Our next speaker is better known to the Eastern Region members as an author than as a lecturer because he is the co-author of a very excéllent text on plant propagation. It gives me a great deal of pleasure to present to you Dr. Dale Kester, who will give us some of his observations and conclusions on the effects of temperature in plant propagation.

TEMPERATURE AND PLANT PROPAGATION

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The pattern of temperature exposure resulting from radiation from the sun to the earth is perhaps the most significant environmental factor that controls plant growth and development and thereby determines what kinds of plants grow and where they grow (26). Likewise, control of temperature is one of the most important tools of the plant propagator. Or perhaps, we could better say that lack of temperature control can be the major limiting factor for plant propagation and subsequent growth of the plant for whatever use we make of it.

Temperature control is achieved by propagators in many ways, utilizing either the natural environment, artificial environments, or both. We can achieve control by locating our operations where the natural temperature regime is favorable and grow plants adapted to that location. We time our operations during the year when proper temperatures are available. We use many artificial methods to control temperature for both heating and cooling: greenhouses, phytotrons, coldframes, hotbeds, bottom heat, refrigerators, mulches, shading, mist systems, sprinkling, reflective materials, such as whitewash, etc.

To exploit these potentials of temperature control we need to know a great deal about engineering aspects of heat production, heat transfer and heat loss. We also should know something about the effects of temperature on the basic biology of the plant. As practical propagators, we need, most of all, to know the temperature requirements of particular plants and plant processes.

PLANT ADAPTATION

My purpose is to discuss some effects of temperature on the basic biological processes of plants as a background for more detailed discussions concerning individual kinds of plants and procedures that will be covered in other parts of these meetings. First, let us recognize that specific growth requirements of plants have resulted from evolution through many generations in a natural environment where such characteristics contributed to survival. Such requirements become more or less fixed into the genetic system and are passed along to the offspring even when shifted to a new environment and whether or not the plant now needs them. When we transplant such plants to new areas and subject them to the demands of modern horticultural production, such requirements may be limiting. What can happen and, in fact, has happened is that through the same process of selective evolution as occurs in nature, plants adapted to the requirements of culture systems have gradually developed. This is really the essence of plant breeding, a procedure which has been exploited with varying degrees of success.

On what are some of the temperature requirements based? The most obvious is the **annual growth cycles** to which plants are subjected in various parts of the world. Compare, for instance: (a) Belem, Brazil, with a hot tropical area where the temperature stays around 80° F through 12 months of the year; (b) San Francisco, California, having a marine climate with cool (55—60° F) but relatively constant temperatures throughout the year; (c) Davis, California, with a distinct seasonal cycle of hot summers and moderately cool winters, where temperatures go below freezing but rarely less than 15° F; and (d) Ames, Iowa with a similar cycle but where winter temperatures can go as low as —30° F. Quite different kinds of plants grow naturally in each of these areas and, if one takes plants from one area to another, quite different kinds of temperature controls may have to be provided for successful culture.

Superimposed upon the annual cycle is the **daily diurnal fluctuation** in temperature from day to night. Knowledge of such requirements has become widely recognized both through scientific experiments (25) and also through plant growing experiences (20). These daily fluctuations are not only important for optimum growth but can be critical for survival. The lower or night temperature is very often (not always) the essential factor. Recommended night temperatures for indoor culture (20) range from 50° F for such plants as carnations and snapdragons; 60° F for roses and chrysanthemums; and about 70° F for warm season foliage plants. Daytime temperatures would be about 10° F higher. These day-night cycles are also important in locating outdoor production areas (16).

In addition to these two basic temperature cycles, a plant can be subjected to **localized microclimatic** conditions. The temperature of the top of the plant exposed to the sun during the day can be considerably higher than the surrounding air depending upon the degree of shading and amount of exposure; likewise the temperature of the same plant during the night can be considerably lower (due to radiation) than that of the surrounding air, depending again upon the degree of exposure. The temperature of the shoot system in both situations may differ considerably from the temperature of the root system, depending upon the depth grown into the soil and the type and depth of cover on the surface of the soil (26).

