APPLICATION FOR THE DEGREE OF
DOCTOR OF SCIENCE

from

MASSEY UNIVERSITY, PALMERSTON NORTH
NEW ZEALAND

by

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PREFACE

The research papers selected in this application for the Degree of Doctor of Science (Massey University) are based on original research in the field of environmental physiology, especially in the areas of spectral quality, photosynthetic photon flux density (PPFD - "light intensity"), photoperiod (daylength), and temperature (including freezing stress) and their effects on plant growth and development. The aim of this research has been to study how these factors of the environment influence plant growth form and function. The work has been carried out using a combination of controlled environment technology and field based research.

A list of other publications not selected for this application is given in Appendix I to indicate other scientific interests of the candidate. A *curriculum vitae* is attatched as Appendix II.

SUMMARY

The original contributions, contained in the research papers comprising this application, can be summarised as follows :

1. Controlled environment lighting systems, incorporating the use of high-pressure discharge lamps, have been developed which provide considerable advances over fluorescent tube-based systems, particularly with respect to the maximum PPFD values that can be attained.
2. Guidelines for the design of controlled environment lighting systems have been developed, which incorporate consideration of plant responses to the spectral quality of short-wave radiation and the characteristics of the spectral energy distribution of daylight.
3. Different high-pressure discharge lamps have been compared and the most suitable type for plant growth and development has been identified.
4. Plant growth and development for a number of species has been assessed under PPFD's in controlled environments that simulate peak daylight conditions.
5. Phytochrome control of stem elongation was demonstrated, for the first time, to occur in coniferous and other non-herbaceous species.
6. The spectral energy distribution characteristics of a radiata pine forest canopy were described.
7. The sensitivity of reproductive development in grapevine and kiwifruit to PPFD and shadelight spectral quality was defined.
8. The influence of PPFD in determining apple fruit quality characteristics, such as red blush development, soluble solids concentration and fruit size, was described and the importance of correct tree training and pruning was demonstrated on the basis of physiological mechanisms.

9. The influence of temperature on the rates of development of various stages of crop development, has been quantitatively defined for wheat, corn, pigeonpea, Cymbidium orchid, kiwifruit and geranium. The results of this work have made significant contributions to the development of computer-based crop simulation models, on the one hand, and to the selection of appropriate conditions for the efficient use of greenhouses, on the other. They have also assisted in accounting for observations of season-to-season and to year-to-year differences in crop behaviour in the field.

10. Large walk-in controlled environment facilities have been designed that are capable of producing simulated advective frost conditions. The responses of plants to various rates of freeze, rates of thaw, and frost duration options have been described.

11. The seasonality of frost hardiness has been defined, using a range of indices, for radiata pine, feijoa, kiwifruit, and for seven ornamental native plant and eleven ornamental exotic plant taxa. Their frost hardiness responses were related to their sites of origin and to their hardiness ratings established from field observations. The environmental control of frost hardening in radiata pine, particularly the influence of temperature and photoperiod, was described.

12. The range of frost tolerance available from within *Eucalyptus regnans* provenances, and among individuals within polycross families of *Pinus radiata*, were identified. The variation in tolerance within *E. regnans* was related to the site of origin of the provenance, where altitude, latitude and distance-from-sea were shown to be of particular importance.

INTRODUCTION

Modern controlled environment biology is a comparatively new science having its origins in the development of "phytotrons" in the 1950's. Prior to that time, considerable research was carried out in both the field and in greenhouses, but the temporal and spatial variability of those environments, together with the inability to examine the influence of a factor in the absence of control over other factors, severely limited the scope and precision of the work being done at that time. Over the past 40 years, controlled environment science has progressed to a high level of sophistication where the influence of all factors of the environment on plant growth and development can now be examined. However, over that time, considerable development of controlled environment facilities and techniques has had to occur to allow natural environments to be fully simulated. As part of those developments, considerable adaptations of other technologies, such as the choice and use of lamp types which are developed and manufactured for human eye responses rather than for plant growth requirements, has had to take place. This has involved a close association between biological scientists and engineers and, importantly, has resulted in many breakthroughs in the understanding of mechanisms associated with plant growth responses to environmental factors.

The applicant and his colleages have been associated with a number of these developments, the details of which are outlined in the following sections. The main topics covered in this dissertation include plant responses to the spectral quality and intensity of light and its duration (i.e.,photoperiod), and the responses to temperature including those to low temperature stress.

SPECTRAL QUALITY AND PLANT GROWTH: CONTROLLED ENVIRONMENT LIGHTING

Throughout the first 20 years of controlled environment biology, the main constraints to research were those arising from the lighting systems being used at that time. The maximum PPFD attainable in artificially-lit plant growth chambers is largely determined by the types and combinations of lamps that are used. From the late 1940's the main lighting systems in use were based on the fluorescent tube - particularly the cool white type - supplemented with varying amounts (usually 30 % by installed wattage) of incandescent lighting. These systems often had a less than desirable spectral energy distribution over the visible and near infrared wavebands and consequently did not adequately simulate daylight. More importantly, however, they were severely constrained by only being able to produce maximum PPFD's of approximately one-quarter of full daylight values.

