THE EFFECT OF PHOTOPERIOD ON THE ROOTING OF *ABELIA GRANDIFLORA* REHD., 'PROSTRATA' CUTTINGS

by

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ABSTRACT

Abelia grandiflora Rehd., 'Prostrata' plants were maintained under five different photoperiods. After 82 days, cuttings were taken and rooted under the five photoperiods. Stock plants grown under short days produced cuttings which had a higher percentage of rooting than cuttings from long-day stock plants. The photoperiod during rooting had no significant effect on rooting ability. Reducing sugar, total nitrogen and growth regulator content of stock plants and cuttings were assayed initially and during the propagation period. Long-day stock plants contained higher amounts of indoleacetic acid than did short-day stock plants. No correlation was found between amounts of reducing sugars, total nitrogen or growth regulators and the rooting response. Statistical evaluation of the oat coleoptile straight growth bioassay revealed that coleoptile variation within a treatment is not a correct estimate of true experimental error. Large variation between samples (chromatograms) indicated the need for increased replication of samples.

INTRODUCTION

Photoperiodic responses observed in woody plants include flowering, vegetative growth, winter hardening, leaf abscission, leaf coloration and rooting of cuttings (Nitsch 1957b, Wareing 1956). Photoperiod may affect the rooting of cuttings directly during the rooting period or indirectly through its influence on the stock plants (Nitsch 1957b, Waxman 1957). Seasonal variation in rooting ability has been observed in woody plants (Childers and Snyder 1957, Keen 1954, Lanphear and Meahl 1963). Some of these workers have studied the effect of natural variation in photoperiod on rooting ability by removing cuttings at monthly or seasonal intervals from stock plants grown outdoors. The cuttings taken were then rooted under different controlled photoperiods. However, interpretation of such experiments is difficult, as there are many other environmental factors that also vary during the year. Without control over these factors, the true amount of variation in rooting ability attributable to the photoperiod cannot be delimitated.

There are two conflicting reports concerning the effects of photoperiod on the rooting of Abelia grandiflora (Baker and Link 1963, Waxman 1957). In both cases only the photoperiod during rooting was controlled, but in one (Baker and Link 1963) the cuttings were taken at various times during the year.

Inferences have been made that certain levels of various plant constituents are more favorable for root initiation than others, e.g., carbohydrate-nitrogen status of the stock plant (Hartmann and Kester 1960) and the indoleacetic acid (IAA) -kinetin ratio (Skoog and Tsui 1948). In addition, the duration of the photoperiod has been associated with the relative amounts of growth promoters and inhibitors present in plants (Nitsch 1957a, Waxman 1957).

Objectives of this study were: (1) to determine what effect, if any, photoperiod has on the rooting of Abelia grandiflora Rehd., 'Prostrata'; (2) to determine if the effect was due to the photoperiod during rooting, the photoperiod that the stock plants were exposed to prior to removal of the cuttings, or an interaction of the two; (3) to determine if the photoperiod, either directly or indirectly, influenced levels of some essential plant constituents, i.e., reducing sugars, total nitrogen content, and growth regulators; and (4) to determine if there was a correlation between any changes in these plant constituents and the rooting of cuttings.

REVIEW OF LITERATURE

The phenomenon of photoperiodism, first discovered by Garner and Allard in 1920, has been studied intensively. Early studies concerned the dramatic response of flowering in herbaceous species. Later other processes mediated by daylength received attention. In comparison with herbaceous species, woody plants were somewhat inconvenient to work with, and elucidation of the role of photoperiod in their growth and development was suppressed. Nevertheless, photoperiodic control over many diverse processes in woody plants has since been shown. Photoperiodic responses that include winter hardiness, leaf abscission, seed germination, and rooting of cuttings have been reviewed by Wareing (1956) and Nitsch (1957b).

Effects of photoperiod on Abelia grandiflora Rehd. were first reported by Kramer (1937) in conjunction with winter hardiness. Extension of the photoperiod by electric lights stimulated growth in portions of an Abelia hedge. These portions failed to harden prior to the occurrence of freezing weather. A light intensity of less than one foot-candle was sufficient to prevent hardening.

In regards to flowering, Abelia grandiflora is classifed as a long-day plant. Flowering can be induced either by extension of the

daylength to 14 hours or by a light break in the middle of the dark period. Waxman (1957) found that flowering was prevented if far-red light followed the light break. Nitsch and Mowogyi (1961) reported that the number of long days required for flowering varied with the daylength. Flower buds were produced in seven weeks with a 24-hour day, eight weeks with an 18-hour day, and nine weeks with a 14-hour day.

Waxman (1957) and Baker and Link (1963) found internode elongation photoperiodically controlled. Normal internode extension occurred under long days, whereas short days resulted in rosetting of the new growth.

The effect of photoperiod on the rooting of Abelia grandiflora is a disputed issue. Nitsch (1957b) citing Waxman (1957) reported that rooting was increased under long days. However, Baker and Link (1963) disclosed that Abelia grandiflora showed no consistent response to photoperiod, and that a seasonal variation in the rooting ability occurred. Cuttings taken in the middle of June rooted 100% regardless of the photoperiodic treatment whereas only 30-40% of the cuttings rooted when they were taken in November or late April (Baker 1963).

Moshkov and Kocherzhenko (1939) demonstrated that the photoperiod may influence the rooting of cuttings either during the rooting period (directly) or through the stock plants (indirectly). Most studies have been concerned with photoperiodic treatments

during the rooting period. Generally, such studies have shown that long days resulted in an increased percentage and quality of rooting, although in some instances short days enhanced rooting.

One of the earliest works demonstrating the influence of photoperiod on rooting was by Zimmerman and Hitchcock (1929). Extension of the natural photoperiod by six hours increased rooting quality of cuttings of azalea, Andromeda, Camellia, and Ilex species. Rooting percentages of the Ilex species were also influenced. Ilex crenata rooted 100% under long days, but only 45% under the normal photoperiod. Extended photoperiods increased the rooting of Ilex glabra 45% over that of short days while increases in rooting of Ilex opaca were not consistent.

Skinner (1939) reported long days increased the rooting of Rhododendron cuttings by 10%.

Stoutemyer, Close, and O'Rourke (1945) found more rapid rooting of cuttings of Weigela floribunda, Ligustrum ovalifolium, and Chrysanthemum morifolium could be obtained if subjected to continuous illumination during rooting. Citrus aurantium var. myrtifolia rooted better under 16-hour days than under continuous illumination. Conversely, Citrus limon cuttings rooted best under continuous illumination. In both species, however, there were no differences in rooting under either photoperiod unless the cuttings were treated with potassium indole butyrate.

Cornus florida, Magnolia soulangeana, Rhododendron mucronatum, and Weigela florida were among the plants considered by Waxman (1957)

to root more favorably under long days. The effects of photoperiod, which resulted in increased numbers of roots per cutting, were most pronounced on cuttings in active growth.

In a few of the species they studied, Baker and Link (1963) also considered long days during the rooting period as beneficial. In contrast to Waxman's work they felt that long days exerted a greater root-promoting effect on hardwood cuttings.

In eight days, 70% of hop (Humulus lupulus) cuttings rooted under 17-hour daylengths compared to 21% under normal photoperiods (Sykes and Williams 1959). However, at the end of 16 days there was little difference between the two treatments.

Thomas and Wilkinson (1962) reported increased rooting of black currants by extension of the photoperiod. Rooting of single bud cuttings was favored under continuous illumination.

Among cuttings of eight species of woody ornamentals taken in the fall, only Juniperus horizontalis 'Plumosa' rooted significantly better under long days (Lanphear and Meahl 1961). Contrary to Waxman's work, rooting of Rhododendron mucronatum was not favored by long days, although rooting quality was increased if the cuttings were treated with indolebutyric acid. If the cuttings were taken in the winter and subjected to long days during the propagation period, the percentage of rooting was decreased in Juniperus horizontalis 'Plumosa', Rhododendron

mucronatum, Taxus cuspidata 'Nana' and other species. Thus the time of the year that the cuttings were taken determined what effect photoperiod had on rooting.

Later work by Lanphear and Meahl (1963) demonstrated that the reduced rooting of Taxus cuspidata 'Nana' cuttings taken in the winter and rooted under long days could be overcome by the use of indolebutyric acid. This is in agreement with Snyder (1955) who found no significant effect of photoperiod on the rooting of Taxus cuspidata cuttings taken in December and treated with indolebutyric acid.

The results may suggest that levels of endogenous auxins were a limiting factor in the rooting ability of the cuttings. Unfortunately growth habits concurrently observed during the rooting period did not support this hypothesis. Lanphear and Meahl (1963) concluded that the controlling factor of root formation was the growth phase of the cuttings. Earlier bud activity, which restricted root formation, was stimulated by long days and inhibited by short days or indolebutryic acid.

Kamp and van Drunen (1958a) demonstrated a significant improvement in rooting of Hatfield yew under short days. Similarly, cuttings of Pfitzer juniper taken in November also rooted better under short days (Kamp and van Drunen 1958b). Van Drunen and Kamp (1959a) also reported that cuttings of chrysanthemum, Peperomia obtusifolia

variegata, Vinca major variegata, Fittonia argyroneura, and Duranta plumieri rooted better under nine-hour days than under 17-hour days. Later work (van Drunen and Kamp 1959b) revealed an interaction between the photoperiod during rooting and the pH of the rooting medium. At pH values of 5.0 and 6.0 daylength had no effect on rooting of Hatfield yew, but at pH 7.0 short days stimulated significant increases in rooting.

Piringer (1961) considered long days to cause earlier and heavier rooting of Ilex and Buxus species. Heavier rooting was a result of the production of more fibrous roots rather than more main roots. A temperature-photoperiod interaction was considered to play an important role in determining the root system formed. Long days and a propagating medium temperature of 80° F. were conducive to formation of fibrous roots. More main roots were formed at 70° F. regardless of the photoperiod.

Moshkov and Kocherzhenko (1939) found that the photoperiod to which stock plants were exposed prior to the removal of cuttings also determined the rooting response of some species. Cuttings of Salix undulata rooted 100% when taken from stock plants grown under 18-hour days and 0% when taken from stock plants grown under nine-hour days. Long or short days during the rooting period had no effect on the above percentages. In contrast, Salix pierotti cuttings rooted best when taken from stock plants grown under ten-hour days. Moreover, short days during the propagation period increased the rooting of cuttings from

both long and short-day plants. Cuttings from Salix babylonica stock plants subjected to a photoperiod of 14 hours rooted better than cuttings taken from stock plants subjected to either 18 or 10-hour photoperiods. In contrast to S. pierotti, rooting of S. babylonica cuttings was increased by a long photoperiod during propagation.

Similarly, Waxman (1957) reported a twofold increase in the number of rooted cuttings taken from stock plants of Cornus florida rubra subjected to 18-hour days as compared to cuttings taken from plants grown under nine hour photoperiods. The number of roots per cutting was also doubled on cuttings from plants grown under the extended photoperiod.

Benefits of subjecting Pelargonium stock plants to long photoperiods were suggested by Emmerson (1959). Plants grown under continuous illumination yielded increased numbers of cuttings as compared to plants subjected to eight-hour or natural photoperiods. In addition, when the cuttings were subsequently rooted under the natural photoperiod, those from the long-day stock plants showed an increase in rooting ability.

With the exception of Salix undulata, photoperiod does not exert an all-or-nothing response in conjunction with rooting. That is, unlike flowering, rooting is not solely dependent on the photoperiod. In general, favorable daylengths influence rooting quality more than

rooting percentage. Thus photoperiodic treatments must enhance certain factors essential for rooting rather than constituting an absolute control mechanism as in flower initiation. To determine in what manner photoperiod may be augmenting rooting quality, physiological factors in the rooting process must be considered.

Many physiological factors affecting root formation have been reported. An adequate review of these factors has been made by Hartmann and Kester (1960, pp. 185-217). The following discussion has been limited to physiological factors affecting rooting which in turn have been shown to be affected by photoperiod. These include carbohydrates, nitrogenous compounds, growth promoters and inhibitors, vitamins and rooting cofactors.

The logical starting point for such a discussion would be the leaves of the cutting. Young leaves just reaching full size are considered to be the receptors of the photoperiodic stimulus (Nitsch 1957b). Leaves are also the site of synthesis of many of the various factors essential for the rooting of cuttings.

Van Overbeek, Gordon, and Gregory (1946) demonstrated that a main function of the leaf was to provide a source of carbohydrates during the rooting period. Utilizing cuttings of Hibiscus rosa-sinensis, it was shown that the function of the leaves could be entirely replaced by sucrose and ammonium sulfate.

Although this experiment has demonstrated the requirement for carbohydrates during rooting, there are many discrepancies in the literature concerning carbohydrates and rooting of cuttings. Much of the dispute is not concerned with the requirement of carbohydrates for the regeneration of roots, but rather with the correlation between carbohydrate content and the rooting response.

Starring (1923) was of the opinion that carbohydrates were of outstanding importance in the production of roots by tomato and Tradescantia cuttings.

Carlson (1929) concluded that rooting of roses was related to the reserve starch content of the cutting. Cuttings of the easy-to-root variety, Dorothy Perkins, contained a high content of reserve starch, whereas a difficult-to-root variety of pillar rose had a low starch content. However, Brandon (1939) using a multitude of rose varieties failed to correlate starch storage and rooting. Striking examples of this were Rosa setigera which, with an abundant supply of starch, failed to root while 92% of the Rosa canina cuttings, with very little starch storage, had rooted.

Zimmerman and Hitchcock (1929) in their study with holly found no evidence that the presence or absence of starch was a limiting factor in root formation.

