tenance of human diversity should be a paramount aim. As long as our brave new world presents an abundance of choices and as long as we have freedom to choose, so long will human intelligence based upon genetic diversity remain a primary requirement.

Intelligence without integrity will fail. Roderick Seidenberg, in a later book, *Anatomy of the Future* (*10*), puts it well. "... The means rather than the ends of life are in our command." Man requires a challenge and a quest if he is to avoid boredom. The Golden Age toward which we move will soon look tawdry if we no longer see endless horizons. We must, then, seek a change within man himself. As he acquires more fully the power to control his own genotype and to direct the course of his own evolution, he must produce a Man who can transcend his present nature. The Erect Ape-Man had little vision of the power that his 20th-century descendant would wield in really so short a span of evolutionary time. For the Erect Ape-Man a club was the acme of power. Even so, if Man can avoid the ultimate follies which our present powers have bestowed upon us, and can survive a few centuries more, we today can little perceive what he may be. Perhaps the Golden Age of no progress will be but a passing phase and history may resume. We can only hope.

References

1. V. Bush, *Endless Horizons* (Public Affairs Press, Washington, D.C., 1946).
2. G. S. Stent, *The Coming of the Golden Age* (Natural History Press, Garden City, N.Y., 1969).
3. R. Seidenberg, *Posthistoric Man* (Univ. of North Carolina Press, Chapel Hill, 1950). See also B. Glass, "A biologic view of human history," *Sci. Mon.* **73**, 363 (1951).
4. L. B. Meyer, *Music, the Arts and Ideas* (Univ. of Chicago Press, Chicago, 1967).
5. B. Glass, *The Timely and the Timeless* (Basic Books, New York, 1970).
6. D. J. de Solla Price, *Science Since Babylon* (Yale Univ. Press, New Haven, 1961).
7. C. Becker, *Progress and Power* (Stanford Univ. Press, Stanford, Calif., 1936; Vintage Books, New York, 1965).
8. B. Glass, *Science*, **165**, 755 (1969); *Quart. Rev. Biol.* **45**, 168 (1970).
9. R. G. Edwards and R. E. Fowler, "Human embryos in the laboratory," *Sci. Amer.* **223**, 44 (Dec. 1970).
10. R. Seidenberg, *Anatomy of the Future* (Univ. of North Carolina Press, Chapel Hill, 1961).

Dormancy of Trees in Winter

Photoperiod is only one of the variables which interact to control leaf fall and other dormancy phenomena.

Thomas O. Perry

Dormancy phenomena in trees include the yearly loss and renewal of leaves which provide both the scientist and the layman with a fascinating pageant of brilliant colors in the fall and a sequence of delicate green traceries in the spring. The leafless tree in winter is commonly said to be in a condition of rest or dormancy; lack of apparent growth and resistance to injury by cold are characteristics of this period.

Careful observations reveal that "dormancy" involves many unsynchronized phenomena. Terminal buds are formed 2 or more months before active growth in diameter ceases and leaves fall. Leaf primordia are formed inside terminal buds during late summer and early fall. Bud scales can grow minutely during every winter month. Roots can grow whenever soil temperature and moisture content are high enough. Photosynthesis, respiration, transpiration, and other physiological activities continue year-round.

The transitions from a phase of active growth in the early summer to a phase of quiescence to a phase of winter rest, and back to a phase of active growth in the spring are gradual. Different species and different genotypes within species vary in their dormancy phenomena. All of the above facts combine to make the task of defining when a plant is in a dormant state or in a state of active growth just as difficult and just as arbitrary as defining whether an organism is dead or alive. Cautious specialists avoid making a highly restrictive definition for the term dormancy. However, some definitions are necessary for intelligent discussion of a subject; for the purpose of this review, a dormant plant is defined as having two attributes: (i) a period of markedly reduced growth rate with few, or in some cases no, cell divisions in the terminal and lateral meristems of the plant and (ii) a winter chilling requirement. Even when exposed to an environment which favors active growth, a dormant plant is unable to renew promptly active growth without exposure to winter cold, chilling, or other special treatments. Not all authors define dormancy in the same way.

Dormancy can be induced and broken both naturally and artificially by a variety of agents that range from controlled photoperiods and winter cold to urine and gibberellic acid; these various agents evidently act to turn some genes on and turn others off. The understanding of dormancy in plants promises to aid in understanding more general mechanisms of genetic control of growth and development. A Pandora's box of over 2000 references related to dormancy and growth substances is opened by reading a selection of review papers (*1–7*). Indeed, the maze of conflicting observations and reviews concerning dormancy and the related field of plant hormones and growth substances is overwhelming.

This article attempts to review the

The author is professor in the School of Forest Resources, North Carolina State University, Raleigh 27607. The review for this manuscript was made while the author was a Charles Bullard Fellow at Harvard University.

existing knowledge of winter dormancy in trees. Dormancy in seeds, bulbs, tubers, and insects is not discussed although there is excellent reason to believe that several of the control mechanisms involved in the dormancy of these life forms are at least homologous to those in trees. The number of references cited has been deliberately restricted.

Growth and Dormancy Sequence

What follows is a general description of the cycle of growth and dormancy for a typical tree from the northeastern United States. This description can serve as a basis for comparison of the various patterns of dormancy phenomena in particular species and genotypes of a given species.

Healthy, open-grown trees in the northeastern United States increase in height 5 to 15 cm per week during the month of June and early July. Eighty to ninety percent of a tree's growth in diameter occurs during this period with additional increments still being made as late as the middle of August. Some species such as white pine and red oak have all of their leaves preformed in the buds of the previous year. Growth in height and expansion of these preformed leaves are often completed by the end of June. Other species (such as maples, poplars, and birches) are less determinate in their growth habits and continue to grow in height and form new leaves until the middle of August. Regardless of the species, active growth and formation of new leaves ceases long before there is danger of frost; cellulose formation is slowed and lignin formation is accelerated. Fats and starches accumulate in the storage tissues of the plant. The buds grow and assume their winter form. Leaf primordia for the next growing season are formed and the apical meristem forms a characteristic domed shape. This period of imperceptible growth marks the beginning of dormancy or early rest. Active vegetative growth may be artificially renewed during this period (August) by treatment with long photoperiods (short nights) or treatment with excess nitrogen fertilizer, or various shock treatments such as defoliation, severe pruning, or flooding. However, under natural circumstances, with the shortening photoperiods of late summer and nights that are either too hot or too cold, the trees continue to make known and unknown physiological changes until they reach a state of true winter rest or dormancy; the leaves are still healthy and green and are still actively able to conduct photosynthesis, and the tree is now able to withstand brief mild freezing (−5° to −10°C), without injury to the leaves, twigs, or buds, but it cannot resume active growth when exposed to a regime of longer photoperiods and favorable temperatures.