In the late 1950's and early 1960's high-pressure mercury vapour lamps were used in some controlled environment facilities and these lamps did produce higher attainable PPFD's but with coincident poor light quality conditions. Little was known about the amounts of supplementation required from other lamp types and, while the benefits of incandescent lamps were generally understood, there was considerable reluctance to use large numbers of these lamps because of the unacceptable amounts of heat produced. Throughout the 1960's considerable developments were made in the design and manufacture of new types of high-pressure discharge lamps including the mercury-iodide and metal-halide types. These lamps emit energy across the entire visible spectrum and produce a much whiter light than the blue-white light from mercury-vapour lamps. Their potential for use in controlled environments was not apparently recognised overseas and the first trials of these lamps for use in plant growth facilities were carried out in Palmerston North in 1971 (Warrington and Mitchell, 1975). These initial studies showed, on the scale of small reach-in growth cabinets, that as long as some supplemental lighting from incandescent and blue fluorescent lamps was used, then plant growth and development was normal and PPFD values in excess of one-half full daylight values could be readily achieved. The use of these lamps, however, was only possible where plate-glass and water thermal barriers were incorporated between the lamps and the plant growth chamber - this technology had been developed at Plant Physiology Division by the late Dr. Ken Mitchell and his associates in the 1950's and continues to be used to the present.

Subsequent research was focused on the refinement of the information base that enabled the most appropriate lamp type for controlled environment lighting to be identified and the responsiveness of plants, to variation in the distribution of energy across the visible and near-infrared regions of the spectrum, to be defined. These studies (Warrington and Mitchell, 1976; Warrington, Mitchell and Halligan, 1976)

(a) identified the metal-halide lamp type (specifically the Sylvania Metalarc lamp) as being the most suitable high-pressure discharge lamp available for plant growth studies because of its uniform spectral energy distribution and operating efficiency,

(b) recommended that controlled environment lighting systems be designed to have a spectral energy distribution based on that of daylight where the air mass = 2,

(c) demonstrated that plants were highly responsive in their growth form, growth rate and biochemical metabolism to energy in the blue, red and far-red wavebands and that the balance of radiation between these wavebands was critical in determining the responses observed,

(d) identified the red and far-red regions of the spectrum as being the most critical regions for determining plant responses and recommended that lighting systems be evaluated on the basis of the ratio between these two regions. In respect to this point it had been widely assumed, until these studies were carried out, that phytochrome responses in plants would be saturated by the relatively high levels of far-red light being used in controlled environment chambers. It was at about this same time that other workers demonstrated the role of the photoequilibrium of phytochrome in determining some plant growth and development responses in field environments and established that it was primarily the red : far-red ratio of light sources that determined the photoequilibrium. Access to appropriate instrumentation allowed our programmes to assess the suitability of lighting systems for plant growth on these terms but not until a decade later (see below).

An important contribution to the understanding of the use of high-pressure metal-halide lamps for plant growth research was to demonstrate that significant amounts of supplementation from incandescent lamps was required to achieve appropriate red : far-red ratios and satisfactory plant growth and development (Warrington, 1978). The standard lighting system, which is still in operation in the Climate Laboratory 18 years after its development, constitutes a radical departure from the conventional fluorescent-tube based system because of the use of high-pressure discharge lamps but also because it incorporates an installed metal-halide : incandescent lamp ratio of 1 : 1. This ratio is still regarded as excessive by many overseas authorities who regard operating costs rather than proven plant reponses as being the main criterion for lighting system design!

The culmination of the original 5 - 6 years' developmental and plant research work, on the use of high-pressure discharge lamps for controlled-environment lighting, was the publication of a detailed description of the design and operation of the systems used in the Climate Laboratory controlled environment rooms, in the DSIR - designed reach-in cabinets, and in the large Forest Research Institute tree growth rooms (Warrington et al., 1978). This publication has formed the basis of controlled environment lighting systems subsequently designed and built in Canada, the USA and in Australia. Within the Climate Laboratory, the lighting system has now been used without modification for 18 years and well over 100 different plant species have been grown satisfactorily under the system over this period. Most significantly, in all instances the form and type of plant growth and development obtained has closely resembled field-grown material and the results from the controlled environment treatments have been able to be extrapolated directly to field situations, testifying to the sound bases on which the original designs were made.

Few new developments have occurred in lighting technology over the past 20 years and the only other lamp to be developed commercially in this period, with any potential for use in controlled environments, is the high-pressure sodium lamp. This lamp is claimed to have a high operating efficiency based on photophysiology terms (i.e., human eye responses) but it has a poor spectral energy distribution over the important visible and near-infrared wavebands so critical for plant growth. I evaluated plant growth and development under high-pressure sodium based systems (i.e., sodium lamps with supplementation from incandescent lamps and/or in association with multi-vapour lamps) in the mid-1970's but did not publish the results of this work as no real advantages from either a biological or technical standpoint were determined. However the claimed operating efficiencies of high-pressure sodium lamps attracted the attention of commercial growth chamber manufacturers and controlled environment biologists in North America and several facilities installed lighting systems based on this lamp - in all cases the lighting system inevitably incorporated, on a 1 : 1 basis, the use of high-pressure phosphor-coated mercury or multivapour lamps (ironically both very inefficient lamp types). None of these developments appeared to have been carried out with any form of rigorous testing or on the basis of matching the lamp spectra either to plant requirements or to the physical characteristics of daylight - the criteria used in the development of the successful Climate Laboratory systems.

