SOME FACTORS WHICH MAY INFLUENCE ROOT FORMATION IN CONIFER CUTTINGS

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ABSTRACT

Seasonal fluctuations in adventitious root formation capacity of cuttings of Juniperus virginiana L. 'Skyrocket' ("easy-to-root") and J. scopulorum Sarg. 'Pathfinder' ("difficult-to-root"), as indicated by three parameters, was determined over a nine month period from late summer (February) until spring (October). Rootability rose from a low or moderate level in late summer to an optimum in mid winter after an intervening period of low potential and diminished again in spring. A less comprehensive study of Cupressus sempervirens L. 'Swane's Golden' ("easy-to-root") revealed that rootability was high in February and June but low in March. The most marked difference in the pattern of seasonal changes between the two juniper cultivars occurred in the percentage of cuttings rooted, which increased dramatically in J. virginiana 'Skyrocket' in April and remained at high levels before declining sharply in October but remained low in cuttings of J. scopulorum 'Pathfinder' until the optimum was attained suddenly in June and diminished thereafter. Generally more gradual changes occurred in the other parameters.

Air temperature treatments of the stock plants and cuttings induced significant differences in level of rooting achieved in cuttings taken in mid winter. Material of J. virginiana 'Skyrocket' and J. scopulorum 'Pathfinder' from stock plants which had received normal winter chilling had a greater root regeneration potential than

that from plants maintained in a heated glasshouse since autumn. The converse was true for cuttings of J. scopulorum 'Blue Haven' ("very difficult-to-root") and C. sempervirens 'Swane's Golden'. The effect of cutting environment was rather more variable but material which had been exposed to the most favourable parent environment tended to root in greatest numbers in an unheated compared with a heated air environment. Responses of J. scopulorum 'Pathfinder' and C. sempervirens 'Swane's Golden' under controlled environment growth cabinet conditions confirmed these results. The attainment of a high rooting percentage in cuttings of J. scopulorum 'Pathfinder' in mid winter appeared to be dependent to a large extent on exposure of the stock plants to low temperatures. Results from the seasonal study generally coincided with the commonly held opinion that phase of growth may be an important determinant of root formation potential in narrow-leaved evergreens. It was suggested that the promotion of rooting in chilled material of J. virginiana 'Skyrocket' and J. scopulorum 'Pathfinder' may have been associated with the stimulation of shoot activity brought about by that treatment but there was no conclusive evidence to support this.

Analysis of endogenous growth regulator content was conducted in material from different cultivars, temperature treatments and harvest dates. Level of an IAA-like growth promoter seemed to be the least related to differences in rootability. Estimated ABA and total cytokinin content appeared to be inversely related to rootability in several instances.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF PLATES

Abbreviations

Mid Winter Study

Parent Material Treatments.

WP = "warm parent" = parent plant held in a heated glasshouse (18°C) from autumn

WCP = "warm+cold parent" = as for WP plus two weeks winter chilling prior to excision

CP = "cold parent" = parent plant exposed to normal winter chilling

CCP = "cold+cold parent" = as for CP plus two weeks cool-st rage (5°C) of cutting material

Cutting Treatments

WH = "warm propagation house" = cuttings propagated in a heated glasshouse (18°C) over basal heat

CH = "cold propagation house" = cuttings propagated in an unheated glasshouse (approx. 13°C) over basal heat

Growth Cabinet Study

Parent Material Treatments

WP = "warm parent" = parent plants maintained in a warm environment (20°C)

CP = "cold parent" = parent plants maintained in a cold environment (10°C)

Cutting Treatments

WH = "warm propagation house" = cuttings propagated in a warm environment (18°C) over basal heat

CH = "cold propagation house" = cuttings propagated in a cold environment (12°C) over basal heat

CHAPTER 1

INTRODUCTION

1.1 Introduction to the Present Investigation

A vegetative means of propagating certain plants is frequently desirable or necessary and for this purpose the use of stem cuttings is normally the preferred and certainly the most extensively applied method. The utilization of this important means of propagation is often seriously hampered however by a low ability of cuttings of many species to form adventitious roots or by large variations in this ability.

Most species exhibit a degree of seasonal variation in their capacity to root from cuttings and root initiation potential of conifers is often greatly influenced by factors associated with season or state of growth. Adventitious root formation is a complex phenonmenon involving interactions of many environmental and endogenous factors not yet clearly understood although such an understanding could be of great assistance in overcoming some of the difficulties encountered in practice. Research conducted at the New Zealand Nursery Research Centre, Palmerston North, indicated that air temperature at both the stock plant and cutting stages may significantly affect rooting of certain conifer species. The present study was therefore undertaken to investigate:

i) seasonal fluctuations in root formation ability,

ii) the effects of air temperature at the parent material and cutting stages on rooting of the cuttings,

iii) levels of certain endogenous growth regulators in relation to capacity to form roots

in easy- and difficult-to-root conifers and to determine possible relationships between these.

1.2 Description of the Cultivars

Four cultivars were used in the study: Juniperus virginiana L. 'Skyrocket' syn J. scopulorum Sarg. 'Skyrocket' ("easy-to-root"); J. scopulorum Sarg. 'Pathfinder' syn J. virginiana L. 'Pathfinder' ("difficult-to-root"); J. scopulorum Sarg. 'Blue Haven' syn 'Blue Heaven' ("very difficult-to-root"); Cupressus sempervirens L. 'Swane's Golden' ("easy-to-root").

The junipers form a very large and important genus from which which a great many cultivars are derived. J. virginiana (eastern red cedar or pencil cedar) and J. scopulorum (Rocky Mountain juniper) are native to eastern and western North America respectively. Identification of these genetically diverse species is difficult and many hybrids occur between these and other species. The two species are closely allied and some authors believe that J. scopulorum may be only a subspecies of J. virginiana. Although both have given rise to many highly valued ornamental cultivars, these hardy species

are of commercial value in other respects. J. virginiana for instance is used in its country of origin for timber, essential oils and windbreaks, and ultimately forms a large tree. (Bailey, 1928; Haverbeke and Read, 1976).
J. virginiana 'Skyrocket' is of a very narrow, columnar growth habit, with grey-green foliage and has a rather fast rate of growth in comparison with most junipers.
J. scopulorum 'Pathfinder' and J. scopulorum 'Blue Haven' have blue-grey foliage and are of upright, pyramidal growth habit. All have predominantly scale-like leaves although foliage of juvenile, more open appearance is commonly found scattered throughout the plant. A height of approximately 2 - 2.5 m is reached after ten years. Propagation is normally from cuttings except in J. scopuloum 'Blue Haven' which is reported to be grafted in most instances (Harrison, 1975; Bloom, 1972; Proudley, 1977).

The cypresses are valued ornamentals in mild climates and C. sempervirens (Italian cypress), as the common name indicates, originates from southern Europe. C. sempervirens 'Swane's Golden' is a slow growing yellow-gold form of narrow, columnar growth habit and is normally propagated by cuttings. (Harrison, 1975; Proudley, 1977).

CHAPTER 2

REVIEW OF LITERATURE

2.1 Seasonal Fluctuations in Rooting Capacity

Many, if not all, woody species exhibit seasonal fluctuations in their capacity to root from cuttings. The timing of taking cuttings to coincide with their maximum rooting potential can be critical for successful adventitious root formation.

Hardwood cuttings of pip and stone fruit trees generally root moderately well in autumn, after which rooting capacity falls to a low level in midwinter and then rises rapidly in late winter and spring (e.g. Howard, 1966; Tustin, 1976; Bassuk and Howard, 1980). Rooting potential of 'Old Home' pear hardwood cuttings followed the potential of the buds to sprout (Fadl and Hartmann, 1967a) although seasonal rooting response of neither plum (Howard, 1968) nor apple (Swingle, 1929; Bassuk and Howard, 1980) was substantially altered by disbudding. Late winter to early spring was also a better period than late fall or early winter to take hardwood cuttings of Loniceria morrowi, Ligustrum vulgare and Cornus alba (Chadwick, 1931). High levels of rooting potential may exist in softwood material during summer as reported for pip and stone fruit species (e.g. Hartmann et al, 1963; Bush, 1978). Poor rooting has been reported to coincide with periods of rapid shoot growth and flower or fruit production

as in Populus (Nanda and Anand, 1970), Ficus (Anand and Heberlein, 1975) and blueberry (O'Rouke, 1940).

Endogenous factors, changes in which have been associated with seasonal variations in rooting capacity include: auxin content in Salix (Vieitez and Pena, 1968), and in Populus (Smith and Wareing, 1972a, b); the level or mobilization of carbohydrates in Populus (Nanda and Anand, 1970) and Macadamia (Cormack and Bate, 1976); ratio of growth promoters to inhibitors in Vitis (Spiegel, 1955) and cofactor activity in pear (Fadl and Hartmann, 1967a, b, c) and apple rootstock (Bassuk and Howard, 1979, 1980). However the causality of these associations has not been clearly established and their relative importance may vary with species and time of year.

The success of rooting cuttings of most narrow-leaved evergreens appears to be heavily dependent on the season or phase of growth. Optimum rootability is normally attained in winter or early spring prior to or during bud break.

Rooting capacity of Douglas fir (Pseudotsuga menziesii) cuttings varied inversely with bud dormancy, being moderate prior to and lowest during deepest dormancy reached quickly in autumn. Rooting then rose sharply in late winter and spring with emergence from dormancy. Low temperature or auxin treatments failed to stimulate rooting until deepest dormancy had passed (Roberts and Fuchigami, 1973; Roberts et al, 1974; Brix, 1974). Optimum rootabilty of Picea abies was also attained about the time of bud break (Girouard, 1975). Maximum rooting of common juniper (Juniperus communis) and savin (J. sabina) propagated in cold climatic conditions occurred during spring, commencing with "the onset of physical

processes" until "the onset of intensive shoot growth". In a milder climate in which deep dormancy was reportedly not attained, conifers could be propagated almost all year round although the optimum still occurred in spring during bud swelling or, in members of the Cupressaeae, even after the commencement of shoot growth (Ivanova, 1979).

Gordienko et al (1976) also demonstrated that cuttings of savin rooted in greatest numbers in early fall or for a brief period during spring. These were periods in which the root system of the parent plant was more active than the shoot system and endogenous growth promoters predominated over inhibitors in both. Activity of an IAA-like promoter fluctuated seasonally in a manner similar to rooting capacity. Lathrop and Mecklenburg (1971) considered that the seasonal changes in root regeneration potential by cuttings and transplants of Taxus hunnelwelliana appeared to be controlled by the same factors and could partially be explained by root dormancy and/or shoot competition for photosynthates. Rooting potential increased during autumn and winter to a peak in winter and then diminished to a low level in summer. According to Wareing (1970), the roots of many conifers do not seem to show any regular dormancy phase but continue to grow in winter whenever temperatures are suitable. It was noted that the degree to which the shoot is modified at certain times of the year differs between species and that cypresses for instance do not form distinct resting buds. Response to environmental factors also varies with species and geographical race. Shoot growth and root initiation and development apparently continues throughout the summer in some species whereas in others shoot growth occurs in flushes during which rooting is often inhibited. Wareing

(1970) attributed the inverse relationship between shoot and root development to competition between the two systems for photosynthates.

Rooting percentage and root number of Juniperus horizontalis 'Plumosa' and Taxus cuspidata 'Nana' cuttings were highest from early winter to spring. Changes in rootability could not be related to cofactor content of the juniper. Seasonal rooting response was thought to be inversely related to shoot activity and it was suggested that an additional peak during summer, especially pronounced in rooting percentage, may have occurred during a period of summer dormancy which is frequently encountered in evergreen species (Lanphear and Meahl, 1963). However the results obtained by Gordienko et al (1976) showed that although the rooting capacity of savin cuttings had begun to increase again during summer dormancy a peak was not attained until early autumn. The hypothesis of Lanphear and Meahl (1963) that rooting is directly or indirectly associated with growth phase is further supported by the influence of daylength, temperature and IBA (indole butyric acid) treatment on shoot activity and rooting (Lanphear and Meahl, 1961, 1963, 1966). That optimum rootability of Juniperus species generally occurs at some time from early winter to spring is confirmed by Klein (1931), Chadwick and Kiplinger (1938), Hall (1977) and Gil-Albert and Boix, 1978).

Rooting of Chamaecyparis pisifera was greater during summer dormancy than in spring (Gil-Albert and Boix, 1978) although Thomsen (1978) reported Chamaecyparis to root well at any time of year. Sanders (1970) reported that Chamaecyparis, Juniperus and Thuja were propagated commer-

cially in mid to late summer by soft tip cuttings which rooted rapidly, but more commonly in autumn and sometimes later from semi-mature or mature side shoots. Cuttings of Pinus strobus were reported to root most readily during spring and summer with a consistent peak in midsummer while buds were rapidly elongating (Kiang et al, 1974) (c.f. Hartmann and Kester, 1968).

Few authors other than Lanphear and Meahl (1963) and Gordienko et al (1976) have endeavoured to establish possible causal relationships between endogenous factors and rooting capacity of coniferous species. Tognoni et al (1977) demonstrated that the rooting percentage of Picea glauca, which was low in autumn and winter and rose sharply in spring, could be at least partially related to the of a water-soluble rooting promoter. The activity of an acidic root-promoting growth inhibitory fraction as indicated by the mung bean bioassay, the major component of which was apparently ABA (abscisic acid), was considered to show no relationship to rooting but did appear to be inversely related to rooting to a certain extent. Waxman(1978) found that rooting percentage of the difficult-to-root Sciadopitys verticillata was highest in spring and late summer and showed a significant negative correlation with resin exudate.

Although auxin application can considerably enhance rootability this effect is often limited to certain times of the year and does not necessarily substantially alter seasonal rooting periodicity (e.g. Roberts and Fuchigami, 1973). Auxin application may even accentuate the rooting pattern as demonstrated with Juniperus horizontalis 'Plumosa' (Lanphear and Meahl, 1963).

2.2 Environmental Factors Influencing Root Formation

2.2.1 Photoperiod

Photoperiod is known to influence many plant processes (e.g. Vince-Prue, 1977) and is one of the most studied environmental factors in relation to seasonal variation in rooting capacity of cuttings.

In most woody species short days induce dormancy whereas long days promote extension growth. Wareing and Smith (1963) proposed that photoperiod might influence root formation either via an effect on shoot activity or by a direct effect of altered hormone production operating independently of shoot growth.

Long-day treatment of Cornus florida stock plants (Waxman, 1957) and Populus canadensis stock plants and cuttings (Kelly, 1965) enhanced rooting capacity. Rooting percentage and root number in leafy Populus x robusta cuttings were also higher under long than short days and were related in a positive manner to concentration of an IAA (indoleacetic acid) -like factor in the cutting bases rather than the state of apical growth (Smith and Wareing, 1972b). Short days also inhibited root formation (number and length) and enhanced bud formation by Begonia leaf cutting whereas long days had the opposite effect (Heide, 1967). The short-day treatment also decreased auxin and gibberellin-like activity (Heide, 1967) and increased cytokinin activity in leaf extracts (Heide and Skoog, 1967) in comparison with long days. The magnitude of decrease of the auxin: cytokinin ratio was considered ample to induce a change in

the regeneration ability of the leaves. The response to daylength was sufficient to account for at least part of the seasonal variation in regeneration of Begonia (Heide, 1967).

However, of 26 woody species studied, Baker and Link (1963) found few that responded to extended photoperiod and then only when overall rooting was poor due to the use of hardwood material or lack of IBA treatment. Cameron and Rook (1974) also reached the tentative conclusion that daylength had little effect on rooting Pinus radiata although Whitehill and Schwabe (1975) found Pinus sylvestris stock plants grown under short days in late summer and autumn provided a higher percentage of rooted cuttings than plants under natural or extended daylengths. Extended daylengths maintained the plants in continuous growth and was most detrimental to subsequent rootability. Exposure of Ilex crenata parent plants to short days during the growing season enhanced primary root number and root growth of cuttings whereas long-day treatment of cuttings improved the number of secondary roots and root length in comparison with the opposing treatments (Kelly, 1965).

Smith and Wareing (1972b) noted that in general, deciduous woody angiosperms responded favourably to long days whereas if narrow-leaved evergreens responded at all, short days were more benificial to rooting. Although the former may be supported to some extent by references already mentioned, the response of narrow-leaved evergreens appears to vary with species and stage of growth and may be largely associated with growth response.

Autumn cuttings of X Cupressocyparis leylandii receiving

extended photoperiods quickly produced new tip growth and rooted whereas the controls remained dormant and failed to root. Sanders (1970) postulated that meristematic activity, stimulated by long days, initiated production of root-inducing substances in thas species but that successful rooting is able to occur in the absence of a visibly growing meristem in other species in which temperature may be a complicating factor. Similarly, Pseudotsuga menziesii cuttings propagated in autumn and winter under 18 hour compared with 9 hour photoperiods showed significantly higher cambial activity, bud respiration, rooting percentage and quality and hastened bud break. The effect of photoperiod was rather less marked during early dormancy (Roberts et al, 1974). Long days extended the peak rooting period of P. menziesii to a month earlier and substituted in whole or in part for the chilling required to break bud dormancy (Bhella and Roberts, 1974). Lanphear and Meahl (1961) found that extended photoperiods stimulated rooting of Juniperus horizontalis 'Plumosa' to a significant extent and enhanced shoot activity in autumn but had the opposite effect on rooting of cuttings taken in late winter. Other species showed little response to long days other than improved rooting quality in a few species in autumn and enhanced bud activity, although Juniperus chinensis 'Glauca' and Taxus cuspidata 'Nana' also rooted more poorly under this treatment in late winter. IBA application counteracted the effects of long days on bud break and rooting in late winter, an action previously noted by Snyder (1955). Lanphear and Meahl (1963) were able to confirm the effect of photoperiod on rooting of the Taxus sp. but not J. horizontalis 'Plumosa'. In a later trial it was shown

that extended or natural photoperiods at the stock plant or cutting stages inhibited rooting of the juniper during early spring if shoot growth was initiated under these photoperiods, a response involving an interaction with parent plant temperature treatment (Lanphear and Meahl, 1966).

Snyder (1955) reported that although photoperiod did not have a significant effect on root formation by Taxus cuspidata cuttings, subsequent growth of rooted cuttings was superior in those which had made little shoot growth on the propagation bench, as in those under short days. The reduction in shoot growth and thereby less competition for photosynthates was suggested to be the cause of enhanced root growth of Populus cuttings under short days (Eliasson, 1971).

2.2.2 Light Intensity and Quality

Root formation by cuttings is commonly influenced by the level of irradiance to which the parent plant or cuttings are exposed. The portion of the cutting or intended cutting illuminated can have a profound effect on the response elicited.

High levels of irradiance of the stock plant or cutting is frequently reported to supress rooting. Hansen and Eriksen (1974) suggested this phenomenon, as demonstrated with stock plants of Pisum sativum, to be the result of a supraoptimal carbohydrate content in relation to endogenous auxin level due to enhanced photosynthesis. Carbohydrate levels were found to increase and rootability

to decrease with increased levels of irradiance given to Pelargonium x hortorum stock plants (Welander, 1978) and stock plants, and to a lesser degree, cuttings of Pinus sylvestris (Hansen et al, 1978). That the effect of irradiance may be influenced by carbohydrate reserves was considered to be demonstrated by cotyledon removal in pea stock plants which then responded favourably to higher light intensities. The results did not support the supraoptimal carbohydrate theory however (Veierskov et al, 1976).

The benificial effect of exposure of excised pea cutting to high light intensity was suggested by Eliasson (1978) to be due to the depletion of nutrient reserves under low light by the rapid shoot growth made by these cuttings. This response contrasted with that reported previously in Pinus sylvestris cuttings (Hansen et al, 1978) which were considered to have relatively large nutrient reserves.

Greater rates of transpiration and water stress have also been implicated in the effects on rooting of high intensity light treatment of pea stock plants (Rajagopal and Andersen, 1980) and cuttings (Eliasson, 1978).

Low light intensity or shading may be regarded as partial etiolation and have a detrimental effect in regard to application to the leaves (e.g. Kawase, 1965) but a benificial effect directly on the stem, particulaly at the site of root initiation (e.g. Kawase, 1965; Frolich, 1961; Biran and Halevy, 1773a). Etiolation also stimulates the emergence of pre-formed roots (e.g. Shapiro, 1958).

The promotory effect of etiolation at the stock plant stage has been variously associated with, for example, a reduction in tissue differentiation and mechanical

strengthening in Hibiscus rosa-sinensis and red kidney bean (Herman and Hess, 1963), greater retention of auxin in treated tissue of Phaseolus aureus (Kawase, 1965) and greater starch concentration in apple rootstocks (Doud and Carlson, 1972). Delargy and Wright (1978, 1979) proposed that a rooting promoter synthesised in the upper, non-etiolated portion of apple shoots accumulated and increased in activity in the etiolated tissue. Shading of Hibiscus rosa-sinensis stock plants was replaceble by ethephon pre-treatment of the parent plant or IBA application to the cuttings (Johnson and Hamilton, 1977) but auxin application was required for promotion of rooting by low light treatment of apple rootstock parent plants (Christian et al, 1980). The promotory effect of etiolation of an initial flush of growth in apple was maintained to a certain extent in a second, unetiolated flush (Harrison-Murray and Howard, 1980).

As with the stock plant effects, little is known of the inhibitory effects involved in the dramatic reduction in rooting brought about by exposure of the basal portion of the cutting to light during root formation, as demonstrated in Picea abies (Stromquist and Eliasson, 1979). Eliasson (1980) foung auxin application to counteract the negative effect of basal illumination on root number in pea cuttings and hypothesised that light prevents the action of endogenous auxin or low levels of exogenous IAA in root formation but that IBA remains fully active.

The effects of the different components of illumination are not always clearly distinguishable. Loach and Whalley (1978) for instance found the rooting percentage of several

species to increase sharply with increasing mean daily radiation to an optimum of 1.5 $MJ.m^{-2}$. Chadwick (1949) found rooting of several narrow-leaved evergreens to be better under natural than fluorescent light and light colour to influence rooting. Stoutmyer and Close (1946) reported that radiation from the orange-red end of the spectrum appeared to promote rooting of cuttings.

2.2.3 Temperature

The effect of air temperature on rooting may be exerted via the parent plant, during the rooting phase or during an intermediate period of controlled-temperature storage. In addition, cuttings set under glass are usually provided with basal heat.

Spiegel (1955) found that high auxin and low inhibitor levels were associated with ease of root formation in cuttings of Vitis hybrids and that the disappearance of growth inhibitory activity was hastened by cold treatment. It was proposed that in many instances the termination of dormancy by cold may be a prerequisite for an auxin:inhibitor balance favourable to rooting. Chilling the whole cutting or the upper portion while over basal heat stimulated rooting and bud activity, reduced rooting inhibitor levels and increased rooting promoter content in the basal segments of hardwood cuttings of the difficult-to-root 'Bartlett' pear. This treatment was considered to affect rooting by altering growth regulator production by the buds (Fadl and Hartmann, 1967a, b). However a period of warm storage was more

satisfactory for the easily rooted 'Old Home' pear and was associated with the production of a rooting cofactor by the active buds. Stimulation of rooting of hardwood cuttings of Populus x robusta by coolstorage was pronounced only if buds were present and slightly different temperature treatments were required for production of maximum root number and length compared with rooting percentage. Auxin content was greatest in chilled cuttings (Smith and Wareing, 1972a). A pre-propagation heat treatment of 35°C for 18 hours enhanced ethylene production by apple rootstock cuttings (Harrison-Murray et al, 1980) and increased rooting percentage of two of the three clones tested (Howard and Babnik, 1980).

Air temperatures may be manipulated during storage to discourage shoot growth preceding root development. An initial period of warm temperature storage of Cornus and Loniceria hardwood cuttings taken in autumn improved rootability over those receiving only low temperatures, possibly by allowing healing and root development before the rest-breaking chilling period (Chadwick, 1931). Cheffins (1975) recommended that cool air temperatures be provided during root induction of hardwood cuttings in heated bins so as to minimize bud activity, which was found to constitute a drain on carbohydrate reserves and was associated with low levels of cutting establishment.

Leaves from Begonia mother plants grown under high temperatures possessed a lower budding ability and a higher rooting potential than those from plants under lower temperatures. IAA level increased but gibberellin-like activity was affected little by the higher temperature (Heide, 1967).

A high temperature also antagonised the influence of cytokinins in promotion of bud formation and inhibition of rooting and enhanced the auxin effects (Heide and Skoog, 1967). These results supported the hypothesis of Heide (1964) that environmental effects on regeneration potential might be mediated by changes in the ratio of endogenous auxins to cytokinins.

It would appear from the stimulation of rooting associated with coolstorage of hardwood cuttings (e.g. Spiegel, 1955; Fadl and Hartmann, 1967a, b; Wareing, 1972a) that winter chilling received by the stock plant might have an integral role in the increased rootability commonly detected in spring (e.g. Howard, 1966; Tustin, 1976; Chadwick, 1931). However despite marked differences in ambient air and soil temperatures, the seasonal fluctuations in rootability of cuttings from apple rootstock M.26 hedge plants kept under heated polythene from late autumn were largely similar to those found in the controls (Howard and Harrison-Murray, 1980). The effect of chilling may however be of greater importance in other species.

Cold storage of Pseudotsuga menziesii cuttings removed dormancy and significantly increased rooting percentage only of those excised in autumn. The attainment of a critical stage of dormancy appeared to be necessary to enable low temperatures to stimulate rooting, with little benificial effect prior to this during deepest dormancy or later when presumably sufficient natural winter chilling had been received. Maximum rooting required substantially less chilling than did rapid bud burst (Roberts and Fuchigami, 1973; Roberts et al, 1974).

Cuttings of Juniperus horizontalis 'Plumosa' taken in early spring from stock plants held warm conditions for four months after autumn had a slightly higher rooting precentage and significantly higher root number than those from plants held outdoors. Cofactor activity in only one Rf zone was higher in the "warm" compared with the "chilled" material. Cuttings taken in early spring had received more winter chilling prior to being held in a glasshouse and had a lower rooting capacity than those excised earlier. The "chilled" material excised in spring also responded to natural and extended daylengths by producing new shoot growth and rooting significantly less well than under short days, unlike that excised in the preceding month. Lanphear and Meahl (1966) hence proposed that stage of dormancy rather than chilling period per se was the prerequisite for increased rooting capacity and restated a previous conlusion (Lanphear and Meahl, 1963) that factors which encourage a dormant state enhance rooting and those which stimulate active growth inhibit rooting.

Tustin (1977a) reported that cuttings of Juniperus virginiana 'Skyrocket' and J. virginiana 'Pathfinder' propagated in midwinter from plants sujected to normal winter chilling rooted in greater numbers than those from plants kept in a heated glasshouse from early autumn. The converse was true for Cupressus sempervirens 'Swanes Golden'. Intermediate levels of rootability were obtained from plants held in the warm environment which had received two weeks of chilling prior to cutting excision. Rooting of the juniper cuttings was best under cool air temperatures

and rooting of the cypress best in a warm environment.

The highest rooting percentage of interfascicular shoot cuttings of Pinus sylvestris was obtained from dormant plants which had been subjected to short days followed by low temperatures. Coldstorage of the cuttings enhanced rooting of all material including that from actively growing plants which otherwise failed to root. Percent bud burst and rooting potential increased with duration of parent plant cold storage to an optimum of four months. The stock plant state of growth was considered to be the primary determinant of rooting capacity, with bud break but not active shoot growth associated with ease of rooting (Whitehill and Schwabe, 1975).

Seasonal fluctuations in root regeneration potential in cuttings and transplants of Taxus hunnewelliana were reported to be partially determined by root dormancy. The low temperatures needed to break root dormancy appeared to be sensed primarily by the root system and although chilling the shoot system increased later growth of the roots it did not substitute for root chilling (Lathrop and Mecklenburg, 1971). Wareing (1970) reported that root regeneration proceeded much more readily in transplants of certain coniferous species subjected to winter chilling prior to transfer to warm conditions.

Although Pinus radiata cuttings rooted more quickly under a high day/night temperature regime they remained more healthy at lower temperatures, the highest proportion of cuttings eventually rooted being obtained under an intermediate regime of 20/10°C. The lowest night temperature (5°C) was benificial under conditions of water stress

irrespective of day temperature. Air and basal temperatures were essentially the same (Cameron and Rook, 1974). According to Hartmann and Kester (1968) daytime air temperatures of 21 to 27°C and a night temperature of 15°C are satisfactory for rooting cuttings of most species but recommended an initial day temperature of 15°C for Juniperus species.

An elevated temperature at the cutting base can enhance rooting percentage and quality and increase speed of root formation (e.g. Laurie and Stillings, 1949; Poole and Waters, 1971; Brix, 1974). A higher basal than air temperature is often employed at least partially to encourage development of the root system ahead of the shoot system (e.g. Hartmann and Kester, 1968; Cheffins, 1975). Optimum basal temperatures may vary with variety (e.g. Howard and Nahlawi, 1969) or season (e.g. Bhella and Roberts, 1974) but are generally accepted to be in the range of 20 to 25°C (Hartmann and Kester, 1968). The optimum temperature for root elongation may be lower than that for initiation as demonstrated with Chrysanthemum cuttings (Dykeman, 1976).

2.2.4 Moisture

The maintenance of tugidity in cutting material throughout the propagation process is an important factor in the attainment of optimum rooting capacity. All parameters were reduced at low leaf water potentials in cuttings of Rhododendron, Ceonathus and Hebe (Loach, 1977). Whalley

and Loach (1978) confirmed that rooting percentage of Hebe 'Caledonia' decreased with mean leaf water potential. The formation of a significantly greater cutting root number followed a brief period of water stress in Pisum sativum stock plants but prolonged stress induced the opposite effect (Rajagopal and Anderson, 1980b).

Transpiration may be reduced by humidification, misting or application of an antitranspirant coating (e.g. Hartmann et al, 1963; Loach, 1977; Loach and Whalley, 1978; Blain and Dudney, 1978). ABA application reduced water loss and enhanced root growth in Chrysanthemum cuttings (Orton, 1979). Cameron and Rook (1974) reported that the major routes of water uptake in conifer cuttings appeared to be through the cut basal surface and via foliage in contact with the rooting medium.

Wunder (1974) considered that the dominant factor in rooting of Larix leptolepis cuttings was the maintenance of a "relative moisture optimum" in the propagation chamber above which promotion of rooting was lost. Ivanova (1979) reported that cuttings of coniferous species are very sensitive to waterlogging. Most conifers rooted poorly under conditions of constant high humidity (90 - 100%) but otherwise did well under artificial fog. The effects of excessive moisture level in the rooting medium may be partially related to a lack of oxygen at the cutting base (e.g. Zimmerman, 1930; Kordon, 1976).

In addition to enhancing water status (e.g. Cameron and Rook, 1974), natural precipitation or misting of stock plants or cuttings can also influence levels of nutrients, growth regulators and other endogenous factors through

leaching or temperature effects. The improvement in rooting of misted compared with non-misted cuttings of Euonymus alatus 'Compactus' appeared to have been brought about by a delayed induction of dormancy due to leaching of ABA. Content of carbohydrates, certain enzymes and phenolics, C/N ratio and auxin-like activity was also greater in material from misted stock plants (Hemphill and Tukey, 1973; Tukey, 1978). Rutin application replaced the promotional effect of stock plant mist treatment (Lee and Tukey, 1971).

2.3 Other Factors Related to the Selection and Treatment of Material

2.3.1 Juvenility

Distinct juvenile and adult phases occur in seedling plants of most species and maturation or ontogenetical aging is normally accompanied by a sharp decline in the capacity to form adventitious roots. The most juvenile material is found in the lowermost, axial region of the stock plant (e.g. Schaffalitzky de Muckadell, 1954; Zimmerman, 1972; Armson et al, 1975; Kester, 1976).

The changes induced during transition to the adult phase are stable and not normally easily reversed. However rejuvenation or maintenance of the juvenile state and high level of rootability can sometimes be achieved for instance by hard pruning or hedging (e.g. Libby and Hood, 1976) or grafting onto juvenile rootstocks as demonstrated in Hevea brasiliensis (Muzik and Cruzado, 1958) and Psuedotsuga

menziesii (Brix, 1974).

The greater rooting capacity of juvenile material has variously been associated with lower rooting inhibitor content in Populus (Eliasson, 1969) and absence of rooting inhibitors in Eucalytus (Paton et al, 1970; Davidson, 1974), higher carbohydrate content, lower reducing sugar and lower rooting inhibitor levels in Phoenix (Reuveni and Adato, 1974), greater cofactor content in Hedera (Hess, 1961, 1962) and Malus (Quamme and Nelson, 1965) (c.f. Zimmerman, 1963) and less fibre in Hedera (Goodin, 1965) (c.f. Girouard, 1969).

Ontogenetical age can influence seasonal pattern of rootability, as demonstrated in Olea europea in which rooting potential of juvenile material remained high throughout a greater portion of the year than that of adult tissue (Porlingis and Therios, 1976).

2.3.2 Other Cutting Characteristics

Important factors to be considered in the selection of material other than juvenility include the choice between lateral and terminal shoots, portion of the shoot used, age, degree of lignification, size and the inclusion of a heel of older wood.

In the absence of auxin treatnemt branch terminals of Pseudotsuga menziesii rooted in significantly greater numbers during spring than first order laterals. This was attributed to the larger number and size of buds and greater stem diameter of the terminal cuttings (Roberts and Fuchigami, 1973). Girouard (1975) found the suitability of

branch terminal compared with lateral cuttings of Picea abies to vary with the season.

An increasing gradient of rootability was found to exist from top to base of apple shoots (Garner and Hatcher, 1948) whereas the converse situation existed in Liquidambar styraciflua (Bilan, 1974). Although rooting percentage was little different, field survival of rooted cuttings was poorer in tip cuttings than in those from lower regions of Ulmus shoots (Whalley, 1975). In general, tip cuttings may be the most suitable for softwood material, possibly due to a more favourable growth regulator status and lesser degree of differentiation, and basal cuttings more appropriate for hardwood material due to a greater accumulation of carbohydrates and prescence of preformed roots in some species. Softwood cuttings may have the potential to root more quickly and easily than others if provided with suitable conditions (e.g. Hartmann et al, 1963; Hartmann and Kester, 1968). Laterals 5 to 15 cm long with or without a heel and terminal growth of current season's wood have been used successfully to propagate junipers (Hartmann and Kester, 1968). The possible presence of preformed roots was suggested to account for the more stable seasonal rooting pattern in lignified cuttings of old wood compared with semilignified one year old shoots of members of the Cupressaceae. However the younger tissue was more responsive to auxin application (Ivanova, 1979).