Let us consider some of the ways temperature affects some basic plant processes.

RESPIRATION AND PHOTOSYNTHESIS

During respiration, energy storing food materials are broken down to CO_2 and water through a series of chemical reactions and metabolic cycles mediated by enzymes (18). At low temperatures, the respiration rate is very low. We reduce temperature to near or below freezing to preserve dormant plants in storage for long periods of time. As the temperature is raised, respiration goes up at an increasing rate. As temperatures rise to 90 ° to 100 ° F, respiration becomes very rapid, materials are used at a rapid rate and the plant can literally "burn up". As temperatures get higher, into the range of 104° to 120° F, an upper limit is reached, cells are injured, and can be killed. There is a time factor associated with high temperatures. The plant may sustain these high respiration rates for only short periods; after a period of time the rate drops; the higher the temperature, the shorter the time.

This type of exponential response curve is typical of many found in the plant since many of the biological processes within plants are chemical reactions, controlled by enzymes. We can say that for respiration, the Q_{10} is 2 or higher. This means that for every 10 degree C rise in temperature, the reaction increases 2 or more times.

In contrast there are other processes, such as the diffusion of CO_2 into a leaf, photochemical light reactions, dissolving materials into water, etc., that are physical rather than chemical. These have a straight line relationship rather than exponential and have a Q_{10} of 1 to 2. At lower temperatures, enzymatic reactions tend to be limiting, whereas at higher temperatures, these physical processes are limiting, even though enzyme activity can be very high.

PHOTOSYNTHESIS

Light energy, plus water, plus carbon dioxide are converted into chemical products (sugars, proteins, fats, etc.) which are the raw materials to provide energy to run the machinery of the plant, build new parts, or are stored for future use. There are two kinds of reactions. First is a photochemical reaction where light energy is converted into chemical energy. This is a physical reaction with a Q_{10} about 1.4. Secondly, there is a "dark" reaction where this chemical energy is converted into various chemical products the plant uses. This is a typical chemical reaction with a Q_{10} of better than 2. At low temperatures the "dark" reaction is limiting and photosynthesis is low. At higher temperatures photosynthesis tends to level off because light becomes limiting. If one attempts to increase photosynthesis by the use of higher temperatures he must also increase light and, perhaps, the CO_2 supply. If light is reduced by shading at these higher temperatures, photosynthesis may be drastically decreased.

The net effect of temperature on the intact plant, however, results from the balance between photosynthesis and respiration. If respiration loss is greater than that gained through photosynthesis the plant will decrease in weight and may eventually die if kept for long periods at continuously high temperatures. The plant should have plenty of light, an efficient, healthy, leaf system, and adequate food reserves before being subjected to such high temperatures. The optimum temperature varies with different kinds of plants from 20°—35° C(68°—86° F).

This principle can be applied to the contrast between the mist systems which are so widely used today and the closed frame system formerly used (10, 11). An enclosed frame system, which is primarily designed to prevent water loss, is associated with low light intensity and high temperature and results in loss of weight in the plant and often poor rooting. Conditions of this system probably mean that a cutting made from a mature, semi-hardened shoot with adequate food reserves would have a better chance of surviving than a cutting that is more succulent and younger in age although with, perhaps, better rooting potential. In contrast, mist systems produce evaporative cooling that can reduce temperatures to 70°or 80° F in full sun and high light intensities, A wider variety of plant materials can be taken at various stages of maturity for optimum rooting with varying amounts of reserve materials and can not only be rooted but can increase in weight during the rooting period.

A second application is the preparation and hardening-off of plants for transplanting. Moderate temperatures with adequate light should provide maximum food reserves.

In either case, we also must recognize that the optimum temperature conditions will vary with different plants.