The development of lighting systems based on high-pressure sodium lamps in North America led to these lamps being re-evaluated with two visiting overseas scientists in 1981 (Tibbitts, Morgan and Warrington, 1983). This research confirmed the findings of the earlier unpublished work and established the superiority of the high-pressure multivapour lamp over the high-pressure sodium lamp. It also identified some undesirable plant morphogenetic effects arising from the latter. The availability of appropriate instrumentation, for the first time in this research, led to several of the plant growth responses being ascribed to phytochrome control through establishing a close relationship between the particular response and the phytochrome photoequilibrium arising from the spectral energy distribution of a particular lamp combination. Such relationships had not previously been determined for plant responses to controlled environment lighting systems.

A unique contribution arising from the development of lighting systems based on high-pressure discharge lamps was that of providing levels of PPFD equivalent to peak summer daylight in controlled environment systems. Prior to the development of the systems outlined above, the only means of achieving such high PPFD's was through the use of xenon-arc lamps which were technically complicated and expensive to operate. They were, consequently, only used on a small scale in very specialised facilities. The development of new, high-efficiency fluorescent tube types during the 1960's did allow many improvements in controlled environment lighting but the upper-most "light intensities" achievable were approximately 700 μmol m^{-2} s^{-1} or approximately one-third of peak summer daylight values. As a consequence, controlled environment research was perceived to be severely limited in its scope and potential relevance because of that limited lighting capability. Climate Laboratory lighting systems were designed in the mid-1970's by the author to simulate maximum daylight intensities and these were evaluated with respect to plant growth - PPFD's in excess of 2000 μmol m^{-2} s^{-1} were achievable (Warrington, Edge and Green, 1978). This is apparently the only report ever published on plant growth responses to such high controlled lighting levels and it provided an important perspective to the requirements for lighting in plant growth chambers.

PLANT RESPONSES TO SPECTRAL QUALITY AND PPFD: CONTROLLED ENVIRONMENT ASSESSMENT OF FIELD RESPONSES

The focus of this research has been on radiata pine, kauri and rimu, to define forest canopy responses, and on apple, grape and kiwifruit to define strategies for orchard pruning and training.

An important outcome of the research into controlled environment lighting systems was the demonstration that many plant growth and development responses were controlled by the red : far-red ratio of incident light via the mediation of phytochrome in the plant and its established photoequilibrium state. The acquisition of improved equipment for measuring the spectral energy distribution of natural and artificial light sources in 1981 enabled our research to focus on phytochrome-related responses as we were, for the first time, able to calculate photoequilibrium values accurately.

Our studies on radiata pine (Morgan, Rook, Warrington and Turnbull, 1983) were the first to show phytochrome-mediated control of stem elongation in a coniferous species or indeed in any plant other than a herbaceous species. The study was also novel in a number of other respects:

- it used juvenile seedlings, adult plants from rooted cuttings, and "intermediate" material in the form of plantlets arising from tissue culture; the results indicated that all plant classes responded to the spectral conditions and that the responses, therefore, were not restricted to juvenile material or the stage most likely to be influenced by shade-light spectra
- material was grown for long periods of time under the different spectral environments and the results obtained demonstrated that the phytochrome responses were sustainable for many weeks; this is in contrast to experiments carried out up to that time where plants had only been grown for a few days under different spectral treatments
- it showed that responses to red : far-red ratio were linear over a wide range of values - specifically from 1.15 to 4.59. No saturation of responses was determined, therefore, confirming the earlier conclusion that phytochrome responses were determined by the photoequilibrium that was established and that, in controlled environment systems, it was not a matter of saturating phytochrome requirements by providing a certain proportion of lighting via incandescent lamps but that the incandescent supplementation should be adequate to simulate daylight.

However, although this work was very significant from the standpoint of physiology, its relevance to shadelight environments in the field was uncertain as the red : far-red ratios examined were not typical of those occurring under forest canopies. The spectral energy distribution of shadelight at various depths within radiata pine canopies of different tree spacings, including the influence of different sky conditions, was defined as part of this research (Morgan, Warrington and Rook, 1985). Typical shadelight red : far-red ratios within daylight were between 1.16 and 1.22 whereas under shadelight they were between 0.22 and 0.41 under clear sky and between 0.68 and 0.95 under overcast sky conditions. Calculated phytochrome photoequilibrium values in shadelight were approximately 0.35 under clear sky and 0.46 under overcast sky conditions. In each case there appeared to be no differences in these minimum values between the different canopy densities measured.

Imaginative use of different lamp combinations, in association with selective filters, achieved lighting conditions that simulated shadelight conditions at high PPFD values in walk-in controlled environment rooms. This allowed large forest and fruit tree plants to be grown under such conditions for the first time. The first study using this facility allowed large, fruit-bearing pot-grown kiwifruit vines and grapevines to be grown under a range of spectral energy and PPFD conditions (Morgan, Stanley and Warrington, 1985). The results of this research showed the extreme sensitivity of flower induction in both grape and kiwifruit vines to low PPFD conditions and the fact that vines were able to detect both the amount and also the quality of shade light conditions. These results provided a physiological basis for the requirement of summer pruning and clearly showed that canopy design must ensure an adequate display of developing buds to high light conditions if they were to become fruitful. It was suggested that flowering on vines in orchards will be markedly reduced if the daily integral of PPFD to a shoot during summer months is a third or less of incident radiation. An unexpected outcome from this study was the result that internode elongation in either species did not noticeably increase in response to the shadelight regimes. It was suggested that this lack of responsiveness may be related to the climbing growth habits of these vine species and the fact that they can avoid shade environments by growing over the exterior of the vegetative canopies formed by other species. Although kiwifruit and grapevine naturally occur in forest habitats, they grow in open positions on the outer regions of tree canopies or on forest margins.

