INDUCTION OF EARLY FLOWERING OF ORNAMENTAL APPLE TREES

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HORTICULTURISTS have long known that the time of flowering of fruit trees could be hastened by various treatments which inhibit vegetative growth. The blocking of phloem transport from the leaves to the root system has been effected by girdling the trunk of the tree, by grafting on dwarfing rootstocks, or, more recently, by inverting a ring of bark on the trunk of the tree (6). Root pruning or confining the root system in pots also inhibits vegetative growth and promotes flowering. Pot binding has long been used to produce dwarf ornamental trees in Japan, and European foresters have used root pruning to promote early seed production in tree-breeding experiments. The bending of branches in a horizontal position also promotes early fruiting and is the basis for the "Spindlebush" method of training fruit trees in Europe.

The general relationship between growth of trees and the production of flowers and fruits was described by Thomas Andrew Knight (2) as follows: "According to that hypothesis, the true sap of trees is wholly generated in their leaves, from which it descends through their bark to the extremities of their roots, depositing in its course the matter which is successively added to the tree; whilst whatever portion of such sap is not thus expended sinks into the alburnum, and joins the ascending current, to which it communicates powers, not possessed by the recently absorbed fluid. When the course of descending current is intercepted, that necessarily stagnates, and accumulates above the decorticated space; whence it is repulsed, and carried upward, to be expended in an increased production of blossoms, and of fruit. . . . The repulsion of the descending fluid therefore accounts, I conceive satisfactorily, for the increased production of blossoms, and more rapid growth of the fruit upon the decorticated branch." Radioactive tracer tests and chemical analyses of the leaves of dwarfed trees done by graduate students at the Bussey Institution confirm Knight's observations made nearly 140 years ago.

The various methods for promoting earlier flowering and fruiting appear to be related to auxin formation and nutritional balance. The suppression of auxin production or accumulation associated with decreased vegetative growth is generally related to precocious flower and fruit production (1). Nutritional balance also appears to be involved in the production of flower buds. According to Klebs a high ratio of carbohydrates to nitrogen and mineral nutrients promotes flowering (3). This conclusion was supported by the later work of Kraus and Kraybill. More recently Roberts (4) found that flowering of shaded *Xanthium* plants could be hastened by spraying the leaves daily with a sugar solution. Although there is considerable evidence in support of the control of flowering by the carbohydrate-nitrogen ratio, the relationship does not appear to be a simple one (1).

Precocious flowering of apple trees may also be promoted by the physiological incompatibility between the rootstock and the grafted scion variety. Certain rootstock varieties greatly inhibit the growth of the bud or scion of certain horticultural varieties of apples, but if the rootstock variety is used as an interstock on a compatible rootstock the dwarfing effect is greatly reduced. In these cases the dwarfing effect is not due to a poor graft union or to the checking of phloem transport through the dwarfing rootstock stem, but is caused by the interaction between the root system and the scion variety (5).

There is also some evidence that flowering may be induced by a "flowering hormone." This idea was first proposed by Sachs. In 1883 he found that cuttings taken from flowering begonias bloomed much earlier than cuttings taken from plants which had not bloomed. Vöchting grafted adventitious buds of beets into one- and two-year-old roots. The buds on the one-year-old roots produced only vegetative shoots, but those on two-year-old roots produced flowering stems. Cuttings or scions from old trees will usually flower earlier than those from immature trees (3). The grafting of scions from young seedlings on mature fruiting trees to hasten flowering and fruiting of the seedling variety may involve the transmission of a "flowering hormone" from stock to scion, since this method of inducing earlier flowering is not related to the suppression of vegetative growth. Similar evidence for the transmission of a flowering-inducing substance is found in grafts of certain herbaceous plants. Long-day non-flowering plants were induced to flower, even under the influence of long days, by grafting on them short-day variety scions bearing flower buds (1). Although no specific plant substance has been isolated which will stimulate flowering, there is considerable indirect evidence to support Sachs' theory that flowering may be induced by a specific hormone which is formed or accumulated by various internal and external factors.

Experiments with an apomictic variety of ornamental apple variety seem to support the concept of a "flowering hormone." The apple variety used was a hybrid between *Malus Sargenti* and *M. astracanica* designated by the planting number 33340. *Malus Sargenti* when open pollinated is completely apomictic and breeds true from seed. When artificially pollinated with pollen of certain species it does produce some sexual hybrids. The hybrid 33340, like the mother parent, is also apomictic and breeds true from seed. The original hybrid first flowered at the age of six years, and its apomictic seedlings produce flowers at about the same age. Since the hybrid is apomictic it is possible to test the fruiting response of old and young seedling trees which are of identical genetic constitution.

An attempt to induce early flowering by grafting scions from the young one-year-old seedlings on the original fruiting tree was only partially successful. Four grafts were made in 1951. One of the grafted scions flowered in 1953 and again in 1954, but the other three scions have not yet bloomed.

