THE PROPAGATION OF PINUS RADIATA BY CUTTINGS

Influences Affecting the Rooting of Cuttings

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SYNOPSIS

A review of the literature concerned with the formation of adventitious roots in stem cuttings of Pinus species, with particular attention to P. radiata, shows that many influences interact to control root initiation processes, the number of root primordia that form and the rate at which they develop. In P. radiata, roots are initiated in callus tissue produced at the base of a cutting. Material taken from mature trees can be more difficult to root than that from younger plants, particularly if the parent trees are not healthy and vigorous, but here pre-severance treatments, including hormone applications, can assist. Light and temperature climates are important but their effects have not yet been fully investigated. Physiological ageing is another factor not well understood and is important in that it appears that some measure of rejuvenation can be achieved. It is concluded that further advances in understanding rooting processes will come mainly from the use of modern methods of laboratory investigation, particularly from studies carried out in controlled environments.

INTRODUCTION

This paper surveys present knowledge of the influences which affect the rooting of Pinus radiata cuttings and indicates the nature of research investigations in progress.

Pinus species are generally regarded as being among the more difficult plants to grow from stem cuttings (e.g., Audus, 1953; Hartman and Kester, 1959). However, investigations during the past 35 years by Field (1934), Jacobs (1939), Sherry (1942), Mirov (1944), Pawsey (1950), Fielding (1953, 1954, 1963), Libby and Conkle (1966) and Thulin and Faulds (1968) indicate clearly that cuttings taken from young trees of Pinus radiata, particularly from trees less than 10 years old, are very easy to root. Indeed, Fielding (1963) gives his opinion that P. radiata and its close relatives can be more easily grown from cuttings than any other species of pine that have been investigated. Thulin and Faulds (1968) now present evidence that they are able to root cuttings from trees up to at least 15 years of age without difficulty (cf. Jacobs, 1939; Fielding, 1954). The large-scale establishment of clonal plantations of P. radiata becomes a real possibility.

Workable methods have now been developed for rooting stem cuttings of P. radiata, with such success that this species must now be regarded as an easy species to propagate, but an accurate understanding of the processes of root initiation in cuttings of

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Pinus species is still lacking, and there is still a very incomplete knowledge of the influences that affect these processes. The present state of knowledge is rather as described by Nienstadt et al. (1958):

“The mysteries of root initiation (in cuttings) remain mostly unsolved, especially the limitation imposed by parent tree age. We are aware of the important environmental factors governing rooting but we know extremely little of the internal mechanisms controlling root initiation. . . .”

This represents a state of affairs that is often found in forestry: seedlings can be raised in nurseries using methods that have been developed over the years through trial and error, through practical experience, but very few of the facts upon which these practices are based can be stated: systems of silviculture have been developed in the same way. Because of this, forestry is referred to as an art, when it is (or should be) a science! If this position is to be improved, facts must be established and mechanisms and processes understood. Opinions, beliefs, and faith must be replaced by accurate, factual, rational knowledge.

As far as propagation work is concerned, once processes and influences are well understood, it should be possible to improve techniques considerably, thus enabling work to proceed with more confidence and with greater certainty of success.

PROCESSES OF ROOT INITIATION

In cuttings of P. radiata, as in many other species of pine, new roots usually develop from callus produced at the base of the cutting (Jacobs, 1939; Satoo, 1956; Hoffman and Kummerow, 1966; Cameron, 1966). They appear first as small, white, finger-like protuberances which rapidly lengthen, remain succulent and brittle at first but later shrink, harden and become dark in colour, and give rise to lateral roots.