GROWTH-DORMANCY REACTION

Growth, by which I mean a permanent increase in size, length, or weight, is very responsive to temperature. Growth processes are largely biochemical, so that the temperature response curve is something like the photosynthesis-respiration curve. Figure 1 shows a temperature response curve for growth of an apricot fruit. The same curve could just as well be used for germination, root growth, shoot growth, or callus production. There is: (a) a minimum temperature where no growth takes place or is so slow that it isn't practical to measure; and (b) a rapidly increasing response to temperature, in that growth speeds up drastically. There is an optimum temperature where growth is most rapid and maximum response (for example germination) takes place. This is followed (c) by inhibiting effects that may decrease the rate or reduce the response. If the temperature is too high, of course, injury occurs and the entire system breaks down. The most favorable temperatures for growth, however, seem to be considerably lower than the point where injury occurs.

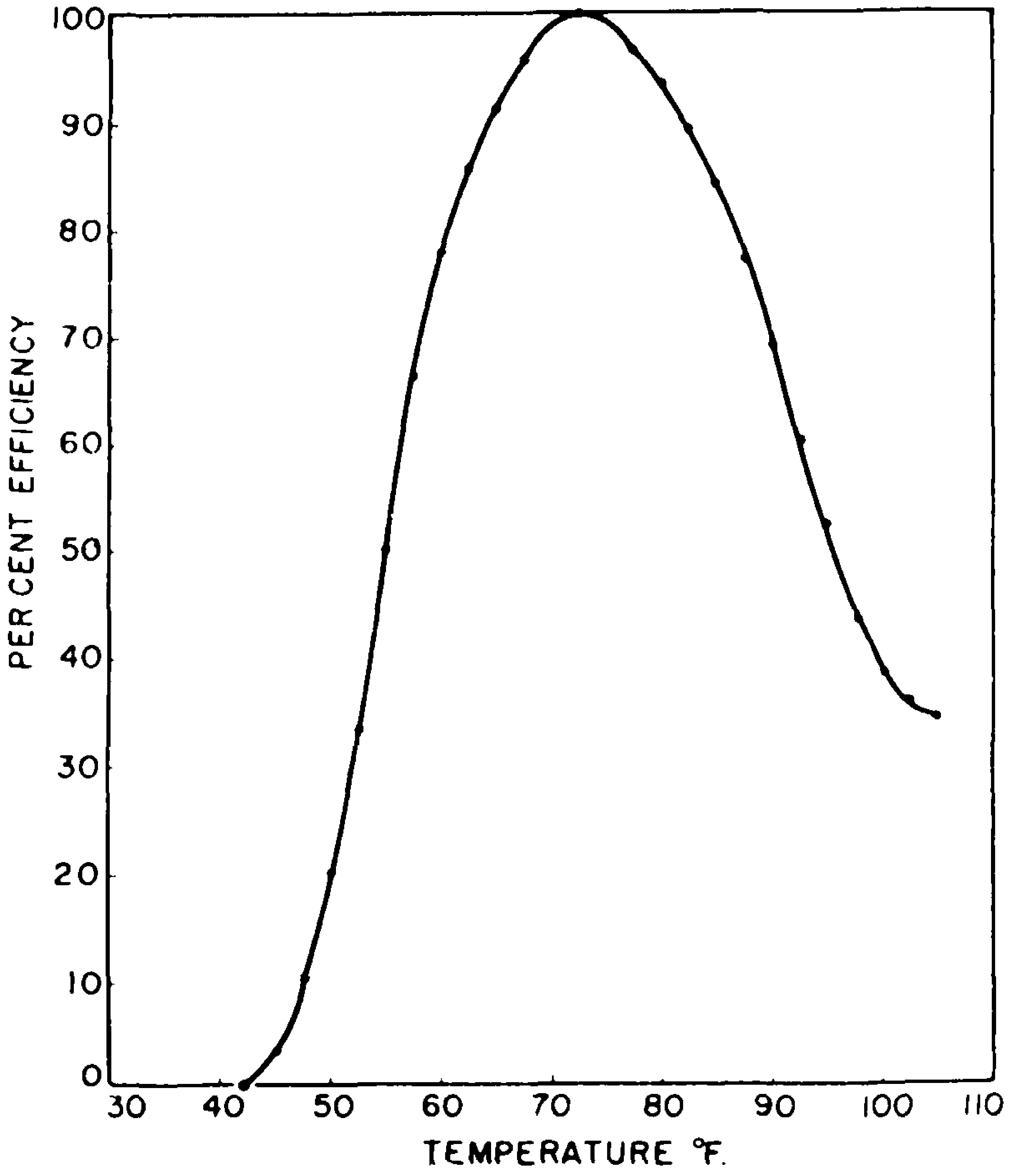

Fig. 1.
The effect of temperature upon growth of an apricot fruit is typical of temperature response curves for many growth phenomenon. From Brown (2).

