THE INFLUENCE OF GIBBERELLIN ON THE VEGETATIVE GROWTH RESPONSES OF CERTAIN WOODY PLANTS SUBJECTED TO VARIOUS PHOTOPERIODS AND THERMOPERIODS, WITH SPECIAL REFERENCE TO CATALPA SPECIOSA

Thesis for the Degree of Ph. D.
MICHIGAN STATE UNIVERSITY
George Randall McVey
1961

This is to certify that the

thesis entitled

THE INFLUENCE OF GIBBERELLIN ON THE VEGETATIVE GROWTH RESPONSES OF CERTAIN WOODY PLANTS SUBJECTED TO VARIOUS PHOTOPERIODS AND THERMOPERIODS, WITH SPECIAL REFERENCE TO CATALPA SPECIOSA

presented by

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has been accepted towards fulfillment
of the requirements for

Ph.D. degree in Horticulture

Major professor

Date

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ABSTRACT

THE INFLUENCE OF GIBBERELLIN ON THE VEGETATIVE GROWTH RESPONSES OF CERTAIN WOODY PLANTS SUBJECTED TO VARIOUS PHOTOPERIODS AND THERMOPERIODS, WITH SPECIAL REFERENCE TO CATALPA SPECIOSA

by GEORGE RANDALL McVEY

Certain woody plants (Catalpa speciosa, Liriodendron Tulipifera, Viburnum Carlesii, Acer saccharum, Pinus sylvestris, Pyracantha coccinea Lalandii, Syringa vulgaris and Euonymus Fortunei vegetus) exhibiting a known photoperiodic response and a broad range of temperature adaptations were selected for this study. The objective was to determine the degree of replacement by gibberellin of the photoperiodically and/or thermoperiodically dependent vegetative responses.

Shoot extension and dry weights of various plant parts, from plants subjected to photoperiods of 9 (short) and 18 (long) hours and night temperatures of 40°F (low) and 70°F (high) in the presence (50 ppm) and absence of gibberellin, were used as a criteria for determining response differences. Radio-phosphorus (P^{32}) was applied to the roots of Catalpa speciosa held at different temperatures, or to the foliage to evaluate alterations in metabolism induced by gibberellin or photoperiod.

Gibberellin simulated the shoot extension responses of long days, low, or high night temperatures in those plants which responded most favorably to these environments. The degree of the replacement was generally greatest in those species which exhibited a rapid and an extended shoot elongation response to long days or high temperatures.

In contrast, an inhibition in dry weight accumulation in the roots, leaves and old shoot wood, accompanied increases in shoot elongation and dry weight of shoots. In species exhibiting a moderate rate of shoot elongation, the replacement of the environmental requirements for vegetative extension by gibberellin was not exaggerated, but was comparable to that of long days or high night temperatures. In addition, the dry weight accumulation in the leaves and roots was not inhibited as extensively as in those plants that exhibited a rapid and extended response to high temperatures and long days. Dormancy of the first flush of growth was delayed by gibberellin in the presence of low night temperatures and short days in Acer saccharum while gibberellin in the presence of low night temperatures prevented dormancy of the second flush of growth in Euonymus Fortunei vegetus and Liriodendron Tulipifera. Gibberellin was also effective in breaking summer dormancy in Acer saccharum at the high night temperatures. Alterations in the metabolism by gibberellin suggest that the principle source of carbohydrates for shoot extension is derived from reserves in the old wood. A gibberellin induced increase in leaf area in some species partially spared the carbohydrate reserves.

Differential rates of uptake and distribution of phosphorus by roots of Catalpa speciosa at different temperatures suggest that the carbohydrates in the roots held at high temperatures were insufficient to supply the energy required for active absorption, but were adequate at the low root temperatures. There was inhibition in phosphorus uptake by the roots of Catalpa speciosa plants pretreated for 6 weeks to long

days and gibberellin, as compared to plants exposed to long days but not treated with gibberellin. There was no inhibition of phosphate uptake after 3 weeks of pretreatment. In Catalpa plants exposed to short days and to gibberellin for 3 weeks, more phosphorus was transported from the roots to the shoots. Thus, gibberellin treatment simulated the long day effect. Six weeks of pretreatment with gibberellin, however, had no effect. These observations, as well as many others, strongly suggest that endogenous levels of growth regulators are in a constant flux throughout the season. Thus the response to gibberellin will vary during the progressive stages of physiological development in a given season.

A control mechanism of growth and development, based on the progressively changing levels of endogenous gibberellins and inhibitors in woody plants is proposed. In the first scheme, plants grown under low night temperatures or long days exhibit, after the initial stage of growth in the spring, an increase in the level of endogenous gibberellins accompanied by a decrease in the level of endogenous inhibitors as the season progresses from spring to fall. In scheme 2, after the initial stages of growth, an exposure of woody plants to high night temperatures or short days results in a reciprocal pattern. As the season progresses from spring to fall there is an increase in the level of endogenous inhibitors accompanied by a decrease in the quantity of endogenous gibberellins.

The relative concentrations, as well as the season of the year when the gibberellin-inhibitor ratio is in balance will vary with the species.

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A delayed balance in the endogenous gibberellin-inhibitor ratio, accompanied by a rapid synthesis or a high concentration of endogenous gibberellins in the spring results in a rapid shoot elongation. Consequently, an exogenous source of gibberellin in the spring results in abnormally rapid vegetative extension accompanied by a marked inhibition of dry weight accumulation in leaves and old wood. In contrast, a slow rate of synthesis of gibberellins in the spring accompanied by either a rapid or a slow balance in the endogenous gibberellin- inhibitor ratio results in a slow rate of vegetative extension for a short or long period of time, respectively. Thus an exogenous application of gibberellin results in a continuation of a moderate rate of vegetative extension beyond the interval of time in which growth would otherwise occur, accompanied by a slight inhibition of dry weight accumulation in leaves and old wood.

THE INFLUENCE OF GIBBERELLIN ON THE VEGETATIVE GROWTH RESPONSES OF CERTAIN WOODY PLANTS SUBJECTED TO VARIOUS PHOTOPERIODS AND THERMOPERIODS, WITH SPECIAL REFERENCE TO *CATALPA SPECIOSA*

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A THESIS

Submitted to the School for Advanced Graduate Studies of Michigan State University of Agriculture and Applied Science in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

Department of Horticulture

1961

TO MY WIFE

Acknowledgements

The author wishes to express his sincere appreciation to Dr. Sylvan H. Wittwer for his accurate guidance, encouragement and invaluable suggestions during the course of this investigation and preparation of the manuscript.

Sincere thanks are expressed to Drs. S. K. Ries, A. L. Kenworthy and D. H. Dewey for their interest and technical assistance during the investigation.

Appriciation is also extended to the members of the guidance committee: Drs. H. Davidson, M. J. Bukovac, C. M. Harrison, G. P. Steinbauer and H. C. Beeskow for their helpful advise.

Grateful acknowledgement is extended to John E. Garver and C. Edward Johnson of the Michigan Department of Agriculture Seed Laboratory, East Lansing, for their cooperation in the investigation.

The author gratefully appreciates the financial assistance of the Chas. Pfizer Co., Brooklyn, New York, that made this study possible.

Finally the author wishes to extend his personal thanks to James A. Simmons, James T. Converse, Mary Y. Chapman and Richard D. Wilson for their assistance during the preparation of the manuscript.

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INTRODUCTION

Since the beginning of time one of man's principle objectives has been to promote and regulate the growth of plants. With the advent of IAA, NAA and 2,4-D and many other chemical substances, possibilities of modifying the behavior of plants for better survival under adverse weather conditions were introduced. Many new substances have been tested to determine their growth regulatory properties. Of primary interest in both applied and basic research are the gibberellins. These compounds have challenged many former concepts held by plant physiologists, necessitating changes in many theories relating to plant growth and development.

In ornamental horticulture, growth regulators offer promising avenues of approach to some of the present day problems. These include the control of flower and fruit development, increasing the rate of growth, expanding the area of adaptation, increasing the rooting and ease of grafting of stem pieces, improving the esthetic value, regulation of the time of dormancy, and as a tool to evaluate the physiology of growth and development.

Research in the above areas has been very limited primarily because of the small number of graduates in ornamental horticulture and the lack of funds. Within the past few years, however, there has been an increasing interest in the response of woody plants to photoperiod and plant growth substances. Findings thus far have been very stimulating for further activity. Home owners are beginning to move the center of their recreation from the playroom to the playlawn. Pride in the lawn

and shrubbery surrounding the home has intensified the demand for more knowledge of woody ornamental plants. There is need to solve such problems as iron chlorosis, sun scald, better methods of transplanting, controlling flowering, reducing maintenance cost, and many others.

The gibberellins, as a tool, offer the possibility of evaluating the growth and development of woody plants. Early research reports with the gibberellins gave strong indications that these chemicals, if properly used, might revolutionize many of our cultural practices and also solve some of the physiological problems encountered in the field of ornamental horticulture. With interest in the gibberellins, it became increasingly evident that research was needed in the field of ornamental horticulture to evaluate these compounds. Preliminary reports presented many interesting possibilities as to how the gibberellins might be of value to the nurseryman. Also, their effects on growth and flowering warranted a re-evaluation of the response of woody ornamental plants to photoperiod and temperature. Consequently, a series of studies were initiated to evaluate the response of several woody plants to gibberellin, photoperiod and temperature separately and in combination. Dry matter accumulation, shoot elongation, leaf area, period of active growth, and node number were used to measure external growth responses, while uptake and distribution of radioactive phosphorus, ash content, and percent nitrogen were indicative of internal changes in plant metabolism.

REVIEW OF LITERATURE

I. Photoperiodism in Woody Plants

A. Shoot Development

The response of woody ornamental plants to photoperiod is not a new concept, since it was reported as early as 1914 by Klebs (1914) that beech, oak, ash and hornbeam grew all winter when placed under continuous lighting. In the early twenties, Garner and Allard (1920) demonstrated conclusively the phenomenon of photoperiodism in plants. They used the term photoperiod to designate the favorable length of day for an organism, and photoperiodism was suggested "to designate the response of organisms to the relative length of day and night".

Early interest in photoperiodism was principally concerned with the flowering response and relatively little attention was given to the vegetative response. In their survey of plant material, Garner and Allard (1923) made note of the vegetative response of Rhus glabra and Liriodendron Tulipifera to long days. Liriodendron Tulipifera was placed in the greenhouse in September and a renewal of growth occurred following exposure to long days. Short days (10 hours) caused a cessation of upward growth.

Almost 15 years elapsed before interest was again directed toward the vegetative response, since the flowering response, as altered by photoperiod, was given first priority. In the late thirties, Gustafson (1938) and Skinner (1939a) reported a vegetative response when cuttings of Leucothoe Catesbaei, Rhododendron ponticum, Rhododendron roseum elegans and Pinus resinosa seedlings were exposed to long days (16 hours of light). In the early forties, interest in this area of study was

intensified by Wareing, Chouard, Kramer, Perlmutter and Darrow. By the late forties and early fifties the real significance of the vegetative response of woody plants to photoperiod was well realized. Nitsch, Downs, Davidson, Borthwick, Kramer, Waxman and others have devoted many hours of study to this area of research. Yet, evidence is still vague and much more work is greatly needed.

According to reports to date, long days will cause shoot elongation of woody plants if the day length is longer than the critical photoperiod. (Klebs, 1914; Garner and Allard, 1920, 1923; Gustafson, 1938; Skinner, 1939b; Perlmutter, 1939; Perlmutter and Darrow, 1942; Wareing, 1948; Wareing, 1950; Shanks and Link, 1951; Piringer and Stuart, 1955; Zahner, 1955; Downs and Piringer, 1958; Nitsch and Nitsch, 1959; Waxman, 1959) At day length of less than the critical duration growth may be proportional to the photoperiod imposed (e.g. Pinus sylvestris) (Wareing, 1948).

A number of methods have been used to prolong day lengths beyond the critical photoperiod such as with continuous electric lighting (Klebs, 1914), an interrupted dark period with one-half hour of light, (Wareing, 1948; Zahner, 1955; Waxman, 1958), or a long day of 16 hours followed by 8 hours of darkness and other degrees of variation between day and night. The optimum photoperiod for minimum growth and vegetative extensions, of course, varies with species, but generally is greater than 12 hours and may be as high as 24 hours in some of the pines (Downs and Piringer, 1958).

A photoperiod longer than the critical day length may cause such varied responses in shoot development as increasing dry weight (Downs and Piringer, 1958; Perlmutter, 1939), increasing internode length and number of nodes (Wareing, 1950), prolonging the phase of juvenile growth

(Downs and Piringer, 1958), eliminating the necessity for freezing temperatures in breaking dormancy (Gustafson 1938), inhibit the development of buds (Piringer and Stuart, 1955), or may not be effective in elongation of shoots which have a predetermined growth (Olmsted, 1942; Wareing, 1948). Excellent reviews concerning the shoot response of woody plants to photoperiod have been prepared by Nitsch (1957a) and Wareing (1956).

B. Root Development

Root development of woody plants as affected by photoperiod has not been as thoroughly investigated as shoot growth. Most of the reports available today are concerned with the rooting of cuttings under long or short days. For instance, (Skinner, 1939a) reported that seven hours of additional light improved the rooting of leaf bud cuttings of Rhododendron, but Snyder (1955) reported no significant effects of long days on the rooting of cuttings or growth of mature Taxus cuspidata plants. Not all plants exhibit increased rooting under long days (Lanphear and Meahl, 1959). Cuttings of Pieris japonica and Pyracantha coccinea Lalandii did not respond to photoperiodic treatment while Euonymus Fortunei coloratus, Ilex crenata convexa, Ilex opaca, Juniperus horizontalis plumosa, and Rhododendron mucronulatum cuttings rooted well under an extended photoperiod.

Root development of established plants of Pinus sylvestris is not affected by the photoperiod (Wareing, 1950). Weaver and Himmel (1929) reported earlier that growth of both tops and roots of certain herbaceous crops were greatly retarded under short days. In contrast, Roberts and Struckmeyer (1946) found that plants which blossom under long photoperiods

have fewer roots, indicating a correlation between flowering and limited root development. The literature is far too deficient in this area to draw any conclusive evidence as to the effect of photoperiod upon root development.

C. Induction and Cessation of Dormancy

One of the principal areas of interest in relation to photoperiod and woody plants is the phenomen of dormancy. Dormancy will be interpreted in the same sense as reported by Doorenbos (1953). "Dormancy is applied to all cases where a living tissue predisposed to elongate does not do so." He subdivides dormancy into three categories:

1 - Imposed dormancy - dormancy imposed by external environmental conditions such as drought or cold.

2 - Summer dormancy - dormancy imposed by internal causes, namely physiological processes inside the plant, but outside the bud, thus an indirect influence of the environment.

3 - Winter dormancy - dormancy also caused by internal causes, but the inhibitor system is inside the bud, thus again an indirect influence of the environment.

Short days will cause the onset of dormancy in many plants while long days delay or break dormancy. (Lammerts, 1943; Chouard, 1946; Wareing, 1948; Wareing, 1951 and 1953; Doorenbos, 1953; Vegis, 1956; Downs and Borthwick, 1956; Downs, 1957; Hellmers, 1959a; and Kawase and Nitsch, 1958) Other plants, such as Pyracantha coccinea, do not become dormant when exposed to short days (Nitsch, 1957b).

Plants induced into dormancy first develop leaves of darker green color, then shoot elongation ceases. (Garner and Allard, 1923; Downs, 1957; and Olmsted, 1951) The terminal bud may die and abscission occurs at the point of blackening just below the bud (e.g. Catalpa), or the terminal bud may just stop expanding leaves and internodes with no bud scales forming (e.g. Liriodendron and Betula). Other species may form a terminal bud completely with bud scales (Downs, 1957). Needle and internode extension is reduced in Pinus sylvestris (Wareing, 1949). Leaf abscission generally follows under naturally induced dormancy with the youngest leaves remaining attached a few days longer (e.g. Sugar maple) (Olmsted, 1951).

The degree of dormancy induced by short days varies with duration under short days, species, and many other factors. Downs (1957) reported two extremes which might exist in dormant plants. Some species develop dormancy which is not broken by long days while in others, growth resumes immediately upon transfer to a long day. Between the two extremes lie some species which resume growth from lower buds and from the terminal bud only if the plant is defoliated and placed under long days. Catalpa when placed under short days becomes dormant but when placed under long days will initiate a new flush of growth as long as the short days imposed do not exceed 2 to 3 weeks. As the number of short days increase, a greater number of long days is required to break dormancy until long days are no longer effective. Liriodendron is not as sensitive to short day inhibition, as growth resumes readily when placed under long days regardless of the number of short days imposed (Downs, 1957).

In contrast Weigela does not require long days to break dormancy since removal of the uppermost fully expanded leaves will cause a resumption of growth even under short days (Downs, 1957).

Kramer (1957a) reported that growth might cease and start again during the growing season several times. If conditions are favorable for the formation of an inhibitor, growth would then cease permanently. In this respect, Doorenbos (1953) reported that summer dormancy was caused by (1) a lack of a stimulus from the roots or (2) an inhibitory influence from the leaves. The second flush of growth (Lammas shoot) may occur so rapidly as to show only a few very short internodes with small leaves which have morphological characteristics different from the first flush. Acer saccharum will initiate a second flush of growth under long days (20 hours) (Olmsted, 1951). Olmsted (1951) also reported that long days will cause a temporary stimulation of buds which are not in deep rest. Irrespective of photoperiod, Acer saccharum will eventually become dormant. The difference being, long days will stimulate a second flush of growth while short days will not. (Olmsted, 1942).

The duration of the short day exposure required to induce dormancy varies with species. Liriodendron will stop growth completely after only ten 8 hour days while Ulmus requires 20 weeks of 8 hour days for the same response. Betula pubescens is almost as sensitive to short days as Liriodendron since less than one week under 10 hour days will slow down growth and is stopped completely after 2 weeks (Kawase and Nitsch, 1958). In general, most woody plants require 4 weeks of 8 hour days before they stop growth (Downs and Borthwick, 1956).

The natural means of breaking dormancy in many woody plants is by chilling during the winter months. The chilling requirements of most woody plants are not known and the chemistry involved in breaking dormancy is even more obscure (Went, 1953). Went (1953) attributed the breaking of dormancy to either (1) starch hydrolysis at low temperature, (2) removal of inhibitors from the buds or branches, or (3) development of growth stimulating substances in the buds. Cool temperatures have been reported to hasten and facilitate the breaking of dormancy (Wareing, 1951) and in some species, cannot be replaced by long days (e.g. Hydrangea macrophylla) (Piringer and Stuart, 1955). In contrast, long days are effective in stimulating growth of non-chilled embryo cultured peach seedlings (Lammerts, 1943), and buds of Fagus sylvatica which do not require a chilling period (Wareing, 1953). Eggert (1951) reported that all buds on the same tree do not require the same degree of chilling to break dormancy. Lateral leaf buds were found to require more chilling in order to break dormancy than terminal or spur leaf buds or flower buds.

Long days are more effective in breaking dormancy during the earlier part of the growing season than the latter. Wareing (1951) reported that seedlings of Pinus sylvestris could be induced into active growth during the summer months by exposure to long days but not during the fall. In the spring, the cambial activity is sensitive to both long and short days provided there is an actively growing shoot present. Short days are only effective at the end of the growing season in inhibiting cambial activity in Pinus sylvestris (Wareing, 1949). Long days appear to be a temporary stimulus for elongation of buds not in deep rest (Olmsted, 1951).

D. Hardiness

Long days are very effective for increasing the rate and total growth of woody plants, but often winter hardiness is reduced. Wareing (1948) found that southern species grown in more northern latitudes exhibited signs of frost damage because of the longer natural photoperiod, whereas northern species grown in the south produced less total growth. As early as 1937, Kramer (1937) found that growth of Abelia which was stimulated by electric lights was killed by freezing temperatures. In contrast, short days will increase maturity in Hydrangea (Piringer and Stuart, 1955). Olmsted (1942) reported that long days will increase cambial activity and decrease frost resistance. Irgens-Moller, (1958) found that plants growing in northern regions of the hemisphere have a greater sensitivity to artificially induced short days. This is an important component to survival in northern latitudes.

E. Leaf Size and Morphology

Leaf size and morphology is markedly affected by photoperiod and intensity of light. Garner and Allard (1920) reported that reduced light intensity tended to increase the superficial area of the foliage of many species. The leaf may be less compact with a reduction in the thickness of the blade. Long days have been reported to increase the leaf area per plant in Vaccinium (Perlmutter and Darrow, 1942) and Pinus sylvestris (Wareing, 1950). Leaf growth under long days can be reduced by the application of an anti-auxin (Lona, 1959). Short days, in contrast to long days, will cause the production of a tougher

textured and thicker leaf in Phaseolus multiflorus. Palisade cells were noticeably longer under short days as compared to long days (Tincker, 1928).

F. Seed Germination

Germination of seeds of woody plants respond in some cases to the photoperiod imposed. Undoubtedly, seeds of many woody ornamentals are photoperiodically responsive but there are very few reports available. Birch (Betula pubescens) was extensively investigated by Black and Wareing (1955) mainly because the non-chilled resting buds of dormant plants were induced to expand by long days. This indicated that possibly seed would respond similarly. Thus it was discovered that birch seed exhibited a definite response to photoperiod. Under long days, or short days followed by a short dark period, germination was greatly increased at 15° C after 8 photoperiodic cycles as compared to short days or long days followed by a long dark period. The photoperiodic effect, however, was not always critical. If the seeds were pre-chilled or germinated at a relatively high temperature (20° C), the necessity for the 8 photoperiodic cycles was negated. The pre-chilling or high temperatures (20°C), however, were not effective unless the seed had previously been exposed to light. Thus it appears that the reactions initiated by the light were promoted at the higher temperature. If a low temperature (5° C) during the light period is used, germination will respond to the photoperiod imposed if the dark period is at a higher temperature (20° C). The higher temperature imposed during the dark period should continue for several days and be imposed immediately after exposure to the photoperiod at lower temperatures for maximum stimulation.

Vaartaja (1956) confirmed the results of Black and Wareing (1955) although his environmental conditions were not as well controlled. In addition, he found that germination was slightly correlated to the illumination intensity. Germination was reduced when the intensity was above or below 800 foot candles at 20 to 30° C irrespective of the photoperiod. At temperatures of 10 to 25° C, a higher light intensity (1000 foot candles) was more favorable.

Stearns and Olson (1958) testing seeds of Tsuga canadensis, found short days of 8 to 12 hours were capable of hastening germination at 22° C. Temperature above or below this optimal range delayed or decreased germination. The effects of high temperatures in inhibiting germination were partially overcome by exposure to long days, but short days were not effective at high temperatures. The short day-high temperature inhibition of seed germination was reversed by placing the seeds at a lower temperature (17° C). As in birch, chilling of the seed replaced the necessity for a photoperiod stimulus to induce germination.

Excised embryos of Betula and Tsuga canadensis seed gave excellent germination in the dark (Black and Wareing, 1955; Stearns and Olson, 1958). This indicates that the pericarp, endosperm or nucellus is important in seed inhibition and that the seed is able to overcome this inhibition when exposed to light.

The effects of red and far red light is operative in seed germination which is responsive to a photoperiodic stimuli. Far red completely nullified the effect of red light when given immediately after birch seeds were exposed to red light. The reversal of red light stimulation of birch seeds at 15° C by far red is no longer effective after 12 hours of exposure to the red light (Black and Wareing, 1955).

In limited studies conducted with woody ornamental seeds, most seem to require a long photoperiod for optimum germination. Tsuga canadensis seeds held at 27° C and Betula pubescens at 15° C gave better germination under long days (16 hours) than under short days (8 hours) (Black and Wareing, 1955; Stearns and Olson, 1958). Earlier reports have shown that seeds of Pseudotsuga (Allen, 1941), Pinus sylvestris, Picea excelsa, Betula verrucosa and Betula pubescens (Sarvas, 1950) germinated more quickly in the light than in the dark. The final germination count of seeds germinated in the dark was reduced only with seeds of Pinus sylvestris. Vaartaja (1952) made similar observations with Betula verrucosa and Pinus sylvestris. These earlier experiments, however, were so designed that it could not be determined if the seeds were photoperiodic or photosensitive. At any rate, germination of almost all seeds tested was improved by the addition of light during germination.

II. Thermoperiodism in Woody Plants

A. Shoot Development

Thermoperiodism (a periodic response that can be induced by temperature cycles) has not been investigated as extensively as photoperiodism. However slight our knowledge of thermoperiodism, its importance in regulating growth in plants should not be overlooked. Went (1959) reported that "one of the most disturbing new facts in photoperiodism is that temperature can substitute for light".

According to Hellmers and Sundahl (1959), Pseudotsuga shows a dramatic response to thermoperiodism. Optimum growth occurred with a

diurnal variation of 10° C (7° C night to 17° C day temperature) while a diurnal variation of 16° C inhibited growth (7° C night and 23° C day temperature). In contrast, growth of Sequoia sempervirens was not altered by diurnal variations. Hellmers (1959b) also reported that Pinus Lambertiana would grow equally well when night temperature ranged from 4° C to 17° C. If the night temperatures exceeded 17° C however, (in conjunction with a 23° C day temperature) dry weight production was decreased. By increasing the night temperatures above 10° C and holding the day temperatures below 10° C, an increase in dry weight could be realized. This condition was also conducive to increasing the root/shoot ratio while higher day temperatures decreased the ratio. Kramer (1957b) also reported a decrease in shoot growth as the night temperature increases. This was especially noticeable in Pinus Taeda whereas Quercus borealis actually showed an increase in shoot growth as the night temperatures increased up to 17° C, but further increase in the temperature resulted in less growth.

The duration of active growth may be reduced by warm nights, while cool night temperatures will delay the onset of dormancy. Kramer, (1957b) reported that Quercus seedlings actually grew 8 weeks longer in the alternating day-night temperature regime as compared to the constant temperature. Kramer felt it was the spread between day and night temperatures which was the important factor in thermoperiodism rather than the actual temperature itself. He found that Pinus Taeda resumed growth early in the season and elongated more rapidly at a higher temperature than those grown at a lower temperature. In contrast, plants held at the lower night temperatures made more growth later in the season. This suggested that the high nights of mid and late summer may be the cause of dormancy (Kramer, 1957a).

B. Root Development

Richardson (1957) conducted extensive studies with Acer saccharinum to determine the effect of shoot temperature in relationship to root elongation. He found that root growth will only occur after the tops have been exposed to low temperatures. Low shoot temperatures resulted in a physiologically active bud which was a prerequisite for root elongation in the spring. The stimulus for the elongation of the roots appear to be formed in the developing buds and leaves, while the root initiating factor is located in the terminal bud.

Root growth in Sequoia sempervirens is not too responsive to thermoperiodism and yet cool nights (7° C) with 23° C day temperatures favored root growth slightly. Pseudotsuga was more responsive to alternating day and night temperatures and exhibited the maximum root growth at 7° C night and 17° C day temperature (Hellmers and Sundahl, 1959). Hellmers also reported that root growth is greater than top growth if day temperatures were less than 10° C, whereas high day temperatures resulted in a shoot/root ratio approaching two (Hellmers, 1959a).

Barney (1951) working with Pinus Taeda related the response of roots to a number of soil temperatures. He found that as the soil temperature increased to a maximum of 25° C, root growth increased, then decreased with further increases in soil temperature. The leaf/root ratio decreased with increasing temperatures up to 20° C, but increased at higher soil temperatures. A sudden rise in temperatures from 20° C to 35° C markedly increased root growth but subsequent growth was greatly reduced and stopped almost completely after 30 hours. By dropping the

soil temperature after this treatment to 20° C, growth of the roots again resumed in 6 days. Transpiration of Loblolly pine was positively correlated to the soil temperature for a short period of time, then gradually leveled off to a stable rate.

Apple and peach roots do not appear to require an alternating temperature for maximum growth. Nightingale (1935) found that the ideal root temperature was 65° F, and any deviation from 65° F resulted in reduced yields of roots and aerial organs.

C. Induction and Cessation of Dormancy

Dormancy as influenced by photoperiod, and in some cases temperature, was discussed previously, but the two environments were not discussed in any great detail together. Downs and Borthwick (1956) working with Ulmus americana, Cornus florida, Liriodendron and Catalpa found in contrast to many other reports that higher temperatures delayed the onset of dormancy under eight hour days. Temperatures lower than 70° F completely inhibited growth even under long days.

The resumption of growth of dormant Betula is markedly affected by temperature and photoperiod. At 23° C long days will break dormancy in 2 to 3 weeks while the leafless shoots remain dormant under short days. In contrast, no growth occurs at 15° C irrespective of photoperiod imposed, (Black and Wareing, 1955).

Bud development is also affected by temperature. Went (1953) reported that buds on Daphne Cneorum are formed at high temperatures but require a low temperature for further development.

III. Effects of Gibberellin on Growth and Development of Woody Plants

A. History

Gibberellin symptoms were first reported by Hori (1898) on rice plants. The disease, which was known as "Bakanae," became a major problem in rice production in the Orient because yields were greatly reduced. Hori described the symptoms as follows,

> "The rice plant becomes taller, with longer internodes and leaf sheaths, leaves were longer, narrower and thinner and the angle the leaf formed with the culm increased. Root growth and tillering is reduced, the plant appears chlorotic. In light infestation, flowering may be 2 to 3 days early but ears are smaller and yields are reduced. Severe infestion leads to adventitious roots, stem curving at the nodes, leaf curl, foot rot and death before flowering."

It wasn't until 1926, however, that Kurosawa (1926) successfully induced "Bakanae" symptoms in rice plants by treating them with a culture medium in which Gibberella fujikuroi had been grown. Twelve years later Yabuta and Sumiki, (1938) successfully crystallized the active ingredient responsible for inducing the Bakanae disease and called it gibberellin A and B ($C_{19}H_{22}O_6$). Research in this area was greatly reduced prior to and during World War II, but immediately afterwards Marth, Audia and Mitchell (1956) under the security of the United States Government began working with this compound on woody plants. Stodola at Northern Regional Laboratories in Illinois in the meantime was attempting to develop the techniques for biological synthesis. In 1956 the story of gibberellin as influencing woody plants was released by Marth, Audia and Mitchell (1956). Experimental quantities of gibberellin were made available in 1955 by Stodola who had perfected the cultural techniques and extraction.

Several reviews on this subject have been written, (Stowe and Yamki, 1957 and 1959; Brian, 1959; Brian, Grove and MacMillan, 1960) and a collection of more than 600 abstracts were published by Stodola (1958). Wittwer and Bukovac (1958) summarized the responses of economic plants to gibberellin.

Gibberellins which have now been characterized as nine distinct chemical structures are gibberellin A_1 ($C_{19}H_{24}O_6$), gibberellin A_2 ($C_{19}H_{26}O_6$), gibberellin A3 ($C_{19}H_{22}O_6$) and gibberellin A_4 ($C_{19}H_{24}O_5$) which are produced by the fungus Gibberella fujikuroi; Gibberellin A_5, A_6 and A_8 were isolated from higher plants by MacMillan, Seaton and Suter (1961). Gibberellin A_7 and A_9 were isolated from the fungus Gibberella fujikuroi by Cross, Galt and Halson (1960) and are closely related chemically to the other gibberellins. Phinney and West (1960) suggested that due to the close structural relationship between GA-3, GA-1 and GA-5, and of GA-2 and GA-4, there may be a close metabolic inter-relationship between these compounds:

$$\text{gibberellin } A_5 \underset{-H_2O}{\overset{+H_2O}{\rightleftharpoons}} \text{gibberellin } A_1 \underset{+2H}{\overset{-2H}{\rightleftharpoons}} \text{gibberellin } A_3$$

$$\text{gibberellin } A_4 \underset{-H_2O}{\overset{+H_2O}{\rightleftharpoons}} \text{gibberellin } A_2$$

No direct evidence for the above reactions has been obtained.

B. Shoot Development

One of the most widely reported responses of woody plants to gibberellin is the accelerated shoot growth accompanied by an increase in internode length (Barton, 1956; Benjamin and Snyder, 1958; Bilan and

Kemp, 1960; Bourdeau, 1958; Bradley and Crane, 1957; Bukovac and Davidson, 1959; Chakravarti and Loshali, 1959; Chakravarti, 1958; Cooper, 1957; Crane, 1957; Donoho and Walker, 1957; Ergle, 1958; Fogle, 1958; Giordano, 1959; Hull and Lewis, 1959; Hull and Klos, 1958; Iwagaki, 1958; Kearns, 1958; Kenworthy and Campbell, 1959; Litvinenko, 1959; Marth, Audia and Mitchell, 1956; Martin and Wiggans, 1959; McVey and Wittwer, 1958; Murphy, 1958; Marth and Smale, 1958; Nishiura and Iba, 1958; Noro and Hirata, 1958; Nitsch, 1957b; Pelton, 1958; Powell, Cain and Lamb, 1959; Robbins, 1957; Sato and Miyajima, 1958; Shidei and Akai, 1958; Scurfield and Moore, 1958; Stuart, Cathey and Asen, 1959; Stuart, 1958; Ueda, Saito, Hashimoto and Ogasawara, 1958; Walker and Donoho, 1959; Weaver and McCune, 1959; Yukawa, 1958).

Growth of physiological dwarfs may be stimulated by application of gibberellin, (Barton, 1956; Donoho and Walker, 1957). Barton, (1956) working with non-after-ripened embryos of Malus Arnoldiana, reported that gibberellin would stimulate shoot elongation. This is also true if half-ripened seeds of Elberta peach are soaked in 100 ppm of gibberellin (Donoho and Walker, 1957).

A number of reports have made reference to the shoot diameter of woody plants treated with gibberellin. The growth of the shoot may be spindly or sturdy, depending on the gibberellin concentration, method of application, and species treated. Foliar sprays of gibberellin on Juniperus chinensis pfitzeriana resulted in long spindly shoots (Benjamin and Snyder, 1958). The degree of after-ripening also alters response to gibberellin. Fogle (1958) found that seeds of sweet cherry, after-ripened for 4 months (normal requirement is 5 to 6 months), produced sturdy plants when treated with 100 ppm of gibberellin, while

seed after-ripened for the full term, grew weak and spindly following treatment. Bradley and Crane (1957) reported that gibberellin stimulated division in the cambial zone of Prunus Armeniaca of the spur branches only, while the main shoots were not affected. Almost all the activity was found along the xylem rays while the phloem tissue was not affected.