The rate at which cuttings form roots depends upon both the physiological condition of the cuttings and the environment in which they are placed. Jacobs (1939) and Fielding (1954) find that in Canberra best results are obtained from cuttings taken in April, May, or June, and these commence to form roots in late October or early November, about the same time that terminal buds show active growth. However, cuttings taken in December or early January and set in the open nursery commence to root before winter (Fielding, 1954). Sherry (1942) records that in South Africa cuttings taken and set in August begin to root in November. Rooting takes place over a period of several weeks, even months, and Libby and Conkle (1966) observe that, the longer a cutting sits without rooting, the less likely it is that it will eventually root—i.e., slowness to root is associated with poor rooting capability. Pawsey (1950) gives evidence that early rooting can be a clonal characteristic. Investigations in New Zealand confirm these observations insofar as work under nursery conditions is concerned (Thulin and Faulds, 1968), but in laboratory experiments in which cuttings from seedling plants are given pre-severance treatments (see later) and then set in controlled environments in growth cabinets, the writer has been able to root them in less than five weeks from time of setting, regardless of time of year.
Much attention has been given to the number of roots that cuttings produce but very little is known of the anatomical structure of these organs. Fielding (1954) records wide differences in the type of root system that cuttings produce and associates variations in this with parent tree, rooting medium, and climate. Experimental results presented by Libby and Conkle (1966) indicate that cuttings from old trees generally produce fewer roots; also that, the longer a cutting takes to root, the smaller the number of roots that eventually form. Libby and Conkle were also able to show that a cold treatment of cuttings for a period of 20 to 50 days before setting improves the speed of rooting and increases the number of roots that form on each cutting. A number of investigators (e.g., Melchior, 1963; Ooyama and Toyoshima, 1965; Libby and Conkle, 1966) give evidence that hormone treatments, particularly with a synthetic hormone, indole butyric acid (IBA), also result in the production of more roots per cutting. Libby and Conkle maintain that the number of roots produced does not increase after first initiation but the writer's experiments show that, if roots are removed as they are produced, new roots form, and this process can be repeated many times. Concerning this, it is a well-established fact that actively-elongating roots produce auxins in a concentration which inhibits the initiation of other roots, including lateral roots (Torrey, 1950; Sinnott, 1960). Sherry (1942) states that rooted cuttings form new roots soon after being planted out. It seems likely that this is induced by root-pruning, intended or accidental, during transplanting. Thulin and Faulds (1968) have applied wrenching techniques to produce excellent root systems on cuttings set in open nursery beds, even on cuttings from mature trees.

The “roots” which appear from callus as white, finger-like protuberances do not become fully differentiated as roots until some time after emergence (Cameron, 1966). They do not at first possess a root-cap, root hairs, a regular vascular system, secondary roots, or indeed any of the structures that characterize a normal root. Reines and McAlpine (1955) make a similar observation for root initiation in Pinus taeda cuttings.

FACTORS INFLUENCING ROOT INITIATION

Effects Attributable to Condition of Parent Tree

Fielding (1953, 1954) reports that individual trees of P. radiata, particularly those over 10 years old, exhibit large differences in the ease with which they can be raised from cuttings, a form of behaviour also reported by Duffield and Liddicoet (1949) for a hybrid, P. atenuradita, and by Ooyama and Toyoshima (1965) for P. thunbergii and P. densiflora. These are observations from experiments repeated in successive years so probably represent genetic differences. Thulin and Faulds (1968) find less evidence of clonal differences in rooting ability. Libby and Conkle (1966) compare the rooting ability of cuttings taken from stands of P. radiata throughout its natural range but find no differences that can be correlated with provenance.

A more important influence insofar as practical propagation work is concerned (since individual trees that prove difficult to propagate
for genetic reasons can be discarded at an early age) is the great effect that the age and health of the parent tree have upon the ability of cuttings to form roots. Jacobs (1939), Sherry (1942), Mirov (1944), and Fielding (1954) present evidence that the ease with which cuttings can be rooted decreases as the parent trees age; for example, Fielding gives data from experiments in which success in rooting fell from 88% for cuttings from trees three years old, to 68% at five years, and 11% at 26 years. Libby and Conkle (1966) report smaller differences than this but only compared material from trees up to 17 years old. Observations of the effect that health of the parent material has on the formation of roots are given by Fielding (1954). It appears that unfavourable climatic conditions during the preceding summer can have adverse effects, as can suppression of the parent tree or branch. It seems likely that age of parent tree may be less important than health of tree, and that the rooting ability of cuttings depends, to a large extent, upon the amount of food reserves present (see Libby and Conkle, 1966). The fact that cuttings from old trees have been reported as being difficult to root is possibly because these possess insufficient quantities of stored carbohydrates, proteins, etc., to support metabolic processes during the period of root initiation. Alternatively, it is possible that age effects only become apparent under conditions of nutritional stress. These speculations require experimental investigation.

The size of cuttings does not appear to be critical, nor the depth at which they are set, nor whether they are partly defoliated or not, since different writers describe the use of rather different practices, all with good success (Jacobs, 1939; Fielding, 1954; Libby and Conkle, 1966; Thulin and Faulds, 1968).

Some attention has been paid to the rooting of fascicle bundles, first by Jacobs (1939) and more recently by Matte and Kummerow (1963), Kummerow (1966) and Sievewright (1967). Generally these appear to root less readily than cuttings; many fail to form callus and of those that do some do not form functional roots or commence shoot growth. Kummerow (1966) and Sievewright (1967) find fascicle shoots from mature trees impossible to root, but these experiments are continuing and may yet meet with success.

Pre-severance Treatments

From the published literature, it seems that very little attention has been given to this aspect although the importance, for rooting processes, of the physiological condition of the cutting is generally recognized. For example, Kelley (1965) shows that the daylength under which the stock plants of Ilex crenulata have been grown affects the rooting ability of cuttings. Kummerow (1966) gives some evidence that the rooting of fascicle shoots of P. radiata are similarly affected.

Recent work at this Institute has proceeded on the assumption that a pre-severance conditioning of cuttings, in which branch material is brought to a set and uniform physiological condition, should reduce considerably the difficulties and and uncertainties of rooting cuttings from old trees. This belief is based on the fact that root initiation and root growth are separate morphogenetic processes, and probably each requires different conditions for
the process to proceed at optimum rates. In genera of trees which are easy to root from cuttings, such as *Populus* or *Salix*, root primordia are usually present in the stem as preformed structures at the time cuttings are taken, so that successful rooting depends mainly upon the provision of conditions favourable for root growth (Hartmann and Kester, 1959). In *Pinus* species, however, as in most conifers, the formation of roots in cuttings takes place in two distinct stages, first, root initiation, then root growth—one must precede the other, and there are reasons for believing that the conditions which favour each process may not be the same. It is convenient and useful to consider root initiation and root growth as separate happenings affected in different ways by different controls. Whereas root growth is greatly affected by environmental factors, root initiation is more directly under the control of nutritional, hormonal, and ontogenetic influences (Allen and McComb, 1955; Nienstadt *et al.*, 1958; Hartmann and Kester, 1959; Sinnott, 1960). These aspects have been, or will be individually discussed.

The modified form of air-layering developed by Thulin and Faulds (1968) as a pre-severance treatment was a logical development from previous work. Jacobs (1939) observed that cuttings rooted more easily if the shoots from which they are taken have been partly broken while still attached to the tree, some time before actual removal. This treatment induces callus growth. Although conventional methods of air-layering work quite well with *P. radiata* (e.g., Melchior, 1963) the roots that form are less satisfactory than those that form on cuttings. Reasons for this have been put forward (Cameron, 1968). The success of girdling, as a pre-severance treatment to induce callus formation, is considered to be a combination of nutritional and hormonal effects, since it involves the removal of a band of phloem tissue, thus interrupting the basipetal movement of photosynthates and growth substances which accumulate in the light-shielded zone at the base of the cutting. Meanwhile the intact xylem maintains a supply of water and nutrients to the shoot. There are also other effects, mainly concerned with root/shoot interrelationships (see Kozlowski) and Winget, 1964), but these will not be considered here.

Removal of the terminal buds from cuttings at time of pre-treatment has a considerable effect on root initiation but the nature and magnitude of this varies with season. These are influences which are not completely understood, although the role of buds in regulating tree growth through the production of growth-promoting and growth-inhibiting substances is well established (Sinnott, 1960; Kozlowski, 1962).

**Influence of Light and Temperature**

Very little is known concerning the ways in which light intensity and photoperiod (daylength) or temperature and thermoperiod (relative day and night temperatures) affect processes of root initiation and growth in stem cuttings of *Pinus radiata*. These are aspects which are being investigated at the Forest Research Institute now that the Institute has a number of growth cabinets in which environmental conditions can be closely controlled.

