EFFECTS OF SOME ENVIRONMENTAL FACTORS ON ROOT REGENERATION POTENTIAL AND GROWTH OF SEEDLINGS OF *PINUS CARIBAEA* MOR. AND *PINUS KESIYA* ROYLE EX GORDON

BY

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ORIGINALITY OF THESIS

Except where acknowledged the research work reported in this thesis is entirely that of the author.

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ABSTRACT

The increasing world demand for wood has prompted wide scale establishment of plantation forests especially in the tropics and subtropics. Successful plantation establishment requires the production of seedlings with high root regeneration potential (RRP) to be planted in an environment which facilitates the production of new roots. This study examines in particular, the fundamental requirements for root regeneration of two economically important *Pinus* species native to the tropics and subtropics. A study of the relationship between photosynthesis and plant RRP was conducted in some of the experiments.

The technique of Stone and co-workers (Stone, 1955; Stone and Schubert, 1959a and 1959b; Krugman and Stone, 1966) was used to assess the RRP of plants grown for a standard length of time in varying conditions of light, nutrients, air and soil temperatures. The results are expressed as root regeneration potential based on number (RRP_N) and as length (RRP_L) of new roots per plant.

In most of the experiments, regenerated roots were classified into newly initiated roots and those which elongated from old roots. It was found that the RRP of plants is dependent upon both its ability to activate the many shoot roots (old roots) left after the root pruning treatment and to initiate new roots on the old roots.

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CHAPTER 1

INTRODUCTION

1.1. *General*

Demand for wood is rising so rapidly that the capacity of many of the traditional sources of wood to maintain supply is now being severely strained. Consumption of wood and wood based commodities has increased in recent decades, largely due to an increasing world population and will continue to rise leading eventually to a substantial world wood deficit (Osara, 1967). The most recent F.A.O. survey shows that there will be a shortfall of about 200 million m^3 of wood by the year 2000; the total demand for wood will be of the order of 4000 million m^3, of which one-third will be required for pulp and paper (Keays and Hatton, 1975). The trends in the world consumption of pulp and paper alone indicates that in 1985 annual consumption will almost double that of 1973 to 800 million m^3 (King, 1975).

To meet these increasing demands for forest products, it is necessary to increase the production of timber by intelligent and intensive management of the present forest resources and by afforesting areas of low productivity. In addition, the F.A.O. has stressed that maximum advantage will have to be taken from fast growth rates in the tropical and subtropical regions to grow more wood.

The bulk of man-made forests are located in the temperate regions despite the fact that the mean annual increments for plantations in these

regions are considerably lower than in the tropics and subtropics. For example, in the north temperate zones and in the Mediterranean countries with a pronounced dry season, the mean annual increment for conifers is between 2 and 5 m^3 per ha per yr; in the tropics and subtropics, the annual increment varies between 15 and 30 m^3 per ha per yr (King, 1975). More specifically, there are many areas lying between 30° north of the equator to 30° south in which *P. caribaea* Mor. gives an annual increment of from 17.5 to 21 m^3 per ha per yr under bark, up to the age of 15 years at least (King, 1975). These rates of growth permit very short rotations of plantation forest, for example, 10 to 15 years for pulpwood; in the temperate they generally take 20 to 30 years.

Within the tropical region, the rising demand by agriculture for the better lowland soils, the low increment of tropical forest, difficulties faced in natural regeneration of the hardwood forests and the rapid utilization of these forests, have focussed increasing attention on plantation forests as a means of meeting timber and pulpwood needs. Because of its variability and adaptation to lowland tropical sites, *P. caribaea* has become the most important pine for commercial plantations in tropical areas (Lamb, 1973).

1.2 *Aim and scope of study*

The present study was of a fundamental nature to study the requirements for root regeneration of two economically important *Pinus* species native to the tropics and subtropics. The effects of some environmental factors on growth were studied with particular emphasis on the root regeneration potential (RRP) of *P. caribaea* Mor., a lowland species, and *P. kesiya* Royle ex Gordon, a montane species. Many workers (Stone and Schubert, 1959a; 1959b; Smith, 1962; Stoeckeler, 1970) have stressed that the initial survival of planted seedlings depends chiefly on the ability of their root systems to regenerate in the first

few weeks after outplanting to re-establish contact with the surrounding soil mass promptly and to tap its water and nutrients. Lack of top development, on the other hand, probably would not become critical in itself during the first year after planting (Stone, 1955). Successful plantation establishment requires the production of seedlings with high RRP to be planted in an environment which facilitates the production of new roots. Knowledge of the response of tree seedlings to the environmental factors can have practical importance in planning species introduction programmes and in selecting suitable nursery and plantation sites. These management practices can reduce the establishment cost, a necessarily high investment incurred in the production of a forest crop (Smith, 1962).

Until recently, soil moisture and soil temperature appeared to be the principal external factors controlling root elongation of undisturbed plants (Morrow, 1950), but recent reports suggest that air temperature (Bagley and Read, 1960) and light intensity (Stone, 1967) may also affect root elongation. Recent nursery practice, especially on the *Pinus radiata* D. Don. in New Zealand (Rook, 1972) has focussed attention on the worth of root pruning to produce 'hardened' seedlings with a mass of fibrous roots capable of rapid proliferation in the field. The ability of root-pruned seedlings to regenerate a new root system following transplanting to the field may be different from the root elongation of undisturbed plants (Krugman and Stone, 1966). We might reasonably expect that all the external factors which influence RRP of undisturbed plants would also exert some influence on the subsequent root regeneration capability of transplanted seedlings. The

impact of nutrient deficiencies, light intensity, and of both air and soil temperatures on the RRP of root-pruned seedlings are evaluated separately in this study.

CHAPTER 2

MATERIALS, FACILITIES AND GENERAL METHODOLOGY

2.1 *Introduction*

This chapter outlines the materials, facilities, experiments conducted and general methodology of the experimental work.

2.2 *Materials*

Two species were used in most of the experiments conducted. One is *Pinus kesiya* Royle ex Gordon which is a montane species and the other *Pinus caribaea* Mor. var. *hondurensis* Barr. and Golf. which is predominantly a lowland species. Both species inhabit tropical and subtropical environments. The natural distribution of the two species and their economic importance are described in Appendix I.

2.2.1 *Pinus kesiya*

Seeds of *Pinus kesiya* were supplied by the Forest Research Institute, Canberra. The seeds were collected near Mount Agapang in the Central Cordillera mountains, Luzon Island, Phillipines at latitude 17° 33' N, longitude 120° 57' E and from an altitude of about 1300m above sea level. Details of the species distribution, climate and economic importance in the Phillipines are given in Appendix IA.

2.2.2 *Pinus caribaea* var. *hondurensis*

Seeds of *P. caribaea* var. *hondurensis* were supplied by the Queensland Department of Forestry, Brisbane. The seeds were collected from open pollinated, high-pruned crop trees in Maryvale, Queensland

at latitude 23° 48' S, longitude 150° 12' E and from an altitude of 20 m above sea level. The species originated from the lowland coastal plain of Belize (British Honduras). Information on the original provenance was not supplied to the author.

Seedlings used in all experiments were grown by the author except for the Air Temperature Experiment (chapter 5). In this experiment the seedlings were grown at Toolara nursery, Queensland in 1974 and shipped to Canberra by air when they were 16 weeks old (from sowing).

Details of the species distribution and climate in Belize are given in Appendix IB. The meterological record of Toolara, Queensland for 1974 is given in Appendix II.

2.3 *Facilities*

All experiments were conducted at the CERES phytotron in Canberra (the facilities of CERES are described in detail by Morse and Evans (1962)). The facilities included open-glasshouses, artificially-lit growth cabinets (type LB), soil temperature units (types I and II) and Infra-red gas analyser (type 225 MK II) manufactured by the Infra-red Development Company, England.

(i) Glasshouses

Both temperature and photoperiod in the glasshouses are precisely controlled. Day and night temperature regimes are alternated in a square wave pattern with day temperature held at one level for eight hours (0830 to 1630 hours) of the daylight period and night temperature held at a level 5° lower for the remaining sixteen hours. The temperature of the rooting medium was found to approximate the ambient air temperature, differing at both day and night by less than 1° C. Relative humidity is always higher than 40 per cent. The photoperiod is extended to 16 hours by low light intensity incandescent lighting with an illumination of 25 fc at plant height.

(ii) Controlled environment cabinets (Type LB)

The LB growth cabinets allow precise control of temperature, photoperiod and light intensity. The cabinet provides constant temperature control at any temperature in the range 0-35^0 C. It is artificially lit by an arched sealed canopy of 28 TL - 33 high output, internal reflector, fluorescent lamps, and four incandescent lamps, which are connected to a time switch for photoperiod control. Light intensity is regulated by switching out pairs of the fluorescent tubes. With new tubes up to 100 watts. m^{-2} (4000 fc) can be obtained in the plane 30 cm below a glass sheet which separates the light panel from the plant-growing space.

(iii) Soil temperature units

Two types of units were used. Type 1 (shown in Fig. 2.1) was installed in a LB cabinet and type II (shown in Fig. 2.2) was situated in the open-glasshouse.

The temperature of each water-bath in both type I and II units was checked twice daily and adjustment made when the temperature was not equal to the set temperature. The temperatures of the rooting medium in both types of water-bath were measured at two points by copper-constantan thermocouples with the cold junction at 0^o C. One thermocouple was placed near the centre of the pot/bath and the second was placed 0.5 cm from the side at half the rooting medium depth. Preliminary studies showed that the vertical differences in soil temperature did not exceed 1.0^o C and lateral differences were usually less than 0.5^o C for all ranges of water-bath temperatures used. All water-baths were stirred continuously by 'Braun' thermomixes to avoid temperature gradients developing in the baths.

(a) Type I units

The first type of soil temperature units were situated in the controlled environment cabinet — two units per cabinet. The diagram of these root tanks (shown in Fig. 2.1) was copied from a CSIRO Division of Plant Industry unit in use at CERES and modified for the present work by the author and J. T. Stupendick. Each unit is a tank containing 8 copper pots in which the seedlings were grown. The bottom of the pots are sealed except for a small hole (1 cm diameter) by means of which they are inserted into two parallel metal pipes (4 pots per pipe) which also act as a drainage system, draining excess water and nutrients from the pots to the outside of the tank. The tank was filled with water and the temperature was lowered by circulating water containing glycol antifreeze from a refrigerated unit through copper coils lining the inside walls of the tank. Each tank was fitted with a 'Braun' thermomix, a thermostatically controlled heating/circulating unit which heated and circulated the water at the desired soil temperature. Adequate spacing between the pots ensured uniform temperature around them.

Each pot has a diameter of 16 cm and depth of 20 cm. The surface inside the copper pots was coated with 'Brushable Hydroseal' (Paboo quality, No. 155) to prevent any toxic effects of copper from affecting the plants. In each pot two seedlings were grown in 1:1 perlite:vermiculite mixture. Competition between plants in the pots was unlikely because they had adequate space, water and nutrients. After transplanting the seedlings to each pot, the top of the pot was covered with aluminium foil to insulate the rooting medium from the ambient environment. Adequate space around the stems of the seedlings ensured sufficient aeration of the roots.

(b) *Type II units*

These units (shown if Fig. 2.2) were kindly made available by Mr. J. D. Williams of CSIRO Division of Plant Industry.

Four water-baths were mounted on a bench fitted with a refrigeration unit underneath. The bench was mobile and the whole system (Fig. 2.2.) could be moved from one glasshouse to another. Subambient soil temperatures were maintained by immersing insulated water-baths in water maintained at a lower temperature than required. The water was cooled by copper coils lining the inside walls of each bath and carrying brine pumped from a tank. The brine was cooled by the refrigeration unit. Insulation and thermostatically-controlled heating by "Braun" thermomix enabled soil temperatures to be heated to the desired temperature and maintained independently of ambient temperature in the glasshouse.

The baths were made of plastic and each bath has a dimension of: length 42 cm, width 27 cm and depth 16 cm. The baths were filled with 1:1 perlite:vermiculite mixture and a maximum of 15 seedlings could be grown in each bath. However, the number was usually restricted to 12 to prevent overcrowding and mutual shading of the seedlings. Competition among the seedlings was unlikely as they were given adequate water and nutrients. Excess water and nutrients were siphoned out of the baths twice daily. When the species were studied simultaneously, each bath was divided into two compartments by a thin sheet of polystyrene and the species grown spearately to prevent competition between species. The seedlings were grown in rows and a cover of compressed asbestos (10.7 cm thick) was fitted between the rows providing efficient insulation of the rooting medium from the ambient environment. Thus, the

Figure 2.1 Two views of type I soil temperature units in LB growth cabinet. A shows that two taps, one for each tank, control the flow of glycol antifreeze from the refrigerator. Note the 4 orange 'drainage' rubber tubes. Each tube is connected to the open end of a hollow metal pipe into which 4 pots are inserted in a row. B shows a closer view inside the baths. Two parallel pipes with holes for insertion of the pots are visible in the tank on the left side. The copper coils which circulate the glycol antifreeze can also be seen inside this tank. The tank on the right side was filled with water. A 'Braun' thermomix heats and circulates the water to a set temperature. A thermometer attached to the thermomix was used to check the temperature of the bath twice daily. Note the thermocouple inside the pot used to check the temperature of the rooting medium.

effects of a range of soil temperature on growth could be studied independently of the direct effects of temperature on the shoot.

Figure 2.1 A

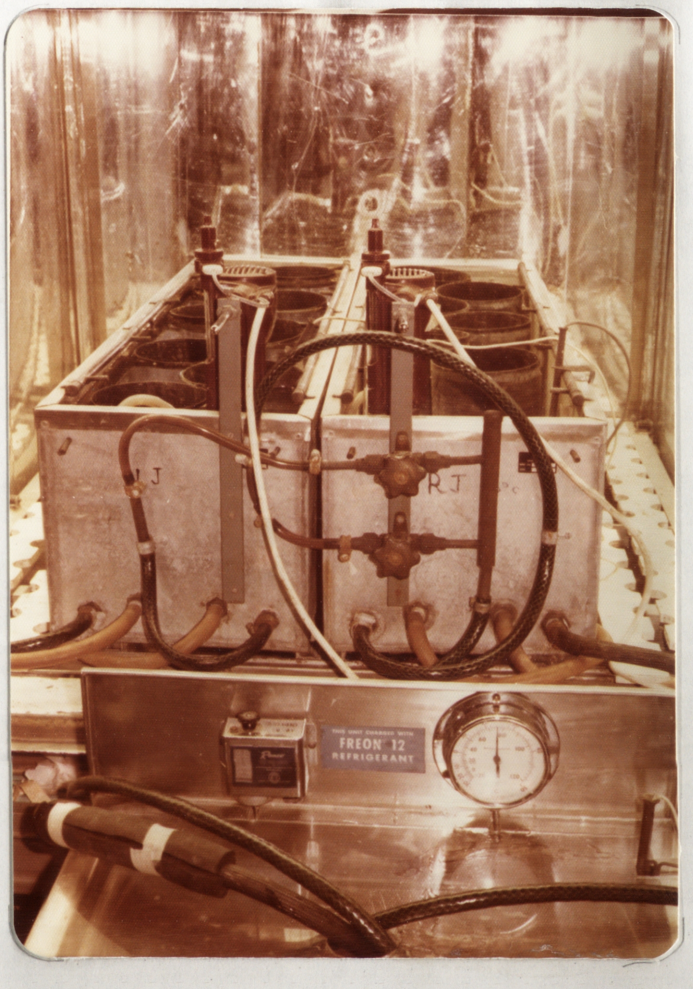

Figure 2.1 B

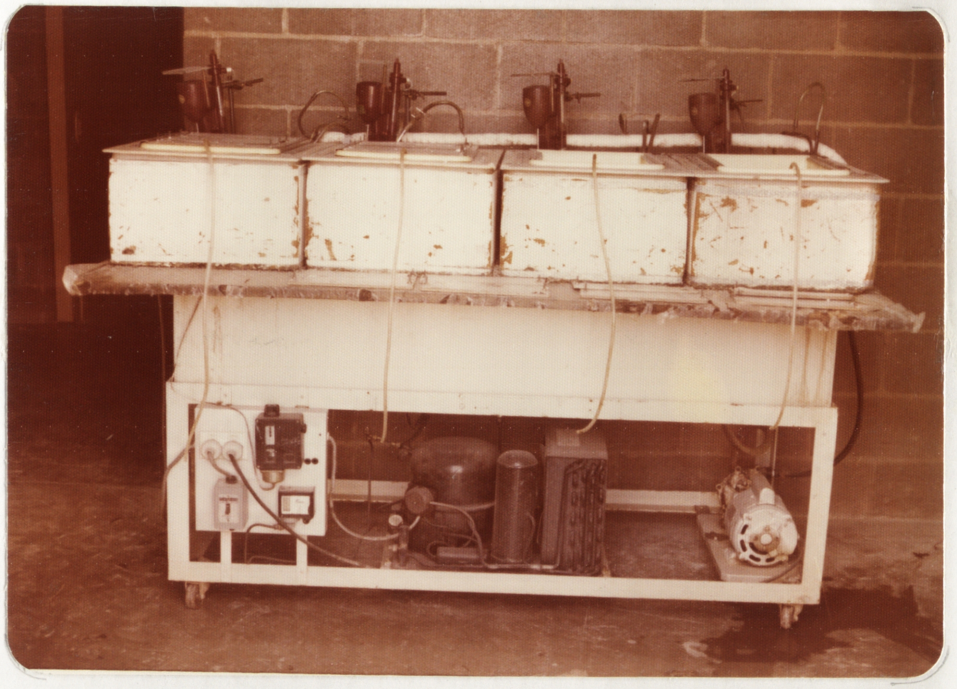

Figure 2.2 Type II soil temperature units. A tank of brine was cooled by the refrigeration unit below and was pumped through copper coils lining the inside walls of each bath. A 'Braun' thermomix, a thermostatically controlled heating/circulating unit heats the water in each bath. A rubber tubing from each bath was used to siphon excess water and nutrients from the rooting medium. Note the compressed asbestos (4 per bath) used for insulating the rooting medium from the ambient environment.

(iv) Gas exchange technique

Air at normal CO_2 concentration (300 p.p.m.) was pumped through a cuvette at a flow rate of 11.5 litres per minute. To enclose the entire crown, a large cuvette (30 x 30 x 50 cm) was used. Samples of air at the rate of 600 ml per min were drawn from the air stream before entering and after leaving the cuvette and passed through the infra-red

gas analyser for differential analysis. Differences in the CO_2 content of the sample and reference streams were displayed on a Tohshin Electron recorder.

Gas exchange was measured at light intensities of 25 watts. m^{-2} (1000 fc) and 75 watts. m^{-2} for Light Intensity Experiment (chapter 4), and at 75 watts. m^{-2} for Soil Temperature Experiment (chapter 6). The air temperature was 27^{o} C. Both the light intensity and air temperature were measured inside the cuvette. Light intensity was measured at plant height using an 'Eel' portable photoelectric photometer while the air temperature was measured by a thermocouple. A fan in the cuvette circulated the air around the plants.

2.4 *General methodology*

2.4.1 *Seed storage and fumigation*

Seed was stored in opaque air-tight containers in the cold (4^{o}C). Both seeds and seedlings were fumigated with methyl bromide on entry into CERES.

2.4.2 *Establishment of seedlings*

(i) Soaking

Seeds were soaked in tap water at room temperature for about 24 hours prior to sowing.

(ii) Sowing

Shallow germination trays with adequate drainage holes were used. Soaked seeds were sown in rows at a depth of about 6 mm in 1:1 perlite: vermiculite medium and lightly watered twice daily. The seeds were germinated either at the Forestry (A.N.U.) glasshouse or at CERES in the 27/22^{o} C glasshouse for 2 - 3 weeks before transplanting.

(iii) Transplanting

The trays were soaked with water to facilitate pricking out of the seedlings. The seedlings were transplanted into 15 cm (6 in) pots (one seedling per pot) and the plants were grown for a few months before use. When grown at CERES, seedlings were established in the 27/22° C glasshouse, firstly because of more space available in that glasshouse, and secondly because Slee (as quoted by Kanchanaburangura, 1976) found that *P. caribaea* var. *hondurensis* showed optimum growth in the seedling stage at 27/22° C day/night air temperature.

(iv) Watering and nutrients

After transplanting, plants grown at CERES were watered daily with modified Hoagland solution (see Appendix III A) in the morning and tap water in the late afternoon. Plants grown in the 33/28° C glasshouse had an additional watering with tap water at noon.

Seedlings grown at the Forestry (A.N.U.) glasshouse were watered twice daily, in the morning and afternoon. The plants were given nutrients once a week with 'Aquasol' (see Appendix III B).

2.4.3 *Selection of seedlings for experiments*

A large number of seedlings of each species were grown initially for an experiment and only those with uniform height, root collar diameter and size of root system were selected. In preliminary trials this was found to be crucial to reduce the variability of the results in root regeneration studies. In addition, it was not possible to use a large sample size because of the physical limitation of space, and more importantly, due to the laborious amount of work involved in removing the white roots at the beginning and end of an experiment. It took about 1 hour per plant to remove the white roots at the start of a treatment and an average of 3 hours to harvest each one.

2.4.4 *Method of assessing root regeneration potential*

The technique of Stone and co-workers (Stone, 1955; Stone and Schubert, 1959a, 1959b; Stone and Benseler, 1962; Stone *et al.*, 1963; Krugman and Stone, 1966) was used to assess the root regeneration potential (RRP) of plants. In essence the technique is a simple one in which seedlings were removed from the growth medium, root-pruned to a standard length and all white root tips were pinched off to simplify recognition of new roots. Subsequently, the seedlings were replanted in different treatment conditions for a standard length of time and then redug and the number and length of new roots measured. The results are expressed as root regeneration potential (RRP) based on total number (RRP_N) and total length (RRP_L) of new roots per plant. For convenience, the amount of new root growth is expressed as RRP when RRP_N gives similar results as RRP_L.

RRP is defined as the capacity of the roots to regenerate and is the sum of the measurements of the lateral root elongation potential and the lateral root initiation potential. However, the origin of the regenerated roots in some of the earlier experiments was not differentiated because of lack of experience at that stage in distinguishing between the two types of root regeneration.

This study evaluates the potential of roots to regenerate when grown in different environmental conditions. In contrast, Stone and co-workers were more concerned in evaluating the RRP of seedlings which initially, were subjected to different environmental conditions or had different growth history. The roots of these seedlings were treated and the plants grown in a standard test environment to determine their RRP. This is, in effect, an evaluation of a potential in retrospect.

In the first major experiment, on the effects of day/night air temperatures (see chapter 5), the roots of the seedlings were pruned to

18cm from the cotyledon at the start of the experiment. Then, all white root tips were pinched off to simplify recognition of new roots at harvest. However, these two practices were found to cause severe water stress to the plants causing needles to die on the seedlings. In all other subsequent experiments, needle death was markedly reduced when the roots were pruned to 20cm from the cotyledon (a common nursery practice) and only white roots $\geq$ 0.5 cm long were pinched off. In the first experiment, the root regeneration period was 6 weeks. However, it was found to be too time consuming to assess the RRP of each plant when grown over this period so the time was shortened to 4 weeks (similar to the method of Stone and co-workers quoted above) in all subsequent experiments. Only new roots which were $\geq$ 2.0 cm long were measured whereas those $\geq$ 1.0 cm long were counted in all experiments conducted to reduce the harvesting time.

2.4.5 *General plant parameters measured*

Parameters commonly measured in most experiments are discussed below while those specific to some experiments are discussed in the relevant sections.

(i) Root collar diameter : the position is defined as 3 cm below the cotyledon. Measurements were made with a vernier caliper at two positions at right angles and the average taken. Plant diameters were measured at the beginning and end of an experiment and the increment determined.

(ii) Shoot height : defined as the distance along the stem, between the root collar and the apical meristem. Some subjectivity was unavoidable due to tight bunching of apical needles around the meristem, thus requiring minimum handling to avoid damage. With practice, it is

possible to recognise a consistent measurement point and accuracy was ± 3 mm. The heights were taken at the beginning and end of an experiment and the increment determined.

(iii) Root regeneration : the parameters are listed as follows:

(a) N : defined as the total number of white roots ⩾ 1.0 cm long, per seedling.

(b) L_{Nir}: defined as the total length of newly initiated roots ⩾ 2.0 cm long, per seedling.

(c) L_{Ore}: defined as the total length of elongation ⩾ 2.0 cm long from old roots, per seedling.

(d) *L : defined as the total length of white roots ⩾ 2.0 cm long, per seedling.

(iv) Dry weight : plant parts -- total root, shoot, and needles (in photosynthesis and respiration experiments) were oven dried (fan circulated air at c. 85°C) for a minimum of 72 hours. Materials were cooled in desiccators to room temperature before weighing. Accuracy was ± 0.0001 g. To avoid moisture imbibition by the dried materials, the exposure time between desiccator and weighing was minimized.

The plant parts were defined as follows:

(a) Shoot : the plant portion above the root collar.

(b) Root : the whole plant portion below the root collar.

(c) Needles : the green portion of the leaves. The dead portion of the needles was not included for expressing the rate of photosynthesis and respiration.

2.4.6 *Calculations and analyses*

(i) Analysis of variance

All data were subjected to analysis of variance to assess the significance of the treatment effects on each parameter. In experiments where two species with similar growth histroy were used, the

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*L = L_{Nir} + L_{Ore}

data were analysed as a two factorial experiment to examine the possibility of interaction between species and treatment on the parameters measured. Moreover, it would also be possible to compare the overall treatment effects and species performance as well as to compare the response of the individual species to treatment effects. Statistical analysis followed Winer (1971) and personal communication with Dr. D. Chant from the Department of Statistics, A.N.U.

(ii) Comparison of mean values

The significance of differences between group means was tested by using Duncan's new multiple range test (Steel and Torrie, 1960; Winer, 1971).

CHAPTER 3

THE EFFECTS OF NUTRIENT DEFICIENCIES ON THE GROWTH AND ROOT REGENERATION POTENTIAL OF *PINUS CARIBAEA* AND *PINUS KESIYA* SEEDLINGS

3.1 *Introduction*

The problems of poor growth due to low fertility are more frequent and serious in the establishment of plantation forests than agricultural crops, because the lands relegated to forestry are often too infertile for agricultural use (Gentle and Humphreys, 1967; Brown and Hall, 1968). It is well-established that trees, like agricultural crops, require a balanced and adequate supply of all the thirteen essential elements for healthy vigorous growth. The essential macronutrients are nitrogen, phosphorous, potassium, calcium, magnesium and sulphur, and the micronutrients are iron, manganese, copper, zinc, boron, molybdenum and chlorine (Epstein, 1972). It is possible that this list will be expanded further with time (Epstein, 1972; Hewitt and Smith, 1975).

Of all the essential elements, N and P are the most universally deficient (Treshow, 1970; Thompson and Troeh, 1973) and are often found to be limiting to the growth of forest trees (Gentle, 1968). Plants appear spindly, pale and are stunted when deficient in N because deficiency of this element limits the production of protein, chlorophyll, and other materials essential for the production of new cells (Thompson and Troeh, 1973).

P is a constituent of nucleoproteins and phospholipids, and the high-energy bonds associated with phosphate groups constitute the chief

medium for energy transfer in plants (Kramer and Kozlowski, 1960). The most common P deficiency symptons include stunting, delayed maturity and bluish or reddish colouration of the leaves due to the abnormally excessive formation of anthocyanin (Treshow, 1970). In conifers, P deficiency can also lead to fused needles (Kramer and Kozlowski, 1960).

The main aim of the experiment described in this chapter was to examine the effects of deficiency in N, P, or both on growth, with particular emphasis on the root regeneration capacity of seedlings of *P. caribaea* and *P. kesiya*. Since tropical soils are nearly always low in N and P (Gourou, 1966; Kalpage, 1974), it could have a useful practical application to know whether any deficiency in these nutrient elements could significantly affect seedlings of these species to regenerate roots vital for successful establishment in the first critical month after outplanting. The use of two species in the experiment provides an opportunity to compare species differences in the response to nutrient deficiencies.

3.2 *Materials and methods*

Seeds of *P. caribaea* and *P. kesiya* were sown in a 27/22° C glasshouse at CERES phytotron (this facility is described in chapter 2) on 1 March, 1975 and grown for 12 weeks till 22 May, 1975. 32 seedlings of uniform height and root collar diameter were selected from each species and grown for another 2 weeks in a growth cabinet. During this acclimatization period all seedlings were given a complete nutrient solution (see Appendix III C) in the morning and distilled water in the afternoon.

The day/night air temperature in the cabinet was 27/22° C and it was synchronized with a 12/12 hour light period in order to simulate

the tropical condition. Light intensity at plant height was 37.5 watts.m^{-2} (1500 fc) measured using an 'Eel' photoelectric photometer (the mean of 5 readings — 4 at the corners and 1 in the centre, was taken). Light intensity level was checked at weekly intervals to ensure constant level throughout the experiment. In addition, the position of the pots in the cabinet was changed at weekly intervals to reduce any experimental error due to 'positional effects'. This was done by alternating the position of the trays as well as the pots within each tray. There were 4 trays in the growth cabinet and each tray carried seedlings from one nutrient treatment. 8 replicates were used in each treatment, hence, each tray contained 16 pots (8 plants for each species).

The plant sizes at the start of the treatment period are presented in Table 3.1. The roots of all seedlings were pruned to 20 cm from the cotyledon and all white root tips $\geq$ 0.5 cm long were pinched off to simplify recognition of new roots. The plants were grown for 4 weeks in full nutrient (F), minus N (-N), minus phosphorous (-P), and minus N and P (-NP). Seedlings were given the above nutrients (see Appendix III C) in the morning and distilled water in the afternoon. At the end of 4 weeks, the plants were harvested and height and diameter increment, root regeneration and dry weight of the various plant parts were determined as described in chapter 2, section 2.4.5. Any morphological differences in the foliage between treatments were compared.

TABLE 3.1 Plant sizes at the start of the 4 week treatment.

Species	Parameter	F	-N	-P	-NP	Mean
P. caribaea (mean for 8 replicates)	Height (cm)	11.9	12.0	12.0	11.4	11.8
	Diameter(cm)	0.25	0.27	0.26	0.27	0.26
P. kesiya (mean for 8 replicates)	Height (cm)	9.9	9.7	10.0	9.8	9.8
	Diameter(cm)	0.28	0.27	0.29	0.26	0.27

3.3 *Results*

The data were analysed on the basis of:

(i) Factor 1 - Nutrients (4 means, 16 observations per mean).

(ii) Factor 2 - Species (2 means, 32 observations per mean).

(iii) Interaction between nutrients and species (8 means, 8 observations per mean).

The identity of the means is as follows:

Factor 1: Full nutrients (F), minus Nitrogen (-N), minus Phosphorous (-P), minus Nitrogen and Phosphorous (-NP).

Factor 2: *P. caribaea* (PC) and *P. kesiya* (PK).

The results of analysis of variance are given in Table 3.2 for the parameters measured in the experiment. There was no interaction between factor 1 (nutrients) and factor 2 (species) indicating a similar response to nutrient treatment in both species.

3.3.1 *Root regeneration*

Root regeneration potential (RRP) based on both number and length of new roots showed no significant difference between treatment means for factor 1 (nutrients). However, there was a highly significant species difference (Table 3.2) due to *P. kesiya* producing more and longer new roots in each treatment (Table 3.3A).

TABLE 3.2 Results of analysis of variance for significance of differences between treatment means for factors 1 and 2 and the interaction between these.

Parameter	Factor 1: Nutrients	Factor 2: Species	Interaction
Root regeneration (per plant)			
Total number of white roots ≥ 1.0cm long	NS	* * *	NS
Total length of white roots ≥ 2.0cm long	NS	* * *	NS
Dry weight (g)			
Root	NS	NS	NS
Shoot	*	*	NS
Total plant	NS	NS	NS
Increment (cm)			
Height	* * *	NS	NS
Root collar diameter	*	NS	NS

P, 0.05 * ; 0.01 * * ; 0.001 * * * ; NS not significant

TABLE 3.3 Ranking of treatment means in ascending order for the different parameters for factors 1, 2 and their interaction. Bracketed means are not significantly different ($P < 0.05$).

	A: Root regeneration (per plant)		B: Dry weight (g)			C: Height & Diameter Increment (cm)	
	Total number (N) of white roots ≥ 1.0cm long	Total length (L) of white roots ≥ 2.0cm long	Root (R)	Shoot (S)	Total Plant (TP)	Height Increment (H)	Diameter Increment (D)
Factor 1: Nutrients	-P 139 F 143 -NP 148 -N 152	F 288 -P 295 -N 328 -NP 330	-NP 0.394 F 0.414 -N 0.450 -P 0.462	-NP 1.219 F 1.332 -N 1.352 -P 1.600	-NP 1.613 F 1.745 -N 1.803 -P 2.062	-N 1.4 -NP 1.4 -P 1.8 F 2.2	-NP 0.05 -N 0.06 -P 0.07 F 0.08
Factor 2: Species	PC 114 PK 178	PC 238 PK 383	PK 0.413 PC 0.447	PC 1.273 PK 1.479	PC 1.720 PK 1.891	PC 1.7 PK 1.7	PC 0.06 PK 0.07
Interaction: Nut. x Spp.	Nut.Spp. N -P PC 86 F PC 92 -N PC 138 -NP PC 138 -NP PK 157 -N PK 166 -P PK 192 F PK 194	Nut.Spp. L -P PC 173 F PC 231 -NP PC 273 -N PC 275 F PK 345 -N PK 381 -NP PK 386 -P PK 418	Nut.Spp. R -NP PK 0.346 F PC 0.390 -N PK 0.399 F PK 0.438 -NP PC 0.442 -P PC 0.455 -P PK 0.469 -N PC 0.502	Nut.Spp. S F PC 1.124 -NP PK 1.152 -N PC 1.262 -NP PC 1.287 -P PC 1.419 -N PK 1.442 F PK 1.540 -P PK 1.780	Nut.Spp. TP -NP PK 1.498 F PC 1.512 -NP PC 1.728 -N PC 1.765 -N PK 1.841 -P PC 1.874 F PK 1.978 -P PK 2.249	Nut.Spp. H -NP PC 1.2 -N PC 1.4 -N PK 1.4 -NP PK 1.5 -P PC 1.8 -P PK 1.8 F PK 2.0 F PC 2.3	Nut.Spp. D -NP PC 0.05 -N PC 0.06 -P PC 0.06 -NP PK 0.06 -N PK 0.07 -P PK 0.08 F PK 0.08 F PC 0.09

3.3.2 *Dry weight*

There was no significant difference in total root and total plant dry weights for factor 1 (nutrients) and factor 2 (species) although there were differences in shoot dry weight for both factors (Table 3.2).