Schneider (1958) revealed that rooting of Mentha cuttings could be greatly improved by immersion in glucose solutions. Similarly

Gregory and Samantarai (1950) concluded that sugars were of primary importance in the initiation of root primordia of isolated bean leaves. The total sugar content of the leaves after seven days was related to the rooting response.

Childers and Snyder (1957) found no consistent relationship between the carbohydrate content of the wood at the time of taking the cuttings and the rooting response of American holly. Greatest rooting occurred in September when the total sugar and reducing sugar content was lowest, but the reverse was not true. Seasonal variation in rooting ability was attributed to some other unknown factor(s).

Machovec and Kopec (1957) contended that the rooting capacity of Rosa gallica var. splendens depended not only on the total sugar content, but also on the type of sugars present. Rooting capacity improved only during flower formation when the monosaccharide content was lowered and the sucrose content was increased. During hip formation the ratio of the sugars was reversed and rooting declined. Thus rooting was proportional to the sucrose content and inversely proportional to the monosaccharide content. In other woody ornamentals studied, a relationship was also found between sugar metabolism and rooting, although it varied with the species.

After Garner and Allard's discovery of photoperiodism, papers concerned with changes in carbohydrate content of plants subjected to

various photoperiods appeared rapidly. Although the papers were mainly concerned with the changes in carbohydrate content in relation to flowering, they are useful in this study to illustrate photoperiodically induced changes in the carbohydrate content of plants.

Many reports of increased carbohydrate levels under long days were made. Among them were reports by Garner, Bacon, and Allard (1924) and Arthur, Guthrie, and Newell (1930). Conversely, Auchter and Harley (1924) found that total carbohydrates in soybeans were slightly higher under 12-hour days than under continuous illumination. Sucrose and total sugar levels were higher under short days. Nightingale (1927) also concluded that carbohydrates accumulated under short days. Soybeans, radishes, and salvia were among the plants studied.

Murneek (1937) found slight differences in total sugars in soybeans under long or short days. During the first 27 days of growth, starch levels were also similar under both photoperiods. After 27 days, starch levels rapidly increased under short days. Correspondingly, total carbohydrates were slightly higher under long days for the first 12 days, but then fell below the levels of the short-day plants.

In many studies it has been assumed that by retaining the light intensity below 50 foot-candles any changes in the carbohydrate content of the plant were phytochrome mediated. Such reports were based on the inference that an increase or decrease in carbohydrates was not

due to changes in the photosynthates produced because the light intensity was below that required for photosynthesis. To provide a sounder foundation for this inference, phytochrome-mediated carbohydrate responses have been reported in etiolated corn leaf sections (Price, Mitrakos and Klein 1963). A decline in starch and sugar levels was enhanced by red light. The response, reversible by far-red light, had a low energy requirement.

Doak (1939) indicated that amino acids had a marked effect on root production. The work substantiated the suggestion of Went, Bonner and Warner (1938) that rooting of some cuttings may be limited by a lack of amino acids. Later, Doak (1940) reported that all nitrogen compounds examined, both organic and inorganic, improved the rooting response of Rhododendron maddeni var. jenkensii to naphthaleneacetic acid. In addition, there was no apparent relationship between the action of the nitrogen compounds and their chemical nature.

Van Overbeek's (1946) previously cited observation that leaves of Hibiscus cuttings were replaceable by sucrose and a nitrogen source, implicated the need of nitrogenous compounds in the rooting process. The nitrogen was equally effective if supplied as arginine or ammonium sulfate.

Besides being essential in the rooting process, nitrogen also affects the rooting of cuttings through its influence on the stock plants.

Haun and Cornell (1951) indicated that nitrogen nutrition of Pelargonium stock plants was important in the rooting of cuttings. Cuttings taken from plants maintained on low and medium nitrogen levels resulted in increased percentages of rooting over those taken from stock plants subjected to high nitrogen levels.

Bosemark (1954) considered the nitrogen supply inversely related to root development. Nitrogen deficiencies produced long slender roots, whereas roots under increased nitrogen levels grew shorter and sturdier.

Nightingale (1927) reported that total nitrogen levels were greater in plants grown under short days than those grown under long days. Arthur, Guthrie, and Newell (1930) also concluded that as day-length was increased total nitrogen levels were increased. In contrast, Murneek (1937) reported that stems and leaves of soybean plants, var. Biloxi, contained more total nitrogen when grown under short days.

While some studies have attempted to assess the role of either carbohydrates or nitrogenous compounds in the rooting process, others have stressed the importance of the ratio of the two. The carbohydrate-nitrogen (C/N) ratio has often been found to have an influence on the rooting ability of cuttings (Hartmann and Kester 1960, pp. 142-195, Pearse 1943). Kraus and Kraybill (1918) were among the early contributors to this concept. Tomato cuttings high in carbohydrates

but low in nitrogen produced many roots; cuttings high in both carbohydrates and nitrogen produced fewer roots. When carbohydrates were present in low quantities in conjunction with high nitrogen levels, no roots were formed.

Schrader (1924) and Reid (1924, 1926) similarly concluded that a high C/N ratio favored the regeneration of roots in tomato cuttings. In view of Arthur, Guthrie, and Newell's previously discussed results, it could be postulated that improved rooting under long days was due to an increased C/N ratio. However, in most cases the possible correlation between chemical constituents and photoperiodism has been quite general. Murneek (1937) reported that the chemical composition varied greatly in relation to other factors, i.e., stage of development, tissues sampled, and time of day. Thus it cannot be definitely stated that photoperiod affects the rooting response through alteration of the C/N ratio. More likely, changes in the C/N ratio are associated phenomenona rather than direct causes.

The voluminous literature reporting the work leading to the discovery of indoleacetic acid and its relation to rooting has been reviewed by many writers. Among the early reviews are those of Pearse (1948) and Boysen-Jensen (1936). Both adequately cover the early concepts of root-forming substances, mechanisms of induced root formation, and practical recommendations for the treatment of cuttings.

The first practical studies of auxins and rooting of cuttings were made by Cooper (1935, 1936, 1938) and Hitchcock and Zimmerman (1936). Since then manuals listing the responses of a myriad of cuttings treated with growth regulators have been compiled (Pearse 1948, Thimann and Behnke-Rogers 1950). Books concerned with auxins and horticulture have been published by Audus (1959), Avery and Johnson (1947), Leopold (1963), and Tukey (1954).

In view of this excellent and extensive coverage of auxins in relation to rooting of cuttings, this discussion will be limited to work pertaining to the influence of photoperiod on endogenous levels of auxins.

Yin (1941) reported that leaves of Phaseolus coccineus and Carica papaya contained a higher amount of auxin when the plants were grown under long days as compared to those grown under short days. Similarly, Zdanova (1941) indicated that leaves of vegetative plants grown on long days contained much more auxin than leaves of photo-induced plants grown under short days.

Cooke (1954) followed the auxin content of several short-day plants during the photoinduction period. More auxin was found in plants under long days, whether they were flowering or vegetative, than in plants growing under short days.

Leopold (1949) found more diffusible auxin in Coleus plants grown under 16-hour days than in those grown under ten-hour days. The difference (78 %) was very highly significant.

Muir and Kuraishi (1963) maintained Hyoscyamus niger and Centaurea cyanus plants in a rosetted condition for 200 days under a daylength of eight hours. Little auxin was present in the plants at this time. If the plants were subjected to long days or treated with gibberellins, there was an increase in the amount of diffusible auxin. Although the increase in auxin levels was elicited by both gibberellins and long days, the auxin produced did not have similar Rf values. The auxin under long days had an Rf of 0.3 to 0.4 while that from plants treated with gibberellins or short days was 0.5 to 0.6.

Nitsch (1957a) reported that sumac plants contained more auxin under long days. Two weeks after the plants were shifted to short days the auxin level became quite low. Similar results in Hedera helix were obtained by Hess (1957).

Waxman (1957) reported that in Cornus florida long days not only increased the amount of growth promoters present but also decreased the amount of growth inhibitors present. In conjunction with these results, rooting was also found to be enhanced under long days. Short days, on the other hand, had the reverse effect on rooting and levels of growth promoters and inhibitors.

Tyce (1957) attempted to correlate the growth-promoting or growth-retarding action of extracts with the rooting capacity of cuttings. Some correlation was found between seasonal variations in the rooting response and content of growth substances. Although both rooting and

levels of growth substances were lower in early dormancy and higher in late dormancy, there was not a good correlation during all of the summer months.

Went, Bonner, and Warner (1938) demonstrated that vitamin B_1 enhanced the rooting of lemon and Camellia cuttings. The cuttings were treated with indoleacetic acid and placed in a sand rooting medium. After one week half of the cuttings were treated with vitamin B_1 (1 mg/l.). At the end of two weeks the vitamin-treated cuttings produced twice as many roots per cutting as did the untreated ones. Other vitamins reported to enhance root formation include nicotinic acid and ascorbic acid (Tukey 1954).

Thimann (1938) considered three known factors to limit the rooting of Pisum cuttings: sucrose, auxin, and biotin. Maximum root formation occurred only if optimum amounts of each factor were present.

Although there have been similar reports of vitamins improving the rooting response (Hemberg 1953, Chadwick and Swartley 1941), they did not receive practical consideration due to the variable results obtained (Pearse 1948). Recently vitamin levels have been shown to be modified by daylength. Perhaps there is some link between photoperiod and rooting via vitamins, as both generally enhance the quality of rooting.

Langston and Leopold (1954) found that biotin, niacin and pantothenic acid levels decreased in barley plants grown under 18

hour days. Riboflavin content remained unchanged regardless of the photoperiod.

Gustafson (1953) reported that the thiamine content of pea, bean, and tomato plants decreased when exposed to long photoperiods. Levels of riboflavin and niacin were increased under long photoperiods.

Witsch (1959) found that the thiamine content of plants increased if they were maintained under photoperiodic conditions conducive to vegetative growth.

The most recent discovery in the physiological aspect of the rooting of cuttings has been made by Hess (1957). Through chromatography and the use of a bioassay utilizing mung bean cuttings and an auxin, the presence of rooting cofactors in extracts of Hedera helix has been ascertained. Their significance in the process of rooting is based on their ability to increase rooting of mung bean cuttings when used in conjunction with indoleacetic acid. The cofactors have been shown to exist in juvenile, easy-to-root forms, but are absent in the mature, hard-to-root forms. Hess (1961) also demonstrated their presence in extracts of Hibiscus rosa-sinensis. The easy-to-root variety contained four rooting cofactors, whereas the difficult-to-root variety contained only two.

Lanphear and Meahl (1963) attempted to elucidate the role of endogenous rooting cofactors in seasonal rooting trends of Juniperus

horizontalis 'Plumosa'. However, there was no apparent relationship between the levels of rooting cofactors and rooting trends.

MATERIALS AND METHODS

Photoperiodic Treatments

Photoperiod Chambers

Chambers to control the photoperiod were constructed in raised benches located in a greenhouse on the University of Arizona campus in Tucson. Each chamber enclosed nine square feet of bench space and was four feet in height. Light barriers between treatments were constructed of frames of thin-walled conduit overlaid with black oil cloth. The compartments were covered with black shade cloth (Knight's Black Sheen obtained from Geo. J. Ball, Inc., West Chicago, Illinois) and secured at each barrier. Maximum light penetration at 5,000 foot-candles through the cloth was two foot-candles; light transmittance through the barriers was excluded.

Selection of a light source for extension of the photoperiod was based on a number of factors. The light source was required to provide light of that quality governing photoperiodic responses, i.e., wavelengths from about 5800 to 7200 A. (red) and wavelengths from about 7200 to 8000 A. (far-red). In addition, adequate illumination (25 foot-candles) without excessive heat was desired.

Gro-Lux fluorescent lamps were selected to partially fulfill these requirements. The Gro-Lux lamp was developed by Sylvania, Salem, Massachusetts, especially for horticultural use. The lamps provided adequate illumination without an excessive temperature increase within the closed chambers. The spectral energy distribution curve for the Gro-Lux lamp is shown in Figure 1; it can be seen to be high in the blue (4300-4900 A.) and red (6300-7000 A.) regions of the light spectrum, but lacking in the far-red (7000-7350 A.) region. The addition of two small incandescent bulbs, with a high proportion of light in the far-red region (Figure 2) provided the entire light spectrum governing photoperiodic responses.

One 20-watt fluorescent and two 15-watt incandescent lamps were used in each chamber. Minimum light intensity for extension of the photoperiod was 24 foot-candles as measured with a Weston light meter, model 603.

The chambers were adapted for propagation by the addition of a mist system and bottom heat; vermiculite (horticultural grade) was used as a propagating medium. The mist was operative between 8:00 AM and 5:00 PM for intervals of five seconds every two minutes. Lead sheathed cables were placed on a layer of coarse gravel and maintained the temperature of the propagating medium at approximately 72° F.

