. For example, Pinus halepensis Mill, native of the Mediteranean area and P. radiata, from coastal California did not respond to photoperiod in the typical manner (Vaartaja, 1959, 1963). In certain species with wide geographic ranges provenances occurring in temperate continental climates respond to photoperiod whereas coastal provenances do not. For example, provenances of Pseudotsuga menziesii and Picea sitchensis (Bong.)Carr. from inland parts of Oregon (latitude 43°N) responded to short days (12 hours) while coastal provenances at the same latitude did not (Vaartaja, 1963).

In lowland forest environments of New Zealand the contrast between summer and winter temperatures is small and it is probable that decreasing temperature rather than decreasing photoperiod controls the onset of dormancy in forest trees. However, it is possible that shoot extension growth is controlled by photoperiod and that tree provenances from different latitudes respond differently to photoperiod. Therefore an experiment was designed to show whether photoperiods of 10h, 15h and 20h affected the shoot extension growth of rimu seedlings from provenances at latitudes of approximately S35°, S37°, S38° and S43° (section 3.2.1). The hypothesis was that seedlings grown at longer photoperiods would have increased shoot extension growth and that those from more southern latitudes would respond more than those from further north.

The shoots of woody plants of temperate zones generally exhibit a definitely periodic growth cycle and episodic rather than continuous growth is almost universal among woody plants (Romberger, 1963). For example, there is usually a decrease or even a cessation of photosynthesis and growth in evergreen conifers in cold winters in the northern hemisphere (Kramer and Kozlowski, 1979) and therefore it was expected that rimu seedlings would cease growth during winter in Rotorua. Most temperate woody plants have an endogenously controlled state of winter dormancy (Kramer and Kozlowski, 1979) the onset of which may be hastened by shortening days (e.g., Wareing, 1950a) or by decreasing temperatures. In one or other of these ways most trees become progressively dormant as winter approaches. There are, however, different forms of winter dormancy in trees and where there

is no resting bud, as in rimu, dormancy can be described simply as "a state in which growth is temporarily suspended" (Wareing and Phillips, 1970). This is also called "quiescence" or "imposed dormancy" as plant inactivity is imposed directly by the environment. Sequoia sempervirens (Lamb) Endl. and Juniperus horizontalis Moench. are other examples of conifers which do not form resting buds and are quiescent during winter (Sterling, 1945; Romberger, 1963) and in such trees exposure to short days does not normally hasten the onset of dormancy. The better known type of dormancy is "physiological dormancy" or "rest" which is only found in trees which form resting buds. This is the type of dormancy which is induced by short days and it can usually only be broken after chilling (Romberger, 1963). While not all trees with resting buds exhibit physiological dormancy, no trees without resting buds are known to become physiologically dormant. Therefore it was expected that winter dormancy in rimu (if it exists) would be merely a state of quiescence imposed by low temperatures and would not require a chilling treatment to be broken. However, it was decided to test this hypothesis in an experiment to show whether rimu seedlings become dormant in winter in Rotorua and whether chilling hastens the breaking of such dormancy.

Because of the close adaptation of certain northern temperate conifers to the growing season of their region of origin early forest geneticists discovered that it was safest to use local seed sources when establishing forest plantations (Wright, 1962). Ecotypes from further north often ceased growth earlier in the growing season than local ecotypes while those from further south continued to grow too long and were susceptible to frost damage in autumn. In general, northern hemisphere provenances from milder regions have longer growing seasons than those from more severe climates (Sweet, 1965; Wright, 1962). As well as differences in annual growth rates caused by genetically controlled differences in length of growing season, there are often differences between conifer provenances in absolute growth rate (Sweet and Wareing, 1968). In the final experiment in section 3.6 provenances from four latitudinally distinct seed sources were grown together in a nursery in Rotorua to discover whether their pattern of seasonal growth is imposed directly by climate or is genetically controlled and determined by their region of origin and also whether their growth rates during the growing season differed.

3.2 Methods

3.2.1 Origins of the Plant Material

Rimu seedlings of five provenances were used in various growth experiments. No seed was available in 1979 when the work was begun as all the seed collected throughout the country in the autumn of 1978 had been sown in different forest nurseries. The seed origins and details of the early treatment of the seedlings are shown in Table 3.2. On arrival at FRI all seedlings were repotted into size 0.48 Fertil peat pots (60 x 60 x 50mm) in 5:2:1 peat:soil:pumice mix with 600 cm^3 fine MagAmp per m^3 and as the plants grew they were repotted (either one or two plants per pot) into solid plastic pots (140 diameter x 120 mm) in the same potting mix with MagAmp. A representative seedling from each provenance is shown in Fig. 3.1 taken in December 1980 when the seedlings were 1 year (Catlins) to 2.5 years old (Puketi). The greatest morphological difference between provenances was between the Waitakere (second from left) and the Westland (second from right) provenances.

Fig. 3.1
A representative seedling from each of the five rimu provenances used in this thesis. Photographed in December 1980.
Left to right: Puketi, Waitakere, Pureora, Westland and Catlins

TABLE 3.2 : THE ORIGINS OF THE RIMU SEEDLINGS WITH DETAILS OF THEIR EARLY TREATMENT

Provenance	Puketi	Waitakere	Pureora	Westland	Catlins
Seed origin	Puketi State Forest	Waitakere Ranges	Pureora State Forest	NZ Forest Service Westland Conservancy	Catlins State Forest Park
Latitude	35°12'S-35°17'S	36°52'S-37°02'S	38°25'S-38°34'S	42°S-44°S	46°30'S
Nursery where seedlings were raised	NZFS Sweetwater Nursery	ARA Hunua Nursery	NZFS FRI Nursery	NZFS Totara Flat Nursery	NZFS Edendale Nursery
Location	Awanui, Northland	Hunua, S.Auckland	Rotorua, Bay of Plenty	Ahaura, Westland	Edendale, Southland
Date of sowing	February/March 1978	Autumn 1978	17 October 1978	April 1978	2 November 1978
Seedbed covering	Fine peat. 50% shade	Glass. 50% shade	Fine sand. 50% shade	Fine chips. 50% shade	Shaded with slats
Further treatment	Pricked out 4 weeks after germination into solid plastic tubes	Pricked out in late Oct 1978 into solid plastic tubes	Pricked out 26 Feb 1979 into peat pots	Sent bare-rooted in sphagnum moss to FRI	Pricked out 18 Nov 1979 into solid plastic tubes

Table 3.2 (continued)

Potting mix	50:50 peat:sand	50:50 peat:sand	5:2:1 peat:soil: pumice	-	Smiths Soils No. 1 Standard potting mix
Fertilisers	Magamp, Dolomite, Superphosphate & trace elements	Osmocote, Uramite Superphosphate, Dolomite, Calcium carbonate	Magamp	Muriate of potash Superphosphate (in seedbed)	-
Shading of potted seedlings	50% shade	Under shade	50% shade	-	-
Transport to FRI, Rotorua	Air	Car	-	Air	Air
Date of arrival	15 March 1979	February 1979	-	20 March 1979	February 1980

3.2.2 Growing Conditions

The potted rimu seedlings were kept in the FRI nursery on benches in shade houses (frames covered with 50% shade cloth) during the summer and a glasshouse bench during the winter from May-September. The glasshouse was whitewashed and the minimum temperature maintained at 10°C. Controlled environment cabinets were used for certain experiments in which only one environmental variable (e.g., irradiance or temperature) was altered between treatments. (Pescod et al, 1962; Warrington et al, 1978.) Other growing conditions are described for individual experiments.

3.2.3 Growth Analysis

3.2.3.1 Methods

For growth analysis experiments in controlled environments a population of potted rimu seeds was sorted into five size classes and sufficient plants of each class for the number of harvests planned (e.g., 8) were placed in each of the experimental treatments (e.g., 5 x 8 = 40 plants). Harvest 1 was taken on Day 1 of the experiment and the remaining harvests at intervals throughout the experimental period. With slow growing rimu seedlings 3-4 week harvest intervals were found to be suitable as insufficient growth occurred during shorter periods. At each harvest plants were cleaned, divided into root and shoot, then either the shoot surface area was measured by the glass bead method (section 3.2.4) or leaves were stripped and the dry weights of leaves, shoots and roots obtained.

Other direct growth measurements were made during, or at the conclusion of experiments. These included measurements of total dry weight, root:shoot dry weight ratios, root-collar diameter, above ground height, and the ratio of root-collar diameter to height (a measure of plant "sturdiness"). In some experiments the number of leaves per 5 mm of stem was counted to determine whether growth was by shoot extension or leaf production. The count was made at least 20 mm behind the tip of the main stem and between branches.

In the photoperiod experiment (section 3.6.1) where shoot extension growth was the most important parameter, it was decided to measure the length of the tallest shoot when held upright even if this was not the leading shoot. At the end of this experiment 10 plants (out

of 35) per provenance from each treatment were dissected and the lengths of each branch and the main stem measured and summed to give total shoot lengths.

3.2.3.2 Treatment of results

The growth of rimu seedlings was examined by growth analysis using polynomial regression functions, the order of polynomial being chosen statistically for each set of data (Hughes and Freeman, 1967; Hunt and Parsons, 1974; Nicholls and Calder, 1973; Hunt, 1978 and 1979). Linear, quadratic and cubic polynomial regressions were calculated to relate Log_e dry weight (W) to time (T) and Log_e leaf area (L), or Log_e leaf weight (Lw) to time. By studying the analysis of variance tables the choice of polynomial was made based on significance tests or, in certain cases, on the decision to use the same degree of polynomial for several sets of data. The various growth parameters; relative growth rate (R), unit leaf rate (E) and leaf area ratio F (or leaf weight ratio Fw) were then calculated. (See Appendix 1 for definitions of R, E, F and Fw.)

Because of variation between replicates at the beginning of the experiments and the fact that the graphs illustrate the fitted values for F (or F_w) and E using data from every harvest, the curves for the various treatments do not all begin at the same point. However, their starting points usually fall within 5% confidence limits.

In all the experiments results indicated that R was constant during the course of the experiment. 5% confidence limits are presented in tables and graphs of results.

In one experiment traditional methods of calculating mean relative growth rate and mean unit leaf rate between two harvests were used (Appendix I) and these results, together with the direct growth measurements and ratios from all experiments, were compared by analysis of variance and Students Newman Kuel's multiple range tests (SNK). Means are tabulated and within a column means sharing the same letter, a, b or c are not significantly different ($p = 0.05$ unless otherwise stated).

3.2.4 Leaf Area Measurement

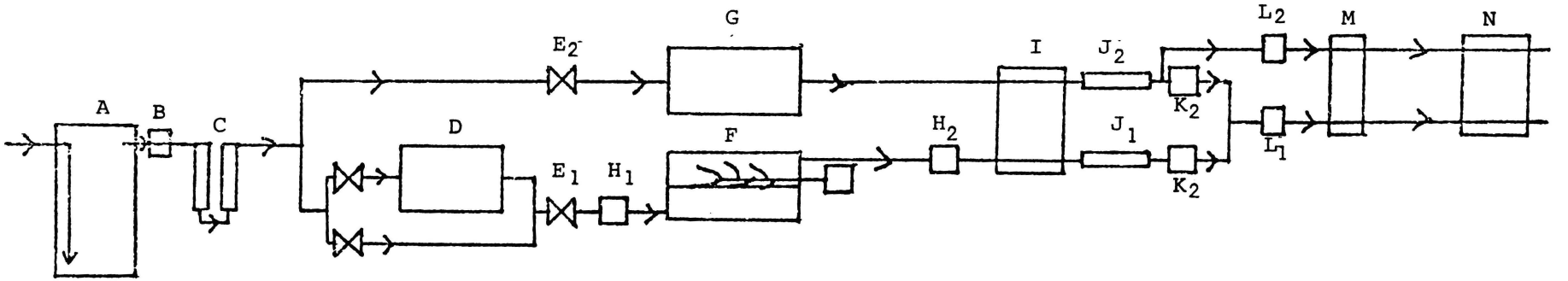
Total surface area of leaves and the stems covered by leaf bases was measured using the technique described by Thompson and Leyton (1971) in which the shoots were suspended from wires, dipped in adhesive (Bostik 645/2, diluted to 10% with 86% perchloroethylene and 4% n-butanol), weighed, covered with fine glass beads (Ballotini Size 14, 80-150 microns, Jencons Scientific Ltd, UK) supported in a fluidised bed (Davies and Benecke, 1980), and reweighed. The method was calibrated using wires of known length and diameter chosen with similar diameters to the main shoot, branches and leaves of the seedlings.

3.2.5 Photosynthesis, Dark Respiration and Transpiration Rate Measurements

3.2.5.1 Methods

Plants to be used for measurement of photosynthesis and dark respiration rates were grown in controlled environments for at least two months before measurements began. Each day a potted seedling was removed from the cabinet near the beginning of the photosynthetic light period and placed in the assimilation chamber. If dark respiration was to be examined the plant was shaded within the cabinet the evening before so that it remained in the correct temperature regime, but did not receive full irradiance when the lights came on in the morning. A standard starting time was used as recommended by Wood and Brittain (1973) to avoid the results being influenced by the diurnal pattern of photosynthesis rate and the plant was left to stabilise for an hour in the assimilation chamber before the first measurement was taken. At least thirty minutes was allowed after each irradiance or temperature change before the next measurement to allow the stomata time to adjust fully to the new conditions. An open system was employed for measuring the rate of CO_2 assimilation by and H_2O loss from the shoot enclosed in the assimilation chamber. A flow diagram of the system is shown in Fig. 3.2. Air from an intake 10 m above ground level was pumped through a 200 litre mixing drum, A, and a glass wool filter to remove dust, at a maximum rate of 20l min^{-1}. The air was divided into two streams, analysis and reference, after being dried in columns of silica gel, C. The reference stream was passed through a chamber of similar

Fig. 3.2 AIR FLOW DIAGRAM



KEY.

A. AIR MIXING DRUM

B. AIR PUMP

C. COLUMNS OF DRY SILICA GEL

D. HUMIDIFYING WATER BATH

E. 1 & 2 FLOW METERS

F. ASSIMILATION CHAMBER

G. REFERENCE CHAMBER

H1. HUMIDITY SENSOR AND THERMOCOUPLE, INGOING AIR

H2. HUMIDITY SENSOR AND THERMOCOUPLE, OUTGOING AIR

I. CONDENSING ICE WATER BATH

J. 1 & 2 COLUMNS OF MAGNESIUM PERCHLORATE TO DRY AIR

K. 1 & 2 SOLENOID VALVES

L. 1 & 2 FILTERS

M. ELECTROMANOMETER

N. I R G A

volume (7.5 litres) to the assimilation chamber. Before the analysis stream was passed into the assimilation chamber it was rehumidified to a pre-determined level by passing part of it through a humidifying bath, D, at room temperature, then re-mixing it with the dry stream. By varying the proportion of wet and dry air the air saturation deficit of the air entering the chamber could be controlled to within $\pm$ 0.1 KPa at 20^{o}C. It was attempted to maintain the deficit in the chamber below 1.0 KPa at all temperatures in all experiments to avoid effects on stomatal resistance. However, this was difficult to achieve in practice. Air flow rates through the chamber were varied up to a maximum of 10 l min^{-1} using flowmeter E..

Temperature and relative humidity of the air entering and leaving the chamber were measured using 48 s.w.g. copper-constantan thermocouples and humidity sensors (Vaisala, Helsinki, Finland), respectively (H).

The perspex assimilation chamber was in two parts clamped together above and below the plant which was supported on a mesh of fine nylon threads (Fig. 3.3). The air entering the chamber, introduced through perforated tubes along the sides, was circulated by a high speed fan (Sprite Roton Inc. USA), G, and its temperature controlled to within $\pm$ 1^{o}C by water jackets. Leaf and air temperatures in the chamber were measured using 48 s.w.g. copper-constantan thermocouples, E, the leaf thermocouple being held against a lower leaf surface using a fine cotton thread.

Teflon tubing was used to carry the air leaving the chamber to avoid leakage of CO_2 (Fig. 3.2). Air in both the reference and analysis streams were passed through a condensing bath, I, set at 0 $\pm$ 1^{o}C and columns of magnesium perchlorate, J, before passing through filters, L, and the infrared gas analyser (IRGA, N) (Unor 2, Germany) working in a differential mode. Pressure differences between analysis and reference air streams were minimised and maintained less than 10 mm water, using an electro-manometer, M (Mercury M10, UK). Approximate flow rates of 1 litre min^{-1} were passed through the IRGA, the rest being bled off to waste. A 1000 watt Halogen-Floodlight lamp (Philips, 12013R) suspended at variable heights above the assimilation chamber provided the light source and the level of irradiance was measured using a silicon cell

Fig. 3.3 DIAGRAM OF LOWER PART OF ASSIMILATION CHAMBER SEEN FROM ABOVE.

KEY.

A. PLANT POT (SUPPORTED IN CLAMP STAND).

B. SLOT FOR PLANT STEM SEALED WITH BLU-TACK (BOSTIK).

C. FINE NYLON MESH SUPPORTING PLANT SHOOT.

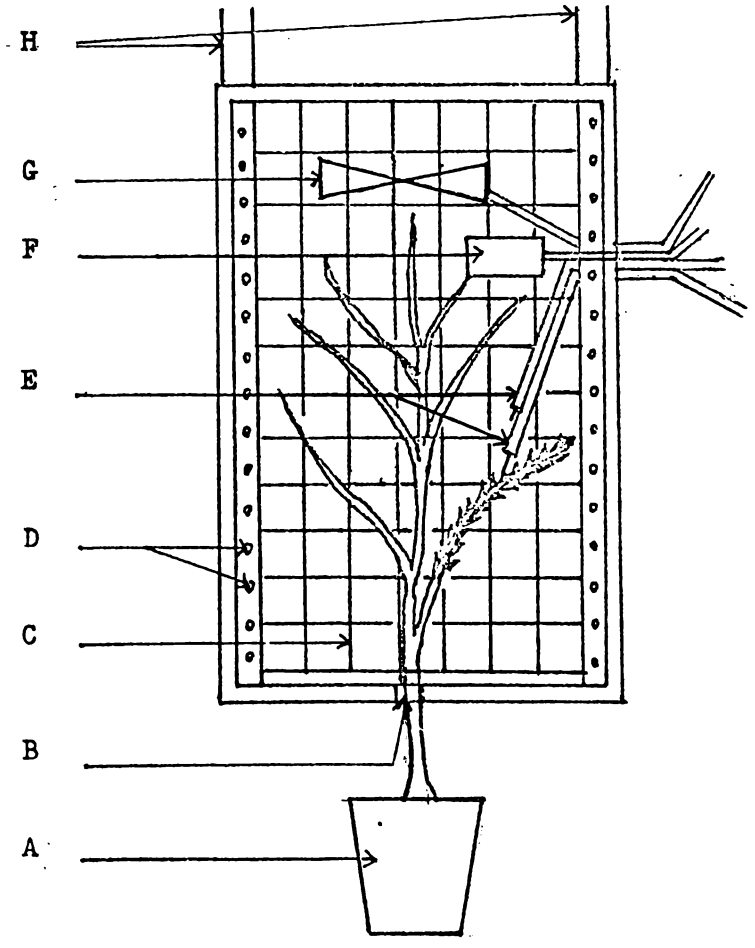
D. SMALL HOLES IN STAINLESS STEEL TUBING THROUGH WHICH AIR ENTERS THE BASE OF THE CHAMBER. AIR LEAVES THE CHAMBER THROUGH SIMILAR PERFORATED TUBES IN THE UPPER SECTION (NOT SHOWN).

E. TWO FINE THERMOCOUPLES (48 swg): ONE ATTACHED TO A LEAF;THE OTHER TO MEASURE CHAMBER AIR TEMPERATURE.

F. SILICON CELL TO MEASURE IRRADIANCE.

G. PLASTIC FAN TO CIRCULATE AIR.

H. AIR INLET PIPES.



(International Rectifier Green Blaze Silicon cell, peak spectral response 500 nm) below a diffusing filter, placed horizontally on the nylon mesh (Fig. 3.3. F). For low irradiances a series of screens of Sarlon shade cloth were placed between the lamp and the chamber. Darkness in the chamber was achieved by screening with black polythene. A 60 mm deep water bath was placed below the lamp to absorb infrared radiation. Calibrations of the flow meters, thermocouples, and humidity sensors were checked at the start of each experiment and the output from the silicon cell was calibrated against a quantum sensor (Lambda Instrument Corp, USA) for wave lengths in the photosynthetically active band, 400-700 nm. Output from the IRGA, humidity sensors, thermocouples and irradiance sensor was recorded on chart recorders, the data read off and calculations made, using a FORTRAN program.

Considering the seedling in the assimilation chamber the transpiration rate, E_t is calculated from:

$$E_t = k_1 (e_o - e_i) . \frac{J}{A} \qquad 3.1$$

where e_i and e_o are the vapour pressures of the air entering and leaving the chamber, J is the flow rate of air through the chamber, A is the leaf (shoot) area, and K_1 is a constant which converts water vapour pressure into a mass concentration of water vapour in air.

Likewise the rate of net potosynthesis, P_n, is calculated from:

$$P_n = k_2 (C_o - C_i) . \frac{J}{A} \qquad 3.2$$

where C_o and C_i are the CO_2 concentrations in the air entering (the reference air stream) and leaving the chamber and k_2 is a constant which converts a volume concentration of CO_2 in air to a mass concentration,

The boundary layer resistance of a seedling in the chamber was calculated using a plaster of Paris replica (Landsberg and Ludlow, 1970). A 48 s.w.g. thermocouple was attached to the seedling in the

position of a leaf and the whole was sprayed with a mixture of plaster of Paris and water. The plaster dried to give a thin coating producing a close replica of the original plant. This was dipped into distilled water and excess water allowed to drip off before the wet replica was sealed into the chamber. From measurements of the vapour pressure of the ingoing and outgoing air, leaf temperature, flow rate and leaf area, the boundary layer resistance was calculated.

Leaf area was measured after the plaster of Paris was removed by gentle shaking. At the flow rates used in the experiments the boundary layer resistance for rimu was calculated to be $0.14\ s\ cm^{-1}$. A boundary layer resistance of $0.1\ s\ cm^{-1}$ was used for P. radiata (Bennett and Rook, 1978; Ludlow and Jarvis, 1971).

3.2.5.2 Treatment of results

It is usual to apply an Ohm's law analogy to the movement of water vapour out of and CO_2 into leaves (Gaastra, 1959) where resistances are calculated in the transfer pathways. In transpiration water evaporates at the xylem ends and the water vapour diffuses through the leaf and stomata to the air outside. The stomatal resistance, $r_{s_{H_2O}}$, refers to the resistances to water vapour diffusion through the stomatal pore which varies with changes in the leaf environment. The boundary layer resistance, $r_{a_{H_2O}}$, is defined as the resistance to diffusion across the thin layer of air close to the leaf surface which depends on windspeed, size, shape and orientation of the leaf. (Sestak et al, 1971, p.571.) The stomatal and boundary layer resistances are in series whereas the cuticular resistance is in parallel with $r_{s_{H_2O}}$. The cuticular resistance depends to some extent on the leaf environment, but its value is generally at least an order of magnitude greater than the $r_{s_{H_2O}}$ (Landsberg et al, 1975). It is assumed that the mesophyll cell walls are always saturated so resistance to water vapour diffusion is zero (Slatyer, 1967).

Following the analysis of Gaastra (1959) the transpiration rate, E_t, of the seedling is given by:

$$E_t = \frac{k_1 \cdot (e_1 - e_o)}{r_{a_{H_2O}} + r_{s_{H_2O}}} \qquad 3.3$$

where e_1 is the water vapour pressure of the air at the sites of evaporation, (assumed to be the saturated vapour pressure at leaf temperature) and e_o is the vapour pressure of the air outside the leaf.

A similar resistance model can be used to describe net photosynthesis rate, P_n, with the diffusion of CO_2 occurring in the opposite direction from water vapour. In photosynthesis carbon dioxide moves from the air into the leaf through the stomata and mesophyll cells to the site of fixation in the chloroplasts.

The boundary layer, and stomatal resistances to CO_2 can be related to the corresponding resistances to water vapour by the ratio of the diffusivities of water vapour and carbon dioxide in air.

The dominant resistance in the flux of carbon dioxide into leaves operates between the sub-stomatal cavity and the sites of fixation. This residual resistance, $r_{r_{CO_2}}$, is the sum of the mesophyll, carboxylation and excitation resistances. Attempts have been made to separate these components in more complex models.

The net photosynthesis rate of the seedling can be calculated:

$$P_n = \frac{k_2 \cdot (C_o - C_{int})}{r_{a_{CO_2}} + r_{s_{CO_2}} + r_{r_{CO_2}}} \qquad 3.4$$

where C_o and C_{int} are the concentrations of CO_2 in the air outside the leaf and at the site of fixation respectively. The CO_2 concentration at the site of fixation is assumed to be zero.

(For some purposes it is more convenient to present the reciprocals of resistance, conductance, and both types of units are widely used in the literature.)

The response of net photosynthesis to irradiance has been described by a rectangular hyperbola where

$$P_n + R_d = \left(\frac{a}{I} + b\right)^{-1} \qquad 3.5$$

where P_n is the net rate of photosynthesis
R_d is the rate of dark respiration
I is the irradiance
and a and b are constants.

This simple model has been used widely and has the advantage that the parameters, a and b, can be related to physiological variables. However, the model makes the assumption that dark respiration is constant at all irradiances and makes no allowance for photorespiration (Ludlow and Jarvis, 1971). Concern has also been expressed that the model does not fit some data perfectly, particularly at the lower irradiances where the response may not be linear as predicted by the model. More complex models have been designed (e.g. Chartier et al. 1970), but these require more detailed measurements to calculate extra parameters. In this thesis the resistance model (Gaastra, 1959) and the rectangular hyperbola (equation 3.5) have been used to separate the effects of the environmental variables on the photosynthesis rate into stomatal and internal components. In this way it can be determined whether a change in photosynthesis rate is caused by stomatal responses or by changes in the mesophyll or chloroplasts. Differences in photosynthesis rate between plants may be due to differences in total resistance to CO_2 uptake or to differences in quantum requirement. The simple rectangular hyperbola model (equation 3.5) enables these differences to be separated. The initial slope of the curve of photosynthesis response to irradiance, a in equation 3.5, gives the increase in the rate of photosynthesis when irradiance is limiting the process. This is called the efficiency of the plant and its reciprocal is referred to as the quantum requirement (Gaastra, 1959). If net photosynthesis, P_n, is expressed μ mol $m^{-2}s^{-1}$ and irradiance in μE $m^{-2}s^{-1}$ the units for quantum requirement are in E mol^{-1}. At high levels of irradiance photosynthesis is light saturated and limited by the transfer of CO_2 from the air to the chloroplasts. This light saturated rate is determined by the total

resistance to CO_2 transfer,

$r_{a_{CO_2}} + r_{s_{CO_2}} + r_{r_{CO_2}}$, b in equation 3.5.

Converting equation 3.5 into the form

$$\frac{1}{P_n + R_d} = a\left(\frac{1}{I}\right) + b \qquad 3.6$$

plotting $\frac{1}{P_n + R_d}$ against $\frac{1}{I}$ gives a linear relationship of slope a, and intercept, b. Knowing a and b the rectangular hyperbola can then be reconstructed in equation 3.5.

In the photosynthesis experiments the responses of photosynthesis to irradiance are illustrated with the actual data points plotted and the curves fitted as described above. Light compensation points were also calculated from the rectangular hyperbola. When

$$P_n = 0, \quad I = \frac{R_d.a}{1-R_d.b}$$

When expressing responses of photosynthesis or dark respiration to temperature, t, for different plants, values were normalised to the maximum rate and the graphs presented show the normalised values with eye fitted curves. Q_{10} ratios of the dark respiration rate between 20° and $30^{\circ}C$ (Steward, 1965) were calculated from curves drawn by eye.

Q_{10} is defined as : $\frac{\text{The rate at } (t + 10)^{\circ}C}{\text{The rate at } t^{\circ}C}$

Light saturated photosynthesis rates, dark respiration rates at $20^{\circ}C$, the reciprocals of stomatal and residual resistances and their ratio, the quantum requirements and compensation points were compared between plants using Student's t-tests or analysis of variance and Students Newman Kuel's multiple range tests (S.N.K.). Means are tabulated and within a column, means which share the same letter, a, b or c are not significantly different. The 0.05 probability level is used unless otherwise stated.

3.2.6 Chlorophyll Analysis

The method used for chlorophyll extraction was described by Hiscox and Israelstam (1979). Material was incubated for four hours at 65°C in dimethyl sulphoxide (DMSO), optical density values were read at 645 and 663 nm in a Pye Unicam Spectrophotometer (SP6-500) against a DMSO standard.

Chlorophyll concentrations were calculated from (Arnon, 1949):

$$\text{Chlorophyll (a+b)} = 8.02\ D_{663} - 20.20\ D_{645}\ \text{mg}\ l^{-1} \qquad 3.7$$

$$\text{Chlorophyll a} = 12.7\ D_{663} - 2.69\ D_{645}\ \text{mg}\ l^{-1} \qquad 3.8$$

$$\text{Chlorophyll b} = 22.9\ D_{645} - 4.68\ D_{663}\ \text{mg}\ l^{-1} \qquad 3.9$$

Concentrations of chlorophylls in mg l^{-1} were converted to mg g^{-1} fresh weight:

$$\text{Chlorophyll concentration} = \frac{Ch}{1000} \times \frac{V}{FWs}$$

where Ch = chlorophyll concentration in mg l^{-1}
V = total volume of DMSO extract in ml
FWs = Fresh weight of the extracted sample in g.

To find the chlorophyll concentrations in mg m^{-2} surface area, the concentration in mg g^{-1} fresh weight is multiplied by the ratio Area:Fresh Weight.

3.2.7 Carbohydrate Analysis

Starch and glucose concentrations (mg g^{-1} dry weight) were measured using a method developed at the Forest Research Institute (K.D. Steele, personal communication). The method uses a commercially prepared kit S.V.R. (single vial reagent, Catalogue Number 870104, Calbiochem-Behring Corporation), and carbohydrares are extracted in ethanol from freeze-dried, ground material.

3.3 Comparison of the net photosynthesis and dark respiration rates of rimu and Pinus radiata seedlings

3.3.1 Methods

CO_2 exchange measurements were compared between Puketi provenance seedlings from the medium treatment (18°C day/12°C night; c360 $\mu E\ m^{-2}\ s^{-1}$) of the night temperature experiment (section 3.5) and P. radiata seedlings grown in the same chamber for 8 weeks. Pine seedlings from the FRI nursery were potted in standard potting mix and plastic pots (section 3.2.1). Pine and rimu seedlings were similar in height (approximately 200 mm) at the beginning of the experiment. Five rimus and four pines were used for measurements of photosynthesis response to irradiance and three replicates of each species for measurements of dark respiration response to temperature.

3.3.2 Results

Curves showing the response of net photosynthesis rate to irradiance for rimu and pine are shown in Fig 3.4. Different symbols represent measured data points for each replicate seedling and lines are fitted using rectangular hyperbolae (section 3.2.5.2). Curves of all five rimu seedlings lie well below the lowest pine curve, although replicate curves of both species cover quite a wide range of values. Whereas maximum net photosynthesis in rimu is reached between 250 and 350 $\mu E\ m^{-2}\ s^{-1}$, the pine curves do not reach an asymptote even at the maximum irradiance (1000-1200 $\mu E\ m^{-2}\ s^{-1}$). This shows that photosynthesis was light saturated in rimu at low irradiances, but in pine saturation was not achieved in this experiment. This was possibly due to more self shading in the denser pine foliage than in rimu.

The mean maximum photosynthesis rate of the pine seedlings measured in this experiment was nearly five times higher than the mean light saturated rate for rimu (Table 3.3) and light saturated rates of pine would have been even higher. At almost all irradiances photosynthesis rates of pine seedlings were higher than those of rimu seedlings (Fig. 3.4). Light compensation points of both species

TABLE 3.3 : A COMPARISON OF THE LIGHT SATURATED (OR MAXIMUM MEASURED) PHOTOSYNTHESIS RATES AND DARK RESPIRATION RATES OF RIMU AND PINE SEEDLINGS AT 20°C. QUANTUM REQUIREMENTS AND LIGHT COMPENSATION POINTS ALSO SHOWN (Mean Values) n = number of replicates

Species	n	Quantum Requirement	Photosynthesis Rate		Dark Respiration Rate		Light Compensation Point
		E mol^{-1}	μmol m^{-2} s^{-1}	g m^{-2} h^{-1}	μmol m^{-2} s^{-1}	g m^{-2} h^{-1}	μE m^{-2} s^{-1}
Rimu	5	53.3 a	1.1 b	0.18 b	0.44 a	0.07 a	30.8 a
P. radiata	4	45.5 a	5.0 a	0.79 a	0.76 a	0.12 a	36.8 a

Fig. 3.4
The response of net photosynthesis (P_n) rate to irradiance (I). The symbols represent the measured data points for the replicate seedlings and the lines are the fitted rectangular hyperbolae. Each curve ends close to the final data point for that replicate.
——— Rimu; ····· Pine.

Fig. 3.5
The relationship between $\frac{1}{P_n + R_d}$ and $\frac{1}{I}$. The symbols represent the calculated data points for the replicate seedlings as in Fig.7.1. The lines are the linear regressions.
——— Rimu; ····· Pine.

Fig. 3.4

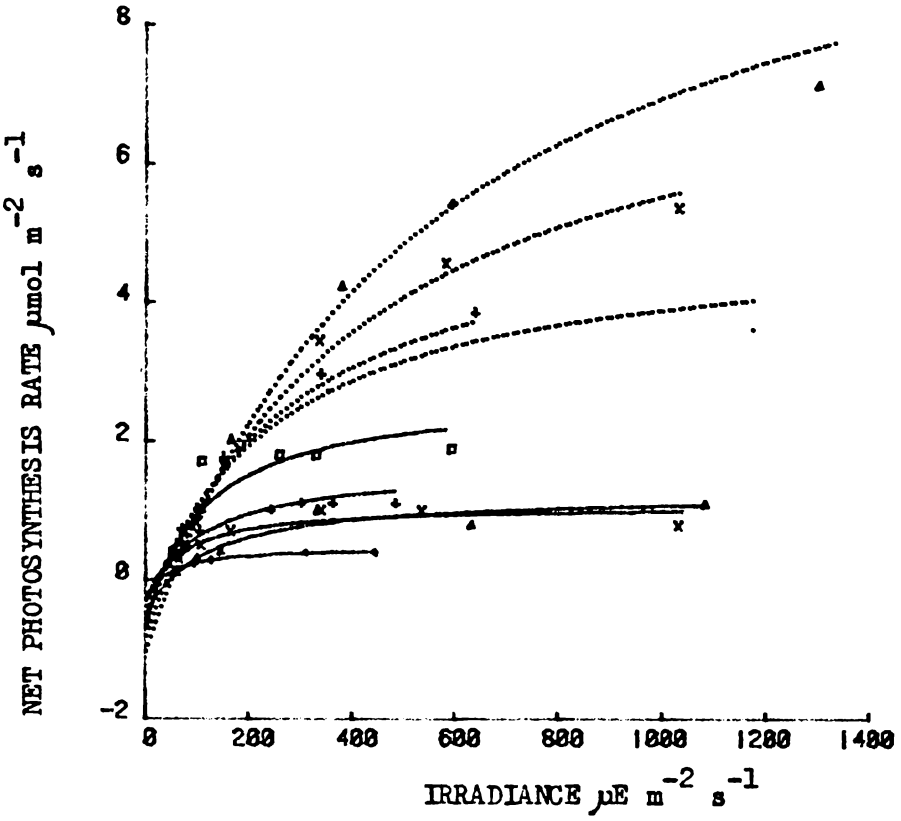
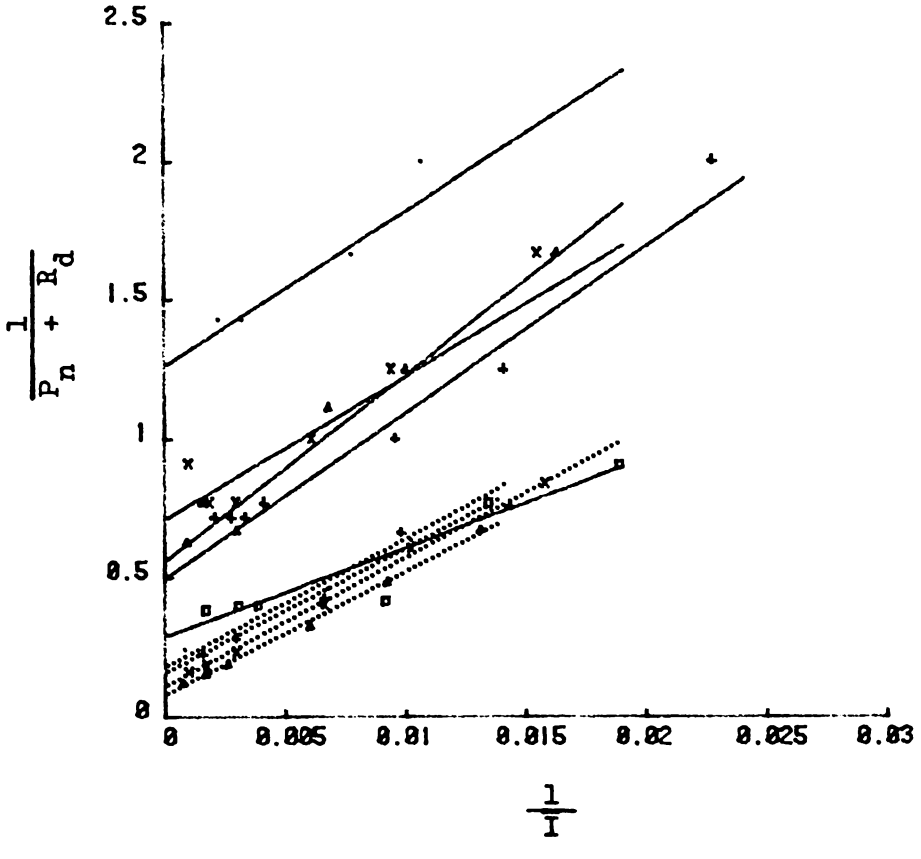

NET PHOTOSYNTHESIS RATE μmol m^{-2} s^{-1}
8
6
4
2
0
-2
0
200
400
600
800
1000
1200
1400
IRRADIANCE μE m^{-2} s^{-1}

Fig. 3.5


$\frac{1}{P_n + R_d}$
2.5
2
1.5
1
0.5
0
0
0.005
0.01
0.015
0.02
0.025
0.03
$\frac{1}{I}$

were very low and not significantly different, although the mean for pine was slightly higher than that for rimu (Table 3.3). This indicates that both species are capable of net photosynthesis at extremely low irradiances, but rates of photosynthesis in rimu are lower than those in pine for irradiances of about 150 $\mu E\ m^{-2}\ s^{-1}$ and above.

When data from photosynthesis response to irradiance were re-plotted as described in section 3.2.5.2 the slopes of most replicate lines for both species were almost parallel (Fig. 3.5). This indicates that quantum requirements are similar. The slopes of the lines (α in equation 3.6), the quantum requirements, are shown in Table 3.3.