Finally, as the night temperatures fall progressively lower, cellulase and pectinases are formed in the abscission zone at the base of the leaf stalk (petiole), and these enzymes begin to digest the cell walls of the abscission zones. The chlorophyll of the leaf breaks down, anthocyanins and other phenols accumulate in the leaves, and the beautiful colors of fall become apparent. Some minerals are transferred to the permanent organs of the tree and the leaves fall. In mild years, the leaves often fall several weeks before there is any killing frost. The tree has then (October to November) completed its preparation for winter and is capable of withstanding the combination of dry winter air, frozen ground (from which the tree cannot obtain sufficient water), and temperatures of −50°C or lower. The tree remains in a state of winter rest until it has been exposed to a period of cold weather. The amount of cold or chilling required varies with the genotype and the weather of the preceding season. Freezing temperatures are not required for meeting the chilling requirement. Temperatures near 5°C are most effective. More hours of chilling are required for temperatures greater than or lower than this optimum. Temperatures near 0° or above 10°C are not effective in meeting the chilling requirement and high temperatures negate the effects of previous chilling so that the tree sinks into a deeper condition of rest (*8, 9*). Most of the chilling requirement is met by the end of December, then trees transferred to a warm greenhouse will slowly break dormancy and expand their leaves and renew growth. Additional exposure to cold in January and February will accelerate the renewal of growth after trees are moved into a greenhouse. The transitions from the reversible state of imperceptible growth to the state of "true winter rest" to the state in which the plant is capable of renewed vegetative growth are gradual. However, plant physiologists arbitrarily recognize at least three phases of dormancy: early rest, true rest (winter rest), and after-rest. [See (*4*) for details on the history of the terminology of dormancy.] During the period of after-rest, the buds of some species, like red maple, open, and flowers emerge, and pollination is completed before leaf expansion and renewal of active vegetative growth. In other species these events tend to occur simultaneously.

After the winter chilling requirement has been met, the trees must be exposed to a minimum number of hours of temperatures near 25°C before they expand new leaves and renew active growth. For elms near Chicago this warm temperature requirement amounts to approximately 310 hours at 25°C and temperatures below 10° and above 30°C are ineffective (*8*). During the periods of winter rest and after-rest the plant is making a series of physiological changes similar to those which seed physiologists call after-ripening. Finally, after the exposure to warm temperatures, the leaves emerge from the buds and the terminal and lateral growth of the next year is begun.

Conifers and other evergreen species follow a cyclic pattern of growth and dormancy similar to the one just described. Although they retain most of their leaves and needles for a full year or more, they go dormant in late summer and have a winter chilling requirement. Deviations from this generalized description of growth and dormancy cycles are the rule and not the exception. The relative and absolute timing of flowering, development of leaves or needles, renewed growth in diameter and height varies for different races of the same species and between species of diverse wood anatomy: ring porous (such as oaks, ash, and locust); diffuse porous (like poplar, maple, and birch); coniferous (like pine, spruce, hemlock, and larch) (*4, 10, 11*).

Environmental Factors and Early Dormancy

Plants grown near street lights (or in other locations where the photoperiod is artificially prolonged, or where the dark period is interrupted) continue to grow and form new leaves later than plants not so exposed. The renewal of active growth and leaf formation in response to prolonged daylengths or interrupted dark periods has been repeatedly demonstrated for a vast array of perennial plant species (*6, 12, 13*). The assumption that cessation of growth and development of dormancy are primarily instigated in response to the shortening photoperiods of late summer and early fall is based on such observations.

Photoperiod is doubtless a key agent in controlling the cessation of growth and the development of dormancy. However, there are many reports which suggest that the photoperiodic control of development of dormancy can be bypassed or overridden by temperature, light intensity during the photoperiod, concentration of nutrients in the culture medium, soil moisture supply, and shock treatments.

Tree seedlings often continue growth in height through September, whereas older plants may cease growth in early July. Growth in height of some species is apparently insensitive to photoperiod at any stage of the life cycle (*13*).

Red maple trees (*Acer rubrum*) begin development of dormancy, regardless of the photoperiod, when the night temperatures are much above 25° or below 14°C.

Two aquatic species, frogbit (*Hydrocharis morus ranae*) (*14*) and greater duckweed (*Spirodela polyrrhiza*) (*15*) show a similar regulation of onset of dormancy by temperature.

Trees growing in the vicinity of street lights will drop their leaves eventually and become dormant even though they are exposed to a long photoperiod (*16*). Some tree species growing in warm night temperatures will retain their leaves for long periods even though the photoperiod is short (*17*).

Suppressed trees grown in shaded conditions or under low light intensities in growth chambers tend to begin development of dormancy independently of the photoperiod (*14, 18*).

Good moisture and nutrient supplies can favor prolonged vegetative growth (*19, 20*). Proper nutrition leads to greater resistance to winter injury. However, trees treated with heavy unbalanced doses of nitrogenous fertilizer late in the summer may maintain vegetative growth until they are killed by frost (*2, 5*). This is one reason why orchardists, nurserymen, and gardeners avoid application of high nitrogen fertilizers to perennial plants in late August. Greater duckweed (which in some ways behaves like a tree) becomes dormant even under a 20-hour photoperiod when grown in culture media that do not contain nitrogen (*15*). Defoliation (by man or by insect), temporary flooding, severe wounding, and various other shock treatments induce renewed growth and delay dormancy.

One may speculate that under natural conditions the quantities of nutrients available to plants vary seasonally and that there is a winter recharge and summer depletion of available soil nutrients that parallels the seasonal cycle of moisture supply. Initiation of dormancy is probably the result of interactions between photoperiod, high night temperature, lack of available soil nutrients, and insufficient moisture during July and August. A limiting amount of any of these factors [at least for the species and circumstances just cited (*13–21*)] can stop growth and initiate dormancy processes independently of photoperiod.

