commercially, using basically the same idea.

CHAIRMAN HERMAN SANDKUHLE: Thank you very much, Carl. I'm sorry that we had to rush you through.

THURSDAY AFTERNOON SESSION

October 26, 1961

q The session convened at 1:30 p.m. with Dr. Vernon T. Stoutemyer, Department of Floriculture and Ornamental Horticulture, University of California at Los Angeles, presiding. The subject of this Symposium was: Light in Relation to Plant Propagation.

MODERATOR STOUTEMYER: The amazing thing about light effects is that many people who almost made the important discoveries, didn't. The men who should have made these, I think, were the Germans who dominated plant physiology from 1850 into the beginning of this century. The one who probably should have discovered photoperiodism was a man named Klebs. He almost had it; but two men in the U. S. Department of Agriculture, Garner and Allard, were unquestionably the first to present proof of this phenomenon of photoperiodism.

We are covering many subjects related to light in this discussion, not only photoperiodism, but many other things. I'm sure there are things that we will be doing with light some day in propagation that we're not doing now. For instance, by exposing stock plants to an unbalanced spectrum, you can change completely the type of roots formed, the amount of callus in the relation to the roots, and the ease of rooting.

LIGHT AND PROPAGATION

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The subject of light in propagation is an example of a badly integrated field of knowledge with a conspicuous lack of communication between the workers in basic science and those who represent the applied side of agricultural science and technology. It is also an example of a rather haphazardly worked basic field with many conspicuous gaps in our knowledge. It is difficult to explain why researchers have given so little attention to some of these problems. One example is that almost no information is available on the effects of different light qualities and intensities on the stock plants for cuttings. The voluminous literature on the influence of light on seed germination is somewhat confusing for reasons which will be discussed later, although the rapid progress of recent research is clarifying the situation.

We shall treat four main subjects in our discussion of light. These are:

1. Light and seed germination.
2. Effects of light on stockplants for cuttings.
3. Light and the rooting of cuttings.
4. Etiolation and root formation in stems.

Light and Seed Germination

Around the turn of the century, the great German plant physiologists and botanists accumulated many interesting facts on the effects of light on seeds. Seed testing laboratories have also had to take the effects of light into consideration with their seed testing and germination procedures. For instance they commonly expose grass seeds to light for about four hours a day for best germination. Many light-sensitive seeds will germinate in the dark if given a weak solution of potassium nitrate or a complete mineral nutrient solution. Foresters have known that light is beneficial to the germination of seeds of some pines. According to Burkholder (4) about 1200 different kinds of seeds, many of them important economic plants, have been reported to be light-sensitive. There are many contradictions in the literature. Some of these variations, as with tobacco or Lobelia, are due to the genetic differences of various varieties and species. The results are also influenced by the temperatures used for germination and by the age and condition of the seeds. Light can be inhibitory as well as stimulating.

The investigations of Axenthev (3) aid in explaining the nature of the mechanism of light stimulation of seeds and also the inhibition of another group. He found that both stimulation and inhibition were dependent on the seed coats in some species but not in others.

In seeds which are inhibited by light, this effect depended upon an intact seed coat in Amaranthus retroflexus, Phacelia tanacetifolia, Bromus squarrosus and Androsace maxima. However, in Nigella arvensis, Cucumis melo, C. sativus and Cucurbita pepo the effect did not depend entirely on seed coats.

Among the seeds which are stimulated by light, the effect was due to the intact seed coats in Rumex crispus and Epilobium hirsutum, but the coats played little part in the stimulation of seeds of Oenothera biennis and Silene densiflora.

In all seeds in which the seed coat played an important part, increasing the oxygen in the atmosphere improved germination and reducing it, decreased it. In some of these seeds the effect of the coat was eliminated by pricking a hole in it. These facts suggest that the seed coats act in some cases by reducing the supply of oxygen and that the light changes the permeability. Apparently light increases oxidative processes in some seeds and decreases it in others.

Although light promotes the germination of some seeds, in others it has an inhibiting effect. Thus the seeds of Lallemantia iberica normally germinate well in the dark, but were thrown into secondary dormancy by exposure to light in experiments by Vakulin (18). The seeds germinated when placed in the dark again, but with increasing difficulty as the exposure to light was increased.