High light intensities, both before severance and after cuttings have been set, should be beneficial through maintenance of high
rates of photosynthesis and hence provision of materials to support metabolic processes; but this does not imply that light is an essential requirement for root initiation. Indeed, there is evidence in literature that to darken shoots, as a pre-severance treatment, could benefit root initiation by mobilizing nitrogen within the shoot (Steward et al., 1959). Conditions of photoperiod should be important in that cuttings set in autumn do not normally begin to callus or form roots until after the spring equinox, even under warm greenhouse conditions. Kummerow (1966) found that fascicle shoots of *Pinus radiata* root best in a 12-hour photoperiod. The writer's own experiments are incomplete, but indicate that long-day conditions (16 or more hours continuous illumination in each 24-hour period) achieved by supplementing natural daylight with low-intensity incandescent lamps, increases not only the rate at which adventitious roots form on stem cuttings, but also the number of roots produced. Cuttings held in the dark, with air temperatures maintained at 5°C and the temperature of the rooting medium at 20–24°C, deteriorate and decay without forming any roots.

High temperatures should increase rates of respiration within plant tissue and hence hasten depletion of food reserves, but low temperatures could be expected to restrict rates of photosynthesis and replenishment of photosynthates. What combinations, then, of root and shoot temperature, or of day and night temperature, are optimal, for these are influences which surely affect root initiation? Should root temperature be kept equal to, or higher or lower than shoot temperature? Ooyama and Toyoshima (1965) obtain improved results from using heated beds to root pine cuttings, while Krugman and Stone (1966) show that thermoperiod (in particular, low night temperatures) has an important effect on the root-regenerating potential of ponderosa pine seedlings. Nielsen and Humphries (1966) review the published work on the effects of root temperature on plant growth, and its modification by light intensity and photoperiod.

The Role of Hormones and Inhibitors

The initiation of roots in stem cuttings is controlled by an interaction of plant hormones and hormone inhibitors (Andus, 1953). These are produced mainly from growing points, such as the terminal bud, or if this is absent, from developing dwarf or fascicle shoots. Jacobs (1939) obtained variable results and only slight improvements from the application of commercial hormones to cuttings but Allsop (1950) in similar experiments obtained a slight increase in rooting. Audus (1953) lists *Pinus* among the plants which are difficult to root from cuttings and in which rooting ability is not stimulated by hormone applications (see also Hartmann and Kester, 1959). Fielding (1954) considers that auxin treatments do not assist in rooting cuttings of *P. radiata*, a point of view with which Thulin and Faulds (1968) are inclined to agree. In contrast with this, experiments reported by Melchior (1963), Libby and Conkle (1966), Hoffman and Kummerow (1966), Kummerow (1966) and Sievewright (1967) show that the use of IBA improves both the rate at which roots form and the number that cuttings eventually produce. The writer's own experiments are,
as yet, rather limited in scope, but indicate that fresh preparations of fully active IBA (1% in hydrous lanoline) have very great effects upon both rates of callus formation and root initiation, not only through morphogenetic effects but also through increasing transport of carbohydrates formed in photosynthesis from needles to the site of root formation at the base of a cutting.

Zimmerman (1963) has investigated the presence of rooting cofactors (substances which interact with, and modify the action of rooting hormones) in several *Pinus* species including *P. radiata*. He distinguishes six different substances and finds that these vary with season, and so explains why cuttings set in winter are easiest to root. Ogasawara (1961, 1962) demonstrates the presence of substances which inhibit the rooting of cuttings in extracts from the foliage of *P. densiflora* and *P. thunbergii*; these increase in abundance as trees age, explaining the observed fact that cuttings from old trees are more difficult to root than those taken from young trees.

There is one other aspect to the use of hormones and other growth regulating substances that can be mentioned here. Fielding (1954) reports that cuttings taken during a period of active shoot elongation show a high rate of failure, presumably due to exhaustion of food reserves. Similarly cuttings will sometimes commence terminal growth before any root initiation has occurred, and such cuttings usually fail. Here there is a possibility, as yet unexplored, that chemicals which function as antigibberellins, and thus restrict shoot elongation, could be applied to cutting beds as a spray to retard shoot growth temporarily. Also, if disbudding becomes a routine operation (as a means of bringing cuttings to a uniform physiological condition before setting) then there is a possibility that chemicals which kill or inhibit terminal meristems without having other effects on shoot growth could be used as sprays as part of a pre-severance treatment (Cathey *et al.*, 1966).