Table 3.3B shows that shoot dry weight in -P treatment was significantly greater than -NP but was not significantly different from F and -N. As the -NP treatment did not differ significantly from full nutrient this result is difficult to explain. These dry weight differences would need to be regarded with caution as the treatment period was only 4 weeks and the pre-treatment dry weight would far exceed the dry weight increment during this period. For example, *P. kesiya* produced more and longer new roots than *P. caribaea* in each treatment (Table 3.3A) with lack of difference in total root dry weights (Table 3.3B). This may be attributed to the original mass of roots which far exceed the newly produced roots.

3.3.3 *Height and diameter increment*

Both height and diameter increment showed significant differences between treatment means for factor 1 (nutrients) and not for factor 2 (species) (Table 3.2). There was no significant difference for height increment between F and -P, and between -N and -NP treatments but F and -P were both significantly greater than -N and -NP treatments (Table 3.3C).

For diameter increment, Table 3.3C shows that the increments in -P and F were both significantly greater than in -NP treatment. No significant difference was observed between F, -P, and -N, and between -N and -NP treatments.

3.3.4 *Morphological differences of the foliage*

No colour difference was observed in the foliage between different treatments for each species at harvest.

3.4 *Discussion*

Within each species no significant difference in root regeneration potential (RRP) was found in any of the nutrient treatments.

Some effects on growth were observed. For example, *P. kesiya* seedlings grown in the -NP treatment had significantly less shoot dry weight than seedlings of this species grown in -P treatment; *P. caribaea* seedlings grown in full nutrients had significantly higher height increment than those grown in -N and -NP treatments and significantly higher diameter increment than those grown in -NP treatment. However, none of these treatments had significant effect on root regeneration although in *P. caribaea*, least root regeneration was found in the treatments (F and -P) giving best height growth. The possibility of competition for nutrients (particularly N) being involved in the balance between root and shoot growth must be borne in mind.

Under the conditions of the experiment however, the results indicate that plants had adequate nutrient reserves at the commencement of the treatment for them not to be significantly affected over a 4 week nutrient deficiency treatment. The supply of N and P from the different parts of the plant, for example from old leaves to the growing roots, were unlikely to be restricted because of the high mobility of the elements. Bukovac and Wittwer (1957) in their study on the mobility of many radioactively labelled mineral nutrients applied to leaves of bean plants, classified P to be one of the very mobile elements. N can also be considered as a relatively mobile element as suggested by experiments on deciduous trees when in autumn a considerable part of the element is translocated into the twigs before abscission occurs (Kramer and Kozlowski, 1960).

The treatment would have to be more stringent in order to determine the effects of nutrient deficiency on growth of the two species studied. This could be achieved by a longer treatment period or by first 'starving' the plants from these nutrient elements prior to treatment. The second alternative is more preferable than the first in view of the time involved to assess the root regeneration potential (RRP) of plants grown longer than 4 weeks (see comments in chapter 2 on the problem associated with this).

Nevertheless, it could be argued that the results from this experiment has shown that it is safe to assume no nutrient effect is likely to impair later experiments (in other chapters). Also, the results indirectly support the recommendations of Endean (1967) and Brown and Hall (1968) in the use of fertilizers where they point out thatplant RRP is not significantly affected when grown in a nutrient deficient condition for one month. The results is this experiment also show that *P. kesiya* is superior to *P. caribaea* in its capacity to regenerate roots despite the shorter mean height (see Table 3.1) of the former species. It may be noted that Kha (1966) reported *P. kesiya* survives well in competition on sites which are poor in nutrients or badly degraded.

CHAPTER 4

THE EFFECTS OF LIGHT INTENSITY ON THE GROWTH AND ROOT REGENERATION POTENTIAL OF *PINUS CARIBAEA* AND *PINUS KESIYA* SEEDLINGS AND ON THE PHOTOSYNTHESIS AND RESPIRATION OF *PINUS CARIBAEA*

4.1 *Introduction*

Light is one of the major environmental factors controlling plant growth and is also one of the most readily varied. The effect of light on plant growth depends on its intensity, quality, duration and periodicity, variation in any one of which may affect growth (Kramer and Koslowski, 1960). Light affects tree growth through its direct effects on photosynthesis, respiration, stomatal opening, chlorophyll synthesis, and enzymatic content or kinetics (Logan, 1970). For example, carboxydimutase content, which has been shown by Bjorkman (1967) to be closely correlated to the rates of photosynthesis. The effect of light on cell enlargement and differentiation affect height growth and the general morphology of plants such as, for example, leaf size and thickness, which in turn, affect the rates of photosynthesis and respiration (Logan, 1970).

There is an extensive literature on the effects of light intensity on tree growth and on variations in the response of different species to reduced light intensities but only a few will be cited. Logan (1959) studied the effects of various light intensities from 14, 19, 22, 55 and 100% of full sun on the growth and development of 4-year-old white pine (*Pinus strobus* L.). He found that the dry weight of the roots, shoot, and total plant and, the height and diameter increments increased with increase in light intensity. Further work by Logan (1968) has shown that both the growth and root dry weight of white, red (*Pinus resinosa* Ait.) and Jack (*Pinus banksiana* Lamb) pines and Eastern Larch (*Larix laricina* (Du Roi) K. Koc

grown for four years at 13, 25, 45 and 100% of full sun increased significantly with each increment of light intensity. Hoffmann's (1965, 1966) work with both hardwoods and softwoods also shows clearly that while shading is generally detrimental to growth and root development, the effect varies with species and is thus a mechanism of competition.

Pines generally are especially sensitive to different levels of light intensity (Ferrell, 1953). Best growth and development in some species e.g., ponderosa pine (*P. ponderosa* Laws) (Pearson, 1936) and white pine (Haig, 1936) occurred under full sun while in some others e.g., Douglas fir (*Pseudotsuga menziesi* (Mirb.) Franco.) (Brix, 1970) and Grnad fir (*Abies grandis* (Dougl.) Lindl.) (Haig, 1936), growth was better under partial shade.

Most of the work on the effects of light on plant growth has been done on the aspect of its intensity probably because it is most readily varied and has greater practical application. Such studies can have practical importance in tropical and subtropical countries where shade nurseries produce seedlings for plantation establishment. For example, knowledge on root growth response of seedlings to different light intensities can guide a nurseryman in selecting optimum shade conditions for producing plants with a high root regeneration potential to ensure greater survival when outplanted. The ability of a seedling to regenerate roots rapidly in the first few weeks after outplanting is critical in determining its success (Stone and Schubert, 1959a). Knowledge on the response of tree seedlings to light intensity can also have practical application in the planning of initial espacement of plantation forests.

The objective of the first experiment conducted in this study was to examine the influence of light intensity on the growth and RRP of *P. caribaea* and *P. kesiya* seedlings. The main objective of the second experiment was to determine whether the effect of light intensity on RRP could be explained in terms of photosynthesis. Many workers (e.g. Barney, 1951; Sutton, 1967; Eliasson, 1968) have attributed reduced root growth in plants grown under low light intensity to decreased shoot photosynthesis and reduced supply of the photosynthate to the roots. In addition, Kozlowski and Peterson (1962) also attributed reduced root growth under low light intensity to the curtailment of growth - substance production and deployment from the shoot to the roots.

4.2 *Materials and methods*

Seeds of *P. caribaea* and *P. kesiya* were sown in 1:1 perlite : vermiculite mixture and maintained at 27/22^{o}C in CERES phytotron. The general methodology in seedling establishment and the facilities of glasshouse, growth cabinet, soil temperature units and Infra-red gas analyser were described in chapter 2. Table 4.1 summarizes the details of the two experiments conducted.

Table 4.1 A summary of Experiments 1 and 2 on the effects of light intensity on growth and root regeneration potential of *P. caribaea* and *P. kesiya* seedlings. The photosynthesis and respiration of seedlings were measured in Experiment 2.

Experiment number and date of the 4 weeks treatment	Species used	Mean height and diameter at start of treatment		Age (from sowing) at start of treatment	Treatment light intensity	Sample size per treatment for each harvest/measurement
		Height (cm)	Diameter (cm)			
1 20/6/75 to 18/7/75	PC* PK*	9.4 10.1	0.25 0.26	14 weeks 14 weeks	25, 50 and 75 watts. m^{-2} conducted in three growth cabinets	6 6
2 13/3/76 to 10/4/76	PC	32.0	0.67	20 weeks	Relative light intensity: 16, 50 and 100% sun conducted in an open-glasshouse at CERES	5

* PC -- *P. caribaea*
* PK -- *P. kesiya*

Experiment 1 was conducted in three growth cabinets providing three different light intensities. The day/night temperature was 27/22^{o}C synchronized with a 12/12 hour photoperiod to simulate the tropical condition. Light intensity in the cabinets was measured using an 'Eel' portable photoelectric photometer. To ensure accuracy, five readings (one from each corner and one in the centre) from each cabinet were taken and then averaged to give the cabinet light intensity. The light intensity level from each cabinet was checked at weekly intervals and adjusted if the level fell below the treatment light intensity. Pots in each cabinet were interchanged every week to reduce experimental error due to 'positional effects'. Seedlings were well-spaced out and thus mutual shading between them was negligible.

Experiment 2 was conducted in a 27/22^{o}C open-glasshouse at the CERES phytotron. Unlike in the growth cabinet, the day temperature in the glass house was held for 8 hours of the daylight period and night temperature for the remaining 16 hours. Also, the light intensity in the open-glass-house was much higher than in the cabinet and varied with the time of day. The mean daily radiation over a 12 hour daylight period during the experiment i.e., from 6/3/76 to 10/4/76 (the natural daylength over this period was approximately 12 hours) was calculated as 484 watts. m^{-2} (CSIRO Division of Plant Industry). The photoperiod in the glasshouse is extended to 16 hours by low light intensity incandescent lighting with an illumination of 0.625 watts. m^{-2} (25fc) at plant height.

Shade was provided by green 'sarlon' cloth giving a range of light intensities, measured with an 'Eel' portable photoelectric photometer. The following formula was used:

$$\text{Relative light intensity} = \frac{\text{Light intensity under shade}}{\text{Light intensity at 1200 hour in daylight under clear sky}} \times 100\%$$

The shade cloth was mounted over a wire framework measuring 100cm (length) x 88cm (breadth) x 88cm (height). The two shade frames were located in the same glasshouse with 27/22^{o}C day/night air temperature regime. They were carefully spaced to avoid all neighbouring shading. Control plants (Full sun treatment) were located in the same glasshouse.

To minimize variation in measuring light intensity, the following precautions were observed: (1) all measurements were made only under clear sky condition at around 1200 hours, (2) only maximum readings were taken, (3) each reading was taken at exactly 30cm beneath the shade cloth, and (4) five readings were taken, one from each corner and one in the centre and the average taken.

Experiment 2 was conducted in the open-glasshouse because of the unavailability of growth cabinets. Only one species was used in this experiment due to the physical limitation in the use of the Infra-red gas analyser. Allowance was also made for sufficient replications for each photosynthesis and respiration measurement. *P. caribaea* was chosen instead of *P. kesiya* because of its greater economic importance (see Appendix 1B) and faster growth rate which allowed the experiment to be conducted earlier. In addition, the results in Experiment 1 show that, unlike *P. kesiya*, *P. caribaea* did not show significant differences between treatment means for RRP under the low cabinet light intensities (maximum light intensity achieved was 75 watts. m^{-2}). Hence, it could be interesting to compare the root growth response of this species under higher natural light intensities.

The treatment light intensities for Experiment 2 were 16%, 50% and 100% sun (or Full sun). The light intensities were selected as above in order to determine the growth response of *P. caribaea* over a wide range of light intensity.

As photosynthesis could not be measured under the treatment light intensities in the open-glasshouse, measurements were made under a 'standard' light intensity in a growth cabinet. This posed a major problem because many workers (Loach, 1967; Logan and Krotkov, 1968; Logan 1970) have found that the foliage (or photochemical system) of plants grown in shade were adapted to photosynthesize more efficiently in low light intensity whereas sun leaves were more efficient in high light intensity. To avoid this complication, photosynthesis of *P. caribaea* was measured under two different light intensities in the growth cabinet i.e. first under a high light intensity of 75 watts. m^{-2} and then under a low one at 25 watts. m^{-2} to compare the response under each light intensity.

Plants in Experiment 1 were havested after 4 weeks of growth under the different light intensities whereas those in Experiment 2 had an intermediate harvest for root regeneration after 2 weeks of growth (harvest 1) in addition to the final harvest at 4 weeks (harvest 2). The origins of the new roots were classified into newly initiated roots (L_{Nir}) and those which elongated from old roots (L_{Ore}) in Experiment 2 but not in Experiment 1.

Photosynthesis and respiration of plants in Experiment 2 were measured at an air temperature of 27°C. A total of four measurements, using 5 plants per light intensity treatment for each measurement were made. Measurement 1 was made on plants which had been grown at the different light intensities for 1 week with intact root systems. There were, initially, 15 plants growing in each light intensity treatment but only 5 plants per treatment were sampled for Measurement 1. Subsequent to Measurement 1, the roots of all seedlings in each treatment were pruned to 20cm from the cotyledon and all white root tips $\geq$ 0.5 cm long were pinched off to simplify recognition of new roots.

One day after root pruning , the same 5 seedlings from each treatment measured for photosynthesis and respiration at Measurement 1 were again measured for Measurement 2 to determine the effect of root pruning on these parameters. Measurement 2 could not be made immediately after root pruning because of the limitation in the use of the Infra-red gas analyser.

Measurements 3 and 4 were made at two and four weeks after root pruning. The samplings at Measurements 2, 3 and 4 were destructive since photosynthesis and respiration in this study were expressed as mg CO_2 per gram oven dry weight of green needles.

4.3 *Results*

4.3.1 *Experiment 1*

The data were analysed on the basis of:

(i) Factor 1 - Light intensity (3 means, 12 observations per mean).

(ii) Factor 2 - Species (2 means, 18 observations per mean).

(iii) Interaction between light intensity and species (6 means, 6 observations per mean).

The identity of the means is as follows:

Factor 1 : 25 (1), 50 (2), and 75 (3) watts. m^{-2}.

Factor 2 : *P. caribaea* (Pc) and *P. kesiya* (Pk).

The results of analysis of variance are given in Table 4.2 for the plant parameters measured in the experiment. Most of the parameters showed significant differences between treatment means for both factor 1 and factor 2. In several instances, in plant height increment and the dry weight of roots, shoot and total plant, there were significant interactions.

Any differences between treatments for factor 2 (species) should be treated in the light that *P. kesiya* was taller and had a thicker root collar diameter than *P. caribaea* at the start of the 4 weeks treatment (Table 4.1).

4.3.1.1 *Root regeneration*

Both RRP_N and RRP_L show similar patterns of response to treatment for factor 1 (light intensity) in both species. (Table 4.3A). RRP increased with increasing light intensity from 25 watts. m^{-2} (1) to 75 watts. m^{-2} (3). However, RRP at light intensities 1 and 2 were not significantly different from each other but were both significantly less than at light intensity 3.

Overall RRP in *P. kesiya* exceeded that of *P. caribaea*.

4.3.1.2 *Dry weight*

The root, shoot and total plant dry weights increased with an increase

Table 4.2 : Results of analysis of variance for significance of differences between treatment means for factors 1 and 2 and the interaction between these.

Parameter	Factor 1 : Light Intensity	Factor 2 : Species	Interaction
Root regeneration (per plant)			
Total number of white roots (N) ≥ 1.0cm long	**	*	NS
Total length of white roots (L) ≥ 2.0cm long	**	*	NS
Dry weight (g)			
Root	***	**	**
Shoot	***	***	**
Total plant	***	***	**
Increment (cm)			
Height	NS	NS	*
Root collar diameter	***	NS	NS

P, 0.05 *; 0.01 **; 0.001 ***; NS not significant

TABLE 4.3 Ranking of treatment means in ascending order for the different parameters for factors 1, 2 and their interaction. Bracketed means are not significantly different ($P < 0.05$).

	A: Root regeneration (per plant)		B: Dry weight (g)			C: Height & Diameter Increment (cm)	
	Total number (N) Of white roots ≥ 1.0cm long	Total length (L) of white roots ≥ 2.0cm long	Root	Shoot	Total plant	Height Increment	Diameter Increment
Factor 1: Light Intensity (L.I.)	1 108 2 162 3 283	1 291 2 471 3 691	1 0.264 2 0.451 3 0.930	1 1.045 2 1.555 3 2.776	1 1.309 2 2.006 3 3.705	1 1.2 2 1.4 3 1.6	1 0.07 2 0.09 3 0.14
Factor 2: Species (Spp.)	Pc 139 Pk 230	Pc 393 Pk 576	Pc 0.415 Pk 0.681	Pc 1.216 Pk 2.368	Pc 1.630 Pk 3.050	Pc 1.3 Pk 1.5	Pc 0.92 Pk 0.11
Interaction: L.I. x Spp.	L.I. Spp. N 1 Pc 97 2 Pc 106 1 Pk 120 3 Pc 213 2 Pk 218 3 Pk 353	L.I. Spp. L 1 Pk 280 1 Pc 302 2 Pc 344 3 Pc 534 2 Pk 598 3 Pk 849	L.I. Spp. R 1 Pk 0.246 1 Pc 0.282 2 Pc 0.341 2 Pk 0.561 3 Pc 0.621 3 Pk 1.237	L.I. Spp. S 2 Pc 0.957 1 Pc 0.964 1 Pk 1.126 3 Pc 1.726 2 Pk 2.154 3 Pk 3.826	L.I. Spp. TP. 1 Pc 1.246 2 Pc 1.298 1 Pk 1.372 3 Pc 2.347 2 Pk 2.714 3 Pk 5.063	L.I. Spp. H 1 Pc 1.0 2 Pc 1.3 1 Pk 1.3 3 Pc 1.6 2 Pk 1.6 3 Pk 1.6	L.I. Spp. D 1 Pk 0.06 1 Pc 0.08 2 Pc 0.09 2 Pk 0.10 3 Pc 0.11 3 Pk 0.16

in light intensity from 25 watts. m^{-2}(1) to 75 watts. m^{-2}(3) (Table 4.3B). Root dry weight at light intensity 1 was not significantly different from light intensity 2 but were both significantly less than at light intensity 3. However, the treatment means for both the shoot and total plant dry weights were significantly different from each other at light intensities 1, 2 and 3.

The root, shoot and total plant dry weights of *P. kesiya* were significantly greater than for *P. caribaea*.

4.3.1.3 *Height and diameter increment*

Both the height and diameter increased in growth with an increase in light intensity from 25 watts.m^{-2} to 75 watts. m^{-2} (Table 4.3C). However, there were no significant differences between treatment means for height increment whereas there was a highly significant difference for diameter increment (Table 4.2). Consequently, an increase in light intensity up to high light intensities would increase the 'quality' of planting stock. The height : diameter ratio is an important measure of the 'quality' of planting stock and is one of the primary purposes of root pruning. The diameter increments at light intensities 1 and 2 were not significantly different from each other but both were significantly less than at light intensity 3.

Both height and diameter increment in *P. kesiya* were not significantly different from *P. caribaea*.

4.3.2 *Experiment 2*

4.3.2.1 *Root Regeneration*

The Anova data for Factor 1 i.e. between different light intensities (16%, 50% and 100% sun) at each harvest, and Factor 2 i.e. between Harvests 1 and 2 at each light intensity are presented in Tables 4.4A I and II respectively. The results in Table 4.4AI show that root regeneration was significantly affected by light intensity at harvest 2 but not at harvest 1. Most of the root regeneration parameters showed significant differences between the two harvests at 100% and 50% sun but not at 16% sun (Table 4.4AII).

Table 4.4A Results of analysis of variance for significance of differences between treatment means for the root regeneration parameters in *P. caribaea*. Plants were grown at three relative light intensities: 16%, 50% and 100% Sun for 4 weeks.

I: *Root regeneration (per plant) at harvests 1 and 2*

Parameter	Harvest 1	Harvest 2
Total number of white roots (N)≥ 1.0cm long	NS	*
Total length of newly initiated roots (L_{Nir})≥2.0cm long	NS	*
Total length of elongation from old roots (L_{Ore})≥2.0cm long	NS	*
Total length of white roots ($L=L_{Nir}+L_{Ore}$)≥ 2.0cm long	NS	*

II: *Anova for root regeneration parameters between harvests 1 & 2.*

Parameter	16% Sun	50% Sun	100% Sun
N	NS	*	*
L_{Nir}	NS	*	*
L_{Ore}	NS	NS	NS
L	NS	*	*

P, 0.05* ; NS, not significant

Table 4.4B Ranking of treatment means in ascending order for root regeneration parameters at harvests 1 and 2 respectively. Bracketed means are not significantly different ($P< 0.05$).

Harvest 1								Harvest 2							
N		L_{Nir}		L_{Ore}		$L=L_{Nir}+L_{Ore}$		N		L_{Nir}		L_{Ore}		$L=L_{Nir}+L_{Ore}$	
16%	1	16%	0.5	16%	0.5	16%	1	16%	2	16%	1	16%	2	16%	
50	5	50	5	50	1	50	6	100	255	100	295	50	186	100	54
100	37	100	31	100	22	100	53	50	328	50	360	100	247	50	54

Table 4.5A Results of analysis of variance for significance of differences between treatment means for the dry weight and height and diameter growth in *P. caribaea* at the final harvest . Plants were grown at three relative light intensities: 16%, 50% and 100% Sun for 4 weeks.

Parameter	Significance of F ratio
Dry weight (g)	
Root	NS
Shoot	NS
Total plant	NS
Increment (cm)	
Height	*
Root collar diameter	NS

P, 0.05* ; NS, not significant

Table 4.5B Ranking of treatment means in ascending order for various plant parameters at final harvest . Bracketed means are not significantly different ($P < 0.05$).

Dry weight (g)						Increment (cm)			
Root		Shoot		Total plant		Height		Root collar diameter	
16%	2.030	16%	8.218	16%	10.248	16%	0.1	16%	0.01
100	2.362	50	8.376	100	11.126	100	2.2	100	0.04
50	3.194	100	8.764	50	11.570	50	4.3	50	0.05

The ranking of the root regeneration parameters in Table 4.4B shows that more roots were formed under 100% sun at Harvest 1 but, at Harvest 2, more roots were formed under 50% sun. The differences between 50% and 100% sun, however, were not significant statistically. Almost no root regeneration was obtained under 16% sun at either harvest. Interestingly, the length of newly initiated roots (L_{Nir}) was maximum at 50% sun whereas that from the elongation of old roots (L_{Ore}) was greater at 100% sun at Harvest 2 although again, these differences were not significant statistically. Slightly more of the roots that regenerated at Harvests 1 and 2 resulted from lateral root initiation and subsequent elongation.

4.3.2.2 *Dry weight*

There was no significant difference in the root, shoot and total plant dry weights between the treatment light intensities at the final harvest (Table 4.5A). Largest dry weight for root and total plant occurred at 50% sun while that for shoot, at 100% sun. Smallest dry weight for the three parameters was at 16% sun but none of the differences were significant statistically.

4.3.2.3 *Height and diameter increment*

Results of Anova in Table 4.5A show that height increment was significantly affected by treatment light intensity whereas the root collar diameter was not. Both the height and diameter increments were largest at 50% sun and smallest at 16% sun (Table 4.5B). Height increment at 50% sun was not significantly different from 100% sun but it was significantly greater than at 16% sun. There was no significant difference in height increment between 16% and 100% sun and none of the differences in diameter increment were significant statistically.

4.3.2.4 *Photosynthesis, respiration and the gross photosynthesis - respiratory balance (P_T/R_D).*

The Anova data for Factor 1 i.e.between different light intensities

Table 4.6A Results of analysis of variance for significance of differences between treatment means for the gas exchange parameters in *P. caribaea*. Plants were grown at three relative light intensities:16%, 50% and 100% Sun for 4 weeks. The CO_2 exchange rates of the plants were measured at two light intensities in a growth cabinet viz. 75 watts. m^{-2} and 25 watts. m^{-2}.

I: *Between different relative light intensities (16,50 & 100% Sun) at each measurement.*

Parameter	Measurement 1		Measurement 2		Measurement 3		Measurement 4	
	75w.m^{-2}	25w.m^{-2}	75w.m^{-2}	25w.m^{-2}	75w.m^{-2}	25w.m^{-2}	75w.m^{-2}	25w.m^{-2}
Net photosynthesis (P_N)	* *	* *	* *	* *	NS	NS	* * *	* * *
Dark respiration (R_D)	* * *	-	*	-	*	-	* * *	-
Total photosynthesis (P_T)	* *	*	* * *	* *	NS	NS	* * *	* * *
P_T / R_D	* * *	* * *	NS	NS	NS	NS	* * *	* * *

II: *Between different measurements (1,2,3, & 4) at each relative light intensity.*

Parameter	16% Sun		50% Sun		100% Sun	
	75w.m^{-2}	25w.m^{-2}	75w.m^{-2}	25w.m^{-2}	75w.m^{-2}	25w.m^{-2}
Net photosynthesis (P_N)	* * *	* * *	* * *	* * *	* * *	* * *
Dark respiration (R_D)	* * *	-	* * *	-	* *	-
Total photosynthesis (P_T)	* * *	* * *	* * *	* * *	* * *	* * *
P_T / R_D	* * *	* * *	* *	* * *	* * *	* * *

P, 0.05* ; 0.01** ; 0.001*** ; NS, not significant

Table 4.6B Ranking of treatment means in ascending order for the gas exchange parameters*. Bracketed means are not significantly different ($P < 0.05$).

I: *Between different relative light intensities (16,50 & 100% Sun) at each measurement.*

Measurement	75 watts. m^{-2}								25 watts. m^{-2}					
	P_N		R_D		P_T		P_T / R_D		P_N		P_T		P_T / R_D	
1	16%	17.4	16%	1.4	16%	18.8	100%	7.2	100%	8.3	100%	11.1	100%	4.0
	100	17.5	100	2.8	100	20.3	50	8.6	16	9.8	16	11.2	50	4.9
	50	22.4	50	3.0	50	25.4	16	13.1	50	11.7	50	14.7	16	8.0
2	16%	9.9	16%	2.1	16%	12.0	16%	5.7	16%	4.9	16%	7.0	16%	3.4
	100	15.8	100	2.9	100	18.7	50	6.4	50	7.3	50	10.5	50	3.4
	50	16.8	50	3.2	50	20.0	100	6.5	100	7.6	100	10.5	100	3.6
3	16%	5.4	16%	1.4	16%	6.8	100%	4.2	100%	3.6	16%	5.1	100%	2.5
	100	7.0	100	2.0	50	9.0	50	4.6	16	3.7	100	5.6	50	3.0
	50	7.2	50	2.1	100	9.3	16	5.0	50	4.1	50	6.2	16	3.8
4	16%	0.7	16%	0.2	16%	0.9	16%	4.2	16%	0.4	16%	0.6	16%	2.7
	100	10.2	100	1.8	100	12.0	100	6.8	100	5.3	100	7.1	100	4.0
	50	13.0	50	1.8	50	14.8	50	8.2	50	7.5	50	9.3	50	5.2

* The gas exchange parameters are expressed in mg CO_2/hr/g oven dry weight of green needles

Table 4.6B continued.

II: *Between different measurements (1,2,3 & 4) at each relative light intensity.*

Relative light intensity	75 watts. m^{-2}								25 watts. m^{-2}							
	P_N		R_D		P_T		P_T / R_D		P_N		P_T		P_T / R_D			
16% Sun	4	0.7	4	0.2	4	0.9	4	4.2	4	0.4	4	0.6	4	2.7		
	3	5.4	3	1.4	3	6.8	3	5.0	3	3.7	3	5.1	2	3.4		
	2	9.9	1	1.4	2	12.0	2	5.7	2	4.9	2	7.0	3	3.8		
	1	17.4	2	2.1	1	18.8	1	13.1	1	9.8	1	11.2	1	8.0		
50% Sun	3	7.2	4	1.8	3	9.2	3	4.6	3	4.1	3	6.1	3	3.0		
	4	13.0	3	2.0	4	14.8	2	6.4	2	7.3	4	9.3	2	3.4		
	2	16.8	1	3.0	2	20.0	4	8.2	4	7.5	2	10.5	1	4.9		
	1	22.4	2	3.2	1	25.4	1	8.6	1	11.7	1	14.7	4	5.2		
100% Sun	3	7.0	4	1.8	3	9.1	3	4.2	3	3.6	3	5.7	3	2.5		
	4	10.2	3	2.1	4	12.0	2	6.5	4	5.3	4	7.1	2	3.6		
	2	15.8	1	2.8	2	18.7	4	6.8	2	7.6	2	10.5	4	4.0		
	1	17.5	2	2.9	1	20.3	1	7.2	1	8.3	1	11.1	1	4.0		

* The gas exchange parameters are expressed in mg CO_2/hr/g oven dry weight of green needles

(16%, 50% and 100% sun) at each photosynthesis (P_N and P_T) and dark respiration (R_D) measurement, and Factor II i.e. between different measurements (1, 2, 3 and 4) at each light intensity, are presented in Tables 4.6AI and II respectively. The ranking of these parameters in Tables 4.6B I and II reveals that both net (P_N) and total (P_T) photosynthesis had similar patterns of response to treatment for both Factors I and II. Hence, to avoid repetition of statements, only P_N will be used to describe the response of photosynthesis to treatment in the two studies.

Tables 4.6B I and II reveal that the measurement light intensity in the growth cabinet viz. 75 watts. m^{-2} and 25 watts. m^{-2} did not significantly affect the patterns of response of P_N, P_T and P_R/R_D ratio to different treatments. Hence, the discussion of the results from gas exchange measurements in this experiment are based on parameters measured only at one light intensity i.e. at 75 watts. m^{-2}. This finding eliminates earlier concern that the measurement light intensity could complicate the interpretation of the results due to treatment effects (see section 4.2). Logan and Krotkov (1968) have reported that not all species grown in shade are adapted to photosynthesize more efficiently in low light intensity or vice versa. In addition, most of the literature on adaptations of the photosynthetic mechanisms in plants are concerned with plants which were grown in the treatment light intensity for long periods (e.g. Loach, 1967; Logan, 1970) and sometimes up to 3 years (Logan and Krotkov, 1968). The plants in this study were grown at the various treatment light intensities up to a maximum of 5 weeks only.

Factor 1 :

Effect of relative light intensity on P_N, R_D and P_T/R_D ratio at each measurement.

1. Net Photosynthesis (PN)

Greatest photosynthesis occurred in plants grown at 50% sun and least at 16% sun at all four measurements (Table 4.6B I). However, the differences between treatments were not significant for Measurement 3 but were significant for Measurements 1, 2 and 4 (Table 4.6A I). At Measurement 1, when the plants had intact root systems, P_N at 16% and 100% sun were not significantly different from each other but were significantly less than at 50% sun. At both one day, and four weeks, after the root pruning treatment i.e. at Measurements 2 and 4 respectively, P_N at 50% and 100% sun were not significantly different from each other but were significantly greater than at 16% sun.

2. Dark respiration (R_D)

R_D showed similar patterns of response to light intensity at all four measurements (Table 4.6B I). R_D never differed significantly in plants grown at 50% and 100% sun but was significantly less at 16% sun at all measurements.

3. P_T/R_D ratio

The P_T/R_D ratio, cited as an efficiency index (e.g. Huber, 1964) is total photosynthesis divided by dark respiration. Total photosynthesis was calculated as net photosynthesis plus dark respiration assuming that respiration in the dark equals that in the light. However, it should be noted that in many plants dark respiration is not the same as light respiration (e.g. Treguna *et al.* 1964; Moss, 1966).

Results of Anova in Table 4.6A I show no significant difference between treatment means for Measurements 2 and 3 whereas there were highly significant differences for Measurements 1 and 4 respectively.

At Measurement 1, P_T/R_D ratio was maximum at 16% sun and minimum at 100% sun. The ratios at the three light intensities were significantly different from each other. At Measurement 4, P_T/R_D ratio at 50% and 100% sun were not significantly different from each other but both were significantly less than at 16% sun.

Factor II :

Effect of root pruning on P_N, R_D and P_T/R_D ratio and their recovery with time at each relative light intensity

Results in Table 4.6B II show that root pruning caused a decrease in P_N, R_D and P_T/R_D ratio. The effect of light intensity in which the plants were grown on the recovery trends for each of these parameters are discussed below.

1. *Net photosynthesis (P_N)*

Seedlings from all light intensity treatments showed a drop in P_N immediately following root pruning (Measurement 2 vs. Measurement 1) though the difference was not significant for plants grown in 100% sun. P_N declined further up to 2 weeks after root pruning in all plants (Measurement 3). After this, however, plants grown in 50% and 100% sun showed a recovery in P_N such that the values were higher at Measurement 4 than at Measurement 3. Plants grown under 16% sun showed a continuing decline in P_N to a very low level at Measurement 4.

2. *Dark respiration (R_D)*

R_D increased 1 day after root pruning (Measurement 2 vs. Measurement 1) but the increase was significant only for plants grown in 16% sun. Subsequently, at 2 weeks (Measurement 3) and 4 weeks (Measurement 4) after the root pruning treatment, R_D declined in all plants though the difference between Measurements 3 and 4 was significant only for plants grown at 16% sun.

3. P_T/R_D *ratio*

Seedlings from all light intensity treatments showed a drop in their efficiency of CO_2 assimilation immediately following root pruning (Measurement 2 vs. Measurement 1) though the difference was not significant for plants grown in 100% sun. P_T/R_D ratio declined further up to 2 weeks after root pruning in all plants (Measurement 3). After this, however, plants grown in 50% and 100% sun showed a recovery in their efficiency ratio such that the values were higher at Measurement 4 than at Measurement 3. There was no significant difference in the efficiency ratio between Measurements 4 and 1 for plants grown in 100% sun indicating a complete recovery in their efficiency of CO_2 assimilation. Plants grown under 16% sun showed a continuing decline in their efficiency ratio to a very low level at Measurement 4 though there was no significant difference in the values between Measurements 2, 3 and 4.

