Growth and development of the Rhododendron shoot was studied in detail to establish a morphological time scale for predicting when root regeneration capacity in cuttings would be maximal. Floret diameter proved to be a valuable index to this. Morphological features related to or influencing root regeneration were shoot origin, type of terminal bud, leaf position and size. These were studied in relation to tissue ageing. Rooting response was evaluated on the basis of rooting percentage, root-ball size and leaf rooting-potential (root-ball diameter per 10 cm$^2$ of leaf area).

Stem, leaf-bud and leaf-petiole cuttings of easy-, intermediate- and hard-to-root cultivars were taken at three-week intervals from late June to October in two years to study the influence of morphological features on root regeneration with increasing tissue age. Although modified by cultivar and seasonal growing conditions, rooting of cuttings made from young shoots when florets were small was
better than the rooting from older, more advanced shoots. The coincidence of periods of low rooting response on the morphological time scale for cuttings of different origins showed the advantages of the scale because these periods were not evident on a chronological basis. Although not evident in easy-to-root cultivars, the data suggested an intense competition between developing florets and initiating roots in cuttings of both intermediate- and hard-to-root cultivars. The rooting-potential of leaves on non-flowering cuttings was often several times greater than that of flowering cuttings, but was modified by cultivar influence. The influence of flower initiation on rooting was attributed to competition for critical metabolites, and changes in leaf size and physiology.

Like flower initiation, the influence of shoot origin, leaf position and leaf area seemed more closely related to leaf size than any factor considered. Although not studied in detail, a consistent inverse relationship between leaf size and rooting-potential existed.

Estimating physiological age by means of the morphological time scale appeared to be more reliable than calendar dating for timing the taking of cuttings. The presence of the flower was the chief factor influencing leaf rooting-potential and its influence as well as others, appeared to be related to the leaf’s size and physiological status.
A MORPHOLOGICAL APPROACH TO PREDICTING THE ROOTING-POTENTIAL OF THE RHODODENDRON SHOOT

by

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Date thesis is presented June 10, 1966
Typed by Marion F. Palmateer
Dedication

This thesis is dedicated to my wife and family.
ACKNOWLEDGMENTS

The writer wishes to express his sincere appreciation to Dr. A. N. Roberts for his assistance throughout the investigation and during the preparation of this manuscript.

Appreciation is also extended to the graduate committee for their part in reviewing the manuscript and particularly to Dr. L. T. Blaney for his counsel throughout all phases of the study. Thanks are also due to the many commercial growers who so generously contributed time and plant materials.
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A MORPHOLOGICAL APPROACH TO PREDICTING
THE ROOTING-POTENTIAL OF THE
RHODODENDRON SHOOT

INTRODUCTION

The commercial importance of vegetative propagation can only be comprehended when it is realized that nearly all tree fruits, nuts, cane fruits, strawberries, ornamental trees and shrubs, florist plants other than annuals, bulbous plants, potatoes, rhubarb and asparagus are propagated in this manner. Forest trees have also been propagated vegetatively in Japan.

Woody plants differ greatly in their ease of vegetative propagation. For instance, among cultivars and species of Pyrus, Persea, Vitis, Citrus, Rhododendron, Hedera, Hibiscus and Malus differences in rooting may approach 100 percent. The economics of commercial production of these plants is reason enough for attempting to understand more of the physiology and biochemistry of rooting.

A voluminous literature has been written over the past 40 years on vegetative propagation. Most reports are empirical in nature and deal with the effects of applications of nutrient and growth substances to cuttings. Although many morphological and biochemical factors have been found to influence root regeneration capacity, their importance has differed greatly between plants and plant parts concerned.
Furthermore, the results of many of these investigations, for the most part, have not been reproducible.

A much neglected area of research concerning woody plant propagation has been the relationship between the growth and development of the stock plant and the time of taking cuttings. The time of taking cuttings has usually been based on calendar date with little thought of the importance of physiological age or condition of the plant. The optimum time for taking cuttings has been studied often, but little has been done to relate this timing to physiological age or to establish a workable morphological time scale for greater accuracy. It is believed that the reason for our inability to obtain reproducible results consistently in propagation research has been our inability to obtain samples at the same precise stages of development and physiological condition as those sampled previously. Because of seasonal differences in rate of extension growth and development, a plant part can be quite different physiologically on the same date in separate years.

The question of when to take rhododendron cuttings is confounded by several factors which influence rooting in many plants. These include the influence of the terminal bud, leaf area and leaf position on the stem among several others. A time differential also exists in rhododendron between bud-break of terminal and lateral buds (Figure 5). Furthermore, late-season "lammas" growth is usually produced
early enough to be included in the taking of normal cuttings. It is obvious that large differences in physiological age of shoots can and do exist on a plant at a given time. Moreover, since the time of bud-break in the spring is largely controlled by temperature, the date on which a shoot reaches a certain physiological age may differ drastically from year to year.

With the above problems in mind, the growth and development of the rhododendron shoot was studied in detail to establish, if possible, a morphological time scale for estimating physiological age. With such a scale, times of high and low rooting-potential could be predicted each season with the possibility that results obtained in rooting cuttings one season could be reproduced the next. The clarification of the importance of certain morphological factors influencing rooting was also a major goal of this study. These were shoot origin (terminal or lateral), terminal bud type (flowering or non-flowering), leaf area and the position of the leaf on the stem. Interactions between these factors and tissue age were studied to determine which dominated root regeneration in the easy-, intermediate- and hard-to-root cultivars.

The Rhododendron was chosen because its cultivars exhibit great differences in rootability. A second consideration was its commercial importance in the Northwest and the availability of many cultivars.

Certain terms are defined:
Types of cultivars:

Easy-to-root; normally rooting 80 percent or better under commercial conditions.

Intermediate-rooting; normally rooting 50-80 percent under commercial conditions.

Hard-to-root; normally rooting less than 50 percent under commercial conditions.

Types of cuttings: (Figures 1, 2 and 3)

1. Stem cuttings; made from shoots of the current season and having their full leaf complement and terminal bud.
   a. Flowering terminal cutting; made from a terminal shoot with a flower bud.
   b. Flowering lateral cutting; made from a lateral shoot with a flower bud.
   c. Non-flowering cutting; made from terminal or lateral shoots without a flower bud.

2. Leaf-bud cutting; consists of a small portion of stem tissue, a lateral bud and the subtending leaf.

3. Leaf-petiole cutting; consists of an individual leaf and its petiole.

Root-ball; the mass of fiberous roots and attached rooting media measured in centimeters of greatest diameter.
Figure 1. Flowering terminal shoot (right) and a flowering lateral shoot (left) of *Rhododendron 'Cynthia'*. 
Figure 2. Flowering stem cutting (left), leaf-bud cuttings (center) and leaf-petiole cuttings (right) of *Rhododendron 'Cynthia'*.
Figure 3. Flowering terminal stem cutting (left), flowering lateral stem cutting (center) and non-flowering stem cutting (right) of Rhododendron 'Cynthia'.
Rooting-potential: capacity of a cutting to regenerate and develop a root system and calculated on the basis of root-ball size produced per ten square centimeters of leaf area.

Bud-scales: scale-like leaves (cataphylls) which surround the terminal and lateral apices. In early stages of development these are indistinguishable from the bracts found subjacent to florets or leaf primordia.

Base date: date on which the largest floret in the terminal bud attained a diameter of 1 mm, used as the zero (0) base for the morphological time scale.
REVIEW OF LITERATURE

Rhododendron Growth and Development

Some of this review (identified by an asterisk) is general knowledge to the hobbiiest and commercial grower and is not to be found in the literature. It is mentioned here because the information was germane to a study of growth and development of the Rhododendron.

The Rhododendron, which contains some 350 species, is one of some 70 genera in the Ericaceae. This paper deals primarily with interspecific hybrids of Rhododendron catawbiense Michaux of the Ponticum Series, but other hybrids were considered as well. The parentage of the cultivars used in this study are found in the International Rhododendron Register (1958).

Rhododendron catawbiense is a shrub, 6 feet to less than 20 feet tall, usually of greater spread than height. Flowers are pedicelled in terminal umbel-like racemes. The 15-20 florets in the inflorescence are 1.5 - 2.5 inches wide. The leaves are usually broad at the base, oval to oblong and three to five inches in length (Bailey 1950, Bowers 1936). The shoots terminate in flower or leaf buds (Figure 3). These are not mixed buds and contain only flowers or leaves, respectively. The two types of buds are easily recognized; the flower buds by their larger size and round shape, the leaf buds
by their smaller size and slender conical shape. The leaves on flowering shoots are often larger than those on non-flowering shoots (Figure 4), but this varies with the cultivar. Sometimes the leaf area on flowering shoots may be nearly double than on non-flowering shoots (*). In the spring, terminal shoot buds break about two to three weeks before the lateral shoots buds located beneath the terminal flower buds (Figure 5). This difference in time of bud-break however, is often changed greatly by temperature (*). Elliot (1937) reported that leaf expansion in *Rhododendron ponticum* is completed in the current season, even though the leaves persist for two to three years. Many *Rhododendron* species and cultivars make naturally a second or "lammas" growth flush in late summer or early autumn. The leaves of "lammas" growth usually expand only one-third the first season, completing their expansion the following year. Seldom do these leaves attain normal size. Elliot has also shown that leaves of a few evergreen plants, including *R. ponticum*, occasionally produce a small amount of second-year xylem but no new phloem. Lammas growth leaves were observed to always produce second-year xylem.

Secondary growth is also induced by pinching under long photoperiods in mid-summer or by long photoperiods in the fall and winter (Doorenbos 1953 and 1955, Davidson and Hamner 1957, Wells 1953).

Luyten and Versluys (1921) found that the respective terminal buds commenced leaf and flower initiation at the same time, May 31 to June 8, 1920, which was soon after bud-break in the spring.
Figure 4. Leaf development on flowering (left) and non-flowering (right) shoots of Rhododendron 'Cynthia' (top) and 'Pink Pearl' (bottom). Terminal buds show position of apices.
Figure 5. Relative time of bud-break associated with type of shoot and position of origin. (Upper photo - three elongating shoots from non-flowering terminal buds, note that no lateral buds located beneath flower clusters have started to elongate. Lower photo - left, one of the shoots in upper photo with expanded leaves; right, an elongating shoot from a non-flowering lateral bud that was located beneath the flower cluster in upper right center of upper photo).
Individual florets were borne in the axils of scale-like bracts. By following the development of individual florets, they found that floret length increased from 0 in early June to 7 mm by late September. The size of the buds then remained fairly constant until anthesis in mid-May of the following year. These preformed leaves and flowers expand during April, May or June depending upon the cultivar (*)

Luyten and Versluys (1921) were also the first to make reference to dormancy in *Rhododendron*. They found that floret development stopped in late September, when the florets were 7 - 8 mm long. This cessation of growth was not an imposed dormancy, since temperatures at that time of year were satisfactory for growth. Cathey (1965) reported that storage of rhododendron plants below 50°F for eight to ten weeks satisfied the chilling requirements of the flower buds.

The author and local growers have observed that non-flowering terminal and lateral buds of *Rhododendron* also respond to cold treatment (*). Although long photoperiods promote vegetative growth (Doorenbos 1953 and 1955, Davidson and Hamner 1957), excessive long day treatment, however, resulted in malformed flowers (Davidson and Watson 1959). Davidson and Hamner (1957) also showed that 16- and 24-hour photoperiods would produce up to four flushes of growth, but fewer individual shoots elongated in each successive flush. This indicates a possible chilling requirement in
addition to the stimulating influence of photoperiod.

Influence of Tissue Ageing on Root Regeneration

Tissue age has been shown by many investigators to effect root regeneration in detached plant parts. Gardner (1929) studied 21 species in 12 genera as to the time root regeneration capacity was at a maximum in stem cuttings. In all cases, it decreased with ageing of the tissue. The relationship between tissue age and root regeneration capacity has been studied by: Hitchcock and Zimmerman (1932), Vaccinium and Syringia; Hitchcock and Zimmerman (1938), Lycopersicum; Brandon (1939), Rosa; Gregory and Samantarai (1950), Phaseolus and Hedera; Selim (1956), Perilla; Childers and Snyder (1957), Ilex; Gorter (1957), Coleus; Hartmann and Brooks (1958), Prunus; Visser (1962) Thea; Fernqvist (1962), Ribes; Lamphear and Meahl (1963), Taxus and Juniperus. The optimum age for root regeneration was reported to differ considerably with the genera and generally decreased with increasing tissue age. Notable exceptions were the evergreens, Ilex, Taxus and Juniperus, whose potential was maximum in the autumn and winter.

Chadwick and Gunesch (1936) found that "succulent" and "semi-succulent" cuttings of Rhododendron 'Cunningham's White' rooted best, while "mature" cuttings were much slower. Skinner (1939), using single-eye (leaf-bud) cuttings of rhododendron species and
hybrids, obtained better rooting when the cuttings were made in June through July rather than later in the season. Cuttings of rhododendron species and hybrids taken in October and November by Hitchcock and Zimmerman (1939) required higher concentrations of hormone to promote rooting than those taken earlier. Pridham (1942) investigated the effects of age and cold temperature on rooting of rhododendron leaf-bud cuttings. He found that cuttings still in "active growth" rooted well, while "mature" cuttings rooted poorly. Cuttings from stock plants in early stages of growth stored for six weeks at 40°F showed improved rooting over those not stored. Bridgers (1952 and 1953) rooted two-year-old wood less readily than one-year-old wood. Shammarello (1957), a commercial grower, suggested that cuttings be taken in November or December. Later, Leach (1965) stated that rhododendron cuttings root progressively better the later they are taken in the autumn.

Wells (1953, 1954 and 1955) has shown large differences in rooting of several rhododendron cultivars with respect to the time the cuttings were taken. The rooting percentage of cuttings of some cultivars tended to increase with tissue ageing while others exhibited the opposite tendency.

In general, rhododendron cuttings taken early are most likely to root, yet, many commercial growers insist on waiting until late August, September and even into October before taking cuttings.
Numerous studies have attempted to correlate ageing and root regeneration in cuttings with physiological changes in the tissues. Although Childers and Snyder (1957) showed that the rootability of *Ilex* cuttings was influenced by the time of taking the cutting, it was not correlated with their carbohydrate level. Several workers have noted decreases in vitamin B$_1$ levels as tissues age (Burkholder and McVeigh 1940, Bonner and Bonner 1948). Graham (1958) found that the naturally occurring analogue of adenine in *Prunus* may increase as tissues age. Changes in auxin levels have been investigated by Thimann and Skoog (1934), van Overbeek, Vasquez and Gordon (1947), Humphries and Wheeler (1963) and Dore (1965). All agreed that auxin content decreased with tissue ageing. Humphries and Wheeler (1963) observed also that indole derivatives and gibberellic acid decreased as tissues aged. Hess (1960) has shown that several root-promoting "co-factors" in a Mung Bean bio-assay decreased or became non-existent when *Hedera helix* changed from the easy-to-root, juvenile form to the hard-to-root, mature form. As tissues age the contents of various substances change, and it is generally agreed that most metabolites, especially auxins, tend to decrease as senescence progresses.

