THE USE OF CONTROLLED ENVIRONMENTS IN FORESTRY RESEARCH

K. R. SHEPHERD

Department of Forestry, Australian National University

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ABSTRACT

The use of controlled environments in forestry research makes it possible to analyse the effects on tree growth of one factor while holding others constant. This paper reviews a number of research projects carried out in phytotrons as a means of demonstrating the advantages and limitations of the use of controlled environments in research with nursery planting stock. The phytotron has been a valuable tool in determining the role of temperature particularly in controlling shoot and root growth, especially with regard to frost effects at low temperatures. It is suggested the phytotron could be used more extensively to select genotypes adapted to particular temperature regimes, especially for frost resistance, and for research with herbicides. Use of controlled environments has problems and some of these discussed with particular reference to the CERES phytotron in Canberra, Australia.

INTRODUCTION

Since the establishment of the first phytotron at Pasedena thirty years ago similar facilities for controlling some or all of the more important environmental factors influencing plant growth have become available for use in most centres for plant research. Use of the phytotron cannot provide all of the answers to research problems associated with producing seedlings of tree species for planting out in the forest but it is indeed a very valuable tool. We do need facilities for controlling specific climatic factors if we are to gain a proper understanding of plant response to environment. In the forest the many factors of the environment, such as temperature, photosynthetic irradiance and day length, are confounded so that it is difficult to isolate the contribution of any one to plant growth. The use of controlled environment makes it possible to analyse the effects of varying one factor while holding the others constant. The flexibility and sophistication of the facilities available will increase the effectiveness of this form of analysis.

Controlled environment has long been employed in forest practice, particularly in the field of vegetative propagation (Hartmann and Kester, 1968). Facilities range from the simplest cold frame to completely air-conditioned glasshouses with humidity control, supplementary CO_2 and extended photoperiod. However, the use of such facilities for routine production of nursery seedlings was rare until fairly recently, in contrast to quite widespread use in crop production (Warren Wilson, 1972). Cost militated against extensive use of greenhouse facilities in forestry until the introduction of the portable plastic greenhouse. These facilities are now extensively used in cool temperate regions to shorten the period required to produce seedlings in the nursery (Tinus and McDonald, 1979), to produce large quantities of planting stock from cuttings of species where this was formerly not possible (Kleinschmit, 1974), and even to produce entirely indoors the seed required for nursery use (Lepisto, 1973).

We have been fortunate in Canberra, Australia, to have had the CERES phytotron available for research with tree species (Morse and Evans, 1962). CERES was established as an Australian facility early in the 1960s and has been extensively used by Australian and visiting workers interested in environmental and associated physiological research topics with a wide range of tree species, more particularly those conifer species included in plantations and a number of species of eucalypts. Because of the special association of the Australian National University with training forest research workers from Asia, a number of studies have been concentrated on tropical and sub-tropical species such as teak. The purpose of this paper is to review a number of research projects carried out at CERES and in other phytotrons as a means of demonstrating the advantages and limitations of the use of controlled environment in research with nursery planting stock.

PHYTOTRON FACILITIES

There is little need here to document the range of phytotron facilities available to the plant research worker engaged in investigations into problems of plantation establishment, and, more particularly, nursery stock. The first detailed account of the use of phytotron facilities was given by West (1957) and several descriptions of new installations have been published since (see for example Morse and Evans, 1962; von Wettstein, 1967; Kramer, Hellmers and Downs, 1970; Nitsch, 1972; and for a review see Downs and Hellmers, 1975). In principle these facilities are similar, consisting of either air-conditioned glasshouses with natural lighting supplemented with artificial light to extend the natural daylength as at CERES, or of large air-conditioned rooms with artificial lighting as at the Department of Scientific and Industrial Research at Palmerston North, New Zealand. A wide range of temperature regimes can be employed. Smaller cabinets with fine control of the environment are also usually available, mostly with artificial lighting but, as in CERES in Canberra, some are positioned in the naturally-lit glasshouse and use shutters for daylength control with or without supplemental incandescent lighting.