The mean quantum requirement for rimu was only slightly higher than that for pine. Rimu was, therefore, a little less efficient at using light energy to fix CO_2, but the difference was not significant. In Fig. 3.5 the intercepts of the lines fall into two groups, those of the rimu seedlings being higher than those of the pines. The intercept, (b in equation 3.5), is related to the total resistance to CO_2. When light is no longer limiting the reaction photosynthesis rate becomes limited by the resistance to CO_2 diffusion into the leaf. The total resistance to CO_2 of rimu seedlings was much greater than that of pines. Subtracting boundary layer and stomatal resistances from total resistance to CO_2 transfer (equation 3.4) enabled separate comparison of stomatal and internal resistances between the species. The $r_{s_{H_2O}}$ were found to be very similar for the two species, but there was a very large difference between the $r_{r_{CO_2}}$ (Table 3.4). Mean $r_{r_{CO_2}}$ of rimu seedlings was about thirteen times that of pines and, whereas in pine $r_{s_{H_2O}}$ and $r_{r_{CO_2}}$ were approximately equal in value, in rimu $r_{r_{CO_2}}$ was more than thirteen times as great as $r_{s_{H_2O}}$. Light saturated photosynthesis rate in rimu seedlings

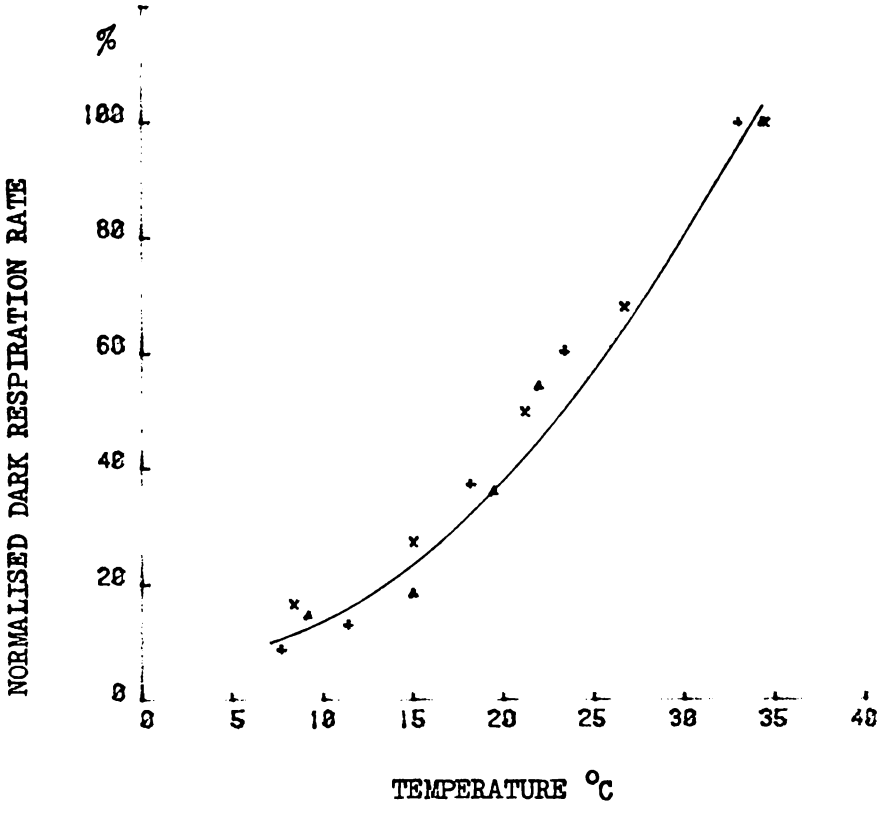
was, therefore, severely limited by residual resistance to CO_2 diffusion transfer.

Dark respiration rate was measured at approximately 20°C at the end of each day when photosynthesis rate response to irradiance was measured. Mean dark respiration rate at 20°C of pine was found to be somewhat higher than that of rimu, although these differences were not significant (Table 3.3). The response of dark respiration rate to increasing temperature was also found to be rather similar in both species (Fig. 3.6 a. and b) and Q_{10} values for dark respiration rate between 20° and 30°C were not significantly different, although the mean Q_{10} for pine, 2.2, was slightly higher than that for rimu, 1.9.

TABLE 3.4 : MEAN RESISTANCES TO WATER VAPOUR AND CARBON DIOXIDE TRANSFER FOR RIMU AND PINUS RADIATA SEEDLINGS GROWN IN THE SAME CONTROLLED ENVIRONMENT. n = number of replicates

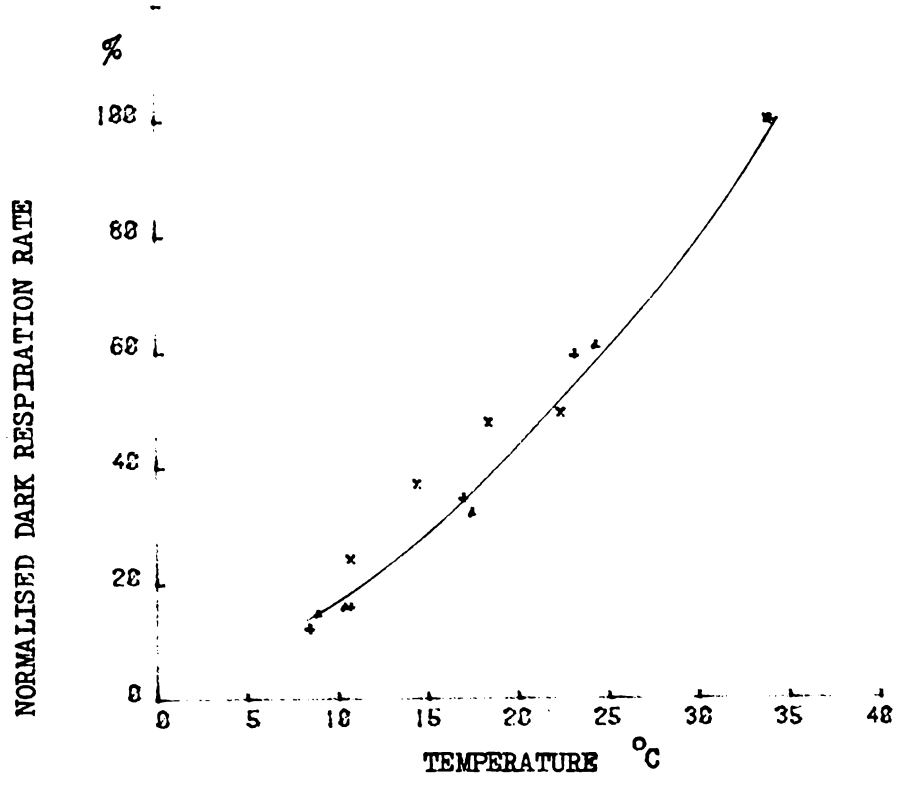
Species	n	$r_{s_{H_2O}}$ s cm^{-1}	$r_{r_{CO_2}}$ s cm^{-1}	$r_{r_{CO_2}}:r_{s_{H_2O}}$
Rimu	5	7.52 a	100.00 a	13.42 a
P. radiata	4	8.05 a	7.35 b	1.09 b

Fig. 3.6 a. PINE



The response of dark respiration rate (R_d) to temperature.
The symbols represent the normalised data points for the replicate seedlings. The curves were fitted by eye.

Fig. 3.6 b. RIMU



3.3.3 Discussion

The mean light saturated rate of photosynthesis found in this experiment for rimu seedlings was low in comparison with the maximum rate found in Pinus radiata. These rates (0.2 and 0.8 $gCO_2\ m^{-2}\ h^{-1}$ respectively) are expressed on a total leaf area basis whereas many published rates are expressed on a single leaf area basis. An approximate conversion to single surface area gives 0.4 and 1.6 g $CO_2\ m^{-2}\ h^{-1}$ for rimu and pine seedlings respectively and these rates can be compared with those listed by Larcher (1969) for conifer seedlings expressed on single leaf areas. The alpine species Pinus cembra L. had the lowest rates (0.4-0.7g $CO_2\ m^{-2}\ h^{-1}$) and the sun-leaves of Pseudotsuga menziesii the highest rates (0.7-1.2g $CO_2\ m^{-2}\ h^{-1}$). Rimu, therefore, had a light saturated photosynthesis rate comparable with the lowest published rates while the rate for pine was high in comparison with other confiers.

Rates of net photosynthesis and dark respiration in plants are affected by the interactions of many variables both in the environment surrounding the plant and within individual leaves. Because these variable factors affect the rates of CO_2 exchange between the plant and the environment comparisons of these rates between different plants should ideally be made in the same conditions. For example, Helms (1976) suggests that some of the differences in published photosynthesis rates of various tree species may be due to differences in the measurement irradiances. However, even in the same measurement conditions, rates may vary within a single species depending on the age of the plant, the age and position of the foliage and the time of year. In Pinus radiata, for example, the light saturated photosynthesis rate of 0-1 year old foliage of a 7 m tall tree grown in a controlled environment room was 0.15g $CO_2\ m^{-2}\ h^{-1}$ while that of 1-2 year old foliage on the same tree was 0.5g $CO_2\ m^{-2}\ h^{-1}$ at 15°C (Rook and Corson, 1978). However, in an 8 m tall tree of the same species growing in a forest stand, at 16-18°C on a partially cloudy day, much higher light saturated rates were measured in first year sun-leaves: 0.9-1.0 g $CO_2\ m^{-2}\ h^{-1}$ (Benecke, 1980). (Rates expressed on total leaf surface areas.)

The fact that the rate found here for Pinus radiata is higher than the rate found for that species by Rook and Corson (1978) is probably because net photosynthesis rates in tree seedlings tend to be higher than in mature trees (Larcher, 1969) because of the smaller proportion of non-photosynthetic respiring woody tissue in seedlings relative to mature trees.

Many of the light saturated photosynthesis rates shown by Larcher (1969) for conifers are expressed on a foliage dry weight basis only and these range from the high rates found in Larix decidua (L) Mill. and Metasequoia glyptostroboides Hu and Cheng (two deciduous species) to low rates found in seedlings of the very widespread North American fir Abies balsamea Mill and the slow growing Rocky Mountain species Pinus aristata Englemann. Rimu, with low light saturated rates of photosynthesis, is both widespread and slow growing.

There was found to be little difference between the quantum requirements of rimu and pine seedlings (Table 3.3). Pine was slightly more efficient than rimu, but also had a somewhat higher dark respiration rate.

In all plants at very low irradiances photosynthesis occurs so slowly that it fails to utilise all the CO_2 evolved by the plant in respiration. With increasing irradiance the photosynthesis rate increases until a point is reached where photosynthetic gains balance respiratory losses of CO_2 and there is no net exchange. This is light compensation point which may vary with species, type and age of leaf, growing irradiance and temperature. In this experiment there was shown to be very little difference between the compensation points of rimu and pine seedlings which had been grown together at an irradiance of approximately 360 $\mu E\ m^{-2}\ s^{-1}$. 360 $\mu E\ m^{-2}\ s^{-1}$ is a relatively low irradiance, close to light saturation level for photosynthesis rate in rimu seedlings, but well below that for P. radiata, and was used because rimu had grown slightly better in this than in higher or lower irradiances in another experiment (section 3.4). Compensation point for pine, 37 $\mu E\ m^{-2}\ s^{-1}$, is similar to that shown by Benecke (1980) for first year sun needles on an 8 m tree growing in a forest stand (approximately 25 $\mu E\ m^{-2}\ s^{-1}$).

Having established that the light saturated rate of photosynthesis in rimu seedlings is low in comparison with pine seedlings and with published rates for other conifers, but that the efficiency of the light reaction, light compensation point and dark respiration rates are similar in rimu and pine seedlings (Table 3.3), the various resistances to CO_2 diffusion were examined. There was little difference between stomatal resistances, but the most obvious difference between the species was found to be their residual resistances, that of rimu being about thirteen times as great as that of pine (Table 3.4). The methods used in the present analysis did not allow various components of this internal leaf resistance to be separated. However, one component, mesophyll resistance, has been shown to be larger in thin leaves because of the decreased surface area of the reduced number of layers of mesophyll cells (Nobel et al, 1975). Rimu has much smaller leaves than pine and possibly the larger residual resistance is partly caused by the smaller surface area of mesophyll cells present in these small diameter leaves. Another component of residual resistance is the carboxylation resistance which depends on the availability and activity of the enzymes involved in carboxylation. Tsel' Niker (1979) suggested that the low photosynthesis rates of forest trees may be caused by low carboxylation activity and this may be a contributing cause of the very high residual resistance found in the rimu seedlings. Further investigation would be necessary to elucidate this point which is examined in more detail in section 3.7. Whatever the cause of the high residual resistance in rimu, it contributes to the very low photosynthesis rate even at high irradiance. On the other hand the quantum requirement and dark respiration rate of this shade tolerant species are similar to those of the much faster growing P. radiata.

3.4 The effect of growing irradiance on the growth and photosynthesis of rimu seedlings

3.4.1 Methods

(a) The effect of extremely low irradiance on the growth of two year old rimu seedlings in the nursery

Two year old Catlins provenance seedlings were repotted into standard plastic pots and potting mix nine months before the experiment began. On 15 July 1981, ten seedlings were placed under each of three shade frames 0.85 m high x 0.75 m wide x 1 m long. Frames were covered with 5, 2 and 1 layers of black Sarlon shadecloth giving relative irradiances of approximately 1% (0.78 $\pm$ 0.21%; I_1), 17% (16.66 $\pm$ 4.70%; I_{17}) and 42% (41.86 $\pm$ 5.51%; I_{42}) full sunlight. Irradiances within each shade frame and in the open were measured using a quantum sensor (section 3.2.5.1) on ten occasions close to midday on clear, sunny days and the irradiances of the three treatments were calculated as a percentage of the irradiance in full sunlight. Mean values and 5% confidence intervals are presented. Temperatures and relative humidities were measured in each frame and in the ambient air on three occasions. The RH of the treatments varied within 4% of each other and of the ambient air and the temperature variation was within 1°C. The frames were placed where they would not shade each other. Each group of seedlings was selected to be as similar as possible and a fourth similar group was chosen on day 1 for the first growth analysis harvest. Also on day 1 heights and root collar diameters of all seedlings were measured. After 7 months (8 February 1982) these parameters were remeasured and increments calculated. Seedlings were then harvested and mean relative growth rates ($\overline{R}$), mean unit leaf rates ($\overline{E}$) and leaf weight ratios calculated using traditional methods of growth analysis (Appendix 1). For these calculations seedlings were paired arbitrarily, e.g. the smallest seedling from the first harvest was paired with the smallest seedling from each treatment at the second harvest, and so on. Root:shoot ratios and ratios of diameter to height were also calculated (section 3.2.3.1).

(b) The effect of irradiance on the growth of one year old rimu seedlings in a nursery bed

Rimu seed from Pureora Forest was sown in beds in the FRI nursery, Rotorua, in October 1978 and seedlings shaded with 50% Sarlon shade cloth supported on wire hoops 500 mm above the bed. In mid October 1979, when seedlings were approximately 35 mm tall and unbranched 3 m of bed was chosen with an even cover of seedlings: 1 m shaded with 1 layer of 30% shade cloth giving approximately 73% (73 $\pm$ 3.72%; I_{73}) full sunlight; 1 m shaded with 1 layer of 50% shade cloth giving 60% (60 $\pm$ 11.17%; I_{60}); and 1 m shaded with 2 layers of 50% shade cloth giving 28% (28 $\pm$ 11.16%; I_{28}). Irradiance at plant height, temperature and relative humidity in each shade treatment and in the open beside the bed were measured at 1100 hours on 3 clear days. The temperature of the I_{73} treatment was an average 1.65 $\pm$ 0.49^{o}C higher than that of the I_{28} treatment, the I_{60} treatment temperature being intermediate. Relative humidity was more variable being highest in different treatments on each measurement occasion, but the maximum recorded difference in relative humidity between treatments was 8%. Forty-eight representative seedlings in each treatment were marked and 8 growth analysis harvests made at 3-4 week intervals. Six seedlings were removed at each harvest, their heights, number of leaves per 5 mm stem, number of branches, shoot surface areas and dry weights measured, and growth analysis performed.

(c) The effect of growing irradiance in controlled environments on the growth and photosynthesis of rimu seedlings

Two year old Puketi provenance seedlings were repotted, two per pot in standard plastic pots and potting mix for two months before the experiment began and placed on the glasshouse bench in May so that growth was not checked by decreasing outdoor temperatures before the experiment began in June 1980. Three controlled environment cabinets were used with the day/night temperature regime 20^{o}/13^{o}C; 70% relative humidity (constant); 12 hours photosynthetic radiation; one hour incandescent light before and after the photosynthetic period giving a 14 hour photoperiod. Irradiances used in the three treatments were: low, 140 μE m^{-2} s^{-1} (I_{140}), medium, 385 μE m^{-2} s^{-1} (I_{385}) and high, 650 μE m^{-2} s^{-1} (I_{650}). The experiment ran for 5 months. Growth analysis was performed (6

harvests x 5 replicates per harvest); heights, root collar diameters and root:shoot ratios were measured at the end of the experiment; photosynthesis rate responses to irradiance and temperature were examined and chlorophyll concentrations measured.

3.4.2 Results

(a) The effect of extremely low irradiance on the growth of two year old rimu seedlings in the nursery

Seedlings grown for seven months from July to February at 1% full sunlight did not die nor show any signs of shoot tips dying back. In late spring (November-December) they put on a flush of new bright green spring growth which contrasted with the dark brownish green of their old growth. In comparison, seedlings grown at 17% and 42% full sunlight were bright green by December and remained that colour until February. However, mean relative growth rate ($\overline{R}$) of the 1% seedlings was negative as were their mean net assimilation rate ($\overline{E}$) and dry weight increment (Table 3.5). A minimal amount of diameter growth occurred in these etiolated seedlings, but root growth and development was very poor compared with the I_{17} and I_{42} seedlings. Root growth improved with increased growing irradiance and the root:shoot ratios increased significantly with each increase in irradiance. The ratio of diameter to height also increased with irradiance, the I_{42} plants having significantly higher ratios than the other two treatments (Table 3.5). This ratio is a measure of the sturdiness of the seedlings.

Although there was very little diameter growth in the I_1 plants and their dry weights actually decreased during the seven months, nevertheless they did grow in height and their height increment was somewhat greater than that of the I_{42} plants (Table 3.5). The medium irradiance I_{17} plants had the greatest height increment although, due to variation of replicates within each treatment, differences in height increment were not significant.

With decreasing growing irradiance leaf weight ratio (F_w) of plants increased (Table 3.5) as they invested an increasing proportion of their photosynthate in leaf production.

TABLE 3.5 : MEAN GROWTH PARAMETERS OF RIMU SEEDLINGS GROWN AT 1%, 17% AND 42% FULL SUNLIGHT FOR SEVEN MONTHS IN THE NURSERY

Treatment	n	$\bar{R}$	$\bar{E}$	F_w	Dry weight increment	Height increment	Root collar diameter increment	Diameter: height ratio	Root: shoot ratio
% sunlight		$gg^{-1}day^{-1} \times 10^{-2}$	$gg^{-1}day^{-1} \times 10^{-2}$		g	mm	mm		
1	10	-0.03 b	-0.26 b	0.41 a	-0.32 b	28.3 a	0.08 b	0.012 b	0.37 c
17	10	0.26 a	0.67 a	0.37 b	2.89 a	41.8 a	0.61 a	0.012 b	0.46 b
42	10	0.24 a	0.69 a	0.31 c	2.49 a	22.8 a	0.76 a	0.014 a	0.59 a

Plants grown in the highest irradiance, I_{42}, therefore were sturdier with better developed root systems and larger diameters than I_{17} and I_1 plants, but their relative growth rates and unit leaf rates were no higher than those of I_{17} plants. In fact the dry weight increment of the I_{42} plants was slightly lower than that of the I_{17} plants. An increase in irradiance from 17% to 42% full sunlight was not sufficient to cause an increase in relative growth rate, unit leaf rate, height or dry weight increment after seven months growth. On the other hand the seedlings grown at only 1% of full sunlight were tall and spindly with high leaf weight ratios, very poor root development and had a slight decrease in dry weight during the 7 months.

(b) The effect of irradiance on the growth of one year old rimu seedlings in a nursery bed

The growth in dry weight of small rimu seedlings was increased markedly by higher growing irradiances. Fig. 3.7 is a photocopy of the largest seedling taken from each shade treatment at the end of the experiment (18 March). This clearly shows improved growth in the I_{73} and I_{60} treatments compared with that in the I_{28} treatment. The difference between the seedlings from the two higher irradiances is less conspicuous, but root development is better in the I_{73} plant and shoot lengths are also marginally longer. Mean values of various growth parameters are shown in Table 3.6. Overall fitted relative growth rate (R) between mid October and mid March increased with increased growing irradiance, although owing to within treatment variation these differences were not significant. However, as can clearly be seen in Fig. 3.8 growth rate increased in all treatments from about day 80 (early January) and from 5 February to 18 March growth rate in the I_{73} and I_{60} seedlings increased more rapidly than in the I_{28} plants. Mean relative growth rates ($\overline{R}$) between these dates at the latter part of the growing season were significantly higher in the two higher growing irradiance treatments (Table 3.6). (The dip in the dry weight curves between 5 February and 18 March was probably due to smaller than average seedlings being harvested on that occasion, particularly from the low irradiance treatment.) The higher $\overline{R}$'s at the end of the summer caused increased

Fig. 3.7

TABLE 3.6 : MEAN GROWTH PARAMETERS OF SMALL RIMU SEEDLINGS GROWN AT 28%, 60% AND 73% FULL SUNLIGHT FOR FIVE SUMMER MONTHS IN A NURSERY BED

Treatment	n	R (8 harvests) October to March	$\bar{R}$ between 5 Feb & 8 Mar	Dry weight increment	Height increment	Leaves/ 5 mm stem	Branch number	Root:shoot ratio
% sunlight		$gg^{-1}day^{-1} \times 10^{-2}$ ± 5% confidence intervals	$gg^{-1}day^{-1} \times 10^{-2}$	mg	mm			
28	6	1.24 ± 0.13 a	0.93 c	139.2 b	83.2 c	11.00 a	1.00 b	0.33 a
60	6	1.29 ± 0.13 a	1.21 b	192.8 a	105.3 b	10.83 a	3.33 ab	0.28 a
73	6	1.31 ± 0.13 a	1.62 a	242.5 a	124.4 a	9.82 a	4.67 a	0.32 a

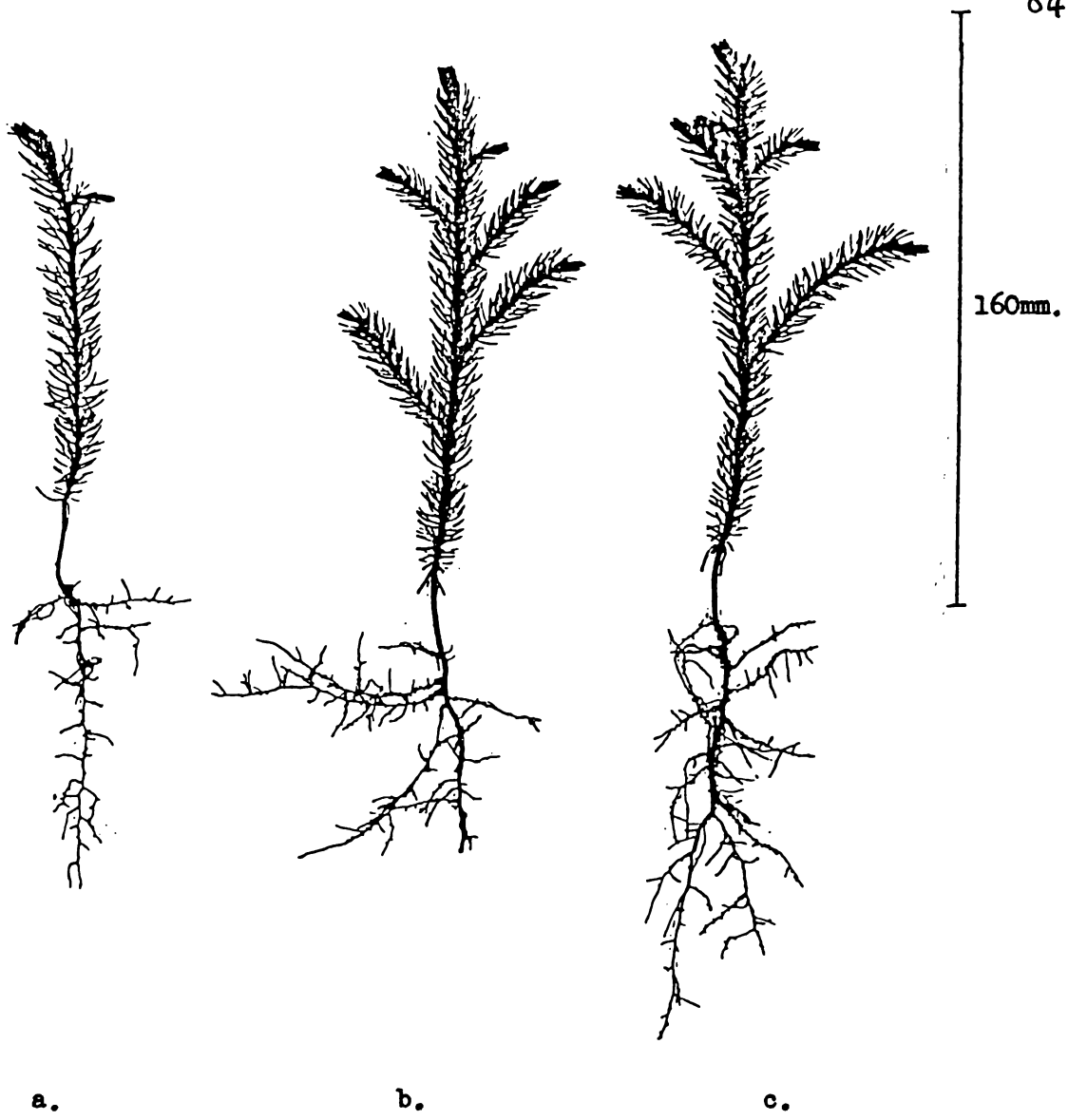


Fig. 3.7
Photocopies (reduced) of the largest seedling taken from each of the irradiance treatments in the nursery at the end of the experiment;
a. Low, 28% full sunlight;
b. Medium, 60% full sunlight;
c. High, 73% full sunlight.

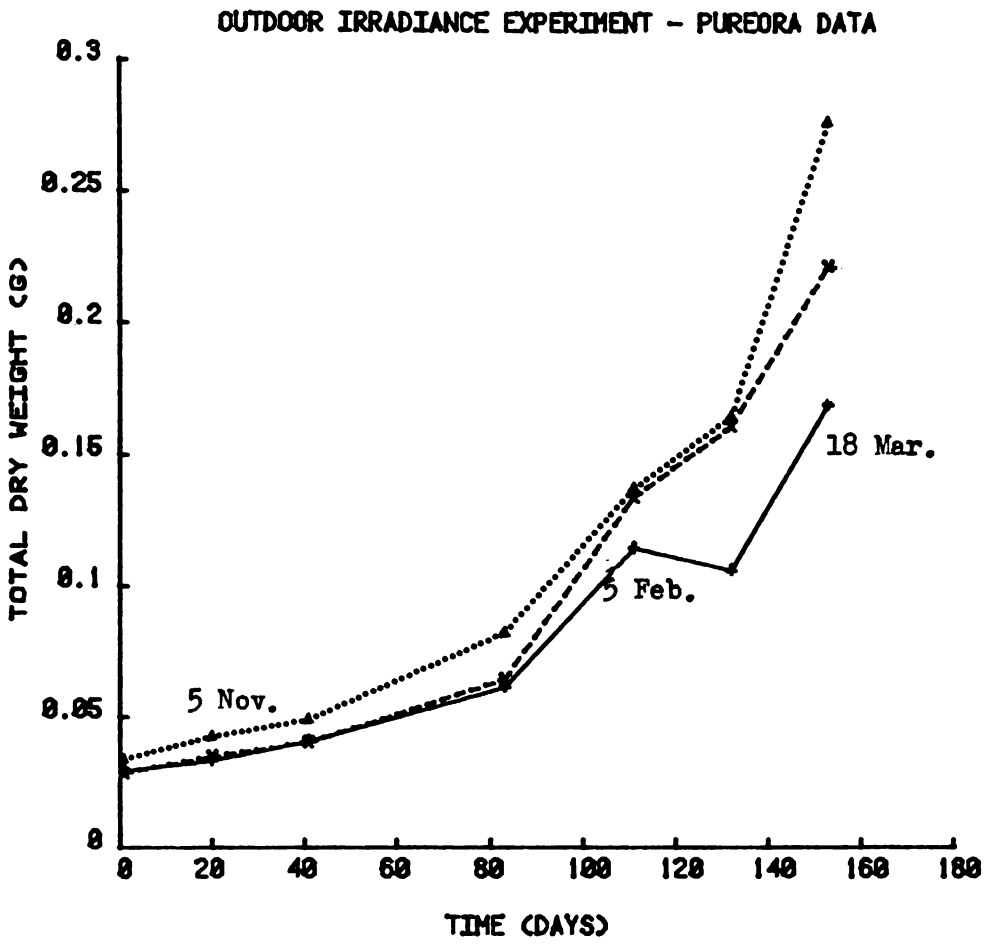


Fig. 3.8

The increase in total dry weight with time of seedlings from the three irradiance treatments in the nursery.

+ —— + Low, 28% full sunlight: x ---- x Medium, 60% full sunlight:
Δ ·····Δ High, 73% full sunlight:

dry weight increment and height increment in the plants grown at higher irradiance. Higher irradiance also caused an increase in the number of branches (Fig. 3.7 and Table 3.6). Increased growing irradiance did not cause an increase in root:shoot ratio in this experiment, however. The proportion of root dry weight to shoot dry weight was similar in all treatments (Fig. 3.7).

There were fewer leaves per 5 mm stem in the taller I_{73} and I_{60} plants indicating that part of the increased height growth was caused by internode extension rather than by the production of new leaves. However, leaf area ratios were increasing throughout summer in the two higher irradiances (Fig 3.9). In these faster growing young seedlings at higher irradiances leaf production was outstripping overall dry weight increase whereas in the I_{28} plants this was not the case and the leaf area ratio of these plants decreased slightly during the summer.

While leaf area ratios of the I_{73} and I_{60} plants increased during the growing season (Fig. 3.9) their unit leaf rates decreased (Fig. 3.10). Unit leaf rate of the slower growing I_{28} plants, on the other hand, increased slightly during the experiment and was higher than those of the I_{73} and I_{60} plants by the end of the summer.

(c) The effect of growing irradiance in controlled environments on the growth and photosynthesis of rimu seedlings

Chlorophyll analysis

The most obvious result of growing two year old rimu seedlings in three controlled irradiances was that their colour changed. They had all been green at the beginning of the experiment, but after about 6 weeks it was apparent that seedlings in 650 $\mu E\ m^{-2}\ s^{-1}$ and, to a slightly less extent in 385 $\mu E\ m^{-2}\ s^{-1}$, were becoming yellowish while those in 140 $\mu E\ m^{-2}\ s^{-1}$ were becoming darker green. By the end of five months these differences were more marked and a typical pair of seedlings from each treatment is illustrated in Fig. 3.11. The colour difference between the I_{650} and I_{385} plants was slight and chlorophyll a + b concentration was very similar in these two higher irradiance treatments, but was more than twice as high (on both leaf area and fresh weight bases) in plants grown at 140 $\mu E\ ^{-2}\ s^{-1}$. Chlorophyll a:b ratios, however, remained remarkably constant in all treatments (Table 3.7). As well as being darker green, leaves

Fig. 3.9
The progressive change in Leaf Area Ratio,F, with time, of seedlings grown at three irradiances in the nursery.
+ —— + Low, 28% full sunlight; x ---- x Medium, 60% full sunlight;
△ ·····△ High, 73% full sunlight.
Bars represent 5% confidence limits.

Fig. 3.10
The progressive change in Unit Leaf Rate,E, with time, of seedlings grown at three irradiances in the nursery. Symbols and lines as in Fig. 3.9.

Fig. 3.9 OUTDOOR IRRADIANCE EXPERIMENT - PUREORA

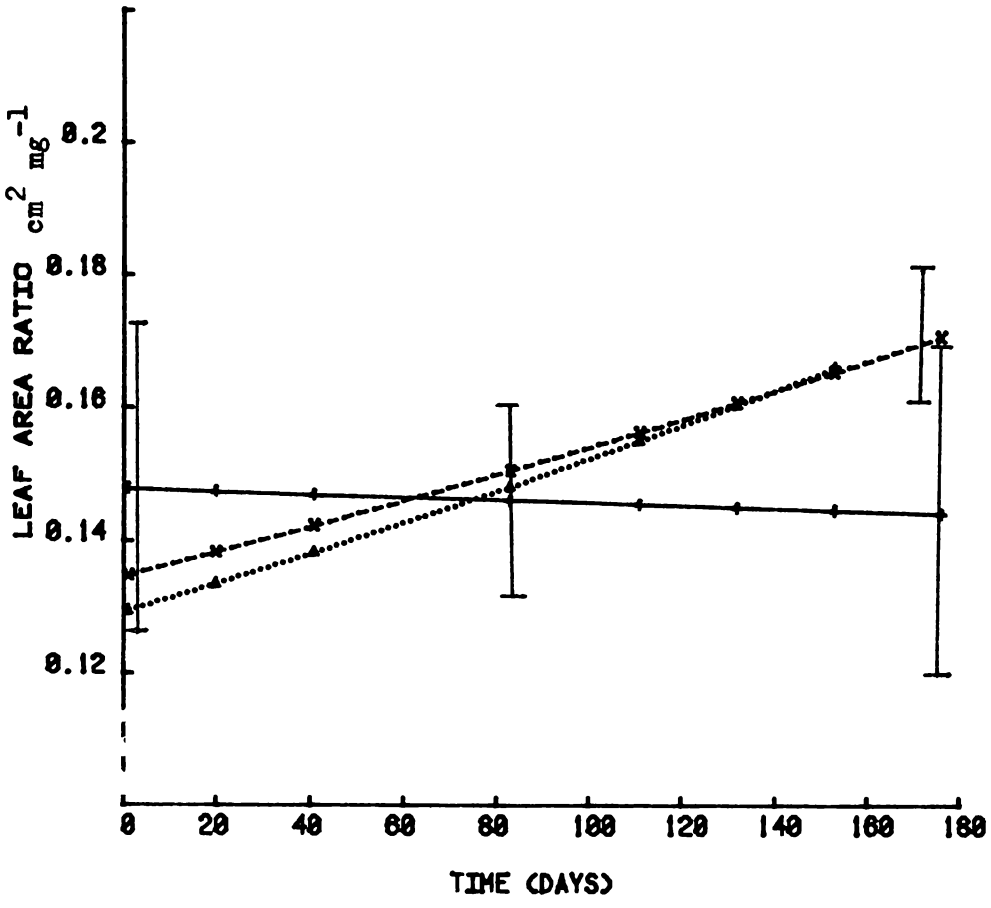
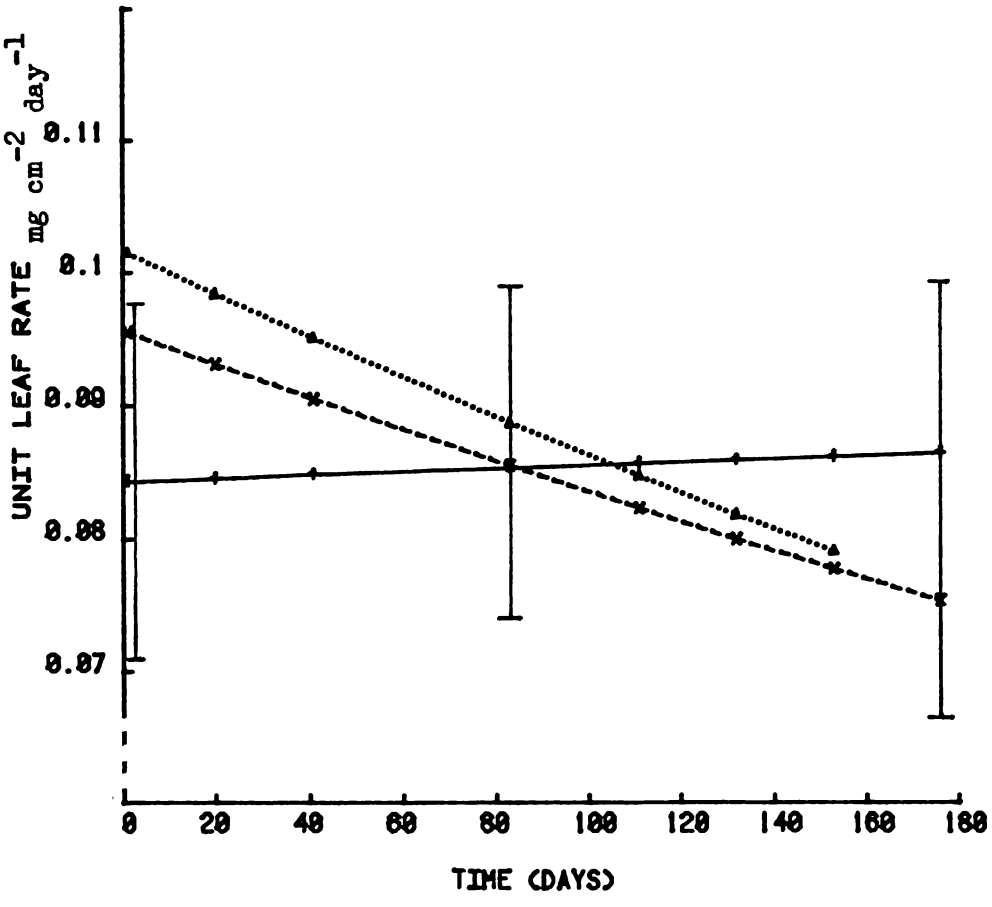


Fig. 3.10 OUTDOOR IRRADIANCE EXPERIMENT - PUREORA



of seedlings grown in low light were longer, thinner and softer than those grown at higher irradiances (Fig. 3.12).

TABLE 3.7 : MEAN CHLOROPHYLL CONCENTRATIONS OF NEW FOLIAGE OF RIMU SEEDLINGS GROWN FOR FIVE MONTHS AT THREE IRRADIANCES IN CONTROLLED ENVIRONMENTS

Treatment	n	Chlorophyll a + b		Chlorophyll a:b
$\mu E\ m^{-2}s^{-1}$		$mg\ g^{-1}$ fresh weight	$mg\ m^{-2}$ surface area	
140	5	0.69 a	76.0 a	3.08 a
385	5	0.28 b	31.7 b	2.91 a
650	5	0.26 b	32.6 b	3.09 a

Growth analysis

Data from destructive harvesting of five plants from each irradiance treatment on six occasions during 5 months were analysed for the important growth parameters. Relative growth rates and dry weights at the end of the experiment (Table 3.8) both indicate that I_{385} plants grew faster than those grown in higher or lower irradiances. However, as the plants were very variable in dry weight at the beginning of the experiment, high variance was carried through and differences in growth rate and final dry weight failed to show significance ($p = 0.05$).

Relative growth rate is determined by the relationship between leaf weight ratio (F_w) and unit leaf rate (E) (Appendix 1). In this experiment leaf weight ratios of plants from all three irradiance treatments declined throughout the experiment (Fig. 3.13), that of the faster growing I_{385} plants falling most rapidly from 0.59 to 0.35. The F_w of low irradiance, I_{140} plants declined at the slowest rate, from 0.58 to 0.45 and from about day 30 onwards these plants had the highest ratio of leaf weight to total weight, i.e. they invested a larger proportion of photosynthate in leaf production and leaf growth than plants grown at higher irradiances. In woody seedlings such as these leaf weight ratios tend to decrease because of the increasing proportion of non-assimilatory supporting tissue. On the other hand, in this experiment unit leaf rates (E) all increased with time (Fig. 3.14). Once again, because of the initial

Fig. 3.11

A typical pair of seedlings from each irradiance treatment.

Left to right: 140 , 385 and 650 $\mu E\ m^{-2}s^{-1}$.

Fig. 3.12

A typical leaf from each irradiance treatment.

Left to right: 140 , 385 and 650 $\mu E\ m^{-2}s^{-1}$.

The longest leaf is approximately 10mm long.

variation amongst replicates within each treatment, these differences were not significant, but throughout the experiment the greatest unit leaf rates were found in the medium irradiance plants and the rate of increase in E was greatest in these plants also. The higher relative growth rate and total dry weight in the medium treatment were associated with this higher, rapidly increasing unit leaf rate which rose from 1.4 mg mg^{-1} day^{-1} x 10^{-2} to 2.4. The unit leaf rate of I_{650} plants increased from 1.1 to 1.6 while that of I_{140} plants remained lower throughout and only increased from 1.0 to 1.3 (Fig. 3.14).