**Influence of Flowers on Rooting**

Bayley as early as 1913, according to Selim (1956), stated that
rooting of cuttings was generally depressed by the presence of flowers. Woycicki (1938) found that flowers inhibited rooting in *Dahlia*, *Pelargonium*, *Dianthus*, *Chrysanthemum*, *Hydrangea* and *Fuchsia* cuttings. Grace (1939) found differences in rooting of *Picea excelsa* cuttings depending on whether they bore male or female flowers. O'Rourke (1940 and 1944) reported similar results with *Vaccinium*. The rooting ability of horseradish root cuttings was also found to be low during periods of flowering (Dore 1953). More recently, similar results have been reported with *Camellia* (Hieke 1961) and *Taxus* (Davidson 1965).

Kemp (1948) suggested that the presence of flowers in rhododendron inhibited rooting. DeBoer (1953), Bridgers (1952 and 1953) and Ticknor (1960) obtained reduced rooting when flowers were present on rhododendron cuttings. DeBoer (1953) arranged the types of rhododendron cuttings in a decreasing order of rootability: non-flowering stems with and without the terminal bud, flowering stems without the terminal bud and flowering stems with the terminal bud.

Turezkaya, as reviewed by Selim (1956), found that the root regenerating capacity in cuttings of *Perilla nankinesis* and *Soja hispida* decreased with flower initiation and disappeared completely during anthesis. She also found that heteroauxin applied to cuttings with open flowers induced rooting. Cuttings with more advanced stages of flower and fruit development could not be stimulated to root.
She was of the opinion that the developing flower, fruit, or both mobilized all available plant auxin leaving none for root initiation. Selim (1956) found that flowering was inhibitory to rooting in the short-day *Perilla crispa* and long-day *Trifolium pratense*, but not in the day-neutral *Lycopersicon esculentum*. His explanation was similar to Turezkaya's. He believed *Lycopersicon* was not affected because it maintained a normal auxin supply through its vegetative apex.

Engelbrecht and Conrad (1961) and Conrad (1961) demonstrated indoleacetic acid (IAA) mobilization to metabolic centers created by kinetin applications. Mobilization of such metabolites as carbohydrates (Stuart and Marth 1937, Alexander 1938) and carbohydrates and nitrogenous compounds (Stuart 1938, Doak 1941) to growth centers as a result of the presence of endogenous or exogenously applied auxin has been demonstrated. In addition, Donnalley and Rahn (1961), Linscott and McCarty (1962), Hill, Lackman and Maynard (1963) and Clor, Crafts and Yamaguchi (1964) found various herbicides to be mobilized by such "sinks". Stuart (1938) noted that the intensity of mobilization of carbohydrates and nitrogenous compounds was positively correlated with increased concentrations of the applied auxin.

It has been accepted generally that flowering and vegetative activities in many plants are antagonistic. Murneek (1926) found that the vegetative and flowering conditions of *Lycopersicon esculentum*
were highly competitive in that the development of fruit greatly reduced vegetative growth. Several workers have obtained similar results, Eaton (1931) with *Gossypium*, and Leopold, Niedergang-Kamien and Janick (1959) with *Glycine max*.

When Loomis (1937) defoliated *Zea mays*, the developing kernels were found to be capable of producing the strongest "sink" in the plant, since metabolites were mobilized from as far as six to eight feet away from the developing ear and were transported both basipetally and acropetally in the stem.

Gustafson (1939) and Luckwill (1948) have detected large amounts of diffusible auxin in seeds. Nitsch (1961) showed that more auxin diffused from detached fruit than from non-flowering apices on the same plant and non-flowering apices on defruited plants. When Skok (1957) deflowered *Helianthus annuus*, the acropetal movement of C\(^{14}\) labeled compounds was reduced by nearly 50 percent. Leopold and Gurensey (1953) and Naqvi and Gordon (1965) demonstrated that the presence of terminal flowers caused a loss of strict basipetal auxin movement in cuttings of *Coleus*.

As mentioned previously, rhododendron growers have observed that leaves on flowering shoots are generally larger than those on non-flowering shoots. Leaf size varies with cultivars, but in many instances the flowering shoots possess nearly twice the leaf area of comparable non-flowering ones. Gorter (1957) determined that
the inhibited rooting in *Coleus* caused by flowering was the direct result of flowering reducing the leaf area. From the time of floral initiation, she found that leaf area and rooting decreased progressively at each successive node. If she made the leaf area constant by trimming the leaves, rooting was similar at each node throughout the plant. Thomas (1961) showed that the leaves of *Chenopodium amaranticolor* decreased in size after flow initiation, but their expansion was actually stimulated during the flower initiation process. Only the leaves which were expanding during flower initiation were stimulated to expand to more than normal size. Leaves expanding after flower initiation was completed were inhibited and expanded less than normal. From the data of other workers, Thomas concluded that this phenomenon also occurs in several other species. Recently, Humphries and Wheeler (1963) showed that leaf expansion takes place as auxin levels begin to drop, maximum expansion being associated with the lowest levels of auxin. Gibberellic acid was also found to decrease as the leaf area increased.

**Influence of Leaves on Rooting**

Bouillenne and Went (1933) very early showed that substances other than auxin originating in the leaves controlled the growth of roots. Since then many substances have been shown to influence root initiation and extension. Van Overbeek, Gordon and Gregory (1946),
working with Hibiscus, found that the function of the leaf in rooting could be replaced almost entirely by the addition of sucrose and an organic or inorganic form of nitrogen.

Various studies have shown that isolated leaf petioles will form roots following proper hormone treatment (Yarwood 1946). Hagemann (1932) was able to root leaf cuttings of 785 out of 1204 species, including monocotyledons, dicotyledons and gymnosperms. Gregory and van Overbeek (1945) rooted leaf-petiole cuttings of easy- and hard-to-root Hibiscus. They found that the petioles of easy-to-root cultivars produced many roots, but only one leaf-petiole cutting rooted out of 50 of the hard-to-root cultivar. These results were attributed to a much reduced substrate level in the leaves of the hard-to-root cultivar. Jusufov (1961) found that the rooting ability of the leaves of 13 woody and herbaceous ornamental species directly reflected that of the stems.

Although the above evidence strongly suggests that the leaf is the sole key to good rooting, the studies of Halma (1931) and Mes (1951) with Citrus, Ryan, Frolich and Kinsella (1958) with several woody ornamentals and Gillespie (1957) with Persea have shown that the stem tissue from which the roots arise has a strong bearing on rootability.

Halma (1926) found that leaf area reduction in Citrus cuttings reduced both the number of roots and the degree of root extension.
Cooper (1938) defoliated *Citrus* cuttings at various times before, during and after a 20-hour indoleacetic acid treatment. The number of root initials and their subsequent extension depended on how long the leaves were left attached. Because defoliation prior to treatment with indoleacetic acid was the only treatment which significantly reduced root initiation, he concluded that substances from the leaves controlled initiation. He assumed that initials present on cuttings defoliated prior to treatment were produced by some substance already in the stem at the time of defoliation. Because of the long treatment time, one might suspect that the decreased root initiation exhibited by the early defoliated cuttings might possibly be due to a lack of indoleacetic acid uptake rather than the translocation of some specific substance from the leaves. This possibility was substantiated by Richardson (1958). He found that a substance produced in the apical meristem of *Acer saccharinum*, and replaceable by indoleacetic acid, controlled root initiation, while one or more substances produced in the leaves controlled root elongation. Halma (1926) with *Citrus*, Calma and Richey (1930) with *Coleus*, Esper and Roof (1931) with woody ornamentals, Selim (1956) with *Perilla*, Gregory and Samantarai (1950) with *Phaseolus* and *Hedera*, Gorter (1957) with *Coleus* and Visser (1962) with *Thea* agree that root extension is determined primarily by the quantity of leaf surface.

The role of the leaf in rooting, therefore, appears to be one of
control of root growth, while root initiation appears to be controlled primarily by auxin supply, whether from an endogenous or exogenous source.

Many of the influences of tissue ageing can also be demonstrated in leaves. The effects of ageing on the rootability of *Lycopersicon esculentum* petioles was demonstrated by Hitchcock and Zimmerman (1938). They found the second petiole from the apex had the highest rooting ability which decreased with age or distance from the apex. Gregory and Samantarai (1950) observed similar responses in *Phaseolus vulgaris* and *Hedera helix*.

Photosynthetic ability of the leaves was found to decrease with increasing tissue age (Tazak 1959 and Saeki 1959).

Selim (1956) demonstrated differences in rooting ability of *Perilla* stem sections taken from various positions along the stem. These stem sections were further divided into treatments consisting of combinations in which leaves and lateral buds were removed. The results showed that the rooting ability of the stem sections depended upon the tissues which contributed most towards the extension of the root. For example, in treatments where leaves were left on the cuttings, position one, nearest the apex, was most efficient in producing roots. Where leaves were removed and stem and bud tissues were the only photosynthetic surface, cuttings from the basal stem position possessed the highest rooting ability. In the first case, the
leaves played the dominant role with respect to root growth, while in the latter, the green stem was the only contributor towards root extension. This indicates that the physiology, with respect to the production of various biochemical substances, differs greatly between tissues and their relative positions on the stem.

Thimann and Skoog (1934) and van Overbeek, Vasquez and Gordon (1947) showed decreasing auxin levels in leaves, buds and stems with ageing of *Vicia faba* and *Ananas sativus*, respectively. Several authors have reported changes in vitamin levels as tissues age (Burkholder and McVeigh 1940, Bonner and Bonner 1948 and Vergnano 1959). In a review by Dore (1965) it was reported that the rooting response of *Streptocarpus* leaves of different ages was closely related to the variations in the auxin content of the whole plant. Furthermore, the importance of position and age in determining rooting ability of *Tradescantia albiflora* leaves was demonstrated. It was shown that fully expanded young leaves possessed the greatest potential for root regeneration. High thiamine, ascorbic acid and auxin levels were associated with this position as well as rapid utilization of tryptophane.

The above evidence points to a definite positional effect on the stem axis with respect to rooting ability. The position of highest rooting was usually near the apex but this was not always the case. Positions of highest rooting ability have also been associated with
highest auxin, vitamin and photosynthetic levels.

This review indicated that many morphological and physiological factors affect rooting ability. Moreover, the influence of these factors differs greatly with plant and plant part. Although stem tissue has been found to influence rooting ability, the major controlling mechanism appears to be present in the leaves and flowers and is further influenced by ageing.
METHODS AND MATERIALS

Sources and Types of Cuttings

Plant materials were obtained from the Oregon State University campus at Corvallis, Oregon, or from commercial growers at Portland, Oregon. Most came from the latter source. Stem cuttings were taken from 5 - 25 year-old stock plants growing in full sun to partial shade. Before treatment, stem cuttings were segregated according to shoot origin (terminal or lateral), leaf number and size, vegetative or reproductive state and apparent development of the terminal flower bud. At this time, leaf-bud or leaf-petiole cuttings were also prepared if needed. The leaf-petiole cutting consisted of a leaf and its petiole. The leaf-bud cuttings consisted of a small portion of stem tissue, a lateral bud and its subtending leaf. The leaves from an individual stem were always handled as a unit. The length of the stem cuttings varied with the cultivar, but were usually less than five inches.

Propagation Techniques and Facilities

The two lowest leaves on stem cuttings were removed to facilitate placement of the cutting in the propagation bench. This was done only when necessary. In general, leaf area was not reduced by cutting the leaves in half, as is done in commercial practice.
Exceptions to this procedure are mentioned when applicable to special treatments. A one-inch wound was sliced along the base of all stem cuttings. Leaf-bud and leaf-petiole cuttings were not wounded. All cuttings, with exceptions mentioned later, were treated with 1.0 percent indolebutyric acid (IBA) plus 0.2 percent naphthalenacetic acid (NAA) in talc. Spacing in the propagation bench varied with the size of the cutting. The usual spacing was about three and one-half inches in the row and six inches between rows. The propagating benches were located in a greenhouse equipped with intermittent misting and maintained at 60°F minimum and 70°F maximum temperatures. Evaporative coolers were used during the summer months to maintain moderate day-time maximums. The rooting medium consisted of one-fourth Canadian Peat and three-fourths Number 16 mesh Del Monte quartz sand and was controlled thermostatically at 72° - 75°F.

**Plant Growth Analysis**

**Leaf Development**

In early studies, leaf area was estimated on the basis of leaf length. Estimates were made more accurate later by tracing leaf samples on graph paper and plotting the areas obtained against blade length for computing regressions. Leaf area was then determined
from the standard curves developed for each cultivar.

As mentioned in the literature review, most investigators have considered leaf position on the stem on the basis of the individual leaf. In the Rhododendron, the leaf complement is determined several months before they expand. Furthermore, it was impossible to obtain large samples of cuttings with uniform leaf numbers. For these reasons, the stem cuttings were arbitrarily divided into four positions, each containing approximately 25 percent of the leaf complement. The actual number of leaves in each position depended on the stem's leaf complement (Figures 6 and 7). Figure 6 is the diagram used in determining the leaf complement at each of four positions on shoots with varying leaf numbers. Although this system has some obvious disadvantages, it seemed the best way to evaluate the importance of leaf position.

**Floret Development**

The increasing diameter, measured in millimeters, of the largest floret in the developing terminal bud was used as a morphological time scale for estimating physiological age. The floret was chosen because it was the only organ of the shoot that progressively increased in size throughout the period being studied. Size increments in newly initiated leaves were followed with length measurements but are not reported. The degree of error in measuring floret
Figure 6. Diagram representing the method used in determining leaf position and leaf number per position of *Rhododendron* stem cuttings. Vertical points represent the total number of leaves per stem, each point representing a leaf, each triangular segment a position on the stem. A cutting having seven leaves would have the following breakdown: two leaves in position 1, two in two, one in three and two in position four.
Figure 7. Number of leaves per position on flowering (top row) and non-flowering (bottom row) shoots of Rhododendron 'Cynthia'. Positions are numbered basipetally from the apex.
development was much less than for young leaves, since the total increase in length of the latter was only 2.0 - 2.5 mm as compared to 5.0 - 6.0 mm increase in floret diameter during the same period of time.

**Tissue Ageing**

Tissue age was considered both on a calendar date and on a physiological basis. The physiological age of the shoot or cutting was estimated from the growth in diameter of the largest floret in the terminal bud. Calendar date was used to compare sample age in a given season, while the morphological time scale, based on days from a base date in floret growth, was used to compare tissues of similar physiological age in the same or different seasons. The base date used in estimating physiological age was arbitrarily set as that time when the floret reached 1 mm in diameter. Shoot age was then calculated as days beyond this point of morphological development. This morphological scale was arbitrarily selected because earlier points of departure, such as the start of flower initiation, would have required detailed sectioning and microscopic examination of the apices.