There is much experimental data to show that the most favorable temperature range for root growth and root initiation in many plants is about 70° F, or slightly higher (4, 12, 13, 19, 23). (Fig. 2). Below this temperature, root growth is reduced and the rate lessened. If temperatures go above 75° or 80° F, at least for many plants, some inhibition and root injury can result.

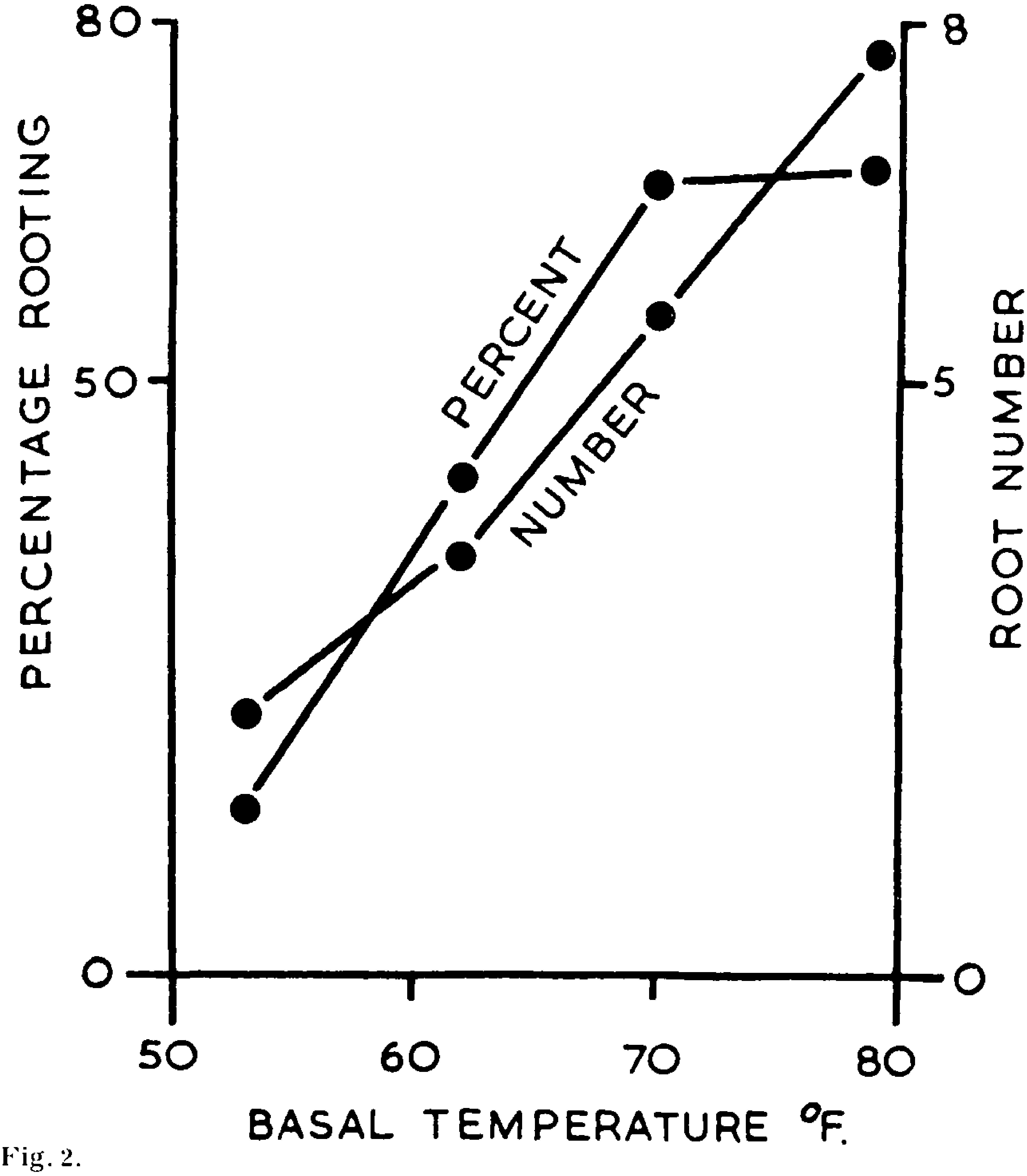

Fig. 2.
Effect of temperature on root initiation in 'EM 26' apple hardwood cuttings (From data of Howard, *J. Hort. Sci.* 43: 23-31. 1968).

Most of these data deal with so-called cool-season plants and may not hold for warm-season plants. For instance, some recent data on the effects of temperature on growth of different citrus rootstock species show that several of them responded to increasing temperature up to 90° F (21). A recent study reporting temperature effects on sunflower roots (3) showed that growth rate increased up to 77° F, declined at higher temperatures, and completely stopped at about 100° F. Growth rate depended upon (a) number of cells dividing, (b) speed of cells dividing, and (c) increase in length of cells. At temperatures less than 77° F temperature affected rate of cell division. Above this temperature, cell division continued to increase up to 85° to 95° F but the number of cells dividing and the size of cells decreased. This shows that both low temperature and high temperature decreased growth but for different reasons.

How about shoot growth? We have already discussed the importance of day-night fluctuations on growth in general. For rooting cuttings, recommendations based on much practical experience have been that the shoot temperature should be less than the root temperature (6). Stated another way, the top temperature should be the optimum for the plant, with bottom heat to give a 10° F differential (20). The explanation for this temperature differential has been that new shoots and leaves may develop before roots form and the cutting is subject to increased desiccation. One might suspect that these recommendations are more important in the absence of a mist system. If we lower the temperature of the tops by mist, we can also drastically reduce root temperature, particularly in continuous mist. Bottom heat may be desirable to keep root temperature from going too low. Certainly the temperature relationships between shoot and root within a mist system might be quite different than in a non-mist environment.

Heide (8) in a series of experiments involving root and shoot initiation on begonia leaves showed that differential temperatures of top and root may produce physiological differences (Fig. 3). Increasing temperature increased rooting but decreased shoot initiation. Temperature differences produced a difference in the physiology of the plant. Higher temperatures were associated with