Independent Phenomena

Cessation of growth, preparation for leaf fall, development of cold hardiness, and winter rest, all take place at approximately the same time (late August through September in New England; late September through December in the southeastern United States). Since they occur at the same time, the assumption has been made that the phenomena are causally connected. Determinate species, such as spruce, white pine, and red oak, may form terminal buds by the end of June, but some activity of the apical meristem, including the development of leaf primordia, can continue for several months (*4*). Cell division in the cambium (lateral meristem) and growth in diameter continue for several months after terminal buds have been formed and growth in height has ceased. When treated with the sequence of long photoperiod and cold night temperatures, box elder (*Acer negundo*) and viburnum (*Viburnum plicatum tomentosum*) cease active growth and develop a considerable ability to tolerate freezing (−10° to −30°C). These plants renew vegetative growth, without chilling treatment, when returned to an environment of warm nights and days. Only plants subjected to a regime of short photoperiods and cold nights developed a true winter rest. The plants retain their leaves under both treatments (*22*).

Red maples from the Everglades of Florida cease active growth and drop their leaves in the fall but are unable to withstand any freezing temperatures and have no winter chilling requirement (*23*). Red maples from New York State develop a true winter rest and require a month or more of chilling before they can resume active growth.

Thus, at least for the examples cited above, the phenomena of dormancy (cessation of growth, development of cold hardiness, winter rest, and leaf fall) can be separated either genetically or by manipulation of the environment. Many other physiological changes take place during the dormancy phase of plant life. A restrictive definition of dormancy which does not include these physiological changes is of limited value.

Behavior of Different Parts of a Tree during the Rest Period

Not all parts of a dormant tree have a true winter rest or chilling requirement. Feeder roots of most trees apparently grow throughout the year when the soil temperatures and moisture content are high enough (*4*).

Lilacs have paired buds. Exposure of a single bud of a pair to the fumes of ethylene chlorohydrin (or other rest-breaking chemicals) induces it to grow, while the untreated bud of the pair remains dormant (*24*).

The cambium is capable of renewing growth even though it is not exposed to chilling or chemical treatments (*24*). On the basis of similar observations some workers infer that the cambium does not have a true winter rest (*20*). Other workers disagree (*11*).

There is a vast and conflicting literature on the dormancy of the cambium and the pattern of initiation of new growth in diameter. Many observations indicate that the renewed growth activity is first initiated in the terminal buds and that indoleacetic acid and gibberellic acid and other growth substances move downward and act to renew the growth in the lateral buds, branches, and trunk of the tree (*25, 26*). Other observations show that the sequence of renewed growth activity is first initiated in the base of the tree trunk and proceeds upward through the

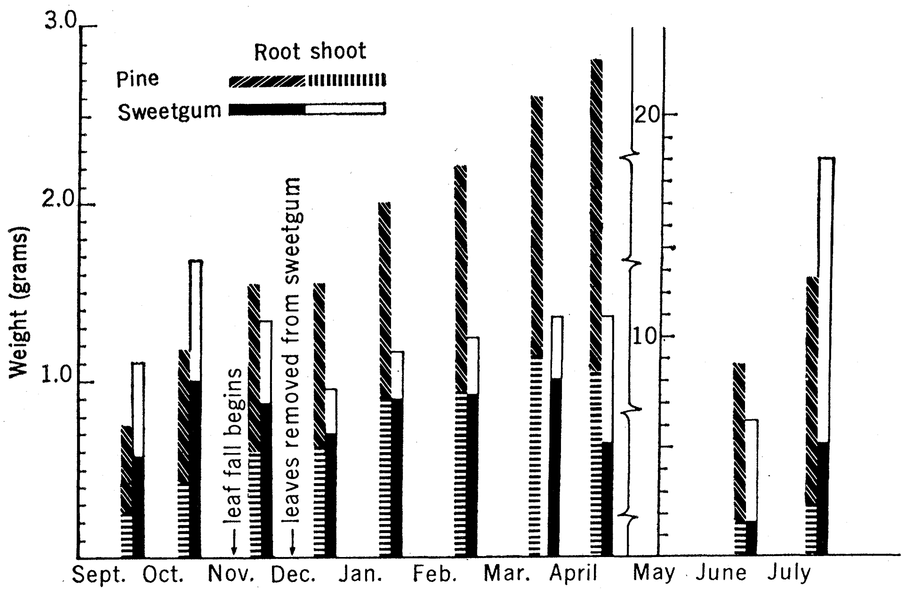

Fig. 1. Changes in dry weight by sweet gum and pine seedlings during the winter months. Although the sweet gum seedlings were without leaves from 20 December through 1 April they increased in weight by 42 percent. The pine seedlings increased in weight by 68 percent during this same period. The *t*-tests comparing sweet gum weights at different dates indicate that the changes in total weight were significant at the 5 percent level for every interval except that between 1 April and 24 April. The changes in root weight and shoot weight and root-shoot ratio were significant at every measurement interval. The pine seedlings made significant changes in weight in every measurement period except for the period between 20 November and 20 December.

branches and twigs to the buds (*11, 27*). The cambia of the diffuse porous trees (genera: *Acer, Tilia, Betula,* and others) may require the presence of buds for renewed growth, whereas the cambia of ring porous trees (genera: *Quercus, Fraxinus, Robinia,* and others) may not (*26*).

The time of dormancy or winter rest is definitely not a period of inert existence for the buds or any other part of the tree. Although there is no significant growth in length (internodal elongation), buds grow in size and in some instances contain cells which divide (*4, 28*). As winter chilling progresses, there is a change in the kinds of enzymes, the number of enzymes, and the form of enzymes (isoenzymes) present in the buds. The concentrations of polyphenoloxidase and phenols are reduced. The concentrations of catalases and hydrolases increase. The concentration of fats, anthocyanins, naringenin, and a number of growth-inhibiting substances is reduced (*29*).