Figure 4.1 Effect of light intensity on RRP_L and root (R), shoot (S) and total plant (TP) dry weights of *P. caribaea* (—) and *P. kesiya* (---) seedlings grown for 4 weeks under three different light intensities in growth cabinets.

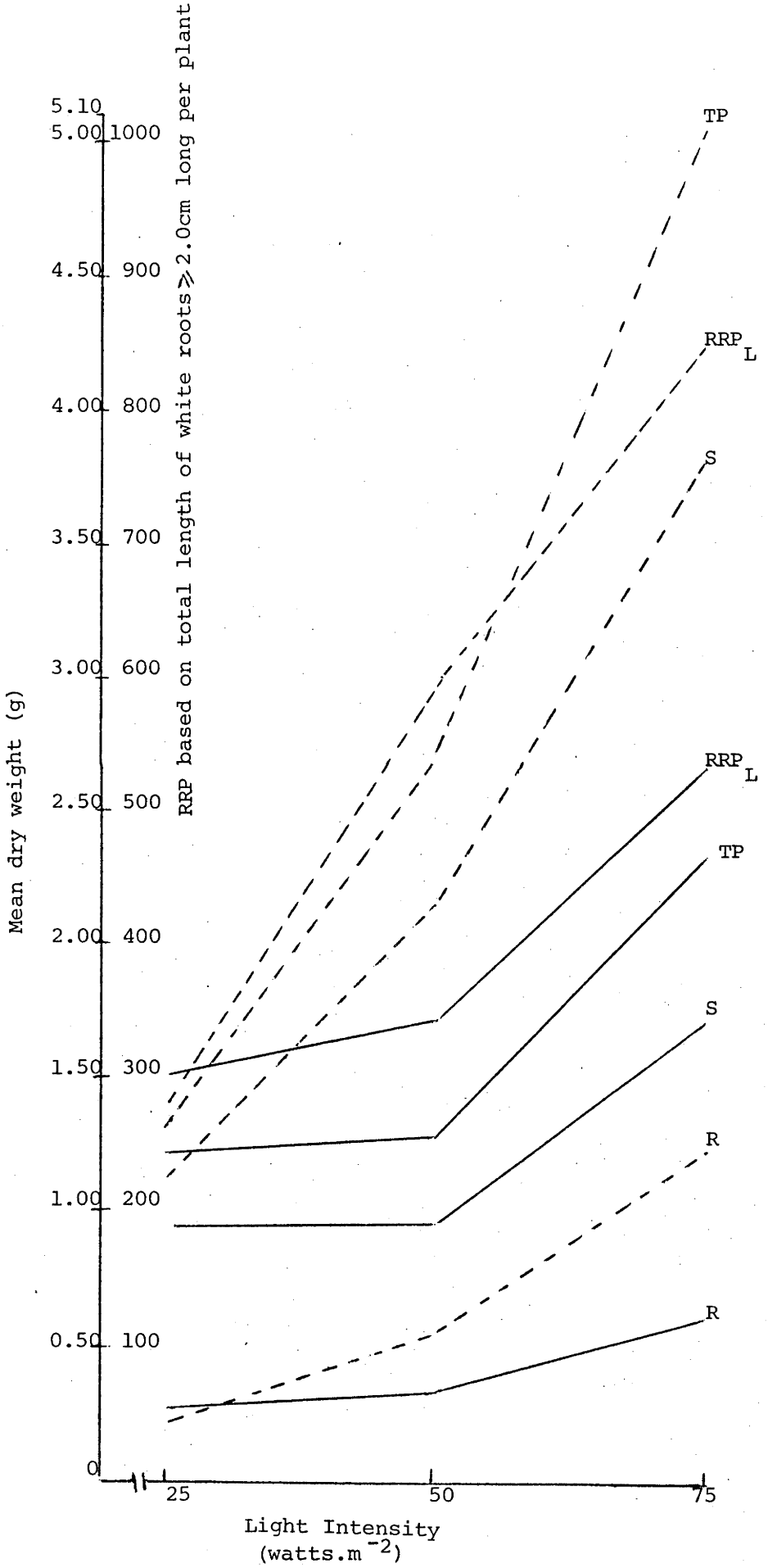


Figure 4.2 Effect of light intensity on photosynthesis and respiration of *P. caribaea* seedlings at four different measurements. (1-O, 2-x, 3-□, 4-△).

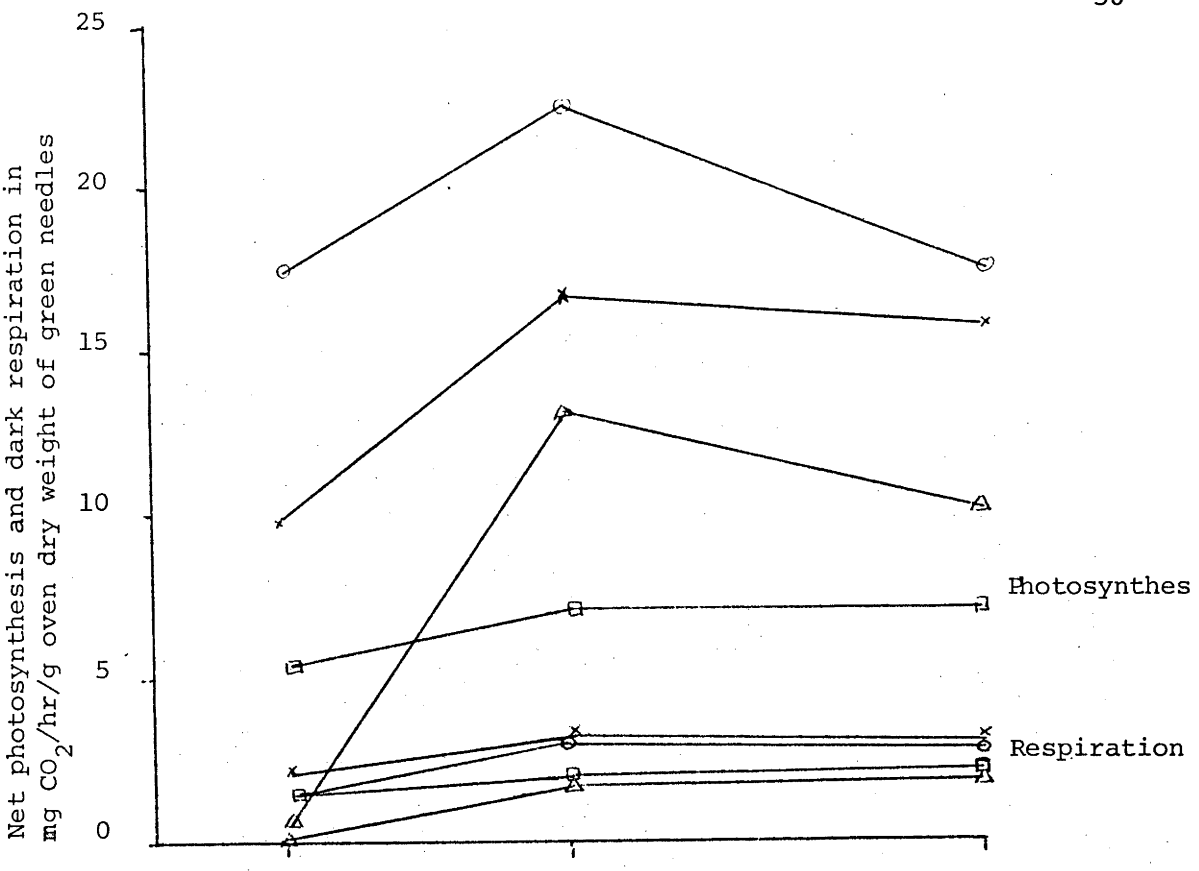
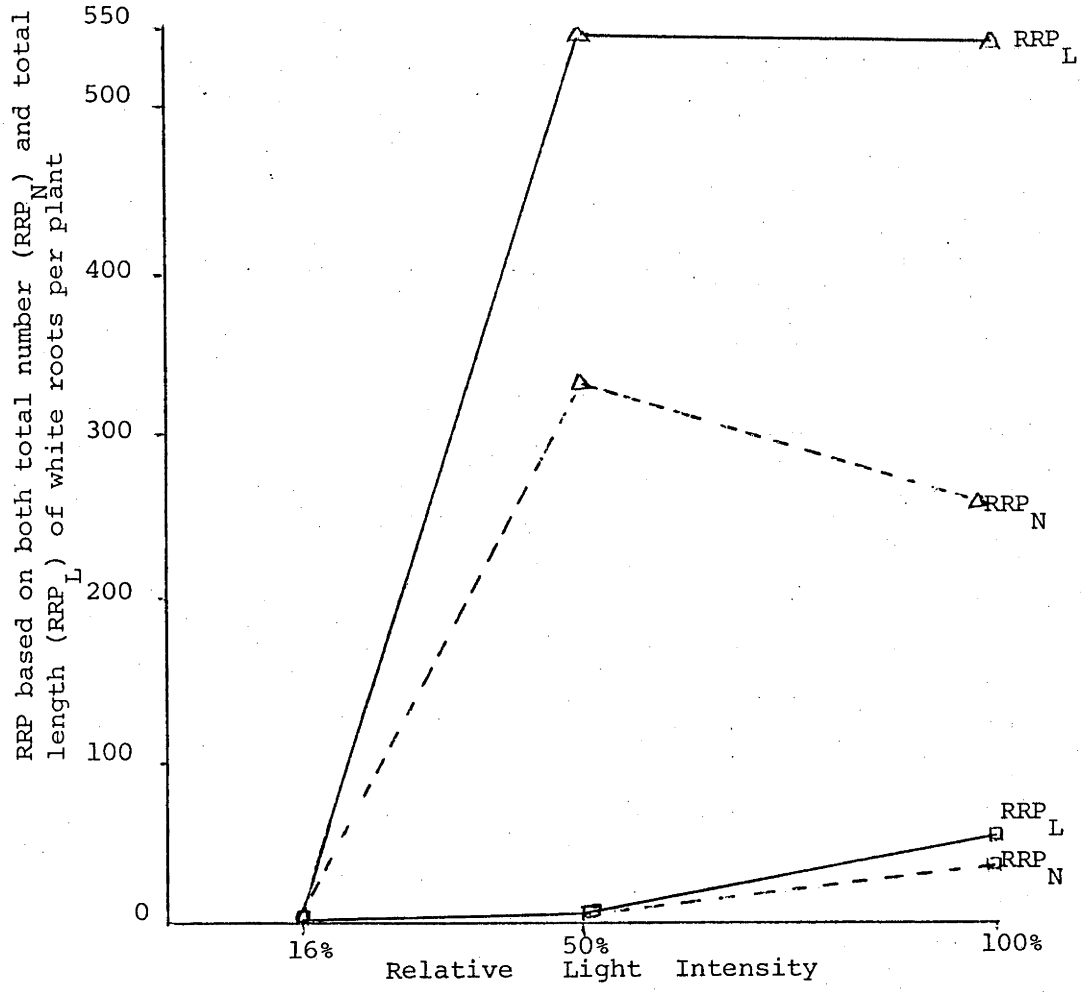


Figure 4.3 Effect of light intensity on RRP_N (---) and RRP_L (—) of *P. caribaea* seedlings at 2 weeks (□) and 4 weeks (△) after root pruning. Photosynthesis and respiration of the plants (see Fig. 4.2) were measured prior to the assessment of root regeneration.



4.4 *Discussion*

4.4.1 *Root regeneration potential and growth*

RRP, dry matter production and height and diameter increments in both *P. caribaea* and *P. kesiya* seedlings in Experiment 1 increased with an increase in irradiance from 25 to 75 watts. m^{-2}.

Some differences in growth were observed between the two species. For example, *P. kesiya* seedlings grown at 75 watts. m^{-2} had significantly greater RRP and diameter increment than at 25 watts. m^{-2}; the root, shoot and total plant dry weights of *P. kesiya* increased significantly with an increase in irradiance from 25 to 50 watts. m^{-2} and from 50 to 75 watts. m^{-2} (Table 4.3). The nature of the response in both RRP and dry weight differed between the two species (Figure 4.1). In *P. caribaea*, an increase in irradiance from 25 to 50 watts. m^{-2} resulted in very little increase in RRP and dry weight whereas a further increase in irradiance to 75 watts. m^{-2} resulted in a sharp increase in the parameters. In contrast to *P. caribaea*, the increase in RRP and dry weight in *P. kesiya* was nearly proportional to the increase in irradiance.

Results in Experiment 1 show that *P. kesiya* is superior to *P. caribaea* in both RRP and dry matter production. It is unlikely that these differences were due to the greater mean height of *P. kesiya* at the start of the treatment (Table 4.1) since the results in an earlier study (chapter 3 have also shown that *P. kesiya* was superior to *P. caribaea* despite being shorter in height.

In Experiment 2, RRP of *P. caribaea* at the end of the fourth week (harvest 2) was far less at 16% sun than at the higher light intensities (Table 4.4B). RRP was very low at the end of the second week (harvest 1) at all light intensities and showed no significant differences between treatment means. The results indicate that heavy shade (16% sun) was very unfavourable for root growth in *P. caribaea* seedlings whereas part

shade (50%) could enhance root growth. Although the RRP at 50% shade in this experiment was not significantly greater than at 100%, a trend is present to show some justification for growing the species under partial shade in tropical nurseries to encourage development of a larger root system in the plants before outplanting.

Root, shoot and total plant dry weights and diameter increment in *P. caribaea* were not significantly affected by the light intensities under which the plants were grown (Tables 4.5A and B). These results are different from the findings of Wadsworth and Lawton (1968) who found that the mean height and diameter increments and dry matter production in 12-week-old *P. caribaea* seedlings at Ibadan (tropical Nigeria) showed significant differences between the relative light intensities : 1, 5, 25 and 100% sun. Optimum light intensity for height and diameter increments and for dry matter production in that study was at 100% sun. The differences in the results between the two studies may be attributed to the fact that plants in Wadsworth and Lawton's experiment had intact root systems, were younger, and the experiment was conducted for 8 weeks. The mean daily radiation for a 12 hour daylight period at Ibadan (tropical Nigeria) when the experiment was conducted was, however, similar to that in this study i.e. 484 watts. m^{-2}.

The differences in results between Experiment 1 (conducted in growth cabinets) and Experiment 2 (conducted in open-glasshouse) may be attributed to the differences in experimental conditions (see Materials and methods). It is likely that the increase in RRP and growth in both *P. caribaea* and *P. kesiya* seedlings with increasing light intensity in Experiment 1 was due to the low cabinet light intensity which limited growth. In addition, the seedlings in Experiment 1 were younger and smaller than in Experiment 2 (Table 4.1).

Origin of new roots

Results in Experiment 2 (Table 4.4B) show that the regeneration of a new root system in *P. caribaea* seedlings depended upon both the elongation of the old roots (L_{Ore}) already present and the initiation and elongation of new laterals (L_{Nir}). This agrees with the findings of Stone and Schubert (1959a) in *Pinus ponderosa* Laws. seedlings. The results also show that L_{Nir} was somewhat greater than L_{Ore} at both 50% and 100% sun treatments. Stone *et al.* (1962) reported that plants whose RRP is determined mainly by the initiation and elongation of new roots (originating in callus tissue, or in the pericycle) rather than by lateral root elongation may be able to tolerate more damage to the roots during lifting from the nursery and during shipping, storage and replanting in the field.

4.4.2 *Effect of light intensity on P_N, R_D and P_T/R_D ratio at each measurement*

The results from this study show a parallelism between photosynthesis and the plants' capacity to regenerate roots. Both P_N and RRP were best at 50% sun followed closely by 100% sun and low at 16% sun by the end of 4 weeks after the root pruning treatment (Figures 4.2 and 4.3). Whether or not there is a causal relationship between P_N and RRP is open to conjecture. If there is a relationship it is more likely that P_N controls the amount of root regeneration rather than vice versa because P_N at Measurement 2, one day after root pruning, has already fallen significantly in plants grown in 16% sun compared with those grown under higher light intensities (Table 4.6B 1). At this time, no new roots would have formed. Nevertheless, the requirement for roots for P_N is suggested by the fact that P_N is not low in intact plants grown in 16% sun (Measurement 1, Table 4.6B I).

In general, shoot respiration and the efficiency ratio (P_T/R_D) showed similar patterns of response to light intensity as photosynthesis

at Measurements 2, 3 and 4 (Table 4.6B I). These results indicate that photosynthesis was much more affected by changes in light intensity than dark respiration following root pruning and subsequent root regeneration.

4.4.3 *Effect of root pruning on P_N, R_D and P_T/R_D ratio and their recovery with time at each light intensity*

Root pruning reduced P_N, R_D and P_T/R_D ratio at all light intensities (Figure 4.2 and Table 4.6B II).

The reduction in photosynthesis could be attributed to a plant water deficit which can develop when its ability to absorb water is reduced by root pruning. Kramer (1969) reported that moisture supply affects photosynthesis indirectly by influencing stomatal closure and impeding uptake of CO_2. The presence of many dead needles on the seedlings after root pruning is circumstantial evidence of a decrease in water uptake. In addition, the removal of part of the root system reduced the size of the sink which can reduce photosynthesis by the build-up of photosynthates in the leaves (Nielsen, 1971; Troughton, 1971; Ziemer, 1971).

Photosynthesis of plants grown at 50% and 100% sun began to recover, though not completely, by the end of the fourth week after root pruning (Table 4.6B II). This was accompanied by a rapid increase in plant RRP at these light intensities (Figures 4.2 and 4.3). Seedlings grown at 16% sun did not show any recovery in photosynthesis (Table 4.6B II; Figure 4.2). Photosynthesis continued to decrease significantly from Measurement 2 onwards and reaching the lowest level at Measurement 4. Practically no new roots were regenerated at this light intensity and the plants appeared to be dying (wilting) by the end of the fourth week after root pruning treatment. These results indicate that 16% sun must be below the critical light intensity for survival of *P. caribaea* seedlings after root pruning. Thus, again there is a parallelism between photosynthesis and RRP but similar difficulties to those discussed earlier (section 4.4.2) in determining whether or not there is a causal relationship between the two processes remain.

Overall, P_N is lowered more over all measurement periods after root pruning in plants grown under 16% sun than in the higher light intensities (Table 4.6B II). Root pruning in itself affects P_N more in plants grown under 16% sun than under the higher light intensities (Measurement 2, Table 4.6B I). Thus an immediate effect of root pruning is influenced by the light regime under which plants have been grown. At Measurement 3 for P_N (Table 4.6 B I) and harvest 1 for RRP (Table 4.4B) both of which were made two weeks after root pruning, there were no differences between P_N and although the differences in RRP were not different statistically there is a strong trend towards plants grown under 100% sun regenerating roots more vigorously. After a further 2 weeks (Measurement 4, Table 4.6 B I; and harvest 2, Table 4.4 B) P_N in plants grown under 16% sun has dropped to negligible proportions whereas P_N of plants grown under higher light intensities has increased. At this time, the plants grown under 16% sun have produced almost no roots whereas those grown under higher light intensities have regenerated many roots. It appears therefore that there is a clear relationship between light intensity, photosynthesis and root regeneration but the nature of this relationship remains obscure.

4.5 *Conclusion*

Root regeneration, dry matter production and height and diameter increments, in both *P. caribaea* and *P. kesiya* increased proportionally with an increase in light intensity when the experiment was conducted in growth cabinets where, the highest light intensity achieved was only 75 watts. m^{-2}. In contrast, root regeneration and growth of *P. caribaea* were adversely affected in seedlings grown in 16% sun but 100% sun was no better than 50% sun when the experiment was conducted in an open-glasshouse using natural light as the source of light energy. At full sun, the mean daily radiation for a 12 hour daylight period during

the experiment was calculated as 484 watts. m^{-2} -- much higher than in the growth cabinet.

A heavy shade of 16% sun appears to be below the critical light intensity for survival of root-pruned *P. caribaea* seedlings. On the other hand, partial shade (50% sun) was no worse and could even have been better than growth under full sun. This could justify the practice in many tropical and subtropical nurseries for growing the species under partial shade.

Effects of treatment on root regeneration and growth were strongly paralleled by effects on photosynthesis but the nature of this relationship remains obscure.

CHAPTER 5

THE EFFECTS OF VARIOUS COMBINATIONS OF DAY AND NIGHT AIR TEMPERATURES ON THE GROWTH AND ROOT REGENERATION POTENTIAL OF *PINUS CARIBAEA* AND *PINUS KESIYA* SEEDLINGS

5.1 *Introduction*

Temperature is one of the most critical factors of the environment influencing growth (Treshow, 1970) and distribution of trees (Daubenmire, 1974) by altering rates of various important physiological processes such as photosynthesis, respiration, transpiration, translocation, enzymatic activity and cell division and cell elongation (Treshow, 1970). The cardinal temperatures * for growth vary with species, stage of plant development, part of plant (Daubenmire, 1974), the period of exposure to the temperature and other environmental factors (Troughton, 1957 ; Sutton, 1967).

Active plant growth is generally confined to a temperature range from about 10^{o} C to 40^{o} C (Treshow, 1970). Within this narrow range of temperatures coniferous species show marked differences in their temperature requirements for seedling growth (Hellmers and Sundahl, 1959). These differences are connected with not only mean temperature but also with response to fluctuations in day, night and diurnal temperatures (Hellmers and Sundahl, 1959), and total daily heat units which, both independently and through their interactions, affect growth (Hellmers, 1966a).

In some species, e.g. loblolly pine (*Pinus taeda* L.) (Kramer, 1957) and red fir (*Abies magnifica* A. Murr.) (Hellmers, 1966a) the effect of temperature on growth is mainly determined by thermoperiodicity, i.e. the

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* Cardinal temperatures are the minimum below which a function is not detectable, the maximum above which it is not detectable, and the optimum at which the function progresses at maximum velocity (Daubenmire, 1974).

differential between day and night temperature; in others, e.g. redwood (*Sequoia sempervirens* D. Don) (Hellmers, 1962; 1966b) by the day temperature; in still others, e.g. Digger pine (*Pinus sabiniana* Dougl.) (Hellmers, 1962) and Engelmann spruce (*Picea engelmannii* Parry) (Hellmers *et al*, 1970) by night temperature; and in still another type, e.g. Jeffrey pine (*Pinus jeffreyi* Grev. and Balf.) (Hellmers, 1963) by the total daily degree-hours.

The main aim of this experiment was to study the effect of air temperature on root regeneration capacity of *Pinus caribaea* Mor. and *Pinus kesiya* Royle ex Gordon. A consideration of the effect of temperature on root regeneration potential could aid in understanding some of the more fundamental requirements for root regeneration.

Since the ability of a seedling to regenerate roots rapidly in the first few weeks after outplanting is critical in determining its success (Stone and Schubert, 1959a), a knowledge of root regeneration response to temperature could have practical importance in the planning of suitable planting season (or month). A knowledge of the response of tree seedlings to temperature can also have practical importance in planning species introduction programmes and in selecting suitable nursery and plantation sites. Indeed, the success or failure of a species is often determined by the maximum and minimum temperatures where it is planted (Treshow, 1970).

The seeds of *P. kesiya* in this experiment originated from a montane environment at an altitude of about 1300m above sea level (a.s.l.) in the Central Cordillera mountains, Luzon Island, Phillipines (see chapter 2). In contrast, *P. caribaea* is a lowland species occurring at an altitude below 300 m a.s.l. in its natural range (Mirov.1967; Lamb, 1973). The seeds used in this experiment originated from the lowland coastal plain of Belize (British Honduras; information on the original provenance was not supplied

to the author, see chapter 2). Thus, the use of these two species provide an opportunity to compare the temperature response of a montane and low - land species.

5.2 *Materials and methods*

Seeds of *P. kesiya* were sown in a mixture of 1:1 perlite: vermiculite in the 27/22° C glasshouse at CERES phytotron (this facility is described in chapter 2). At 10 weeks of age, 100 seedlings of uniform height (7.5 ± 0.5cm) and root collar diameter (0.22 ± 0.02cm) were selected for the experiment.

Seedlings of *P. caribaea* were supplied from Toolara nursery (Queensland) when they were 16 weeks old. The seedlings were totally immersed in 0.5% solution of Diazinon, a normal quarantine procedure, before being shipped to Canberra. The seedlings were grown in the 27/22° C glasshouse at the CERES phytotron for a further 10 weeks after which 100 seedlings of uniform height (11.1 ± 1.0cm) and root collar diameter (0.26 ± 0.02cm) were selected for the experiment.

The roots of the seedlings were pruned to 18 cm from the cotyledon and all white root tips were pinched off to simplify recognition of new roots. The height and root collar diameter were taken and the seedlings were then subjected to 10 different combinations of day/night temperature regime (see Table 5.1) for 6 weeks, from 20 October, 1974 to 1 December, 1974. 10 seedlings from each species were used for each treatment.

After 6 weeks, the seedlings were harvested. The height and root collar diameter were taken and the increment over the 6 week period calculated. The shoots were severed at the root collar and oven dried (fan circulated air at c. 85° C) for a minimum of 48 hours before the dry weight was taken. The roots of each plant were carefully washed with a fine spray of water and put into a small plastic bag (1 plant per bag) filled with

water and stored at 2° C. This practice enabled the assessment of root regeneration of the plants — a very time consuming process, to be done gradually without decreasing the precision of the results due to root growth while awaiting harvest. The new roots were still clearly recognisable even after 3 weeks in cold storage. All white roots ≧ 1.0cm long were counted and the lengths of those ≧ 2.0cm long were measured. Total root, shoot and total plant dry weights were also taken.

All data were subjected to analysis of variance to assess the significance of the treatment effects on each parameter. The significance of differences between group means was tested using Duncan's new multiple range test (Steel and Torrie, 1960; Winer, 1971). It should be noted that the sample sizes for *P. kesiya* at harvest were unequal due to the death of 3 seedlings in both treatments 33/28° C and 33/22° C. However, since the sample sizes at harvest were not markedly different from each other, the average (harmonic mean) sample size was calculated and Duncan's new multiple range test adapted for use in comparing for significance of differences between group means. The method is described by Winer (1971).

For height and diameter increment, only the means of eight treatments could be statistically compared in each of the species. Treatments 21/22° C and 24/16° C were not included because it was not possible to calculate their respective sums of squares. This was due to an accident at harvest resulting in loss of plant labels and consequently it was not possible to measure the height and diameter increment of the same plant.

Table 5.1 Day/night air temperature treatments and the corresponding daily degree-hours.

Four of the treatments (*) were obtained in open-glasshouses while other temperature combinations (#) were obtained by moving trolleys containing 20 plants from one glasshouse to another at 0830 and 1630 hours.¢

Night temperature (°C)	Day temperature (°C)			
	21	24	27	33
16	* 424	# 448	# 472	# 520
19		* 496		
22	# 520	# 544	* 568	# 616
28				* 712

¢ Total daily degree-hours ≡ total amount of heat in 24 hours ≡ day temperature °C x daylight in hours + night temperature °C x nightlength in hours.

5.3 *Results*

This experiment was conducted earlier than any other experiment reported in the thesis. It was observed that pruning of the plant roots to 18 cm from the cotyledon and removing all the white roots at the start of the treatment period caused too much moisture stress in most of the plants as shown by needle death. Three *P. kesiya* plants died in each of the warmer day/night air temperature combinations i.e. 33/28° C and 33/22° C. It is likely that the severe root pruning impeded water absorption sufficient to cope with the transpiration at the high temperatures. It was also realized that the root growth period of 6 weeks had to be shortened to reduce the time taken to assess root regeneration.

Colour of new root growth

Temperature affected the colour of new roots in both species. Roots grown under cold conditions were white in colour. An increase in either day or night temperature generally resulted in the production of light tan coloured roots. However, it was not difficult to differentiate between new and old roots in any temperature treatments.

Table 5.2 Results of analysis of variance for significance of differences between treatment means of the measured parameters in *P. caribaea*.

Parameter	Significance of F ratio
Root regeneration (per plant)	
Total number of white roots ≥ 1.0cm long	* * *
Total length of white roots ≥ 2.0cm long	* * *
Dry weight (g)	
Root	* * *
Shoot	* * *
Total plant	* * *
Increment (cm) #	
Height	NS
Root collar diameter	* * *

P, 0.001 * * * ; NS, not significant.

Only means of 8 treatments were compared. Treatments 21/22° C and 24/16° C were not included (see section 5.2 for the reason).

TABLE 5.3 Ranking of treatment means in ascending order for the different parameters of *P. caribaea* seedlings grown for 6 weeks under the air temperature regimes shown in Table 5.1. Bracketed means are not significantly different ($P < 0.05$).

A: *Root regeneration (per plant)*

B: *Dry weight (g)*

C: *Height & Diameter Increment (cm)*

Total number (N) of white roots ≥ 1.0cm long	Total length (L) of white roots ≥ 2.0cm long	Root	Shoot	Total plant	Height Increment	Diameter Increment
33/28 66	33/28 147	33/28 0.342	33/28 1.108	33/28 1.450	33/28 3.5	33/16 0.07
33/16 110	33/16 227	33/16 0.405	33/16 1.392	33/16 1.797	33/16 4.8	33/28 0.09
33/22 136	33/22 297	33/22 0.491	33/22 1.472	33/22 1.963	33/22 4.9	33/22 0.10
21/22 158	21/22 359	21/22 0.510	21/22 1.505	21/22 2.015	21/16 5.0	24/22 0.12
24/19 159	24/22 360	24/22 0.624	24/19 1.781	24/22 2.349	24/19 5.3	24/19 0.13
24/22 174	24/19 422	24/19 0.635	24/22 1.825	24/19 2.416	24/22 5.3	21/16 0.15
24/16 199	27/22 505	27/22 0.702	27/22 2.042	27/22 2.744	27/16 5.6	27/22 0.16
21/16 215	24/16 542	27/16 0.820	27/16 2.259	27/16 3.078	27/22 6.5	27/16 0.18
27/22 228	21/16 605	21/16 0.827	21/16 2.379	21/16 3.206		
27/16 261	27/16 613	24/16 0.856	24/16 2.502	24/16 3.358		

Figure 5.1 Root regeneration of *P. caribaea* seedlings plotted over the difference between day and night air temperatures (thermoperiod).

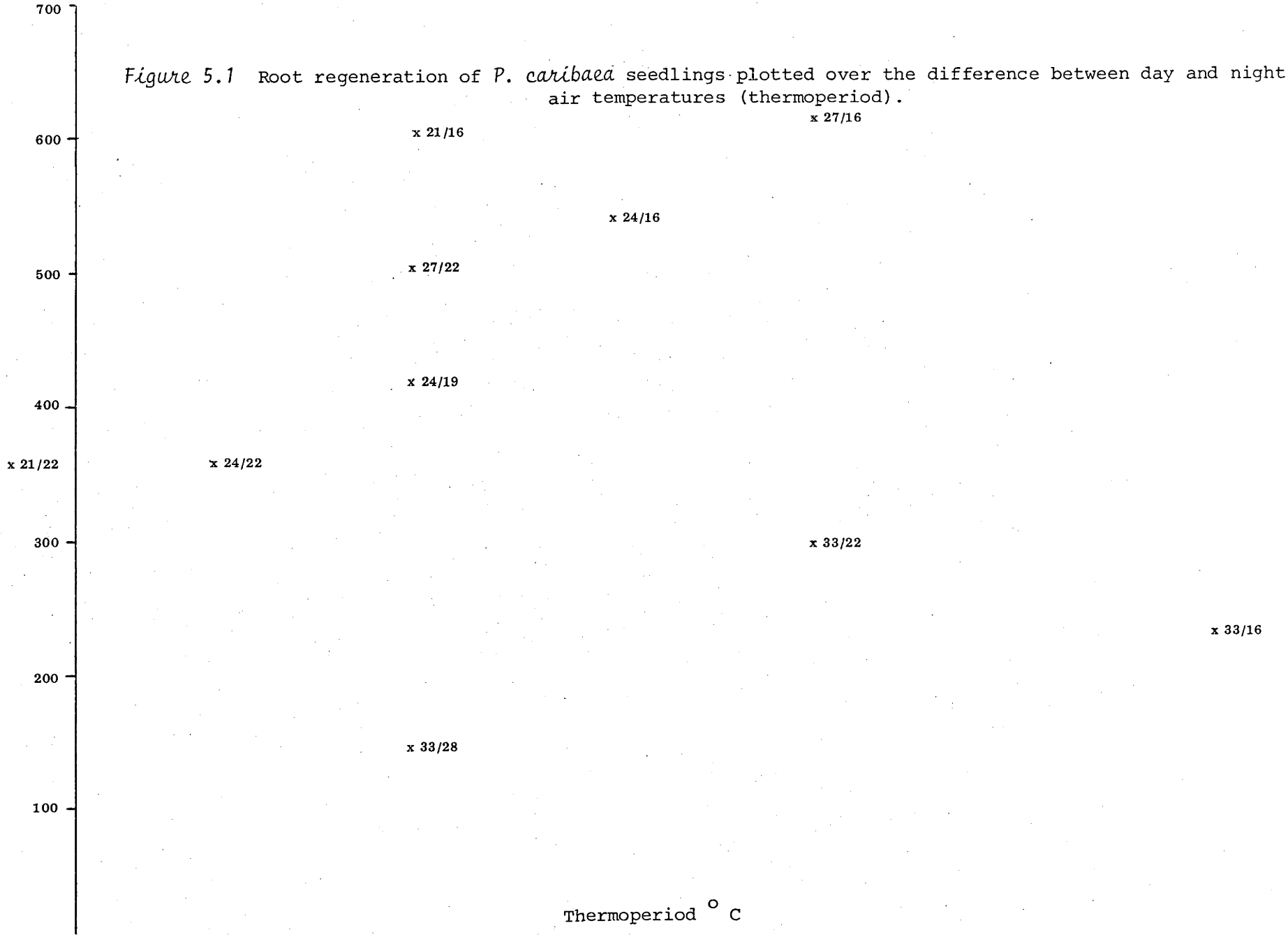


Figure 5.2 Linear regression of root regeneration of *P. caribaea* seedlings on daily degree-hours.