Mean heights of seedlings from the three irradiance treatments were similar to each other (Table 3.8). (Height differences illustrated in Fig. 3.11 are coincidental - plants were chosen to represent colour differences rather than height differences.) I_{140} plants were marginally taller than I_{650} plants whereas I_{385} plants, which had the highest relative growth rates, unit leaf rates and total dry weights, were approximately 12 mm shorter in mean height. The additional growth at 385 μE m^{-2} s^{-1} was thus not in height but in diameter and root growth (Table 3.8). I_{385} plants had the largest root collar diameters, with I_{650} plants intermediate and I_{140} plants smallest. (This is the same order as R, E and dry weight.) I_{385} plants were therefore somewhat shorter, but larger in diameter as indicated by their ratio of diameter:height (Table 3.8). This ratio is a measure of plant sturdiness and Table 3.8 shows that I_{385} plants were the most sturdy followed by I_{650} plants. I_{140} plants were significantly less sturdy with slightly greater height and smaller diameter.

Finally, the root:shoot ratio of I_{385} plants was significantly greater than that of I_{140} plants (Table 3.8) while the I_{650} root:shoot was intermediate. Higher root:shoot ratio indicated better root development in the medium irradiance treatment. In all parameters, except height, I_{385} plants showed the best growth followed by I_{650} plants. Low light, I_{140} plants grew less well in all parameters except height.

TABLE 3.8 : MEAN GROWTH PARAMETERS OF TWO YEAR OLD PUKETI PROVENANCE RIMU SEEDLINGS GROWN FOR 5 MONTHS IN THREE IRRADIANCES IN CONTROLLED ENVIRONMENTS. Relative humidities and temperature regimes were the same in all three treatments: 20°C/13°C; constant 70% R.H., 14 hour photoperiod

Treatment	n	R (harvests)	Dry weight	Height	Root collar diameter	Diameter: height ratio	Root:shoot ratio
$\mu E\ m^{-2}s^{-1}$		$gg^{-1}day^{-1} \times 10^{-2}$ ± 5% confidence intervals	g	mm	mm		
140	5	0.59 ± 0.32 a	2.10 a	210 a	2.60 a	0.012 b	0.37 b
385	5	0.83 ± 0.30 a	3.12 a	198 a	3.34 a	0.017 a	0.75 a
650	5	0.60 ± 0.31 a	2.71 a	209 a	3.04 a	0.015 a	0.51 ab

Fig. 3.13
The progressive change in Leaf Weight Ratio, F_w, with time, of seedlings grown at three irradiances in controlled environment cabinets.
+ ——+ Low, 140 uE m^{-2} s^{-1}; x- - -x Medium, 385 uE m^{-2} s^{-1};
△....△ High, 650 uE m^{-2} s^{-1}.

Bars represent 5% confidence limits.

Fig. 3.14
The progressive change in Unit Leaf Rate, E, with time, of seedlings grown at three irradiances in controlled environment cabinets.
Symbols and lines as in Fig. 3.13.

Fig. 3.13 INDOOR IRRADIANCE EXPERIMENT

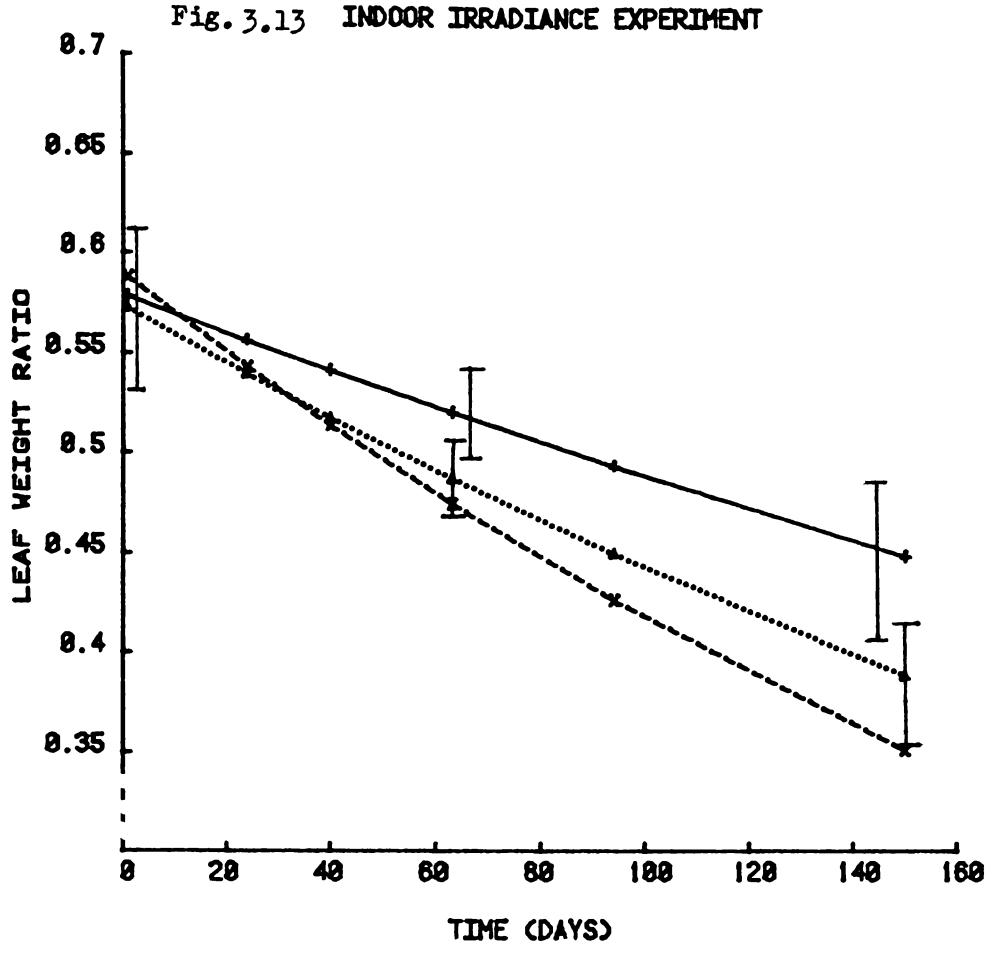
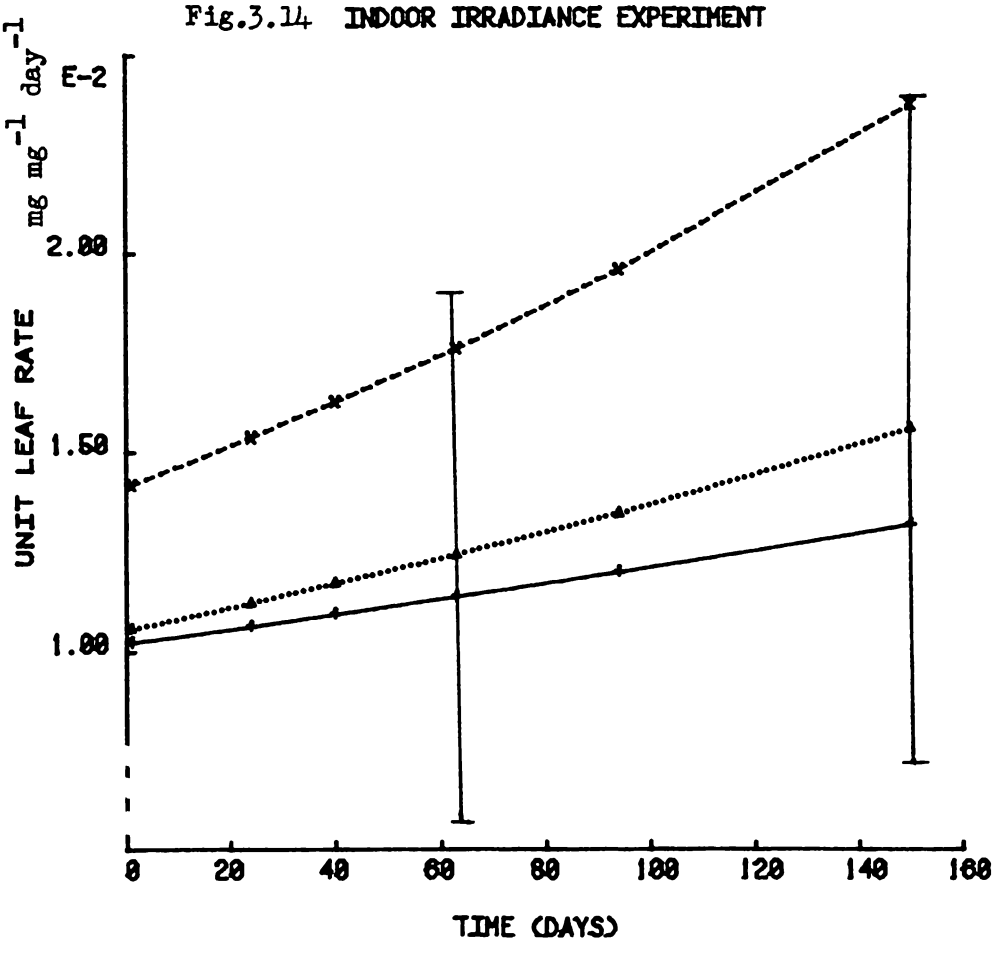


Fig.3.14 INDOOR IRRADIANCE EXPERIMENT



Gas exchange measurements

The responses of net photosynthesis rate to irradiance of seedlings from the three treatments were found to be very similar to each other (Fig. 3.15 a-c). Light saturation was reached at approximately 400 $\mu E\ m^{-2}\ s^{-1}$ in all treatments and light saturated photosynthesis rates fell between about 1.8 and 2.8 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$. Rationships between

$$\frac{1}{P_n + R_d} \quad \text{and} \quad \frac{1}{I}$$

are illustrated in Fig. 3.16 a-c and there is little difference in the intercepts between the three treatments, indicating a similarity between the plants in total resistance to CO_2 diffusion into the leaves. However, the slopes of the lines are very different indicating differences in quantum requirement at low irradiances. Mean quantum requirements are shown in Table 3.9. I_{140} seedlings had significantly lower quantum requirements than I_{650} plants showing that they were more efficient at fixing CO_2 at low irradiances. The quantum requirement of I_{385} plants was intermediate in value. The lower the growing irradiance, therefore, the more efficient were the seedlings at fixing CO_2 when light was limiting.

When light was not limiting, however, (above about 400 $\mu E\ m^{-2}s^{-1}$) seedlings from all three treatments had very similar rates of photosynthesis (Table 3.9, Fig. 3.15 a-c). The mean light saturated photosynthesis rate of I_{385} plants was slightly lower than that of the other two treatments and there was less variation between replicates from this treatment (Fig. 3.15b).

Mean dark respiration rates at 20°C are slightly higher in I_{385} plants (Table 3.9), the rates for I_{650} plants being intermediate between these and I_{140} plants. In Fig. 3.15 a-c the light compensation point is the point where net photosynthesis rate is zero. Mean values for light compensation point are given in Table 3.9. Light compensation points of plants from all three treatments are very low, but that of the I_{140} plants, with lower quantum requirements (greater efficiency) and dark respiration rates, is significantly lower than those of I_{385} or I_{650} plants.

TABLE 3.9 : THE MEAN QUANTUM REQUIREMENTS, LIGHT SATURATED PHOTOSYNTHESIS AND DARK RESPIRATION RATES AT 20°C, AND LIGHT COMPENSATION POINTS FOR RIMU SEEDLINGS GROWN AT THREE IRRADIANCES IN CONTROLLED ENVIRONMENT CABINETS

Treatment	n	Quantum Requirement	Photosynthesis Rate		Dark Respiration Rate		Ligh Compensation Point
$\mu E\ m^{-2}s^{-1}$		E mol^{-1}	μ mol $m^{-2}s^{-1}$	g $m^{-2}h^{-1}$	μ mol $m^{-2}s^{-1}$	g $m^{-2}h^{-1}$	$\mu E\ m^{-2}s^{-1}$
140	4	17.8 b	2.7 a	0.43 a	0.46 a	0.07 a	9.2 b
385	5	26.2 ab	2.4 a	0.38 a	0.59 a	0.09 a	19.1 a
650	5	36.2 a	2.7 a	0.43 a	0.50 a	0.08 a	20.6 a

Fig.3.15 a - c.

The response of net photosynthesis rate to irradiance of seedlings grown at three irradiances.

a. 140 $\mu E\ m^{-2}\ s^{-1}$

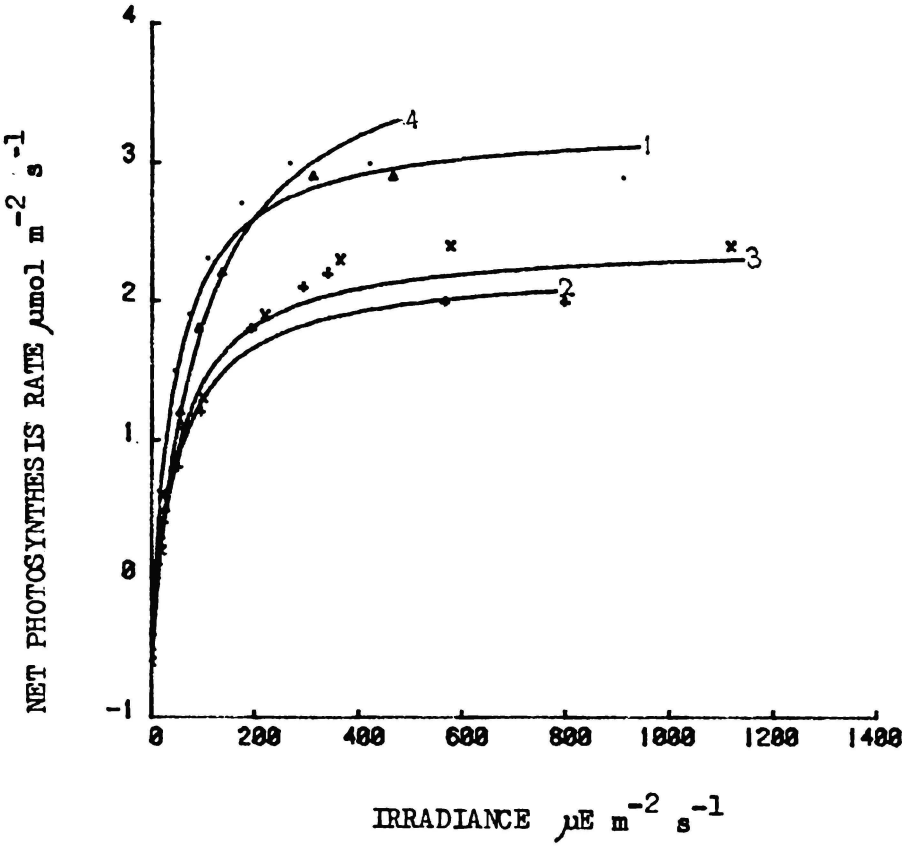
b. 385 $\mu E\ m^{-2}\ s^{-1}$

c. 650 $\mu E\ m^{-2}\ s^{-1}$

The symbols represent the measured data points for the replicate seedlings and the lines are the fitted rectangular hyperbolae, identified by replicate number.

Replicate number.	Symbol.
1	·
2	+
3	×
4	△
5	□

Fig3.15 a. 140 μE m^{-2} s^{-1}



b. 385 μE m^{-2} s^{-1}

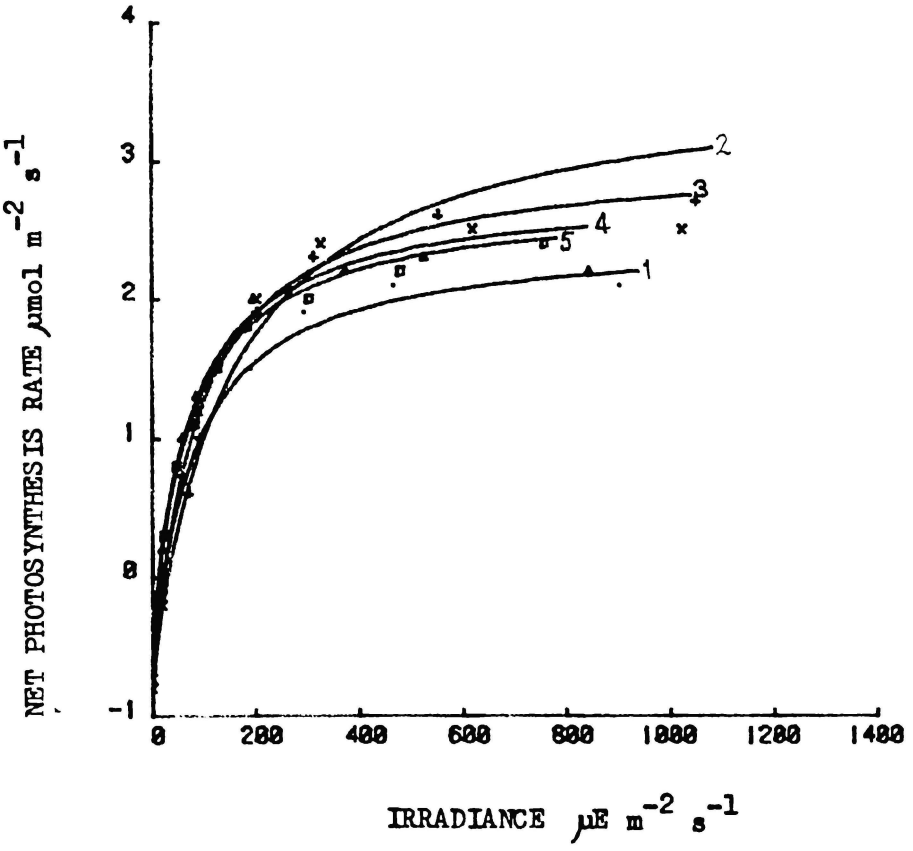


Fig. 3.15 c. 650 $\mu E\ m^{-2}\ s^{-1}$

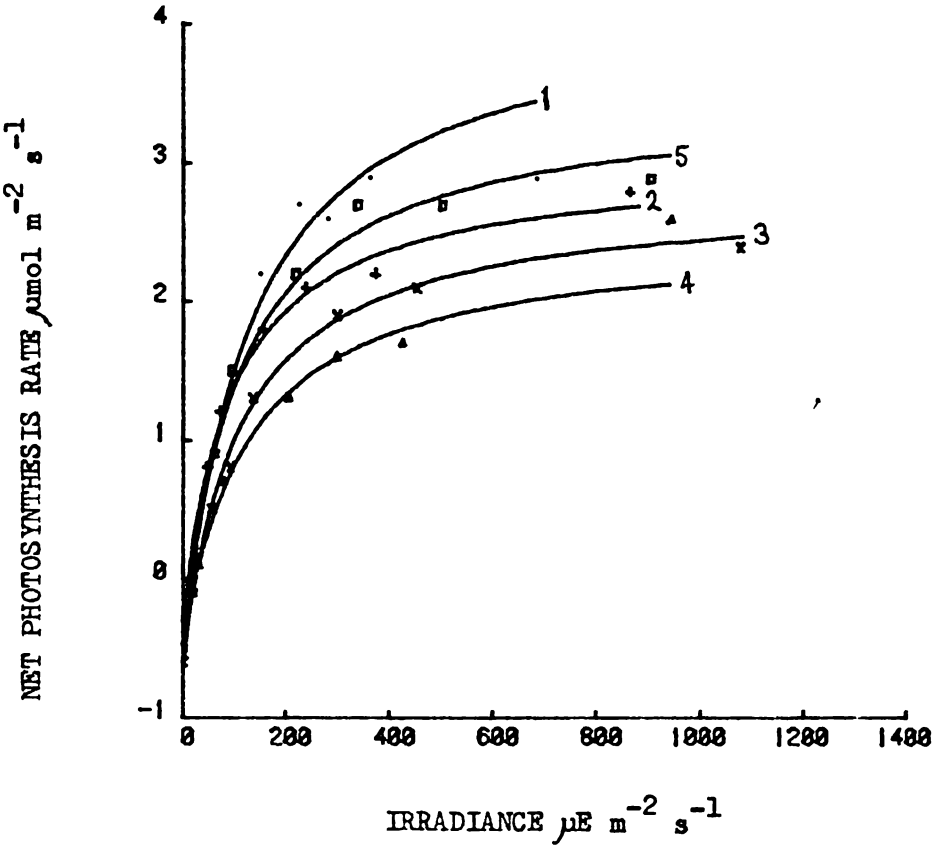


Fig. 3.16 a. - c.

The relationships between $\frac{1}{P_n + R_d}$ and $\frac{1}{I}$ for seedlings grown at three irradiances. The symbols represent the calculated data points for the replicate seedlings and the lines are the linear regressions identified by replicate number. (Replicate symbols as in Fig. 3.15).

Fig. 3.16 a. 140 μE m^{-2} s^{-1}

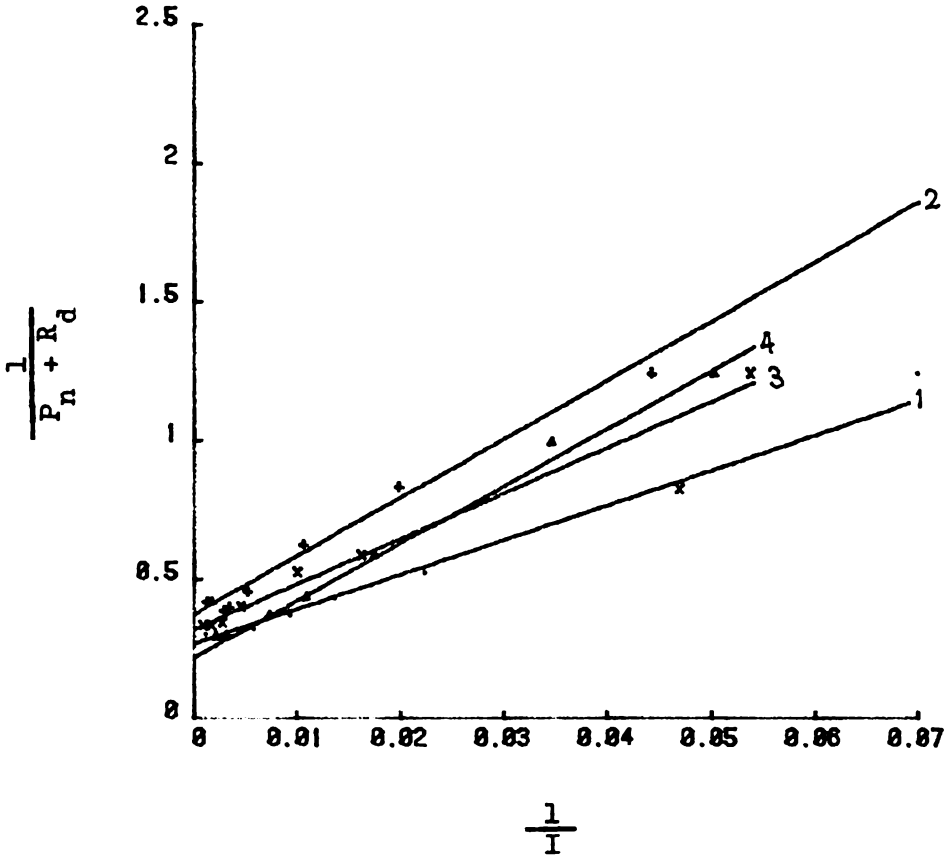


Fig. 3.16 b. 385 μE m^{-2} s^{-1}

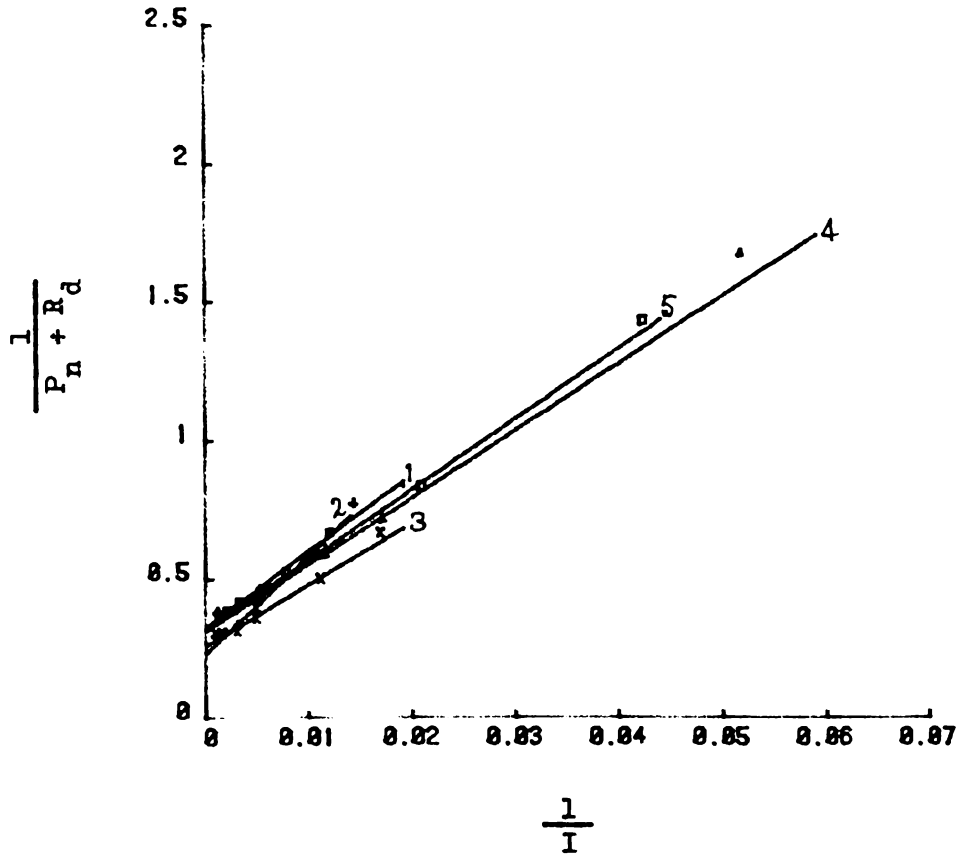
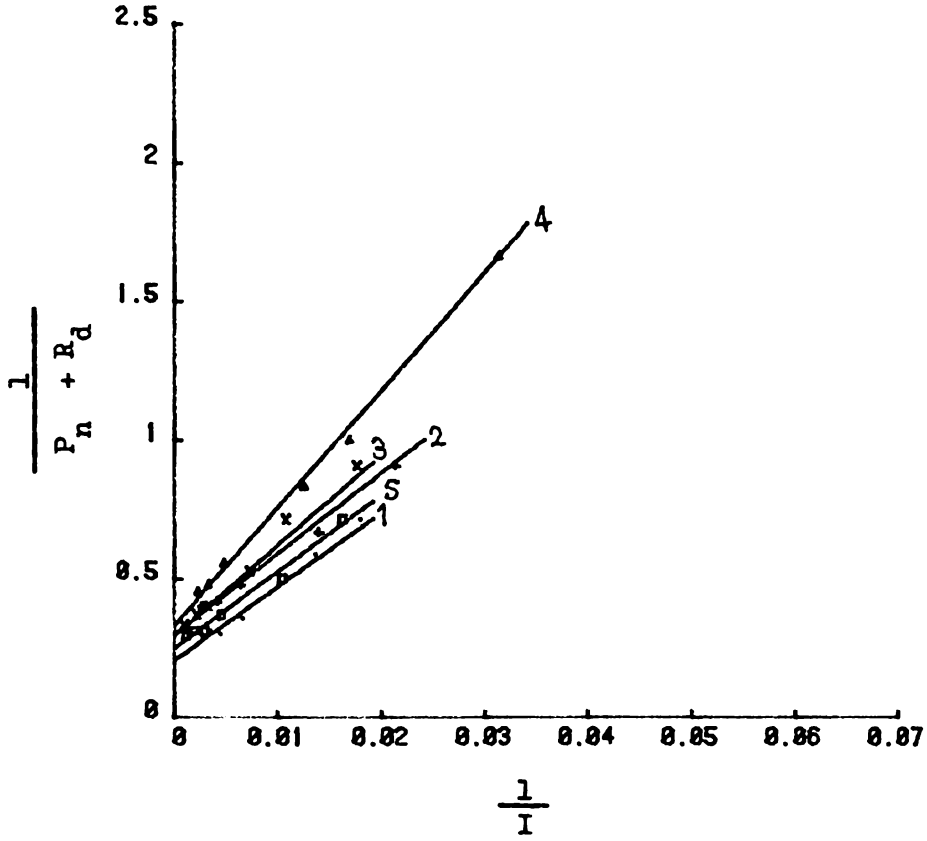


Fig.3.16 c. 650 μE m^{-2} s^{-1}



To examine what limits the light saturated photosynthesis rate the various resistances to CO_2 diffusion into the leaf were studied and resistances and their ratios are shown in Table 3.10. Stomatal resistance tended to increase with growing irradiance whereas residual resistance tended to decrease. In all cases residual resistance was more than twice as great as stomatal resistance and the ratio $r_{r_{CO_2}} : r_{s_{H_2O}}$ was highest at lowest growing irradiance, indicating that photosynthesis rate was limited more by the internal leaf resistance than by stomatal resistance. The ratio of resistances decreased somewhat with increasing growing irradiance, but none of the differences in resistances or their ratios were significant.

TABLE 3.10 : MEAN RESISTANCES TO H_2O AND CO_2 OF RIMU SEEDLINGS GROWN AT THREE IRRADIANCES. Resistances are calculated at light saturated rates of photosynthesis

Treatment	n	$r_{s_{H_2O}}$	$r_{r_{CO_2}}$	$r_{r_{CO_2}} : r_{s_{H_2O}}$
$\mu E\ m^{-2}\ s^{-1}$		S cm^{-1}	S cm^{-1}	
140	4	7.49 a	34.72 a	5.13 a
385	3	11.36 a	33.67 a	2.98 a
650	3	11.59 a	23.81 a	2.70 a

The response of photosynthesis to increasing temperature is shown in Fig. 3.17 a-c. Characteristically photosynthesis increases to a maximum rate between 18° and 22°C and then decreases as temperature increases further. Photosynthesis probably reaches zero between 35° and 40°C. Seedlings from all three irradiances responded in a similar way. Above about 22°C the increase in dark respiration rate counteracts any further increase in gross photosynthesis rate caused by increasing temperature and consequently net photosynthesis rate begins to decline. These seedlings were grown at day temperatures of 20°C and maximum rates of photosynthesis at saturating irradiance were found close to this temperature.

Fig. 3.17 a - c
The response of net photosynthesis rate to temperature of seedlings grown at three irradiances. The symbols represent the normalised data points for the replicate seedlings. The curves were fitted by eye. Measurements were made at approximately 1000 $\mu E\ m^{-2}\ s^{-1}$.

Fig. 3.17 a. 140 $\mu E\ m^{-2}\ s^{-1}$

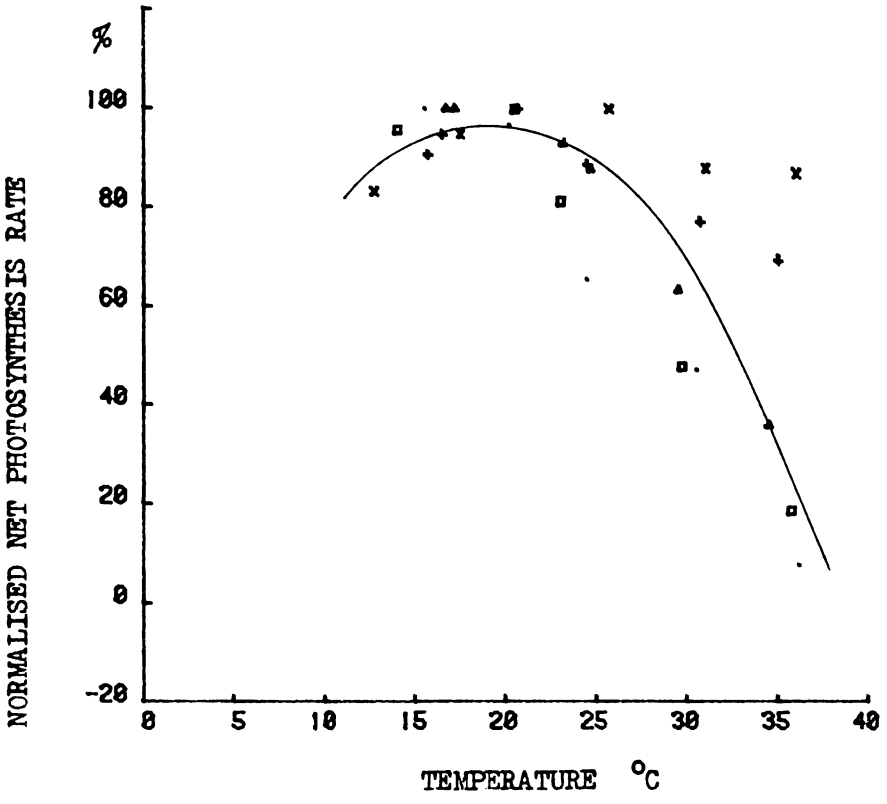


Fig. 3.17 b. 385 $\mu E\ m^{-2}\ s^{-1}$

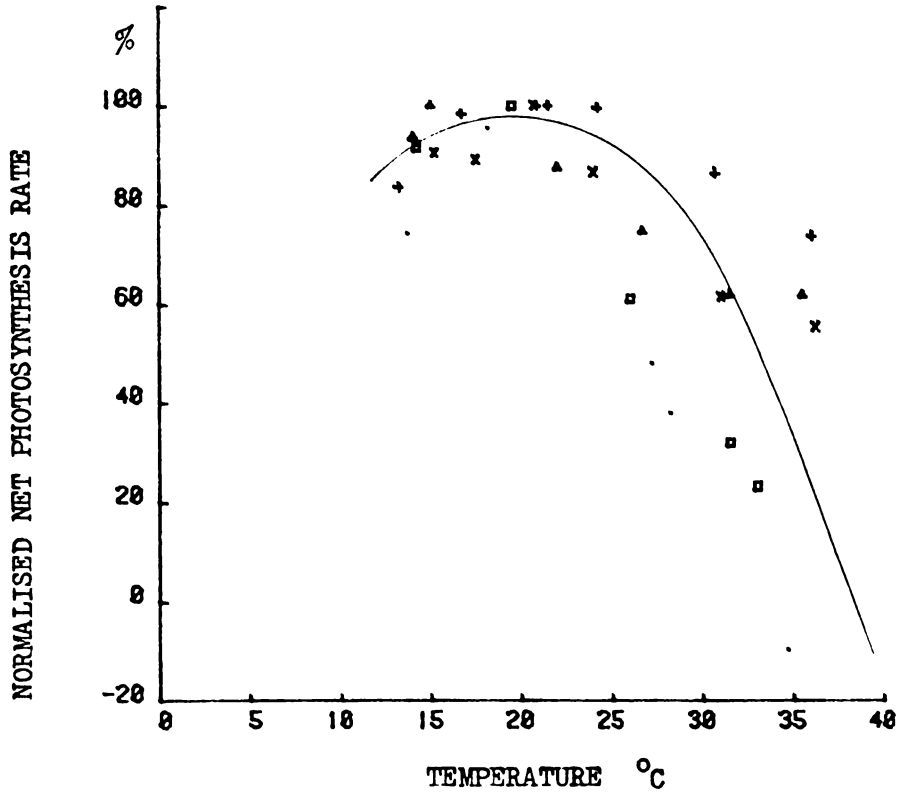
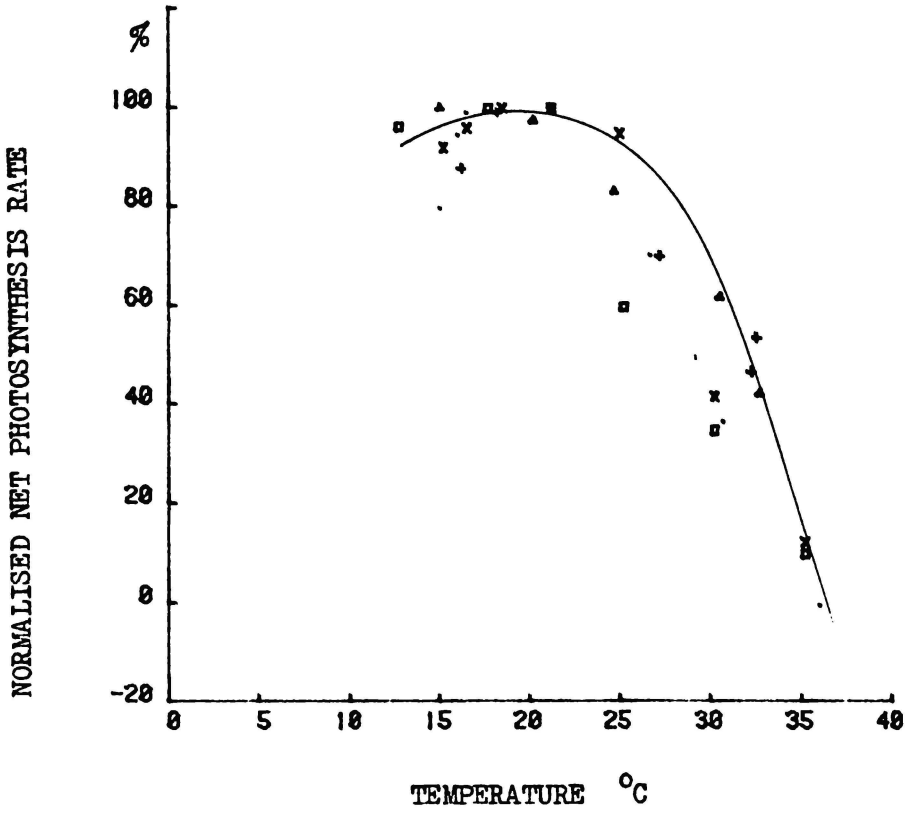


Fig. 3.17 c. 650 $\mu E\ m^{-2}\ s^{-1}$



3.4.3 Discussion

The seedlings of rimu are known to be shade tolerant and to persist for many years at relatively low light intensities on the forest floor. Their light compensation point is low - about 20 $\mu E\ m^{-2}\ s^{-1}$ when grown at irradiances between 385 and 650 $\mu E\ m^{-2}\ s^{-1}$ (Table 3.9), and may be even lower, e.g., 9 $\mu E\ m^{-2}\ s^{-1}$ when grown at 140 $\mu E\ m^{-2}\ s^{-1}$ in controlled conditions. It is probable that compensation point was reduced even further in seedlings grown in 1% full sunlight as the irradiance in this treatment was often lower than 20 $\mu E\ m^{-2}s^{-1}$ and the plants survived.

However, after seven months (July to February), two year old seedlings grown in 1% full sunlight had negative mean relative growth rates and net assimilation rates, although their leaf weight ratios were higher than those of plants grown at 17% and 42% sunlight (Table 3.5). It is possible that continued growth in the very low irradiance would lead to a further increase in leaf weight ratio and a subsequent increase in relative growth rate until positive growth was achieved. It should be noted that these seedlings were grown in a well balanced potting mix and kept well watered, whereas in nature seedlings at such a low irradiance would be competing with surrounding vegetation for water, mineral nutrients and space.

Shade grown seedlings have much weaker root systems than plants grown in higher irradiances (Table 3.5) and consequently it is estimated that in nature the minimum irradiance at which they could survive would be between 1% and 2% full sunlight. This compares with the minimum light intensities found to be necessary for the establishment of seedlings of tanekaha and kauri. Tanekaha seedlings did not occur below 1.8% and kauri below 1.5% full sunlight (Bieleski, 1959a). Light compensation point for kauri seedlings at normal temperatures in semi-controlled conditions was estimated to be approximately 2% full sunlight (Bielseki, 1959b).

In common with shade tolerant seedlings of many forest trees rimu seedlings are very slow growing, but growth rates are increased by increased growing irradiance. Growth rates of seedlings of several other conifers are shown in Table 3.11 for comparison (Jarvis and Jarvis, 1964).

