THE RELATION OF VEGETATIVE PROPAGATION TO TOPOPHYSIS, CYCLOPHYSIS AND PERIPHYSIS IN FOREST TREES

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INTRODUCTION

Vegetative propagation by means of rooting cuttings, air-layerings, and grafting is an important tool of the forest geneticist and tree breeder. Its role in the production of clonal material for various purposes is well accepted. However, the success and results obtained with the use of vegetatively-produced material is often masked by three little-investigated phenomena. These phenomena have been coined, topophysis, cyclophysis, and periphysis (Molisch, 1915; Seeliger, 19244; Busgen and Munch, 1929).

Some workers familiar with vegetatively-produced forest plant material have recognized the above mentioned phenomena. Cuttings, air-layerings, and grafts from different individuals, species or genera, crown sections, or branch orders may have been observed as behaving quite differently when grown in uniform environments. These behaviors do not seem to coincide with the performance that horticulturists have found in the vegetative propagation of special ornamental varieties of woody trees (fastigiate, weeping, dwarf, "broom", "snake", and other forms). Recognition must be given to workers such as Molisch (14), Goebel (5), Seeliger (18), Busgen and Munch (2), and others who recognized and clearly defined the problem,, Workers today are especially confronted with this problem in the establishment of seed orchards and clonal test areas, and in the use of vegetatively-produced plant material for reforestation and similar purposes.

TERMINOLOGY

Topophysis. The term topophysis was first introduced by Molisch. Busgen and Munch refer to it as the "characters of the parts of the tree which are determined by position." Topophysis, in the sense of Molisch and others who adopted the term, refers to the branch order (first, second, third) and/or to terminals in contrast to laterals.

Cyclophysis. Seeliger introduced the term cyclophysis to describe the shoot individuality as related to different stages of life (physiological ages), first mentioned by Goebel. Cyclophysis also covers Baur's (1) term of "strongly induced modification" for fixed developmental stages of trees (ability to flower, sexual separation of flowers in different tree parts, sun and shade leaves, etc.). These modifications or stages are unalterable or alterable only with great difficulty.

Periphysis. Busgen and Munch introduced the term periphysis to describe "characters induced by the influence of environment without necessarily connecting it with the idea of prolonged duration of induced characteristics." The effects of climatic, physiographic, edaphic, and biotic agencies would be included here.

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In regard to vegetatively-produced material, the phenomena are herein described:

Topophysis - the local position effect exhibited in plants originating from different branch orders in the same crown section.

Cyclophysis - the physiological age effect exhibited in plants originating from the same branch order in different crown sections.

Periphysis the environmental and/or the rootstock effect exhibited in plants growing under different environments and/or on other than their own root systems.

TOPOPHYSIC INFLUENCES[1]

In American literature, Mirov (12) and Smith, Haddock, and Hancock (19) seem to be the first to report the importance of local position effect on the performance of individual rooted cuttings. Kleinschmidt (9) observed differences in the branching characteristics of four-year-old Abies alba rooted cuttings taken from different branch orders. After six years, rooted cuttings of first order laterals still resembled branches; first order terminals produced plants of normal tree form. In contrast, almost complete orthotrophic plants were derived from first order laterals rooted from five-year-old Picea abies.

Herrmann (7) reports significant differences between the growth of ten-year-old seedlings and cuttings or buddings of Picea abies and Pseudotsuga menziesii. He points out that the topophysic effect is more pronounced if the cuttings or scions are collected from the flowering portions of the tree. Kleinschmidt makes a similar statement and he thinks that the branching habit of rooted cuttings of spruces becomes more pronounced with the advancing age of the tree from which the cuttings are taken.

Exotic Abies species grafted on four-year-old balsam fir rootstocks at Syracuse have performed quite differently after four years from grafting, depending on branch order. All scionwood was from the center crown section of trees in the 20-to 30-year age class. Grafted first order laterals became orthotrophic in the second year, while second order and third order laterals still retain more or less the original branch habit. Grafts from 25-year-old Douglas firs, all from the top crown section, exhibited orthotrophic development in a few years from first order lateral scionwood; grafts from higher order laterals showed plagiotrophic development.