Giordano (1959) also reported an increase in stem diameter of Eucalyptus with increased concentrations of gibberellin from 5 to 200 ppm. Scurfield and Moore (1958) reported a similar response. Hull and Klos (1958) noted an increase in shoot diameter when 1 year old Montmorency cherry trees were sprayed with 100 ppm on May 7, June 1, and weekly until August 7. Gibberellin caused an increase in the trunk diameter of 1 year old Montmorency cherries which had been grown in the greenhouse and then transferred to the field on May 21 for treatment (Hull and Lewis, 1959). Ergle (1958) and Sato and Miyajima (1958) reported that gibberellin treatment resulted in an increase in stem diameter of cotton, and Cryptomeria and Populus seedlings, respectively.

Shoot diameter may also be reduced as reported by Kearns (1958) when Robinia Pseudoacacia was treated with gibberellin on July 24 and August 14. Marth, Audia and Mitchell (1956) reported that, generally, one would expect some plants to produce very thin threadlike stems while others would produce thicker stems. Apple trees sprayed with 1000 ppm, twice weekly, developed shoots of smaller diameter (Powell, Cain and Lamb, 1959). Iwagaki (1958) noted that 1000 ppm applied to the spur of pear, peach, and Malus sieboldii Rehd seedlings resulted in slender stems. Nishiura and Iba (1958) also reported a smaller stem diameter as compared to non-treated controls when orange seedlings were sprayed with 10 to 100 ppm between May 13 and August 29 with 6 applications of gibberellin.

The stem diameter of the new growth was initially smaller but gradually increased in thickness later in the season. Suyama, Yamasaki and Kubota (1958) observed spindly growth following a root soaking or foliar treatment of apple seedlings with 20 to 100 ppm of gibberellin.

Wareing (1958) working with one year old pot grown seedlings of Acer Psuedo-Platanus, Populus nigra, Fraxinus excelsior discovered a relationship between gibberellin and IAA in xylem development. By applying IAA to disbudded shoots of the above species, a narrow zone of new xylem with lignified vessels was produced as compared to no new wood in the control. When gibberellin was applied to the disbudded shoot, new wood with small unlignified cells with no sign of vessels was produced. If gibberellin and IAA were applied simultaneously, a wide zone of new wood with fully lignified vessels with intervening fibrous tissue developed. This approximated normal wood. Wareing felt that normal xylem development would involve the interaction of both endogenous IAA and native gibberellin.

Lateral shoot growth is markedly affected by gibberellin treatment. It may be increased or inhibited, depending on species, method of application, concentration of gibberellin, and temperature. Benjamin and Snyder (1958) and Bilan and Kemp (1960) both reported a decrease in lateral shoot growth of conifers (Juniperus chinensis Pfitzeriana and Pinus Taeda, respectively) when treated with gibberellin. In contrast, Cooper (1957) reported increased growth of lateral buds in the new shoots of grapefruit trees treated with a 1 percent solution of gibberellin. The following year, Cooper and Peynado (1958) reported that elongation of Citrus shoots resulted from a series of flushes from

lateral buds close to the apex. Hull and Lewis (1959) also observed that gibberellin induced lateral bud growth of Montmorency cherries in the distal region of the previous flush of growth.

Marth, Audia and Mitchell (1956) surveyed numerous woody plants and found that there was a reduction in the number of laterals developing in Buxus sempervirens, while Citrus exhibited an increase in lateral bud development as reported by Cooper (1957). Euonymus Fortunei vegetus, when treated May 4th with 100 ppm and at weekly intervals until August 21, exhibited a marked reduction in the total number of shoots per plant (McVey and Wittwer, 1958). Young apple seedlings treated twice weekly with 1000 ppm of gibberellin showed an increase in the number of growing points per tree (Powell, Cain and Lamb, 1959).

Lateral shoot growth development may be dependent on concentration and temperature as reported by Donoho and Walker (1957). They found that when two year old peach trees were treated with 500 to 1000 ppm nearly all growth occurred from the terminal bud, whereas with 100 ppm of gibberellin, more lateral growth occurred. This was especially true when trees were held at 40° F as compared to 65° F. Nishiura and Iba (1958) found that the deleterious effect of gibberellin in stimulating axillary buds could be avoided by treating only the growing tips of orange seedlings. A temporary stimulation of spurs of persimmons by low concentrations (20 to 100 ppm) was reported by Sato and Hirose (1958). Yokozawa and Yasui (1958) found low concentrations of gibberellin (25 to 100 ppm) caused a permanent increase in elongation of spurs of Masui Dauphine fig. The rate of appearance of lateral buds was increased by treating Populus with 50 to 1000 ppm of gibberellin from 2 to 6 times (Sato and Miyajima, 1958).

Cooper and Peynado (1958) postulated a mechanism of action of gibberellin in stimulating axillary development which was related to the IAA concentration. It is known that shoots of citrus which are actively growing, produce copious amounts of auxin. He further stated that auxins cause inhibition of lateral buds. Therefore, gibberellin may act in some way to deplete the inhibitory concentration of auxin in buds. Kato (1958) reported that gibberellin increased the bud growth of peas so greatly that the inhibition of applied auxin was nullified. Gibberellin also counteracted the stimulating effect of auxin in root formation. When IAA was applied in concentrations that promoted growth, gibberellin acted additively.

Fresh and dry weights of woody plants are markedly altered by gibberellin. A number of reports had shown an increase in fresh and dry weight of shoots (Benjamin and Snyder, 1958; Hull and Lewis, 1959; Scurfield and Moore, 1958; and Chakravarti, 1958). Benjamin and Snyder (1958) found that when seeds of Quercus Robur were soaked in 100 ppm for 24 hours there was a significant increase in fresh and dry weights of the seedlings. If a lower (10 ppm) or higher (1000 ppm) concentration was used no response or deleterious effects, respectively, would result. Chakravarti (1958) also reported an increase in dry weight of Sesamum indicum seedlings from seed treated with gibberellin (1 to 100 ppm).

Hull and Lewis (1959) treated one year old Montmorency cherry trees with gibberellin (100 to 1000 ppm) on May 21, (prior to this period, the trees had been in the greenhouse and had completed their first flush of growth for the season) which resulted in a significant increase in fresh and dry weight of the tops.

Scurfield and Moore (1958) attributed the increase in stem weight to the alteration in the relative weights of stem, root and leaves. When young seedlings of Eucalyptus were treated with gibberellin there was an increase in the weight of the stem, but the leaves and roots weighed less. Ergle (1958) reported a similar redistribution of dry weight in cotton plants. At low concentration (10 and 100 micrograms per plant) gibberellin caused an increase in stem weight with little or no effect on leaf and root dry weights. If, however, a higher concentration was used (1000 ppm) there was a marked reduction in leaf weight, together with the weight of the entire plant. At the higher concentrations the stem diameter was smaller than the controls but the dry weight was not altered.

A few investigators have reported a decrease or no change in fresh and dry weight following gibberellin treatment. Benjamin and Snyder (1958) reported a reduction in fresh and dry weight of the tops of Juniperus chinensis pfitzeriana. Young apple seedlings treated with 1000 ppm of gibberellin exhibited an increase in linear growth and a reduced root/top ratio but there was no significant change in the dry weight per tree (Powell, Cain and Lamb, 1959). Bamboo shoots also failed to show an increase in shoot weight when treated with 40 to 200 ppm of gibberellin (Ueda, Saito, Hashimoto and Ogasawara, 1958).

Node number may be increased or not affected by gibberellin treatment. Seed of Quercus palustris soaked in 100 ppm of gibberellin produced a greater number of leaves upon germination as compared to those soaked in water (Benjamin and Snyder, 1958). Litvinenko (1959) reported a similar condition if young seedlings of Ligustrum vulgare and Pyracantha coccinea were treated with .0025 percent "Ukranian

Gibberellin". McVey and Wittwer (1958) noted a significant increase in the node number of Euonymus Fortunei vegetus, Forsythia "Arnold Dwarf", Ligustrum obtusifolium vicari and Phellodendron amurense following gibberellin treatment. A repeat application of 100 ppm or a single application of 1000 ppm was more effective in increasing the node number than lower concentrations of gibberellin. Nitsch (1957b) found the same to be true with Acer palmatum. Young apple seedlings (Powell, Cain and Lamb, 1959) and Eucalyptus (Scurfield and Moore, 1958) also exhibited an increase in node number.

Other reports indicate that there is no increase in node number following gibberellin treatment. McVey and Wittwer (1958) reported that Magnolia Soulangeana, Berberis Thunbergi "Crimson Pygmy" and Viburnum Opulus nanum exhibited increased growth with no increase in node number following gibberellin treatment. Marth, Audia and Mitchell (1956) also observed a number of woody plants which failed to exhibit an increase in node number following gibberellin treatment.

Anatomical studies following gibberellin treatment have shown a change in the rate of cell division. Prunus Armeniaca spurs sprayed with gibberellin exhibited increased cell division in the cambial zone, but there was a reduction in the size of bud development on the spur branches. (Bradley and Crane, 1960). They also reported a retardation in bud development following gibberellin treatment during full bloom or at the beginning of pit hardening. The higher the dosage, the greater the elongation, but the more retarded the bud development. Gibberellin inhibited cell division in lateral bud apices while the terminal was relatively immune. Bud scales and leaf primordia failed to form or eventually disintegrated if formed when the gibberellin was

applied (Bradley and Crane, 1957). Wareing (1958) reported a similar condition could be induced in Acer Pseudo-Platanus, Populus nigra and Fraxinus excelsior. A number of studies have been carried out on herbaceous plants which support the concept that gibberellin induces an increase in the rate of cell division (Feucht and Watson, 1958; Geulach and Haesloop, 1958; Sachs, Bretz and Lang, 1959).

The action of gibberellin is not long lasting. A continuous supply of gibberellin must be available to induce continuous elongation. Chakravarti and Loshali (1959), working with Hamelia patens which has two different types of growth (winter rosette leaves of the terminal shoots and normal summer elongated internodes) found that gibberellin will cause a summer type growth when applied to winter rosette leaves. The effect is not long lasting since growth will revert back to a winter type growth within a month.

McVey and Wittwer (1958) reported that a continuous supply of gibberellin was required to stimulate continuous growth of Forsythia "Arnold Dwarf", Ligustrum obtusifolium vicari and Euonymus Fortunei vegetus. In contrast, a single spray application of 1000 ppm was adequate in stimulating continuous elongation in Magnolia Soulangeana. The elongation of terminal internodes of control plants tends to decrease as the plant approaches dormancy, whereas Euonymus Fortunei vegetus and Magnolia Soulangeana treated with a single application of gibberellin at 1000 ppm, or a repeat treatment of 100 ppm in the case of Magnolia, exhibited an increase in the length of the internodes as the plants went into dormancy. Fujita (1958) reported an initial stimulation of hop plants with 10 or 50 ppm of gibberellin but later growth was retarded and within 20 days there was no difference between control and

treated plants. Sato and Hirose (1958) reported a similar retarding effect of gibberellin on spur branches of Fuyu persimmons. In contrast, a 1 percent lanolin mixture of gibberellin applied to 2 to 3 year old Cornus, Acer, Catalpa and Aesculus caused continuous growth for 18 months in the greenhouse at 60 to 100° F.

Chakravarti (1958) supported the finding that repeat treatments are required for continuous internode elongation. He states that with a cessation of application of gibberellin there was a decrease in the length of the subsequently formed internodes when compared to the corresponding ones in the non-treated plants. Chakravarti felt that this may be caused by a reduction in the rate of synthesis of endogenous growth factors (Chakravarti and Loshali, 1959). Phinney (1956) also reported that a continuous supply of gibberellin was required to maintain a normal type of growth for dwarf mutant corn seedlings.

Gibberellin has also been reported to affect the development of the terminal buds of woody plants. Chakravarti and Loshali (1959) reported that when Lawsonia alba was treated with 100 to 200 ppm of gibberellin, elongation of the shoot terminated in death of the terminal meristem. McVey and Wittwer (1958) also reported a similar response in Berberis Thunbergii "Crimson Pygmy" treated with 100 ppm weekly. A number of authors have found that gibberellin will initiate a second flush of growth in woody plants (Hull and Lewis, 1959; Fogle, 1958; McVey and Wittwer, 1958). Murphy, (1958) reported no apparent growth response to gibberellin during the growing season when poplar trees were treated with 1 to 1000 ppm. After growth had terminated in September, a fall application of 60 to 1000 ppm to the vascular system resulted in a second flush of growth. Gibberellin induced a greater number of growth

flushes to occur in Red Blush grapefruit tree with a reduction in the period of dormancy between the first and second flush of growth. The terminal bud of grapefruit trees which is normally abscised, remained intact following gibberellin treatment (Cooper and Peynado, 1958). Nelson (1957) in contrast, reported that the terminal bud of Platanus desiccated after a substantial increase in growth rate over the control had been obtained.

Juvenility has been induced in several woody ornamentals treated with gibberellin. Cooper and Peynado (1958) reported that Red Blush grapefruit trees sprayed with 1000 ppm produced unusually long shoots which bore long thorns (characteristic of juvenility). Robbins (1957) also reports a reversal to the juvenile stage of leaf development in Hedera canarienis variegata following treatment with 10 micrograms of gibberellin per plant. In contrast, Scurfield and Moore (1958) found an alternate leaf arrangement and falcate-lanceolate shaped leaves when Eucalyptus was treated with gibberellin. These characteristics are typical of the adult phase of development and appeared much earlier in the development of the plant as compared to plants not treated with gibberellin. Chakravarti and Loshali (1959) felt that a "Gibberellin-like" material might be responsible for changes in leaf arrangement. He reported that Linaria marocanna (an annual) treated with gibberellin in the vegetative phase of development, developed an alternate leaf arrangement. The non-treated plants produced a whorled leaf arrangement in the vegetative phase and an alternate arrangement in the inflorescence.

An interesting report by Hull and Klos (1958) which has not been observed elsewhere in woody plants, was the response of virus yellows and ring spot stunted plants of young Montmorency cherry trees to gibber-

ellin. Gibberellin (100 ppm) caused stimulation of vegetative elongation to slightly offset ring spot virus and had a marked effect on overcoming stunting induced by cherry yellows virus.

In contrast to the rapid elongation of deciduous woody plants to gibberellin, most conifers fail to show any striking increase in shoot elongation. Kearns reported a significant increase in height of Pinus Strobus treated with 100 to 1000 ppm at weekly intervals for 4 consecutive weeks. Pseudotsuga taxifolia, Picea Abies, Pinus Banksiana, Pinus sylvestris and Picea glauca failed to respond to gibberellin concentration as high as 20,000 ppm for the latter three species and 100 to 1000 ppm in the former two species (Kearns, 1958). Nelson (1957) treated Pinus Strobus and Cupressus arizonica with 0.1 percent lanolin paste of gibberellin and found no growth response. Knight (1958) reported no response of Picea Engelmannii or Tsuga heterophylla with 10 to 1000 ppm of gibberellin repeated numerous times. Westing (1959) found a large number of conifers failed to respond to gibberellin. Marth, Audia and Mitchell (1956) were able to stimulate shoot elongation in Pinus virginiana, Pinus Taeda and Picea glauca if the gibberellin was applied as a lanolin paste at a concentration of 0.25 to 1.0 percent to a wounded area of the stem. Shidei and Akai (1958) reported that Larix gave only a slight response to gibberellin.

The response of woody plants to gibberellin is dependent on a number of factors, some of which are the physiological stage of development, degree of establishment of the plant, and method of application. Marth, Audia and Mitchell (1956) reported that the greatest response of woody plants to gibberellin occurred when it was applied to shoots that had just begun to elongate. Sato and Miyajima (1958) found that

Melasequoia glyptostroboides exhibited an increase in growth following gibberellin treatment only during the initial stage of development. In contrast, McVey and Wittwer (1958) and Murphy (1958) reported no increase in the rate of shoot extension of the first flush of growth in Euonymus Fortunei vegetus and Poplar, respectively, but gibberellin greatly influenced the second flush of growth. Kearns (1958) reported that Acer saccharum failed to respond to concentrations of 10 to 1000 ppm in late July and early August, but exhibited a growth response in early July following a foliar spray of 20,000 ppm of gibberellin. Nelson (1957) also reported that the oak responded to gibberellin immediately following the first flush of growth. Nelson (1957) placed 11 different species of one year old woody plants in the greenhouse in December under 16 hour photoperiods, he found that a 0.1 percent spray of gibberellin caused marked stem elongation with no spindly weakened stems such as is typical in many plants treated with gibberellin.

Wilting following gibberellin treatment was observed in Ligustrum (McVey and Wittwer, 1958) and in Populus (Murphy, 1958) following a foliar spray of 100 ppm of gibberellin. Wilting, however, was only temporary, lasting 1 to 2 weeks after first observed. In contrast, Nelson (1957) reported that 11 different woody plants treated with 0.1 percent gibberellin as a lanolin paste or as a foliar spray in December exhibited less tendency to wilt under a soil moisture stress than non-treated plants.

Genetically dwarfed herbaceous plants show a marked response to gibberellin. Brian (1959) reported that dwarf woody plants also respond remarkably well to gibberellin treatment. McVey and Wittwer, (1958) found that dwarf forms of Barberry (Berberis Thunbergii "Crimson Pygmy")

and Forsythia (Forsythia "Arnold Dwarf") exhibited the most dramatic responses to gibberellin. Pelton (1958) also found that a genetically controlled dwarf alpine plant (Potentilla) responded to either gibberellin or a transfer to lower altitudes both causing marked stimulations in growth. Shidei and Akai (1958) treated dwarf plants of Robinia Pseudoacacia, Liquidambar formosana and Acer palmatum TH., with gibberellin resulting in a noticeable response.

Not only may gibberellin stimulate shoot elongation but it may in contrast inhibit shoot development. McVey and Wittwer (1958) reported that high concentration of gibberellin (100 to 1000 ppm) caused a retardation of growth of Taxus cuspidata. Nickell and Tulecke (1959) exposed numerous isolated plant tissues to gibberellin. In general, the plant tissues tested showed no response. In some cases, however, there was a marked inhibition of growth by low levels of gibberellin. Pear trees treated with 100 to 1000 ppm were inhibited in their development with less total linear growth than controls (Powell, Cain and Lamb, 1959). Schoedle (1958) and Sato and Miyajima (1958) also reported that Pseudotsuga menziesii was inhibited in its development when sprayed with 125, 500 or 1000 ppm of gibberellin.

C. Root Development

Several investigators have reported that gibberellin reduces the rate of growth and development of roots of woody plants. Rood development of apple seedlings may be greatly retarded with a resulting decrease in the root/top ratio following treatment with 1000 ppm of gibberellin (Powell, Cain and Lamb, 1959). Suyama, Yamasaki and Kubota (1958)

also reported that root growth was suppressed by gibberellin when apple seedlings were soaked overnight in 20 ppm or sprayed with 20 to 100 ppm.

Benjamin and Snyder (1958) and Scurfield and Moore (1958) reported a reduction in fresh and dry weight of the roots following treatment of Juniperus chinensis Pfitzeriana and Eucalyptus seedlings, respectively, with gibberellin. Concentrations as low as 25 ppm of gibberellin were effective in reducing root weight of Eucalyptus.

Rooting of cuttings may be affected by gibberellin. Miller (1959) treated Salix cuttings, collected at monthly intervals, with .01 to 100 ppm of gibberellin. He found that gibberellin was only effective during the normal fall depression of root induction. During periods of high rooting capacity gibberellin was not effective. Sato and Miyajima (1958) reported that gibberellin inhibited appearance of roots and rooting of Chamaecyparis obtusa. If, however, gibberellin and naphthaleneacetic acid (NAA) were used simultaneously, the rooting induced by NAA was increased by gibberellin. In contrast, Marth and Smale (1958) treated cuttings of Hydrangea with IAA and gibberellin and found that gibberellin reduced the ability of the cuttings to respond to IAA. Rooting of cuttings of Rosa, Juniperus, Ligustrum and Pyracantha was also reduced when treated with 10 to 100 ppm of gibberellin. Gray (1957) supported Marth and Smale's (1958) findings when studying the effects of gibberellin on cuttings of Chinese Hibiscus treated with indolebutyric acid (IBA). In contrast, he found that gibberellin stimulated rooting of intact bean and tomato plants treated with IBA. Rooting was also improved in Coleus with gibberellin.

Root growth and development on intact plants may be stimulated by gibberellin depending on the concentration and species treated. Sato

and Miyajima (1958) found that high concentrations of gibberellin (4 to 7 applications of 400 ppm) promoted root elongation of Cryptomeria seedlings. Donoho and Walker (1957) reported an increase in root growth from half ripened Elberta peach seeds soaked in 20 to 200 ppm. When higher concentrations were employed, little root extension occurred. Stowe and Yamaki's review (1957) stated that Azaki bean roots were stimulated by gibberellin. An unsubstantiated report revealed that gibberellin B promotes root growth. Dry weight of roots of the Montmorency cherry was not altered by gibberellin treatment when applied to one year old seedlings which had made their first initial flush of growth prior to treatment with 100 to 1000 ppm of gibberellin (Hull and Lewis, 1959). In contrast, when excised embryos of Pinus Lambertiana were grown in contact with agar containing 3×10^{-7} and 3×10^{-5} molar gibberellin there was a 45 percent increase in root growth after 45 days. Root growth however, during the remaining 16 days paralleled that of the controls (Brown and Gibbord, 1958).

Size of the root and light intensity may play an important role in response of woody plants to gibberellin. Total yield and quality of roots of Derris elliptica were reduced if roots of treated plants were less than 6 millimeters in diameter. If however, the diameter of the roots was greater than 6 millimeters there was an increase in the diameter, quality, and yield of roots when gibberellin was applied as a root treatment of 100 milligrams per plant. Gibberellin decreased the fresh weight of roots and stems, but increased the root/top ratio (Moore, 1959). Richardson (1958) also reported that the size of the root affects their response to gibberellin. Growth of roots of Douglas fir seedlings, greater than 5 millimeters in initial length were markedly affected by

gibberellin applied to the roots. As the initial root length increased from 5 millmeters to 10 millimeters, the optimum concentration of gibberellin for promoting growth decreased from 10 to 5 ppm. Richardson (1958) also found that the inhibiting influence of 4000 lux of light on root growth could be completely overcome by 3 ppm of gibberellin. The initial response of roots to 8 ppm of gibberellin was much greater in the light than in the dark. In this respect, Hejnowicz (1958) reported that protochlorophyll was present in root tips of many different species and was destroyed by red and blue light. Light also inhibited growth of roots at an action spectrum similar to the spectrum of protochlorophyll destruction.

D. Induction and Cessation of Dormancy

Dormancy of woody plants has been studied for many years, but since the advent of gibberellin, more emphasis has been devoted to this area. It has been reported that gibberellin will delay the abortion or setting of terminal buds in woody plants. Cooper (1957) found that a 1 percent solution of gibberellin would delay the abortion of the terminal bud of grapefruit. He later reported that gibberellin delayed but failed to prevent dormancy from occurring in Red Blush grapefruit trees Cooper and Peynado, 1958). Yukawa (1958) also found this to be true in Satsuma orange seedlings. Hull and Klos (1958) reported that a foliar spray of gibberellin (100 ppm) caused a three week delay in terminal dormancy of Prunus. Kearns (1958) found that the terminal buds of Douglas fir seedlings set 6 weeks later than the buds of the control plants following treatment with 100 to 1000 ppm of gibberellin. Forsythia "Arnold Dwarf" and Phellodendron amurense also failed to initiate a

terminal bud until 2 or 3 weeks after the control, when treated with 100 ppm of gibberellin (McVey and Wittwer, 1958). Nitsch (1957) reported that abscission of the terminal bud of sumac under short days could be prevented by the addition of gibberellin.

Gibberellin also induces abortion or desiccation of terminal buds. McVey and Wittwer (1958) found that 20 to 40 percent of the terminal buds of Phellodendron amurense abscised when treated weekly with 10 to 100 ppm of gibberellin. Desiccation of the terminal buds of Forsythia "Arnold Dwarf", Prunus tomentosa and Berberis Thunbergii "Crimson Pygmy" occurred following treatment with 100 ppm at weekly intervals throughout the summer starting in early May. The growing points of Platanus occidentalis seedlings and Quercus were injured following 23 days of shoot elongation stimulated by 1 percent gibberellin in a lanolin paste applied to the main shoot (Nelson, 1957). He further stated that the terminal buds of Quercus did not desiccate but tended to form on a partially elongated internode. Soost (1959) also reported twig dieback on Clementine mandarin one month after treatment with 100 or 500 ppm of gibberellin. In contrast to many reports, Weaver (1959) found that gibberellin applied in the autumn prolonged the dormancy of buds of Vitis vinifera. The higher the gibberellin concentration, the longer the development of buds was delayed.

Low temperature exposure is essential for breaking dormancy of many woody plants. Yet, gibberellin has been shown to replace the low temperature requirement of dormant epicotyls of tree peony (Barton and Chandler, 1957). Oohata and Shiraki (1958) reported that the leaf buds of Prunus mume opened earlier in the spring when sprayed with 50 ppm of gibberellin repeated three times in late January. Barton (1956) also

reported that low temperature requirements needed for elongation of non-after-ripened embryos of Malus Arnoldiana could be replaced with gibberellin. Azaleas for forcing are normally stored at 40° F for 8 to 12 weeks to break the dormancy, then an additional 4 to 6 weeks at 60° F is required for forcing. Gibberellin (1000 ppm) will completely replace the cold treatment being more effective at higher temperatures (70° F) than at 60° F. Fewer applications are required in mid-winter than during late fall forcing, (Boodley and Mastalerz, 1959).

The physiological stage of development influences the response of woody plants to gibberellin. Donoho and Walker (1957) reported that as the chilling requirement for Elberta peach trees decreased, the optimum concentration of gibberellin for breaking dormancy also decreased. Fogle and McCrory (1959) found a similar condition to be true when Lambert cherry seeds were after-ripened in the presence of gibberellin. Terminal buds of Quercus and Acer which had their cold requirements satisfied, were induced to break one to two weeks earlier when treated with gibberellin (Marth, Audia and Mitchell, 1956). Prince (1958) in support of Donoho and Walker (1957), reported that eight varieties of Georgian peaches which had received 100 hours of the chilling requirements necessary to break their rest period, showed growth responses to contrations as low as 100 ppm of gibberellin. Stuart (1957), working with Hydrangea macrophylla also found that gibberellin was more effective in breaking dormancy if the plants cold requirement had already been partially satisfied. Apple trees held at 40° F for 2 or 4 weeks broke dormancy following gibberellin treatment, but only small tufts of leaves developed (Walker and Donoho, 1959).

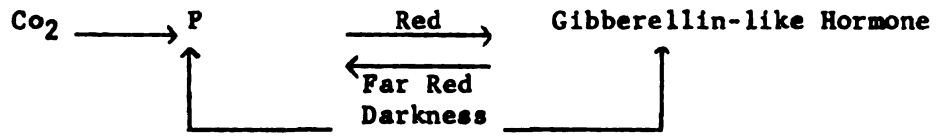
Dormancy, broken by gibberellin, may be only temporary and eventually the plant may revert to a dormant condition. Fogle (1958) treated rosetted Prunus seedlings, with 100 ppm of gibberellin as a foliar spray 6 weeks after germination, which had developed from non-after-ripened embryos. A lateral bud was forced into active growth but the shoot rosetted again after 3 to 4 weeks. A second application of gibberellin again broke dormancy and induced active growth for another month while some shoots grew continuously.

Completely dormant plants of Hydrangea macrophylla can have their cold requirements satisfied in at least two ways. Gibberellin and IAA (1 milligram each per plant) if applied prior to flower initiation will enable the plant to bypass the cold requirement needed for flowering. If, however, the plant is already dormant, defoliating the plant plus the addition of gibberellin to the soil or terminal buds will break dormancy (Stuart, 1958).

A number of woody plants will resume growth from dormant buds when treated with gibberellin. Bukovac and Davidson (1959) reported that photoinduced dormancy (9 hour days) of Weigela was inhibited following a single application of 50 ppm of gibberellin while the controls became dormant. Bourdeau (1958) reported a similar response for Pinus elliotti which had been induced into dormancy by short days. He found that if a 0.1 percent solution of gibberellin was applied at weekly intervals the cessation of photo-induced dormancy occurred within one month after the initial gibberellin treatment. Winter twigs of Fagus sylvatica, which normally require long days to break dormancy, were induced into vegetative elongation by 50 ppm gibberellin while the controls under short days at 17° to 19° C exhibited only a slight vegetative response (Lona and Borghi, 1957).

Brian (1958) proposed a mechanism of action for gibberellin in inducing a photoperiodic response with respect to flowering. The following scheme might also be applicable to vegetative response of woody plants.

> "In response to light, gibberellin-like hormones are formed in leaves, a physiologically inactive precursor (P) being intermediary. The hormone is converted slowly back to (P) in the dark and more rapidly in far red.



> Thus in a long day plant, gibberellin-like hormones induce flowering, but flowering takes place in short day plants only at low levels of gibberellin."

Apical dominance may be negated in some species and intensified in others depending on the concentration of gibberellin imposed. Marth, Audia and Mitchell (1956) reported that generally, the main stem is the first to elongate following gibberellin treatment with no apparent stimulation to the lateral buds. As the rate of elongation of the main axis decreases, there is a simultaneous increase in lateral bud elongation (e.g. Citrus and snapdragon). McVey and Wittwer (1958) reported a similar condition in Hydrangea arborescens grandiflora and Berberis Thunbergii "Crimson Pygmy" following weekly application of 100 ppm of gibberellin. Walker and Donoho (1959) however, found that higher concentrations of gibberellin (500 or 1000 ppm) would stimulate growth from the terminal bud and had little or no affect on lateral bud elongation in partially dormant peach trees.

E. Hardiness

Frost resistance is increased in some cases, while in others there is a reduction in frost tolerance. Marth and Smale (1958) found that English boxwood was more susceptible to frost injury when subjected to out-of-door winter temperatures following gibberellin treatment. Kearns (1958) reported a similar condition for black locust sprayed with 100 or 1000 ppm of gibberellin. High concentrations of gibberellin (200 ppm) were injurious to orange seedlings with a delay in maturity resulting (Yukawa, 1958).

Allsopp (1959) presented a hypothesis which might account for the variation in hardiness reported for plants following treatment with gibberellin:

> "The increase in growth vigor following gibberellin treatment might be expected to increase the rate of heteroblastic development (aging) in cases where the appearance of the adult characteristic is dependent on the enlargement of the apical meristem, while an increased utilization of carbohydrates might lead to a delay in the appearance of adult characteristics when their formation is dependent on an increasing accumulation of soluble carbohydrates in the developing organs."

F. Leaf Size and Morphology

Leaf size and weight may be markedly reduced following gibberellin treatment. Benjamin and Snyder (1958) found that leaf size of Quercus Robur was reduced when seeds were soaked 24 hours in gibberellin before planting. McVey and Wittwer (1958) reported that Magnolia Soulangeana, Phellodendron amurense, Berberis Thunbergii "Crimson Pygmy", Hydrangea arborescens grandiflora, Prunus tomentosa, Thuja occidentalis Hoveyi

and Viburnum Opulus nanum produced smaller leaves following weekly treatments of 100 ppm beginning in early May and continuing throughout the summer. Other investigations dealing with herbaceous plants have shown a decrease in leaf size and weight following gibberellin treatment (Haesloop and Greulach, 1958; Gray, 1957; and Ergle, 1958).

Leaves are generally longer and narrower following treatment of woody plants with gibberellin. Bukovac and Davidson (1959) reported an increase in length but a decrease in width of Weigela leaves treated with 50 ppm irrespective of the photoperiod imposed. Chakravarti and Loshali (1959) noted a temporary change in leaf shape from ovate to lanceolate which persisted for only a month in Hamelia patens. Cooper and Peynado,(1958), Kearns (1958), Marth, Audia and Mitchell (1956), Nelson (1957), Scurfield and Moore (1958), Stuart (1958), Walker and Donoho (1959), Yakushiji, Yamaguchi and Yamanaka (1958), Noro and Hirata (1958) and Chakravarti (1958) all reported an increase in length with a subsequent decrease in width of leaves treated with gibberellin. Chakravarti and Arora (1958) noted a similarity between removal of cotyledons and response to gibberellin in Sesamum indicum. Both methods of treatment caused the pair of leaves developing just above the cotyledons, to exhibit prominent concavities on both sides near the apex, as compared to the ovate control leaves.

Numerous reports have shown an increase in leaf size and weight but most of these reports have delt primarily with herbaceous plants (Gray, 1957; Humphries, 1958; Kuraishi and Hashimoto, 1957; Scott and Liverman, 1957; and Njoku, 1958). Takizawa and Kano (1958) and Sawada and Yakuwa (1958) treated mulberry in late summer and apple trees at full bloom with 50 and 100 ppm of gibberellin, respectively, with a resultant

increase in leaf size and dry weight. Mulberry leaves were increased in size by twofold. Apple leaves exhibited an increase in area and fresh and dry weight, with no effect on the water content of the leaves. McVey and Wittwer (1958) reported that low rates of gibberellin (10 ppm in early spring) would increase the size of leaves of Magnolia Soulangeana, Hydrangea arborescens grandiflora, Euonymus Fortunei vegetus, Prunus tomentosa and Viburnum Opulus nanum. Marth, Audia and Mitchell (1956) also observed an increase in leaf width in a number of woody plants treated with gibberellin.

Leaf thickness and surface morphology may be altered following gibberellin treatment. McVey and Wittwer (1958) noted that Prunus tomentosa sprayed with 10 to 1000 ppm produced leaves that appeared thinner and less tomentose. Nitsch (1957b) also reported a reduction in leaf thickness in Acer palmatum treated with 5 micrograms of gibberellin. The reduction was attributed to a decrease in mesophyll tissue.