Equally dramatic results were obtained with radiata pine when the spectral quality of the light was extended to simulate shadelight conditions (Warrington, Rook, Morgan and Turnbull, 1989). The results showed that radiata pine was typical of many shade-intolerant species, having the ability to elongate its stem markedly in response to shade conditions therefore allowing it to compete effectively against neighbouring plants and retain the display of photosynthetic leaf area under high light conditions. In contrast, the native species *Dacrydium cupressinum* Lamb. (rimu) was shown to be shade-tolerant, therefore requiring competing neighbouring plants to be removed if it is to grow at its maximum potential.

PLANT RESPONSES TO PPFD : FIELD RESPONSES

The understanding obtained of plant responses to PPFD under controlled environment conditions allowed new initiatives to be taken in the study of similar responses in the field. In particular, the influence of light environment in determining the yield and quality of apples under both New Zealand and North American conditions has been studied. Earlier research investigated the influence of summer pruning on the fruit quality characteristics of 'Gala' apple (Morgan, Stanley, Volz and Warrington,1984). The main contribution of this work was to show the independence of changes in red skin colour development from the progressive changes in background colour. Summer pruning increased the percentage of red blush, but not background colour, within the treatments examined. The percentage of red blush, fruit soluble solids concentration and fruit fresh weight were all shown to be highly correlated positively with PPFD penetration through the canopy. Response curves of these relationships were published which showed that the main changes in quality and fruit size occurred where transmitted PPFD was lower than approximately 15 to 20% of above-canopy values. Differences in quality apple production and differences in effectiveness of summer pruning on commercial orchards could be attributed to the influence of tree training and pruning and their effects on light transmission through the tree canopies (Warrington, Stanley, Volz and Morgan, 1984).

Another contribution of this research has been the recognition that transmission of light through the tree to individual fruit bearing sights was the key factor which influenced the size and quality of fruit being produced - this approach is in contrast to that used in Europe where the main emphasis has been in studying light interception by canopies with the primary goal of maximising light interception per unit orchard land area. Partitioning of the tree into regions (upper-inner, lower-outer etc.) provided an insight into the relative productivity of different positions within the canopy and led to the publication of results relating the orientation and position of fruiting laterals to canopy light penetration, yield, and fruit quality in "Granny Smith" apple (Tustin, Hirst and Warrington, 1988). These results established a physiological basis for replacement pruning of fruiting laterals where vertical and horizontal laterals are retained in preference to pendant laterals which, irrepective of canopy position, never receive more than 15 % of the incident PPFD.

TEMPERATURE AND PHOTOPERIOD EFFECTS ON PLANT GROWTH : CROP RESPONSES

An understanding of plant growth and development responses to environmental factors such as temperature and daylength is essential if crop development and performance in different climatic zones and in different cropping seasons is to be predicted and the consequences of management decisions assessed. These relationships between climate and crop growth are discussed in detail in McPherson, Gandar and Warrington, 1980. The influence of environment must also be understood if plant behaviour in greenhouses is to be optimised over the range of environmental and cultural conditions that can be controlled. Traditionally investigations of plant growth responses in controlled environment research facilities have been limited to the study of only three or four levels of a factor, such as temperature, and treatments are run for comparatively short periods of time in the order of days and weeks rather than months. It has also been typical for only one stage of development to be investigated, usually vegetative growth, with little emphasis on the influence of environment over two or even three phases, such as vegetative growth, flowering, and fruiting or grain fill. Our studies have attempted to redress these shortcomings by taking a much more comprehensive approach to environmental studies as outlined below.

In a detailed study on the influence of temperature on spring wheat growth and development (Warrington, Dunstone and Green, 1977), the most important temperature effects were found during the ear development phase. Plants grown at low temperature during this time had long culms, large flag leaves and more potentially fertile florets in each spikelet whereas those grown at high temperatures had high levels of floret abortion. The number of florets which produced harvestable grains, and the weight of those grains at maturity, were affected by temperature during the grain growth stage. This study assisted in identifying the key temperature factors that influence grain yield in spring wheats and the importance of adjusting sowing date to optimise the coincidence of ideal temperatures with the various phases of crop development.

An important contribution to the understanding of the effects of environment on plant growth was the publication of a series of papers describing the response of various growth stages of corn to temperature and photoperiod (Warrington and Kanemasu, 1983 a, b, c). These papers, written from work primarily carried out to provide quantitative desciptions of plant development, have been used extensively in simulation models of corn growth responses to climate. The descriptions of seedling emergence, tassel initiation and anthesis (Warrington and Kanemasu, 1983 a), supplied details of the responses of these developmental stages to temperature and provided direct information of the basis on which degree-day models are based - particularly the shape of the development - temperature response curve and the base temperature for each development stage. Equally the description of leaf initiation and appearance responses to temperature (Warrington and Kanemasu, 1983 b) has allowed the expansion of the photosynthetic surface to be defined.

This research on corn resulted in a number of other important breakthroughs in the understanding of plant responses to temperature. Firstly, a technique was applied which allowed the individual contribution of discrete components of the diurnal temperature pattern to be taken into account. This technique allowed the true response of a plant's development stage to temperature to be defined rather than representing that as a response to mean daily temperature. Consequently the principles underlying thermoperiodicity in plants could be challenged and the actual reasons for the responses previously observed could be advanced. Secondly, the temperature thresholds for growth were defined and the differences in growth between the minimum mean temperature, the minimum day temperature and the minimum night temperature were defined - this confirmed the acute sensitivity of corn (and other C4 photosynthesis plants) to minimum temperatures while the plant is under high light conditions. Thirdly, the advantages of defining the growth responses to temperature in rate rather than duration terms were identified.