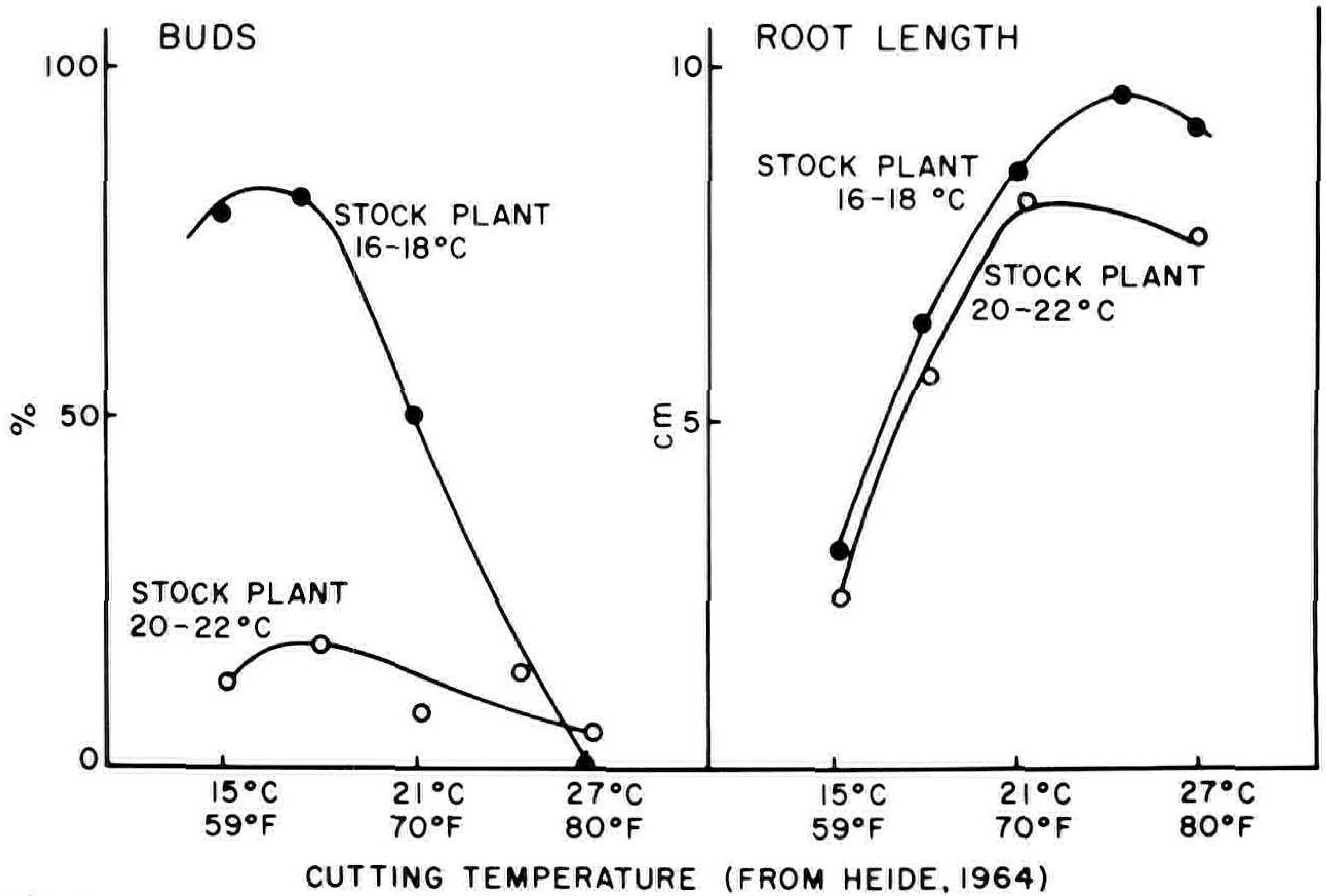

Fig. 3.
The effect of temperature on bud and root initiation in begonia leaves. From Heide (8).

high auxin / kinin ratios whereas lowering the temperatures reduced it. The applications of kinetin materials to these cuttings at the higher temperature increased bud formation (9).

Callus formation in grafting is also strongly influenced by temperature, but different species differ in the range of temperatures within which callus production takes place (15).

Relationship of temperature to growth rates as described is only a part of the story. We must consider the growth-dormancy relationship. Few plants (at least perennial plants) grow continuously but grow and cease growth in cycles of growth and dormancy. How does lowering the temperature affect growth? Many tropical plants exposed to 40° to 50° F, not only cease growth but develop permanent chilling injury; others, such as citrus, exposed gradually to low temperatures cease growing and become dormant. If properly hardened, they can withstand considerable freezing. When temperature increases these plants start to grow again. Deciduous trees and shrubs of the temperate zone enter dormancy as temperatures gradually lower in the fall. Other factors, as shortened days, also are factors. The buds of these plants, in addition to being dormant, will have developed a rest period which started earlier in the summer when temperatures were high. This rest period prevents the buds from growing until such time as the rest period is overcome by prolonged exposure to moderately cool temperatures (that is, 32° to about 45° F(. Such plants can withstand considerable freezing, e.g. down to 0° F. A fourth group of plants exists which not only go dormant and develop a rest period, but have the ability to develop hardiness to extremely low temperatures (—30° F, for instance) if they are first exposed to a period of time to temperatures around 0° F (24).