The flow and pattern of air movement are carefully controlled, temperature can be programmed as desired and daylength can be extended in glasshouses, or controlled as desired in growth rooms and cabinets. Relative humidity is difficult and costly to control and is usually controlled only to a minimum level (40% in CERES (Morse and Evans, 1962); 50-70% at Pasadena, and no perfect control was achieved at Gif, in France (Nitsch, 1972)). For complete humidity control plants can be grown in cabinets designed for this purpose, such as the LBH Type in CERES (Morse and Evans, 1962). Plants are usually grown in an artificial root medium, such as perlite and vermiculite, with adequate water provided and nutrients added by way of a balanced nutrient solution. The temperature of the root medium is usually not controlled, following the square wave pattern of the day/night ambient air temperature regime, so that special facilities are required to maintain separate control (Abod *et al.*, 1979). It is also difficult to manipulate soil moisture availability in a phytotron without special equipment. Nutrient availability can, however, be modified by manipulating the formula of the nutrient solution.

In controlled environment facilities one of the most significant features is the near absence of problems with predators and disease. With proper phytosanitary precautions the problems can be kept to a minimum as the root medium is usually sterile and insects can be kept out or eliminated by fumigation. Red spider (*Tetranychus* sp.) has proven to be a difficult mite to deal with in CERES, as at Gif (Nitsch, 1972).

Conventional phytotrons pose problems for research workers concerned with tall plants such as sugar cane or some tropical grasses, and with trees. Of particular interest, therefore, is the facility for research in controlled environment with trees up to 7 m tall built at the Forest Research Institute, Rotorua (Forest Research Institute, 1973).

SHOOT GROWTH

Controlled environment is a valuable tool for the study of shoot growth and in acquiring some understanding of the climatic factors which might limit the use of a species as an exotic in plantation. The development of pine shoots is quite varied but environments place restraints on growth, especially by imposing climatic barriers (Lanner, 1976). Plantations of exotic species have frequently resulted in considerable economic gain, as with *Pinus radiata* D.Don in Australia and New Zealand (Scott, 1960). However, some experiences with other species have been less rewarding, as, for example, with *P. caribaea* Morelet. This species has been successfully planted in Queensland, Australia (Hawkins *et al.,* 1978) and in Fiji (Rennie, 1974) but has suffered deformity in the wet tropical lowlands (Slee *et al.,* 1976; Waring, 1971). Part of the reason for this is now thought to be due to disruption of the natural patterns of apical growth, a conclusion reached after long and careful observation of seedlings of *P. elliottii* Engelm, later of *P. caribaea,* grown under a range of temperature-daylength regimes in the CERES phytotron (Slee and Shepherd, 1972; 1977). These studies, combined with field observations, led to the generalised hypothesis that the differentiation of floral primordia in *P. caribaea* is disrupted at high temperatures and short daylengths. This leads to growth abnormalities which render *P. caribaea* generally unsuited to lowland areas within 5° of latitude of the equator (Slee, 1977b). The early work, using controlled environment to define carefully the stages of growth in the shoot apex, now forms the basis of extended studies in the field on growth morphology in tropical and subtropical conifers (Slee, pers. comm.).

SEEDLING GROWTH

Investigations into seedling growth in controlled environments can serve two particular objectives for the worker concerned with seedling nursery stock. First, for studies of growth processes *per se,* and second, for studies on the effects of treatments applied to the seedlings under conditions where all other effects are held constant. Before the second approach can be followed with assurance it is desirable to understand the basic growth patterns of the species under conditions of controlled environment. For example, the temperature regime, or regimes, selected for a seedling growth study will depend on whether the objective is to study temperature effects *per se* or to study some other factor while maintaining a favourable temperature regime (Downs and Hellmers, 1975 p. 27).