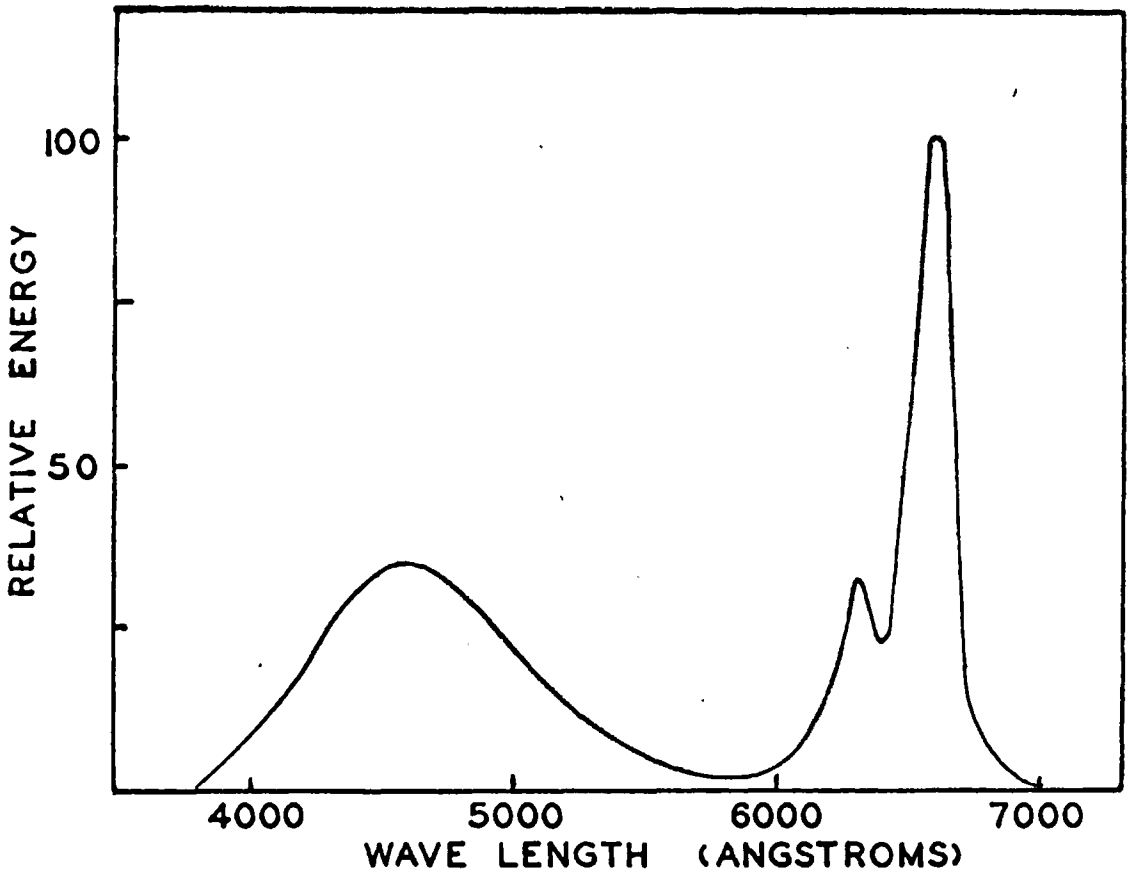


Figure 1. Spectral energy distribution for Gro-Lux fluorescent lamps (from Mpelkas).

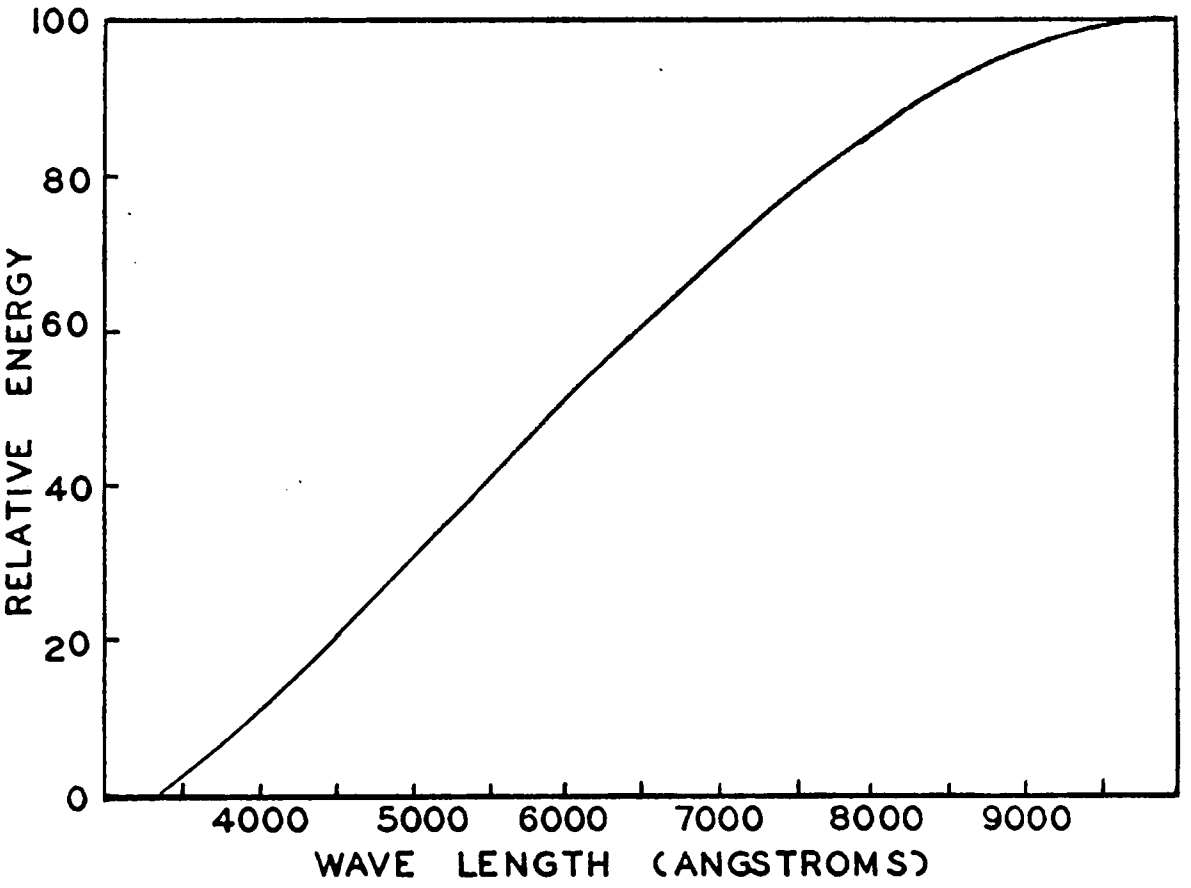


Figure 2. Spectral energy distribution for incandescent lamp (from Downs, Piringer and Wiebe 1959).

Photoperiodic Regimes

Five photoperiodic treatments were used in both photoinduction of the stock plants and rooting of cuttings. The photoperiods consisted of 9, 12, 18, and 24-hour daylengths and a 9-hour daylength with a 3-hour interruption in the middle of the dark period. Hereafter the latter treatment will be referred to as 9i. This treatment was essentially the same as the 18-hour photoperiod in that the maximum length of the dark period was six hours. All of the chambers, regardless of the photoperiodic treatments, were opened at 8:00 AM and closed at 5:00 PM.

Greenhouse temperatures were maintained at 60° F. at night and a minimum of 75° F. during the day. Temperature differences between the closed chambers were a maximum of 3° F. within replications and 5° F. between replications.

Stock Plants

One hundred and eighty, one-gallon, container-grown Abelia grandiflora 'Prostrata' plants were purchased from Monrovia Nurseries, Azusa, California. From these, 135 uniform plants were selected for use in the experiment. On September 4, 1963, nine stock plants were randomly chosen and placed in each of the fifteen chambers.

Initially the light intensity at the surface of the plants varied from 36-50 foot-candles. The plants were maintained under the photoperiodic treatments for 82 days.

Cuttings

On November 23, 1963, terminal cuttings were removed from the stock plants. The maximum number of uniform cuttings, 6-8 inches in length, were harvested from each stock plant. Cuttings taken from stock plants within a single photoperiodic treatment were divided into five equal groups and randomly assigned to each of the five rooting photoperiods. The cuttings were not treated with root-inducing chemicals.

Experimental Design and Statistical Analysis

A randomized complete block design was used for the portion of the experiment concerned with photoinduction of the stock plants. The five treatments were replicated three times.

The design was expanded to a 5 x 5 factorial when the photoperiodic treatments during rooting were introduced. Thus within any one of the five rooting photoperiods there were cuttings from all five stock plant treatments. The cuttings were kept within groups with respect to the stock plant treatment, but the groups were randomly arranged in the rooting chamber. Thus with both the stock plant photoperiod and the cutting photoperiod considered, there were 25 photoperiodic treatment combinations applied to the cuttings. The 25 treatments were replicated three times. The design for one replicate is shown in Figure 3.

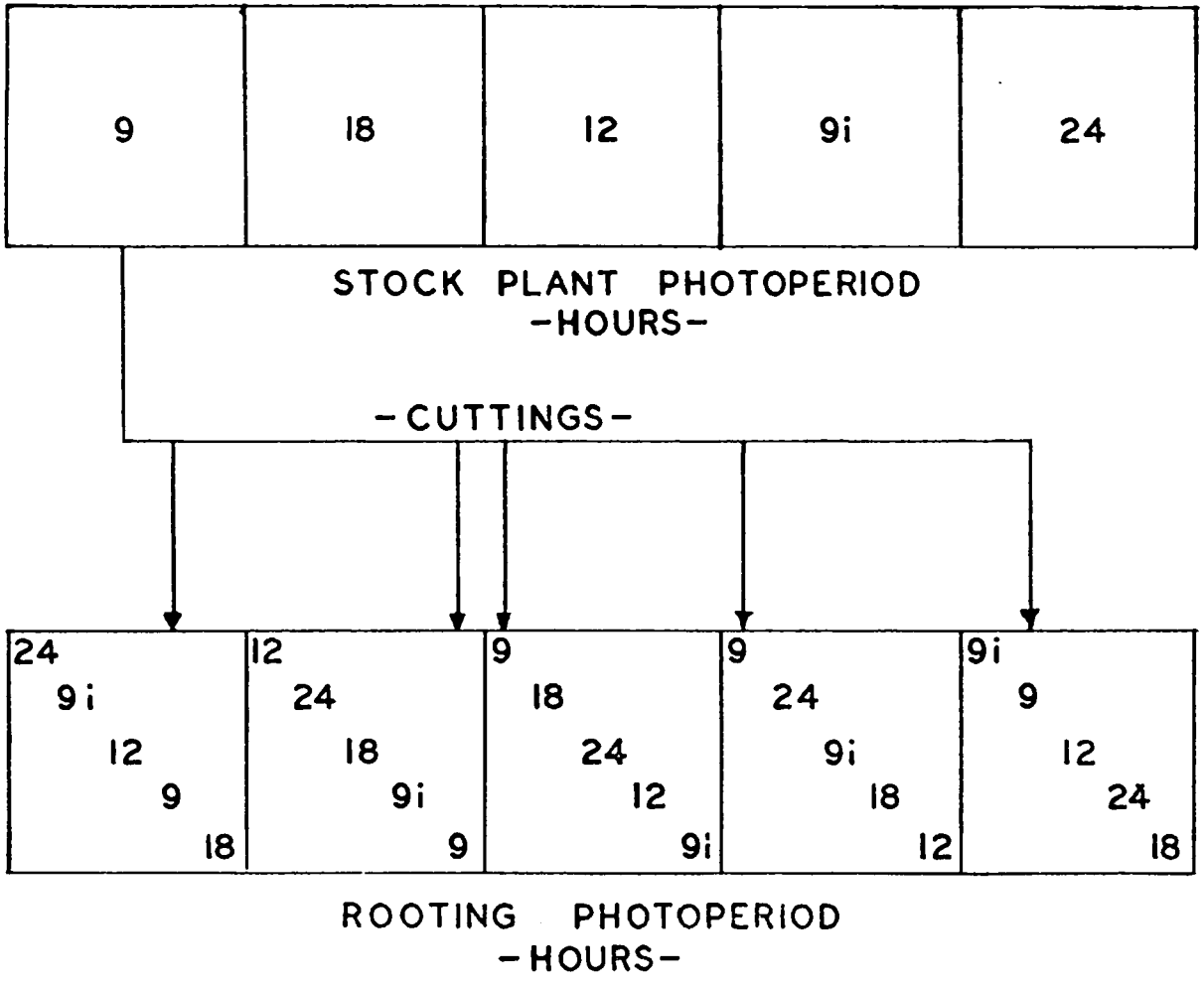


Figure 3. A graphical illustration of the experimental design showing the stock plant photoperiod treatments and subsequent allocation of cuttings to rooting photoperiods.

Evaluation of Rooting

On February 29, 1964, the cuttings were removed from the propagation bench and the percentage of rooted cuttings was determined. Rooted cuttings were further evaluated for quality of rooting. Initially rooting quality was evaluated by the technique utilizing methylene blue as described by Dunham (1958). This method proved to be inadequate for detecting obvious visual differences and a rating system was adopted. The method of ranks was evaluated by Mahlstede and Lana (1958) and found to be accurate in determining the rooting response of cuttings. The rooted cuttings were ranked as follows:

I	lightly rooted	2 points
II	medium rooted	3 points
III	heavily rooted	4 points

A mean rating for each treatment was obtained by dividing the number of points scored by the number of rooted cuttings in the treatment. Unrooted cuttings did not penalize a particular treatment as only rooted cuttings were considered. This presented a truer picture of rooting quality which was not confounded by the already measured percentage of rooting.

Chemical Analyses

Sampling and Preparation of Plant Material

Samples of the cuttings for chemical analyses were taken at three times: (1) initially, upon removal from the stock plants, (2) after one week in the propagation bench, and (3) upon termination of the rooting period. The first sampling period served a twofold purpose; it provided data concerning levels of the plant constituents within the stock plants, in addition to providing the initial levels of the cuttings.

At each sampling date, twenty cuttings were randomly selected from each treatment. Ten of the cuttings were placed in plastic bags and quick frozen with Dry Ice. These samples were stored at -20° C. until needed for growth regulator analyses. The remainder of the cuttings were oven dried overnight at 70° C. After drying, the leaves were separated from the stems and ground to 40 mesh in a Wiley mill. Prior to chemical analysis these samples were again dried at 70° C. All chemical analyses were conducted on leaf samples.