Mirov (13) raises the question as to whether cuttings of pine can develop into straight trees. From clonal test areas in Sweden, Larsen's (11) "tree shows" in Denmark, Greene's (6) work with slash pine, and young clonal test units of red pine and white pine at Pack Forest (New York), indications are that branch order in Pinus--especially two-needled pines—is much less pronounced than in Abies, Picea, and Pseudotsuga (figure 1). Larix appears to be intermediate between Pinus and Picea, in this respect, since the change from plagiotrophic to orthotrophic growth normally occurs after a period of five or more years, depending upon the age of the ortet. At Syracuse, grafts from older white pines form less straight stems than those from younger trees, at least during the first few years.

In making the above general statements, we must realize that topophysis is not completely divorced from cyclophysis. Interactions between the two phenomena occur and are not easily separated.

[1] The original translation from the German used the terms "topophytic, cyclophytic and periphytic."

Figure 1. Five-year-old Pseudotsuga menziesii grafts obtained from a 25-year-old tree. (A) Scion collected from first order laterals, top crown section. (B) Scion collected from third order laterals, top crown section.

CYCLOPHYSIC INFLUENCES

Schaffalitzky De Muckadell (16) found that in European beech the age of the apical meristem (physiological age) is of much greater importance than branch order in the growth behavior of vegetatively-produced plants. This also seems to hold true for many other hardwoods and conifers. His experiments with grafts from the leaf-retaining section (lower crown) in comparison with those of the non-retaining section (upper crown) are good examples of cyclophysis.

The performance and non-flowering condition of grafts or cuttings from lower epicormics also indicate the existence of age-zoze effects, i. e., cyclophysis in trees. The juvenile characteristics of grafts or cuttings from epicormics are expressed by fast growth. Schrock (17) compared cuttings from an old Pop ulus berolinensis tree in relation to the height where they were obtained in the tree crown. He found that the growth of the cuttings increased with increasing distance from the stem base up to 4.5 m (13.5 feet) and decreased from there on. The ability to strike roots increased also with increasing height up to the same distance from the stem base. Grace (4) and others have obtained similar results with regard to rooting Norway spruce cuttings. Cuttings obtained from the lower crown section rooted better than those from upper regions.

Lehnert (unpublished) found that severed root suckers of aspen collected close to the main stem grew faster than those from more distant portions of the root. Leaf characteristics differed on suckers taken from near the main and those taken towards the root tip. This suggests that physiological age-zones exist within the root system of a tree.

Cyclophysis is very pronounced in clonal test areas of many species. Ramets taken from younger ortets are more vigorous than those taken from older octets. This has been found by a number of workers such as Hoekstra and Johansen (8). Kleinschmit, Herrmann, and many others.

It should be mentioned here that results obtained in some poplar test plantations must be considered inconclusive when those plantations were established with vegetatively produced plants (cuttings). In most instances the "physiological age effect" or "crown section effect" was not taken into account when the cuttings were collected and planted.

It follows also that the absolute tree age which we use in all our records can mean very little. What is important in our work are the physiological conditions of a tree, i.e., its physiological a e. To determine the exact physiological tree age or the physiological age o a certain crown section is very difficult or impossible because the criteria used for their determination are not entirely due to internal conditions but very often highly influenced by environment.

Cyclophysis is often closely connected with the problem of resistance to diseases and insect attacks. It is well known that certain species exhibit resistances to certain agencies in youth and lose this resistance with age. Their ramets behave accordingly. This has been found in Ulmus where young plants are resistant to Dutch elm disease but older plants are not. A reverse situation is given in Thuja plicata (Sogaard, 20) where young seedlings were killed or severely damaged by fungal attack, Cuttings of older trees were however highly resistant.

It has been observed in a few cases that grafts or cuttings derived from older trees have rejuvenated, i.e., have shown juvenile characters expressed by leaf form, lack of flower production, growth form, etc. In many cases this rejuvenation is due to very favorable site conditions, or in the case of grafts, a very strong and favorable rootstock (periphysis). However, in some of these cases of rejuvenation, which are mostly temporary, no attention has been paid to the crown section from which these plants were derived. Scions and cuttings obtained from physiologically young crown zones should, and do, behave as young plants.