A number of studies have been undertaken to study the basic effects of temperature on growth of *P. radiata* seedlings (Cremer, 1968; Florence and Malajczuk, 1970; Hellmers and Rook, 1973) and for favourable growth a day temperature of 20° to 25°C is indicated with a night temperature at least 5°C and preferably 10°C lower. The effects of temperature on photosynthesis were studied by Rook (1969); and of temperature on root growth by Stupendick and Shepherd (1980). Similar analyses have been made for *P. caribaea* and some other tropical pines (Basri, 1976; Slee, 1977a; Bacon and Bachelard, 1978; Abod *et al.,* 1979). Optimum temperatures for growth are given for a number of other conifers in Tinus and McDonald (1978, p. 187). Temperature requirements have been investigated for a number of eucalypt species, including *E. deglupta* Blume (Davidson, 1972), *E. camaldulenses* Dehnh. (Awe, 1973), *E. nitens* Maiden (Shepherd *et al.,* 1976), *E. sieberi* L. Johnson (Shepherd and Banks, unpubl. data), *E. cloeziana* E. Muell. (Turnbull, 1979), and for a group of species by Awang (1977). Paton (in prep.) has examined the question of temperature response in eucalypts. The behaviour of teak in controlled environment has been investigated by Ko Ko Gyi (1972), Kanchananburangura (1976), and Pinyopusarerk (1979).

The species noted above may now be grown in controlled environment or greenhouses at near maximum growth rates with some degree of assurance. The purpose may be to raise seedlings commercially, as discussed by Tinus and McDonald (1978, p. 91), or for experimental purposes where other treatments are to be imposed. An understanding of the pattern of temperature response also allows a more meaningful interpretation of observed field responses, as, for example, with the effects of root pruning and root wrenching in nursery beds, or the uptake of fertiliser added at the time of planting as discussed by Stupendick and Shepherd (in press). A particularly interesting example of a procedure for estimating photosynthetic temperature response in the field from phytotron observations is provided by Slatyer (1977).

FROST STUDIES

As with studies of shoot growth, growth studies with seedlings can be used as a diagnostic tool, to pin-point weaknesses in plants, and to identify important climatic factors responsible for these (McWilliam, 1966). Use of the phytotron is more likely to suggest the environment in which the plant will not succeed. One such avenue for profitable research with nursery seedlings has been to study frost tolerance. Controlled frost treatments may be applied to nursery stock conditioned in various ways, either in the nursery (Rook *et al.,* 1976; Menzies, 1977), or under precise climatic control within a phytotron (Timmis, 1976). The investigations with *P. radiata,* using advective frost (Robotham *et al.,* 1978), have been useful in defining the seasonal tolerance limits in radiata pine to a single frost (—6°C in summer and between —10 and —12.5°C in winter) and revealing that consecutive frosts and high day temperatures increase damage. Early planting prior to the development of maximum frost tolerance could lead to heavy losses if a period of clear weather and severe frosts followed planting, a situation not uncommon in Australia.

Little emphasis has been given in Australasia to hardening of *P. radiata* planting stock for cold temperature storage after lifting, although some attention was given to this question by Rook *et al.* (1974). In northern temperate countries much attention has been given to this problem as frost and snow prevent open-root planting during the greater part of the dormant season so that either autumn or spring planting is necessary (Brown, 1973). Cold storage can extend the planting season into spring as seedlings remain dormant while stored. In Australia and New Zealand *P. radiata* planting takes place in winter while seedlings are dormant as snow or frozen soil is rarely a problem. In Australia particularly, considerable losses can be sustained due to drought where early or late planting is practised. One incentive for cold storage would be to enable excess nursery stock to be held over for use the following year but to date this has not become accepted practice and warrants some research.