Nitrogen Analysis

The micro-Kjeldahl method of nitrogen determination of plant tissue as described in Official Methods of Analysis of the Association of Official Agricultural Chemists (1955) was used. The method was not applicable to material containing N-N or N-O linkages. The total nitrogen content was expressed as a percent of the dry weight.

Sugar Analysis

Reducing sugars were determined by oxidation with ferricyanide and titration with cerric sulfate (Hassid 1936). A modification of the original procedure which used Setopaline C as the indicator was used in the analyses (Hassid 1937). The method was accurate for quantities between 0.3 and 3.5 mg of reducing sugars. Results were expressed as a percent of the dry weight.

Growth Regulator Analysis

Growth regulator analyses were conducted on all of the stock plant treatments. Samples of the cuttings were limited to only those taken after the cuttings were in the propagation bench one week. At this time only cuttings subjected to the four possible combinations of 9 and 18-hour photoperiodic treatments were taken. These treatments were:

(1) 9-hour stock plant photoperiod - 9-hour rooting photoperiod.

(2) 9-hour stock plant photoperiod - 18-hour rooting photoperiod.

(3) 18-hour stock plant photoperiod - 9-hour rooting photoperiod.

(4) 18-hour stock plant photoperiod - 18-hour rooting photoperiod.

These treatments were considered indicative of long and short-day combinations.

Frozen leaf samples were combined with Dry Ice and ground to 20 mesh in a Wiley mill. The mixture was then lyophilized for 10 hours.

A 0.5-gram portion of the dried material was extracted with 50 ml of peroxide free ether at -10° C. for 15 hours. Peroxides were removed from the diethyl ether by shaking with a 5% ferrous sulfate solution. The extract was filtered through glass wool and concentrated under an air stream. The aqueous solution remaining was taken to dryness under reduced pressure. The dried sample was then taken up in 0.5 ml of 95% ethanol. Re-suspension of the extract was facilitated by placing the sample on a horizontal shaker for 1 hour.

Aliquots of the extract were transferred to Whatman No. 1 MM paper strips with a micro-syringe. Ascending chromatography was used; the solvent system was isopropanol (8) - ammonia (1) - water (1) (v/v). All chromatograms were run in individual test tubes to prevent sublimation of the indolic growth regulators between chromatograms (Nitsch and Nitsch 1960). The strips were equilibrated above the solvent for 15 hours. Glass rods inserted through rubber stoppers held the chromatograms in place and allowed them to be lowered into the solvent following equilibration. Equilibration and development of the chromatograms were done in the dark at room temperature. After the solvent front had ascended 20 cm, the strips were air-dried for one hour and cut into ten 2-cm sections.

The chromatogram sections were biologically assayed using the sensitized oat coleoptile test (Nitsch and Nitsch 1956). Brighton oats were soaked for two hours and then rinsed repeatedly with distilled

water. The seeds were germinated on Whatman No. 3 MM filter paper discs supported by a Syracuse watchglass in a covered crystallizing dish. The seeds were placed around the circumference of the paper with the embryos pointing out and up, and were germinated at 75° F. and 100% RH. Each day, prior to the removal of the coleoptiles, the seeds were subjected to one hour of red light to inhibit elongation of the first internode. After 72 hours, coleoptiles between 20 and 30 mm were selected. Sections 4.5 mm in length were removed 3.0 mm behind the tip with a hand coleoptile cutter. The coleoptile sections, with the primary leaf remaining inside, were presoaked in a manganese sulfate solution (1 mg/l. of $MnSO_4 \cdot H_2O$) for three hours. After presoaking, the coleoptile sections were transferred to 60-mm petri dishes containing a chromatogram section in 2 ml of a 2% sucrose solution buffered at pH 5.0 (K_2HPO_4 1.794 gm/l. + citric acid monohydrate 1.019 gm/l.). Prior to this the petri dishes containing the sucrose solution and chromatogram section were placed on a horizontal shaker for 30 minutes to elute the growth regulators. Five coleoptile sections were used for each chromatogram section. Chromatograms were run in duplicates, each with 1 λ aliquots. Blank chromatogram sections were used as a control and segments of chromatograms containing 50 γ/l. of indoleacetic acid were used for growth comparisons. The sections were incubated in the dark at 75° F. and 100% RH for 20 hours. Growth was then measured to 0.1 mm with an ocular micrometer.

An analysis of variance was conducted on the elongation of the control coleoptiles run each day. A non-significant F test indicated a homogeneous population. Therefore, growth of the individual treatment coleoptiles was expressed as the difference from the grand mean of the controls. There were two different grand means used; one for the initial analysis of the stock plant treatments, and one for the second analysis made after the cuttings were in the propagation bench for one week. Statistical analysis of the difference employed the analysis of variance of a factorial design. Dunnett's procedure (Steel and Torrie 1960, pp. 111-112) of comparing all means with a control was utilized for comparing elongation of the controls with that of the treatment (Rf) means. Confidence limits were placed on the average coleoptile elongation at each Rf value by the formula:

$$CL = (\bar{x}_i - \bar{x}_o) \pm t_{.05}\ (\text{Dunnett's})\ s\sqrt{2/r.}$$

and entered on the graphs illustrating the results.

RESULTS

Effect of Photoperiod on Growth Characteristics

Stock Plants

A striking difference between stock plants maintained under long and short days was the extent of internode elongation. Plants receiving an excess of 12 hours of light displayed normal leaf development and internode elongation. Those receiving 12 hours of light or less continued to produce new leaves, but without any pronounced internode elongation which resulted in rosetting. Comparison of representative plants maintained under the various photoperiods is shown in Figure 4. Photographs were taken at the end of eleven weeks of photoperiodic treatment.

Lateral branching was somewhat enhanced under long days and suppressed under short days.

A slight interveinal chlorosis was noted in those plants maintained under long days. Plants grown under short days remained dark green.

Visible flower buds were not initiated under long days by the end of eleven weeks.

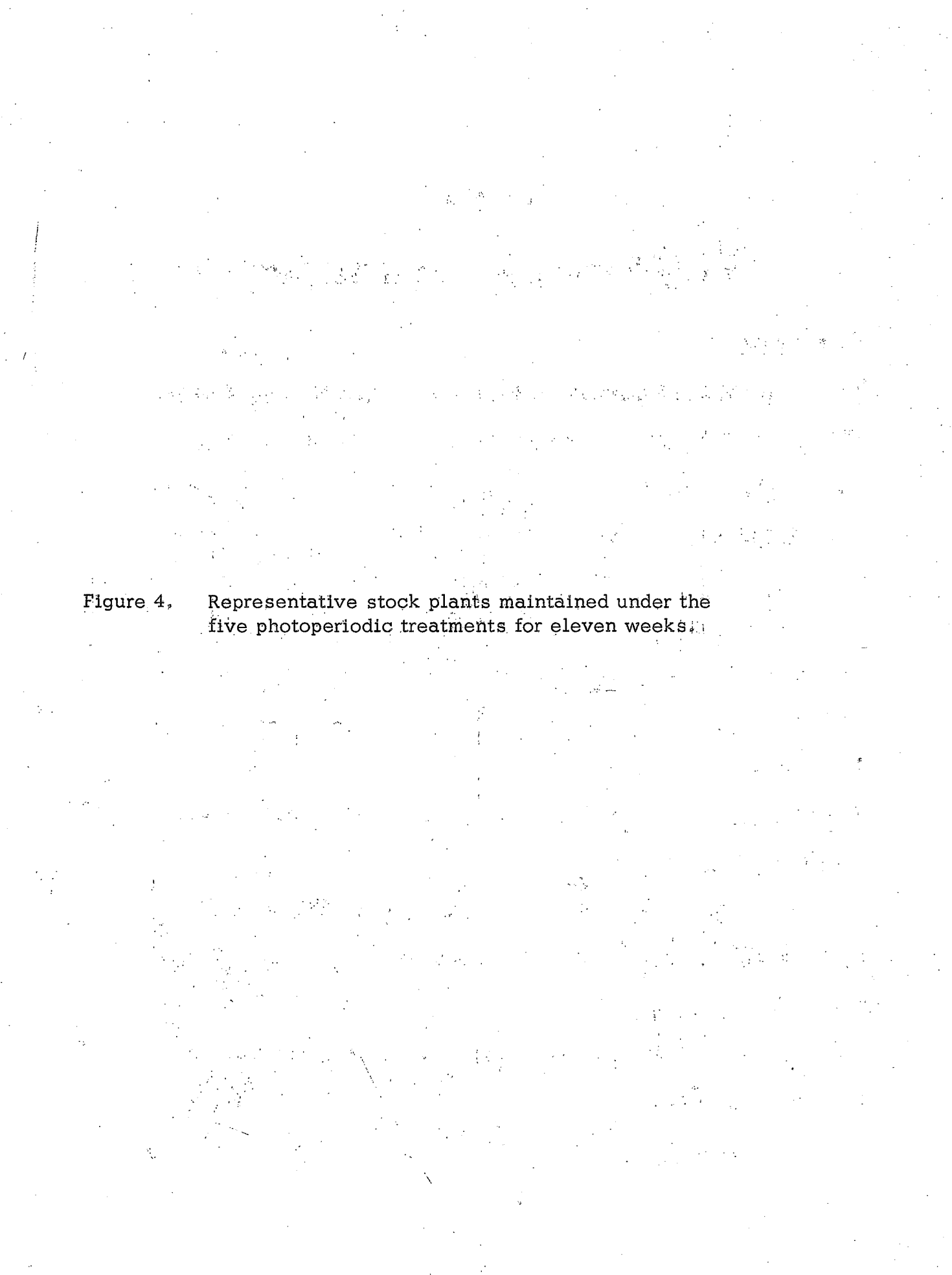


Figure 4. Representative stock plants maintained under the five photoperiodic treatments for eleven weeks.

Cuttings

Differences in internode elongation of the cuttings were also evident during the propagation period. Characteristic rosetting of growth occurred in cuttings placed under short photoperiods. Cuttings from short-day plants under long-day rooting photoperiods resumed normal internode elongation. Areas of old growth were unaffected and regions of rosetting were followed by regions of elongation.

Some cuttings, apparently from the same stock plant, bore visible flower buds after one week in the propagating bench.

Effect of Photoperiod on Rooting of Cuttings

Percent of Rooting

As shown in Table 2, the analysis of variance of rooting percentages, photoperiod had a significant effect on the number of cuttings that rooted. Significant differences in rooting percentages were attributable to the photoperiod that stock plants were grown under prior to removal of cuttings. Cuttings from stock plants maintained under short days (9 and 12 hours) had a significantly higher percentage of rooting than cuttings taken from long-day stock plants (9i, 18 and 24 hours). Thirty-seven percent of the cuttings taken from 18-hour stock plants rooted; 53% of the cuttings from 12-hour stock plants rooted, with the means of other photoperiods intermediate. Separation

TABLE 1.--Percent rooting of Abelia grandiflora 'Prostrata' cuttings as affected by photoperiod.[a]

Rooting Photoperiod (hours)	Stock Plant Photoperiod (hours)				
	9	12	9i	18	24
9	51.67[b]	47.67	41.67	37.00	46.67
12	47.33	54.67	37.00	32.00	34.00
9i	39.67	58.33	35.33	36.33	44.67
18	45.33	51.00	58.33	45.67	45.67
24	53.33	53.00	40.33	34.00	41.67

[a]Each value is the mean of three replications.

[b]Standard error of a treatment mean ($s_{\bar{x}}$) = 6.87%.

TABLE 2.--Analysis of variance of rooting percentage of Abelia grandiflora 'Prostrata' cuttings.

Source	d.f.	SS	MS	F
Replications	2	3,892.5	1,946.3	
Stock plant photoperiod	4	2,158.6	539.7	3.81**
Rooting photoperiod	4	557.9	139.5	0.98
S x R	16	1,642.2	102.6	0.72
Error	48	6,799.5	141.7	
TOTAL	74	15,050.7		

**Indicates significance at 1% level.

of stock plant photoperiod means by Duncan's multiple range test is given in Table 3. Each mean is an average of fifteen values; the five photoperiods to which the cuttings were subjected during rooting, each of which was replicated three times. Separation of the over-all stock plant treatment means into each of the five rooting photoperiod components is presented graphically in Figure 5.

Alteration of photoperiod during propagation had no significant effect on rooting percentages. Although the 18-hour photoperiod during rooting was slightly more favorable than others, there were no significant differences among the treatments. Treatments means are ranked in Table 3; no trends favoring long or short photoperiods exist.

Rooting Quality

The analysis of variance of rooting quality, Table 5, indicated that the density of the root system produced was also significantly affected by photoperiod treatments received by stock plants. Stock plant photoperiods separated the cuttings into two significantly distinct classes: short-day and long-day treatments (Table 6). Short-day treatments (9 and 12 hours) produced cuttings with the highest quality of rooting. Cuttings from these two treatments received a mean quality rating of 3.4, which was between medium and heavily rooted. Cuttings from stock plants subjected to long days (9i, 18 and 24 hours) had a mean of 2.9, which was the lightly rooted class.

TABLE 3.--Separation of rooting percentage means by Duncan's multiple range test.

	Stock Plant Photoperiods (hours)				
	18	9i	24	9	12
Mean value[a]	37.00[b]	42.53	42.53	47.47	52.93
Significance at 5%[c]	_____	_____		_____	
		_____			
Significance at 1%	_____				
		_____			

	Rooting Photoperiods (hours)				
	12	9i	24	9	18
Mean value[a]	41.00	42.87	44.47	44.93	49.20
Significance at 5%	_____				_____

[a]Mean of 15 observations.