One must be careful in using the term rejuvenation in reference to vegetatively-produced plant material. A true rejuvenation would require that physiologically old plants or plant parts change to physiologically young plants or plant parts, and continue to perform as such. Cases of true rejuvenation are rare.

PERIPHYSIC INFLUENCES

The rootstock effect on grafts is here considered as an environmental effect and thus a periphysic influence. Voluminous horticultural literature is available on the effects of rootstocks on flowering, fruiting, and dwarfing.

Forest geneticists and tree-breeders can learn much from the outstanding research done at such stations as the East Mailing Research Station, England.

The effects of site, photoperiod, and climate on tree performance is well known to foresters Silviculturalists are even more familiar with the variability of seed crops within the same species under different environmental conditions. Frolowa (3) believes that the available water can change the ratio of male to female flower production in plants, The effects of the en vironment on different vegetatively-produced plants may favor flower production on one clone and not another. This has been found true in fruit trees (10) and should lead to individual flower stimulation procedures in seed orchards.

There are many cases of incompatibility or delayed incompatibility in homoplastic grafts which are growing on a genetically "strange" rootstock of the same species. Incompatibility or delayed incompatibility can be hereditary, but also periphysic. It is logical to assume that there are many stages between complete compatibility and full incompatibility which would influence the performance of grafts.

The influence of the degree of compatibility in heteroplastic grafts is even more pronounced. It has been found in our grafting experiments that in red pine grafting the "take" was much better on Scotch pine rootstocks. Certain grafted Betula and Castanea species have made better growth on other stock species than on their own species.

There is still speculation among foresters as to whether dwarf rootstocks are superior to regular rootstocks, with regard to their effect on total flowering and seed setting. Heimburger (personal communication) has found that rootstocks produced by early-flowering parents of aspen have an effect on the time of initiation and amount of flowering in grafted scions.