G. Plant Composition

Gibberellin can significantly alter the chemical composition of woody plants. Hull and Lewis (1959) working with one year old Montmorency cherry trees grown in sand cultures, reported a significant decrease in boron and calcium and an increase in nitrogen in the leaves. Powell, Cain and Lamb (1959) treated apple seedlings with 1 to 1000 ppm of gibberellin twice weekly. All concentrations of gibberellin decreased the percent nitrogen in the leaves while only high levels of gibberellin (1000 ppm) decreased the calcium and magnesium content. Potassium was increased in the leaves following treatment with 1000 ppm but all

other levels of gibberellin (1, 10 and 100 ppm) decreased the percent potassium in the leaf tissue. Ergle (1958) also reported a decrease in protein nitrogen, total nitrogen and percent ash in leaves, stems and petioles when cotton plants were sprayed with 1000 micrograms of gibberellin.

At lower rates of gibberellin, there was an increase in total nitrogen as well as total ash in the stem plus petioles. Straus and Epp (1960) working with tissue cultures of Cupressus funebris reported a possible increase in the utilization of nitrogen when plant parts were treated with 1.0 ppm of gibberellin. He postulated that gibberellin may somehow be concerned with nitrogen metabolism since gibberellin permitted three times the amount of growth (no organic nitrogen added), as compared to the basal medium alone. Gibberellin may enhance the utilization by plants of organic and inorganic nitrogen sources.

Reports on the composition of herbaceous plants as affected by gibberellin have occurred in the literature (Morgan and Mees, 1958; Wittwer, Bukovac and Grigsby, 1957), but few reports have dealt with gibberellin affects on composition of woody ornamentals. Some studies concerning the chemical composition of fruit of various citrus species have been reported (Hield, Coggins and Garber, 1958).

Numerous elements in woody plants are not changed following gibberellin treatment. Hull and Lewis (1959) reported no change in the phosphorus potassium, magnesium, manganese, iron and copper content of one year old Prunus plants treated with 100 to 1000 ppm of gibberellin. Powell, Cain and Lamb (1959) also reported no change in the phosphorus content of apple leaves treated twice weekly with 1 to 1000 ppm of gibberellin.

H. Chlorosis

Some degree of chlorosis often accompanies gibberellin treatment of woody plants. Conifers, though not greatly stimulated vegetatively, do exhibit some degree of chlorosis following gibberellin treatment (Bilan and Kemp, 1960; Kearns, 1958; McVey and Wittwer, 1958). In contrast to conifers, deciduous woody plants generally exhibit an increase in vegetative extension which is accompanied by a chlorotic condition following gibberellin treatment. McVey and Wittwer (1958) reported marked chlorosis by the first of July in Prunus tomentosa sprayed weekly with 100 ppm of gibberellin. Plants sprayed once with 100 ppm in early May, however, did not show a marked chlorosis until September.

Chlorosis is temporary in Phellodendron amurense if the gibberellin treatment is not repeated. Buxus microphylla, in contrast to other woody ornamental plants treated, produced darker green leaves following weekly applications of 100 ppm of gibberellin. Only 10 ppm repeated weekly caused chlorosis which was not evident until late in the season (McVey and Wittwer, 1958). Weaver and McCune (1959) observed a chlorotic condition in grapes treated with gibberellin which was only temporary. The chlorotic condition became more intense as the concentration increased. Numerous other reports have noted a chlorotic condition accompanying gibberellin treatment (Bukovac and Davidson, 1959; Noro and Hirata, 1958; Suyama, Yamasaki and Kubota, 1958).

Chlorosis may be a result of pigment dilution or reduced chlorophyll synthesis in herbaceous crops. Ullmann and Krekule (1957) reported a 30 percent decrease in chlorophyll content of lettuce seedlings

per unit dry weight. Wolf and Haber (1960) supported the above findings and attributed the chlorosis of young wheat plants entirely to a chlorophyll dilution (synthesis of chlorophyll failed to keep pace with the increase in cell expansion). These findings support a theory that chlorosis induced by gibberellin is in part related to nutritional deficiencies. In this respect Dancer and Oyer (1958) were able to prevent chlorosis by the application of small quantities of certain mineral elements. If chlorosis had already been induced prior to application of certain minerals it could only be reduced. They also noted that chlorosis did not ensue if the gibberellin was applied to the primary leaves of beans, yet if applied to the tri-foliate leaves, chlorosis was induced. Stowe and Yamaki (1957) reported in their review that that gibberellin actually decreases the percent chlorophyll and chloroplast content. They stated that the degree of chlorosis was associated with the nutritional level of the plant.

I. Seed Germination

The response of germinating seeds has probably been investigated as thoroughly as any area concerning the gibberellins. Gibberellin will stimulate the rate of germination of seeds of woody plants. Litvinenko (1959) soaked fresh seeds of apple, pear and dogwood in a 0.2 percent solution of gibberellin for 24 hours. All species treated with gibberellin exhibited an increase in germination of 30 to 60 percent as compared to the controls. Tod (1958) evaluated numerous herbaceous seeds and found that gibberellin (25 ppm) was effective in inducing germination. He noted that seeds which normally germinate fairly freely were inhibited

at high concentrations of gibberellin. Benjamin and Snyder (1958) soaked seeds of Quercus Robur 24 hours in gibberellin, and found a positive correlation between the concentration of gibberellin and the rate of germination. The final percent germination was not affected. Martin and Wiggans (1959) reported that pecan seeds soaked for 8 days in 5000 ppm showed an increase in the rate of emergence and the total percent germination.

Many seeds require a period of chilling to induce seed germination. Gibberellin has been reported to completely or partially substitute for the chilling requirement of many seeds. Donoho and Walker (1957) stimulated germination of partially stratified peach seeds by soaking for 24 hours in 100 to 200 ppm of gibberellin. If higher concentrations of gibberellin were used, germination was inhibited. Sweet cherry seeds responded similarly when soaked in 100 ppm of gibberellin (Fogle, 1958). In contrast, Mes (1959) reported that non-stratified and partially stratified seeds of peach soaked in gibberellic acid showed no improvement in germination. Richardson (1959) working with seeds of Douglas fir reported that non-stratified seeds required a lower concentration of gibberellin for optimum germination than stratified seed. Richardson attributed this difference to a dilution of the gibberellin in the stratified seeds. Gibberellin (3 to 10 ppm) was most effective in stimulating germination, with evidence of a depressing effect on germination at higher concentrations. The total germination was not affected.

STATEMENT OF THE PROBLEM

That gibberellin will replace or partially replace the vegetative phases of development which are controlled by the photoperiod and/or thermoperiod was assumed. In this investigation two general areas of plant growth and development as affected by gibberellin are considered, (1) vegetative phases of plant growth and development and (2) metabolic phases of growth and development which are controlled by the photoperiod and/or thermoperiod. The problem is to ascertain whether gibberellin will (1) replace the vegetative and metabolic phenomena which are controlled by the photoperiod and/or thermoperiod and (2) if the degree of replacement is dependent on the photoperiodic and/or thermoperiodic sensitivity of the plants investigated.

The first area of investigation (vegetative modifications by gibberellin on plant responses controlled by the photoperiod and/or temperature) can be divided into three areas (1) vegetative modification of shoot growth and development (2) modification of the induction and cessation of dormancy and (3) accumulative vegetative modification by gibberellin. A logical approach for investigation of this area should include the selection of woody plants which vary in their degree of response to photoperiod and/or thermoperiod. These plants could be exposed to different photoperiods and thermoperiods in conjunction with their treatment with gibberellin.

The second area of investigation (metabolic modifications by gibberellin on plant responses controlled by either photoperiod and/or temperature) can also be divided into three phases (1) modification of the chemical composition (2) modification of foliar absorption and transport of phosphorus (3) modification of root absorption and transport of phosphorus.

Investigation of the metabolic modifications by gibberellin should be conducted on a woody plant which is very responsive to gibberellin, photoperiod and temperature and is also easily propagated. The modifying influence of gibberellin on the chemical composition should be a long term experiment (2 to 3 months) while foliar or root absorption of a radioactive mineral nutrient should be on a short term basis. An isotope which is readily available, actively absorbed, easily transported, and would reflect the movement of carbohydrates within the plant would be desirable. Accordingly an isotope of phosphorus^{32} and Catalpa speciosa were selected for these investigations since they closely conformed to the above specifications.

A mechanism of the modifying influence of gibberellin on growth and development of woody plants is proposed with certain practical implications.

EXPERIMENTAL

I. VEGETATIVE MODIFICATIONS BY GIBBERELLIN

A. Materials and Methods

1. Plant Material and Cultural Techniques

Special equipment and plant material was required to study the response of woody plants to gibberellin, photoperiod and temperature. Eight woody plants (Catalpa speciosa, Liriodendron Tulipifera, Viburnum Carlesii, Acer saccharum, Pinus sylvestris, Pyracantha coccinea Lalandii, Syringa vulgaris and Euonymus Fortunei vegetus) were selected in accordance to their photoperiodic response as reported by Nitsch (1957a) (Table I). The physiological age, method of propagation, and zone of hardiness varied with species (Table I). All plants were locally grown except Catalpa speciosa and Syringa vulgaris which were shipped from Iowa. The plants were selected for uniformity to reduce variability of response to imposed treatments.

During late March and early April all plant material was placed in 6 inch clay pots containing a well mixed 3-1-1 loam, peat, sand mixture. Following bud break, 2 buds exhibiting good vigor were allowed to develope on each shrub while the trees were allowed to develope only one shoot per plant. The plants of Pinus sylvestris and Acer saccharum were so small that two plants were placed in each pot where only one plant of the other species was used. The plant material was all in excellent vigor at the initiation of the experiment on April 26, 1958 at which time the variables gibberellin (0 or 50 ppm), photoperiod

TABLE I The Photoperiodic Response, Hardiness Zone, Description at the Time of Treatment, and Early Chronology of Certain Woody Plants

Photoperiodic Response (Nitsch 1957a)	Latin Name (Bailey 1954)	Hardiness Zone (Wyman 1949 and 1951)	Description at Time of Treatment		Early Chronology		
			Height (cms)	Shoot* Development	Age and Method of Propagation	Growth Initiated (date)	Initial Treatment (date)
I. Long Days Prevent the Onset of Dormancy.							
1. Short days cause dormancy							
a. Long days cause continuous growth	Catalpa speciosa, Warder.	4	15-20	1	1 year Seedling	4-22	4-26
	Liriodendron Tulipifera, L.	4	15-20	1	1 year Seedling	4-25	5-10
	Viburnum Carlesii, Hemsl.	4	13-18	2	1 year Grafted	4-14	4-26
b. Long days cause periodic growth	Acer saccharum, Marsh.	3	13-18	1	1 year Seedling	4-17	4-26
	Pinus sylvestris, L.	2	13-18	2	2 year Seedling	4-22	4-26
2. Short days do not cause dormancy	Pyracantha coccinea, Roem. Lalandii, Dipp.	6	15-30	1	1 year Cutting	4-22	4-26
II. Long Days do not Prevent the Onset of Dormancy	Syringa vulgaris, L.	3	13-18	2	1 year Cutting	4-27	5-10
III. Not Classified	Euonymus Fortunei, Hand.-Maze. vegetus, Rehd.	5	15-30	3	2 year Cutting	4-13	4-26

* 1 Buds breaking 2 New shoot growth 1 to 2 cms. long 3 New shoot growth 5 to 9 cms. long

(9 (short) or 18 (long) hours) and night temperature (40 (low) or 70 (high) ^{o}F) were imposed on all plants except Liriodendron and Syringa which were not incorporated into the experiment until May 10. The experiment was terminated in mid-September, 1958 (Figure 1).

To assure adequate fertility all plants were fertilized with a completely soluble fertilizer (20-20-20), each 6 inch pot receiving 100 milliliters of a solution containing ½ ounce/gallon/application. One application was given on each of the following dates; May 5, 28, June 18 and August 12, 1958. This was equivalent to .074 grams for each major element per application, giving a total of .296 grams of N, P_2O_5 or K_2O per 6 inch pot.

An adequate watering schedule was followed to prevent wilting and yet allow proper soil aeration. Generally, the plants required daily watering with the application being applied during mid-day. During the period of watering, the plants were adequately syringed to cool the foliage and reduce wilting of the leaves during the extreme heat of the day. Each plant was hand watered to assure a sufficient and uniform water supply.

To control insects, all plants were sprayed with Lindane (1,2,3, 4,5,6, Hexachlorocyclohexane) at the rate of 1 tablespoon per gallon, on May 5, 23 and June 12, 1958. Mildew was controlled on Syringa and Catalpa in mid-August by a solution of Isothan (Laurylisoquinolinium bromide).

2. Environmental Conditions

Temperature control was not easily achieved since controlled environment facilities to handle such large quantities of plant material

Figure 1 Plant Growing Area. Plants in flats were transferred into a refrigerated compartment (40°F) at 5:00 pm and returned to the growing area at 8:00 am.

Figure 1

were not available. To insure as much control of temperature as possible all plant material was subjected to the same day temperatures with only the night temperature (15 hours, 5 pm to 8 pm) being varied. The low night temperature (40°F) was obtained by moving half of the plants, which were placed on 36 x 48 inch flats, to a refrigerated storage room. The plants were moved on a dolly which could be placed under the flats and hoisted to allow the legs to ride 1 inch above the concrete flooring (Figure 2-A). The entire operation required 30 minutes, with this time slightly less when the plants were again returned to their day position. Night temperatures for plants grown under the high night temperatures were above that found in the area during a particular season of the year, because the plants were covered at 5 pm with a heavy black velveteen cloth which trapped the heat of the day and prevented the cooling influence of the night. Artificial lighting during part of the night also added heat to the area. The fluctuation of day and night temperatures during the season is shown in Figures 3 and 4.

To obtain an adequate control of the photoperiod and assure that the photosynthetic time was equal among the treatments, all plants were covered at 5 pm and uncovered at 8 am. Long days (18 hours) were extended by using 50 watt incandescent bulbs which were automatically turned on at 5 pm and off at 2 am. Two bulbs, 2½ feet above the soil level, with 10 inch white enamel finished reflectors were used for each 3 x 4 foot area. This allowed 25 to 50 foot candles at the soil level. As the plants grew in height the intensity increased as they approached the lights. Short days (9 hours) were obtained by an adequate system of screening out the light produced by the supplemental lights as shown in

Figure 2 Methods Employed in Satisfying the Thermoperiodic and Photoperiodic Requirements.

A) Plants were moved to a refrigerated compartment by a manually operated dolly.

B) Plants were placed in the refrigerated compartment (40°F) which was divided into short and long day areas.

C) Plants growing at the higher night temperature. Dividers were placed in position at 5:00 pm to provide proper day length between photoperiodic treatments (9 and 18 hours).

D) All plants were darkened at 5:00 pm with a black velveteen cloth. A laminated black and white plastic, with the white side up, was placed over the black velveteen cloth to reduce heat buildup in the early morning or evening. The coverings were removed at 8:00 am each day.

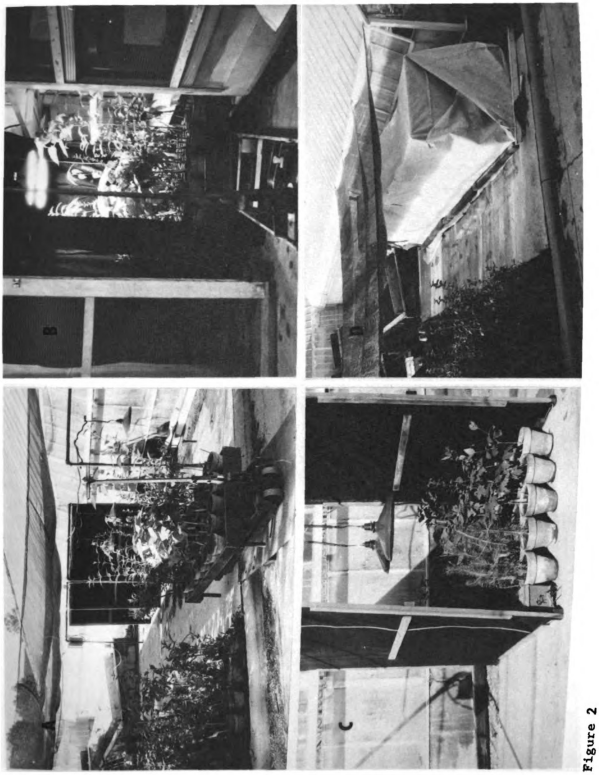


Figure 2

Figure 3 Maximum, Minimum and Hourly Temperatures Averaged Weekly for Eight Woody Plants Subjected to Low and High Night Temperatures.

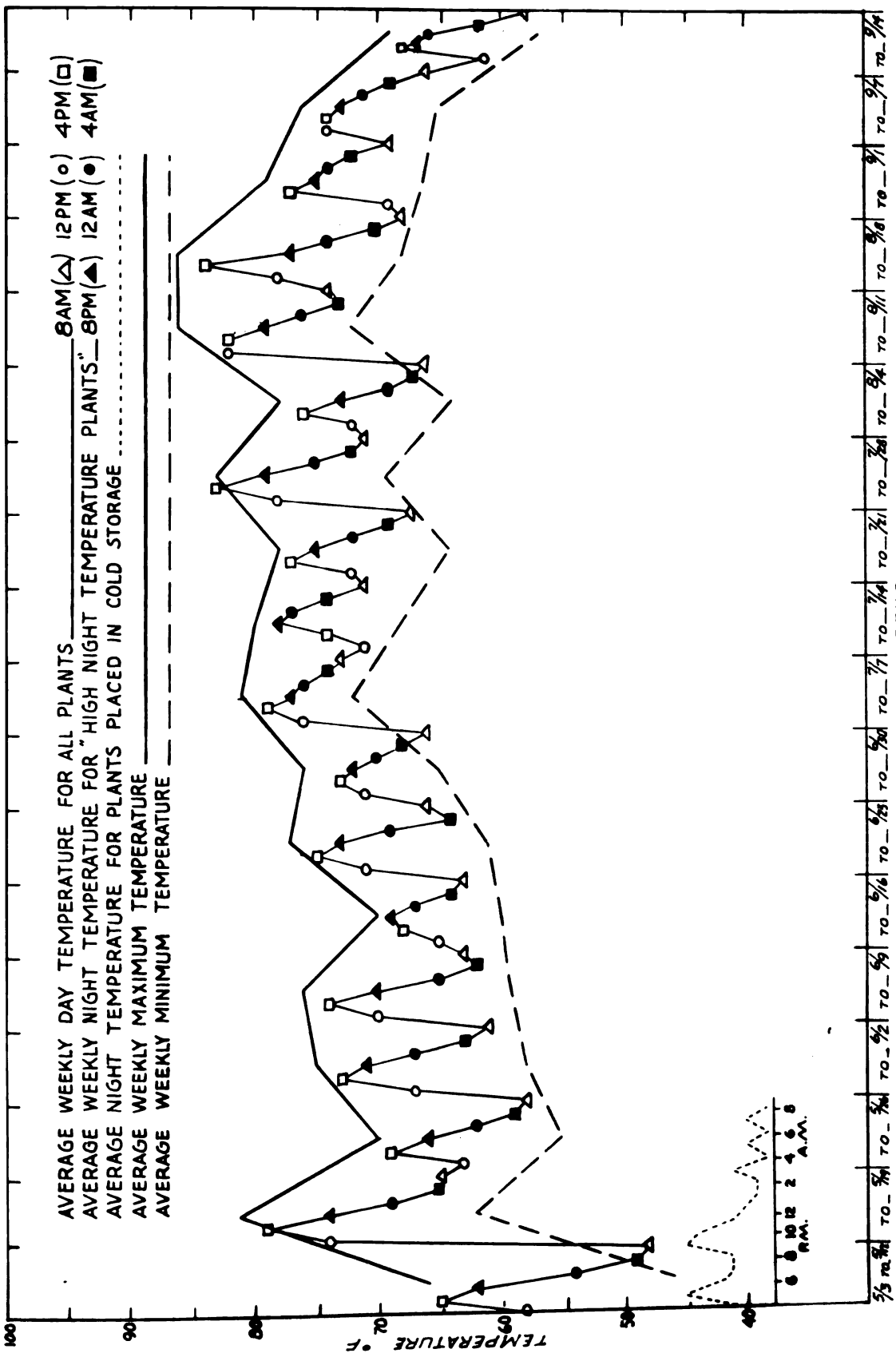

AVERAGE WEEKLY DAY TEMPERATURE FOR ALL PLANTS
AVERAGE WEEKLY NIGHT TEMPERATURE FOR "HIGH NIGHT TEMPERATURE PLANTS"
AVERAGE NIGHT TEMPERATURE FOR PLANTS PLACED IN COLD STORAGE
AVERAGE WEEKLY MAXIMUM TEMPERATURE
AVERAGE WEEKLY MINIMUM TEMPERATURE
8AM(△) 12PM(○) 4PM(□)
8PM(▲) 12AM(●) 4AM(■)
TEMPERATURE °F
100
90
80
70
60
50
40
WEEKS
5/3 TO 5/9 TO 5/16 TO 5/23 TO 5/30 TO 6/6 TO 6/13 TO 6/20 TO 6/27 TO 7/4 TO 7/11 TO 7/18 TO 7/25 TO 8/1 TO 8/8 TO 8/15 TO 8/22 TO 8/29 TO 9/5 TO 9/12
6 8 10 12 2 4 6 8
P.M. A.M.

Figure 3

Figure 4 Typical Air and Soil Temperatures During a Selected 24 Hour Period for Plants Exposed to Low and High Night Temperatures.

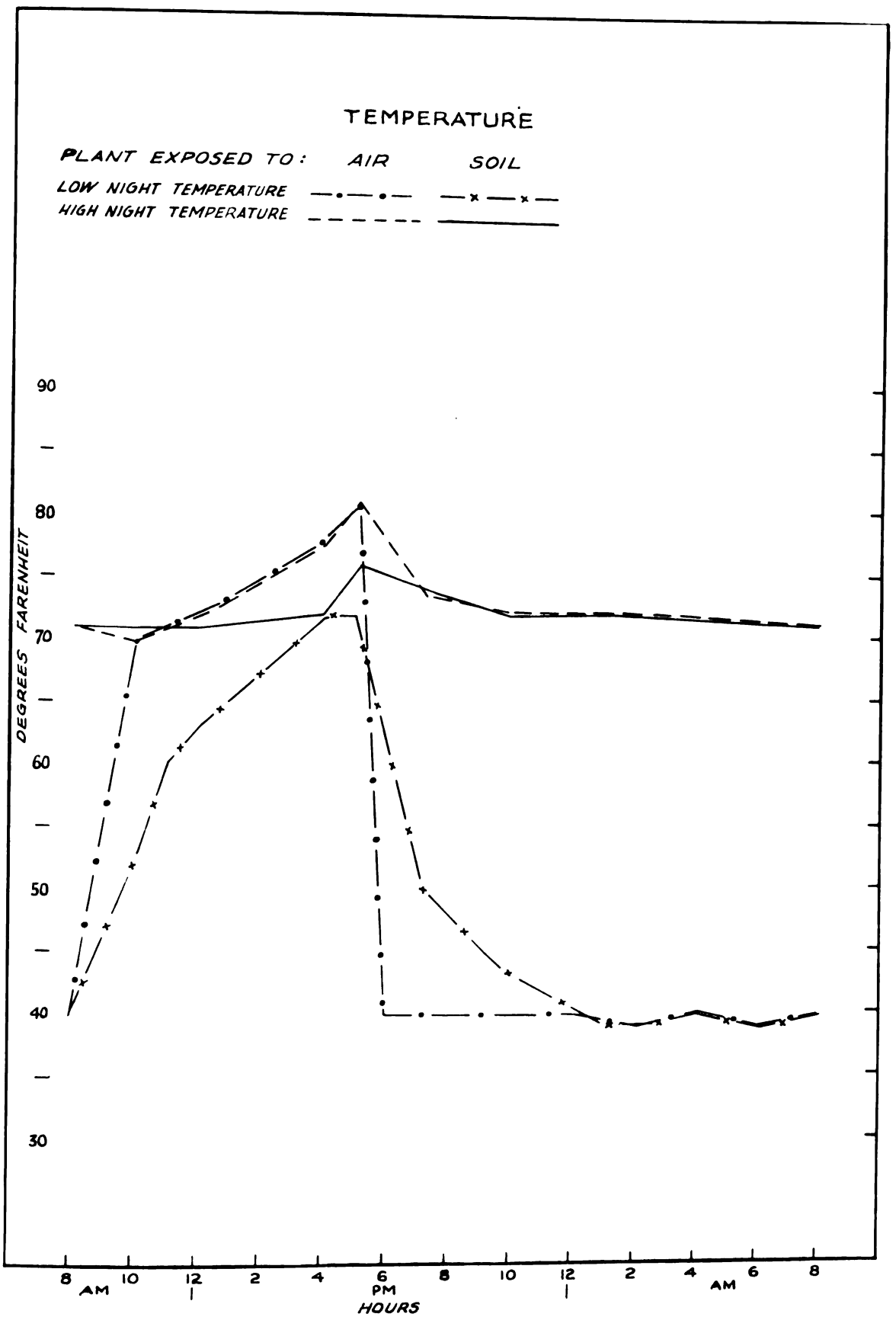

TEMPERATURE
PLANT EXPOSED TO: AIR SOIL
LOW NIGHT TEMPERATURE
HIGH NIGHT TEMPERATURE
DEGREES FARENHEIT
90
80
70
60
50
40
30
8 AM 10 12 2 4 6 PM 8 10 12 2 4 6 AM 8
HOURS

Figure 4

Figure 2-C. Air circulation was sufficient to prevent temperature buildup under the long day regime.

Plants held daily at the 40°F temperature from 5 pm to 8 am were segregated by black velveteen cloth into 6 areas, thus providing 3 long day and 3 short day locations (Figure 2-B). Plants on the outside and exposed to the high night temperatures were divided similarly to obtain the desired photoperiods. The outdoor area was covered with a black velveteen cloth followed by laminated black and white plastic (white side out, to reduce heat buildup in the early morning). The coverings prevented photosynthesis and screened out any light which might have come from the sun, street lights or cars (Figures 2-C and D).

The variables under test in this experiment necessitated an area in close proximity to the refrigerated storage room thus allowing rapid transfer and placement of the plants receiving the 40°F night temperature. An area between two greenhouses running north and south, measuring 16 x 20 feet was selected. The area was covered with a 4 inch slab of concrete to allow operation of a dolly for removal and return of the plants exposed daily to 40°F from 5 pm to 8 am. The entire outdoor plant growing area was covered by a luminite shading material which produced 50 percent shade and appreciably reduced the daytime temperature. The netting was suspended 6 feet above the cement to allow room for recording data (Figure 1). This location was only 70 feet from the refrigerated storage which was located inside of the Michigan State University Horticulture Building.

3. Method of Treatment

Gibberellin was applied at the rate of 50 ppm as an aqueous spray to the foliage until runoff. The solution, containing 0.1 percent Tween 20, was applied between 3 and 4 pm on April 26 and for 4 consecutive weeks thereafter. Two genera (Liriodendron and Syringa) did not receive the initial treatment until May 10 as they were not available at the earlier date of application. Four genera, Viburnum, Acer, Pinus and Pyracantha received a sixth treatment on August 11. A self-contained air pressure container delivered the spray under 100 pounds of pressure. In place of the Tween 20 wetting agent, all pine seedlings were sprayed with a 2 percent solution of Volck oil to allow greater penetration of the gibberellin.

Plants which were sprayed with gibberellin or the surfactants only (controls) were removed from the plant growing area to a shaded location for treatment. After the chemicals were applied uniformly to the foliage of the plants, they were allowed to dry in the shade before returning to the growing area. Consequently the rate of drying was reduced possibly insuring better uptake. Mechanical injury of the foliage prior to treatment was avoided in so far as possible.

4. Data Recorded

Shoot elongation and number of nodes were recorded at weekly intervals from April 24 through June 21, then again on July 24. The last shoot elongation measurements were taken on September 5, 1958. Final harvest and measurements occurred between the 9th and 16th of

September. Weekly notes as to the development of the plants were taken, with a detailed description on July 24, 1958. Shoot extension and node number were recorded from the base of the current season's shoot to its apex with stem diameter measurements taken on the shoots at the mid-point of the current season's growth. All leaf blades (petiole discarded) of the current season's shoot growth were removed and counted. This also permitted a recording of the dry weight per leaf.

At the termination of the experiment the plants were dismantled into five parts - leaves, new shoot growth, new root growth, old shoot growth, and old root growth. The five parts were placed in paper bags, and dried thoroughly in a forced air drying oven at 70°C. In addition to the above data, the total dry weight per plant, dry weight per centimeter of the new shoot growth, number of flushes of growth, the dates of induction and cessation of dormancy, average internode length (Pinus not included) and shoot-root ratio were analyzed.

Leaf area per plant was determined for all genera except Pinus. This value was obtained by determining the correlation between leaf area and dry weight. Six representative leaves, 2 each from the lower middle and upper nodes of the new shoot growth were selected from 3 replicate plants of each genera which were exposed to the different treatments. The leaf area was determined by placing the leaf in a light tight chamber which permitted the recording of the percent light transmitted through a clear window glass. The reduction of the light transmitted through the glass by the leaf was recorded, and converted to leaf area in centimeters. Subsequent dry weights of each leaf allowed a test for a correlation between leaf dry weight and area. The correlation was highly significant for all genera. By knowing the weight of the leaves per plant, the total leaf area could be readily calculated.

5. Analysis of Variance

A high speed computer ("The Mistic" at Michigan State University) was employed for the analysis of variance. A program tape (P-10) prepared by Dr. W. C. Jacob at the University of Illinois was used. This facility permitted detailed calculations that would have been virtually impossible in the time available using a standard hand calculator.

Each species was analyzed separately using a split plot design as no program tapes were available which could handle a 4-way interaction (species x temperature x photoperiod x gibberellin). The photoperiod was replicated three times assuring a valid test for the photoperiodic response. In contrast, the temperature was not replicated, but was adequately controlled to justify the evaluation of the effects of temperature on growth. Genera were randomized within the randomized photoperiods with the control and treated plants of each variety, adjacent to each other to reduce variation.

Within each photoperiod replicate were two single pot samples containing one plant for each genera, the exception being Acer and Pinus in which two plants comprised a sample. A total of 4 shoots were measured for the two single pot samples of all species with the exception of one shoot per sample for Catalpa and Liriodendron. Thus either 2 or 4 shoots were averaged to give values for each replication. In the case of the old shoots, and old and new roots, only 2 samples were averaged in the values for each replication, except with Acer and Pinus, in which 4 samples were averaged for each replication.

Since only two variables for each treatment (gibberellin (0 to 50 ppm), photoperiod (9 and 18 hours) and night temperature (40 and 70°F) were tested, a significant "F" test indicated significant difference resulting from treatment. Consequently a least significant difference (LSD) was not required to determine differences (Snedecor and Cochran, (1956).

6. Catalpa speciosa Seed Germination

Catalpa speciosa seed germinated at different temperatures following gibberellin treatment might give supporting evidence to the modifying influence of gibberellin on the vegetative response in woody plants. Consequently seed from pods of Catalpa speciosa were collected on September 15, 1959 from locally grown trees for germination studies. Prior to placing the seeds under test, they were soaked in aerated solutions of 0, 1, 10, 100 and 1000 ppm of gibberellin for 24 hours on September 16, 1959. The seeds were dried at room temperature and placed in bottles until ready for use. On September 22, the seeds were placed in two germinators held at a constant 68°F and on an alternating day-night temperature of 86°F for 8 hours and 68° for 16 hours during the dark period. Treatments were replicated four times.

Thirty seeds were placed in each 5 inch Petri dish containing a moistened filture paper for germination. The seeds were watered with tap water during the germination test. The temperature was adequately controlled in standard germination equipment furnished by the Michigan Department of Agriculture Seed Testing Laboratory. The percent germination was recorded periodically until germination was complete or no further evidence of germination was apparent. A standard analysis of variance, utilizing Duncan's multiple range test, was used to determine significance. (Duncan, 1955).

B. Results

1. Vegetative Modifications of Shoot Growth and Development

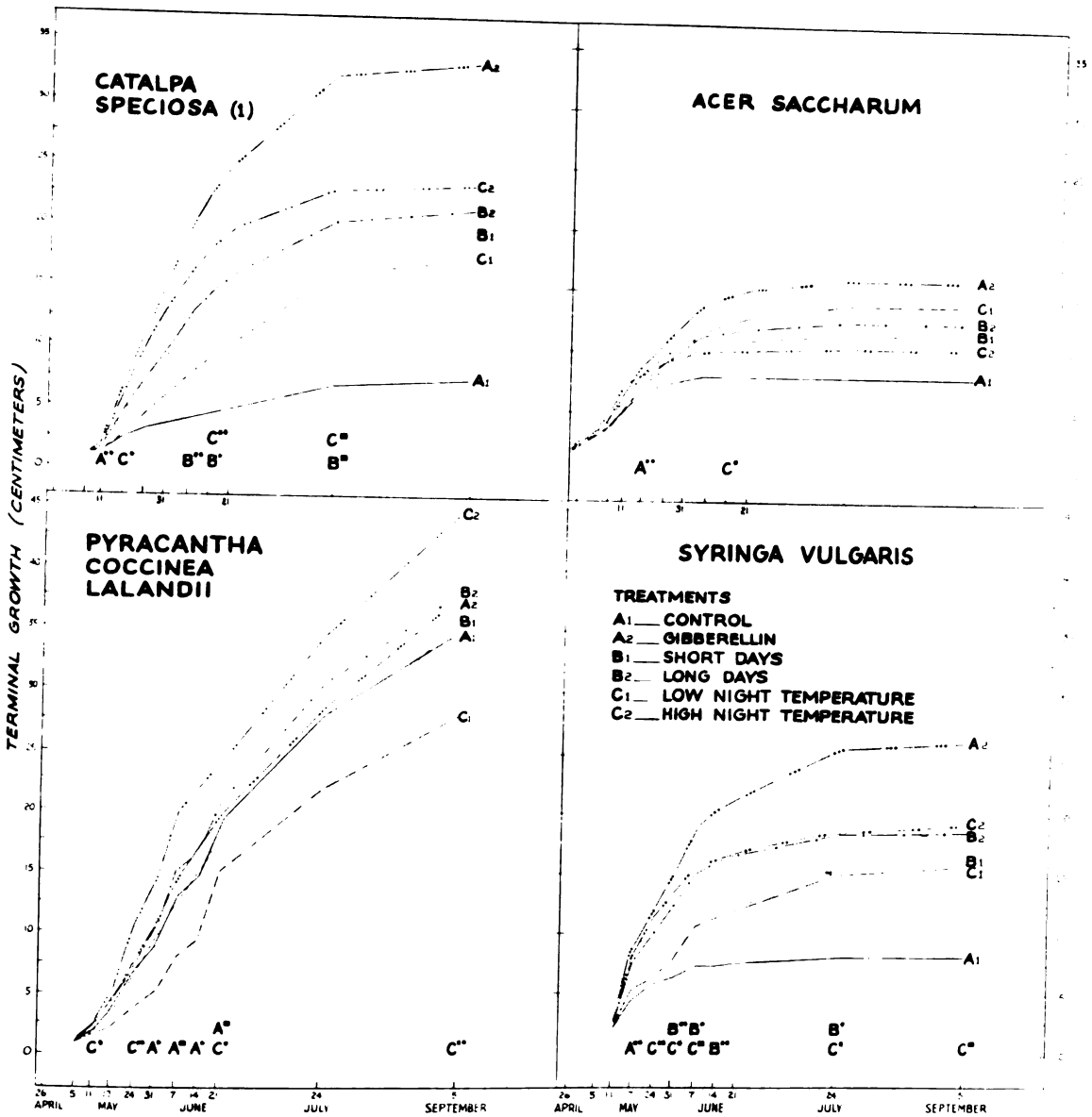
a. Shoot Extension

Figures 5 and 6 present a summary of the modifying influence of gibberellin, photoperiod and temperature on shoot elongation during the season, for eight woody plants. A perusal of the data illustrates the degree, rapidity and duration of shoot extension resulting from the variables imposed within and between species.