During the second season of study, shoots were tagged shortly after bud-break in the spring. Depending on the position of the bud, bud-break occurred at widely different times, resulting in shoots of
several calendar and physiological ages. By tagging the shoots at a set stage of development for the cultivar, calendar age could be determined for a given shoot at any time during the year. Furthermore, by using only tagged shoots in sampling for physiological age, floret development was highly uniform within each sampling.

Rooting Response

Root initiation was evaluated on a percentage basis while root development was measured by root-ball size. Cuttings exhibiting even the smallest root were considered rooted on both bases. Root-ball size was measured to the nearest 0.5 cm. Cuttings showing only slight rooting were recorded as having a 0.5 cm root-ball. Rooting-potential, on the other hand, was used to express the efficiency of the leaf in root regeneration and was defined as the root-ball, in centimeters of diameter, produced per ten square centimeters of leaf area. This factor was computed because it correlated the physiological capacity to form roots with the morphological feature of leaf area.

Statistical Interpretation

The statistical methods used in interpreting the data are those used by Li (1961). All analyses were based on the analysis of variance, single degree of freedom and least significant difference tests. All percentage values were transformed to degrees prior to analysis.
RESULTS

Environmental Influences on Rooting and Floret Growth

This experiment was done to determine the influence of air temperature and photoperiod on rooting and floret growth. Such information was needed, because cuttings were to be rooted under various natural photoperiods in later tests. Also, floret growth was to be used as an estimate of physiological age, since the florets enlarged progressively during the period to be studied.

Methods and Materials

Stem cuttings of Rhododendron 'America' and Catawbiense album were taken at three commercial plantings at Portland, Oregon. Using the three sampling locations for replication, ten flowering cuttings from each location (total 30) were used in each of the following five treatments:

1. normal or prevailing day length with 65°F air temperature (ND 65),
2. eight hours of natural light followed by eight hours of artificial light with 65°F air temperature (LD 65),
3. eight hours of natural light with 65°F air temperature (SD 65),
4. sixteen hours of artificial light with 40°F air temperature
   (LD 40),

5. eight hours of artificial light with 40°F air temperature
   (SD 40).

The cuttings were matched as to leaf number and apparent degree of floret development to increase sampling uniformity. Cuttings taken July 22, 1964, were wounded and given the standard hormone treatment prior to light-temperature treatments. The 65°F treatments were rooted in the mist propagation house, while the 40°F treatments were rooted in heated beds constructed in a growth chamber. Rooting temperatures in both situations were 70°-75°F. The light-temperature treatments consisted of natural, 8- and 16-hour photoperiods in combination with 65°F or 40°F air temperatures. Light was supplied by 100-watt, white, incandescent lamps (100 ft. c.) in the propagation house and a combination of Gro-lux fluorescent and white incandescent lamps (350 ft. c.) in the growth chamber. Short-day conditions were controlled with time clocks in the growth chamber and covering with black plastic covered boxes in the propagation house. Small blowers in the plastic covered boxes slowly circulated outside air and maintained temperatures similar to that in the propagation house.

Diameters of florets from dissected terminal buds on 30 cuttings, a quantity equivalent to one treatment, were measured at the beginning of the study. After completion of the rooting treatments,
the terminal buds of all cuttings were similarly examined to determine the increase in floret diameter. Rooting response, measured on October 11, 1964, after 81 days of treatment, was evaluated on the basis of percent rooting and root-ball size.

Cuttings in the 40°F growth chamber could not be syringed as often as those in the propagation house, thus increasing the possibility of experimental error from partial dessication, but such a condition was not apparent.

Results

The data (Figures 8 and 9) show that percent rooting and root-ball size were not influenced by photoperiod. A 40°F air temperature, on the other hand, significantly reduced percent rooting and root-ball size, regardless of cultivar. Comparison of the data (Figures 8 and 9) indicates that root initiation was not influenced as much as root extension by low air temperature. This was not unexpected, since root initiation was primarily dependent upon hormone treatment and the warm temperature of the rooting medium. Root development and extension, on the other hand, were more dependent on synthates translocated from the leaves. The combined effects of low light intensity and low air temperature undoubtedly reduced the quantity of synthates reaching the root initials. On the other hand, the temperature of the rooting medium was not influenced by the low air
Figure 8. Rooting percentage of stem cuttings of *Rhododendron* 'America' □ and *Catawbiense album* △ as influenced by photoperiod and air temperature.

* Treatments associated with the same letter are not significantly different at 1%.
Figure 9. Root-ball diameter on stem cuttings of *Rhododendron 'America'* and *Catawbiense album* as influenced by photoperiod and air temperature.

* Treatments associated with the same letter are not significantly different at 1%.
temperature, thus the rooting percentage was about 40 percent of normal. Many other roots were undoubtedly initiated but had not elongated sufficiently to be recognized, thus lowering rooting percentage. The reduced rooting may also have resulted from the low light intensity in the growth chamber. However, differences in rooting between the 8- and 16-hour photoperiods with 40°F air temperatures do not support this conclusion (Figures 8 and 9).

Although floret growth was unaffected by photoperiod, it was almost completely inhibited by low air temperature (Figure 10).

The conclusion from this study was that photoperiod had little or no influence on rooting or floret growth in cuttings during the period of normally rapid floret growth. Low air temperature, 40°F, on the other hand, stopped floret growth and significantly inhibited rooting of cuttings. Therefore, slight fluctuations in propagation house temperature and changes in photoperiod were not considered critical in subsequent experiments.

Influence of Tissue Ageing on Rooting of Stem Cuttings

Various workers have observed decreased rooting with tissue ageing, yet others found rhododendron shoots rooted more readily in the autumn.

The principal aim in the study was to determine the importance of tissue ageing in root regeneration in stem cuttings, and at the same
Figure 10. Increase in floret diameter on stem cuttings of Rhododendron 'America' and Catawbiense album during an 81 day rooting period as influenced by photoperiod and air temperature.

*Treatments associated with the same letter are not significantly different at 1% level.
time establish floret growth as a morphological index of tissue aging. This was an attempt to replace the exceedingly variable index based on calendar date. Leaf expansion and stem elongation were not thought to be reliable indices, since these are accomplished in three to four weeks. The growth in diameter of the florets, it was thought, would be correlated with the various physiological changes taking place in the shoots. It was also assumed that the rate of development would be indicative of physiological alterations brought about by internal or external factors and would therefore be reliable in predicting physiological age. Such alterations would not be evident in organs that had completed their growth. Although calendar age may be measured from any point in time, indexing physiological age requires systematically correlating the development of an organ with the physiological changes occurring in the plant.

Methods and Materials

Stem cuttings of easy-to-root 'Cynthia', intermediate-rooting 'Pink Pearl' and hard-to-root 'Britannia' cultivars were obtained from 10 - 25-year-old stock plants growing in full sun. Cuttings were collected at two locations at Portland, Oregon. The locations were used as replications. Thirty-two cuttings of each cultivar were collected at three-week intervals from June 22 to November 26, 1964, a total of seven samples. Each sample consisted of about 12
flowering and four non-flowering cuttings. The samples were divided into 24 cuttings for rooting tests and eight cuttings for dissection of the terminal buds to determine floret diameter at the time of sampling. In this way the progressive growth of the index floret on the stock plant was plotted for the season. The 24 cuttings in the rooting test were wounded, hormone treated, and placed in the propagation bench for a period of 100 days. The hormone treatments were as follows:

1. cuttings taken on June 22 (sample 1) were treated with 0.5 percent indolebutyric acid (IBA) plus 0.1 percent naphthaleneacetic acid (NAA) in talc,

2. cuttings taken July 13 (sample 2) were treated with 0.75 percent IBA plus 0.15 percent NAA in talc,

3. all other cuttings (samples 3-7) were treated with the standard 1.0 percent IBA and 0.2 percent NAA in talc.

The lower IBA-NAA concentrations, used on samples 1 and 2, were necessary because of the succulence of the cuttings. Percent rooting, root-ball size and diameter of the largest floret in the terminal bud were recorded after 100 days, thus giving an index of floret growth during the rooting period. Table 1 presents the dates on which the various samples were placed in and removed from the cutting bench. Data on rooting response are given with both calendar age and age based on the morphological time scale (floret growth)
Table 1. Dates when stem cuttings of *Rhododendron* 'Cynthia', 'Pink Pearl' and 'Britannia' were placed in (samples 1-7) and removed from (samples 1'-7') the propagation bench. Rooting time 100 days.

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<thead>
<tr>
<th>Sample number</th>
<th>Sampling and Recording Dates</th>
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<td>June</td>
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Results

Progressive ageing of easy-to-root 'Cynthia' shoots had no major influence on rootability with the exception of sample 5', whose roots were much less developed (Figure 11). On the other hand, the rootability of intermediate-rooting 'Pink Pearl' and hard-to-root 'Britannia' tended to decrease with ageing (Figures 12 and 13). 'Pink Pearl' sample 5' and 'Britannia' samples 4' and 5' also developed small root-balls. Tissue ageing most pronouncedly influenced the more difficult-to-root cultivars, as shown by the loss in rooting capacity by 'Pink Pearl' and 'Britannia' cuttings.

Figure 14 shows the progressive increase in floret size in the terminal flower buds of the three cultivars. The growth of the largest floret in the bud was followed in samples 1'-7 while the shoot was attached to the stock plant (Figures 11, 12 and 13). Samples 1'-7'reflect the growth and development of this floret during the 100 days the cuttings were in the propagating bench. The close fit of the two 'Pink Pearl' curves (Figures 12 and 14) suggests that the growth rates of the 'Pink Pearl' florets on the detached cutting and on the intact stock plant were the same. It also reflects the relatively strong mobilization power of the developing flower bud. Floret growth in 'Cynthia' cuttings taken early in the season (samples 1'-3') was somewhat
Figure 11. Rooting response in *Rhododendron 'Cynthia'* stem cuttings as related to sampling date and floret growth (physiological age).

* Treatments associated with the same letter are not significantly different at the 5% level.
Figure 12. Rooting response in *Rhododendron* 'Pink Pearl' stem cuttings as related to sampling date and floret growth (physiological age).

*Treatments associated with the same letter are not significantly different at the 5% level.*
Figure 13. Rooting response in *Rhododendron* 'Britannia' stem cuttings as related to sampling date and floret growth (physiological age).

*Treatments associated with the same letter are not significantly different at the 5% level.*
Figure 14. Progressive increase of floret size on stem cuttings of three *Rhododendron* cultivars taken at three-week intervals from June 22 to October 26, 1964. Floret size recorded at the time of taking cuttings (1-7) and again after 100 days in the propagation bench (1'-7').
inhibited, and 'Britannia' florets were inhibited even more, (samples 1'-3') (Figures 11, 12 and 13).

These differences in floret growth rate are interpreted as indicative of the relative mobilizing power of the developing flowers during the growing season, and they may be indicative of physiological changes within the cutting. That the florets of 'Pink Pearl' showed a greater growth rate in all samples may indicate the existence of a stronger "sink" in the flowers of this cultivar than in those of the other cultivars. Perhaps, this explains the very poor rooting obtained with sample 5' of 'Pink Pearl' (Figure 12) and 'Cynthia' (Figure 11). If there is intense competition between developing florets and newly forming roots, it would be expected that one of these processes might be inhibited. Where the developing florets establish a strong "sink", the development of the root-ball and possibly percent rooting would be reduced. 'Britannia', on the other hand, rooted best early in the season when floret growth was generally much slower than in the other cultivars (Figures 13 and 14). Because of the lack of strong mobilizing capacity early in the season, better rooting might be anticipated at that time. Flower primordia in 'Britannia' were not visible under low power magnification at the time of the first sample, but the total number of primordia in the apex indicated that flower initiation had taken place. More will be said concerning this point in the next study. On several occasions
a reversal from the reproductive to the vegetative condition occurred in the apex following detachment of the cutting from the stock plant. This was shown by the initiation of four to five florets followed by the initiation of four to six leaves. Such reversal was observed only in the more difficult-to-root cultivars, 'Pink Pearl' and 'Britannia', and occurred only when cuttings were taken during the earliest stages of floret growth (samples 1 and 2). This phenomenon is quite common in those cultivars whose lateral buds frequently initiate flowers.

The use of floret growth to predict physiological changes in the tissues appeared more reliable than chronological age. This was evident when comparing base dates (the florets reached 1 mm in diameter) in the three cultivars for establishing the morphological time scale. The data in Figures 11, 12 and 13 show that July 23, 29 and 31 were the base dates for 'Cynthia', 'Pink Pearl' and 'Britannia', respectively. Although the growth rate of the florets differed somewhat after this point, it was obvious that on any given date the stage of development of any two cultivars might differ widely and could not be predicted by calendar date. This fact becomes increasingly clear later in the paper. All three cultivars showed reductions in rooting response at approximately 40 - 50 days from the base date in floret growth. Since reduced rooting was evident in sample 5' in all cases, this effect might be considered as experimental error. Later studies, however, indicated possible intraplant
competition occurring at this time, particularly in 'Pink Pearl' and 'Britannia'.

The importance of tissue ageing to rooting capacity seemed to depend primarily on the cultivar and was most evident in intermediate and hard-to-root types. It should be noted that early cuttings (samples 1' and 2') of all cultivars treated with the lower hormone concentrations rooted as readily as the later cuttings (sample 3') which received the standard hormone treatment. This indicated an optimum root regeneration capacity in these younger tissues. Hitchcock and Zimmerman (1939) found that higher concentrations of hormone were required later in the season than earlier to promote rooting in Rhododendron.

### Flower Initiation as Related to Shoot Elongation

Luyten and Versulys (1921) indicated that flower initiation in rhododendron occurs quite early in the shoot's developmental cycle. Thomas (1961) reported that flower initiation in Chenopodium favored enlargement of leaves expanding at the time of initiation, but expansion of subsequent leaves was inhibited by the flowers.

Leaf area has been shown by many workers to be positively correlated with the initiation and growth or roots on cuttings, yet reports indicate that flowering cuttings root poorly. Leaf size and total area is much greater on flowering than on non-flowering shoots.
of several species. The situation can exist, therefore, where the rooting response of flowering cuttings with large leaf areas is often less than that of the non-flowering cuttings with smaller leaf areas.

The purpose of this test therefore, was to determine the time of flower initiation in Rhododendron as it relates to stem and leaf elongation.

Methods and Materials

A single plant of Rhododendron "Roseum Elegans" was dug and moved into the greenhouse on February 2, 1965. It was approximately four by four by four feet in size and contained more than 100 terminal flower buds. The plant was forced into flower at 60°-65°F under prevailing day lengths. Flowers were removed as they withered. A single, large lateral bud was marked on stems possessing terminal flower buds. These lateral buds were located in the axils of leaves at the second or third position from the apex. This particular lateral bud position was selected because previous observations of the growth pattern of this cultivar strongly suggested that flowers were produced most often on shoots arising from this position. Shoot development from these lateral buds was followed by periodic sampling for a period of 38 days. The length of the developing shoot axis, the number of primordia initiated in the apex and the length of the largest leaf were recorded on each sampling
date. The morphological composition of the apex was determined by dissection under low power binoculars. Forty-eight lateral buds were marked and studied in this manner, five being sampled every seven to ten days. Since some buds developed malformations and were generally weak, only 30 of the most uniform buds were actually used. A single sample of five shoots produced from non-flowering terminal buds was also dissected to get some indication of floret initiation in these as compared to shoots produced from lateral buds.