A heel of older wood has variously been reported to assist or be of no significance in rooting of juniper cuttings (e.g. Snyder, 1952). Cuttings of Juniperus chinensis 'Hetzii' from current season's wood rapidly formed vigorous

root systems and rootability of two year old wood was raised to an acceptable level by the inclusion of a heel (Hall, 1977). Edwards and Thomas (1979) reported that rooting of non-heel cuttings of Chamaecyparis lawsoniana and Juniperus cultivars from current season's growth was superior to that of heel cuttings.

Tip cuttings of Juniperus virginiana 'Skyrocket' 15 cm in length rooted significantly better than those 8 or 25 cm in length. Number, length and dry weight of roots and rapidity of root formation were positively correlated with length of rose cuttings (Azimi and Bisgrove, 1975). Chemlar (1974) found that pole-size to very short cuttings of easily rooted Salix species were readily propagated.

2.3.3 The Presence of Buds and Leaves

Buds and leaves are commonly regarded as important sources of auxin and other rooting substances. Leaves are attributed with providing nutrients and growth regulators during root initiation (e.g. Bouillenne and Went, 1933; Went, 1938; van Overbeek et al, 1946; Altman, 1972; Middleton et al, 1980).

The presence of vegetative buds also frequently appears to enhance rooting, particularly when emerging from dormancy (e.g. Roberts and Fuchigami, 1973; Roberts et al, 1974). This phenomenon has been associated with increased levels of rooting promoters including auxin and cofactor-like substances, and reduced inhibitor levels (e.g. Spiegel, 1955; Fadl and Hartmann, 1967a,b,c; Smith and Wareing,

1972a). However, disbudding has been reported as having little or no effect on seasonal fluctuations in rooting capacity of plum (Howard, 1968) and apple (Bassuk and Howard, 1980) but in the absence of exogenously supplied auxin prevented the spring optimum of rootability in Psuedotsuga menziesii (Roberts and Fuchigami, 1973).

The presence of buds were essential for rooting of pea cuttings (Went, 1934) but only in the first few days, coinciding with root initiation (Eriksen, 1973). Buds, including those that are growing, may influence rooting in a negative manner by producing inhibitors or by competing for metabolites and in a positve manner by providing growth regulators conducive to rooting and enhancing cambial activity (e.g. Biran and Halevy, 1973b; Fadl and Hartmann, 1976a,b; Fischer and Hansen, 1977). Rooting of Dahlia cuttings was inversely related to growth rate of the buds and removal of vegetative and flower buds enhanced rooting (Biran and Halevy, 1973b). The presence of flower buds or the flowering phase is normally considered detrimental to rooting (e.g. O'Rouke,1940; Kraus, 1953).

2.3.4 Additional Cutting Treatments

Additional wounding, normally in the form of the removal of a thin slice of bark from one side of the cutting base, is frequently employed and has been found to stimulate rooting in a wide range of species including Juniperus species (e.g. Snyder, 1953; Edwards and Thomas, 1979). It has been proposed that this treatment may enhance rooting

by aiding processes such as the absorption of water, penetration of applied rooting substances, proliferation of new cells, accumulation of rooting promoters and nutrients, release of wound-induced rooting stimuli or the removal of physical barriers to root emergence (Hartmann and Kester, 1968; Lamb et al, 1975). The pre-severence treatment of girdling often increases rootability which has been largely attributed to the accumulation of factors such as photosynthates (Cameron, 1970) and cofactors (e.g. Stoltz and Hess, 1966) from the upper portion of the shoot.

Basal pH (Cormack, 1965; Brukel and Johnson, 1969) and cutting orientation (e.g. Nanda et al, 1969) can also influence rooting, the polar transport of auxin a possible determining factor in the latter.

2.4 Growth Regulators, Cofactors and Nutrients

2.4.1 Auxins

Endogenous IAA has been studied extensively in relation to root formation and has been recognized for many years as an important promoter of this process (e.g. Went, 1934; Thimann and Went, 1934; Kogl et al, 1934).

Rooting potential and level of endogenous auxin have been found to be related in a positive manner in a wide range of genera including Salix (Vieitez and Pena, 1968), Malus (Tustin, 1976), Pisum (Eliasson, 1980) and a range of other herbaceous species (Odom and Carpenter,

1965). However this has not always been the case as demonstrated in Salix (Tyce, 1957), Dahlia (Biran and Halevy, 1973b) and Rhododendron (Foong, 1977).

Exogenously supplied auxins are used extensively to improve rooting of cuttings, the synthetic auxins NAA (napthaleneacetic acid) and IBA being the most stable and suitable for this purpose (e.g. Middleton et al, 1980). Although auxin application significantly improved rooting at certain times of the year, the seasonal pattern of rootability was affected relatively little in Juniperus horizontalis 'Plumosa', Taxus cuspidata 'Nana' (Lanphear and Meahl, 1963) of Psuedotsuga menziesii (Roberts and Fuchigami, 1973). As with other growth regulators, optimal concentration varies with other factors such as season in Pinus strobus (Kiang et al, 1974) or photoperiod as demonstrated in Populus spp. (Kumar, 1978). Klahr and Still (1974) noted that optimal IBA level for root number often exceeded that for rooting percentage in Tilia. Studies of hardwood apple cuttings indicated that IBA acted as an IAA protectant (Tustin, 1976). The ratio of growth regulators, such as auxin:inhibitor (e.g. Spiegel, 1955; Gordienko et al, 1976) and auxin:cytokinin (Heide, 1965, 1967, 1968; Heide and Skoog, 1967) may be of prime importance in the determination of rooting potential rather than absolute level.

IAA is reported to be transported basipetially and to accumulate at the cutting base (e.g. Mohammed and Eriksen, 1974; Greenwood and Goldsmith, 1970). While auxin may enhance carbohydrate production in the leaves and stimulate mobilization to the site of root initiation (e.g. Nanda and

Anand, 1970; Altman, 1972), these effects may be of secondary importance to the probable triggering effect of auxin on adventitious root formation (e.g. Jain and Nanda, 1972; Smith and Wareing, 1972a).

Four distinct stages of adventitious root formation have been described: a) the initiation of groups of meristematic cells; b) the differentiation of these tissues into recognizable root primordia; c) the extension and emergence of the roots; d) the development of roots outside the cutting (e.g. Argylos, 1959). The various stages may have differing levels of sensitivity to a range of factors and might be subdivided further. Auxin is reported to be active at more than one stage of adventitious root formation (Went, 1939; Smith and Thorpe, 1975; Mitsuhashi-Kato, 1978). Mullins (1970) reported that the promotive effect of auxin is lost if application is delayed.

It has not been established conclusively if auxin necessarily acts in the free state as indicated in Pinus lambertiana embryos (Greenwood et al, 1974) or in a bound or conjugated form, for example as an auxin - phenol complex (e.g. Fadl and Hartmann, 1967a,b,c).

2.4.2 Gibberellins

Gibberellins are regarded primarily as inhibitors of root formation by cuttings and tissue culture explants (e.g. Bachelard and Stowe, 1963; Murashige, 1964; Mitsuhashi-Kato et al, 1978).

Inhibition does not always result from gibberellin application however, the final effect sometimes shown as being dependent on factors such as concentration or light intensity as in pea (Hansen, 1975) or stage of initiation as in Pinus radiata (Smith and Thorpe, 1975). Whereas low levels are occasionally promotory, high levels invariably inhibit or retard rooting (e.g. Sircar and Chatterjee, 1973, 1974; Hansen, 1975; Jansen, 1967). Non-competitive antagonism between gibberellins and auxins in relation to rooting was found to occur in pea and bean cuttins. GA and auxin also had opposing effects on shoot extension growth (Brian et al, 1960).

An early theory which attempted to explain the inhibitory effect of gibberellin on rooting concerned the diversion of nutrients away from the rooting zone by shoot growth stimulated by gibberellin action (e.g. Brian, 1957; Sircar and Chatterjee, 1974). However, Brian et al (1960) found that the effects of gibberellin on root regeneration and shoot growth could be dissociated. The influence of exogenously supplied gibberellin appeared to be primarily due to a direct, localized effect involving the prevention of the early organized cell divisions. Murashige (1964) similarly found retardation of early root and shoot primordia formation in tobbaco tissue cultures to occur under concentrations of gibberellin which did not completely inhibit cell division or vascularization. The effect of exogenous gibberellin was found to be weaker when applied at later stages of root formation (e.g. Brian, 1960; Jansen, 1967; Sircar and Chatterjee, 1974).

2.4.3 Cytokinins

Another group of plant hormones known to mainly inhibit root initiation is that of the cytokinins, most information having been obtained through experiments involving the supply of exogenous cytokinin to explants and cuttings.

The ratio of cytokinin to auxin has been demonstrated to be of great importance to regeneration in tissue cultures. A high cytokinin:auxin ratio promoted bud formation and inhibited rooting in tobacco callus cultures (Skoog and Miller, 1957) and Begonia leaf cuttings (Heide, 1965) whereas a low ratio had the opposite effect. Very low concentrations of either hormone promoted the effect of the other. Low cytokinin levels also promoted and high levels inhibited rooting of pea cuttings (Eriksen, 1975). Kinetin had a negative effect on rooting when applied to the base of Acer cuttings but a positive effect if applied to the leaves (Bachelard and Stowe, 1963).

Easily rooted Rhododendron (Foong, 1977) and Populus (Okoro and Grace, 1978) varieties contained lower levels of endogenous cytokinin than difficult-to-root varieties. Conversely, Tustin (1976) found no relationship between varietal or seasonal differences in rootability of apple rootstocks and cytokinin activity.

Exogenously supplied cytokinin inhibited only the pre-initiation stages of rooting of pea (Eriksen, 1974) and Pinus radiata (Smith and Thorpe, 1975) cuttings. Earlier, Humphries and Maciejewska-Potapczk (1960) had proposed that kinetin affected root initiation at an early stage by influencing the type of cell produced rather than by

inhibition of cell division. This is also consistent with results obtained by Skoog and Miller (1957), Heide (1965) and Chandra et al (1973).

2.4.4 Abscisic Acid

Abscisic acid is generally regarded as an inhibitor of plant processes but, as with other growth regulators, the ultimate effect on adventitious root formation may vary with other factors such as concentration or plant species.

Exogenously supplied ABA inhibited rooting in Begonia leaf cuttings (Heide, 1968) and Rhododendron explants (Pierek and Steegmans, 1975). Conversely, ABA application enhanced rooting of Hedera helix and mung bean (Chin et al, 1969) and Pisum sativum (Rasmussen and Anderson, 1980) although in the latter root emergence was delayed by concentrations exceeding 10^{-4}M ABA. Chin et al (1969) reported that ABA could partially overcome gibberellin - induced inhibition of rooting but not that caused by kinetin.

Higher levels of ABA were present in cuttings of an easy-to-root compared with a difficult-to-root variety of Rhododendron in all seasons (Foong, 1977). A low level of endogenous growth inhibitor and high auxin content, giving a high auxin:inhibitor ratio, were associated with ease of rooting in Vitis (Spiegel, 1955) and Juniperus (Gordienko et al, 1976).

The growth inhibitory fraction of pip and stone fruit extracts (Challenger et al, 1964), Pinus radiata bud extracts (Zabkiewicz and Steele 1974) and Picea glauca and

Chamaecyparis lawsoniana (Tognoni et al, 1977) stimulated rooting in the mung bean bioassay. In the latter case the inhibitors, of which the major component was tentatively identified as ABA, were not considered to be the prime causal factor of the difference of rootability between the two species or in P. glauca during different seasons, although seasonal fluctuations in inhibitor content and rooting capacity appeared to show some inverse relationship. Eliasson (1969) reported that the bases of easily rooted suckers of Populus tremula contained lower levels of growth inhibitors than the less easily rooted sprouts from the crown.

2.4.5 Ethylene

Ethylene, structurally the simplest of known plant hormones, was found by Zimmerman and Hitchcock (1933) to stimulate both adventitious root formation and the emergence of preformed roots in several species. Formation of secondary roots and root hairs was also promoted but shoot formation was not. Similar effects were produced by other unsaturated hydrocarbon gases.

Subsequent studies involving exogenously supplied ethylene or ethrel and endogenous ethylene level, as conducted with mung bean (Krishnamoorthy, 1970), Pelargonium, Coleus (Maleike, 1977),and Salix (Kawase, 1971) have largely confirmed the promotory effect on root initiation up to optimum concentrations. Mullins (1970) found ethylene to promote emergence of latent roots from mung bean hypocotyls but inhibit adventitious root formation.

root initiation was promoted when rates of ethylene evolution were low in relation to auxin level. It was suggested that a feedback mechanism between the two hormones might be involved. Retardation of root extension by ethylene has been noted in some instances (Krishnamoorthy, 1970; Drew et al, 1979). Rajagopal and Anderson (1980) reported that ethylene did not appear to be the major controlling factor in root initiation in pea cuttings.

Ethrel acted synergistically with IAA on rooting of mung bean cuttings and overcame the inhibitory effect of GA_3 and kinetin on root number but not root length (Krishnamoorthy, 1970). A synergistic interaction with IAA was also found to occur in tomato cuttings (Roy et al, 1972).

2.4.6 Cofactors

A component of the postulated 'rhizocaline' complex other than auxin and translocated from the leaves was characterized as an ortho-dihydroxy phenol (Bouillenne and Bouillenne-Warland, 1955; Went, 1938). Girdling and grafting experiments offered confirmation of the requirement for a non-auxin factor (e.g. Cooper, 1935; Gregory and van Overbeek, 1945; van Overbeek and Gregory, 1945).

The rooting capacity of easy- and difficult-to-root forms of Hedera helix and Hibiscus rosa-sinensis appeared to be unrelated to growth inhibitor or growth promoter content but could be related to the prescence and

concentration of four groups of substances, "rooting cofactors", which appeared to act as cofactors for IAA in promotion of rooting (Hess, 1959; 1960; 1962). The constituents of cofactors include phenolic, acidic and lipid-like components (e.g. Girouard, 1969; Heuser and Hess, 1972; Heuser, 1976; Foong, 1977). Varietal and seasonal differences in rooting potential have been related to cofactor content in, for instance, Rhododendron (Lee et al, 1969) and pear (Fadl and Hartmann, 1967a,b,c).
Total cofactor activity was found to be relatively stable throughout the year and therefore could not account for seasonal fluctuations in rooting capacity of Juniperus horizontalis 'Plumosa'. It was suggested that cofactor content might determine rooting potential attainable but that this was limited by other factors such as cofactor mobilization (Lanphear and Meahl, 1963). Cofactors did not appear to be the prime cause of limited rooting in pecan (Taylor and Odom, 1970), Dahlia (Biran and Halevy, 1973c) or apple (Tustin, 1976).

Application of cofactor-like substances has been reported to stimulate rooting of Euonymous (Lee and Tukey, 1971) and apple (Bassuk and Howard, 1980). Rooting capacity of apple was increased at a time of year when rooting was normally poor. Although phenolics (e.g. Hess; 1962; Heuser, 1976), have been found to be associated with root initiation in a postive manner, Foong (1977) also found many extracted from Rhododendron inhibited rooting in the mung bean bioassay. The ultimate effect of a cofactor-like component of apple tissue in the mung bean bioassay was similarly dependent on concentration (Tustin, 1976).

Condensation products of oxidized phenolics and auxin have been suggested to be the true or at least the most active inducers of root initiation (e.g. Leopold and Plummer, 1961; Fadl and Hartmann, 1967a,b,c; Haissig, 1974b). Cofactors may protect IAA from destruction (e.g. Zenk and Muller, 1963; Bastin, 1966; Hackett, 1970) or sensitize cells to auxin (e.g. Gorter, 1969).

2.4.7 Nutrients

The most studied aspect of nutrient status in relation to adventitious root formation is that of carbohydrate content. Changes in starch and sugar levels indicate that the processes of starch hydrolysis, basipetal transport and subsequent utilization of sugars occur after cutting excision and during root formation (e.g. Stuart, 1938; Smith *et al*, 1940; Breen and Muraoka, 1973; Haissig, 1974c; Okoro and Grace, 1976).

Positive relationships have been demonstrated between rooting capacity and endogenous levels of, for instance, total carbohydrate or sugar in *Hibiscus* (Stoltz and Hess 1966), *Chrysanthemum* (Stoltz, 1968), *Phoenix* (Reuveni and Adato, 1974) and pea (Eliasson, 1978) and starch content in *Hydrangea* (Molnar and La Croix, 1972). Okoro and Grace (1976) however found no indication that carbohydrate content was a causal factor in the difference in rootability between *Populus* species. Seasonal changes in total non-structural carbohydrate appeared to be of significance only in the more difficult to root of two *Macadamia*

integrifolia varieties, and in which rooting capacity was greatest in winter when carbohydrate levels were highest (Cormack and Bate, 1976). Carbohydrate status and rooting can sometimes be improved by girdling (e.g. Cameron, 1970).

Exogenously supplied sugars seemed to promote rooting only if endogenous levels were limiting (Lovell et al, 1974; Eliasson, 1978). Supraoptimal levels may be the cause of rooting inhibition under high light intensity (e.g. Hansen and Eriksen. 1974). A suitable carbohydrate content appears to be necessary for optimal rooting but with the inductive effect of IAA still required (e.g. Jain and Nanda, 1972; Smith and Wareing, 1972a). Under conditions of sub-optimal sucrose concentration, IAA increased rooting percentage but not root number in Pinus lambertiana embryo cuttings (Greenwood and Berlyn, 1973).

Root initiation and development require nitrogen for nucleic acid and protein synthesis and there is a level of nitrogen below which rooting fails to occur or does so at a reduced rate (Haissig, 1974c).

A high carbohydrate:nitrogen (C/N) ratio has been considered to be benificial to rooting (e.g. Reid, 1924; Evans, 1971) although absolute levels of both factors (e.g. Starring, 1923) and the form of nitrogen (e.g. Reid, 1924; Thiamann and Portasse, 1941) are probably at least as important.

Mineral nutrients such as boron and magnesium are important for root formation and growth although their specific functions have not all been clearly established. Boron, for instance, has been suggested to be involved in

auxin biosynthesis (e.g. Middleton *et al*,1980) whereas Hirsch and Torrey (1980) proposed that its role in root development might rather be in the maintenance of cell membrane integrity. The efficacy of exogenous nutrient supply appears to be largely determined by the nutrient status of the cutting, with treatment of most benifit to low nutrient status material as demonstrated for example, in cuttings of *Ilex crenata* (Tichnor and Roberts, 1968) and *Pisum sativum* (Eliasson, 1978).

CHAPTER 3

MATERIALS AND METHODS

3.1 Source, Preparation and Treatment of Cutting Material

Four cultivars were employed in the study: Juniperus virginiana 'Skyrocket' ("easy-to-root"); J. scopulorum 'Pathfinder' ("difficult-to-root"); J. scopulorum 'Blue Haven' ("very difficult-to-root"); Cupressus sempervirens 'Swanes Golden' ("easy-to-root"). Material was provided by the New Zealand Nursery Research Centre, Palmerston North, from stock plants of approximately five years in age and maintained by standard nursery practice.

3.1.1 Seasonal Study

Lateral tip cuttings of current season's growth, 15 cm and 12 cm in length of J. 'Skyrocket' and J. 'Pathfinder' respectively, were taken in the last week of each month from late summer (February) until spring (October). Lower leaves were removed and the cuttings lightly wounded before being dipped in 2.0% IBA in talc and planted in trays of peat:pumice (1:1 v/v) in three replicates of eight cuttings each. A split-plot in time experimental design was used, with cultivar designated as the main plot factor and month of excision as the subplot (Steele and Torrey, 1960; Little and Hills, 1978). The cuttings were placed over basal heat of 21 $\pm 2^{\circ}C$ in an unheated glasshouse and watered in.

Thereafter the cuttings were provided with moisture as required including a thorough watering once a week, and in the case of cuttings taken in February and March, light intermittent mist.

After 10 weeks the cuttings were lifted and data recorded. As in all the trials, data on number of cuttings rooted, number of roots per cutting and mean total root length per cutting were analysed statistically and appropriate tests of significance applied, primarily Duncan's New Multiple Range Test. The last - mentioned parameter was considered the most suitable non-destructive measure of root mass per cutting. Samples of rooted cuttings from each month were grown on in plastic tubes in a glasshouse for evaluation of subsequent growth.

Cuttings of C. 'Swanes Golden' of about 10 cm in length were harvested in February, March and June and treated as described above.

3.1.2 Growth Cabinet Study

Stock plants of J. 'Pathfinder' and C. 'Swanes Golden' were placed in "Temperzone" controlled environment cabinets during the summer prior to the midwinter trial. One group of plants was kept at 20 $\pm 2^{\circ}C$ (WP) and the temperature of the other group gradually lowered over a week then maintained at 10 $\pm 2^{\circ}C$ (CP). A 10 hour photoperiod, light intensity of approximately 120 $W.m^{-2}$ from mercury halide HID lamps, and a relative humidity of 70 $\pm 5\%$ were provided. The plants

were rotated at intervals.

After five weeks, cuttings were taken, prepared as outlined in the seasonal trial and planted in four replicates of eight cuttings each according to a split-plot design (Steele and Torrey, 1960; Little and Hills, 1978). Cuttings from each parent plant environment were split into two groups and subjected to growth cabinet air temperatures of 18 ± 2°C (WH) or 12 ±2°C (CH), a light intensity reduced by shading to approximately 40 $W.m^{-2}$ at cutting height, a 10 hour photoperiod and a relative humidity of 80 ±5%. The cuttings were sprinkled with water as necessary and the trays rotated at intervals.

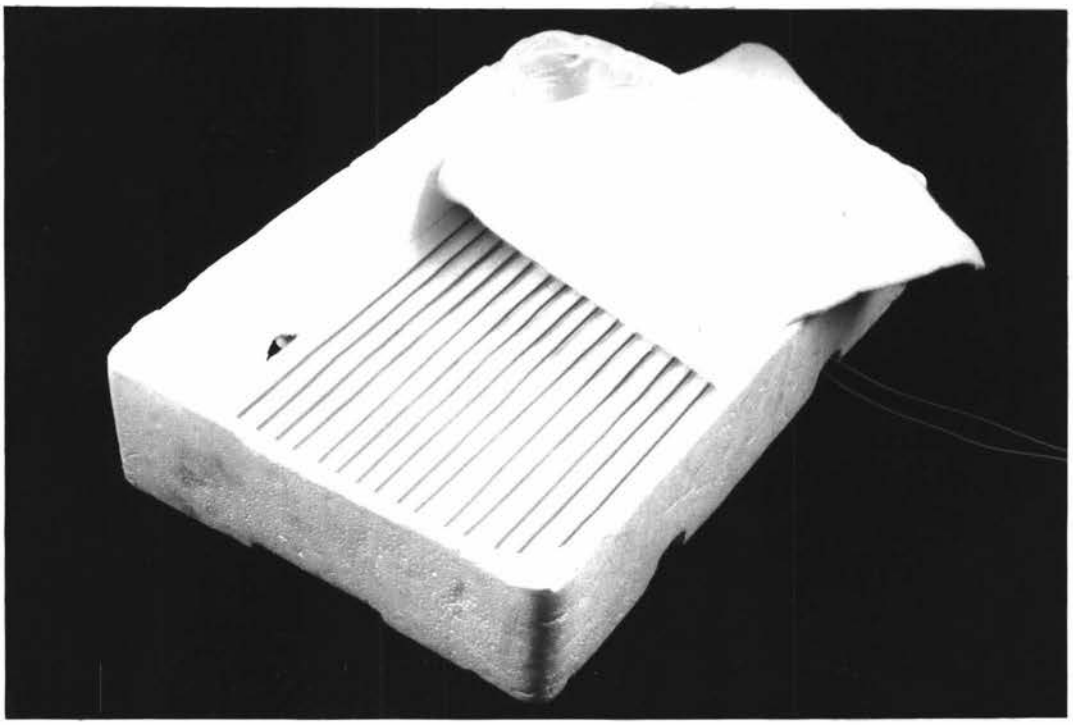
To provide basal heat for the cuttings, containers were made from polystyrene trays (49 cm x 32 cm x 10 cm) lined with electric blanket cables enclosed between layers of capillary felt (Plate 1) into which the cutting trays were placed. The polystyrene trays were in turn placed on drainage trays. A 0.25 KvA isolating transformer was included in the system and the temperature at the cutting bases thermostatically controlled at 21 ±2°C.

The cuttings were lifted after eight weeks and data recorded for later analysis.

3.1.3 Midwinter Study

Parent material and cuttings of J. 'Skyrocket', J. 'Pathfinder', J. 'Blue Haven' and C. 'Swanes Golden' were subjected to one of a number of air temperature treatments.

Plate 1. A propagation tray (49 cm x 32 cm x 10 cm) used for the provision of basal heat to cuttings in the growth cabinets



The "cold parent" (CP) plant treatment consisted of normal winter chilling and "warm parent" (WP) plants were maintained in a glasshouse at 18± 2°C from early autumn (March). Where additional material was available, plants were removed from the warm glasshouse environment and exposed to outdoor temperatures for two weeks prior to cutting excision, thus comprising the "warm+cold parent" (WCP) plant treatment. Alternatively, shoots were excised from plants exposed to normal winter chilling and coolstored in darkness for two weeks at 5 ±1°C thereby providing the "cold+coolstored parent" (CCP) material.

Cuttings were taken in late June and treated as described for the seasonal study. Cuttings of J. 'Blue Haven' were approximately 15 cm in length. Cuttings from each parent environment were divided into two groups and placed over bottom heat of 21± 2°C in either an unheated glasshouse with air temperatures of about 13 ±4°C during the rooting period, comprising the "cold propagation house" (CH) environment, or a heated glasshouse generally kept at 18 ±2°C but ranging up to 22°C for brief periods and which provided the "warm propagation house" (WH) environment. A split-plot experimental design was employed, with parent material environment of prime interest and designated as the subplot factor.

After 10 weeks the cuttings were lifted, data recorded for later analysis and a sample of rooted cuttings grown on for subsquent evaluation of growth.

3.2 Endogenous Growth Regulator Analyses

Cutting samples taken at the same time as those for the propagation trials were lyophylised and stored in air-tight jars in a deep freeze until required for analysis of endogenous growth regulator activity.

3.2.1 Extraction and Initial Purification

A 5 g sample of finely ground, lyophylized tissue was suspended in 100 ml of chilled 80% aqueous methanol, giving a ratio of approximately 1 g fresh weight to 10 ml aqueous MeOH. This was extracted at 1°C for 16 hours with intermittent agitation. The supernatant was decanted and extraction of the residue repeated with changes of 50 ml 80% aqueous MeOH for 4 hours each, giving a final volume of 200 ml. The extracts were vacuum filtered through Whatman No. 1 filter paper using a Buchner funnel, the residue rinsed, and the filtrate reduced to approximately 25 ml of the aqueous phase on a rotary evaporator at 27°C, shielded from direct light.

The aqueous residue, made up to 50 ml with rinsings of distilled water from the evaporating flask, was transferred to centrifuge tubes and stood at 1°C overnight to precipitate chlorophyll and lipids. The extract was then centrifuged at 23,000 x g for 40 min at 1°C, the supernatant poured off, and the residue and tubes rinsed with a few mls of cold distilled water.

The extract, adjusted to pH 6.0, was slurried with 8 g of dry, washed polyclar AT for 1 hour at 4°C to remove

phenolics.

The polyclar AT (an insoluble form of polyvinlpyrrolidone) had been sieved to give a size range of 125μ - 250μ diameter and slurried in five times its own volume of distilled water, allowed to settle for 15 min and the fines decanted off. This was repeated a further six times after which the polyclar was dried in a vacuum oven at about 40°C.

The extract and polyclar slurry was filtered through Whatman No. 1 filter paper under vacuum, rinsed with a total of 100 ml distilled water at pH 6.0, and the combined filtrate centrifuged at 20,000 x g for 10 min.

The clear aqueous phase was adjusted to pH 3.0 with 50% HCl and shaken with three separate equal volumes of peroxide-free diethyl ether for 5 min each. The bulked ether fraction was shaken for 5 min with 10% by volume distilled water at pH 3.0 to remove any remaining cytokinins from the ether phase. The combined aqueous partitions and backwash were retained for the separation of cytokinins.

The ether fraction was reduced under vacuum to 150 ml, which included approximately 40 ml of rinsings from the evaporating flask, and extracted with two 50 ml aliquots of 5% sodium bicarbonate at pH 8.0 shaken for 5 min each. The sodium bicarbonate fraction was then acidified to pH 3.0 with 50% HCl and partitioned three times with equal volumes of diethyl ether.

The acidic ether fraction obtained was reduced to dryness on a rotary evaporator, redissolved in 100% redistilled methanol and transferred to a sample vial in which it was dried under vacuum in the dark. (Recovery of a 0.25 mg

"spike" added at the beginning of the extraction process indicated that recovery of IAA or ABA was at least 65% and 75% respectively in the methonal rinse). The vial was capped and stored in a deep freeze until required for chromatography. This fraction contained the acidic growth regulators.

The combined aqueous fraction and backwash from the first acidic ether fraction was adjusted to pH 8.0 with 50% NH_4OH and partitioned three times with equal volumes of water-saturated n-butonol. The butonol fraction was then taken to dryness in vacuo and the residue taken up in several mls of absolute methanol and transferred to a vial. After the sample was dried under vacuum the vials were sealed and stored in a deep freeze until required. Cytokinin activity was determined from this fraction.

3.2.2 Paper Chromatography

Auxins and Acidic Inhibitors

The residue of the acidic ether fraction was dissolved in 0.5 ml acetone:metanol (1:1 v/v). The sample vial was rinsed with a further 0.4 ml which was also taken up in the same pippette. The extract was applied to prewashed Whatman No. 3 chromatography paper to give a 15 cm wide streak and dried with the aid of a cold airstream to reduce spreading. The paper was developed in isopropanol: ammonia:water (10:1:1 v/v) in a descending manner and left at room temperature in the dark until the solvent front had travelled 20 cm. The chromatogram was air-dried for 1 hour

then dried under vacuum overnight. The chromatogram was then cut into 10 equal transverse strips plus a control strip from behind the origin, ready to be bioassayed.

Butonol-Soluble Cytokinins

The procedure for chromatography of the butonol fraction was the same as for the acidic ether fraction except that the solvent system used was n-butonol:ammonia (4:1 v/v). After initial drying the chromatogram was lightly sprayed with distilled water to assist with the removal of butonol which may have been inhibitory in the bioassay, and dried under vacuum overnight.

3.2.3 Bioassays

Avena Coleoptile Bioassay

The tissue extracts were assayed for auxin-like activity by the procedure employed by Tustin (1976) which is a combination of the methods of Sirios (1967) and Burstrom (1973).

Seeds of the oat cultivar 'Brighton' were soaked for 15 hours in 0.1% hydrogen peroxide, rinsed and spread evenly over moist filter paper in a plastic tray. The tray was covered with a sheet of glass and placed in a darkroom under red light for 24 hours at 25°C. The seeds were then left in darkness for a further two days until the coleoptiles were 2 to 3 cm in length. Using a precision double-

bladed guillotine, 5 mm sections were cut 3 mm from the tip. The coleoptile sections were soaked in Burstrom's buffer (Appendix 1) for 1 hour before use.

The chromatogram strips were rolled lightly, placed in glass vials (40 x 25 mm) and 2 ml of Burstrom's buffer added to each. After each vial had ten coleoptiles added it was capped with a plastic top with a needle hole in the centre. All manipulations of the coleoptiles were carried out in a dark-room under a green safelight. The vials were placed on a vertical turntable rotating at approximately 1 r.p.m. for 6 hours in darkness at 25°C. The vials were then removed and the coleoptiles killed by the addition of 2 ml of 10% methanol. Coleoptile length was measured with the aid of a photographic enlarger at 3X magnification.

A standard series of IAA solutions in a log dilution series 0.001 to 10 μg/ml was run concurrently with each bioassay. A strip of washed chromatography paper was included in each standard vial. A typical standard curve from which activity was determined is shown in Appendix 2. Percent growth was calculated as:

$$\% \text{ growth} = \frac{\text{growth coleoptile} - \text{growth control}}{\text{growth control}}$$

Triticum Coleoptile Bioassay

The procedure of Nitsch and Nitsch (1956) was employed to assay the extracts for ABA-like inhibitors.

Wheat seed of the cultivar 'Aotea' was soaked in tap water for 2 hours and spread on moist filter paper in a

plastic tray. The tray was covered with a sheet of glass and left in a dark-room at 25°C for 3 days by which time the coleoptiles were 2 to 3 cm long. Ten mm sections were cut 3 mm from the coleoptile tips and floated in distilled water for 3 hours before being loaded into the bioassay vials.

The chromatogram zones were rolled lightly and each placed in glass vials (40 x 25 mm) to which 2 ml of phosphate-citrate buffer (Appendix 1) was added. Under a green safelight, ten coleoptiles were placed in each vial which was then capped and left in darkness at 25°C on a turntable run at approximately 1 r.p.m. After 20 hours the vials were removed and 2 ml of 10% MeOH added to kill the coleoptiles. The length of the coleoptiles was measured as described for the Avena coleoptile bioassay.

Standards of ABA 0.001 to 10 μg/ml were run concurrently with each bioassay, a strip of washed chromatography paper included in each vial. A typical standard curve is shown in Appendix 2. Percent growth inhibition was calculated as:

$$\% \text{ growth inhibition} = \frac{\text{growth coleoptile} - \text{growth control}}{\text{growth control}} .$$

Radish Cotyledon Bioassay

Cytokinin activity in the butonol fraction was determined by the radish cotyledon bioassay of Letham (1971).

Radish seed, Rhaphanus sativus L. cv. Long Scarlet, Market Strain, retained by a 2 mm sieve was soaked for 5 min in a 0.3% sodium hypochlorite solution and rinsed thoroughly. The seed was germinated at 25°C in darkness on well-wetted filter paper in a plastic tray covered with a sheet of glass. After 42 hours the smaller cotyledon was excised from each seedling. Eight cotyledons of uniform size, about 6 mg, were placed with the upper surface in contact with the paper chromatogram zones which had been cut into pieces and placed in Petri dishes (9 cm diam.) containing 3 ml distilled water at pH 6.5. The Petri dishes were placed on moist filter paper in a plastic tray and covered with a sheet of glass. After 72 hours at 25°C under continuous, low fluorescent light the cotyledons were blotted dry and weighed.