A significant response to gibberellin treatment (0 or 50 ppm) and night temperatures (40 or 70°F) was evident at various periods during the growing season for all species. In contrast, Acer saccharum, Pyracantha coccinea Lalandii and Euonymus Fortunei vegetus failed to respond to the photoperiods imposed (9 and 18 hours) (Figures 20, 22 and 24). In this respect the above species generally failed to respond markedly to gibberellin treatment. This was particularly evident in Pyracantha coccinea Lalandii and less apparent in Acer saccharum and Euonymus Fortunei vegetus.

Four species (Catalpa speciosa, Liriodendron Tulipifera, Viburnum Carlesii and Syringa vulgaris) exhibited a marked response to gibberellin throughout the growing season (Figures 17, 18, 19 and 23). The similarity in the response to the variables imposed on these species is interesting. Note that in all 4 species the same sequence of response to treatments is evident ($A_2 \rightarrow C_2 \rightarrow B_2 \rightarrow B_1 \rightarrow C_1 \rightarrow A_1$) although differences between treatments were not always significant. The shoot elongation for plants treated with gibberellin (50 ppm), high night temperature

Figure 5 Comparative Growth Rates of Terminal Shoots of *Catalpa*, *Acer*, *Pyrancantha* and *Syringa* as Influenced by Gibberellin, Photoperiod and Temperature.

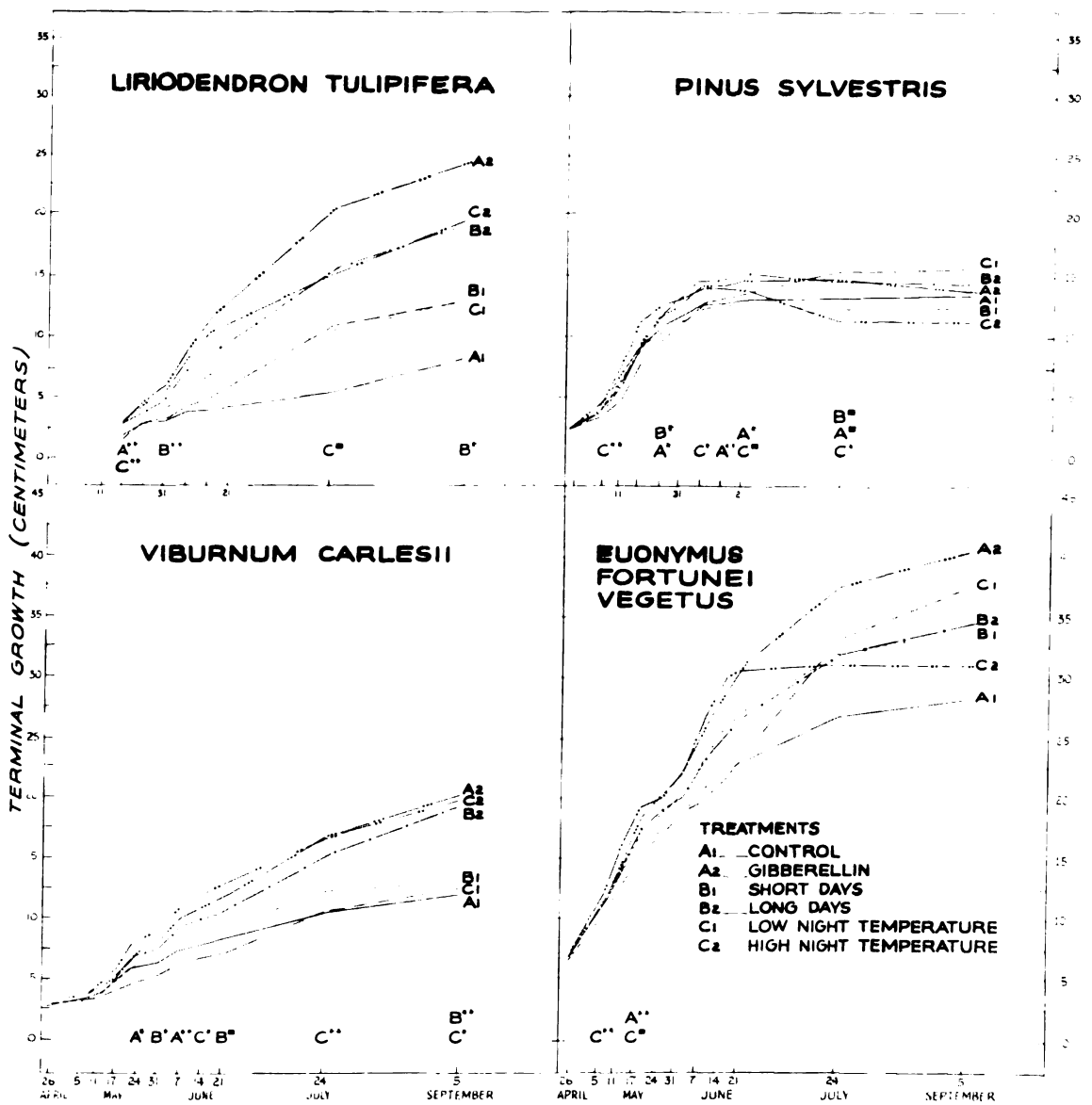


(1) *MULTIPLY SCALE BY 2 TO OBTAIN TRUE VALUE*

* OR ** *SIGNIFICANT DIFFERENCE BETWEEN TREATMENTS SHOWN BY THE LETTERS (A, B OR C) AT THE 5 OR 1 PERCENT LEVELS, RESPECTIVELY, AT DATE INDICATED, OR AT ALL DATES NOTED LATER IN THE SEASON. IF THE LETTER IS FOLLOWED BY A SQUARE (■), THE TREATMENT IS NO LONGER SIGNIFICANT.*

Figure 5

Figure 6 Comparative Growth Rates of Terminal Shoots of Liriodendron, Pinus, Viburnum and Euonymus as Influenced by Gibberellin, Photoperiod and Temperature.



* OR ** *SIGNIFICANT DIFFERENCE BETWEEN TREATMENTS SHOWN BY THE LETTERS (A, B OR C) AT THE 5 OR 1 PERCENT LEVELS, RESPECTIVELY, AT DATE INDICATED, OR AT ALL DATES NOTED LATER IN THE SEASON. IF THE LETTER IS FOLLOWED BY A SQUARE (■), THE TREATMENT IS NO LONGER SIGNIFICANT.*

Figure 6

($70^{o}F$) or long days (18 hours) is very similar particularly in Viburnum Carlesii and Liriodendron Tulipifera. This relationship is also true for Catalpa speciosa and Syringa vulgaris, but in contrast, the response to gibberellin is more dramatic than the photoperiodic or thermoperiodic response observed (Figures 5 and 6).

Acer saccharum and Euonymus Fortunei vegetus exhibited the above trend for a short time during the spring. Later the sequence of shoot elongation was altered, ($A_2 \rightarrow C_1 \rightarrow B_2 \rightarrow C_2 \rightarrow A_1$) with gibberellin (50 ppm) low night temperature ($40^{o}F$) and long days (18 hours) approximating a similar response, although the differences were not always significant between the temperature treatments. Pinus sylvestris could be grouped with the above two species, at least through July 24th. Subsequently, gibberellin caused death of the plants at the high temperatures. Pyracantha coccinea Lalandii failed to follow the above two patterns of growth, common for all other species. In contrast, shoot extension was more evident under high night temperature ($70^{o}F$) than any of the other variables imposed (Figures 5 and 22).

The rapidity of response of shoot elongation to the variables imposed varied between species but again a pattern of response emerged (Figures 5 and 6). Catalpa speciosa, Syringa vulgaris, Liriodendron Tulipifera responded to gibberellin one to two weeks after the initial treatment but failed to respond to photoperiod (9 or 18 hours) until 6, 3 and 3 weeks, respectively, after the initiation of the experiment. The above species responded to the thermoperiodic treatment one week after the response to gibberellin was observed, except with Liriodendron in which the response occurred simultaneously to temperature and gibberellin (Figures 5 and 6).

Viburnum Carlesii which had previously been grouped with the above species did not respond to gibberellin (50 ppm) until 4 weeks after treatment. It is of interest to note that a similarity still exists between these 4 species; a response to gibberellin was always evident prior to or during the response to the other variables (low or high night temperature, long or short days.

Acer saccharum, Pyracantha coccinea Lalandii, and Pinus sylvestris were slow to respond to gibberellin treatment. This was particularly evident in Pyracantha coccinea Lalandii (Figures 5 and 6). In the latter 2 species and also Euonymus Fortunei vegetus, the shoot responded more rapidly to the temperature treatment (40 and 70°F) than gibberellin (0 and 50 ppm). (Figure 5 and 6).

The duration of elongation as influenced by gibberellin (0 or 50 ppm), photoperiod (9 or 18 hours) and night temperature (40 or 70°F) are shown in figure 5 and 6. It is of interest to note that gibberellin had an influence on growth in Liriodendron Tulipifera, Viburnum Carlesii and Euonymus throughout the growing season which was comparable to the long day and high temperature (low temperature in the case of Euonymus). In contrast, gibberellin did not cause an increase in growth of Catalpa and Syringa after mid-July and in Acer after late June (Figure 5 and 6). The shoot elongation response to photoperiod and temperature followed a comparable pattern. Pyracantha which failed to respond to photoperiod was influenced by gibberellin during late May and early June only.

It is of interest that those species which exhibited the greatest shoot elongation following gibberellin treatment could be classified in two groups (I.-1.-a. and II.) which are shown in Table 1. In

contrast, species in group I.-1.-b. and I.-2 were least responsive to gibberellin treatment. Euonymus should be placed in group I.-1.-b with Acer and Pinus in this investigation.

A differential response of shoot extension to gibberellin treatment at the different night temperatures is shown in Figure 7. It appears that the action of gibberellin is reduced in some manner under low night temperature in Catalpa, Liriodendron, Viburnum and Syringa. Note that the duration of the interaction in Catalpa and Liriodendron is apparent only until July 24, whereas Viburnum and Syringa responded differently to gibberellin under the different night temperatures until the termination of the experiment in September.

The general lack of a significant interaction between gibberellin (50 ppm) and night temperature (40 or 70°F) is of interest in Acer, Pinus, Pyracantha and Euonymus. If compounds were present within these species to counteract the action of gibberellin or shoot elongation they were ineffective except in certain instances. Note that on May 24 there was a greater response to gibberellin at the higher than at the lower temperature in Acer. As the season progresses this interaction was no longer apparent. In contrast Pinus and Pyracantha failed to respond differentially to gibberellin treatment early in the season but did so late in the summer. The action of gibberellin on Pinus under high night temperature was so intense during July that death ensued.

The implication in Figure 7 is that species which respond most favorably to a low night temperature (e.g. Pinus, Euonymus and Acer, note Figure 5 and 6) do not respond differentially to gibberellin when

grown under different night temperature regimes. Apparently the inhibition by high night temperature is not very intense in these species except during specific periods of the growth cycle.

In contrast, in those species responding most markedly to high night temperature (Catalpa, Liriodendron, Syringa and Viburnum) the inhibitory influence of low night temperatures is not completely overcome by gibberellin (50 ppm) (Figures 5, 6 and 7). In Catalpa and Liriodendron however, the inhibitory influence of the low night temperature on the shoot growth response was no longer apparent after July 24. It also appears that inhibitors accumulate in plants under high night temperatures thus reducing the action of gibberellin. In this respect, on August 12, Pyracantha, Pinus, Viburnum and Acer were sprayed with 50 ppm in hopes of stimulating additional growth. As shown in Figure 7, only 1 species appeared to be affected (Pyracantha). Apparently the action of gibberellin was inhibited at the cool temperature while this was not apparent at the higher night temperatures. In contrast the failure of Acer, Viburnum and Pinus to respond differential to gibberellin would indicate that the endogenous inhibitors had accumulated in the shoots irrespective of the night temperature or photoperiod. There also exists the possibility that the concentration of gibberellin was insufficient to overcome the endogenous inhibitor within the plant.

The inhibitory influence of short days on shoot elongation can easily be over ridden by gibberellin resulting in a similar growth response irrespective of the photoperiod imposed in all species. One exception was Syringa, in which a greater response to gibberellin was observed under long days from June 7 to 21.

Figure 7 The Modifying Influence of Gibberellin on the Thermoperiodic Response of Shoot Extension in Certain Woody Plants.

* or ** Significant interactions at the 5 or 1 percent levels, respectively.

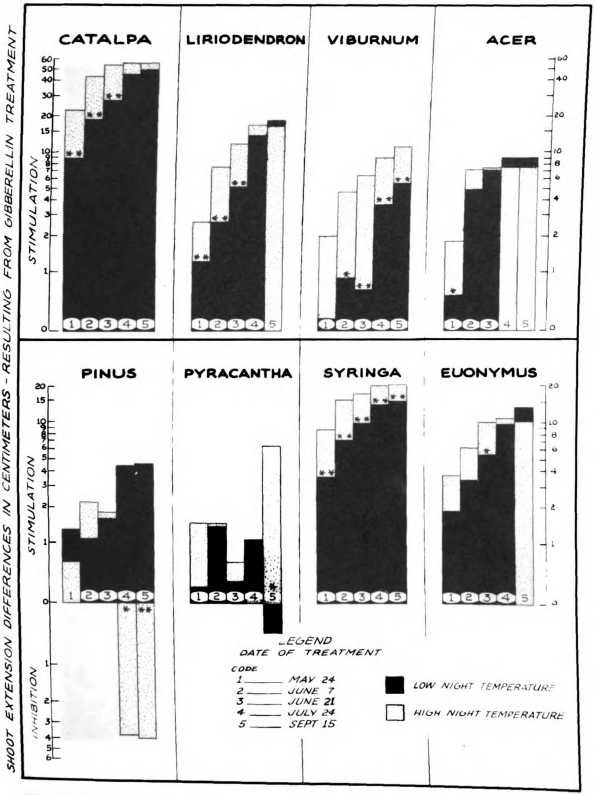

SHOOT EXTENSION DIFFERENCES IN CENTIMETERS - RESULTING FROM GIBBERELLIN TREATMENT
CATALPA
LIRIODENDRON
VIBURNUM
ACER
PINUS
PYRACANTHA
SYRINGA
EUONYMUS
STIMULATION
INHIBITION
LEGEND
DATE OF TREATMENT
CODE
1 ____ MAY 24
2 ____ JUNE 7
3 ____ JUNE 21
4 ____ JULY 24
5 ____ SEPT 15
LOW NIGHT TEMPERATURE
HIGH NIGHT TEMPERATURE

Figure 7

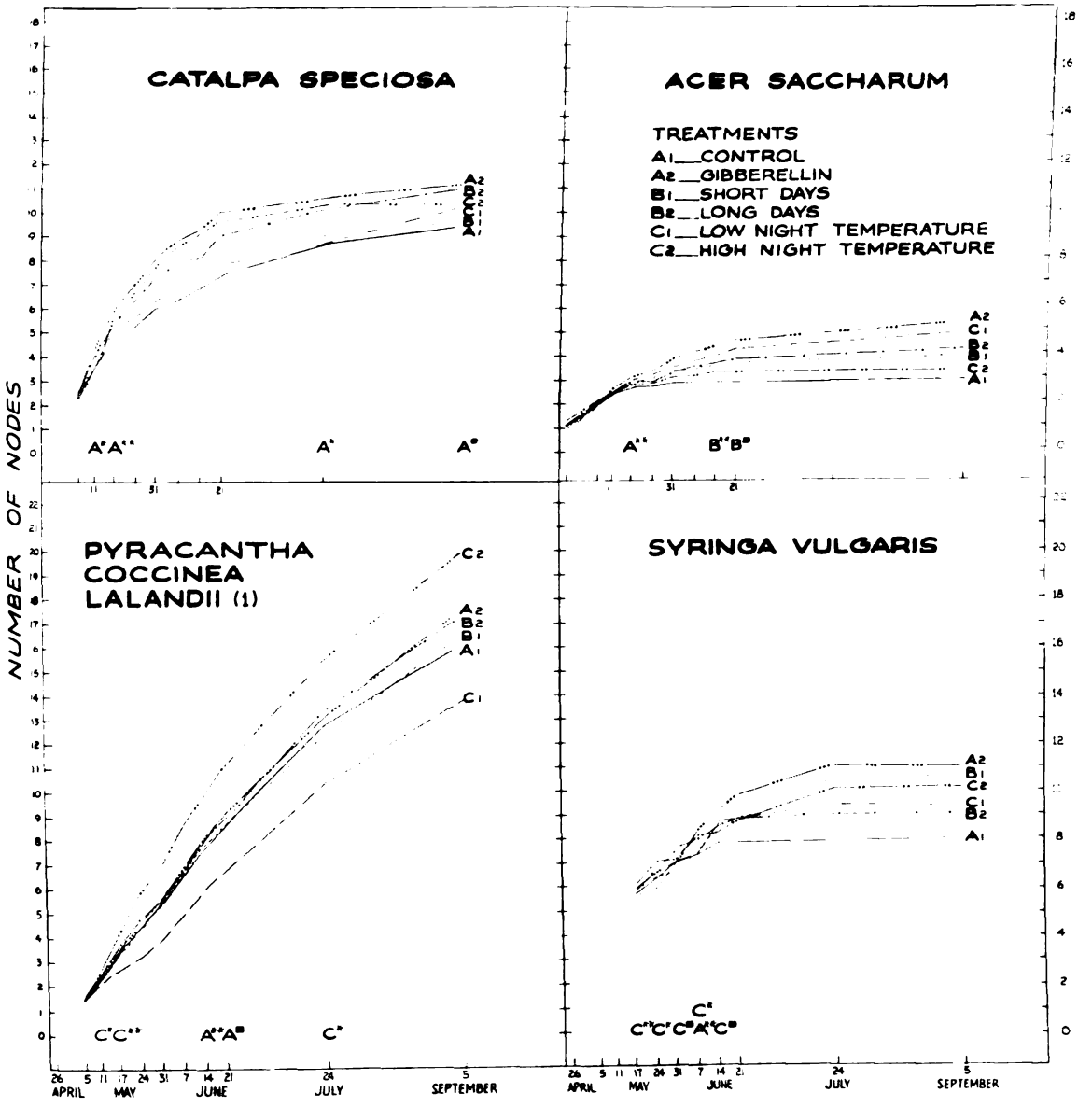
A greater shoot elongation to the long day regime was evident at the higher night temperatures throughout the growing season in Liriodendron and Viburnum (Figures 18 and 19). Shoot elongation of Pinus and Syringa, however, was greatest under the long day regime irrespective of the night temperatures (Figure 17, 21 and 23). Euonymus and Catalpa exhibited a greater shoot growth response to long days under the high night temperature as compared to the low night temperature regime only, on June 14 and May 24 respectively.

b. Node Formation

Node formation was altered by gibberellin (50 ppm) in all species at some period during the growing season as shown in Figures 8 and 9. The degree, rapidity and duration of response to gibberellin (0 or 50 ppm) as well as, photoperiod (9 or 18 hours) and night temperature (40 or 70°F) are shown. The response of node formation to the variables imposed followed a very similar pattern as found in shoot elongation. Generally, however, the differences were not as evident (Figures 5, 6, 8 and 9).

In contrast to the response of shoot elongation to gibberellin, node formation generally responded more rapidly to high night temperatures (e.g. Liriodendron and Syringa) and long days (e.g. Viburnum) than to the gibberellin treatment. Euonymus, Pyracantha, Catalpa and Acer approximated the same rapidity of response to gibberellin in both node formation and shoot elongation. The duration of response to the variable imposed follows a similar pattern in all species as exemplified by shoot extension.

Figure 8 Comparative Rates of Node Formation in Terminal Shoots of Catalpa, Acer, Pyracantha and Syringa as Influenced by Gibberellin, Photoperiod and Temperature.

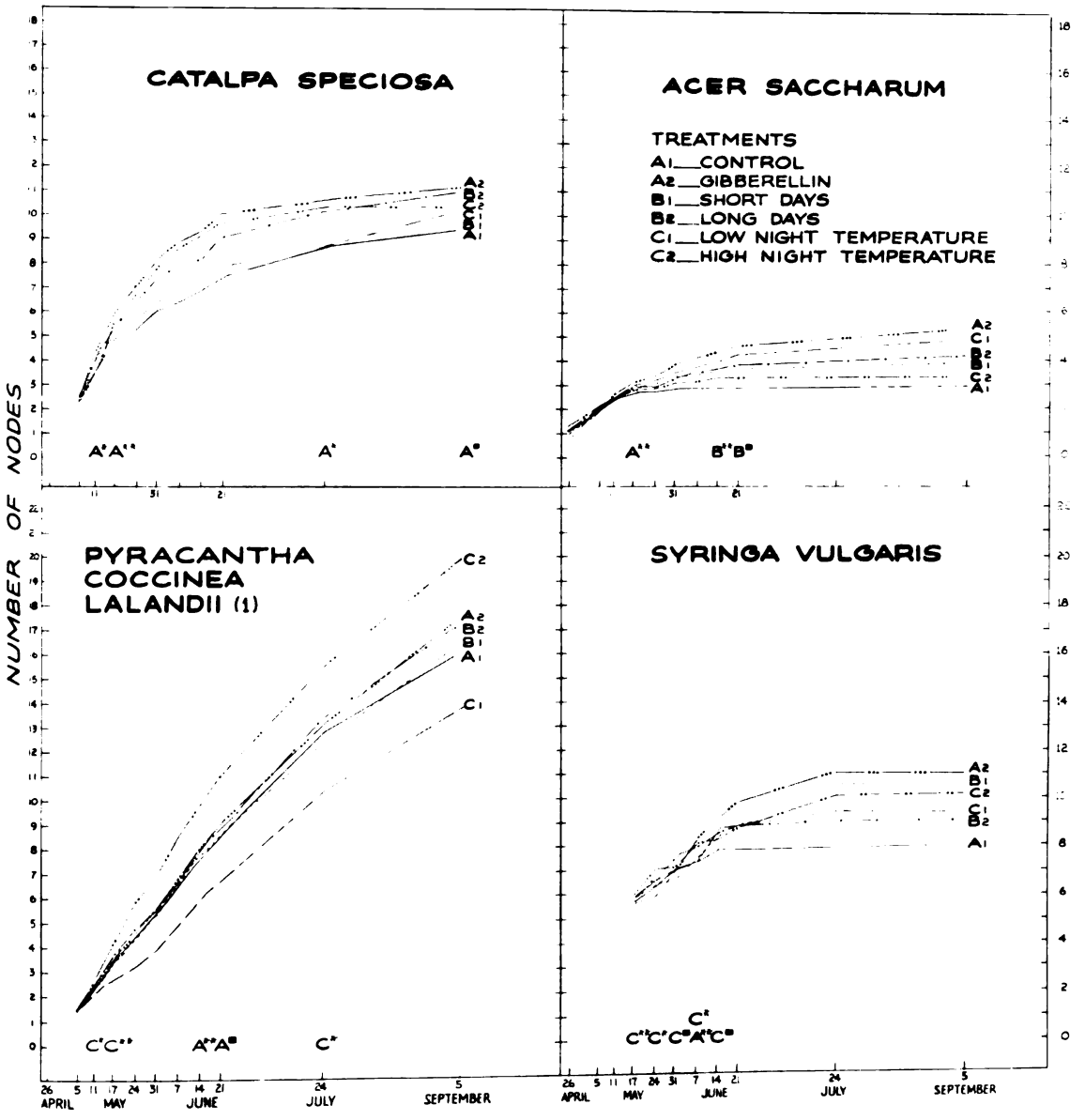


(1) MULTIPLY SCALE BY 2 TO OBTAIN TRUE VALUE

* OR ** SIGNIFICANT DIFFERENCE BETWEEN TREATMENTS SHOWN BY THE LETTERS (A,B OR C) AT THE 5 OR 1 PERCENT LEVELS, RESPECTIVELY, AT DATE INDICATED OR AT ALL DATES NOTED LATER IN THE SEASON. IF THE LETTER IS FOLLOWED BY A SQUARE (■), THE TREATMENT IS NO LONGER SIGNIFICANT.

Figure 8

Figure 8 Comparative Rates of Node Formation in Terminal Shoots of Catalpa, Acer, Pyracantha and Syringa as Influenced by Gibberellin, Photoperiod and Temperature.

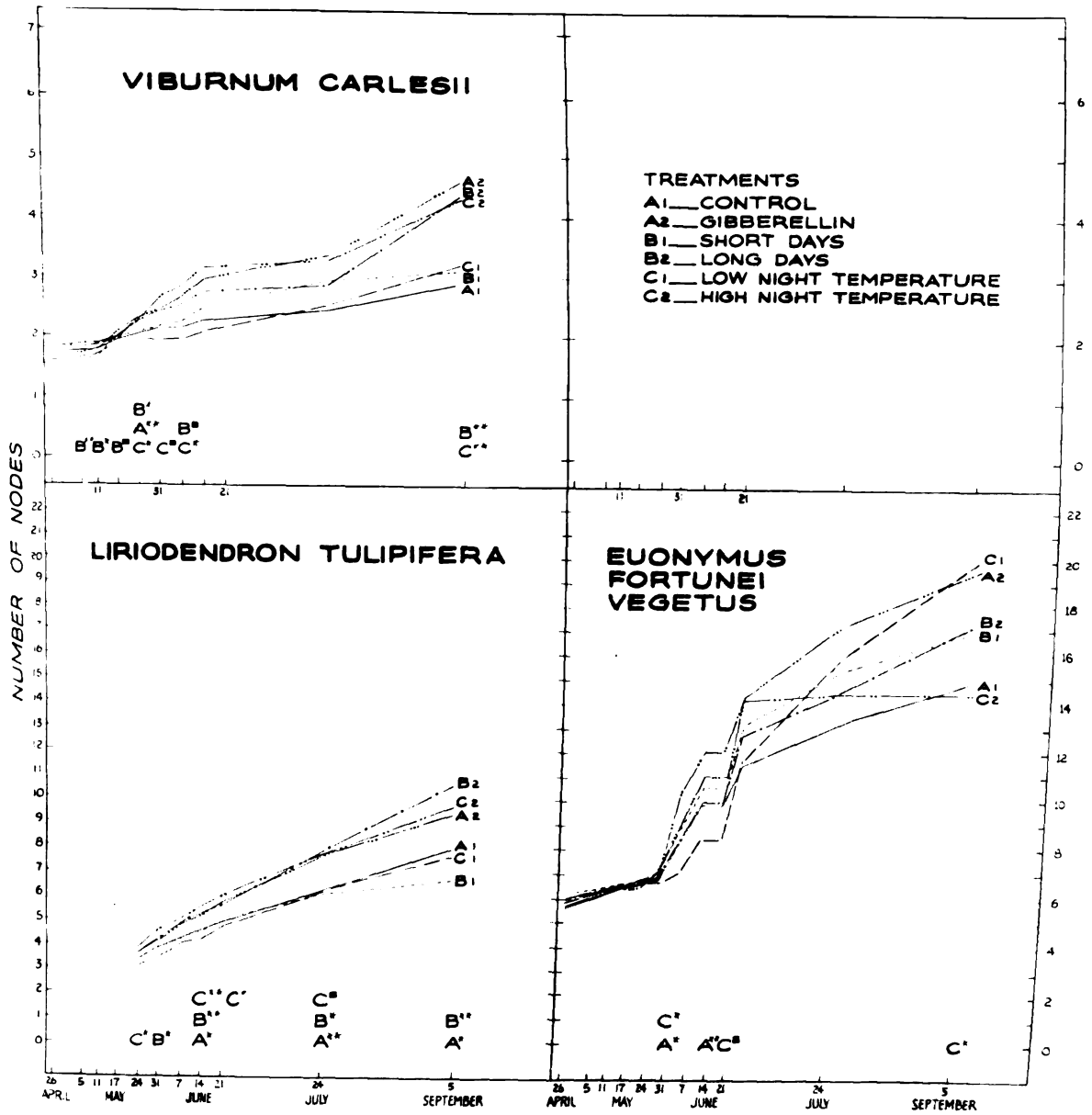


(1) MULTIPLY SCALE BY 2 TO OBTAIN TRUE VALUE

* OR ** SIGNIFICANT DIFFERENCE BETWEEN TREATMENTS SHOWN BY THE LETTERS (A, B OR C) AT THE 5 OR 1 PERCENT LEVELS, RESPECTIVELY, AT DATE INDICATED OR AT ALL DATES NOTED LATER IN THE SEASON. IF THE LETTER IS FOLLOWED BY A SQUARE (■), THE TREATMENT IS NO LONGER SIGNIFICANT.

Figure 8

Figure 9 Comparative Rates of Node Formation in Terminal Shoots of Viburnum, Liriodendron and Euonymus as Influenced by Gibberellin, Photoperiod and Temperature.



* OR ** SIGNIFICANT DIFFERENCE BETWEEN TREATMENTS SHOWN BY THE LETTERS (A, B OR C) AT THE 5 OR 1 PERCENT LEVELS, RESPECTIVELY, AT DATE INDICATED, OR AT ALL DATES NOTED LATER IN THE SEASON. IF THE LETTER IS FOLLOWED BY A SQUARE (■) THE TREATMENT IS NO LONGER SIGNIFICANT.

Figure 9

The significant response to the variables imposed early in the season, does not necessitate a significant response throughout the growing season. It is of interest to note that in Viburnum and Euonymus the response of shoot extension or node formation to night temperature (40 or 70°F) was not significant in mid-June but was significant earlier and later in the season (Figure 6).

The degree, variation in duration, and rapidity of response to gibberellin, (0 or 50 ppm) photoperiod (9 and 18 hours) or night temperature (40 or 70°F) illustrates that plants are not always physiologically receptive to these variables (Figures 5, 6, 8 and 9).

Interactions between gibberellin (50 ppm) and night temperature (40 or 70°F) as influencing node formation are shown in Figure 10. There is a marked similarity between Figures 7 and 10, illustrating again that the response in shoot elongation and node number to gibberellin (50 ppm) are very similar.

The differential response of node formation to gibberellin (50 ppm) under the different temperature regimes is well illustrated in Acer and Viburnum and less evident in Syringa and Euonymus. In contrast to the response of shoot elongation to gibberellin (50 ppm) at different night temperatures, node formation in Acer was greater under the low night temperature regime following gibberellin treatment. Syringa exhibited a greater response to gibberellin under the high night temperature during the latter part of the season only (Figure 10). The formation of nodes of Catalpa, Liriodendron and Pyracantha were affected similarly by gibberellin treatment irrespective of the night temperature imposed.

Figure 10 The Modifying Influence of Gibberellin on the Thermoperiodic Response of Node Formation in Viburnum, Acer, Syringa and Euonymus.

* or ** Significant interactions at the 5 or 1 percent levels, respectively.

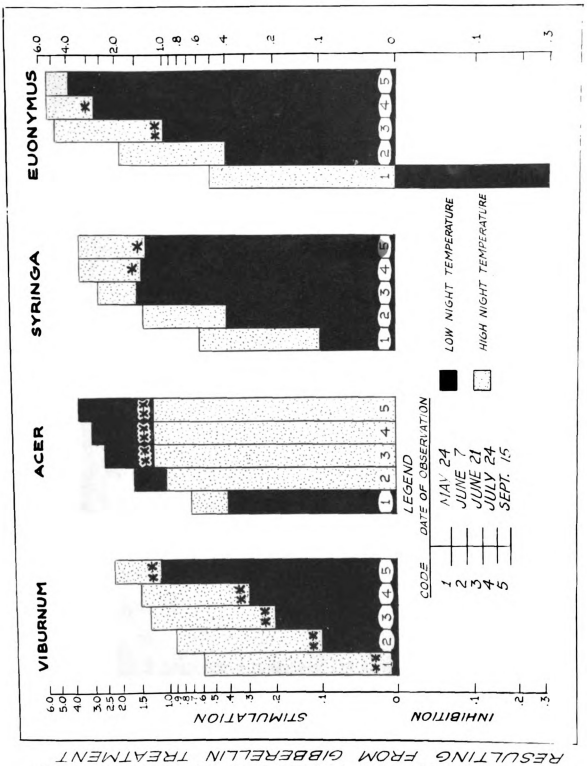

NODE FORMATION DIFFERENCES IN CENTIMETERS RESULTING FROM GIBBERELLIN TREATMENT
VIBURNUM
ACER
SYRINGA
EUONYMUS
STIMULATION
INHIBITION
LEGEND
DATE OF OBSERVATION
CODE
1 MAY 24
2 JUNE 7
3 JUNE 21
4 JULY 24
5 SEPT. 15
LOW NIGHT TEMPERATURE
HIGH NIGHT TEMPERATURE

Figure 10

The effects of gibberellin on node formation in the various woody plants were in almost all cases completely independent of the photoperiod imposed (9 or 18 hours). This is in marked contrast to the interaction observed between gibberellin (50 ppm) and night temperature (40 and 70°F) (Figure 10). This illustrates that the temperature modifies the response of plants to gibberellin to a greater extent than the photoperiod.

c. Degree of Replacement by Gibberellin of the Environmental Factors Which Influence Shoot Elongation and Node Formation

The effectiveness of gibberellin in replacing or partially replacing the response of shoot elongation or node formation to photoperiod (9 or 18 hours) or night temperature is (40 or 70°F) summarized in Figures 11 and 12. These figures illustrate conclusively that (1) gibberellin will replace or partially replace the effects of photoperiod or thermoperiod on shoot elongation and node formation and (2) the degree of replacement varies with species.