The results obtained also showed that an increase in photoperiod lengthened both the time between sowing and tassel initiation and that between tassel initiation and anthesis in a similar, almost equal, manner. Sensitivity to photoperiod was not altered by temperature. These responses were largely due to an increase in leaf number (0.71 leaves per addition hour) even though both leaf-initiation and leaf-appearance rates increased with an increase in photoperiod.

A detailed description of the response of photosynthesis in corn to varying temperature regimes has also been published (Bennett, McPherson and Warrington, 1983). The influence of growth temperature, acclimation temperature (i.e., the temperature to which plants were transferred to for 24 h), and measurement temperature were all defined. The measurement temperature had the greatest single effect on photosynthetic rate, which increased 2-3 fold between 16 and 35 °C.

Research similar to that outlined above for corn has also been carried out for the tropical legume *Cajanus cajan* (L.) Millsp. (pigeonpea) where the primary objective was to achieve an understanding of the environmental control of flowering so that rapid generation turnover techniques could be used in breeding programmes (McPherson, Warrington and Turnbull, 1985). The rate of development from sowing to flower bud initiation varied among the 11 cultivars examined. Responses to temperature were all strongly curvilinear with optima between 20 and 24 °C. The rate of development from sowing to flowering showed a similar pattern. The effect of daylength on the rate of development was greatest between sowing and flower bud initiation, with greatest sensitivity between 12 and 14 h. Extensive use was made of the discrete rate analysis technique to interpret the data obtained in this study, allowing the underlying temperature response curves to be identified from otherwise confusing patterns arising from the evaluation of responses based on mean temperatures. The rate of development between sowing and flower bud initiation in a given environment varied among cultivars approximately in accordance with their maturity rankings established from field trials in India, particularly over the 20-28 °C range, indicating the direct relevance of these controlled environment results to field situations.

As indicated above with both corn and pigeonpea, an understanding of the underlying responses of plant development processes to temperature can help to explain, or challenge, the basis of phenomena such as thermoperiodicity, and identify ways in which day and night temperature regimes can be optimised for plant growth responses or for minimising energy consumption in greenhouses. Thermoperiodicity was also examined in soybean where it was shown that plants grown under different day/night temperature regimes did not differ greatly in growth rates, in rates of physiological processes such as photosynthesis, or in the diurnal courses of these processes. However, this study did show marked depression of net photosynthesis rates where high concentrations of starch accumulated in the leaf tissue during the latter part of the day temperature (and photo-) period (Warrington, Peet, Patterson, Bunce, Haslemore and Hellmers, 1977).

Detailed analysis of the temperature requirements for growth and flower development in *Pelargonium x hortorum* Bailey (geranium) identified a number of ways in which significant energy or time savings could be made in the commercial production of this greenhouse pot-plant. One option for energy savings was identified through the use of "split-night" temperature regimes (White and Warrington, 1984a) - a technique that had been evaluated previously on only three or four other crops. Carefully selected temperature regimes with wide day/night differentials, and consequent low energy consumption, but the same means as constant temperature regimes, were shown to produce equivalent growth and development but with considerable energy savings (White and Warrington, 1984b). The influence of the growth regulator chlormequat was also evaluated in these studies and although it suppressed most vegetative growth characteristics it did not alter any of the flower development responses. Flower development was also unaffected by supplemental CO_2 but in this instance growth characteristics were enhanced. Subsequent work (White and Warrington, 1988) identified the optimum daily light integral and temperature conditions for this crop and presented the relationships between temperature and the rates of development to macrobud from seedling emergence and to anthesis from macrobud. Overall these results showed how a greenhouse production schedule for this crop could be reduced from about 120 days to about 42 days.

Similar studies have shown how the selection of appropriate temperature regimes can enhance flower production in greenhouse-grown Cymbidium orchids (Powell, Caldwell, Littler and Warrington, 1988).

Temperature also plays an important role in the growth and development of tree and vine crops. Studies have defined the temperature optimum for vegetative growth in kiwifruit and have identified its sensitivity to chilling temperatures especially under high PPFD conditions (Morgan, Warrington and Halligan, 1985). The response of kiwifruit pollen produced and evaluated under various temperature conditions has also been defined (Jansson and Warrington, 1988). Highest pollen germination was obtained under the warmest plant growth regimes and declined as development temperature decreased. Maximum percentage germination occurred at incubation temperatures between 22 and 28 °C with little germination at or below 13 °C or above 35 °C. Budbreak and flowering in kiwifruit have also been shown to be very temperature sensitive (Warrington and Stanley,1986). The proportion of budbreak was shown to be highest under cool temperature regimes but under these conditions it occurred over a prolonged period. Conversely, the proportion of fruitful shoots was highest under the warm temperature regimes. A 1 °C drop in mean daily temperature between budbreak and flowering resulted in a 5 day delay in flowering for the male cultivar 'Matua' and a 7.5 day delay in the female cultivar 'Hayward'. These results agree well with differences in flowering time for plants grown at different altitudes where the lapse rate would result in temperature differences of the order required to produce the observed flowering response. Related subsequent work (McPherson, Stanley and Warrington, 1988) has expanded this understanding further.