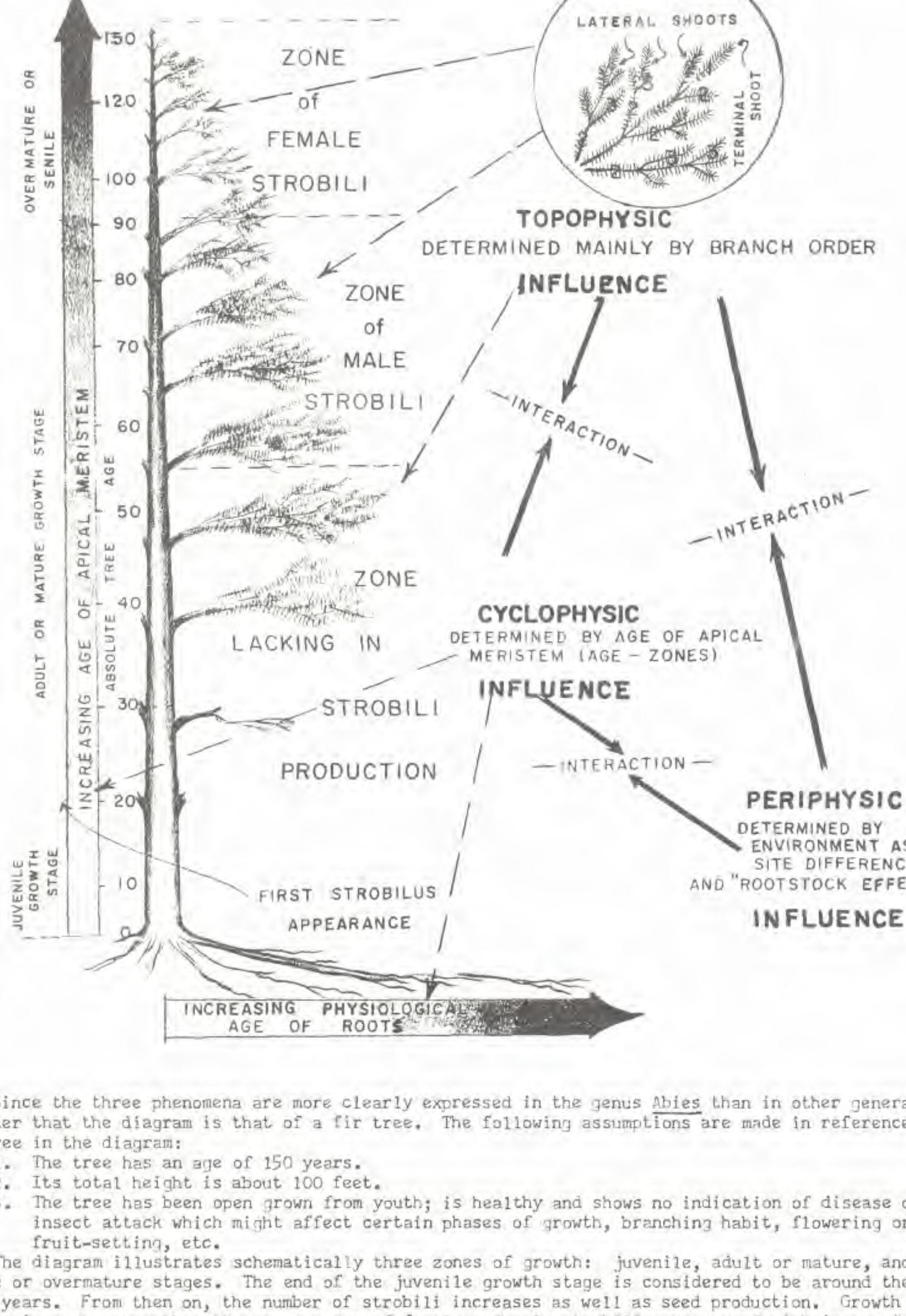
INTERACTION BETWEEN THE THREE PHENOMENA

There is no doubt that, in many instances, a close interaction exists between two or all three of the above mentioned phenomena, In *Hedera*, for example, cyclophysis and periphysis are both effective in the expression of the adult form only in old age and in full sunlight. Busgen and Munch summar izes the interaction in relation to the heredity of a given plant by saying, "The topo-, cyclo-, and periphysis of the parts of plants are naturally different for different species, and indeed, for different individuals. Internal heredity factors prescribe even in the fertilized egg cell of the incipient plant the characteristics for all its parts, for every age and for all possible external circumstances. We have already learned of these internal forces passing over with the germ plasm under the conception of 'genotype'. Genotype, environment, age, and part of the plant together determine imperatively the characteristics of all the plant members, and so the whole phenotype."

If we apply Munich's statement to our subject matter situation, we immed iately begin to realize that the performance of rooted cuttings, air-layerings, or grafts must be, to varying degrees, determined by topophysis, cyclophysis, and periphysis. To illustrate the interaction between the three phenomena more clearly, a diagram has been developed (figure 2).

FIGURE 2

DIAGRAM SHOWING THE GROWTH STAGES AND BRANCH ORDER OF A 150 YEAR OLD FIR TREE AND THEIR RELATIONSHIP TO TOPOPHYSIS, CYCLOPHYSIS AND PERIPHYSIS.



Since the three phenomena are more clearly expressed in the genus Abies than in other genera, consider that the diagram is that of a fir tree. The following assumptions are made in reference to the tree in the diagram:

1. The tree has an age of 150 years.
2. Its total height is about 100 feet.
3. The tree has been open grown from youth; is healthy and shows no indication of disease or insect attack which might affect certain phases of growth, branching habit, flowering or fruit-setting, etc.

The diagram illustrates schematically three zones of growth: juvenile, adult or mature, and senile or overmature stages. The end of the juvenile growth stage is considered to be around the age of 20 years. From then on, the number of strobili increases as well as seed production. Growth progresses in such a way that the crown zones of female and male strobili move upward with increasing age. These zones of female and male flowering are most clearly expressed in the genus Abies and to a lesser degree in the genera Picea and Pinus.