With seeds of tomato, a subject which has also been recognized to be inhibited by the action of light, the seeds were illuminated by Aneli (2) through a filter vessel 2 cm. thick containing a 0.01 per cent aqueous solution of methylene blue. This passed the whole blue spectrum and one-third of the violet end and the usual depression of the germination occurred, and percentages ranging from 0 to 28.5, depending on the variety, were obtained from samples of seed which normally germinated about 96 per cent in darkness. Biochemical studies which were made on these seeds showed that respiration was reduced under blue irradiation, and disaccharides decreased in amount at first but afterwards increased. On the contrary, in seeds germinated in darkness, the increase was in the monosaccharides as the starch decreased.

Some other examples of seeds inhibited by light are Nigella, Celosia and certain species of Amaranthus, although light is helpful to some of the latter if dormant.

The experiments of Flint and McAlister (6) at the Smithsonian Institution of Washington, D. C., demonstrated that the wavelengths between 5,200 and 7,000 angstroms were effective with light-sensitive lettuce seed in promoting germination. The critical wavelength within the most effective range was about 6,700 A. The light which appeared to be most effective was the same as that which is absorbed most abundantly by chlorophyll and the authors were able to demonstrate the presence of chlorophyll in the seed. It is now known that red light promotes germination of some seeds but the far red inhibits it.

This work was later continued brilliantly by a group of scientists at the USDA Plant Industry Station at Beltsville, Maryland, who separated the influence of red and far red light and were able to develop an action spectrum for the effects which seemed to relate these effects to the same action spectrum for the control of flowering in plants. An unstable pigment, phytochrome, was discovered and partially characterized, although much work may be needed before its chemical structure will be known completely.

At the U. S. Plant Introduction Garden at Glenn Dale, Maryland, the head propagator, Mr. Albert Close, handled thousands of seeds of little known plants from all over the world. Seeds were usually sown on shredded and sifted sphagnum moss, either living or dead, and the seeds were covered very lightly, or not at all, so that a little light would be available for the seeds which would benefit by it. The seed flats were covered with glass or with plastic in wooden frames and were covered with newspapers so that the light was quite subdued.

The 1961 Yearbook of the U. S. Department of Agriculture is devoted to the subject of seeds. On page 93 an instance is cited of birch seeds which will not germinate on a forest floor beneath a leafy canopy, but will germinate in an opening which receives direct sunlight. This is interpreted as a response to the filtering out of the red light, but not the far-red by the leaves of the trees.

Effects of Light on Stock Plants

The modification of the quality or quantity of light on stock plants has a profound effect on stock plant behavior and also on the rooting of cuttings taken from them. Abbot (1) found that a plant of *Pandanus* grown under light rich in the red end of the spectrum and poor in the blue proliferated buds and produced an exceptional number of offshoots.

Stoutemyer and Close (15) illuminated stock plants of *Gordonia oxillaris* and *Cinchona* with various qualities of light from fluorescent tubes and compared the callus and root formation with that produced on cuttings from greenhouse grown stock plants. With the latter and with stock plants grown under daylight tubes, callus formation was excessive and roots were light. Plants grown under blue fluorescent tubes produced the heaviest rooting and lightest callus. In this experiment, the results were clear cut and striking, but unfortunately this line of work has never been continued either by the speaker or by others.

A moderate reduction of light on stock plants may increase the ease of rooting of cuttings. Thus cuttings of certain varieties of roses grown outdoors in sun root poorly, but may root better when the stock plants are grown in partial shade, according to a famous nurseryman of a past generation, Thomas Meehan (9). This rule is not invariable. L. B. Stewart, the famous propagator of the Botanical Garden at Edinburgh, took cuttings from plants in both sun or shade according to the requirements of the individual plant. Thus cuttings of *Escallonia* were taken from plants in full sun, but cuttings of *Clematis montana* were taken from plants in shade.

The reason why plants which are grown under low light intensities often supply cuttings which are rooted more easily than those from plants grown in full sun may be related to the established fact that solar radiation tends to inactivate auxin. This is particularly true of the short wave lengths of the spectrum.