Photosynthesis and respiration continue throughout the winter, especially when the temperatures rise above 5°C. These phenomena have long been recognized for evergreen species (*30*). The bark, twigs, and branches of deciduous trees contain a large amount of chlorophyll, and they too are capable of carrying on photosynthesis whenever the temperatures are above freezing (*31*). Leafless sweet gum seedlings (*Liquidambar sytraciflua*) increased in dry weight by 42 percent from 20 December to 1 April in Raleigh, North Carolina, in spite of night temperatures which were frequently −5°C or lower. Loblolly pines (*Pinus taeda*) which usually retain needles for 2 years or more, increased 68 percent in weight during this same period (Fig. 1).

Control Centers of Dormancy Phenomena

Much work has been done on the location of the receptors and control centers of dormancy phenomena (*13*). Trees with buds exposed to long photoperiods, while their leaves were exposed to short photoperiods, were unable to renew growth. Similar trees, with leaves removed, were able to renew growth when exposed to long photoperiods. Thus, both leaves and buds must be exposed to long photoperiods before buds in the early rest can renew growth (*13*).

The wavelengths of light (red and far red) which control the photoperiodic regulation of dormancy and flowering are apparently the same and are absorbed by the plant pigment phytochrome. Phytochrome is present in the leaves and twigs of many species (*32*).

Renewed growth is correlated with the disappearance of inhibitors from the buds and increased concentrations of growth stimulators (*7, 33*). Such findings are criticized because some inhibitors are concentrated in the scales of dormant buds rather than in the apical meristem. However, bud scales and leaf primordia may be centers of growth control. Bud scales make slow growth throughout the winter, and show active growth long before there is evidence of active growth or cell division in the apical meristem (*28, 34*). Some research indicates that apical meristems may not be able to grow in artificial culture media unless a minimum number of leaf primordia are attached (*35*). Recently, isolated meristems of Norway spruce (*Picea abies*) have been cultured and produce new leaf primordia (*36*).

As mentioned earlier, twigs of dormant plants conduct active photosynthesis during the winter months and could, themselves, be important receptors and sites of dormancy regulation. Although there is much evidence for the concept of a control center of dormancy processes in buds and leaves, the possibility that other plant parts may be involved is not excluded.

Breaking Dormancy with Chemical Reagents and Shock Treatments

A wide variety of chemical and shock treatments can hasten renewed vegetative growth of dormant plants: potassium cyanide, potassium thiocyanate, urea, thiourea, ether, ethylene, ethylene chlorohydrin, acetone, alcohol, ethyl acetate, potassium chloride, other simple salts, and so forth. The list of reagents used is long and their structures are dismayingly diverse (*6, 24, 37*). Many of the early workers were unaware of the chilling requirements of plants, and it is not clear to what degree winter chilling requirements were met before chemical treatments began, hence it is not always clear whether the growth during after-rest was accelerated or whether true winter rest was broken by the treatments. Denny and Stanton (*24*) appear to be the first workers to recognize clearly that previous growth conditions and chilling treatments could modify the effectiveness of the chemicals tested for breaking dormancy. Unless chilled, some genera, such as *Viburnum*, do not break dormancy following treatment with any of the reagents Denny and Stanton used (*24*).

The action of chilling in breaking winter rest is not understood. Many species, and races of species, do not have a true chilling requirement. The interaction of high and low temperatures, the restricted ranges of temperature above or below which growth cannot be renewed, and the variation with time are most confusing (*6*). The careful studies with elm indicate that at least two temperature-sensitive enzyme systems may be involved (*8*). One set of enzymes is either synthesized or active at temperatures near 5°C and the other at temperatures near 25°C.

Hot water baths, anaerobic conditions, and exposure to high intensity lights have also been used to "break dormancy." The common feature of all the treatments used to break dormancy is that they are severe. Often the temperatures or chemical concentrations used border on being lethal. Many of the chemicals used are poisonous at relatively low concentrations.

Plant Hormones and Growth Substances

A number of known and unknown growth stimulators (indoleacetic acid, gibberellic acid, ethylene, and others) decrease in concentration in the fall and increase in concentration with chilling treatments and renewal of growth in the spring. The correlation between these accumulations and decreases has led to the hypothesis that the phenomena of dormancy in trees result from changes in the balance of inhibitor and stimulator concentrations. Several reviews introduce the topic and present hypotheses about these and other growth-promoting and inhibiting substances—inositol, sorbitol, leucoanthocyanins, and so forth (*4, 6, 7, 38, 39*).

There is evidence that substances synthesized in one part of a plant move to another part and regulate its growth and development. During early rest, birch (*Betula pubescens*) leaves, exposed to short days, inhibit the growth of buds exposed to long days. The buds will renew growth when the leaves are removed (*17*). The work of Wareing and his colleagues (*40*) suggests strongly that abscisic acid is the primary inhibitor synthesized in the leaves of plants in response to short photoperiods. Application of abscisic acid to leaves and growing tips (*Acer pseudoplatanus, Betula pubescens*) induces the formation of bud scales. The demonstration of abscisic acid in the honeydew of aphids feeding on willow stems is evidence for the transportation of abscisic acid between plant parts (*41*).

Abscisic acid may function in concert with indoleacetic acid, cytokinins, gibberellic acid, and ethylene to stimulate processes of senescence and leaf abscission (*42, 43*). The processes involved are not well understood (*1*).

Gibberellic acid is one of the few substances for which hormonal action is clearly demonstrated. Gibberellic acid formed in one plant part can move to another plant part where it acts on genes to induce the formation of a number of enzymes, including the starch-digesting enzyme, α-amylase (*5*). However, treatment with simple sugars does not induce break of dormancy, and the role of gibberellic acid in renewed