Kinetin standards from 0.001 to 1.0 μg/ml were run concurrently with each bioassay. A typical standard curve is shown in Appendix 1.

CHAPTER 4

RESULTS

4.1 Seasonal Fluctuations in Root Formation Capacity

Changes in the rootability of cuttings of J. virginiana 'Skyrocket' (easy-to-root) and J. scopulorum 'Pathfinder' (difficult-to-root) were followed over the nine months from late summer (February) to spring (October) as outlined in Materials and Methods. Cuttings of C. sempervirens 'Swanes Golden' were also taken in Feruary, March and June. Data analysed included mean number of cuttings rooted, mean number of roots per cutting and mean total root length per cutting. Additional values were calculated on a per rooted cutting basis and of mean root length for comparison. New shoot growth made by the juniper cuttings was also recorded at lifting.

4.1.1 J. virginiana 'Skyrocket'

The mean number of J. 'Skyrocket' cuttings rooted was low in February and had diminished a little further in March but rose dramatically in April, remaining at high levels until an equally sudden drop occurred in October (Figure 1). No significant differences were detected from April to September inclusive although cuttings taken in April, June and August rooted in significantly greater numbers than those in Febrary, March or October (Table 1a). For analysis of variance refer to Appendix 3. All cuttings harvested in June formed roots.

The greatest number of roots per cutting (Table 1b, Figure 2) was produced in June and was significantly different from mean root number of cuttings taken in

Table 1a. Mean number of cuttings rooted/8

Cultivar	Month of Excision					
	Feb	Mar	Apr	May		
J.'Skyrocket'	2.00_{bcA}	1.33_{bcA}	7.67_{aA}*	6.67_{abA}		
J.'Pathfinder'	3.00_{bA}	1.67_{bcA}	1.00_{bcA}	0.67_{bcA}		
Mean	2.50_{cdBCD}	1.50_{deCD}	4.33_{abAB}	3.67_{bcABC}		
	Jun	Jul	Aug	Sep	Oct	Mean
	8.00_{aA}	6.00_{abA}*	7.67_{aA}	6.00_{abA}	1.00_{cA}	5.16**
	7.00_{aA}	0.33_{bcA}	4.00_{abA}	0.33_{bcA}	0.00_{cA}	2.00
	7.50	3.17_{bcdBC}	5.83_{aA}	3.17_{bcdBC}	0.50_{eD}	

Table 1b. Mean number of roots per cutting

Cultivar	Month of Excision					
	Feb	Mar	Apr	May		
J.'Skyrocket'	0.63_{bcA}	0.21_{cA}	2.96_{aA}	2.38_{abA}*		
J.'Pathfinder'	0.92_{a}	0.33_{a}	0.17_{a}*	0.17_{a}		
Mean	0.77_{bcdCD}	0.27_{cdCD}	1.56_{abBCD}	1.27_{bcBCD}		
	Jun	Jul	Aug	Sep	Oct	Mean
	5.84_{aA}	3.58_{aA}	4.13_{aA}	2.25_{abA}	0.21_{cA}	2.46*
	1.88_{a}	0.04_{a}**	1.17_{a}	0.04_{a}	0.00_{a}	0.52
	3.86_{A}	1.81_{abBC}	2.65_{aAB}	1.15_{bcdBCD}	0.10_{dD}	

Table 1c. Mean total root length per cutting (mm)

Cultivar	Month of Excision					
	Feb	Mar	Apr	May		
J.'Skyrocket'	16.13_{cB}	0.96_{cB}	124.69_{bAB}	139.71_{bAB}		
J.'Pathfinder'	26.46_{bAB}	0.54_{bB}	9.54_{bAB}*	5.42_{bAB}*		
Mean	21.29_{bCD}	0.75_{bD}	67.12_{aBC}	72.56_{aBC}		
	Jun	Jul	Aug	Sep	Oct	Mean
	227.95_{aA}	212.08_{bAB}	264.79_{abAB}	36.25_{cB}	4.25_{cB}	119.65*
	168.71_{aA}**	2.00_{bB}**	97.50_{abAB}	0.33_{bB}	0.00_{bB}	34.50
	223.33_{A}	107.04_{aB}	181.15_{A}	18.29_{bCD}	2.13_{bD}	

Tables 1(a-c). Variation in a) mean number of cuttings rooted b) mean number of roots per cutting and c) mean total root length per cutting of J.'Skyrocket' and J.'Pathfinder' with month of excision. Means followed by same lower or upper case character not significantly different at the 5% or 1% levels of significance within the same cultivar. Means within the same month significantly different at the * = 5% and ** = 1% levels of significance.

February, March or October. Intermediate values were obtained in other months. The mean number of roots per rooted cutting exhibited a less erratic, more gradual decline after June (Figure 2b).

Similarly, mean total root length per cutting (Table 1c, Figure 3a) was significantly greater in June than in any other month except August and was very significantly greater than in February, March, September or October. Although intermediate levels were obtained in April and May, all values from April to August inclusive were significantly greater than those of the preceding or following months. The return to low values of mean total root length per cutting in spring occurred a month earlier than in mean number of roots per cutting. Unlike the corresponding value on the per cutting basis, mean total root length per rooted cutting did not fall in July (Figure 3b).

Shoot activity apparent at lifting increased from that first visible in June-excised cuttings until all cuttings had made new shoot growth in August (Tables 2a and b). Values for October were not included since tip wilting or death had occurred in several cuttings, rapid shoot elongation having taken place soon after cutting excision in most instances. Investigation of individual cuttings failed to show any consistent relationship between parameters of rooting and those of shoot activity. Shoot growth in the stock plants had not fully ceased by February and had recommenced by or shortly after the October harvest date.

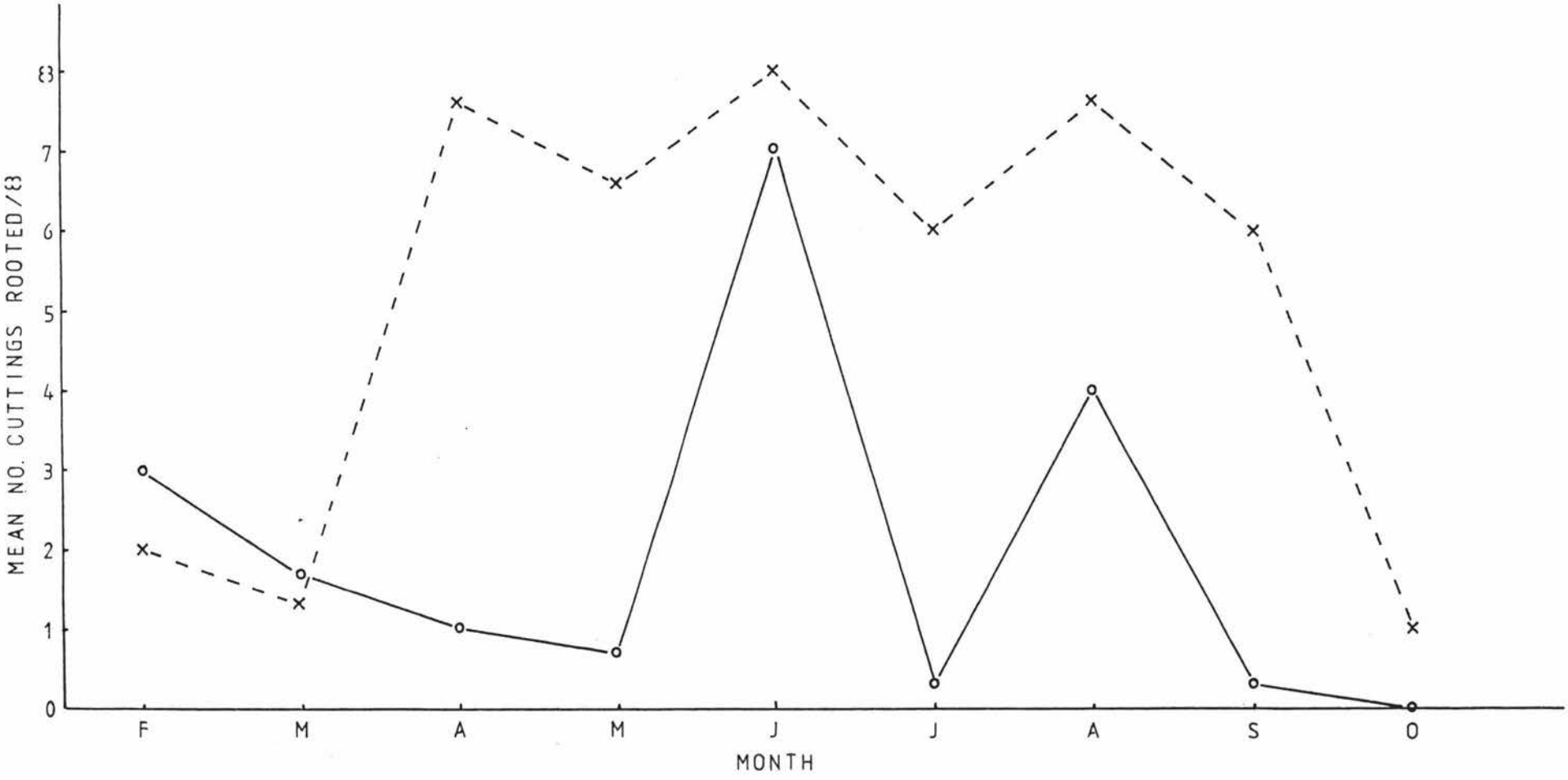


Figure 1. Seasonal fluctuations in mean number of J. 'Skyrocket' (x--x) and J. 'Pathfinder' (o—o) cuttings rooted.

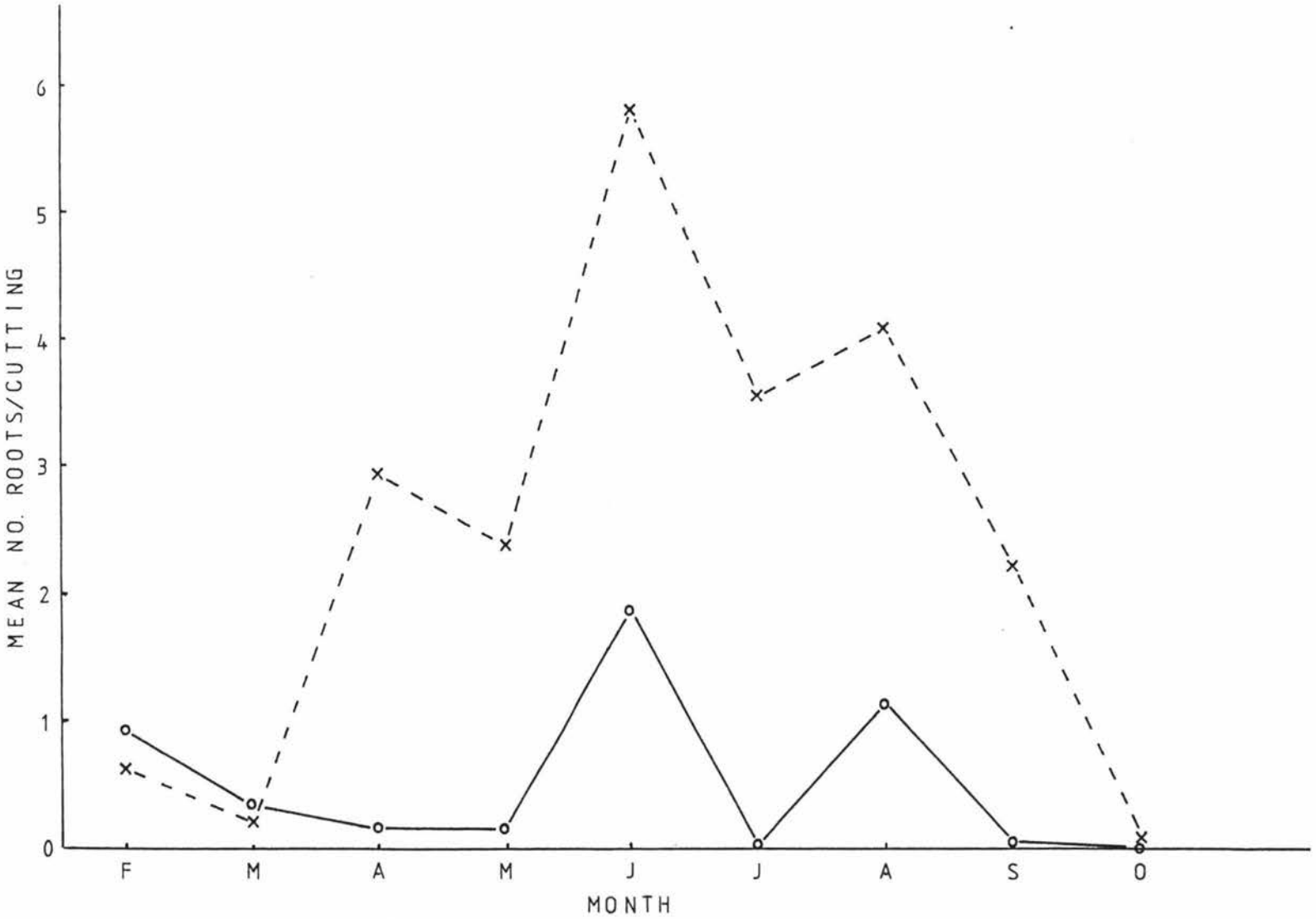


Figure 2a. Seasonal fluctuations in mean number of roots per cutting of J. 'Skyrocket' (x-x) and J. 'Pathfinder' (o-o).

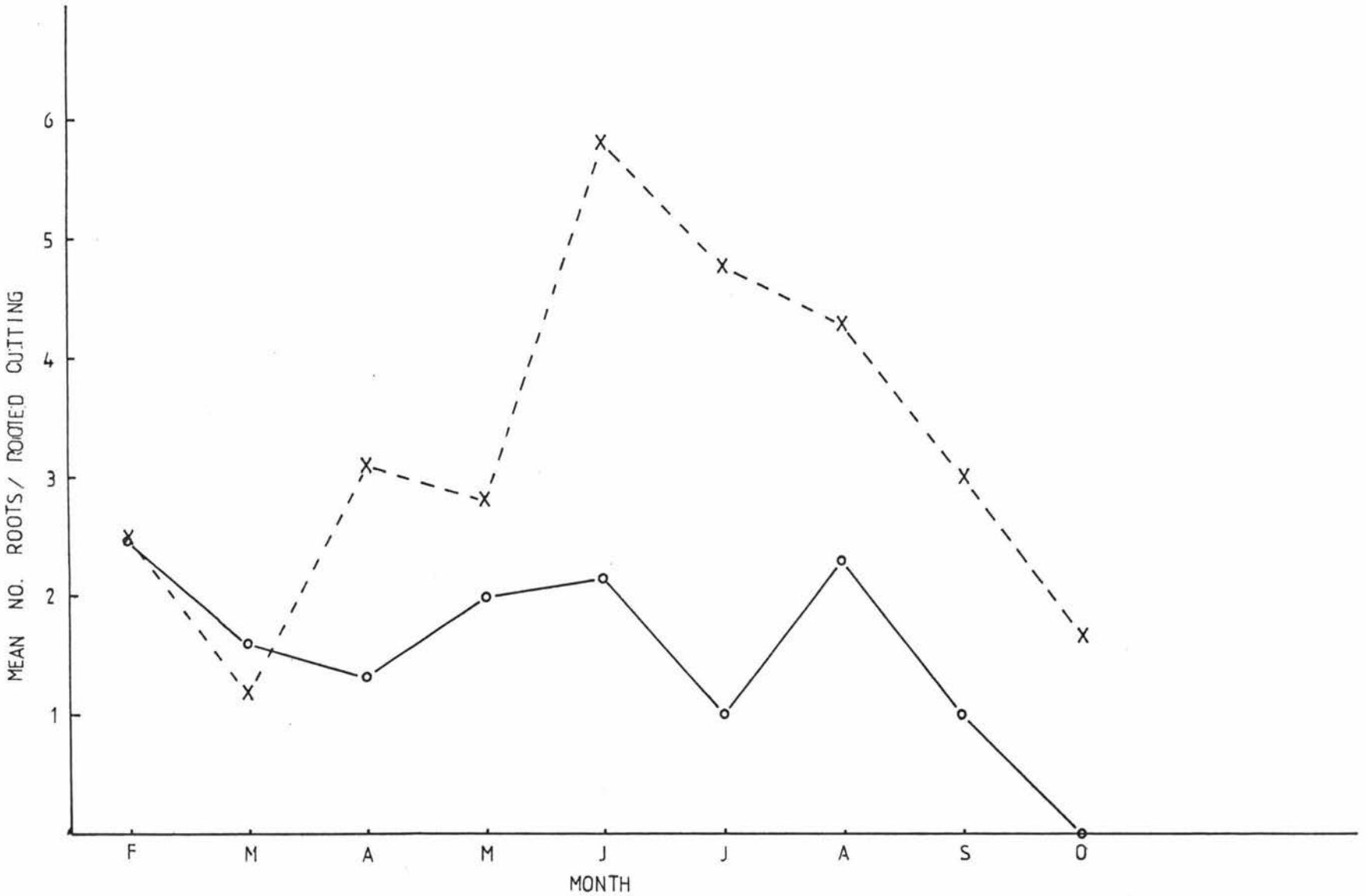


Figure 2b. Seasonal fluctuations in mean number of roots per rooted cutting of J. 'Skyrocket' (x--x) and J. 'Pathfinder' (o—o).

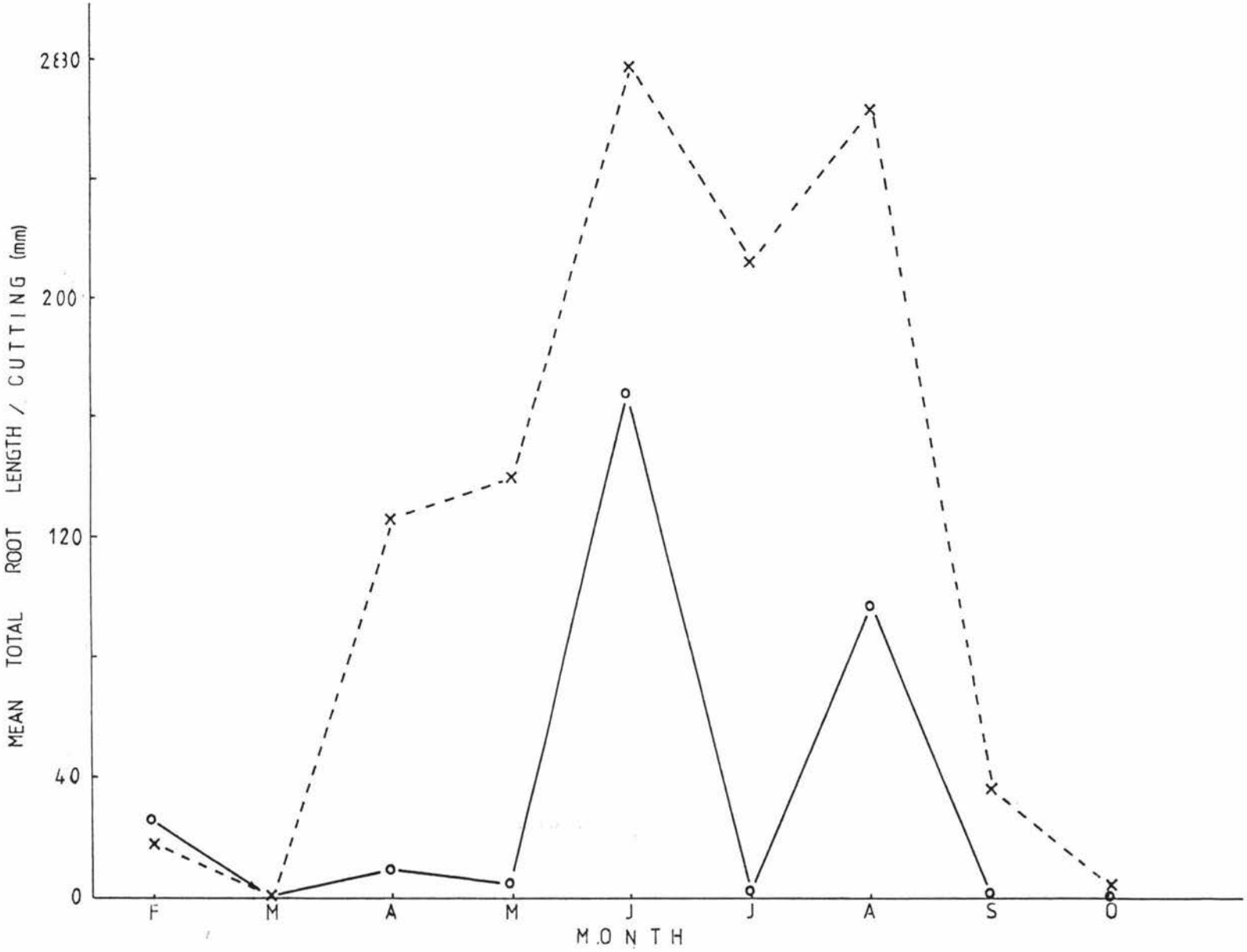


Figure 3a. Seasonal fluctuations in mean total root length per cutting of J. 'Skyrocket' (x---x) and J. 'Pathfinder' (o—o).

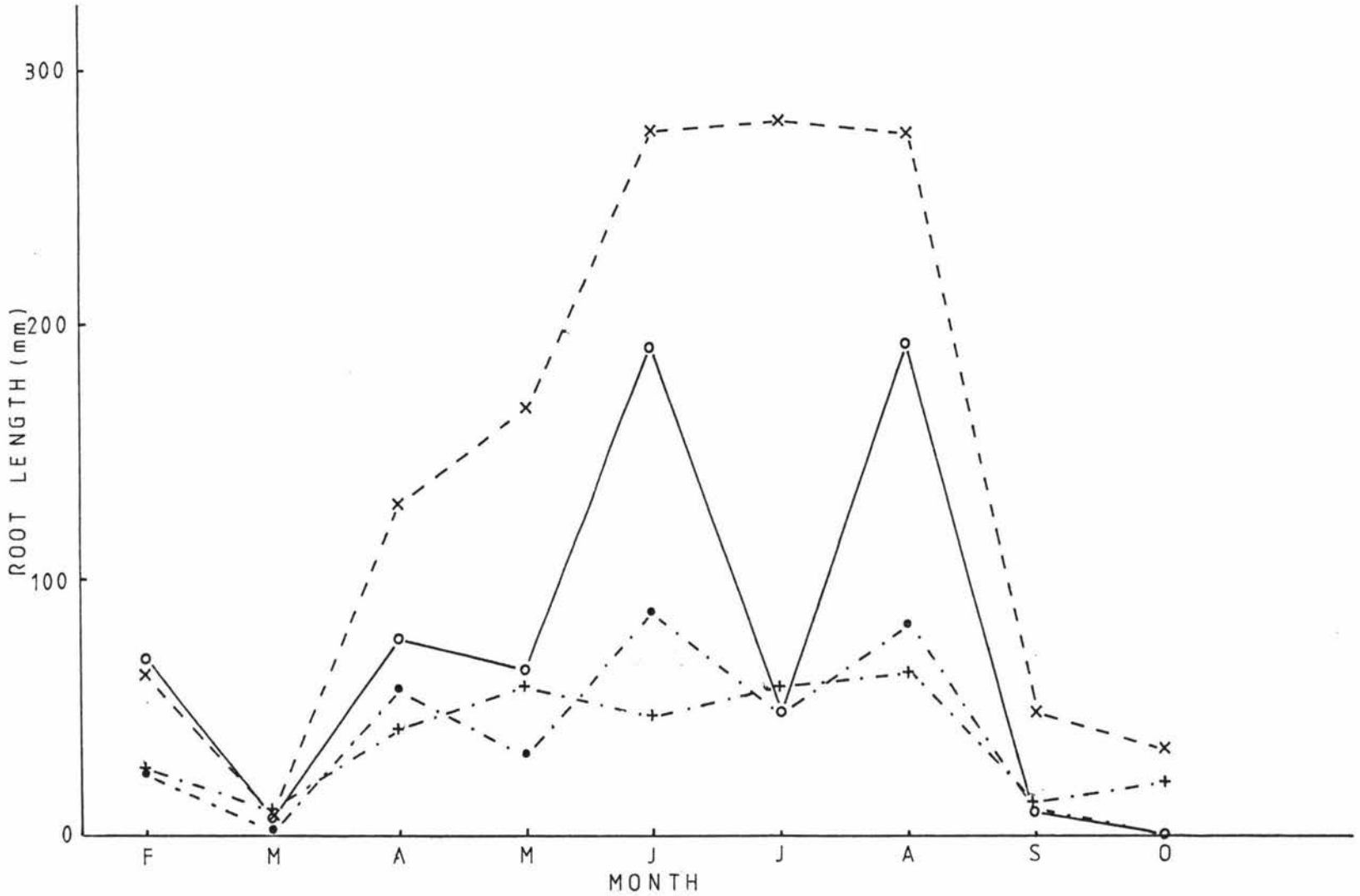


Figure 3b. Seasonal fluctuations in mean total root length per rooted cutting and mean root length of J. 'Skyrocket' (x--x ;+---+) and J. 'Pathfinder' (o—o ;•---•).

Table 2a. Mean number of cuttings showing new shoot growth/8

Cultivar	Month of Harvest			
	Jun	Jul	Aug	Sep
J.'Skyrocket'	0.33	4.67	8.0	8.0
J.'Pathfinder'	3.33	0	7.67	8.0

Table 2b. Mean shoot growth per cutting (mm)

Cultivar	Month of Harvest			
	Jun	Jul	Aug	Sep
J.'Skyrocket'	0.42	2.38	4.04	5.50
J.'Pathfinder'	1.0	0	4.0	8.25

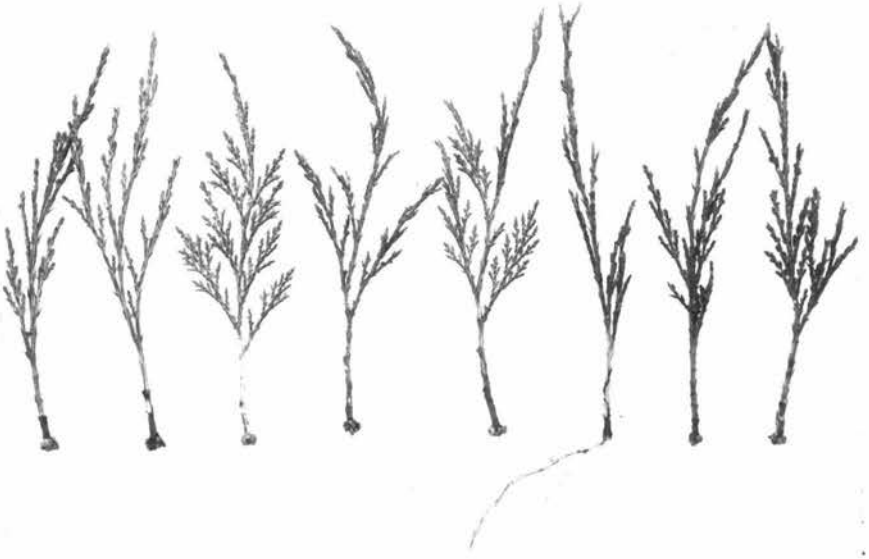
Tables 2(a,b). Variation in shoot activity of J.'Skyrocket' and J.'Pathfinder' cuttings at lifting as indicated by a) mean number of cuttings showing new shoot growth and b) mean shoot growth per cutting with month of excision.

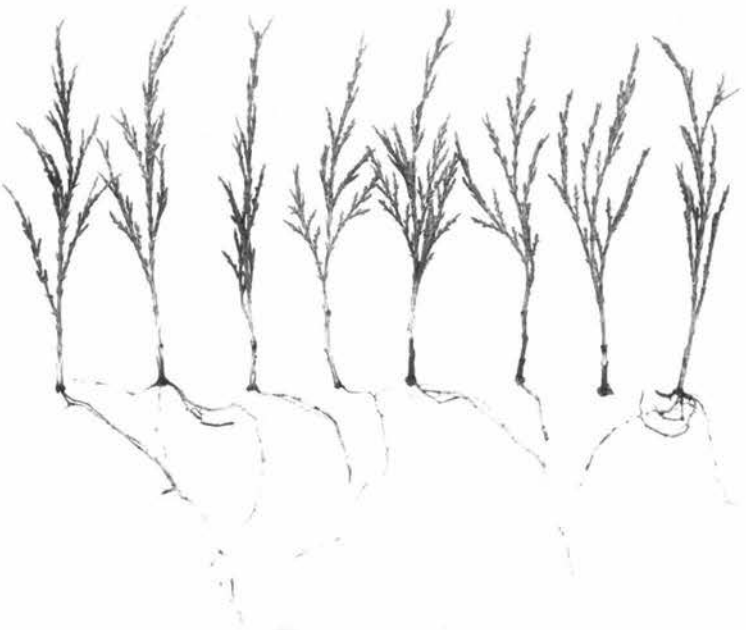
4.1.2 J. scopulorum 'Pathfinder'

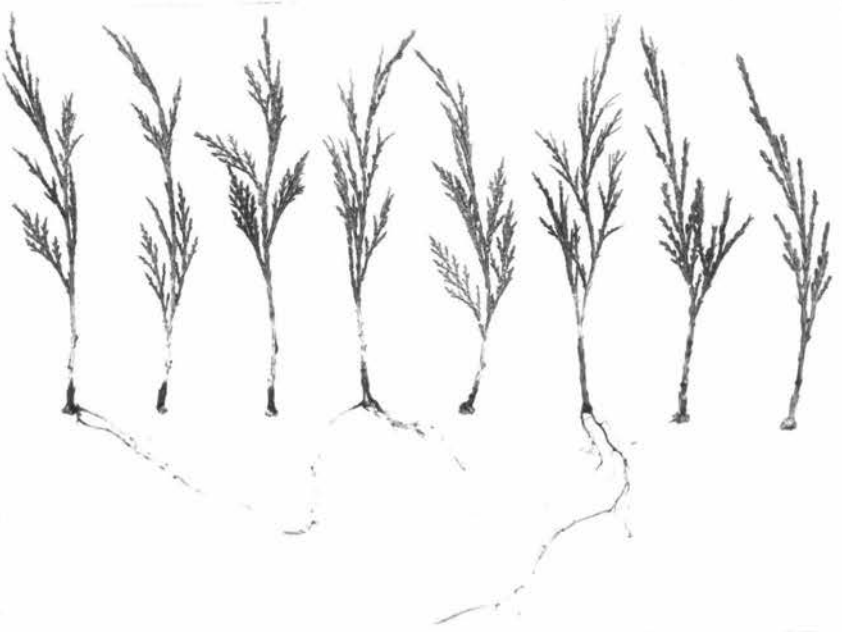
The mean number of cuttings rooted gradually diminished from an intermediate level in February to a low in May. An abrupt rise in June produced a high level of rooting which was significantly different from that in all other months with the exception of August (Table 1a, Figure 1, Plate 2). The intermediate level encountered in August was preceded and followed by low levels of rooting which then remained low in spring. No cuttings rooted in October.

No significant differences between months were found in mean number of roots per cutting although seasonal fluctuations were similar to those of mean number of cuttings rooted (Table 1b, Figure 2a). The mean number of roots per rooted cutting varied relatively little but exhibited a slightly different pattern in that means obtained in February and August exceeded that in June slightly and an increase was detected in May, a month

Plate 2. Photographic representation of the mean number of J. scopulorum 'Pathfinder' cuttings rooted 10 weeks after excision in April (top), June (centre) and August (bottom). Magnification approx. X 0.42.







earlier than in the corresponding data per cutting (Figure 2b). It was noted that prior to June roots invariably emerged through the side wound but did so less frequently in cuttings excised in later months. This was in contrast with the situation in J. 'Skyrocket' in which the proportion of roots emerging through the wound increased after March.

Mean total root length per cutting was significantly greater in June than in any other month except August and was different from that obtained in March, July, September and October to a highly significant degree (Table 2c, Figure 3a). Mean total root length per rooted cutting and mean root length had begun to improve by April (Figure 3b).

Bud break had taken place in just over half the cuttings taken in June and in almost all those from August by the time they were lifted. No new growth was present in material from July. Tip wilting and death occurred in a few cuttings which had made most extension growth in September and in a greater number in October but to a lesser extent compared with J. 'Skyrocket'.

4.1.3 Comparison of J. virginiana 'Skyrocket' and J. scopulorum 'Pathfinder' within the same Month.

The mean number of J. 'Skyrocket' cuttings rooted exceeded that of J.'Pathfinder' in every month except February (Figure 1). Significant differences between the two cultivars were found in April and July (Table 1a). The difference between the grand means was highly significant.

Mean root number per cutting and mean total root length per cutting were also greater in J.'Skyrocket' than in J.'Pathfinder' in every month except for the marginal difference in February (Figures 2a and 3a). Significant differ-

ences between the two varieties were found in April and May and a highly significant difference in July with regard to both parameters (Tables 1b and c). A highly significant difference in mean total root length per cutting also existed in June. Mean root length of J.'Pathfinder' followed a similar but more erratic seasonal pattern than J.'Skyrocket' (Figure 3b).

More cuttings of J.'Pathfinder' than J.'Skyrocket' showed shoot activity at the time of lifting the June cuttings although both shoot and root-forming activity had diminished again in the July cuttings of J.'Pathfinder' (Tabes 2a and 1a-c). J.'Pathfinder' cuttings taken in September had made more shoot growth prior to lifting than those of J.'Skyrocket' (Table 2b).

4.1.4 C. sempervirens 'Swanes Golden'

Cuttings of C.'Swanes Golden' rooted well in February and June but poorly in March (Figures 4a-c). All parameters analysed were slightly, but not significantly, superior in February than June although mean root length was greater in June (416 mm) than in February (246 mm). The mean number of cuttings rooted and mean number of roots per cutting obtained in March were lower than those in the other two months to a highly significant extent but mean total root length per cutting was not significantly different (Tables 3a-c).

Cuttings excised in June had made new shoot growth by the lifting date but as this was not always readily distinguishable the data has not been included.