Results

Curve 1 in Figure 15 shows the average stem length of laterally produced shoots on various sampling dates. Under these growing conditions, shoot elongation was completed in approximately 24 days, with shoot length increasing from 4.2 to 120 mm during that time. Curve 2 shows the progressive increase in length of the largest leaf, which is usually found in the middle of the shoot. Here again, leaf elongation occurred quite rapidly requiring under these greenhouse conditions only 24 days from bud-break. Curve 3 shows the progressive increase in number of new bud-scales and primordia in the newly forming terminal buds. The number of new bud-scales and primordia increased from 0 to about 22 in only 24 days (Figure 15). Since 'Roseum Elegans' shoots normally initiate 15 to 17 bud-scales before initiating flower or leaf primordia, the remaining 10 - 12
Figure 15. Stem and leaf elongation in relation to time of flower initiation in *Rhododendron 'Roseum Elegans'*. Stock plant forced in a 60° - 65°F greenhouse from February 2, 1965 to dates shown. Each point represents an average of five shoots.
initials observed by May 1 (Figure 15) were either leaf or bud-scales at the bases of which florets were initiated. Although flower primordia were not evident under low power magnification at the time, their presence was later verified by the heavy set of flowers on the shoots remaining on the stock plant. In addition, a sample of these remaining shoots was dissected the following spring after the terminals were fully developed. It was found that an average of 16.4 bud-scales and 17.4 florets was initiated on these shoots produced by lateral buds during April, 1965. This indicated a total of 34 bud-scales was initiated in April, 1965, of which 17 had flowers initiated at their bases. Floret initiation was, therefore, probably still occurring as late as mid-May, 1965, on the test plant (Figure 15).

The above work was done using only shoots produced from lateral buds located beneath flowering terminals. A single sample of five shoots produced from non-flowering terminal buds, which had begun growth prior to the lateral shoots, was similarly dissected. This was done to compare floral initiation on terminal and lateral shoots. At the time of sampling, April 10, 1964, the stock plant was in full flower and the non-flowering terminal buds had elongated to approximately 30-40 mm in length. Other non-flowering terminals were much further advanced at this time. The results indicated that flower initiation was quite similar in terminal and lateral shoots. It was found that 12 of the necessary 14 – 17 terminal bud-scales had
been produced by the time the new shoot had elongated to 30-40 mm. This was about the same as found in the lateral shoots of the same length (Figure 15).

It was concluded that flower initiation and leaf and stem elongation occurred rapidly and concurrently with the latter two being completed in approximately 24 days under greenhouse conditions. Development was quite similar in both terminal and lateral shoots. Since flower initiation and stem and leaf elongation were taking place at the same time, it was impossible from this study to determine if one process directly influenced the other or not. Thomas (1961) cited information that flower initiation in some plants was accompanied by a short-lived stimulation to leaf expansion in those leaves expanding at the time of initiation. These results agreed with his, in that the leaves of rhododendron which normally attain greatest size on flowering shoots were expanding at the time of flower initiation.

The present study leads to the conclusion that, under these experimental conditions, flower initiation began when the stem and largest leaf were about one-half elongated and continued even after they were fully elongated.

It seems plausible to expect that the time of flower initiation could vary considerably with respect to the number of leaves expanded, if grown under different environmental conditions. At one
extreme, flower initiation could occur before any leaves were fully expanded, or at the other, several leaves might be expanded. The significance of this point will be discussed in later studies.

**Influence of the Terminal Bud on Rooting-Potential**

Numerous reports have indicated that flowers inhibit rooting of cuttings, and this has been observed also in *Rhododendron* propagation. DeBoer (1953) found that flower removal partially but not entirely removed this inhibition.

A large leaf surface has been found essential for maximum root growth on cuttings. Since the leaves of flowering shoots are much larger than those of non-flowering shoots, it might be expected that the former would root better. A situation exists, however, where flowering cuttings possessing a relatively larger leaf surface than non-flowering ones, do not root as well.

The purposes of this test were to determine the influence of the terminal bud on rooting and to compare the rooting-potential of leaves from flowering and non-flowering shoots.

**Methods and Materials**

Two types of 'Pink Pearl' cuttings were taken at the Lewis-Brown Horticultural Farm near Corvallis, Oregon on February 2, 1965. A total of 16 stem cuttings, four replications of four cuttings
each, were used in each treatment of stem cuttings. In the case of the leaf-petiole cuttings, all the leaves from 16 shoots, four replications of four shoots each, were used in each treatment. The leaf-petiole cuttings consisted of individual leaves cut near the base of the petioles so that no stem or lateral bud tissue remained with the leaf. For analytical purposes, the leaf-petioles from a single stem were handled as a unit. In the case of stem cuttings, none of the leaves were removed and in no case was the leaf area reduced.

The stem cuttings were wounded, hormone treated, and placed in propagating benches as previously specified. Leaf-petiole cuttings were handled similarly, but without additional wounding. Rooting response was determined May 27, 115 days after sticking the cuttings.

The following treatments were used (Figure 16):

1. stem cuttings from flowering shoots with terminal bud intact,
2. stem cuttings from flowering shoots with terminal bud removed,
3. stem cuttings from non-flowering shoots with terminal bud intact,
4. stem cuttings from non-flowering shoots with terminal bud removed,
5. leaf-petiole cuttings from flowering shoots,
6. leaf-petiole cuttings from non-flowering shoots.
Figure 16. Types of cuttings used in determining the influence of the terminal bud on rooting of *Rhododendron* 'Pink Pearl'.

(From upper left to right, 1-4)

1. Flowering stem cutting.
2. Flowering stem cutting with the terminal bud removed.
3. Non-flowering stem cutting.
4. Non-flowering stem cutting with the terminal bud removed.
5. Leaf-petiole cuttings from flowering shoots (lower left).
6. Leaf-petiole cuttings from non-flowering shoots (lower right).
Results

Although the differences in rooting percentage were not significant, differences did occur in the degree of root development (Tables 2 and 3). Stem cuttings from non-flowering shoots made greater root extension than did those from flowering shoots.

The removal of the terminal flower bud tended to promote better rooting, although bud removal did not result in significant differences between treatments. The rooting-potential of the flowering shoots with the terminal bud removed approached that of the leaf-petiole cuttings from flowering shoots (Table 4). This would indicate that the inhibiting factor controlled by the flower resides not in the stem tissue but more likely in the leaf and terminal bud.

The influence of the terminal flower bud may be explained on the basis of its strong mobilizing power. In a previous study this mobilizing power was shown when floret growth in 'Pink Pearl' cuttings, which had been in the propagation bench for 100 days, was not reduced. DeBoer (1953) also found that terminal flower removal promoted a slight increase in rooting of flowering shoots of \textit{R. catawbiense grandiflorum}. In her study, non-flowering cuttings were not benefited by similar treatments. The non-flowering cuttings in this study reacted similarly. The rooting capacity of these cuttings was influenced more by leaf size than by the presence or absence of the
Table 2. Rooting percentage of stem and leaf-petiole cuttings of flowering and non-flowering shoots of *Rhododendron 'Pink Pearl'.* Propagation time 115 days.

<table>
<thead>
<tr>
<th>Cutting source</th>
<th>Leaf-petiole cuttings</th>
<th>Stem Cuttings</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>%</td>
<td>Without terminal bud</td>
</tr>
<tr>
<td>Non-flowering shoots</td>
<td>83.3</td>
<td>100.0</td>
</tr>
<tr>
<td>Flowering shoots</td>
<td>82.1</td>
<td>81.3</td>
</tr>
</tbody>
</table>

Differences not significant

Table 3. Diameter of root-ball on stem and leaf-petiole cuttings of flowering and non-flowering shoots of *Rhododendron 'Pink Pearl'.*

<table>
<thead>
<tr>
<th>Cutting source</th>
<th>Leaf-petiole cuttings cm</th>
<th>Stem Cuttings</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Without terminal bud</td>
</tr>
<tr>
<td>Non-flowering shoots</td>
<td>6.1 ab*</td>
<td>7.5 a</td>
</tr>
<tr>
<td>Flowering shoots</td>
<td>4.4 cb</td>
<td>3.1 c</td>
</tr>
</tbody>
</table>

*Treatments associated with the same letter were not significantly different at the five percent level, (LSD = 2.8).*
terminal bud (Tables 4 and 5). It should be noted that, the greater the total leaf area per stem, the poorer the rooting-potential in non-flowering cuttings. This relationship, however, did not apply to flowering stem or leaf-petiole cuttings. The exact nature of this was not understood, but was considered in more detail in later tests.

Statistically, leaf-petiole cuttings from both flowering and non-flowering shoots rooted similarly, however, non-flowering cuttings always tended to root better than flowering cuttings (Tables 3 and 4). Rooting response of leaf-petiole cuttings was found to be an indicator or "bio-assay" of the rooting-potential of stem tissues. Gregory and van Overbeek (1945) and Jusufov (1961) have found this also to be true of other species of plants.

Results of this study support the conclusion that flowers strongly inhibit rooting. This inhibition finds expression in increased leaf size with accompanying reduction in root-potential. Removal of the terminal bud, although alleviating the inhibition somewhat, did not remove the inhibitory influence completely, since it was found to reside also in the leaf.

**Influence of Leaf Position and Leaf Area on the Rooting of Stem Cuttings**

Previous studies in this series and those of others point up the importance of leaves in rooting cuttings. Moreover, it has been
Table 4. Rooting-potential of stem and leaf-petiole cuttings of flowering and non-flowering shoots of Rhododendron 'Pink Pearl'.

<table>
<thead>
<tr>
<th>Cutting source</th>
<th>Stem Cuttings</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Leaf-petiole</td>
<td>Without</td>
<td>With</td>
</tr>
<tr>
<td></td>
<td>cuttings cm</td>
<td>terminal bud cm</td>
<td>terminal bud cm</td>
</tr>
<tr>
<td>Non-flowering shoots</td>
<td>0.51 ab*</td>
<td>1.82 a</td>
<td>0.85 b</td>
</tr>
<tr>
<td>Flowering shoots</td>
<td>0.26 c</td>
<td>0.21 c</td>
<td>0.15 c</td>
</tr>
</tbody>
</table>

*Treatments associated with the same letter were not significantly different at the five percent level (LSD = 0.55).

Table 5. Leaf area per stem of stem and leaf-petiole cuttings of flowering and non-flowering shoots of Rhododendron 'Pink Pearl'.

<table>
<thead>
<tr>
<th>Cutting source</th>
<th>Stem Cuttings</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Leaf-petiole</td>
<td>Without</td>
<td>With</td>
</tr>
<tr>
<td></td>
<td>cuttings cm²</td>
<td>terminal bud cm²</td>
<td>terminal bud cm²</td>
</tr>
<tr>
<td>Non-flowering cuttings</td>
<td>119</td>
<td>45</td>
<td>88</td>
</tr>
<tr>
<td>Flowering cuttings</td>
<td>170</td>
<td>159</td>
<td>136</td>
</tr>
</tbody>
</table>
shown that the rooting-potential of a leaf is influenced by its position on the stem. Commercial propagators commonly reduce the leaf surface of cuttings before placing them in propagation beds to reduce transpiration and to conserve space.

The purpose of this test was to determine the importance of leaf position and leaf surface in rooting stem cuttings.

**Methods and Materials**

Stem cuttings of *Rhododendron 'Cynthia', 'Elizabeth' and 'Unique'* were taken from plants five to ten years of age growing in partial shade on the Oregon State University campus on August 19, 1964. Ten cuttings, replicated three times for each cultivar, were used in each of five treatments. Each treatment consisted of approximately seven flowering and three non-flowering cuttings. They were wounded, given the standard hormone treatment and placed in the propagation bench.

The leaves on these stem cuttings were treated as follows:

1. normal complement of leaves on stem,
2. upper half of leaf complement removed,
3. lower half of leaf complement removed,
4. upper half of leaf complement removed plus the distal one-half of each remaining leaf,
5. lower half of leaf complement removed plus the distal
one-half of each remaining leaf.

Rooting response was measured on the basis of rooting percentage and root-ball diameter 82 days later.

Results

Many factors influencing rooting do so by affecting root extension rather than initiation. This was the case here, since no differences were observed in percent rooting as a result of treatment. Large reductions in leaf surface, as estimated from leaf length, were accompanied by only small changes in root-ball size. A 60 percent reduction in leaf length (treatment 1 vs. 5) reduced root-ball size in 'Cynthia' cuttings (Figure 17) by only 26 percent. Similarly, 68 and 66 percent reductions in leaf length in some treatments of 'Elizabeth' and 'Unique' reduced by 23 and 39 percent their root-ball sizes, respectively (Figures 18 and 19). The greater reduction noted in the latter cultivar would be expected because of its lower inherent rooting-potential. With each of the three cultivars, maximum root growth occurred when all leaves were retained on the cutting (treatment 1). In general, those treatments which retained the upper leaves (treatments 3 and 5) resulted in slightly more root development than those which had only their lower leaves (treatments 2 and 4). Although no significant differences occurred between treatments retaining upper and lower leaves, four of the six combinations
Figure 17. Effect of leaf removal on leaf area per cutting (leaf length), rooting percentage and root-ball diameter on stem cuttings of *Rhododendron 'Cynthia'*. Differences in root-ball size and rooting percentage were not significant.
Figure 18. Effect of leaf removal on leaf area per cutting (leaf length), rooting percentage and root-ball diameter on stem cuttings of *Rhododendron* 'Elizabeth'.

* Treatments associated with the same letter are not significantly different at the 5% level (LSD - 1.2 for root-ball size).
Figure 19. Effect of leaf removal on leaf area per cutting (leaf length), rooting percentage and root-ball diameter on stem cuttings of *Rhododendron* 'Unique'.

*Treatments associated with the same letter are not significantly different at the 5% level (LSD = 1.1 for root-ball size).*
exhibited slightly larger root-ball development where the upper leaves were retained. The easy-to-root cultivars showed little of this characteristic, while it was more striking in the intermediate-rooting cultivar 'Unique'. The lack of response of 'Cynthia' and 'Elizabeth' would be expected because of the inherently higher rooting-potential in all their leaves.

It was concluded that leaf area plays an important role in root development, but leaf surface could be reduced considerably without seriously reducing root extension.

Data in Figures 17, 18 and 19 suggested that leaf removal from cultivars with low rooting potentials adversely effected root growth more than similar treatments with easy-to-root cultivars. The data further suggested that cuttings possessing upper leaves root slightly better than those with equal leaf area but with only lower leaves.

Influence of Leaf Position and Nutritive Treatment on Rooting of Detached Leaves

It was shown in the preceding experiment that the contribution of a leaf to rooting of the stem was influenced by the position of the leaf on the stem. This corroborated the observations of Hitchcock and Zimmerman (1938) and Jusufov (1961) with herbaceous and woody plants. Doak (1939, 1940) van Overbeek, Gordon and Gregory (1946), Berg (1957) and Graham (1958) have shown rooting to be increased
and in some cases to be decreased by various amino acids, nitrogenous substances, sugars and vitamins applied to cuttings.