Since environmental factors about the parent plant influence greatly the internal condition of the part of the plant which is to be made into a cutting, they are among the most important considerations in the rooting of cuttings. This is the reason why cuttings of a plant may be difficult to root in one country, but easy in another. Altitude may also be a factor in rooting, and sometimes cuttings from plants grown near sea level are hard to root, although those grown a short distance away near the top of a high mountain may be rooted easily. Probably this is not directly related to light quality.

Cuttings taken from stock plants grown under glass usually root much more freely than those taken from plants of the same species grown outdoors. The causes may include the greater humidity under glass or the screening out of ultra-violet rays by the glass or possibly the higher temperatures. At any rate, cuttings of many woody plants which are exceedingly difficult to root may strike easily when taken from stock plants which have been forced under glass. This is almost always one of the most useful procedures for the rooting of difficult plants.

Light and the Rooting of Cuttings

Not long ago the noted plant physiologist, Frits Went, suggested that a blue or purpled glass or plastic would be more efficient in plant growing structures than clear glass. It is interesting to note that as far as propagation is concerned this idea was prevalent in some circles both in Europe and in America. In 1845, Neumann, the propagator of the famous botanic garden at Paris, reported that bell jars of blue glass were often preferred to those of the ordinary clear greenish glass for covering cuttings during the process of rooting. (11) Grape cuttings were reported by "Thoth" (16) to root more quickly when covered by blue or violet tinted glass than when under clear glass.

The addition of supplementary artificial light over cutting beds has occasionally been demonstrated to increase root production in cuttings under certain circumstances. Chouard (5) found that supplementary lighting increased root production in cuttings of pea. Under orange glass the roots were numerous and little branched, but under blue glass the roots were longer, fewer and more branched. Leaf cuttings of Brimeura (Hyacinthus amethystina) produced the best bulbs under neon lights but mazda bulbs likewise increased rooting.

Since the light intensity is a highly important factor in the rooting of greenwood cuttings it is not unlikely that in the future an increasing use will be made of objective measurements of the light intensity within propagating structures by means of various types of illuminometers.

When the speaker was working at Glenn Dale, Maryland, measurements were made at noon of the light intensity within outdoor propagating frames, in which cuttings of azaleas were rooting with excellent uniformity and ease. The light intensity within the frame at noon as measured by a Weston illumination meter was never much over 250 to 300 foot candles. Measurements made within propagating cases in a north lean-to greenhouse used for summer propagation gave similar readings. The normal intensity of noonday sun in this locality is over 10,000 foot candles.

Although these conditions were not proved to be entirely optimal they certainly approached this condition, which shows the desirability of a considerable reduction of the light over cuttings in frames. Traub and Marshall (17) found an even lower light intensity to be beneficial in rooting cuttings of payaya, and only 100 to 200 foot candles of light were maintained over the cuttings in the propagating frame. On the other hand, the introduction of mist propagation has given an entirely new impetus toward the use of high light intensities, even to the use of unscreened or unshaded sunlight. The rooting of cuttings with full sun under mist is now quite common and many cuttings do quite well with such a treatment.

Since length of day has a considerable effect on both the vegetative and reproductive processes of plants, it would indeed be surprising if photoperiodism did not also influence the rooting of cuttings of plants in some degree. In some experiments with southern species of woody plants transported to more northerly latitudes, the rooting of cuttings was improved when the day length for the parent plants was decreased to that normal in their native habitats. Nevertheless, the cuttings of most species rooted better when the propagating bed which Moshkov and Kocherzhenko (10) used was illuminated continuously.

Etiolation and Root Formation in Stems

The etiolation of shoots, which is accomplished by growing them in darkness, is a particularly effective treatment for the rooting of cuttings of plants which are otherwise difficult or impossible to root. The etiolation of the stems is undoubtedly one of the chief factors responsible for the exceptional success of layers with recalcitrant plants. The effectiveness of etiolation can be enhanced by applying ringing or notching treatments at the same time.