[b]Standard error of either a stock plant or rooting photoperiod mean ($s_{\bar{x}}$) = 3.07%.

[c]Means underscored with the same line are not significantly different at the probability level indicated.

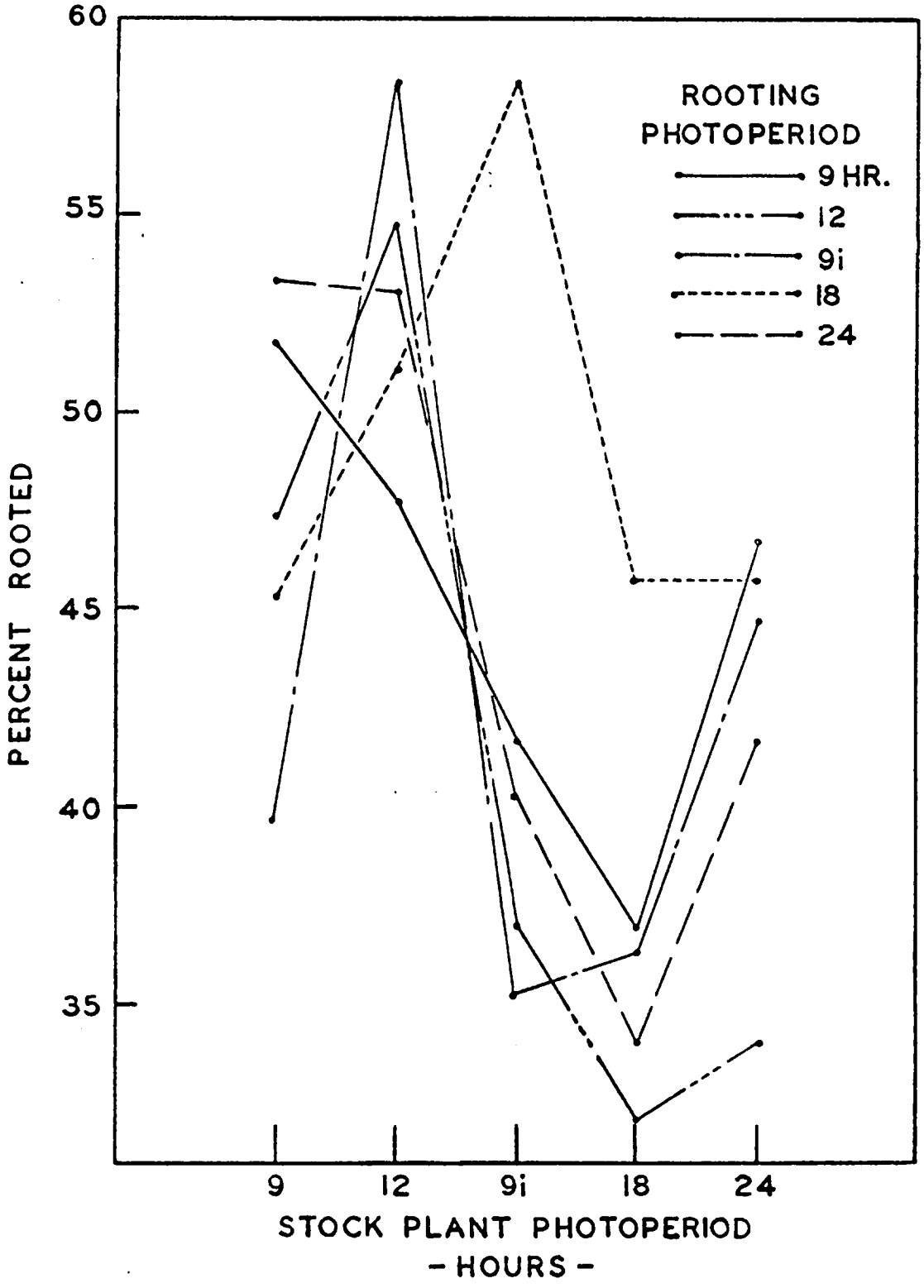


Figure 5. Percent rooting of Abelia grandiflora 'Prostrata' cuttings as affected by photoperiod.

TABLE 4. --Evaluation of rooting quality of Abelia grandiflora 'Prostrata' cuttings as affected by photoperiod.[a]

Rooting Photoperiod (hours)	Stock Plant Photoperiod (hours)				
	9	12	9i	18	24
9	3.46[b]	3.66	2.92	2.90	2.90
12	3.48	3.50	2.94	2.76	2.81
9i	3.37	3.31	2.69	2.82	2.89
18	3.36	3.15	3.16	3.03	2.83
24	2.94	3.26	3.10	3.03	2.91

[a]Each value represents the mean of three replications.

[b]Standard error of a treatment mean ($s_{\bar{x}}$) = 0.18.

TABLE 5.--Analysis of variance of rooting quality of Abelia grandiflora 'Prostrata' cuttings.

Source	d.f.	SS	MS	F
Replications	2	1.4231	0.7116	
Stock plant photoperiod	4	3.5018	0.8755	9.55**
Rooting photoperiod	4	0.2001	0.0500	0.51
S x R	16	1.4671	0.0917	0.94
Error	48	4.6672		
TOTAL	74	11.2593		

**Indicates significance at 1% level.

TABLE 6. --Separation of rooting quality means by Duncan's multiple range test.

	Stock Plant Photoperiods (hours)				
	24	18	9i	9	12
Mean value[a]	2.86[b]	2.91	2.96	3.32	3.38
Significance at 5%[c]	_____				
				_____	
Significance at 1%	_____				
				_____	

	Rooting Photoperiods (hours)				
	9i	24	12	18	9
Mean value[a]	3.02	3.05	3.10	3.11	3.17
Significance at 5%	_____				

[a]Mean of fifteen observations.

[b]Standard error of either a stock plant or rooting photoperiod mean ($s_{\bar{x}}$) = 0.08.

[c]Means underscored with the same line are not significantly different at the probability level indicated.

Rooting quality of cuttings from stock plant treatments under each of the five subsequent propagation photoperiods is presented graphically in Figure 6. Photographs of representative cuttings from each of the 25 individual treatments are shown in Figures 7 to 11.

The photoperiods during the propagation period had no significant effect on rooting quality. Although interactions between stock plant photoperiods and propagation photoperiods were non-significant, it appeared that cuttings from short-day stock plants did best under short-day rooting photoperiods. Conversely, cuttings from long-day stock plants rooted best under long-day rooting photoperiods (see Figure 6).

Effect of Photoperiod on Chemical Constituents

Reducing Sugar Content

Reducing sugar content of the stock plants was not significantly influenced by photoperiodic treatments (Table 10). Reducing sugar levels under the different daylengths ranged from 2.07% to 2.31% with a standard error of a difference between treatment means ($s_{\bar{d}}$) of 0.21%. Thus, initially all cuttings had essentially the same reducing sugar content.

After one week in the propagation bench, there was a general decline in reducing sugars, although in some treatments the levels of sugars increased. Significant differences in sugar levels at this time were due to photoperiodic treatments received during propagation, not

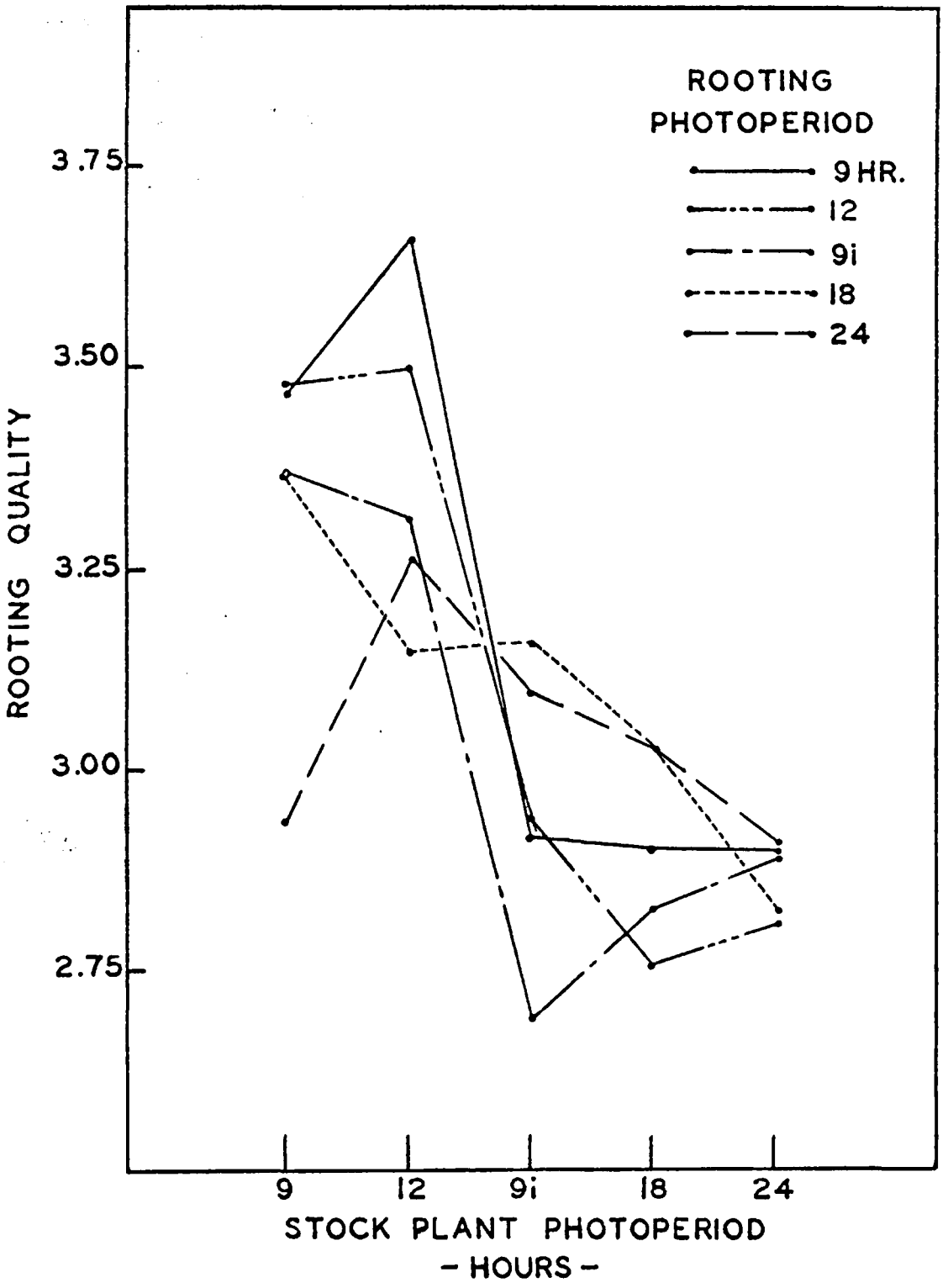
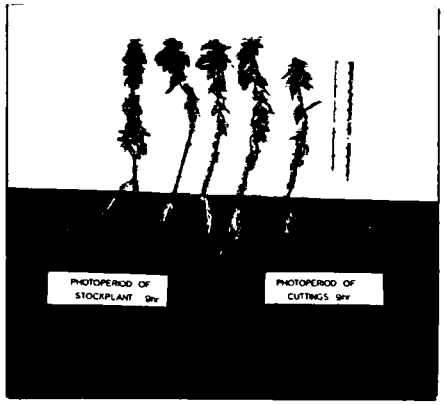


Figure 6. Rooting quality of Abelia grandiflora 'Prostrata' as affected by photoperiod.