Gibberellin was more efficient in replacing the influence of long days than that of high temperatures on shoot extension, in Catalpa, Liriodendron and Viburnum. This relationship was not as apparent in Syringa. Viburnum in contrast to Catalpa and Liriodendron exhibits only a partial replacement earlier in the season but by July 24 complete replacement of the high night temperature by gibberellin was evident.

Shoot elongation in Pinus and Acer under low or high night temperatures is of interest. As shown in Figures 5 and 6, the shoot elongation of Pinus and Acer was greater under the low night temperatures

than the higher night temperature regime. Consequently the comparison, with the addition of gibberellin, should be between the response of high night temperature plants treated with gibberellin as compared to the low night temperature controls. As shown in Figure 11, gibberellin completely replaced the effects of low night temperatures in both Acer and Pinus. In the case of the latter species replacement was complete until June 14 at which time gibberellin became toxic. In Acer, gibberellin did not become toxic but continued to substitute for the low temperature affect throughout the season (Figures 21 and 23).

Gibberellin was not effective in substituting for the high night temperature response in Pyracantha (Figure 11) except on May 31. And yet this species responds markedly to high night temperatures. This is difficult to explain since most all plants that respond to photoperiod or thermoperiod respond to gibberellin.

Gibberellin replaced the effects of long days or high night temperature on node formation. In contrast to the substitution of gibberellin for the control of shoot elongation by photoperiod and temperature, only a partial replacement of nodal formation was evident in Liriodendron. Viburnum and Syringa grown at low night temperatures and treated with gibberellin simulated a node formation response which was typical at high night temperatures (Figure 12).

Gibberellin was effective in replacing the influence of low night temperature (which stimulated node formation, see Figure 9) in Euonymus for a major part of the season. However, in September, gibberellin applied to plants under the high night temperature was only partially effective in replacing the low night temperature response (Figure 12.) Possibly at the higher night temperatures an inhibitor accumulates in the

Figure 11 The Extent to Which Gibberellin Replaced the Photoperiodic and Thermoperiodic Response of Terminal Growth in Certain Woody Plants During the Growing Season.

* A significant replacement or partial replacement of the photoperiodic or thermoperiodic response by gibberellin at the 5 percent level.

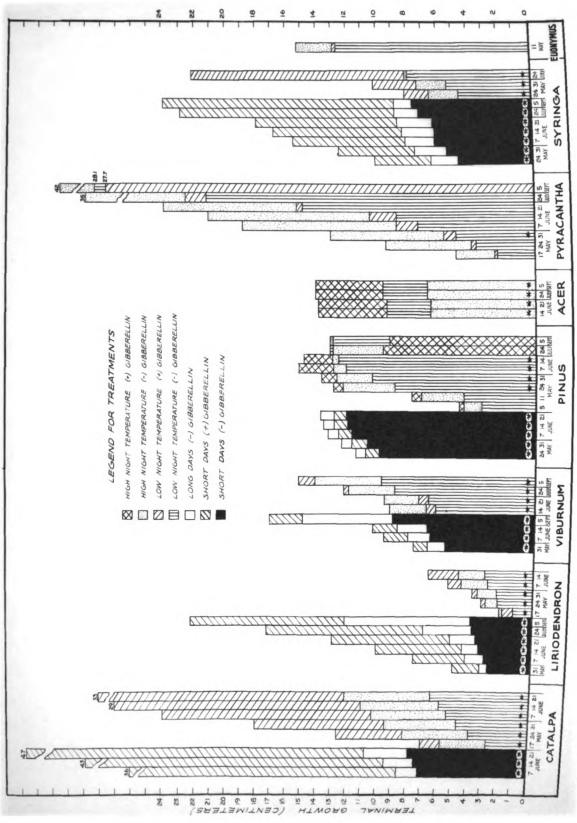

TERMINAL GROWTH (CENTIMETERS)
LEGEND FOR TREATMENTS
HIGH NIGHT TEMPERATURE (+) GIBBERELLIN
HIGH NIGHT TEMPERATURE (-) GIBBERELLIN
LOW NIGHT TEMPERATURE (+) GIBBERELLIN
LOW NIGHT TEMPERATURE (-) GIBBERELLIN
LONG DAYS (-) GIBBERELLIN
SHORT DAYS (+) GIBBERELLIN
SHORT DAYS (-) GIBBERELLIN
CATALPA
LIRIODENDRON
VIBURNUM
PINUS
ACER
PYRACANTHA
SYRINGA
EUONYMUS

Figure 11

Figure 12 The Extent to Which Gibberellin Replaced the Photoperiodic and Thermoperiodic Response of Node Formation in Certain Woody Plants During the Growing Season.

* A significant replacement or partial replacement of the photoperiodic or thermoperiodic response by gibberellin at the 5 percent level.

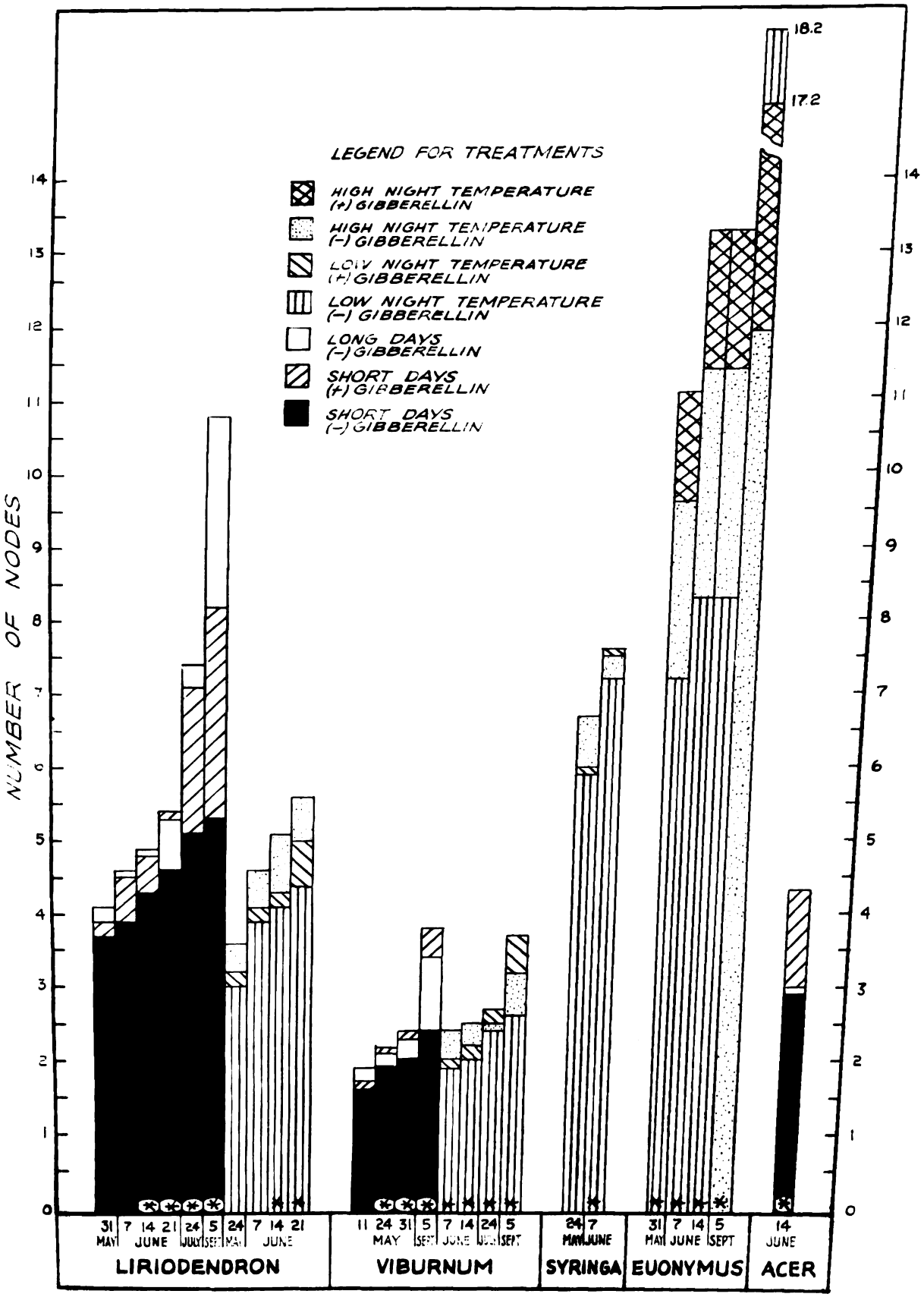

LEGEND FOR TREATMENTS
HIGH NIGHT TEMPERATURE (+) GIBBERELLIN
HIGH NIGHT TEMPERATURE (−) GIBBERELLIN
LOW NIGHT TEMPERATURE (+) GIBBERELLIN
LOW NIGHT TEMPERATURE (−) GIBBERELLIN
LONG DAYS (−) GIBBERELLIN
SHORT DAYS (+) GIBBERELLIN
SHORT DAYS (−) GIBBERELLIN
NUMBER OF NODES
18.2
17.2
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
31 MAY 7 14 21 JUNE 24 JULY 5 SEPT
24 MAY 7 14 21 JUNE
LIRIODENDRON
11 24 31 MAY 5 SEPT 7 14 JUNE 24 JUNE 5 SEPT
VIBURNUM
24 MAY 7 JUNE
SYRINGA
31 MAY 7 14 JUNE 5 SEPT
EUONYMUS
14 JUNE
ACER

Figure 12

buds which prevents the full expression of the gibberellins late in the season.

2. Modifications of the Induction and Cessation of Dormancy

a. Breaking of Dormancy in Buds

Dormancy in buds of woody plants, as influenced by gibberellin under various environmental conditions, is shown in Figure 13 and Table II. A statistical evaluation of the duration of the first flush of growth was possible in only Viburnum, Acer, Syringa and Euonymus. Catalpa failed to initiate a terminal bud which was well defined. Liriodendron and Pinus initiated a terminal bud in late May and early June, irrespective of treatment.

A statistical evaluation of the duration of the second flush of growth was not possible since the response was not consistent between replicates. Figure 13 illustrates the general relationship between treatments for the majority of the observation recorded.

The first flush of growth was statistically altered in Acer by all three variables imposed as shown in Table II. The modification in the duration of the first flush of growth however, can be attributed to only one of the eight treatments imposed, (short days and low temperatures in the presence of gibberellin). This three way interaction was significant for the duration of the first flush of growth in Acer, as shown in Figure 13 and 20. Apparently the principle factors responsible for the induction dormancy in Acer are over balanced under short days and low temperatures in the presence of an exogenous supply of gibberellin.

TABLE II Duration of the First Flush of Growth of Certain Woody Plants as Modified by Gibberellin, Photoperiod and Temperature

	Gibberellin		Photoperiod (hours)		Temperature (°F)	
	-	+	9	18	40	70
Genera						
Viburnum	34[a]	39	38	36	32	42
Acer	37	46**	46	37*	47	36**
Syringa	67	68	69	66	87	47**
Euonymus	24	22	24	23	23	23

a Values represent number of days after April 25.

* or ** Values for a given genera and treatment are significant at the 5 and 1 percent levels, respectively.

Figure 13 Modifying Influence of Gibberellin, Photoperiod and Temperature on the Number of Growth Flushes, Period of Dornancy and Shoot Extension of Acer, Euonymus, Syringa and Liriodendron.

Treatments

Code	Gibberellin (50 ppm)	Photoperiod (hours)	Night Temperature (^{o}F)
1	-	9	40
2	-	18	40
3	-	9	70
4	-	18	70
5	+	9	40
6	+	18	40
7	+	9	70
8	+	18	70

* Values represent shoot extension in centimeters from April 26 to September 15.

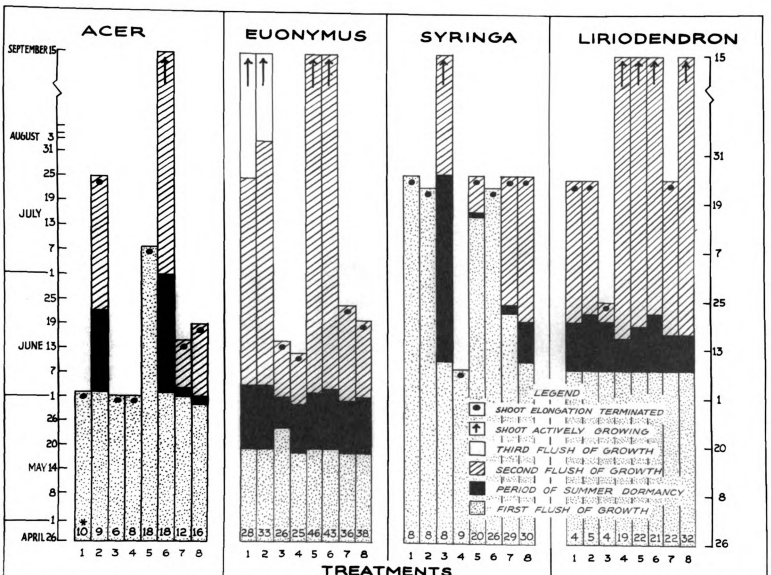

ACER
EUONYMUS
SYRINGA
LIRIODENDRON
SEPTEMBER 15
AUGUST 3
31
25
19
JULY
13
7
1
25
19
JUNE 13
7
1
26
20
MAY 14
8
1
APRIL 26
10 9 6 8 18 18 12 16
28 33 26 25 46 43 36 38
8 8 8 9 20 26 29 30
4 5 4 19 22 21 22 32
1 2 3 4 5 6 7 8
TREATMENTS
LEGEND
SHOOT ELONGATION TERMINATED
SHOOT ACTIVELY GROWING
THIRD FLUSH OF GROWTH
SECOND FLUSH OF GROWTH
PERIOD OF SUMMER DORMANCY
FIRST FLUSH OF GROWTH

Figure 13

The first flush of growth of the control plants grown under long days and low temperatures terminated in early June and produced a second flush of growth after 3 weeks of dormancy. The initial flush of the control plants under the low night temperature short day regime also terminated in early June, but failed to initiate a second flush of growth. Gibberellin applied to the long day-low temperature plants was not effective in delaying dormancy of the first flush of growth and had no effect on the duration of the dormancy period. The control plants under long day and low temperatures, terminated in late July, while dormancy of the second flush of growth of gibberellin treated plants under a comparable environment was delayed indefinitely. Gibberellin in the presence of low temperature and long days appears to be instrumental in delaying dormancy of the second flush of growth (Figure 13).

Under the high night temperature regime, gibberellin did not delay dormancy in Acer but was effective in causing a second flush of growth which terminated after 2 or 3 weeks.

It is of interest that in Euonymus, gibberellin was effective in preventing dormancy of the second flush of growth which normally occurs under low night temperatures but was ineffective under the high night temperatures. A third flush of growth was initiated in the control plants growing under the low night temperature, indicating that dormancy was not very intense (Figure 13).

Gibberellin was effective in breaking dormancy in buds of Syringa under the low night temperature-short day regime, but had no influence on plants under low night temperatures and long days. It would appear that in control plants grown under low night temperatures dormancy is

delayed, while under high night temperatures, dormancy is induced earlier in the season. The second flush of growth of the control plant under high night temperatures and short days would indicate that short days are instrumental in initiating a second flush of growth. Note that gibberellin was also more effective in initiating a second flush of growth, in the presence of the higher night temperatures and short days (Figure 13). A second flush of growth was induced by gibberellin under the high night temperature-long day regime but the period of dormancy was greater under this environment, indicating a more intense quiescence.

Dormancy of the first flush of growth in Liriodendron was apparently not too intense, since gibberellin caused continuous growth under all environments except short days and high temperature. Note that plants under the long day-high night temperature regime produced a second flush of growth which grew continuously. Cessation of growth of the second flush was delayed in control plants under the low night temperatures, irrespective of the photoperiod, and hastened in the short day-high temperature plants. A low night temperature appears to be instrumental in delaying dormancy.

It is of interest to note that in Syringa, although the duration of the first or second flush of growth was altered by the temperatures imposed (40 or 70°) the final hight was not altered (comparison of treatments 1, 2 and 3 with 4) (Figure 13). This growth response was also evident in Acer (comparison of treatment 1 with 2, 5 with 6) This relationship was not as evident in Euonymus for a longer duration of growth generally resulted in an increase in length of the shoot.

Termination of shoot elongation in Liriodendron, Catalpa and Pinus occasionally was caused by desiccation of the growing tip. This was only evident at the higher night temperatures in Catalpa. Gibberellin was not effective in altering the frequency of desiccation. Gibberellin was instrumental in causing desiccation of the buds in Pinus and Liriodendron, in all of the secondary shoots of Pinus irrespective of the environment, and in 6 out of a possible 24 terminal buds in Liriodendron, which was most evident under the higher night temperatures.

b. Breaking of Dormancy in Seeds

The effects of gibberellin on dormancy in seeds of Catalpa followed a similar pattern as was evidenced in the growth of Acer and Euonymus buds. A constant temperature of 68°F prevented germination almost completely, but with the addition of gibberellin the rate and total germination increased appreciably (Table III). Under the alternating day and night temperatures, the rate of germinating was also increased, but in comparison to the constant temperature regime, the total germination was not affected by gibberellin treatment. It would appear that the alternating day and night temperatures were instrumental in the synthesis of a growth promoting compound. Note the addition of gibberellin to seeds under the constant temperature gave a germination response between 11 and 14 days comparable to the non-treated controls under the alternating day and night temperature (Table III).

TABLE III Periodic and Total Germination of *Catalpa speciosa* Seed Within Specific Time Intervals After Seeding, as Modified by Temperature and Gibberellin

Gibberellin Seed Treatment (ppm)	Percent Germination Within Each Time Interval in Days After Seeding					
	1-10	11-14	15-17	18-21	22-28	Total Germination
			68° F Constant Temperature			
0	**	2.3	2.7	2.7	5.7	13.4
1		2.3	3.3	5.0	2.3	12.9
10		4.0	15.3	15.7	5.7	40.7
100		9.7	20.0	12.0	4.0	45.7
1000		22.7	25.0	7.0	3.3	58.0
			86° - 68° F Alternating Day-Night Temperatures			
0	3.3	21.7	56.0	8.3	**	89.3
1	2.7	21.0	57.7	6.7		88.1
10	7.0	67.7	12.7	7.7		95.1
100	7.3	61.0	21.0	3.3		92.6
1000	9.3	76.6	10.0	2.3		98.2

* Values connected by a solid line are not significantly different at the 5 percent level.

** No seeds germinated within this time interval.

3. Accumulative Vegetative Modifications by Gibberellin

a. Shoot Extension and Dry Weight of Shoots

Numerous measurements of the shoot growth response to gibberellin (0 or 50 ppm), photoperiod (9 or 18 hours), or night temperature (40 or 70°F) are shown in Figure 14 along with other data to be discussed later. It is apparent that the growth of shoots respond dramatically to gibberellin treatment in all species except Pinus and Pyracantha. Note that the shoot extension (1) shoot-root ratio (6) and the dry weight of the new shoot wood (9) increased in most of the species studied following gibberellin treatment (50 ppm). The number of nodes initiated (3) and the internode length (4) were also increased by gibberellin when a significant response occurred, but the frequency in response among species was reduced. The dry weight per centimeter of the new shoot growth (8) and the stem diameter (2) were not greatly altered by gibberellin treatment. However, when a significant response to gibberellin did occur, the dry weight per centimeter (8) was reduced in Catalpa but was increased in Pinus. The stem diameter (2) was generally increased whenever a significant response to gibberellin was evident (e.g. Pinus, Liriodendron, Viburnum) except with Catalpa in which the diameter of the shoot was less (Figure 14).

In all species, if a significant response to photoperiod occurred, long days resulted in an increase in shoot growth (9) were the most frequent growth responses to be affected by long days. This was particularly evident in Liriodendron, Viburnum and Syringa.

Figure 14 Growth Differences of Certain Woody Plants, that Developed Between April 26 and September 15, as Influenced by Gibberellin, Photoperiod and Temperature.

Legend

1. Shoot Extension
2. Stem Diameter
3. Node Number
4. Internode Length
5. Leaf Area Per Plant
6. Shoot-Root Ratio of New Wood
7. Dry Weight Per Leaf
8. Dry Weight Per Centimeter of New Shoot Growth
9. Dry Weight of New Shoot Growth
10. Dry Weight of Old Shoot Growth
11. Dry Weight of New Root Growth
12. Dry Weight of Old Root Growth
13. Total Dry Weight Per Plant

* Only values exhibiting significant growth differences between gibberellin (50 ppm) and no gibberellin, short (9 hours) and long days (18 hours), and low ($40^{o}F$) and high night temperatures ($70^{o}F$) are included in the figure.

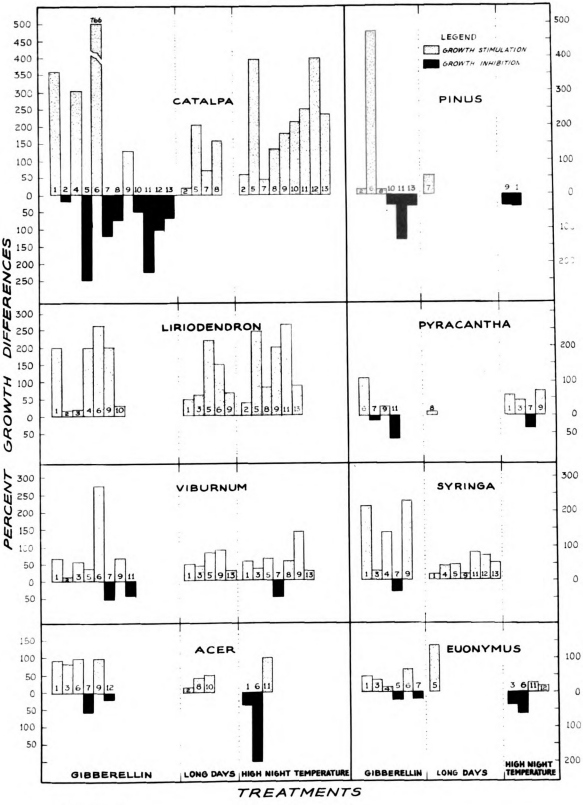

CATALPA
PINUS
LIRIODENDRON
PYRACANTHA
VIBURNUM
SYRINGA
ACER
EUONYMUS
LEGEND
GROWTH STIMULATION
GROWTH INHIBITION
PERCENT GROWTH DIFFERENCES
GIBBERELLIN
LONG DAYS
HIGH NIGHT TEMPERATURE
TREATMENTS

Figure 14

High night temperatures generally altered the growth of the shoots in a greater number of species than the long day regime. The dry weight accumulation of the new shoot growth (9) was markedly affected by high night temperatures, and was significantly increased in Catalpa, Liriodendron, Viburnum and Pyracantha, but was inhibited in Acer and Pinus. Node number (3) and dry weight per centimeter of the new shoot growth (8) were not as markedly affected by high night temperature, although differences were apparent in 3 of the species studied.

Dry weight of the old shoot wood was not altered to any great extent by any of the variables imposed. However, gibberellin was instrumental in inhibiting dry matter accumulation in the old shoot wood of Catalpa and Pinus. In contrast, an increase was realized in Liriodendron. Long days or high night temperatures increased the dry weight accumulation in the old shoot wood of Acer and Catalpa, respectively. It became apparent that the majority of the growth phenomena affected by either gibberellin, long days or high night temperatures as compared to no gibberellin, short days and low night temperatures, are associated with the growth and development of the shoot.

b. Leaf Area and Dry Weight of Leaves

In contrast to the increase in growth of shoots, dry weight accumulation in leaves of all species (except Liriodendron and Pinus) was inhibited following gibberellin treatment (Figure 14). Although dry matter accumulation of leaves was inhibited, the increase in the number of leaves initiated (3) compensated for the smaller leaves produced in Viburnum, Acer and Syringa (Figures 19, 20 and 23). This compensatory

affect was not evident in Catalpa, Pyracantha and Euonymus (Figure 17, 22 and 24). Long days or high temperature, in contrast to short days or low temperature, generally caused an increase in leaf area per plant (5) and leaf dry weight (7) in Catalpa (Figure 17), while only an increase in the leaf area per plant (5) was evident in Liriodendron and Viburnum (Figure 18 and 19).

c. Root Dry Weight

Associated with a general inhibition of dry weight accumulation in leaves by gibberellin was an inhibition of the dry weight accumulated in the newly initiated roots of some species. This was particularly evident in Catalpa and Pinus and less so in Viburnum and Pyracantha (Figure 14, 17, 21, 19 and 22). Liriodendron, Syringa and Euonymus were not affected (Figures 18, 23 and 24). Two species (Catalpa and Acer) exhibited an inhibition in dry weight accumulation in the old root wood following gibberellin treatment. The inhibition in Catalpa was very evident while Acer was only slightly affected.

Long days, as compared to short days, had little or no influence on the dry matter accumulation in the species studied, except in Syringa in which an increase in both old and new root dry weight was realized under long days (Figure 23). High night temperatures were much more effective in altering dry matter accumulation in roots. As shown in Figure 14, the new roots accumulated a greater quantity of dry matter at the higher, as compared to the lower, temperature in Catalpa, Liriodendron, Acer and Euonymus, while the other species were not

affected (Figures 17, 18, 20 and 24). Dry weight of the old root wood was increased by a high night temperature as compared to a low night temperature in only Catalpa and Euonymus.

d. Total Dry Weight

The total dry weight accumulation as modified by gibberellin (0 or 50 ppm), photoperiod (9 or 18 hours), or temperature (40 or 70°F) is shown in Figure 14. It is of interest that not one species treated with gibberellin exhibited an increase in total dry weight accumulation. It appears that there is an accumulation of dry weight in the shoot at the expense of the roots and leaves. Liriodendron, in contrast to all other species, exhibited no inhibition in growth following gibberellin treatment, and yet there was no increase in total dry weight. In contrast to other species the total dry matter accumulation in Catalpa and Pinus was inhibited by gibberellin.

Total dry weight accumulation in Viburnum and Syringa was increased to a greater extent under long than short days. High night temperature, as compared to low night temperature, stimulated dry weight increases in Liriodendron, Viburnum and Catalpa.

Figure 15 summarizes the interaction between gibberellin and photoperiod or gibberellin and temperature for the various vegetative responses. It is of interest to note that under the short day regime there was less inhibition (e.g. Catalpa) or a greater stimulation in the growth index (Liriodendron, Pinus and Euonymus) following gibberellin treatment. This generalization holds true for the growth responses under low night temperatures. For example, the inhibition of growth at high night

temperatures by gibberellin is reduced (e.g. Catalpa) or results in a greater stimulation of growth under low night temperature in Liriodendron, Acer (node number (3) and shoot-root ratio (6)), Pinus and Euonymus (stem diameter (2) and internode length (4)). In Viburnum, Pyracantha and Syringa this relationship is not evident since a greater response to gibberellin is observed at the higher than under the lower night temperature regime.

A perusal of Figure 15 shows a greater inhibition of growth following gibberellin treatment occurring more frequently under high temperatures or long days than under low night temperatures or short days. Conversely a greater stimulation in growth occurs, in general, under short days or low temperature as compared to long days or high temperatures. The growth stimulation of gibberellin under low night temperatures occurs most frequently when shoot extension (1) node number (3) shoot-root ratio (6) and dry weight of the new shoot growth are used as criteria for response. Under short days the growth stimulation of gibberellin occurs most frequently in number of nodes initiated (3) and leaf area per plant (5). Conversely the greatest frequency of inhibition of growth under high night temperature is with respect to stem diameter (2), dry weight of the old root growth (12), and total dry weight per plant (13). Inhibition from gibberellin treatment under long days was most frequent in the initiate of nodes (3), leaf area per plant (5), and dry weight per leaf (7).

The modifying influence of low and high temperatures or long and short days on the growth responses to gibberellin is puzzling. It would appear that under short days an inhibitor is modifying the influence

Figure 15 The Modifying Influence of Gibberellin on the Photoperiodic and Thermoperiodic Responses of Various Plant Parts in Certain Woody Plants.*

* Only growth responses exhibiting significant interactions between gibberellin (0 or 50 ppm) and photoperiod (9 or 18 hours) or gibberellin (0 or 50 ppm) and night temperature (40 or 70°F) are included in this figure.

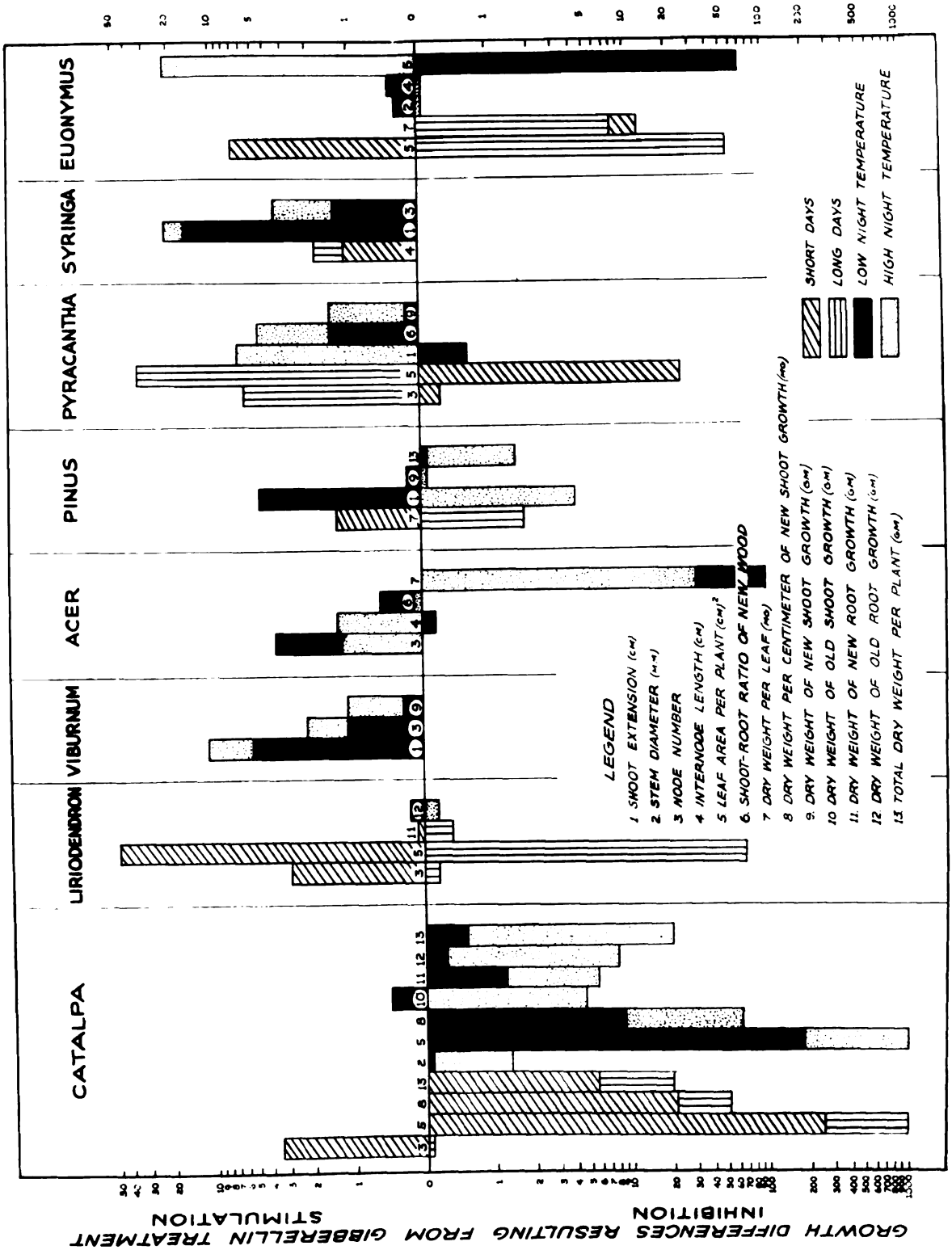

GROWTH DIFFERENCES RESULTING FROM GIBBERELLIN TREATMENT
INHIBITION
STIMULATION
CATALPA
LIRIODENDRON
VIBURNUM
ACER
PINUS
PYRACANTHA
SYRINGA
EUONYMUS
LEGEND
1 SHOOT EXTENSION (cm)
2 STEM DIAMETER (mm)
3 NODE NUMBER
4 INTERNODE LENGTH (cm)
5 LEAF AREA PER PLANT (cm)²
6 SHOOT-ROOT RATIO OF NEW WOOD
7 DRY WEIGHT PER LEAF (mg)
8 DRY WEIGHT PER CENTIMETER OF NEW SHOOT GROWTH (mg)
9 DRY WEIGHT OF NEW SHOOT GROWTH (gm)
10 DRY WEIGHT OF OLD SHOOT GROWTH (gm)
11 DRY WEIGHT OF NEW ROOT GROWTH (gm)
12 DRY WEIGHT OF OLD ROOT GROWTH (gm)
13 TOTAL DRY WEIGHT PER PLANT (gm)
SHORT DAYS
LONG DAYS
LOW NIGHT TEMPERATURE
HIGH NIGHT TEMPERATURE

Figure 15

Figure 15 The Modifying Influence of Gibberellin on the Photoperiodic and Thermoperiodic Responses of Various Plant Parts in Certain Woody Plants.*

* Only growth responses exhibiting significant interactions between gibberellin (0 or 50 ppm) and photoperiod (9 or 18 hours) or gibberellin (0 or 50 ppm) and night temperature (40 or 70°F) are included in this figure.