TABLE 3.11 : RELATIVE GROWTH RATES OF CONIFER SEEDLINGS FOR COMPARISON WITH RATES FOUND IN RIMU (after Jarvis and Jarvis, 1964)

Species	Age Years	Relative growth rate $g\ g^{-1}\ day^{-1} \times 10^{-2}$	Growing irradiance
Pinus sylvestris	1	3.3	Not known
	2	2.2	Not known
	5	0.3	Not known
Larix kaempferi	4	1.4	Not known
Picea abies	4	0.8	Not known
Agathis australis	1	1.2	40% sunlight
Dacrydium cupressinum	1	1.3	73% sunlight
	2	0.8	385 $\mu E\ m^{-2}\ s^{-1}$

Relative growth rates in woody plants tend to decrease with increase in dry weight because of the increasing proportion of structural material and in the experiments described in this chapter relative growth rates of rimu seedlings ranged from - 0.03 $g\ g^{-1}\ day^{-1} \times 10^{-2}$ for second year woody seedlings grown at 1% sunlight, to 1.3 $g\ g^{-1}\ day^{-1} \times 10^{-2}$ for small, soft first year seedlings grown at 73% sunlight. In first year kauri seedlings Bieleski (1959b) found relative growth rates ranging from 0.28 $g\ g^{-1}\ day^{-1} \times 10^{-2}$ for plants grown at 2% sunlight, to 1.2 $g\ g^{-1}\ day^{-1} \times 10^{-2}$ for plants grown at 40% sunlight. In both rimu and kauri increased growing irradiance up to a certain level caused an increase in growth rate and the relative growth rates are similar to those found in other shade tolerant tree seedlings (Bieleski, 1959b; Jarvis and Jarvis, 1964). Growth rates in 1 year old rimu seedlings at 73% sunlight were similar to those of 1 year old kauri at 40% sunlight (Table 3.11). Growth rates of 2 year old rimu were low in comparison with 2 year old Pinus sylvestris seedlings. Rimu growth rate were as low in two year old seedlings as the rates found in four year old Picea abies seedlings.

In very small rimu seedlings growth rate increased with irradiance up to the relatively high light intensity of 73% sunlight (Table 3.6). In larger seedlings grown at relatively lower irradiances, however,

there appeared to be an optimal irradiance above which growth rate either remained the same (Table 3.5) or decreased (Table 3.8). Light saturated photosynthesis rates for plants from three irradiance treatments were very similar, approximately 0.4 g CO_2 m^{-2} h^{-1} which is within the range given for shade plants (Tables 3.1 and 3.9).

In many species light saturated photosynthesis rates increase with increasing growing irradiance, but this was not the case in rimu. Seedlings grown at low irradiance (140 μE m^{-2} s^{-1}) and high irradiance (650 μE m^{-2} s^{-1}) had rates very slightly higher than those of seedlings grown at medium irradiances (385 μE m^{-2} s^{-1}). On the other hand, best relative growth rates were found in seedlings grown at medium irradiance (Tables 3.9 and 3.8).

In many species dark respiration rate decreases at low growing irradiance, but there was only a slight decrease in dark respiration rate in rimu seedlings grown at low irradiance (Table 3.9) and plants grown at high irradiance also had slightly lower dark respiration rates than those grown at medium irradiance. The slighly lower light saturated net photosynthesis rate found in plants grown at medium irradiance may have been caused by their higher dark respiration rate. In this experiment, therefore, seedlings grew most vigorously at medium rather than at high irradiance.

Rimu seedlings did respond in a manner typical of many other plants, however, by decreasing their light compensation point and quantum requirement when grown at low irradiance (Table 3.9). The quantum requirement of approximately 18E mol^{-1} for rimu seedlings grown at 140 μE m^{-2} s^{-1} (low light) is comparable with that found in the herbaceous shade tolerant plant Alocasia macrorrhiza Schott. of approximately 14E mol^{-1} (Bjorkman et al., 1972b).

In certain species high growing irradiance causes an increase in stomatal frequency which in turn causes a decrease in stomatal resistance (e.g., Atriplex patula L. (Bjorkman et al 1972a)) but in rimu there was a slight increase in stomatal resistance with increased growing irradiance (Table 3.10). Examination of epidermal peels and scanning electron micrographs of rimu leaves from the three treatments showed no evidence of increased numbers of stomata per

unit area in leaves grown at higher irradiance. The surface of leaves from all treatments appeared similar (not illustrated).

In some experiments increased residual resistances have been measured in plants grown at low irradiances. Some workers have related such increases to changes in the morphology of the leaf, thicker sun leaves having more mesophyll cell layers and therefore greater mesophyll cell surface area and consequently lower mesophyll resistance (e.g., Nobel et al., 1975), while others have indicated that reduced enzyme activity at low irradiances may be responsible for increased residual resistance (e.g., Bjorkman, 1967; Bjorkman et al., 1972a; Tsel' Niker, 1979). In rimu seedlings there was a slight increase in residual resistance with decreasing growing irradiance (Table 3.10), but as has been mentioned, this was not accompanied by a decrease in light saturated photosynthesis rate. The morphology of the leaves of rimu seedlings responded to growing irradiance in a typical manner (Fig. 3.12), those grown in low light being longer, thinner and softer than those grown in high light. There was also a higher concentration of chlorophyll a + b in shade grown leaves (Table 3.7). Chlorophyll concentrations in rimu leaves from all treatments were low relative to other species (Table 3.12) and there appeared to be quite marked chlorosis in plants grown in both the medium and high irradiances. Chlorophyll concentration in medium and high irradiance plants was similar to each other and only about half that in the green plants from the low irradiance treatment. Chlorosis due to high light intensity is common in many plants and affects plants which normally grow in the shade to a greater extent (Treshow, 1970). Most plants have abundant chlorophyll and normally only in very young leaves of most species or in leaves of aurea varieties are chlorophyll concentrations sufficiently low for rates of photosynthesis and growth to be affected (Gabrielsen, 1948). Optimal chlorophyll concentrations for photosynthesis are between 40-50 mg m^{-2} surface area (Gabrielsen, 1948) and in these rimu seedlings the concentrations were 76 mg m^{-2} for plants grown at 140 $\mu E\ m^{-2}\ s^{-1}$ but only 32 mg m^{-2} for plants grown at both 385 and 650 $\mu E\ m^{-2}\ s^{-1}$. The increased quantum requirements of plants grown at medium and high irradiance, relative to those grown at low irradiance, were probably related to their very low (sub-optimal) chlorophyll concentrations (Table 3.9).

TABLE 3.12 : CHLOROPHYLL CONCENTRATIONS OF SEVERAL SPECIES FOR COMPARISON WITH CONCENTRATIONS FOUND IN RIMU. The same extraction method was used in all species (after Hiscox and Israelstam, 1979)

Species	Chlorophyll a + b mg g^{-1} fresh weight
Pisum sativum	2.6
Pelargonium hortorum	2.2
Citrus lemonii	2.3
Pinus sylvestris	1.4
Dacrydium cupressinum (Grown at 140 $\mu E\ m^{-2}\ s^{-1}$)	0.7
Dacrydium cupressinum (Grown at 385 $\mu E\ m^{-2}\ s^{-1}$)	0.3

In many plants the proportion of chlorophyll b increases relative to chlorophyll a with decreasing growing irradiance (Goodchild et al., 1972; Leopold and Kriedemann, 1975). Chlorophyll b improves the utilisation of light between 450 and 480 nm and light in this waveband is relatively abundant on the forest floor (Rabinowitch, 1945). The ratio of chlorophyll a:b was, however, not affected by growing irradiance in the experiment with rimu seedlings in controlled environments and this is believed to be because the quality of the light was not altered by the shade screens in the same way in which light is altered as it passes through a forest canopy.

Plants grown at low irradiances usually have a higher proportion of foliage than plants grown at higher irradiances (e.g., Boardman, 1977) and in this respect the larger, woody rimu seedlings were typical (Table 3.5 and Fig. 3.13). Together with increased leaf weight ratios, plants grown at low irradiance often have poorly developed root systems (Spurr and Barnes, 1973). In kauri seedlings, for example, there was a decrease in root:shoot ratio with decreasing growing irradiance in semi-controlled conditions (Bieleski, 1959b). This decrease in root development at low growing irradiance was also shown in the root:shoot ratios of woody rimu seedlings (Table 3.5).

Similarly, the root:shoot ratio was lower in woody rimu seedlings grown at 140 μE m^{-2} s^{-1} compared with those grown at 385 μE m^{-2} s^{-1} (Table 3.8), but a further increase in growing irradiance (to 650 μE m^{-2} s^{-1}) caused a reduction in root:shoot ratio. In small soft seedlings grown at relatively high irradiances there was no decrease in root:shoot ratio with decreasing irradiance (Table 3.6). The poor development of roots in tree seedlings grown in low irradiance can be a critical factor in their survival. When light is reduced by larger trees the roots of these trees reduce the available soil moisture and in times of drought shade grown seedlings often die of desiccation. The fact that the root:shoot ratio of small rimu seedlings did not vary with irradiance down to 28% sunlight, implies that an inadequate root system would not be the main limiting factor for survival of rimu seedlings at this irradiance. At very low light intensities, however, root development of small rimu seedlings would probably be reduced and this would limit their establishment especially in drought-prone sites.

Small rimu seedlings grown at high irradiances (60% and 73% sunlight) developed more branches than those grown at low light intensity (28% sunlight) (Table 3.6). Open grown rimu trees are bushier with more numerous, heavier branches than trees grown in partial light (e.g., Nicholls, 1976). When rimus which have grown up in the shade of a canopy finally break through into full sunlight above the canopy, they often become multi-leadered and heavily branched (Lloyd, 1960).

Woody rimu seedlings grew taller in 17% sunlight than in 42% sunlight (Table 3.5) and even weak seedlings grown in only 1% sunlight grew somewhat more in height than those grown at 42%. Many tree species, conifer and angiosperm, make as much or more height growth when grown in the shade as when grown in full sunlight (Spurr and Barnes, 1973). Under a leaf canopy the light which penetrates to the forest floor is relatively rich in far-red wavelenghts (700-775 nm) and in many tree seedlings far-red enriched light causes the stems to elongate more than normal white light of the same irradiance (Salisbury and Ross, 1978). In many species grown beneath a plant canopy there is a simultaneous retardation in the amount of branching and consequently the plant expends a greater proportion of its photosynthate in growing upwards (towards the top of the canopy) than

when unshaded (Salisbury and Ross, 1978). However, the quality of light in the experiments with rimu was probably not altered by the shade cloth in the same way as light is altered by passing through a leaf canopy and so the cause of increased height growth at reduced irradiance may not have been far-red enrichment.

From the foregoing it can be seen that rimu seedlings respond to growing irradiance in ways typical of many shade tolerant plants. In small seedlings growth rate is increased by increased irradiance up to relatively high light intensities, but in larger seedlings growth rate increases up to a certain optimal level, above which there is no further increase, at least in the short term. How does this information correspond with what is known about the regeneration of rimu in nature?

Rimu is a very versatile species which is not restricted to any one regeneration method, but is capable of becoming established and surviving in a wide variety of situations. On the one hand the seedlings are shade tolerant and may grow extremely slowly in very low irradiances (close to 2% sunlight), surviving with very little dry weight increment for many years until a gap is created in the canopy which increases the irradiance (and decreases root competition) and allows the small rimu to increase their growth rate to some extent. Alternatively, rimu seedlings readily become established alongside forest margins and in small forest clearings where conditions of irradiance are intermediate between heavy shade and full sunlight. On the other hand the seedlings are also capable of establishing and growing in fully exposed sites where they may act as pioneering colonisers, for example, following fire. The regeneration of rimu in different environments will be discussed further in Chapter 4.

Because of the ability of the species to establish, persist and grow slowly for hundreds of years in a very wide range of environments, many of which would not be tolerated by more rapidly growing tree species, rimu is an extremely ubiquitous forest tree occurring in a great many forest communities (Nicholls, 1976).

3.5 The effect of temperature on the growth and photosynthesis of rimu seedlings

3.5.1 Methods

a. The effect of different temperature regimes on the growth of small rimu seedlings.

Puketi and Pureora seedlings were established in the glasshouse and transferred (3 April 1979) to three controlled environment treatments: low $17^{o}/9^{o}C$, medium $22^{o}/14^{o}C$ and high $27^{o}/19^{o}C$, all with 15 hours photoperiod and c.600 $\mu E\ m^{-2}\ s^{-1}$ irradiance. (Relative humidity was uncontrolled.) Puketi seedlings were approximately 12 months old with an initial mean height of 118.5 mm and were potted in solid plastic tubes in 50:50 peat:sand; Pureora seedlings were approximately 5 months old with an initial mean height of 36.3 mm and were potted in peat pots in standard potting mix (Table 3.2 and section 3.2.1). Sequential harvests for growth analysis were made over 65 days: Puketi, 19 harvests; Pureora, 12 harvests.

b. The effect of night temperature (Thermoperiod) on the growth, photosynthesis and dark respiration of rimu seedlings.

2.5 year old Puketi and 2 year old Waitakere seedlings were potted 2 per pot and grown in the glasshouse for four months until December 1980, when they were transferred to three controlled environment cabinets with: 70% relative humidity (constant); 12 hours photosynthetic radiation, approximately 360 $\mu E\ m^{-2}\ s^{-1}$ at plant level; 14 hour photoperiod with one hour of incandescent light before and after the photosynthetic period; day temperature $18^{o}C$ in all treatments; night temperature $5^{o}C$ (low, NT_5), $12^{o}C$ (medium, NT_{12}), and $20^{o}C$ (high, NT_{20}). The experiment ran for six months. Five sequential harvests were made for growth analysis using Waitakere seedlings. Beginning four months after treatments commenced, Puketi seedlings were used for measurement of responses of photosynthesis rate to irradiance and dark respiration rate to temperature. Chlorophyll concentrations were measured in new foliage from five replicates from each treatment and starch and glucose concentrations were measured in roots and shoots of seedlings from the NT_5 and NT_{12} treatments.

3.5.2 Results

a. The effect of different temperature regimes on the growth of small rimu seedlings.

For such slow growing plants 65 days was probably too short a period for the full effects of the various temperature regimes to become apparent. However, Puketi seedlings were only about 14 months old at the end of the experiment and Pureora plants only 7 months so the two month period of the experiment was a relatively large proportion of the plants' lives. Many of the small Pureora seedlings died during the experiment especially in the high treatment. This was probably because the peat pots dried out too rapidly in the controlled environment cabinet at high temperatures. However, surviving Pureora seedlings grew best in the high regime (Table 3.13b). The low treatment seedlings from both provenances turned brown after about five weeks, but although they had the lowest relative growth rates, they did not die (Table 3.13 a and b).

Puketi Provenance

In these larger seedlings highest R was found in the medium temperature regime. High treatment R was intermediate between this and low treatment R, but high treatment plants had the smallest dry weight and height increments of the three treatments (Table 3.13a). None of these differences were significant however, owing to the variable nature of the plants at the beginning of the experiment and their slow growth rates.

Leaf area ratio (F) of Puketi seedlings grown in the high temperature regime increased rapidly during the experiment (Fig. 3.18) and after 30 days was significantly higher than those of the other two treatments. Leaf production was therefore greatly increased by warm temperatures in these seedlings. In the medium treatment, on the other hand, F remained more or less constant throughout the experiment and in the low treatment there was a slight decrease in leaf area ratio.

TABLE 3.13 : MEAN GROWTH PARAMETERS OF 12 MONTH OLD PUKETI AND 5 MONTH OLD PUREORA RIMU SEEDLINGS GROWN FOR 65 DAYS IN THREE CONTROLLED TEMPERATURE REGIMES. 15h Photoperiod and 600 μE m^{-2} s^{-1} irradiance

a. Puketi (Initial mean dryweight 180.9 mg; mean height 118.5 mm)

Treatment Day°C/Night°C	n	R $g\ g^{-1}\ day^{-1} \times 10^{-2}$ $\pm$ 5% confidence intervals	Dry weight increment mg	Height increment mm	Root collar diameter mm	Diameter: height ratio	Root: shoot ratio
17/9	5	0.82 $\pm$ 0.34 a	184.3 a	7.40 a	1.72 a	0.014 a	0.47 a
22/14	5	1.04 $\pm$ 0.32 a	188.8 a	8.90 a	1.52 a	0.013 a	0.54 a
27/19	5	0.93 $\pm$ 0.32 a	141.6 a	5.20 a	1.56 a	0.012 a	0.53 a

b. Pureora (Initial mean dry weight 16.04 mg; mean height 36.3 mm)

17/9	5	1.52 $\pm$ 0.30 a	28.2 a	9.6 b	0.91 a	0.019 a	0.38 a
22/14	5	1.70 $\pm$ 0.34 a	33.7 a	12.0 b	0.89 a	0.018 a	0.32 a
27/19	5	1.73 $\pm$ 0.28 a	37.1 a	23.3 a	0.98 a	0.017 a	0.33 a

Unit leaf rate, E, of Puketi plants from the medium treatment was more or less constant throughout the experiment and consistently (though not significantly) higher than those of the other two treatments (Fig. 3.19). Unit leaf rate of the high treatment plants decreased somewhat throughout and was lowest of the three treatments by the end of the experiment. This was probably caused by the rapidly increasing proportion of new leaves which were not fully developed and therefore not capable of maximum rates of photosynthesis. Unit leaf rate of the low treatment plants increased very slightly throughout the experiment.

The larger, woody Puketi seedlings, therefore, grew best in the medium temperature regime in which they had the highest relative growth rate, unit leaf rate, and dry weight increment.

Pureora Provenance

Small, soft seedlings from an upland forest in the central North Island responded to growing temperature somewhat differently from larger woody Puketi seedlings from Northland. Relative growth rate, dry weight and height increment all increased with increasing growing temperature (Table 3.13 b), although in most cases the differences were not significant. Height increment was significantly increased in the high temperature regime, however, and root collar diameter was also highest in this treatment, but there was little difference in root collar diameter between the medium and low treatments. (Had diameter increments been measured the trends in diameter growth for both provenances may have been different.)

The root:shoot ratio of Pureora seedlings was highest in the low treatment while ratios in the medium and high treatments were very similar to each other (Table 3.13b).

In all treatments leaf area ratio (F) of small Pureora seedlings was increasing with time (Fig. 3.20) and (as in the Puketi provenance), plants in the high temperature regime were increasing their leaf area ratio at a faster rate than those in the medium and low treatments. Leaf area ratios of plants from the three treatments were all significantly different from each other after 38 days and that of the

Fig. 3.18
The progressive changes in Leaf Area Ratio, F, with time, of seedlings grown in three temperature regimes. Puketi.
+ —— + Low, 17°C/9°C; x ----- x Medium, 22°C/14°C;
Δ···· Δ High, 27°C/19°C.

Bars represent 5% confidence limits.

Fig. 3.19
The progressive changes in Unit Leaf Rate, E, with time, of seedlings grown in three temperature regimes. Puketi.
Symbols and lines as in Fig. 3.18.

Fig. 3.18 TEMPERATURE EXPERIMENT - PUKETI

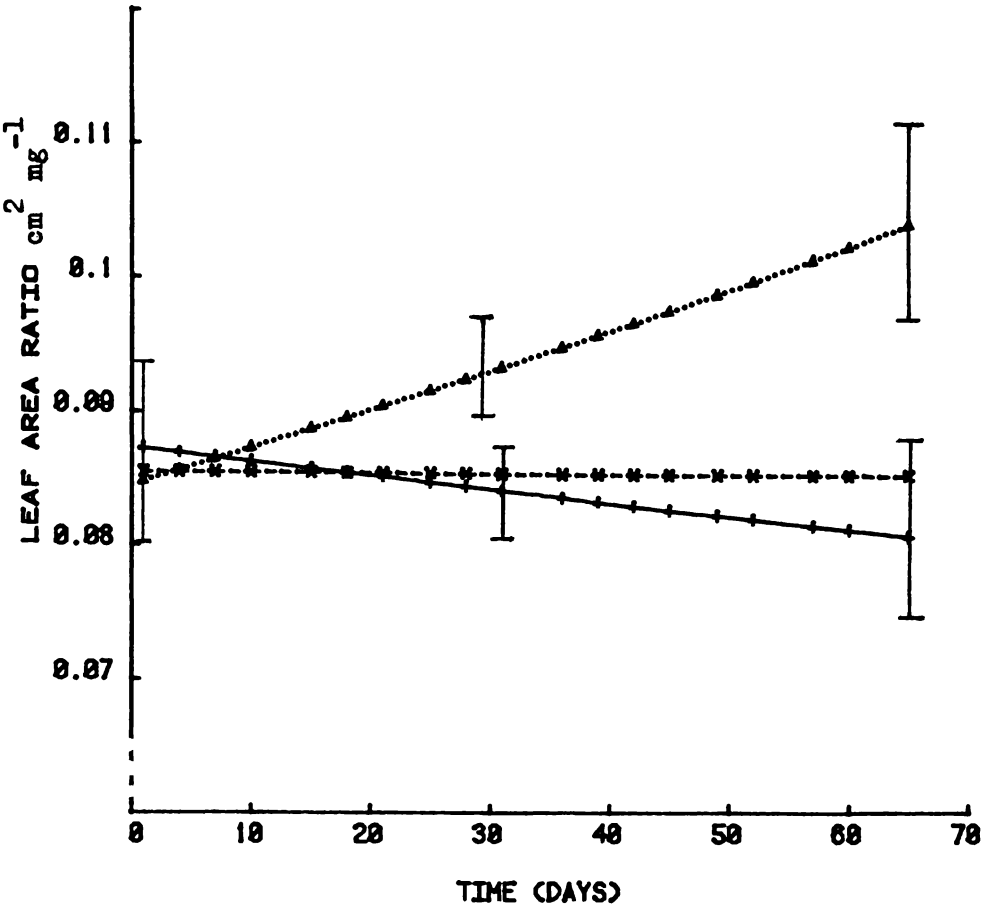


Fig. 3.19 TEMPERATURE EXPERIMENT - PUKETI

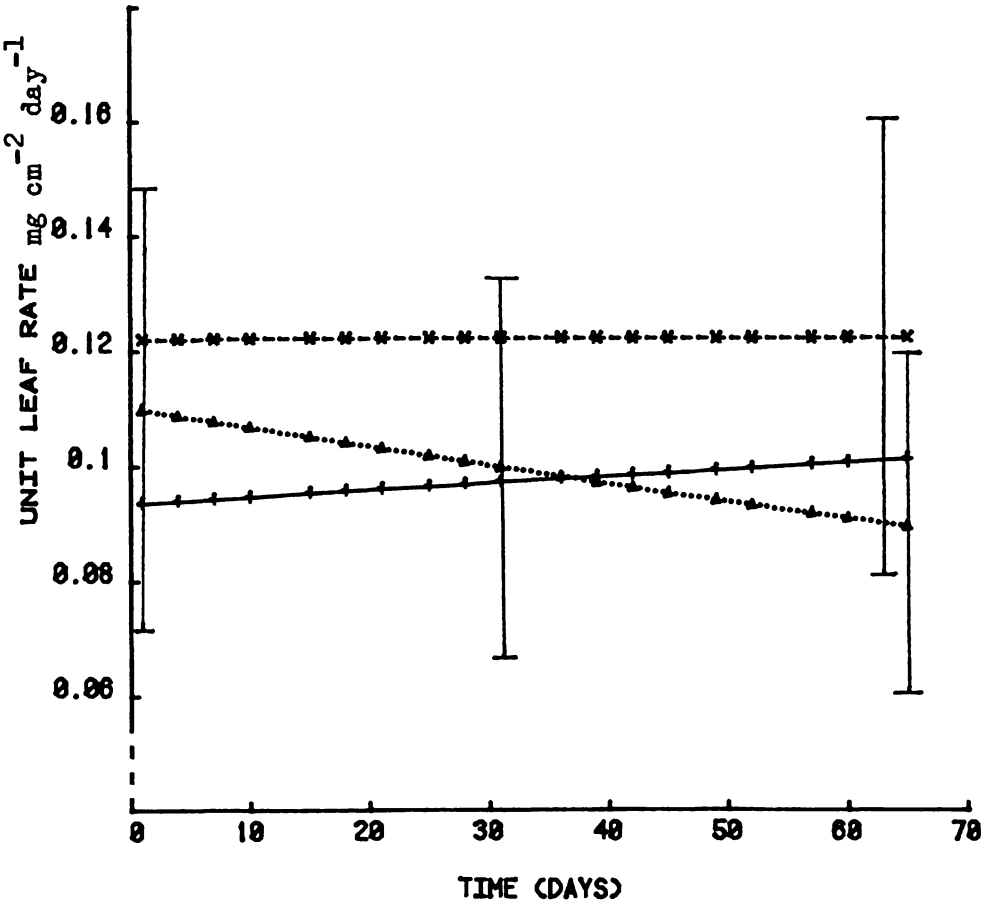


Fig. 3.20

The progressive changes in Leaf Area Ratio,F, with time, of seedlings grown in three temperature regimes. Pureora.

+ —— + Low, 17° C/9°C: x ---- x Medium, 22°C/14°C:

Δ ····· Δ High,27°C/19°C:

Bars represent 5% confidence limits.

Fig. 3.21

The progressive changes in Unit Leaf Rate,E, with time, of seedlings grown at three temperature regimes. Pureora.

Symbols and lines as in Fig. 3.20.

Fig. 3.20 TEMPERATURE EXPERIMENT - PUREORA

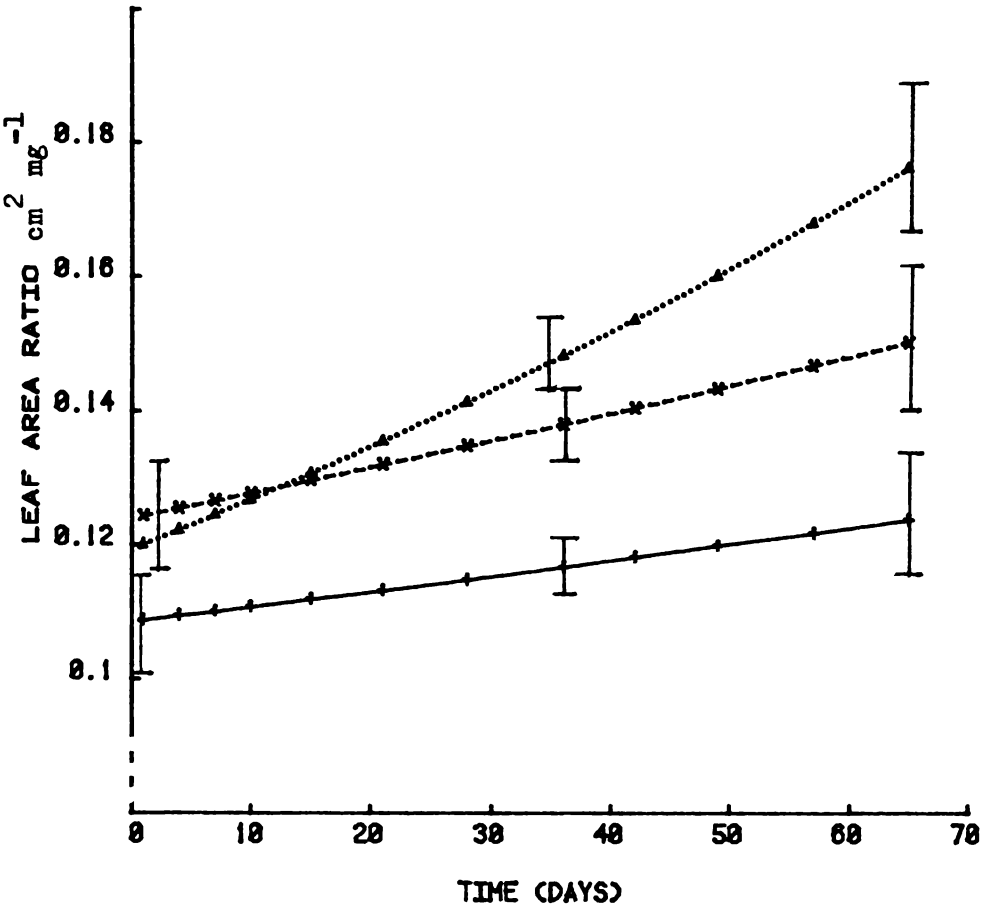
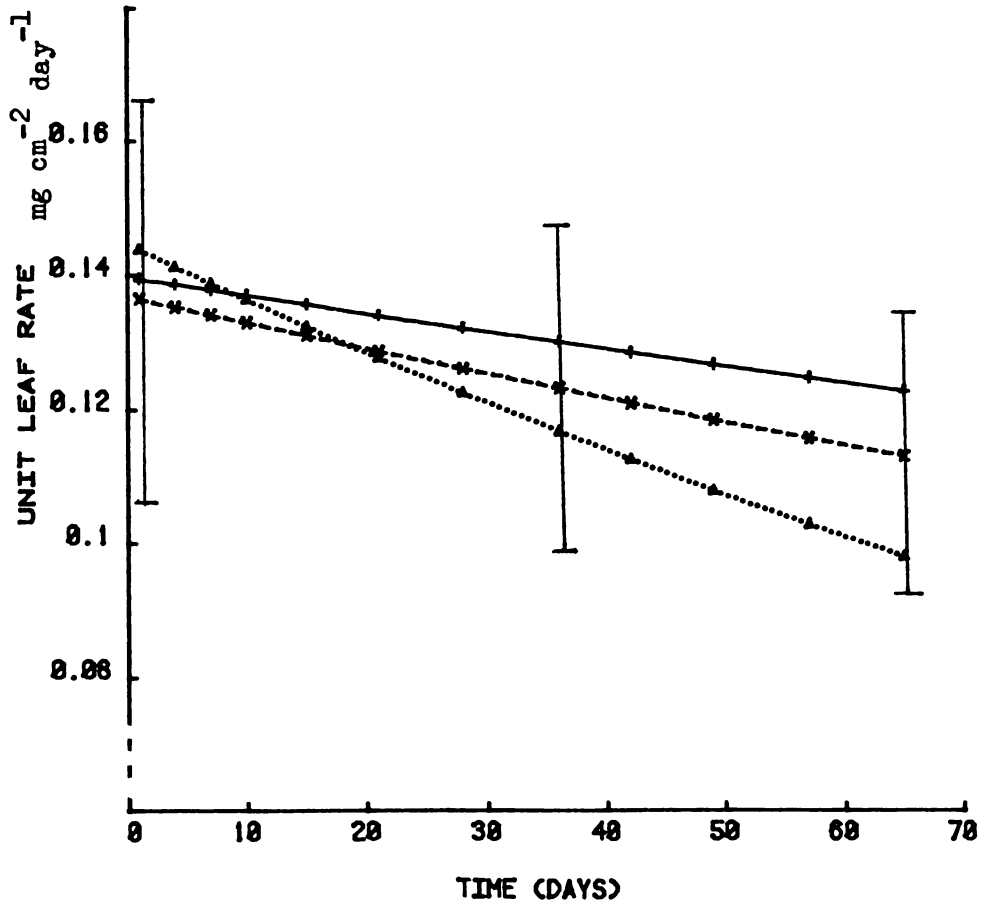


Fig. 3.21 TEMPERATURE EXPERIMENT - PUREORA



low treatment plants was at a consistently lower level throughout the experiment. Plants in the low temperature regime, therefore, were producing fewer new leaves than plants from the medium and high regimes. In both provenances high temperatures promoted the production of new leaves.

In Pureora seedlings unit leaf rates decreased with time in all treatments (Fig. 3.21) and the rate of decrease was related to the rate of increase in leaf area ratio (Fig. 3.20). Although the differences were not significant, by the end of the experiment the unit leaf rate of low treatment plants was highest, that of medium treatment plants intermediate, and that of high treatment plants lowest.

Small Pureora seedlings therefore grew best in the high temperature regime which they would seldom, if ever, experience in Pureora.

b. The effect of night temperature (Thermoperiod) on the growth, photosynthesis and dark respiration of rimu seedlings.

Chlorophyll analysis

A change in foliage colour after about 6 weeks was one of the most obvious results of the experiment (Fig. 3.22). $5^{o}C$ night temperature (NT_5) plants became distinctly brown while NT_{20} plants became dark green and NT_{12} plants were intermediate in colour: a slightly brownish green. In this respect Puketi provenance seedlings from further north (used for gas exchange measurements) were affected more than Waitakere seedlings (used for growth analysis). Several NT_5 Puketi plants eventually died (after five or six months) and certain branches of others died back, but no NT_5 Waitakere seedlings suffered any die back at all. There was no sign of any insect or fungal disease in the plants which died.

The chlorophyll a + b concentrations of Puketi seedlings from the three treatments were all significantly different from each other on both leaf area and fresh weight bases (Table 3.14) with dark green NT_{20} plants having the highest concentrations, and brown NT_5 plants the lowest concentrations. Chlorophyll a:b ratios were,

however, unaffected by treatment (Table 3.14) and remained more or less constant.

TABLE 3.14 : MEAN CHLOROPHYLL CONCENTRATIONS OF NEW FOLIAGE OF RIMU SEEDLINGS GROWN FOR SIX MONTHS AT THREE NIGHT TEMPERATURES IN CONTROLLED ENVIRONMENTS. Day temperature 18°C; Irradiance 360 $\mu E\ m^{-2}\ s^{-1}$. Puketi provenance.

Treatment	n	Chlorophyll a + b		Chlorophyll a:b
Night temperature °C		mg g^{-1} fresh weight	mg m^{-2} surface area	
5	5	0.32 c	36.2 c	3.7 a
12	5	0.38 b	43.8 b	3.7 a
20	5	0.50 a	57.1 a	3.5 a

Fig. 3.22

A typical pair of Puketi seedlings from each of the night temperature treatments.

Left to right: 20°, 12° and 5°C

Growth analysis

Waitakere provenance plants were used for growth analysis because insufficient Puketi plants were available. Destructive harvesting of five plants per treatment was performed on five occasions during the six month experiment. Relative growth rates and total dry weights of seedlings increased with increasing night temperature (Table 3.15) although differences were not significant owing to variation between replicates. Root:shoot ratios on the other hand did not show a consistent trend, but were highest in the medium night temperature plants.

TABLE 3.15 : RELATIVE GROWTH RATES (5 HARVESTS), MEAN DRY WEIGHTS AND ROOT:SHOOT RATIOS OF SEEDLINGS GROWN AT THREE NIGHT TEMPERATURES. Day temperature 18°C: Irradiance 360 $\mu E\ m^{-2}\ s^{-1}$

Treatment Night temp °C	R mg mg^{-1} day^{-1} x 10^{-2}	Dry weight g	Root:shoot ratio
5	0.78 ± 0.32 a	10.24 a	0.42 a
12	0.98 ± 0.34 a	12.36 a	0.48 a
20	1.08 ± 0.28 a	16.16 a	0.40 a

Leaf dry weights rather than leaf areas were measured in the two year old woody seedlings used in this experiment. As is usually the case in woody plants leaf weight ratios (F_w) in all treatments decreased with time (Fig. 3.23). Leaf weight ratios of NT_5 plants were decreasing more rapidly than F_w of NT_{12} and NT_{20} plants and by the end of the experiment the highest F_w was in the NT_{20} plants and the lowest in the NT_5 plants. Leaf production relative to total dry weight increase, therefore, was highest in plants grown in warm night temperatures and lowest in plants grown in cold night temperatures. Unit leaf rate (E) was increasing in all three treatments, but throughout the experiment highest E was found in NT_{20} plants and lowest in NT_5 plants (Fig. 3.24). High night

Fig. 3.23

The progressive changes in Leaf Weight Ratio, Fw, with time, of seedlings grown at three night temperatures.

+ ———— + Low, 5°C night temperature;

x - - - - -x Medium, 12°C night temperature;

Δ.....Δ High, 20°C night temperature.

Bars represent 5% confidence limits.

Fig. 3.24

The progressive changes in Unit Leaf Rate, E, with time, of seedlings grown at three night temperatures.

Symbols and lines as in Fig. 3.23.

Fig. 3.23 NIGHT TEMPERATURE EXPERIMENT

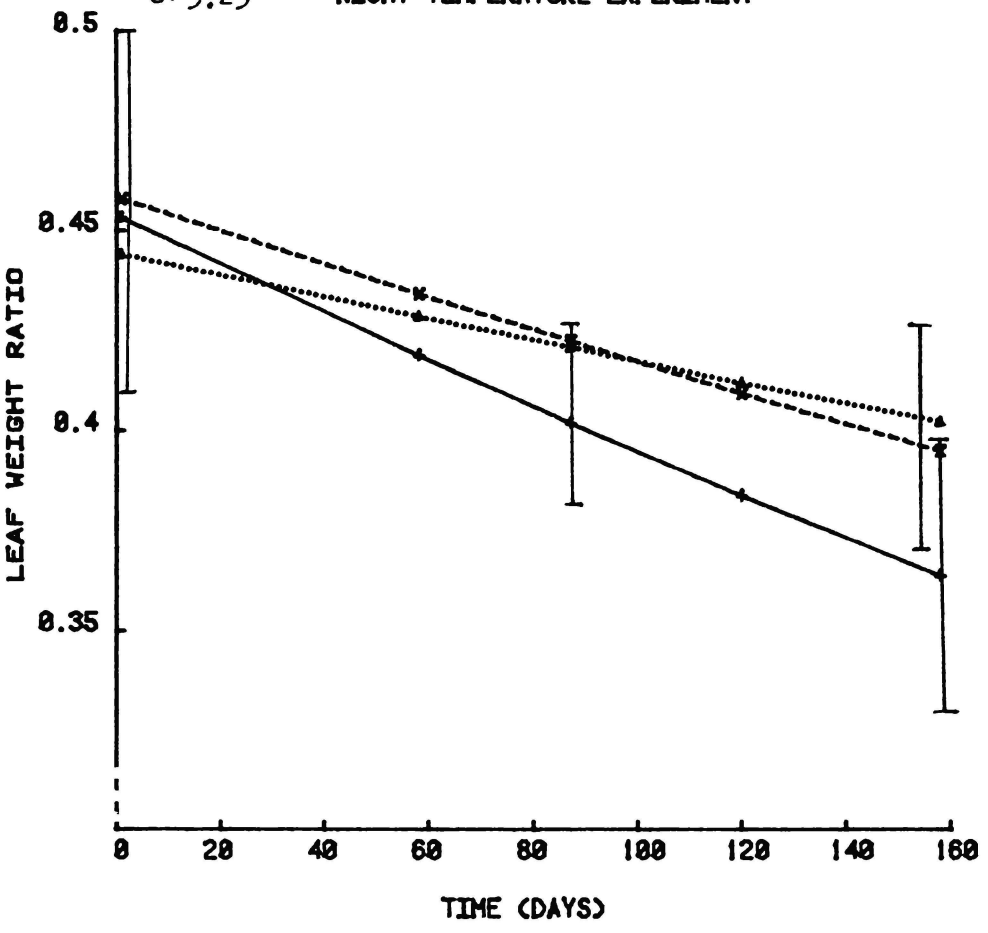
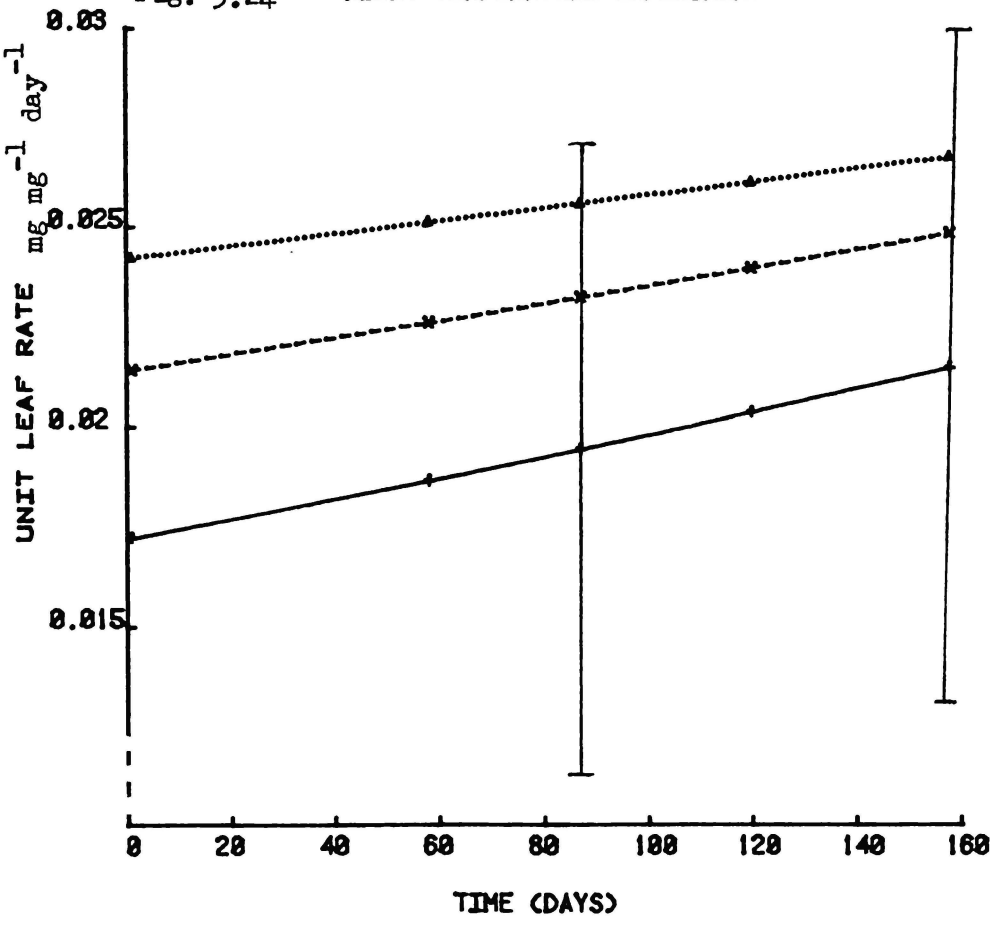


Fig. 3.24 NIGHT TEMPERATURE EXPERIMENT



temperature, therefore, caused increased growth in these two year old Waitakere seedlings. NT_{20} plants had higher relative growth rates, total dry weights, leaf weight ratios and unit leaf rates at the end of the experiment and chlorophyll concentrations were also higher in Puketi provenance NT_{20} plants.