The purposes of this test were: first, to determine the importance of leaf position; second, its interaction with the effects of certain vitamin and nutritive substances on rooting of leaf-bud cuttings; and third, to verify earlier observations that leaf-bud and leaf-petiole cuttings reflect the rootability of stem cuttings.

Methods and Materials

Stem cuttings of *Rhododendron* 'Roseum Elegans', 'Unique', 'Sappho' and 'Gomer Waterer' were taken from four separate locations at Portland, Oregon, on September 11, 1964. Five stem cuttings of each cultivar, or all the leaves from five stem cuttings with three replications, were used in each treatment. Both flowering and non-flowering cuttings were used, but in a ratio of approximately 4:1. Leaf position on the stem was determined by dividing each stem into four sections, each containing about 25 percent of the leaf complement, thus facilitating the comparison of stems with different leaf numbers (Figure 6). Although this system had obvious disadvantages, it was necessitated by the difficulty of obtaining large samples with uniform leaf numbers. Leaf positions one and four were assigned to the apical and basal positions on the stem, respectively.

The portion of the study designed to determine the effects of
certain vitamin and nutritive substances on the rooting response of leaf-bud cuttings from different stem positions was arranged as a four by eight factorial, replicated three times in each cultivar. The eight treatments for leaf-bud cuttings were as follows:

1. (control),
2. vitamin $B_1$ at 5 ppm,
3. vitamin $B_6$ at 5 ppm,
4. nicotinic acid at 5 ppm,
5. cocoanut milk at five percent,
6. arginine at 50 ppm,
7. mixture of all the above at the original concentrations,
8. mixture of all the above at one-fifth the above concentrations.

The vitamin and nutritive substances were dissolved in 0.5 percent agar and applied at the rate of about 0.3 ml to the mid-rib of leaf-bud cuttings. Treatment applications were started three weeks after standard hormone treatment and placement in the propagation bench, and were repeated at two-week intervals for three applications. Applications were made at 5:00 P.M., after the mist system was off for the night. The agar was slowly washed away by mist action the following day.

The stem, leaf-bud and leaf-petiole cuttings used in that part of the study to determine the influence of cutting type on ...
rooting-potential, received only the standard hormone treatment. All leaves from an individual stem cutting used as leaf-bud or leaf-petiole cuttings were handled as a unit in interpreting results.

Rooting response was evaluated on the basis of rooting percentage, root-ball size and rooting-potential. Data for the three replications were recorded November 18, December 5 and December 23, respectively because of the large number of samples.

Results

The data (Table 6) show conclusively that leaf-bud or leaf-petiole cuttings reflect equally well the rootability of the stems. Leaf cuttings can therefore be used as a reliable index of the percent rooting of the shoots. The data are averages of either 60 stem cuttings or the leaves from 60 stem cuttings in the case of leaf-petiole and leaf-bud cuttings (Tables 6 and 7). The influence of leaf position on rootability was best illustrated by the cultivar 'Roseum Elegans' (Figure 20). Although clonal differences with respect to rootability would be expected, the more consistent results obtained with 'Roseum Elegans' was attributed to the single location from which these cuttings were obtained. Cuttings of the other cultivars came from three locations and were pooled before sampling, a procedure which undoubtedly increased experimental error.

The differences in root-ball size for the various leaf positions
Table 6. Rooting percentages of stem, leaf-bud and leaf-petiole cuttings of four *Rhododendron* cultivars.

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Type of Cutting</th>
<th>Cultivar average</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Stem</td>
<td>Leaf-bud</td>
</tr>
<tr>
<td>'Roseum Elegans'</td>
<td>100.0</td>
<td>96.7</td>
</tr>
<tr>
<td>'Unique'</td>
<td>66.7</td>
<td>50.6</td>
</tr>
<tr>
<td>'Gomer Waterer'</td>
<td>53.3</td>
<td>76.7</td>
</tr>
<tr>
<td>'Sappho'</td>
<td>73.3</td>
<td>47.6</td>
</tr>
<tr>
<td>Cutting average</td>
<td>73.3 c*</td>
<td>67.9 c</td>
</tr>
</tbody>
</table>

*Values associated with the same letter are not significantly different at the five percent level.*

Table 7. Rooting percentages of leaf-bud cuttings from four positions on the stems of four *Rhododendron* cultivars.

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Leaf Position</th>
<th>Cultivar average</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1 2 3 4</td>
<td></td>
</tr>
<tr>
<td>'Roseum Elegans'</td>
<td>96.9 96.5 93.4 90.1</td>
<td>94.2 a*</td>
</tr>
<tr>
<td>'Unique'</td>
<td>57.3 55.0 56.8 50.1</td>
<td>54.8 c</td>
</tr>
<tr>
<td>'Sappho'</td>
<td>49.9 50.0 54.8 52.4</td>
<td>51.8 c</td>
</tr>
<tr>
<td>'Gomer Waterer'</td>
<td>74.9 80.7 78.7 76.7</td>
<td>77.8 b</td>
</tr>
<tr>
<td>Position average</td>
<td>69.8d* 70.6d 70.9d 67.3d</td>
<td></td>
</tr>
</tbody>
</table>

*Values associated with the same letter are not significantly different at the five percent level.*
Figure 20. Root-ball diameter □ (cm) and rooting-potential □ (cm) of leaf-bud cuttings of four *Rhododendron* cultivars for four positions on the cutting. Leaf positions are numbered basipetally from the apex.

*Treatments associated with the same letter are not significantly different at the 5% level. Letters apply only to individual cultivars.*
(Figure 20) was probably due to root growth resulting from differences in metabolic activity with respect to position and age rather than the result of differences in rooting percentage (Table 7). The rooting-potential of leaves from position one was significantly better than those from other positions in 'Roseum Elegans' and 'Sappho'. It appeared that the rooting-potential of leaves in positions 2, 3 and 4 in all cultivars were similar (Figure 20). These results substantiate those of the previous test concerning leaf position and root regeneration in stem cuttings. At the stage of growth of the stock plants used, terminal leaves possessed a greater rooting-potential than leaves from the lower portions of the stem.

No consistently significant interactions were found between vitamin or nutrient treatments and leaf position. Nicotinic acid, cocoanut milk, arginine and the two mixtures significantly increased rooting in 'Roseum Elegans', while vitamin $B_6$ and the low concentration of the mixture promoted a significant increase in 'Sappho'. The (+) plus and (-) minus symbols in Table 8 indicate only whether the root-ball produced was greater or less than the treatment mean. In general, 'Roseum Elegans' and 'Sappho' were stimulated by all the vitamin or nutrient treatments, while 'Gomer Waterer' and 'Unique' were generally inhibited. Berg (1957) reported promotion and inhibition of rooting from vitamins and amino acids applied to rhododendrons. He also found vitamin $B_1$ inhibited rooting in 'Gomer
Table 8. Effect of vitamin and nutrient treatments on rooting (1) of leaf-bud cuttings of four Rhododendron cultivars.

<table>
<thead>
<tr>
<th>Cultivars</th>
<th>Treatments</th>
<th>Vitamins</th>
<th>Nicotinic acid</th>
<th>Cocoanut milk</th>
<th>Arginine HCl</th>
<th>Mixture (2)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>B1  B6</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Full 1/5 Full</td>
</tr>
<tr>
<td>'Roseum Elegans'</td>
<td>+ + + + +</td>
<td>+ 1%</td>
<td>5%</td>
<td>1%</td>
<td>1%</td>
<td>1% 1%</td>
</tr>
<tr>
<td>P</td>
<td>+ + + + +</td>
<td>+ 5%</td>
<td></td>
<td>1%</td>
<td>1%</td>
<td>1% 1%</td>
</tr>
<tr>
<td>'Sappho'</td>
<td>B + + 1%+ +</td>
<td>- +</td>
<td></td>
<td>5%*</td>
<td>+ +</td>
<td>1%</td>
</tr>
<tr>
<td>P</td>
<td>+ + 1%+ +</td>
<td>+ +</td>
<td></td>
<td>- +</td>
<td>+ 1%</td>
<td></td>
</tr>
<tr>
<td>'Gomer Waterer'</td>
<td>B - 1%+ +</td>
<td>5%* + +</td>
<td>-</td>
<td>+ -</td>
<td>- - +</td>
<td></td>
</tr>
<tr>
<td>P</td>
<td>- - - -</td>
<td>- -</td>
<td>-</td>
<td>- -</td>
<td>- - +</td>
<td></td>
</tr>
<tr>
<td>'Unique '</td>
<td>B - - + +</td>
<td>5% - -</td>
<td>-</td>
<td>- -</td>
<td>- - +</td>
<td></td>
</tr>
<tr>
<td>P</td>
<td>+ + + + +</td>
<td>+ +</td>
<td></td>
<td>- -</td>
<td>- - +</td>
<td></td>
</tr>
</tbody>
</table>

1 Root-ball diameter, (+) greater than control, (-) less than control, (5% and 1%) levels of significance, (*) significant inhibition.

2 Concentration in mixture equalled sum of individual treatment concentrations or equalled 1/5 of the sum.

3 B -- root-ball diameter
   P -- rooting-potential.
Waterer'. The variable responses obtained from the applications of vitamins and organic nutrients calls attention to the probable biochemical and physiological differences existing between cultivars of *Rhododendron*. The results (Table 8) would lead one to assume that high rooting-potential may be closely related to the ability of the cultivar to utilize numerous biochemical substances in its metabolism, as illustrated by the responsiveness of 'Roseum Elegans'.

**Root Regeneration as Related to Tissue Ageing and Morphological Development**

The previous experiments have attempted to analyze several factors influencing rooting-potential. For the most part, each factor was observed at one stage of plant development. The purpose of this test was to examine in one experiment the major factors influencing rooting. Rooting was observed under a uniform environment, but with changing physiological and calendar age of the cutting source. Physiological age was estimated by using the increase in diameter of the largest floret in the terminal bud as a morphological index. The factors studied included the cultivar, tissue age, shoot origin, type of terminal bud, leaf position on the stem and leaf area.

**Methods and Materials**

Stem cuttings of four cultivars were obtained from two locations
Figure 21. Root-balls on leaf-petiole cuttings of *Rhododendron* 'Roseum Elegans'. 
at Portland and one near Corvallis, Oregon. Each cultivar was sampled at a single location to avoid experimental error because of differences in environment, age of the stock plant and other source variables.

The following Rhododendron cultivars and types of cuttings were used:

'Cynthia'—easy-to-root; from ten-year-old plants growing in partial shade near Corvallis, Oregon; each replication consisting of three flowering terminal and five flowering lateral cuttings.

'Pink Pearl'—intermediate-rooting; from 20-year-old plants growing in full sun at Portland, Oregon; each replication consisting of four flowering terminal and four flowering lateral cuttings.

'Roseum Elegans'—easy-to-root; from three-year-old plants growing in full sun near Portland, Oregon; each replication consisting of four flowering and four non-flowering cuttings; flowering cuttings were from a mixture of terminal and lateral shoots.

'Britannia'—hard-to-root; from 20-year-old plants growing in full sun at Portland, Oregon; each replication consisting of four non-flowering and four flowering terminal cuttings; flowering cuttings were from a mixture of terminal and lateral shoots.

The differences in number and type of cuttings were necessitated by a lack of sufficient materials. Terminal and lateral shoots were tagged at a uniform stage of growth on May 28, 1965 to assure that
cuttings taken later in the season would be of comparable age and terminal bud development. For example, on this date, shoots from non-flowering terminals of 'Britannia' were elongating rapidly and the expanding leaves were generally oriented parallel to the shoot axis. A few leaves were assuming a position perpendicular to the axis. At the same time, shoots from lateral buds were just beginning to elongate. The first cuttings were taken approximately one month after tagging.

Forty-eight stem cuttings from stock plants of each of the four cultivars were sampled at three locations. Three replications of 16 cuttings each were taken at three-week intervals on six dates from June 25 to October 8 (Table 9). Leaf-petiole cuttings were prepared from half of the stems in each sample. The size of the largest floret in the terminal buds of these latter stems was used to follow floret growth on the stock plant. The remaining half of the sample was rooted as stem cuttings. After the stem cuttings had rooted, floret length and diameter were measured to determine floret growth during the rooting period. The types of samples taken and the methods used in evaluating their rooting responses are presented in Figure 22.

As in previous tests, stem cuttings only were wounded. All cuttings were given standard hormone treatment before placement in the propagation bench. Those taken June 25 and July 16 (samples 1 and 2), however, were treated with reduced concentration as in the
Table 9. Dates on which cuttings of the four *Rhododendron* cultivars were placed in (sample 1-6) and removed from (samples 1'-6') the propagation benches.

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Sample Number</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1-1'</td>
<td>2-2'</td>
<td>3-3'</td>
<td>4-4'</td>
<td>5-5'</td>
<td>6-6'</td>
</tr>
<tr>
<td>'Cynthia'</td>
<td>6/25-10/5</td>
<td>7/16-10/26</td>
<td>8/6-11/16</td>
<td>8/27-12/7</td>
<td>9/17-12/28</td>
<td>10/8-1/18</td>
</tr>
</tbody>
</table>
Figure 22. Factors studied and methods of evaluation used in determining the root regeneration response of four Rhododendron cultivars sampled tri-weekly from June 25 to October 8, 1965.
previous year, because high concentrations of hormone injure or kill succulent tissues.

Rooting response was evaluated on the basis of percent rooting, root-ball size and rooting-potential. Cutting age was determined chronologically by calendar date and estimated physiologically by the morphological time scale. The base date of the morphological time scale was arrived at as in previous studies, i.e., the date the largest floret was 1 mm in diameter (Table 10). To allow for inherent differences in root regenerating capacity, the rooting responses of 'Roseum Elegans', 'Cynthia', 'Pink Pearl' and 'Britannia' were recorded after 95, 102, 109 and 109 days, respectively, in the propagating bench. Sampling dates and dates on which cuttings were placed in and removed from the propagation benches are given in Table 9.

The order of discussion of the results is in terms of floret growth, and rooting response of stem and leaf-petiole cuttings since earlier determinations showed that much of the leaf surface could be removed without reducing root-ball size. However, rooting-potential was used in evaluating the rooting response of leaf-petiole cuttings.

Results

Floret Growth. Data presented in Figures 23, 24, 25 and 26 represent the progressive increase in floret size on the stock plants.
(samples 1-6) and on cuttings during the rooting process (samples 1'-6'). These growth curves show considerable differences between cultivars in their morphological development on any given date.

There was a three to four week difference in the time terminal and lateral flowering shoots of both 'Cynthia' and 'Pink Pearl' (Figures 23 and 24) took to reach the 1 mm floret size. The dates when the florets were 1 mm in diameter (Table 10) were used as base dates in estimating physiological age. Floret growth in diameter in all cultivars was found to cease at about 6 to 7 mm. This is believed to correspond to the beginning of their dormant period and corroborates work by Luyten and Versluys (1921).