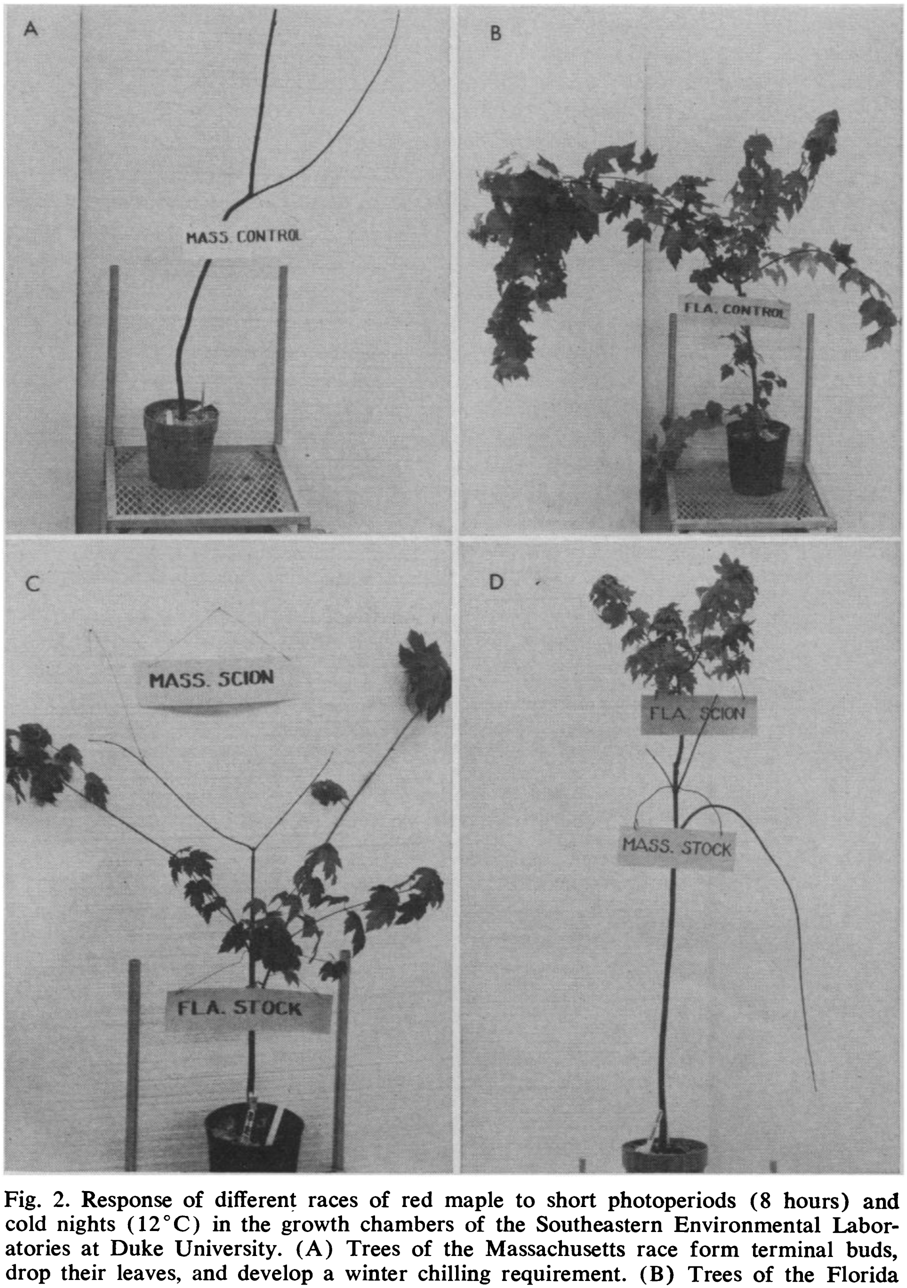

Fig. 2. Response of different races of red maple to short photoperiods (8 hours) and cold nights (12°C) in the growth chambers of the Southeastern Environmental Laboratories at Duke University. (A) Trees of the Massachusetts race form terminal buds, drop their leaves, and develop a winter chilling requirement. (B) Trees of the Florida race do not make these responses and continue to grow and form new leaves. (C and D) Stocks and scions of grafts between the Massachusetts and Florida races respond independently of each other. There is no evidence of movement of "dormancy hormones" from stock to scion.

growth may involve additional factors. Application of gibberellic acid to leaves of box elder (*Acer negundo*) grown in short photoperiods and low temperatures, prevents the development of cold resistance (*44*).

The concentration of gibberellic acid in buds increases as they expand in the spring; the increase in concentration is most rapid after the chilling requirement has been met. The changing concentration of gibberellic acid may be a secondary, rather than a causal, factor in the breaking of dormancy (*10*).

In some species gibberellic acid is reported to hasten the renewal of vegetative growth in the spring whereas it is reported to have no effect on other species (*38*). Experiments with greater duckweed (*Spirodela polyrrhiza*), an aquatic perennial that has a chilling requirement and dormancy patterns similar to trees, indicate that conflicting observations regarding the role of gibberellic acid in dormancy may be due to genetic variation within and between species: one unchilled clone of greater duckweed could be induced to break dormancy in less than 7 days when treated with a combination of long photoperiods and gibberellic acid (10 μg/ml). Another unchilled clone required the same concentration of gibberellic acid, long photoperiods, and 48 days for complete break of dormancy. All greater duckweed clones broke dormancy in less than 7 days after chilling treatment of 1 month even without gibberellic acid. Long photoperiods were not required for break of dormancy after chilling (*15*).

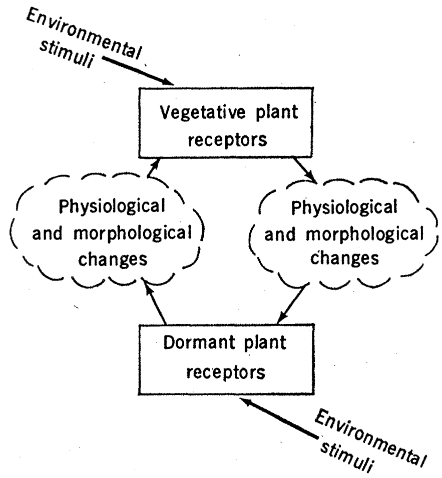

Fig. 3. Cyclic diagram of seasonal transition from a condition of active vegetative growth to a condition of dormancy. Dormancy involves three arbitrary phases: early rest, winter rest, and after-rest. Table 1 lists some of the stimuli and physiological processes involved in the cycle.

Similar conflicting observations make interpretation of the role of indoleacetic acid and other growth substances in dormancy difficult. For the present, we can only state that their concentrations vary with the degree of vegetative activity in plants. In which instances do these parallels reflect causal relationships? In which instances do they reflect mere secondary correlations?