It is concluded, then, that auxins and other growth-regulating substances are important and can affect the rooting of cuttings in a number of ways, but rational use or manipulation of any of these is not yet possible. A first step would be an investigation of natural variation in hormones and growth inhibitors in plant tissue, their variation with season and age of tree, and the effect of these on root initiation.

**Season of Setting and Method of Setting Cuttings**

Jacobs (1939) records that April, May, and June are the best months for setting cuttings in Canberra, for this avoids the hot, dry weather common in February and March. Fielding (1954) agrees, and observes that the poorest results are obtained from cuttings collected during the spring from vigorously growing branches. Most of the other writers have restricted their work to the setting of autumn-collected cuttings (*e.g.*, Mirov, 1944; Pawsey, 1950) but the recent experiments of Thulin and Faulds (1968) include the preparation and setting of cuttings at all times from November to June. The pre-severance treatments they are using appear to eliminate seasonal effects to a considerable extent.

Jacobs also finds that cuttings can be stored for up to a week before setting without harm while Fielding (1954) can store cuttings,
under moist, cold conditions, for up to five months. Libby and Conkle (1966) make a more detailed investigation of the effects of refrigeration and conclude that cold storage for 20 to 50 days may actually be beneficial, increasing the speed of rooting and giving an increase in the number of roots produced by each cutting. The possibility of using cold storage as a post-severance, pre-setting treatment should be investigated further.

Most writers have used whatever facilities they have at hand, or whatever facilities they are familiar with, to handle cuttings of *P. radiata*. Thus, Fielding (1954; 1963) gives recommendations for potting mixtures, tubing procedures, weeding, and watering for the system he has developed for raising cuttings in metal tubes, which suit the conditions prevailing in Canberra, while Thulin and Faulds (1968) find that simpler methods work well in Rotorua. These are hardly physiological problems. Mist sprays are invaluable as a means of reducing the wilting of cuttings set under summer conditions or in a greenhouse and experiments are at present in progress to find out whether particular chemicals reputed to reduce rates of foliar transpiration can be used as sprays or dips to reduce the initial wilting of cuttings (Cameron, unpublished records).

Jacobs (1959) states that cuttings root best if the foliage is left intact and this is also the practice advocated by Fielding (1954) and Thulin and Faulds (pers. comm.). It is unlikely that this is a critical point, for Ooyama and Toyoshima (1965) defoliate the bases of cuttings of other *Pinus* species before setting without any adverse effects becoming apparent. Libby and Conkle (1966) surface-sterilize the bases of cuttings and score them to promote callus formation but whether or not such treatments have any real value is not apparent from their report.

**Rejuvenation**

The nature, significance, and complexity of aging and rejuvenation as physiological processes associated with the vegetative propagation of woody plants cannot be fully discussed here. Jacobs (1939) states that rooted cuttings appear to undergo a degree of rejuvenation and that sometimes primary leaves are produced as well as occasional juvenile buds. Fielding (1954) finds that hedged trees remain physiologically juvenile in that cuttings taken from these root more readily than cuttings from unhedged trees of the same age. Similarly, cuttings from cuttings (*i.e.*, second and third generation clones) are easier to root than cuttings of the same physiological age taken from trees raised from seedlings, and Ooyama and Toyoshima (1965) show that cuttings from second generation trees root more readily than the original cuttings. These appear to be rejuvenation phenomena, but it has already been pointed out (above) that nutritional influences may also be involved.

Observations such as these provide hope that, through the use of cuttings taken from hedged trees, themselves raised from cuttings, any problems encountered in rooting cuttings taken from old trees can be substantially reduced.
THE FACTORS AFFECTING ROOT AND STEM GROWTH IN ROOTED CUTTINGS

The problems of obtaining adequate root growth appear to be small compared with the manifold problems of root initiation. Nor are there any reasons for believing that the general environmental influences which control and modify the root growth of cuttings differ in any way from those required for root growth in seedlings. These are fully discussed by Burström (1954) and Kramer and Kozlowski (1960, pp. 428-536).