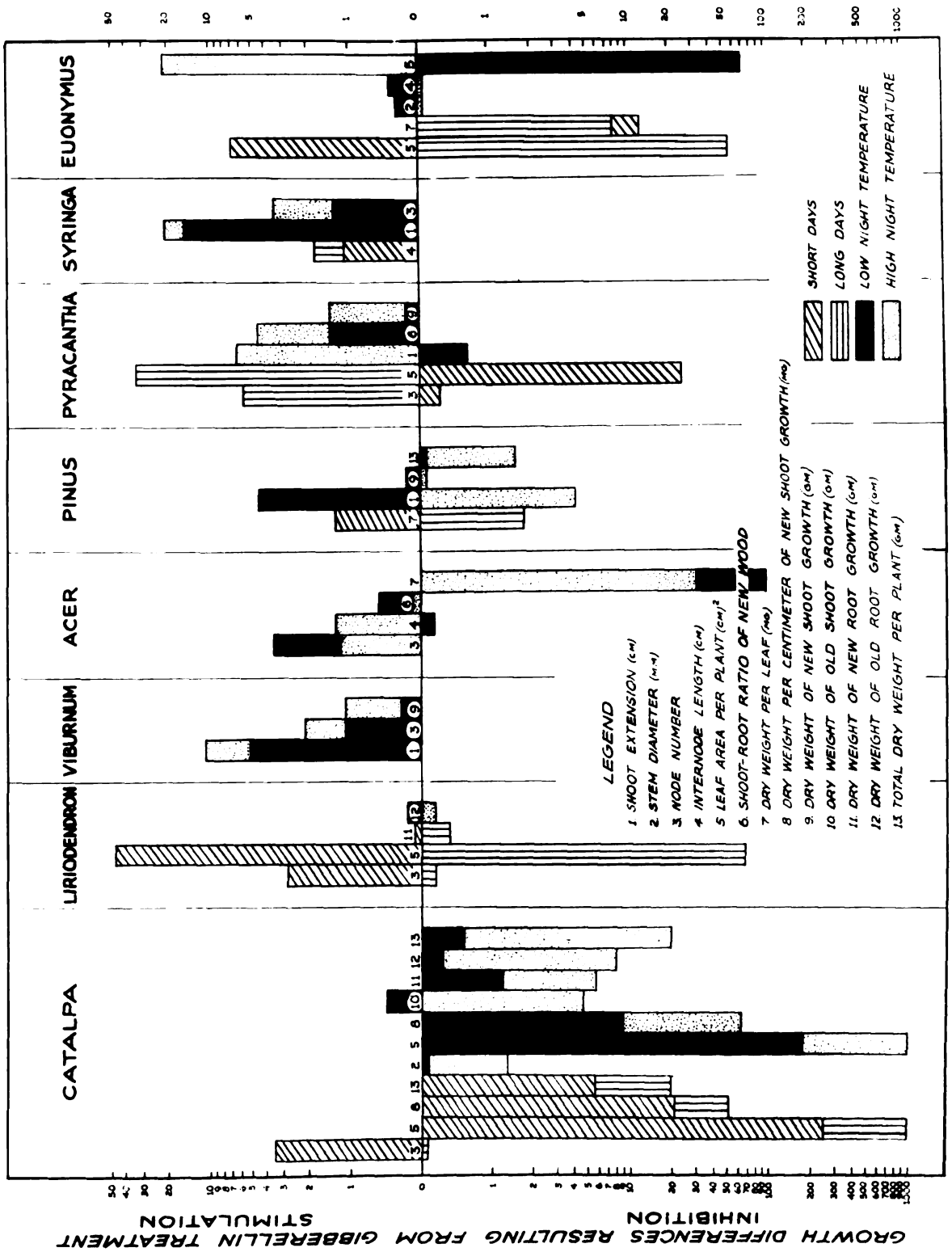
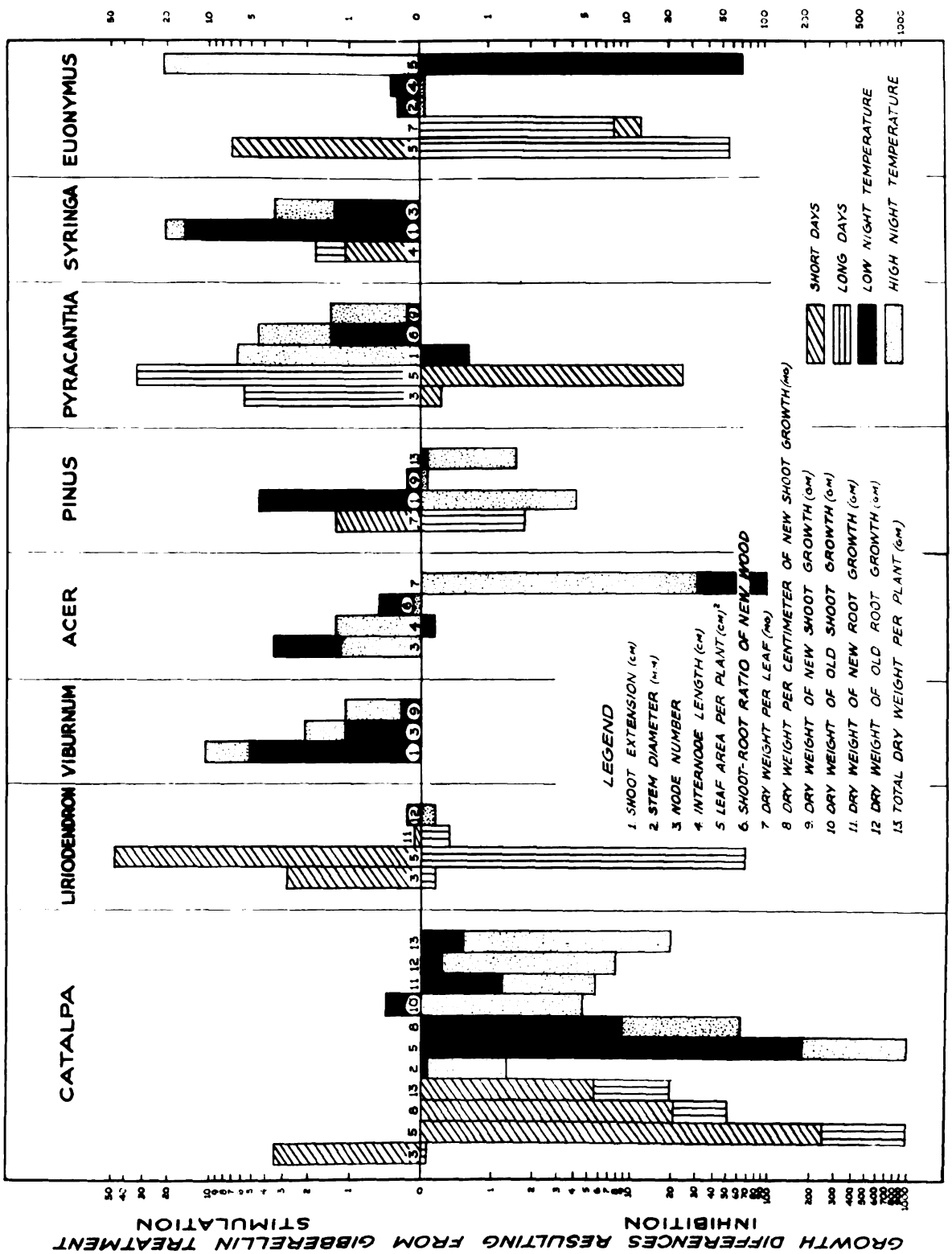

GROWTH DIFFERENCES RESULTING FROM GIBBERELLIN TREATMENT
INHIBITION
STIMULATION
CATALPA
LIRIODENDRON
VIBURNUM
ACER
PINUS
PYRACANTHA
SYRINGA
EUONYMUS
LEGEND
1 SHOOT EXTENSION (cm)
2 STEM DIAMETER (mm)
3 NODE NUMBER
4 INTERNODE LENGTH (cm)
5 LEAF AREA PER PLANT (cm)²
6 SHOOT-ROOT RATIO OF NEW WOOD
7 DRY WEIGHT PER LEAF (mg)
8 DRY WEIGHT PER CENTIMETER OF NEW SHOOT GROWTH (mg)
9 DRY WEIGHT OF NEW SHOOT GROWTH (gm)
10 DRY WEIGHT OF OLD SHOOT GROWTH (gm)
11 DRY WEIGHT OF NEW ROOT GROWTH (gm)
12 DRY WEIGHT OF OLD ROOT GROWTH (gm)
13 TOTAL DRY WEIGHT PER PLANT (gm)
SHORT DAYS
LONG DAYS
LOW NIGHT TEMPERATURE
HIGH NIGHT TEMPERATURE

Figure 15

Figure 15 The Modifying Influence of Gibberellin on the Photoperiodic and Thermoperiodic Responses of Various Plant Parts in Certain Woody Plants.*

* Only growth responses exhibiting significant interactions between gibberellin (0 or 50 ppm) and photoperiod (9 or 18 hours) or gibberellin (0 or 50 ppm) and night temperature (40 or 70°F) are included in this figure.


GROWTH DIFFERENCES RESULTING FROM GIBBERELLIN TREATMENT
INHIBITION
STIMULATION
CATALPA
LIRIODENDRON
VIBURNUM
ACER
PINUS
PYRACANTHA
SYRINGA
EUONYMUS
LEGEND
1 SHOOT EXTENSION (cm)
2 STEM DIAMETER (mm)
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9 DRY WEIGHT OF NEW SHOOT GROWTH (gm)
10 DRY WEIGHT OF OLD SHOOT GROWTH (gm)
11 DRY WEIGHT OF NEW ROOT GROWTH (gm)
12 DRY WEIGHT OF OLD ROOT GROWTH (gm)
13 TOTAL DRY WEIGHT PER PLANT (gm)
SHORT DAYS
LONG DAYS
LOW NIGHT TEMPERATURE
HIGH NIGHT TEMPERATURE

Figure 15

of gibberellin, while under long days the inhibition of gibberellin is not apparent and consequently results in a greater inhibition of dry weight accumulation (e.g. Catalpa, Pinus and Euonymus). Low night temperatures correspond to short days in that an inhibitor under this environment appears to prevent the full expression of gibberellin in Catalpa, Liriodendron, Viburnum, Pyracantha, Syringa and Euonymus (stem diameter (2) internode length (4)). In contrast high night temperatures generally inhibit the action of gibberellin in Acer and Euonymus (leaf area per plant (5)).

e. Degree of Replacement by Gibberellin of Environmental Factors Which Influence the Accumulative Vegetative Growth Responses

The extent of the replacement of the thermoperiodic and photoperiodic responses by gibberellin is shown in Figure 16. The plant parts responding to a photoperiodic or thermoperiodic treatment generally were associated with shoot development (Figure 14). As shown in Figure 16, gibberellin partially or completely substituted for long days or high temperatures in Catalpa, Liriodendron, Viburnum and Syringa. Low night temperatures which stimulated the shoot growth of Acer and Euonymus to a greater extent than high night temperatures could be partially replaced by gibberellin treatment.

It is of interest to compare Figures 14 and 16. As shown in Figure 14 all species except Pyracantha, Viburnum and Pinus exhibited an increase in dry weight of the new root under long day and/or high night temperatures in comparison to short days and low night temperatures. It is apparent that gibberellin is ineffective in replacing the influence of the above

environmental factors (Figure 16) except in Liriodendron in which a partial replacement was accomplished. The dry weight per centimeter of the new shoot growth is also increased by high night temperatures and/or long days in Catalpa, Liriodendron, Pyracantha and Acer (Figure 14). Here again gibberellin is completely ineffective in substituting for this response.

Total dry weight was also increased in the former three species in addition to Syringa under high night temperatures while the growth of the latter was also increased under long days (Figure 14). A persual of Figure 16 again illustrates the inability of gibberellin to substitute for certain vegetative phenomena controlled by environmental factors. Generally, gibberellin was effective in substituting for the environmental control of shoot growth, but had little or no influence in replacing the effects of long days or high night temperature on growth of roots, dry weight per centimeter of new shoot growth, or total dry weight per plant.

Figure 16 The Extent to Which Gibberellin Replaced the Photoperiodic and Thermoperiodic Responses of Specific Vegetative Phenomena in Certain Woody Plants.

* A significant replacement or partial replacement of the photoperiodic or thermoperiodic response by gibberellin at the 5 percent level.

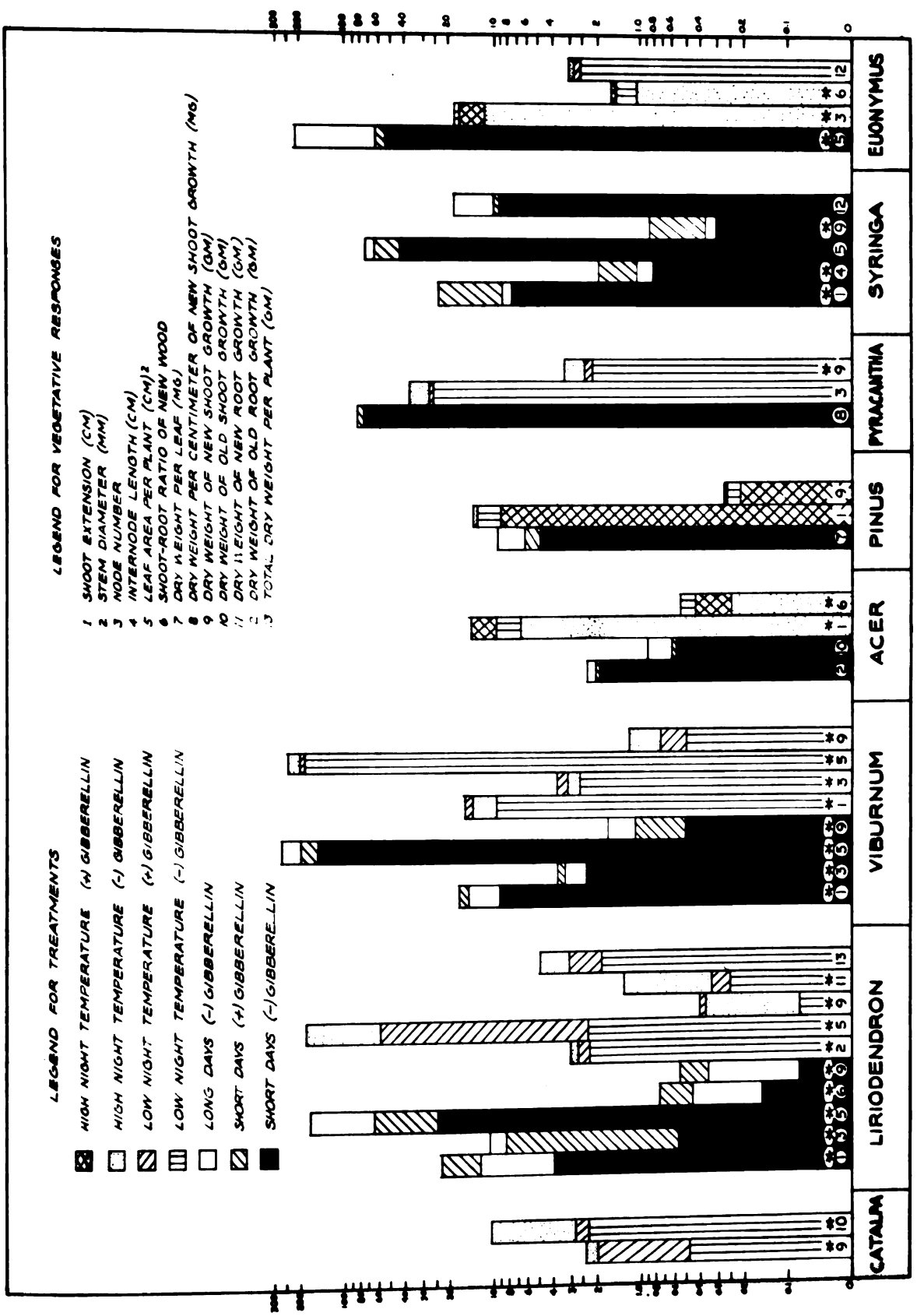

LEGEND FOR TREATMENTS
HIGH NIGHT TEMPERATURE (+) GIBBERELLIN
HIGH NIGHT TEMPERATURE (-) GIBBERELLIN
LOW NIGHT TEMPERATURE (+) GIBBERELLIN
LOW NIGHT TEMPERATURE (-) GIBBERELLIN
LONG DAYS (-) GIBBERELLIN
SHORT DAYS (+) GIBBERELLIN
SHORT DAYS (-) GIBBERELLIN
LEGEND FOR VEGETATIVE RESPONSES
1 SHOOT EXTENSION (CM)
2 STEM DIAMETER (MM)
3 NODE NUMBER
4 INTERNODE LENGTH (CM)
5 LEAF AREA PER PLANT (CM)²
6 SHOOT-ROOT RATIO OF NEW WOOD
7 DRY WEIGHT PER LEAF (MG)
8 DRY WEIGHT PER CENTIMETER OF NEW SHOOT GROWTH (MG)
9 DRY WEIGHT OF NEW SHOOT GROWTH (GM)
10 DRY WEIGHT OF OLD SHOOT GROWTH (GM)
11 DRY WEIGHT OF NEW ROOT GROWTH (GM)
12 DRY WEIGHT OF OLD ROOT GROWTH (GM)
13 TOTAL DRY WEIGHT PER PLANT (GM)
CATALPA
LIRIODENDRON
VIBURNUM
ACER
PINUS
PYRACANTHA
SYRINGA
EUONYMUS

Figure 16

Figure 16 The Extent to Which Gibberellin Replaced the Photoperiodic and Thermoperiodic Responses of Specific Vegetative Phenomena in Certain Woody Plants.

* A significant replacement or partial replacement of the photoperiodic or thermoperiodic response by gibberellin at the 5 percent level.

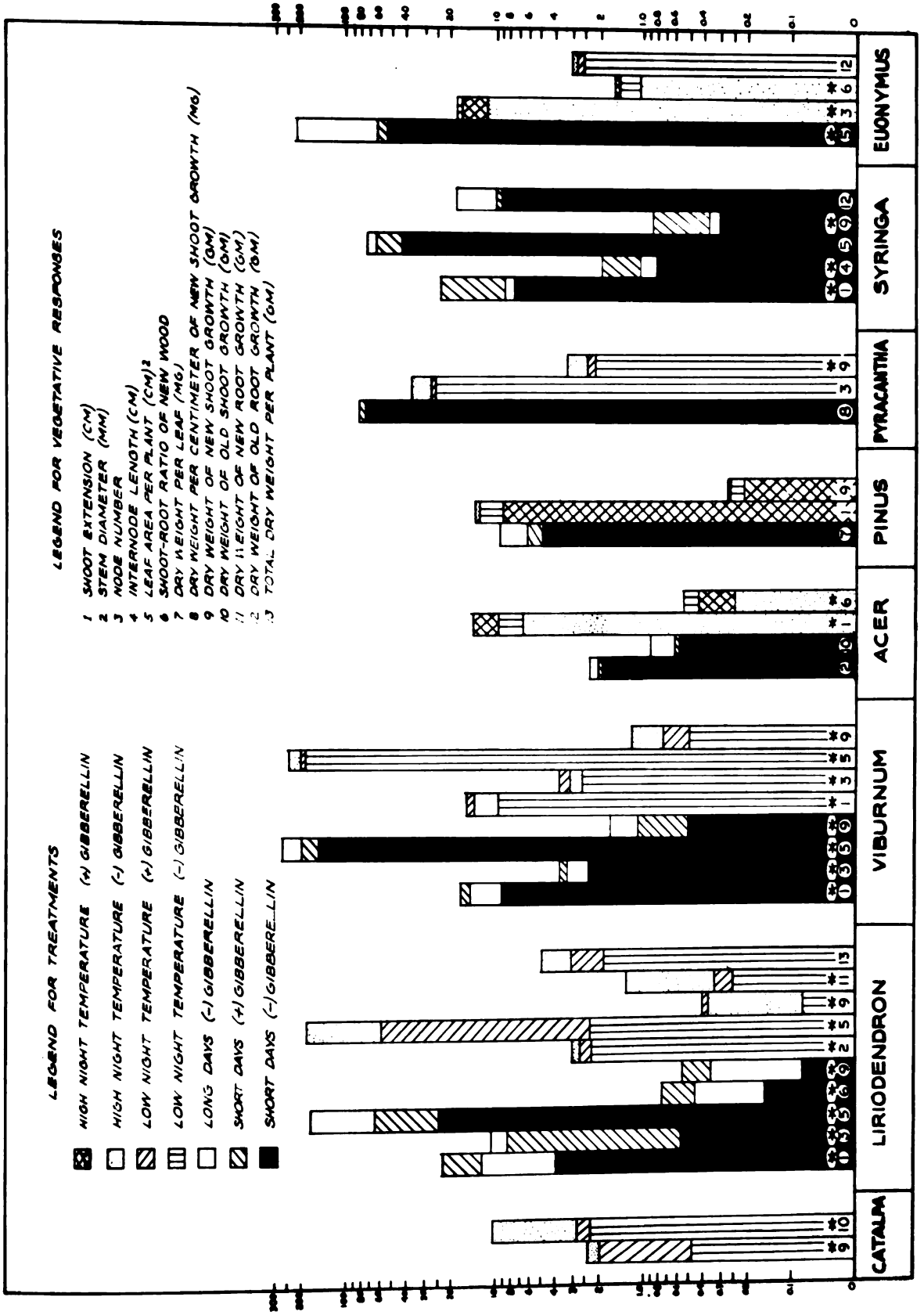

LEGEND FOR TREATMENTS
HIGH NIGHT TEMPERATURE (+) GIBBERELLIN
HIGH NIGHT TEMPERATURE (-) GIBBERELLIN
LOW NIGHT TEMPERATURE (+) GIBBERELLIN
LOW NIGHT TEMPERATURE (-) GIBBERELLIN
LONG DAYS (-) GIBBERELLIN
SHORT DAYS (+) GIBBERELLIN
SHORT DAYS (-) GIBBERELLIN
LEGEND FOR VEGETATIVE RESPONSES
1 SHOOT EXTENSION (CM)
2 STEM DIAMETER (MM)
3 NODE NUMBER
4 INTERNODE LENGTH (CM)
5 LEAF AREA PER PLANT (CM)²
6 SHOOT-ROOT RATIO OF NEW WOOD
7 DRY WEIGHT PER LEAF (MG)
8 DRY WEIGHT PER CENTIMETER OF NEW SHOOT GROWTH (MG)
9 DRY WEIGHT OF NEW SHOOT GROWTH (GM)
10 DRY WEIGHT OF OLD SHOOT GROWTH (GM)
11 DRY WEIGHT OF NEW ROOT GROWTH (GM)
12 DRY WEIGHT OF OLD ROOT GROWTH (GM)
13 TOTAL DRY WEIGHT PER PLANT (GM)
CATALPA
LIRIODENDRON
VIBURNUM
ACER
PINUS
PYRACANTHA
SYRINGA
EUONYMUS

Figure 16

Figure 17 - 24 Modifying Influences of Gibberellin, Photoperiod and Temperature on Root, Shoot and Leaf Development in Certain Woody Plants

Legend for Figures 17 through 24

Woody Plants

	Figure
Catalpa speciosa	17
Liriodendron Tulipifera	18
Viburnum Carlesii	19
Acer saccharum	20
Pinus sylvestris	21
Pyracantha coccinea Lalandii	22
Syringa vulgaris	23
Euonymus Fortunei vegetus	24

Treatments

Code	Gibberellin (50 ppm)	Photoperiod (hours)	Night Temperature (^{o}F)
1	-	9	40
2	-	18	40
3	-	9	70
4	-	18	70
5	+	9	40
6	+	18	40
7	+	9	70
8	+	18	70

Leaf Arrangement

Left to Right, one leaf was collected from each node of a representative plant for each treatment, from the proximal to the distal end of the new shoot.

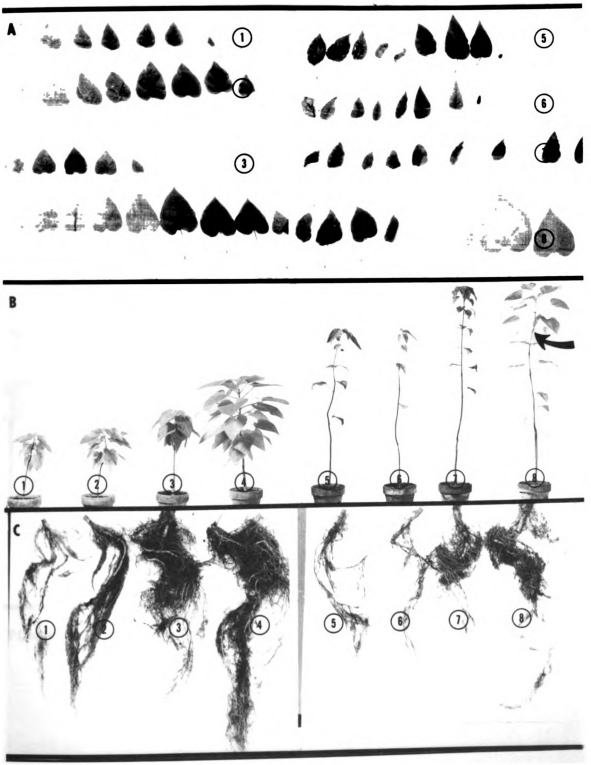


Figure 17. Catalpa speciosa

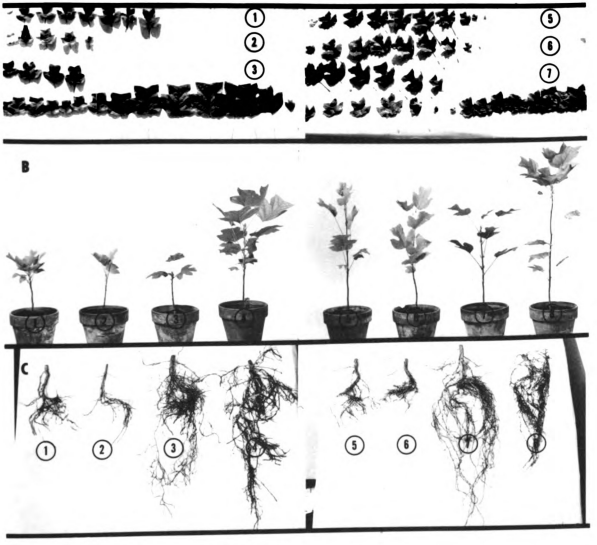


Figure 18. Liriodendron Tulipifera

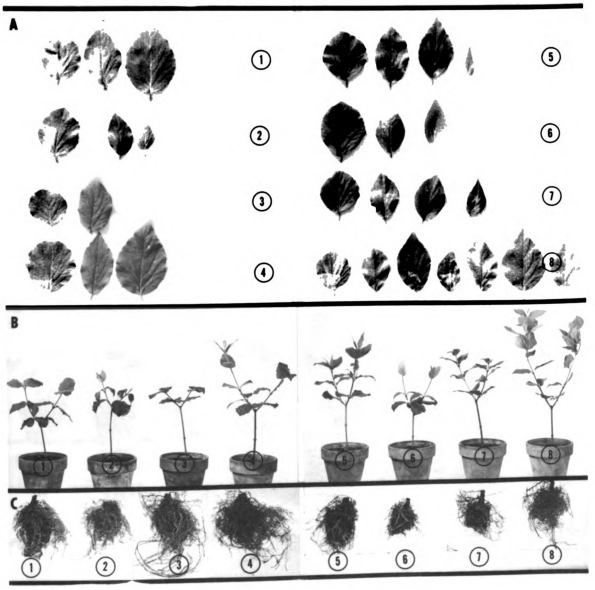


Figure 19. Viburnum Carlesii

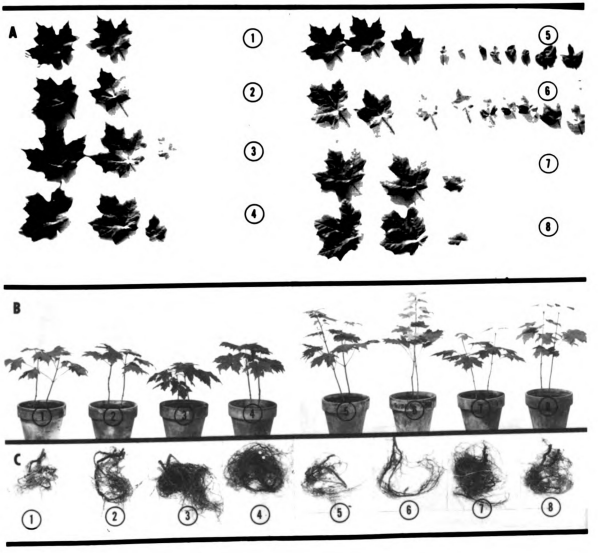


Figure 20. Acer saccharum

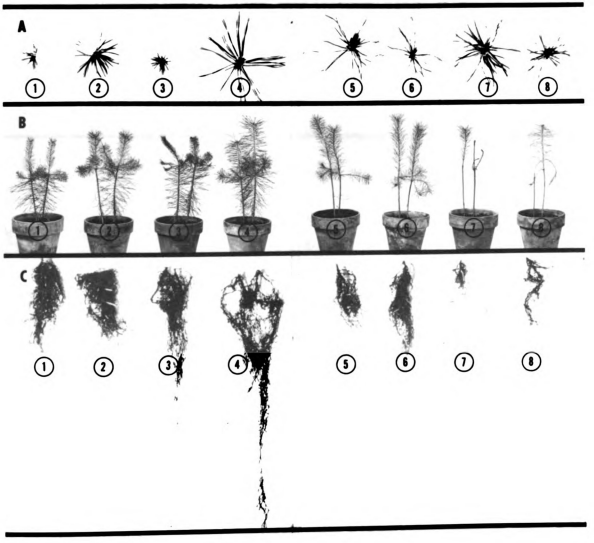


Figure 21. Pinus sylvestris

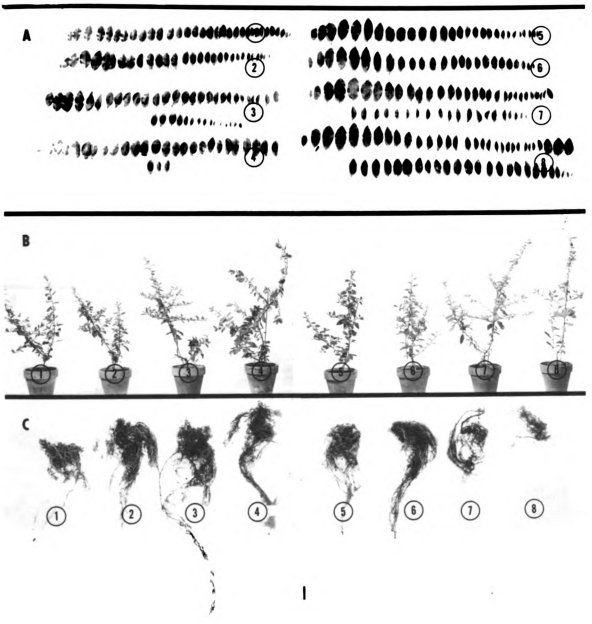


Figure 22. Pyracantha coccinea Lalandii

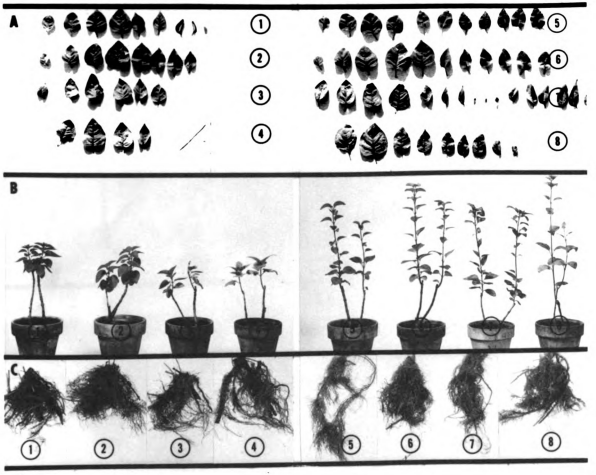


Figure 23. Syringa vulgaris

Figure 24. Euonymus Fortunei vegetus

II. ALTERATIONS IN THE METABOLISM OF *CATALPA SPECIOSA* AS INFLUENCED BY GIBBERELLIN

A. Modifications of the Chemical Composition

1. Materials and Methods

In the previous study *Catalpa speciosa* exhibited a marked response to all variables imposed, consequently this species was selected for chemical analysis. Routine nitrogen and percent ash determinations were made on the various plant parts previously mentioned. Half or one gram samples of finely ground (20 mesh) dried plant material were used. The standard Kjeldahl method was employed for nitrogen. The percent ash was determined by recording the difference between weights of an oven dried sample before and after ashing in a muffle furnace at 550°C for 8 hours.

2. Results

The influence of gibberellin (0 or 50 ppm), photoperiod (9 or 18 hours) and night temperature (40 or 70°F) on the chemical composition (ash and nitrogen) of Catalpa is recorded in Table IV. Two obvious responses to gibberellin are evident, (1) an increase in the ash content of the old and new roots, (2) an increase in the nitrogen content of the leaves and new roots but an inhibition of nitrogen accumulation in the old shoots. The inhibition of the nitrogen content of the old shoots was more pronounced under short days, consequently simulating a long day response. In contrast, the accumulation of nitrogen in the new roots following gibberellin treatment was more evident under long days and approximated the normal accumulation under short days. Nitrogen accumulation was inhibited in the old shoots and roots to a greater extent under long days than short days. High night temperatures as compared to low night temperatures cause a decrease in nitrogen in the new roots and increase the ash of the new roots and leaves.