Table 10. Base dates used in estimating physiological age. These are the dates on which the diameter of the florets reached 1 mm.

<table>
<thead>
<tr>
<th>Cultivar and kind of shoot</th>
<th>Base Date</th>
</tr>
</thead>
<tbody>
<tr>
<td>'Cynthia'</td>
<td></td>
</tr>
<tr>
<td>Flowering terminal cuttings</td>
<td>June 4</td>
</tr>
<tr>
<td>Flowering lateral cuttings</td>
<td>July 13</td>
</tr>
<tr>
<td>'Pink Pearl'</td>
<td></td>
</tr>
<tr>
<td>Flowering terminal cuttings</td>
<td>June 18</td>
</tr>
<tr>
<td>Flowering lateral cuttings</td>
<td>July 13</td>
</tr>
<tr>
<td>'Roseum Elegans'</td>
<td></td>
</tr>
<tr>
<td>Flowering lateral and terminal cuttings combined</td>
<td>July 3</td>
</tr>
<tr>
<td>'Britannia'</td>
<td></td>
</tr>
<tr>
<td>Flowering lateral and terminal cuttings combined</td>
<td>July 10</td>
</tr>
</tbody>
</table>
'Cynthia': The continued growth of the florets was apparently inhibited by the developing root-ball on flowering lateral cuttings taken early in the season (samples 1' and 2'). Floret growth in sample 1' from lateral cuttings was extremely variable and was not plotted. Rooting did not influence floret growth on flowering terminal cuttings (Figure 23). These characteristic responses no doubt reflected the greater leaf surface on terminally produced cuttings (Figure 23) and the smaller floret size in the lateral cuttings. Data in Figure 23 show that the leaf surface of flowering terminal cuttings of 'Cynthia' was nearly double that of flowering lateral cuttings. The leaf surface of the latter was possibly too small to serve adequately the combined needs of the growing florets and the new root system. If the mobilizing ability of one set of organs was not greater than the other, a reduction in growth of both organs would be expected. This would likely occur most in a cultivar like this, where the power of the terminal to mobilize nutritive substances is weak. Furthermore, if cuttings were taken early (samples 1 and 2), when the floret was small and possibly its mobilizing power was weak, similar inhibition could occur.

'Pink Pearl': Because floret growth on flowering lateral cuttings from sample 1' was extremely variable, the data were not plotted. This variability was probably due to the small leaf surface and floret size as with 'Cynthia' (Figures 23 and 24). Floret growth
Figure 23. Increase in floret size on flowering terminal (---) and flowering lateral (-----) stem cuttings of *Rhododendron 'Cynthia'* taken at three week intervals from June 25 to October 8, 1965. Floret size recorded at the time of taking cuttings (1-6) and again after 102 days in the propagation bench (1'-6').
Figure 24. Increase in floret size on flowering terminal (——) and flowering lateral (-----) stem cuttings of *Rhododendron* 'Pink Pearl' taken at three-week intervals from June 25 to October 8, 1965. Floret size recorded at the time of taking cuttings (1-6) and again after 109 days in the propagation bench (1'-6').
on cuttings in sample 2' was not retarded. It was the only cultivar whose buds were not inhibited on this sample date (Figures 23, 24, 25 and 26). Apparently, flower buds of 'Pink Pearl' have a high mobilizing power, and successfully compete with the roots for common growth substances. The strong "sinks" developed by the flower buds were further evinced by the smoothness of the floret growth curves (Figure 24).

'Roseum Elegans': When cuttings were taken in late June and mid-July (samples 1' and 2'), floret growth on the cuttings, as in 'Cynthia', was apparently slowed by the rooting process (Figure 25). The florets apparently were unable to mobilize sufficient substrates.

'Britannia': Floret growth was similar to 'Cynthia' and 'Roseum Elegans' in that samples 1' and 2' were greatly inhibited, apparently by root-ball development. Again, the smallness of the florets at the time of sampling undoubtedly contributed to their weak mobilizing power and resulting growth retardation.

When floret diameter was less than 1 mm at the time of the first sampling, growth of the floret on the cutting was always inhibited in the propagation bench (Figures 23, 24, 25 and 26), indicating that florets of this size had a weak capacity for mobilization. The size of the meristematic center also bears directly on the strength of the "sink". The influence of the "massed meristem" has been shown in Zea mays by Loomis (1937).
Figure 25. Increase in floret size on stem cuttings of *Rhododendron 'Roseum Elegans'* taken at three-week intervals from June 25 to October 8, 1965. Floret size recorded at the time of taking cuttings (1-6) and again after 95 days in the propagation bench (1'-6').
Figure 26. Increase in floret size on stem cuttings of *Rhododendron* 'Britannia' taken at three-week intervals from June 25 to October 8, 1965. Floret size recorded at the time of taking cuttings (1-6) and again after 109 days in the propagation bench (1'-6').
Influence of Shoot Origin and Age on the Rooting of Stem Cuttings. 'Cynthia': Figures 27 and 28 compare the rooting of flowering terminal and lateral cuttings of increasing physiological and calendar age, whose respective base dates for the morphological time scale were June 4 and July 13. The 39-day difference between the two dates made the rooting response of the two types of cuttings correspond at samples 1' and 3', respectively. Reduced root-ball development was noted at 63 and 24 days beyond the base dates for terminal and lateral cuttings, respectively. Percent rooting was high in all cuttings and did not change consistently throughout the season. The low points in rooting percentage occurred when the florets were 3.5 and 4.0 mm in diameter in terminal and lateral cuttings, respectively (Figure 27).

Figure 28 replots the above data by sampling and calendar date. In general, both types of stem cuttings tended to produce larger root-balls with shoot ageing. Flowering terminal cuttings rooted somewhat better throughout the season than did lateral cuttings. The former had 22 to 57 percent greater leaf surface than the latter, yet produced only slightly larger root-balls at each sampling (Figure 28). Although rooting-potential was not calculated, the data in Figure 28 show clearly that the smaller leaf surface of lateral cuttings supplied a greater rooting-potential to the stems than the larger leaf surface of the terminal cuttings. It is clear also that
Figure 27. Rooting percentage (□) and root-ball size (△) of flowering terminal and lateral stem cuttings of *Rhododendron 'Cynthia'. Floret growth used as a morphological time scale for age comparisons.

*No significant differences were found.
Figure 28. Leaf area per stem and effects of shoot age on percent rooting and root-ball size of flowering terminal (△) and lateral (○) stem cuttings of Rhododendron 'Cynthia'.

* No significant differences were found.
percent rooting is less indicative of rooting response than the degree of root development expressed by root-ball size. No significant differences in rooting with respect to cutting origin or date of sampling were found.

'Pink Pearl': The rooting response of flowering terminal and lateral cuttings of different ages are compared on morphological and calendar bases in Figures 29 and 30, respectively. When floret size was used as a measure of age, flowering terminal and lateral cuttings were comparable when sampled at 1' and 2', respectively, a difference of about 24 days (Figure 29). Although cutting age did not appear critical to rooting percentage or root-ball size, periods of weak response in the latter occurred. These appeared at 49 and 45 days from the base date for the terminal and lateral cuttings, respectively. Periods of intense competition between the developing florets and the root system could account for these low points. Inhibition of rooting by floret development was not apparent when the data were compared on a simple chronological basis (Figure 30), and inhibition appeared to be due to experimental error. The advantages, therefore, of using floret growth as the basis for a morphological time scale in establishing shoot and cutting age are quite apparent.

Like 'Cynthia', 'Pink Pearl' cuttings from lateral shoots always rooted better than those from terminals, even though they had
Figure 29. Rooting percentage (□) and root-ball size (△) of flowering terminal and lateral stem cuttings of Rhododendron 'Pink Pearl'. Floret growth used as a morphological time scale for age comparisons.

*No significant differences were found.
Figure 30. Leaf area per stem and effects of shoot age on percent rooting and root-ball size of flowering terminal (△) and lateral (○) stem cuttings of Rhododendron 'Pink Pearl'.

* Significant differences at the 5% level were found only for percent rooting between types of cuttings in samples 1, 2, 3 and 6.
less leaf-surface (Figures 29 and 30).

Influence of Shoot Age and Type of Terminal Bud on the Rooting of Stem Cuttings. 'Roseum Elegans': In general, the rooting capacities of flowering and non-flowering stem cuttings were constant throughout the season except for the flowering cuttings of samples 5' and 6' (Figure 31). The figure shows that reduced rooting of flowering cuttings late in the season was due to reduced initiation and root extension. Evidence of disease was noted in these latter samples and they are not considered further. Flowering cuttings had 30-54 percent more leaf surface than non-flowering cuttings taken at the same times, but rooted better in only two of the six samples. Of these, sample 4 had 54 percent more leaf surface than the corresponding non-flowering cuttings. Although rooting-potential was not calculated, it was obvious that the root regenerating capacity of non-flowering cuttings was superior to that of flowering cuttings. Because of the large variability within samples, differences in rooting with shoot age and type could not be detected.

'Britannia': The rooting of flowering terminal cuttings was practically the same for all sampling dates, but significant differences in rooting occurred in non-flowering cuttings. Flowering terminal cuttings had a much greater leaf surface, but rooted substantially better in only one case (Figure 32). Rooting response, as in 'Roseum
Figure 31. Leaf area per stem and effects of shoot age on percent rooting and root-ball size of flowering (△) and non-flowering (○) stem cuttings of *Rhododendron 'Roseum Elegans'.

No significant differences were found.
Figure 32. Leaf area per stem and effects of shoot age on percent rooting and root-ball size of flowering (△) and non-flowering (○) stem cuttings of *Rhododendron 'Britannia'*.  

* Points within a cutting type associated with the same letter are not significantly different at the 5% level.
'Roseum Elegans', was nearly always greater in the non-flowering cuttings. The apices of the non-flowering series of cuttings were examined at the end of the rooting periods and showed that all cuttings in sample 2' and two-thirds in sample 3' were actually flowering cuttings instead of non-flowering as planned; therefore, these samples are not considered further.

Non-flowering cuttings with their corresponding smaller leaf areas generally tended to root better than flowering cuttings in both cultivars. This is similar to the earlier findings with 'Pink Pearl' (Tables 2, 3, 4 and 5).

The data for both types of cuttings were not plotted on a morphological time scale because, as yet, the development of flowering and non-flowering terminal buds cannot be correlated. However, floret growth, rooting percentage and root-ball size of the flowering terminal cuttings of these two cultivars were compared on a morphological basis (Figure 33). July 3 and July 10 were the base dates of 'Roseum Elegans' and 'Britannia', respectively. The data in Figure 33, as in Figures 14, 27 and 29, further confirm the large differences in morphological development between cultivars. Although major differences in rooting related to ageing were not observed in 'Roseum Elegans', root-ball size in sample 3' of 'Britannia' was much lower, as was the rooting percentage in sample 2' (Figure 33).
Figure 33. Rooting percentage (□) and root-ball size (△) of flowering terminal stem cuttings of *Rhododendron* 'Roseum Elegans' and 'Britannia'. Floret growth used as a morphological time scale for age comparisons.

* No significant differences were found.
Influence of Shoot Age and Leaf Position on the Stem on the Rooting of Leaf-petiole Cuttings from Flowering Terminal and Lateral Shoots. 'Cynthia': The rooting responses of leaf-petiole cuttings taken from flowering terminal and lateral shoots are shown in Figures 34 and 35. The root-ball size in samples 1', 2' and 3' increased with increasing shoot age and may have been caused by the progressively higher concentrations of IBA-NAA used with these first three samples. The increased rooting may, therefore, be related more to hormone treatment than to tissue age. The rooting-potential of leaf-petiole cuttings from flowering lateral shoots was only slightly greater than that from flowering terminal shoots. The leaf surface of the former was also somewhat smaller, corresponding to the findings obtained in rooting stem cuttings of 'Cynthia' (Figures 27 and 28).

Leaf position on the stem appeared to cause few significant differences. In most cases (Figures 35, 40 and 41), however, leaves in position one in addition to having the smallest leaf surface had the greatest rooting-potential. The rooting percentage for each sample is shown in Table 11. The reduced root initiation in the first sample was undoubtedly due to the low concentration of hormone used. Rooting percentage tended to be less in leaves positioned lower on the stem. In general, shoot age was not a consistent factor influencing rooting of this cultivar.
Figure 34. Influence of shoot age (expressed as days on morphological scale) and leaf position on the shoot, on root-ball size made by leaf-petiole cuttings from flowering terminal and lateral shoots of *Rhododendron* 'Cynthia'.
Figure 35. (a) Influence of shoot age (expressed as days on morphological scale) and leaf position on the shoot, on rooting-potential of leaf-petiole cuttings taken from flowering terminal and flowering lateral shoots of *Rhododendron* 'Cynthia'.

(b) Leaf area as related to leaf position and shoot age at the time of taking cuttings.
Table 11. Rooting percentage of leaf-petiole cuttings of three *Rhododendron* cultivars as influenced by cutting age, origin, type of terminal bud and leaf position on the stem.

<table>
<thead>
<tr>
<th>Cultivar and Type of Cutting</th>
<th>Sampling Date</th>
<th>Position</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>6/25</td>
<td>7/16</td>
</tr>
<tr>
<td>'Cynthia'</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Flowering</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Terminal</td>
<td>34a</td>
<td>99b</td>
</tr>
<tr>
<td>Lateral</td>
<td>53a</td>
<td>87b</td>
</tr>
<tr>
<td>'Pink Pearl'</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Flowering</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Terminal</td>
<td>49a</td>
<td>61ab</td>
</tr>
<tr>
<td>Lateral</td>
<td>63ab</td>
<td>47a</td>
</tr>
<tr>
<td>'Roseum Elegans'</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Flowering</td>
<td>92ab</td>
<td>99c</td>
</tr>
<tr>
<td>Non-flowering</td>
<td>91a</td>
<td>99a</td>
</tr>
<tr>
<td>Average</td>
<td>64</td>
<td>82</td>
</tr>
</tbody>
</table>

*Values within cutting types associated with the same letter are not significantly different at the five percent level.*
'Pink Pearl': Root-ball size for both types of cuttings tended to be small early in the season (samples 1' and 2') as in 'Cynthia'. This was again undoubtedly due to the lower hormone concentration received by these samples. Root-ball size of leaf-petiole cuttings from flowering terminal shoots tended to decrease with increasing shoot age, but differences were generally not significant. Those of flowering lateral shoots, however, did not change significantly with increasing shoot age (Figure 36).

The leaf surface on cuttings from flowering lateral shoots was somewhat less than that from flowering terminal shoots (Figure 37). As with 'Cynthia', leaves from flowering lateral shoots had a greater rooting-potential and smaller leaf size. Although leaf position on the shoot had little influence on rooting-potential, leaves from position one tended generally to respond more, as in 'Cynthia' (Figures 37, 40 and 41). Rooting percentage was influenced only slightly by leaf position or age of the tissue (Table 11).