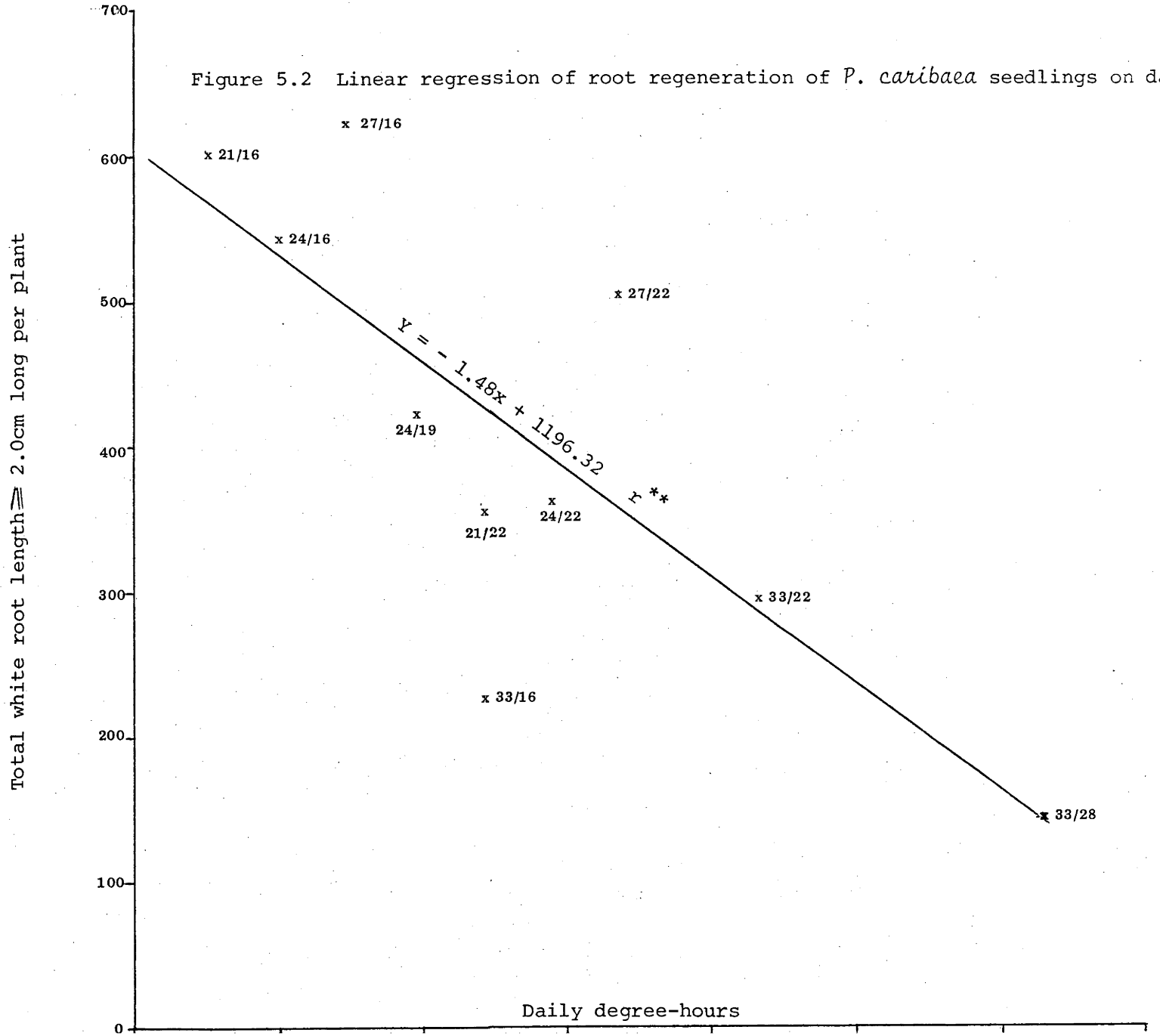


Table 5.4 Linear correlation and regression of various plant parameters in *P. caribaea* with daily degree-hours.

Parameters	Correlation coefficient (r)	Linear regression equation Y = mx + c
White root number	-0.790 * *	Y = -0.48x + 424.54
White root length	-0.793 * *	Y = -1.48x + 1196.32
Root dry weight	-0.782 * *	Y = -0.002x + 1.510
Shoot dry weight	-0.791 * *	Y = -0.004x + 4.120
Total plant dry weight	-0.792 * *	Y = -0.006x + 5.640
Diameter increment #	-0.540 NS	

Table 5.5 Results of analysis of variance for significance of differences between treatment means of the measured parameters in *P. kesiya*.

Parameter	Significance of F ratio
Root regeneration (per plant)	
Total number of white roots ≥ 1.0cm long	* * *
Total length of white roots ≥ 2.0cm long	* * *
Dry weight (g)	
Root	* * *
Shoot	* * *
Total plant	* * *
Increment (cm) #	
Height	* * *
Root collar diameter	* * *

P, 0.01 * * ; 0.001 * * * ; NS, not significant.

Only means of 8 treatments were compared. Treatments 21/22° C and 24/16° C were not included (see section 5.2 for the reason).

TABLE 5.6 Ranking of treatment means in ascending order for the different parameters of *P. kesiya* seedlings grown for 6 weeks under the air temperature regimes shown in Table 5.1. Bracketed means are not significantly different ($P < 0.05$).

A: *Root regeneration (per plant)*

B: *Dry weight (g)*

C: *Height & Diameter Increment (cm)*

Total number (N) of white roots ≥ 1.0cm long	Total length (L) of white roots ≥ 2.0cm long	Root	Shoot	Total plant	Height Increment	Diameter Increment
33/16 15	33/16 28	33/16 0.115	33/16 0.551	33/16 0.666	33/16 1.0	33/16 .01
33/28 30	33/28 71	33/28 0.116	33/28 0.597	33/28 0.713	27/16 1.1	27/16 .04
33/22 38	33/22 98	33/22 0.138	33/22 0.612	33/22 0.750	21/16 1.2	21/16 .04
21/16 47	21/16 117	27/22 0.239	21/16 0.858	21/16 1.104	27/22 1.6	27/22 .04
21/22 64	21/22 126	21/16 0.246	27/16 0.877	27/22 1.122	24/22 1.9	33/22 .07
27/22 89	27/22 151	21/22 0.252	27/22 0.883	27/16 1.132	33/22 2.3	24/22 .07
27/16 89	27/16 184	27/16 0.255	21/22 0.990	21/22 1.242	24/19 2.4	24/19 .08
24/16 101	24/16 188	24/16 0.272	24/19 0.997	24/19 1.301	33/28 2.5	33/28 .09
24/22 111	24/22 193	24/19 0.304	24/16 1.031	24/16 1.303		
24/19 160	24/19 322	24/22 0.339	24/22 1.073	24/22 1.412		

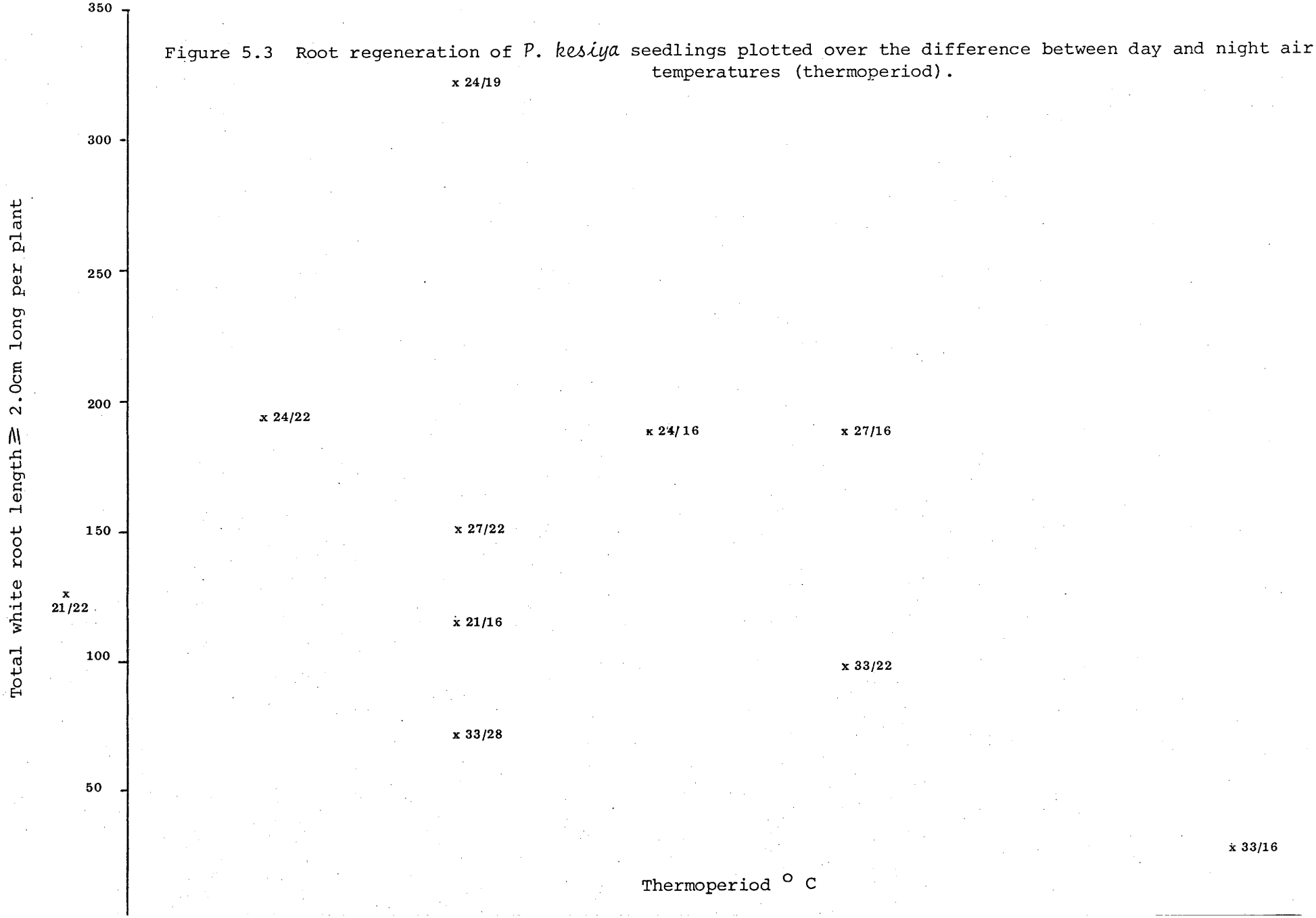
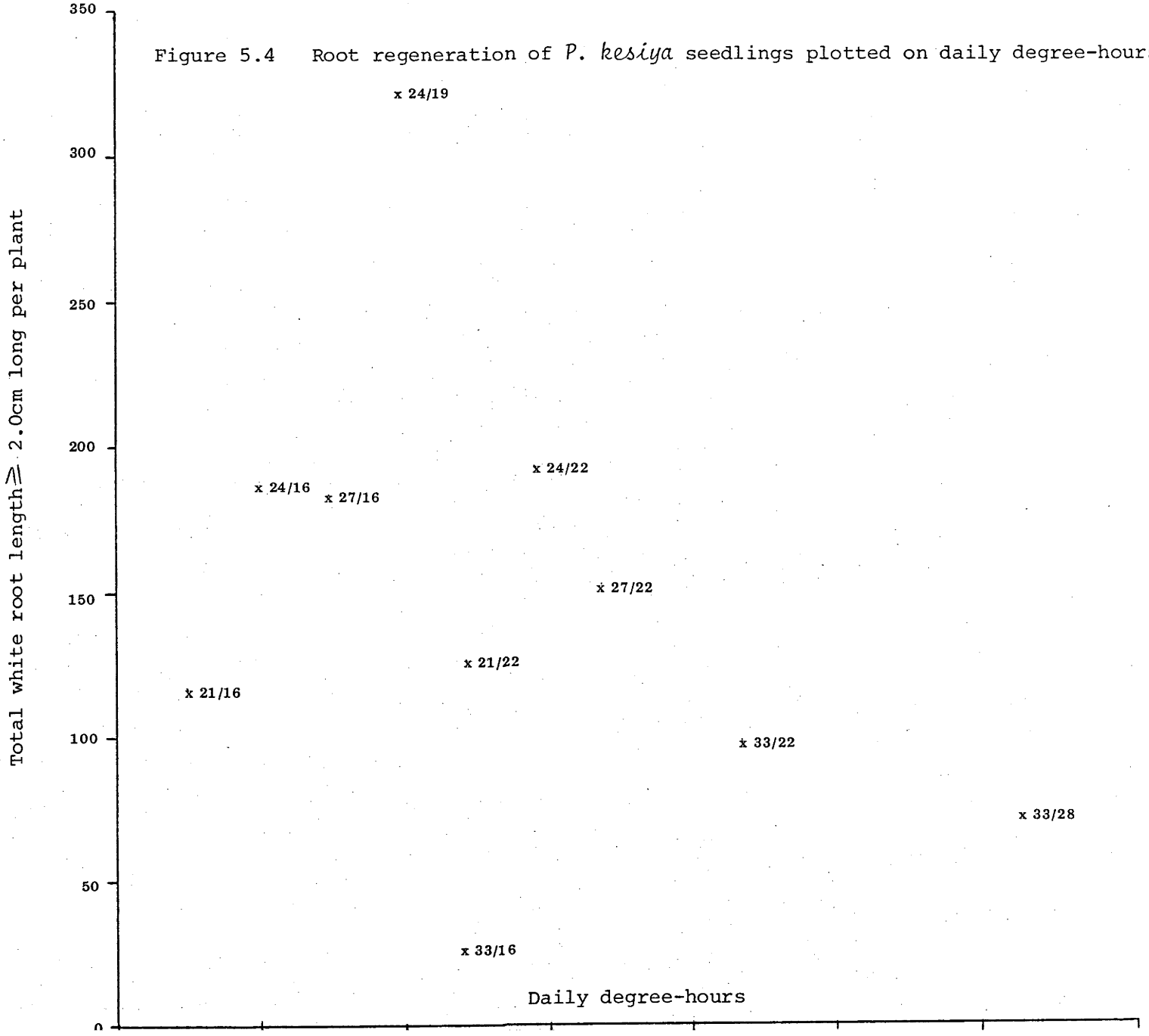


Figure 5.3 Root regeneration of *P. kesiya* seedlings plotted over the difference between day and night air temperatures (thermoperiod).

Figure 5.4 Root regeneration of *P. kesiya* seedlings plotted on daily degree-hours.



5.3.1 *Effects of temperature on the growth and RRP of P. caribaea*

Analysis of variance revealed highly significant differences between treatment means for all of the measured parameters except for height increment (Table 5.2).

5.3.1.1 *Root regeneration*

In general, root regeneration based on both number and length of white roots had a similar pattern of response to temperature (Table 5.3A). Maximum root regeneration potential was at 27/16^{o} C and minimum potential at 33/28^{o} C. 16^{o} C night temperature was most favourable for root regeneration under moderate day temperatures. 33^{o} C day temperature was least favourable for root growth irrespective of any night temperature combination.

Root regeneration did not exhibit any clear relationship with a day-night temperature change (thermoperiod) as shown in Figure 5.1. However, a plot of root regeneration on daily degree-hours in Figure 5.2 showed evidence of a negative linear relationship between them. Analysis of the data revealed a highly significant linear correlation between root regeneration and the total amount of heat that the plants received in 24 hours (Table 5.4). The root regeneration potential was increased when plants were exposed to lower heat sum between 400 to 500 daily degree-hours (Figure 5.2).

5.3.1.2 *Dry weight*

The root, shoot and total plant dry weights show similar patterns of response to temperature (Table 5.3B). Maximum dry matter production occurred at 24/16^{o} C and minimum production at 33/28^{o} C. 16^{o} C night temperature was most favourable to growth under favourable day temperature, and day temperatures of 33^{o} C gave poorest growth irrespective of night temperatures.

In general, the response in terms of dry weight were similar to those of root regeneration (Tables 5.3A and B). As in root regeneration, the root, shoot and total plant dry weights did not show any clear relationship with thermoperiod but showed a negative linear relationship with heat sum. The linear correlation coefficients for root, shoot and total plant dry weights with heat sum were all significant at the 99% confidence level (Table 5.4). Dry matter production was favoured when plants were exposed to lower heat sum between 400 to 500 daily degree-hours (see Tables 5.1 and 5.3B).

5.3.1.3 *Height and diameter increment*

There was no significant difference between treatment means for height increment (Table 5.2) possibly because of so much variation within the treatment means for the differences to be detected. However, there was a similar trend in height increment to diameter increment (Table 5.3B). For example, 27^{o} C day temperature was most favourable for both height and diameter growth whereas 33^{o} C day temperature gave poorest growth. For diameter increment, the best temperature was 27/16^{o} C and poorest temperature was 33/16^{o} C. It may be noted that since there was no significant change in height whereas there was in diameter with change in temperature, the height : diameter ratio would be decreased under favourable day/night air temperature regime. The height : diameter ratio is an important measure of the 'quality' of planting stock and is one of the primary purposes of root pruning.

Diameter increment did not appear to have any clear relationship with either thermoperiod or daily heat sum. Analysis of the data (treatments 21/22 and 24/16^{o} C were not included) did not reveal any significant correlation between them.

5.3.2 *Effects of temperature on the growth and RRP of P. kesiya*

The Anova data revealed highly significant differences between treatment means for all of the measured parameters (Table 5.5).

5.3.2.1 *Root regeneration*

In general, root regeneration based on both number and length of white roots had a similar pattern of response to temperature (Table 5.6A). Root regeneration at 24/19^{o} C was significantly greater than at any other temperature. 24^{o} C day temperature was most favourable for root regeneration under any night temperature combination. Poorest root regeneration occurred at 33/16^{o} C; 33^{o} C day temperature was least favourable for root regeneration irrespective of the night temperature combination.

The day temperature had a more pronounced effect on root regeneration in *P. kesiya* than the night temperature. This is evident in Table 5.6A which shows that changes in day temperature from 33, 21, 27 and 24 ^{o} C increased both the number and length of white roots in that order.

Root regeneration in *P. kesiya* did not appear to have any clear relationship with either thermoperiod or daily heat sum as shown in Figures 5.3. and 5.4. respectively. Analysis of the data did not reveal any significant correlation between them. However, Figure 5.4 shows that the absence of a correlation between root regeneration and daily heat sum was largely due to treatments 24/19^{o} C and 33/16^{o} C which gave the optimum and minimum root regeneration respectively.

5.3.2.2 *Dry weight*

In general, the root, shoot and total plant dry weights showed similar patterns of response to temperature (Table 5.6B). 33^{o} C day temperature produced significantly less dry matter than any other day temperature. 24^{o} C day temperature was most favourable for dry matter production under any night temperature combination.

As in root regeneration, the root, shoot and total plant dry weights did not show any clear relationship with either thermoperiod or daily heat sum. Analysis of the data for each of the dry weight parameters did not reveal any significant correlation between them.

5.3.2.3 *Height and diameter increment*

In general, both height and root collar diameter increment showed similar patterns of response to temperature (Table 5.6C). Best increment occurred at 33/28^{o} C and poorest at 33/16^{o} C. 16^{o} C night temperature was least favourable for growth in size under any day temperatures whereas a high day temperature of 33^{o} C under moderate night temperature was most favourable.

Both height and diameter increment did not appear to have any clear relationship with either thermoperiod or daily heat sum. Analysis of the data for each of the parameters (treatments 21/22 and 24/16^{o} C were not included) did not reveal any significant correlation between them.

Figure 5.5 Comparison of the root regeneration potential of *P. caribaea* and *P. kesiya* as affected by various combinations of day/night air temperatures.

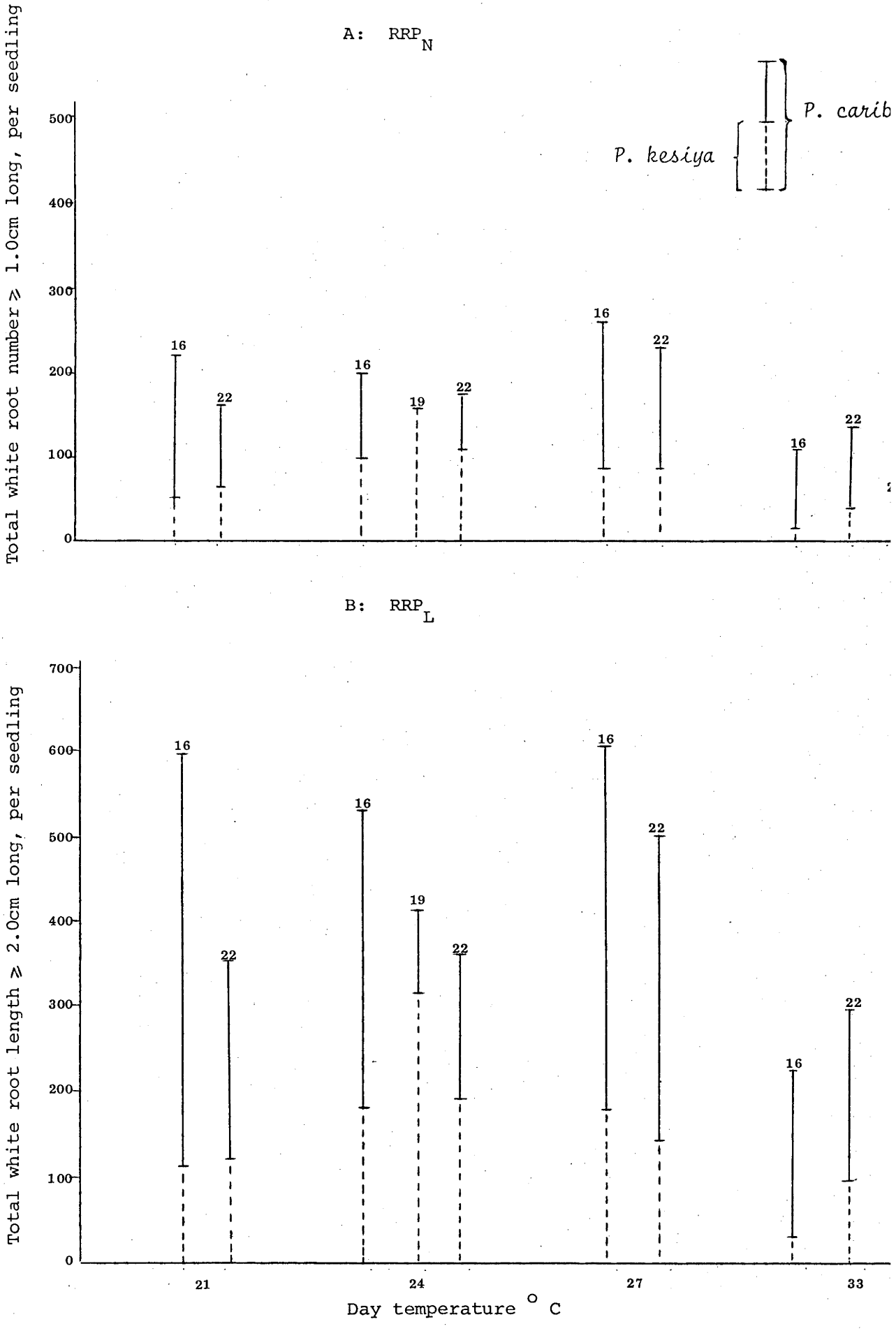


Figure 5.6 Comparison of the dry weight of *P. caribaea* and *P. kesiya* seedlings as affected by various combinations of day/night air temperatures.

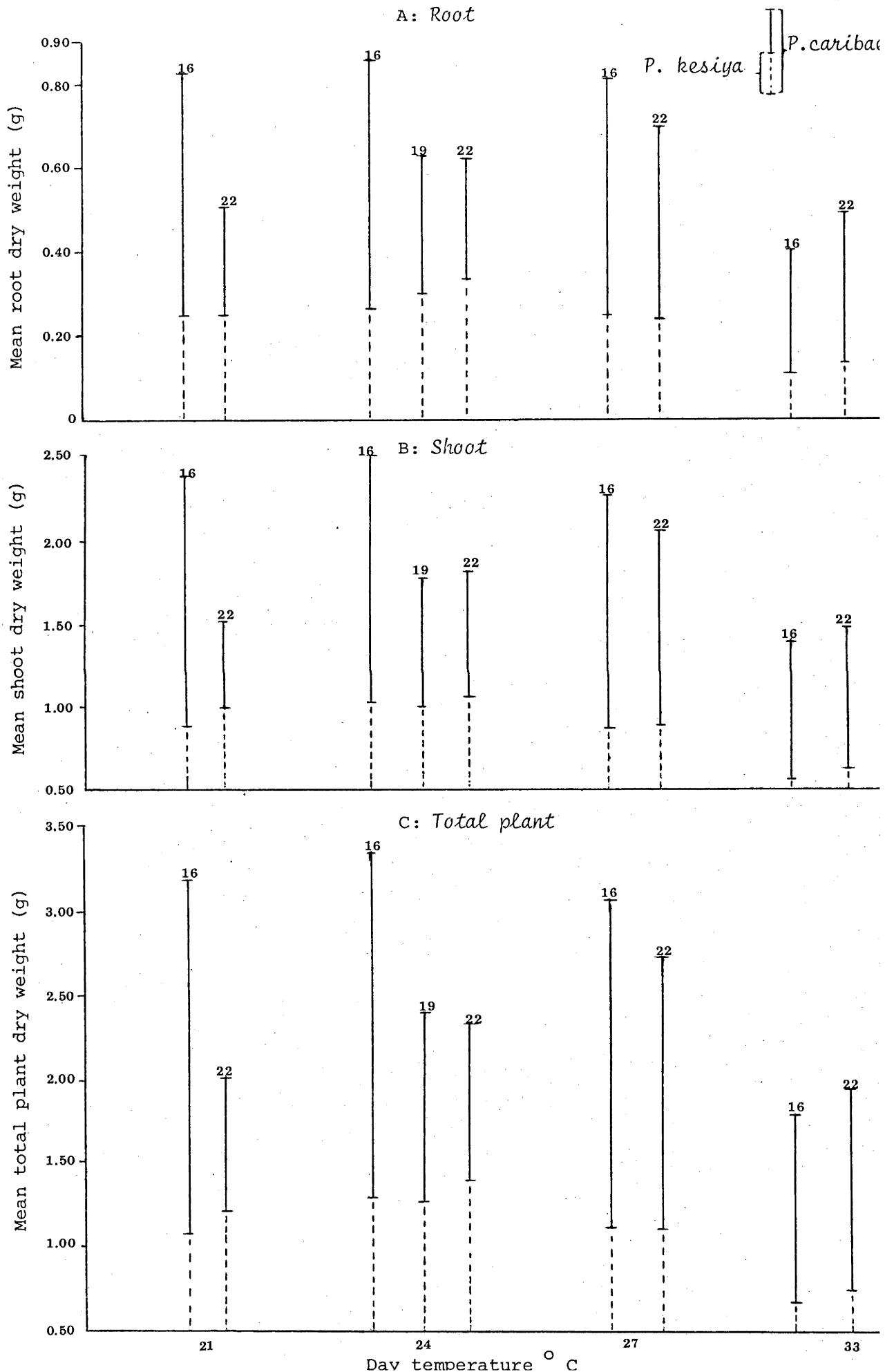
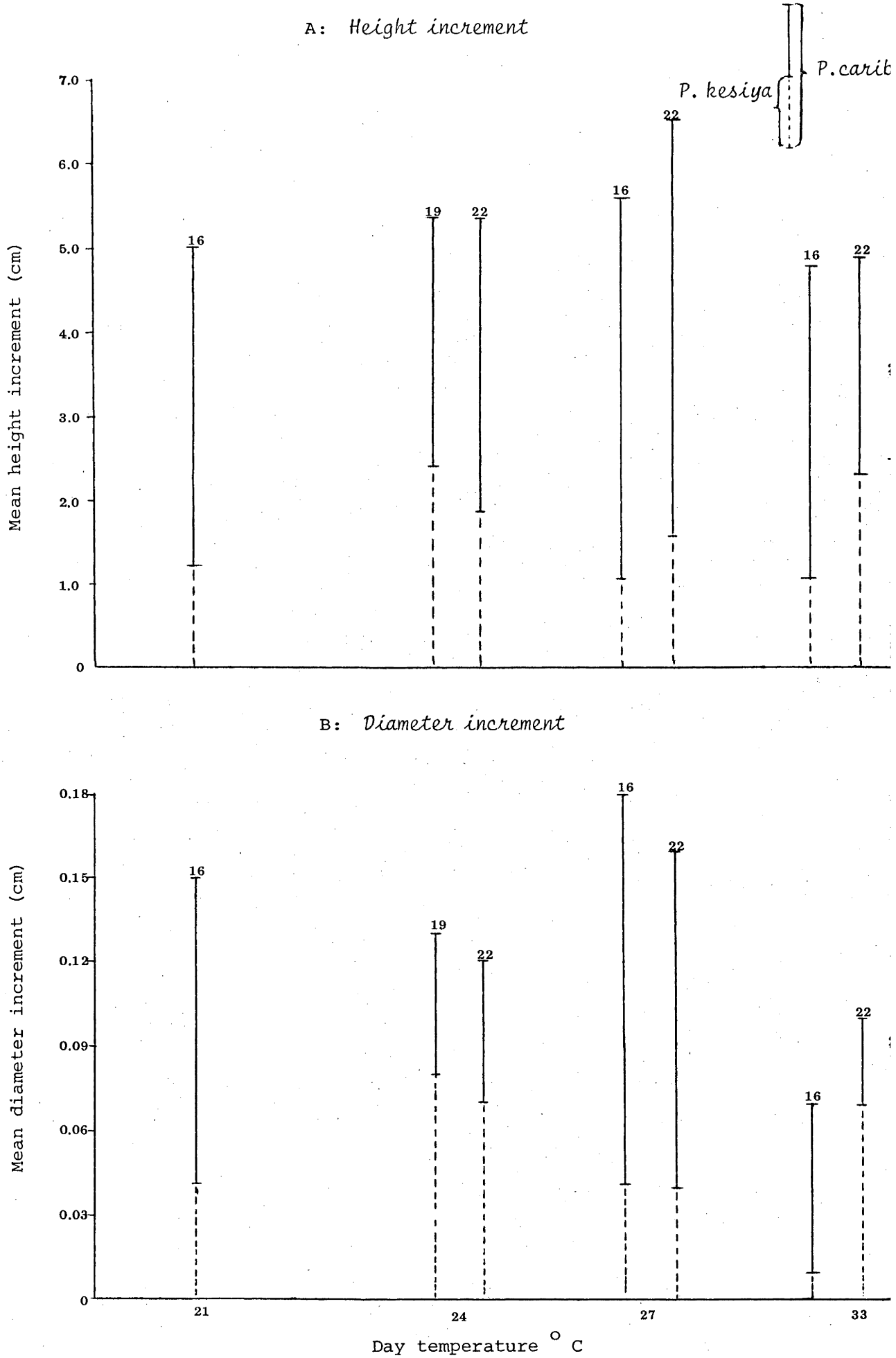


Figure 5.7 Comparison of the height and diameter increments of *P. caribaea* and *P. hesiya* seedlings as affected by various combinations of day/night air temperatures.



5.4 *Discussion*

Both the root and shoot of plants in this study were subjected to the same temperature (± 1.0° C). Hence, there would be no complications due to a temperature gradient between root and shoot in any of the treatments. Evans (1963) reported that a temperature gradient between the root and shoot could have significant physiological consequences on the plants. These possibilities are studied in Chapter 6.

The effects of temperature on root growth could either be due to its direct effect on the metabolic activity of the roots or indirectly through its effect on the crown, or both. Kozlowski (1971) stated that root growth is regulated to a large degree by products produced by shoots and thus it also varies with the environment of the crown. Nevertheless, there was evidence in this experiment of the direct effects of temperature on roots. For example, it was observed that regenerated roots grown under cooler conditions were whiter in colour than those grown in the warmer condition. This observation is similar to those of other workers (e.g. Hellmers, 1966a; Rook and Hobbs, 1976).

In comparing the two species it should be remembered that they had a different growth history and were of different age and size at the start of the treatments. For example, *P. caribaea* was 1.5 times taller than *P. kesiya* at the start of the experiment. This difference in size is reflected in the results in Figures 5.5, 5.6 and 5.7 which show that the former species had a greater amount of root growth, dry weight, and height and diameter increment. Hence, between species comparison is restricted to the relative patterns of response to different temperatures and not to the absolute growth data.

Both day and night temperatures had a marked effect on growth of the two species studied. There are striking similarities and differences in the response of the various measured parameters both within and between species. The general similarities between root regeneration potential based on number (RRP_N) and length (RRP_L) of new roots in both *P. caribaea* and *P. hesiya* are consistent with the findings of Stone and co-workers (Stone and Schubert, 1959a; Krugman and Stone, 1966). The results indicate that either one of the criteria could be used in root regeneration studies. The use of only one of the criteria, especially that of RRP_N has the advantage of reducing the time and labour in assessing the RRP but Stone and co-workers usually use both criteria to increase the precision of the results.

Root regeneration and dry matter production in *P. hesiya* and, all of the measured parameters in *P. caribaea* showed that 33°C day temperature was least favourable for growth. The decrease in growth due to high temperature may result from excessive respiration which decreases carbohydrates (Kramer, 1957), from decreased rate of photosynthesis, from excessive transpiration which causes wilting or from a combination of these (Kramer and Kozlowski, 1960). Many workers (Langridge, 1963; Cremer, 1968; Treshow, 1970) have reported that beyond about 30°C, the rate of and balance between physiological processes deteriorates sharply. For example, Decker (1944) has shown that the apparent photosynthesis in both loblolby pine and red pine (*P. resinosa* Ait.) began to decline rapidly above 30°C because respiration continued to increase above that temperature while actual photosynthesis did not. Therefore exposure of trees to high temperatures may cause decreased growth because of respiratory loss of large amounts of carbohydrates which otherwise would be available for growth.

The temperature regime at which the seedlings were grown altered the distribution of growth within the plant. For example, root regeneration and

the dry weights of root, shoot and total plant show similar patterns of response to temperature but were different from those of height and diameter growth in both *P. caribaea* and *P. kesiya* respectively (Figures 5.5, 5.6 and 5.7).