Gas exchange measurements

When plants had been growing in the treatments for four months gas exchange measurements were commenced. Five replicate Puketi seedlings from each treatment were used to examine the response of photosynthesis rate to decreasing irradiance at 20°C. Two replicates from the low night temperature treatment (NT_5) were found not to be absorbing CO_2 at 20°C even at a saturating irradiance of 1000 $\mu E\ m^{-2}\ s^{-1}$. They were alive, however, and their rates of dark respiration at 20°C were similar to rates found in the other seedlings which were fixing CO_2 at 20°C. The two non-photosynthesising seedlings were entirely brown in colour, whereas the other three replicates from the NT_5 treatment had slightly green foliage. These three replicates had a mean light saturated photosynthesis rate which was only slightly lower than that of seedlings from the medium night temperature treatment (NT_{12}) (Table 3.16). The curves of response of photosynthesis to irradiance for each replicate from the three treatments are shown in Fig. 3.25 a-c. For most replicates light saturation occurred a little below 400 $\mu E\ m^{-2}\ s^{-1}$ (growing irradiance was approximately 360 $\mu E\ m^{-2}\ s^{-1}$) and light saturated rates of photosynthesis were between 0.5 and 1.5 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$. There was more variation in seedlings from the NT_{12} treatment (Fig. 3.25 b), however, where light saturated photosynthesis rate of replicate 5 was less than 0.5 and that of replicate 1 was greater than 1.5 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$. Although there was no significant difference between light saturated photosynthesis rates of seedlings from the three treatments, the trend was towards increased rate with increasing night temperature (Table 3.16).

Lowest mean dark respiration rate at 20°C was found in plants from the 20°C night temperature treatment (Table 3.16). Highest mean dark respiration rate at 20°C, however, was found in plants from the medium treatment (NT_{12}) rather than from the low night temperature treatment which might have been expected.

TABLE 3.16 : THE MEAN QUANTUM REQUIREMENTS, PHOTOSYNTHESIS AND RESPIRATION RATES AND LIGHT COMPENSATION POINTS FOR RIMU SEEDLINGS GROWN AT THREE NIGHT TEMPERATURES. Day temperature 18°C; Irradiance 360 uE $m^{-2}s^{-1}$

Treatment	n	Quantum Requirement	Photosynthesis Rate		Dark Respiration Rate		Light Compensation Point
Night Temp °C		E mol^{-1}	μ mol $m^{-2}s^{-1}$	g $m^{-2}h^{-1}$	μ mol $m^{-2}s^{-1}$	g $m^{-2}h^{-1}$	μE $m^{-2}s^{-1}$
5	5	70.5 a	1.0 a	0.16 a	0.39 a	0.06 a	34.4 a
12	5	53.3 a	1.1 a	0.18 a	0.44 a	0.07 a	30.8 ab
20	3	41.6 a	1.3 a	0.19 a	0.26 a	0.04 a	12.8 b

Fig. 3.25 a. - c.

The response of net photosynthesis rate to irradiance of seedlings grown at three night temperatures. Measurement temperature 20°C.

a. 5°C

b. 12°C

c. 20°C

The symbols represent the measured data points for the replicate seedlings and the lines are the fitted rectangular hyperbolae, identified by replicate number.

Replicate number.	Symbol
1.	•
2.	+
3.	x
4.	Δ
5.	□

Fig. 3.25 a. 5°C

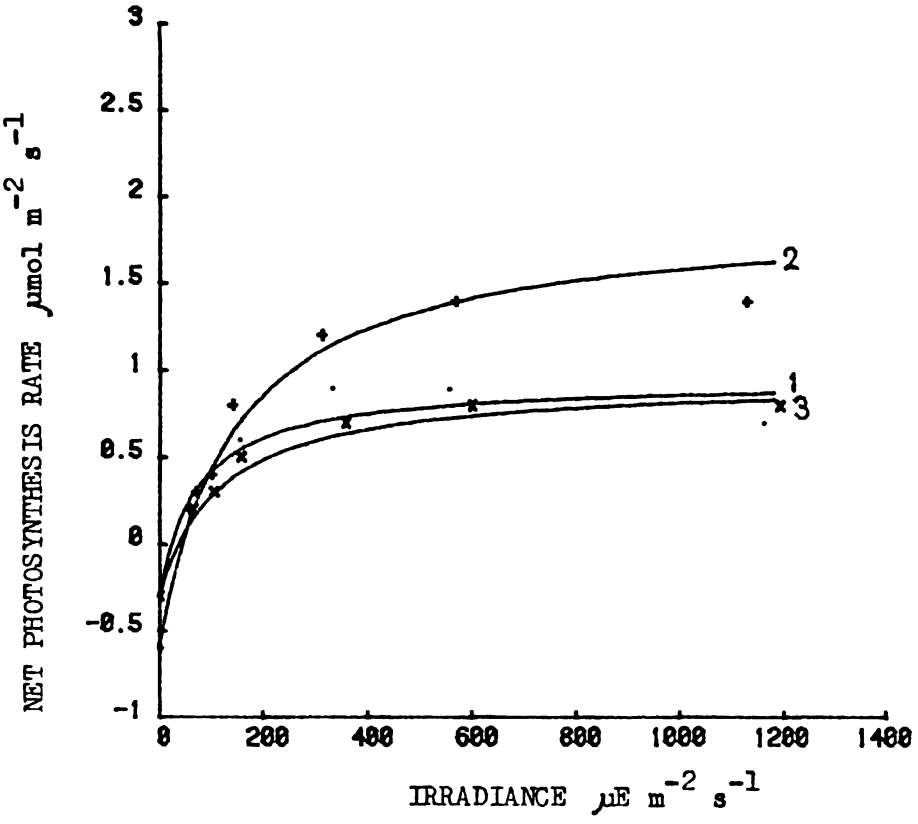


Fig. 3.25 b. 12°C

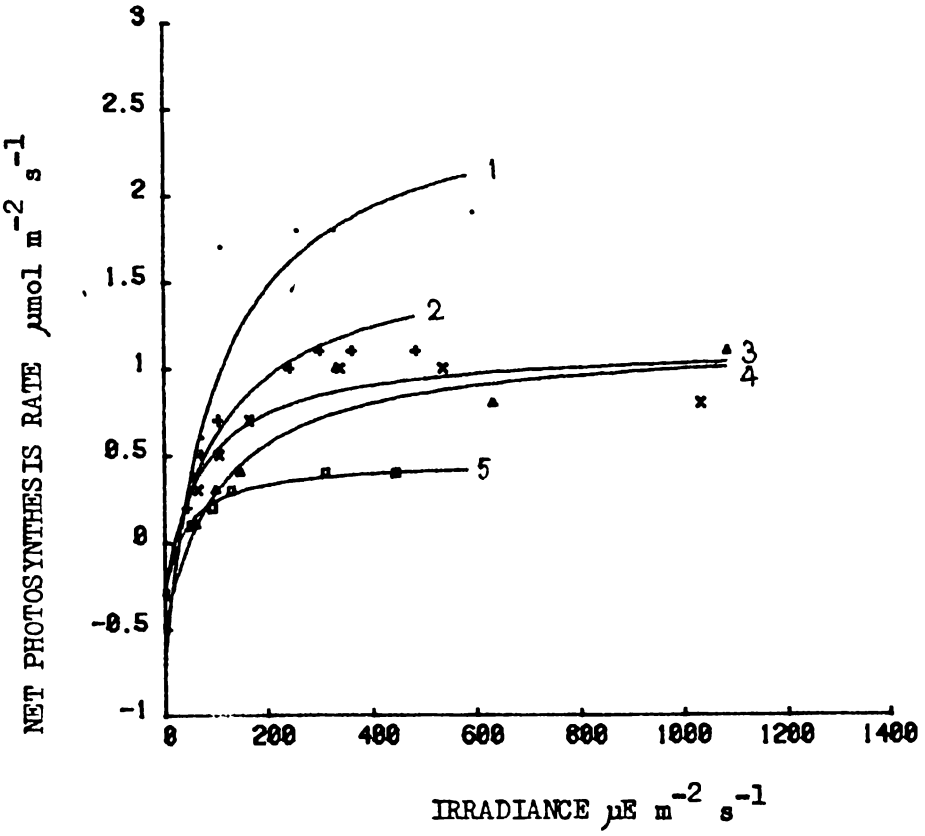
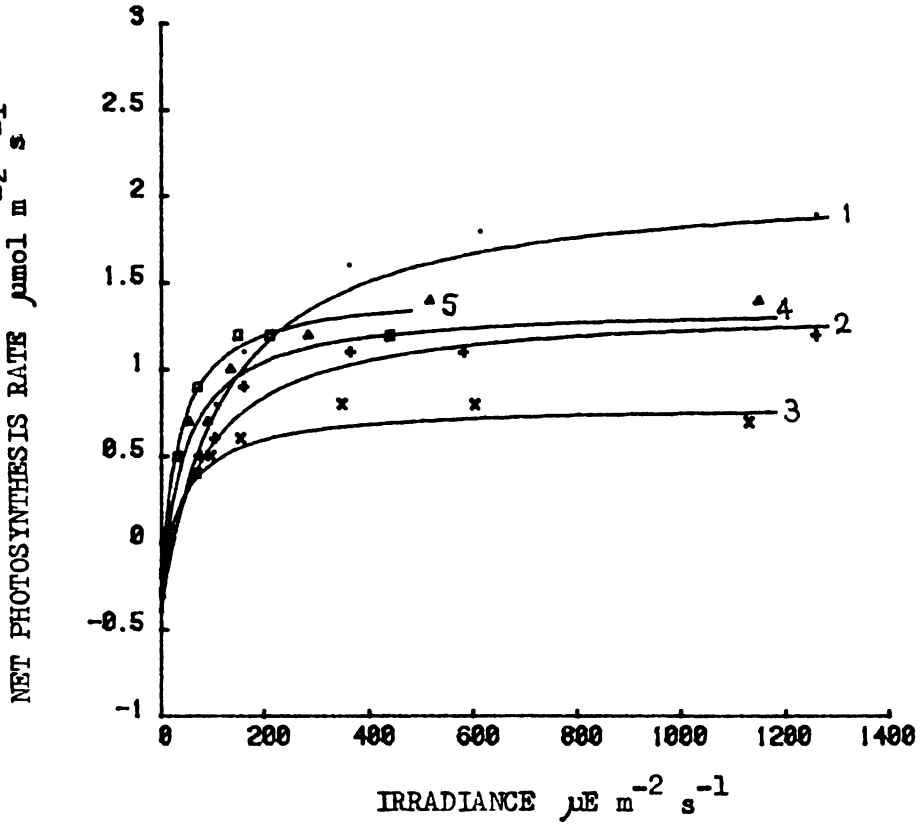


Fig. 3.25 c. 20°C


NET PHOTOSYNTHESIS RATE μmol m^{-2} s^{-1}
3
2.5
2
1.5
1
0.5
0
-0.5
-1
0
200
400
600
800
1000
1200
1400
IRRADIANCE μE m^{-2} s^{-1}
1
2
3
4
5

Relationships between $\frac{1}{P_n + R_d}$ and $\frac{1}{I}$

are illustrated in Fig. 3.26 a-c. Even between replicates within each treatment there is variation amongst these linear regression lines in both slope (representing the quantum requirement) and intercept (representing the total resistance to CO_2 at saturating irradiance). However, mean quantum requirements, calculated from slopes of the regressions, show decreasing quantum requirement (increasing efficiency) with increasing night temperature, although differences are not significant (Table 3.16).

Light compensation points were calculated from rectangular hyperbolae (equation 3.5, section 3.2.5.2) and mean light compensation point of NT_{20} plants was significantly lower than that of NT_5 plants while that of NT_{12} plants was intermediate (Table 3.16). In summary, plants grown at 18°C days and 20°C nights, had slightly higher light saturated photosynthesis rates, lower dark respiration rates at 20°C, lower quantum requirements when light was limiting photosynthesis and significantly lower light compensation points than plants grown at lower night temperatures (12° and 5°C).

The boundary layer and stomatal resistances were subtracted from total resistances (calculated from the intercepts, Fig. 3.26) and comparisons made of stomatal and residual resistances between treatments (Table 3.17). Residual resistances were all very high and increased with decreasing night temperature. Stomatal resistances, on the other hand, were lower and did not follow any obvious trend. The ratios $r_{r_{CO_2}} : r_{s_{H_2O}}$ indicate the relative importance of each of these resistances in limiting the light saturated rate of photosynthesis.

Fig. 3.26 a - c.

The relationship between $\frac{1}{P_n + R_d}$ and $\frac{1}{I}$ for seedlings grown at three night temperatures. The symbols represent the calculated data points for the replicate seedlings and the lines are the linear regressions identified by replicate number.

(Replicate symbols as in Fig.3.25).

Fig. 3.26 a. 5°C.

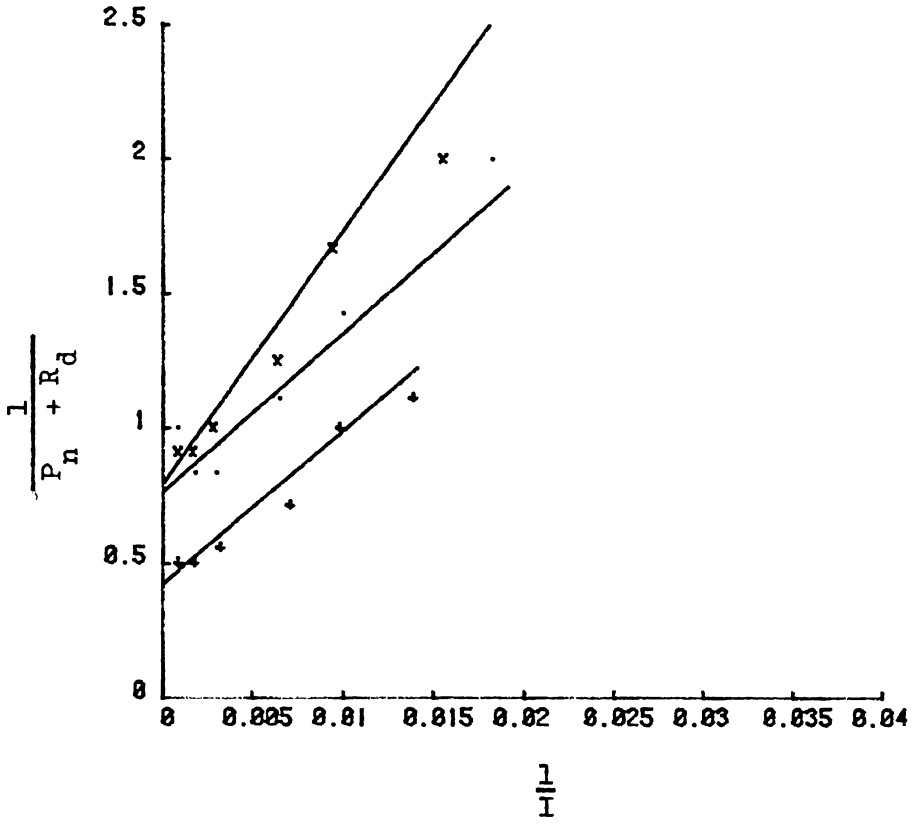


Fig. 3.26 b. 12°C

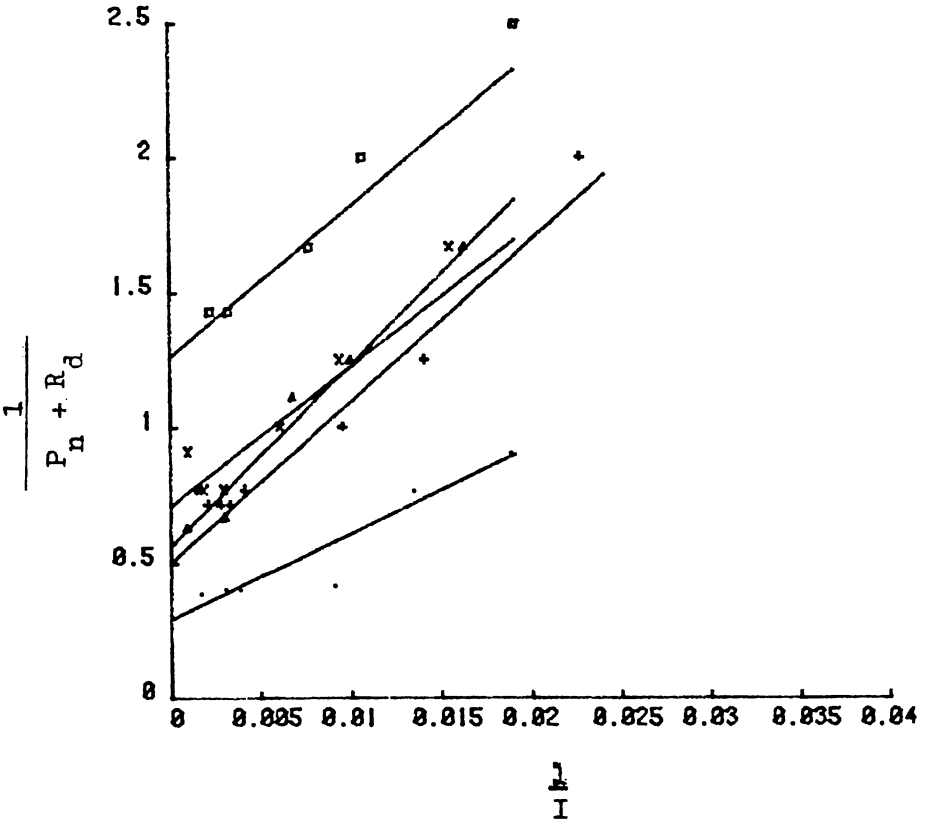
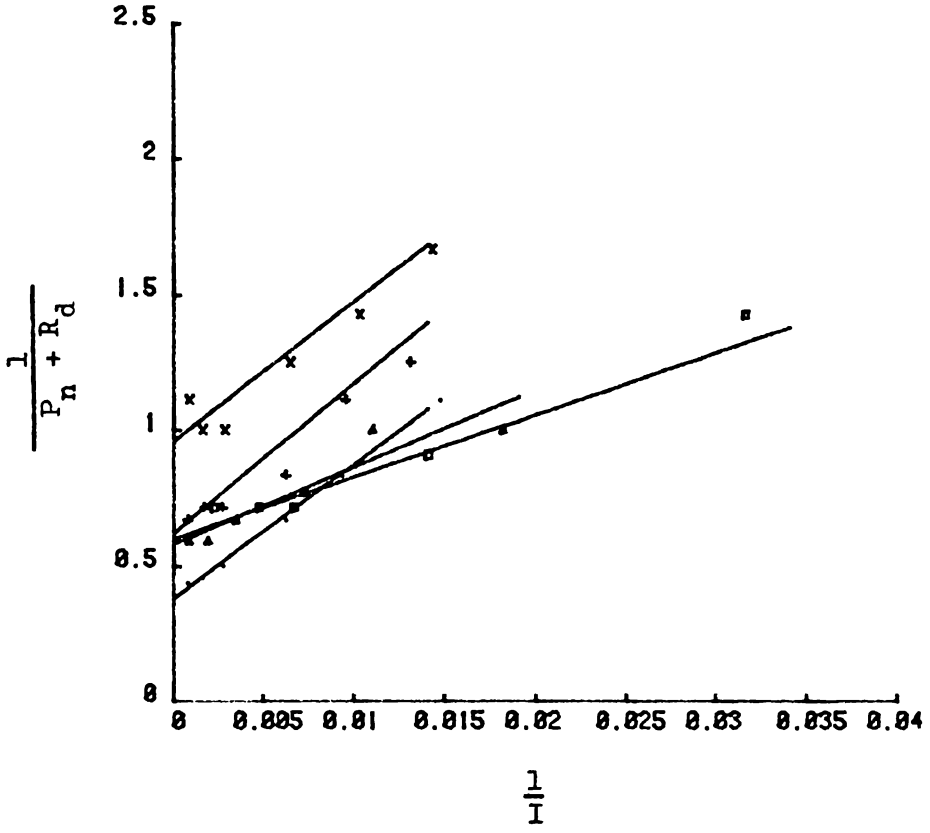


Fig. 3.26 c. 20°C


2.5
2
1.5
1
0.5
0
0
0.005
0.01
0.015
0.02
0.025
0.03
0.035
0.04
$\frac{1}{P_n + R_d}$
$\frac{1}{I}$

All ratios were greater than unity, but the lowest was found in plants from the NT_{20} treatment where $r_{s_{H_2O}}$ was relatively large and $r_{r_{CO_2}}$ relatively small compared with the other two treatments (Table 3.17). There were no significant differences between any of the resistances or ratios owing to the large amount of variance and low number of replicates.

TABLE 3.17 : MEAN RESISTANCES TO H_2O AND CO_2 OF RIMU SEEDLINGS GROWN AT THREE NIGHT TEMPERATURES. Resistances are calculated at light saturated rates of photosynthesis. Day temperature 18°C; Irradiance 360 uE m^{-2} s^{-1}

Treatment Night Temp. °C	n	$r_{s_{H_2O}}$ s cm^{-1}	$r_{r_{CO_2}}$ s cm^{-1}	$r_{r_{CO_2}} : r_{s_{H_2O}}$
5	2	12.35 a	142.86 a	10.93 a
12	5	7.52 a	100.00 a	13.42 a
20	4	21.28 a	58.82 a	2.75 a

The response of dark respiration rate to increasing temperature was examined in three Puketi seedlings from each treatment (Fig. 3.27 a-c). Dark respiration rate increases rapidly with temperature between 10° and 35°C and there were no marked differences between treatments. Q_{10} values for dark respiration rate between 20° and 30° for plants from the 5°, 12° and 20°C night treatments were 2.0, 1.9 and 1.7 respectively (not significantly different). Q_{10} ratio, therefore, decreased slightly with increasing night temperature. This can also be seen in Fig. 3.27 a-c by the slight decrease in the slope of the curves with increasing night temperature.

Carbohydrate analysis

As has been mentioned, after about five months at 5°C night temperature several Puketi seedlings died, certain shoots of several other plants died back, and two of the five replicates used to examine gas exchange were not absorbing CO_2 at high irradiances, although their dark respiration rates were similar to other seedlings. Therefore, it was believed that continued low minimum

Fig.3.27 a. - c.
The response of dark respiration rate to temperature of seedlings grown at three night temperatures.
The symbols represent the normalised data points for the replicate seedlings. The curves were fitted by eye.

Fig. 3.27 a. 5°C

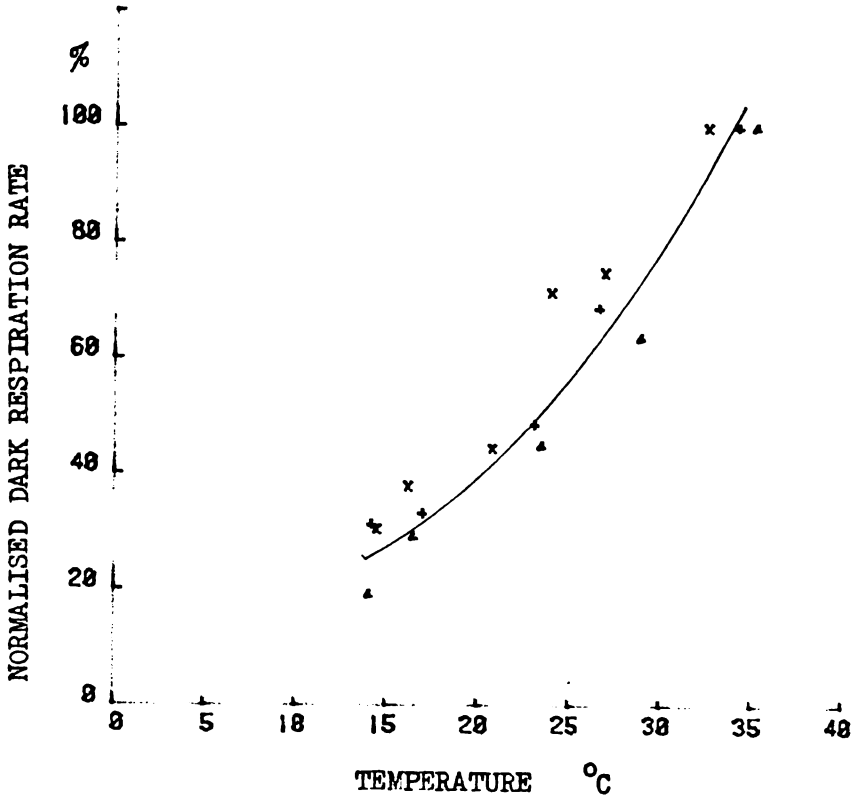


Fig. 3.27 b. 12°C

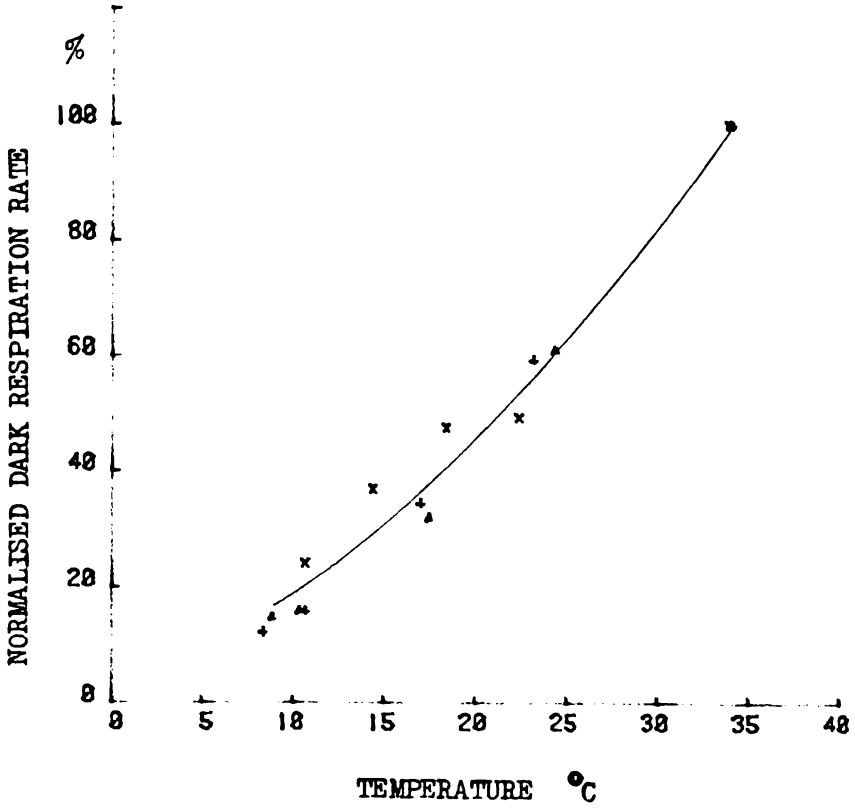


Fig. 3.27 c. 20°C

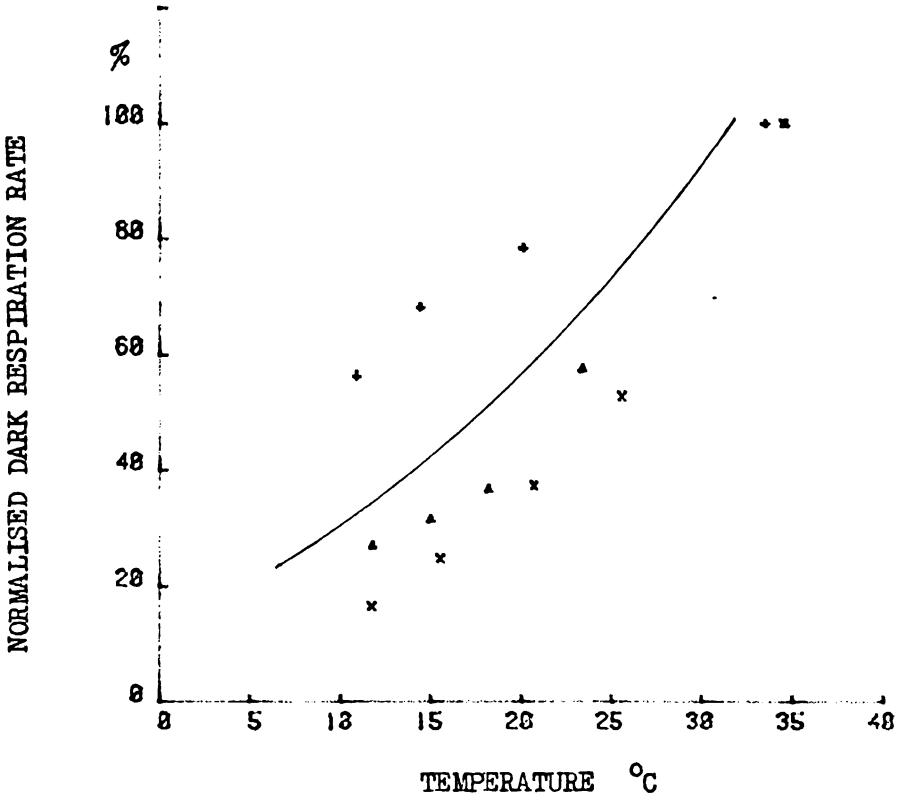

%
100
80
60
40
20
0
NORMALISED DARK RESPIRATION RATE
0
5
10
15
20
25
30
35
40
TEMPERATURE °C

TABLE 3.18 : CARBOHYDRATE CONCENTRATIONS OF RIMU SEEDLINGS GROWN FOR SIX MONTHS AT 5° and 12°C NIGHT TEMPERATURE. Day temperature 18°C; Irradiance 360 $\mu E\ m^{-2}\ s^{-1}$

Treatment Night Temp. °C	Starch concentration mg g^{-1} dry weight		Glucose concentration mg g^{-1} dry weight	
	Shoots	Roots	Shoots	Roots
5	35 b	16 b	16 a	12 a
12	47 a	28 a	16 a	9 a

temperature might be limiting photosynthesis in certain of the Puketi seedlings possibly because of disruption of the chloroplasts. Residual resistance to CO_2 diffusion transfer in the brown NT_5 plants was very high in the three which were still fixing CO_2. To examine whether reduced photosynthesis was causing carbohydrate starvation, starch and glucose concentrations of shoots and roots of brown NT_5 seedlings were measured and compared with those of greener seedlings from the 12°C night temperature treatment. Material analysed was from living plants from the Puketi provenance. Although there were no differences in glucose concentrations, Table 3.18 shows significantly more starch in roots and shoots of green NT_{12}, than in those of brown NT_5 plants, indicating that more carbohydrates were available for conversion into storage products in the green seedlings.

3.5.3 Discussion

Rimu grows throughout New Zealand in lowland forests with relatively mild, equable, maritime climates. In both experiments in this section seedlings grown at higher temperatures at least up to a certain optimal level showed increased growth rates and were greener in colour than seedlings grown at lower temperatures. Green seedlings from the warm night temperature (part b) with a mean daily temperature of 18.8°C had significantly more chlorophyll than seedlings grown at cooler temperatures (Table 3.14). They also had somewhat lower quantum requirements, higher photosynthesis rates, lower dark respiration rates and significantly lower light compensation points than less green seedlings grown in cooler

nights. Similarly, the dry weights and relative growth rates of seedlings grown at warm nights were higher (Table 3.15). Woody Puketi seedlings grew best in the medium temperature regime (part a) with a mean daily temperature of 19°C in which they had the highest relative growth rate, dry weight and height increment. Small soft Pureora seedlings on the other hand, grew best at higher mean daily temperatures (24°C) in the 27°C/19°C regime and in these plants relative growth rate, dry weight and height increments all increased with increasing temperature. These differences in the responses of the two groups of seedlings are believed to be related to their size difference and to be caused by the ontogenetic stage of development rather than by provenance. This illustrates the fact that the optimal temperature for growth may change with the age of a plant.

As tree seedlings become woody their relative growth rate decreases with increasing dry weight because of the increasing proportion of supportive tissue relative to photosynthetic tissue. For this reason the relative growth rates of the larger Puketi seedlings were much smaller than those of the soft Pureora seedlings and consequently dry weights of Puketi plants only approximately doubled in 65 days, whereas dry weights of Pureora plants approximately trebled. Similarly heights of Puketi plants only increased by 6% or 7%, whereas heights of Pureora plants increased by between 28% (low temperature) and 64% (high temperature) (Table 3.13 a and b). (The different potting mixes and pots may also have influenced these results.)

In both the small and larger seedlings, however, leaf production was increased in the high temperature regime (Figs. 3.18 and 3.20). Increased relative growth rate at higher temperatures in the small Pureora seedlings was related to high and increasing leaf area ratio (Table 3.13 b and Fig. 3.20) even though this was related to low unit leaf rate (Fig. 3.21). While the production of new leaves increases the leaf area ratio of a plant, it tends to decrease the unit leaf rate because developing leaves have higher respiration rates and therefore lower net photosynthesis rates than fully developed leaves and so increasing leaf area ratios are often associated with decreasing unit leaf rates.

On the other hand, in the larger Puketi plants grown at medium temperatures high relative growth rate was related to high unit leaf rate (Table 3.13 a and Fig. 3.19). The high relative growth rate of woody seedlings grown at high night temperature was also related to high unit leaf rate and these plants had a less rapidly decreasing leaf weight ratio compared with seedlings grown in lower night temperatures (Table 3.15 and Figs. 3.23, 2.34). Warm temperatures therefore increase leaf production in rimu seedlings and may also increase unit leaf rate. Leaf production was also increased by higher temperatures in Douglas fir seedlings (Sorensen and Ferrell, 1973).

In the larger Puketi seedlings grown in the high temperature regime leaf area ratio was increasing very rapidly (Fig. 3.18). Possibly high dark respiration rates offset the growth potential caused by this increased leafiness. If the respiration rate had acclimated to the high temperatures after a longer period of time an increase in relative growth rate might have resulted.

Rimu seedlings grown in regimes with low night temperatures ($9^{o}C$ and $5^{o}C$) turned brown after five or six weeks. Rimu seedlings also become brown as temperatures fall with the approach of winter. Low minimum rather than low mean daily temperature appears to cause browning as the mean daily temperature in the low night regime was $12.6^{o}C$ and that in the $17^{o}C/9^{o}C$ regime was $14^{o}C$. It is probable that anthocyanins are involved in the brown pigmentation, but their function is not known. However, the browning is accompanied by the breakdown of chlorophyll (Table 3.14 and Fig. 3.22). Even rimu seedlings grown at $12^{o}C$ night temperature were browner and had significantly less chlorophyll than those grown at $20^{o}C$ night temperature and the heat sum rather than thermoperiod seems to be important for chlorophyll production and breakdown.

Winter chlorosis is a common phenomenon in conifers and many assume a yellow-green colour resembling nitrogen deficiency, but caused by a disruption of the photosynthetic apparatus and a breakdown of chloroplasts. However, this usually occurs following frost (Treshow, 1970; Kramer and Kozlowski, 1979), whereas in rimu browning and chlorophyll loss occurs in the absence of frost. In loblolly and

white pine (Pinus strobus L.) the concentration of chlorophyll a + b shows a seasonal trend with low levels in winter but, as occurred also in the experiment with rimu, the chlorophyll a:b ratio remained constant throughout the year (McGregor and Kramer, 1963). The disorganisation of chloroplasts and breakdown of chlorophyll which occurs in cold winters is often the cause of a decline in photosynthesis in conifers (Kramer and Kozlowski, 1979). In loblolly and white pine seedlings McGregor and Kramer (1963) also found a winter increase in the total resistance to CO_2 diffusion, although it was not known whether the stomatal or the residual resistance, or both, were responsible for the increase. In rimu seedlings grown at $5^{o}C$ night temperature the residual resistance to CO_2 was very high (Table 3.16) and was the predominant resistance limiting light saturated rates of photosynthesis (ratio $r_{r_{CO_2}} : r_{s_{H_2O}} = 10.9$). The increased residual resistance was related to slightly reduced light saturated rates of photosynthesis in these rimus (Table 3.15). Continued exposure to low night temperatures may have caused a disorganisation of chloroplasts as well as a breakdown of chlorophyll in some of the rimu seedlings, which might have been the reason why two of the Puketi plants were not fixing CO_2 at saturating irradiances at $20^{o}C$. Genetic differences between replicates may have caused more rapid chloroplast disorganisation in certain plants. The high residual resistance of the three remaining replicates from the $5^{o}C$ night temperture regime was possibly caused by partial breakdown of chloroplasts and the higher quantum requirement and light compensation point in these plants may have been related to their low chlorophyll concentrations (Tables 3.16 and 3.14).

It is possible that certain Puketi seedlings died and some branches of other seedlings died back because they were starved of carbohydrates. As the residual resistance to CO_2 increased, photosynthesis may have ceased and respiration continued until stored carbohydrates were unavailable. The rimus grown at $5^{o}C$ night temperatures which were still alive had significantly less starch in their roots and shoots than seedlings grown at $12^{o}C$ nights, leading to the conclusion that low night temperature resulted in less carbohydrates being available for conversion into starch.

The dark respiration rate of plants grown at low temperatures is often higher at any given temperature than the respiration rate of plants grown at higher temperatures (Sorensen and Ferrell, 1973). Likewise, the Q_{10} for respiration rate of plants grown at low temperatures is usually higher than that of plants grown at higher temperatures. This was the case in rimu (Table 3.16) where dark respiration rates at 20°C of seedlings grown at 5°C and 12°C night temperatures were higher than the rate of seedlings grown at 20°C night temperature. Similarly the Q_{10} for respiration rate was higher for plants grown at lower night temperatures.