A number of studies into frost tolerances of eucalypts have indicated where species are more likely not to succeed by defining likely climatic limitations. These studies have employed the frost room built by the Botany Department, Australian National University, which simulates a radiation frost (Aston and Paton, 1973). Plants have been preconditioned either in CERES or in growth cabinets (Paton, 1972; Awe and Shepherd, 1975; Wilkinson, 1976). Frost tolerance in eucalypt seedlings has been found to be confined to relatively mild sub-zero temperatures compared with those tolerated by many cool temperate species. Of considerable interest is the recent suggestion that dehardening of shoots of some eucalypts involves active roots, as the process is delayed in very cold or waterlogged soils in spite of warm shoot temperatures (Paton *et al.,* 1979). Paton (1978) notes "the temperature-dependent photoperiodic responses in some *Eucalyptus* species are clearly very small" suggesting they "have not evolved photoperiodic induction of winter dormancy as an adaptive character". The low level of photoperiodic response in *Eucalyptus* (and also possibly in *P. radiata*) probably explains why so little emphasis has been placed on this avenue of research in tree seedlings in Australia and New Zealand, in marked contrast to northern temperate countries (see, for example, Lanner, 1976; Timmis, 1976; and Glerum, 1976).

PROPAGATION WITH STUMPS

A stump, or root and shoot cutting, is a taproot with a short stem used for planting. Stump planting is an accepted method of propagation in forest practice but surprisingly little is written on the physiological processes involved. Our research interest in propagation with stumps has concerned teak (*Tectona grandis* L.f.) for which species stump planting is a long established practice (Champion and Pant, 1932), and for *E. camaldulensis,* a species planted this way since the turn of the century, but the method has been accorded little attention in the literature (Jacobs, 1955; FAO, 1956).

Kaosa-ard (1977) investigated some of the physiological aspects of teak stump sprouting using the CERES phytotron facilities and employing temperature regimes known from previous work to favour the growth of teak (Ko Ko Gyi, 1972). Teak seedlings lifted and stumped at full dormancy were known to have a relatively higher sprouting potential than those lifted earlier and could be stored for some time before planting. Phytotron trials defined the role of temperature regimes in inducing high sprouting potential and demonstrated neither a positive correlation between the amount of stored carbohydrates in the stump nor between the size of stumps and the vigour of sprouts. The mobilisation of reserves, mediated possibly through hormonal relationships, appeared to govern sprouting vigour.

Preliminary experiments with *E. camaldulensis* stump replanting in the glasshouse established the capacity of this species to be propagated by this method under a range of environmental conditions (Sa-ardavut, 1979). Successful rooting of cuttings is known to require a favourable temperature of the root medium of 18° to 27°C (Hartmann and Kester, 1968) but excessively high soil temperatures will result in the death of the cuttings. Controlled environment was used to investigate the effects of temperaure on sprout and root development from stumps where the ambient air and soil temperature were separately controlled, using the equipment detailed in Abod *et al.* (1979). The air and soil temperature combinations tested and some of the results of these tests are shown in Fig. 1. There were marked differences in sprout and root growth both due to temperature regime and between provenances. A fuller analysis of these experiments is being prepared (Sa-ardavut and Shepherd, in prep.).

OTHER USES FOR CONTROLLED ENVIRONMENT

This paper has reviewed briefly the range of research work with tree seedlings carried out during the past few years, particularly in CERES. A number of other uses could be made of controlled environment which have so far not received much attention in CERES, or possibly elsewhere. McWilliams (1966) notes how the provision of standard reproducible environments is of value in reducing environmental variance and increasing the precision with which estimates can be made of the genetic component of variability. Agriculturalists have put this possibility to good use in crop breeding where selections are needed to obtain genotypes adapted to a particular climatic attribute. Little use has yet been made of controlled environment for this purpose in forestry, for example in breeding for frost resistance as suggested by Menzies (1977).