The temperature optima for root regeneration and dry matter production in *P. caribaea* occurred in a cool night temperature (16° C) under moderate day temperatures. It is tempting to speculate that the cool night temperature allows the seedlings to conserve carbohydrates by reducing respiration. Hellmers and Rook (1973) explained that respiration may be subdivided into metabolic respiration and maintenance respiration, thus, the cool night temperature could possibly boost growth by reducing the rate of maintenance respiration or reducing the wastage of photosynthate by some other means, such as inhibiting the production of secondary products. Lundegardh (1931) and Kramer (1957) have stressed the importance of low night temperatures in conserving food by reducing its use in respiration.

Increased growth with decreased night temperatures has been observed in several other species by Went (1953). He attributed this to increased translocation of food to the growing regions (Went, 1944), but this is questioned by other investigators (Hewitt and Curtis, 1948; Swanson and Bohning, 1951). For example, Swanson and Bohning (1951) found that the translocation of sucrose from bean leaves was maximum at petiole temperatures between 20-30° C. In addition, Hewitt and Curtis (1948) found that translocation of carbohydrates decreases only above 30° C.

In contrast to *P. caribaea*, *P. kesiya* was more responsive to the day temperature; best root regeneration and dry matter production occurred at 24° C day temperature under any night temperature combination (Figures 5.5 and 5.6). The mean annual temperature in the natural habitat of *P. Kesiya* in the Phillipines is about 25° C (23° C January to 28° C in May,

see Appendix IA) and fluctuates little throughout the year. The fact that a day temperature of 24° C was best for root regeneration and dry matter production (and height and diameter growth) could be attributed to the species adaptation to the climate in its native habitat. Steward (1969) reported that a plant's optimal temperature usually agree very closely with the temperatures to which the plants are subjected in nature.

It seems probable that a day temperature of 24° C was most favourable for the manufacture of food by photosynthesis in *P. kesiya*. The observation that root regeneration at 24/19° C was significantly greater than at any other temperature suggests that the night temperature must have played an important role in regulating the use of the manufactured food. Searle (1973) commented that plant reaction to day temperature can be markedly affected by the night temperature for it is at night that growth and developmental responses within the plant mainly take place. Probably, the observed optimum root regeneration at 24/19° C in this study reflects an optimum balance between carbohydrate formation in photosynthesis, loss in respiration and its use in root regeneration.

In general, both height and diameter growth in *P. caribaea* showed different patterns of response to temperature from *P. kesiya* (Figure 5.7). Best height and diameter growth in *P. caribaea* occurred at 27° C day temperature. Slee, according to Kanchanaburangura (1976) also found that the species grew best in height and diameter at 27° C day temperature. Unlike root regeneration and dry matter production the day temperature had a larger effect on height and diameter growth in *P. caribaea* than the night temperature. This is evident in Table 5.3C which shows that height and diameter growth were determined primarily by day temperature irrespective of night temperature. Brix (1971) and Daubenmire (1974) have stressed that the effects of temperature on growth varies with the part of the plant.

The best recorded height and diameter increments in *P. kesiya* occurred at 33/28° C and 24/19° C (Table 5.6C). However, whereas 24/19° C was also best for RRP and close to optimum for dry matter production, 33/28° C was most unfavourable for RRP and dry matter production. The increased growth in height and diameter at 33/28° C and 33/22° C could be a reflection of the greater amount of photosynthate present for apical meristem and cambium at the expense of root growth and foliage dry matter production. It is generally recognised that the apical meristem is at an advantage compared to the roots under conditions of limiting photosynthate availability (Hellmers and Rook, 1973). Unlike root regeneration and dry matter production the night temperature had a larger effect on height and diameter growth in *P. kesiya* than the day temperature. This is evident in Table 5.6C which shows that both height and diameter growth were determined primarily by night temperature. The fact that 33/16° C was least favourable for height and diameter growth whereas 33/28° C and 33/22° C were more favourable could be attributed to the unfavourable effect of the cool night temperature. Hellmers and Rook (1973) reported that root growth in *P. radiata* (D. Don) was encouraged compared to shoot growth at low night temperatures but this was not shown in the RRP in this study.

There was a strong linear relationship between daily heat sum and root regeneration potential and the dry weight of root, shoot and total plant in *P. caribaea*. Optimum root regeneration and dry matter production were attained under a low heat sum i.e. 424 to 472 daily degree-hours. The day/night temperature combinations of 21/16, 24/16 and 27/16° C which favoured root regeneration and dry matter production fell in that range. No significar correlation was exhibited between the daily heat sum and height and diameter increments in *P. caribaea*, nor was there any significant correlation with any of the measured parameters in *P. kesiya*.

The daily heat requirement for optimum growth of seedlings has now been studied for several forest species (Hellmers, 1962; 1963; Brix, 1971) but there appears to be no common response to temperature. Hellmers (1963) working with Jeffrey pine found that the total daily degree-hours was the dominant temperature measure in determining maximum dry weight production. He found that best growth was obtained under a lower daily heat sum, in the range of 300-400 daily degree-hours from a range of 96 to 576 degree-hours. The best growth in *P. caribaea* was also found at a low heat sum but the limits of the data here were 424 and 712 degree-hours.

To find an explanation for the control that the total daily degree-hour exerts over root regeneration and dry matter production is as complicated a task as to explain growth itself. This is so because many processes, including photosynthesis, anabolism, respiration, and translocation, are involved and each is temperature-dependent. Additional work is needed on the relation between temperature and individual processes before the role of temperature in tree growth can be completely understood.

5.5 *Conclusion*

Extrapolation from controlled environments to the field and from individuals to communities is difficult (Evans, 1963). In the field, temperature varies continuously, and some or all of the other growth controlling factors (e.g. water, nutrients, light) are often limiting and thus likely to modify the influence of temperature. Nevertheless, it can be suggested that good growth in both of the species tested takes place in the range of temperatures in the mid-twenties. It can also be reasonably suggested that growth and root regeneration in *P. caribaea* are better in a cool night temperature (16^{o} C) whereas that in *P. kesiya* under a moderate day temperature (24^{o} C).

Root regeneration and dry matter production showed similar optimum temperature requirements in both *P. caribaea* and *P. kesiya* respectively. However, the optimum temperature requirements as well as the patterns of response to temperature in *P. caribaea* differed from *P. kesiya*. This is consistent with differences in their respective natural habitats.

CHAPTER 6
THE EFFECTS OF AIR AND SOIL TEMPERATURES ON THE GROWTH AND ROOT REGENERATION POTENTIAL OF *PINUS CARIBAEA* AND *PINUS KESIYA* SEEDLINGS

6.1 *Introduction*

How are the root regeneration and growth of *P. caribaea* and *P. kesiya* seedlings affected by air and soil temperatures? Results from an earlier study (chapter 5) showed that there were significant differences in growth response to air temperature both within and between the two species In that study, however, only the air temperature was controlled and the soil temperature was in equilibrium with the air so that the effects could not be separated. Growth of higher plants, however, is a function of both the aerial and the soil temperatures. Thus, in this study, both the air and soil temperatures were controlled and varied independently to examine the influence on the growth and root regeneration potential of *P. caribaea* and *P. kesiya* seedlings.

An effort was made to determine whether the regenerated root system develops from a rapid elongation of the short laterals already present, or from newly initiated laterals originating in the pericycle. This has an important practical application. For example, if the root system develops primarily from the elongation of lateral roots present at time of lifting, particular care must be taken to protect the lateral roots during lifting, shipping, storage, and replanting to prevent breakage and desiccation. If, on the other hand, the root system develops from lateral roots initiated after the seedling is planted in the field, the protection of lateral roots present when the seedling is lifted from the nursery is not as critical

Besides a direct effect on the growth of roots (Stone *et al.*, 1962; Lyford and Wilson, 1966) and shoot (Humphries, 1967; Brouwer and Levi, 1969), soil temperature also affects plant growth indirectly by affecting the soil microflora as well as the physical properties of soil such as soil air, soil moisture and soil nutrients (Richards *et al.*, 1952; Nielsen, 1971) For example, low soil temperature decreases the diffusion of soil air (Richards, *et al.*, 1952); decreases water uptake by plants by the combined effects of increased viscosity of the water and reduced permeability of the root membranes (Babalola *et al.*, 1968; Keller, 1972); and decreases the uptake, assimilation and translocation of nutrients by the plants (Nielsen, 1971). The results in chapter 3 indicate that it is safe to assume no nutrient deficiency effect is likely to impair the experiments in this chapter. Also, it is unlikely that the effect of soil temperature on the soil microflora or aeration would complicate the experiments because the roots were grown in a sterile and porous 1 : 1 perlite : vermiculite mixture.

Root tissues of many plants are more sensitive to temperature extremes than the shoot (Daubenmire, 1974) and soil temperature is more critical in survival than is foliage temperature (Nielsen, 1971). Roots of most plants are usually produced at temperatures below the optimum for tops (Nielsen, 1971), and Walker (1970) showed that different parts of the corn plant have different optimum soil temperatures. The optimum soil temperature, which depends on the other environmental conditions and on their duration, vary from species to species (Cooper, 1973) and with age and size of plant (Hellmers, 1963).

The roots of forest trees do not have an inherent dormant period (Kramer and Kozlowski, 1960; Bilan, 1967) and continue to grow if the soil temperature is between $5^{o}$and 35^{o} C (Richards *et al.*, 1952). Favourable

soil temperatures may induce shoot growth despite unfavourable air temperature condition (Nielsen, 1971). Canon (1971) stated that the soil temperature may be expected to influence shoot growth to the extent that it affects the development and functioning of the root system. Cooper (1973), in a review of the influence of soil temperature on plant growth, states that soil temperatures can profoundly affect rates of growth and concomitant processes, and the distribution of growth within the plant. It has been suggested that roots exert a stimulating action on the growth of shoots not entirely dependent upon the absorptive functions of the roots and perhaps attributeable to some growth-promoting substance developed within the roots. Temperature may influence the formation and transfer of this growth substance.

The ability to regenerate new roots largely determines the seedling's effectiveness in obtaining water and mineral salts from the soil. An understanding of the root growth response of tree seedlings to different soil temperatures can have practical significance in the choice of season of planting when the soil temperature is suitable for rapid root regeneration of seedlings outplanted from a nursery. If there is sufficient time for the plant to grow, as in the tropics and subtropics, then the part of the season with the most favourable temperature (both air and soil) could be selected. In cool temperate climates where plantingtime is often governed by seasonal moisture patterns it may be important to plan fertilizer additior to correspond with rapid root growth and hence rapid nutrient uptake.

The importance of the temperature of the rooting medium for good root development in cuttings is generally recognized, and propagating boxes are often provided with bottom heat. In practical situations, there are a number of management techniques which can be used to moderate the temperature of root zones. Certain practices like tilling, mulching and irrigation (with warm or cold water) have been used to help stimulate root

regeneration of planted seedlings (Richards *et al.*,1952; Nielsen, 1971). Soil temperature effects are now being used as a screening tool in plant breeding.

Notwithstanding, comparatively little attention has been given to evaluating the importance of soil temperature as a factor in plant growth. Accordingly, it is very difficult and in most cases impossible to evaluate from published ecological data the contribution of soil temperature to the observed plant growth responses. Soil temperature has not been emphasized in studies of plant development partly because of the difficulty in controlling soil temperature and evaluating its effects (Heninger and White, 1974).

Root temperatures are believed to approach closely those of their immediate surroundings (Daubenmire, 1974). This means that in the field, at any given time a single root system is exposed to a considerable range in temperature and that each part is subject to a continually changing temperature (Richards *et al.*, 1952; Nielsen, 1971 ; Daubenmire, 1974). This continual variation in soil temperature with depth and with time poses a formidable obstacle in attempting to relate soil temperatures to the observe growth of plants. It may be noted, however, that the whole plant root system in the experiments in this chapter was exposed to the same soil temperature set.

6.2 *Materials and methods*

The materials and methods of 5 separate experiments are described in this chapter. Table 6.1 summarizes the experiments arranged in chronological order. The details of the experiments are described below.

Experiment 1 was carried out in an LB type growth cabinet using type I soil temperature units (see chapter 2). The day/night air temperature was $27/22^{o}$ C synchronized with a 12/12 hour light period to simulate the tropical condition. Light intensity at plant height was 50 watts.m^{-2} (2000 fc)

Table 6.1 A summary of experiments on the effects of air and soil temperatures on growth and root regeneration potential of *P. caribaea* and *P. kesiya* seedlings. The plant water status of *P. caribaea* was measured in Experiment 4 and the photosynthesis and respiration in Experiment 5.

Experiment number and date of the 4 weeks treatment	Day/night air temperature °C	Soil temperature °C	Species used	Age (from sowing) at start of treatment	Mean height (cm) at start of treatment		Mean diameter (cm) at start of treatment		Sample size per treatment for each harvest/measurement
					Pc*	Pk#	Pc*	Pk#	
1 19/6/75 to 17/7/75	27/22	10,15 20,25	Pc & Pk	17 wk	13.2	8.5	0.24	0.22	6 for each species
2 26/7/75 to 23/8/75	21/16	10,15, 20,25	Pc & Pk	21 wk	13.3	13.0	0.28	0.28	same as above
3 5/9/75 to 3/10/75	24/19	10,15 20,25	Pc & Pk	14 wk	15.4	11.3	0.30	0.26	same as above
4 18/11/75 to 16/12/75	33/28	15,20 25,30	Pc	17 wk	27.7	-	0.64	-	6
5 27/2/76 to 2/4/76	27/22	15,20 25,30	Pc	19 wk	36.4	-	0.73	-	5

measured using an 'Eel' portable photoelectric photometer. Light intensity level was checked at weekly intervals to ensure a constant level throughout the experiment.

In contrast to experiment 1, all subsequent experiments were conducted in open-glasshouses using natural lighting and type II soil temperature units (see chapter 2). This was mainly due to the ease in obtaining these facilities at CERES. Use of the type II soil temperature units allowed a more extensive range of experiments to be carried out at the time this work was done. It should be noted that, unlike in the growth cabinet, the day temperature in the glasshouse was held for 8 hours of the daylight period and night temperature for the remaining 16 hours. Light intensity in the open-glasshouse is much higher than in the cabinet and varies with the time of day. Also, the photoperiod in the glasshouse is extended to 16 hours by low light intensity incandescent lighting with an illumination of 0.625 watts.m^{-2} (25 fc) at plant height.

The air temperatures in Experiments 2,3,4 and 5 were selected because they were the 'standard' day/night air temperature regimes in the open-glasshouses at the CERES phytotron in which the type II soil temperature units could be situated. In addition, the effects of these air temperatures on the growth and RRP of *P. caribaea* and *P. kesiya* seedlings have been studied in chapter 5 and the results have shown that within each species there were significant differences in growth and RRP for air temperature. It would thus be informative to determine the interaction of different soil temperatures with each of these air temperatures.

The minimum soil temperature used was 10^{o} C, firstly because Treshow (1970) reported active plant growth generally occurs at temperatures greater than that, and secondly, because it was thought unlikely the soil temperature would be lower than 10^{o} C in the tropics and subtropics. In Experiments 4 and 5 the 10^{o} C soil temperature was omitted and 30^{o} C was

included for two reasons. Firstly, because the results in the earlier three experiments (Tables 6.4B, 6.2B and 6.3B) all show that there was no significant difference in RRP of *P. caribaea* between 10° and 15° C. Secondly, the RRP of *P. caribaea* in all the three experiments was maximum at 25° C, hence, the soil temperature in experiments 4 and 5 was increased to 30° C to determine whether the RRP would further increase or decrease at this temperature.

It was not possible to conduct all of the five experiments using seedlings of exactly the same size and age due to space limitations in the 27/22° C glasshouse at CERES (Table 6.1)). Hence, seedlings in Experiments 1 and 2 were initially grown at the Forestry glasshouse (A.N.U.) but were brought to CERES and grown in the 27/22° C glasshouse 2 weeks before the start of each experiment. Seedlings in Experiments 3, 4 and 5 were germinated and grown in the 27/22° C glasshouse at CERES. In addition, the seedlings in each of the experiments were germinated and grown at different times (or seasons) of the year.

Only one species was used in Experiments 4 and 5. The physical limitations of space in type II soil temperature units and in the use of Infrared gas analyser facilities in Experiment 5 necessitated the use of only one species, making due allowance for sufficient replications for each photosynthesis and respiration meausrements. Also, the results of Anova in Experiments 1, 2 and 3 (Tables 6.4A, 6.2A and 6.3A) showed that there was no interaction between factor 1 (soil temperature) and factor 2(species) indicating a similar response to soil temperature treatments in both *P. caribaea* and *P. kesiya*.

P. caribaea was chosen instead of *P. kesiya* in Experiments 4 and 5 because of its faster growth rate which would allow the experiments to be conducted earlier. In addition, the species has a greater economic importance in the tropics and subtropics (see Appendix IB).

Plants in Experiments 1, 2,3 and 4 were harvested after 4 weeks of growth under the different soil temperatures whereas that in Experiment 5 had an intermediate harvest for root regeneration at 2 weeks of growth period (harvest 1) in addition to the final harvest at 4 weeks (harvest 2). Photosynthesis and respiration measurements were made in plants of Experiment 5 and they will be described separately in chapter 7. It should also be noted that the relative leaf water content of plants in each soil temperature in Experiment 4 was determined at the final harvest and the method will also be described separately in chapter 7.

In Experiments 2 to 4, the origin of the regenerated roots was classified into newly initiated roots and those which elongated from old roots. Roots were not classified in Experiment 1 because of lack of experience at this stage in distinguising between the two types of root regeneration.

A comparison of RRP based on length of new roots $\geq$2.0 cm long (RRP_L) and RRP based on length of new roots $\geq$1.0cm long (RRP_1) was made in Experiment 2 to determine whether the two criteria give similar results in describir the root growth response of seedlings to different soil temperatures. The results (see Table 6.2B I and section 6.3.1.1) show that RRP_L and RRP_1 gave similar patterns of response in each species. RRP in all subsequent experiments was based on new root growth $\geq$ 2.0cm long to reduce measurement time, but without affecting the precision of the results significantly.

6.3 *Results*

All data were subjected to analysis of variance to assess the significance of the treatment effects on each parameter. In Experiments 1, 2 and 3 (see Table 6.1) where two species were used, the data were analysed on the basis of:

(i) Factor 1 — Soil temperature (4 means, 12 observations per mean).

(ii) Factor 2 — Species (2 means, 24 observations per mean).

(iii) Interaction between soil temperature and species (8 means, 6 observations per mean).

The significance of differences between group means in all experiments was tested by using Duncan's new multiple range test (Steel and Torrie, 1960).

6.3.1 Effects of the interaction between day/night air temperature of 21/16° C and the soil temperatures : 10° (1), 15° (2), 20° (3) and 25° C (4) on the growth and RRP of *P. caribaea* and *P. kesiya* seedlings.

The results of Anova given in Table 6.2A reveal that most of the parameters had significant differences between treatment means for factor 1 (soil temperature) but not for factor 2 (species). Except for height increment, there was no significant interaction in all of the measured parameters indicating a similar response to treatment in both species. Both species had a similar growth history, mean height and root collar diameter at the start of the treatment (Table 6.1).

6.3.1.1 *Root regeneration*

The data are presented in Table 6.2 BI.

Root regeneration based on length of new roots $\geq$ 1.0cm long (l_{Nir} , l_{Ore} , l) gave similar patterns of response to that based on length $\geq$2.0cm long (L_{Nir}, L_{Ore}, L) for both factors 1 and 2, and within each species This indicates that conclusions to be drawn from these would be similar regardless of which measurement was used.

Both RRP_N and RRP_L showed similar patterns of response to treatment for factor 1 (soil temperature) and factor 2 (species). There was no significant difference in RRP, L_{Nir} and L_{Ore} for factor 2.

RRP increased with increase in soil temperature from 10^{o} to 25^{o} C although there was no significant difference in RRP between 10^{o} and 15^{o} C, and 15^{o} and 20^{o} C respectively. The elongation from old roots (L_{Ore}) was always markedly greater than the elongation from newly initiated roots (L_{Nir}) at every soil temperature in both *P. caribaea* and *P. kesiya*.

6.3.1.2 *Dry weight*

The shoot and total plant dry weights showed no significant difference between treatment means for factor 1 (soil temperature) (Table 6.2BII). There was, however, a highly significant species difference due to *P. kesiya* having greater shoot and total plant dry weights than *P. caribaea* although the two species had similar mean height and root collar diameter at the start of the treatment. There was no significant difference in root dry weight for factor 2 (species) (Table 6.2 B II).

There was a clear trend for root, shoot and total plant dry weights to increase with increase in soil temperature from 10^{o} to 25^{o} C but only root dry weight at 10^{o} C was significantly less than at 20^{o} and 25^{o} C; there was no significant difference in the weight between 15^{o}, 20^{o} and 25^{o} C

6.3.1.3 *Height and diameter increment*

Both height and diameter increment showed significant differences between treatment means for factor 1 (soil temperature) (Table 6.2A). The two parameters increased in growth with increase in temperature from $10^{o}$to 25^{o} C (Table 6.2B III). Height increment at 25^{o} C was significantly greater than at 10^{o} and 15^{o} C; there was no significant difference in the increment between 10^{o}, 15^{o} and 20^{o} C. There was no significant difference in diameter increment between 10^{o} and 15^{o} C and between 20^{o} and 25^{o} C but the increment in the latter two treatments exceeded the former two.

There was no significant difference between treatment means in height increment for factor 2 (species) whereas in diameter increment, *P. kesiya* grew significantly more than *P. caribaea* (Table 6.2 B III).

Table 6.2A Results of analysis of variance for significance of differences between treatment means for factors 1 and 2 and the interaction between these. Plants were grown at 21/16°C day/night air temperature and under four different soil temperatures : 10° (1), 15° (2), 20° (3), & 25°C (4).

Parameter	Factor 1: Soil temperature	Factor 2: Species	Interaction
Root regeneration (per plant)			
Total number of white roots (N) ≥ 1.0cm long	* * *	NS	NS
Total length of newly initiated roots (l_{Nir}) ≥ 1.0cm long	* *	NS	NS
Total length of elongation from old roots (l_{Ore}) ≥ 1.0cm long	* * *	NS	NS
Total length of white roots ($l = l_{Nir} + l_{Ore}$) ≥ 1.0cm long	* * *	NS	NS
Total length of newly initiated roots (L_{Nir}) ≥ 2.0cm long	* *	NS	NS
Total length of elongation from old roots (L_{Ore}) ≥ 2.0cm long	* * *	NS	NS
Total length of white roots ($L = L_{Nir} + L_{Ore}$) ≥ 2.0cm long	* * *	NS	NS
Dry weight (g)			
Root	*	NS	NS
Shoot	NS	* * *	NS
Total plant	NS	* *	NS
Increment (cm)			
Height	*	NS	*
Root collar diameter	* *	*	NS

P, 0.05* ; 0.01** ; 0.001*** ; NS, not significant

Table 6.2B Ranking of treatment means in ascending order for various plant parameters for factors 1 and 2 and their interaction. Bracketed means are not significantly different ($P < 0.05$).

I: *Root regeneration (per plant)* *

	N	l_{Nir}	l_{Ore}	$l = l_{Nir} + l_{Ore}$	L_{Nir}	L_{Ore}	$L = L_{Nir} + L_{Ore}$
Factor 1:	1 3	1 2	1 4	1 6	1 0.5	1 1	1 2
Soil Temperature (S.T.)	2 38	2 25	2 66	2 91	2 16	2 49	2 66
	3 58	3 47	3 140	3 187	3 35	3 108	3 143
	4 100	4 59	4 286	4 345	4 50	4 237	4 287
Factor 2:	Pc 44	Pk 27	Pc 102	Pc 134	Pk 21	Pc 81	Pc 111
Species (Spp.)	Pk 56	Pc 40	Pk 146	Pk 171	Pc 30	Pk 117	Pk 138
Interaction: S.T. x Spp.	S.T. Spp. N	S.T. Spp. l_{Nir}	S.T. Spp. l_{Ore}	S.T. Spp. l	S.T. Spp. L_{Nir}	S.T. Spp. L_{Ore}	S.T. Spp. L
	1 Pk 2	1 Pk 0.8	1 Pk 3	1 Pk 4	1 Pk 0.5	1 Pc 1	1 Pk 2
	1 Pc 4	1 Pc 2	1 Pc 4	1 Pc 7	1 Pc 1	1 Pk 1	1 Pc 2
	2 Pc 31	2 Pk 16	2 Pc 46	2 Pc 81	2 Pk 8	2 Pc 35	2 Pc 61
	2 Pk 46	3 Pk 21	2 Pk 86	2 Pk 103	3 Pk 15	2 Pk 64	2 Pk 71
	3 Pk 57	2 Pc 36	3 Pc 125	3 Pk 175	2 Pc 25	3 Pc 88	3 Pk 142
	3 Pc 60	4 Pc 50	3 Pk 154	3 Pc 198	4 Pc 39	3 Pk 128	3 Pc 143
	4 Pc 80	4 Pk 68	4 Pc 233	4 Pc 283	3 Pc 55	4 Pc 199	4 Pc 237
	4 Pk 120	3 Pc 73	4 Pk 338	4 Pk 407	4 Pk 60	4 Pk 276	4 Pk 336

* N is the total number of white roots ≥ 1.0cm long
l is the total length of white roots ≥ 1.0cm long
L is the total length of white roots ≥ 2.0cm long

Table 6.2B continued.

II: *Dry weight (g)* III: *Height & Diameter increment (cm)*

	Root	Shoot	Total plant	Height Increment	Diameter Increment
Factor 1: Soil Temperature (S.T.)	1 0.359	1 1.498	1 1.858	1 1.6	1 0.04
	2 0.477	2 1.659	2 2.106	2 1.8	2 0.04
	3 0.507	3 1.850	3 2.358	3 2.2	3 0.06
	4 0.571	4 2.069	4 2.640	4 2.8	4 0.07
Factor 2: Species (Spp.)	Pc 0.467	Pc 1.458	Pc 1.925	Pc 2.0	Pc 0.05
	Pk 0.475	Pk 2.081	Pk 2.556	Pk 2.2	Pk 0.06
Interaction: S.T. x Spp.	S.T. Spp. R	S.T. Spp. S	S.T. Spp. TP	S.T. Spp. H	S.T. Spp. D
	1 Pk 0.333	1 Pc 1.271	1 Pc 1.657	1 Pk 1.4	1 Pc 0.03
	1 Pc 0.386	2 Pc 1.398	2 Pc 1.793	1 Pc 1.8	2 Pc 0.04
	2 Pc 0.395	3 Pc 1.535	3 Pc 2.026	2 Pk 1.8	1 Pk 0.05
	3 Pc 0.491	4 Pc 1.628	1 Pk 2.060	2 Pc 1.9	3 Pc 0.05
	2 Pk 0.499	1 Pk 1.727	4 Pc 2.225	3 Pk 2.1	2 Pk 0.05
	3 Pk 0.524	2 Pk 1.920	2 Pk 2.419	3 Pc 2.4	3 Pk 0.07
	4 Pk 0.545	3 Pk 2.166	3 Pk 2.690	4 Pk 2.8	4 Pc 0.07
	4 Pc 0.597	4 Pk 2.511	4 Pk 3.056	4 Pc 2.8	4 Pk 0.08

6.3.2 Effects of the interaction between day/night air temperature of 24/19° C and the soil temperatures : 10° (1), 15° (2), 20° (3) and 25° C (4) on the growth and RRP of *P. caribaea* and *P. kesiya* seedlings.

Results of Anova in Table 6.3A reveal that most of the parameters show highly significant differences between treatment means for both factor 1 (soil temperature) and factor 2 (species) with no interaction between them. However, any significant difference between treatment means in the measured parameters for factor 2 should be viewed in the light that *P. caribaea* was taller and had a thicker root collar diameter than *P. kesiya* at the start of the treatment (Table 6.1).

6.3.2.1 *Root regeneration*

Both RRP_N and RRP_L showed similar patterns of response to treatment for factors 1 and 2 (Table 6.3BI). RRP increased with increase in soil temperature from 10° to 25° C. The RRP at 10° and 15° C were not significantly different from each other but were both significantly less than at 20° and 25° C. RRP at 25° C was significantly greater than at any other temperature. A similar pattern of response was exhibited for both L_{Nir} and L_{Ore} as that for RRP. L_{Ore} was greater than L_{Nir} at 10°, 15° and 20° C but was less than L_{Nir} at 25° C.

RRP and L_{Ore} in *P. caribaea* were both significantly greater than in *P. kesiya*. There was no significant species difference in L_{Nir}.

6.3.2.2 *Dry weight*

Root, shoot and total plant dry weights increased with increase in soil temperature from 10° to 25° C (Table 6.3 B II). The root dry weight at 15° C was significantly greater than at 10° C and the dry weights in both treatments were significantly less than at 20° and 25° C. There was no significant difference in the root dry weight between 20° and 25° C. Shoot dry weight was not significantly affected by the different soil

temperatures. For total plant dry weight, there was no significant difference between 10^{o} and 15^{o} C, between 15^{o} and 20^{o} C, and between 20^{o} and 25^{o} C. However, the dry weight at 25^{o} C was significantly greater than at 10^{o} and 15^{o} C and that at 20^{o} C was significantly greater than at 10^{o} C.

The root, shoot and total plant dry weights in *P. caribaea* were each significantly greater than in *P. kesiya* (Table 6.3 B II).

6.3.2.3 *Height and diameter increment*

Both height and diameter increments showed similar patterns of response to treatment for factor 1 (soil temperature) and factor 2 (species) (Table 6.3B III). The growth in height and diameter increased with increase in temperature from 10^{o} to 25^{o} C. There was no significant difference in the increment between 10^{o} and 15^{o} C and between 20^{o} and 25^{o} C but the increments at the latter two temperatures were significantly greater than at the former two.

Overall height and diameter increments in *P. caribaea* exceeded that of *P. kesiya*.

Table 6.3 A Results of analysis of variance for significance of differences between treatment means for factors 1 and 2 and the interaction between these. Plants were grown at 24/19° C day/night air temperature and under four different soil temperatures : 10° (1), 15° (2), 20° (3), and 25° C. (4).

Parameters	Factor 1: Soil temperature	Factor 2: Species	Interaction
Root regeneration (per plant)			
Total number of white roots (N) ≥ 1.0cm long	* * *	* *	NS
Total length of newly initiated roots (L_{Nir}) ≥ 2.0cm long	* * *	NS	*
Total length of elongation from old roots (L_{Ore}) ≥ 2.0cm long	* * *	* * *	NS
Total length of white roots ($L = L_{Nir} + L_{Ore}$) ≥ 2.0cm long	* * *	*	NS
Dry weight (g)			
Root	* * *	* * *	NS
Shoot	NS	* * *	NS
Total plant	*	* *	NS
Increment (cm)			
Height	* * *	* * *	NS
Root collar diameter	* * *	* * *	NS

P, 0.05* ; 0.01** ; 0.001***; NS, not significant

Table 6.3B Ranking of treatment means in ascending order for various plant parameters for factors 1 and 2 and their interaction. Bracketed means are not significantly different ($P < 0.05$).

I: *Root regeneration (per plant)*

	N	L_{Nir}	L_{Ore}	$L = L_{Nir} + L_{Ore}$
Factor 1: Soil temperature (S.T.)	1 11 | 2 56 | 3 151 | 4 247	1 0.5 | 2 31 | 3 180 | 4 504	1 4 | 2 48 | 3 208 | 4 325	1 4 | 2 79 | 3 388 | 4 829
Factor 2: Species (Spp.)	Pk 95 | Pc 135	Pk 169 | Pc 188	Pk 101 | Pc 192	Pk 264 | Pc 378
Interaction: S.T. x Spp.	S.T. Spp. N	S.T. Spp. L_{Nir}	S.T. Spp. L_{Ore}	S.T. Spp. L
	1 Pc 10 | 1 Pk 11 | 2 Pk 32 | 2 Pc 80 | 3 Pk 113 | 3 Pc 189 | 4 Pk 224 | 4 Pc 270	1 Pc 0.3 | 1 Pk 0.9 | 2 Pk 18 | 2 Pc 44 | 3 Pk 80 | 3 Pc 279 | 4 Pc 431 | 4 Pk 577	1 Pc 2 | 1 Pk 6 | 2 Pk 19 | 2 Pc 78 | 3 Pk 146 | 4 Pk 229 | 3 Pc 270 | 4 Pc 420	1 Pc 1 | 1 Pk 7 | 2 Pk 37 | 2 Pc 122 | 3 Pk 226 | 3 Pc 548 | 4 Pk 807 | 4 Pc 852

Table 6.3B continued.

II: *Dry weight (g)*

III: *Height & Diameter Increment (cm)*

	Root	Shoot	Total plant	Height Increment	Diameter Increment
Factor 1: Soil temperature (S.T.)	1 0.393	1 1.969	1 2.362	1 2.1	1 0.05
	2 0.541	2 2.134	2 2.675	2 2.7	2 0.06
	3 0.721	3 2.292	3 3.013	3 4.1	3 0.09
	4 0.764	4 2.425	4 3.189	4 5.0	4 0.10
Factor 2: Species (Spp.)	Pk 0.401	Pk 1.728	Pk 2.129	Pk 2.2	Pk 0.05
	Pc 0.810	Pc 2.682	Pc 3.491	Pc 4.7	Pc 0.10
Interaction: S.T. x Spp.	S.T. Spp. R	S.T. Spp. S	S.T. Spp. TP	S.T. Spp. H	S.T. Spp. D
	1 Pk 0.277	1 Pk 1.570	1 Pk 1.847	1 Pk 1.1	1 Pk 0.03
	2 Pk 0.333	2 Pk 1.688	2 Pk 2.021	2 Pk 1.3	2 Pk 0.05
	3 Pk 0.489	3 Pk 1.804	3 Pk 2.293	3 Pk 3.0	3 Pk 0.06
	4 Pk 0.503	4 Pk 1.850	4 Pk 2.353	1 Pc 3.0	1 Pc 0.06
	1 Pc 0.509	1 Pc 2.368	1 Pc 2.878	4 Pk 3.4	2 Pc 0.07
	2 Pc 0.749	2 Pc 2.580	2 Pc 3.329	2 Pc 4.1	4 Pk 0.07
	3 Pc 0.953	3 Pc 2.779	3 Pc 3.732	3 Pc 5.2	3 Pc 0.12
	4 Pc 1.026	4 Pc 2.999	4 Pc 4.026	4 Pc 6.6	4 Pc 0.13

6.3.3 Effects of the interaction between day/night air temperature of 27/22° C and the soil temperatures : 10° (1), 15° (2), 20° (3) and 25° C (4) on the growth and RRP of *P. caribaea* and *P. kesiya* seedlings.