Table 1. Some stimuli and metabolic processes reported to be involved in the cycle of transformations from the vegetative condition to the dormant condition and back to the vegetative condition (see Fig. 3).

A. Stimuli which act on plants in a vegetative condition

1. Radiant energy: light intensity during the photoperiod: length of the day and night; red–far-red shifts of phytochrome receptor
2. Temperatures: High day temperatures, low night temperatures
3. Nitrate and nutrient content of the culture medium
4. Availability of water and other unknown variables

B. Morphological and physiological changes during transition from the vegetative condition

1. Stop cellulose synthesis; accelerate lignin and starch synthesis
2. Accumulate anthocyanins, phenols, fats, dormin, and other growth inhibitors
3. Stop the synthesis of some enzymes and accelerate the synthesis of others
4. Induce formation and terminal buds, migration of minerals from leaves, and formation of abscission layers in leaf stems
5. Stop cambial activity

C. Stimuli (natural and artificial) which act on the dormant plant to accelerate transition back to vegetative state

1. Chilling treatments: 30- to 90-day exposure to temperatures less than 6°C, natural winter cold
2. High temperatures; hot water baths, natural high temperatures
3. Natural chemical agents: abscisic acid, kinetin, IAA, GA, ethylene
4. Artificial chemical agents: chloroform, ether, ethanol, acetaldehyde, CO_2, anaerobic conditions, nitrate, thiourea, and many others
5. Long photoperiods: 16 to 20 hours (longer photoperiods than are normal for the season)
6. Other variables

D. Physiological and morphological processes and changes in dormant plant before renewal of active and vegetable growth

1. Dissipation of fats, phenols, abscisic acid, and various other pigments and growth inhibitors
2. Increased concentrations of IAA, GA, and other growth promoters
3. Elimination of some enzymes and the formation of others
4. Slow growth of bud scales with a very few cell divisions
5. Photosynthesis, respiration, and transpiration (via lenticels) whenever temperatures permit

Invoking a hormonal control of dormancy phenomena may be unjustified in some instances: If the topmost bud or leader of a young tree is cut away, the buds at the tips of the lower branches will resume growth and one of these lower branches will assume the role of generating the main stem. It should also be noted, conversely, that extensive pruning, removal of the lateral buds, or severe wounding will induce the terminal buds to grow. If the leaves of a tree in early dormancy are removed, the quiescent buds open and new leaves form. These and similar observations are cited as evidence that dormancy-inducing substances are synthesized in one part of a plant and are transferred to other parts where they regulate the processes of growth and the development of dormancy. Are responses of the type described above due to the removal of inhibitors or due to the action of substances created de novo as a result of shock treatment?

Conclusive proof or disproof of hormone-like action for abscisic acid or other growth substances is most difficult to achieve. Indeed, there are a number of common observations which indicate that different parts of a tree are able independently to grow, go dormant, and initiate new growth:

1) Lamb (*45*) observed the red maple leaves which were formed as a prolonged growth response to shock of heavy August pruning. These leaves remained on the tree until December while the leaves formed during the normal growing season fell from the trees in October. Leaves on the side of a tree nearest a street light are retained longer than leaves on the side away from the light. These and similar observations indicate the formation of abscission layers by different leaves on a plant is somehow determined by the age and physiological condition of the particular leaf rather than by substances transported from other parts of the tree.

2) There is a mutant of European beech (*Fagus sylvatica*) which has pendulous branches. The buds open and the leaves of this mutant develop much later in the spring than the buds and leaves of a normal plant. A double graft was made so that the root system

and lower branches of the resulting plant were normal, the middle stem and branches pendulous, and the upper stem and branches normal (by Syrach Larson, Royal Danish Arboretum). The leaves generated on the normal sections of the tree continued to emerge and grow at an earlier date than the leaves generated on the mutant middle section of the tree. Figure 2 illustrates this genetic variation in dormancy and lack of influence of stock on scion for red maple. Interracial grafts of cottonwood (*Populus deltoides*) behave in a similar fashion.

3) As mentioned earlier, treatment of a single bud with a rest-breaking chemical, such as ethylene chlorohydrin, induces the treated buds to grow while the untreated portions of the plant remain dormant (*24*).

The observations described above are not compatible with the concept of a series of hormones that move from one part of a plant to another to regulate the processes of dormancy. Under some conditions, at least, different parts of a plant develop and terminate the condition of dormancy independently.

The phenomena of dormancy are many and can be mediated by an array of environmental triggers (temperature, photoperiod, moisture, nutrition, and others) (Table 1 and Fig. 3). One is forced to conclude either that dormancy processes are initiated by several receptors or that the receptor which triggers the morphological and metabolic changes of dormancy is sensitive to several stimuli other than photoperiod. Genetic evidence indicates that a large number of genes are involved and hence a large number of enzymes and regulating substances may also be involved (*46*).

Research with barley (*47*) and with tobacco pith (*1*) and duckweed indicate that gibberellic acid, indoleacetic acid, and kinetin can alter the enzyme patterns of plants (Fig. 4). These and similar observations suggest that various environmental stimuli may act directly on the genes or on a number of receptor substances (such as phytochrome) which in turn act to produce changes in the enzymes and regulator substances involved in dormancy. Perhaps dormancy genes can be reversibly "turned on and off." Such reversible control of developmental processes is not possible with animals. For this reason work with the dormancy phenomena has the exciting prospect of elucidating many of the mechanisms of gene action.

Scientists (who seek for general principles and useful simplifications) are searching the maze of conflicting observations about dormancy in the hope of finding a single receptor that acts through some pyramid of affector substances to control all of the processes involved. Phytochrome and abscisic acid are the current foci of attention in this search. However, the phenomena of dormancy are many, are separated in time, and are further separable by manipulating either the environment or the genotype. Phytochrome and abscisic acid undoubtedly play key roles in some phenomena of dormancy. Which ones? And to what degree?

Summary

Early dormancy involves a number of phenomena: cessation of active growth, formation of terminal buds, formation of abscission layers in leaves, development of cold resistance, development of winter rest (a chilling requirement), and leaf fall. The buds of some tree species (or some races of a species) have a true rest or winter chilling requirement; usually the roots do not; perhaps the cambium does not. There is a wide range of genetic variation within and between species in response to photoperiod, winter chilling, water nutrients, and other environmental factors which affect the dormancy condition of plants.