The arrow to the left of the tree indicates the increasing age of the apical meristem, being oldest in the tip of the crown and youngest just above the ground. 1/ The horizontal arrow shows the increasing physiological age of the roots. If we consider cuttings or grafted scions from a certain crown section, differences in their behavior may be due to both differences in age and to branch order. Material taken from first order terminals and from one-year-old wood graft better and behave differently than that taken from various lateral orders and two-or three-year-old wood.

The interaction among the three phenomena is normally triangular, as illustrated in the diagram. It seems possible, however, to isolate through specially designed experiments one phenomenon from the others. Research on this matter has been started at Syracuse.

1/ See footnote on p. 48

HEREDITY EFFECT

In the discussion of the general problem, the work of horticulturists in vegetatively duplicating ornamental varieties of plants was mentioned. These are cases where the genotypic influences are so strong that the three phenomena are masked or fully overshadowed. Similar cases in the genera Pseudotsuga, Picea, and other genera are known (Figure 3).

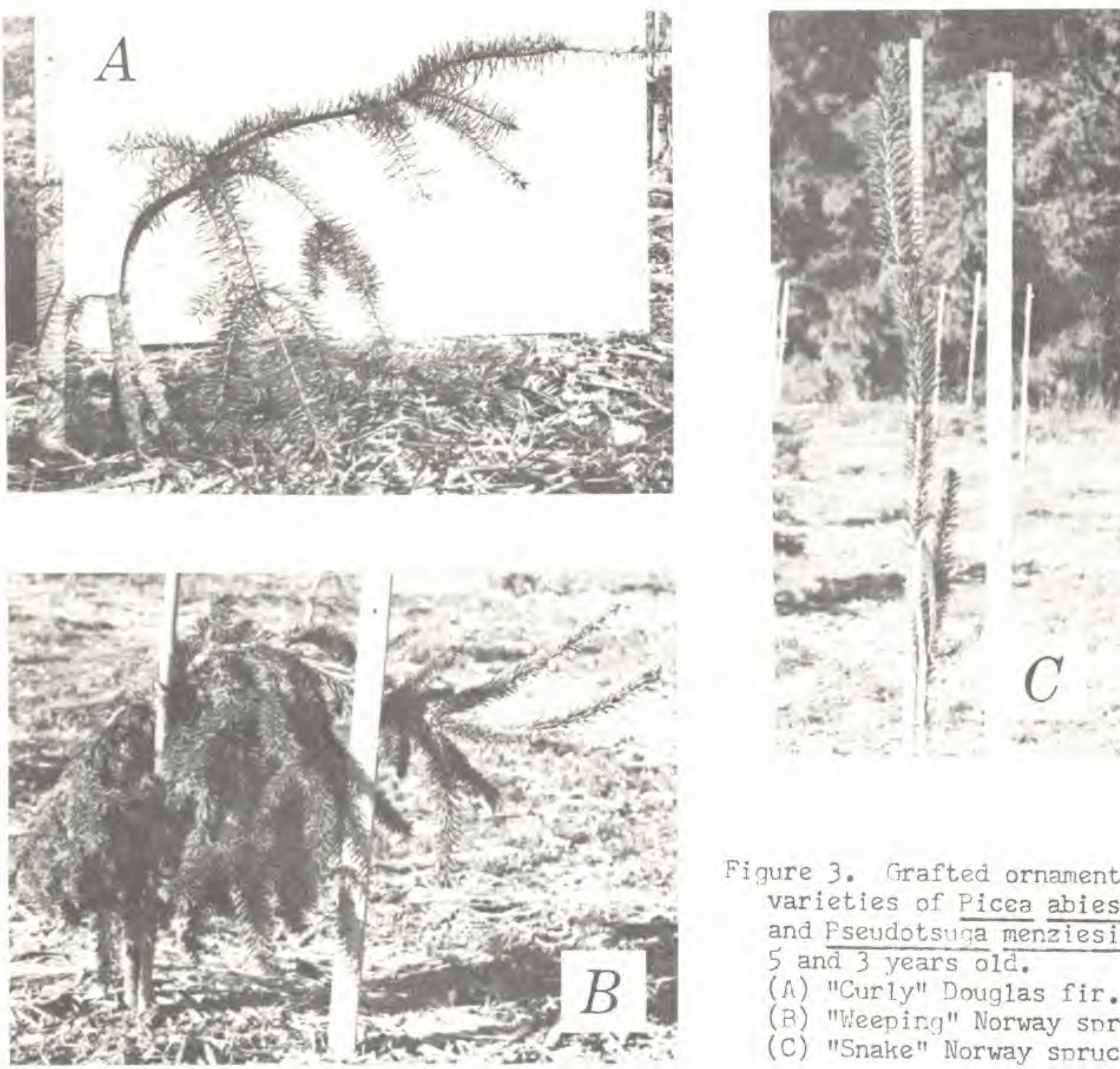


Figure 3. Grafted ornamental varieties of Picea abies and Pseudotsuga menziesii, 5 and 3 years old.
(A) "Curly" Douglas fir.
(B) "Weeping" Norway spruce.
(C) "Snake" Norway spruce.

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It should be mentioned here that there are workers who doubt that the meristem changes during its life time and ages. They feel, I quote Robbins (1) . . . "that the differentiation of a meristem is determined by the materials which come to it by the balance of the plant." "Evidence to support each of these viewpoints . . . aging and non-aging . . . can be presented."

We still will accept the "aging theory" as most people do. Actual aging, or non-aging on the other hand, has little or no bearing on our discussion since only the effects caused by the meristem and not its change or non-change are here under consideration.

Additional qualitative and quantitative characters which seem to be under strong genetic influence and thus allow up to neglect, to varying degrees, the three phenomena might include: chloritic needle color, if this color is hereditary and not environmental, winter needle color in Scotch pine, needle length and leaf form, the color of strobili and flowers, early and late flushing, early and late flowering, spiral grain, bark color and design, gum and sugar production, various resistances, branch angle, and others. We have to consider also that the genetic make-up expresses itself more strongly in some species or genera than in others.

APPLICATIONS