This experiment was conducted in the growth cabinet. The experimental conditions have been described in the materials and methods.

Results of Anova in Table 6.4A reveal that most of the parameters show highly significant differences between treatment means for both factor 1 (soil temperature) and factor 2 (species) with no interaction between them. However, as in the previous experiment (air temperature 24/19° any significant difference between treatment means in the measured parameters for factor 2 should be viewed in the light that the *P. caribaea* plants were taller and had a thicker root collar than *P. kesiya* at the start of the treatment (Table 6.1).

6.3.3.1 *Root regeneration*

Both RRP_N and RRP_L gave similar patterns of response to temperature for factor 1 (soil temperature) and factor 2 (species) (Table 6.4 BI). RRP increased with increase in soil temperature from 10° to 25° C. There was no significant difference between 10° and 15° C but the RRP in both treatments were significantly less than at 20° C and 25° C. RRP at 25° C was significantly greater than at 20° C.

Overall RRP in *P. caribaea* exceeded that of *P. kesiya*.

6.3.3.2 *Dry weight*

The root, shoot and total plant dry weights increased with increase in temperature from 10° to 25° C (Table 6.4 BII). There was no significant difference in root dry weight between 10° and 15° C and between 20° and 25° C but the weights at the latter two treatments were significantly greater than at the former two. Shoot dry weights at 10°, 15° and 20° were not significantly different from each other but the weight at 25° C was significantly greater than at 10° and 15° C. The total plant dry weight at 25° C was

significantly greater than at 10° and 15° C whereas that at 20° was significantly greater than at 10° C. There was no significant difference in total plant dry weight between 10° and 25° C.

Overall root, shoot and total plant dry weights in *P. caribaea* exceeded that of *P. kesiya*.

6.3.3.3 *Height and diameter increment*

Both the height and diameter growth increased with increase in soil temperature, reaching a maximum at 25° C (Table 6.4 B III). However, there was no significant difference between treatment means for diameter increment. For height increment, the increments at 10°, 15° and 20° C were not significantly different from each other but were significantly less than at 25° C.

Height and diameter increments in *P. caribaea* were both significantly greater than in *P. kesiya*.

Table 6.4A Results of analysis of variance for significance of differences between treatment means for factors 1 and 2 and the interaction between these. Plants were grown at 27/22° C day/night air temperature in the growth cabinet and under four different soil temperatures : 10° (1), 15° (2), 20° (3) and 25° C (4).

Parameters	Factor 1: Soil temperature	Factor 2: Species	Interaction
Root regeneration (per plant)			
Total number of white roots (N)≧ 1.0cm long	* * *	* *	NS
Total length of white roots (L)≧ 2.0cm long	* * *	* *	NS
Dry weight (g)			
Root	* * *	* * *	NS
Shoot	* *	* * *	NS
Total plant	* * *	* * *	NS
Increment (cm)			
Height	* * *	* * *	*
Root collar diameter	NS	* *	NS

P, 0.05* ; 0.01**; 0.001***; NS, not significant

Table 6.4B Ranking of treatment means in ascending order for various plant parameters for factors 1 and 2 and their interaction. Bracketed means are not significantly different ($P < 0.05$).

I: *Root regeneration (per plant)* II: *Dry weight (g)* III: *Height & Diameter Increment (cm)*

	N	L	Root	Shoot	Total plant	Height Increment	Diameter Increment
Factor 1: Soil Temperature (S.T.)	1 17	1 17	1 0.237	1 0.827	1 1.064	1 0.7	1 0.05
	2 38	2 61	2 0.300	2 0.836	2 1.132	2 0.8	2 0.05
	3 82	3 225	3 0.420	3 0.966	3 1.386	3 0.9	3 0.06
	4 117	4 349	4 0.469	4 1.174	4 1.643	4 1.6	4 0.07
Factor 2: Species (Spp.)	Pk 41	Pk 117	Pk 0.297	Pk 0.704	Pk 1.000	Pk 0.6	Pk 0.05
	Pc 86	Pc 209	Pc 0.414	Pc 1.198	Pc 1.612	Pc 1.4	Pc 0.07
Interaction	S.T.Spp. N	S.T.Spp. L	S.T.Spp. R	S.T. Spp. S	S.T.Spp. TP	S.T.Spp. H	S.T.Spp. D
Soil x Species Temperature (S.T.) (Spp.)	1 Pk 2	1 Pk 1	1 Pk 0.175	2 Pk 0.616	1 Pk 0.837	1 Pk 0.4	1 Pk 0.4
	2 Pk 22	2 Pk 23	2 Pk 0.263	1 Pk 0.662	2 Pk 0.879	2 Pk 0.6	2 Pk 0.5
	1 Pc 32	1 Pc 35	1 Pc 0.299	3 Pk 0.698	3 Pk 1.039	3 Pk 0.6	3 Pk 0.5
	3 Pk 44	2 Pc 99	2 Pc 0.328	4 Pk 0.838	4 Pk 1.247	4 Pk 0.8	4 Pk 0.6
	2 Pc 56	3 Pk 144	3 Pk 0.341	1 Pc 0.992	1 Pc 1.291	1 Pc 1.0	1 Pc 0.6
	4 Pk 97	4 Pk 303	4 Pk 0.409	2 Pc 1.057	2 Pc 1.385	2 Pc 1.1	2 Pc 0.6
	3 Pc 121	3 Pc 310	3 Pc 0.498	3 Pc 1.234	3 Pc 1.732	3 Pc 1.2	3 Pc 0.6
	4 Pc 136	4 Pc 393	4 Pc 0.529	4 Pc 1.510	4 Pc 2.039	4 Pc 2.4	4 Pc 0.09

6.3.4 Effects of the interaction between day/night air temperature of 27/22° C and the soil temperatures : 15°, 20°, 25° and 30° C on the growth and RRP of *P. caribaea* seedlings.

This experiment was conducted in the open-glasshouse. The experimental conditions have been described in the materials and methods. It may be noted that the RRP of the plants was determined at two harvests i.e. at 2 weeks (harvest 1) and 4 weeks (harvest 2) of growth respectively. Photosynthesis and respiration measurements were made at 4 stages during the treatment period and the results are presented in chapter 7.

6.3.4.1 *Root regeneration*

Results of Anova in Table 6.5 A I show that there are highly significant differences between all treatment means at both harvests 1 and 2 respectively. Table 6.5A II shows that the treatment means of each parameter were significantly different between the two harvests.

The ranking of the parameters of harvests 1 and 2 in Tables 6.5B shows that both RRP_N and RRP_L gave similar patterns of response to soil temperature. Optimum RRP at both harvests occurred at 25° C and minimum RRP at 15° C. However, the RRP at 15°, 20° and 30° C at harvest 1 were not significantly different from each other whereas at harvest 2, the RRP at 30° C was significantly greater than at 15° and 20° C.

In general, both L_{Nir} and L_{Ore} showed similar patterns of response as RRP at both harvests 1 and 2 respectively. In one instance, at harvest 2, L_{Ore} was optimum at 30° C instead of at 25° C as in L_{Nir} and RRP. L_{Nir} was markedly greater than L_{Ore} in all treatments at both harvests.

6.3.4.2 *Dry weight*

Maximum root, shoot and total plant dry weights at final harvest (harvest 2) occurred at 25° C and minimum weight occurred at 15° C (Table 6.6B). The root dry weights at 15°, 20° and 30° C were not significantly different from each other but were significantly less than at 25° C. The difference between treatment means for both shoot and total plant dry weights was less marked.

Table 6.5A Results of analysis of variance for significance of differences between treatment means for the root regeneration parameters in *P. caribaea*. Plants were grown at 27/22° C air temperature in the open-glasshouse and under four different soil temperatures : 15, 20, 25 and 30° C.

I: *Root regeneration (per plant) at harvests 1 and 2.*

Parameter	Harvest 1	Harvest 2
Total number of white roots (N) ≥ 1.0cm long	* *	* * *
Total length of newly initiated roots (L_{Nir}) ≥ 2.0cm long	* *	* * *
Total length of elongation from old roots (L_{Ore}) ≥ 2.0cm long	* * *	* * *
Total length of white roots ($L = L_{Nir} + L_{Ore}$) ≥ 2.0cm long	* *	* * *

II: *Anova for root regeneration parameters between harvests 1 and 2.*

Parameter	Soil temperature ° C 15	20	25	30
N	*	* *	* *	* * *
L_{Nir}	*	*	* *	* * *
L_{Ore}	* *	* *	*	* * *
$L = L_{Nir} + L_{Ore}$	*	*	* *	* * *

P, 0.05* ; 0.01** ; 0.001***

Table 6.5B Ranking of treatment means in ascending order for root regeneration parameters at harvests 1 and 2 respectively. Bracketed means are not significantly different ($P < 0.05$).

Harvest 1								Harvest 2							
N		L_{Nir}		L_{Ore}		$L=L_{Nir}+L_{Ore}$		N		L_{Nir}		L_{Ore}		$L=L_{Nir}+L_{Ore}$	
$15^{o}C$	1	$15^{o}C$	1	$15^{o}C$	1	$15^{o}C$	2	$15^{o}C$	23	$15^{o}C$	23	$15^{o}C$	7	$15^{o}C$	30
20	19	30	7	20	4	30	11	20	114	20	133	20	44	20	177
30	19	20	13	30	4	20	17	30	240	30	284	25	134	30	521
25	120	25	102	25	39	25	141	25	328	25	704	30	237	25	838

Table 6.6A Results of analysis of variance for significance of differences between treatment means for the dry weight and height and diameter growth in *P. caribaea* at the final harvest.#

Plants were grown at 27/22°C day/night air temperature in the open-glasshouse and under four different soil temperatures : 15, 20, 25 and 30° C.

Parameter	Significance of F ratio
Dry weight (g)	
Root	*
Shoot	*
Total plant	*
Increment (cm)	
Height	*
Root collar diameter	* *

P , 0.05* ; 0.01**

Table 6.6B Ranking of treatment means in ascending order for various plant parameters at the final harvest#. Bracketed means are not significantly different ($P < 0.05$).

Dry weight (g)						Increment (cm)			
Root		Shoot		Total plant		Height		Root collar diameter	
15°C	2.140	15°C	8.120	15°C	10.259	15°C	2.6	15°C	0.02
20	2.211	20	8.750	20	10.961	20	3.1	20	0.03
30	2.287	30	9.308	30	11.595	25	3.6	25	0.08
25	3.629	25	10.982	25	14.611	30	6.1	30	0.10

Harvest 2

6.3.4.3 *Height and diameter increment*

Maximum height and diameter growth occurred at 30° C and minimum growth at 15° C (Table 6.6B). Height increment at 30° C was not significantly different from 20° and 25° C but was significantly greater than at 15° C. No significant difference in height growth was observed between 15°, 20° and 25° C.

There was no significant difference in diameter increment between 15° and 20° C and between 25° and 30° C respectively, but the increments at the latter two treatments were significantly greater than at the former two.

6.3.5 Effects of the interaction between day/night air temperature of 33/28° C and the soil temperature : 15°, 20°, 25° and 30° C on the growth and RRP of *P. caribaea* seedlings.

It should be noted that the water status of the seedlings in each soil temperature was determined at the final harvest in this experiment. Both the method and results are described in chapter 7 and discussed together with the results on photosynthesis.

6.3.5.1 *Root regeneration*

Both RRP_N and RRP_L showed similar patterns of response to soil temperature (Table 6.7B I). Maximum RRP occurred at 30° C and minimum RRP at 15° C. RRP at 20°, 25° and 30° C were not significantly different from each other but were significantly greater than at 15° C.

L_{Nir} showed a similar pattern of response to temperature as RRP and was always greater than L_{Ore} at all soil temperatures.

6.3.5.2 *Dry weight*

There was a trend for root, shoot and total plant dry weight to increase with increase in soil temperature from 15° to 30° C (Table 6.7 B II) but there was no significant difference between treatment means.

6.3.5.3 *Height and diameter increment*

Both height and diameter growth increased with increase in soil temperature from 15° to 30° C (Table 6.7 BIII). The height increments at 15°, 20° and 25° C were not significantly different from each other but were significantly less than at 30° C. For diameter increment, however, there was no significant difference between 15° and 20° C and between 25° and 30° C but the increments at the latter two treatments were significantly greater than at the former two.

Table 6.7A Results of analysis of variance for significance of differences between treatment means for various plant parameters of *P. caribaea*. Plants were grown at 33/28° C day/night air temperature and under four different soil temperatures : 15°, 20°, 25° and 30° C.

Parameters	Significance of F ratio
Root regeneration (per plant)	
Total number of white roots (N) ≥ 1.0cm long	* *
Total length of newly initiated roots (L_{Nir}) ≥ 2.0cm long	* * *
Total length of elongation from old roots (L_{Ore}) ≥ 2.0cm long	*
Total length of white roots ($L=L_{Nir}+L_{Ore}$) ≥ 2.0cm long	* *
Dry weight (g)	
Root	NS
Shoot	NS
Total plant	NS
Increment (cm)	
Height	*
Root collar diameter	*

P, 0.05* ; 0.01**; 0.001 *** ; NS, not significant

TABLE 6.7B Ranking of treatment means in ascending order for various plant parameters of *P. caribaea*. Bracketed means are not significantly different ($P < 0.05$).

I: *Root regeneration (per plant)*

N		L_{Nir}		L_{Ore}		$L=L_{Nir}+L_{Ore}$	
15°C	102	15°C	77	15°C	57	15°C	134
20	253	20	319	25	165	20	536
25	255	25	383	30	175	25	548
30	314	30	473	20	217	30	648

II: *Dry weight (g)*

Root		Shoot		Total plant	
15°C	1.190	15°C	4.141	15°C	5.331
20	1.345	20	4.162	20	5.507
25	1.376	25	4.319	25	5.695
30	1.483	30	4.513	30	5.996

III: *Height & Diameter increment (cm)*

Height Increment		Diameter Increment	
15°C	4.3	15°C	0.04
20	5.6	20	0.04
25	5.6	25	0.07
30	8.4	30	0.10

Figure 6.1A Effect of air and soil temperatureson RRP_N of *P. caribaea* seedlings.

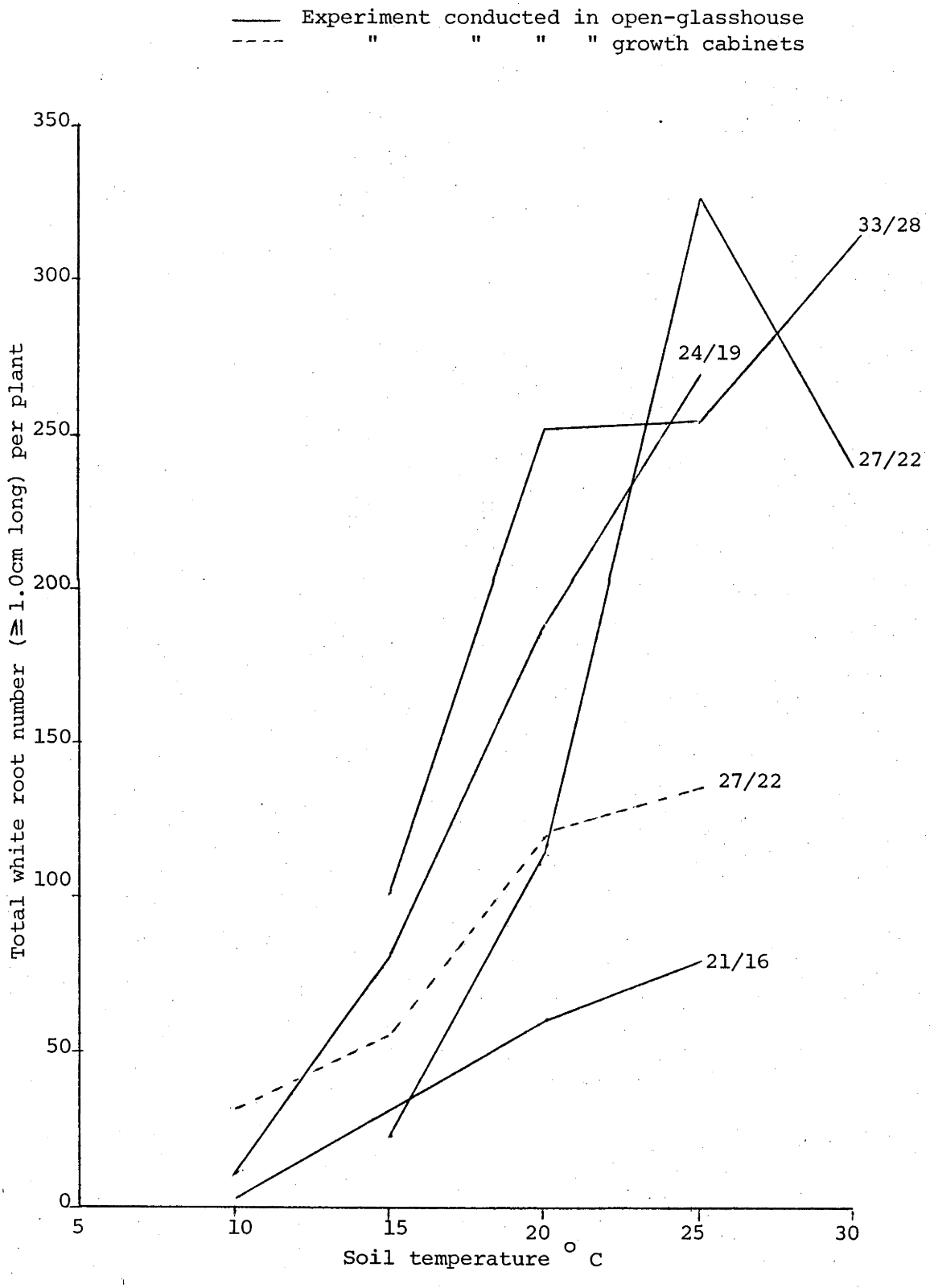


Figure 6.1B Effect of air and soil temperatures on RRP_L of *P. caribaea* seedlings.

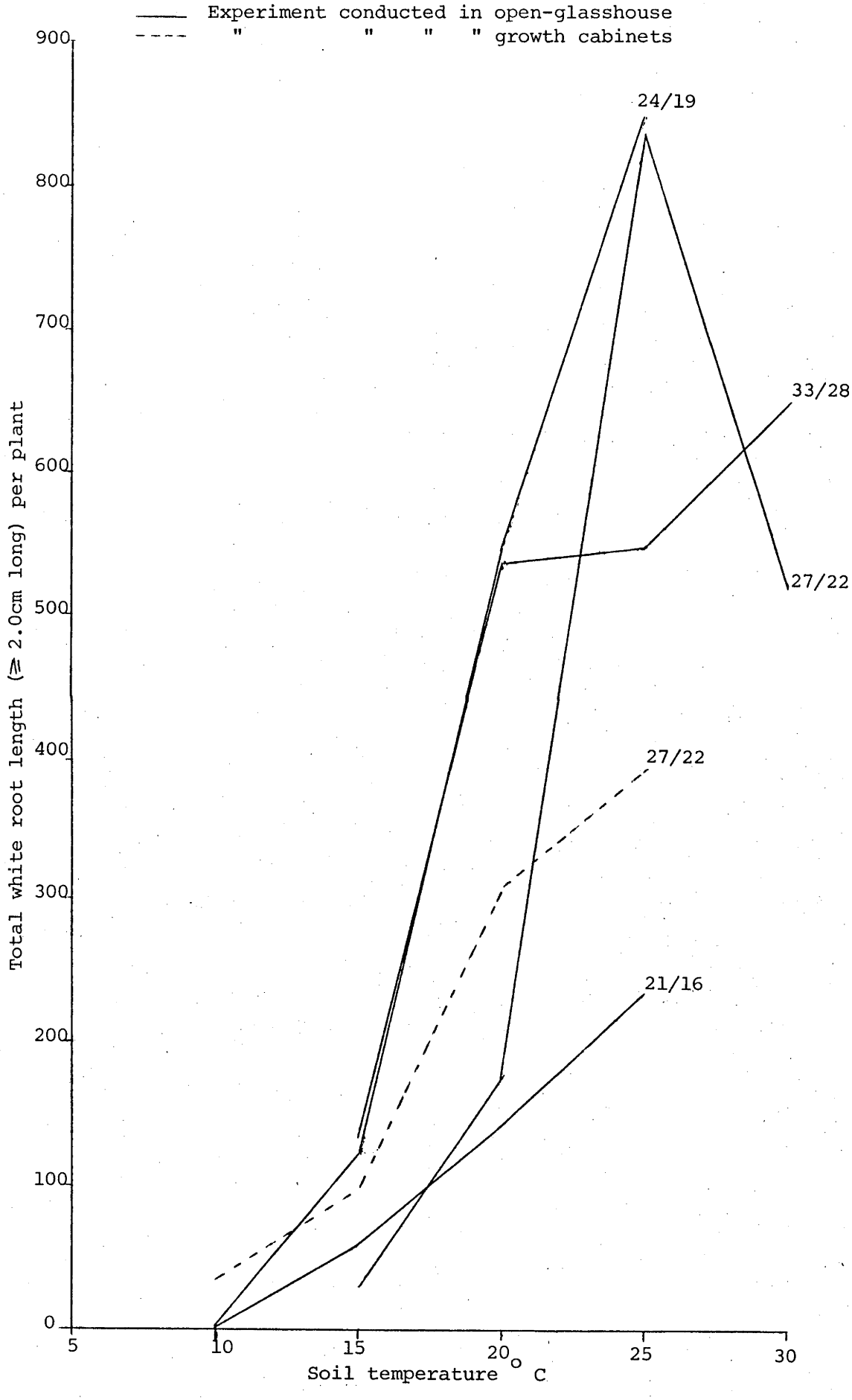


Figure 6.2A Effect of air and soil temperatures on RRP_N of *P. kesiya* seedlings.

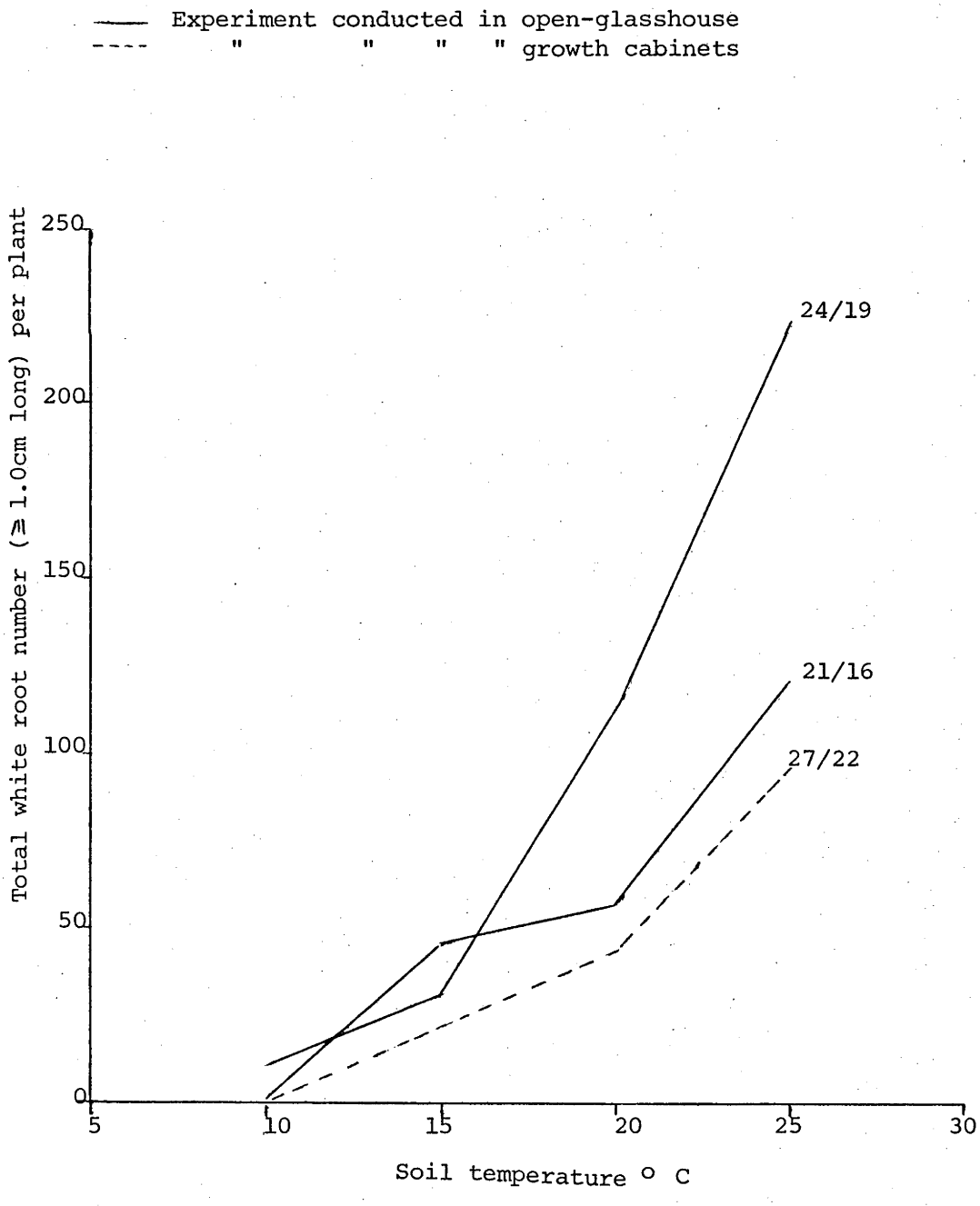
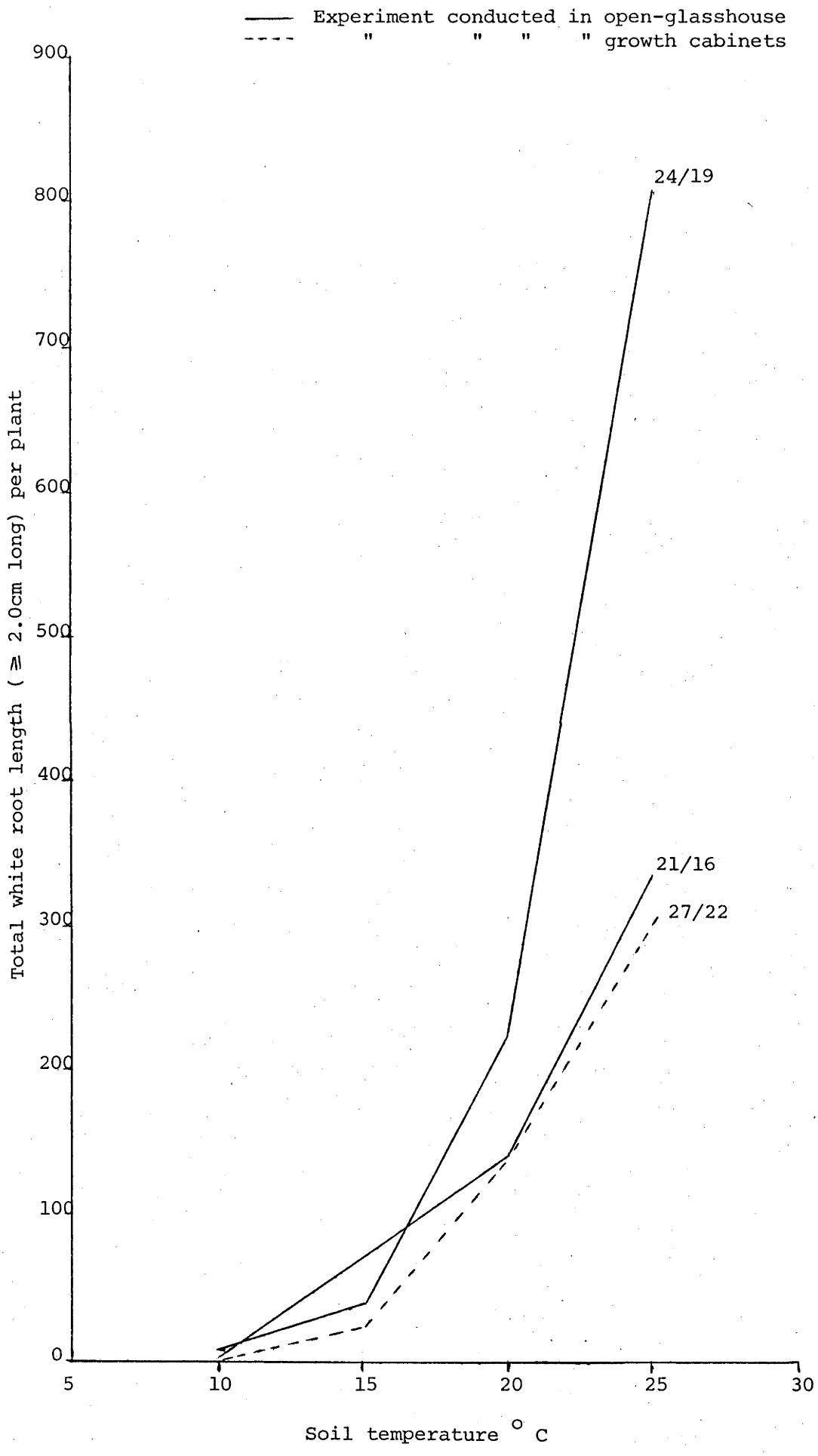


Figure 6.2B Effect of air and soil temperatures on RRP_L of *P. kesiya* seedlings.



6.4 *Discussion*

6.4.1 *Root regeneration*

The results of this study show that soil temperature accounts for most of the differences in RRP under a wide range of air temperatures. Root regeneration was very low at 10° C, and only marginally better at 15° C. There was a substantial increase in root growth with an increase in soil temperature to 20° C, irrespective of the air temperatures for plant shoots. Root regeneration increased even more sharply with an increase in soil temperature to 25° C. The experiments are not extensive enough to distinguish between the effects of soil temperatures of 25° C and 30° C on the root growth. The optimum temperature for root regeneration of the two species tested appears to be within this range, irrespective of air temperatures of the order of 21/16° to 33/28° C day/night.

Barney (1951), in his extensive work with soil temperature on root elongation of loblolly pine (*P. taeda.L*) found a soil temperature of 25° C to be optimum for seedlings from North Carolina. He also reported decreased root growth in the seedlings at 30° C and above. Stone and Schubert (1959a) in their study on the effect of soil temperature on root growth of ponderosa pine (*P. ponderosa* Laws.) found that maximum growth occurred at 25° C, but the study was confined to a temperature range of 10° to 25° C. Both Barney, and Stone and Schubert reported practically no root growth at 10° C. Bowen (1970), noted more root regeneration in radiata pine (*P. radiata* D. Don) seedlings at 27° C soil temperature than at 15° C. The air temperature in the experiments conducted by these authors was not controlled. In summary, the findings from this study are consistent with the literature that the root zone temperature between 25° and 30° C is most favourable for root growth of Pinus species under a wide range of air temperatures.

Roots grown in the cool soil conditions in this study were shorter, thicker and whiter than those grown in warmer conditions i.e. 20°, 25° and 30° C soil. This finding is in agreement with other published literature

(e.g. Hellmers, 1963; Sutton, 1967; Cooper, 1973; Rook and Hobbs, 1976). In an earlier study (chapter 5) it was found that regenerated roots grown under cooler conditions were whiter in colour than those grown in the warmer conditionsand it was discussed that this was evidence to show that the effect of the temperature on RRP could be due to both its direct effect on the roots and to its effect on the crown. In that study, however, soil temperature was in equilibrium with the air temperature so that their effects could not be separated. This study shows that increasing the soil temperature will result in the production of more new roots which, at the same time, are darker in colour due to increased maturation (Barney, 1951; Richards *et al.*, 1952). The findings confirm the discussion in chapter 5 that the effects of temperature on root growth was due to its direct effect on the metabolic activity of the roots in addition to its effect on the crown. It may be noted however, that the new roots from all soil temperature conditions in this study were still recognizable at harvest, possibly because of the short treatment period

Relatively low soil temperatures retard root growth and slow maturation, whereas relatively high temperatures accelerate both processes (Street, 1966). Burstrom (1941), in his study on the effects of different soil temperatures on the root growth of wheat found that the increase in root length was mainly a result of an accelerated rate of cell division. However, Barney (1947) reported that the amount of embryonic tissue, the cell size and the number of mitotic figures in loblolly pine roots appeared to be nearly equal between 5^{o} and 30^{o} C soil temperatures. Barney (1951) also reported that the root tips of loblolly pine seedlings grown between 5^{o} and 30^{o} C soil differed very little in general appearance and under microscopic examination. Low soil temperature probably acts in many ways to reduce the rate of root growth by reducing the metabolic activity in the roots (Street, 1966; Guinn and Gunter, 1968). Reduced metabolic activity

in the roots could result in the restriction of the production of metabolites necessary for cell division. It has been reported (Street 1966) for example, that thermal inactivation of growth could in many cases be partly overcome by addition of single well-known metabolites such as glutamic acid, tannic acid, thiomin, biotin, and nicotinic acid.

Results of this study show very marked effects of soil temperature on RRP at all air temperatures but the root regeneration response of seedlings grown at a cooler air temperature of 21/16° C is very much less at the higher soil temperature of 20° and 25° C in both species (Fig.6.1A & B and 6.2 A & B). It is of interest to compare the relative effects of air and soil temperature as shown in chapter 5 and in this chapter. In chapter 5, the air and soil temperatures were essentially the same; the results show that:

(i) both day and night temperatures had a marked effect on RRP of *P. caribaea* and *P. kesiya*,

(ii) RRP of *P. caribaea* was greatest at a cool night temperature (16° C) under moderate day temperatures (21°, 24°, 27° C) whereas that of *P. kesiya* was greatest at a day temperature of 24° C. in combination with night temperatures of 16°, 19° and 22° C but was optimum at 24/19° C.,

(iii) 33° C day temperature was least favourable for root regeneration in both species under any night temperature (16°, 22°, 28°C) combination.