Forestry is a major user of agricultural chemicals yet little use has been made of controlled environment in herbicide research. Most of this work in Australia has been in field conditions where environmental variation is great. Screening studies on susceptibility of the plantation tree species or of resistant weed species to new chemicals might possibly be carried out with reduced cost and increased efficiency in controlled environment.

PROBLEMS FOR PHYTOTRON USERS

Two particular aspects of temperature response studies in phytotrons deserve comment. One is the effect of age of the seedlings, as a number of studies suggest the temperature regime for optimum growth may change as the seedlings age (Hellmers and Rook, 1973; Eldridge, 1969; Green, 1969) and certainly a physiological response such as root regeneration following root-pruning is sensitive to the age of the seedlings treated (Stupendick and Shepherd, 1980). An important aspect of this problem is the possibility of seedling response being confounded by drought stress when plants, which have grown well in the early months of a study, are retained in pots too small to maintain an adequate water balance at all times. Likewise, air flow patterns in cabinets and photosynthetic irradiance at the plant leaf surface will alter as seedlings develop with age.

The second aspect deserving comment concerns the seasonal effects of operating in open glasshouses facilities. In CERES we have concluded from a number of studies with eucalypts that experimental results can be confounded by variations in incoming

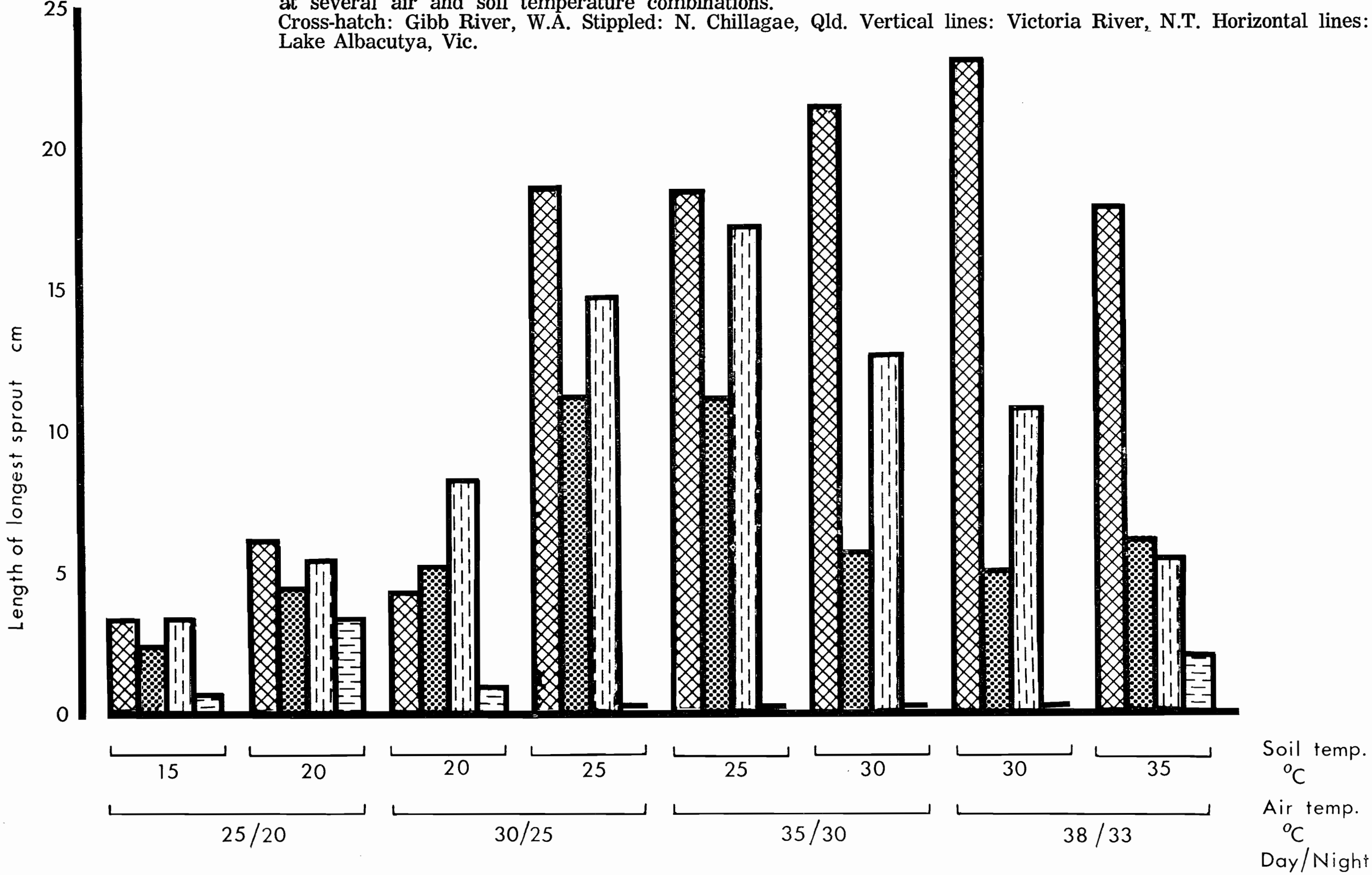

FIG. 1—Length of the longest sprout of replanted stumps of four provenances of **Eucalyptus camadulensis** maintained at several air and soil temperature combinations.
Cross-hatch: Gibb River, W.A. Stippled: N. Chillagae, Qld. Vertical lines: Victoria River, N.T. Horizontal lines: Lake Albacutya, Vic.

radiation during the year, an effect confirmed by others working with tree species (Slee, pers. comm.; Paton, pers. comm.). The effect has been found to be critical in studies with teak, a species which requires very highlight values for maximum photosynthesis, and some of the work of earlier investigators (Ko Ko Gyi, 1972; Kanchananburangura, 1976) could not be repeated with assurance (Pinyopusarerk, 1979). One associated effect (Paton, pers. comm.) is a direct result of the watering system in CERES as the temperature of the mains water supply varies considerably during the year and this affects plant growth. There is no provision in CERES for equilibration of the irrigation water in tanks within the glasshouse to the ambient temperature, as described for the phytotron at Duke University (Downs and Hellmers, 1975, p. 26).