TEMPERATURE EFFECTS AND PLANT GROWTH: LOW TEMPERATURE (FROST) STUDIES

Low temperature frost conditions provide a major limitation to the growth and development of many agricultural, horticultural and forestry species in many countries including New Zealand . In the field the incidence of frost events is unpredictable and the duration and extent of the frost are largely uncontrollable. Research techniques have been developed to allow plant responses to low temperature stresses to be studied in the laboratory but in most instances studies are restricted to evaluating the responses of detatched twigs or plant parts rather than allowing for the study of intact plants or plant populations (Warrington and Rook, 1980).

The design of a walk-in room-scale controlled frost facility in the Climate Laboratory provided a unique facility for studying whole-plant responses to low temperature frost conditions (Robotham, Lloyd and Warrington, 1978). These facilities have been intensively used over the past decade by a large number of workers from New Zealand, Australia and Canada and results of the research have contributed widely to improving our understanding of the mechanisms of frost hardiness development and to defining the thresholds of frost tolerance of various plant species. The use of the facilities was enhanced by developing standardised screening techniques that took cognisance of the influence of freezing and thawing rates and the effects of frost duration (Warrington and Jackson, 1981). All studies were carried out by building on previously-published research and techniques which were evaluated and summarised in a review (Warrington and Rook, 1980).

An early study during this period (Green and Warrington, 1978) provided much-needed information on the seasonality of frost hardening and dehardening in radiata pine, and on the threshhold temperatures for injury throughout the year. The development of frost injury assessed visually was related to a physiological index of cell membrane damage as measured by diffusate electro-conductivity. This study then led to a detailed investigation of the influence of daylength and temperature on hardiness development in radiata pine and provided some of the first evidence for the relationships between hardiness development and environment in a coniferous species (Greer and Warrington, 1982). This work also demonstrated how the environment at a nursery site could influence hardiness development in seedling stock and indicated the desirability of using nursery sites adjacent to, or in a climate type similar to, the forest planting site to ensure that planting stock would transfer and establish successfully.

The ultimate objective of this research has been to develop quantitative descriptions and eventually "models" of how environmental factors control hardiness in radiata pine. Most recently, Greer, Stanley and Warrington (in press) have shown, for the first time, how the rate of change in photoperiod appears to be the way in which the plant determines the onset of autumn and winter conditions to modify its endogenous cold tolerance level.

The marked upsurge in interest in horticultural crops in New Zealand over the past two decades has led to a demand for information on the environmental requirements of those crops in order to define the best regions for their production. Minimum winter temperatures and the incidence of early autumn and late spring frosts can often be the factor that limits crop distribution most unless some form of protection is provided. In response to this demand, the seasonal frost tolerance of feijoa (Stanley and Warrington, 1984) and of kiwifruit (Pyke, Stanley and Warrington, 1986) were described - both the temperature that caused initial injury (the frost hardiness temperature) and the temperature that caused death (the lethal temperature) were defined at each season throughout the year.

In a similar manner to the constraint of plant distribution in New Zealand, the distribution and survival of plants in overseas countries is also determined by the low temperature limits reached. Ornamental plants which may grow well in New Zealand and have considerable export potential may not be suitable for export unless they tolerate the climate in the importing country. This is particularly the case with native plants which have evolved in our largely maritime environment and for which frost tolerance limits have not been defined. In studies conducted over the past four years, the seasonal frost tolerance limits of ornamental plants in seven native plant taxa and in eleven exotic plant taxa have been defined and the ecological significance of their cold hardiness limits discussed (Warrington and Stanley, 1987; Stanley and Warrington, 1988). Within some native plant species, such as *Pittosporum tenuifolium* Sol. ex Gaertn. considerable differences in frost tolerance among cultivars were defined which could be attributed to their altitude of origin and, therefore, indicated scope for breeding and selection of enhanced frost tolerance. In contrast, in other species such as *Leptospermum scoparium* J. R. et G. Forst., no differences in frost tolerance among cultivars were detected apparently because of the very limited base of genetic/ecotypic origin of the ornamental material currently being grown. In these species a more extensive range of material will need to be screened to establish if more extreme cold tolerance is available among natural types.

These studies also -

(a) related the ranking of plant species and their absolute levels of frost hardiness with tolerance levels established from field observations and their classification within broad cold hardiness zones,

(b) showed, within the range of material examined, how plants which have evolved in the comparatively mild oceanic climates of Australasia have not developed the considerable hardiness levels of species which have evolved in the more extreme climates of continental Europe and America,

(c) showed that evergreen, broadleaved plant species do not have the capacity to harden to the extent attained by deciduous plant species, and

(d) showed how the hardiness levels attained by different coniferous species were related to their centre of origin and that their consequent hardiness could span the range covered by both evergreen and deciduous broadleaved plants.

The importance of defining the genetic variability within a species for frost tolerance was recognised in several other studies. A major evaluation of the range of frost tolerance available, among 38 provenances of *Eucalyptus regnans* F. Muell. identified the sites of origin of the most-hardy material as being the interior, upland sites of south-central Tasmania and the high altitude (> 900m) regions of Victoria. Mathematical descriptions of these relationships were determined. Close agreement between field and laboratory rankings of the provenances was shown, illustrating the value of the controlled environment tests in screening material of this nature. Gains of up to 2.5 °C in winter frost tolerance could be made by selecting the most frost tolerant provenance for use in improvement programmes (Rook, Wilcox, Holden and Warrington, 1980).