Shoot ageing, although adversely affecting somewhat the rooting of leaf-petiole cuttings from flowering terminal shoots, was of little overall importance in root regeneration in 'Pink Pearl' and 'Cynthia'. High rooting-potential in the leaves of both cultivars was again associated with the terminal position and small size. The relationship of small leaf size and high rooting-potential was quite obvious (compare (a) and (b) in Figures 35 and 37).
Figure 36. Influence of shoot age (expressed as days on morphological scale) and leaf position on the shoot, on root-ball size made by leaf-petiole cuttings from flowering terminal and lateral shoots of *Rhododendron* 'Pink Pearl'.
Figure 37. (a) Influence of shoot age (expressed as days on morphological scale) and leaf position on the shoot, on rooting-potential of leaf-petiole cuttings taken from flowering terminal and flowering lateral shoots of *Rhododendron* 'Pink Pearl'.

(b) Leaf area as related to leaf position and shoot age at the time of taking cuttings.
Influence of Shoot Age and Leaf Position on the Stem on the Rooting of Leaf-petiole Cuttings from Flowering and Non-flowering Shoots of 'Roseum Elegans'. The rooting response of leaf-petiole cuttings changed little with ageing of the source shoot (Figure 38). The cuttings from flowering shoots rooted slightly better than those from non-flowering shoots, but this was not consistent. Leaf-petiole cuttings from non-flowering shoots followed the same pattern observed with leaves from flowering lateral shoots of 'Cynthia' and 'Pink Pearl', i.e., a smaller leaf area but a higher rooting-potential (Figure 39). In a similar study in 1964, leaves in position one had the highest capacity for root regeneration, whether based on total roots per cutting or per unit of leaf surface. However, leaves in position four had the highest rooting-potential as well as the smallest leaves in this test (Figures 39, 40 and 41). As with 'Cynthia' and 'Pink Pearl', positions on the stem with the smallest leaves had the highest rooting-potentials. Although the relationship of small leaf area to high rooting-potential was significant in only a few leaf positions (Figures 39 and 41), it seemed of considerable importance and should be studied further. There are 36 possible combinations of leaf position and ageing in the present test, i.e., six sampling dates x two types of cuttings x three cultivars. The inverse relationship of leaf size and rooting-potential was perfect in seven of the combinations, that is, as the leaf size in the four positions decreased,
Figure 38. Influence of shoot age and leaf position on the shoot, on root-ball size made by leaf-petiole cuttings from flowering and non-flowering shoots of *Rhododendron* 'Roseum Elegans'.
Figure 39. (a) Influence of shoot age and leaf position on the shoot, on rooting-potential of leaf-petiole cuttings taken from flowering and non-flowering shoots of *Rhododendron* 'Roseum Elegans'.

(b) Leaf area as related to leaf position and shoot age at the time of taking cuttings.
Figure 40. Influence of leaf position on the stem for the entire season on root-ball diameter (cm) of leaf-petiole cuttings from flowering terminal, flowering lateral, and non-flowering shoots of three Rhododendron cultivars. *No significant differences were found.
Figure 41. Influence of leaf position on the stem for the entire season on rooting-potential (cm) of leaf-petiole cuttings from flowering terminal □, flowering lateral □□ and non-flowering □□ shoots of three Rhododendron cultivars.
rooting-potential increased. The probability of this happening in any one sample of four leaf positions and four rooting-potential values is 1:24. There were also many other combinations in which this relationship between the largest and smallest leaves in a single sample held true. 'Roseum Elegans' was most inconsistent, since its leaves differed little in size between the four leaf positions (Figure 39). Therefore, the relationship of leaf area to rooting-potential could be easily misinterpreted.

As in the other cultivars, there was no reduction in root initiation with ageing of the leaf tissues (Table 11), suggesting that ageing was not responsible for the decreased rooting noted in 'Roseum Elegans' stem cuttings late in the season (Figures 31 and 33).

The morphological time scale used in the 1965 studies permitted comparison of flowering cuttings from shoots of different origins and ages. Although imperfect, it was a valuable first step in determining physiological age. The mobilizing power of the florets was again demonstrated by their continued growth in the propagation bench. This is shown graphically by the smooth curves in the figures, particularly in 'Pink Pearl' samples 6 to 1' (Figure 24).

The influence of shoot origin was consistent throughout in that stems or leaves from non-flowering or flowering lateral shoots had greater rooting capacities than those from flowering terminal shoots. In general, shoot ageing did not influence rootability in the 1965
tests, however, a slight reduction in root-ball size occurred in flowering terminal leaf-petiole cuttings of 'Pink Pearl'. Since leaf-petiole cuttings were essentially free of bud and stem influences, sampling variability was found to be less of a problem than with stem cuttings. Therefore, it is believed that the former would be a better measure of the influence of tissue ageing.

In general, the leaves from non-flowering and flowering lateral shoots were smaller than those from flowering terminal shoots but their rooting-potentials were greater. Leaves nearest the shoot apex usually had the highest rooting-potentials, but data for 'Roseum Elegans' suggested that the rooting-potential of the leaf-petiole cuttings was more closely allied to leaf size than to position on the stem. Although the latter seemed contradictory to previous studies, high rooting-potential was always associated with those shoots or positions having the smallest leaves. Although shoot origin, type of terminal bud and leaf position on the stem may be related to rooting in other ways, their primary influence on rooting seems to be through leaf size. The possible reasons for small leaves having higher rooting-potentials are considered later.
DISCUSSION AND CONCLUSIONS

The primary purposes of this study were to determine the stage of growth and development when the rooting-potential of the shoot was maximum and, if possible, to develop a method of identifying this stage in different cultivars and growing seasons. Detailed growth analyses of developing shoots on stock plants and their rooting responses as cuttings were used to correlate rooting-potential with morphological development. This required replacing unreliable calendar dating in establishing tissue age by a morphological time scale based on floret diameter. The morphological features related to shoot age and influencing rooting-potential were shoot origin, type of terminal bud, leaf position on the stem and leaf size.

It became apparent that morphological timing had limitations, but it was an improvement over simple calendar dating in predicting time of maximum rooting-potential. These limitations originate no doubt in the interplay between heredity and environment which is expressed in rate of floret growth and physiological status of the tissues at any given time.

The leaf has been found to be the sole source of substances necessary for rooting (Hagemann 1932, Gregory and van Overbeek 1945, and Jusufov 1961), and in the present study to be indicative of the rooting capacity of shoots (Tables 3, 4 and 6). A large leaf
surface has always been associated with maximum rooting response (Calma and Richey 1930, Gregory and Samantarai 1950, Gorter 1957, and Visser 1962). These conclusions with qualifications are supported by the present study, however, any factor influencing growth, development or biochemistry of the leaf would be expected to alter its rooting-potential.

A schema presenting several morphological features influencing rooting-potential and their interactions is given in Figure 42. Although possibly oversimplified, it serves as a working hypothesis for interpreting and understanding the observations made in these studies.

Environment

Because the environment of the stock plant could be expected to influence the rate of growth, morphological development and rooting capacity of the shoot, the importance of controlling photoperiod and temperature was considered. Variations in photoperiod had no effect on rooting or floret growth (Figures 8, 9 and 10). But when air temperature was lowered from 65°F to 40°F, rooting decreased about 40 percent and floret growth was almost completely stopped. In subsequent testing, therefore, greenhouse temperatures were controlled closely but photoperiod was ignored.
Figure 42. Schema representing the major factors influencing rooting-potential.
Ageing Based on Calendar Date

The time to take cuttings has been studied by many researchers and commercial growers interested in finding the time of maximum root regeneration. Although the problem has been discussed at length in trade journals and to a lesser extent in research papers, the time to take rhododendron cuttings has never been clearly resolved. The present study has shown timing to be as dependent on the cultivar as on seasonal growing conditions. In 1964, the rooting of intermediate-rooting 'Pink Pearl' and hard-to-root 'Britannia' generally decreased with ageing of the shoots, while rooting of easy-to-root 'Cynthia' did not change. It appeared that the detrimental effects of ageing increased with the inherent difficulty of rooting the cultivar. Because leaves of hard-to-root cultivars have an inherently low rooting-potential, they would more likely be adversely affected by unfavorable conditions than would leaves of easy-to-root cultivars. Results with easy-to-root 'Cynthia' in 1964 and 1965 were similar, but were quite different from the other cultivars. Ageing had little influence on any of the cultivars in 1965.

Leaf-petiole cuttings, taken at the same three-week intervals as were stems in 1965, gave more uniform and accurate measurements of rooting response than the stems. This was probably due to larger sample size. Although the analyses were made on a stem
basis in both cases, the failure of a few leaves to root would not influence averages to the same extent as would a stem's failure in the smaller samples. Each sample consisted of five stems or all the leaves from five stems. The use of leaf-petiole cuttings made possible also the elimination of stem and bud tissue influences on root regeneration. For these reasons, the results obtained from leaf-petiole cuttings more accurately measured the influence of tissue ageing on rooting-potential. In contrast to 1964, shoot ageing in 1965 had little or no effect on the rooting response of stem or leaf-petiole cuttings. In both years, early samples (samples 1' and 2') of most cultivars rooted well in spite of reduced hormone treatment. It appeared that rooting-potential was high in the young shoots when floret growth was just starting. This suggests that taking cuttings early might avoid problems brought on later in the season by poor environmental conditions.

U. S. Weather Bureau climatological records (1964 and 1965) for April through October at the Portland, Oregon, airport show the average temperature in 1964 to be 3.4°F below and in 1965 0.4°F above normal, a difference of almost 4°F. Possibly more important was the fact that these months had nearly ten percent more sunshine in 1965 than in 1964. During May and June when most shoot growth occurred, there were 11 and 20 percent more sunshine in 1965 than in 1964, respectively. The rooting results in these two years indicated
that tissue ageing affected rooting more in hard-to-root cultivars than in the less difficult ones. In 1965, a season favorable to maintenance of a high rooting-potential in the leaves, ageing would not be as limiting as in 1964, a less favorable season. Any factor reducing leaf rooting-potential would be expected to influence hard-to-root cultivars to a greater extent than easy-to-root ones. Ageing might be important in years when other factors, not clearly defined in 1964, tended to become limiting.

**Physiological Ageing**

To estimate and correlate physiological ageing to maximum rooting-potential of the tissues for timing the taking of cuttings, the data were plotted on a morphological time scale whose base date was the date when floret diameter reached 1 mm. This approach showed that periods of low root development, occurring as much as three weeks apart on a chronological scale, actually coincided with certain stages of floret development.

Rooting response in 'Pink Pearl' for the two seasons was plotted against floret diameter (Figures 12 and 29). In 1964, a single period of low rooting occurred at sample 5' (Figure 12), while in 1965 similar periods occurred in sample 3' of flowering terminal and sample 4' of flowering lateral cuttings (Figure 29). These three samples corresponded to calendar dates of 9/14/64, 8/6/65 and
8/27/65, respectively. On a morphological basis, however, these low periods of root development corresponded to 47, 49 and 45 days from the base date, respectively. Corresponding diameters of the florets at the end of these periods were 3.5, 2.9 and 4.3 mm. The differences between the two years were due primarily to the much earlier time of bud-break in the spring of 1965. The differences in 1965 were due to the different times of bud-break for terminal and lateral shoots, respectively. 'Pink Pearl' cuttings in 1964 consisted of a combination of flowering lateral and flowering terminal shoots. In 1965 the two types were handled separately. The floret diameter of 3.5 mm in 1964, as would be expected, almost equalled the 3.6 mm average diameter of the two separate groups sampled in 1965. The 1.4 mm difference in floret size in the two 1965 samples was due to different growth rates on terminal and lateral cuttings (Figure 29). The lateral cuttings developed much faster even though growth started later in the season.

'Britannia' cuttings showed two periods of slightly below average root-ball development at samples 4' and 5' in 1964 and at sample 3' in 1965. Both years, the cuttings consisted of a combination of flowering terminal and lateral shoots. The calendar dates on which these three samples were taken were 8/24/64, 9/14/64 and 8/6/65, respectively. The early August date in 1965, was again due to the early bud-break that year. On the morphological time scale,
these low periods in root development occurred 24 and 45 days in 1964 and 27 days in 1965 after the 1 mm base date, when corresponding floret diameters were 1.8, 3.6 and 2.9 mm, respectively. Again the 2.7 mm average floret diameter in 1964 almost equalled the 2.9 mm diameter in 1965. As with 'Pink Pearl', the periods of low root development, average floret size and days after 1 mm base date corresponded favorably in the two years.

Reductions in root-ball size in 'Cynthia', unlike in 'Pink Pearl' and 'Britannia', could not be correlated with morphological development.

These periods of low rooting capacity probably coincide with periods of intense competition between the developing florets and the developing root system for substances found in limited supply, such as vitamins, co-factors and hormones. They may be related to periods of high metabolic activity and rapid growth of the terminal bud and may coincide with mega- or microsporogenesis or other high energy requiring processes.

The lack of correlation between floret growth and rooting in 'Cynthia' was undoubtedly due to the greater rooting-potential of its leaves and the moderately weak mobilizing power of its florets. Conversely, the 'Pink Pearl' florets had a strong mobilizing power and its leaves had a medium rooting-potential. 'Britannia', on the other hand, had florets of moderate mobilizing power like 'Cynthia', but
leaves of very low rooting-potential. This would indicate that a
cultivar must possess either a low rooting-potential in the leaves or
a very strong mobilizing power in the florets to demonstrate the
above competition.

Leaf-petiole cuttings, free of competing buds, did not show
periods of reduced rooting. Possibly, removal of the terminal bud
at sampling, eliminated competition. In 1964 when ageing played a
major role, the inhibitory effects of intraplant competition caused
significant differences in rooting. But in 1965 when ageing had es-
sentially no influence, the differences were smaller.

In view of the consistent correlation in the two years between
specific stages of floret growth, reduced rootability with number of
days after the 1 mm base date in individual cultivars, these specific
changes in rooting capacity were probably due to intraplant competi-
tion and not experimental error as suggested by calendar dating.
These results indicate that tissue ageing per se may not be a major
factor affecting shoot rootability in all seasons. The stage of develop-
ment of the terminal flower bud, however, may be important as a
growth center competitive to rooting.

Because the periods of low rooting response were chrono-
logically as much as three weeks apart but coincided on the morpho-
logical time scale, the data for 'Pink Pearl' and 'Britannia' (Figures
12, 13, 29 and 33) clearly show the morphological time scale to be
superior to calendar dating for predicting shoot rootability.

Florets grew over a longer period of time and were somewhat larger at the end of the season in 1965 than in 1964. The different rates of floret growth on terminal and lateral cuttings and lengths of growing seasons limit somewhat the usefulness of the morphological time scale (Figures 14, 23, 24, 25 and 26). A more reliable index could be developed if the physiological basis for the competition could be determined. Anther and ovary development would be prime candidates for investigation. Such events as bud development, pollen production and anther growth were found by Erickson (1948) to be correlated in the growth and development of Lilium longiflorum.