It is well known that different provenances often have different cardinal temperatures for growth (e.g., Spurr and Barnes, 1973) and there appeared to be a slight provenance difference in the response to low night temperature between the more northern Puketi seedlings and those from Waitakere. None of the Waitakere seedlings died or had any branches die back, although they did turn brown and grew less well in the cold night treatment.

From these two experiments it is concluded that rimu seedlings become brown in low minimum temperatures and their growth rates are reduced. Continued exposure to low temperature may eventually cause the death of rimu seedlings possibly due to carbohydrate starvation. Nevertheless, it is apparent from the distribution of rimu in New Zealand that the seedlings can establish in a relatively wide range of climates and seedlings were shown to be able to survive and grow for two months in a 10°C range of day/night regimes between 17°C/9°C and 27°C/19° (Table 3.13).

It is believed that growth rate in rimu is more dependent on the heat sum (hours x temperature) than the thermoperiod (day/night temperature differential). In the thermoperiod experiment rimu seedlings from Puketi forest in Northland and Waitakere Ranges, Auckland, grew best at warm day and night temperatures (18°C day/20°C night) with a mean daily temperature of 18.8°C (heat sum 452 degree hours). The mean daily temperature in the northern parts of New Zealand where these provenances originated ranges from approximately 10°C in winter to 17.5°C in summer (Coulter, 1975).

The mean daily temperatures of the regimes in the earlier experiment (part a) were 14°C, 19°C and 24°C and Puketi seedlings grew best in the medium treatment. Small soft seedlings from Pureora (where the mean daily temperature in summer is only about 15°C) grew best in the warm regime, but this difference in response to growing temperature is believed to be ontogenetic and not caused by provenance.

If the assumption is correct that heat sum is more important in promoting growth in rimu than day-night temperature differential and there are no provenance differences in this respect, seedlings might be expected to have higher relative growth rates in the warmer parts of New Zealand.

The growth of certain other conifers is known to be affected by the total heat sum in 24 hours irrespective of whether days or nights are warmer. Examples include eastern hemlock (Tsuga canadensis), Jeffrey pine (Pinus jeffreyi A.Murray) and Calabrian pine (P. halepensis var brutia (Tenore) Elwes and Henry) (Spurr and Barnes, 1973). However, a temperature alternation between day and night often promotes the production of new tissue and shoot growth in trees (Larcher, 1980; Spurr and Barnes, 1973). Low night temperature may increase root growth and reduce respiration rate, which, in turn, reduces carbohydrate loss (Sutcliffe, 1977). The day-night temperature requirements for optimal growth of a particular plant are often related to the environmental conditions under which the species or population has evolved. Plants from continental regions, where there are large day-night temperature differences, usually develop best when nights are 10-15°C lower than days, e.g., loblolly pine and Douglas fir seedlings and red fir (Abies magnifica A. Muir). In the latter example a 13°C thermoperiod (days warmer than nights) was more important to height growth than the actual temperatures or heat sum (Spurr and Barnes, 1973). In some conifers night temperature is more important than day temperature in determining growth. For example, Picea engelmannii (Parry) Engelm., a timberline species, grew best in cool days with relatively warm nights (Spurr and Barnes, 1973), and Pinus sabiniana Dougl., a native of California grew better in 17°C nights than in either 7° or 26°C nights regardless of

day temperature whereas Pinus radiata, native of Monterey, California, grew best in low night temperatures (5°C) regardless of day temperature between 17°C and 29°C (Hellmers and Rook, 1973). In other conifers, by comparison, day temperature is more important than night temperature in determining growth (e.g., Sequoia sempervirens D.Don., Endlicher) and there are also species which grow best at constant temperature (e.g., young trees of Picea sp.) (Spurr and Barnes, 1973). A few unusual plants have been shown by experiment to grow best when nights are warmer than days (e.g., Pinus ponderosa Dougl.) (Larcher, 1980). It is therefore difficult to predict how a certain species will respond to changes in day temperature or night temperature or thermoperiod and even within one species, provenances from different regions may have different optimal growing temperatures which are related to the climates in their regions of origin.

Although optimal temperature for growth often varies with the age of the plant as well as the time of year and previous plant history, and therefore comparisons should be made with caution, it is interesting to note results of earlier work on the effect of temperature on the growth of indigenous conifer seedlings. In kauri the optimal temperature for seed germination and initial growth of seedlings (the vital stage of the life cycle) was shown to be 25°C (Barton, 1978) and in tanekaha seedlings growth was optimal at about 26.5°C (Pook, 1960). Small rimu seedlings were able to increase their growth rate up to slightly higher daytime temperatures (27°C) whereas larger, woody seedlings had somewhat lower optimal temperatures for growth. In kauri seedlings root:shoot ratios increased with decreasing growing temperature (Bieleski, 1959c) and in the small rimu seedlings the greatest root:shoot ratio was also found at the lowest growing temperature. Root growth is often greater at lower temperatures (Sutcliffe, 1977). While relative growth rate in rimu seedlings seems to be affected more by heat sum than by thermoperiod, root growth may be under thermoperiod control. In the thermoperiod experiment the medium night temperature treatment (18°C day/12°C night) gave the highest root:shoot ratio, the low night treatment (18°C day/5°C night) an intermediate ratio, and

the high night regime (18°C day/20°C night) a slightly lower ratio. Root growth in rimu seedlings was apparently stimulated by a thermoperiod of 6°C or by night temperature of 12°C (Table 3.15). It might have been further stimulated by a larger thermoperiod (e.g., 13°C), but the 5°C night temperature used with a 13°C thermoperiod caused the plants to become brown and slowed the overall relative growth rate.

The temperature regimes used in the experiments described here were not designed to kill the rimu seedlings and further experiments would have to be performed to discover the minimum heat sum or mean daily temperature rimu seedlings could survive in.

In summary it was shown that seedlings survived and grew in a 10°C range of temperature regimes and that the growth rate of small soft seedlings increased with temperature up to a mean daily temperature of 24°C whereas larger woody seedlings grew best in a mean daily temperature of about 19°C in both a regime of 22°C/14°C (15 hour photoperiod) and 18°C/20°C (14 hour photoperiod). The establishment of rimu seedlings is limited to regions where minimum winter temperatures do not remain low for too long and the most rapid growth of seedlings occurs in warm climates. In Chapter 4 the responses of rimu seedlings to temperature are discussed in relation to the establishment and distribution of the species.

3.6 Photoperiod, dormancy and the seasonal pattern of growth in rimu seedlings

3.6.1 Methods

a. The effect of photoperiod on the shoot extension growth of four provenances of rimu seedlings.

Puketi, Waitakere, Pureora and Westland seedlings were established in the glasshouse in 100 x 200 mm polythene planter bags in standard potting mix and bags placed on wet sphagnum in seed boxes. Plants were placed in three controlled environment treatments: day/night temperatures 22°C/14°C; relative humidity 70% (constant); photosynthetic irradiance (c.600 μE m^{-2} s^{-1}) 10h; photoperiods 10h (short day), 15h (medium day), and 20h (long day). The non-photosynthetic light used to extend the medium and long photoperiods was provided by mercury vapour quartz halogen incandescent lamps which produce more far-red radiation than fluorescent lamps. Far-red light is involved in plant detection of photoperiod by phytochrome (e.g., Whatley and Whatley, 1980). For three months the supplementary irradiance was about 12 μE m^{-2} s^{-1}, but this was reduced to 9 μE m^{-2} s^{-1} for the remaining 1.5 months because it was believed rimu seedlings could lower their light compensation point below 12 μE m^{-2} s^{-1} and therefore any differences in growth might be due to additional photosynthesis rather than photoperiod. The temperature regime was the one which gave best growth in woody seedlings in section 3.5.1a.

Similar populations of 35 seedlings per provenance were placed in each treatment and the height of their tallest shoot measured at approximately 4 weekly intervals. After 5 months total shoot lengths and shoot surface areas of 10 seedlings per provenance from each treatment were measured and the number of leaves per 5 mm stem counted.

Forty extra Waitakere seedlings were grown in each treatment and used for growth analysis (8 harvests x 5 replicates).

b. Dormancy

First year Pureora seedlings growing in a nursery bed were examined (section 3.2.1).

A. Each month from late March to early September 1979, 10 seedlings were collected from the bed, measured to check representativeness, and their leaves counted to determine whether growth was by leaf production or internode extension. The dormant period was determined by lack of height growth.

B. On the same dates as in A seedlings were removed from the bed and potted in standard mix in peat pots set in sphagnum in a seed box. Heights of at least 35 seedlings were measured and the box placed on a glasshouse bench with a minimum temperature of $10^{o}C$. Eight weeks after the final seedlings were potted (29 October), all surviving seedlings were remeasured.

C. On the same dates as in A a second box of seedlings was prepared, heights measured, and the box placed in the dark in a cool room at $4 \pm 2^{o}C$ for four weeks, after which it was placed on a glasshouse bench. Boxes in the glasshouse were misted daily for two weeks until they developed new roots. Four weeks after the final box was put in the glasshouse (29 October) all surviving seedlings were remeasured.

Survival rates of seedlings in B and C were calculated and results expressed as percent survival. Height growth was expressed per week in the glasshouse (time in the cool room excluded).

c. The seasonal pattern of growth of four provenances of rimu seedlings in the FRI nursery, Rotorua.

Seedlings from Puketi, Waitakere, Pureora and Westland provenances were overwintered in a glasshouse, hardened off outside under 50% shade cloth and lined out in a nursery bed prepared with 50 kg ha^{-1} MagAmp fertilizer with 0.6 kg ha^{-1} Propazine and 6 kg ha^{-1} Chlorthal in 500l ha^{-1} water. Seedlings were planted out on 15-17 October 1979, spaced at 10 cm x 20 cm, each provenance in 8 replicate blocks distributed at random along a uniform bed. Additional Pureora seedlings were used as buffer trees between experimental provenance trees and surrounding the bed, and each row contained 5 buffer and 4 provenance trees, 9 rows per block. The bed

was shaded by 50% shade cloth on wire hoops c.60 cm high, but after 12 months shade was removed (during November 1980). However, it was believed growth was set back by full exposure so 30% shade cloth was applied supported on 85 cm high wooden frames for the second 12 months.

Approximately monthly from November 1979 - November 1980, then less frequently until November 1981, one provenance tree was harvested from each block (8 replicates x 4 provenances = 32 trees). The 5 largest replicates of each provenance were used for growth measurements and the rest discarded. All harvests were made near the middle of the month.

Weather data was provided by the Forest Research Institute from the Whakarewarewa Weather Station, latitude 38°10'S, longitude 176°16'E. As seedlings were kept well watered in dry weather, rainfall was not included in the weather summaries.

3.6.2 Results

a. The effect of photoperiod on the shoot extension growth of four provenances of rimu seedlings.

Seedlings of the four provenances were different in mean height at the beginning of the experiment (Fig. 3.28), the Waitakere plants being nearly twice as tall as the others. After several weeks in controlled environments all seedlings were growing relatively fast and their leading shoots began to droop. Branching began in all treatments after three weeks and by six weeks some branches were found to be much longer than the leading shoot when held upright. For the sake of consistency it was therefore decided to measure the length of the tallest shoot held vertically against a ruler. By the end of the experiment leading shoots had straightened up again in most plants. Seedlings of mean height from each provenance and photoperiod were photographed at the end of the experiment (Figs. 3.29 a-d). It can be seen that many lateral branches

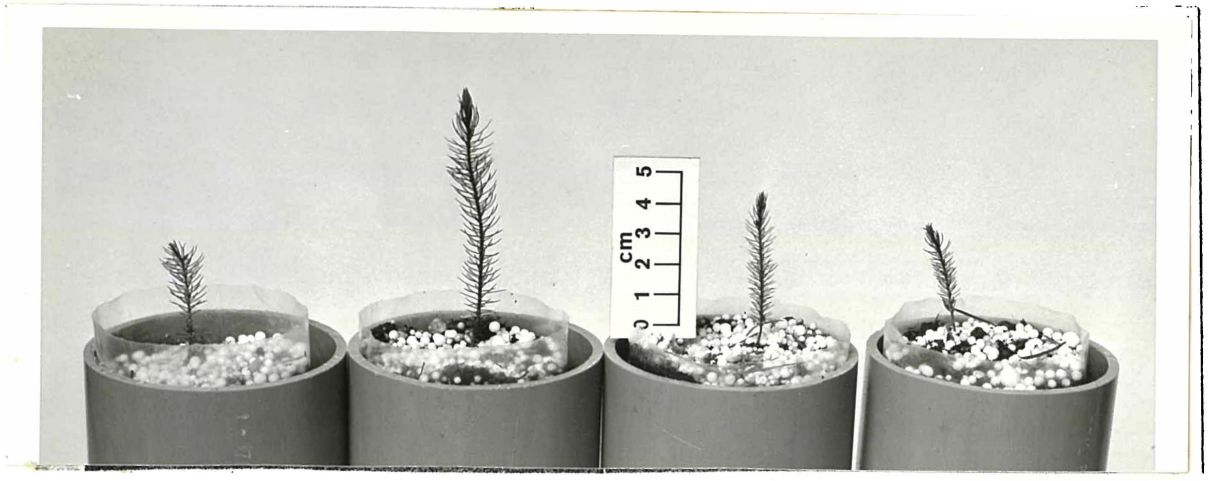


Fig. 3.28

A plant of mean height from each of the four provenances at the start of the photoperiod experiment (Section 3.6.2 a)

Left to right: Puketi, Waitakere, Pureora, Westland.

Fig. 3.29 a-d.

A plant of mean height from each photoperiod at the end of the experiment.

Left to right: 10h , 15h and 20h days.

Fig.3.29 a. Puketi provenance.

Fig. 3.29 b. Waitakere provenance.

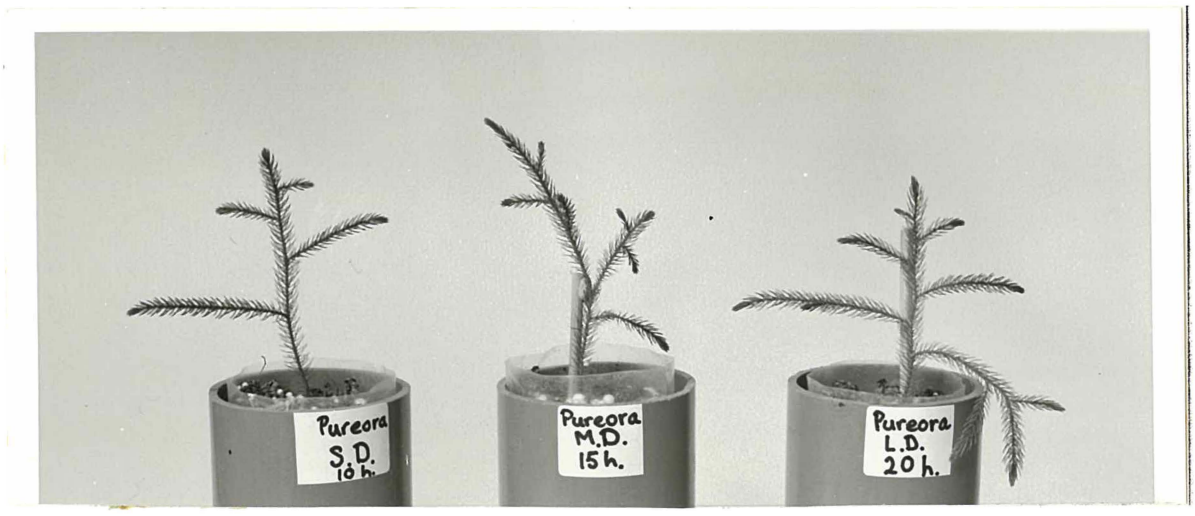


Fig. 3.29 c. Pureora provenance.

Fig. 3.29 d. Westland provenance.

Fig. 3.30 a - d.
The increase in mean height of the tallest shoots of seedlings grown for 4·5 months at three photoperiods.

a. Puketi.
b. Waitakere.
c. Pureora.
d. Westland.

x —— x Short Day.
+ —— + Medium Day.
△ —— △ Long Day.

Fig. 3.30

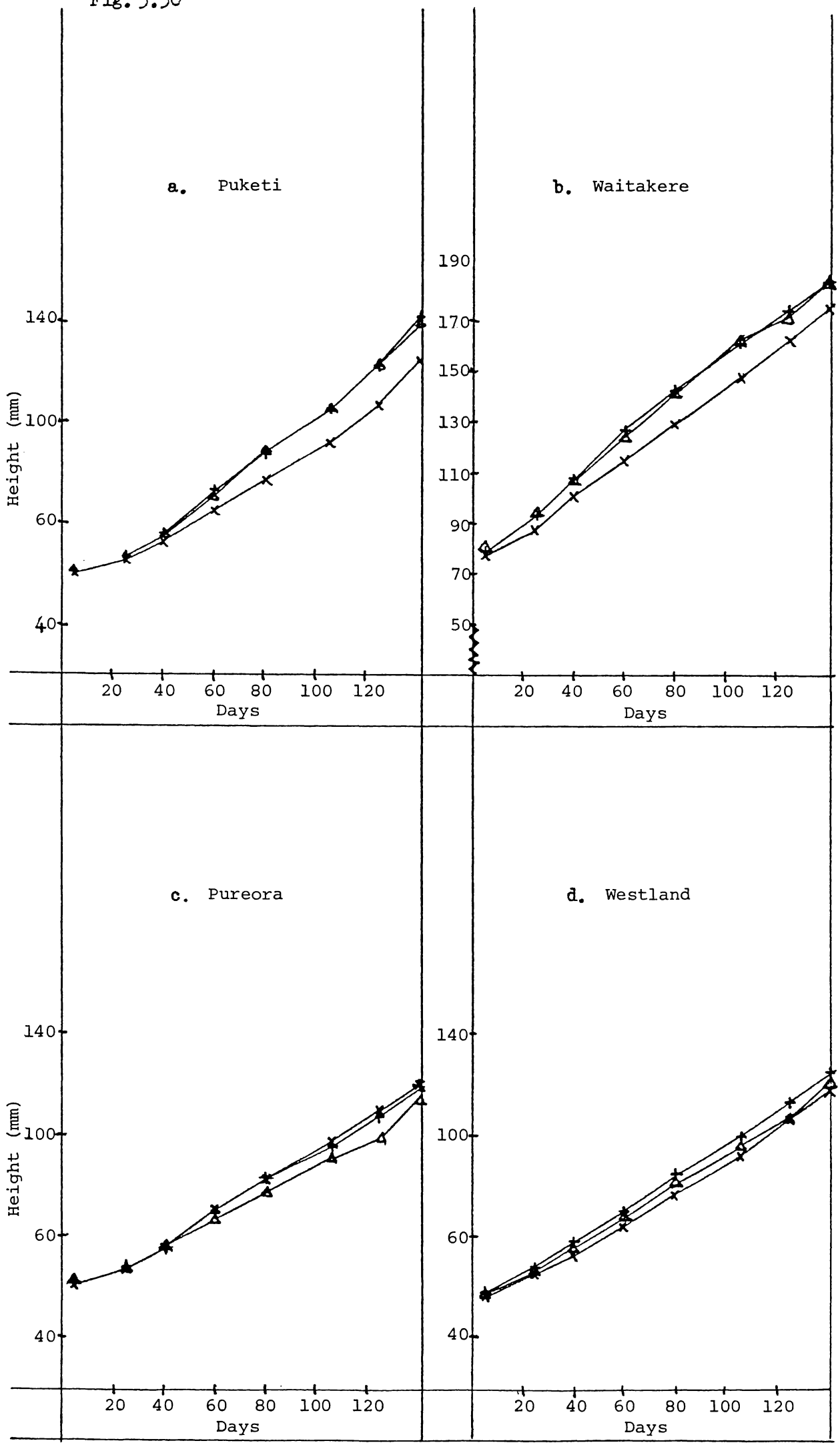

a. Puketi
b. Waitakere
c. Pureora
d. Westland
Height (mm)
Days
20 40 60 80 100 120
40 60 100 140
50 70 90 110 130 150 170 190

TABLE 3.19 : MEAN HEIGHTS OF SEEDLINGS FROM FOUR PROVENANCES AFTER 4.5 MONTHS GROWING AT SHORT, MEDIUM AND LONG DAY LENGTHS. Day/night temperature 22°C/14°C; 70% Relative humidity; c.600 μE m^{-2} s^{-1} Irradiance

		Provenance							
		Puketi		Waitakere		Pureora		Westland	
Photoperiod	Hrs	n	Height (mm)	n	Height (mm)	n	Height (mm)	n	Height (mm)
Short Day	10	33	122.6 b	35	174.5 a	26	119.1 a	30	125.5 a
Medium Day	15	34	140.2 a	35	186.8 a	30	119.2 a	31	127.5 a
Long Day	20	35	138.4 a	35	184.3 a	31	114.6 a	33	124.0 a

TABLE 3.20 : MEAN TOTAL SHOOT LENGTHS OF SEEDLINGS FROM FOUR PROVENANCES AFTER 4.5 MONTHS GROWING AT SHORT, MEDIUM AND LONG DAY LENGTHS. n = 10. Controlled environment regime as in Table 3.19

		Provenance			
		Puketi	Waitakere	Pureora	Westland
Photoperiod	Hrs	Shoot length (mm)	Shoot length (mm)	Shoot length (mm)	Shoot length (mm)
Short Day	10	396.7 b	558.3 a	269.5 a	331.4 a
Medium Day	15	564.3 a	652.8 a	278.1 a	357.0 a
Long Day	20	598.4 a	589.9 a	362.1 a	308.4 a

are as long or longer than the leading shoots. The height measurements shown in Figs. 3.30 a-d and Table 3.19 represent the height above ground of the longest shoot, not necessarily the leading shoot. The increase in mean height with time of seedlings grown in the three photoperiods is shown in Figs. 3.30 a-d. Both Puketi and taller Waitakere seedlings grew faster in medium and long days than in short days (Fig. 3.30 a and b) and because this was observed the supplementary irradiance in the 15 and 20 hour photoperiods was reduced after 90 days. However, there was little if any change in

the pattern of growth in the remaining 50 days. In contrast to Puketi and Waitakere provenances, Pureora seedlings had somewhat slower height growth in long days than in both short and medium days (Fig. 3.30 c), and in Westland seedlings height growth was fastest in medium days with long days giving intermediate growth and short days slowest growth (Fig. 3.30d). These results may have been influenced by the decision to measure the longest shoot rather than the leading shoot. Possibly fewer Pureora seedlings had branches which were longer than the leading shoot.

Mean heights of seedlings at the end of the experiment are shown in Table 3.19. Medium and long day Puketi plants were significantly taller than short day plants and the same trend was apparent in the Waitakere seedlings also. In Pureora plants the trend was different: although medium days gave the greatest height growth as in the Puketi and Waitakere provenances, Pureora plants grown in short days were almost as tall whereas the shortest plants were grown in long days. This trend was the same also in the Westland seedlings: greatest height growth in 15 hour days, followed by 10 hour days, with least height growth in 20 hour days. Differences in the Waitakere, Pureora and Westland provenances were not significant however (Table 3.19).

At the end of the experiment total shoot lengths (that is the sum of the lengths of the main stem and all branches), were measured in a sample of 10 trees per provenance from each photoperiod. The 10 seedlings closest to mean height for each provenance and treatment were chosen. As mean heights of the provenances were all different at the beginning comparisons between provenances were not made. Mean total shoot lengths of each provenance and treatment are shown in Table 3.20. In Puketi plants long and medium days gave a significant increase in total shoot extension. A similar trend was repeated in the Pureora provenance: long day $>$ medium day $>$ short day. It is believed that total shoot length is a more accurate measure of shoot extension growth in rimu than height based on the longest shoot held upright.

Mean numbers of leaves per 5 mm stem for seedlings from different provenances and treatments are shown in Table 3.21. Leaf numbers were compared within and between provenances and although differences between treatments within the Puketi, Waitakere and Westland provenances were not significant, Pureora seedlings had significantly more leaves per unit stem in the short and long days than any of the other provenances in any treatment. Why this should be is not known. Differences in rate of internode extension growth result in different numbers of leaves per unit stem length. Shoot extension growth may be a combination of new leaf production and internode extension. Higher numbers of leaves per unit stem, as in long and short day Pureora plants, indicate relatively less internode extension growth.

Mean surface areas of shoots of plants from each provenance and treatment are shown in Table 3.22. In all four provenances the trend was the same: long day $>$ medium day $>$ short day. In Puketi plants long and medium day surface areas were significantly greater than short day areas and in Pureora plants long day areas were significantly greater than medium or short day areas. In Waitakere and Westland plants differences were not significant.

Growth analysis was only performed on Waitakere provenance plants because of limited space in the controlled environment chambers. Relative growth rates (R) followed the same trend as shoot areas: long day $>$ medium day $>$ short day (Table 3.23). Differences were not significant, however. The higher R in long day plants was caused by increasing unit leaf rate (E) (Fig. 3.32). Unit leaf rate rather than leaf area ratio (F) determined relative growth rate in the three treatments (Figs. 3. 31, 3.32 and Table 3.23). In short days leaf production was outstripping overall dry weight increase and F increased with time; in medium days F was more or less constant throughout and in long days dry weight was increasing relatively faster than leaf production and F decreased with time. By comparison unit leaf rates at the end of the experiment followed the same trend as relative growth rates.

TABLE 3.21 : MEAN NUMBER OF LEAVES PER 5 mm STEM OF SEEDLINGS FROM FOUR PROVENANCES AFTER 4.5 MONTHS GROWING AT SHORT, MEDIUM AND LONG DAYLENGTHS. n = 10 Controlled environment regime as in Table 3.19

Photoperiod	hours	Provenance			
		Puketi	Waitakere	Pureora	Westland
		No. leaves/5 mm stem	No. leaves/5 mm stem	No. leaves/5 mm stem	No. leaves/5 mm stem
Short day	10	11.3 b	11.2 b	15.0 a	12.8 b
Medium day	15	11.5 b	12.3 b	12.9 b	13.3 b
Long day	20	11.3 b	11.8 b	15.0 a	12.9 b

TABLE 3.22 : MEAN SHOOT SURFACE AREA OF SEEDLINGS FROM FOUR PROVENANCES AFTER 4.5 MONTHS GROWING AT SHORT, MEDIUM AND LONG DAYLENGTHS. Controlled environment regime as in Table 3.19

Photoperiod	hours	Provenance							
		Puketi		Waitakere		Pureora		Westland	
		n	Area (cm^2)	n	Area (cm^2)	n	Area (cm^2)	n	Area (cm^2)
Short day	10	10	46.6 b	10	79.6 a	10	30.8 b	10	39.0 a
Medium day	15	5	85.0 a	10	102.1 a	9	39.0 b	10	43.3 a
Long day	20	5	91.8 a	5	107.4 a	10	54.3 a	10	44.6 a

TABLE 3.23 : THE RELATIVE GROWTH RATES (8 Harvests; n = 5) OF WAITAKERE PROVENANCE SEEDLINGS GROWN AT SHORT, MEDIUM AND LONG DAYLENGTHS. Controlled environment regime as in Table 3.19

Photoperiod	hours	R ($g\ g^{-1}\ day^{-1} \times 10^{-2}$)
Short day	10	1.30 $\pm$ 0.2 a
Medium day	15	1.43 $\pm$ 0.2 a
Long day	20	1.51 $\pm$ 0.2 a

Fig. 3.31

The progressive changes in Leaf Area Ratio, F, with time, of seedlings grown at three photoperiods.

+ ——— + Short Day, 10h;

x ------ x Medium Day, 15h;

△ ......△ Long Day, 20h.

Bars represent 5% confidence limits.

Fig. 3.32

The progressive changes in Unit Leaf Rate, E, with time, of seedlings grown at three photoperiods.

Symbols and lines as in Fig. 3.31.

Fig. 3.31

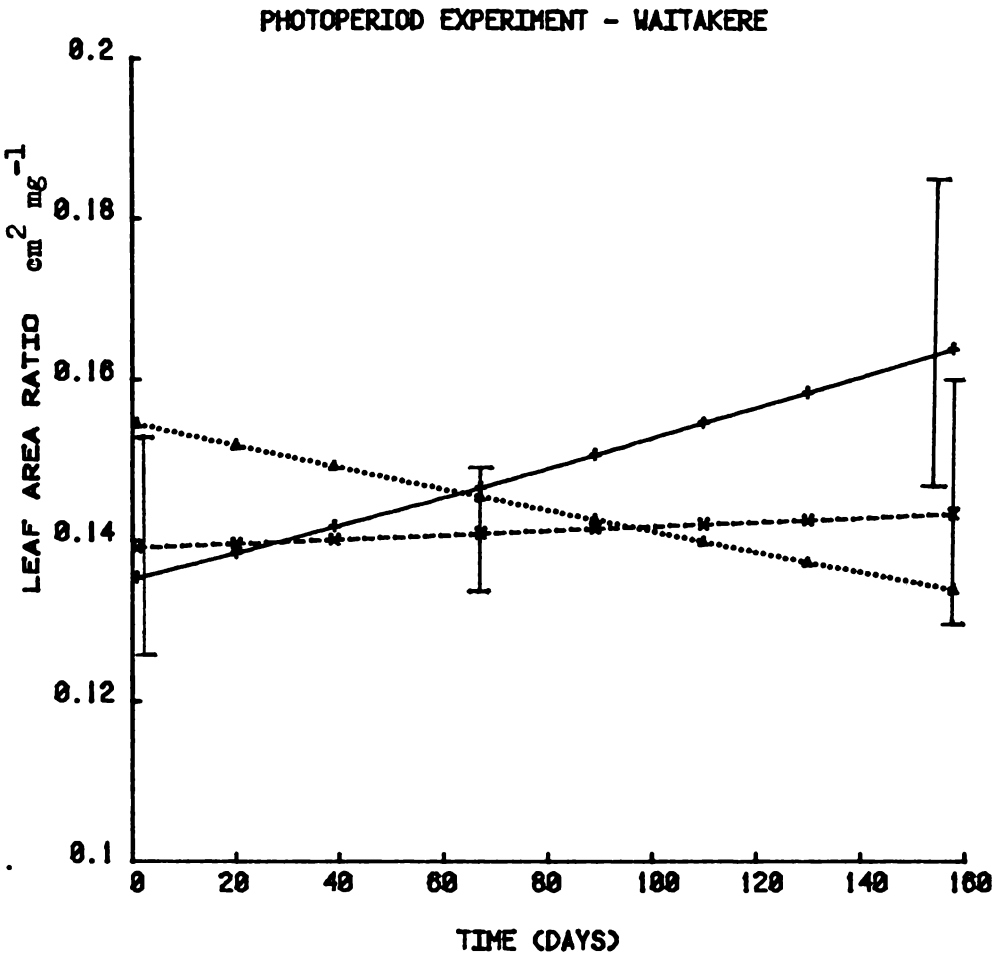
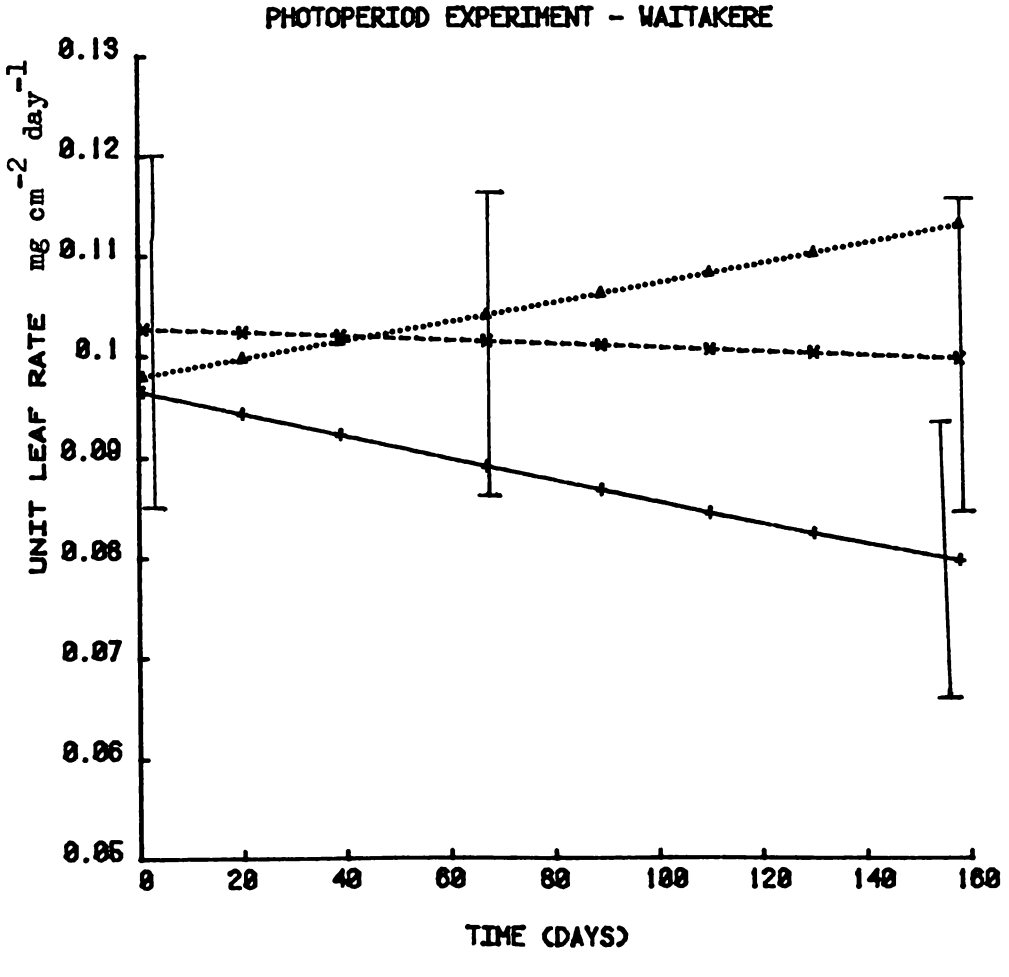


Fig. 3.32



To summarise: in the three North Island provenances growth was somewhat greater in longer photoperiods.

Relative growth rate in Waitakere seedlings was apparently increased by increased photoperiod.

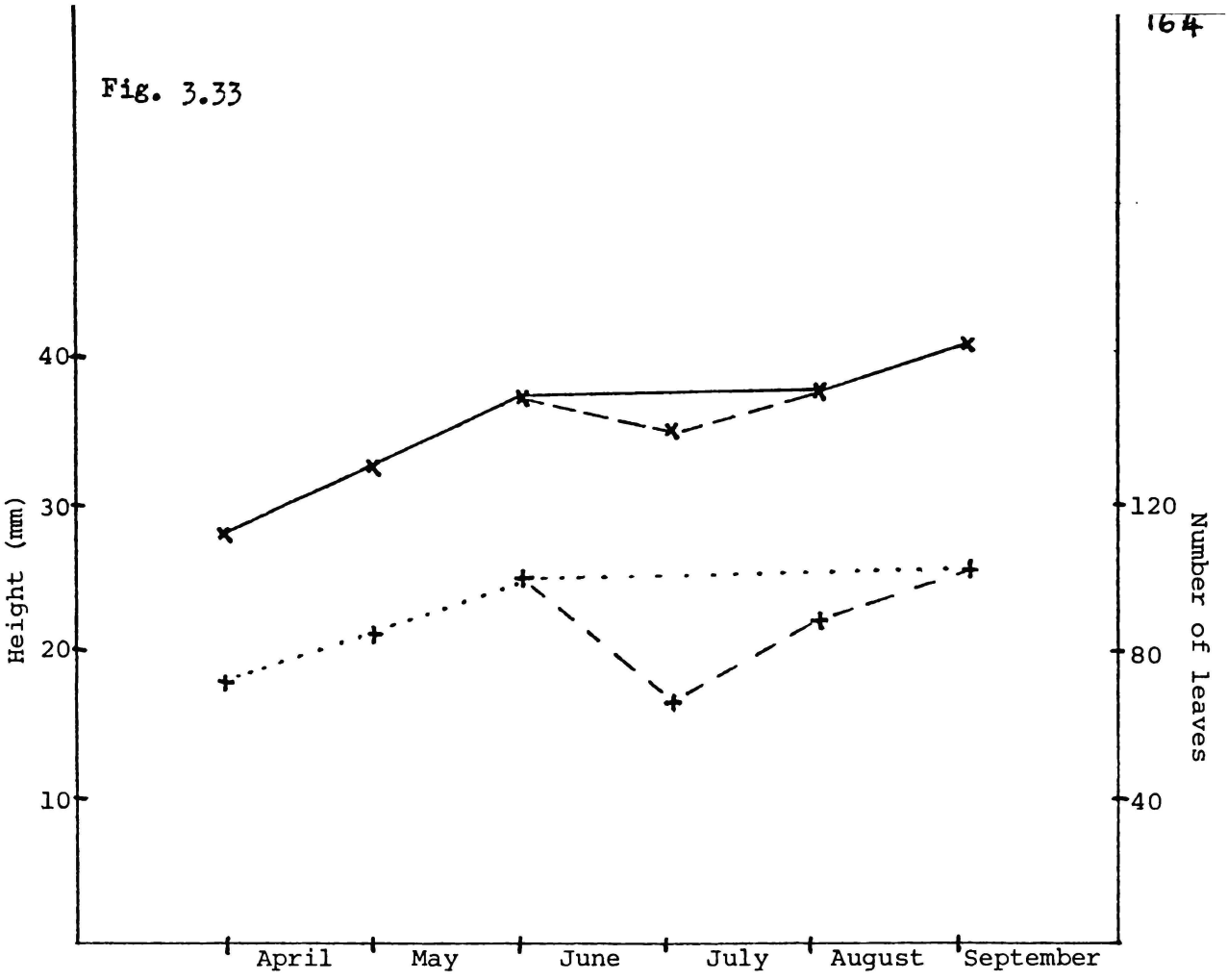
b. Dormancy

The aim of this experiment was firstly to discover whether and for how long rimu seedlings became dormant in winter in Rotorua and secondly, whether a chilling treatment hastened the breaking of dormancy. Mean heights and leaf numbers of 10 seedlings collected monthly from late March to early September (Part A) are shown in Fig. 3.33. Dashed lines indicate that the sample measured in early July was below average for the population. Height growth and leaf production continued at a constant rate from March until early June when both ceased. Height growth apparently recommenced after winter in August at a rate similar to its former one, but leaf production had not resumed by September. The apparent earlier resumption of height growth may have been due to sampling error or it may have been real and caused by internode extension rather than leaf production. There was a linear relationship between height and leaf number for the whole period: Height (mm) = 8.9 + 0.3 (leaf number), $r^2 = 0.94$.

The difference in size of seedlings collected from the nursery in late April and early September is illustrated in Fig. 3.34 a and b. There appears to have been some growth in diameter and in root systems, as well as in height and leaf number during the winter period.

Results of parts B and C are presented together. Height growth rate (per week in the glasshouse) of seedlings without and with a four week chilling treatment are shown in Fig. 3.35. Where height growth appears negative (seedlings potted on 3 July and 3 September for chilling treatment) the means which growth rates are derived from are

Fig. 3.33



Mean height and leaf number of seedlings lifted from the nursery throughout the winter.

x———x Height (mm).

+ .....+ Leaf number.