When the RRP in *P. caribaea* grown at 21/16° C air temperature in chapter 5 is compared with the RRP at 15° C soil and 21/16° C air in chapter 6, the results show that the RRP in the earlier study (RRP_N* = 36, RRP_L* = 101cm) was markedly greater than in this study (RRP_N* = 8, RRP_L*=15cm)

RRP* refers to the RRP per week since it is not possible to compare the absolute values of RRP in chapters 5 and 6 due to the differences in the duration of the treatment i.e. 6 weeks in chapter 5 and 4 weeks in chapter 6.

despite the smaller size of the seedlings in the earlier study. RRP in the earlier study was also markedly greater than the optimum RRP at 25^{o} C soil (RRP_N* = 20, RRP_L* = 59cm) in this study. It was discussed in chapter 5 that a cool night temperature of 16^{o} C was favourable for root regeneration either due to a decrease in the rate of maintainence respiration in both roots and shoot or by increased translocation of photosynthates from the shoot to roots, or both. Soil temperature of 15^{o} C in this study was constant whereas in the earlier study it was 21^{o} C for 8 hours in the day and 16^{o} C for the remaining 16 hours. This may explain the reduced root growth at 15^{o} C soil temperature in this study despite the similar favourable air temperature with the earlier study. A warm soil temperature (21^{o} C) may be required for part of the 24 hour cycle to increase the metabolic activity of the roots and to provide a source - sink relationship from the shoot to roots. Cool soil may be favourable at night for increased translocation of the photosynthates from the shoot to roots in addition to reducing respiration. The decreased root growth at the optimum soil temperature of 25^{o} C in this study compared to the earlier study may be due to the soil temperature being too high at night.

It should be noted however, that the experiment in chapter 5 was conducted in summer (20 October to 1 December, 1974) when the natural daylight intensity was high whereas the Experiment 2 ($21/16^{o}$ C air) in this study was conducted in winter (26 July to 23 August, 1975) when the light intensity was low. These seasonal differences could have a significant influence on both the amount of root regeneration and its response to the air and soil temperatures. It was established in chapter 4 that photosynthesis of *P. caribaea* seedlings grown in 50% Sun and Full Sun (in summer) was not significantly different but were both significantly greater than in 16% Sun. RRP also increased with an increase in photosynthesis. Earley and Cartler (1945) found that the intensity of shoot illumination was the

controlling factor determining the magnitude of root growth response in soybeans to each increment of soil temperature.

It is interesting to compare the root growth response to soil temperature in *P. caribaea* growing at 27/22° C air in the open-glasshouse and in the growth cabinet. In the open-glasshouse, the increase in RRP with increase in soil temperautre from 15° C to 20° and from 20° to 25° C were both greater in magnitude than the corresponding increases in the growth cabinet (Fig. 6.1 A & B). These differences could be due to the higher light intensity in the open-glasshouse. Thus the reduced root regeneration response of both *P. caribaea* and *P. kesiya* seedlings grown at 21/16° C air at higher soil temperatures of 20° and 25° C (Fig. 6.1 A & B and 6.2 A & B) may have been due to the reduced natural light intensity when the experiment was conducted.

In chapter 5, a day temperature of 24° C was found to be favourable for root regeneration in *P. kesiya* seedlings irrespective of the night temperature, possibly due to the temperature being optimum for photosynthesis. It is known that the photosynthetic products produced by the shoot should be translocated away from the leaves so as not to impede photosynthetic activity (Richards *et al.*, 1952;Hartt, 1965; Nielsen, 1971). The results in this study showed optimum RRP in *P. kesiya* at 25° C soil under 24/19° C air. This suggests the direct effect of the day temperature of 24° C on the roots in an earlier study was also responsible for increasing the shoot photosynthesis by creating a large sink in the roots. In chapter 5 the day/night temperature combination of 24/19° C was optimum for root regeneration in *P. kesiya* compared to 24/16° and 24/22° C. One would expect the optimum soil temperature in this study to have occurred at 20° C soil under 24/19° C air but this did not occur possibly because the soil temperature of 20° C was kept constant over a 24 hour cycle instead of 16 hours as in chapter 5. It seems that a high soil temperature of about 24° C in the day

is required to enhance root regeneration. In the earlier study when the air/soil day temperature was 24° C, the RRP in *P. kesiya* at 16° and 24° C night temperatures were similar. In this study, the RRP at 15° C soil was markedly less than at 20° C soil with a day air temperature of 24° C.

Thirty three ° C day air temperature was found to be least favourable for root regeneration in both *P. caribaea* and *P. kesiya* under any night temperature combination in the studies reported in chapter 5. The decreased root growth was attributed to a decreased rate of photosynthesis and increased respiration of both root and shoot under the high day temperature. However, the results in this study have shown that at 33/28° C air, an increase in soil temperature from 15° to 30° C increased RRP (in *P. caribaea*). This suggests that the low RRP at 33° C day temperature in chapter 5 was more likely to be due to the direct effect of the high soil temperature of 33° C during the 8 hour part of the day. Stupendick (1977, unpublished data at Forestry Department, A.N.U.) has shown that *P. radiata* seedlings have no capacity to regenerate roots at 35° C soil.

Both the air and soil temperaturesaffect the plants' RRP in this study but the effect of soil temperature was more crucial than the air. There appears to be an 'optimum response surface'for root regeneration with air temperature about 25° to 33° C and soil temperature about 25° to 30° C (see Table 6.8). The air temperature also has an influence on the patterns of root growth response to soil temperature. Root growth at high soil temperature is further enhanced if the air temperature is also high (Fig. 6.1 A & B and 6.2 A & B). This is inconsistent with the findings of Hellmers (1963) that low air temperature combined with warm soils stimulated root elongation in redwood (*Sequoia sempervirens* (D. Don)) seedlings.

The reason may be attributed to species differences. In addition, the root growth response of seedlings to air and soil temperatures depends on their age and size (Stone and Benseler, 1962; Hellmers, 1963) and the season (Stone and Schubert, 1959a; Stone *et al.*, 1962) when the experiment is conducted. The seedlings in both *P. caribaea* and *P. kesiya* in the experiments in this study differed in age and size.

Some differences in root growth response to soil temperature were observed between *P. caribaea* and *P. kesiya*. At 21/16° C air, the RRP in *P. caribaea* at 25° C soil was not significantly greater than at 20° C soil whereas it was significantly greater in *P. kesiya* (Table 6.2 BI); at 27/22° C air (growth cabinet experiment), the RRP in *P. caribaea* at 20° C soil was significantly greater than at 15° C soil but it was not in *P. kesiya* (Table 6.4BI). These differences in the root growth response could not have been due solely to differences in size because the two species had similar mean height and root collar diameter at the start of the treatment under 21/16° C air temperature (Table 6.1)

RRP in *P. caribaea* at 21/16° C air was not significantly greater than in *P. kesiya* (Table 6.2 BI) but it was significantly greater at 24/19° C (Table 6.3 BI) and 27/22° C (growth cabinet experiment) (Table 6.4BI) air respectively. These differences at the latter two air temperatures could be attributed to *P. caribaea* plants being larger than *P. kesiya* at the start of the treatment.

Origin of new roots

The regeneration of a new root system by transplanted *P. caribaea* and *P. kesiya* seedlings is dependent, after root pruning, upon both the elongation of the old roots (L_{Ore}) already present and the initiation and elongation of new laterals (L_{Nir}). This is in agreement with the findings of Stone and Schubert (1959a) in ponderosa pine seedlings.

Table 6.8 Effect of air and soil temperatures on the origin of new roots in *P. caribaea* and *P. kesiya* seedlings based on the length of white roots ≥2.0cm long per plant.

Species	Air temperature °C	SOIL TEMPERATURE °C														
		10°			15°			20°			25°			30°		
		L_{Nir}*	L_{Ore}#	L¢	L_{Nir}	L_{Ore}	L	L_{Nir}	L_{Ore}	L	L_{Nir}	L_{Ore}	L	L_{Nir}	L_{Ore}	L
P. caribaea	21/16	1	1	2	25	35	60	55	88	143	39	199	238			
	24/19	<1	2	2	44	78	122	279	270	549	431	420	851			
	27/22				23	7	30	133	44	177	704	134	838	284	237	521
	33/28				77	57	134	319	217	536	383	165	548	473	175	648
P. kesiya	21/16	<1	1	1	8	64	72	15	128	143	60	276	336			
	24/19	1	6	7	18	19	37	80	146	226	577	229	806			

* L_{Nir} is total length of newly initiated roots ≥2.0cm long per plant

\# L_{Ore} is total length of elongation from old roots ≥2.0cm long per plant

¢ $L = L_{Nir} + L_{Ore}$ = total length of white roots ≥2.0cm long per plant

Results in Table 6.8 show that both the air and soil temperatures affect the type (origin) of new roots formed. Few roots of either type (L_{Nir} or L_{Ore}) were formed at 10^{o} and 15^{o} C soil irrespective of the air temperature. At soil temperature of 20^{o} C, more roots were formed but large numbers were not favoured until the air temperature was $24/19^{o}$ C. At $21/16^{o}$ C air, mainly old roots elongate. An air temperature greater than $21/16^{o}$ C was required for good root growth, with the one important exception that at 25^{o} C soil and $21/16^{o}$ C air, about 200cm of new roots elongated from old roots which is close to the maximum possible for L_{Ore} (i.e. about 300cm), but few new roots were initiated.

At air temperature of $24/19^{o}$ C and soil temperature of 20^{o} C, L_{Ore} was similar ranging from 200 to 400 cm, but L_{Nir} varied more markedly. Under these conditions, initiation and elongation of new laterals is favoured more than the elongation from old roots. A soil temperature of 20^{o} C as well as air temperature of 24^{o} C are required for more new roots to be initiated. These results suggest that a seedling which has been root pruned will have a potential to produce about 200 to 400 cm roots from the severed root ends at favourable air/soil temperature combinations, a rapid proliferation of new laterals will take place, and within the conditions of the present experiments, the newly initiated laterals can be about twice the length of elongation from old roots.

In the earlier part of the discussion on root regeneration, it was stated that there is an 'optimum response surface'for RRP with air temperature about 25^{o} to 33^{o} C and soil temperature about 25^{o} to 30^{o} C. The study on the origin of the new roots formed shows that this 'optimum response surface'is mainly a function of the response by the plant in initiating new laterals.

6.4.2 *Dry weight*

The results of Anova did not reveal highly significant differences between treatment means for the dry weight parameters. This may be attributed to the short duration of the treatment period (4 weeks). Nevertheless, there are consistent trends in the results to indicate that, as in root regeneration, the soil temperature and not the air temperature or its differential with the soil temperature accounted for most of the differences in the dry weights of the two species studied. Dry weight of the various plant parts increased with increasing soil temperature to a maximum at soil temperatures in the range of 25^{o} to 30^{o} C.

The root, shoot and total plant dry weights in both *P. caribaea* and *P. kesiya* showed similar patterns of response to soil temperature in all the experiments conducted. The effect of low soil temperatures in reducing dry matter production observed in this study is in agreement with other studies on a variety of plant species reviewed by Cooper (1973). Hearth and Ormrod (1965) reported that an increase in the soil temperature of rice from 16^{o} to 32^{o} C increased sheath lengths, the size of leaf lamina and the number and size of stomata. Earley and Cartter (1945) concluded that soil temperatures from about 22^{o} to 27^{o} C appeared to be most favourable for maximum dry weight production of both roots and tops when soybean plants were grown under a great variety of aerial conditions. Whiteman *et al.*, (1963) and Hartt (1965) reported that sugar cane (*Saccharum officinarum*) yields are affected more by soil temperature than by air temperature and the optimum was in the range of 25^{o} - $3o^{o}$ C. Soil temperatures between 25^{o} and 30^{o} C are also favourable for dry matter production under a wide range of air temperatures for *P. caribaea* and *P. kesiya*.

Little information could be found in the mechanisms through which soil temperatures affect dry matter production. Possible explanations include the effects of soil temperature on translocation of carbohydrate

for growth, the changes in endogenons levels of hormones in the tissues, carbohydrate storage, and the metabolic activities of the roots and shoot. Hartt (1965) found that translocation from the leaves of sugar-cane was decreased and congestion occurred which interfer ed with photo-synthesis at suboptimum soil temperatures. Other factors which could also affect dry matter production are amino-acid and hormone supplies. Rates of amino-acid and hormone production and supply from the roots to the shoots have been shown to decrease at low soil temperature (Street, 1966; Barton and Robinson, 1973; Lavender *et al.*, 1973).

Some growth differences were observed between *P. caribaea* and *P. kesiya* in each of the experiments where both species were used (see Table 6.1). For example, at 21/16° C air temperature, both the shoot and total plant dry weights in *P. caribaea* were not significantly affected by the different soil temperatures whereas in *P. kesiya*, both the shoot and total plant dry weights at 10° C were significantly less than at 25° C (Table 6.2 BII). Also, at 21/16° C air temperature, the shoot and total plant dry weights in *P. kesiya* were both significantly greater than in *P. caribaea*. These dry weight differences between the two species did not affect the RRP as shown by the results that the RRP in *P. kesiya* was not significantly greater than in *P. caribaea* (see Tables 6.2 BI and II).

6.4.3 *Height and diameter increment*

In general, both the height and diameter incrementsof *P. caribaea* and *P. kesiya* seedlings increased with increasing soil temperature at all the air temperature regimes studied. In constrast to root regeneration and dry weight, maximum height and diameter increments in *P. caribaea* occurred at 30° C soil temperature at both the 27/22° C and 33/28° C air temperatures. Daubenmire (1974) has reported that the optimum temperature for growth may vary with the different parts of the plant. Lavender and Overton (1972)

and Rook and Hobbs (1976) have also reported increased height growth in Douglas fir (*Pseudotsuga menziesi* (Mirb.) Franco) and radiata pine (*P. radiata* (D. Don)) seedlings respectively, with increase in soil temperature.

It is clear that as in root regeneration and dry matter production, the soil temperature is a key factor in controlling height and diameter growth in the two species studied. As in root regeneration, both height and diameter responses to soil temperature differed in *P. caribaea* growing at 27/22° C air temperature in the open-glasshouse and in a growth cabinet. The results suggest that the degree of response to soil temperature differences will tend to be accentuated at higher radiation levels as the cabinet only supplied about a tenth-sunlight radiation of the period that the glasshouse experiment was conducted.

Results in Table 6.1 show that in general, *P. caribaea* grew faster than *P. kesiya* in height and diameter under a wide range of environmental conditions. However, *P. caribaea* had a different pattern of response to *P. kesiya* with respect to height and diameter increment in each of the experiments conducted. This is best demonstrated for the 21/16° C air temperature treatment since both species were of the same height and root collar diameter at the start of the experiment (Table 6.1) thus the growth differences may not be attributed to differences in seedling size. For example, Table 6.2 B III shows that both the height and diameter increments in *P. kesiya* at 25° C soil were significantly greater than at 15° C soil but not for *P. caribaea*.

Height and diameter growth of young seedlings are indeterminate requiring both the initiation of new primordia and their expansion (Kozlowski, 1971). The effect of a decrease in the rate of amino-acid and hormone production in the roots and their supply to the shoots at relatively

low soil temperatures (Street, 1966; Cooper, 1973) may have interfered with the processes controlling height and diameter growth. In addition, low soil temperatures reduce the rate of photosynthesis (see chapter 7) and thus the supply of carbohydrates needed for growth. However, growth is such a complex of processes that the effect of low temperature on either physical or chemical processes alone is probably inadequate to account for the slower growth.

6.5 *Conclusions*

1. Soil temperature is more important than air temperature in affecting both the RRP and growth of the two species studied. All of the growth parameters measured in both species increased with increasing soil temperature and the optimum temperature appears to be within the range of 25^{o}-30^{o}C irrespective of air temperatures. However, the air temperature does have some influence on the pattern of root growth response to soil temperature. There appears to be an 'optimum response surface' for RRP with air temperature about 25^{o} to 33^{o}C and soil temperature about 25^{o} to 30^{o}C. This 'optimum response surface' is mainly a function of the response by the plant in initiating new laterals. At lower than optimum temperature combinations root regeneration is mainly from old root ends. At favourable temperature combinations a rapid proliferation of new roots result in very high RRP.

2. Roots grown at 10^{o} and 15^{o}C soil temperatures were shorter, thicker and whiter whereas those grown at higher temperatures tended to be longer, thinner and darker in colour.

3. The regeneration of a new root system by transplanted *P. caribaea* and *P. kesiya* seedlings was dependent, after root pruning, upon both the elongation of old roots (L_{Ore}) already present and elongation of new laterals (L_{Nir}). At favourable air/soil temperature combinations, and within the conditions of the present experiments, the newly initiated laterals can be about twice the length of elongation from old roots.

CHAPTER 7

THE EFFECT OF SOIL TEMPERATURE ON PHOTOSYNTHESIS, RESPIRATION AND WATER RELATIONS OF *PINUS CARIBAEA* SEEDLINGS

7.1 *Introduction*

In the previous chapter it was shown that soil temperature has a marked effect on root regeneration, far greater than but not entirely independent of air temperature. Is this because of a reduction in photosynthesis, a reduction of translocation due to low soil temperature or is some other causal mechanism involved? The role of photosynthesis was explored in one of the experiments reported in chapter 6. The experiment was designed to determine whether there was any apparent correlation between the patterns of photosynthesis for plants subjected to root pruning and the subsequent root regeneration. At the same time some attempt was made to ascertain the water status of root-pruned plants.

7.2 *Materials and methods*

The plants involved were those used in Experiments 4 and 5 in chapter 6. Plants in Experiment 5 which were grown at 27/22^{o}C day/night air temperature in the open-glasshouse were used for photosynthesis (and dark respiration) measurements. An earlier study in chapter 5 had shown that best root regeneration and height and diameter growth of *P. caribaea* was obtained from seedlings grown at a day temperature of 27^{o}C.

A study on the effect of soil temperature on the relative leaf water content (RLWC) of *P. caribaea* seedlings was also included in this study. RLWC of *P. caribaea* in each soil temperature treatment was determined at final harvest in Experiment 4 where the air temperature was 33/28^{o}C. The high air temperature provides a high evaporative demand and any obstacle imposed by the different soil temperature to water absorption or conduction in the

plants can be more easily discerned. An attempt was made to relate the results of this experiment with that of photosynthesis. Keller (1972) and Turner and Jarvis (1976) have reported that a reduction in leaf water potential of plants may reduce the rate of photosynthesis by increasing stomatal resistance to CO_2 uptake.

7.2.1 *Photosynthesis and dark respiration*

Both the method and the facilities involved in measuring photosynthesis and dark respiration of plants have been described in chapter 2. The type I soil temperature units were used to control the soil temperature of plants during the photosynthesis and respiration measurements.

Photosynthesis and dark respiration were measured at an air temperature of 27°C in a growth cabinet. Photosynthesis was measured at a light intensity of 75 watts. m^{-2} (3000 fc). The plants were transferred from type II soil temperature units in the 27/22°C glasshouse to type I units in the growth cabinet for photosynthesis and respiration measurements. To facilitate the transfer of seedlings from type II to type I units, and to reduce the time of exposure of the soil to the air temperature during the transfer, each seedling was grown in a 15cm (6 in) diameter plastic bag (with drainage holes). Photosynthesis and respiration measurements were made about 1 hour after the plants had been transferred into the type I units to ensure the roots had reached the set temperature.

A total of four measurements of photosynthesis and respiration using 5 plants per soil temperature treatment for each measurement were made in the experiment. Measurement 1 was made on plants which had been grown at the different soil temperature for 1 week with intact root systems. There were, initially, 15 plants growing in each soil temperature but only five plants per treatment were sampled for Measurement 1. Subsequent to Measurement 1, the roots of all seedlings in each treatment were pruned to 20cm from the cotyledon and all white root tips $\geq$ 0.5cm long were pinched off. RRP of the plants was determined at two harvests i.e. at two weeks

(Harvest 1) and 4 weeks (Harvest 2) (chapter 6).

One day after root pruning, the same 5 seedlings from each treatment measured for photosynthesis and respiration at Measurement 1 were again measured to determine the effect of root pruning on these parameters (Measurement 2). These measurements could not be made immediately after root pruning because of limitations on the use of the Infra-red gas analyser.

Measurements 3 and 4 were made at two weeks and four weeks after root pruning respectively. The samplings at Measurements 2, 3 and 4 were destructive and photosynthesis and respiration were expressed as mg CO_2 per gram oven dry weight of green needles.

7.2.2 *Determination of the relative water content of P. caribaea foliage*

The procedure described is a modification of that of Clausen and Kozlowski (1965).

Two fasciles from each plant were detached and bulked for each treatment (6 plants per treatment) at the end of the 4 week treatment period. The leaves were sampled at 50 percent height of the plant and samplings were made at 1500 hours. Wood (1969) found the relative water content (RWC) of *Pinus radiata* D. Don leaves varied with height and age of needles, and Williams (1975) found that the RWC of *Pinus caribaea* Mor. var. *hondurensis* Barr. and Golf. varied with time of sampling and was minimum at 1500 hours. The sheath of the detached fasciles were removed by severing the needles with a sharp razor blade at the point just above the sheath. The needles were immediately transferred into tared, tightly stoppered 2.5cm x 1.0cm test-tubes with their bases immersed in 5ml of tap water. The fresh weight of the samples were then determined.

The test-tubes were stored in the dark at a constant temperature of 27°C until the leaves attained full turgidity. This was achieved within 48 hours. After saturation, the leaves were removed, surface dried with Kleenex tissue papers and transferred into another set of tared, tightly stoppered test-tubes. The turgid weight of the samples were determined

immediately, and later their oven dry weights were obtained. The RLWC of the leaves from each treatment was calculated and expressed as a percentage as follows:

$$\text{RLWC (\%)} = \frac{\text{Fresh weight - Oven dry weight}}{\text{Turgid weight - Oven dry weight}} \times 100$$

7.3 *Results*

The Anova data for Factor 1 i.e. between different soil temperatures (15°, 20°, 25° and 30°C) at each photosynthesis (P_N and P_T) and dark respiration (R_D) measurements, and Factor II i.e. between different measurements (1,2,3 and 4) at each soil temperature, are presented in Tables 7.1A I and II respectively. The ranking of these parameters in Tables 7.1 B I and II reveals that both net (P_N) and total (P_T) photosynthesis had similar patterns of response to treatment for both Factors 1 and II. Hence, to avoid repetition of statements, only P_N will be used to describe the response of photosynthesis to treatment in the two studies.

Results on the water relations of *P. caribaea* grown at 33/28°C air temperature and under different soil temperatures (15, 20, 25 and 30°C) at final harvest are presented in Table 7.2.

7.3.1 *Photosynthesis, respiration and the gross photosynthetic - respiratory balance (P_T/R_D)*

Factor 1 :

Effect of soil temperature on P_N, R_D and P_T/R_D ratio at each measurement

1. *Net photosynthesis (P_N)*

P_N increased with an increase in soil temperature from 15 to 30°C at all the four measurements. However, the differences between treatments were not significant for Measurements 1 and 2. At Measurement 3, P_N at 15, 20 and 25°C were not significantly different from each other but were significantly less than at 30°C whereas at Measurement 4, P_N at 20 and

Table 7.1A Results of analysis of variance for significance of differences between treatment means for the gas exchange parameters. Plants were grown at 27/22° C day/night air temperature in the open-glasshouse and under four different soil temperatures: 15°, 20°, 25° and 30° C.

I: *Between different soil temperatures (15, 20, 25 and 30 °C) at each measurement.*

Parameter	Measurement 1	Measurement 2	Measurement 3	Measurement 4
Net photosynthesis (P_N)	NS	NS	* *	* * *
Dark respiration (R_D)	NS	NS	NS	NS
Total photosynthesis (P_T)	NS	NS	* *	* * *
P_T / R_D	NS	NS	* *	* * *

II: *Between different measurements (1, 2, 3, & 4) at each soil temperature.*

Parameter	Soil temperature ° C 15	20	25	30
Net photosynthesis (P_N)	* * *	* * *	* * *	*
Dark respiration (R_D)	* * *	* * *	* *	*
Total photosynthesis (P_T)	* * *	* * *	* * *	*
P_T / R_D	* * *	* * *	* *	NS

P, 0.05* ; 0.01** ; 0.001*** ; NS, not significant

Table 7.1B Ranking of treatment means in ascending order for the gas exchange parameters. Bracketed means are not significantly different ($P < 0.05$).

1: *Between different soil temperatures (15^0, 20^0 25^0 & 30^0 C) at each measurement.*

Measurement	Net photosynthesis (PN) $mgCO_2/hr/g$*	Dark respiration (RD) $mgCO_2/hr/g$	Total photosynthesis (PT) $mgCO_2/hr/g$	P_T / R_D
1	15^oC 17.1	15^oC 2.2	15^oC 19.3	25^oC 8.2
	20 18.7	20 2.2	20 20.9	30 8.3
	25 18.8	25 2.6	25 21.4	15 8.8
	30 19.1	30 2.6	30 21.7	20 9.5
2	15^oC 13.1	15^oC 2.4	15^oC 15.5	30^oC 6.2
	20 13.7	20 2.6	20 16.3	25 6.3
	25 14.7	25 2.7	25 17.4	20 6.3
	30 16.1	30 3.0	30 19.1	15 6.4
3	15^oC 6.1	15^oC 1.4	15^oC 7.5	15^oC 5.3
	25 8.2	20 1.6	25 9.8	25 6.1
	20 8.5	25 1.6	20 10.1	20 6.3
	30 13.6	30 2.0	30 15.6	30 7.8
4	15^oC 6.2	15^oC 1.4	15^oC 7.6	15^oC 5.4
	20 10.7	20 1.6	20 12.3	20 7.7
	25 12.4	25 1.8	25 14.2	25 7.8
	30 16.1	30 2.0	30 18.1	30 9.4

* g is over dry weight of green needles in gram.

Table 7.1B continued.

II: *Between different measurements (1,2,3 & 4) at each soil temperature.*

Soil temperature	P_N		R_D		P_T		P_T / R_D	
15°C	3	6.1	3	1.4	3	7.5	3	5.3
	4	6.2	4	1.4	4	7.6	4	5.4
	2	13.1	1	2.2	2	15.5	2	6.4
	1	17.1	2	2.4	1	19.3	1	8.8
20°C	3	8.5	3	1.6	3	10.1	3	6.3
	4	10.7	4	1.6	4	12.3	2	6.3
	2	13.7	1	2.2	2	16.3	4	7.7
	1	18.7	2	2.6	1	20.9	1	9.5
25°C	3	8.2	3	1.6	3	9.8	3	6.1
	4	12.4	4	1.8	4	14.2	2	6.3
	2	14.7	1	2.6	2	17.4	4	7.4
	1	18.8	2	2.7	1	21.4	1	8.6
30°C	3	13.6	3	2.0	3	15.6	2	6.6
	4	16.1	4	2.0	4	18.1	3	7.3
	2	16.1	1	2.6	2	19.1	4	8.5
	1	19.1	2	3.0	1	21.7	1	8.7

* g is oven dry weight of green needles in gram.

25°C were not significantly different from each other but both were significantly greater than at 15°C and significantly less than at 30°C.

2. *Dark respiration (R_D)*

The rate of dark respiration was not significantly affected by soil temperature at all four measurements. There was, however, a clear trend of increase in respiration with increasing soil temperature from 15 to 30°C at all the measurements.

3. *P_T/R_D ratio*

P_T/R_D ratio, cited as an efficiency index (e.g. Huber, 1964) was not significantly affected by the soil temperature at Measurements 1 and 2. There was, however, a highly significant difference between treatment means at Measurements 3 and 4 and the patterns of response at these measurements were similar to that of P_N. At Measurement 3, P_T/R_D ratio at 15, 20 and 25°C were not significantly different from each other but were significantly less than at 30°C whereas at Measurement 4, the ratios at 20 and 25°C were not significantly greater than at 15°C and significantly less than at 30°C.

Factor 2 :

Effect of root pruning on P_N, R_D and P_T/R_D ratio and their recovery with time at each soil temperature

Results in Table 7.1B II show that in general, root pruning caused a decrease in P_N, R_D and P_T/R_D ratio. The effect of soil temperature on the recovery trends for each of these parameters with time are discussed below.

1. *Net photosynthesis (P_N)*

The recovery patterns in P_N were similar at all the four soil temperatures. P_N was maximum at Measurement 1 (when the plants had intact root systems) and decreased at Measurement 2 (1 day after root pruning) reaching a minimum at Measurement 3 (2 weeks after root pruning) and increased at Measurement 4 (4 weeks after root pruning). In contrast

with plants grown at 15°, 20° and 25°C, plants grown at 30°C soil temperature showed complete recovery at Measurement 4 i.e. there was no significant difference in P_N between Measurements 1 and 4. Also, the decrease in P_N at Measurement 2 was significant at 15°, 20° and 25°C soil but not at 30°C soil.

At 25°C soil, P_N at Measurement 2 was not significantly different from Measurement 4 but both were significantly greater than at Measurement 3. On the other hand, at 15° and 20°C soil, P_N at Measurement 2 was significantly greater than at Measurements 3 and 4 but there was no significant difference in P_N between the latter two measurements. There was no significant difference in P_N between Measurements 2, 3 and 4 at 30°C soil.

2. *Dark respiration (R_D)*

Dark respiration increased 1 day after root pruning (Measurement 2) but decreased 2 weeks (Measurement 3) and 4 weeks (Measurement 4) later at all soil temperature treatments. The increase in R_D from Measurement 1 to 2 was significant for soil temperatures of 15 and 20°C but not for 20° and 25°C. R_D did not show a recovery in any of the soil temperature treatments even at 4 weeks after root pruning as indicated by the fact that R_D at Measurement 4 was significantly less than at Measurement 1. However, there was no significant difference in R_D between Measurements 3 and 4 at all soil temperatures.

3. *P_T/R_D ratio*

In general, root pruning decreased the efficiency of CO_2 assimilation by seedlings at all soil temperatures. However, the trends clearly show a recovery in efficiency with time after root pruning. In contrast to plants grown at 15, 20 and 25°C soil, P_T/R_D ratio of plants grown at 30°C soil was not significantly affected by root pruning. Plants grown at 15°, 20° and 25°C soil did not show complete recovery in their efficie

in CO_2 assimilation at 4 weeks after root pruning. These results are due to the fact that P_T is affected much more by root pruning than R_D and the efficiency ratio is basically controlled here by the changes in P_T.

7.3.2 *Water status of the seedlings*

The relative leaf water content (RLWC) at the four soil temperatures at final harvest are presented in Table 6.7C. There was a trend of declining water status in the seedlings with increasing soil temperature but the difference between treatments were relatively slight. Williams (1975) reported that the RLWC associated with a permanently wilted condition in seedlings of this species is approximately 54 percent. His data of the RLWC of *P. caribaea* plants grown at field capacity (and with intact root systems) was 80 percent. Based on these reports, it would appear that no serious plant water stress existed in any of the soil temperature treatments at the final harvest in this study.

Table 7.2 Relative leaf water content of *P. caribaea* seedlings determined from each soil temperature treatment at the final harvest. Plants were grown at 33/28°C day/night air temperature and under four different soil temperatures.

Soil temperature °C	15	20	25	30
RWLC (%)	88.2	80.8	78.7	77.9

Figure 7.1 Effect of soil temperature on photosynthesis and respiration of *Pinus caribaea* seedlings at four different measurements (1-0, 2-x, 3-□, and 4-△).