One aspect, however, that merits special mention, is the effect of root wrenching. This has been discussed but is of such importance that it bears repetition. Whereas Jacobs (1939) and Fielding (1954) report that cuttings from old trees produce only a few long straggling roots, which results in a check in growth for one or two years after cuttings have rooted, regular and severe wrenching of nursery-set cuttings induces excellent root systems within the first growing season after setting, even in cuttings from old trees (Thulin and Faulds, 1968).

As far as shoot growth is concerned, terminal cuttings (set with terminal buds intact) exhibit growth patterns closely resembling those of grafts (adult scions grafted on to seedling stocks). The needles produced during the first growing season, however, are generally much shorter and more rigid than those of grafts. Where the cuttings are subterminal in origin, or where the terminal buds have been removed, abnormal shoot growth patterns may result. If lateral buds are present, these take over and then subsequent shoot growth more or less resembles that of normal cuttings with intact terminal buds, but if the cutting possesses no formed buds then no shoot growth can occur until one or more of the fascicle bundles near the tip of the cutting develop as actively growing shoots. Often this does not happen until near the end of the first growing season, and in some cuttings, particularly those taken from old trees, fascicle shoots fail to form and the cuttings become blind and moribund (Fielding, 1954). The full effects of disbudding on the shoot growth of cuttings have not yet been fully determined, nor has it yet been ascertained whether or not the adverse effects of disbudding can be overcome by applications of hormones or other growth-regulating substances, so promoting the developing of fascicle buds.

LABORATORY METHODS OF INVESTIGATION

Most investigations that have been reported of the rooting of P. radiata cuttings are nursery or greenhouse experiments and consist mainly of evaluating the effects of particular treatments. The main exceptions are the studies of Zimmerman (1963) in which an assessment was made of growth-regulating substances within the plant, of Hoffman and Kummerow (1966), and Cameron (1966; 1968) in which anatomical studies were made of root initiation in cuttings, and of Kummerow (1966) in which controlled environments were used to investigate the rooting of fascicle shoots. Future advances in knowledge will mainly come from investigations of causal mechanisms.

The writer wishes to give particular emphasis to the value of experiments in controlled environments. A full investigation of
the effects of light intensity, photoperiod, temperature, and thermoperiod (see earlier) could be completed in a relatively short space of time, and, this accomplished, prescriptions could then be given for the conditions under which cuttings should be set to favour root initiation. Extended experiments should make it possible to define the effect of environmental conditions upon the separate processes of root initiation and root growth, as well as establish facts on which to base any preconditioning treatments before cuttings are severed from the parent tree. Investigations of this kind have been commenced in the Forest Research Institute laboratories, in growth cabinets which provide full control of the factors listed above, and also in controlled-temperature glasshouses.

A second line of investigation which will be commenced as soon as suitable instrumentation becomes available, probably early in 1968, is a full and detailed study of the physiological changes that take place in cuttings from time of actual severance, through the period of root initiation, until the cuttings are fully rooted. Satoo (1956) shows that in cuttings of conifers severance causes rates of photosynthesis and transpiration to fall to low levels but these rise again as callus forms. Yusufow et al. (1965) record changes in chlorophyll content, starches, vitamins, etc., in cuttings; these all fall after severance but increase again as cuttings root. Similar studies for *P. radiata*, in which such things as photosynthesis, respiration, translocation, transpiration, changes in pigmentation, and variation in food reserves are measured, would provide an understanding of the internal changes that accompany root initiation. Once these are understood, it should be possible to modify the conditions under which cuttings are taken and set to accommodate these processes.

Another subject that requires investigation under laboratory conditions is the variation in the complex of substances in the plant that regulate growth and development—auxins, gibberellins, cytokinins—and their interaction with co-factors and inhibitors. A preliminary inquiry has already been commenced into the presence and activity of substances which function to inhibit root initiation, and the variation in the amount of these with age of tree and season. This study will be extended as staff, equipment, and laboratory space permit, to cover other aspects.

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