Shoot Origin

Other factors appeared to modify the influence of shoot age on rooting-potential. In addition to springtime temperatures, whether the shoot is terminal or lateral determines the time of bud-break. As mentioned in the literature review, shoots of as many as three or four ages may be present on the stock plant at one time. For example, shoots produced from terminal non-flowering buds may break into growth two to four weeks ahead of those from lateral buds. Lammas growth, that is normally initiated in the autumn, is initiated early enough to be included in the normal taking of cuttings.

This study clearly points out the superior capacity for root
regeneration in non-flowering versus flowering shoots. The import-
tance of shoot origin is further emphasized by the fact that rooting
capacity is greater in flowering shoots from lateral buds than flow-
ering shoots of the same age from terminal shoots. Origin of the cut-
ting also influences rooting-potential to some degree through leaf
size. Throughout this study small leaves have had higher rooting-
potentials than larger leaves. The relationship of shoot origin to
these other factors affecting rooting has significance in commercial
propagation, since cuttings may be readily selected on the basis of
origin and leaf size.

Leaf Position

A leaf's position on the stem determines its physiological and
chronological age. Since shoots were fully elongated in 25 to 30 days
under greenhouse conditions, the difference in calendar age between
leaves on the stem was relatively small. Physiologically, however,
leaf age on an individual stem may vary greatly. Several workers
have reported differences in the capacity of leaves from various posi-
tions to produce biochemical substances. In most cases, these dif-
f erences were undoubtedly due to physiological ageing rather than
calendar age. In general, the youngest leaves nearest the terminus
of the stem have the greatest capacity for producing auxins, vitamins
and steroids, while the physiologically older leaves mainly produce
sucrose and become progressively less influential (Burkholder and McVeigh 1940, Bonner and Bonner 1948, Hartt et al. 1963, Hartt and Kortschak 1964, Hartt, Kortschak and Burr 1964 and Biddulph and Cory 1965). In the present study high rooting-potential was most often associated with apical leaves capable of producing formative substances. This conclusion was further substantiated by the fact that stems with upper leaves only (Figures 17, 18 and 19) tended to root better than those with lower leaves only. This pattern was followed generally by leaf-bud and leaf-petiole cuttings during the 1964 and 1965 seasons (Figures 20, 40 and 41).

**Leaf Area**

The quantitative aspect of leaf surface in promoting root growth in cuttings has been demonstrated by numerous workers and was also evident in this study (Figures 17, 18 and 19). Total leaf surface per se was evidently not the key to rooting capacity, because small leaves contributed more to root development than larger leaves when root-ball sizes were compared on the basis of unit leaf surface. This latter measure of rootability has been referred to as rooting-potential. Although not studied specifically, the inverse relationship between leaf size and rooting-potential was often unmistakable (Figures 35, 27 and 39). In general, as leaf size increased, rooting-potential decreased. Perhaps leaf size reflects the content of natural auxin in
the leaf. Elliot (1937) has shown that the always smaller than normal leaves of lammas growth in *Rhododendron ponticum*, produce second-year xylem. Numerous studies reviewed by Leopold (1964) have shown xylem production to be positively correlated with either natural or exogenously supplied auxin. Perhaps the small leaves of lammas growth are able to produce auxin in their second year of growth.

Humphries and Wheeler (1963) have shown that leaf expansion in *Phaseolus vulgaris* increases with decreasing auxin levels. Thomas (1961) has shown increased leaf expansion accompanying flower initiation in *Chenopodium*, possibly indicating decreasing auxin levels in leaves of flowering shoots. Turezkaya (Selim 1956) and Selim (1956) were of the opinion that developing flowers inhibited root initiation by mobilizing plant auxins. Throughout this study, cuttings with small leaves had higher rooting capacities than those with larger leaves, whether these cuttings were from flowering or non-flowering shoots. This relationship of small leaf size to high rooting-potential is logically explained, therefore, on the basis of a longer retention of the capacity for cell division and synthesis of auxins and other biochemical substances necessary for rooting.

The superior rooting-potential of basal leaf-petiole cuttings (position four) in 'Roseum Elegans' in 1965, although seemingly contradictory was actually in agreement with all previous work. This position bore the smallest leaves on the stem (Figure 39), as did
position one in 'Cynthia' and 'Pink Pearl' (Figures 35 and 37). These results confirm the importance of leaf position on the stem, but show that leaf size contributes even more to the physiological state of the leaf.

**Time of Flower Initiation**

It is difficult to account for leaves in position four on shoots of 'Roseum Elegans' being smallest, but it may be related to the time of flower initiation. Thomas (1961) showed that flower initiation in *Chenopodium* stimulated expanding leaves to expand more than normal. Those leaves expanding after flower initiation was completed were inhibited and expanded less than normal.

The present study showed flower initiation in the greenhouse began when elongation of the stem and largest leaf was about half completed. It is possible that at least one or more bottom leaves were fully expanded prior to flower initiation and were no longer sufficiently plastic to respond to the flowering stimulus. Seasonal differences in temperature and light conditions during shoot elongation may influence greatly the number of fully expanded leaves by the time of flower initiation. This could account for the greater variability in leaf size on flowering shoots and could account for the small leaves in position four of 'Roseum Elegans' in 1965 (Figures 31 and 39). Perhaps the rooting-potential of the foregoing leaves was not
influenced physiologically by the presence of the flower. They may have retained many of the biochemical properties associated with leaves on non-flowering shoots, including better rooting-potentials. Here again, the primary effect is on leaf size and accompanying leaf physiology.

Flower

In addition to the influence of time of flower initiation, flower development influences rooting-potential. Intraplant competition between the florets and developing root system resulting from differential mobilizing powers have already been discussed. In 'Pink Pearl' and 'Britannia' this apparent competition occurred when the diameters of their respective florets averaged about 3.5 mm and 3.0 mm, about 47 and 43 days after the base dates, respectively. Had samples been taken more frequently than at three-week intervals, the correlations would have been closer.

The influence of mobilization was seen both years in floret growth. Floret growth of the intermediate-rooting cultivar 'Pink Pearl' was not inhibited on the cutting during the rooting period (Figures 12 and 24), while it was in easy- and hard-to-root cultivars having greater and lesser rooting-potentials (Figures 11, 13, 23, 25 and 26). This suggests that the mobilizing power is independent of leaf rooting-potential. Growth of 'Pink Pearl' florets was not
inhibited during rooting in sample 2' and only occasionally in sample 1' in the two years. In all other cultivars it was definitely inhibited when cuttings were rooted from these early samples. When the floret was less than 1 mm in diameter at the time of taking the cutting, further growth of the floret was somewhat retarded except for 'Pink Pearl' in 1964 (Figure 12), thus showing low mobilizing power at this stage of development (Figures 11, 13, 23, 25 and 26). This strong mobilizing power of 'Pink Pearl' florets was shown also by the relatively poor root-ball development and the lower rooting-potential of flowering compared to non-flowering shoots (Tables 3 and 4).

The physiological explanation for this competition and mobilization is not known, although Turezkaya (Selim 1956) and Selim (1956) suggested that auxin mobilization by the developing flower may lower the level in the shoot below the optimum for root initiation. Engelbrecht and Conrad (1961) and Conrad (1961) have shown that a localized application of kinetin can establish a "sink" that can mobilize auxin. Prior to these reports, only auxin and related hormone-type herbicides were known to promote mobilization.

The author is of the opinion that flowers either mobilize an auxin precursor away from the leaf or flower initiation modifies auxin production in the leaf itself. Mobilization by the flower may be eliminated by removing the terminal flower bud at the time of
taking cuttings. Rooting of leaf-petiole cuttings, which have no flower buds of course, was not inhibited at times when inhibition was evident on intact flowering stem cuttings.

The primary influence of the flower is not believed to be due to its strong mobilizing power, but rather to changes in leaf biochemistry brought about by flower induction and initiation. The first visual indication of possible biochemical changes in the leaf brought about by flower initiation is the increased leaf size followed later by rapid growth of the flower bud. The increased leaf size was accompanied by decreased rooting-potential.

Biochemical changes associated with flowering have been reported by many workers. Reviews by Hillman (1962) and Searle (1965) show that flower initiation is primarily controlled by DNA and RNA. Numerous substances, such as steroids, lipids and many unidentified compounds in plant extracts, have been shown to be altered by floral induction. Floral induction has altered basipetal auxin movement (Leopold and Guernsey 1953, Naqvi and Gordon 1965). Harada and Nitsch (1959) reported changes in various growth substances with flower initiation and development. Hess (1960) extracted four "co-factors" in large amounts from easy-to-root, non-flowering Hedera helix that promoted rooting in a Mung Bean bio-assay. The "co-factors" were nil or were in very low concentration in the hard-to-root reproductive form.
Many biochemical changes are known to occur during flower initiation in many species of plants. Whether the absence or presence of some substance during flower initiation inhibits root initiation and growth is not known. Any explanation of the reduction in leaf rooting-potential resulting from flower initiation should include the following observations from this study and the literature:

1. flower initiation increases leaf size,
2. leaf expansion is negatively correlated with auxin supply,
3. rooting-potential decreases with increasing leaf size,
4. the loss of rooting-potential is apparent shortly after flower initiation,
5. the time of flower initiation is critical since its influence on the leaf varies with leaf age,
6. rooting-potential of non-flowering cuttings may be several times greater than that of flowering cuttings,
7. losses in leaf rooting-potential because of the presence of flowers, remain even though the flower buds are removed from stem cuttings and even when rooting leaf-petiole cuttings where the influence of both the flower and stem tissues are removed.

Such losses in rooting-potential cannot be explained solely on the basis of mobilization as suggested by Turezkaya (Selim 1956) and Selim (1956). It is conceded that during floral initiation and a specific
stage of floret development, mobilization may play a major role in leaf expansion and the inhibition of root growth as shown by 'Pink Pearl' and 'Britania' (Figures 12, 13, 29, 30, 32 and 33). This partial loss of leaf rooting-potential on flowering shoots, and in leaf-petiole cuttings taken from them, cannot be explained solely on the basis of a mobilization phenomenon. The only explanation which can include all the responses in the above list assumes that the basic physiology of the leaf is changed irreversibly by flowering in such a way that the rooting-potential is more or less lost. Although it is not known exactly what biochemical changes occur, the literature suggests several possibilities. For example, leaves from flowering and non-flowering shoots might differ in their synthesis of vitamins. Audus (1959) reviewed evidence that roots cannot synthesize certain vitamins, particularly $B_1$, $B_6$ and nicotinic acid. Under conditions of low natural production of these by the shoot, root initiation and growth would necessarily be inhibited. The Camellia has been shown to be influenced in this manner (Bonner and Greene 1938 and 1939, Went, Bonner and Warner 1938). Skoog (1944) and Skoog and Tsui (1948) have shown the importance of hormone balance in the production of roots, buds and callus. These investigations and others cited by Elliot (1937), Thomas (1961) and Humphries and Wheeler (1963) point out the occurrence of major biochemical changes which can profoundly influence leaf rooting-potential.
Cultivar and Interactions

The influence of the cultivar has been apparent in the variable responses obtained in individual tests. The easy-to-root cultivars, 'Cynthia', 'Roseum Elegans' and 'Elizabeth', were not influenced greatly by any factor studied. Cuttings can be taken at any time, from any type of shoot, withstand drastic leaf removal, and still root acceptably by commercial standards. Handling procedures for this group are not critical because of their high rooting-potential.

Intermediate-rooting cultivars, particularly those related to 'Pink Pearl', should be handled with more care. Since florets of 'Pink Pearl' and probably its hybrids have a high mobilizing power, cuttings should be taken before the diameter of the florets reach 1 mm. This size is usually reached about 45 days after bud-break, near July 1 in most seasons. Florets on terminal shoots reach this size first, because these shoots start growing earlier. Terminal bud removal should also be practiced to prevent competition later with the new root system. Non-flowering and flowering lateral shoots with small leaves should be used in preference to flowering terminal cuttings or those with large leaves. No more than about 20 percent of the total leaf surface should be removed, and only the basal leaves should be removed.

Hard-to-root cultivars like 'Britannia' must be handled so as
to take advantage of all factors favoring rooting. The cuttings should be taken before the florets reach 1 mm in diameter and should consist principally of non-flowering wood. Small-leaved, flowering lateral shoots may be used, but heavy terminal shoots should be avoided. Terminal bud removal should be practiced. Because of the very low rooting-potential of the leaves of this group, no leaves should be removed unless absolutely necessary. All cuttings should of course be wounded and hormone treated.

The inadequacy of measuring tissue age by calendar date has been evident. The morphological time scale should be a valuable first step in determining tissue age, but additional research is needed to increase its accuracy. The optimum time for taking cuttings appears to be before the florets reach 1 mm in diameter, since these small florets appear less competitive to rooting and the tissues seem most responsive to root initiation. The morphological time scale also suggests that the developing florets and developing root system are intensely competitive at about 40-50 days after the 1 mm diameter base date. Floret size during this period ranged from 2.5 to 4.0 mm in several cultivars. The data suggest that cuttings, particularly of intermediate and hard-to-root cultivars, should not be taken at that time. The terminal bud should be removed in these cultivars because the rooting of leaf-petiole cuttings did not show reductions in root-ball development as did stem cuttings taken at the same times.
Flower initiation influenced the rooting-potential of the cuttings more than any other factor. It affected rooting primarily by influencing the rooting-potential of the leaf. Flower initiation probably affects the biochemistry of the leaf in such a way as to prevent further synthesis of substances necessary for root initiation and development. That rooting-potential is not simply a condition predictable morphologically or even biochemically without consideration of the numerous factors involved has been shown. These factors must also be considered in relation to the cultivar, since cultivars differ in their reaction to the various factors.

The goals of commercial propagators are not necessarily oriented to the use of cuttings which are easiest to propagate. The primary goal with easy-to-root cultivars should be the propagation of a cutting that will develop into a well-branched plant in the shortest time. This necessitates the use of flowering cuttings only. Flowering shoots normally develop several large lateral buds capable of producing the desired plant in much less time than non-flowering shoots (Figure 43). In the normal growth and development of the non-flowering shoot, only one lateral bud enlarges, therefore, cuttings from such shoots do not produce well-branched plants unless they are pruned or pinched at the right time.

The primary goal with hard-to-root cultivars is to root the cuttings. Much more attention, therefore, must be given to selecting
Figure 43. Lateral bud growth on flowering and non-flowering stems of *Rhododendron* 'Pink Pearl' and 'Cynthia'.

1. Non-flowering stem of 'Pink Pearl'.
2. Flowering stem of 'Pink Pearl'.
3. Non-flowering stem of 'Cynthia'.
4. Flowering stem of 'Cynthia'.

1 2 3 4
shoots that root quickly. For these reasons, the selection of cuttings and the time of taking them must be based on knowledge of the inherent growth characteristics, the factors controlling rooting-potential and the goal of the propagator.
BIBLIOGRAPHY


Murneek, Andrew Edward. 1926. Effects of correlation between vegetative and reproductive functions in the tomato (Lycopersicon esculentum). Plant Physiology 1:3-56.