It is evident that the various plant parts responded differently to gibberellin treatment. The modifying influence of gibberellin on the distribution of the ash and nitrogen in Catalpa strongly suggested an alteration in the normal metabolism. The accumulation of nitrogen in the new roots following gibberellin treatment approximated a short day and/or a low temperature response. In contrast the accumulation of nitrogen in the old shoots, and possibly new shoots (not significant), resembled a long day response. This is difficult to explain. It appears that the reduction in nitrogen movement out of the roots associated with

TABLE IV Modifying Influence of Gibberellin, Photoperiod and Temperature on the Distribution of Nitrogen and Ash in Catalpa speciosa (Values Expressed as Percentages of Dry Weight)

	Treatments						Significant Interactions							
	Gibberellin		Photoperiod (Hours)		Temperature (°F)		Temperature x Photoperiod				Gibberellin x Photoperiod			
							40° F		70° F		9 Hours		18 Hours	
Percent Ash	-	+	9	18	40	70	9hrs	18hrs	9hrs	18hrs	-	+	-	+
Leaf	6.2	6.3	6.4	6.0	5.3	7.2**								
New Shoots	2.6	2.4	2.3	2.7	2.6	2.4								
Old Shoots	2.1	2.5**	2.3	2.4	2.4	2.3					2.3	2.3	2.0	2.8
Old Roots	2.4	3.1**	2.8	2.8	2.7	2.9								
New Roots	6.6	8.1*	7.3	7.3	6.6	8.0*								
Percent Nitrogen														
Leaf	2.22	2.74**	2.56	2.44	2.40	2.60								
New Shoots	0.91	0.74	0.86	0.78	0.84	0.81								
Old Shoots	0.69	0.59*	0.76	0.52**	0.60	0.68	0.65	0.55	0.86	0.50	0.85	0.67	0.53	0.52
Old Roots	0.78	0.80	0.95	0.63**	0.73	0.85	0.81	0.65	1.09	0.62				
New Roots	1.38	1.68**	1.60	1.46	1.66	1.40*					1.51	1.69	1.24	1.68

* or ** Values for a given plant part and treatment are significant at the 5 or 1 percent levels, respectively.

an increased ash content of the roots and old shoots following gibberellin treatment, would indicate that the normal transport of minerals to the aerial portion of the plant is being inhibited. Conversely, assuming the nitrogen and ash content to be the total inorganic solids, it would appear that gibberellin induces carbohydrates to move out of the new and old roots and old shoots and to some extent out of the leaves, into the newly developing shoots.

B. Modifications of Foliar Absorption and Transport

1. Modifications by Gibberellin and Photoperiod

a. Materials and Methods

A responsive test plant was required to evaluate the modifying influence of gibberellin on metabolic activity controlled by photoperiod and/or temperature in woody plants. Catalpa speciosa was selected as it is sensitive in growth to all three factors. The species is easy to culture since it germinates within two weeks from freshly harvested seed (collected locally), thus requiring no stratification, as is the case with many woody plant seeds. The freshly harvested seed was sown in beach sand in 12 by 18 inch flats and lightly covered with sand. The flats were placed in a greenhouse under short days at 68°F night temperature and 70 to 85°F day temperature. Uniform seedling emmergence occurred within 10 days. The seedlings were watered with tap water for 4 to 5 weeks at which time they were large enough for testing.

Uniform seedlings were carefully washed out of the sand so as to not injure the root system, and transferred to light tight aerated solution culture containers in the greenhouse previously described (Asen, Wittwer and Teubner, 1954). A 0.5 strength Hoagland's solution was selected as the growing medium. Each aerated culture (1 gallon) contained 4 small seedlings with the leaves at the first node generally 1½ centimeters wide and 3 centimeters long with the second nodal leaves just appearing.

The seedlings were placed under two photoperiods (8 and 16 hours) and half of the plants were treated with a foliar spray of gibberellin

(50 ppm) until runoff. To prevent any desiccation of the foliage by high sunlight intensity, one layer of cheesecloth was placed over the entire experimental area.

The day length was extended by using 60 watt lights placed 2 feet above the seedlings producing 50 to 75 foot candles at plant level. Short days (8 hours) were provided by placing a black velveteen cloth between the photoperiodic treatments as well as over all the plants at 4 pm and was removed at 8 am. To prevent heat build-up under the cloth, a fan facing outward was placed at each end of the growing area under the black velveteen cloth to increase air circulation. The night temperatures were maintained at 70°F with day temperatures fluctuating between 70° and 90° F.

Fifteen days after treatment two plants from each jar were removed and weighed immediately to determine total fresh weight prior to P^{32} treatment. The plants were then severed into leaves, stem and root to determine the fresh weight of the individual plant parts. Two plants were averaged to give a value for each of the six replicates. Estimates of variability between treatments were determined by analysis of variance employing a split plot design. The remaining two plants which had not been harvested were used for determining the effects of gibberellin and photoperiod upon uptake and distribution of radiophosphorus (P^{32}) applied to a single leaf at the second node. The upper surface was treated at mid-leaf on the mid-vein with a drop (0.02 ml) of radiophosphorus (0.2 percent H_3PO_4 P^{32} labeled, pH adjusted to 3.5 with Ammonium hydroxide) prepared with an activity of 16 microcuries per milliliter. This solution was delivered from a no. 20 gauge stainless

steel needle mounted on a tubercullin syringe. The entire operation required 30 minutes (3:15 to 3:45 pm). It was a sunny day with a temperature of 92°F during the treating period.

Five days after applying the radio-phosphorus, the treated leaves were harvested (3:15 to 3:45 pm) using the "leaf washing technique" (15 ml of distilled water per leaf collected in a 50 milliliter beaker for counting) (Jyung 1959). The remaining portion of the plant was severed into three areas; above the treated leaf, aerial portion below the treated leaf, and the roots. Values for each of the three replications were determined by averaging two samples. The plant parts and the P^{32} washed from the leaf were placed in 50 milliliter beakers for drying in a forced air oven at 70°C.

Since the samples were small, self absorption by the plant tissue was negligible. The samples were crushed with a rubber stopper to assure uniform geometry for the radio-assay. Care was taken to prevent loss of the radioactive plant material, or transfer to the end-window of the G-M tube. All samples were counted for 3 minutes, using an end-window G-M tube, and standard scaler circuit. The final count was corrected for background. The analysis of variance was determined on the percent uptake of radio-phosphorus and percent transported of the total absorbed. A split plot design with photoperiods as the main plots and gibberellin treatments as subplots was employed.

b. Results

In the previous experiment it was apparent that gibberrllin modified the normal distribution of the ash and nitrogen constituents in Catalpa speciosa. Thus, uptake and distribution of radio-labeled phosphate by leaves of Catalpa treated with gibberellin under different photoperiods would be of interest. The data in Table V shows that neither photoperiod nor gibberellin altered the percent uptake or subsequent distribution of foliar applied P^{32}. There was, however, a significant interaction between gibberellin and photoperiod which resulted in a greater percent uptake of P^{32} under the long day-gibberellin treatment (not shown in table). The fresh weight accumulated in the shoots was increased, accompanied by a decrease in fresh weight of the roots following gibberellin treatment. This response was not evident under long or short days. It was anticipated that gibberellin would stimulate a greater movement of phosphorus out of the leaves to accomodate the increased growth of the shoots, this however was not the case. Since the percent uptake of P^{32} after 5 days was very minute it is possible that the duration of the experiment should have been longer.

TABLE V Foliar Uptake and Distribution of P^{32} (Harvested 5 Days After P^{32} Treatment) and Vegetative Growth by Catalpa speciosa as Modified by Gibberellin and Photoperiod (Gibberellin and Photoperiod Imposed Two Weeks Prior to P^{32} Treatment)

Uptake and Distribution	Photoperiod (hours)		Gibberellin (ppm)	
	8	16	0	50
Percent Uptake	2.3	2.9	2.2	3.0
Percent Transported of Total Absorbed	51.7	32.5	42.0	42.1
Growth Response (Fresh Weight in Grams and Height in Centimeters)				
Roots	.37	.42	.43	.39**
Shoots	.35	.37	.32	.40**
Leaves	.62	.69	.68	.62
Total	1.34	1.48	1.43	1.41
Height	10.3	10.6	8.5	12.4**

** Values for a given plant part and treatment are significant at the 1 percent level.

2. Modifications by Gibberellin and Leaf Position

a. Materials and Methods

The negative results obtained in the previous experiment warranted a study of the influence of leaf position and gibberellin on the uptake and distribution of radioactive phosphorus. Similar cultural techniques in germinating the Catalpa speciosa seed were used as previously described. When the first two leaves were partially to fully expanded, the seedlings were carefully removed from the sand germinating medium and selected for uniformity. They were then transferred to aerated solution cultures in the greenhouse as previously described containing 0.5 strength Hoagland's solution.

After 13 days in solution cultures, uniform plants were treated with a foliar spray of 0 or 50 ppm of gibberellin. The air temperature was 76°F and the sky was cloudy. The following day the upper leaf surface was treated with P^{32} precisely as described in the previous experiment. One leaf at either the first, second or third node above the cotyledons was treated so the affects of leaf position on absorption and transport might be determined. The plants were 7 to 9 centimeters tall and the leaves averaged 5, 7 and 1½ centimeters in length at the first, second and third nodes, respectively, when the labeled phosphorus was applied. Plants were harvested 6, 24, 96 hours, 8 and 16 days after treatment, utilizing the "leaf washing technique" (Jyung, 1959). The plants were harvested, dried and prepared for counting as previously described. Duncan's multiple range test was employed to determine differences, utilizing a randomized block design with four replications (Duncan, 1955).

b. Results

A further evaluation of foliar absorption as modified by gibberellin was desired since the duration of the previous experiment might have been insufficient to obtain differences. As shown in Table VI, gibberellin (50 ppm) did not have an influence on the percent uptake, percent transported of total absorbed, or the relative distribution within the plant, during the entire 16 day period. Leaf position and gibberellin treatments did not interact, consequently ruling out the effects of leaf age on uptake and distribution of P^{32} as influenced by gibberellin. Leaf position was in some instances, a factor in altering the uptake and transport of P^{32}. The leaves at the first node were most efficient during the first four days of the experiment, while those at the first and third nodes were most efficient after 8 days in increasing the uptake and distribution of radio-labeled phosphorus (Table VI).

All of the gibberellin treated plants responded markedly to treatment, indicating that 50 ppm was sufficient to cause a difference in growth. This experiment, in conjunction with the previous study illustrates that gibberellin fails to cause an increase in the phosphorus movement out of the leaves but greatly stimulated fresh weight accumulation within the shoots.

It has been demonstrated that phosphate movement parallels the movement of carbohydrates out of plant leaves (Biddulph, 1940; Colwell, 1942; Kazaryan, Avundzhyan and Gabrielyan, 1955; and Kendall, 1954). This would indicate that the carbohydrates associated with the increased

dry matter accumulation in the shoots are translocated principally from the stored reserves accumulated during the previous season. An increase in the leaf area might compensate for the greater demand of carbohydrates in the newly developing shoots, consequently the reserve carbohydrates in the old wood would be partially to completely spared.

TABLE VI Rate of Uptake and Distribution of Foliar Applied P^{32} by Catalpa speciosa as Affected by Leaf Position and Gibberellin (50 ppm 24 Hours Prior to P^{32} Treatment)

Time of Harvest (Days)	Percent Uptake					Percent Transported of Total Absorbed					P^{32} Transported Above Treated Area/ Below Treated Area				
	Leaf Position (Node)			Gibberellin (ppm)		Leaf Position (Node)			Gibberellin (ppm)		Leaf Position (Node)			Gibberellin (ppm)	
	1st	2nd	3rd	0	50	1st	2nd	3rd	0	50	1st	2nd	3rd	0	50
.25	6.2	1.7	3.6	4.8	2.9	23.4	32.4	24.0	19.1	34.2	2.5	0.9	1.6	2.8	0.6
1	6.8[a]*	3.0[b]	3.1[b]	3.9	4.7	8.6	5.1	7.6	8.7	5.5	0.7	1.1	1.5	1.2	1.0
4	6.6	4.8	6.7	5.9	6.2	11.4[a]	5.4[b]	5.1[b]	7.0	7.7	1.3	1.1	0.5	1.2	0.7
8	7.5	4.5	9.1	5.2	8.9	8.5[b]	3.1[a]	12.2[b]	9.3	6.5	2.1	3.0	6.3	3.1	4.5
16	10.7	5.8	8.1	7.4	9.1	14.5	10.2	15.6	11.5	15.4	1.8	6.5	1.0	1.9	4.3

* Values at a given harvest time and within each observation (percent uptake or percent transported of the total absorbed) under a particular treatment (leaf position or gibberellin) indicated by the same letter or not lettered, are not significantly different at the 5 percent level.

C. Modifications of Root Absorption and Transport

1. Rate of Absorption and Transport as Influenced by Gibberellin

a. Materials and Methods

The rate of root absorption and transport of radio-phosphorus was studied to further evaluate the modifying influence of gibberellin on the metabolic processes in woody plants. Catalpa speciosa was again selected as the test plant. Seeds collected from locally grown Catalpa trees on November 25, 1958, were sown in flats of sand under short days at 70°F night temperature in a greenhouse. Five weeks after seeding uniform seedlings were selected in the first and second leaf stage and the sand gently washed from the roots, taking precautions to prevent root injury.

The seedlings were placed in aerated water cultures as described previously. Subsequently, the plants were treated with a foliar spray of gibberellin (0, 50 or 500 ppm). Five days after the gibberellin had been applied the seedlings were transferred to 7 inch test tubes containing 60 milliliters of 0.5 strength Hoagland's solution with a specific activity of .0166 microcuries of radio-phosphorus per milliliter. The five day preconditioning period in the distilled water allowed sufficient time for the broken roots to callus, and depletion of the root phosphorus to assure maximum uptake of the P^{32}. The root temperature was held constant at 62°F $\pm$ 2°. The minimum night air temperature was 70°F, while the day temperature ranged from 70° to 85°F.

Each of the four double plant replicates in a randomized block design were segregated into aerial and root portions. To eliminate a

possibility of contamination of the aerial portion by the P^{32} in the root media, the plants were severed above the cotyledons. The plants were harvested at various time intervals (15 minutes, 1, 3, 12, 48 and 96 hours) after placement in the radioactive solution. After harvesting, the roots were rinsed in distilled water and placed in 50 milliliter beakers for drying in a forced air oven at 70°C. Self absorption was not a problem with such small samples, but the geometry was considered prior to counting.

Three replicate samples (1 ml) of the treating solution were analyzed for radioactivity and total phosphorus, using the standard A.O.A.C. method for phosphorus determinations (Horwitz, 1960). These two values plus the dry weight per sample made possible the determination of the micrograms of phosphorus taken up per unit dry weight as well as the total per plant part as shown below.

$$\frac{\text{counts per minute (cpm)}}{\text{micrograms per milliliter}} = \text{cpm/micrograms} \qquad \text{therefore}$$

$$\frac{\text{cpm/plant part}}{\text{cpm/microgram}} = \text{microgram/plant part}$$

Duncan's multiple range was employed to determine if differences were significant (Duncan, 1955).

b. Results

The movement of reserve materials out of the older plant parts is suggested as being one of the principle sources of carbohydrates for the newly developing shoot, as demonstrated in the previous experiment. A valid test of this hypothesis would require incorporation of a carbon labeled carbohydrate into the plant, preferably prior to dormancy and absiccion of the leaves. Following the breaking of dormancy the plant would then be treated with gibberellin and harvested to determine if gibberellin caused an increase in movement of the reserve carbohydrates from the old wood to the newly developing shoots. Since time did not allow such a long term experiment, an alternate approach already discribed was taken.

The results are present in Table VII. It is important to note that gibberellin caused an increase in the percent of phosphorus translocated to the shoot from the root on a per plant basis, but not on a per unit dry weight basis after 96 hours in the P^{32} solution. A general inhibition of P^{32} uptake by gibberellin was observed on a unit dry weight basis, although it was not always significant. This was particularly evident after the plant roots had been exposed to P^{32} for one hour. It would seem that the overall efficiency of uptake and distribution of P^{32} on a plant basis is not reduced. On the contrary, on a unit dry weight basis the efficiency of uptake appears to be reduced following gibberellin treatment.

TABLE VII Rate of Uptake and Distribution of Phosphorus by Roots of Catalpa speciosa as Modified by Gibberellin (Foliar Application of Gibberellin 5 Days Prior to P^{32} Treatment)

Micrograms of Phosphorus Accumulated for Two Plants												
	Root			Shoot			Total			Percent in Shoot		
Gibberellin (ppm)	0	50	500	0	50	500	0	50	500	0	50	500
Time of Harvest (Hours)												
0.25	1.02	1.74	1.53	0.14	0.12	0.14	1.16	1.87	1.67	13.7	7.0	13.4
1	3.01	2.30	1.36	0.12	0.13	0.15	3.13	2.43	1.51	4.6	5.5	10.1
3	5.68	5.65	5.38	0.27	0.37	0.20	5.95	5.90	5.58	4.7	4.9	3.8
12	13.35	13.53	13.40	1.00	1.05	0.95	14.25	14.60	14.37	8.2	7.2	7.3
48	33.86	27.87	29.19	6.89	6.73	7.50	40.75	34.60	36.68	17.2	18.4	20.1
96	65.96	52.39	59.08	25.19	21.10	32.09	91.15	73.49	91.22	27.3^{a}	28.6^{a}	35.0^{b}
Micrograms of Phosphorus Accumulated per Gram Dry Weight												
0.25	11.7	19.9	31.9	8.3	7.2	6.6	20.0	25.9	38.5	41.5	27.8	17.1
1	42.6^{a*}	27.8^{b}	14.9^{b}	7.6	5.9	7.9	50.2^{a}	33.7^{b}	22.8^{b}	15.1	17.5	34.6
3	59.3	65.2	62.1	13.5	13.0	10.4	72.8	78.2	72.5	18.5	16.6	14.3
12	161.8	170.9	172.4	54.5	43.2	55.5	216.3	214.1	227.0	25.2	20.2	24.4
48	405.0	375.1	348.1	278.6	303.2	262.1	683.6	678.3	610.2	40.8	44.7	43.0
96	789.7	625.5	643.9	953.1	701.6	791.8	1742.8	1327.1	1435.7	54.7^{a}	52.9^{b}	55.2^{a}

* Values at a given harvest time and plant part, indicated by the same letter or not lettered, are not significantly different at the 5 percent level.

2. Rate of Absorption and Transport as Influenced by Gibberellin and Root Temperature

a. Materials and Methods

The effects of root temperature on uptake and distribution as modified by gibberellin might partially explain the interactions between gibberellin and temperature in the previous experiments relating to vegetative modifications by gibberellin. Consequently seedlings of Catalpa speciosa, cultured and prepared for treatment as previously described, were treated with a foliar spray of gibberellin (0 and 500 ppm). Four days later the plants in their first and second leaf stage were transferred to 7 inch test tubes containing an aerated solution of radio-phosphorus as previously stated. The root temperatures were controlled within $\pm$ 2°C by a cooled and heated water bath. Four root temperatures (5, 10, 15 and 20°C) were maintained during the 48 hour exposure to the radio-phosphorus.

The plants were harvested, prepared for radioactivity and dry weight determinations, as previously described. The micrograms absorbed per unit dry weight and per plant part were also determined according to procedures already mentioned in previous experiments. Temperature coefficients (Q-10) of phosphorus absorption by the roots were readily calculated from the above information.

Eight single plant replicates were incorporated in a split plot randomized block design. Root temperatures (5, 10, 15 or 20°C) were the main plot and gibberellin (0 or 500 ppm) the sub plots. Duncan's multiple range test for differences among means was employed. (Duncan, 1955).

b. Results

In the previous experiment the implication was that gibberellin would inhibit the uptake of phosphorus on a unit basis. Consequently, a further evaluation of the effects of gibberellin on the uptake of phosphorus by roots, in conjunction with various root temperatures, should substantiate or refute this hypothesis. This phase of the investigation gives strong evidence supporting the possibility that gibberellin increases plant growth at suboptimal temperatures.

As shown in Table VIII, the overall efficiency of uptake is generally reduced on a per plant as well as a per unit dry weight basis by gibberellin treatment. However, the percent transported to the shoot was not altered. This relationship was, however, not consistant under the various root temperature regimes. It is of interest to note in Table VIII, that an increase in temperature results in a subsequent increase in phosphorus uptake by roots of the control plants on a unit weight basis. If, however, gibberellin treated plants are placed under similar root temperatures, the rate of uptake with increasing temperature is not as rapid. Therefore, the rate of uptake and distribution is not altered at the lower root temperatures, (5 or 10°C) but is markedly reduced at the higher root temperatures. This would imply that a mechanism associated with active absorption of phosphorus has been modified.

The root temperature coefficients for data in Table VIII are shown in Table IX. The data clearly illustrate that gibberellin caused a marked reduction in the root temperature coefficients on a unit weight basis for the roots, shoots and total plant. In contrast the percent

phosphorus translocated to the shoot under the different root temperatures was not modified by gibberellin treatment. The reduction in the temperature coefficients for root uptake on a plant basis was only apparent between the 5-15°C range and not influenced by the 10-20°C range.

TABLE VIII The Effects of Root Temperature on the Uptake and Distribution of Phosphorus by Roots of *Catalpa speciosa* as Modified by a Foliar Spray of Gibberellin (Exposed for 2 Days to P^{32} Solution and Treated 6 Days Prior to Harvest with Gibberellin)

	Root Temperature (°C)				Gibberellin (ppm)	
	5	10	15	20	0	500
Micrograms of Phosphorus Accumulated for Two Plants						
Plant Parts						
Root	13.3*	17.0	24.6	33.1	24.7^a	19.3^b
Shoot	1.5	2.1	4.9	10.9	5.3^a	4.6^a
Total	14.8	19.1	29.5	44.0	30.0^a	24.0^b
Percent in Shoot	10.1	11.0	16.6	24.8	17.7^a	19.2^a
Micrograms of Phosphorus Accumulated per Gram Dry Weight						
Root	162.7	185.6	273.6	358.4	271.5^a	218.6^b
Shoot	48.7	68.5	136.0	311.3	163.3^a	118.9^b
Total	211.4	254.1	403.3	669.6	434.8^a	337.5^b
Percent in Shoot	23.0	27.0	33.7	46.5	37.6^a	35.2^a

Interactions of Gibberellin and Temperature

	Gibberellin				
Root	-	161.7^a	195.7^a	325.7^b	402.8^c
	+	163.5^a	175.5^a	221.6^a	313.9^b
Shoot	-	53.5^a	67.5^a	169.7^b	362.6^c
	+	44.0^a	69.4^a	102.3^a	260.0^b
Total	-	215.2^a	263.2^a	482.6^b	765.4^c
	+	207.6^a	245.0^a	323.9^a	573.9^b

* Values for the same plant part not connected by a common line or letter (horizontal comparisons) are significantly different from each other at the 5 percent level.

TABLE IX Root Temperature Coefficients for Uptake and Distribution of Phosphorus by Roots of *Catalpa speciosa* as Modified by Gibberellin

Micrograms of Phosphorus Accumulated for Two Plants	Gibberellin	
	-	+
Plant Part		
Root	2.3[a]*	1.9[a]
Shoot	4.7[a]	4.1[a]
Total	2.6[a]	2.2[a]
Percent in Shoot	2.1[a]	2.0[a]
Interaction of Gibberellin and Temperature		
Root — Temperature Range (°C)		
5 - 15	2.6[a]	1.9[b]
10 - 20	2.0[a]	2.1[a]
Micrograms of Phosphorus Accumulated Per Gram Dry Weight		
Root	2.2[a]	1.7[b]
Shoot	4.6[a]	3.2[b]
Total	2.9[a]	2.0[b]
Percent in Shoot	1.8[a]	1.6[a]

* Values for the same plant part not connected by a common line or letter (horizontal comparisons) are significantly different from each other at the 5 percent level.

2. Rate of Absorption and Transport at Different Root Temperatures as Influenced by Preconditioning to Gibberellin and Photoperiod

a. Materials and Methods

Previous findings warranted an investigation of the influence of root temperature on the uptake of P^{32} by plants which had been preconditioned to gibberellin and photoperiod for a longer period. Consequently, seedlings of Catalpa were transplanted to 4 inch pots containing a 50-50 muck soil mixture. Half of all the plants were treated with a foliar spray of gibberellin (100 ppm) and exposed to long (18 hours) or short (9 hours) days. The photoperiod was extended by both incandescent and fluorescent lamps which produced 50 foot candles at pot level. Short days were provided by moving the plants to a dark room at 5 pm and returning the plants to their day positions at 8 am.

Three and six weeks after the initiation of the experiment, 80 uniform plants (20 from each environment) were gently removed from the soil in the pots and placed in a pan of tap water. These plants were then transferred to aerated cultures for 4 days containing 0.5 strength Hoagland's solution. This procedure permitted callus formation where roots might have been broken in the transfer from the soil to the solution cultures. After the 4 day healing period, plants were transferred to the test tubes containing the radioactive phosphorus and 0.5 strength Hoagland's solution as previously described (Figure 25 and 26). Root temperatures in the water bath containing the test tubes were maintained at 50 and 68°F $\pm$ 2°F. The root temperature was replicated twice to assure a valid test for the temperature response and a duplicate

sample for each treatment was randomized within. The air temperature was maintained at $68^{o}F \pm 2^{o}F$ during this period. Consequently, a split plot design with temperature as the main plot and precondition treatments as the subplot was utilized. Duncan's multiple range test was employed to determine if the differences among means were significant.

The first and second harvests were made 3 and 12 hours respectively after P^{32} treatment. The plants were segregated into two parts, roots and shoot, with the division at the cotyledonary node. This point of segregation was essential to reduce the possibility of contamination from the radioactive root media. The plant roots were rinsed in distilled water prior to placement in 50 milliliter beakers and air dried at $70^{o}C$ prior to counting, using the counting procedures and equipment previously described.

Since the plants were relatively large in the above experiments, self absorption became a problem. Self absorption was corrected by determining the relationship of the activity before and after ashing of 16 different samples representing a range in weights for both the shoots and roots. The standard A. O. A. C. method for preparing plant material for phosphorus determination was followed (Horwitz, 1960). A well defined curve was obtained between dry weight of the sample and activity. This correlation precluded further ashing. Consequently, the remaining dryed samples were analyzed for activity without ashing. The self absorption was corrected by adjusting the activity of a given sample weight to fit the curve. Total micrograms per plant and per gram dry weight were determined as previously described.

Figure 25 A Refrigerated and Heated Water Bath for Exposing *Catalpa* to Various Root Temperatures and P^{32} Solutions.

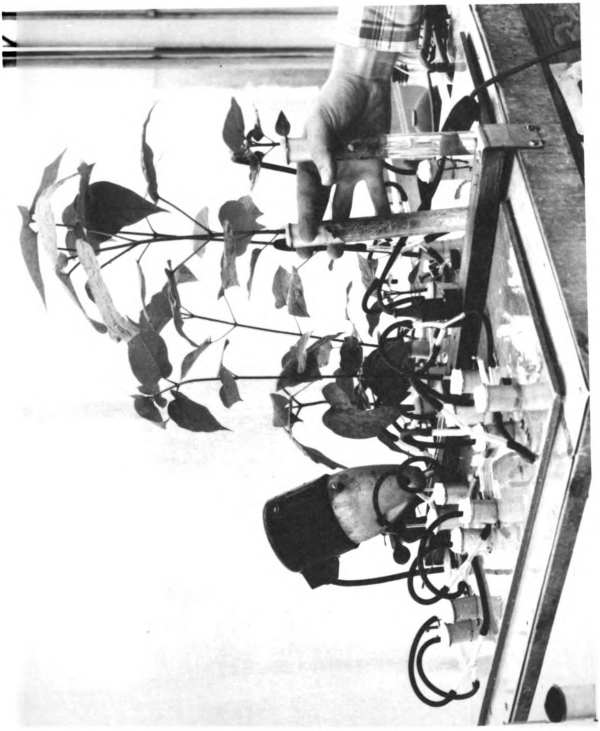


Figure 25

Figure 26 Catalpa speciosa Seedlings Precondition to Gibberellin (100 ppm as a Foliar Spray) and Photoperiod (9 and 18 hours) During an Interval of Six Weeks.

	Treatments	
Code	Gibberellin	Photoperiod (hours)
A	-	9
B	+	9
C	-	18
D	+	18

Figure 26

b. Results

The modifying influence of gibberellin on the rate of uptake at various root temperatures was indicative of young seedling as illustrated in the previous experiment. Evaluation of the effects of gibberellin, in conjunction with various photoperiods, on the uptake of phosphorus at different root temperature in older plants should confirm or refute previous findings in addition to giving new information. The results of this investigation are shown in Tables X and XI.

At least 6 weeks of preconditioning to gibberellin (0 or 100 ppm) or photoperiod (9 or 18 hours) were required to alter the uptake of phosphorus by roots. As shown in Table XI the accumulation of phosphorus by roots after 12 hours in the P^{32} solution, on a per plant or per unit dry weight basis, was generally inhibited following a preconditioning to gibberellin under a long day regime, as compared to the long day control plants. This inhibition was not apparent in treated plants under short days as compared to the short day controls.

The percent phosphorus translocated to the shoot from the root was not greatly altered after six weeks of preconditioning but was markedly affected in plants preconditioned for 3 weeks to gibberellin (100 ppm) or photoperiod (9 or 18 hours) (Table X). Two general observations are evident, (1) gibberellin temporarily inhibited the percent of phosphorus transported to the shoots which normally increases at the higher root temperature, irrespective of the photoperiod imposed, and (2) gibberellin applied to plants under short days partially substituted for the percent of phosphorus translocated to the shoots under a long

day regime. This was apparent at the 12 hour harvest only (Table X). It became evident that root temperature was only effective in altering the percent of phosphorus transported to the shoots in younger plants and that gibberellin will modify this effect. The partial substitution by gibberellin, of the long day effect on the percent transported to the shoots, is only evident in young plants also (3 weeks of pre-conditioning). As the plant matures the influence of root temperature is no longer effective in altering the uptake and distribution of phosphorus, but photoperiod (9 or 18 hours) becomes the controlling factor. Gibberellin inhibited uptake of phosphorus under long days but had no influence on the uptake of root applied P^{32} by plants exposed to short days.

TABLE X The Modifying Influence of Three and Six Weeks of Preconditioning to Gibberellin and Photoperiod on the Percent of Phosphorus Translocated to the Shoots from the Roots of Catalpa speciosa Exposed to Different Root Temperatures

		Three Weeks of Preconditioning to Gibberellin and Photoperiod								Six Weeks of Preconditioning to Gibberellin and Photoperiod			
		Micrograms of Phosphorus Per Plant				Micrograms of Phosphorus Per Gram Dry Weight				Micrograms of Phosphorus Per Plant		Micrograms of Phosphorus Per Gram Dry Weight	
Hours of P^{32} Treatment		3	12	3		3	12	3		3	12	3	12
Root Temperature (°C) [1]				10	20			10	20				
Preconditioning Treatment													
Photoperiod (hours)	Gibberellin												
9	-	8.4[a]*	11.7[a]	2.8[a]	13.9[a]	8.0[ab]	11.9[a]	2.7[a]	13.2[a]	6.1[a]	10.1[a]	10.1[ab]	16.9[a]
9	+	4.6[a]	17.8[ab]	3.1[a]	6.2[b]	4.5[a]	17.3[ab]	2.9[a]	6.1[b]	9.2[a]	11.7[a]	12.4[a]	19.8[a]
18	-	11.3[a]	20.2[b]	6.2[a]	16.4[a]	10.0[b]	19.5[b]	5.9[a]	15.1[a]	9.7[a]	19.1[a]	6.2[b]	13.0[a]
18	+	8.0[a]	23.7[b]	8.7[a]	7.3[b]	7.6[b]	23.7[b]	8.3[a]	6.8[b]	8.7[a]	18.6[a]	6.0[b]	14.1[a]

* All values indicated by the same letter within each column are not significantly different from each other at the 5 percent level.

1 The effects of root temperature were not included if the differences were not significant.

TABLE XI The Modifying Influence of Six Weeks of Preconditioning to Gibberellin and Photoperiod on the Uptake and Distribution of Phosphorus by Roots of Catalpa speciosa

Preconditioning Treatment		Micrograms of Phosphorus Per Plant				Micrograms of Phosphorus Per Gram Dry Weight			
		Root		Total Accumulation		Root		Total Accumulation	
Photoperiod (hours)	Gibberellin	Hours of P^{32} Treatment 3	12	3	12	3	12	3	12
9	-	9.7^{a}*	29.1^{a}	10.3^{a}	32.7^{ab}	16.5^{a}	44.2^{a}	18.5^{a}	53.8^{a}
9	+	10.8^{a}	23.5^{a}	11.8^{a}	28.8^{a}	20.6^{ab}	50.0^{ab}	23.7^{ab}	64.3^{a}
18	-	52.5^{b}	98.8^{b}	58.3^{b}	128.6^{c}	82.2^{c}	133.8^{c}	88.4^{c}	158.8^{b}
18	+	37.5^{b}	54.4^{c}	40.6^{b}	70.6^{b}	57.9^{cb}	87.6^{b}	61.2^{cb}	106.6^{ab}

* All values indicated by the same letter within each column are not significantly different from each other at the 5 percent level.

DISCUSSION

I. General Considerations

The premise of this thesis originated from reports that gibberellin could partially or completely replace the effects of long days or cool temperatures on the vegetative response of woody plants. At the initiation of this investigation in the spring of 1958, only seven reports on this subject had been published. In only one of these studies (Lockhart and Bonner, 1957) were plants which had been treated with gibberellin subjected to various photoperiods under different night temperature regimes. As of this writing no further reports have been published relating to the effects of gibberellin, photoperiod and temperature in combination, on the vegetative growth of woody plants.

The premise that gibberellin will substitute for long days or cool temperatures in woody plants needed further investigation. Consequently, a group of plants of a known photoperiodic response were selected (Table I). In addition, these plants also exhibited a broad range in thermoperiod response. Two criteria for determining differences induced by gibberellin, photoperiod or temperature treatments were used; (1) alterations in vegetative growth (2) alterations in metabolism.

The replacement or partial replacement of the photoperiodic response in woody plants by gibberellin has been widely reported (Alleweldt, 1959; Bourdeau, 1958; Bukovac and Davidson, 1959; Hudson, 1958; Lockhart and Bonner, 1957; Lona and Borghi, 1957; Nitsch, 1957b). On the other hand gibberellin was ineffective in simulating long day conditions in some plants, (Lockhart and Bonner, 1957; Nitsch, 1957b) and actually accelerated dormancy in others (Brian, Petty and Richmond, 1959a and b; Weaver, 1959).