CONCLUSIONS

Controlled environments have a very useful role in research in plant growth and can be especially useful in solving problems associated with raising nursery planting stock. Nursery seedlings are of a size particularly suited to phytotron investigations. Few problems are encountered due to plant size as can occur when very large plants, such as sugar cane or small trees, are grown in these facilities.

However, phytotrons do have limitations and these should be taken into account when designing experiments. Air relative humidity is difficult and costly to control and soil moisture regimes are difficult to manipulate, especially with the artificial root media usually employed. Hence, water stress is a difficult variable to take into account. Special facilities will be required to control shoot and root temperature separately. Care must be taken to allow for different responses from plants of different ages. In naturally-lit glasshouses incoming solar radiation varies with season and can confound results, as can the temperature of the mains water supply if this is not equilibrated to the glasshouse temperature regime.

Where careful procedures are followed the phytotron can, and has, provided useful answers to a range of problems. For example, the growth pattern of *P. caribaea* in the lowland tropics can now be more readily interpreted following studies of shoot growth in controlled environment. A better understanding is also possible of the processes of hardening and root regeneration in *P. radiata* following a series of phytotron trials. A number of factors influencing the growth and natural distribution of eucalypts have been investigated in a similar way, particularly the signifiance of low temperatures. Experimental "plantings" of stumped seedlings in controlled environments has aided in an understanding of the factors which might influence success in the use of this method of plantation establishment in areas where access is difficult and plant transport costly. There appears to be considerable scope for the use of phytotrons in the future, for example in screening planting stock for frost resistance in a search for cold hardy genotypes.

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