Clonal testing is a field in which topophysis, cyclophysis, and periphysis have to be considered. These phenomena are of great importance also in establishment of clonal seed orchards and in the production of planting stock. Clonal testing and the production of planting stock normally require that individuals produced should not greatly differ in form, size, and growth from sexually produced trees. For clonal seed orchard material, the form, size, height, and diameter growth are generally of secondary importance. Here, flower and seed production are more important.

The value of clonal testing is still questioned by some workers. This author feels that clonal testing can reveal valuable information about the genetical make-up of certain tree characters under test. Some characters under strong genetic control may be correctly evaluated in a clonal test. However, above mentioned effects of the phenomena may lead to invalid conclusions in the case of height and diameter growth and other characteristics.

Only completely comparable material might give some meaningful information. This means that the vegetatively-produced material compared must originate from branches of the same age class, branch order, crown section, and be produced in the same way. The uniformity of rootstocks in source, size, height and diameter, weight and other characteristics does not eliminate the fact that one individual plant might obtain a more favorable root system than another, in the case of grafts. In spite of these limitations, it is felt that clonal testing (in conjuction with progeny testing) has a valuable place in forest genetics work. However, to have all required information of our selections based exclusively on the performance of clonal material and to assume that all visible and measurable characteristics are transferred to the progeny, is certainly out of the question.

CONCLUSIONS

Concluding the discussion on topophysis, cyclophysis, and periphysis and the genetic effect on vegetatively-produced plants, a few general statements might be made:

1. Cyclophysis deserves special interest because it seems to have the strongest effect on vegetatively-produced plant performance, followed by topophysis and finally periphysis.
2. Close interaction among the three phenomena makes separation of individual effects difficult. Topophysis seems to be more pronounced in plants originating from physiologically older trees and crown sections.
3. The topophysic and cyclophysic effects are more clearly expressed in tree species of the genera Pseudotsuga, Picea, and Abies than in the genus Pinus.

4. In most hardwoods, cyclophysis seems most important since scions and cuttings express their physiological conditions more clearly than their branch conditions.

5. Clonal testing has a valuable place in forest genetics research when the materials under test are fully comparable. Collection of scionwood for clonal seed orchards should be made from the flowering parts of the tree; for clonal testing and the production of planting stock from juvenile parts of trees.

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