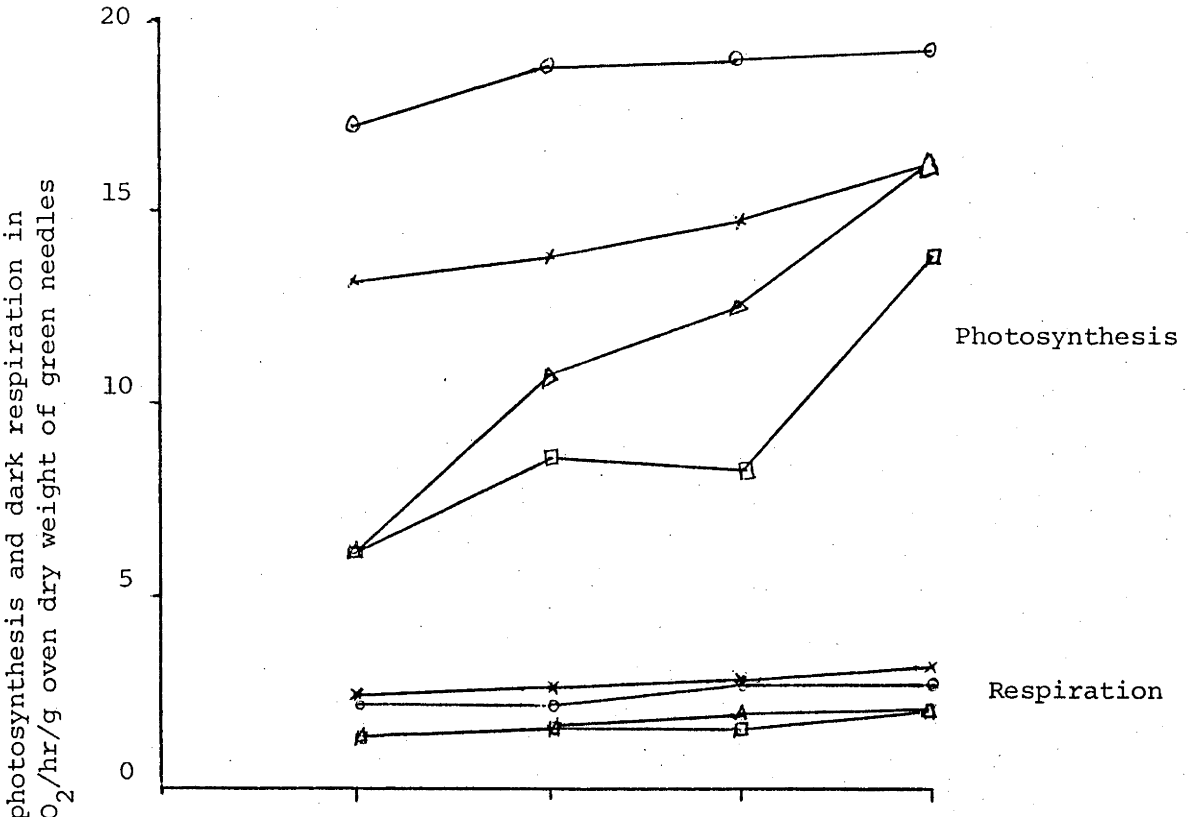
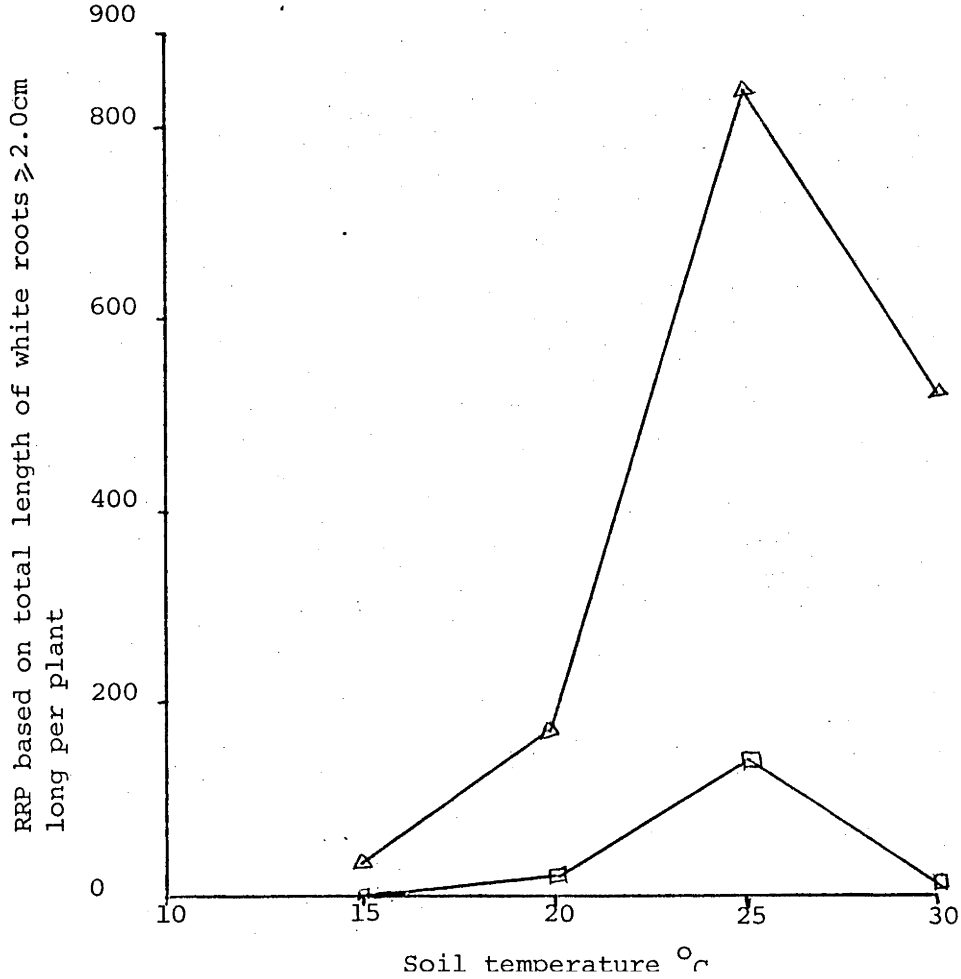


Figure 7.2 Effect of soil temperature on RRP_L of *P. caribaea* seedlings at 2 weeks (□) and 4 weeks (△) after root pruning. Photosynthesis and respiration of the plants (see Fig 7.1) were measured prior to the assessment of root regeneration.



7.4 *Discussion*

7.4.1 *Effect of soil temperature on P_N, R_D and P_T/R_D ratio at each measurement*

The results from this study show that an increase in soil temperature from 15° to 25°C increased both P_N (Figure 7.1) and RRP (Figure 7.2). The increase in P_N with increasing soil temperature is very small in seedlings with intact root systems but becomes increasingly pronounced with time after root pruning. P_N continued to rise at 30°C soil whereas RRP reached an optimum at 25°C. Hence it appears that the increase in photosynthesis with increasing soil temperature cannot be linked directly to the changes in RRP at different soil temperatures. Neither does it seem likely that the increase in RRP is due to increased photosynthesis. The nature of the relationship between RRP and photosynthesis was also found to be obscure in an earlier study in chapter 4 (Light Intensity Experiment). However, the effect of soil temperature and light intensity on root regeneration were strongly paralleled by the consequent effect on photosynthesis.

Shhot respiration also increased with increasing soil temperature but the magnitude of the change in R_D was very much less than the change in photosynthesis hence making it unlikely that the decrease in RRP at 30°C soil temperature was caused by excessive shoot respiration. The effect of soil temperature on shoot respiration was not determined in this study. According to Keller (1972), soil temperature has a more significant effect on root than on shoot respiration. Keller (1966) working on *Picea abies* (L.) Karst. and *Pinus sylvestris* seedlings found a Q_{10} of about 2 over a soil temperature range of 10° to 30°C. He concluded that high soil temperature has an overall depressing effect on root dry matter production because respiratory losses increase more than do photosynthetic gains. It is possible that increases in root respiration also influenced RRP at higher soil temperatures in the present study but no evidence was obtained on this point.

In chapter 6 it was pointed out that (i) soil temperature can affect the translocation of photosynthates from shoot to roots and (ii) soil temperature has a direct effect on the metabolic activities in the roots. For example, low soil temperature retards the production and/or translocation of root-produced growth - regulating compounds such as cytokinins (Guinn and Hunter, 1968) from roots to shoot. This could have a resultant effect on photosynthetic activity.

Went (1944) working with tomato plants found that the amount of sugar translocated in the plants gradually decreased as the temperature was raised from 8^{o} to $26^{o}C$. Based on this finding, it may be postulated that the decreased RRP at $30^{o}C$ soil in this study despite the increase in photosynthesis was due to decreased translocation of photosynthates from the shoot to the roots. From this hypothesis one would expect greater translocation of photosynthates from shoot to roots at lower soil temperatures and increased root growth. On the contrary, the RRP at 15^{o} and $20^{o}C$ soil was found to be significantly less than at 25^{o} and $30^{o}C$ soil (Table 6.5B, chapter 6).

Barney (1951) has reported that reduced root growth (elongation) at a low soil temperature ($5^{o}C$) in loblolly pine seedlings was not due to lack of carbohydrates, but inability to use them. Nevertheless, it should be noted, as pointed out in chapter 5, investigators differ in their findings on the influence of temperature on translocation i.e. whether translocation is enhanced at low temperatures and decreased at high temperatures or vice versa. The temperature gradient between the root and shoot in this study made it more difficult to speculate on the translocation patterns involved in the distribution of assimilates. Possibly, the observed maximum RRP at $25^{o}C$ soil reflects an optimum balance between the translocation of photosynthates from shoot to roots and their use in root regeneration.

It is possible that the increase in photosynthesis with an increase in soil temperature in this study could be due to the increased production of root-produced growth - regulating compounds necessary for photosynthesis. Oritani (1963) suggested that roots may in some way influence RNA systhesis and thereby control protein level of the leaf with a resultant effect on photosynthetic activity. Street (1966) concluded in his review that it is not necessary to postulate that the sole determining effect of roots on the tops is through their function as sinks for carbohydrate produced by the tops.

Relative leaf water content (RLWC) was collected only once at the final harvest, and only in the experiment under 33/28°C air temperature. There was a trend of declining RLWC in the seedlings with increasing soil temperature from 15° to 30°C whereas, photosynthesis increased with an increase in the soil temperature. These results are inconsistent with the general view that a decrease in RLWC decreases photosynthesis in plants (Wood and Brittain, 1973). It might well be that at the relative leaf water content's observed the plants were not under any undue water stress.

7.4.2 *Effect of root pruning on P_N, R_D and P_T/R_D ratio and their recovery with time at each soil temperature*

Root pruning reduced photosynthesis at all soil temperatures. The reduction in the rate of photosynthesis after root pruning might well be attributed to plant water deficit. The presence of many dead needles on the seedlings after root pruning is circumstantial evidence of a decrease in water uptake leading to a water saturation deficit and subsequent stomatal closure which reduces photosynthesis (Kramer, 1969; Keller, 1972; Wood and Brittain, 1973). In addition, the removal of part of the root system reduced the size of the sink for photosynthates and could thus have caused a reduction in shoot photosynthesis due to a build-up of photosynthates in the leaves (Troughton, 1971; Nielsen, 1971; Ziemer, 1971).

Photosynthesis did not recover at the end of the second week at any soil temperature treatment despite the initiation and elongation of new roots at the higher soil temperatures (Fig. 7.1 and 7.2). Possibly, the root growth was not then adequate to provide a significant change in the rate of water uptake or to increase the size of the sink significantly. Both photosynthesis and RRP increased by the end of the fourth week (Fig. 7.1 and 7.2). Photosynthesis remained relatively high and returned more rapidly to the pre-root pruning levels at 25° and 30°C soil where root regeneration was also greatest. However, as evidenced by an optimum RRP at 25°C soil temperature whilst photosynthesis continued to increase up to 30°C soil, there is no direct relationship between RRP and photosynthesis.

A comparison of Tables 7.1B I and II show that shoot respiration (R_D) was much more affected by the root pruning treatment than by soil temperature. This is consistent with the findings of Babalola *et al.* (1968) which showed R_D of radiata pine was much more affected by soil water tension than by soil temperature. Nevertheless, this study revealed little correlation between R_D and plant RRP following root pruning (Figures 7.1 and 7.2).

In general, P_T/R_D ratio shows similar patterns of response as photosynthesis following root pruning at each soil temperature (Table 7.1B II). This is because photosynthesis was much more affected by root pruning than R_D and the efficiency ratio is basically controlled by the changes in P_T. There was no indication of a disturbance in the gross-respiratory balance in the plants to explain the differences in the rate of root regeneration following root pruning at each soil temperature (Figure 7.2).

7.5 *Conclusions*

1. An increase in soil temperature increases both RRP and photosynthesis of root-pruned seedlings but RRP was optimum at 25°C soil whereas photosynthesis peaked at 30°C. These results indicate that RRP cannot be linked

directly to photosynthesis. Soil temperature may have a direct effect on photosynthesis not entirely dependent on its effect on the size of the root sink.

2. Root pruning reduced P_N, R_D and P_T/R_D ratio dramatically over 24 hours. The most obvious cause was an increased water saturation deficit and subsequent stomatal closure. Removal of part of the sink for photosynthates leading to congestion in the leaves may also have contributed to reduced photosynthetic activity.

3. The effect of soil temperature on shoot respiration (R_D) was not significant. In contrast, R_D was significantly affected by root pruning. However, there was little correlation between R_D and plant RRP.

4. Gross photosynthesis (P_T) was much more affected than R_D by soil temperature and root pruning, and the efficiency ratio (P_T/R_D) was basically controlled by P_T. There was no indication of a disturbance in the gross-respiratory balance in the plants.

CHAPTER 8

CONCLUSIONS

1. Root growth depends on a number of environmental factors of which the most important from the range of factors tested appears to be soil temperature. Root regeneration and growth of *P. caribaea* and *P. kesiya* seedlings are inhibited under limiting conditions of light, and of both air and soil temperatures.

2. The air and soil temperatures interact with each other to affect plant RRP. There appears to be what might be termed an 'optimum response surface' for RRP with air temperature about 25° to 33°C and soil temperature about 25° to 30°C. This 'optimum response surface' is mainly a function of the response by the plant in initiating new laterals. At lower than optimum temperature combinations root regeneration is mainly from the old root ends. At favourable temperature combinations a rapid proliferation of new roots result in very high RRP.

3. It is suggested that nursery grown *P. caribaea* and *P. kesiya* seedlings have a greater potential to regenerate more roots and consequently to have an increased chance of survival when outplanted in an environment where both the air and soil temperatures are above 20°C. The potential of *P. caribaea* seedlings to regenerate roots may be increased when grown under partial shade in the nursery. The application of fertilizers in the field may not be needed in the first few weeks after outplanting if the plants have an adequate reserves of N and P but further research would be needed to determine the longer term need for nutrient additions.

4. The effect of light intensity and soil temperature on root regeneration and growth were strongly paralleled by the consequent effect on photosynthesis but the nature of the relationship between the two factors remains obscure.

5. The short treatment period of 4 weeks did not reveal any significant differences in height and diameter increments and dry matter production of plants as a result of treatments. It would be desirable if a better estimate of root pruning effects on height and diameter growth and dry weight production could be obtained. However, lengthening the period would incur much time and labour to assess the plants' RRP. Perhaps, the use of a rhizometer - a recent photo-electric device for measuring root surface areas (Anon., 1967; Morrison and Armson, 1968) could be a useful apparatus for estimating RRP of plants grown for longer periods. In addition, the use of such apparatus enables root regeneration studies in plants to be conducted with intact root systems.

6. Root regeneration and growth in *P. caribaea* showed similar optimum requirements for light, air and soil temperatures as *P. kesiya*. However, the patterns of response of the measured parameters to each of the factors tested differed in some respects between the two species. When seedlings of the two species used were of similar size at the start of a 4 week treatment, *P. kesiya* showed a greater capacity to regenerate roots and produce more plant dry matter than *P. caribaea*. There were however, few differences in height and diameter growth between the two species over the treatment period although, the results showed that *P. caribaea* grew faster than *P. kesiya* in height and diameter over a wide range of environmental conditions prior to the root pruning treatment.

APPENDIX I

Natural distribution, climate and economic importance of *Pinus kesiya* Royle ex Gordon and *Pinus caribaea* Mor. with particular emphasis to the region where the seed used in the experiments originated.

A. *P. kesiya*

(i) *Natural distribution*

P. kesiya is a complex of south-east Asian three-needled pines. It includes *P. khasya* Royle from Assam, Tibet, Burma, Laos, Yunnan and Vietnam; *P. insularis* Enlicher from the Phillipines; *P. langbianensis* A. Chev. from South Vietnam and probably *P. Yunnanensis* Franchet from China (Lamb and Cooling, 1967). The distribution is shown in Figure 1a.

(ii) *Natural distribution in the Phillipines*

The species "occurs in the Phillipines on the island of Luzon between lat. 15° 30' N and 18° 15' N at altitudes from 450 m to 2450 m as shown in Fig. 1b. The principal occurrence is in the Central Cordillera mountain range in Northern Luzon but smaller stands are found in the Caraballo and Zambales mountains" (Turnbull, 1971).

(iii) *Climate in their natural habitat in Phillipines*

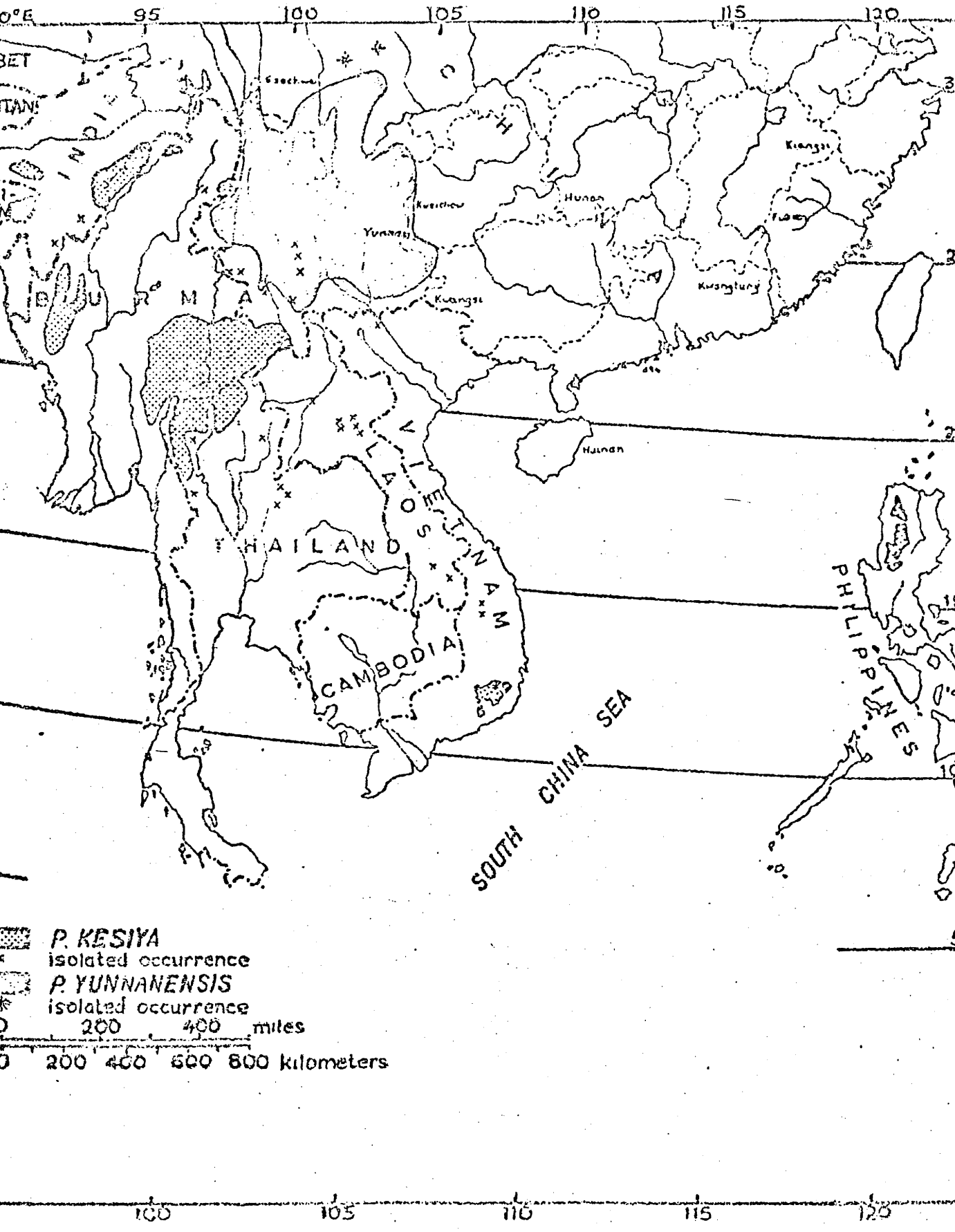
The climate is monsoonal, with a dry season from 5 - 7 months. Rainfall during the wet season (April to November) is 3000 - 5000 mm.

Average temperature fluctuates little throughout the year. At elevations above 1500 m the average annual temperature is about 18°C (17°C in January to 19°C in May) and below 1500 m about 25°C (23°C in January to 28°C in May).

(iv) *Economic Importance*

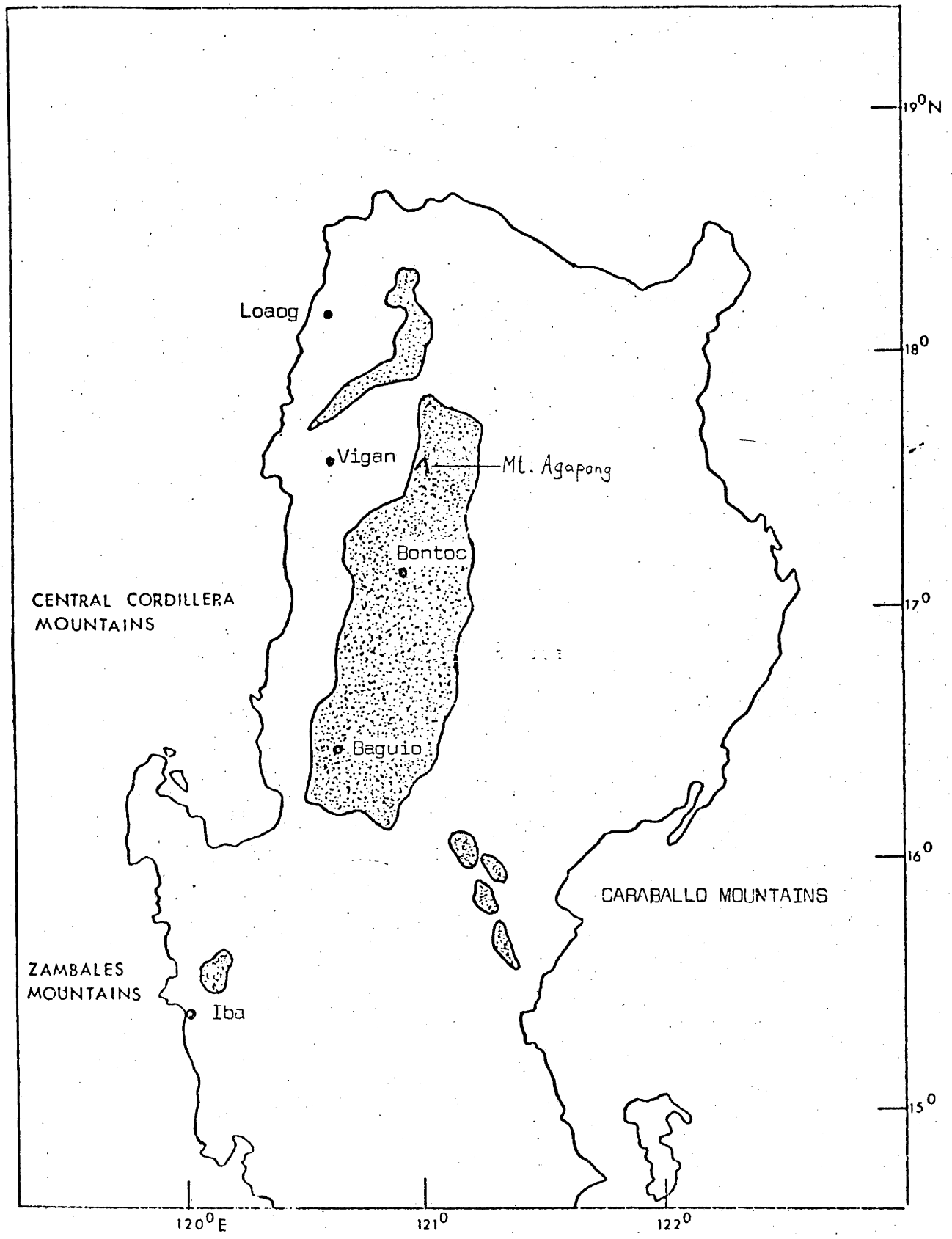
As a montane species with a considerable geographic and altitudinal range *P. kesiya* has a potential place in afforestation projects of middle and high altitudes in tropical and subtropical areas especially where there is a long dry season. It is an important species in the Phillipines as a mining timber and general purpose softwood lumber. It provides protection for several large water-sheds and attempts are being made to supplement natural forests with plantations in the important water-sheds.

gure 1a. Natural distribution of *Pinus kesiya* (modified by Shelbourne*) from Critchfield and Little, 1966).



*C.J.A. Shelbourne, Forest Research Institute, Rotorua, New Zealand.

Figure 1b. Natural distribution of *P. kesiya* in Northern Luzon, Phillipines, with locations of seed collections near Mount Agapang (source: Turnbull, 1971).



B. *P. caribaea* Mor. var. *hondurensis* Barr. and Golf.

(i) *Natural distribution*

P. caribaea var. *hondurensis* grows in the Bahamas Islands, western Cuba, Isle de Pinos, Honduras, Guatemala, Nicaragua and Belize (British Honduras), ranging in altitude from sea-level to 300 m (Mirov. 1967). The natural distribution of *P. caribaea* Mor. is shown in Figure 1c.

(ii) *Natural distribution in Belize (British Honduras)*

The species "occurs between lat. 16° 30' N to lat. 18° N mainly on the coastal plain about 25 km from the coast" (Lamb, 1973).

(iii) *Climate in Belize (British Honduras)*

The climate varies from moist tropical rain forest to savannah types with dry to semi-dry winter periods. Winter temperature is c. 13°C and summer temperature c. 29°C (Luckhoff, 1964).

(iv) *Economic Importance*

"Because of its variability and adaptation to lowland tropical sites the species has become the most important pine for commercial plantations in tropical areas. Trials are in progress in nearly every tropical country with a suitable climate for growing the species" (Lamb, 1973). A summary of plantation programmes of the species is presented in Table 1. Lamb (1973) summarized that the big centres of Caribbean pine plantations are likely to be in Brazil, lowland tropical Africa, Queensland, Fiji and possibly eastern India. Smaller centres of development exist in Uganda, Surinam, Trinidad, Venezuela, Jamaica, Sri Lanka, Malaysia, Madagascar and the Pacific Islands.

lc. (source: Lamb, 1973).

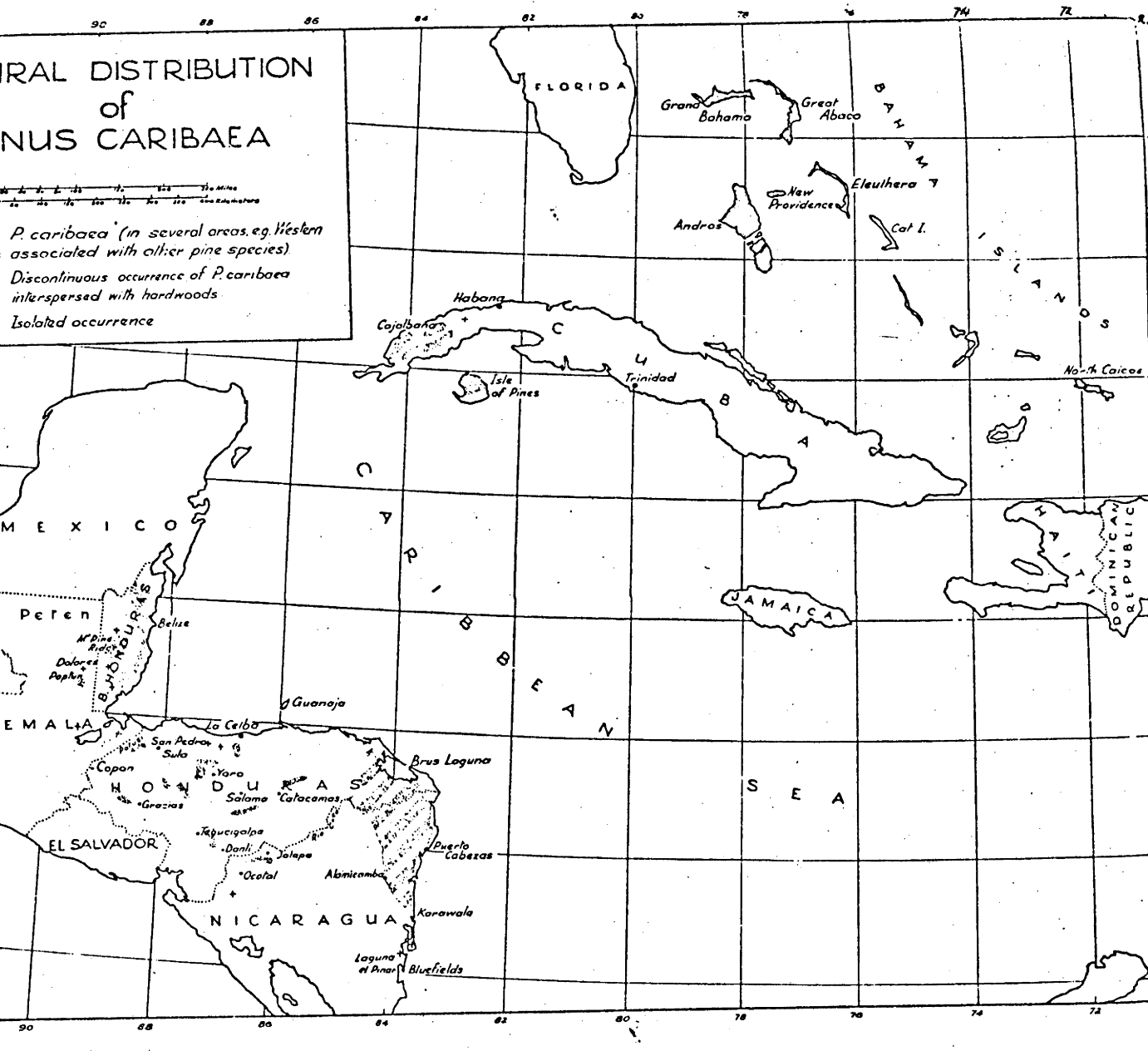


TABLE 1. Summary of Plantation Programmes of *P. caribaea* (source: Lamb 1973).

Country	Area planted up to 1970		Current rate of planting		Estimated rate in 1975		Remarks
	Acres	Hectares	Acres	Hectares	Acres	Hectares	
P. caribaea var hondurensis							
Australia (Queensland)	8,000	3,238	750	304	1,500	607	
Australia (N.Territories)	small	-	small	-	1,000	404	Future success in plantations depends on avoidance of Mastotermes sites
Brazil (Para)	-	-	small	-	1,000	404	Jari River
Brazil (Sao Paulo)	4,000	1,619	7,000	2,833	7,000	2,833	
Brit.Solomon Island Prot.	small	-	small	-	200	81	
Congo (Brazzaville)	1,500	607	1,235	500	2,470	1,000	Many trials in progress
Fiji	11,500	4,654	2,400	971	10,000	4,047	Chip export project + local sawn timber
French Guiana	small	-	200	81	500	203	
Guyana	450	182	100	40	200	81	
India	small	-	100	40	500	203	E. Ghats and Kerala
Jamaica	7,000	2,833	2,000	809	3,000	1,214	
Madagascar	-	-	250	101	1,750	690	
Malaysia	small	-	200	81	1,000	404	
Nigeria	-	-	small	-	1,000	404	Many trials in progress
S.Africa	10,000	4,047	small	-	-	-	
Surinam	10,000	4,047	2,470	1,000	2,470	1,000	
Tanzania	6,700	2,712	1,200	486	10,000	4,047	Mainly coastal plain pulp scheme
Trinidad	6,000	2,428	1,000	405	1,000	405	
Uganda	small	-	200	81	500	203	
Venezuela	200	81	2,000	810	4,000	1,620	
Total var hon.	65,350	26,448	21,105	8,542	49,090	19,850	
P.caribaea var bahamensis							
Australia (Queensland)	1,080	437	250	101	500	202	
Brazil (Sao Paulo)	6,000	2,428	7,000	2,833	7,000	2,833	Seed supply may limit expansion till local supplies become available
Madagascar	-	-	100	40	100	40	
S.Africa	860	348	-	-	-	-	
Tanzania	small	-	1,200	486	2,100	850	
Total var bah.	7,940	3,213	8,550	3,460	9,700	3,925	
P. caribaea var caribaea							
Australia (Queensland)	780	316	300	121	600	243	Seed offered for sale by Cuban Government April 1972
Brazil (Sao Paulo)	4,000	1,619	7,000	2,833	7,000	2,833	
S.Africa	1,000	405	-	-	-	-	
Total var carib.	5,780	2,340	7,300	2,954	7,600	3,076	
Total P. caribaea	79,070	32,001	36,955	14,956	66,390	26,851	

Appendix II Metereological record at Toolara Forest Station, Queensland.

January - September, 1974.

	J	F	M	A	M	J	J	A	S
Mean maximum temp. ^{o}C	28.6	29.0	27.5	27.5	23.8	21.8	21.6	22.5	23.3
Mean minimum temp. ^{o}C	21.0	20.1	19.3	14.6	11.2	8.2	6.3	7.9	7.5
Mean R.H.(%) at 1500 hours	76.2	64.4	74.2	61.1	62.0	58.7	42.8	43.2	50.9
Total rain for month (mm)	649.9	115.4	336.8	60.6	174.7	18.1	17.0	58.1	64.0

Source: Queensland Department of Forestry, Brisbane.

Appendix III A

Composition of modified Hoagland solution

The nutrient solution is based on (No. 2) solution (E. J. Hewitt, Sand and Water Culture Methods used in the Study of Plant Nutrition, 2nd Edition 1966, pp. 187-193) with some modification to the minor elements.

Composition			Elements		
$Ca(NO_3)_2.4H_2O$	950	mg/l	N	211.7	mg/l
$(NH_4)H_2PO_4$	120	"	P	32.2	"
KNO_3	610	"	K	235.9	"
$MgSO_4.7H_2O$	490	"	Ca	160.9	"
H_3BO_3	0.6	"	Mg	48.3	"
$MnCl_2.4H_2O$	0.4	"	Na	3.61	"
$ZuSO_4.7H_2O$	0.09	"	S	66.7	"
$CuSO_4.5H_2O$	0.05	"	Cl	0.143	"
H_2MoO_4	0.02	"	Fe	5.007	"
$Co(NO_3)_2.6H_2O$	0.025	"	B	0.105	"
$FeSO_4.7H_2O$ (chelated with EDTA)	24.9	"	Co	0.005	"
NaOH	6.3	"	Mn	0.111	"
			Cu	0.013	"
			Zn	0.02	"
			Mo	0.012	"

Appendix III B

Composition of Aquasol — a commercial fertilizer.

Analysis : N : P : K Ratio 20 : 5 : 18

	%
Nitrogen (N) as mono-ammonium phosphate	2.0
Nitrogen (N) as potassium nitrate	6.0
Nitrogen (N) as urea	12.0
Total Nitrogen (N)	20.0
Total phosphorous (P) as mono-ammonium phosphate	5.0
Total potassium (K) as potassium nitrate	18.0
Zinc (Zn) as zinc sulphate	0.05
Copper (Cu) as copper sulphate	0.06
Molybdenum (Mo) as sodium molybdate	0.0015
Sulphur (S) as sulphates	0.40
Manganese (Mn) as manganese sulphate	0.15
Iron (Fe) as sodium ferric EDTA	0.12
Boron (B) as sodium borate	0.012
Magnesium (Mg) as magnesium sulphate	0.18

Appendix III C

Chart for mixing nutrient solutions in Nutrient Experiment (Chapter 2) showing number of ml per litre.

	Complete	-N	-P	-NP
1 M Ca $(NO_3)_2 .4H_2O$	5	-	5	-
1 M Mg $SO_4 .7H_2O$	2	2	2	2
1 M $KH_2 PO_4$	1	1	-	-
1 M KNO_3	5	-	5	-
Fe complex	1	1	1	1
* Micronutrients	1	1	1	1
1 M Ca $Cl_2 .6H_2O$	-	5	-	5
1 M KCl	-	5	1	6

* The micronutrient stock solution is 0.046M H_3BO_3, 0.009M $MnCl_2.4H_2O$, 0.0008M $ZnCl_2$, 0.0003M Cu $Cl_2.2H_2O$, and 0.0001 M $Na_2 MoO_4 .2H_2O$.

Source: E. P. Bachelard,
Senior Lecturer
at the Forestry
Department, A.N.U.

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