Figure 7. Representative cuttings from the five stock plant photoperiods rooted under a nine hour photoperiod.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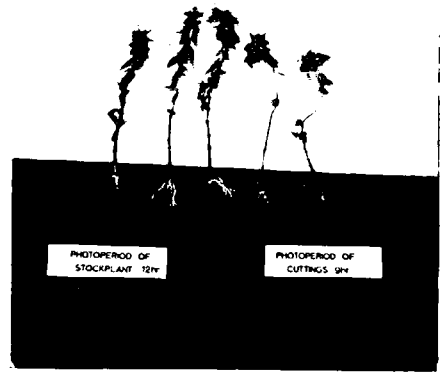
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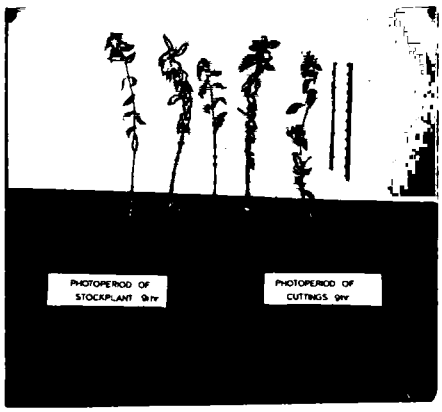
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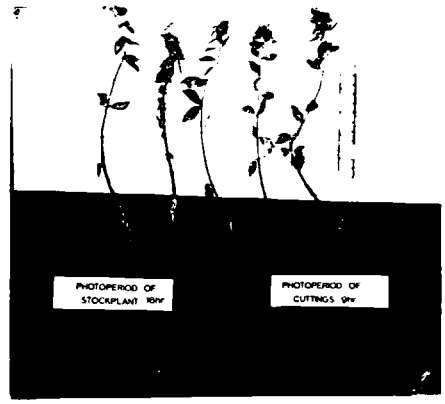
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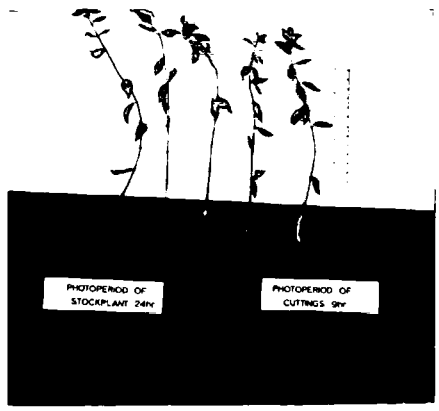
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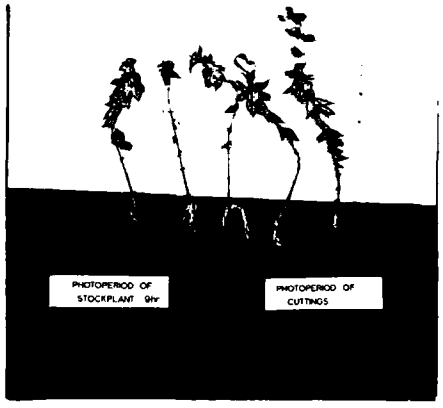
Figure 8. Representative cuttings from the five stock plant photoperiods rooted under a 12-hour photoperiod.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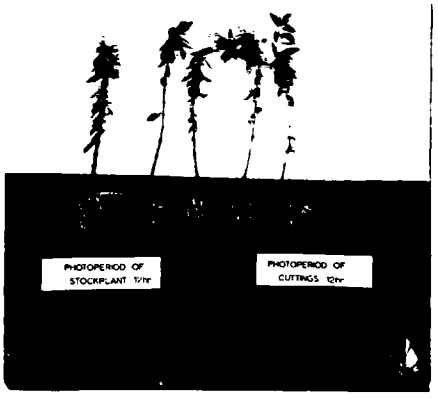
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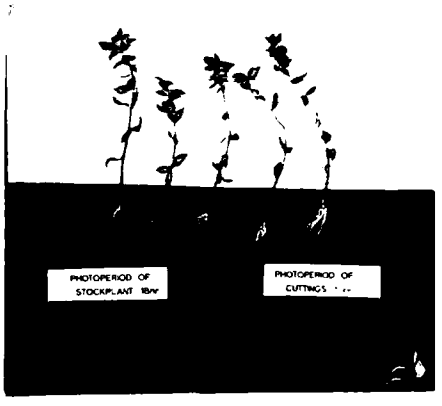
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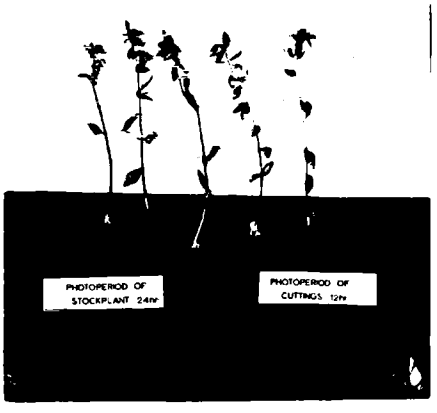
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Figure 9. Representative cuttings from the five stock plant photoperiods rooted under a 9i-hour photoperiod.


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PHOTOPERIOD OF STOCKPLANT 12hr
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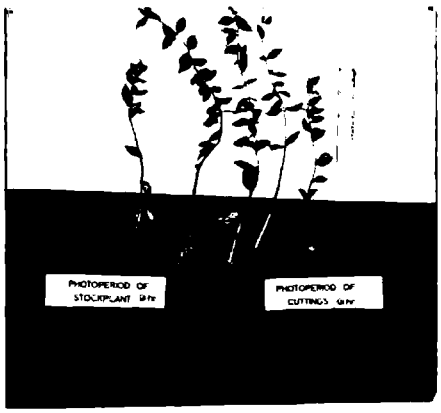
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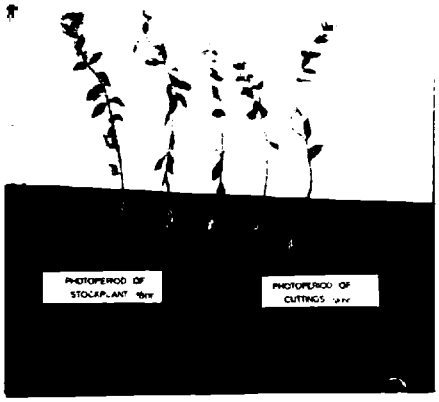
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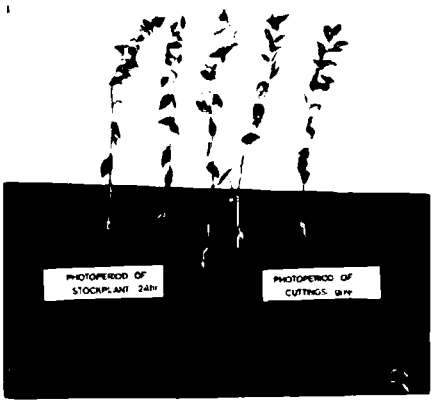
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Figure 10. Representative cuttings from the five stock plant photoperiods rooted under an 18-hour photoperiod.


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PHOTOPERIOD OF STOCKPLANT 12hr
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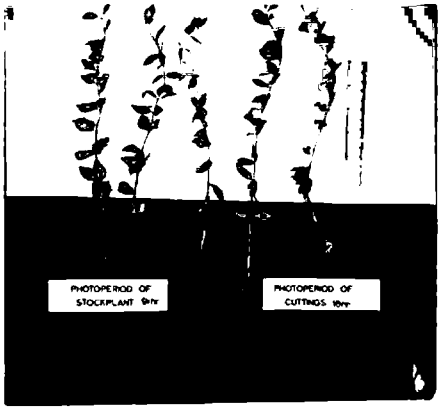
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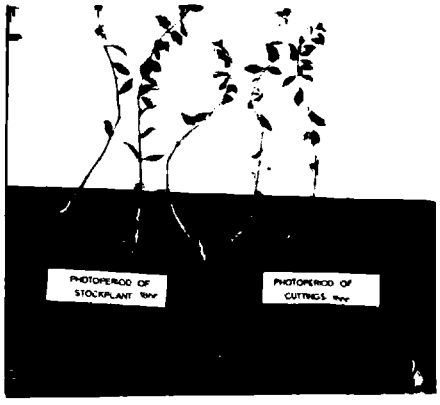
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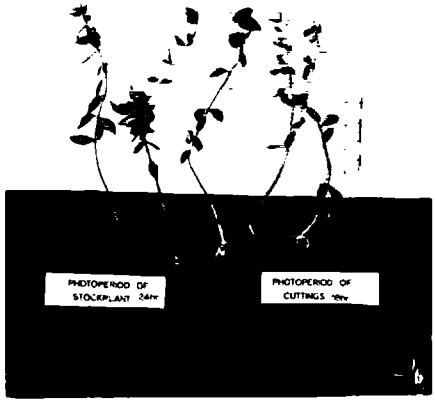
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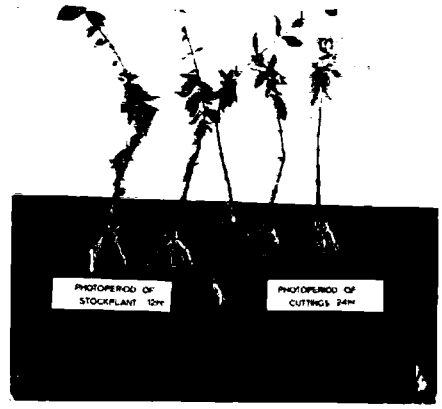
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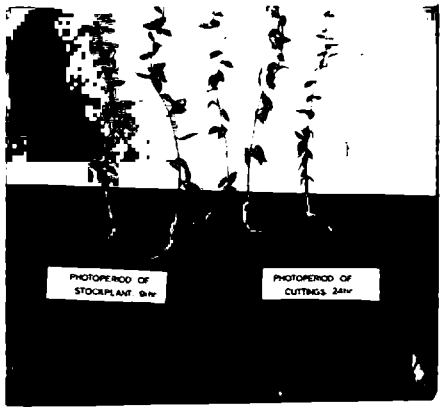
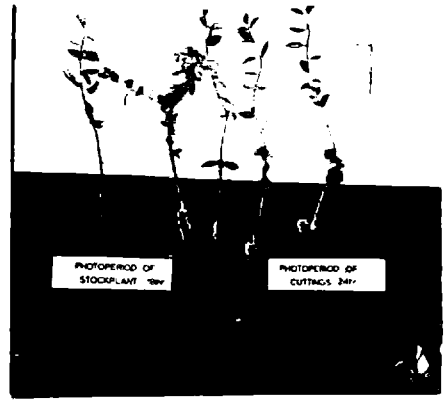

PHOTOPERIOD OF STOCKPLANT 9hr
PHOTOPERIOD OF CUTTINGS 24hr


PHOTOPERIOD OF STOCKPLANT 12hr
PHOTOPERIOD OF CUTTINGS 24hr

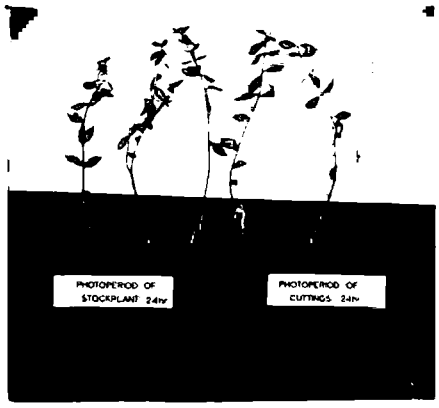

PHOTOPERIOD OF STOCKPLANT 24hr
PHOTOPERIOD OF CUTTINGS 24hr

TABLE 7.--Percent reducing sugar content of Abelia grandiflora 'Prostrata' stock plants as affected by photoperiod.[a]

	Stock Plant Photoperiod (hours)				
	9	12	9i	18	24
% Reducing Sugars	2.07[b]	2.17	2.10	2.17	2.31

[a]Each value is the mean of three replications.

[b]Standard error of a treatment mean ($s_{\bar{x}}$) = 0.15%.

TABLE 8.--Percent reducing sugar content of Abelia grandiflora 'Prostrata' cuttings after one week in the propagation bench.[a]

Rooting Photoperiod (hours)	Stock Plant Photoperiod (hours)				
	9	12	9i	18	24
9	2.61[b]	2.16	1.86	2.69	2.52
12	2.18	2.06	1.86	1.76	1.95
9i	2.62	2.21	1.77	1.67	1.95
18	1.97	1.74	1.20	1.50	1.54
24	1.28	1.84	1.67	1.88	1.77

[a]Each value is the mean of three replications.

[b]Standard error of a treatment mean ($s_{\bar{x}}$) = 0.25%.

TABLE 9. --Percent reducing sugar content of Abelia grandiflora 'Prostrata' cuttings after eleven weeks in the propagation bench.[a]

Rooting Photoperiod (hours)	Stock Plant Photoperiod (hours)				
	9	12	9i	18	24
9	0.60[b]	0.66	1.02	0.99	0.91
12	0.91	0.79	1.05	0.81	0.88
9i	0.75	0.85	0.96	0.88	0.90
18	0.92	1.04	1.03	0.95	1.02
24	0.93	0.89	1.06	0.94	1.13

[a]Each value is the mean of three replications.

[b]Standard error of a treatment mean ($s_{\bar{x}}$) = 0.10%.

TABLE 10.--Analysis of variance of reducing sugar content of Abelia grandiflora 'Prostrata' stock plants.

Source	d.f.	SS	MS	F
Replications	2	0.3480	0.174	
Photoperiod	4	0.1025	0.026	0.40
Error	8	0.5190	0.065	
TOTAL	14	0.9695		

TABLE 11.--Separation of percent reducing sugar means of five photoperiodic treatments of Abelia grandiflora 'Prostrata' stock plants.

	Stock Plant Photoperiods (hours)				
	9	9i	12	18	24
Mean value[a]	2.07	2.10	2.17	2.17	2.31
Significance at 5%[b]	_____				

[a]Mean of three observations.

[b]Means underscored with the same line are not significantly different at the probability level indicated.

previous stock plant treatments. Reducing sugar content ranged from 1.59% to 2.37%. Cuttings from the two longest photoperiods, 18 and 24 hours, had the lowest content, while cuttings receiving 12 or less hours of light had the highest levels. Cuttings receiving 12 continuous hours of light had essentially the same sugar content as those receiving 12 hours of light in two portions (9i photoperiod). Analysis of variance and separation of means is presented in Tables 12 and 13.

When cuttings were removed from the propagating bench at the end of eleven weeks, reducing sugar levels were again assayed. Trends were essentially opposite of those established at the previous sampling date. Two basic differences were evident. Photoperiodic treatments received by stock plants had a significant effect on reducing sugar levels, with no significant effects due to the photoperiod during rooting. Secondly, the order of magnitude of the reducing sugar levels was an inverse of the second sampling. That is treatments which produced highest sugar levels previously were lowest at this sampling date. This was true whether rooting or stock plant photoperiods were considered.

Total Nitrogen Content

Photoperiodic treatment of stock plants did not significantly alter nitrogen content based on percent of dry weight (Table 19). Total nitrogen content ranged from 1.46% to 1.62% with higher values from long-day treatments and lower values from short-day treatments.

TABLE 12.--Analysis of variance of percent reducing sugar content of Abelia grandiflora 'Prostrata cuttings after one week in the propagation bench.