The genetic potential for improvement in frost tolerance has also been evaluated in radiata pine (Menzies, Burdon, Holden and Warrington, 1987). Some families within a polycross population were shown to be consistently more frost resistant (tolerant) than others. The potential to produce frost-resistant populations within New Zealand breeding programmes was, therefore, defined and the rates of gain in resistance were quantified.

CODA

The work described in this dissertation is continuing in each of the areas of environmental physiology outlined above. The physiological principles that determine the differences in productivity and fruit quality characteristics of different apple tree training systems are being defined and are being translated into recommendations to growers that will result in improved orchard productivity. Similarly, light interception and transmission characteristics are being studied in orchards established at different tree planting densities in order to define optimum fruit production methods based on sound physiological and environmental principles. Temperature studies are continuing with kiwifruit with further investigation of the influence of temperature on budbreak, flowering, and on the development of fruit maturity, being carried out. Continued analysis of the corn data set obtained previously is allowing a quantitative description of leaf elongation and expansion rates to be prepared. With regard to greenhouse crops, research is being concluded which will define the environmental requirements for vegetative growth and flower production in *Nerine* and *Zantedeschia* cultivars and identify cultural regimes which will allow crop scheduling and optimum productivity.

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PAPERS CITED IN THIS APPLICATION

Warrington, I.J. and K.J. Mitchell. 1975. The suitability of three high intensity lamp sources for plant growth and development. J. Agric. Engng. Res. 20: 295-302.

Warrington, I.J. and K.J. Mitchell. 1976. The influence of blue- and red-biased light spectra on the growth and development of plants. Agric. Meteorol. 16: 247-262.

Warrington, I.J., K.J. Mitchell and G. Halligan. 1976. Comparisons of plant growth under four different lamp combinations and various temperature and irradiance levels. Agric. Meteorol. 16: 231-245.

Warrington, I.J., R.L. Dunstone and L.M. Green. 1977. Temperature effects at three development stages on the yield of the wheat ear. Aust. J. Agric. Res. 28: 11-27.

Warrington, I.J., M. Peet, D.T. Patterson, J. Bunce, R.M. Haslemore and H. Hellmers. 1977. Growth and physiological responses of soybean under various thermoperiods. Aust. J. Plant Physiol. 4: 371-380.

Green, L.M. and I.J. Warrington. 1978. Assessment of frost damage in radiata pine seedlings using the diffusate electro-conductivity technique. N.Z. J. For. Sci. 8: 344-350.

Robotham, R.W., J. Lloyd and I.J. Warrington. 1978. A controlled environment room for producing advective white or black frost conditions. J. Agric. Engng. Res. 23: 301-311.

Warrington, I.J. 1978. Controlled environment lighting - high pressure discharge lamp based systems. Proc. of Growth Chamber Environments Symp. XXth Int. Hort. Congr., Sydney, Australia. August 22, 1978. Phytotronic Newsletter No. 19, p.15-27. 77pp.

Warrington, I.J., T. Dixon, R.W. Robotham and D.A. Rook. 1978. Lighting systems in major New Zealand controlled environment facilities. J. Agric. Engng. Res. 23: 23-36.

Warrington, I.J., E.A. Edge and L.M. Green. 1978. Plant growth under high radiant energy fluxes. Ann. Bot. 42: 1305-1313.

McPherson, H.G., P.W. Gandar and I.J. Warrington. 1980. Matching the crop to the environment. In Symp. "Temperature and plant productivity in New Zealand", Agron. Soc. of N.Z. and N.Z. Soc. Plant Physiol. Christchurch, August 20-24, 1979. Proc. Agron. Soc. N.Z. 1979, 9: 71-78.

Rook, D.A., M.D. Wilcox, D.G. Holden and I.J. Warrington. 1980. Provenance variation in frost tolerance of *Eucalyptus regnans* F. Muell. Aust. For. Res. 10: 213-238.

Warrington, I.J. and D.A. Rook. 1980. Evaluation of techniques used in determining frost tolerance of forest planting stock: A Review. N.Z. J. For. Sci. 10: 116-132.

Warrington, I.J. and A.K.H. Jackson. 1981. Injury to radiata pine as influenced by freezing and thawing rate, and low temperature duration. N.Z. J. For. Sci. 11: 37-44.

Greer, D.H. and I.J. Warrington. 1982. Effect of photoperiod, night temperature and frost incidence on development of frost hardiness in *Pinus radiata*. Aust. J. Plant Physiol. 9: 333-342.

Bennett, K.J., H.G. McPherson and I.J. Warrington. 1983. Effect of pre-treatment temperature on the response of photosynthesis in maize to current temperature. Aust. J. Plant Physiol. 9: 773-781.

Morgan, D.C., D.A. Rook, I.J. Warrington and H.L. Turnbull. 1983. Growth and development of *Pinus radiata* D. Don.: the effect of light quality. Plant, Cell and Environment 6(9): 691-701.

Tibbitts, T.W., D.C. Morgan and I.J. Warrington. 1983. Growth of lettuce, spinach, mustard and wheat plants under four combinations of high-pressure sodium, metal halide and tungsten-halogen lamps at equal PPFD. J. Amer. Soc. Hort. Sci. 108: 622-630.

Warrington, I.J. and E.T. Kanemasu. 1983a. Corn growth responses to temperature and photoperiod. I. Seedling emergence, tassel initiation and anthesis. Agron. J. 75: 749-754.