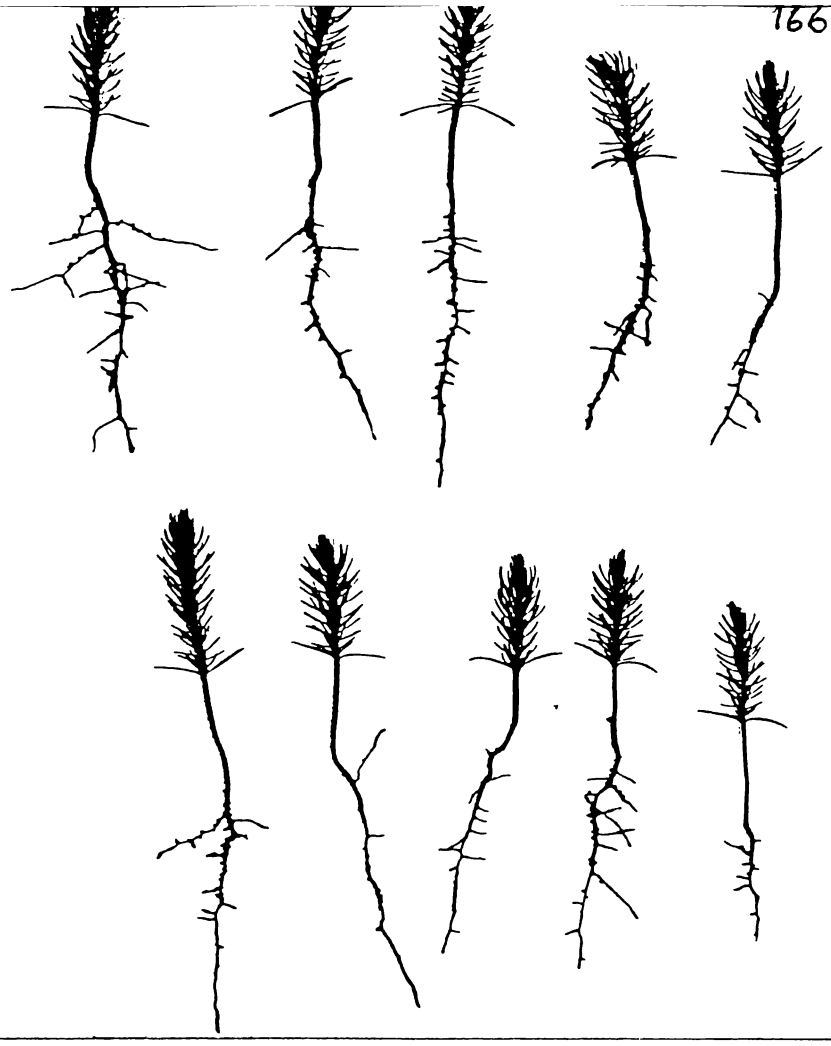
Fig. 3.34

Photocopies (reduced) of first year rimu seedlings before and after winter.

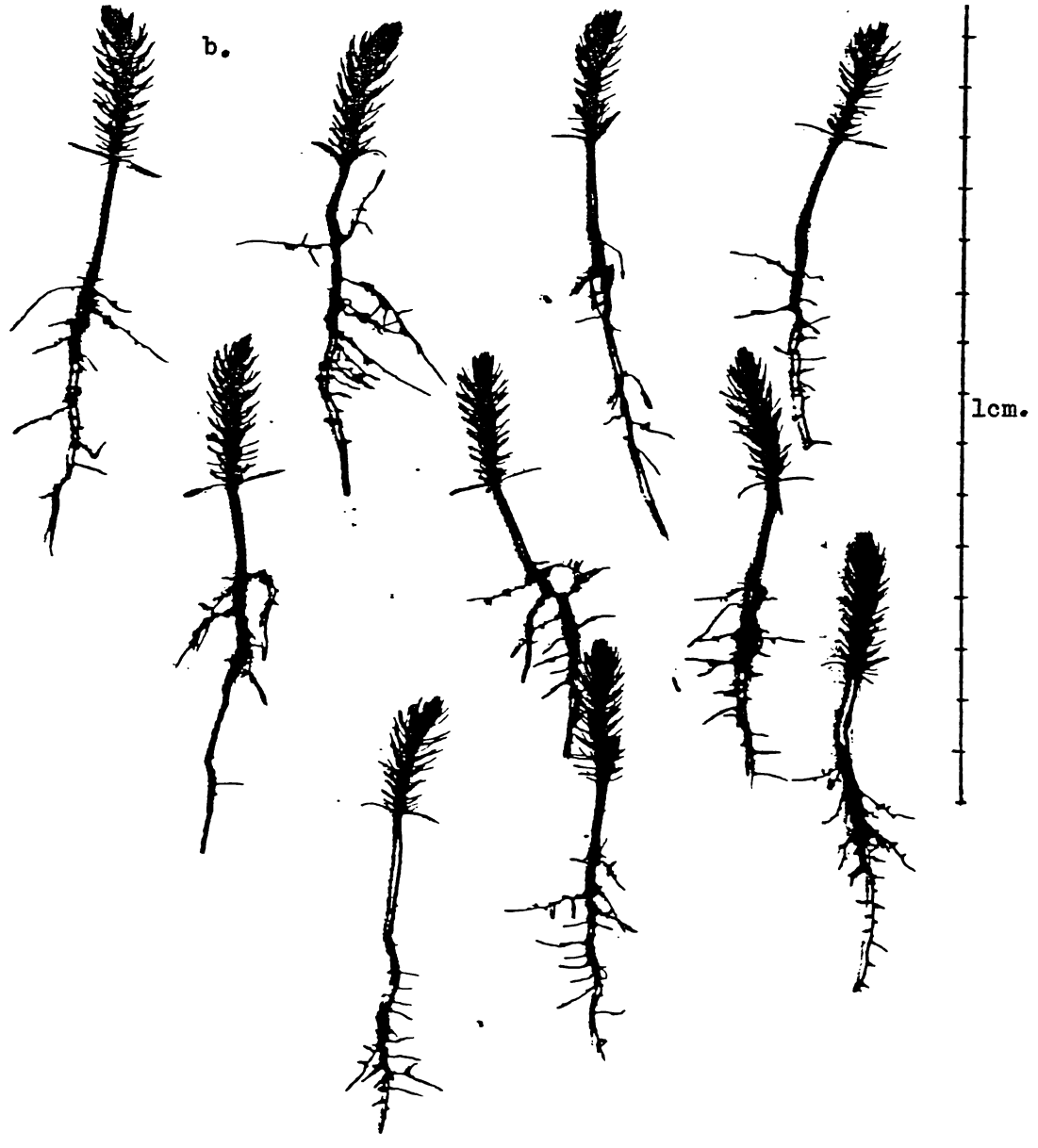
a. Seedlings lifted from nursery bed 27 April.

b. Seedlings lifted from nursery bed 3 September.
(Scale applies to a. and b.)

Fig. 3.34 a.



b.



of reduced numbers of replicates following 80% and 60% mortality. Height growth rate of chilled seedlings potted on 28 May may also be doubtful as it is derived from a reduced number of replicates following 70% mortality.

For unchilled seedlings height growth rate was related to the length of time plants had been in the glasshouse. The longer seedlings experienced a minimum temperature of 10^{0}C the greater their height growth rate. Seedlings potted on 3 July, when they were apparently dormant in the nursery bed, recommenced height growth without any requirement for further chilling.

Height growth rate of seedlings which had been chilled for four weeks was also apparently related to the length of time they were in the glasshouse, although, due to heavy mortality and consequently reduced numbers of replicates on which mean height growth rates were based, this trend was not so apparent. Chilling did not hasten the breaking of dormancy in rimu seedlings. On the contrary, height growth rate was retarded following a four week chilling treatment (Fig. 3.35).

The chilling treatment used was apparently too long for small rimu seedlings. A shorter chilling period in an environment including several hours of photosynthetically active radiation each day might have caused lower mortality. The percent survival rate of seedlings without and with a chilling treatment is shown in Fig. 3.36. Four weeks in the dark at 4^{o}C caused high mortality amongst small rimu seedlings, especially those collected from the nursery in late May, early July and early September. Some of the difference in survival from month to month was probably due to differences in handling and in the weather on the day seedlings were lifted from the nursery.

c. The seasonal pattern of growth of four provenances of rimu seedlings in the FRI Nursery, Rotorua.

Seedlings of each provenance had been raised in different nurseries (Table 3.2, section 3.2.1) and consequently were different in size at the beginning of the experiment. A representative seedling from each provenance collected in November 1979, is illustrated in Fig. 3.37.

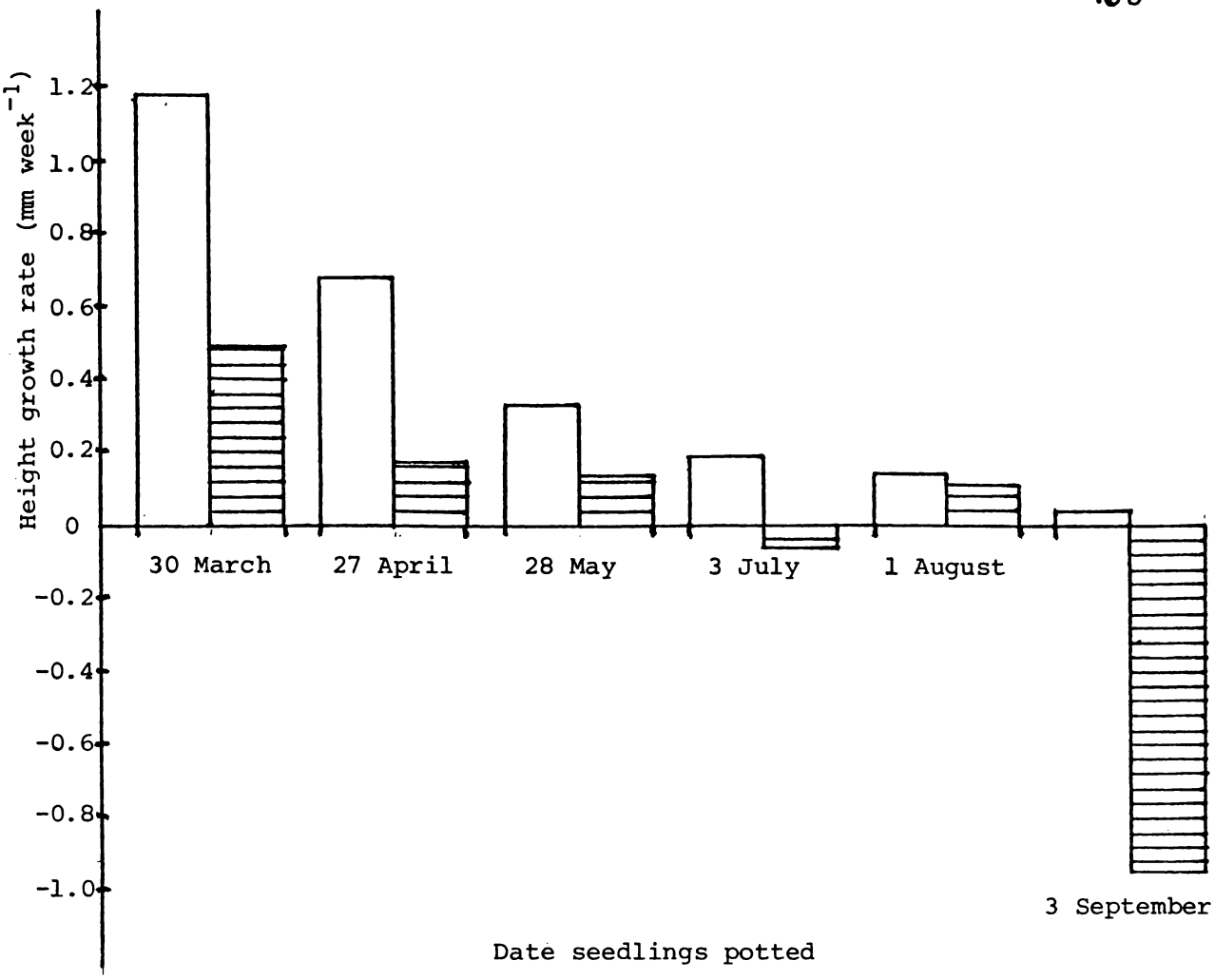


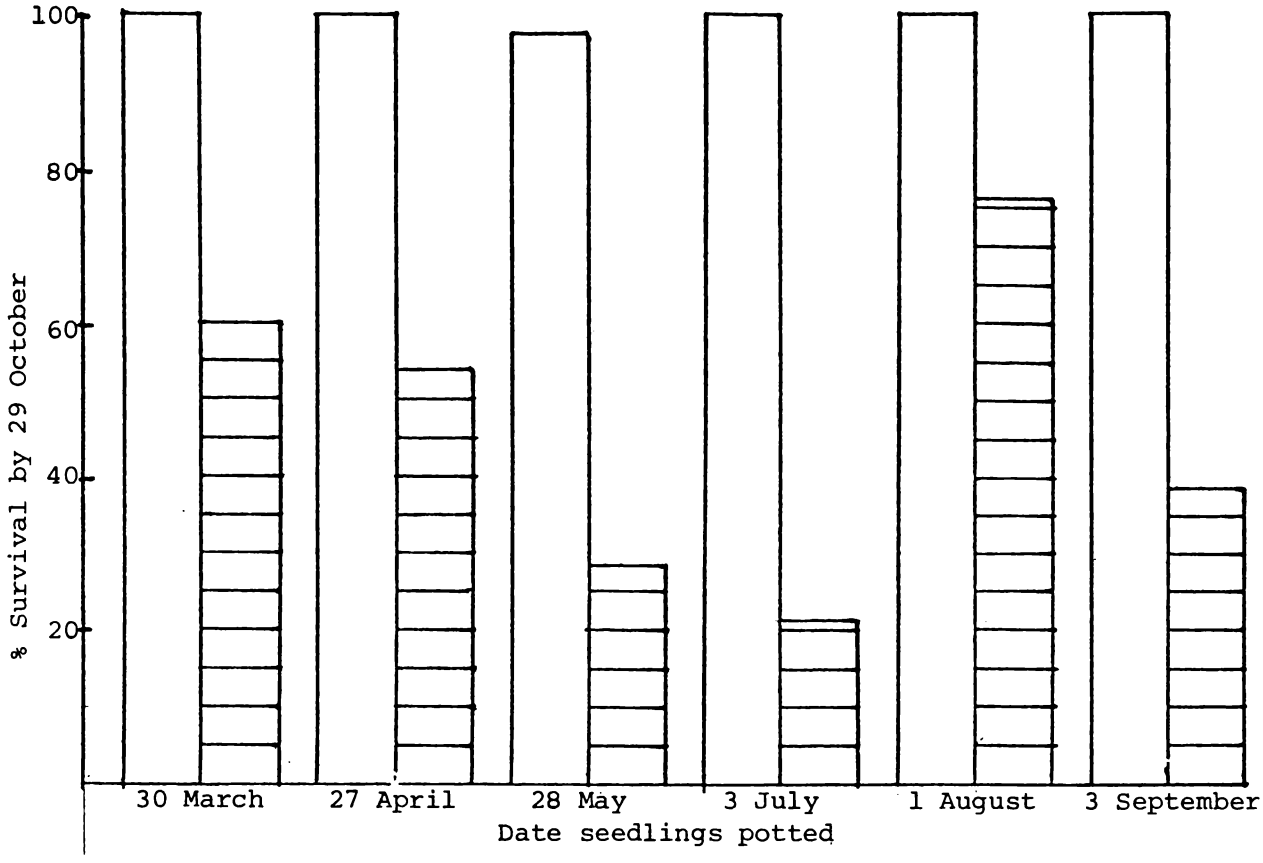
Fig. 3.35

The height growth per week in the glasshouse of seedlings lifted from the nursery throughout the winter. Measurements were made on 29 October, 1979.

Without chilling treatment.

With chilling treatment.

Fig. 3.36



The percentage survival of seedlings lifted from the nursery throughout the winter.

Without chilling treatment.

With chilling treatment.

Because of the size differences it was not possible to compare growth rates of the four provenances, but their seasonal patterns of growth were derived by plotting mean size against month for each provenance. The experiment continued for two years to discover whether the growth pattern altered as the seedlings became older.

The pattern of increase in total dry weight with time for the four provenances is shown in Fig. 3.38. Because of the size variation of seedlings within each provenance and because destructive harvesting was used, the graph fluctuates. On certain harvests seedlings above or below average size were collected. For example, smaller than average plants were harvested during July 1981, for Puketi and Waitakere provenances and during August 1981, for Pureora and Westland provenances.

The initial differences in mean size of the four provenances were maintained: Puketi > Waitakere > Pureora > Westland. (These size differences are related to the temperature and length of growing season in the nurseries where the seedlings were raised.) For all provenances the pattern of dry weight growth follows the same trend.

Monthly weather summaries for Rotorua during the two years of the experiment are shown in Table 3.24. Mean tempterature warmed steadily from October to January and February (the hottest months) and then fell more rapidly to reach a minimum in June, July and August. As temperatures fell with the approach of winter, rimu seedlings became brown in colour, the Westland provenance browning earlier and greening later in the season than the other provenances. Browning began to be apparent from May onwards and seedlings were still brown in October, except for new bright green leaves at the shoot tips. They were all fully green by December.

In the first summer (November 1979-February 1980) dry weight growth was slow in all provenances as they developed new roots in the nursery bed. Growth rate increased a little in late summer and growth continued until temperatures dropped suddenly in June with the onset of frosts (Fig. 3.38, Table 3.24) when growth ceased, probably until late September or October, when mean temperatures were above $10^{o}C$ and there were no more frosts. Dry weight growth rate was

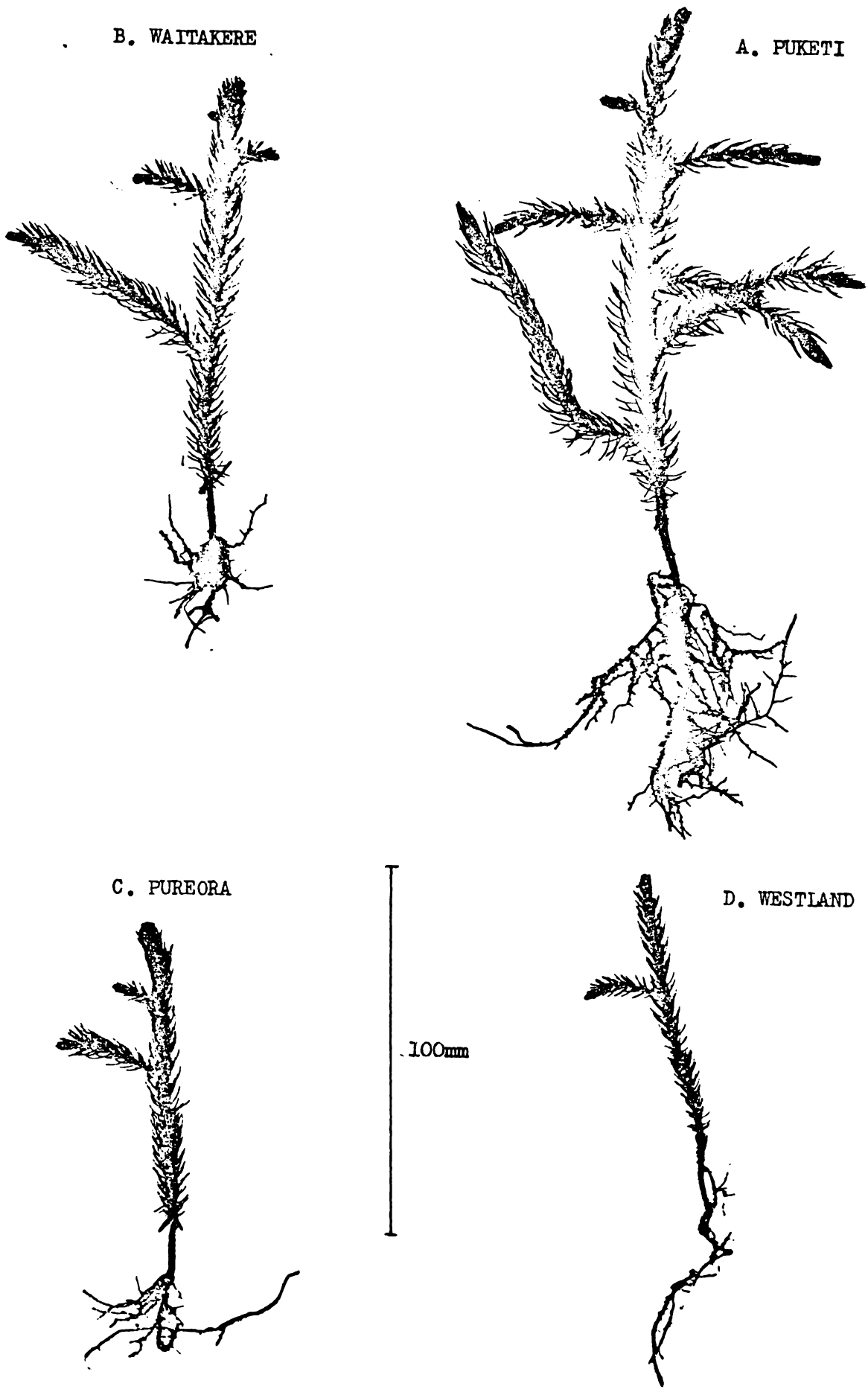
TABLE 3.24 : MONTHLY WEATHER SUMMARIES DURING THE TWO YEARS RIMU SEEDLINGS WERE GROWN IN THE FOREST RESEARCH INSTITUTE NURSERY. WHAKAREWAREWA STATION LAT. 38°10'S long. 176°16'E. The bed was watered during dry periods and rainfall is omitted from the table.

Month and year	Number of days with screen frost	Number of days with ground frost	Mean Temperature °C	Range Mean max. - mean min.	Highest Max. T°C	Lowest Min. T°C
Oct 1979	0	1	11	8.8	21.6	1.0
Nov 1979	0	0	13.5	8.5	22.4	4.6
Dec 1979	0	0	15.1	10.3	24.4	5.8
Jan 1980	0	0	17.0	8.7	28.3	7.0
Feb 1980	0	0	19.0	9.9	28.4	9.5
Mar 1980	0	0	13.0	9.4	23.2	3.6
Apr 1980	0	0	10.3	9.8	23.0	0.5
May 1980	0	0	10.4	8.6	18.3	2.5
Jun 1980	4	12	6.6	8.3	16.0	- 2.9
Jul 1980	12	15	6.1	8.7	15.1	- 3.0
Aug 1980	5	9	6.6	8.6	15.5	- 2.5
Sep 1980	1	3	9.4	8.0	19.2	- 0.5
Oct 1980	0	2	11.8	9.0	22.5	1.0
Nov 1980	0	2	14.0	9.0	24.9	3.1
Dec 1980	0	0	16.6	9.4	27.8	5.4
Jan 1981	0	0	18.8	10.1	26.4	7.8
Feb 1981	0	0	16.5	8.8	24.6	8.3
Mar 1981	0	0	14.4	7.5	24.5	4.3
Apr 1981	0	0	13.2	9.8	21.5	4.8
May 1981	1	6	9.8	9.2	19.7	- 0.2
Jun 1981	4	7	7.9	7.3	17.3	- 1.5
Jul 1981	3	14	6.7	8.5	14.6	- 1.2
Aug 1981	2	16	6.7	8.5	14.9	- 1.6
Sep 1981	0	4	7.6	7.5	15.0	0.1
Oct 1981	0	4	10.7	8.9	20.6	0.8
Nov 1981	0	2	12.1	9.3	20.8	3.4

Fig. 3.37

Photocopies (reduced) of representative seedlings from the four provenances at the beginning of the experiment. (November, 1979).

Fig. 3.37



fairly steady from October or November 1980 until February 1981 when the rate increased and growth continued at this higher rate apparently until May or June. It is believed that growth ceased from June until October 1981 as in the previous year. There is some indication that Westland seedlings were later than the other provenances in resuming dry weight growth after winter in both 1980 and 1981 and this may have been related to their remaining brown for longer.

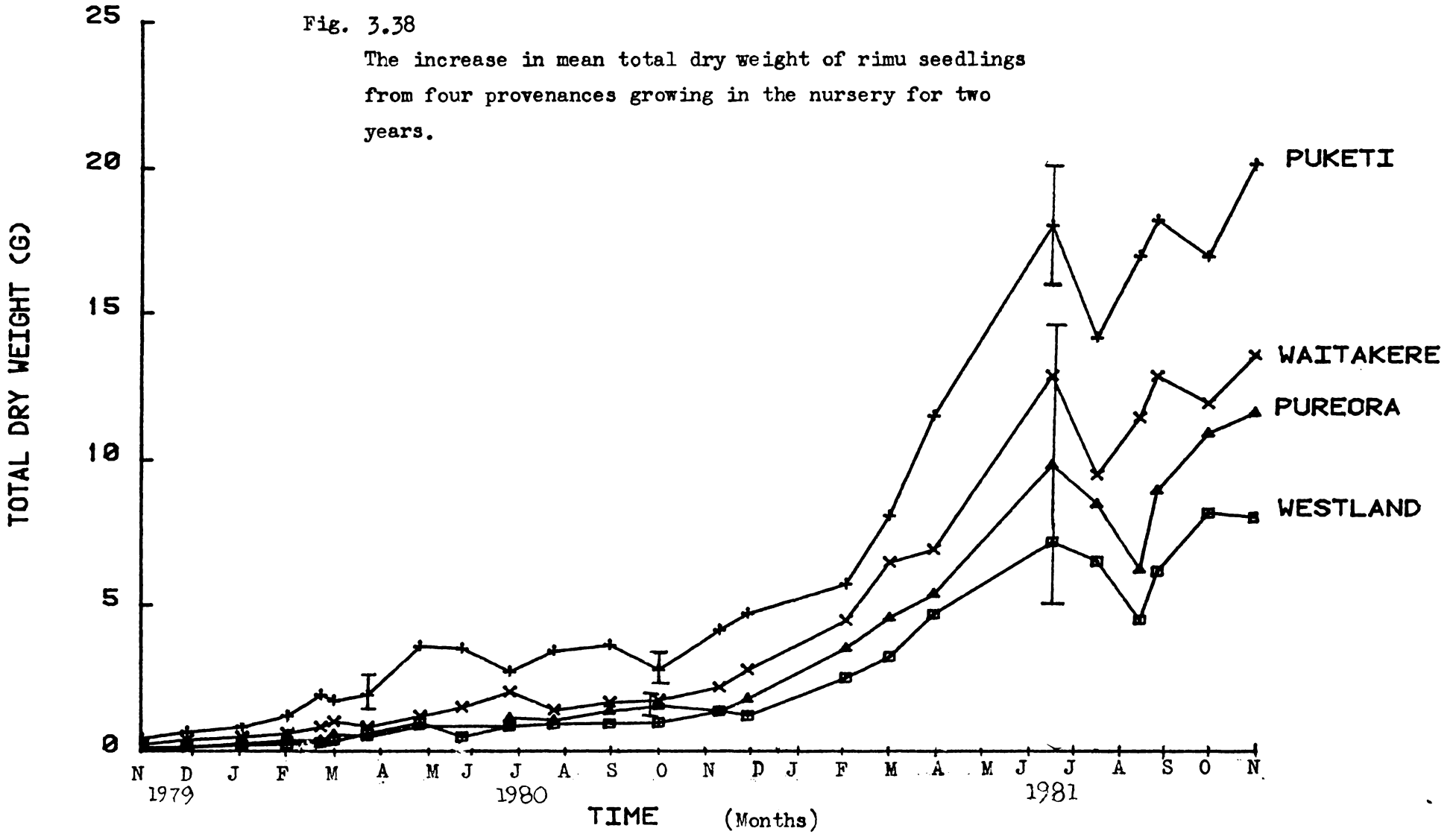
In both years, therefore, dry weight growth was slow between October or November and February and fastest in the later part of the season from February until May or June. Little or no dry weight growth occurred between June and September (at least in 1980).

The pattern of height growth during the two years is shown in Fig. 3.39. Although destructive harvesting resulted in somewhat erratic height growth curves for the four provenances, it is believed that they all followed a similar pattern. Height growth was slow in the early part of summer 1979-1980, but the rate increased in about January or February and growth continued until May or June. There was little or no height growth from June until November when it recommenced slowly as temperatures rose and seedlings lost their brown colour. Between December 1980 and February 1981 (the hottest months) height growth rate was most rapid in all provenances. It then slowed, but remained at a fairly steady rate from February to June. It is probable that no height growth occurred in any of the provenances between June and November 1981.

The pattern of growth in root collar diameter during the two years is shown in Fig. 3.40. Diameters grew slowly at first in all provenances and the growth rate increased in all but the Pureora provenance in December 1979. Growth rate was then fairly steady throughout summer and autumn, although it may have increased in the Puketi seedlings in April 1980 (Fig. 3.40). In all provenances diameter growth probably ceased in June 1980, and recommenced slowly in October, the same time as dry weight growth resumed and a month earlier than height growth. Diameter growth rate increased as temperatures warmed with a rapid rise in the Puketi and Waitakere provenances during November 1980 and good growth during the hottest months, December 1980 to February 1981. Growth continued steadily,

Fig. 3.38

The increase in mean total dry weight of rimu seedlings from four provenances growing in the nursery for two years.



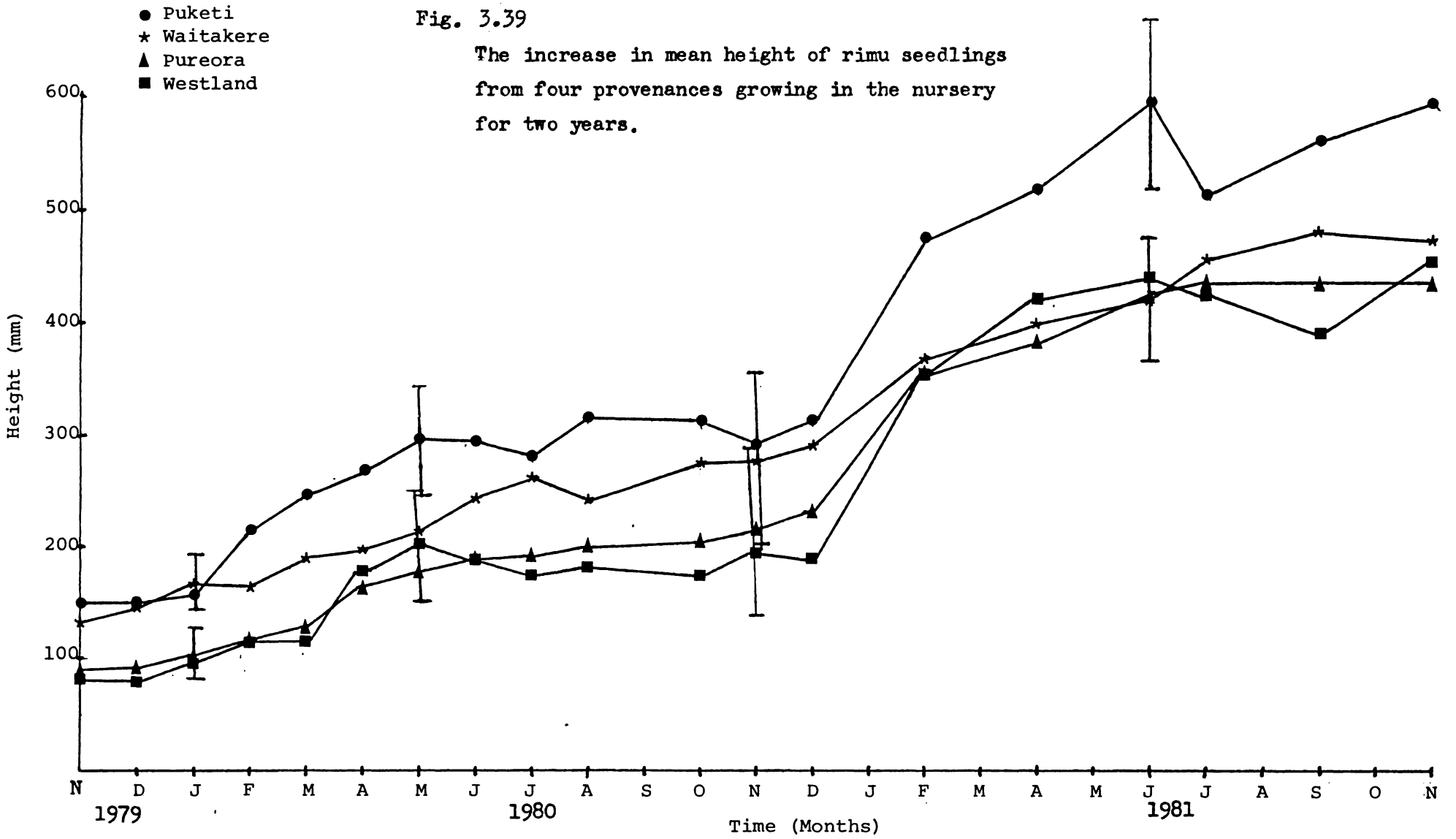


Fig. 3.39

The increase in mean height of rimu seedlings from four provenances growing in the nursery for two years.

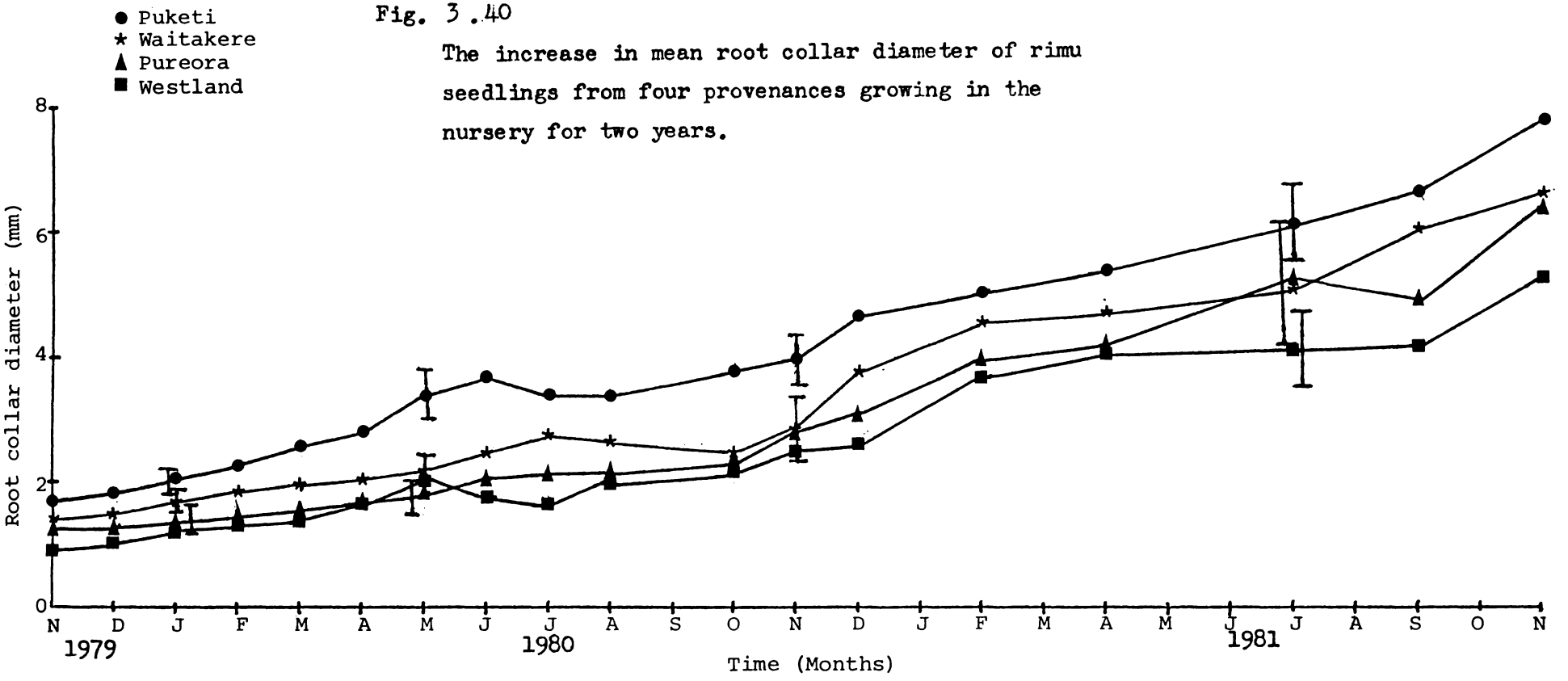


Fig. 3.40

The increase in mean root collar diameter of rimu seedlings from four provenances growing in the nursery for two years.

probably until June. The high value for Pureora seedlings in July 1981 is believed to be erroneous. Insufficient measurements were made during winter 1981, and in Fig. 3.40 Puketi and Waitakere plants appear to have continued diameter growth from July to September, but this is considered unlikely. Diameter growth probably began again slowly in October as in 1980.

The increase in diameter growth rate which occurred in the larger Puketi and Waitakere plants during November 1980, may have been caused by the removal of shade cloth during that month, although the smaller Pureora and Westland plants did not appear to be affected.

To summarise: All four provenances had similar seasonal patterns of growth. Growth in dry weight, height and diameter was related to mean monthly temperature and there was probably no growth between June and September. Dry weight and diameter growth recommenced in October and growth rates increased with temperature: dry weight growth rate was highest in late summer and autumn, from February to May while diameter growth rate was fairly steady throughout summer and autumn. Height growth apparently resumed after the winter dormant period somewhat later than diameter and dry weight growth and was greatest in the hottest months.

3.6.3 Discussion

Rimu seedlings showed only a slight response to photoperiod which is typical of many trees from warm-temperate climates (Vaartaja, 1963). Shoot extension growth was increased by increased photoperiod in two provenances. This could be interpreted as a true photoperiodic effect caused by the far-red enriched low irradiance supplementary light acting on phytochrome prior to the dark period, (e.g., Whatley and Whatley, 1980), and resulting in increased shoot extension growth. But on the other hand, as well as shoot extension growth and shoot surface area being increased by increased photoperiod, relative growth rate was also increased in the one provenance in which it was measured. The fact that longer days caused higher relative growth rates suggests the possibility that additional photosynthesis may have been involved. For the first 90 (out of 140) days the irradiance of the supplementary light used in the medium and long day treatments was approximately 12 $\mu E\ m^{-2}\ s^{-1}$. It is possible that

light compensation point was below this value and the seedlings were able to utilise the additional energy for photosynthesis. However, if this were the case the extra photosynthate created by each plant each day would have been very small as the irradiance was very low.

An alternative theory is that relative growth rate was altered by photoperiod affecting the way in which the photosynthate was utilised. This was found to be the case in seedlings of lobolly pine (McGregor et al., 1971). In this species there was no significant difference in net photosynthesis or dark respiration rate per unit of fascicle length between seedlings grown in short days (9.5 hours) and long days (15 hours). However, plants from different photoperiods varied in the way in which photosynthate was utilised. Long photoperiods apparently caused the production of more photosynthetic tissue from a given amount of photosynthate, rather than causing an increase in photosynthesis rate per unit foliage length. This additional photosynthetic tissue (i.e., increased leaf weight ratio) led to increased relative growth rates in lolbolly pine seedlings grown in long days.

In rimu seedlings, on the other hand, the increased relative growth rate in plants grown in long days was related to their increasing unit leaf rates and not to higher leaf weight ratios (Table 3.23, Figs. 3.31 and 3.32). Leaf weight ratio in these long day plants was decreasing throughout the experiment. Increased unit leaf rate in rimu seedlings grown in long days may have been caused either by the supplementary irradiance being above compensation point or, (probably more likely), by a true photoperiodic response.

Photoperiod thus affects the growth of different plants in different ways: long days may cause increased relative growth rate either by increasing unit leaf rate (as in rimu) or by increasing leaf weight ratio (as in loblolly pine).

The photoperiodic responses in rimu seedlings were small compared with responses found in many northern hemisphere conifers, especially from inland continental regions above latitude 40^{o}N, and although there were slight differences between provenances in their response to photoperiod, these were not the typical differences one would

expect in northern hemisphere species. Instead of the greatest response to photoperiod occurring in provenances from the highest southern latitude (Westland), the reverse was true and the greatest increase in shoot extension growth was found in the Puketi provenance from the lowest latitude.

Few conifer or angiosperm trees from warm or warm temperate climates in both northern and southern hemispheres have been shown to respond to photoperiod by becoming dormant in short days as is typical of trees from high northern latitudes (Vaartaja, 1963). On the other hand, shoot growth in these species may be increased by longer photoperiods, but these responses are usually very small compared with trees which survive the harsh winters of northern continental areas (Paton, 1978).