During the period of winter rest there are many metabolic and developmental processes going on in the buds and twigs. These processes include respiration, photosynthesis, some cell division, enzyme synthesis, production of growth stimulators, and dissipation of growth inhibitors.

Dormancy of trees can be divided arbitrarily into three phases: early rest, winter rest, and after-rest. Each of these phases is marked by a distinct set of physiological processes. The transition between the three phases is gradual. Some processes of after-rest

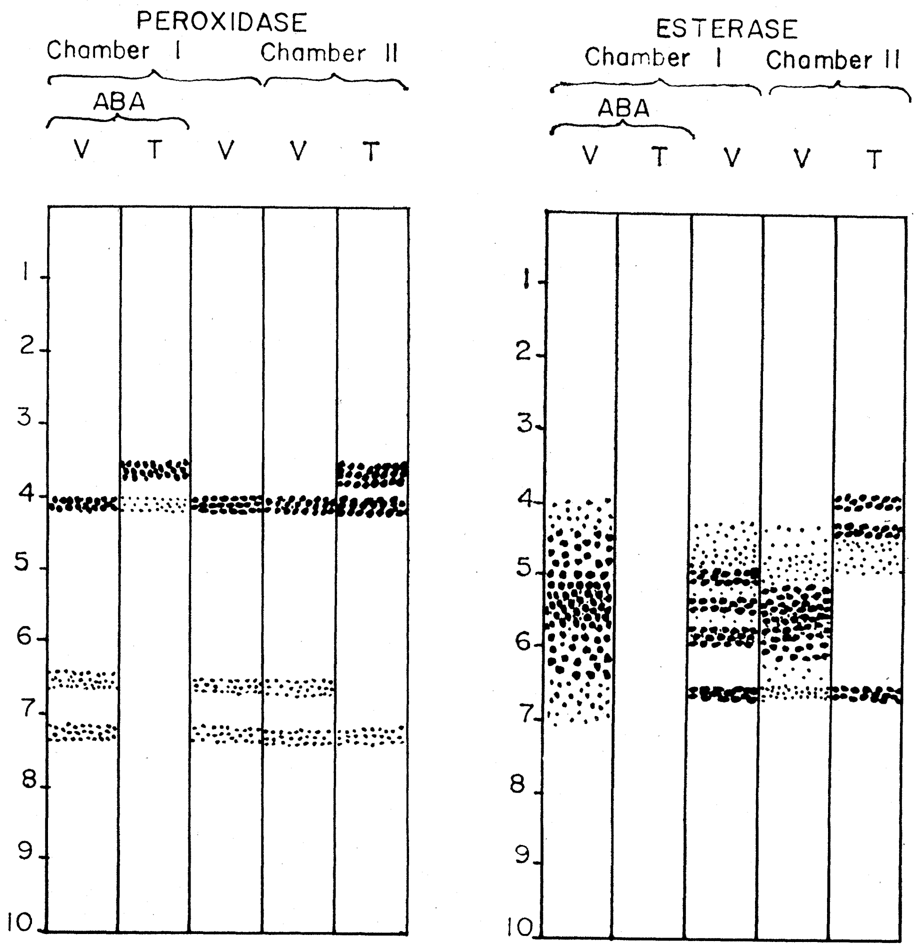

Fig. 4. Altered isoperoxidase and isoesterase patterns for a single clone of *Spirodela polyrrhiza* treated with varying combinations of photoperiod, night temperature, and abscisic acid. Chamber I, 20-hour photoperiod, 23°C phototemperature, 17°C dark temperature. Chamber II, 8-hour photoperiod, 23°C phototemperature, 12°C dark temperature. *V*, vegetative fronds forming turions. *T*, turions (dormant bodies). ABA treatment, 1 μg/ml. Different genotypes and different enzymes give different responses.

can proceed even though the winter chilling requirement (winter rest) of a tree has not been completed fully.

Evidence from grafting experiments and chemical treatments to break winter rest, and studies of genetic variability indicate that the processes and phenomena of dormancy are at least partially independent of each other. Different buds and branches and other parts of the same plant may initiate dormancy, break dormancy, and renew vegetative growth independently.

Initiation and cessation of dormancy can be triggered by a number of environmental variables: photoperiod, temperature, nutrition, water, an array of chemicals, and shock treatments. Dormancy regulation must either involve a variety of receptors or involve receptors that are responsive to a variety of stimuli. Unless dormancy is defined in a highly restricted sense (that is, possession of chilling requirement), it is hard to conceive of a single receptor or regulator that controls all of the phenomena of dormancy. A large number of genes are definitely involved and hence a large number of enzymes. The kinds of enzymes, their numbers, and their concentrations can be regulated by manipulating the environment.

References and Notes

1. A. W. Galston and P. J. Davies, *Science* **163**, 1288 (1969).
2. J. Levitt, in *Hardiness in Plants*, J. Levitt, Ed. (Academic Press, New York, 1956).
3. T. T. Kozlowski, *Bot. Rev.* **30**, 334 (1964).
4. J. Romberger, *U.S. Dep. Agr. Tech. Bull. No. 123* (1963).
5. I. M. Vasil-yev, *Wintering of Plants* (American Institute of Biological Sciences, Washington, D.C., 1961).
6. A. Vegis, *Annu. Rev. Plant Physiol.* **15**, 185 (1964).
7. P. F. Wareing, C. F. Eagles, P. M. Robinson, in *Colloq. Intern. No. 123 Centr. Nat. Rech. Sci., Paris* (1964), pp. 377–386.
8. G. T. Jones, thesis, Univ. of Chicago (1938).
9. W. H. Chandler, in *Deciduous Orchards* (Lea & Febiger, Philadelphia, ed. 2, 1951), p. 40.
10. P. P. Larson, in *Tree Growth*, T. T. Kozlowski, Ed. (Ronald Press, New York, 1962), pp. 97–117.
11. C. M. Stewart, *Tappi* **40**, 244 (1957).
12. H. A. Borthwick and S. A. Hendricks, *Science* **132**, 1223 (1960).
13. P. F. Wareing, *Annu. Rev. Plant Physiol.* **7**, 191 (1956).
14. A. Vegis, *Symb. Bot. Upssal.* **14**, 1 (1955).
15. T. O. Perry, *Plant Physiol.* **43 (11)**, 1866 (1968).

→ E. B. Matzke, *Amer. J. Bot.* **23**, 446 (1936).

17. P. F. Wareing, *Physiol. Plant.* **7**, 261 (1954).
18. T. T. Kozlowski and T. A. Peterson, *Bot. Gaz.* **124**, 146 (1962).
19. T. D. Rudolph, *Forest Sci. Monogr. No. 6* (1964); R. Zahner, J. E. Lotan, W. D. Baughman, *Forest Sci.* **10**, 361 (1964).
20. M. Büsgen and E. Münsch, in *The Structure and Life in Forest Trees*, translated by T. Thomson (Wiley, New York, ed. 3, 1931), p. 104.
21. T. O. Perry, *Forest Sci.* **8**, 336 (1962).
22. R. M. Irving and F. O. Lanphear, *Plant Physiol.* **42**, 1191 (1967).
23. T. O. Perry and Chi Wu Wang, *Ecology* **41**, 785 (1960).
24. F. E. Denny and E. N. Stanton, *Proc. Amer. Soc. Hort. Sci.* **77**, 107 (1928).
25. K. Ladefoged, *Kgl. Danske Videnskab. Selskab. Biol. Skr.* **7 (3)**, 1 (1952).
26. P. F. Wareing, *Physiol. Plant.* **4**, 546 (1951).
27. J. E. Lodewick, *N.Y. State Coll. Forest. Syracuse Univ. Tech. Publ. No. 23* (1928).
28. T. O. Perry and W. R. Simons, *Forest Sci.* **13** (4), 400 (1967).
29. F. V. Coville, *J. Agr. Res.* **20**, 151 (1920); G. Klebs, *Bot. Zentralbl.* **119**, 426 (1912); J. Parker, *Protoplasma* **48**, 147 (1957); T. O. Perry, *J. Forest.*, in press.
30. W. Tranquillini, *Mitt. Forstl. Bund. Mariabrunn* **60**, 501 (1963).

→ L. C. Pearson and D. B. Lawrence, *Amer. J. Bot.* **45**, 383 (1958).

32. S. B. Hendricks and H. W. Siegelman, in *Comprehensive Biochemistry*, M. Florkin and E. S. Stotz, Eds. (Elsevier, Amsterdam, 1967), vol. 27, pp. 211–235.
33. T. Hemberg, *Physiol. Plant.* **2**, 37 (1949); C. H. Hendershott and D. R. Walker, *Amer. Soc. Hort. Sci.* **74**, 121 (1959).
34. R. Zahner, personal communication.
35. E. Ball, *Growth* **24**, 91 (1960).
36. J. A. Romberger, R. J. Varnell, C. A. Tabor, *U.S. Dep. Agr. Tech. Bull. No. 1409* (1970).
37. W. L. Howard, *Univ. Mo. Agr. Exp. Sta. Bull. No. 1* (1910), p. 101.
38. H. Smith and N. P. Kefford, *Amer. J. Bot.* **59**, 1002 (1964).
39. P. F. Wareing, in *Trends in Plant Morphogenesis*, E. G. Cutter, Ed. (Longmans, Green & Co., London, 1966).
40. J. W. Cornforth, B. V. Milborrow, G. Ryback, P. F. Wareing, *Nature* **205**, 1269 (1965); C. F. Eagles and P. F. Wareing, *Physiol. Plant.* **17**, 697 (1964).
41. G. V. Hoad, *Life Sci.* **6**, 1113 (1967).
42. L. N. Lewis and J. C. Bakhshi, *Plant Physiol.* **43 (3)**, 359 (1968).
43. A. E. DeMaggio, and J. A. Freeberg, *Can. J. Bot.* **47**, 1165 (1969).
44. R. M. Irving and F. O. Lanphear, *Plant Physiol.* **43**, 9 (1968).
45. G. H. Lamb, *Mon. Weather Rev. Suppl. II* (1915).
46. H. B. Kriebel, in *Proc. Soc. Amer. Forest.* (Memphis, Tennessee, 1956), pp. 79–82; J. S. Olsen and H. Nienstaedt, *Science* **125**, 492 (1957); H. Iregens-Moller, *Forest Sci.* **4**, 325 (1958); S. S. Pauley and T. O. Perry, *J. Arnold Arboretum* **35**, 167 (1954).

→ J. E. Varner and G. R. Chandra, *Proc. Nat. Acad. Sci. U.S.* **52**, 100 (1964).

48. Supported in part by NSF grant GB 7153.

Magnetic Resonances and Waves in Simple Metals

Transparencies of alkali metals near cyclotron and spin resonances reveal many-body interactions.

W. M. Walsh, Jr.

The high reflectivity of smooth metal surfaces is among their most familiar physical properties. At room temperature, electromagnetic radiation is efficiently reflected at all frequencies below the ultraviolet region. Since this screening or skin-effect phenomenon results directly from the metal's large electrical conductivity, it is somewhat of a paradox that purification and cooling to liquid helium temperatures both greatly increase the direct current (d-c) conductivity and yet create "windows" or regions of partial transparency in the audio, radio, and microwave frequency ranges. In fact the windows are *magneto*transparencies which require the presence of strong magnetic fields to curl the conduction-electron trajectories into cyclotron orbits. These changes in trajectory seriously modify the screening characteristics of the conduction electrons.

The ability of ionized gases or fluids (plasmas) to support a variety of harmonic disturbances (waves) and to transmit them many wavelengths is well known (*1*). The study of such phenomena in semiconductors, semimetals, and metals—solid-state plasma physics—has become an active branch, during the past decade, of the investigation of the electronic properties of solids (*2*). Research activity has been particularly fruitful in the case of the simplest metals—the light alkali metals sodium and potassium—in which the greatest variety of wave propagation phenomena has been observed; also the nearly total absence of band-structure complexities in these metals greatly facilitates comparison of theory and experiment. In this article the various plasma and spin-wave excitations thus far discovered in the alkali metals are

The author is head of the Solid State and Physics of Metals Research Department of the Bell Telephone Laboratories, Murray Hill, New Jersey 07974.