Warrington, I.J. and E.T. Kanemasu. 1983b. Corn growth responses to temperature and photoperiod. II. Leaf initiation and leaf appearance rates. Agron. J. 75: 755-761.

Warrington, I.J. and E.T. Kanemasu. 1983c. Corn growth responses to temperature and photoperiod. III. Leaf number. Agron. J. 75: 762-766.

Morgan, D.C., C.J. Stanley, R. Volz and I.J. Warrington. 1984. Summer pruning of Gala apple: the relationships between pruning time, radiation penetration and fruit quality. J. Amer. Soc. Hort. Sci. 109: 637-642.

White, J.W. and I.J. Warrington. 1984a. Effects of split-night temperatures, light, and chlormequat on growth and carbohydrate status of *Pelargonium x hortorum.* J. Amer. Soc. Hort. Sci. 109: 458-463.

White, J.W. and I.J. Warrington. 1984b. Growth and development responses of *Pelargonium x hortorum* to temperature, light integral, CO_2, and chlormequat. J. Amer. Soc. Hort. Sci.: 109: 728-735.

Warrington, I.J., C.J. Stanley, R. Volz and D.C. Morgan. 1984. Effects of summer pruning on Gala apple quality. The Orchardist of N.Z. 57: 518-522.

Stanley, C.J. and I.J. Warrington. 1984. Seasonal frost tolerance of Feijoa (*Feijoa sellowiana* Berg.) N.Z. J. Agric. Res. 12: 315-317.

Morgan, D.C., I.J. Warrington and E.A. Halligan. 1985. Effect of temperature and photosynthetic photon flux density on vegetative growth of kiwifruit (*Actinidia chinensis* Planch.) N.Z. J. Agric. Res. 28: 109-116.

Morgan, D.C., I.J. Warrington and D.A. Rook. 1985. Some observations on the spectral distribution characteristics of short-wave radiation within *Pinus radiata* D. Don canopies. Plant, Cell and Environment 8: 201-206.

McPherson, H.G., I.J. Warrington and H.L. Turnbull. 1985. The effects of temperature and daylength on the rate of development of pigeonpea. Ann. Bot. 56: 597-611.

Morgan, D.C., C.J. Stanley and I.J. Warrington. 1985. The effects of simulated daylight and shadelight on vegetative and reproductive growth in kiwifruit and grapevine. J. Hort. Sci. 60: 473-484.

Warrington, I.J. and C.J. Stanley. 1985. The influence of pre- and post-budbreak temperatures on flowering in kiwifruit. Proceedings of ISHS Symposium on Physiology of Productivity of Subtropical and Tropical Tree Fruits, Brisbane, 12-17 May, 1985. Acta Horticulturae 175: 103-107.

Pyke, N.B., C.J. Stanley and I.J. Warrington. 1986. Kiwifruit: frost tolerance of plants in controlled frost conditions. N.Z. J. Expt. Agric. 14: 443-447.

Menzies, M.I., R.D. Burdon, D.G. Holden and I.J. Warrington. 1987. Family variation and potential for genetic gain in frost resistance of *Pinus radiata*. New Forests 3: 171-186.

Powell, C.L., K.I. Caldwell, R.A. Littler and I.J. Warrington. 1988. Effect of temperature regime and nitrogen fertiliser level on vegetative and reproductive bud development in Cymbidium orchids. J. Amer. Soc. Hort. Sci. 113: 552-556.

Warrington, I.J. and C.J. Stanley. 1987. Seasonal frost tolerance of some ornamental indigenous New Zealand plant species in the genera *Astelia, Dicksonia, Leptospermum, Metrosideros, Phormium, Pittosporum* and Sophora. N.Z. J. Exptl. Agric. 15: 357-365.

White, J.W. and I.J. Warrington. 1988. Temperature and light integral effects on growth and flowering of hybrid geraniums. J. Amer. Soc. Hort. Sci. 113: 354-359.

Stanley, C.J. and I.J. Warrington. 1988. Seasonal frost tolerance of some ornamental evergreen broad-leaved and coniferous tree and shrub species. N.Z. J. Expt. Agric. 16: 239-248.

Jansson, D.M. and I.J. Warrington. 1988. The influence of temperature during floral development and germination *in vitro* on the germinability of kiwifruit pollen. N.Z. J. Expt. Agric. 16: 225-230.

Tustin, D.S., P.M. Hirst and I.J. Warrington. 1988. Influence of orientation and position of fruiting laterals on canopy light penetration, yield, and fruit quality of 'Granny Smith' apple. J. Amer. Soc. Hort. Sci. 113: 693-699.

McPherson, H.G., C.J. Stanley, I.J. Warrington and D. Jansson. 1988. Dynamics of budbreak and flowering. Proceedings National Research Conference 1988, Special Publication No. 2, New Zealand Kiwifruit, New Zealand Kiwifruit Authority, Auckland. p. 9-11.

Warrington, I.J., D.A. Rook, D.C. Morgan and H.L. Turnbull. 1989. The influence of simulated shadelight and daylight on growth, development and photosynthesis of *Pinus radiata, Agathis australis* and *Dacrydium cupressinum.* Plant, Cell and Environment (in press).

Greer, D.H., C.J. Stanley and I.J. Warrington. 1989. Photoperiod control of the initial phase of frost hardiness development in *Pinus radiata*. Plant, Cell and Environment (submitted for publication).