Since most methods of etiolating stems also change other growth factors such as temperature and humidity, the exact part played by the exclusion of light is not always easy to measure. However, there can be no doubt of the inhibitory action of light on the rooting of cuttings of certain plants. The chemical and anatomical changes produced by etiolation are not clearly understood at present. However, some important observations have been made by Smith (14) which aid in the comprehension of the process. As tissues increased in age, the proportion which is highly lignified became greater. Etiolation changed some of the tissues back to a condition resembling that of the younger and more active portions. The tissues were softened, especially the pith and fibers, and meristematic activity was promoted, particularly in vascular rays, which often play an important part in rooting.

Kuster (8) has reviewed the literature on the changes produced in stems by etiolation. He concluded that the etiolation of stems depresses the development of mechanical strengthening tissues and also the vascular conducting elements. Parenchyma was less differentiated and the development of highly specialized units such as hairs, was suppressed. The large amount of undifferentiated tissue in etiolated stems favors root formation, and although large, vacuolated cells can divide, undoubtedly the advantage of having as many cells as possible in an undifferentiated condition is great.

Etiolation has been considered by Priestley (13) to delay lignification of pericyclic cells and to keep them more actively meristematic. One significant difference following etiolation was observed in shoots of broad bean, pea or potato which, when grown in darkness produced a functional endodermis with Casparian strips, although shoots produced in the light formed a simple starch sheath.

One other change noticed by Priestley and Ewing (12) in apical shoot meristems after etiolation which also suggests root structure is that the growth of the superficial meristem is diminished and fewer folds occur resulting in a decreased development of lateral leaf initials.

Priestley (13) made some observations which have an important bearing on the greater ability of etiolated stems to form roots. In darkness the fatty substances released from the dividing meristem cells tended to remain in these cells instead of going to build up the cuticle, thus resulting in a thinner cuticle. The free passage of food was hindered and the meristem did not form the folds which ordinarily differentiate into leaves. Thus the meristem of the shoot, because of a change in nutrition, resembled that of the normal root more closely.

In the root, the fatty substances do not reach the cuticle and air passed in freely. These substances were oxidized and formed a relatively impervious layer in the endodermis, which kept much of the passage of nutritive materials within this layer. Priestley and his associates have laid much emphasis upon the existence of endodermal leaks which determine the regions of root formation.

The effects of etiolation on the food reserves of tissues have been studied, but the interpretations placed on the results do not always agree. In studies on Clematis by Smith (14), starch practically disappeared from the pith, xylem parenchyma and vascular rays and was also reduced in the cortex of stems of clematis defoliated and wrapped with black paper for 10 days to three weeks. A starch sheath was present but without Casparian strips, thus indicating that this was not a true functional endodermis. Walls of fiber cells were reduced in thickness. In these experiments, the reduction of the carbohydrates changing the carbohydrate-nitrogen ratio was considered to be an important factor in changing a resting cell into an actively meristematic cell. Shading of the entire cutting does not accomplish this, since the carbohydrate is reduced without increasing nitrogen and the cutting is therefore weakened.

On the other hand, according to Hicks (7) etiolation did not reduce starch in stems of willow, Salix viminalis, but the reducing sugars were diminished. Cells were more elongated in etiolated tissue and sometimes were thicker.

From a biochemical standpoint, the available information is certainly inadequate and out of date. A modern approach, using more advanced methods of the subject, studying the metabolic changes which the treatment produces might throw much new light on the subject.

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MODERATOR STOUTEMYER: Our next speaker in this symposium is a man in the USDA Beltsville group working on light, at the Plant Industry Station. I would say there's no group in the world that is as far advanced in work on light and on this strange pigment, phytochrome. We don't know what it is yet, but we know it's there; it's a pigment, but it's very unstable, it shifts back and forth from the exposure to the light. It is part of the mechanism of a built-in time clock.

Our first speaker got his Master's Degree at the University of Minnesota, and later his Ph. D. at the University of Maryland. He was in pomology for a while at Minnesota after he got his doctor's degree, and then went to the USDA at Beltsville about a decade ago where he has participated in some of the work on photoperiodism. He has worked especially with woody plant mechanisms as regulated by light, and will lead us in this discussion today - Dr. Albert A. Piringer, Jr.: