THE RELATIONSHIP OF JUVENILITY TO PLANT PROPAGATION

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The subject of juvenility in plants is receiving increasing attention from propagators, horticulturists and foresters both from academic interest and practical necessity. A worldwide study group for horticulturists, foresters, and pomologists interested in juvenility has been formed under the auspices of the International Society for Horticultural Science. In 1975, two international symposia were held, one in Beltsville, MD., U.S.A. and one in Berlin, Germany (17)[a].

Most interest in juvenility focuses on 3 significant practical problems. First, how can one maintain or increase the rooting potential and regenerate hard-to-root cultivars by vegetative propagation? Second, how can one shorten the juvenile period to bring about early flowering to speed up breeding programs for fruit, nut and forest crops? Thirdly, how can one avoid (or utilize) the variability in growth performance and morphological appearance that sometimes characterizes juvenile growth

Relationships, such as the effect of juvenility on rootstock behavior, may also be important but are not well understood. Likewise, seed production of forest trees must be conducted to retain the long juvenile period important in this crop.

CONCEPTS OF JUVENILITY IN RELATION TO LIFE CYCLES

Understanding and finding solutions to the above problems for specific plants requires basic understanding of the life cycle of the plant because it is only in this context that juvenility makes sense. Thus, we must distinguish between the life cycle of an individual plant started from seed (Fig. 1) and a life cycle of an individual plant started vegetatively from a bud or a cutting (Fig. 7) (4).

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[a] References are made by number to specific publications; names identify papers in the 1975 Symposia that deal specifically with the subject under discussion.

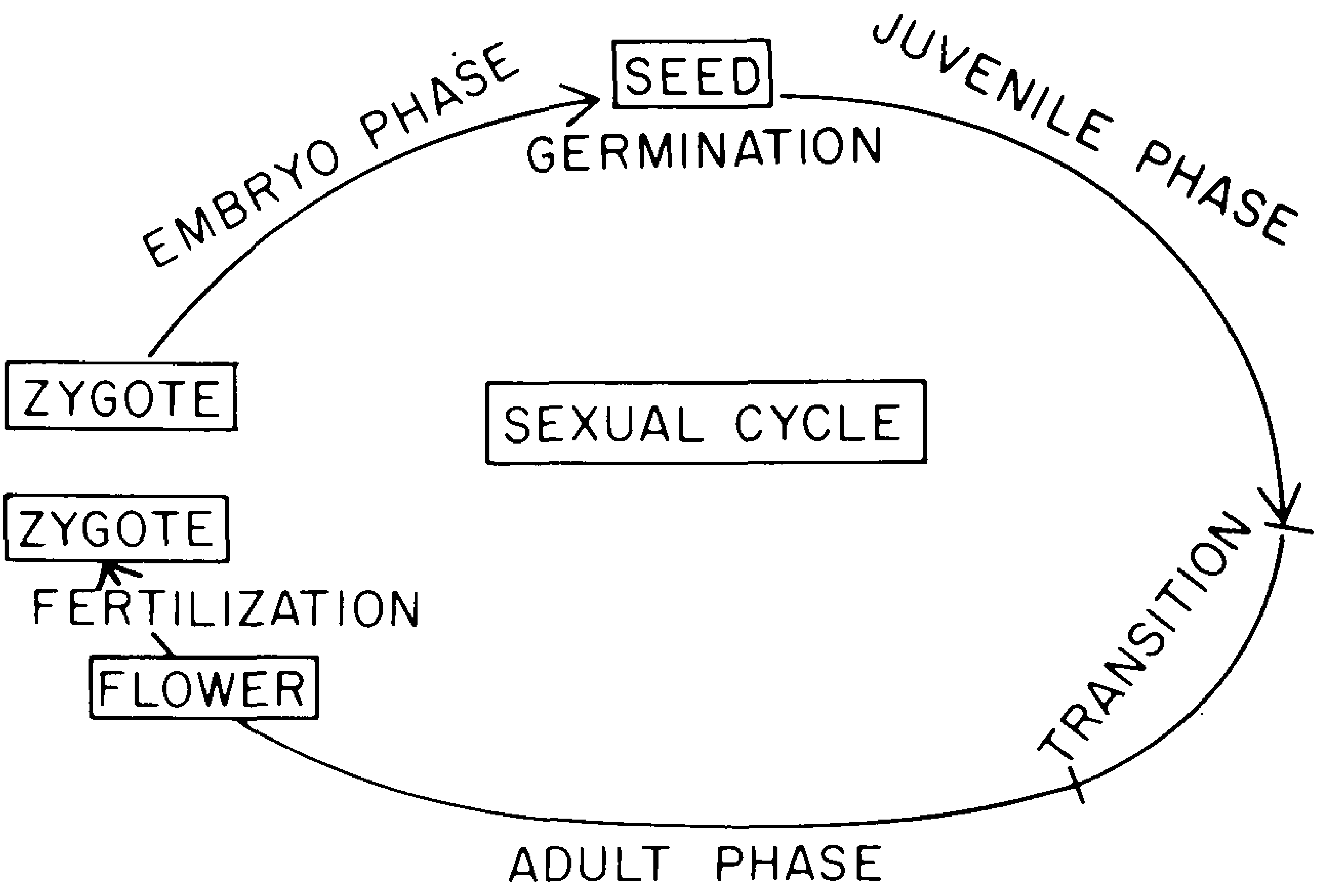

Figure 1. Development cycle of a plant grown from seed. Shows the distinction between the juvenile phase and adult phase.

Seedling life cycles. (Figs. 1 and 2).

1. The cycle begins with a single cell, normally the *zygote*, which is the first cell originating from fertilization of the egg by a sperm cell. (Sometimes, however, the cycle could begin with another cell as in *nucellar embryos* or unreduced sex cells, as in *apomictic embryos*.) This first phase involves growth of the embryo within the mother plant and is terminated by germination of the seed.

2. The growth phase immediately following germination is defined as *juvenile* and is a period of growth in size and volume resulting from cell division in the meristems. It is part of the concept of juvenility that these growing points cannot initiate flower buds at this stage. In some plants unique morphological characters, as thorns, distinct leaf shapes, etc., may be present in the juvenile phase. These may be useful as "markers" to identify changes in phase.

3. A *transitional* phase follows the juvenile phase and involves an internal shift from strictly vegetative to reproductive in which flower buds can be initiated. Sometimes there are abrupt changes in appearance of the plant; in others, the change may be gradual and the time when it begins difficult to identify precisely.

4. Eventually the plant becomes fully reproductive and produces flowers, fruits and disseminates seeds. This is the

adult phase. Production of new seeds repeats the sexual cycle and creates a new generation.

Terminology is important in the context of juvenile to adult changes. It seems desirable to avoid the terms "age" or "aging". Rather the consensus among workers in this field is to use the term "maturation" for the process and to refer to the reproducing plant as "adult" or "mature", rather than "old".

Eventually, the plant becomes senescent and dies. In some cases this follows because growing points produce only flowers and fruits and none are left to regenerate shoots. In an annual, all shoots become flowering in one season and the plant dies thereafter. Some bamboos and some Agave plants may be juvenile for many years — 50 to 100 — then suddenly become reproductive, flower, and die after seeds are produced. Perennial plants continue to live year after year because only some of the shoot buds become reproductive, but other buds remain vegetative (not necessarily juvenile) and continue the existence of the plant.

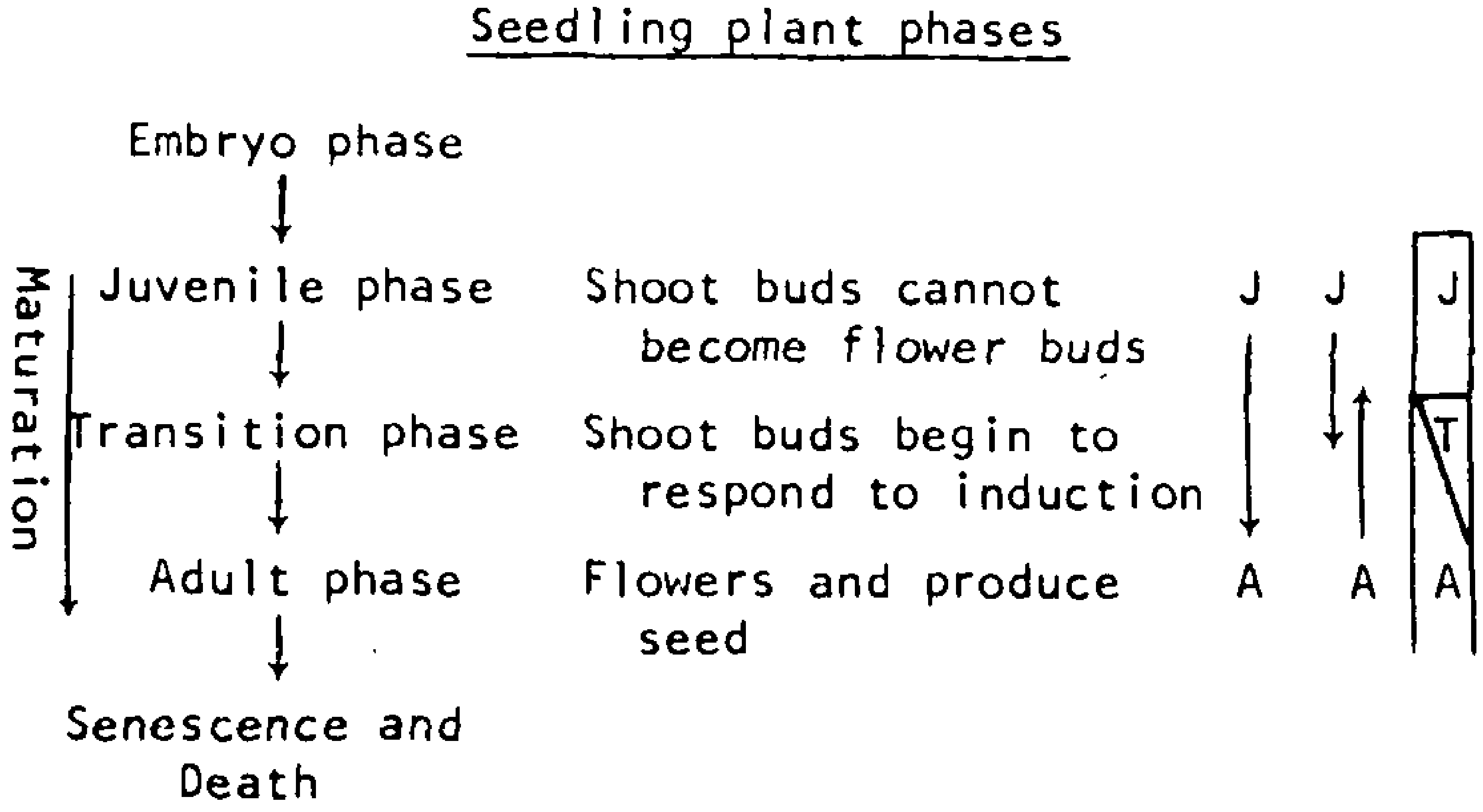

Figure 2. Phase of maturation from juvenile to eventual death. Change may be considered as a gradual shift from juvenile to adult, J → A, 2 distinct overlapping phases, or 3 separate phases — juvenile, transitional and adult.

Juvenility and growth patterns. Plant growth and development proceeds in individual growing points (meristems) in the tips of shoots and roots, and in lateral points in axils of leaves. Some of the cells in these meristems continue to divide to produce new cells and thus continue to expand the plant; others remain behind to become stems, leaves, roots, etc. More and more new growing points are produced at nodes as the plant increases in size and complexity (Borchert, Lord, 17).

With time, these growing points become separated from each other and progress through the maturation phases at different rates. Various research efforts are now being made to establish the relative importance of the internal control system within the growing point itself, the surrounding environment, and the hormonal influence of the nearby leaves, other growing points, and the roots for determining the phase of maturation (Wareing, Hackett, Schwabe 17).

Juvenility is related significantly to propagation in several ways. First, control of maturation from juvenile → adult is largely a function of the development of the growing point. Thus the duration of the juvenile phase is determined by number of cell divisions achieved by the vegetative meristem (and the number of nodes) rather than chronological time. Keeping juvenile plants growing continuously at their maximum rate with optimum growing conditions, e.g., continuous light, long days, adequate nutrition, increased CO_2, etc., — will allow the growing points to literally *grow their way* through the juvenile period in the shortest time and result in early flowering. Aldwinckle (17) brought apple seedlings into flower in the greenhouse in 16 months compared to 3 to 8 years for plants growing in the field. Similarly, Zimmerman (16) found certain (apomictic) crabapples to have a juvenile phase of 75 to 80 nodes irrespective of the time required to attain this height. Similar response from growing seedling plants rapidly in controlled environments have been shown for pear (14), birch (Longman 14), and spruce (Young 17) and the principle is probably universally applicable (Fig. 3). Growth and development has also been stimulated greatly in annuals by environmental controls applied as early in their life cycle as possible (4). Even excised embryos of some peach cultivars respond to long photoperiods and increased temperature (6).

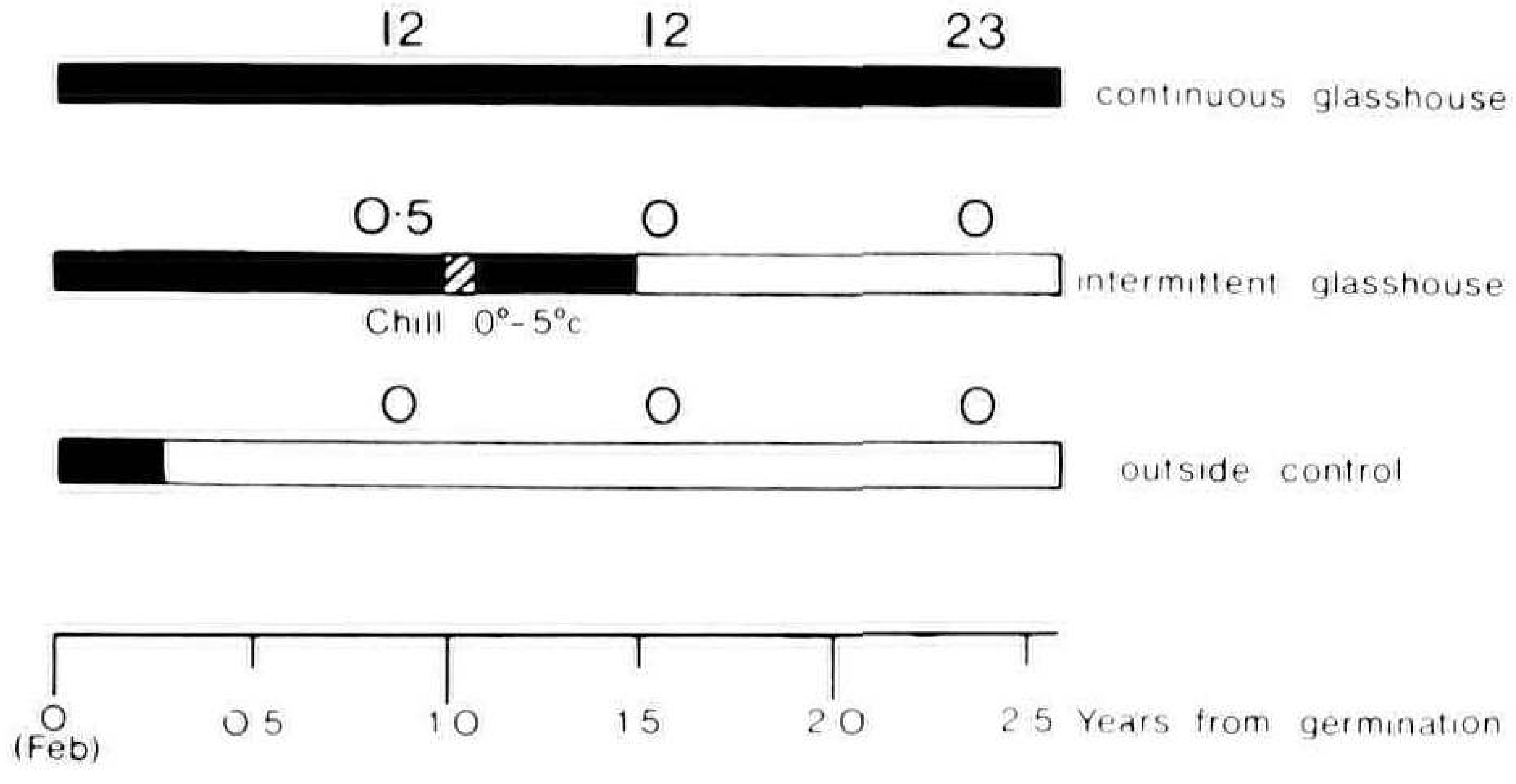

Figure 3. Effect of growing conditions on flowering in *Betula verrucosa seedlings*. *Dark* = heated greenhouse, light = out-of-doors. Numbers refer to mean numbers of catkins per plant. (from Longman, 17).

The second application is that different parts of the plant tend to remain juvenile and others adult, as shown in Fig. 4. This phenomenon has been known in the horticultural literature as *topophysis* (4). It leads to a paradox in terminology in that the oldest part of the plant, from standpoint of chronological age (base), actually remains the youngest in terms of maturation. Likewise, the youngest part in time (top and extremities of branches) may be the oldest in maturation.

Fig. 4 could depict a ten-year-old apple or citrus tree which grows very vigorously, with fruiting only at the top and extremities of the branches. Or it could be a 25 year old pine or spruce tree with cone production very high in the tops of the tree. However, it could also be a tobacco plant of one year duration with lateral shoot buds at the lower nods and flower buds only at the upper nodes. McDaniel and Hsu (17) found that, for a given tobacco plant a certain number of nodes was required to flower. If the nodes were removed as cuttings in consecutive order from base to tip, the cuttings from the base produced new vegetative shoots but the upper ones produced flowers. New shoots required about the same number of nodes to flower as did the original shoot at that node. It can be said that the individual bud "remembered" its position and continued to express the potential for that position even when separated from the original seedling plant.

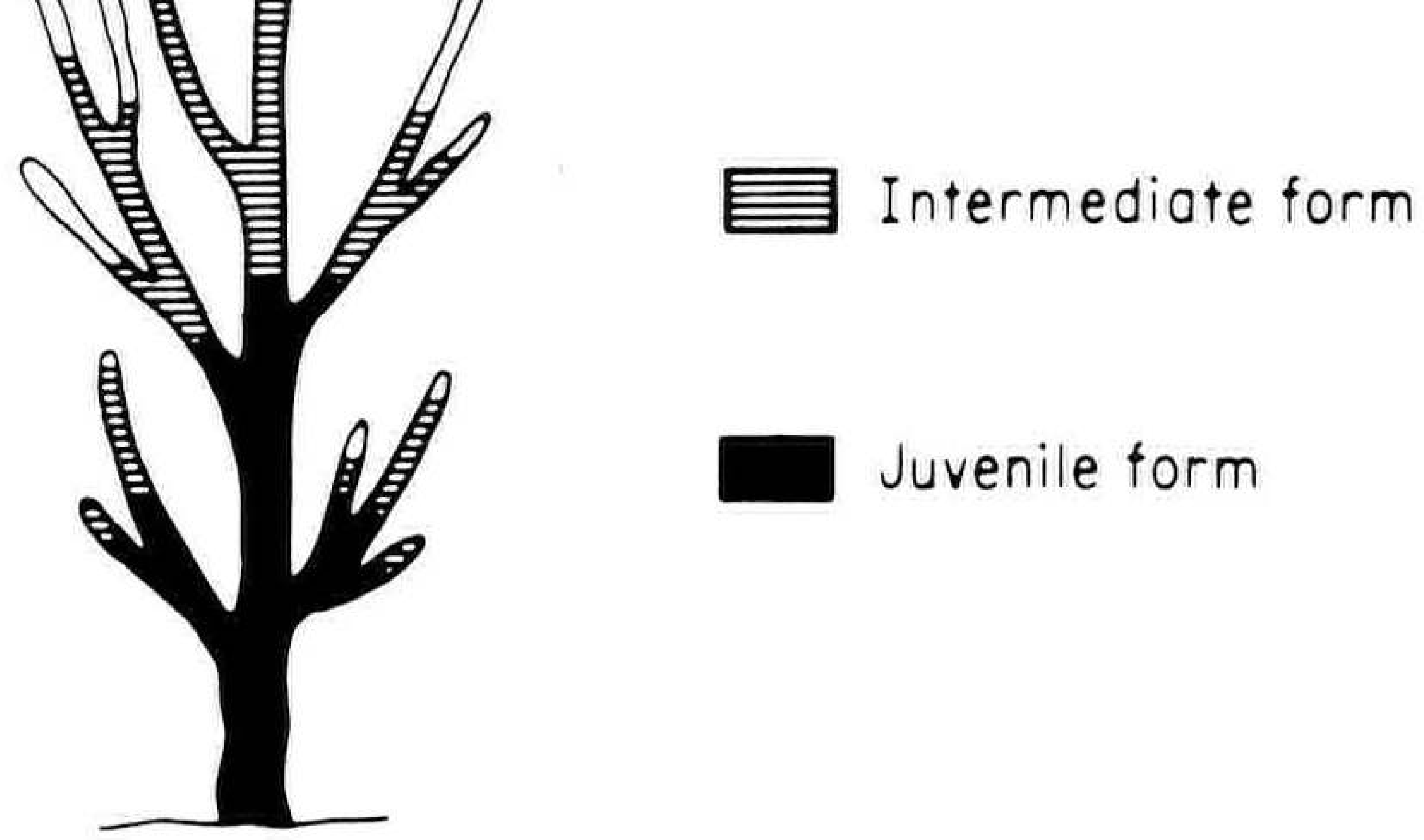

Figure 4. Variations in location of different maturation phases on a mature seedling plant.

Fig. 5 shows variations in three important characteristics: rooting potential, flowering, and shoot vigor associated with juvenility (Borchert, 17). The level of maturation is indicated in the top of the graph by change in leaf characteristics as "markers". In this sense "age" (maturity) must be identified as number of nodes or cell division.

For plants, such as many woody trees, e.g., conifers, etc., the rooting potential may drop sharply with maturation (A). Other species and individual seedlings, however, may show the pattern of A^1 which indicates that significant rooting potential is retained in the adult phase, providing that appropriate propagation procedures are followed. Most plants probably fall between these extremes. Ability to initiate flowers marks the termination of the juvenile state (B) but there may be plant species or cultivars where the distinction can not be so sharply defined (B^1). Likewise more vigorous growth is associated with the juvenile phase (C). In some plants the difference in growth habit may be very striking — those propagated vegetatively from the adult phase may be bushy and with much lateral branching whereas those from juvenile tissue grow upright with a central leader.

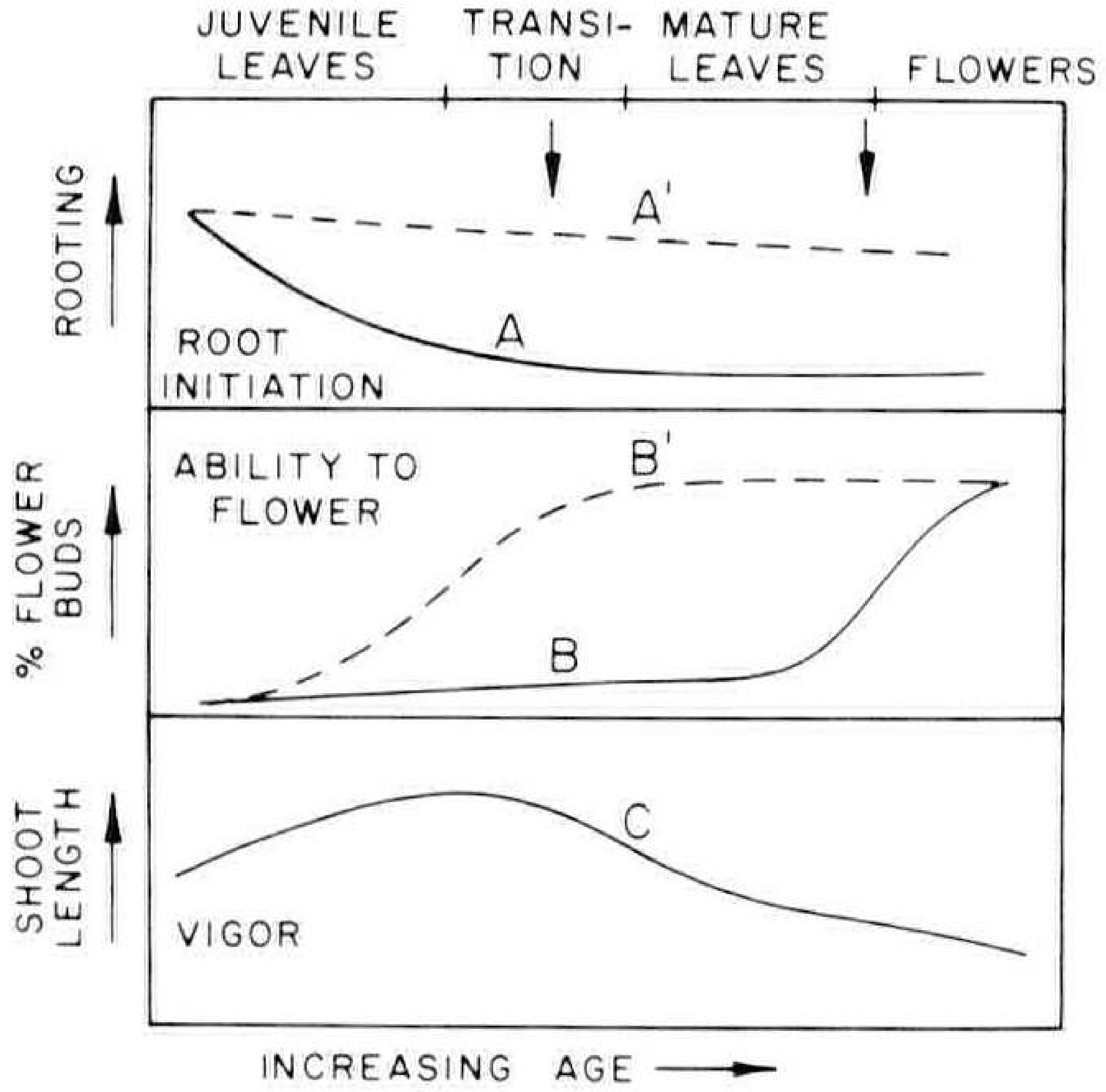

Figure 5. Changes in potential for *rooting, flowering* and *vigor*, in relation to maturation are measured here as node number, not as chronological age. Leaf morphology (top of graph) is used as a "marker" to indicate phase change. Arrows indicate when significant changes had occurred. (See text for further explanation).

Juvenility and evolution. If one considers that a distinct juvenile period has value to a plant in nature, one can understand why various juvenile characters exist. Consider the following examples:

a. In the crowded forest environment, it is a distinct advantage, if not a necessity, for a tree to have initially strong, upright, vigorous growth without flowering in order to compete with its neighbors for light.

b. It is a distinct advantage to be able to regenerate or resprout from near the base of the plant to permit survival after fire or browsing animals.

c. It would be a distinct advantage to have thorns (apple, pear, citrus), scale-like (junipers, etc.) or spiny (holly) leaves to ward off browsing animals in the forest.

d. It would be a distinct advantage for a plant in the midst of a dense jungle or forest, to be a vine, grow along the ground until it reaches a stake or tree, grow upward, twine around the support until it reaches the top where it reaches sun and air. Note the *Hedera helix* (Fig. 6).

Numerous other examples could be cited but all underscore the evolutionary advantage of juvenile characters in which the plant not only has such morphological characteristics but also has the flexibility to produce them when needed and shut them off when not.

In the dogma of modern genetics, the basic control mechanism of the cell resides in the DNA molecules of the chromosomes. These molecules are the same for all cells in the plant. However, the information utilized from such basic molecules differs in different development stages and in different organs of the same plant. At this time our understanding of gene regulation in higher plants is very limited.

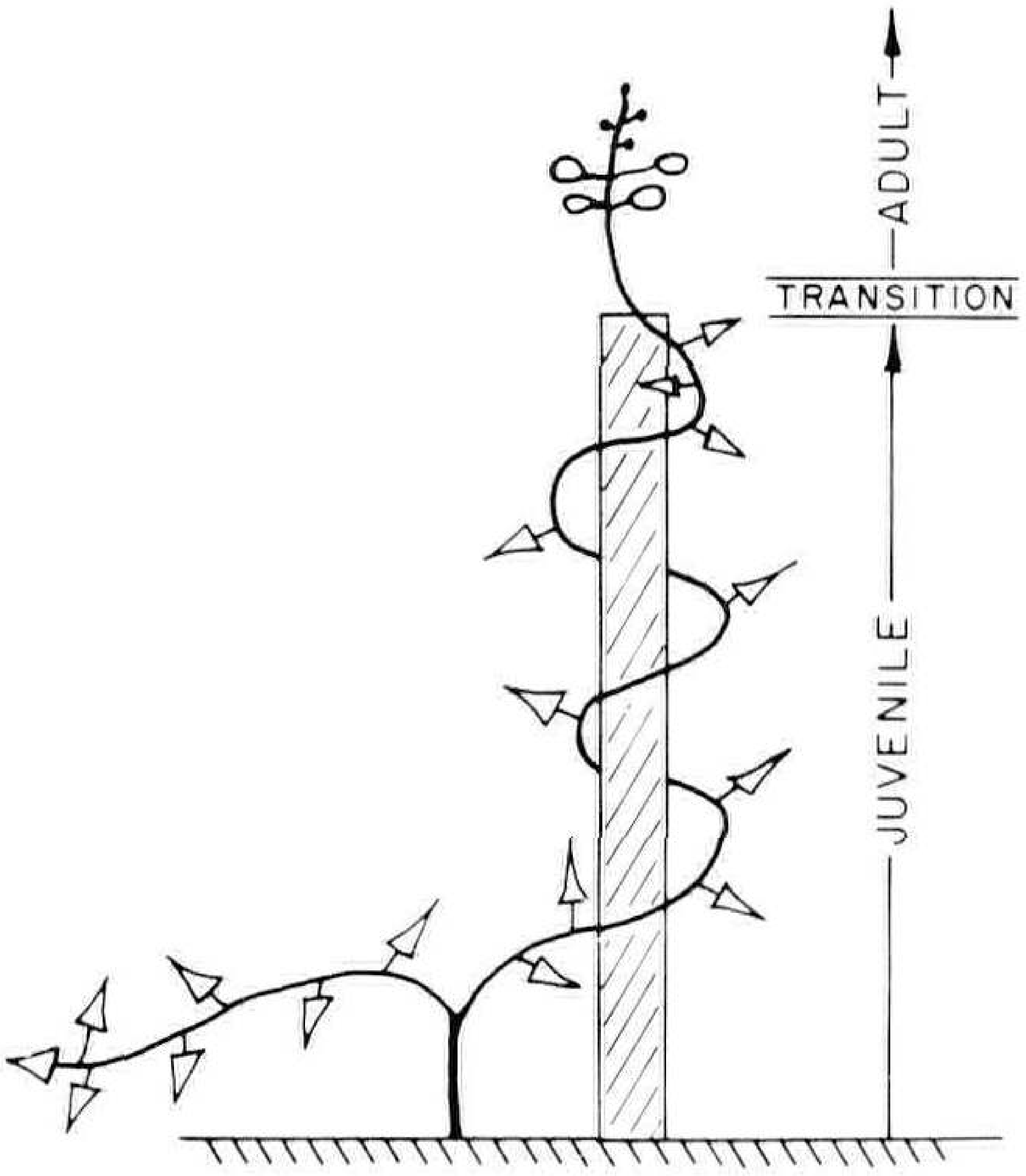

Figure 6. Diagram of an ivy plant (*Hedera*) showing how phase change may be correlated with growth habit.

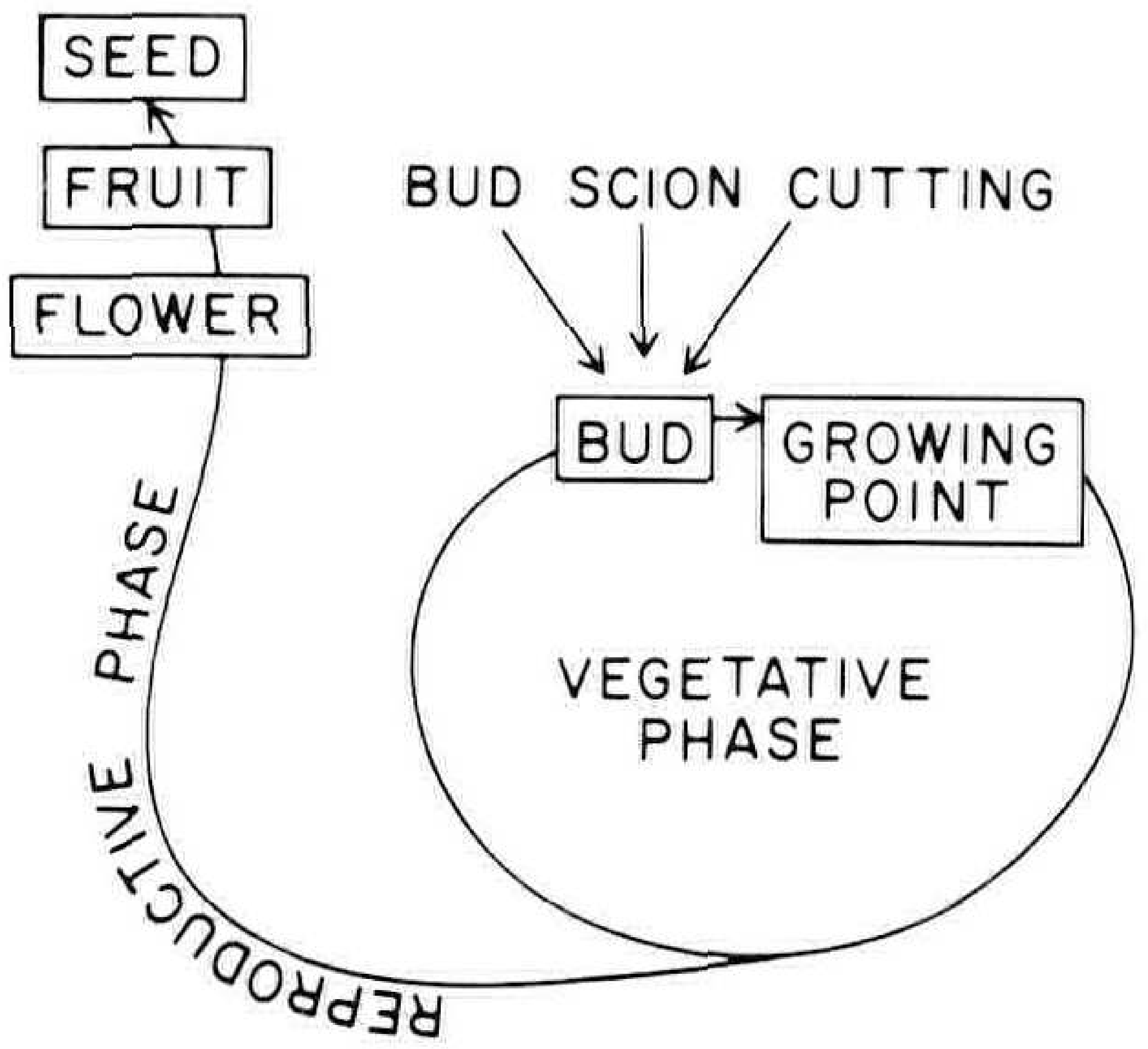

Figure 7. Growth cycle of a vegetatively propagated plant in the "adult" phase. Many growing points remain vegetative (not juvenile) and maintain the plant as a perennial. Others become reproductive, become flowers, fruits, and then die.

The vegetative life cqcle. Consider now the vegetative — reproductive life cycle of the plant shown in Fig. 7. Such a plant may start as a bud or a cutting removed from any part of a seedling plant as shown in Fig. 8. The plant could be grown on its own roots, as in a cutting; or as a scion grafted to a rootstock which, in turn, could either be a seedling or an own-rooted cutting. Continued vegetative propagation produces a group of plants referred to as a *clone* and which could become a named *cultivar*. Since control of juvenility is in the growing point, the new plant could start either as juvenile or adult depending on source of the bud or tissue. Plants propagated vegetatively from juvenile tissue show juvenile characteristics and buds and cuttings derived from mature plants retain those characteristics.

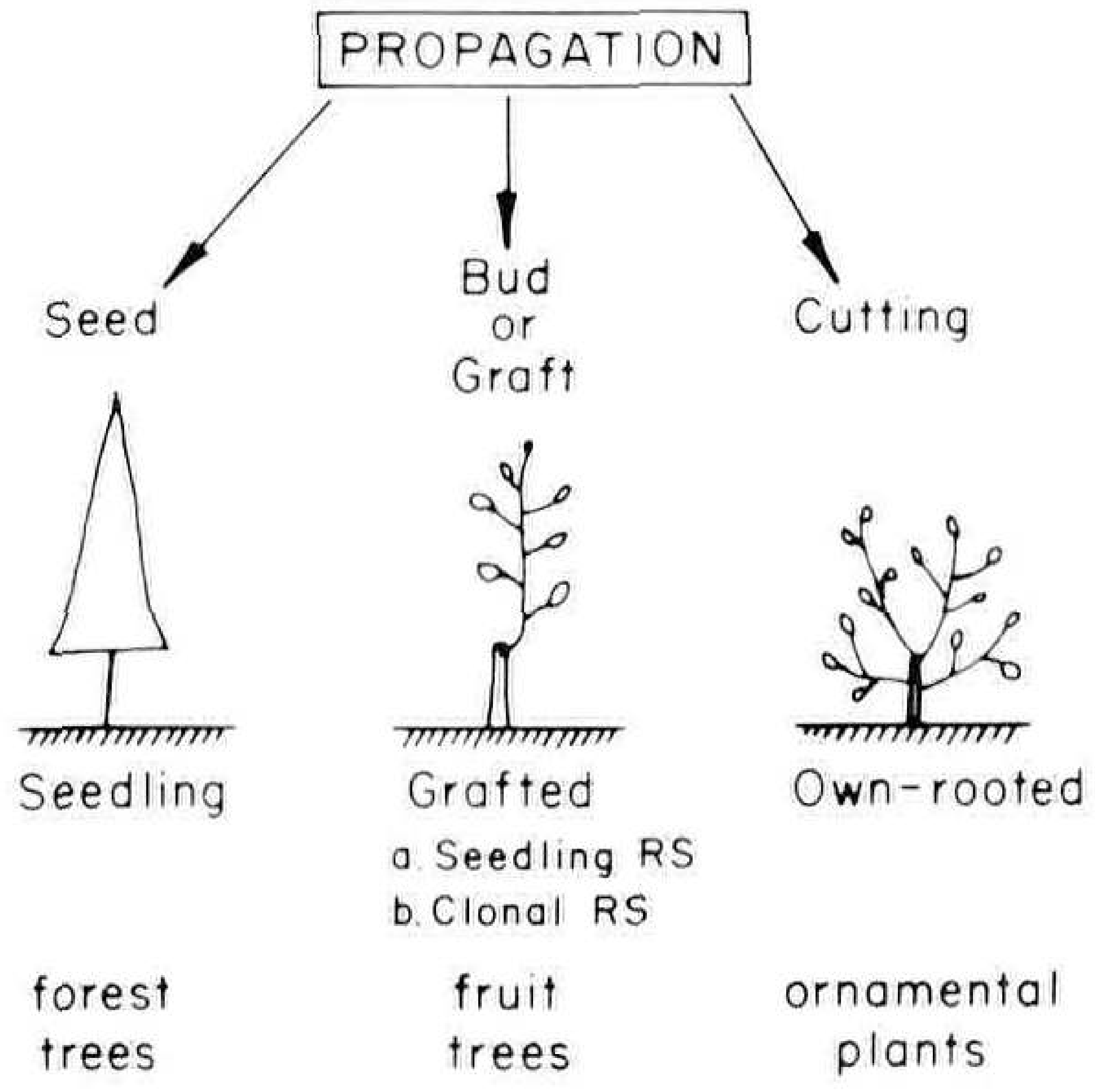

Figure 8. Different forms of plants may be produced depending upon whether they are propagated by seed or are vegetatively propagated.

The growth cycle of the vegetatively propagated adult plant, therefore, is fundamentally different from the seedling cycle (Fig. 9). Two phases are recognized — a vegetative phase and a reproductive phase. In the vegetative phase, shoot tips may resemble those in the juvenile phase (at least superficially) but can now respond physiologically to flower-inducing stimuli. A certain amount of elapsed time and a certain amount of growth may be needed before flowering is initiated. Many of the horticultural practices, such as chemical regulation, grafting to dwarfing stocks, girdling, growth reduction, etc., are effective in inducing initiation of flowering. In contrast to their effect in the juvenile phase, environmental and management conditions that produce excessive vigor, such as high nitrogen, heavy pruning, etc., may delay flowering and fruiting. These are the opposite conditions that are effective in promoting the juvenile phase to induce flowering.

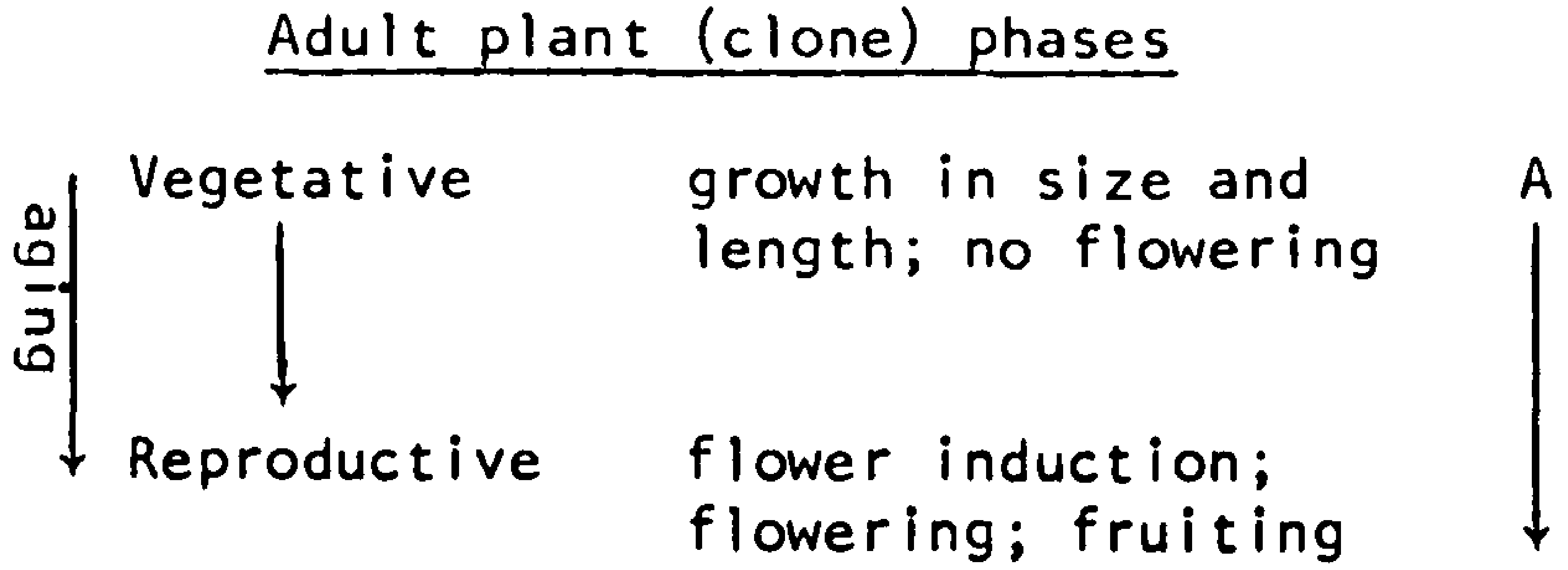

Figure 9. Phases of development of a vegetatively propagated clone in an adult phase. The process of change may be referred to as "aging" rather than "maturation", as shown in Fig. 2.

Probably most fruit tree growers have never seen a juvenile fruit tree since all grafted cultivars are in the adult phase. Whether or not vegetatively propagated nursery stock is juvenile or mature would depend on what growth form was selected in the initial development of that material.

Both the specific character associated with juvenility and the cellular control mechanism that controls the timing appears to be genetically controlled and inherited. Fruit tree cultivars that bear precociously tend to produce seedling offspring with short juvenile periods (Visser 17). Ease-of-rooting is inherited and varies greatly within seedling populations and may not be dependent on being in the juvenile phase.

Melchoir (17) found that in seedling populations of *Chamaecyparis pisifera* various foliage types associated with the juvenile phase was inherited but the time when these leaf characters changed was not necessarily related to the time of flowering. In some plants, the character and the timing may be independent of each other; in others they may be associated.

JUVENILITY AND REGENERATION BY CUTTINGS

The fact that cuttings from juvenile plant material initiate adventitious roots and shoots more readily than adult or mature material is well known. Our concern is to utilize this principle in propagating potential cultivars either as own-rooted plants or as rootstocks, which as adult material are difficult to propagate vegetatively.

1. **Selection of juvenile material.** Juvenile shoots may arise from the base of mature plants, appearing as watersprouts, or suckers from the roots or near the surface of the ground at the root/stem junction. Such material has been rooted successfully in such species as chestnuts (Vietez, 17), oaks (Morgan, 17), eucalyptus (3), black walnuts (2), and pecans (8), among others. However, if this procedure is to be of practical value, one must be able to continue to produce such juvenile material of selected clones in quantity sufficient to meet commercial needs. This means some method of maintenance in a stock block or some other procedure must be used to preserve the necessary rooting potential.

2. **Hedging and heavy pruning of stock plants.** This procedure would appear to be an essential part of a program dependent on utilizing juvenile material. Otherwise the natural tendency toward maturation may result in the loss of rooting potential. Whether or not heavy pruning and hedging involves rejuvenation to the juvenile phase or simply the stimulation of vegetative shoots to a condition more favorable to rooting, is difficult to answer. Stool beds have been cited as an example of induced juvenility, although the rejuvenating influence of this treatment may vary with the cultivar. What is essential is that the rooting potential be stabilized at a required level.

Hedging for propagation materials has important uses in forestry, as in Monterey pine (Libby 17) and other forest trees. Work with olive provides another example (12), where better rooting potential comes from basal shoots on stock plants.

The program for fruit tree rootstock development and associated propagation systems at the East Malling Research Station, England provides another example where hedging plays a key role (personal communication). New potential rootstocks originate as seedling plants, grow first in the greenhouse and then are transplanted to the nursery six inches apart where they remain for two years. (Note that close spacing and attending slow growth tend to retain the juvenile phase). After preliminary screening, seedling selections are transplanted to a hedge row, planted 1 to 1 1/2 feet apart, and cut to a height of 1 1/2 to 2 feet. Propagation tests for ease of rooting are then made on this material and, within the group of plants selected for propagation potential, rootstock tests are conducted. Again, it may be an academic question whether this process involves selection of individual easy-to-root clones completely independent of the juvenile phase, or whether the process involves a stabilization of juvenile phase. Nevertheless, the point is that the selection for ease of propagation precedes selection for horticultural characteristics.

3. Reversion or reinduction of the juvenile phase from adult material.

a. *Initiation of adventitious shoots on roots or sphaeoblasts.* Shoots arising adventitiously on roots or stems (sphaeroblasts) are characteristically juvenile in appearance and can often be rooted easily. Schwabe (17) reported that he and students had developed roots on a few cuttings of hard-to-root, adult 'Lord Lamborne' apple; these produced a continuous supply of adventitious shoots which could then be detached and rooted. Although such plants were juvenile in appearance and rooted readily, they flowered within 2 years and would respond readily to flower-inducing treatments. The possibility that one can separate the genetic control of flowering and rooting in the same clone, as these results suggest, offers exciting possibilities for future work.

b. *Reversion through applied chemicals.* The fact that biochemical differences can be measured between juvenile and adult material has been shown by numerous investigators. For instance, the existence of rooting co-factors in conjunction with auxin has been demonstrated on juvenile material (Heuser, 17). Gibberellins and perhaps other growth promoting substances, as auxins, have been associated with juvenile growth whereas growth inhibiting substances, as abscisic acid, and other naturally occurring inhibitors have been associated with the adult phase. In such cases, it is not certain whether their presence are causes or effects.

Nevertheless, it has been possible to rejuvenate adult ivy (*Hedera*) with gibberellic acid (Hackett, 17). Furthermore, this reversion can be prevented by abscisic acid. GA applied to pear, citrus, acacia and some *Prunus* species can produce thorny, vigorous juvenile-like growth but it is uncertain if actual reversion occurred because no repropagation tests were made. On the other hand, early flowering has been induced in mango by ethephon, an effect that was reversed by GA (Chacko, 17). To further confuse the issue, applications of GA to many conifer species will produce cones (female flowers). This latter discovery appears to have significant application to seed production practices in forest trees (Pharis, *et al.* 17).

One of the potentially significant developments reported at Beltsville, (Wardell, 17) and since published (15) involved experiments in which extracts shown to contain DNA from the flowering adult phase of a tobacco plant were injected into another tobacco plant and produced flowering. Extracts of a plant in the juvenile phase failed to do so. One of the essential aspects of the experiment was that foliage of the juvenile portion had to be removed before the extract would be effective. The implications of these findings are that the control of the maturation phases may indeed be located in chromosomes at the informational sites of the DNA molecules, and procedures could be developed to program or deprogram plants to whatever phase one wanted. Further the foliage is shown to have a controlling influence and the relative amounts of each may have to be evaluated. Future experiments will determine the validity of these implications.

c. *Grafting effects.* A third way by which reversion has been produced is by grafting. However, results have been so conflicting with different plants that at present it is impossible to establish definite principles. Grafting scions of seedling plants to dwarfing precocious rootstocks can sometimes stimulate flower induction but the scions must have reached a particular stage of maturation before this happens. There is a possibility, however, that the juvenile foliage has an inhibiting effect on flowering and must be removed.

On the other hand, these are indications that reversion of mature scions is possible. For example, grafting adult ivy scions to juvenile stocks has produced reversion in new shoots (Hackett, 17), providing the temperature was sufficiently high. Seedling rootstocks often invigorate scion cultivars grafted to them whereas clonal rootstocks may be dwarfing and induce precocity. Monselise has shown with nucellar seedling material in citrus that this invigorating effect can be attributed to a juvenility influence (10). More directly applicable to propagators is the situation in rubber (*Hevea brasiliensis*); rooting of mature clones has been enhanced by grafting to juvenile plants (11). Success of developing easy-to-root clones of eucalyptus and limbe has recently been reported by grafting of mature shoots to juvenile seedling stocks (7).

4. **Tissue culture, micropropagation and juvenility.** Many species of herbaceous plants are now being propagated successfully by tissue culture and shoot-tip culture. Successful propagation of woody species in vitro is more difficult and has been achieved in relatively few species, such as, easy-to-root clones of aspen (14). Selecting juvenile tissue may be important, if not essential for success of this material.

The two methods — tissue culture and shoot tip culture — are fundamentally different in that in tissue cultures completely new adventitious shoots, roots, or small embryos (embryoids) are produced from callus. In micropropagation with shoot tips, growth takes place from meristems and axillary buds which are already present, although sometimes adventitious shoots may also arise in the process. Thus, these shoot tips can retain either the juvenile or adult phase depending upon the source of explant. On the other hand, the possibility exists that the adventitious shoots and embryos regenerated through tissue culture may be juvenile. Whether or not such juvenile material would be horticulturally useful would depend on the needs of the propagator and the use of the plants.

Explants of juvenile tissue (embryos, seeds, nucellus) have been used to achieve regeneration of shoots in tissue cultures in almond (9), apple (1), and *Acacia koa* (13). Abbott and Whiteley cultured juvenile shoot tips of germinating apple seedlings and produced basal callus and *both* axillary and adventitious meristems. Shoot tips from greenhouse-grown adult apple cultivars, on the other hand, produced basal callus and *only* axillary meristems; the number of shoots was less than from juvenile material. Success with non-juvenile material may require the addition to the medium of certain naturally occurring materials, such as phloridzin, or related compounds, as phloroglucinol, as reported by Jones (5) for apple shoot tips. In all cases, the process of propagation is a 2-stage affair, first, the shoots are initiated (whether axillary or adventitious) and secondly, these are removed and rooted.

The juvenile and adult phases apparently are present in certain tissue cultures, as ivy (Hackett, 17). This is significant for basic studies. The possibility of controlled modifications of phases *in vitro* is suggested in a report of propagation of certain early flowering birch seedling by tissue culture (Hubtinen, 17). Seedlings produced by breeding several generations of early flowering birch plants were apparently so precocious and adult that all buds became flowering and none remained vegetative to maintain the normally perennial nature of the plant; vegetative propagation was impossible. However, tissue cultures regenerated plantlets readily. However, when grown to flowering, the regenerated plants had apparently re-established the perennial habit. The ability to produce vegetative shoots was regained and the excessive flowering tendency was reduced. This suggests that the juvenile → adult changes may be reversible under particular conditions of tissue culture.

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