Source	d.f.	SS	MS	F
Replications	2	0.5783	0.2892	
Stock plant photoperiod	4	1.6971	0.4243	2.11
Rooting photoperiod	4	5.6687	1.4172	7.05**
S x R	16	3.4827	0.2177	1.08
Error	48	9.6551	0.2011	
TOTAL	74	21.0819		

**Indicates significance at 1% level.

TABLE 13.--Separation of percent reducing sugars of Abelia grandiflora 'Prostrata' cuttings as influenced by photoperiod. After one week in the propagation bench.

	Stock Plant Photoperiods (hours)				
	9i	18	24	12	9
Mean value[a]	1.67[b]	1.90	1.95	2.00	2.13
Significance at 5%[c]	_____				
		_____			
Significance at 1%	_____				

	Rooting Photoperiods (hours)				
	18	24	12	9i	9
Mean value[a]	1.59[b]	1.69	1.96	2.04	2.37
Significance at 5%	_____				
		_____			
			_____		
					____
Significance at 1%	_____				
		_____			

[a]Mean of 15 observations.

[b]Standard error of either a stock plant or rooting photoperiod mean ($s_{\bar{x}}$) = 0.12%.

[c]Means underscored with the same line are not significantly different at the probability level indicated.

TABLE 14.--Analysis of variance of reducing sugar content of Abelia grandiflora 'Prostrata' cuttings after eleven weeks in the propagation bench.

Source	d.f.	SS	MS	F
Replications	2	1.4926	0.7463	
Stock plant photoperiod	4	0.4215	0.1054	3.48*
Rooting photoperiod	4	0.3072	0.0240	2.53
S x R	16	0.3840	0.0303	0.79
Error	48	1.4552		
TOTAL	74	4.0605		

*Indicates significance at 5% level.

TABLE 15. --Separation of percent reducing sugar means of Abelia grandiflora 'Prostrata' cuttings as influenced by photoperiod. After eleven weeks in the propagation bench.

	Stock Plant Photoperiods (hours)				
	9	12	18	24	9i
Mean value[a]	0.82[b]	0.85	0.92	0.97	1.02
Significance at 5% level[c]	_____	_____	_____	_____	
		_____	_____	_____	
			_____	_____	
Significance at 1% level	_____	_____			
		_____	_____		

	Rooting Photoperiods (hours)				
	9	9i	12	18	24
Mean value[a]	0.84	0.87	0.89	0.99	0.99
Significance at 5% level	_____	_____	_____	_____	

[a]Mean of 15 observations.

[b]Standard error of either a stock plant or rooting photoperiod mean ($s_{\bar{x}}$) = 0.05%.

[c]Means underlined with the same line are not significantly different at the probability level indicated.

TABLE 16.--Total nitrogen content of Abelia grandiflora 'Prostrata' stock plants as influenced by photoperiod. In percent of dry weight.[a]

	Stock Plant Photoperiod (hours)				
	9	12	9i	18	24
% Total Nitrogen	1.48[b]	1.46	1.62	1.59	1.51

[a]Each value is the mean of three replications.

[b]Standard error of a treatment mean ($s_{\bar{x}}$) = 0.06%.

TABLE 17.--Total nitrogen content of Abelia grandiflora 'Prostrata' cuttings after one week in the propagation bench. In percent of dry weight.[a]

Rooting Photoperiod (hours)	Stock Plant Photoperiod (hours)				
	9	12	9i	18	24
9	1.59[b]	1.56	1.57	1.57	1.51
12	1.74	1.59	1.75	1.61	1.64
9i	1.60	1.56	1.62	1.58	1.53
18	1.63	1.50	1.74	1.47	1.55
24	1.59	1.52	1.71	1.52	1.55

[a]Each value is the mean of three replications.

[b]Standard error of a treatment mean ($s_{\bar{x}}$) = 0.07%.

TABLE 18.--Total nitrogen content of Abelia grandiflora 'Prostrata' cuttings after eleven weeks in the propagation bench. In percent of dry weight.[a]

Rooting Photoperiod (hours)	Stock Plant Photoperiod (hours)				
	9	12	9i	18	24
9	1.62[b]	1.34	1.31	1.21	1.25
12	1.45	1.43	1.31	1.30	1.21
9i	1.41	1.33	1.17	1.26	1.25
18	1.39	1.29	1.20	1.17	1.11
24	1.29	1.28	1.13	1.12	1.14

[a]Each value is the mean of three replications.

[b]Standard error of a treatment mean ($s_{\bar{x}}$) = 0.04%.

TABLE 19.--Analysis of variance of nitrogen content of Abelia grandiflora 'Prostrata' stock plants as influenced by photoperiod.

Source	d.f.	SS	MS	F
Replications	2	0.0385	0.0193	
Photoperiod	4	0.0618	0.0155	1.61
Error	8	0.0768	0.0096	
TOTAL	14	0.1771		

TABLE 20.--Separation of percent total nitrogen content of Abelia grandiflora 'Prostrata' stock plants as influenced by photoperiod.

	Stock Plant Photoperiods (hours)				
	12	9	24	18	9i
Mean value[a]	1.26	1.48	1.51	1.59	1.62
Significance at 5% level[c]					

[a]Mean of three replications.

[b]Means underscored with the same line are not significantly different at the probability level indicated.

After one week in the propagation bench, there was a general accumulation of nitrogen in the cuttings over levels present when cuttings were first taken. This was true except for cuttings from 18-hour stock plants. Although there were significant differences due to stock plant photoperiods (Table 21), the results could not be generalized solely to long or short days. Results ranged from 1.55% under 12- and 18-hour treatments to 1.68% under the 9i-hour treatment. At this time, photoperiods that cuttings were subjected to during rooting had no significant effect on the nitrogen content of the cuttings (Table 21).

With the exception of the 9-hour stock plant photoperiod - 9-hour rooting photoperiod treatment, nitrogen levels at the end of 11 weeks decreased below initial levels. Photoperiod treatments applied to both stock plants and cuttings were responsible for highly significant differences between treatments (Table 23). As either series of treatments increased in daylength there was corresponding decrease in amount of total nitrogen.

Preliminary Studies on Growth Regulator Analysis

In establishing a calibration curve for elongation of coleoptiles at various concentrations of indoleacetic acid, it was noted that the response was not linear. After reaching a maximum point of 50 γ IAA/l., elongation was not strictly linear but peaked and declined erratically. To determine the optimum concentration of extract to use, aliquots of

TABLE 21.--Analysis of variance of nitrogen content of Abelia grandiflora 'Prostrata' cuttings as influenced by photoperiod. After one week in the propagation bench.

Source	d.f.	SS	MS	F
Replications	2	0.2493	0.1247	
Stock plant photoperiod	4	0.2054	0.0514	3.52*
Rooting photoperiod	4	0.1061	0.0265	1.82
S x R	16	0.1017	0.0064	0.44
Error	48	0.7016	0.0146	
TOTAL	74	1.3641		

*Indicates significance at the 5% level.

TABLE 22.--Separation of percent total nitrogen content of Abelia grandiflora 'Prostrata' cuttings as influenced by photoperiod. After one week in the propagation bench.

	Stock plant photoperiods (hours)				
	12	18	24	9	9i
Mean values[a]	1.55[b]	1.55	1.56	1.63	1.68
Significance at 5% level[c]	_____			_____	

	Rooting photoperiods (hours)				
	9	9i	18	24	12
Mean values[a]	1.56	1.58	1.58	1.58	1.67
Significance at 5% level	_____				____

[a]Mean of 15 observations.

[b]Standard error of either a stock plant or rooting photoperiod mean ($s_{\bar{x}}$) = 0.03%.

[c]Means underscored with the same line are not significantly different at the probability level indicated.

TABLE 23.--Analysis of variance of nitrogen content of Abelia grandiflora 'Prostrata' cuttings as influenced by photoperiod. After eleven weeks in the propagation bench.

Source	d.f.	SS	MS	F
Replications	2	0.3533	0.1767	
Stock plant photoperiod	4	0.6294	0.1574	26.67**
Rooting photoperiod	4	0.2628	0.0657	11.14**
S x R	16	0.1380	0.0086	1.46
Error	48	0.2812	0.0059	
TOTAL	74	1.6647		

**Indicates significance at the 1% level.

TABLE 24. --Separation of percent total nitrogen of Abelia grandiflora 'Prostrata' cuttings as influenced by photoperiod. After eleven weeks in the propagation bench.

	Stock Plant Photoperiods (hours)				
	24	18	9i	12	9
Mean values[a]	1.19[b]	1.21	1.22	1.33	1.43
Significance at 1% level[c]	_____	_____	_____	____	____

	Rooting Photoperiods (hours)				
	24	18	9i	12	9
Mean values[a]	1.19	1.23	1.28	1.34	1.34
Significance at 1% level	_____	_____	_____	_____	_____

[a]Mean of 15 observations.

[b]Standard error of either a stock plant or rooting photoperiod mean ($s_{\bar{x}}$) = 0.02%.

[c]Means underscored by the same line are not significantly different at the probability level indicated.

varying concentrations were chromatographed. Results indicate that 1 λ aliquots gave optimal growth responses.

Subsequently, the first replication of stock plant treatments was run at two concentrations: 1 λ and 5 λ. The 1 λ aliquots repeatedly gave the best results and were used throughout the remainder of the study.

It was also desirable to check the Rf of endogenous indoleacetic acid to determine if it had the same Rf as commercially prepared indoleacetic acid. To locate the compounds the chromatograms were sprayed with p-dimethylaminobenzaldehyde (0.5 gms/100 ml 95% ethanol + 1 ml conc. HCl). The minute quantities of indolic compounds present in the extract failed to react with the location reagent. Commercially prepared indoleacetic acid was then added to the extract and the resultant mixture was chromatographed. In the presence of the extract, the Rf of indoleacetic acid was consistently slightly lower than that of pure indoleacetic acid. The Rf of pure IAA was .375; in the presence of the extract it was .360. However, it still remained in the section of the chromatogram from Rf 0.3 to 0.4. With each set of chromatograms run during the study, a control with IAA was also chromatographed to check the Rf of IAA. The spot was never out of the 0.3 to 0.4 section.

Growth Regulator Content

Histograms of the results of bioassays of extracts from stock plants are illustrated in Figure 14. Each value is the average elongation

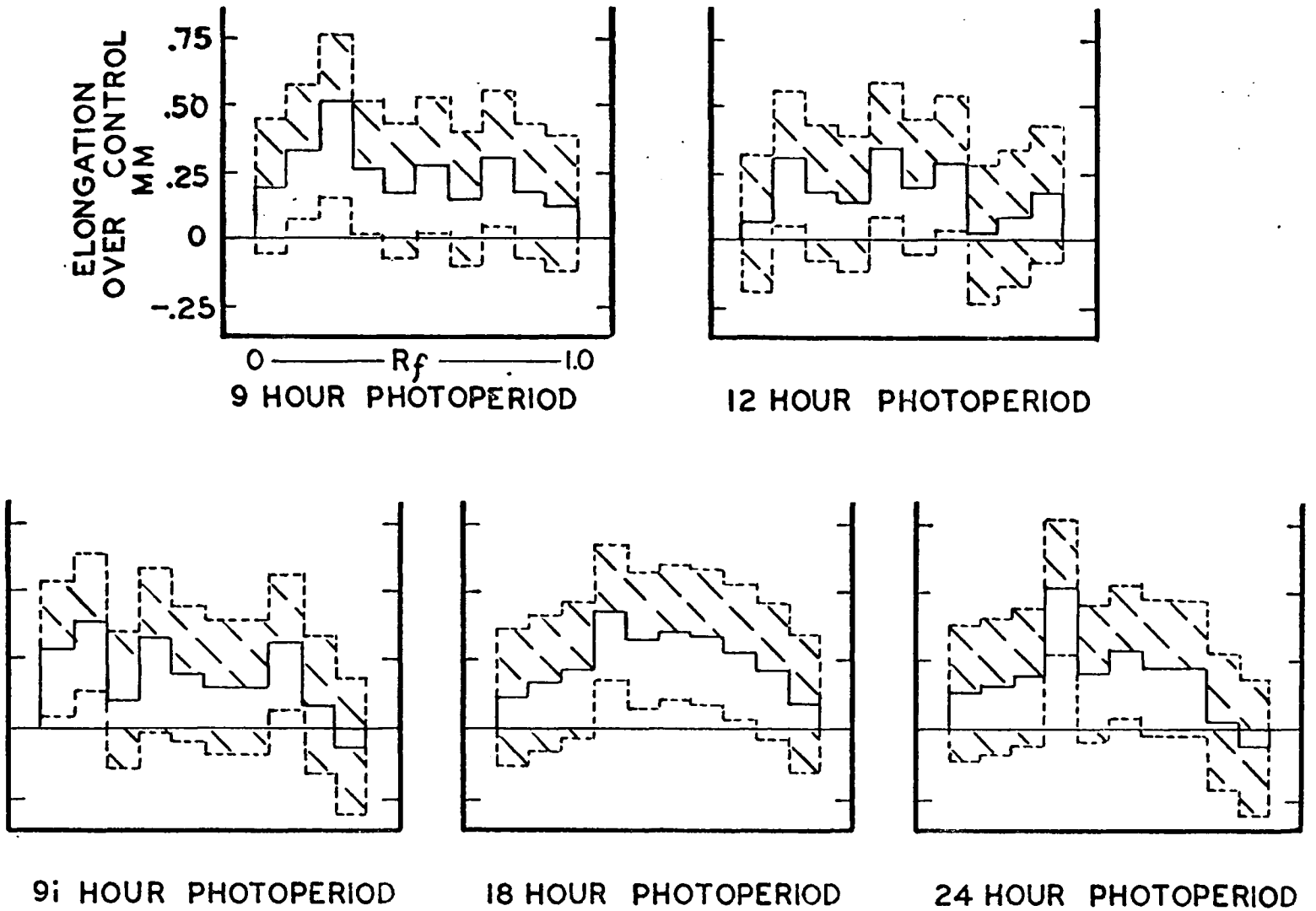


Figure 12. Distribution of growth regulators in extracts of stock plants from five different photoperiods.

of 30 coleoptiles for individual Rf regions. Solid lines are observed values; dashed lines represent 95% confidence bands on these values as established by Dunnett's procedure. The Rf of indoleacetic acid is between 0.3 and 0.4. Under long-day treatments, this region of the chromatograms promoted coleoptile elongation that was very highly significantly different from that of the control. Under 9-hour days, elongation is just slightly above that of the control, while under 12-hour photoperiods elongation was not significantly different from the control.