The tendency for gibberellin to simulate the thermoperiodic response in woody plants has also been observed (Donoho and Walker, 1957; Fogle and McCrory, 1959; Prince, 1958; Stuart, 1957; Barton and Chandler, 1957; Oohato and Shiraki, 1958; Boodley and Mastalerz, 1959). The degree of chilling, season of the year and species predicts the concentration of gibberellin required to simulate the thermoperiodic response (Donoho and Walker, 1957; Fogle and McCrory, 1959; Marth, Audia and Mitchell, 1956; Prince, 1958; Stuart, 1957). The findings presented herein possibly will lend additional insight into the mechanisms controlling growth and developing in woody plants.

It would be presumptuous to assume that gibberellin will completely parallel responses induced by variations in the photoperiod or thermoperiod. In this respect Steward and Shantz (1959) have presented their interpretation of the complexity of growth and development as follows:

> "There can be no question that many substances and extracts cause rapid cell multiplication, and the causal substances need to be specified. However, obvious problems are created if one regards one aspect of growth (cell enlargement) to be promoted wholly or predominantly by the class of substances known as auxins and another aspect of growth (cell division) to be stimulated by another class of substances to be known as kinins. These names alone do not lead to understanding, on the contrary they may lead to confusion".

II. Replacement or Partial Replacement of the Photoperiodic or Thermoperiodic Requirements by Gibberellin

The similarity within and the variation among the responses of photoperiodic groups (Table I) to gibberellin is striking. It would be erroneous to assume however that the replacement of these responses by gibberellin were similar throughout all plant parts. Evidence presented indicates that gibberellin is ineffective in completely or even

partially simulating a photoperiodic or thermoperiodic response in all plant parts, particularly roots and leaves. In this respect, Lockhart (1961) reported a relationship in irradiated Pisum seedlings which is pertenant to this investigation.

> "The same red far-red photochemical process affects various morphological responses of plants in addition to stem length. In the same plants, i.e., Pisum seedlings, irradiation affects stem length, leaf development, epicotyl hook opening, and rate of node formation. Gibberellin treatments will completely reverse the effects of radiation on stem growth, but it has no effect on these other photomorphogenic responses. Therefore, applied gibberellin does not act directly on the initial photochemical act, or even on subsequent thermochemical processes which are common to all these reactions. Rather, gibberellin must act on the terminal reactions controlling stem growth. It clearly does not influence. any reaction common to all these photomorphogenic processes."

Interactions between gibberellin and photoperiod, and even more noticeably between gibberellin and temperature suggest that endogenous stimulants and inhibitors are modifying the action of an exogenous source of gibberellin. Consequently, in discussing the results of this thesis, a theory is wanting to best explain such varied responses to gibberellin as, the marked inhibition of dry weight accumulation in Catalpa, the failure of Pyracantha to respond to gibberellin, the death of Pinus, held at high temperature, the delay of dormancy under cool temperatures and short days in Acer, and many others.

III. Interrelationships Between Gibberellin and Endogenous Growth Regulators

A. Modifying Influence of the Photoperiod on Gibberellin Action

Conflicting reports on the response of certain woody plants to gibberellin would indicate an interaction between the exogenous supply

of gibberellin and the endogenous growth regulators. Throughout the literature there are conflicting reports on the response of woody plants to gibberellin. It is evident that the quantity of gibberellin applied is an important factor, and yet, the physiological stage of development of the plants treated with gibberellin markedly modifies or intensifies the responses as well (Donoho and Walker, 1957; Fogle and McCrory, 1959; Marth, Audia and Mitchell, 1956; Prince, 1958; Stuart, 1957; Moore and Bonde, 1958).

More specifically, Bukovac and Davidson (1959) reported that under short days the stimulating effect of gibberellin on shoot elongation diminishes in 3 to 4 weeks but gibberellin continued to be effective under long days. Stuart (1957) found the effectiveness of gibberellin in breaking dormancy of Hydrangea macrophylla to be increased if the plants had already had the cold requirement partially satisfied. In this respect Moore and Bonde (1958) reported a synergistic response between gibberellin and vegetative vernalization in promoting vegetative growth of dwarf telephone peas. Lona (1957) in contrast reported a similarity in action of gibberellin and high night temperature in stem elongation of Perilla. Biochemical evaluation of growth regulating substances within stem tips of plant grown under different photoperiods and treated with gibberellin, revealed the presence of both growth-promoting and growth-inhibiting substances (Nitsch and Nitsch, 1959). Thus both indirect evidence and actual extraction studies have indicated the importance of endogenous growth relating compounds on growth and development of plants treated with gibberellin.

The biological importance of gibberellin produced by the fungus Gibberella fujikuroi increased as wide spread evidence indicated the

occurrence of gibberellin-like substances in higher plants (West and Phinney, 1956; Phinney, West, Ritzel and Neely, 1957; Radley, 1958; and Lona, 1957). Recently, MacMillan and Suter (1958) succeeded in isolating the first pure gibberellin from immature seeds of a higher plant. Kawarada and Sumiki (1959) have also isolated gibberellin A_1 from water sprouts of Citrus unshui. There is little doubt that the endogenous supply of gibberellins and growth inhibitors greatly modifies the response of woody plants to their environment, and to chemical treatments.

One should not assume that one theory of the mechanism of gibberellin action in modifying the growth and development of different woody plants would explain all the varied responses observed. Genetic tendencies, carbohydrate reserves, respiration patterns and many other physiological differences might play an important role in influencing the differences observed in this study. However, the relationships between endogenous gibberellins and inhibitors presented herein best explain the differences in growth patterns which resulted from gibberellin treatment to woody plants exposed to different photoperiods and thermoperiods. The size of angle A and the relative position of the vertex will predict the response of the various species to an exogenous supply of gibberellin (Figure 27).

The general lack of an interaction between the photoperiods imposed and gibberellin on shoot elongation can be explained using the theory presented. The difference in the relative concentration of endogenous gibberellin and inhibitors between plants grown under long days as compared to short days is very slight (Angle A decreases). Consequently

the addition of an exogenous source of gibberellin in the spring overrides the influence of the endogenous growth regulators resulting in a similar response to gibberellin, irrespective of the photoperiod imposed.

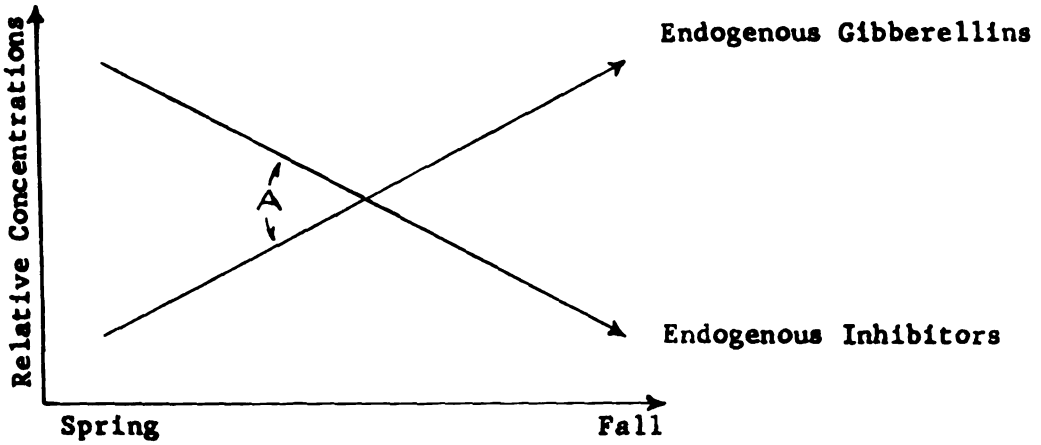
In figure 15, it is apparent that an interaction between gibberellin and photoperiod does greatly modify the leaf area per plant, (5) and less frequently modifies the dry weight per leaf (7). In this respect it has been reported that maturing leaves are the receptive organs of the photoperiodic stimuli (Wareing, 1956; Nitsch and Nitsch, 1959). Long days have been reported to increase the leaf area per plant in blueberry (Perlmutter and Darrow, 1942) and Pinus sylvestris (Wareing, 1950). Accumulating evidence would indicate that far red light or darkness which inhibits leaf expansion, also inhibits a portion of the effect of gibberellic acid on leaf expansion (Liverman, 1959). This evidence suggests that an inhibitor produced under short days (darkness) modifies the action of gibberellin (Scheme II). In contrast, the relative relationship of gibberellin to an inhibitor under long days approximates that relationship found in Scheme I. The lack of endogenous inhibitors, particularly later in the season, in conjunction with increased levels of endogenous and in these tests exogenous sources of gibberellin causes a marked unbalance in the gibberellin inhibitor ratio. This results in an inhibition of the total leaf area per plant and dry weight per leaf.

In this respect, it is of interest that an increased leaf expansion in woody plants, following treatment with small quantities of gibberellin, occurred in late summer (Sawada and Yakuwa, 1958) or early spring (McVey and Wittwer, 1958). However, higher rates of gibberellin in the spring,

Figure 27 Proposed Mechanism of Action Controlling the Growth and Development of the Eight Woody Plants Investigated.

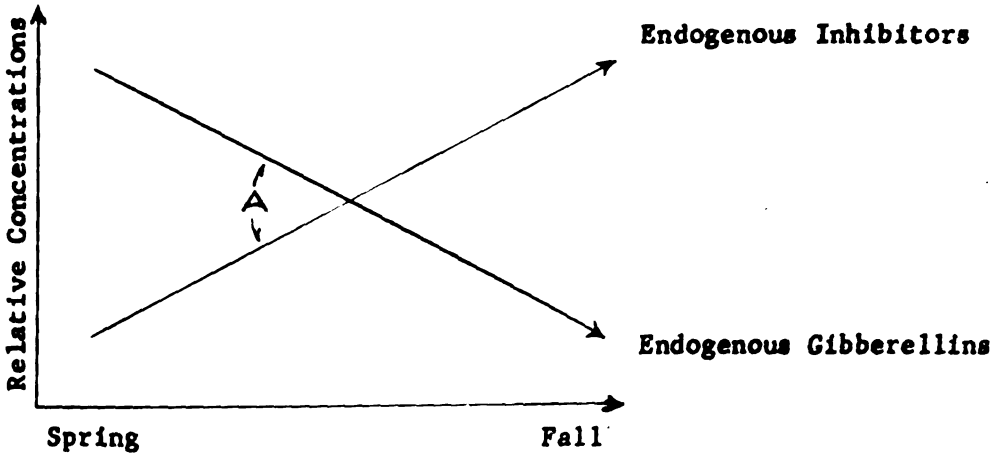
Scheme I

Plants Under Low Night Temperatures or Long Days



Scheme II

Plants Under High Night Temperatures or Short Days



or reduced rates in the summer, resulted in an inhibition of leaf expansion (McVey and Wittwer, 1958; Scurfield and Moore, 1958; Powell, Cain and Lamb, 1959; Suyama, Yamasaki and Kubota, 1958).

Gibberellin applied to plants under a short day regime generally caused an increase in leaf expansion as compared to those plants placed under a long day regime (Fig 15, 17, 18, 21, and 24). If an inhibition in leaf dry weight accumulation does occur following treatment with gibberellin, it is generally more evident under the long day regime as compared to that found in plants under the short day regime (Figure 17).

In this respect a few of the rapidly growing Catalpa plants under the long day high temperature regime were injured in late June by the heat of the incandescent bulbs used to extend the photoperiod. As shown in Figure 17, an axillary bud developed and elongated but in contrast to the treated plants under the same environment which had not been injured, the leaves which developed closely resembled leaves of the check plants. This accident in cultural techniques would indicate that inhibitors which accumulated during the period of axillary bud development moderated the subsequent action of gibberellin on the expanding leaves.

The actual cause of the inhibition of leaf expansion by gibberellin is not known. It is highly probable that the high concentration of gibberellin in relation to the endogenous inhibitors cause a marked increase in the rate of respiration. In this respect Kato (1956 and Coulombe and Paquin (1959) have reported a marked increase in the rate of respiration in pea and tomato foliage following gibberellin treatment.

In Pyracantha, as compared to the other plants studied gibberellin caused an increase in the leaf area per plant under long days while a reduction in leaf area occurred following gibberellin treatment to plants under short days (Figure 15). In order to explain this reversal in the the trend, it would appear that the balance between the endogenous gibberellin and inhibitor is very delicate (Angle A greatly reduced). The increase in leaf area following gibberellin treatment under long days would indicate that an inhibitor was moderating the action of gibberellin, whereas under short days this was not the case. This is the reverse of other plants studies, in which short days generally moderated the action of gibberellin to a greater extent than long days.

To explain this difference we note in Figure 5 that Pyracantha exhibited no photoperiod response in respect to shoot elongation. It is possible that within theplant a similar balance between gibberellin and inhibitor is maintained irrespective of the photoperiod. However, the mechanism of maintaining the balance varies. It is postulated that the synthesis of endogenous gibberellin in the leaf is dependent and the inhibitor concentration is independent of influence of long days on growth. Plants grown under the short day regime would exhibit a reciprocal relationship. If this relationship does exist, the addition of gibberellin would be destroyed at a greater rate under long days than short days. The inhibitor, which is synthesized under short days, would not greatly modify the addition of an exogenous source of gibberellin. The end result would be a moderation of gibberellin effect on leaf expansion by long days with the reciprocal relationship evident

under short days. In this respect it has been suggested that the mechanism responsible for the synthesis of the endogenous gibberellin is blocked by light (Lockhart, 1959). As previously mentioned a high gibberellin-inhibitor ratio might result in an increased rate of respiration.

This relationship might also explain the greater inhibition of dry weight accumulation in leaves of Euonymus treated with gibberellin under short days as compared to long days (Figure 15). Note in Figure 5 and 6 that neither Pyracantha or Euonymus respond to photoperiod treatment. It appears that plants which exhibit little or no response to photoperiod exhibit a similar response to gibberellin. If, however, there is a response to gibberellin in plants which do not exhibit a marked response to photoperiod the response is greater under long days. If gibberellin causes an inhibition in dry weight accumulation in plants which fail to respond markedly to photoperiod, the inhibition is more evident under short days than under the long day regime. (e.g. Pyracantha and Euonymus Figure 15).

Leaf area per plant and dry weight per leaf of Acer and Viburnum following gibberellin treatment were not differentially affected by the photoperiodic treatment imposed. This would indicate that the endogenous sources of gibberellin and inhibitor are relatively equal in amounts within the leaves. Consequently a similar response to an exogenous source of gibberellin results.

B. Modifying Influence of the Thermoperiod on Gibberellin Action

In contrast to the effect of photoperiod, the response of shoot development and dry weight accumulation in various plant parts to gibberellin, was greatly modified by temperature. A perusal of Figures 4, 5, 6, 7, 8, 9 and 10, strongly supported the theories previously discussed. All plants under high night temperature showed a more rapid rate of shoot elongation in the spring in contrast to those under low night temperature. As the season progresses the rate of shoot elongation of plants under high night temperatures decreased while shoot elongation of plants under low night temperatures increased. This decrease in the rate of shoot elongation under high night temperatures accompanied by an increase rate at the lower night temperature as the season progressed was not evident in Pyracantha, Liriodendron and Viburnum.

Scheme I and II fit into the above pattern of shoot extension evident under the low and high night temperatures. The addition of an exogenous supply of gibberellin also lends strong supporting evidence to the mechanism controlling shoot elongation in the woody plants investigated. A differential response of shoot elongation to the thermoperiod following gibberellin treatment is evident early in the spring. As the season progresses the rate of elongation under high night temperatures decreases while the shoot extension under low night temperatures increases following gibberellin treatment.

Viburnum and Syringa exhibited greater growth at the end of the season under high as compared to low night temperatures. However, the interactions were not as evident at the end of the season as they were during mid-spring (Figure 7). Employing the schemes I and II, it would appear

that the rate of synthesis of endogenous gibberellins under the low night temperature as compared to high night temperatures is increased as the season progresses. Therefore, the addition of gibberellin to plants under the low night temperature would result in a greater shoot elongation response than plants under the high night temperatures, thus accounting for the reduction in the interaction observed. In contrast, early in the spring the quantity of endogenous gibberellin was synthesized at a much faster rate under the high night temperature as compared to the low night temperature. This resulted in a greater increase in the rate of shoot elongation in Viburnum and Syringa. An exogenous source plus a relatively high endogenous source of gibberellin (Scheme II, angle A increased) resulted in a growth pattern of the shoots which could not be over-taken by the low temperature gibberellin treated plants. The rates of shoot elongation of Viburnum and Syringa under low and high temperatures during early spring and mid-summer bare out this hypothesis.

Theoretically Liriodendron should have shown an interaction between gibberellin and temperature during the entire growing season, since the rate of shoot extension under high and low temperatures in Viburnum and Liriodendron is very similar (Figure 6). However, this was not the case (Figure 7). To explain this lack of conformity to the theory proposed is not difficult. Gibberellin caused desiccation of some terminal buds of Liriodendron at the higher night temperature. Consequently gibberellin treated plants grown under the lower night temperature rapidly over-took the elongation of shoots occurring under the higher night temperature regime.

The shoot elongation response of Pyracantha induced by gibberellin under the various temperature regimes greatly challenges the schemes presented (Figure 7). The lack of a significant interaction during the first 3 months of the experiment would indicate that the endogenous gibberellins and inhibitors are closely balanced (Angle A greatly reduced).

Employing the previous explanation used to explain the interaction between gibberellin and photoperiod on the growth responses of Pyracantha will suffice. That is, under high night temperatures the production of endogenous gibberellins are controlled by the temperature while the synthesis of the endogenous inhibitors are not. The reverse is true for the synthesis of endogenous gibberellins and inhibitors under low night temperatures. Consequently, the addition of gibberellin to plants under the higher night temperature results in a growth stimulation of the shoots. The exogenous source of gibberellin in combination with the endogenous source is slowly destroyed by the mechanisms which are operative under high night temperatures, consequently a slight acceleration in shoot elongation results. In contrast plants under low night temperatures do not possess this system to destroy or make gibberellin inoperative, thus an inhibition in growth results. A failure of an interaction earlier in the season would indicate that the mechanism for destroying an exogenous supply of gibberellin is operative in plants under both low or high night temperatures.

Pinus also failed to respond markedly to gibberellin treatment early in the season, but in mid-July death of plants treated with gibberellin under high night temperatures occurred. It is difficult to explain this response. Possibly under high night temperatures, there is a rapid

accumulation of inhibitors as the season progresses. In this respect the shoot extension of Pinus in early June under high night temperatures is markedly reduced but not so under low night temperatures. This supports the above schemes. It is postulated that gibberellin increases the sensitivity of plant tissue to endogenous inhibitors. Gibberellin has been reported to induce abortion or disiccation of terminal buds in other woody plants, (McVey and Wittwer, 1958; Nelson, 1957; Soost, 1959). Clor, Currier and Stocking (1958) also reported an increase in the sensitivity of bean plants to 2,4-D following gibberellin treatment. Weaver (1959) reported a prolonged dormancy in buds of Vitus vinifera with increasing amounts of gibberellin. It appears that the sensitivity of some tissues to the endogenous inhibitors may be increased by the presence of gibberellin.

The interaction of the accumulative vegetative responses to gibberellin and temperature can be explained amply by the schemes presented. Note in Figure 15 that under the high night temperature regime, Catalpa plants treated with gibberellin exhibited a greater inhibition in growth than those under the low night temperatures. This relationship was not evident in Viburnum and Syringa. Explanation of this difference by the schemes presented is as follows: In Catalpa there is a rapid increase in endogenous gibberellin synthesis in the early spring. The accumulation of an inhibitor to over balance the concentration of gibberellin is not apparent until late June or early July (Figure 5, Treatment C_2). The rate of synthesis of endogenous gibberellin is as rapid in Syringa, but in contrast to Catalpa, the accumulation of the inhibitor complex occurs much more rapidly; about the first of June (Figure 5, Treatment C_2).

The rate of inhibitor accumulation consequently controls the action of gibberellin. In one case, (Catalpa), the reduced rate of synthesis of the inhibitor in conjunction with a rapid rate of synthesis of the endogenous gibberellins results in uncontrolled growth (Figure 17). While in Syringa the growth is moderated by a rapid production of endogenous inhibitors. To explain this relationship in respect to scheme II would necessitate both a change in position of the vertex and the degree of angle A. For example, the position of the vertex would shift to the right and the angle would increase for Catalpa. In contrast, for Syringa the vertex would have to move to the left with relatively no change in the position of angle A.

Viburnum, in contrast to Syringa does not accumulate an inhibitor under high night temperatures. However, the rate of elongation of the shoot is greatly reduced, as compared to Syringa and Catalpa. This would imply that it is not essential for an inhibitor to be produced to prevent the deleterious effects following gibberellin treatment. On the contrary, a relatively low quantity of endogenous gibberellin will permit the addition of an exogenous source of gibberellin without resulting in the inhibition of growth. Graphically presented, the shift in the vertex would be to the right, but the angle A would be greatly reduced. Shoot elongation which was greater under higher night temperature than under lower night temperatures would suggest a greater production of endogenous gibberellin under the higher as compared to the lower night temperature. The reduction of angle A allows the addition of an exogenous source of gibberellin under either low or high temperatures without a deleterious effect resulting (Figure 27).

Acer, Pinus and Euonymus generally exhibited an increased growth under low temperature, but in contrast to Viburnum, the rate of elongation under high night temperatures was inhibited later in the season. Possibly a rapid accumulation of inhibitors in Acer, Pinus and Euonymus under high night temperatures (Figures 5 and 6, Treatment C_2) reduced the action of gibberellin. In some cases gibberellin might increase the sensitivity of the cells. Consequently resulting in an inhibition in growth from the high concentration of inhibitors present.

The induction and cessation of dormancy as shown in Figure 13 strongly supports the concept presented. Note that under high night temperatures as compared to low night regime (treatment 7 and 8) gibberellin was much less effective in preventing induction of dormancy in Acer, Euonymus, Syringa and Liriodendron. In the latter species this was only evident under high night temperature-short day regime illustrating the importance of photoperiod in this overall scheme of dormancy.

It would appear that the synthesis of gibberellin in shoots of plants is not as temperature dependent as that of seeds. In this respect, note in Table III that the total germination under alternating day and night temperatures was not altered following gibberellin treatment. In contrast the shoot extension of Catalpa and Syringa was greatly stimulated as compared to the check under the low night temperature regime. This would indicate that the synthesis of gibberellin in seeds is relatively high, or conversely the distruction of inhibitors are relatively rapid resulting in a total germination. However, in terminal shoots of plants there appears to be a strongly moderating influence of endogenous

inhibitors within the plant which prevents full expression of the endogenous gibberellin regardless of the environmental exposure. In Liriodendron and Viburnum however the ultimate achievement is similar to that of germination of Catalpa seed under optimum conditions, that is, the total growth was similar under either long days, high night temperatures, or gibberellin treatment. This would imply that there is a complete utilization of the endogenous gibberellins synthesized under the long days or high night temperatures, during the shoot extension period.

It would appear that a high production of gibberellin in conjunction with a reduced rate of synthesis of an inhibitor within the seed (increase in the angle A with the vertex removed to the left in scheme I) might result in poor germination following gibberellin treatment. In this respect Tod (1958) reported that seeds which were difficult or erratic germinators exhibited an increase in germination following treatment with gibberellin. In contrast, seeds which normally germinate fairly freely were inhibited by high concentrations of gibberellin. Donoho and Walker (1957), also reported an increase in germination with low concentrations of gibberellin applied to partially stratified seed, if however a high concentration was used, germination was inhibited. Richardson (1959) reported a depressing effect of gibberellin on germination of Pseudotsuga taxifolia with higher concentrations in comparison to low concentration of 3 to 10 ppm of gibberellin.

The concept of a gibberellin-inhibitor balance as a mechanism controlling growth has been present elsewhere (Lockhart, 1961; Wareing and Villiers, 1961; Nitsch and Nitsch, 1959). It is of interest to note that "gibberellin-like" substances were present in larger amounts in plants grown under long days than those exposed to a short day regime.

(Chailakhian, 1961). In this respect Brain and Hemming, (1961) reported an increase in the response of plants to a exogenous source of gibberellin as the length of the previous photoperiod increased. Not only is the photoperiod effective in modifying the synthesis of an endogenous source of gibberellin but the thermoperiod might play an important role. Wareing and Villiers (1961) reported that chilling of dormant Fraxinus seeds resulted in an increase in the concentration of a growth promoter accompanied by a reduction in the inhibitor concentration. Donoho and Walker, 1957; Fogle and McCrory, 1959; Marth, Audia and Mitchell, 1956; Prince, 1958; Stuart, 1957, also reported the optimum concentration of gibberellin for breaking dormancy decreased as the period of exposure to chilling temperatures increased.

IV. Alterations in the Metabolism by Gibberellin

A. Modifications of Mineral Absorption and Distribution

1. Dry Weight Distribution

Alterations in the distribution of the dry weight in woody plants following gibberellin treatment have been widely reported (Benjamin and Snyder, 1958; Hull and Lewis, 1959; Scurfield and Moore, 1958; Powell, Cain and Lamb, 1959). The degree of alterations in dry weight distribution appears to be dependent on the time of application, physiological stage of development, species, and concentration of gibberellin (Hull and Lewis, 1959; Benjamin and Snyder, 1958; Chakrevarti, 1958; and Ergle, 1958). More specifically, Ergle (1958) reported an in-

crease in stem weight with little or no effect on leaf and shoot dry weight with small quantities of gibberellin (10 to 100 micrograms). If a large quantity of gibberellin were used, there was a marked reduction in leaf weight together with that of the entire plant. Scurfield and Moore (1958) reported a similar condition in Eucalyptus but in contrast the shoot weight increased concurrently with a reduction in leaf and root weight. The physiological stage of development as shown by Fogle (1958) in his studies with after-ripened Sweet cherry seeds, also greatly modifies the response of shoot growth to gibberellin.

Evidence present in Figures 14 and 15 illustrate many of the varied dry weight modifications in woody plants resulting from gibberellin treatment.

The marked increase in dry weight of the newly developing shoot of most species studied, accompanied by an inhibition in root, leaf and occasionally old shoot growth development, would necessitate an alteration in the normal distribution of the plant constituents. The rapidly developing shoots resulting from gibberellin treatment can obtain the carbohydrates required from two sources, the leaf, or reserve carbohydrates in the older wood. It is of interest to note that Hayashi (1961) reported a reduction in the reducing and total sugars in the roots of rice plant treated with gibberellin with a subsequent increase in the reducing sugars in the shoots. If there is a reduction in leaf area, the carbohydrate required for shoot extension would come basically from the stored reserve. In contrast, if the leaf area is not reduced, the reserve carbohydrate would be partially spared. To illustrate this point, note in Figure 14, that a reduction in the leaf area per plant (5) in Catalpa resulted in a subsequent reduction in the dry weight of the old

wood. However, as shown in Figure 15, the inhibition in leaf expansion was not as evident under low night temperatures or short days. This resulted in an actual increase in the dry weight of the old shoot under a low night temperature regime, following gibberellin treatment. The dry weight of the old wood was generally spared when the leaf expansion or leaf area was greater under one environment than another, following gibberellin treatment.

2. Mineral Distribution in Catalpa speciosa

Evidence presented would strongly suggest that the nitrogen metabolism within the roots of Catalpa speciosa treated with gibberellin simulates that of short days and low temperatures. In contrast, it is suggested by the data that the reciprocal relationship is true for the shoots. This relationship might partially explain the greater inhibition of growth under long days or high temperatures following gibberellin treatment. That is, a reduced rate of transport of nitrogen to the shoot following gibberellin treatment which normally occurs under long day and high temperature, would result in a nitrogen deficiency in the shoots of plants. This response, associated with an increased carbohydrate movement to the shoot, which was suggested by the data in Table IV, would result in an increased C/N ratio in the shoots or conversely a decreased C/N ratio in the roots.

An increased carbohydrate content in the shoot would necessitate a decrease in the ash content. This, however, was not evident, suggesting that gibberellin caused an increase in the utilization of the carbohydrates translocated to the shoots. Consequently, the difference

between the percent ash in the leaves and new shoots was not significant. In this respect, high night temperatures caused an increase in the ash content in the leaves, suggesting that gibberellin treatment simulated the response of high night temperatures. Evidence has appeared in the literature indicating an increase in the rate of respiration following gibberellin treatment, (Nielsen and Bergquist, 1958; Paleg, 1960).

3. Absorption and Transport of Labelled Phosphorus in *Catalpa speciosa*

Evidence is presented which strongly suggests that gibberellin or photoperiod does not alter the movement of labeled phosphorus out of the leaves of *Catalpa* seedlings. In contrast to the photoperiodic response, which was not apparent in the young seedlings, gibberellin greatly stimulates growth of the shoot with a subsequent reduction in root weight (Table V). This evidence would suggest that the greater quantity of photosynthate utilized in the synthesis of organic constituents, within the rapidly developing shoot, came from the reserves accumulated in the root and old shoot wood. In this respect, Alvin (1960) reported that the inhibition of dry weight accumulation in roots of beans treated with gibberellin could be controlled by the addition of a 10 percent sucrose solution.

A relationship between the metabolism of nutrient uptake and vegetative growth of *Catalpa speciosa*, suggests possible causes for the differential growth response to gibberellin under various thermoperiodic and photoperiodic regimes. The inhibition of nutrient uptake and distribution by roots of young seedlings following gibberellin treatment

might suggest that a reduction in root surface caused the inhibition observed. However, a differential rate of uptake at different root temperatures rules out this possibility.

The uptake of anions, such as phosphates are generally accumulated metabolically in relation to enhanced aerobic respiration. However, it is now recognized that phosphates can be absorbed by non metabolic pathways. (Steward and Sutcliffe, 1959). If we assume that the quantity of photosynthates moving to the roots are reduced as a result of gibberellin treatment, it is evident that at higher temperatures a greater quantity of the photosynthates would be needed to compensate for the increased rate of respiration. Consequently, a reduction in uptake at the higher temperature following gibberellin treatment would result. In contrast, at lower temperatures the rate of respiration in the root would not be greatly accelerated thus the supply of photosynthate would be sufficient to provide the energy required for active uptake. The reduced rate of uptake under high root temperatures might explain the greater inhibition of growth in Catalpa speciosa under high as compared to low night temperatures.

Uptake and distribution of phosphorus, as affected by gibberellin is mediated by the photoperiod imposed on young seedlings of Catalpa (3 weeks of preconditioning to gibberellin and photoperiod). The percentage of phosphorus translocated to the shoot following gibberellin treatment was increased to a greater extent under short than long days. As the plants matured, the uptake of phosphorus by the roots of plants treated with gibberellin was inhibited to a greater extent under long than short days. This relationship would indicate a similarity between the metabolic

and the vegetative aspects of growth as modified by gibberellin. It is of interest that the proposed schemes (I and II) might partially explain the differences observed. In young seedlings, the balance between endogenous inhibitors and gibberellin under short days is represented in Scheme I, while those under long days is represented by Scheme II. Consequently, the addition of an exogenous supply of gibberellin to plants under short days results in an increased growth response which is moderated by the inhibitor present. After 6 weeks of preconditioning the inhibitor content is so intense under short days that the exogenous source of gibberellin is masked. In contrast, the inhibition of uptake under long days by roots of Catalpa plants preconditioned for six weeks, as compared to those preconditioned for 3 weeks, would indicate that the balance between the endogenous inhibitor and gibberellin was sufficient to moderate the effects of an exogenous source of gibberellin after 3 weeks, but not so after 6 weeks of preconditioning.

An increase in the gibberellin-inhibitor ratio could result in an increased rate of respiration in the shoots and therefore a reduced rate of uptake, because of an insufficient supply of photosynthate moving to the roots.

In contrast to findings reported herein, Linck and Sudia (1960) reported an increase in the quantity of phosphorus absorbed by roots of bean plants treated with 1 ppm of gibberellin. The rate and method of application might account for the discrepancy in results.

SUMMARY

Certain woody plants (Catalpa speciosa, Liriodendron Tulipifera, Viburnum Carlesii, Acer saccharum, Pinus sylvestris, Pyracantha coccinea Lalandii, Syringa vulgaris and Euonymus Fortunei vegetus) exhibiting a known photoperiodic response and a broad range of temperature adaptation were selected for this investigation. Two aspects of plant behavior were followed. The plants were subjected to photoperiods of 9 (short) and 18 (long) hours, thermoperiods of 40°F (low) and 70°F (high) night temperatures and to sprays of gibberellin at 0 and 50 ppm for the evaluation of the various vegetative growth responses. Alterations in metabolism were determined by using a radio-labeled source of phosphorus applied to the foliage or roots of Catalpa speciosa. These plants were subjected to various photoperiods, gibberellin concentrations and root temperatures prior to or during the P^{32} treatment.

Gibberellin simulated a shoot extension response which is typical of long days or cool night temperatures. In addition, gibberellin replaced the affect of high night temperatures on shoot elongation in plants which grew more favorably under this regime. The photoperiodic response of vegetative shoot elongation was replaced to a greater extent by gibberellin than the thermoperiodic response. Although gibberellin could replace the shoot elongation which was stimulated by the various environmental regimes imposed, replacement was not evident in leaf, root and old shoot wood dry weights.

Differential responses to gibberellin under the various photoperiods and thermoperiods imposed indicated an interaction between endogenous

growth regulators and an exogenous source of gibberellin. A mechanism for the hormonal control of growth and development in the woody plants investigated is proposed.

Alterations in the metabolism of Catalpa speciosa by gibberellin suggest that the reserves in the old wood are the primary source of carbohydrate in the shoot which is induced to elongate rapidly. These reserves may be partially spared by an increase in the leaf area per plant.

Phosphorus uptake and distribution by the roots of Catalpa speciosa seedlings was altered by gibberellin at the high but not at the low root temperatures. The phosphorus distribution in the young short day gibberellin treated Catalpa plants was similar to those not treated under long days. In contrast, as the plants matured, gibberellin was effective in inhibiting the uptake and distribution of phosphorus only under the long day regime.

Both induced vegetative growth responses and alterations in the metabolism suggest that endogenous growth regulators modify the effects of an exogenous source of gibberellin. The degree of modification depends on the rapidity, duration, and extent of the response to the imposed photoperiod or thermoperiod.

It is suggested that the endogenous growth regulators associated with the various stages of growth and development strongly modify the responses of certain woody plants to gibberellin. An understanding of the photoperiodic and thermoperiodic responses of plants would allow one to predict the response and possibly the concentration of gibberellin required to obtain optimal growth of all plant parts with no loss of aesthetic value.

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