If the rest period has disappeared by the end of the winter season, the buds on the plant will respond to warm temperatures and grow. If the rest period is still in effect to some degree, growth may be delayed or sluggish to some extent, The significant point to us, as propagators, is that the physiology of the stock plant we are going to use in propagation changes throughout the year along with the shoot's ability to initiate roots. Timing of propagation operations is closely related to the stage of dormancy of the plant(6).

High temperatures can have an inhibiting effect on growth in many instances. Many kinds of seeds show dormancy, at least when freshly harvested, if germination is attempted at about 75° F or higher. At lower temperatures they will germinate without difficulty. Some kinds of seed requiring chilling, such as apple, also are adversely affected by high temperatures and fail to germinate except at moderate temperatures (14). Some seedlings of this group also show severe inhibition of leaves and stems if exposed to high temperatures at early stages of germination (21).

CHANGE IN NATURE OF PLANT (MORPHOGENESIS)

A third significant kind of effect produced by temperature are those cases where a more or less permanent change in the morphology (appearance or structure) of the plant is induced.

This effect is well illustrated by temperate zone bulbs (6,18). Flower and bulb development takes place in well-defined stages beginning with changes of vegetative buds to flowering buds. Progress from one stage to the next depends on exposure to a particular temperature for a certain length of time. Successful bulb production depends upon an understanding of this cycle.

Flowering is induced by exposure to cold in a number of plants. This reaction can be described as a signal the plant receives from the environment to the genetic system of the plant which causes a complete change in the physiology of the plant (18). These changes from a vegetative to a reproductive state can come about in the germinating embryo of some winter cereals (vernalization) or it may occur in the end of first season in the life cycle of biennial crop, e.g. celery.

The olive is an example of a woody plant that has a winter cold requirement to induce flowering (5). Trees may grow beautifully in the tropics but remain vegetative and never flower unless they receive an adequate number of days of the proper chilling regime.

HOST-PARASITE RELATIONSHIP

Much of our discussion in plant physiology assumes that temperature is affecting only the process or plant with which we think we are dealing. In practice, the natural environment or the propagating area with which we are concerned is an ecological system which may include a multitude of other organisms that we don't realize are there, such as fungi, bacteria, insects, viruses, etc. All of these organisms have their own temperature requirements. At certain temperatures these may be particularly active and pathogenic, whereas at others, they are inhibited. The success of a particular propagation technique may be partly due to control of the other organisms (1).

For example, Leach (17) showed that the temperature response in germination can depend on the relative germination rates of the seed as well as that of "damping-off" organisms, *Rhizoctonia* and *Phythium*, which are most active at 20° to 30° C. Consequently, seeds of cool season plants that germinate at lower temperatures can escape them. Because of this effect, treated seed in sterilized media may have different temperature responses than if they are placed in untreated conditions. We had some experience with this problem during 1969 when we were testing stored hardwood cuttings of *Prunus* species at various temperatures. Root initiation was actually best at 68° F but, because of the susceptibility to decay of the material we were using, cutting survival was much less at 68° F than at lower temperatures. On the other hand, 'Marianna' plum cuttings, because of their resistance to these fungi, survived best at 68° F.

This paper has outlined various ways that temperature affects plants. It is the role of the propagator to apply information such as this to conform to the specific requirements of individual kinds of plants.