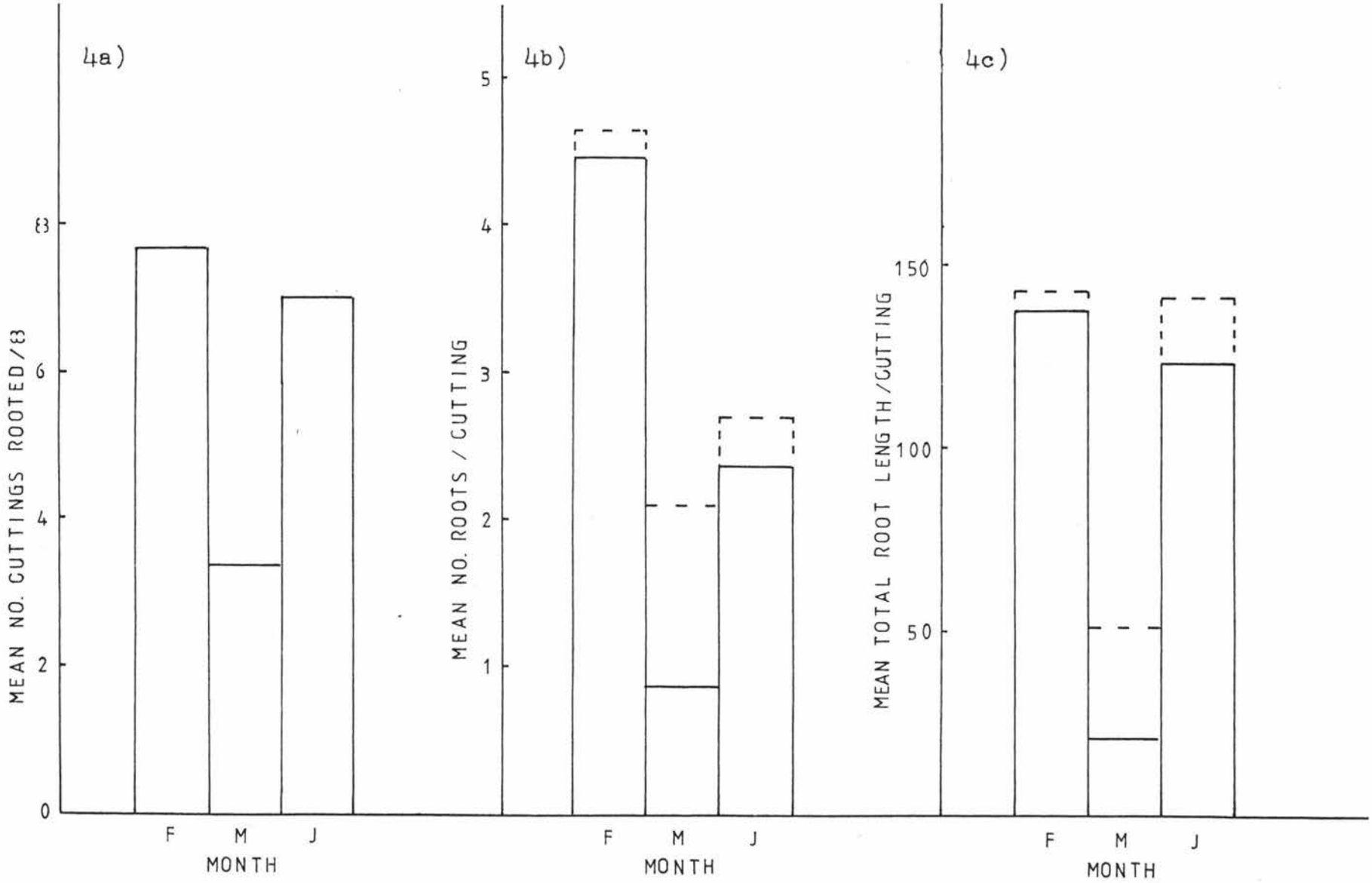


Figure 4(a-c). Variation in a) mean number of cuttings rooted, b) mean number of roots per cutting and c) mean total root length per cutting of C. 'Swanes Golden' with month of excision. □ = mean no. roots/cutting, mean total root length/cutting; ⊡ = per rooted cutting.

Table 3a. Mean number of cuttings rooted/8

Month of Harvest			
Feb	Mar	Jun	Mean
7.67_{aA}	3.33	7.0_{aA}	6.0

Table 3b. Mean number of roots per cutting

Month of Harvest			
Feb	Mar	Jun	Mean
4.46_{aA}	0.88	2.38_{aA}	2.57

Table 3c. Mean total root length per cutting (mm)

Month of Harvest			
Feb	Mar	Jun	Mean
137.5_{a}	21.3_{a}	123.8_{a}	94.2

Tables 3(a-c). Variation in a) mean number of cuttings rooted, b) mean number of roots per cutting and c) mean total root length per cutting of C.'Swanes Golden' with month of excision. Means followed by the same lower- or upper-case character not significantly different at the 5% or 1% levels of significance respectively.

4.1.5 Subsequent Growth of Rooted Cuttings

Substantial gains in growth of the shoot and root systems had been made in cuttings of J.'Skyrocket' taken during February to July inclusive and in cuttings of J.'Pathfinder' taken prior to July (Table 4). These samples of rooted cuttings had made sufficient growth to warrant repotting in midsummer, particularly those of J.'Skyrocket', but for the puposes of this study remained in the same containers. Rather less, but still satisfactory, growth had

been made by autumn in cuttings harvested in most other months. Cuttings of C.'Swanes Golden' from all months were also ready to be potted on in early autumn.

Cultivar	Month of Excision				
	Feb	Mar	Apr	May	
J.'Skyrocket'	478	468	469	356	
J.'Pathfinder'	249	258	235	264	
C.'Swanes Golden'	186	149	-	-	
Jun	Jul	Aug	Sep	Oct	
454	394	238	201	-	
263	207	200	142	-	
146	-	-	-	-	

Table 4. Variation in mean height (mm) above soil level of rooted cuttings of J.'Skyrocket', J.'Pathfinder' and C.'Swanes Golden' with month of excision as recorded in autumn.

4.1.6 Summary of Seasonal Trends

Both varieties of juniper attained maximum rooting capacity as determined by all parameters in June after having fallen from an apparently small peak in late summer. Rootability diminished rapidly again in spring. High rooting percentages were obtained two months earlier in J. 'Skyrocket' than in J. 'Pathfinder' and levels remained high for a longer period in spring. Other parameters of rooting tended to change more gradually. Not only was the favourable period for rooting J. 'Pathfinder' cuttings more brief but rooting was generally more erratic than that of J. 'Skyrocket'. Rootability of J. 'Skyrocket' exceeded that of J. 'Pathfinder' in all months except February. Cuttings of C. 'Swanes Golden' rooted well in February and June but

poorly in March.

Shoot growth had begun by the time of lifting in cuttings of all cultivars taken in June and later months with the exception of those of J. 'Pathfinder' taken in July. Rooted cuttings which had been excised prior to, and in the case of J. 'Skyrocket' including, July had made vigorous root and shoot growth by late summer in the junipers and by autumn in the Cupressus sp.

4.2 Growth Cabinet Study

Stock plants of J.'Pathfinder' and C.'Swanes Golden' were grown in a warm or cold environment for 5 weeks after which cuttings were excised and rooted over basal heat for 8 weeks in warm or cold air temperatures as described in Materials and Methods.

4.2.1 J. scopulorum 'Pathfinder'

Stock plants from the cold environment provided cuttings which rooted in the greatest numbers, and the low air temperature during the rooting phase was also more suitable than the WH environment (Figures 5a, 6a and 7a). Mean number of cuttings rooted was significantly different between the WP WH and CP CH treatments (Table 5a). Trends in mean root number per cutting and mean total root length per cutting were similar to those described above, significant differences again occurring between the WP WH and CP CH treatments (Tables 5b and c). Responses to air temperature were similar in means calculated on a per rooted cutting basis (Figures 5a, 6a and 7a).

It was noted that red pigmentation in the stock plants and cuttings became more highly developed with duration of exposure to low temperatures, but a preliminary investigation involving a visual score of colour intensity indicated no relationship with root number in individual cuttings (c.f. the more detailed study with Acer by Bachelard and Stowe, 1962).

Table 5a. Mean number of cuttings rooted/8

Cutting Environment	Stock Plant Environment		
	WP	CP	Mean
WH	1.25_a	2.50_a	1.88
CH	3.00_a	4.50_a	3.75
Mean	2.13_a	3.50_a	

Table 5b. Mean number of roots per cutting

Cutting Environment	Stock Plant Environment		
	WP	CP	Mean
WH	0.19_a	0.44_a	0.31
CH	0.72_a	1.34_a	1.03
Mean	0.45_a	0.89_a	

Table 5c. Mean total root length per cutting (mm)

Cutting Environment	Stock Plant Environment		
	WP	CP	Mean
WH	0.38_a	3.72_a	2.05
CH	8.69_a	28.16_a	18.42
Mean	4.53_a	15.94_a	

Tables 5(a-c). Growth cabinet study. Variation in rooting of J.'Pathfinder' cuttings with air temperature treatment. Means within same cutting environment followed by same lower- or upper-case character not significantly different at the 5% or 1% levels of significance respectively. Means in the same or different parent material environments indicated by * significantly different at the 5% level; none significantly different at the 1% level.

Table 6a. Mean number of cuttings rooted/8

Cutting Environment	Stock Plant Environment		
	WP	CP	Mean
WH	6.75_{a}	6.25_{a}	6.50
CH	7.75_{aA}	5.50_{A}	6.63
Mean	7.25_{A}	5.88_{B}	

Table 6b. Mean number of roots per cutting

Cutting Environment	Stock Plant Environment		
	WP	CP	Mean
WH	5.09_{a}	4.84_{a}	4.97
CH	8.81_{A} *	4.19_{B}	6.50
Mean	6.95_{aA}	4.52_{bA}	

Table 6c. Mean total root length per cutting (mm)

Cutting Environment	Stock Plant Environment		
	WP	CP	Mean
WH	117.22_{a}	95.97_{a}	106.59
CH	165.38_{A} *	70.00_{B} *	117.69
Mean	141.30_{aA}	82.98_{bA}	

Tables 6(a-c). Growth cabinet study. Variation in rooting of C.'Swanes Golden' cuttings with air temperature treatment. Means within same cutting environment followed by same lower- or upper-case character not significantly different at the 5% or 1% levels of significance respectively. Means in the same or different parent material environments indicated by * significantly different at the 5% level; none significantly different at the 1% level.

4.2.2 C. sempervirens 'Swanes Golden'

All parameters of C.'Swanes Golden' were greatest in WP material, particularly if rooted in the CH environment (Figures 5b, 6b and 7b). Grand means of all parameters were significantly greater in the WP compared with the CP environment, the difference in the mean number of cuttings rooted being highly significant and that in mean total root length significantly different (Tables 6a, b and c). For analysis of variance see Appendix 4. The only other significant difference in mean number of cuttings rooted was found between the WP and CP material in the CH environment, indicating a significant interaction between the stock-plant and cutting environments. The mean number of roots per cutting obtained from WP material under CH conditions was also highly significantly greater when compared with CP material under the same rooting temperatures, and significantly greater than the remaining two treatment combinations (Table 6b). A similar, highly significant difference existed in mean total root length per cutting between WP and CP material in the CH environment and a significant difference between the WP CH and CP WH treatments (Table 6c). Means calculated per rooted cutting followed similar trends although mean root length was marginally superior under WH compared with CH conditions (Figures 5b, 6b and 7b).

4.2.3 Summary

Air temperature at the parent plant and cutting stages significantly effected rooting of both genera. Whereas

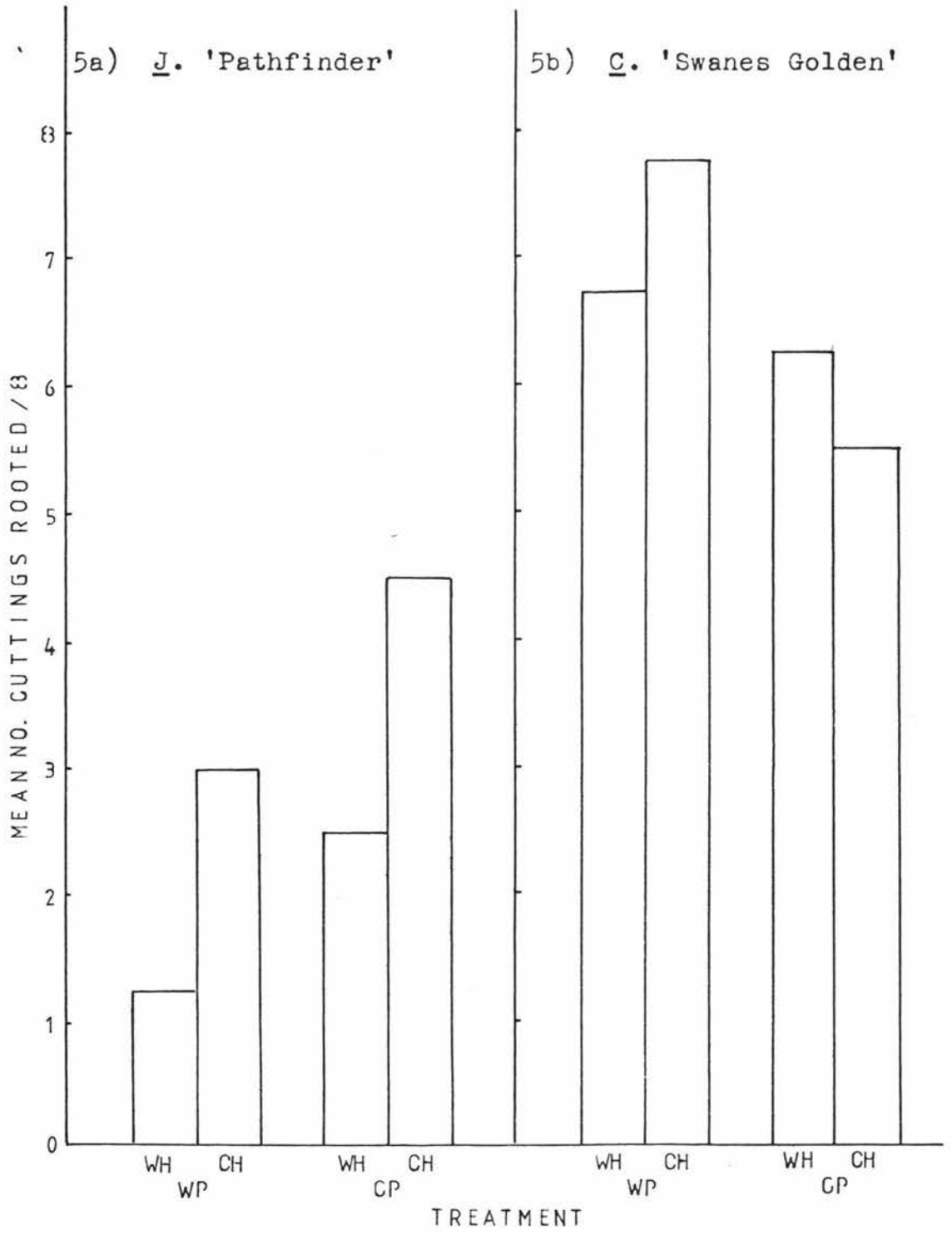


Figure 5(a,b). Growth cabinet study. Variation in mean number of a) J. 'Pathfinder' and b) C. 'Swanes Golden' cuttings rooted with air temperature treatment.

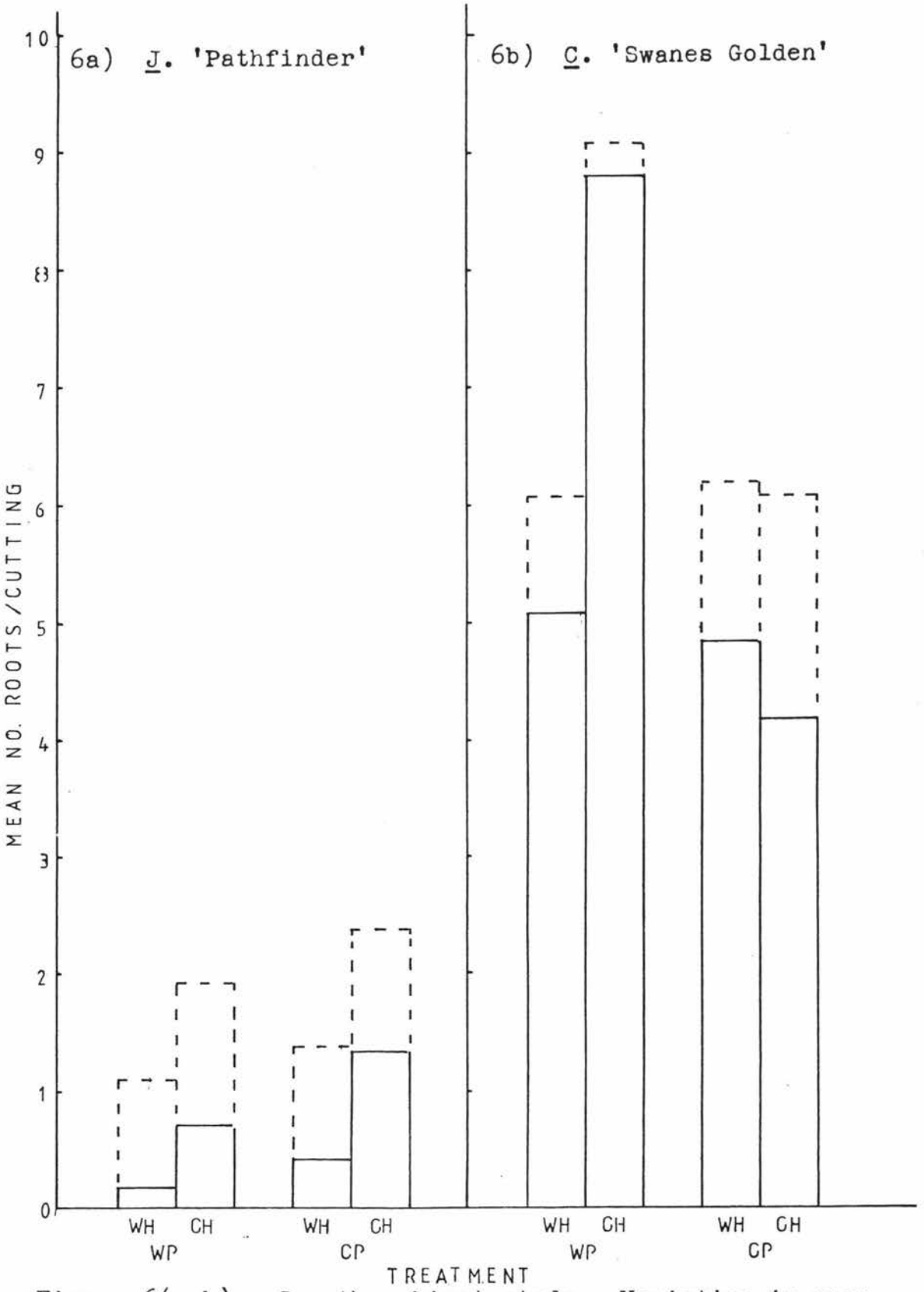


Figure 6(a,b). Growth cabinet study. Variation in mean number of roots per cutting of a) J. 'Pathfinder' and b) C. 'Swanes Golden' with air temperature treatment. □ = mean no. roots/cutting; ⬚ = mean no. roots /rooted cutting.

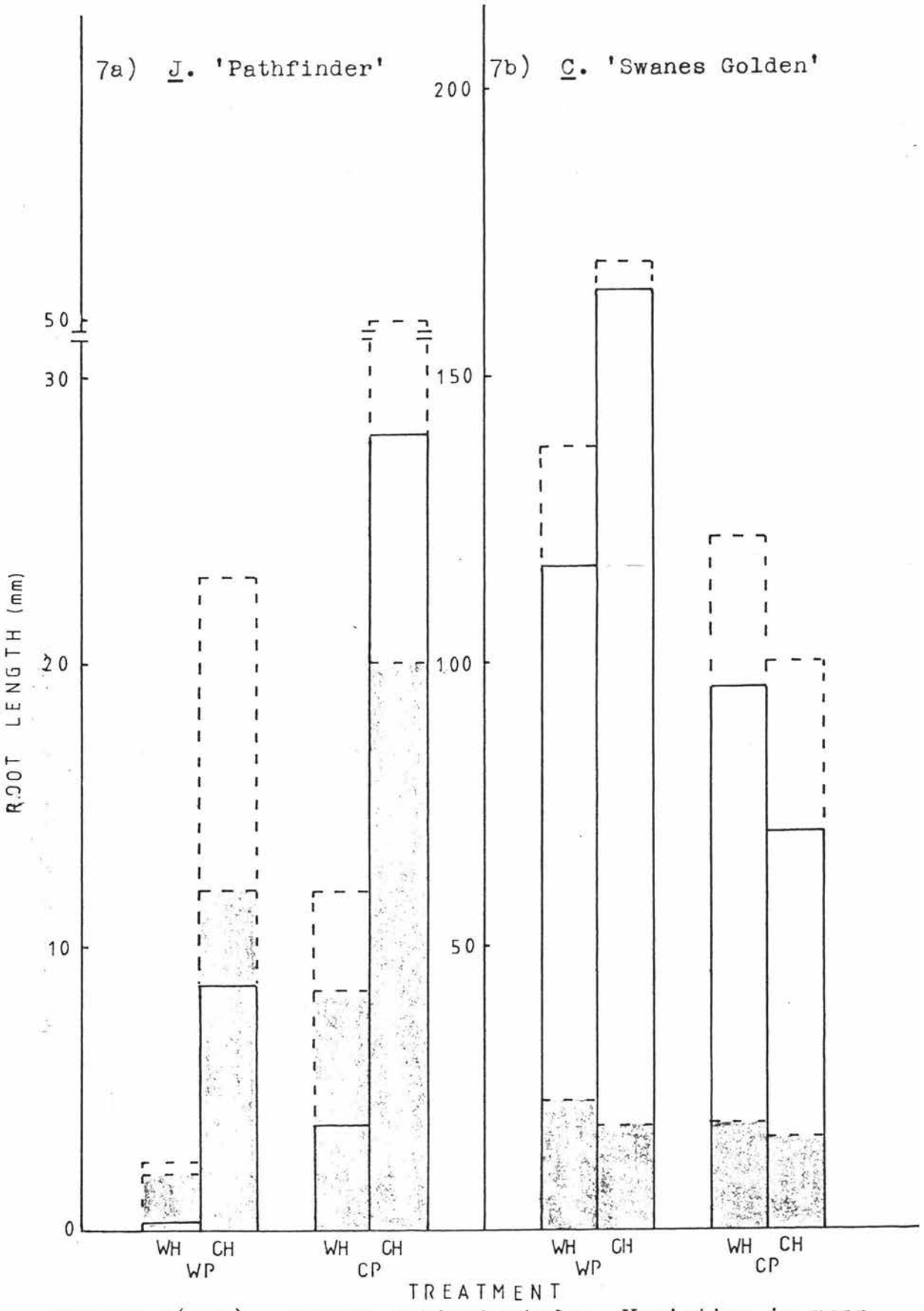


Figure 7(a,b). Growth cabinet study. Variation in mean total root length per cutting and mean root length of a) J. 'Pathfinder' and b) C. 'Swanes Golden' with air temperature treatment. □ = mean tot. root length/cutting, ⁚ = mean tot. root length/rooted cutting; ▪ = mean root length.

cold stock plant and cutting environments were benificial for rooting the juniper cuttings, a warm stock plant environment was more suitable for the Cupressus sp. especially if followed by low air temperatures during rooting. Cuttings of C.'Swanes Golden' in general rooted more readily and profusely than those of J.'Pathfinder'.

4.3 Mid Winter Study

Cuttings of the four cultivars prepared from material exposed to differing air temperature environments were placed in a heated or unheated glasshouse over basal heat as outlined in Materials and Methods. All cultivars were subjected to the "warm" and "cold" parent plant treatments and, where material was available, treatments involving exposure to lower temperatures during the two weeks prior to cutting excision. Shoot growth had commenced in some cuttings approximately 3 weeks before lifting. Samples of rooted cuttings from each treatment were grown on until the following autumn.

4.3.1 *J. virginiana* 'Skyrocket'

Mean number of cuttings rooted was high in all treatments except WCP material in the WH environment. All cuttings from CP stock plants rooted. The WCP WH treatment combination reduced rooting percentage to a highly significant extent when compared with other parent material treatments in the WH environment and also brought about a significant reduction compared with the WCP CH treatment (Table 7a, Figure 8a). For analysis of variance of all cultivars see Appendix 5.

The mean number of roots per cutting and mean total root length per cutting were also greatest in CP material (Figures 9a and 10a). Significant and highly significant differences were found in mean root number and mean total root length per cutting respectively between the WCP WH and CP WH treatments (Tables 7b and c). Mean total root length

Table 7a. Mean number of cuttings rooted/8

Cutting Environment	Parent Material Environment				
	WP	WCP	CP	CCP	Mean
WH	7.67_{aA}	4.33_{*}	8.00_{aA}	7.33_{aA}	6.83
CH	7.67_{a}	7.33_{a}	8.00_{a}	7.00_{a}	7.50
Mean	7.67_{aAB}	5.83_{B}	8.00_{aA}	7.17_{aAB}	

Table 7b. Mean number of roots per cutting

Cutting Environment	Parent Material Environment				
	WP	WCP	CP	CCP	Mean
WH	4.33_{ab}	1.79_{b}	5.88_{a}	4.50_{ab}	4.12
CH	3.38_{a}	3.50_{a}	5.83_{a}	3.67_{a}	4.09
Mean	3.85_{ab}	2.65_{b}	5.85_{a}	4.08_{ab}	

Table 7c. Mean total root length per cutting (mm)

Cutting Environment	Parent Material Environment				
	WP	WCP	CP	CCP	Mean
WH	219.19_{aAB}	37.83_{B} *	239.38_{aA}	170.00_{aAB}	166.62 *
CH	229.75_{a}	194.38_{a}	227.96_{a}	234.21_{a}	234.07
Mean	224.75_{a}	116.10_{b}	258.67_{a}	202.10_{ab}	

Tables 7(a-c). Midwinter study. Variation in a) mean number of cuttings rooted, b) mean number of roots per cutting and c) mean total root length per cutting of J.'Skyrocket' with air temperature treatment. Means within the same propagation environment followed by the same lower or upper case character not significantly different at the 5% or 1% levels of significance respectively. Means within the same parent material environment indicated if significantly different at the * = 5% and ** = 1% levels.

Table 8a. Mean number of cuttings showing new shoot growth/8

Cutting Environment	Parent Material Environment				
	WP	WCP	CP	CCP	Mean
WH	1.33_{aA}	1.33_{aA}	4.33_{A} **	1.33_{aA}	2.08 *
CH	0.00_{a}	0.33_{a}	0.33_{a}	1.67_{a}	0.58
Mean	0.67_{a}	0.83_{a}	2.33_{a}	1.50_{a}	

Table 8b. Mean shoot growth per cutting (mm)

Cutting Environment	Parent Material Environment				
	WP	WCP	CP	CCP	Mean
WH	0.33_{A}	0.54_{A}	2.58 **	0.33_{A}	0.95
CH	0.00_{a}	0.04_{a}	0.04_{a}	0.25_{a}	0.08
Mean	0.17_{aA}	0.29_{aA}	1.31	0.29_{a}	

Tables 8(a and b). Midwinter study. Variation in a) mean number of cuttings showing new shoot growth and b) mean shoot growth per cutting of J.'Skyrocket' with air temperature treatment. Means within the same propagation environment followed by the same lower or upper case character not significantly different at the 5% or 1% levels of significance respectively. Means within the same parent material environment indicated if significantly different at the * = 5% and ** = 1% levels.

per cutting was also greater in the CH than the WH rooting environments to a significant degree in the WCP material and between the grand means. Mean root length was highest under CH conditions regardless of parent material treatment. Mean root number per cutting was slightly higher in the WH compared with the CH environment except for WCP material.

A sample of cuttings indicating the range of rooting obtained is shown in Plate 3.

The mean number of cuttings showing active shoot growth at lifting was significantly greater in CP compared with other parent material under WH conditions (Tables 8a and b, Figures 11a and 12a). On comparison of grand means, shoot growth by CP material was highly significantly greater than that made by cuttings of other parent material. The mean number of cuttings showing shoot activity was greater in the WH than the CH environment in all except CCP material and this difference was highly significant in CP material and significant on comparison of the grand means. Mean shoot growth was also greater in the WH compared with the CH propagation environment in each case and to a highly significant extent in CP material. By far the greatest amount of shoot activity occurred in the CP WH treatment combination and none in the WP CH combination.

Strong growth in both the shoot and root systems had been made in rooted cuttings from all treatments by autumn.

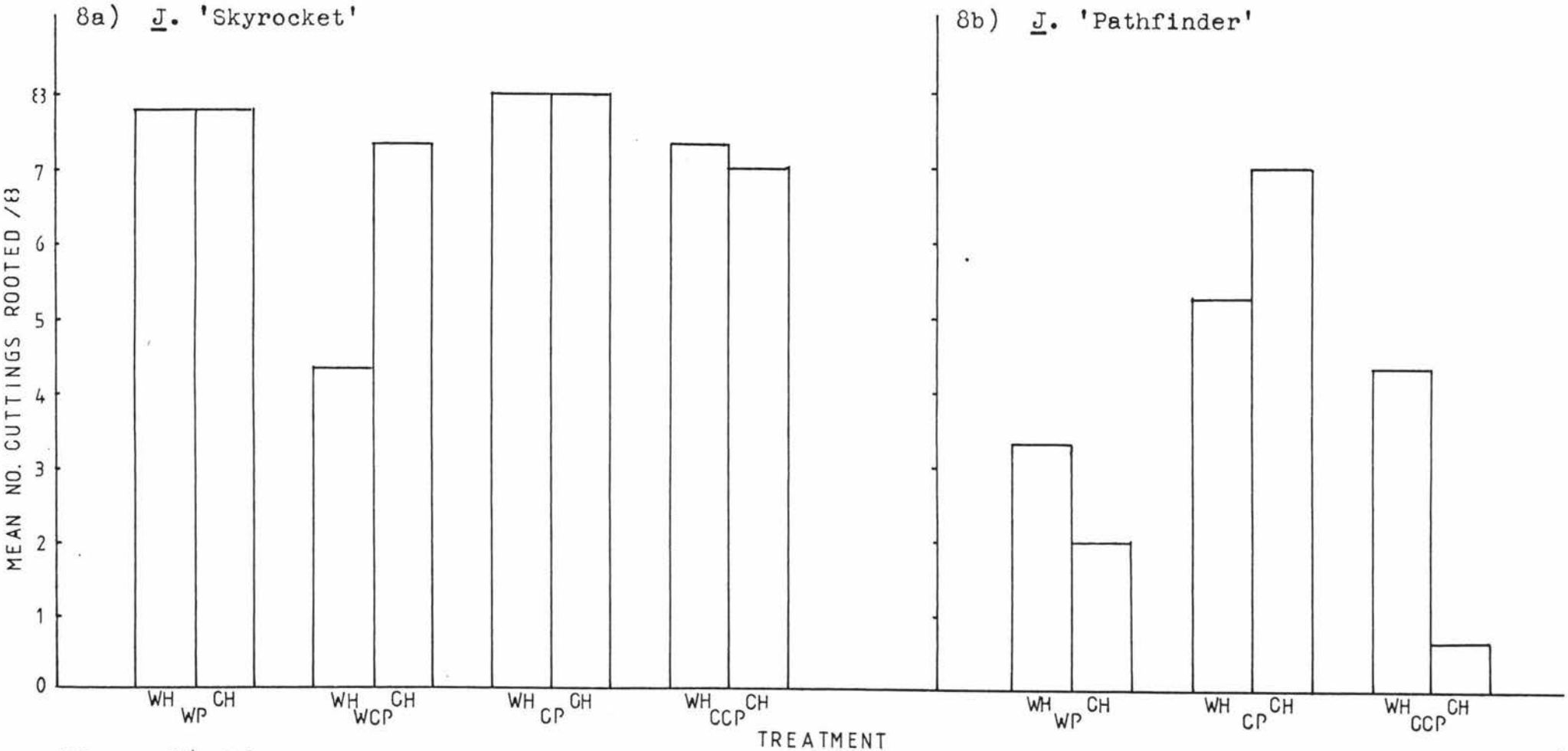


Figure 8(a,b). Variation in mean number of a) J. 'Skyrocket' and b) J. 'Pathfinder' cuttings rooted with air temperature treatment.

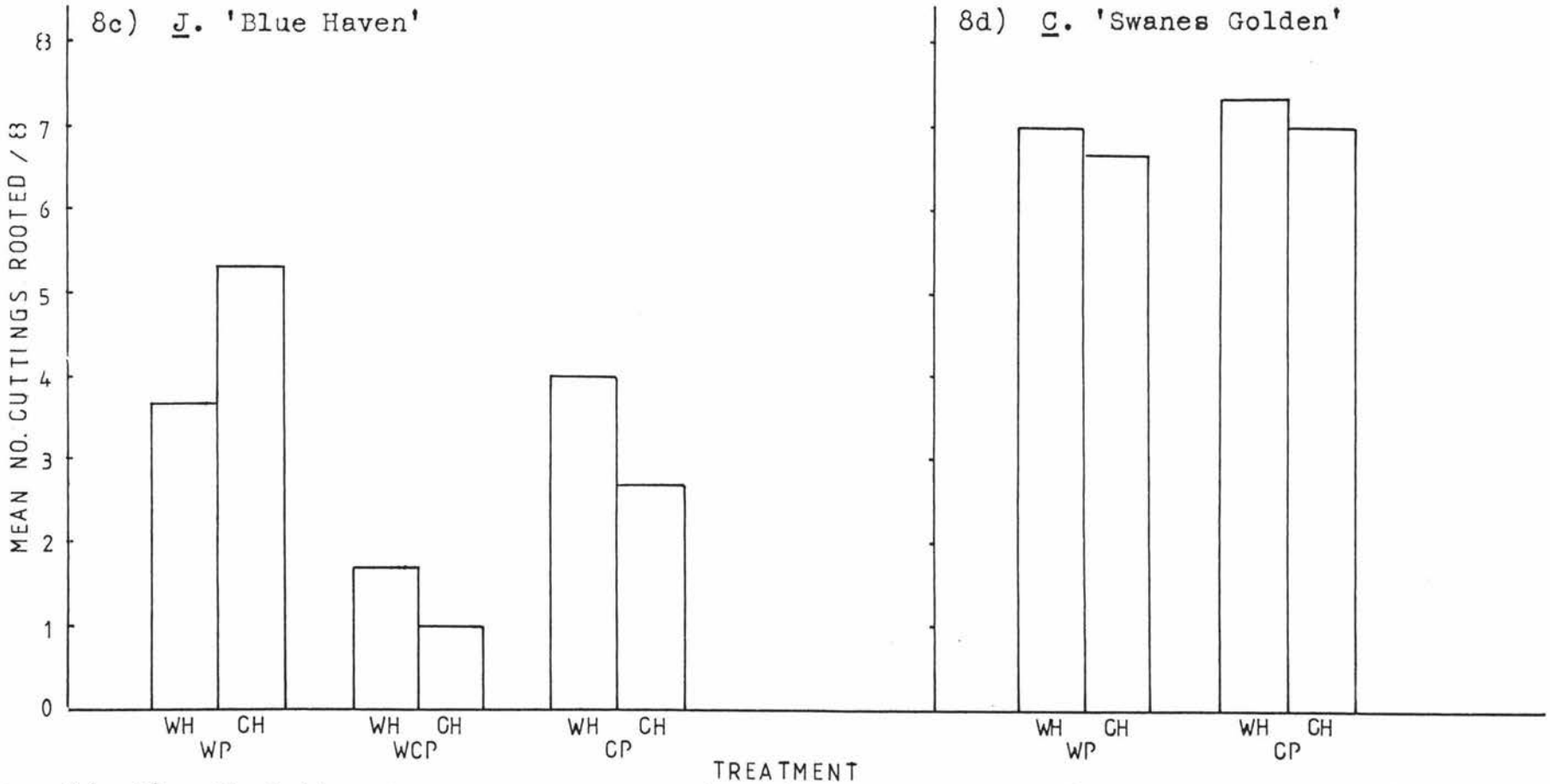


Figure 8(c,d). Variation in mean number of c) J. 'Blue Haven and d) C. 'Swanes Golden' cuttings rooted with air temperature treatment.

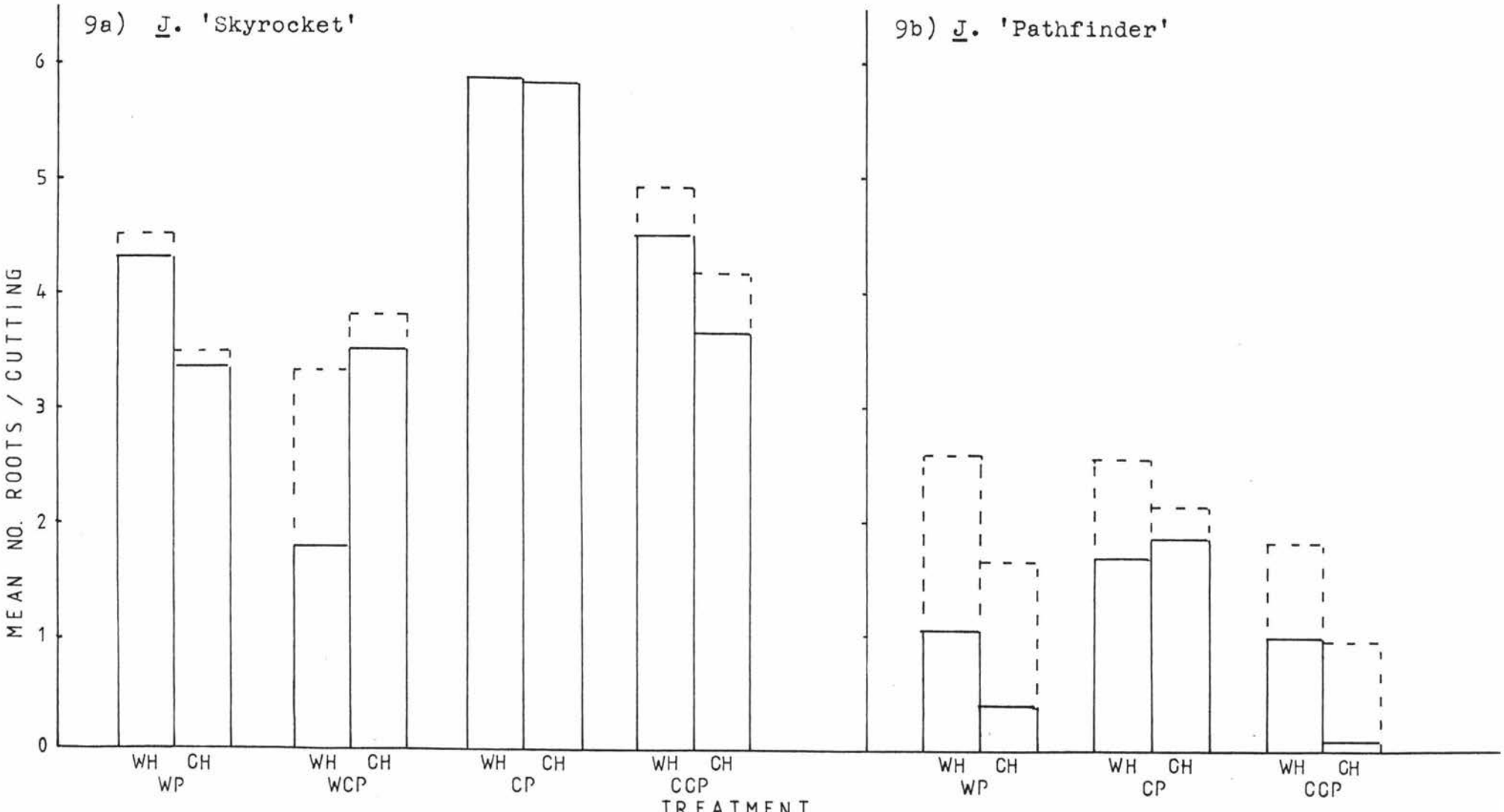


Figure 9(a,b). Variation in mean number of roots per cutting of a) J. 'Skyrocket' and b) J. 'Pathfinder' with air temperature treatment. □ = mean no./cutting; ⁚ = mean no./rooted cutting.

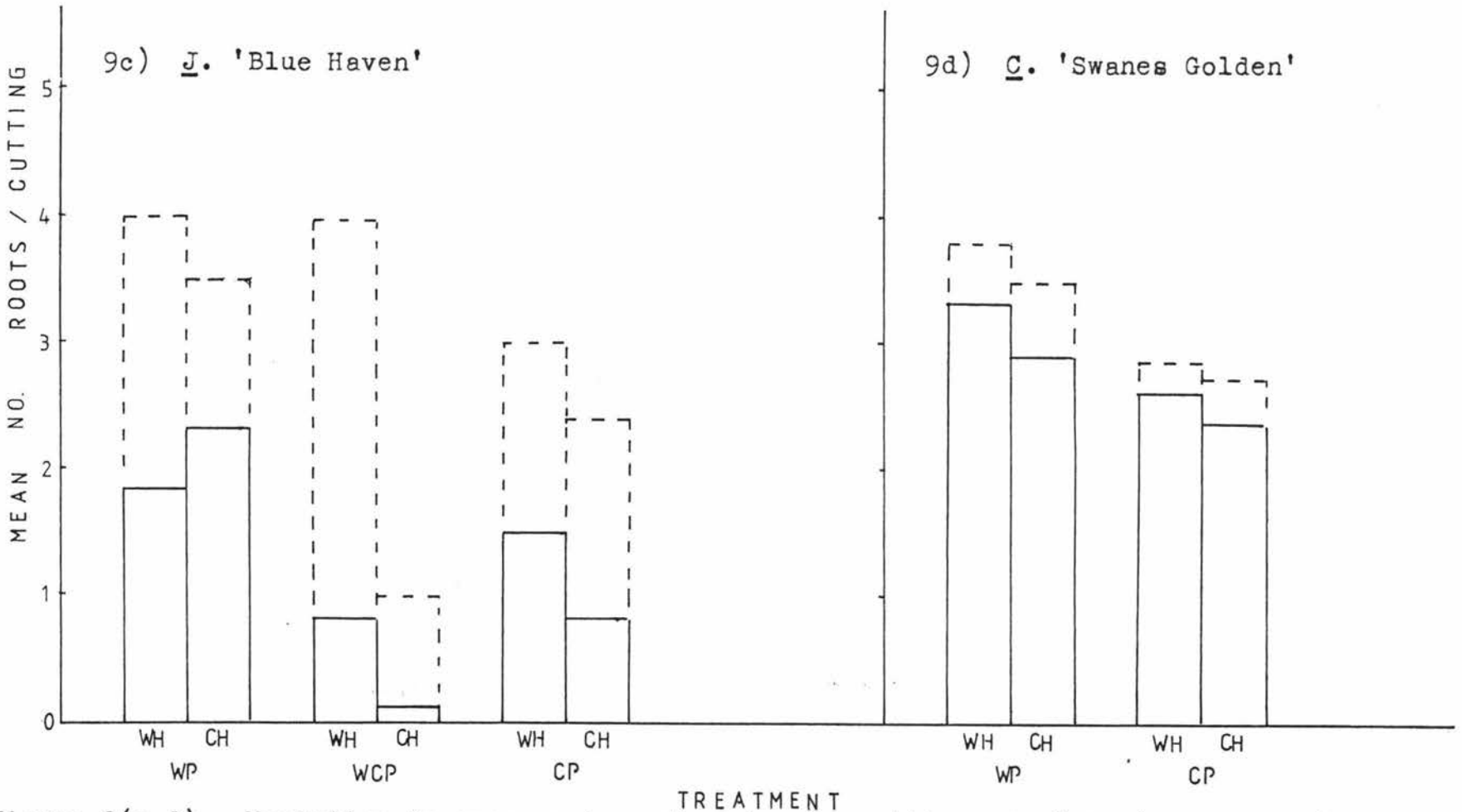


Figure 9(c,d). Variation in mean number of roots per cutting of c) J. 'Blue Haven' and d) C. 'Swanes Golden' with air temperature treatment. □ = mean no./cutting; ⊡ = mean no./rooted cutting.

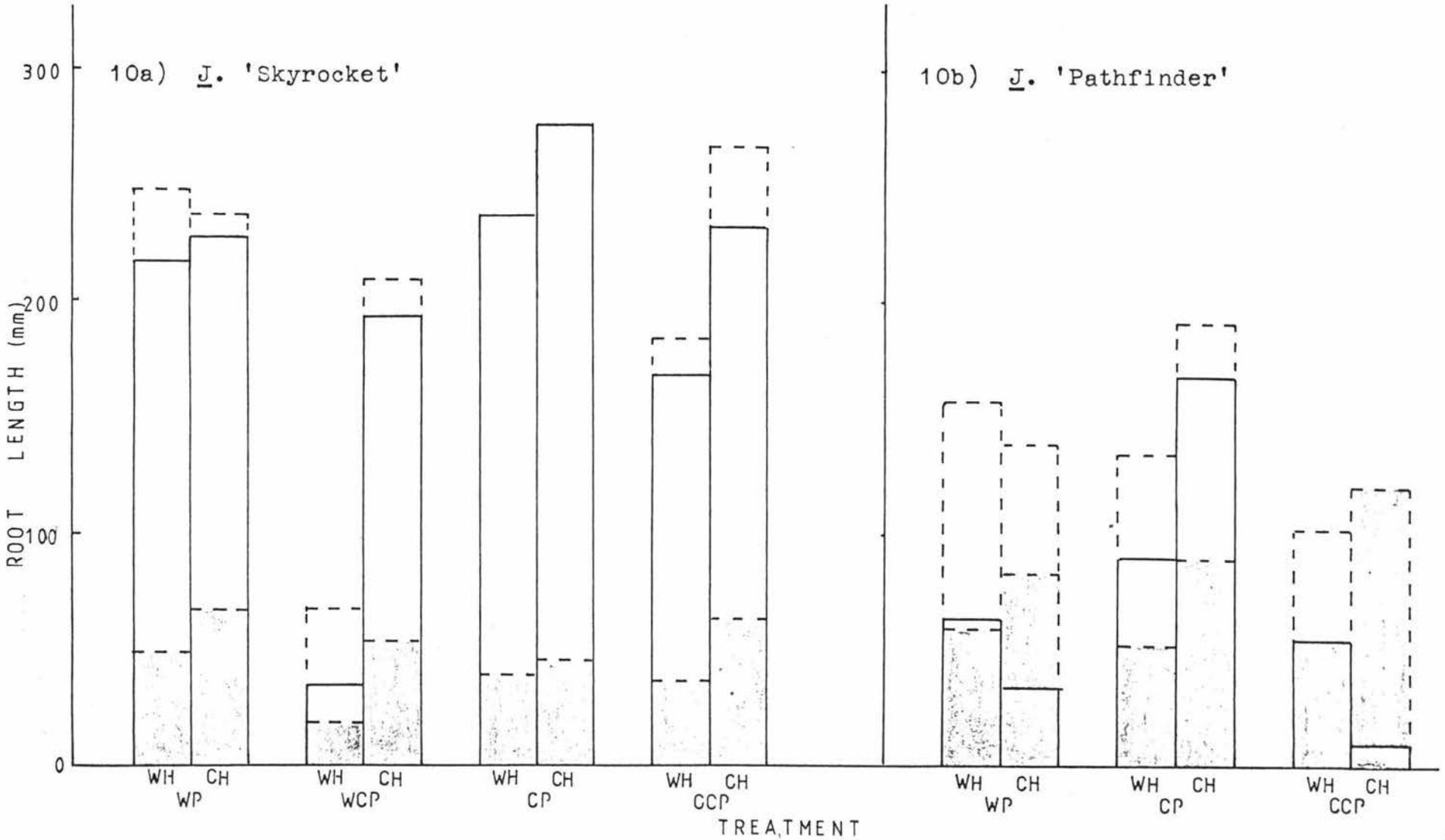


Figure 10(a,b). Variation in mean total root length per cutting and mean root length of a) J. 'Skyrocket' and b) J. 'Pathfinder' with air temperature treatment. □ = mean total root length/cutting; ▯ = mean total root length/rooted cutting; ▩ = mean root length.

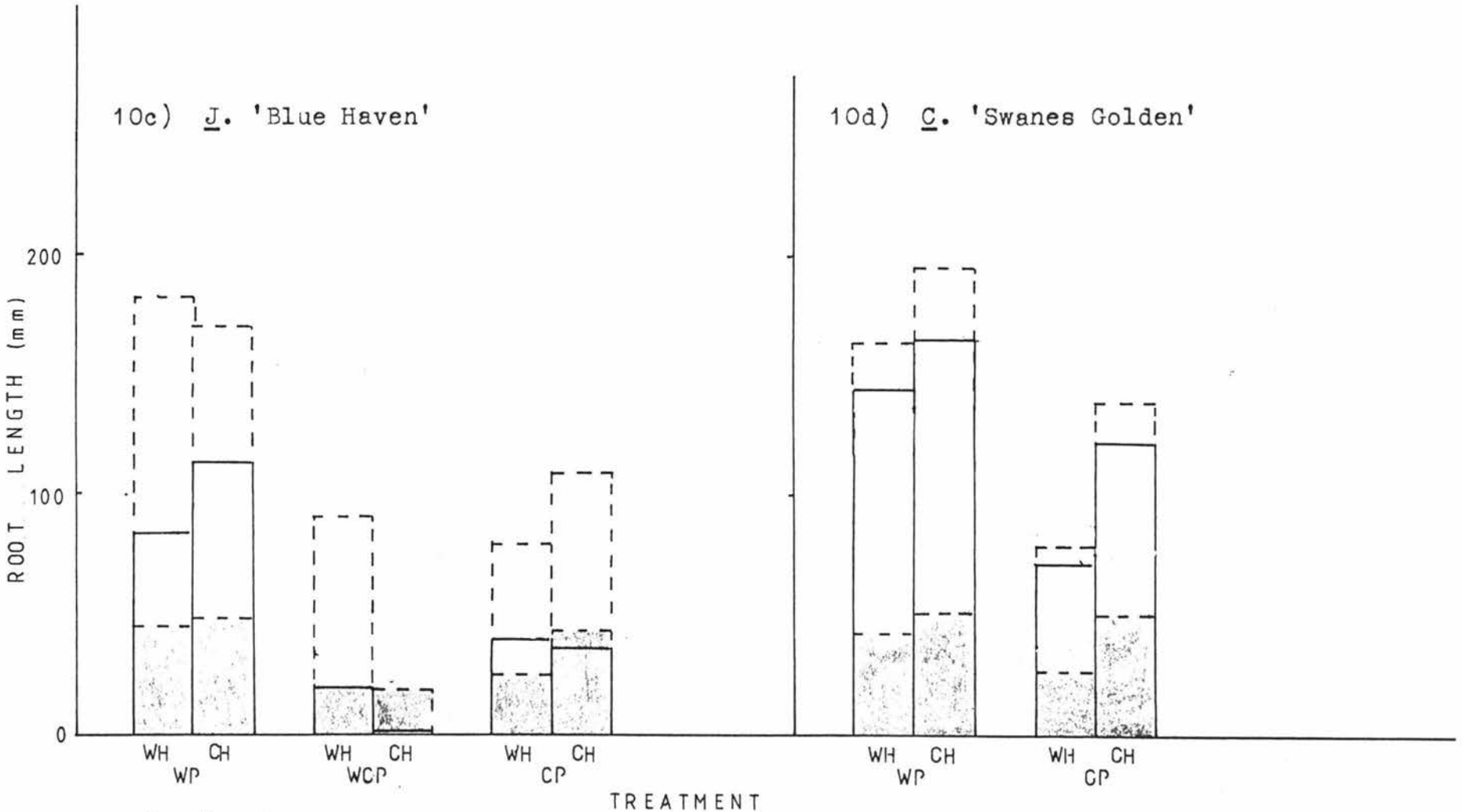


Figure 10(c,d). Variation in mean total root length per cutting and mean root length of c) J. 'Blue Haven' and d) C. 'Swanes Golden' with air temperature treatment.
□ = mean tot. length/cutting; ▯ = mean tot. length/rooted cutting; ▪ = mean root length.

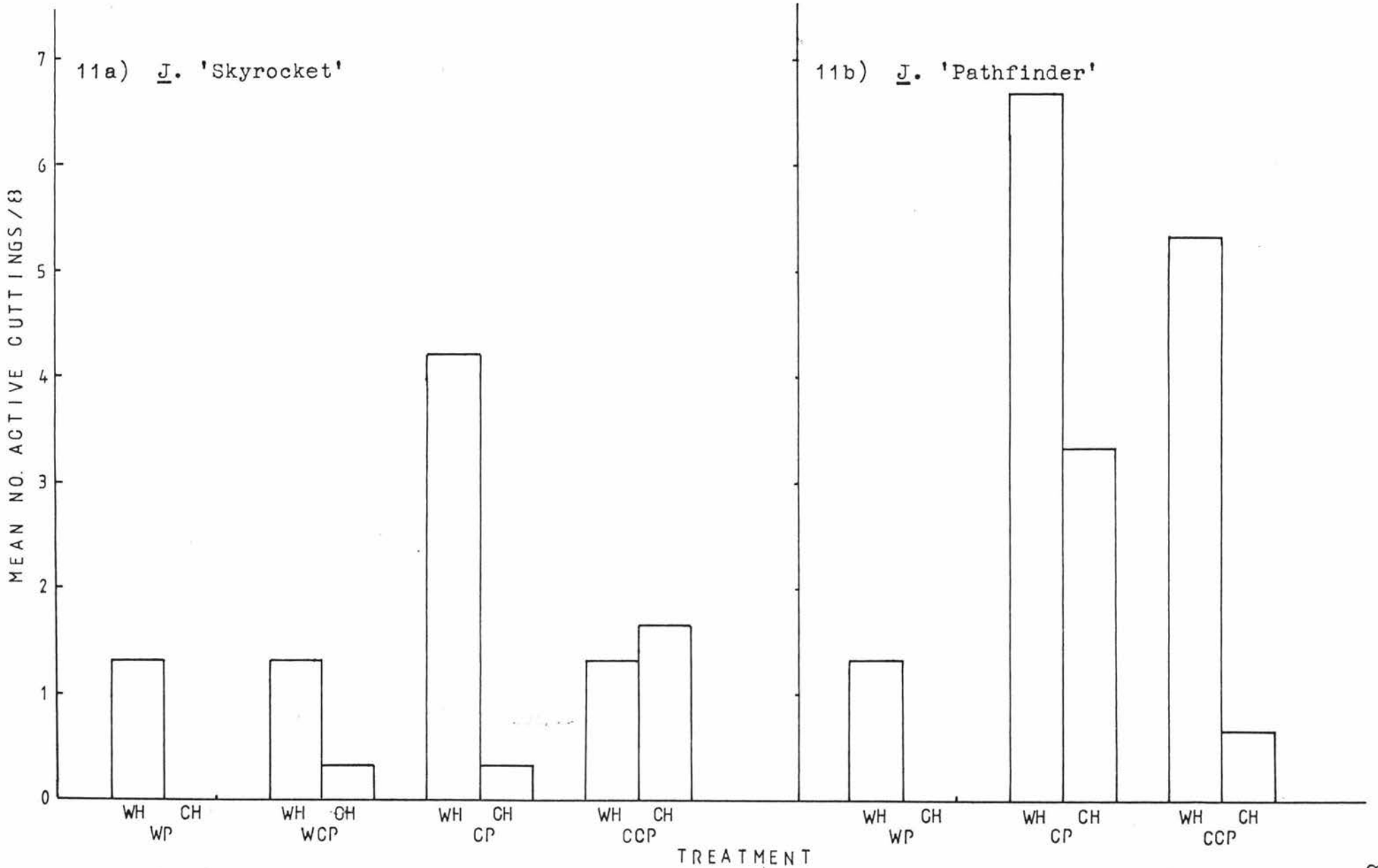


Figure 11(a,b). Variation in mean number of cuttings of a) J. 'Skyrocket' and b) J. 'Pathfinder' showing active shoot growth with air temperature treatment.

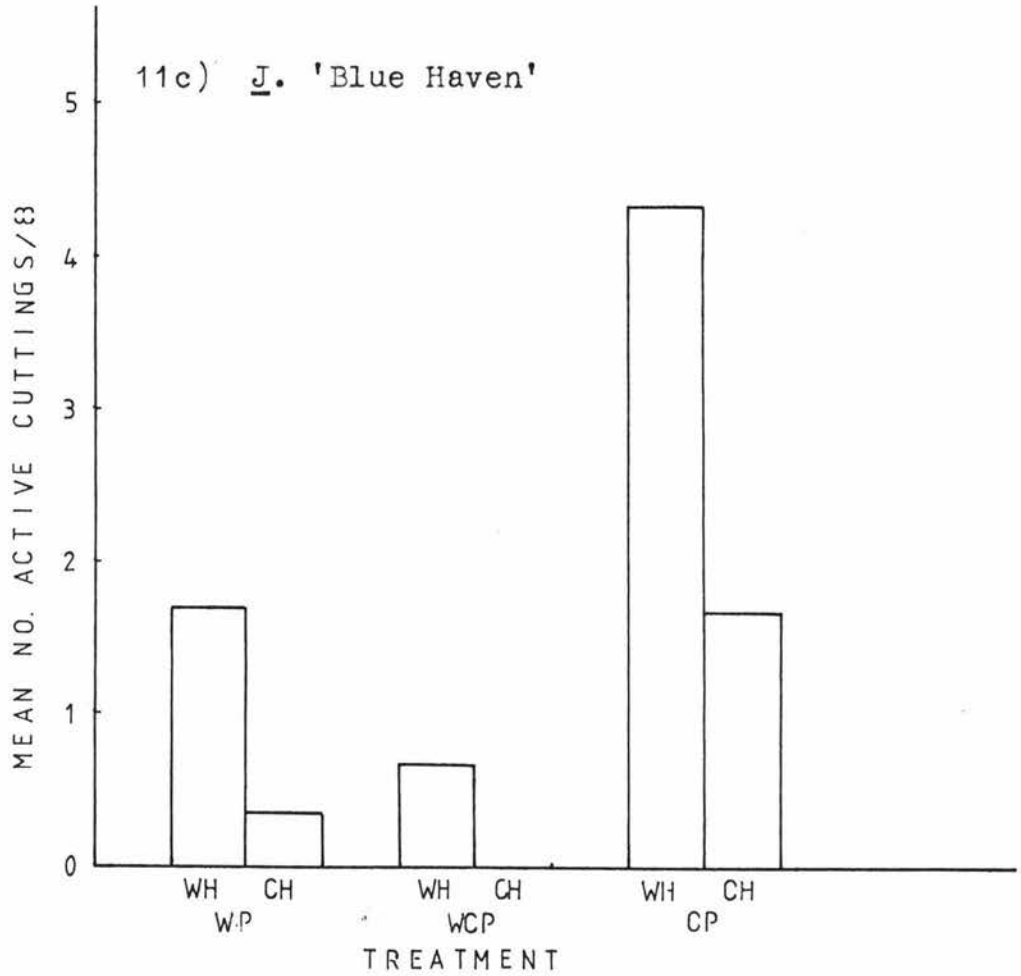


Figure 11c. Variation in mean number of J. 'Blue Haven' cuttings showing active shoot growth with air temperature treatment.

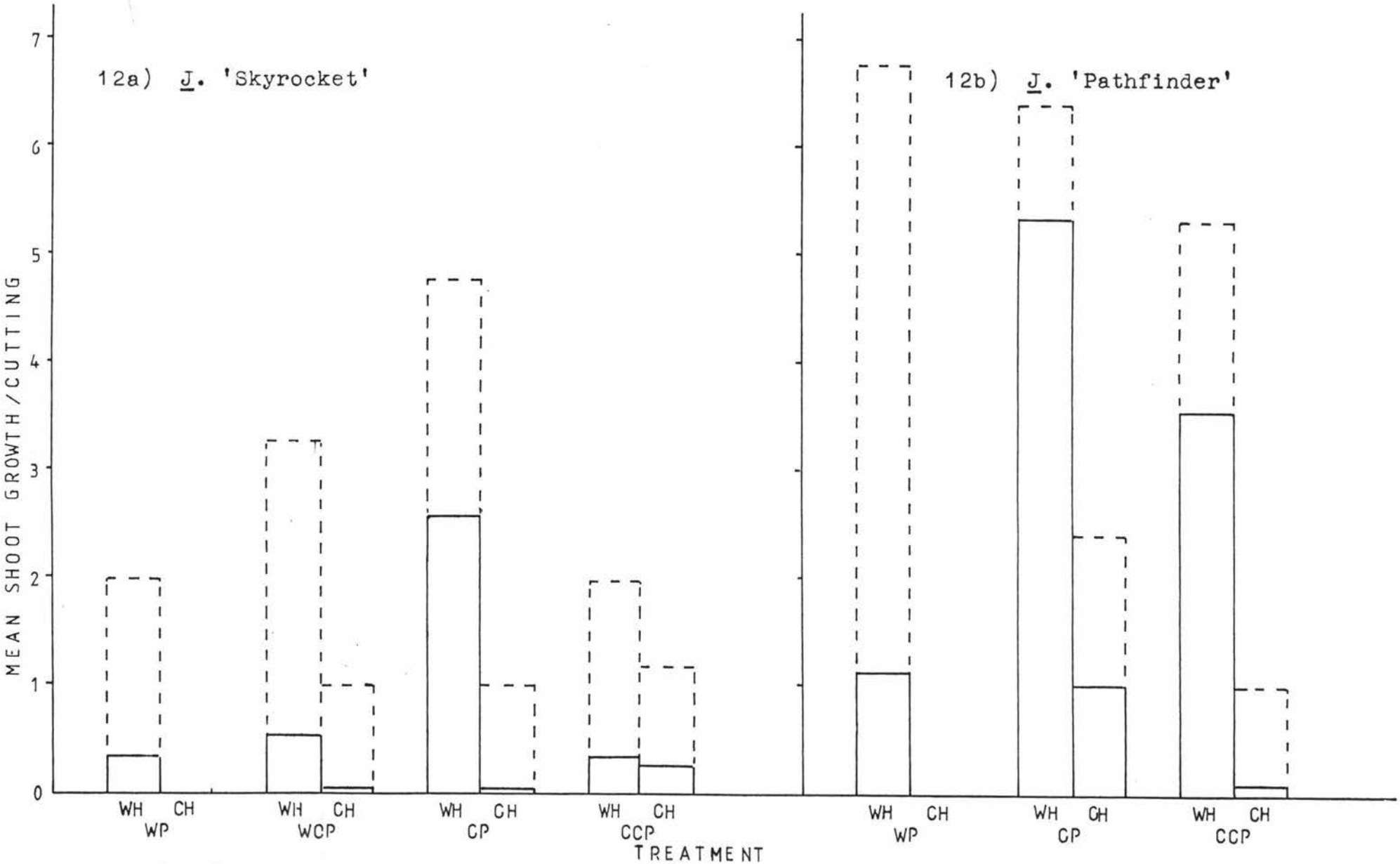


Figure 12(a,b). Variation in mean shoot growth per cutting of a) J. 'Skyrocket' and b) J. 'Pathfinder' with air temperature treatment. ▢ = mean growth/cutting; ⬚ = mean growth/cutting with active shoot growth.

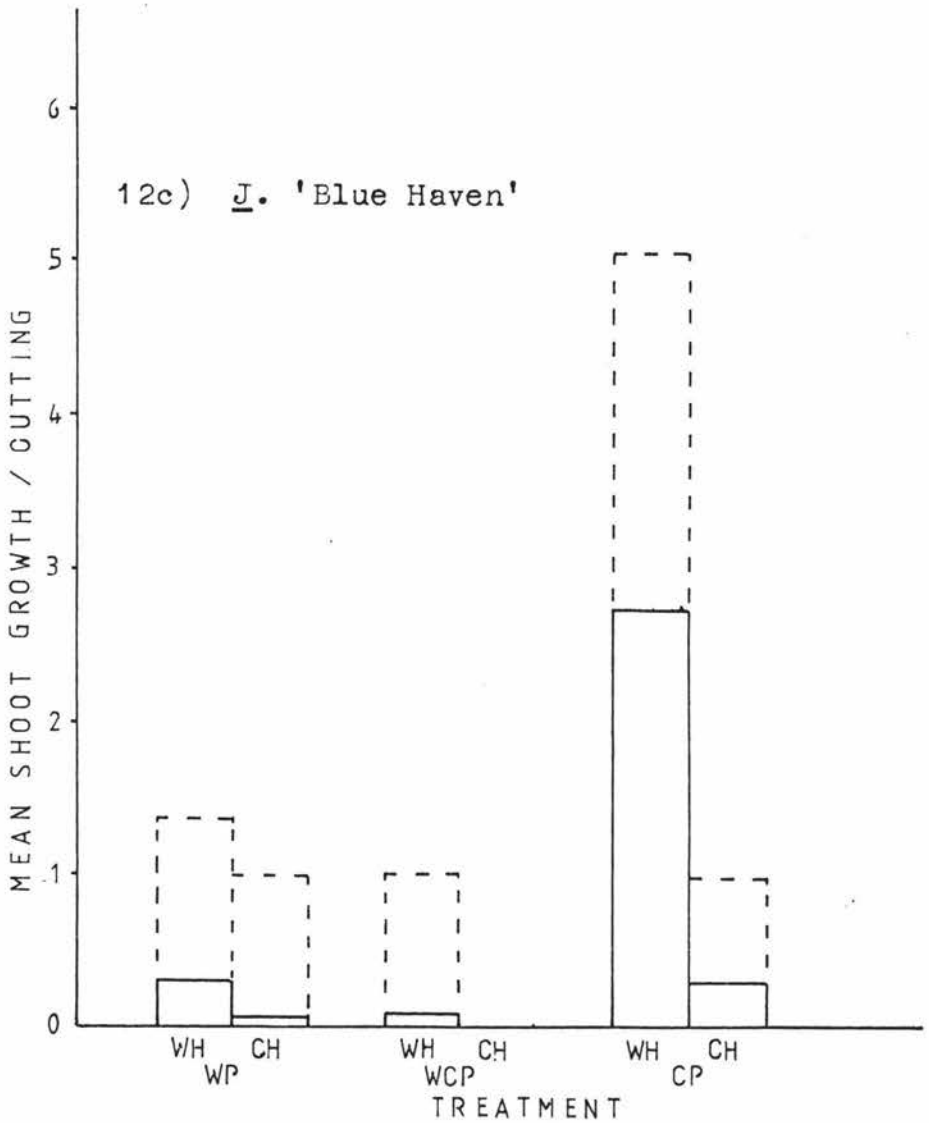


Figure 12c. Variation in mean shoot growth per cutting of J. 'Blue Haven' with air temperature treatment. □ = mean growth/cutting; ⁚ = mean growth/cutting with active shoot growth.

4.3.2 *J. scopulorum* 'Pathfinder'

The most successful parent material treatment was that of natural winter chilling, particularly if followed by low air temperatures during rooting. The CP CH material rooted in highly significantly greater mean numbers than other parent material in the CH environment (Table 9a, Figure 8b). The difference between the CP and other parent material treatments was also highly significant on comparison of grand means. The WH environment provided significantly better conditions for rooting CCP material than did the CH environment.

No significant differences were found in the mean number of roots per cutting although the CP, and to a lesser extent WH, grand means were slightly superior (Table 9b, Figure 9b). Mean number of roots per rooted cutting was higher in the WH compared with the CH rooting environment for each parent material treatment.

Mean total root length per cutting was significantly greater in CP material than in either of the other stock plant treatments when rooted under CH conditions (Table 9c, Figure 10b). The grand means indicated that a significant reduction of rooting potential had been brought about by the CCP treatment when compared with the CP treatment. No significant differences were found between propagation house environments although mean root length was consistently greater in the CH environment.

The range of rooting obtained is shown in Plate 5.

The mean number of cuttings with active shoot growth and the amount of shoot growth per cutting was greatest in

Table 9a. Mean number of cuttings rooted/8

Cutting Environment	Parent Material Environment			
	WP	CP	CCP	Mean
WH	3.33_{a}	5.33_{a}	4.33_{a*}	4.33
CH	2.00_{aA}	7.00	0.67_{aA}	3.22
Mean	2.67_{aA}	6.17	2.50_{aA}	

Table 9b. Mean number of roots per cutting

Cutting Environment	Parent Material Environment			
	WP	CP	CCP	Mean
WH	1.08_{a}	1.71_{a}	1.00_{a}	1.26
CH	0.42_{a}	1.88_{a}	0.08_{a}	0.70
Mean	0.75_{a}	1.79_{a}	0.54_{a}	

Table 9c. Mean total root length per cutting (mm)

Cutting Environment	Parent Material Environment			
	WP	CP	CCP	Mean
WH	65.92_{a}	91.13_{a}	56.21_{a}	71.08
CH	35.08_{aA}	168.71	10.25_{aA}	71.35
Mean	50.50_{aAB}	129.92_{A}	33.23_{aB}	

Tables 9(a-c). Midwinter study. Variation in a) mean number of cuttings rooted, b) mean number of roots per cutting and c) mean total root length per cutting of J.'Pathfinder' with air temperature treatment. Means within the same propagation environment followed by the same lower or upper case character not significantly different at the 5% or 1% levels of significance respectively. Means within the same parent material environment indicated if significantly different at the * = 5% and ** = 1% levels.

Table 10a. Mean number of cuttings showing new shoot growth/8

Cutting Environment	Parent Material Environment			
	WP	CP	CCP	Mean
WH	1.33_{B}	6.67_{aA} *	5.33_{aAB} **	4.44 **
CH	0.00_{bA}	3.33_{aA}	0.67_{abA}	1.33
Mean	0.67_{B}	5.00_{aA}	3.00_{aAB}	

Table 10b. Mean shoot growth per cutting (mm)

Cutting Environment	Parent Material Environment			
	WP	CP	CCP	Mean
WH	1.13	5.33_{A} **	3.54_{A} *	3.33 *
CH	0.00_{a}	1.00_{a}	0.08_{a}	0.36
Mean	0.56_{B}	3.17_{A}	1.81_{AB}	

Tables 10(a and b). Midwinter study. Variation in a) mean number of cuttings showing new shoot growth and b) mean shoot growth per cutting of J.'Pathfinder' with air temperature treatment. Means within the same propagation environment followed by the same lower or upper case character not significantly different at the 5% or 1% levels of significance respectively. Means within the same parent material environment indicated if significantly different at the * = 5% and ** = 1% levels.

material of CP origin (Figures 11b and 12b) which was highly significantly different from that of WP origin on comparison of the grand means (Tables 10a and b). Mean number of cuttings showing new shoot growth obtained from WP material was significantly and highly significantly lower than those of CP material in the cold and warm propagating houses respectively. Mean shoot growth per cutting in each parent material treatment was significantly different under WH conditions and between the grand means and that of WP material was reduced to a highly significant extent compared with the other parent material treatments under WH conditions. Mean shoot growth per active cutting was high in the WP WH treatment combination but otherwise followed similar trends to that on a per cutting basis.

Shoot activity was lower under CH than WH conditions in all material and between grand means to a significant or highly significant degree in all but WP material.

Rooted cuttings from each treatment had made good growth by the following autumn.

4.3.3 *J. scopulorum* 'Blue Haven'

Stock plants which had received the WP treatment in general showed the greatest rooting potential and WCP the lowest. Air temperature treatments during the rooting phase produced no significant differences in material from the same parent plant environment. The mean number of cuttings rooted from CP material was marginally higher under warm air temperatures during rooting and was significantly greater than the number of WCP WH cuttings rooted (Table 11a, Figure 8c). In the CH environment however, WP material

Table 11a. Mean number of cuttings rooted/8

Cutting Environment	Parent Material Environment			
	WP	WCP	CP	Mean
WH	3.67_{abA}	1.67_{bA}	4.00_{aA}	3.11
CH	5.33_{A}	1.00_{aB}	2.67_{aAB}	3.00
Mean	4.50	1.33_{A}	3.33_{A}	

Table 11b. Mean number of roots per cutting

Cutting Environment	Parent Material Environment			
	WP	WCP	CP	Mean
WH	1.83_{a}	0.83_{a}	1.50_{a}	1.39
CH	2.33_{a}	0.13_{a}	0.83_{a}	1.10
Mean	2.08_{a}	0.48_{a}	1.17_{a}	

Table 11c. Mean total root length per cutting (mm)

Cutting Environment	Parent Material Environment			
	WP	WCP	CP	Mean
WH	84.04_{a}	19.04_{b}	40.42_{ab}	47.83
CH	114.50_{A}	2.25_{aB}	36.75_{aAB}	51.17
Mean	99.27_{A}	10.65_{aB}	38.58_{aAB}	

Tables 11(a-c). Midwinter study. Variation in a) mean number of cuttings rooted, b) mean number of roots per cutting and c) mean total root length per cutting of J.'Blue Haven' with temperature treatment. Means within the same propagation environment followed by the same lower or upper case character not significantly different at the 5% or 1% levels of significance respectively. Means within the same parent material environment not significantly different.

Table 12a. Mean number of cuttings showing new shoot growth/8

Cutting Environment	Parent Material Environment			
	WP	WCP	CP	Mean
WH	1.67_{aA}	0.67_{aA}	4.33^{*}	2.22
CH	0.33_{abA}	0.00_{bA}	1.67_{aA}	0.67
Mean	1.00_{aA}	0.33_{aA}	3.00	

Table 12b. Mean shoot growth per cutting (mm)

Cutting Environment	Parent Material Environment			
	WP	WCP	CP	Mean
WH	0.29_{aAB}	0.08_{aB}	2.75_{A}	1.04
CH	0.04_{a}	0.00_{a}	0.21^{*}_{a}	0.08
Mean	0.17_{aA}	0.04_{aA}	1.50_{A}	

Tables 12 (a and b). Midwinter study. Variation in a) mean number of cuttings showing new shoot growth and b) mean shoot growth per cutting of J.'Blue Haven' with temperature treatment. Means within the same propagation environment followed by the same lower or upper case character not significantly different at the 5% or 1% levels of significance respectively. Means within the same parent material environment indicated if significantly different at the * = 5% level; none significant at the 1% level.

rooted in significantly greater numbers than other parent material and was highly significantly different from WCP CH cuttings in this respect. On comparison of grand means, cuttings of WP origin rooted very significantly better than those from the other stock plant treatments and all means were significantly different. Of a small sample of unrooted cuttings that had been retreated with IBA, reinserted in rooting medium and placed in the unheated environment, two-thirds had formed roots when lifted 8 weeks later.

No significant differences were found in the mean number of roots per cutting although cuttings of WP origin again produced the best results (Table 11b, Figure 9c). Mean root number per rooted cutting was consistently higher in the WH compared with the CH environment.

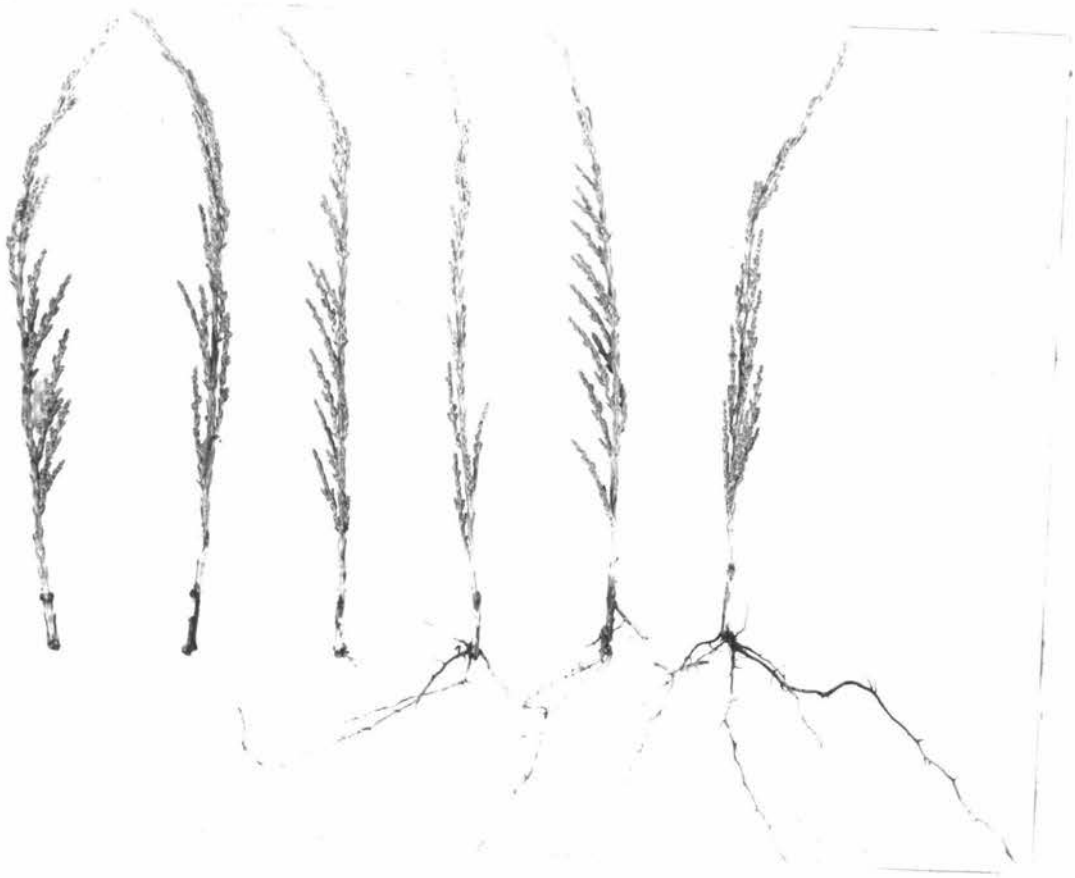
Mean total root length per cutting was greatest in WP material especially in the CH environment in which WP material was significantly different from CP material and highly significantly different from WCP material (Table 11c, Figure 10c). Mean total root length of WP cuttings was similarly significantly and highly significantly greater than CP and WCP material respectively on comparison of the grand means. Cuttings of WP plants also had a significantly greater mean total root length per cutting than those of WCP plants when rooted under warm conditions.

The range of root formation is shown in Plate 4.

The response of shoot activity to air temperatures was similar to that of the other two junipers in the over-pattern except that least activity occurred in the WCP material in J.'Blue Haven' (Figures 11c and 12c). The

Plate 3. A sample showing the range of root formation obtained over all temperature treatments 10 weeks after excision of J. virginiana 'Skyrocket' cuttings in mid winter. Magnification approx. X 0.55.

Plate 4. A sample showing the range of root formation obtained over all temperature treatments 10 weeks after excision of J. scopulorum 'Blue Haven' cuttings in mid winter. Magnification approx. X 0.53.



number of cuttings showing bud growth in CP material was greater than that in the other parent material to a significant extent in the CH environment and to a highly significant extent in the WH environment. On comparison of the grand means the number of cuttings with new shoot growth in CP material was also highly significantly greater than in material from other parent plant treatments. Mean shoot growth by CP cuttings was significantly different from the others in the WH environment and between grand means and highly significantly different from the WCP material under WH conditions (Table 12b). Shoot activity was greater in the WH than the CH environment regardless of parent material treatment although the difference was only significant in CP material.

By the following autumn, vigorous growth of both the shoot and root systems had occurred in all rooted cuttings grown on.

4.3.4 C. sempervirens 'Swanes Golden'

No significant differences were found between treatments in any of the rooting parameters (Tables 13a, b and c). CP material and the WH environment did however produce slightly greater mean numbers of cuttings rooted than did WP material or the CH propagation environment (Figure 8d). In comparison, mean root number per cutting and the mean total root length per cutting were higher in the WP material. The WH environment enhanced mean root number per cutting but had the opposite effect on mean total root length per cutting and mean root length (Figures 9d and 10d). The range of rooting obtained is depicted in Plate 6.

Table 13a. Mean number of cuttings rooted/8

Cutting Environment	Parent Material Environment		
	WP	CP	Mean
WH	7.00_a	7.33_a	7.17
CH	6.67_a	7.00_a	6.83
Mean	6.83_a	7.17_a	

Table 13b. Mean number of roots per cutting

Cutting Environment	Parent Material Environment		
	WP	CP	Mean
WH	3.33_a	2.63_a	2.98
CH	2.29_a	2.38_a	2.65
Mean	3.12_a	2.50_a	

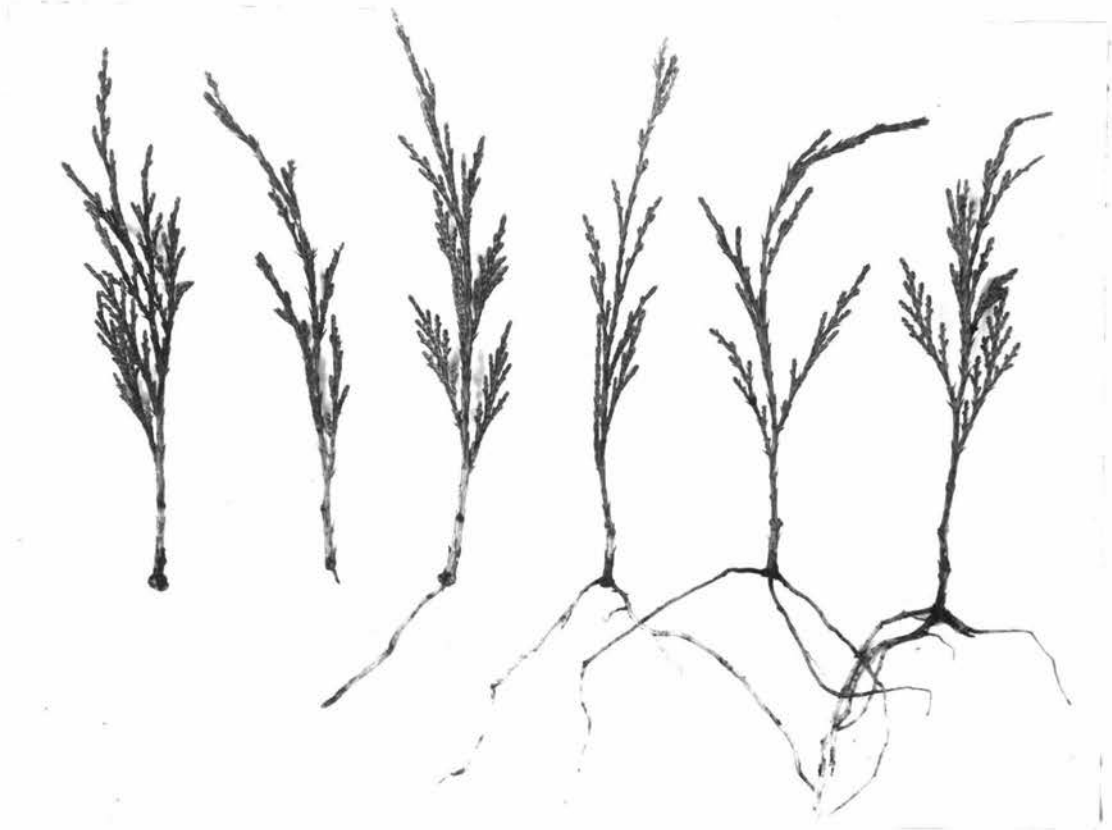
Table 13c. Mean total root length per cutting (mm)

Cutting Environment	Parent Material Environment		
	WP	CP	Mean
WH	144.88_a	73.21_a	109.04
CH	164.50_a	123.75_a	144.13
Mean	154.69_a	98.48_a	

Tables 13(a-c). Midwinter study. Variation in a) mean number of cuttings rooted, b) mean number of roots per cutting and c) mean total root length per cutting of C.'Swanes Golden' with air temperature treatment. Means within the same propagation or parent material environments not significantly different at the 5% level of significance.

Plate 5. A sample showing the range of root formation obtained over all temperature treatments 10 weeks after excision of J. scopulorum 'Pathfinder' cuttings in mid winter. Magnification approx. X 0.58.

Plate 6. A sample showing the range of root formation obtained over all temperature treatments 10 weeks after excision of C. sempervirens 'Swanes Golden' cuttings in mid winter. Magnification approx. X 0.50.



Data obtained concerning shoot activity was not analysed as the new shoot growth was not always readily distinguishable. Shoot extension growth was however apparent in at least 40% of the cuttings in all treatments.

Rooted cuttings from all treatments had made good growth by the following autumn.

4.3.5 Comparison of Parameters of Rooting and Shoot Growth

In most instances mean root length was greater in the CH than the WH environment whereas mean shoot growth per cutting and mean root number, particularly per rooted cutting, showed the opposite response (Figures 9, 10 and 12). Values from individual cuttings of J.'Skyrocket' plotted against each other indicated that only a low negative relationship might exist between mean root length and shoot growth and between mean root length and root number (Appendix 6). No relationship was evident between root number or total root length and shoot growth, or bud break and rooting. Possible relationships between parameters in other cultivars were no more clearly discernable on preliminary investigation than in J.'Skyrocket'.

4.3.6 Summary

Rooting capacity, as reflected in the three parameters, was greatest in CP material of J.'Skyrocket' and J.'Pathfinder' but greatest in WP material of J.'Blue Haven' and C.'Swanes Golden' although no significant differences were detected between treatment means in the latter. The parent material treatments that involved a two week period of chilling prior to cutting excision, WCP and CCP, reduced

rooting capacity in comparison with the corresponding treatments lacking the concluding drop in temperature. The reduction brought about by the WCP treatment aside, parent material treatment had the least effect on the mean number of cuttings rooted in the two most easily rooted cultivars, J.'Skyrocket and C.'Swanes Golden' but brought about significant differences in the remaining two cultivars. Shoot activity was also most evident in naturally chilled material and decreased in the other parent material treatments with decreasing exposure to low temperatures, with the exception of the low level of activity in WCP material of J.'Blue Haven'. J.'Pathfinder' showed greater overall shoot activity than the other junipers.

The effect of propagation house air temperature on the mean number of cuttings rooted varied but cuttings previously subjected to the optimum parent environment [illegible] maximum rooting percentages under CH conditions in the two difficult-to-root junipers. Mean total root length, or more often mean root length, was greater in a CH than a WH environment whereas mean root number and mean shoot growth per cutting were promoted more under WH conditions. There was little evidence of readily discernable relationships between parameters in individual cuttings however.

Rooted cuttings from all treatments had made good growth by the following autumn in both the root and shoot systems.

4.4 Growth Regulator Analyses

Cuttings harvested simultaneously with those for the glasshouse trials were freeze-dried and stored for subsequent determination of endogenous growth regulator levels as outlined under Materials and Methods.

4.4.1 Auxin

Activity of an acidic growth promoter was detected in Rf zones 0.3 - 0.5, corresponding to the zones covered by an IAA marker spot (e.g. Appendix 7). Promoter content of these zones was determined utilizing the Avena coleoptile bioassay and expressed as μg equivalent of IAA per 5g dry weight of plant tissue (Figure 13).

IAA-like activity in J. 'Skyrocket' and J. 'Pathfinder' cuttings from the seasonal study was highest in February and only slightly lower in April but had dropped to approximately half this in June. Levels were very similar in J. 'Skyrocket' and J. 'Pathfinder', with that of J. 'Skyrocket' normally the higher of the two by a small margin. Determination of growth promoter activity in cuttings of C. 'Swanes Golden' was hindered due to the fact that Avena coleoptiles exposed to the Rf 0.5 zone became flaccid and glassy . This did not appear to be due to excessively high levels of IAA as levels of activity in the Rf 0.3 - 0.4 zones were quite normal in comparison with the other extracts, the appearance of the coleoptiles exposed to Rf 0.5 being similar to that described by Smith and Wareing (1972a) for mesocotyl sections affected by inhibitors

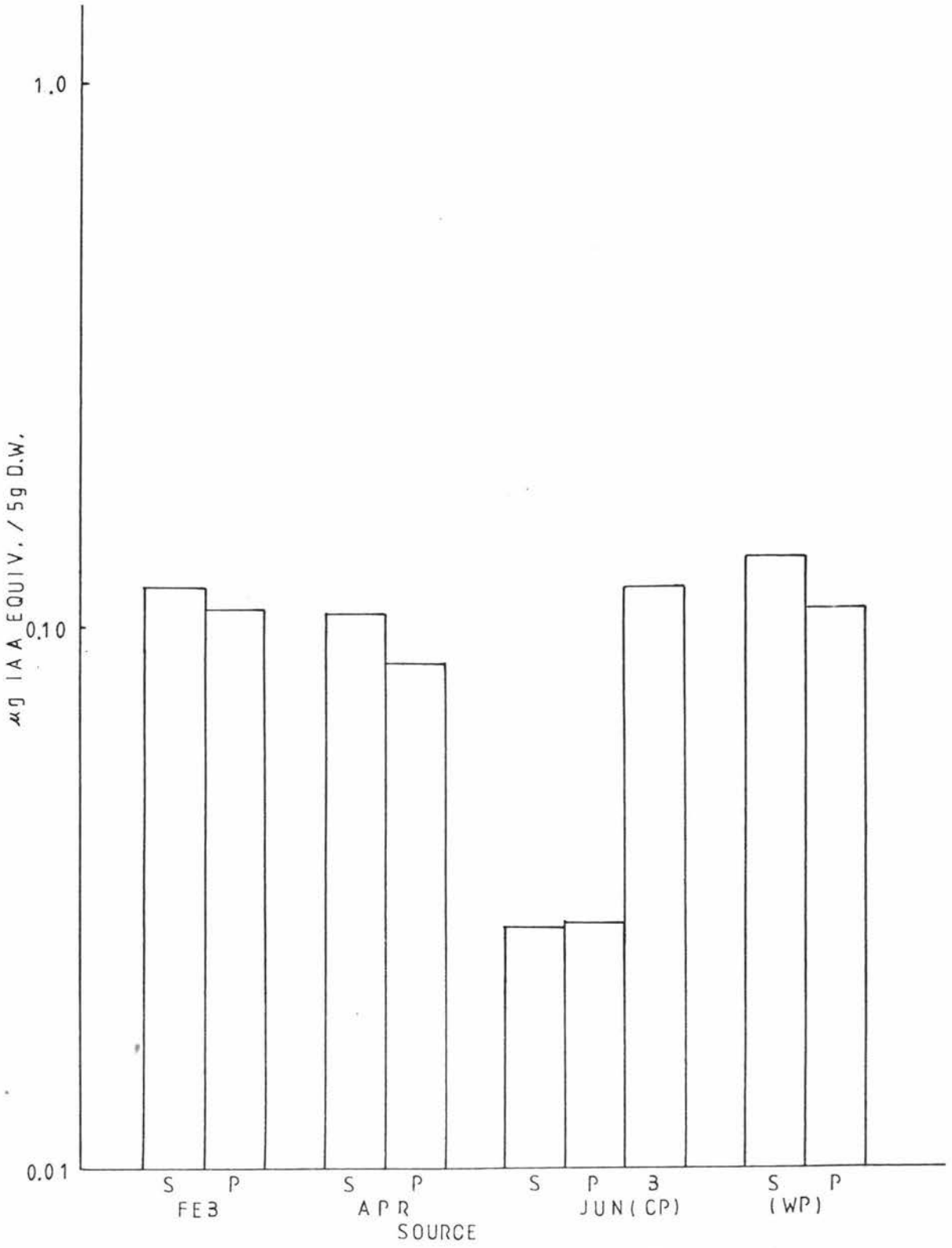


Figure 13. Levels of an IAA-like growth promoter detected in cutting tissue from different sources. Expressed as μg equivalent of IAA per 5g tissue dry weight. S = J. 'Skyrocket', P = J. 'Pathfinder' and B = J. 'Blue Haven'.

in poplar. Growth promotion in the Rf 0.3 - 0.4 zones was however slightly greater in February (4.20×10^{-2} μg) than June (2.64×10^{-2} μg). Levels of auxin activity in cuttings of J. 'Skyrocket' and J. 'Pathfinder' from stock plants subjected to the WH treatment and harvested in June was higher than that in samples from plants which had received natural winter chilling and were similar to those obtained in earlier months.

On comparison of IAA-like activity in the different cultivars on June, the greatest level of activity was detected in cuttings of J. 'Blue Haven'.

4.4.2 Growth Inhibitory Activity

The greatest proportion of growth inhibitory activity, as determined by the Triticum coleoptile bioassay, was confined to the zones of Rf 0.6 - 0.8 and coincided with an ABA marker spot (e.g. Appendix 7). Inhibitor concentration was expressed as μg equivalent of ABA per 5 g dry weight of cutting sample (Figure 14).

ABA-like activity in J. 'Skyrocket' and J. 'Pathfinder' cuttings was greatest during February and had diminished by a factor of ten by April. Levels had risen a little again by June. Samples of C. 'Swanes Golden' contained similar, relatively low levels of activity in both February and June. Inhibitor content of J. 'Pathfinder' was slightly greater than that of J. 'Skyrocket' in June but similar in other months.

Almost equal levels of ABA-like activity were detected in WP and CP material of J, 'Skyrocket'. Activity in WP

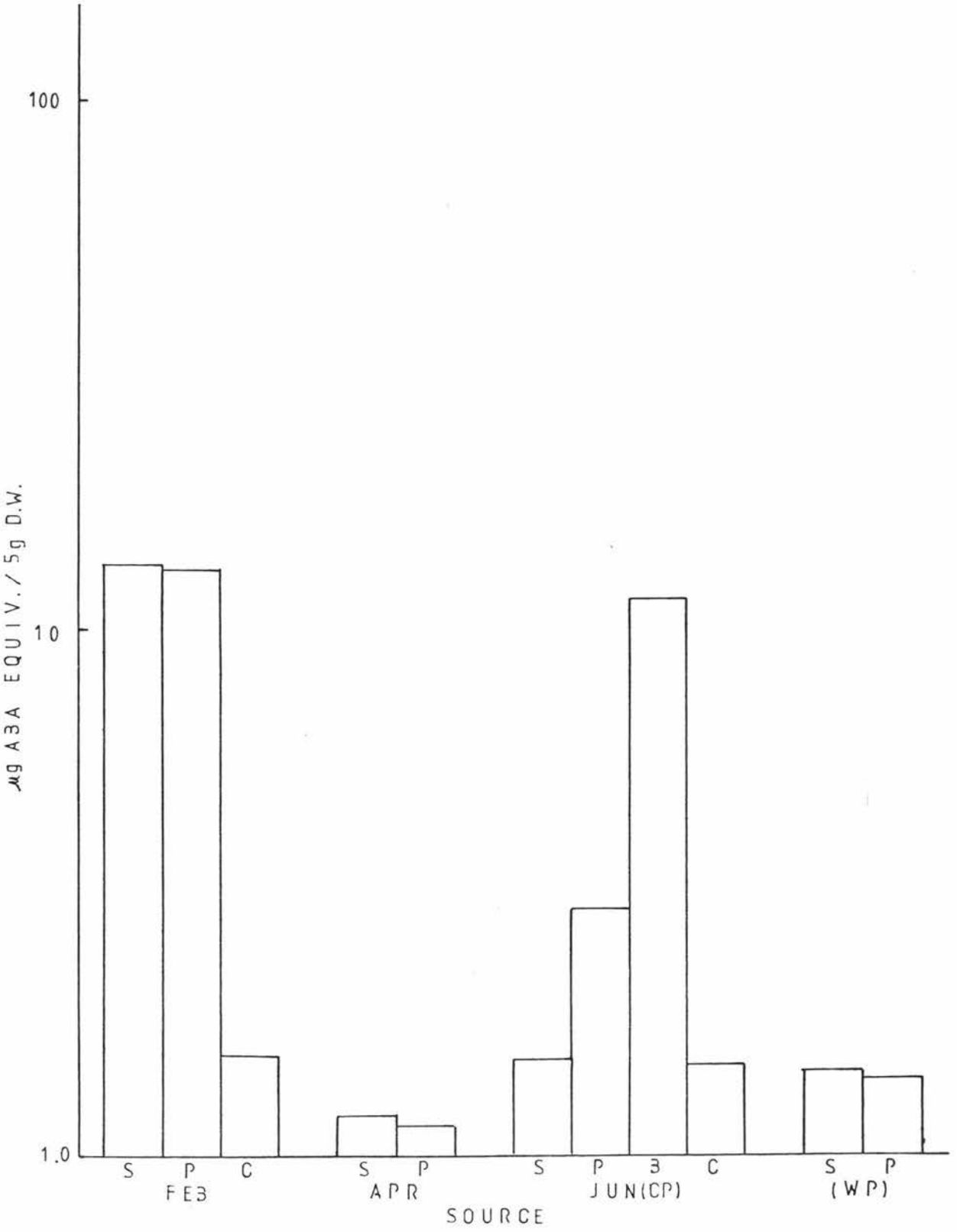


Figure 14. Levels of an ABA-like growth inhibitor detected in cutting tissue from different sources. Expressed as µg equivalent of ABA per 5g tissue dry weight. S = J. 'Skyrocket', P = J. 'Pathfinder', B = J. 'Blue Haven' and C = C. 'Swanes Golden'.

material of J. 'Pathfinder' was a little lower than that in CH material and almost identical to the level detected in WP cuttings of J. 'Skyrocket'.

Comparison of values obtained in the different cultivars in midwinter revealed that the greatest amount of inhibitory activity was found in J. 'Blue Haven' followed by an estimated content of less than fifty percent of this in J. 'Pathfinder'. Nearly equal levels were detected in J. 'Skyrocket' and C. 'Swanes Golden', approximately one-tenth that of J. 'Blue Haven'.

4.4.3 Cytokinin Activity

Peaks of cytokinin activity as detected in the radish cotyledon bioassay occurred in three main areas of the chromatograms (Appendix 8) and total activity was estimated as μg equivalent of kinetin per 5 g dry weight (Figure 15).

The pattern of changes in cytokinin content from late summer to midwinter differed between J. 'Skyrocket' and J. 'Pathfinder'. Activity in J. 'Skyrocket' samples dropped from a high level in February to a low level in April, constituting a ten-fold reduction in content, and returned to a high again in June. J. 'Pathfinder' cytokinin content however was at an intermediate to high level in February and increased a little in April before falling to a low level in June. A high level of cytokinin activity was detected in cuttings of C. 'Swanes Golden' during February and only a slightly higher level in June.

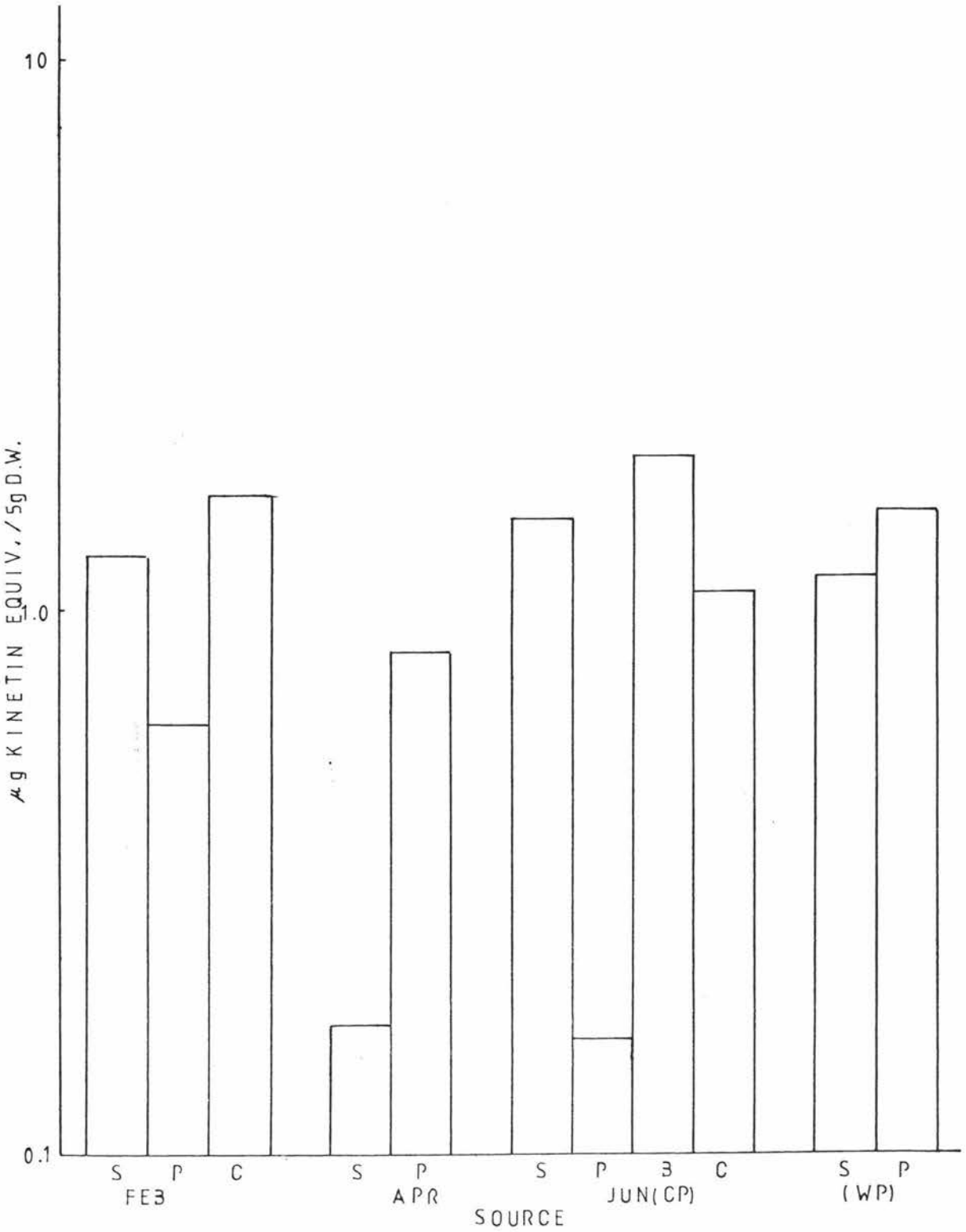


Figure 15. Levels of total cytokinin activity detected in cutting tissue from different sources. Expressed as µg equivalent of kinetin per 5g tissue dry weight. S = J. 'Skyrocket', P = J. 'Pathfinder', B = J. 'Blue Haven' and C = C. 'Swanes Golden'.

WP material of J. 'Skyrocket' contained a little less activity than cuttings from naturally chilled stock plants whereas activity in WP material of J. 'Pathfinder' exceeded that in CP material amounting to a ten-fold difference in estimated cytokinin content. Cytokinin activity of WP material was slightly higher in J. 'Pathfinder' than J. 'Skyrocket'.

The highest total cytokinin content in parent material exposed to normal winter temperatures and harvested in June was estimated in samples from J. 'Blue Haven'. Slightly lower levels were detected in J. 'Skyrocket' and C. 'Swanes Golden' and a considerably lower level in J. 'Pathfinder'.

4.4.3 Summary

Estimated IAA content showed relatively little variation between sources of cutting material but was lowest in samples of J. 'Skyrocket' and J. 'Pathfinder' taken in June after exposure to winter chilling.

Cuttings of J.'Skyrocket' and J. 'Pathfinder' contained the greatest amount of ABA-like activity in February, which was also notably higher than the activity detected in C. 'Swanes Golden' at that time. The highest level of estimated ABA content in June occurred in J. 'Blue Haven' followed by J. 'Pathfinder' and then J. 'Skyrocket' and C. 'Swanes Golden'. Activity in WP material was similar to that in CP material.

The greatest difference detected in growth regulator content between samples of J. 'Skyrocket' and J. 'Pathfinder' excised in the same month was in estimated total cytokinin

level. Over all treatments and cultivars, the lowest values were obtained from J. 'Skyrocket' in April and J. 'Pathfinder' in June. Levels in all other samples were relatively high, with marginally the highest found in J. 'Blue Haven' at the midwinter harvest date.

CHAPTER 5

DISCUSSION

5.1 Seasonal Fluctuations in Root Formation Potential

The pattern of changes in ability to form roots as determined over all parameters of rooting in cuttings of the easy-to-root J. 'Skyrocket' compared with the difficult-to-root J. 'Pathfinder' over the nine month trial period was similar in that rooting potential improved from a relatively low or moderate level in late summer (February) to an optimum in mid winter (June) after an interval of poor rooting. Rooting potential then diminished again in spring (Figures 1-3; Tables 1a-c). Cuttings of both cultivars taken in August showed root formation next most extensive to that achieved in June. The less comprehensive study of C. 'Swanes Golden' indicated that fluctuations in rooting resembling those found in the junipers from late summer to mid winter might also exist in that cultivar (Figures 4a-c; Tables 3a-c). In contrast to the junipers however, rooting capacity was very high in February as well as in June.

An optimum of root initation ability during winter or spring, sometimes preceded by smaller peak(s) in summer or autumn is the normal pattern in species of a wide range of genera (e.g. Howard, 1966; Vieitez and Pena, 1968; Roberts and Fuchigami, 1973; Girouard, 1975; Tustin, 1976; Tognoni et al, 1977). The realization of maximum rooting potential in juniper cuttings at some time during winter or

spring has often been reported (e.g. Klein, 1931; Chadwick and Kiplinger, 1938; Lanphear and Meahl, 1963; Gordienko et al, 1976; Hall, 1977; Ivanova, 1979). An additional peak during summer or autumn has also been recorded (Lanphear and Meahl, 1963; Gordienko et al, 1976).

The most marked difference in seasonal pattern of rootability between the two junipers concerned the number of cuttings rooted, which is perhaps the parameter of foremost interest to the commercial propagator. High levels were attained in J. 'Skyrocket' two months earlier and continued for a month longer than in J. 'Pathfinder', spanning a period of six months. Whereas rooting percentage of J. 'Skyrocket' rose abruptly in April (96%) from the low in March (17%), that of J. 'Pathfinder' continued to decline even further (8% in May) until the optimum was suddenly reached in June (88%). Although rootability of J. 'Pathfinder' was marginally superior to that of J. 'Skyrocket' in February, June was the only time a rooting percentage comparible to those of J. 'Skyrocket' during the later period occurred in J. 'Pathfinder'. The mean number of J. 'Pathfinder' cuttings rooted in that month was significantly greater than in any other month except August while no significant differences in this parameter occurred in J. 'Skyrocket' from April to September inclusive (Table 1a, Figure 1).

Generally more gradual changes were encountered in the other parameters relating to root number and length (Tables 1a and b; Figures 2a,b and 3a,b). Steady changes in these parameters occurred in J. 'Skyrocket' before and, in mean root number at least, after the optimum in June. Small

improvements in these parameters, more so an a per rooted cutting basis, were also noted in J. 'Pathfinder' prior to June although mean root number remained relatively low all year. At this point it might be noted that the differences observed in proportion of roots emerging through the wound area on the cuttings (Section 4.1.2) was, in the case of J. 'Pathfinder', unlikely to be due to crowding of the roots in cuttings excised later in the year (Figure 2b) but perhaps brought about by physiological differences in response to wounding. Whereas mean number of roots per cutting of J. 'Skyrocket' was significantly lower in March and October than in any other month except February, mean total root length obtained in September after a sharp decline was in addition to those in the earliest months significantly less than at other harvest dates (Tables 1b,c). Significant and highly significant differences were also detected in mean total root length per cutting of J. 'Pathfinder' between the optimum obtained in June and the early and later months in the study, as in J. 'Skyrocket'. The greatest differences in rooting potential between the two cultivars occurred in April and July when significant and highly significant differences were found in all parameters (Tables 1a-c).

Such seasonal variations in the capacity of cuttings to form roots may be attributed to a direct influence of environmental factors or to the state of plant growth; most investigations of narrow-leaved evergreens have indicated the latter alternative (e.g. Lanphear and Meahl, 1963; 1966; Roberts et al, 1974; Whitehill and Schwabe,

1975; Ivanova, 1979).

Although optimum rooting and shoot extension growth both occurred in cuttings of J. 'Skyrocket' and J. 'Pathfinder' excised in June, the decline in rooting capacity during spring may have been associated with the approach and recommencement of shootgrowth. New growth was first noted in cuttings of both cultivars taken in June approximately seven weeks after setting, activity at time of lifting increasing in successive harvest dates (Tables 2a,b). The exception to this was the abscence of shoot activity associated with a very low level of rooting in J. 'Pathfinder' cuttings taken in July, for which there was no obvious explanation, the cuttings being normal in appearance with a little callus formed at the bases. Almost all cuttings of both cultivars excised in August had made new shoot growth by the time of lifting. The greater amount of shoot growth made by cuttings of J. 'Pathfinder' compared with J. 'Skyrocket' taken in September may have contributed to the reduction in all parameters of J. 'Pathfinder' in that month whereas only mean total root length and mean root length of J. 'Skyrocket' had reached a low level (Figures 1-3).

The first signs of new growth in the stock plants were evident by the October harvest date and rapid shoot growth commenced in most cuttings shortly after setting. This event coincided with the dramatic reduction in the mean number of J. 'Skyrocket' cuttings rooted and the lowest levels of other parameters of rooting encountered in this cultivar since autumn (Figures 1-3). All cuttings of J. 'Pathfinder' failed to root.

A sharp decrease in rooting potential of narrow-leaved evergreens in spring has frequently been associated with the onset of (rapid) shoot growth (e.g. Lanphear and Meahl, 1963; Gordienko et al, 1976; Girouard, 1975; Ivanova, 1979). Any negative influence exerted by shoot growth on root formation might reasonably be expected to be more powerful the closer to the time of cutting excision it occurs. However there was little clear evidence of relat-ionships between parameters of rooting and shoot growth except in the mid winter study (to be discussed in the next section) in which a negative relationship of only low magnitude was detected between mean root length and shoot growth in cuttings of J. 'Skyrocket' under WH conditions, conditions in which shoot growth was more advanced. Factors which might accompany active shoot growth by the cutting and inhibit root initiation and/or growth include an unfavourable growth regulator (e.g. Gordienko et al, 1976; Whitehill and Schwabe, 1975) or nutrient (e.g. Cheffins, 1975; Nanda and Anand, 1970; Wareing, 1970) status. Competition for nutrients may be particulary important if photosynthesis is greatly reduced until after root formation as reported by Cameron and Rook (1974). The presence of soft, rapidly elongating shoot growth particularly prior to root formation, may induce a state of water stress in the cutting, normally considered to be most detrimental to rooting (e.g. Loach, 1977; Whalley and Loach, 1978; Cameron and Rook, 1974). Warmer temperatures encountered in the latter part of the year may have compounded these effects by increasing rates of respiration and transpiration. The tip wilting and death which occurred in several cuttings

taken in late spring might also have been brought about by water stress and depletion of nutrients. This may have been alleviated to a certain extent by mist application, as was provided in February and March, although Girouard (1975) reported that succulent elongating cuttings of Picea abies tended to wilt on warm summer days, remaining bent and rooting poorly even under mist.

Complex physiological changes unfavourable to rooting might also have preceded the recommencement of shoot growth and have brought about the decline in mean root number on cuttings of J. 'Skyrocket' and rooting percentage of J. 'Pathfinder' in early spring (Figures 1 and 2a,b). Mean total root length and mean root length of J. 'Skyrocket' cuttings diminished little until the sudden decrease in September (Figures 3a and b) which may have been largely due to increased competition from the shoot system for nutrients as shoot growth was quite well advanced when the cuttings were lifted. Similarly, mean total root length per rooted cutting and mean root length of J. 'Pathfinder' was greatly reduced in cuttings excised in September.

Lanphear and Meahl (1963) had proposed that rooting of Juniperus horizontalis 'Plumosa' cuttings was inhibited during periods of growth and suggested that the peak in rootability during summer may have occurred during "a period of summer dormancy, characteristic of many evergreen species". A high percentage of rooting was indeed reported in Chamaecyparis pisifera cuttings during summer dormancy (Gil-Albert and Boix, 1978) but rooting capacity of

Juniperus sabina was low during summer dormancy and increased with resumption of stock plant growth, especially root growth, to a peak later in autumn (Gordienko et al, 1976). It appears from various reports that activity of the stock plant root system may be implicated in the cycles of cutting rootability in narrow-leaved evergreens, with high rooting potential occurring during periods of root activity particularly when this is high in relation to activity of the shoot system as has been reported to occur in early spring before bud break (Gordienko et al, 1976; Lathrop and Mecklenburg, 1971; Wareing, 1970). Such a relationship could equally well have occurred in the material in this study.

The low or moderate levels of rooting obtained from J. 'Skyrocket' and J. 'Pathfinder' during extension growth in February (Figures 1-3) might be considered to constitute a small peak, and which might have been higher in January. A high level of root forming ability was attained in C. 'Swanes Golden' in February, with the mean number of cuttings rooted (96%) slightly greater than in June (88%) and highly significantly greater than that in March (42%). No shoot extension growth was detected in plants of C. 'Swanes Golden' during this period the following summer and therefore may lend some support to the proposal of Lanphear and Meahl (1963) that factors which stimulate active growth inhibit rooting and those which inhibit growth enhance rooting of certain narrow-leaved evergreens. However, a simple inverse relationship with growth cannot explain all the fluctuations in rooting capacity encountered, particularly during the autumn/winter

period. The changes in rooting potential during this period from early autumn to mid winter and the possible causal factors were of prime interest in the present investigation.

The very low level of rooting potential indicated by all parameters encountered in March (Figures 1-3) occurred about the time of cessation of growth in the junipers. A similar period of very poor rootability has also been demonstrated in, for example, Juniperus horizontalis 'Plumosa' (Lanphear and Meahl, 1963), Psuedotsuga menziesii (Roberts and Fuchigami, 1973) and Picea glauca (Tognoni et al, 1977). The processes of root initiation and development are complex and involve many factors, any one or more of which may limit rooting potential (Chapter 2). The rise in rooting capacity subsequent to the low level in autumn therefore involved the removal (e.g. inactivation or production) of certain limiting factor(s) until maximum rooting was attained in mid winter after which the same or different, as dicussed earlier, limitations were imposed. Certain requirements relating to environmental factors, such as photoperiod or temperature, and/or phase of growth may have to be fulfilled for maximum root formation potential to be achieved although the ultimate effect must operate via changes in endogenous factors. The period of very poor rooting reported in Psuedotsuga menziesii coincided with early, deepest dormancy as measured by cambial activity, respiration and time to bud break. The subsequent rise in rooting potential was associated with removal of bud dormancy until an optimum in potential was reached prior to bud burst (Roberts and Fuchigami, 1973;

Roberts et al, 1974; Bhella and Roberts, 1974). Rooting percentage of Pinus sylvestris was also found to parallel release from dormancy (Whitehill and Schwabe, 1975). Different species and geographical races may exhibit differences in response to environmental factors and in addition, degree of dormancy attained may vary with species and location or climate (e.g. Wareing, 1970; von Rudloff, 1975; Ivanova, 1979). Unlike most conifers, the species used in this study are noted for the absence of distinct resting buds (e.g. Wareing, 1970; Haverbeke and Read, 1976). The Cupressus species in particular, reported to originate from southern Europe and be more suited to cultivation in mild climates, may never attain dormancy comparible to that in species requiring a period of rest-breaking winter chilling although all species employed in this investigation ceased growth in winter even under glasshouse conditions. It might be added that plants of C. 'Swanes Golden' grown on under moderately warm conditions recommenced growth in winter after brief exposure to extended photoperiods whereas the junipers did not (observation). However the similarity in pattern of most reports of seasonal periodicity in rootability (e.g. Lanphear and Meahl, 1964; Roberts and Fuchigami, 1973; Tognoni et al, 1977; Gordienko et al; 1976; Ivanova, 1979) is such that it is reasonable to assume that similar, although perhaps not entirely identical, factors are operating in each case. In addition, Ivanova (1979) noted that conifers under mild climatic conditions could, in contrast to those in a colder climate, be propapagated almost year round but that the optimum rootability still occurred about the time

of bud break.

The requirements for attainment of a high rooting percentage in J. 'Skyrocket' (Figure 1) were apparently met relatively early and continued for a number of months but the requirements for maximum root number and length (Figures 2a,b and 3a,b) appeared to be achieved more gradually and retained for a shorter period in spring. Although root number and length, particularly per rooted cutting, showed a small improvement in late autumn, the attainment of maximum rooting potential in J. 'Pathfinder' so abruptly in mid winter indicates that not only is an endogenous state favourable for root formation achieved much later than in J. 'Skyrocket' but that the induction of such a state may be be more dependent on, for instance, the fulfilment of certain environmental or growth requirements. The possible involvement of temperature is dicussed in the next section.

Although rootability was generally no greater in autumn than spring, growth of rooted cuttings grown on until the following autumn was superior in those that had been propagated before early spring (Table 4). This was probably mainly due to the earlier cuttings having been established (a little root growth was noted in a few cuttings during winter) before the onset of shoot growth, high temperatures and the accompanying demands for moisture and nutrients in spring. The desirability for minimum shoot growth during root formation in regard to subsequent growth of rooted cuttings was reported by Snyder (1955). In cases where this difference in growth might be

of importance, cuttings of J. 'Skyrocket' would be better harvested in mid winter or a little earlier, regardless of the continued high level of rootability in August. The limited period of suitably high rooting potential that occurred in the present study in J. 'Pathfinder' would outweigh this consideration in most instances.

5.2 Air Temperature Treatment

The effect of air temperature treatments at the parent material and cutting stages were investigated primarily in relation to possible involvement of this factor in the seasonal changes in the capacity of the cuttings to form roots.

Exposure to low temperatures during autumn has been considered to improve rootability in a range of genera, including Vitis (Spiegel, 1955), pear (Fadl and Hartmann, 1967a), Populus (Smith and Wareing, 1972a) and Pinus (Whitehill and Schwabe, 1975). This has not always been the case however (e.g. Lanphear and Meahl, 1966; Howard and Harrison-Murray, 1980) and in addition, Fadl and Hartmann (1967a) found easy- compared with difficult-to- root cultivars of pear to respond differently to temperature treatments. The mean number of cuttings of J. 'Skyrocket' that formed roots was high in material taken from stock plants which had received normal winter chilling and from those which had been held in a warm environment since autumn (Figure 8a; Table 7a). A smaller proportion of cuttings of J. 'Pathfinder' from WP stock

rooted than those of CP origin to a highly significant extent under cool propagation air temperatures (Table 8a). The magnitude of response in each cultivar was comparible to the seasonal differences in mean number of cuttings rooted and mean root number that occurred between autumn and mid winter. Mean root number per cutting and mean total root length per cutting of J. 'Skyrocket' showed a greater response to parent plant environment and cutting environment temperatures than did the mean number of cuttings rooted (Figures 8a, 9a, 10a, Tables 7a,b,c). Only small changes occurred in mean root number on cuttings of J. 'Pathfinder' (Figure 9b, Table 9b) but mean total root length was greatest in CP material, highly significantly greater than material sujected to other parent environments if propagated under CH conditions (Figure 10b, Table 9b). Therefore the most important responses to temperature occurred in mean number of cuttings rooted of J 'Pathfinder' and mean number of roots per cutting of J. 'Skyrocket'. In contrast, rooting capacity of J. 'Blue Haven' and C. 'Swanes Golden' was greater in WP than CP material although not to a significant extent in C. 'Swanes Golden' (Figures 8c,d - 10c,d, Tables 11a-c, 13a-c). Results obtained in the growth cabinet study of J. 'Pathfinder' and C. 'Swanes Golden' coincided with those of the mid winter study in most respects (Figures 5-7, Tables 5 and 6) and the general effects of parent plant environment on rooting confirmed the results obtained by Tustin (1977a) with these cultivars.

The proportion of cuttings of WCP origin that formed roots was reported by Tustin (1977a) to be intermediate

between the WP and CP means. However stock plant treatments in the present study involving exposure to lower temperatures during the two weeks prior to excision, comprising the WCP and CCP treatments, reduced rooting capacity in all cultivars in comparison with the corresponding treatment without the additional chilling (WP, CP), to a highly significant extent in some cases (Figures 8-10, Tables 7, 9, 11). This phenomenon may have been brought about by stress arising from the sudden drop in temperature, especially in plants from the warm environment which would not have been winter-hardened. Conditions experienced by the plants in the previous study (Tustin, 1977a) may have been relatively mild. The return to a warm environment during root formation further reduced rooting of J. 'Skyrocket' cuttings of WCP material. The additional chilling might also have brought about a general reduction in shoot activity, as suggested by the data on shoot activity (Figures 11 and 12. Tables 8,10,12) in some instances.

In addition to the attainment of optimum rootability of J. 'Skyrocket' and J. 'Pathfinder' cuttings by stock plant chilling, this treatment also induced the greatest degree of shoot activity, as indicated by the number of cuttings showing new shoot growth and the amount of growth made by the time the cuttings were lifted (Figures 11 and 12, Tables 8,10,12). Significant and highly significant differences in shoot activity were found on comparison of WP and CP material in all the junipers. Cuttings of J. 'Pathfinder' showed a greater response to temperature and more shoot activity over all than those of

J. 'Skyrocket'. The apparent relationship between shoot activity in the junipers and parent material treatment was fairly well-defined, with activity increasing the greater the duration of exposure to low temperatures. The exception to this was the CCP material, which showed next most activity after CP material, possibly due to stress factors as mentioned previously or other factors related to storage. Resumption of shoot growth was therefore stimulated by, but did not have an absolute requirement for, chilling at the stock plant stage. This response has been reported in a number of species and Roberts et al (1974) found that long days could substitute at least in part for the low temperature requirement for breaking bud dormancy and that both low temperatures and long days could enhance rooting in cuttings of Psuedotsuga menziesii at cetain times during winter or spring. Extended photoperiods also induced the resumption of active shoot growth and greatly enhanced rooting of X Cupressocyparis leylandii cuttings taken in autumn (Sanders, 1970). These and other reports suggest that although the resumption of shoot growth in spring may have a detrimental effect on rootability, a certain degree of activity is benificial to root iniation (e.g. Lanphear and Meahl, 1961; Whitehill and Schwabe, 1975; Bhella and Roberts, 1974). Mean shoot growth was more advanced and the number of cuttings with shoot activity apparent was higher in the warm compared with the cold propagation environment (Figures 11, 12, Tables 8, 10, 12). Greater expression of the differences in shoot activity induced by the parent material treatments were permitted in cuttings under WH conditions. In addition, the differences

brought about by the propagation environments were significant or highly significant in CP material of all juniper cultivars.

Response of root formation capacity in relation to propagation environment was rather more variable within each cultivar than response to parent environment. Cuttings which had received the stock plant treatment most conducive to root formation in each juniper cultivar produced the maximum mean number of cuttings rooted when provided with cool air temperatures during the rooting phase in J. 'Pathfinder' and J. 'Blue Haven' whereas those from less favourable parent environments responded better to the WH treatment (Figure 8b,c, Tables 9a and 11a). Mean number of cuttings rooted of C. 'Swanes Golden' and J. 'Skyrocket' was high in all material regardless of propagation environment, with the excetion of WCP of J. 'Skyrocket' as discussed earlier. The parent/cutting environment interaction also occurred in J. 'Pathfinder' and C. 'Swanes Golden' under growth cabinet conditions (Figure 5a,b, Tables 5a and 6a). If indeed a certain level of shoot activity or associated factors is promotory to root initiation, a possible explanation of the parent/cutting environment interactions may be that the most favourable level of shoot activity for initiation and formation was most nearly achieved in the CP treatment for J. 'Skyrocket' and J. 'Pathfinder' and in the WP environment for J. 'Blue Haven' and that further shoot activity, detrimental to rooting, was limited in the cool propagation environment. Cuttings from other treatments may have required WH conditions to raise activity or associated

factors to an acceptable level. However if this was the case in J. 'Blue Haven' (Figure 8c), one would have expected that CP material which would presumably have exceeded the desired amount of chilling, to also root better in CH conditions. Rather than have exceeded a "desirable" amount of chilling however, the responses to and requirements for certain environmental or endogenous factors may be quite different in J. 'Blue Haven' and C. 'Swanes Golde ' compared with the other cultivars, as Fadl and Hartmann (1967a) found in regard to temperature storage treatment on rootability of different cultivars of pear. The suitability of each propagation environment also varied in regard to effect on root number or root length (Figures 9 and 10, Tables 7, 9, 11 and 13). Mean root number, particularly per rooted cutting, was often slightly higher in the WH compared with the CH environment whereas mean root length and to a much lesser extent, mean total root length showed the opposite tendancy. The general level of activity or factors associated with a certain level of shoot activity may have also enhanced the number of roots formed but may have subsequently, for instance, caused a mobilization of nutrients required for root growth away from the roots. One would however also expect competition between roots for metabolites to increase as numbers increase. There was little evidence of clearly defined relationships between parameters of rooting or shoot activity in individual cuttings apart from the slight negative relationships indicated between shoot growth and mean root length, and mean root length and root number in J. 'Skyrocket'.

Cuttings of Juniperus horizontalis 'Plumosa' in the study by Lanphear and Meahl (1966) rooted more readily from stock plants held in a warm environment since autumn until excision late in winter than from those which had remained outdoors. This might at first seem to be in conflict with the results obtained in this study in relation to J. 'Skyrocket' and J. 'Pathfinder'. However, it seems possible that if an optimum stage of release from dormancy or activation of growth processes for root initiation exists (e.g. Roberts et al, 1974; Whitehill and Schwabe, 1975; Gordienko et al, 1976), this may have been exceeded in the chilled material of J. horizontalis 'Plumosa'. The chilled material responded to extended or natural daylengths by producing new shoot growth and rooting more poorly than if provided with short days or in comparison with material under warm conditions in which bud break was retarded. This explanation may be given further support in that rooting potential of that cultivar in an earlier study (Lanphear and Meahl, 1963), treated with the same concentration of IBA, had begun to diminish by late winter. In addition, whereas long days and the ensuing activation of shoot growth were associated with poor rooting in spring, the effect tended to be more favourable in autumn (Lanphear and Meahl, 1961). Lanphear and Meahl (1966) proposed that "stage of dormancy rather than the chilling period, is the prerequisite factor for the increased root-forming capacity". Results obtained by Whitehill and Schwabe (1975) and Roberts et al (1974) tended to confirm this. Rooting of Psuedotsuga menziesii cuttings could be enhanced by low temperature storage only during a specific period in late

autumn. Response of the root system to temperature may have been a further complicating factor in the present study.

Future studies could include effects of differential root/shoot temperatures in stock plants, and early chilling.

5.3 Endogenous Growth Regulators

Effects of environment must ultimately act via endogenous changes and of the many factors found to be implicated and interact in the complex process of adventitious root formation changes in growth regulator levels or balance are frequently associated with changes in potential to form roots (Chapter 2).

Auxin is widely regarded as an important promoter of root initiation (e.g. Went, 1939; Mullins, 1970; Smith and Wareing, 1972b; Smith and Thorpe, 1975; Mitsuhashi-Kato, 1978) and increased auxin or auxin:inhibitor content has been found to be associated with improved rootability, including improvements apparently brought about by seasonal changes or low temperature treatments (e.g. Spiegel, 1955; Smith and Wareing, 1972a;b; Vieitez and Pena, 1968; Gordienko et al, 1976). That has not always been the case however (e.g. Foong, 1977) and of the growth regulators investigated in the present study changes in IAA-like activity with season or temperature treatment (Figure 13) showed little relationship to changes in rooting capacity. Differences in content between cultivars also seemed unrelated to rooting potential although estimated levels were normally marginally higher in J. 'Skyrocket' than J. 'Pathfinder'. The decline in content from late summer to winter was in agreement with the results obtained

by Gordienko et al,(1976) with Juniperus sabina but the peaks in rooting potential during spring and autumn coincided with peaks in auxin activity. With regard to seasonal fluctuations in rootability of Juniperus spp. Lanphear and Meahl (1966) found that these could not be accounted for by cofactor level which remained relatively static in J. horizontalis 'Plumosa' but suggested that cofactor content may determine maximum rooting potential attainable which is limited by other factors, possibly including mobilization of cofactors.

ABA is generally regarded as in inhibitor of growth processes including root formation although positive relationships between endogenous ABA level and rooting (Section 2.4.4). An inverse relationship between rootability and ABA content could at least partially account for seasonal changes in rooting potential in J. 'Skyrocket' and the high level of rooting obtained from cuttings of C. 'Swanes Golden' in February and June but could not account for the reduction in rootability in WP material or that attained by J. 'Pathfinder' during April (Figure 14). On comparison of the four cultivars in June, a consistent inverse relationship between estimated ABA concentration and rootability was found, with a high level in J. 'Blue Haven', an intermediate level in J. 'Pathfinder' and low levels in J. 'Skyrocket' and C. 'Swanes Golden'. Only ABA showed a consistent relationship with rooting capacity in this respect.

Cytokinins are also normally considered to be inhibitory to root initiation at least if present in high concen-

trations (Section 2.4.3). Although total cytokinin activity was not easily related to cultivar differences in rooting in June and high levels were detected in C. 'Swanes Golden' in February and June, this was the only growth regulator which could account for the reduction in rooting brought about by the WP treatment. The seasonal fluctuations in rooting capacity of J. 'Pathfinder' were also consistently related only to estimated cytokinin content. (Figure 15). The greatest difference in rooting potential between J. 'Skyrocket' and J. 'Pathfinder' occurred in April (Tables 1a-c), coinciding with the large difference in cytokinin content between these two cultivars. Seasonal changes in content of the other growth regulators tended to be similar in J. 'Skyrocket' and J. 'Pathfinder' and cytokinin content was also similar in cutting samples other than those obtained in April, therefore it appears that cytokinin concentration may contribute to the difference in seasonal patterns of rooting potential encountered. The high level of rootability of J. 'Skyrocket' cuttings during April, particularly in rooting percentage, may have been assisted by a relatively higher auxin:inhibitor ratio. However, cytokinin level had returned to a high level in J. 'Skyrocket' at the time of optimimum rootability in June. Other factors may have allowed this easily rooted cultivar to attain a high level of rooting even under conditions of high endogenous cytokinin at this time.

5.4 Conclusion

The general pattern of seasonal fluctuations in rootability of cuttings of J. 'Skyrocket' and J. 'Pathfinder' coincided with most patterns reported to occur in narrow-leaved evergreens. The hypothesis that adventitious root formation in such plants is largely controlled directly or indirectly by growth phase was supported to some extent by the differences in rooting capacity during different seasons or after exposure to different temperatures and state of shoot growth associated with these differences. Exposure of stock plants of J. 'Skyrocket' and J. 'Pathfinder' to chilling temperaures apparently contributes at least in part to the attainment of optimum rootability in mid winter although the specific responses or requirements for optimum rooting may vary with cultivar as indicated in J, 'Blue Haven'. The response to parent plant temperature , although limited, was the opposite in C. 'Swanes Golden' to that of J. 'Skyrocket' and J. 'Pathfinder' and a difference was again found in the seasonal pattern of root formation potential. The effect of temperature of the cutting environment tended to be more variable than that of parent plant environment and appeared to interact with parent environment in some instances.

Although differences in rootabilty did not appear to be related to level of the endogenous IAA-like component, levels of ABA and cytokinin-like activity appeared to be inversely related to rootability in several instances.

APPENDICES

Appendix 1. Buffer Solutions

1a. Phosphate-citrate buffer for the Triticum coleoptile bioassay.

K_2HPO_4	4.485 g
Citric acid monohydrate	2.547 g

The above dissolved in 250 ml distilled give a 10 X concentrated solution. Dilute 1 in 10 when required and add 2 g sucrose per 100 cm^3. Check that pH = 5.3 and adjust if necessary.

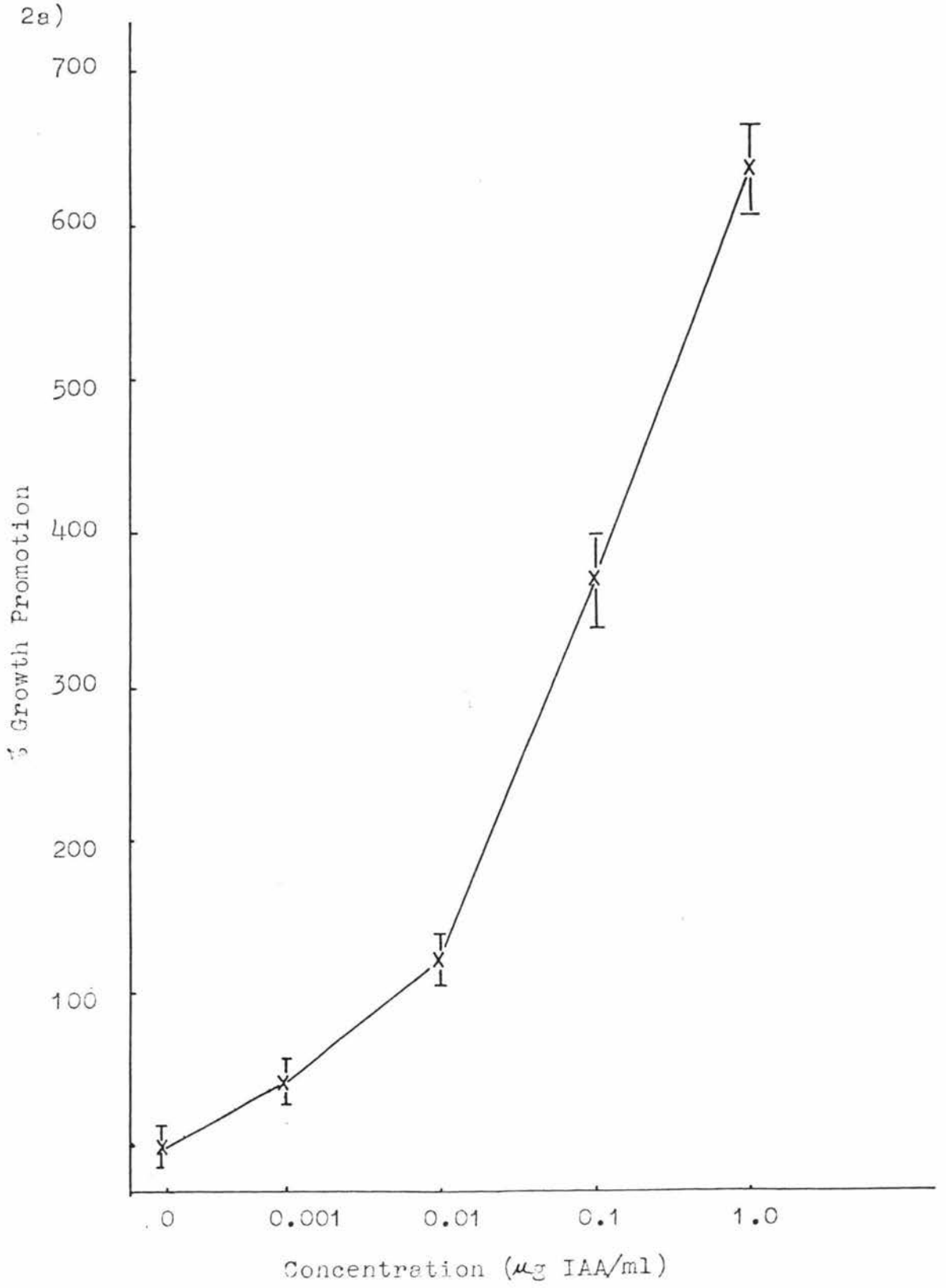
1b. Burström's Basal Buffer.

KH_2PO_4	10^{-3} mol/l
$Ca(NO_3)_2$	10^{-4} "
$MgSO_4$	10^{-5} "
Glucose	16 g/l

Citric acid (0.1 M) is used to adjust the pH to 5.6.

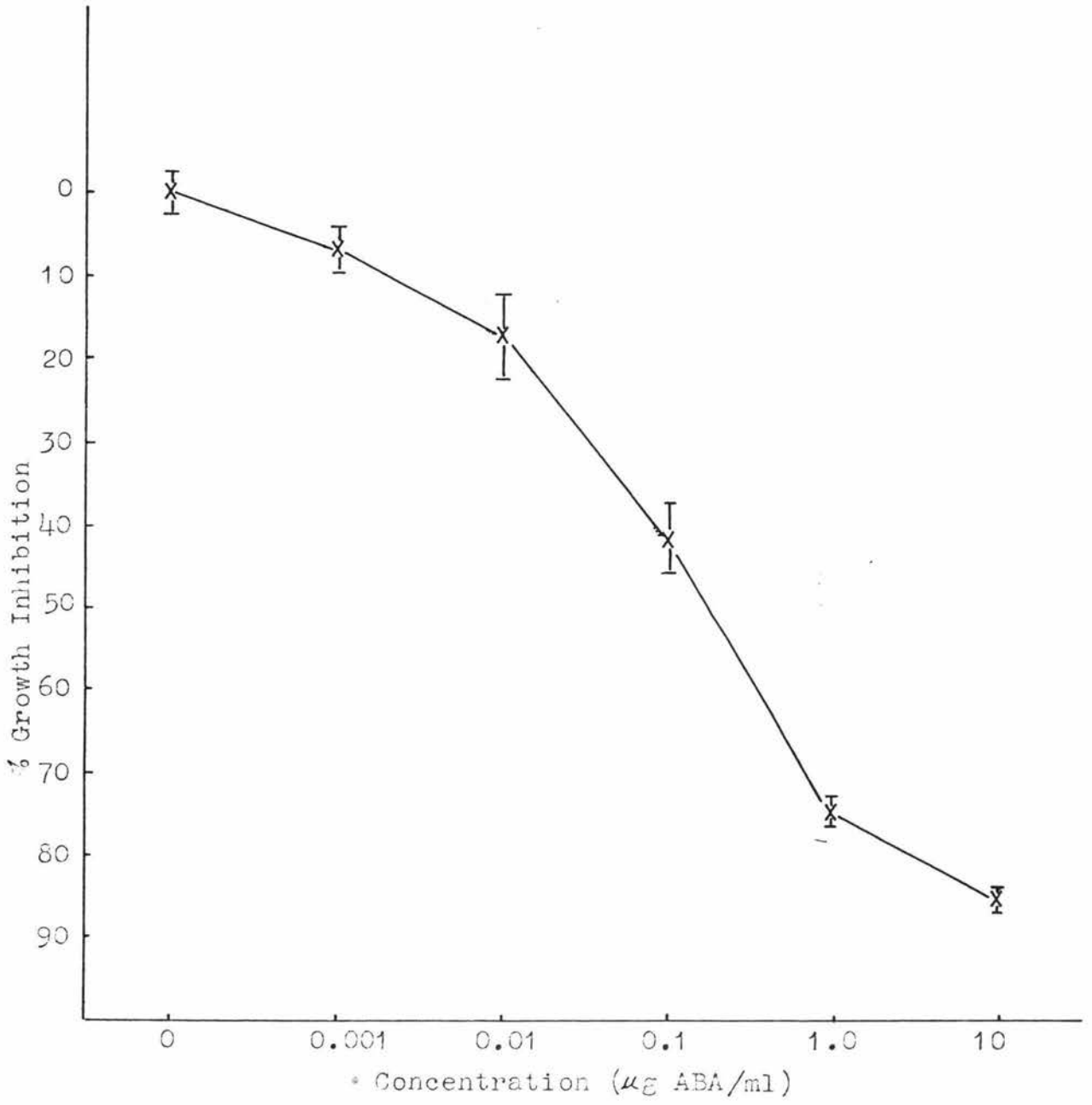
Appendix 2. Standard Curves

2a)



A standard curve for Avena coleoptile response to IAA. Standard errors shown.

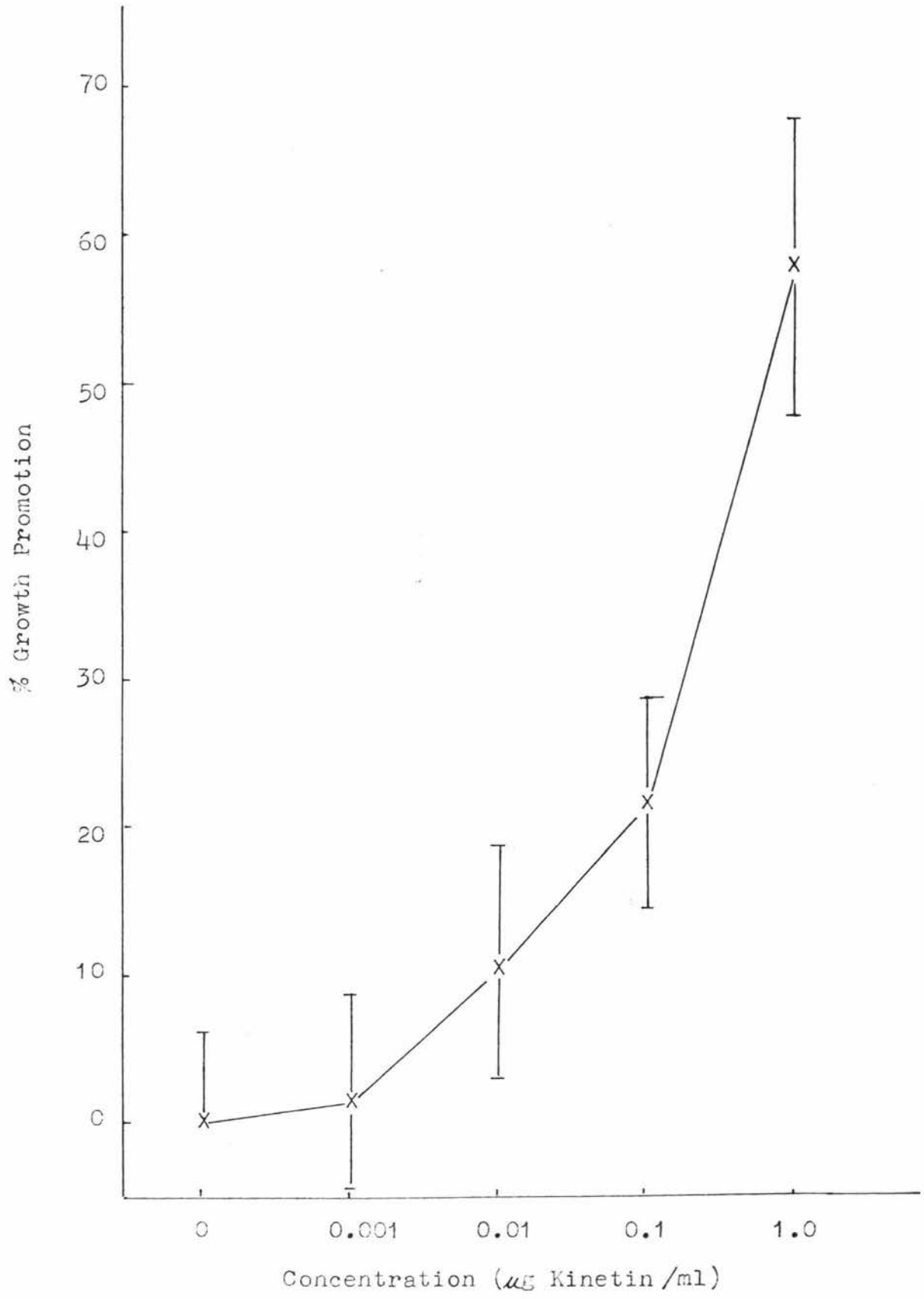
2b)



A standard curve for Triticum coleoptile response to ABA.

Standard errors shown.

2c)



A standard curve for radish cotyledon expasion growth in response to kinetin.

Standard errors shown.

Appendix 3. Seasonal Study Analysis of Variance

3a) Mean number of cuttings rooted/8

Analysis of variance for the whole year

Source Variation	df	SS	MS	F
Blocks, R	2	0.26	0.13	
Varieties, A	1	133.80	133.80	7341.34**
Error (a)	2	0.04	0.02	
Months, B	8	218.04	27.25	14.37**
Interaction, AB	8	108.37	13.55	7.14**
Error (b)	32	60.70	1.90	

Analysis of variance for each month

Source of Variation	df	Feb SS	Feb MS	Mar SS	Mar MS
Blocks, R	2	3.00	1.50	1.00	0.50
Varieties, A	1	1.50	1.50	0.17	0.17
Error	2	1.00	0.50	2.33	1.17

Apr SS	Apr MS	May SS	May MS	Jun SS	Jun MS
1.33	0.67	4.33	2.17	3.00	1.50
66.67	66.67	54.00	54.00	1.50	1.50
5.33	2.67	7.00	3.50	3.00	1.50

Jul SS	Jul MS	Aug SS	Aug MS	Sep SS	Sep MS
4.33	2.17	4.33	2.17	8.33	4.17
48.17	48.17	20.17	20.17	48.17	48.17
2.33	1.17	2.33	1.17	6.33	3.17

Oct SS	Oct MS
1.00	0.50
1.50	1.50
1.00	0.50

3b) Mean number of roots per cutting

Analysis of variance for the whole year

Source of Variation	df	SS	MS	F
Blocks, R	2	1.35	0.67	
Varieties, A	1	50.84	50.84	42.83 *
Error (a)	2	2.37	1.19	
Months, B	8	66.80	8.35	10.74 **
Interaction, AB	8	31.20	3.90	5.02 **
Error (b)	32	24.88	0.78	

Analysis of variance for each month

Source of Variation	df	Feb		Mar	
		SS	MS	SS	MS
Blocks, R	2	0.72	0.36	0.005	0.003
Varieties, A	1	0.13	0.13	0.023	0.023
Error	2	0.22	0.11	0.109	0.055

Apr		May		Jun	
SS	MS	SS	MS	SS	MS
0.11	0.05	0.48	0.24	11.36	5.68
11.72	11.72	7.33	7.33	23.52	23.52
0.56	0.28	0.79	0.39	9.02	4.51

Jul		Aug		Sep	
SS	MS	SS	MS	SS	MS
0.20	0.10	1.28	0.64	1.04	0.52
18.79	18.79	13.14	13.15	7.32	7.32
0.10	0.05	1.53	0.77	0.94	0.47

Oct	
SS	MS
0.07	0.03
0.07	0.07
0.07	0.03

3c) Mean total root length per cutting

Analysis of variance for the whole year

Source of Variation	df	SS	MS	F
Blocks, R	2	1,277.18	638.59	
Varieties, A	1	97,818.59	97,818.59	88.56 *
Error (a)	2	2,208.86	1,104.43	
Months, B	8	307,956.06	38,494.51	32.92 **
Interaction, AB	8	77,495.38	9,686.92	8.28 **
Error (b)	32	37,419.69	1,169.37	

Analysis of variance for each month

Source of Variation	df	Feb SS	Feb MS	Mar SS	Mar MS
Blocks, R	2	1912.32	956.16	0.42	0.12
Varieties, A	1	160.17	160.17	0.26	0.26
Error	2	140.56	70.28	2.10	1.05

Apr SS	Apr MS	May SS	May MS	Jun SS	Jun MS
529.49	264.74	2651.39	1325.70	12094.89	6047.45
19889.28	19889.28	27051.38	27051.38	17901.15	17901.15
2000.33	1000.17	2068.10	1034.05	30.64	15.32

Jul SS	Jul MS	Aug SS	Aug MS	Sep SS	Sep MS
1418.15	709.07	461.08	230.54	520.77	260.39
66202.51	66202.51	42147.21	42147.21	1935.01	1935.01
1119.15	559.57	15407.33	7703.67	505.27	252.64

Oct SS	Oct MS
21.81	10.91
27.09	27.09
21.81	10.91

3d) Analysis of variance for C.'Swanes Golden'

Mean number of cuttings rooted/8

Source of Variation	df	SS	MS	F
Blocks, R	2	0.67	0.33	
Month	2	32.67	16.33	36.79 **
Error	6	2.67	0.44	

Mean number of roots per cutting

Source of Variation	df	SS	MS	F
Blocks, R	2	0.70	0.35	
Month	2	19.45	9.73	2.71
Error	6	21.53	3.59	

Mean total root length per cutting

Source of Variation	df	SS	MS	F
Blocks, R	2	2,618.03	1,309.02	
Month	2	24,219.77	12,109.89	0.86
Error	6	84,380.15	14,063.36	

Appendix 4. Analysis of Variance for the Growth Cabinet Study.

4a) J.'Pathfinder'

Mean number of cuttings rooted/8

Source of Variation	df	SS	MS	F
Blocks, R	3	3.19	1.06	
Cutting Env, A	1	14.06	14.06	9.00
Error (a)	3	4.69	1.56	
Parent Env, B	1	7.56	7.56	6.60 *
Interaction, AB	1	0.06	0.06	0.05
Error (b)	6	6.88	1.15	

Mean number of roots per cutting

Source of Variation	df	SS	MS	F
Blocks, R	3	0.46	0.15	
Cutting Env, A	1	2.07	2.07	6.18
Error (a)	3	1.00	0.33	
Parent Env, B	1	0.77	0.77	2.26
Interaction, AB	1	0.14	0.14	0.42
Error (b)	6	2.03	0.34	

Mean total root length per cutting

Source of Variation	df	SS	MS	F
Blocks, R	3	210.23	70.08	
Cutting Env, A	1	1,072.56	1,072.56	8.58
Error (a)	3	375.13	125.04	
Parent Env, B	1	520.41	520.41	2.33
Interaction, AB	1	260.02	260.02	1.17
Error (b)	6	1,338.75	223.12	

4b) C.'Swanes Golden'

Mean number of cuttings rooted/8

Source of Variation	df	SS	MS	F
Blocks, R	3	5.19	1.73	
Cutting Env, A	1	0.06	0.06	0.04
Error (a)	3	4.19	1.40	
Parent Env, B	1	7.56	7.56	5.76
Interaction, AB	1	3.06	3.06	2.33
Error (b)	6	7.88	1.31	

Mean number of roots per cutting

Source of Variation	df	SS	MS	F
Blocks, R	3	2.29	0.76	
Cutting Env, A	1	9.38	9.38	2.28
Error (a)	3	12.35	4.12	
Parent Env, B	1	23.77	23.77	9.44 *
Interaction, AB	1	19.14	19.14	7.60 *
Error (b)	6	15.11	2.52	

Mean total root length per cutting

Source of Variation	df	SS	MS	F
Blocks, R	3	417.83	139.28	
Cutting Env, A	1	492.29	492.29	0.57
Error (a)	3	2,569.34	856.45	
Parent Env, B	1	13,601.39	13,601.39	10.53 *
Interaction, AB	1	5,494.51	5,494.51	4.25
Error (b)	6	7,749.33	1,291.56	

Appendix 5. Analysis of Variance for the Midwinter Study

5a) J.'Skyrocket'

Mean number of cuttings rooted/8

Source of Variation	df	SS	MS	F
Blocks, R	2	0.08	0.04	
Cutting Env, A	1	2.67	2.67	3.37
Error (a)	2	1.58	0.79	
Parent Env, B	3	16.33	5.44	6.76 **
Interaction, AB	3	11.00	3.67	4.55 *
Error (b)	12	9.67	0.81	

Mean number of roots per cutting

Source of Variation	df	SS	MS	F
Blocks, R	2	0.43	0.21	
Cutting Env, A	1	5.99×10^{-3}	5.99×10^{-3}	4.15×10^{-3}
Error (a)	2	2.88	1.44	
Parent Env, B	3	31.16	10.51	4.41
Interaction, AB	3	7.15	2.38	0.71
Error (b)	12	40.20	3.35	

Mean total root length per cutting

Source of Variation	df	SS	MS	F
Blocks, R	2	314.54	157.27	
Cutting Env, A	1	27,295.25	27,295.69	32.77 *
Error (a)	2	1,665.90	832.95	
Parent Env, B	3	66,502.80	22,167.60	4.06 *
Interaction, AB	3	18,085.45	6,028.48	1.10
Error (b)	12	65,579.46	5,464.96	

Mean number of cuttings with new shoot growth/8

Source of Variation	df	SS	MS	F
Blocks, R	2	0.58	0.29	
Cutting Env, A	1	13.50	13.50	36.00 *
Error (a)	2	0.75	0.38	
Parent Env, B	3	10.33	3.44	2.14
Interaction, AB	3	14.83	4.94	3.07
Error (b)	12	19.33	1.61	

Mean shoot growth per cutting

Source of Variation	df	SS	MS	F
Blocks, R	2	0.52	0.26	
Cutting Env, A	1	4.49	4.49	13.17 *
Error (a)	2	0.68	0.34	
Parent Env, B	3	5.14	1.71	9.20 **
Interaction, AB	3	5.76	1.92	10.29 **
Error (b)	12	2.24	0.19	

5b) J. 'Pathfinder'

Mean number of cuttings rooted/8

Source of Variation	df	SS	MS	F
Blocks, R	2	0.11	0.05	
Cutting Env, A	1	5.56	5.56	2.70
Error (a)	2	4.11	2.06	
Parent Env, B	2	51.44	25.72	12.51 **
Interaction, AB	2	21.44	10.72	5.22 *
Error (b)	8	16.44	2.06	

Mean number of roots per cutting

Source of Variation	df	SS	MS	F
Blocks, R	2	0.43	0.21	
Cutting Env, A	1	1.00	1.00	1.46
Error (a)	2	1.38	0.69	
Parent Env, B	2	5.37	2.69	1.37
Interaction, AB	2	0.97	0.48	0.25
Error (b)	8	3.92	1.96	

Mean total root length per cutting

Source of Variation	df	SS	MS	F
Blocks, R	2	1,184.67	592.34	
Cutting Env, A	1	0.31	0.31	6.37×10^{-5}
Error (a)	2	9,826.70	4,913.35	
Parent Env, B	2	31,907.52	15,953.76	7.73 *
Interaction, AB	2	13,622.74	6,811.37	0.82
Error (b)	8	16,520.04	2,065.01	

Mean number of cuttings with new shoot growth/8

Source of Variation	df	SS	MS	F
Blocks, R	2	2.78	1.39	
Cutting Env, A	1	43.56	43.56	783.93 **
Error (a)	2	0.11	0.06	
Parent Env, B	2	56.44	28.22	12.24 **
Interaction, AB	2	8.44	4.22	1.83
Error (b)	8	18.44	2.31	

Mean shoot growth per cutting

Source of Variation	df	SS	MS	F
Blocks, R	2	0.40	0.20	
Cutting Env, A	1	39.75	39.75	47.07 *
Error (a)	2	1.69	0.84	
Parent Env, B	2	20.36	10.18	20.64 **
Interaction, AB	2	8.25	4.13	8.37 *
Error (b)	8	3.94	0.49	

5c) J. 'Blue Haven'

Mean number of cuttings rooted/8

Source of Variation	df	SS	MS	F
Blocks, R	2	1.44	0.72	
Cutting Env, A	1	0.06	0.06	6.62×10^{-3}
Error (a)	2	16.78	8.39	
Parent Env, B	2	30.78	15.39	11.79 **
Interaction, AB	2	7.44	3.72	2.85
Error (b)	8	10.44	1.31	

Mean number of roots per cutting

Source of Variation	df	SS	MS	F
Blocks, R	2	4.43	2.21	
Cutting Env, A	1	5.14	5.14	0.85
Error (a)	2	12.06	6.03	
Parent Env, B	2	2.51	1.26	0.26
Interaction, AB	2	9.79	4.89	1.43
Error (b)	8	27.29	3.41	

Mean total root length per cutting

Source of Variation	df	SS	MS	F
Blocks, R	2	2,425.61	1,212.81	
Cutting Env, A	1	50.02	50.02	0.02
Error (a)	2	6,084.99	3,042.49	
Parent Env, B	2	24,635.24	12,317.62	12.02 **
Interaction, AB	2	1,784.81	892.40	0.87
Error (b)	8	8,200.73	1,025.09	

Mean number of cuttings with new shoot growth/8

Source of Variation	df	SS	MS	F
Blocks, R	2	1.44	0.72	
Cutting Env, A	1	10.89	10.89	15.08
Error (a)	2	1.44	0.72	
Parent Env, B	2	23.11	11.56	20.80 **
Interaction, AB	2	3.11	1.56	2.80
Error (b)	8	4.44	0.56	

Mean shoot growth per cutting

Source of Variation	df	SS	MS	F
Blocks, R	2	2.02	1.01	
Cutting Env, A	1	4.13	4.13	4.09
Error (a)	2	2.02	1.01	
Parent Env, B	2	7.61	3.80	4.89 *
Interaction, AB	2	5.66	2.83	3.64
Error (b)	8	6.22	0.78	

5d) C. 'Swanes Golden'

Mean number of cuttings rooted/8

Source of Variation	df	SS	MS	F
Blocks, R	2	1.50	0.75	
Cutting Env, A	1	0.33	0.33	0.57
Error (a)	2	1.17	0.58	
Parent Env, B	1	0.33	0.33	2.00
Interaction, AB	1	0.00	0.00	0.00
Error (b)	4	0.67	0.17	

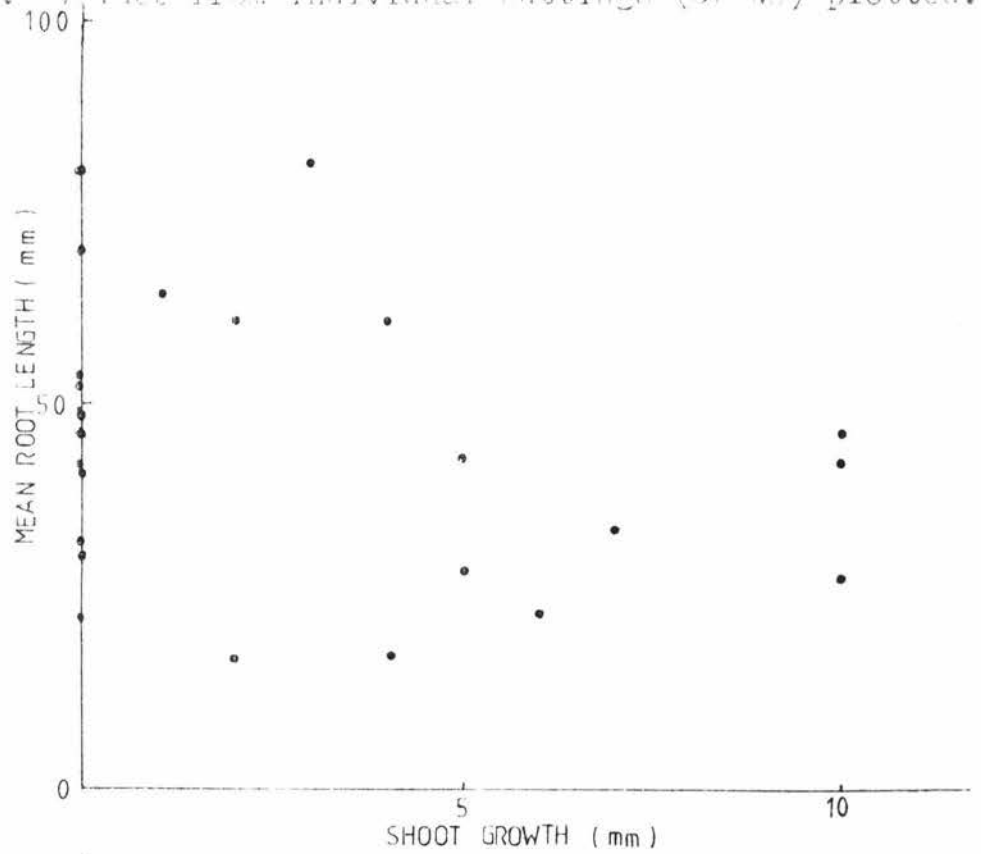
Mean number of roots per cutting

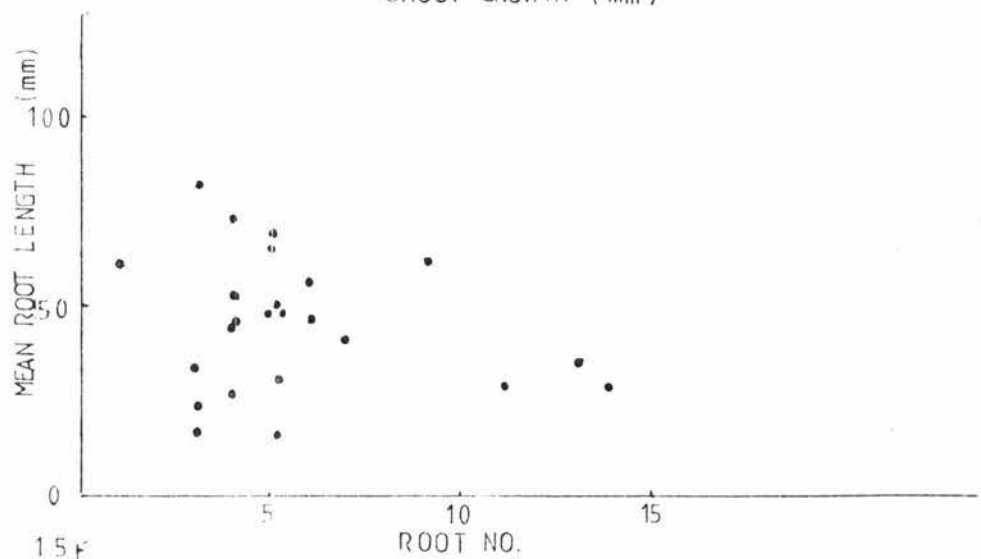
Source of Variation	df	SS	MS	F
Blocks, R	2	2.50×10^{-8}	1.25×10^{-8}	
Cutting Env, A	1	0.33	0.33	0.26
Error (a)	2	2.57	1.29	
Parent Env, B	1	1.17	1.17	0.90
Interaction, AB	1	0.02	0.02	0.02
Error (a)	4	5.23	1.31	

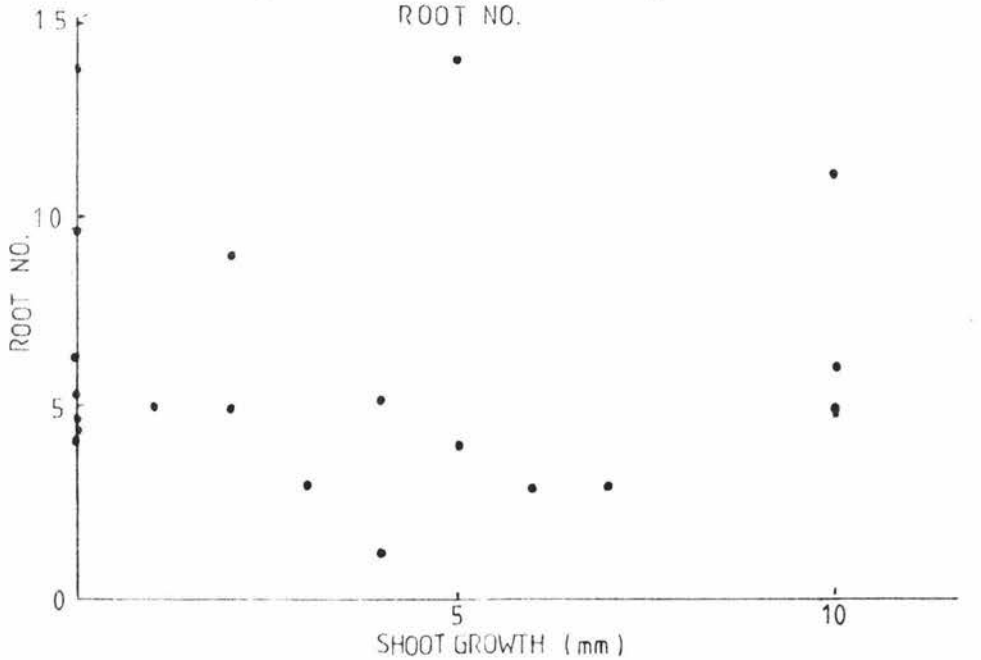
Mean total root length per cutting

Source of Variation	df	SS	MS	F
Blocks, R	2	8,146.59	4,073.30	
Cutting Env, A	1	3,692.52	3,692.52	1.26
Error (a)	2	5,847.44	2,923.72	
Parent Env, B	1	9,478.12	9,478.12	2.27
Interaction, AB	1	716.89	716.89	0.17
Error (b)	4	16,707.06	4,176.77	

Appendix 6. Relationship between parameters in *D. virginiana* 'Shamrocket'. Values from individual cuttings (CP VI) plotted.

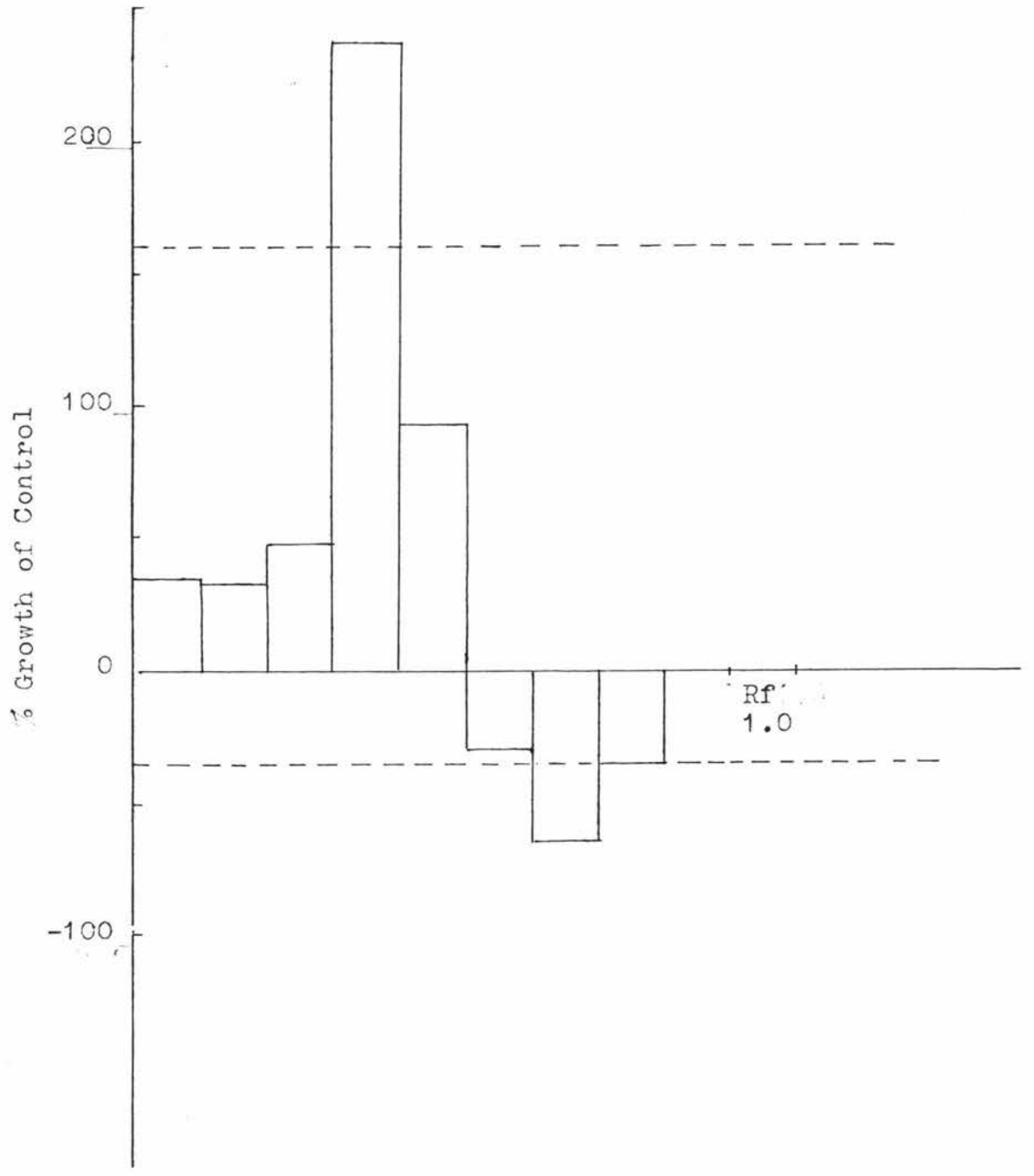






Appendix 7. Chromatograms.

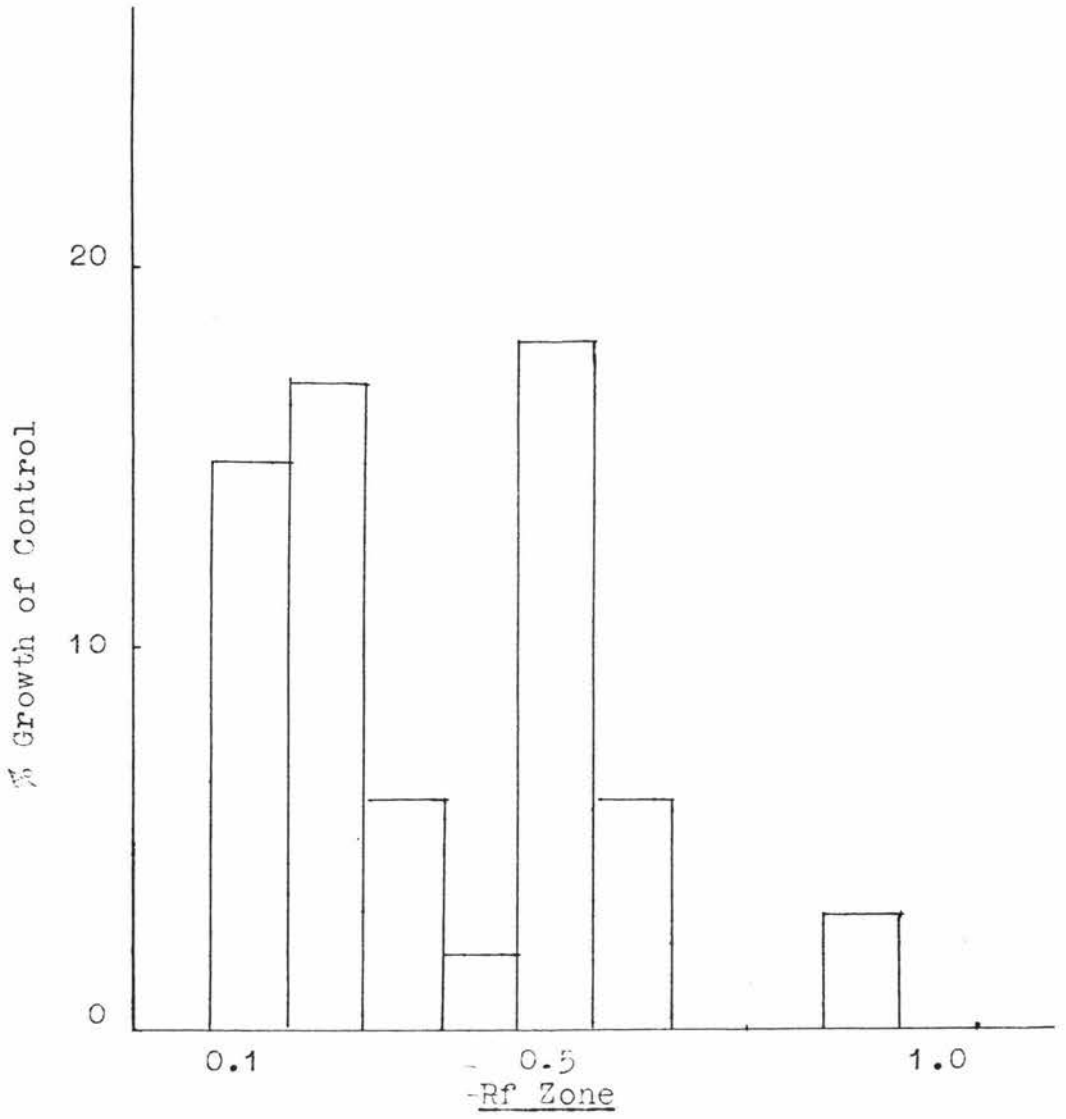
Typical example showing the major zones of activity of acidic growth promoters and inhibitors.



Activity in stem tissue of J. 'Skyrocket' excised in April. $LSD_{0.05}$ indicated.

Appendix 8. Chromatograms.

Typical example indicating major areas of cytokinin-like activity.



Activity in stem tissue of J. 'Skyrocket' excised in April. Relatively more activity located about Rf 0.9 in some other samples.

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