Photoperiodic responses in trees are often temperature dependent and this should be considered when interpreting the results of a photoperiod experiment performed at a single temperature regime (Paton, 1978). With the use of factorial combinations of temperature and photoperiod Paton (1978) was able to reveal day length optima for growth in cetain species of Eucalyptus which rarely occured at more than one growing temperature for any species or provenance. It is likely that various provenances of rimu would also show different optimal day lengths for growth in different temperature regimes. This may account for some of the differences between provenances found in this experiment.

Short days (10 hours) did not cause dormancy in rimu seedlings. It is possible that shorter days might have done so, although it is believed that even very short days (e.g., 5 hours) would not cause dormancy in rimu at the temperature regime used ($22^{o}C/14^{o}C$). However, a combination of short or shortening days with low or decreasing mean temperatures probably would cause dormancy in rimu seedlings. In the maritime climate of much of lowland New Zealand even at latitudes higher than $40^{o}S$, winter cold and frost are less extreme than in inland regions of large continents at similar northern latitudes. Also the change from autumn to winter tends to be gradual and at low altitudes the first frosts are usually preceded by a slow decrease in mean temperature. Therefore rimu does not

become frost tolerant a long time in advance of the first autumn frosts as do trees indigenous to continental regions at high northern latitudes where the change in seasons is rapid. If the end of the growing season in rimu was limited by decreasing photoperiods and growth rate began to decline following the summer equinox, as days become progressively shorter, growth would be severely limited. As can be seen in Figs. 3.38-3.40 most dry weight, height and diameter growth in rimu seedlings occurs from December onwards throughout the hottest months of summer, following the equinox, and growth continues right through late summer and autumn until mean temperatures suddenly drop with the first frosts, usually in June in Rotorua. This is similar to the growth pattern in first year Pinus radiata seedlings in which most height and diameter growth occurs from late December until about mid April in Rotorua (van Dorsser, 1981).

In the Rotorua nursery first year Puroera seedlings did not change colour noticeably with the approach of winter, but height growth and leaf production ceased suddenly in June 1979, when mean monthly temperatures fell from 9.4°C (in May) to 7.6°C and lowest minimum temperatures fell from -0.8°C to -1.6°C. In the same nursery four provenances of seedlings in their second growing season gradually turned brown from about May onwards and ceased height, diameter and dry weight growth similarly in June 1980, when mean monthly temperatures fell from 10.4°C to 6.6°C (Table 3.24). It is concluded that growth in rimu seedlings ceases when mean daily temperatures fall below about 7° or 8°C and all provenances responded to the cooling temperatures of winter in a similar way.

Browning, on the other hand, is caused by low minimum temperatures. Seedlings become brown before the first frosts of the winter and the brown colour may be associated with cold or frost tolerance. In the two experiments in which rimu seedlings were grown in the nursery throughout winter they were protected from severe frosts by shade cloth, but Beveridge (1962), found no damage to rimu seedlings attributable to frosts in the Pureora nursery. Foliage from mature rimu trees collected in mid-winter (July) at an altitude of 90 m in Westland had a freezing resistance of -8°C (Sakai and Wardle, 1978) and small rimu trees are apparently unharmed by frosts, although rimu does not establish in very frosty sites (Katz, 1980). It is possible

that first year seedlings do not become as frost hardy as older seedlings and that establishment of rimu in the open is thus limited to less frost-prone sites or to warmer seasons. However, the fact that first year seedlings did not become distinctly brown, as did older seedlings, does not necessarily mean they were any less cold or frost tolerant. Older rimu trees do not become obviously brown in winter although they are reasonably frost and cold tolerant, but the size or age at which plants change from being winter-brown to being winter-green is not known.

If dormancy in rimu seedlings is simply a state of quiescence imposed by low temperatures, it follows that in climates with mild winters they may not become dormant at all. This is the case in Sweetwater Nursery at Awanui near Kaitaia where rimu seedlings continued to grow slowly throughout winter in mean monthly temperatures not less than $10^{o}C$, with only one or two very light frosts occurring in June or July (J.H. Nicholson, pers.comm). Seedlings from Puketi, where the climate is only a little cooler than Kaitaia were able to survive and grow in Rotorua as well as (or better than) those from Pureora where the climate is much colder and frostier. There did not appear to be any obvious genetic differences in response to changing seasons of rimu provenances from distinctly different latitudes and climates.

Low temperature imposed dormancy in rimu does not require a chilling treatment to be broken (section 3.6.2 b.). Small green seedlings resumed growth soon after being moved to warmer temperatures and this is typical of plants which experience imposed rather than physiological dormancy (Romberger, 1963). However, older seedlings which were distinctly brown from May until the end of October, did not resume growth after winter until they began to lose their brown colour, although mean monthly temperatures had risen above $10^{o}C$ by October (Table 3.24). Growth rates increased in December when plants were fully green and mean temperatures were above $15^{o}C$. The slow return to green colouration in spring or early summer apparently delays the beginning of the growing season. The loss of brown colouration occurs gradually and may be controlled by heat sum (hours x temperature), although increasing photoperiod might also be involved.

There were some apparently genetic differences between certain provenances in the time they began to turn brown, the depth of the brown colour and the time they began to turn green again. For example, Westland seedlings were brown for a longer period during winter and even in January and February were a more bronze-green colour than the other provenances.

While handling seedlings during the course of these studies certain morphological differences between provenances were recognised (Fig. 3.1). Westland seedlings in particular differed from seedlings of the three North Island provenances. (Seedlings from a fifth provenance, used in one experiment in section 3.4 were from Catlins, Southland and more closely resembled those of the North Island provenances, especially Pureora.) Westland seedlings appeared more spindly with shorter, more rigid branches. Their leaves were shorter and sharper to touch than those of the other provenances when grown in the same conditions. Waitakere seedlings also were usually easy to distinguish from the other provenances. In particular their appearance contrasted with that of the Westland seedlings as they were bushier with longer, drooping branches and longer, softer leaves than those of the other provenances. A simple trial was made to determine whether these differences between the Westland and Waitakere provenances were obvious to other people. Five people with little experience of rimu seedlings, independently sorted 60 randomly arranged potted seedlings (30 from Westland; 30 from Waitakere) into groups of similar looking plants. Two scored 90% correct and the mean result was 85.3% showing that morphological differences between provenances were obvious in most seedlings. The trial was made in December when colour differences were minimal and all seedlings had been grown together under 50% shade cloth for 12 months.

Slight differences between provenances were observed in the rate of increase in dry weight, height and diameter with seasonal changes (Figs. 3.38, 3.39 and 3.40). However, it was difficult to determine whether differences were due to provenance or to ontogenetic stage as seedlings were different in size at the start of the experiment. Larger trees have higher absolute growth rates than smaller trees as can be seen by comparing the slope of the dry weight curve for one provenance between February and June 1980 with the slope between February and June 1981 (Fig. 3.38).

To summarise: the seasonal pattern of growth in rimu seedlings is primarily determined by temperature, although increased photoperiod may cause slightly increased shoot extension growth and increase the relative growth rate and unit leaf rate. Low minimum temperatures cause browning in seedlings after the first year, but growth continues in brown seedlings until mean daily temperatures fall below about 7^{o} or 8^{o}C when dry weight, height and diameter growth ceases. The brown colour may be associated with cold or frost tolerance and it remains late into the spring, apparently causing a delay in the resumption of seedling growth until November in Rotorua. Maximum height and dry weight growth occurs in the hottest months and growth continues throughout late summer and autumn. The pattern of growth of the four provenances was similar, although there were distinct morphological differences between Waitakere and Westland provenances in particular.

3.7 Discussion

The first feature of rimu seedlings which is apparent to the student is their slow growth rate. It is well known that most conifers have slower growth rates than angiosperm trees and within conifers species vary in growth rate. For example (Table 3.11, section 3.4.3) Picea abies L.Karst is much slower growing than Larix kaempferi (Lambert) Carriere at the same age. As tree seedlings increase in size their relative growth rate (R) decreases and two year old rimu seedlings have the same R as four year old Picea seedlings, suggesting that growth rate in rimu is slower than in Picea of the same age. Most New Zealand conifers have slow growth rates and many exotic conifers grow much faster in New Zealand than the indigenous species. The relative growth rate of two year old New Zealand kauri, for example, was the same as for two year old rimu, although the kauri was grown at lower light intensity and it is probable that it would grow somewhat faster than rimu at the same irradiance. This might depend on the ontogentic stage and other environmental conditions, however, as Lloyd (1960) in a study in Russell Forest found that in trees over 4 m high rimu grew faster than kauri (and Phyllocladus trichomanoides) until they reached the forest canopy. Growth rate in rimu, therefore, is similar to or somewhat slower than other New Zealand conifers, and slow compared with certain northern hemisphere conifers.

Why rimu grows slowly is not fully understood, but a contributing factor is its low net photosynthesis rate. Light saturated net photosynthesis rates are limited by the resistances to CO_2 diffusion from the air to the site of fixation in the chloroplast. In comparison with Pinus radiata, rimu seedlings have similar stomatal resistances, but much higher internal leaf resistances (residual resistance) (Table 3.4, section 3.3). The residual resistance in rimu was greatly increased in seedlings growing in low night temperatures (Table 3.17, section 3.5) and in these conditions photosynthesis rates and also relative growth rates were decreased, (Tables 3.16 and 3.15, section 3.5) suggesting a relationship between high residual resistance on the one hand and low net photosynthesis and consequent growth rate on the other. Internal leaf resistance may be separated into mesophyll resistance r_m and "carboxylation resistance", r_x. In the analysis used in this thesis the latter two resistances were included in the residual resistance r_r. Some authors (e.g., Chartier, 1970 seen in Tsel' Niker, 1979)

consider r_m to be the more important component of r_r, but others (e.g., Laisk, 1977 seen in Tsel' Niker, 1979) believe r_x to be the dominant component. It is not possible to measure directly either r_m or r_x, but the former may be calculated from some anatomical features of the leaves and r_x can then be estimated as the residual (Tsel' Niker, 1979). Tsel' Niker (1979) examined the various resistances to CO_2 in several angiosperm tree seedlings grown in a range of irradiances from 90% to 0.5% full sunlight and discovered that in leaves grown in high irradiances the three resistances ($r_a + r_s$, r_m and r_x) were all of the same order of magnitude, but r_x values of light demanding species were usually lower than those of shade tolerant species. When plants were grown at low irradiances, however, r_x values were more than 10 times higher than either $r_a + r_s$ or r_m values. It was concluded that low carboxylation activity is probably the main reason for low photosynthetic rates in forest trees, particularly in shade tolerant tree seedlings.

If mesophyll resistance of rimu leaves was calculated from antomical features, carboxylation resistance could be estimated to confirm whether it was the dominant component of the high residual resistance found in the experiments described here. If, as suggested in section 3.5.3, the very high residual resistance found in seedlings grown at low night temperatures (5^{o}C) was caused by disorganisation of chloroplasts, then it is probable that a high carboxylation resistance was involved.

On the other hand the mesophyll resistance of very small diameter needle shaped leaves may be larger than that of thicker leaves. Nobel et al. (1975) examined the relationships between mesophyll cell surface area and external leaf area for leaves of Plectranthus parviflorus Henckel. grown at different irradiances. In thicker leaves grown in high light intensities the ratio of internal to external leaf area was increased and all observed increases in photosynthesis rate could be accounted for by this increase in mesophyll surface area. It was concluded that the development of a thick mesophyll region with a high internal/external leaf area ratio lowers the liquid phase resistance to CO_2 and leads to higher photosynthetic rates. The reverse may apply in the very small diameter leaves of rimu where a low internal/external area ratio may cause high mesophyll resistance which would contribute to low photosynthesis rates.

It is probable that both low carboxylation activity and low internal/external area ratio are involved in the very high residual resistances measured in rimu seedlings. r_r in rimu seedlings can be modified by growing temperature (section 3.5) and growing irradiance (section 3.4). However, many factors are involved in growth and high residual resistances and consequent low net photosynthesis rates are only part of the reason for rimu's low growth rate. Some of the other very important processes on which plant growth depends are respiration, translocation, root growth and leaf growth and development.

A remarkable attribute of rimu seedlings in nature is their extreme tolerance of a wide range of environments. They survive in conditions of very low irradiance, with root competition from larger plants for soil moisture, nutrients and space, and they can also grow in fully exposed conditions on cleared sites following fires or landslips where they may act as pioneers. It is unusual for a species which can tolerate heavily shaded sub-canopy conditions also to be able to grow in sites exposed to full sunlight. In order to survive for long periods in heavy shade with little or no net growth increment rimu seedlings must have the capacity to remain alive while almost all the carbohydrate fixed in photosynthesis is consumed in maintenance respiration. Like many other shade tolerant species, rimu seedlings grown in low irradiance had lower dark respiration rates than seedlings grown in medium irradiances (although the difference was not significant) (Table 3.9, section 3.4). Reduced dark respiration rate may help to conserve carbohydrates.

When rimu seedlings are grown in different environments of either irradiance or temperature their colour changes. Seedlings are green when grown in warm, shady conditions, but they become yellower in higher irradiances and browner in lower temperatures (Fig. 3.11, section 3.4; Fig. 3.22, section 3.5). Existing foliage and shoots change colour as well as new leaves and both the yellowing and browning are accompanied by a loss of chlorophyll and an increase in quantum requirement and light compensation point (Tables 3.7, 3.9, section 3.4; Tables 3.14, 3.16, section 3.5). Growth rate is reduced in brown plants and may be at least temporarily checked in yellow plants. While it is not known whether colour changes are caused by exposure of pigments which are otherwise

screened by chlorophyll, or whether additional pigments are produced, it is suggested that yellowing may be due to carotenoids which are already present in the plastids while browning may be due to new production of anthocyanins or other brown phenolic compounds. Browning may be associated with cold or frost tolerance, but does not occur in very small first year seedlings nor in older trees.

Rimu seedlings thus appear different in colour depending on their growing conditions and they also modify their morphology to suit the environment, becoming taller with few, long branches and long, thin leaves when grown in the shade and bushier with more, shorter branches and short, thick leaves when grown in the sun (Fig. 3.12, section 3.4).

The ability to survive in conditions of low irradiance, soil moisture and nutrient status, in which many other species would die, enables rimu seedlings to persist for many years in sub-optimal growing conditions beneath a forest canopy. In such severe environments rimu seedlings often suffer dieback of branches and the leading shoot, apparently without insect or pathogen cause. In many cases, however, they are able to survive a limited amount of net growth decrement until conditions are ameliorated, usually by modification of the forest structure by windthrow or natural senescence of a canopy tree in the vicinity (A.E. Beveridge, pers.comm.). Extreme tolerance combined with genetically determined slow growth rate and longevity result in the persistence of rimu seedlings and small trees in the forest sub-canopy for many years.

Depending on the irradiance and relative humidity of the microsite in which it germinates, a small rimu seedling will develop foliage morphology suitable to the immediate environment. If shade-grown seedlings experience a very gradual increase in irradiance (often accompanied by a gradual decrease in relative humidity) as the senescing crown of an overhead canopy tree slowly dies, there is sufficient time for new foliage to grow which is morphologically suited to the changed microsite. Every year the new leaves will be thicker, shorter and more able to tolerate the increasing irradiance than the original long, thin, soft leaves of the shade-grown seedling. If, on the other hand, a shade-grown plant is suddenly exposed to greatly increased irradiance, for example following the windthrow of one or more canopy trees in a

storm, there may be an immediate check in growth rate. Rimu seedlings are tolerant of various growing conditions and many of them survive sudden exposure, but because of their existing shade foliage, increased transpiration rates caused by lower relative humidities may cause stomatal closure and reduce the rate of photosynthesis and subsequent growth, until existing leaves have been modified and new leaves grown which are morphologically suited to the new conditions. Because of this it may take some months for a plant to recover from sudden exposure and return to its original growth rate, but in time the increased irradiance, and probably also reduced root competition, will increase rimu growth rate to some extent. Very small soft rimu seedlings can acclimate to changed growing conditions much more rapidly than older, woody seedlings because their relative growth rate and rate of new leaf production is much more rapid (e.g. Table 3.13 a and b, section 3.5).

In a natural environment such as a forest any increase in irradiance is usually accompanied by a rise in mean daytime temperature. Less solar radiation is absorbed by the canopy than before and therefore the air is warmer in the daytime. Any increase in daily heat sum is likely to increase the growth rate of rimu seedlings. Therefore when seedlings have developed suitable foliage for the changed environment, additional warmth as well as additional photosynthetically active radiation may result in an increase in growth rate. If the canopy opening is too large, however, increased daytime temperatures may be balanced by decreased night temperatures and the more extreme environment in terms of daily temperature range, may cause a decrease in growth rate. Possibly small canopy gaps are more beneficial to rimu seedling growth than large gaps because they allow an increase in day temperature without too great a decrease in night temperature. Also the additional irradiance created by small gaps is insufficient to allow fast growing, light demanding species to establish and compete with rimu for moisture, nutrients and light. Small canopy gaps also allow more shelter from wind and frosts than large clearings. In certain circumstances a small opening in the canopy may immediately increase rimu seedling growth rates by raising the mean daily temperature of the microsite before the shade foliage is altered in response to the increased light.

In a study of the ecology and regeneration of rimu (and other species) in the Longwood Range, Southland, Barthgate (1981) referred to rimu as "warmth-demanding" in comparison with certain other tree species in the area. In the current study the tolerance of rimu to extremes of temperature was not examined, but the species was found to be "warmth-preferring" up to a mean daily temperature of at least 19°C. Small, soft seedlings grew best in warm temperature regimes (mean temperature 24°C) (Table 3.13a, section 3.5) and larger seedlings grew best in warm day and night temperatures (mean temperature 18.8°C) where the night was 2°C warmer than the day (Table 3.15, section 3.5). It was concluded that rimu growth rate was determined by the heat sum or mean daily temperature rather than by thermoperiod. However, rimu growth decreased when the night temperature was very low (5°C) (Table 3.15, section 3.5) and it is believed that growth would be decreased by low night temperatures even if day temperatures were high (e.g., 27°C), and consequently the daily heat sum (and mean temperature) was relatively high because low minimum temperatures cause rimu seedlings to become brown and decrease their growth rate.

The effect of warm temperature on promoting growth in rimu seedlings is apparently cumulative. In small first year seedlings height growth rate increased the longer the plants remained in a glasshouse with a minimum temperature of 10°C.

The increased relative growth rate of seedlings in warm mean daily temperatures is accompanied by a reduction in light compensation point and quantum requirement as is shown in Tables 3.15 and 3.16. This implies that rimu may be able to become established and grow in lower irradiances in localities where the climate is warmer than it can in cooler climates. It is not known whether or not this is the case in nature where there are many other variables.

The seasonal growth pattern is apparently imposed on rimu seedlings by temperature (section 3.6) and for this reason seedlings growing in warmer climates with longer growing seasons should have higher annual growth rates than seedlings growing in cooler climates. There did not seem to be any obvious genetically determined autonomous differences in the general pattern of seasonal growth in the Rotorua nursery between the four provenances examined, in spite of very obvious morphological

differences (section 3.6). There was a slight difference, however, in the way in which the Puketi and Waitakere provenances responded to several months growth in moderate day (18°C) but cold night (5°C)) temperatures (section 3.5). These two provenances seem to differ in tolerance to chilling, the more southern provenance surviving prolonged night chilling better than the one from a warmer northern climate. The other possibility, however, is that the particular Puketi plants used were not in a totally healthy condition at the commencement of this experiment. Support for this suggestion comes from a comparison of the light saturated photosynthesis rates in these Puketi plants and Puketi plants grown in an earlier experiment in different irradiance treatments (Tables 3.16 and 3.9; Figs. 3.25 a-c and 3.15 a-c). Photosynthesis rates in the irradiance experiment (section 3.4.2 c) were more than twice the rates in the night temperature experiment (section 3.5.2 b). Similarly a comparison of residual resistances of the same two groups of Puketi seedlings shows that these were very much higher in plants in the night temperature experiment (Tables 3.17 and 3.10). The lowest residual resistance in the latter experiment (in plants grown in warm nights) was 1.7 times as high as the highest residual resistance in the irradiance experiment. The high residual resistances indicate that these plants may not have been in good health. Why this should be is not known, but could be related to the growing conditions of the plants between the times the two experiments were carried out. Alternately the differences could be due to ontogenetic stage of development. Whatever their cause these differences in light saturated photosynthesis rate and residual resistance between two groups of Puketi provenance rimu seedlings measured within six months of each other illustrate the fact that results of physiological experiments should only be compared with great caution. For example, the comparison of rimu with Pinus radiata was made with the Puketi rimus with low photosynthesis rates and high residual resistances. Had the comparison been made at a different time or with rimus from a different provenance the actual results would probably have been different, although general trends would almost certainly have been similar.

A serious problem in this study of the effects of the environment on rimu seedling growth was the fact that even within each provenance individual plants were extremely variable. Because of this innate variability and

slow growth rate, large numbers of replicates would be needed before significant differences in growth rate caused by different environmental conditions would become apparent. June (1982) also referred to great variability in height growth rate between individual rimu seedlings growing in a Westland forest. The size differences within each provenance used in the present study were probably partly due to the differing time taken for germination of different seeds as well as inherent genetic differences in response to the environment, between individual seedlings.

The use of rooted cuttings or tissue cultured clones of rimu replicates might enable differences in response to environmental variables to be determined more readily, but the results would only indicate the behaviour of the particular cloned individual. The fact that there is such great genetic variability in each generation of rimu, not only in rate of seed germination, but also in growth rate in any particular environment, is of great importance to the survival of the species.

In this chapter the response of rimu seedling growth to different growing irradiances, temperature regimes, photoperiods and changing seasons were examined. The seedlings were shown to be capable of growing in a wide range of irradiances and temperatures, but to grow best, in terms of dry weight increment, at higher irradiances and temperatures while they are small and soft, and at somewhat lower irradiances and temperatures when they become woody. The optimal conditions of irradiance and temperature for growth may be influenced by growing conditions preceding the growth experiment because of the existence at the start of the experiment of foliage morphologically suited to the original conditions. Response to photoperiod varied slightly between provenances, but was much less marked than in most northern hemisphere conifers and all provenances had similar seasonal patterns of growth in terms of dry weight, height and diameter increase.

CHAPTER 4 : GENERAL DISCUSSION

Rimu is a very successful forest tree with a long history in the New Zealand flora. In the 80 million years during which rimu has been abundant throughout the country, New Zealand has been a changing island archipelago surrounded by ocean and therefore experiencing an equable maritime climate (Mildenhall, 1980; Fleming, 1979). During the Tertiary, prior to the cooling of the late Pliocene and the glaciations of the Pleistocene, the climate is believed to have been warmer than (or at least as warm as) the present and rimu, therefore, grew in a sub-tropical to warm temperate climate for much of its history. The fifteen other species of the genus Dacrydium Sol. ex Lamb. emend. de Laub. which are closely related to D. cupressinum all have present day distributions in tropical or sub-tropical climates. They occur in the islands of New Caledonia, Fiji, the Solomons, New Guinea and in Indonesia, Thailand and Southern China (Quinn, 1982). (The remaining New Zealand species which were formerly classified as Dacrydium are not closely related to rimu and have recently been reclassified into new genera (Quinn, 1982).)

Today rimu is widespread throughout most of New Zealand, occurring in many different forest types often as a dominant species (e.g., Nicholls, 1976). It grows in a very wide variety of sites from the edge of swamps to relatively dry slopes and from close to sea level to altitudes of up to 900 m in the north and 450 m in the south and is the most widely distributed of all indigenous forest trees (Nicholls, 1982 in press). The species, therefore, must have the ability to reproduce and become established in many different environments. This thesis examines seed production and the early growth of rimu seedlings in a variety of environmental conditions. Detailed discussions of experimental results have been given in earlier chapters. The present discussion is concerned with reproduction and seedling establishment in rimu in relation to the present day ecology of the species.

Individual mature female rimu trees do not produce seed every year. Generally there are several years between good seed crops, although occasionally two good seed years occur in succession (e.g., Beveridge, 1964; 1973). As has been described in Chapter 2 ovule and seed

production spans two years from the probable time of initiation to the time mature seed are shed in autumn. The production of a large crop of seed uses a large proportion of a forest tree's carbohydrate reserves and often several growing seasons are required to build up these reserves to a level where numerous ovules can be initiated again (Kozlowski, 1962). In rimu, however, even when many ovules are initiated and become visible in late spring, a good seed crop eighteen months later is not guaranteed. Many young ovules, before or after pollination, fail to develop for reasons which are not yet known, but the major cause of the production of empty seed in rimu has been shown to be lack of pollination, followed later by failure of fertilisation (Chapter 2). In certain years a large proportion of rimu seeds are found to be empty, although full-sized and this is almost always due to failure of pollination 15-18 months earlier. Successful pollination in a dioecious, wind pollinated species depends on suitable weather during the short period of pollen shed and ovule receptivity and therefore failure of pollination is commonly caused by wet weather at that time (e.g., Sarvas, 1962).

Despite the infrequency of potentially good seed crops and the production of many empty seed, each female tree produces numerous sound, fully developed seed during its reproductive lifetime of several hundred years and consequently the regeneration of rimu is seldom, if ever, limited by lack of sound seed.

This study did not examine rimu seed dispersal, but it is well known that a large proportion of seed falls below or close to the parent tree, dispersed by gravity and wind (e.g., Franklin, 1968) and that some seed is transported away by frugivorous birds.

Early botanists in New Zealand observed the rapid establishment of rimu along new forest roads and fire induced ecotone areas at the edge of tall forests and formed the opinion that rimu (and other podocarp trees) were light demanding. Because of this they hypothesised that podocarps could not perpetuate themselves in undisturbed mature forests (Cockayne, 1958; Robbins, 1962). Cockayne (1958) however, also noticed that there were often a certain number of small sub-canopy rimu trees and seedlings surviving, although growing extremely slowly in the shade of the mature

forest canopy and these trees he referred to as "lingerers". Seedlings and small tree stages of forest trees which are able to survive and grow under a forest canopy are termed "tolerant" (Spurr and Barnes, 1973) and rimu seedlings fall into this category. While many tree seeds may germinate and the seedlings survive for a few years in the shade of a forest canopy, only tolerant species are able to persist and grow slowly for decades in such a position.

The seed of rimu is relatively small, being only about 4 mm long. Many trees with shade tolerant seedlings, for example miro (Podocarpus ferrugineus G. Benn. ex D.Don) and tawa (Beilschmiedia tawa (A.Cunn) Benth. et Hook.f.) have larger seeds with relatively greater stores of carbohydrates to support the seedling while it becomes established in a shaded microsite where, as well as irradiance being limited, space, water and nutrients are reduced in the soil by the presence of numerous other roots. In comparison with these larger seeded species the initial seedling of rimu is extremely small with a minute radicle which can only penetrate a short distance into the litter on the forest floor before the food reserves in the seed are exhausted. If plant growth is regarded in terms of compound interest, the plant's initial dry weight is its capital investment and the relative growth rate is the current rate of interest (Blackman, 1919; Sweet and Wareing, 1966). Small seeded plants have a smaller initial dry weight than larger seeded plants and are therefore at a disadvantage from the time of germination, even if they have the same relative growth rate. In the case of rimu not only are the initial seedlings very small, but their relative growth rate is very low (see, for example Table 3.11, section 3.4.3).

Many of the rimu seed which fall in autumn close to the parent tree germinate the following spring in a thick layer of leaf litter, but because of their small size and slow growth rate a large proportion of these seedlings succumb to drought during summer as their roots do not have time to penetrate the litter to moister soil below (A.E. Beveridge, pers.comm.). However, certain seedlings which land in damper microsites, succeed on the forest floor and others are able to grow on logs and stumps where root competition is limited (e.g., June, 1982). In these ways some rimu seedlings become established in the shade of their parent's canopy and they may survive, often with little or no net growth increment for many years: the "lingerers" described by Cockayne in 1928 (Cockayne, 1958).

These "lingerers" form a bank of persistent seedlings on the forest floor (or on logs) and are capable of surviving at very low irradiances. In section 3.4 two year old seedlings survived for seven months outdoors in 1% full sunlight and it was concluded that in nature rimu seedlings could establish in irradiances at least as low as 2% full sunlight. When a canopy gap is created in a forest which allows an increase in irradiance, the suppressed "lingerers" respond gradually by increasing their growth rate even after many years in heavily shaded sites (e.g., Beveridge and Franklin, 1977). From the point of view of the survival of the species infrequent seeding is no problem while there is a supply of seedlings surviving for many years below the canopy (Grime, 1979). The experiments in this study were not designed to demonstrate the improvement in growth which occurs when suppressed rimu seedlings are exposed to higher irradiance, but small seedlings were shown to increase their relative growth rates with increased irradiance up to 73% sunlight (section 3.4). Because the seedling can tolerate very low irradiances, but can also grow in high irradiances, rimu trees may be recruited to the forest canopy in several different ways. The species may replace itself in (or above) the forest canopy by slow continuous recruitment: seedlings establish and the trees grow very slowly in the shade, possibly for several hundred years, depending on the height and density of the canopy, eventually growing through and overtopping an existing healthy canopy (Lloyd, 1960). Alternatively, aging canopy trees may senesce and slowly die, allowing an increase in irradiance and causing an increase in rimu growth rate. This type of continuous recruitment was found to be the most frequent type of regeneration in rimu growing in certain sites in North Westland (June, 1982).

This type of recruitment of forest trees into the canopy occurs in forests in many parts of the world. For example, in North America, hemlock trees suppressed by a heavy overhead canopy had diameter growth rates of approximately 0.8 mm $year^{-1}$ for 108 years. When the canopy was removed by logging, however, the diameter growth rate rapidly increased and averaged 6.4 mm $year^{-1}$ for the next 80 years (Marshall, 1927). Similarly in Sweden, small spruce trees, surviving but suppressed beneath a canopy of mature spruce may be only 1000 mm high after 50 years. However, if a storm creates a canopy gap, these dwarfed trees are

able to utilise the additional irradiance (and benefit from the reduced root competition) and rapidly improve their growth rate, greatly increasing their annual diameter and height increments (Sernander, 1936).

Because an increase in irradiance at least up to a certain optimal level, causes an increase in the growth rate of rimu, the creation of canopy gaps may hasten the speed with which rimu seedlings and small trees reach the canopy. This applies particularly where the gap is created to one side of the advanced rimu regeneration and not directly above it (June, 1982). When a canopy gap is formed angiosperm shrubs and trees rapidly grow into a thicket and any rimu seedlings which established either before or immediately after the gap was made are soon suppressed by shading and root competition. Therefore, the creation of a canopy gap may only temporarily increase the growth rate of small rimu trees and seedlings. However, if the gap is small enough, or to one side, the additional irradiance may be sufficient to improve the growth rate of rimu seedlings, but insufficient to allow the establishment of light demanding angiosperm trees and shrubs. Small overhead canopy gaps or larger gaps to one side may thus allow rimu trees to reach the canopy sooner than when no gap is created (June, 1982).

There is other evidence that small, suppressed rimu seedlings respond to increased irradiance by increasing their growth rate. When new forest roads are built, small seedlings already in existence alongside the roads increase their growth rate rapidly in response to the increased light and reduced root competition (A.E. Beveridge, pers.comm.), and similarly, in plantations, if rapidly growing ground and tree ferns are removed, rimu seedlings respond with increased growth rates (Beveridge, 1973).

As well as being able to establish in heavy shade and survive until conditions improve, rimu also establishes and grows well in situations of higher irradiance. For example, new seedlings often germinate and establish on the edges of new forest roads and logging tracks where increased light, together with the scarified soil surface create a suitable microsite (Beveridge, 1973). Beveridge (1962) showed that high light intensities (close to full sunlight) were not harmful to rimu seedlings in a nursery if they were protected from wind and kept well watered, and in the present study small rimu seedlings were shown to grow

well at relatively high irradiances (73% sunlight, section 3.4). The best growth rates in plantations of rimu seedlings were found in canopy gaps of 10 m diameter providing faster growing ferns and shrubs were kept clear (Beveridge, 1973). The indications are, then, that rimu growth increases with increasing growing irradiance and the seedlings are not damaged by high irradiance. However, the maximum growth rates in rimu are low compared with the rates of most ferns and angiosperm shrubs and trees. Therefore, rimu seedlings are usually found in the shade because, even if they establish in the open, faster growing plants soon overtop them. Also, because rimu seedlings have low light compensation points they are shade tolerant and able to survive at low irradiance.

When shade grown rimu seedlings are suddenly exposed to increased irradiance their growth rate may not be increased immediately. There was an initial check in the growth rate of rimu which had established below a kamahi stand when the kamahi canopy was artificially killed. However, after two or three years the growth rate improved (Beveridge, 1973). Best growth rates of woody seedlings in the experiments in section 3.4 were found in the intermediate irradiances used. Had the experiments been continued, after perhaps a year or more the foliage might have been modified to suit the new conditions and growth rates in the high irradiances might have increased. Most field evidence indicates increased growth rates (in diameter at least) with increasing irradiance up to full sunlight.

Although rimu usually establishes in shaded sites for reasons mentioned above, it is also known to be capable of establishing and growing in full sunlight in certain conditions. For example, where forest has been destroyed over a wide area by landslip or burning, rimu may act as a pioneer species (e.g., June, 1982). The rimu seedlings may occasionally develop, without suppression, directly, but slowly into mature forest trees.

As in many other species the shape and form of an individual rimu seedling is partly determined by the conditions in which it was grown. In very low irradiances, close to light compensation point, under a forest canopy, growth is minimal and the plant is weak with small diameter relative to height and a poorly developed root system (e.g.

Fig. 3.7 and Table 3.5, section 3.4). What little growth there is is concentrated in height increase and leaf production. At higher irradiances rimu growth rates increase, but height growth continues to predominate over diameter growth while the seedling is below canopy level and the plant grows relatively tall and slender with few, long, narrow, drooping branches (table 3.5). Lloyd (1960) found that rimu had height growth rates comparable with and sometimes faster than those of kauri and tanekaha when growing beneath a moderately dense canopy, but when rimu broke through the canopy, or the canopy trees began to die and more light was allowed through, rimu's height growth slowed down. Exposed rimu crowns and open grown rimu trees are heavily branched and therefore Lloyd (1960) concluded that a very tall overhead canopy was necessary to produce rimu trees with long clean boles. Similarly Cameron (1960) concluded that a Leptospermum canopy would not have been tall enough to produce the tall mature rimu forests existing in Whirinaki today. It may be possible to detect the successional history of a stand of mature rimu trees from their height and form.

If rimu is able to establish in irradiances from less than 2% to 100% full sunlight what are the features of the environment which limit the distribution of rimu? This thesis did not examine the effect of water or minerals on the growth of rimu seedlings, but the effect of growing temperature was studied. Temperature is one of the most significant features of the environment of a plant and has a major influence on all physiological activities. Because New Zealand is a group of islands most of the low altitude parts of the country have a relatively mild, even, maritime climate, but certain inland areas such as central Otago and parts of inland Southland have a continental type of climate (Coulter, 1975). Rimu is absent from these areas and from high altitudes where there is a wide range of temperature both between day and night and summer and winter (Franklin, 1968; Coulter, 1975).

Seed germination and the initial establishment of the seedlings are the vital stages in determining the limits of distribution of a species, and early growth of rimu seedlings is more rapid at higher temperatures as shown in the small Pureora seedlings (Table 3.13 b). New seedlings must have a long enough growing season to enable them to build up carbohydrate reserves to last through the winter when photosynthesis is reduced or ceases.

Dormancy in rimu seedlings is not triggered by decreasing or short photoperiods, but is imposed directly by low temperatures and therefore the species is restricted to areas which do not experience unseasonal early autumn frosts (section 3.6). Rimu growth continues throughout autumn until mean daily temperatures fall to 7^{o} or 8^{o}C and in seedlings after the first year and for a number of years, browning precedes dormancy in regions of New Zealand with relatively cool winters. Browning is accompanied by a loss of chlorophyll and a decrease in growth rate and apparently delays the resumption of dry weight, height and diameter growth after winter until November or December (sections 3.5 and 3.6).

Prolonged periods of low mean or nighttime temperature (e.g., 5^{o}C) may lead to the cessation of net photosynthesis and ultimately to death in small rimu seedlings thus limiting the locations in which rimu can become established. For example, Barthgate (1981) found that rimu was being replaced by angiosperm trees in the relatively drier parts of the Longwood Range where the range of temperature between seasons is widest. The sudden onset of severe frosts and the coldness of the winter, rather than the temperature range as such, limits rimu regeneration from occurring in regions with more continental or mountain climates (section 3.5). Rimu regeneration is limited to regions where the temperature decreases relatively slowly with the approach of winter, severe autumn frosts are uncommon and low minimum temperatures do not continue for too many months. Different provenances may be adapted to their local climates to some extent as indicated by the death of several Puketi but no Waitakere seedlings in the thermoperiod experiment (section 3.5).

There are some distinct morphological differences between certain provenances of rimu seedlings. In this study three of the most widely separated provenances were most similar to each other in appearance: Puketi (35^{o}S), Pureora (38^{o}S) and Catlins (46^{o}S). The Waitakere provenance, located at latitude 36.5^{o}S, between Puketi and Pureora, was somewhat different from any of the other provenances examined, but the most uniquely distinctive seedlings were from the Westland provenance (42^{o}-44^{o}S). These had shorter, sharper foliage and shorter, less

drooping branches than the other provenances grown in the same conditions and were always less green, being brown for longer in winter and bronze-coloured during summer (section 3.6.3).

In spite of the morphological differences between the provenances used in this study, there were no obvious genetically determined differences in their patterns of seasonal growth. However further, more extensive provenance trials are recommended to confirm these findings as conclusions regarding mature trees should not be made by extrapolation from the behaviour of seedlings (Wareing, 1956).

In the various experiments in this study and in other studies of rimu seedling growth (e.g., Beveridge, 1962; 1973), seedlings have been shown to be always relatively slow growing, but extremely tolerant of a wide range of growing conditions. The regeneration of rimu is seldom limited by inadequate seed production and dispersal and the species is able to establish in many different irradiances and a wide range of temperatures wherever the climate has sufficient rainfall and is not too cold in winter.

The only way in which a slow growing tree such as rimu can survive in competition with numerous faster growing plants is by extreme tolerance combined with longevity. Because of their tolerance the seedlings are able to establish in a wide range of environments and therefore rimu is a generalist species with a wide ecological amplitude. It is inevitable that this tolerant, slow growing, long-lived species will be extremely widely distributed in diverse forest types, and will eventually become dominant in many of them if they remain undisturbed long enough. Prior to the arrival of man, only periods of severe deterioration in the New Zealand climate had limited rimu distribution and dominance of lowland forests during the 80 million years of its history.

APPENDIX 1

GROWTH ANALYSIS FORMULAE

Relative Growth Rate, R

Instantaneous relative growth rate is given by the formula

$$R = \frac{1}{W} \cdot \frac{dW}{dT} \qquad 1$$

where W is the plant dry weight and T is time.

The mean relative growth rate between times T_1, and T_2 is given by the formula

$$\bar{R}_{1-2} = \frac{\log_e W_2 - \log_e W_1}{T_2 - T_1} \qquad 2$$

Unit Leaf Rate, E

Instantaneous unit leaf rate is given by the formula

$$E = \frac{1}{L} \cdot \frac{dW}{dT} \qquad 3$$

where L is the total leaf area. (The assimilatory material may alternately be measured as the total leaf dry weight, Lw.) The mean unit leaf rate between times T_1 and T_2 is given by the formula

$$\bar{E}_{1-2} = \frac{W_2 - W_1}{T_2 - T_1} \cdot \frac{\log_e L_2 - \log_e L_1}{L_2 - L_1} \qquad 4$$

Unit leaf rate has also been called "net assimilation rate".

Leaf Area Ratio, F

Leaf area ratio is given by the formula

$$F = \frac{L}{W} \qquad 5$$

If leaf weight rather than leaf area is measured then the leaf weight ratio is similarly defined as

$$F_w = \frac{Lw}{W} \qquad 6$$

E and F evolved as subdivisions of R so that by definition

$$R = E.F \qquad 7$$

or

$$\frac{1}{W} \cdot \frac{dW}{dt} = \frac{1}{L} \cdot \frac{dW}{dT} \cdot \frac{L}{W} \qquad 8$$

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