LITERATURE CITED

1. Baker, K. F. 1957. Damping-off and related diseases. In UC System for Producing Healthy Container Grown Plants. *University of California Manual* 23. p. 34-51.
2. Brown, D. S. 1953. Climate in relation to deciduous fruit production in California. II. The apparent efficiencies of different temperatures for the development of apricot fruit. *Proc. Amer. Soc. Hort. Sci.* 62: 173-188
3. Burholt, D. R. and J. Vant Hof. 1970. The influence of temperature on the relationship between cell population and growth kinetics of *Helianthus annus* roots. *Amer. J. Bot.* 57:73.
4. Fernqvist, I. 1966. Studies on factors in adventitious root formation. *Ann. Agr. College of Sweden.* 32: 109-244.
5. Hartmann, H. T. 1953. Effect of winter chilling on fruitfulness and vegetative growth in the olive. *Proc. Amer. Soc. Hort. Sci.* 62: 184-190.
6. Hartmann, H. T. and D. E. Kester. 1968. Plant Propagation: Principles and Practices, 2nd Edition. Prentice Hall. 702 p.
7. Hartmann, H. T., W. H. Griggs, and C. J. Hansen. 1963. Propagation of own-rooted Old Home and Bartlett pears to produce trees resistant to pear decline. *Proc. Amer. Soc. Hort. Sci. 82: 92-102.*
8. Heide, O. M. 1964. Effects of light and temperature on the regeneration ability of begonia leaf cutting. *Physiol. Plant.* 17: 789-804.
9. Heide, O. M. 1965. Interactions of temperature, auxins and kinins in the regeneration ability of Begonia leaf cuttings. *Physiol. Plantarum* 18: 891-920.
10. Hess, C. E. 1965. Mist from a cuttings viewpoint. *Proc. Int. Plant Prop. Soc.* 15: 71-73.
11. Hess, C. E. and W. E. Snyder. 1955. A physiological comparison of the use of mist with other propagation procedures used in rooting cuttings. *Rpt. of XIVth Intern. Hort. Cong. Netherlands. p. 1133-1139.*
12. Howard, B. W. 1965. Regeneration of the hop plant *(Humulus lupulus* L.) from softwood cuttings. I. The cutting and its rooting environment. *J. Hort. Sci.* 40: 181-91.
13. Howard, B. W. and N. Nahlawi. 1969. Factors affecting the rooting of plum hardwood cuttings. *J. Hort. Sci.* 44: 303-10.

14. Kester, D. E. 1960. Seed dormancy and its relation to nursery practices. *Proc. Plant Prop. Soc.* 10: 256-266.
15. Kester, D. E. 1965. The physiology of grafting. *Proc. Int. Plant Prop. Soc.* 15: 261-272.
16. Kimball, M. and D. E. Gilbert. 1947. Plant climate mapping: the key to conservation of resources. In: Ground Level Climatology. *Amer. Soc. Adv. of Sci.* p. 67-92.
17. Leach, L. D. 1947. Growth rates of host and pathogens as factors determining the severity of me-emergence damping-off. *J. Agr. Res.* 75: 161-179.
18. Leopold, Carl A. 1964. Plant Growth and Development. McGraw-Hill. 466 p.
19. Marston, M. E. 1969. The use of bottom heat in mist propagation of carnation cuttings. *Hort. Res.* 9: 75-79.
20. Nelson, K. S. 1966. Flower and plant production in the greenhouse. Interstate Printers and Publishers, Inc. Danville, Illinois.
21. Northey, J. E., C. H. Hendershott, and J. F. Gerber. 1968. Effects of three rootstocks and three soil temperatures on growth of 'Orlando' tangelos. *Proc. Amer. Soc. Hort. Sci.* 93: 199-204.
22. Pollock, B. M. 1962. Temperature control of physiological dwarfing in peach seedling. *Plant Physiol.* 37: 190-197.
23. Sykes, J. T. and I. H. Williams. 1959. Factors affecting regeneration from cuttings using mist techniques. *Ann. Appl. Biol.* 47: 631-634.
24. Weiser, C. J. 1965. Principles of hardiness and survival as they apply to newly propagated plants. *Proc. Int. Plant Prop. Soc.* 15: 113-121.
25. Went, F. W. and Lillian Overland Sheps. 1969. Environmental factors in growth and development. In: Plant Physiology. VA. F. C. Steward Ed. Academic Press. p. 299-406.
26. Wilsie, C. P. 1962. Crop adaptation and distribution. Freeman. 448 p.

BILL FLEMER: Thank you very much, Dr. Kester. You have done a masterful job of compressing into too little time the very complex and very important effects of temperature on plant propagation and growth.

Our last paper of the symposium this morning will be presented by Richard Maire and will be concerned with mineral nutrition in plant propagation.