At the other Rf values areas of significant elongation over the control can not be classified as either long or short-day responses in general. Chromatograms of extracts from 9- and 18-hour photoperiods had five regions of significant elongation, 12- and 9i-hour photoperiods had three, and the 24-hour photoperiod had two.

There were no regions of growth inhibition that were significantly different from the control.

Histograms in Figure 15 show that at the end of one week in the propagation bench there was a general decline in the magnitude and number of regions showing significant growth promotion. The most universal response was the decline at the Rf of IAA, where none of the four treatments exhibited a significant increase in growth. Only Rf areas between 0 and 0.3 of the short-day stock plant-short-day rooting

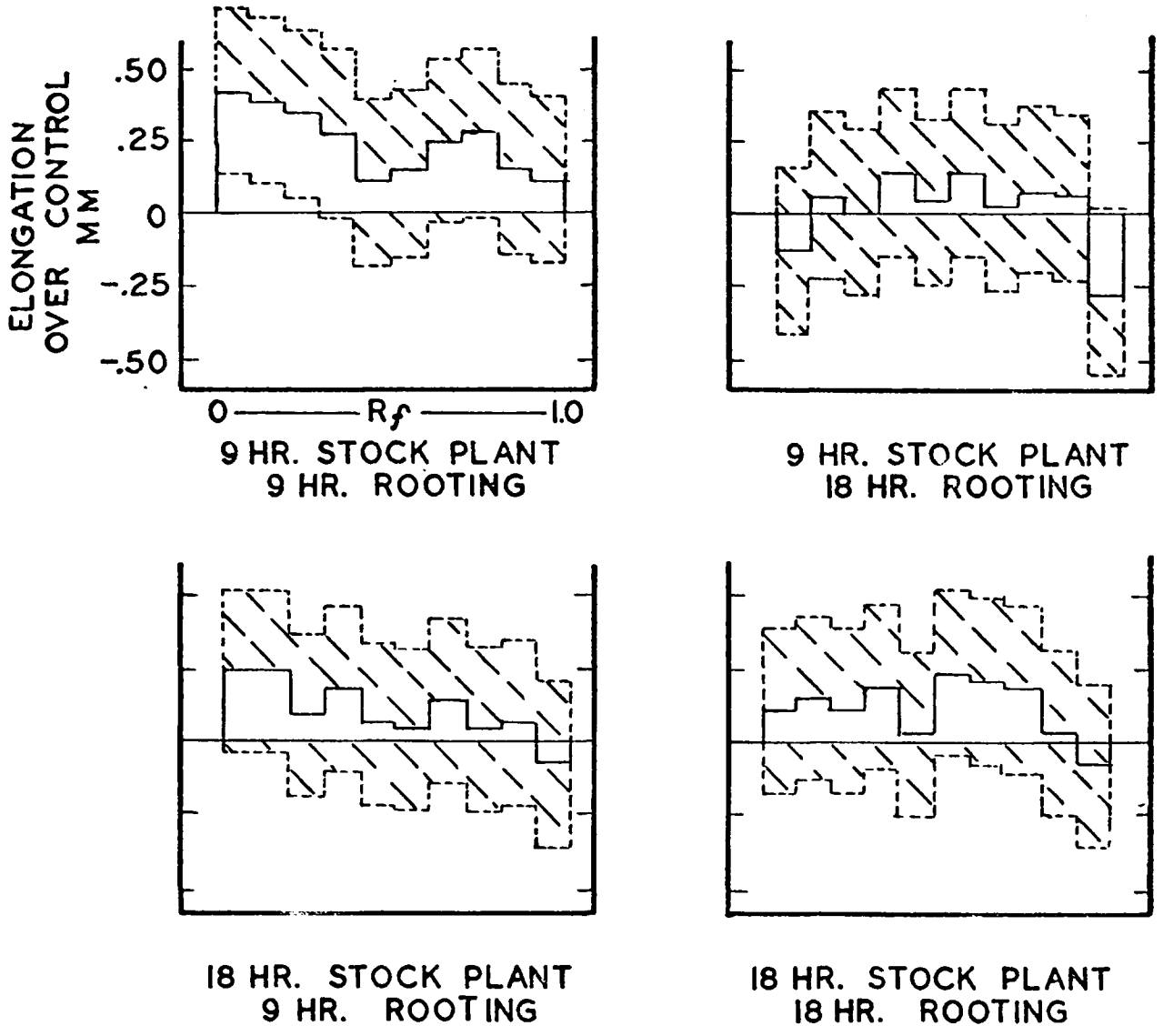


Figure 13. Distribution of growth regulators under four different combinations of 9 and 18 hour stock plant and rooting photoperiods.

photoperiod exhibited significant increases in elongation. All other Rf values of other treatments elicited elongation that was not significantly different from the control. The analysis of variance for this sample is presented in Table 26.

TABLE 25.--Analysis of variance of growth regulator content of stock plants of Abelia grandiflora 'Prostrata' as affected by photoperiod.

Source	d.f.	SS	MS	F
Replications	2	387.316	193.658	
Photoperiod	4	135.804	33.951	0.34
Rf	9	922.401	102.489	2.71*
Rf x P	36	1,222.342	33.954	0.71
Rf x R	18	680.777	37.821	0.93
R x P	8	792.043	99.005	0.60
R x P x Rf	72	3,439.530	47.771	1.18
Sample/Photoperiod	15	2,493.970	166.265	12.94**
Rf x Sample/Photoperiod	135	5,475.130	40.557	3.16**
Coleoptiles[a]	1200	15,417.200	12.848	
TOTAL	1499	30,966.514		

*Indicates significance at 5% level.

**Indicates significance at 1% level.

[a]Standard error of elongation of coleoptiles within any one treatment (Rf section) = 0.16 mm.

TABLE 26.--Analysis of variance of growth regulator content of Abelia grandiflora 'Prostrata' cuttings as affected by photoperiod. After one week in the propagation bench.

Source	d.f.	SS	MS	F
Replications	2	770.735	385.368	
Photoperiod	3	763.050	254.350	2.03
Rf	9	723.597	80.400	1.90
Rf x P	27	527.016	19.519	0.58
Rf x R	18	760.948	42.275	1.24
R x P	6	752.325	125.388	2.55
R x P x Rf	54	1,825.859	33.810	0.99
Sample/Photoperiod	12	590.180	49.182	3.11**
Rf x Sample/Photoperiod	108	3,684.020	34.111	2.16**
Coleoptiles[a]	960	15,192.800	15.826	
TOTAL	1199	27,136.400		

**Indicates significance at 1% level.

[a]Standard error of elongation of coleoptiles within any one treatment (Rf section) = 0.18 mm.

DISCUSSION AND CONCLUSIONS

Effect of Photoperiod on Rooting

Results of the experiment indicate that the photoperiod to which stock plants are subjected prior to the removal of cuttings exerts a greater influence on the rooting of Abelia grandiflora 'Prostrata' cuttings than the photoperiod during rooting. The fact that the rooting photoperiod was non-significant was in agreement with Baker and Link (1963), who found similar results. Although the 18-hour rooting photoperiod resulted in increased rooting over the other photoperiods, differences were not significant. Had Waxman (1957) statistically analyzed his results, similar conclusions might have resulted.

Comparison of this study to the two papers mentioned above may be questionable since rooting ability may vary with species and even varieties. A notable example is Hibiscus rosa-sinensis. In view of inter-varietal differences, comparison of Abelia grandiflora 'Prostrata' to Abelia grandiflora may not be valid. However, the percentage of rooting experienced in this study was comparable to results obtained for Abelia grandiflora in the past. Pearse (1948) lists A. grandiflora as having rooted 93% when treated with indolebutyric acid and 33% when untreated. Similarly, Thimann and Behnke-Rogers (1950) have reported rooting of untreated A. grandiflora cuttings to be 30 and 40%. The over-all rooting

percentage for this study was 44%, and indicates that the rooting of A. grandiflora 'Prostrata' is not apparently different from that of A. grandiflora.

Relationship of Chemical Constituents of Stock Plants to Rooting

Although the stock plant photoperiods had a significant effect on rooting, they did not produce significant differences in the levels of reducing sugars or total nitrogen content of the stock plants. Thus the effects induced upon the cuttings while on the stock plant, but manifested during the rooting process were unlikely to be due to quantitative changes in either of these factors.

Auxin levels present a different picture. Stock plant treatments that had the lowest rooting percentage, long-day treatments, contained relatively more indoleacetic acid than short-day treatments that produced the highest percentage of rooting. However, to conclude that high IAA levels decreased rooting would not be consistent with what is known of plant responses to auxins. It is more probable that although IAA levels were higher under long days some other factor(s) was limiting the rooting ability of the cuttings. These results would be in accord with those of Tyce (1957) who could not correlate auxin content to the rooting response.

Levels of indoleacetic acid were associated with and apparently the cause of internode elongation. Plants under short days, which contained little IAA were rosetted; plants under long days with high amounts

of IAA exhibited appreciable internode elongation. It may be concluded that photoperiodic control of internode elongation is operative through alteration of levels of endogenous indoleacetic acid.

Relationship of Chemical Constituents of Cuttings to Rooting

Fluctuations in the amounts of reducing sugars and total nitrogen after one week were not directly associated with the enhancement of rooting. While 9i- and 18-hour treatments exhibited a similar influence on rooting, responses elicited by the two treatments in changes in levels of sugars and nitrogenous compounds were not similar. In both instances, results of the 9i treatments were more similar to those obtained under 9-hour photoperiods than to those under 18-hour treatments.

Conversely at the end of eleven weeks, sugar and nitrogen levels of 9i treatments were similar to those from 18-hour treatments, both of which were significantly different from the 9-hour treatment. From the results it cannot be unequivocally stated whether sugar and nitrogen levels were or were not photoperiodically controlled. Although reducing sugars were significantly lower and total nitrogen content significantly higher under short days, their relationship to rooting is obscure. Rather than attempt to assess their role in the rooting response, it is just as apt that differences were the results of differences in rooting. The decrease in reducing sugars could have been the result of their utilization in regeneration of roots. Loss of nitrogen from the cuttings by leaching

probably contributed to the reduction in nitrogen content. However, unequal differences suggest that leaching was not solely responsible.

Reduction in growth regulator levels at the end of one week may have been the result of mobilization to the basal portion of the cutting. Nevertheless, growth regulator levels at this time contributed no substantial clues as to causes of differences in the rooting response.

Statistical Evaluation of Bioassay

Estimation of the components of variance indicates that true experimental error is not correctly estimated by coleoptile variation within a treatment. These results are in agreement with the evaluation of the wheat coleoptile test by Walker, Hendershott, and Snedecor (1958). Incorrect estimation of experimental error by coleoptile variation within a treatment can be better realized if the results of this bioassay are compared to those obtained by Nitsch and Nitsch (1956). They concluded that the standard deviation from the mean is usually 0.15 to 0.25. In this study the standard deviation was 0.16, which is quite similar. However, the highly significant difference between samples of the same treatment (Sample/Photoperiod, Tables 25 and 26) and variation in the responses of a given Rf region on similar chromatograms run at different times (Rf x Sample/Photoperiod, Tables 25 and 26), indicates the high variation that exists. Variation that cannot be estimated by merely increasing the numbers of coleoptiles within a given treatment, regardless of the

standard deviation of the coleoptiles. Only through true replication (separate samples) can the precise growth regulator status be secured.

SUMMARY

1. Photoperiod was shown to affect rooting of Abelia grandiflora Rehd., 'Prostrata'. Significant differences in rooting were results of alteration of the photoperiod that stock plants were grown under; alteration of the photoperiod during propagation had no significant effect. There was an increased percentage of rooted cuttings from plants grown under short days than from plants grown under long days. A better quality of root system was also formed on cuttings from short-day plants. Photoperiodic nature of the phenomena was confirmed by the fact that an interrupted night treatment elicited the same response as the long-day treatments.

2. Reducing sugars and total nitrogen content of the stock plants were similar under all photoperiods. Significant differences in reducing sugar and nitrogen levels of cuttings during the propagation period. The role of photoperiod in promoting these differences could not be unequivocally determined. Differences in rooting were probably not determined by quantitative differences in reducing sugars or nitrogenous compounds.

3. Growth regulator analyses utilizing the straight growth oat coleoptile test demonstrated a higher indoleacetic acid content of stock plants under long days than under short days. Other regions of growth

promotion were not common to all long-day or all short-day treatments. There was no indication of the presence of growth inhibitors in any of the extracts. Levels of growth regulators in the leaves of the cuttings diminished after one week in the propagation bench. Results may indicate a mobilization of growth regulators from the leaves to the basal end of the stem.

4. Statistical evaluation of the bioassay indicated that coleoptile variation within a treatment was not a true measure of experimental error. High variation between samples and Rf regions of similar chromatograms indicated the need of increased replications in bioassays.

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