Scions from the fruiting mother tree were grafted on the apomictic seedlings in 1951. The two surviving grafts flowered sparsely in 1953 at the age of three years, but did not flower in 1954. The fact that a scion from a young apomictic seedling grafted on the mature mother tree and the scions from the fruiting tree grafted on the apomictic seedlings produced flowers in the third year, as compared with six years for the seedlings, does suggest the presence of a flowering stimulating substance in the fruiting tree.

More critical evidence was obtained by budding genetically uniform dwarfing rootstocks with buds from both the fruiting hybrid 33340 and its apomictic seedlings. The dwarfing stock used was Ottawa 524 budded on *Malus sikkimensis*, an apomictic species which has been found to be semi-dwarfing when used as a rootstock. In 1951 buds from the hybrid 33340 mother tree and from its apomictic seedlings were budded on uniform rootstocks of Ottawa 524/*M. sikkimensis*.

The resulting trees were grown in the nursery for a year and then transplanted to a test plot. They were spaced six feet apart in a single row, alternating the five "old bud" with the five "young bud" trees. In 1953 one of the "old bud" trees produced flowers and fruits, but no flowers were produced by any of the other trees. In 1954 all of the trees from the "old buds" produced flowers and fruits, while no flowers were produced on any of the trees propagated from buds of the young seedlings. The data regarding flowering, fruiting, and tree size are shown in TABLE 1.

TABLE 1

Performance of trees from buds from an old fruiting tree (O), and from buds of a young apomictic seedling (Y) from the old fruiting tree. Budded in 1951 on Ottawa 524/*Malus sikkimensis*.

Tree Number	Source of Bud	Flower Clusters 1953	Flower Clusters 1954	Fruit 1954	Trunk Caliper cm. June 1954
1.	O	0	15	43	2.2
2.	Y	0	0	0	2.3
3.	O	21	34	103	1.9
4.	Y	0	0	0	2.2
5.	O	0	24	75	2.2
6.	Y	0	0	0	2.3
7.	O	0	42	104	2.2
8.	Y	0	0	0	2.3
9.	O	0	14	54	2.1
10.	Y	0	0	0	2.0
Ave.	O	. .	26	76	2.1
	Y	. .	0	0	2.2

There is no evidence that the initiation of flowering in the "old bud" trees was caused by the suppression of vegetative growth. Tree number 3 from an "old bud" was smaller than the adjacent "young bud" trees (numbers 2 and 4), presumably because it had borne a relatively heavy crop of fruit for such a small tree in the previous year. The four other "old bud" trees, which did not fruit in 1953, were no smaller than the adjacent "young bud" trees. All trees of both lots were identical in morphological characters.

The abundant fruiting of the "old bud" trees in the third year of growth may be due in part to the dwarfing rootstocks, yet the "young bud" trees on the same clonal rootstocks produced no flowers or fruits at the same age. Scions from the fruiting mother tree grafted on 33340 seedlings did produce some flowers the third year, whereas the original hybrid and several of its apomictic seedling progeny did not flower until the sixth year. Although the number of trees tested is small, the consistent results do suggest the transmission of some substance which promotes flowering in the buds or scions from the fruiting tree.

If there is transmission of a flowering hormone or "florigen" through the buds from fruiting trees, one might expect the "florigen" to be transmitted through the apomictic seeds from the mother tree. However, the transmission by vegetative propagation, but not by seed, is not inconsistent with the behavior of the viruses which are transmitted by grafting but not by seed.

The induction of flowering and fruiting can be stimulated in many ways, — by pruning or confining the root system, by grafting onto dwarfing stocks, by ringing or inverting the bark on the trunk of the tree, by knotting the stem, by training the branches in a horizontal position, and in some plants by vernalization or by changing the photoperiod. Only in a few cases has the artificial addition of auxin proved effective in promoting flowering. It is also possible that anti-auxin may play a role in flower induction and that vegetative growth and flowering are controlled by a balance between auxin and anti-auxin, but there is as yet little evidence to support this theory (1).

It seems improbable that all of the various flower-inducing techniques act in the same way. For example, the inversion of a ring of bark on the trunk of a young apple tree undoubtedly inhibits the flow of nutrients to the root system. But the inversion of a ring of bark on one of many branches of a large apple tree also checks vegetative growth and promotes fruiting of the branch involved, but has little or no effect on the rest of the tree. The checking of phloem transport by various means does affect the nutritional balance of the tree, but this is probably only one of a number of factors in promoting flowering.

The apparent transmission of a flowering stimulus by buds from fruiting trees may not be related to the production of flowers and fruits by the tree from which the buds are taken. Differences in tree vigor, size of the leaf associated with the bud, and differences in nutritional balance may be causal factors in promoting earlier fruiting. In order to test some of these possibilities buds from vigorous one-year-old McIntosh whips and buds from mature bearing McIntosh trees were budded on clonal rootstocks in 1951. Eight of each type were planted in a test plot at the Arnold Arboretum's Case Estate in Weston, but none has yet produced flowers. Since the young whips came from buds from a fruiting tree their buds might be expected to transmit the "flowering hormone," even though the whips would not reach the fruiting age for several years.

We have also selected buds in August from a branch which had a section of bark inverted in June, and at the same time taken buds from a normal branch of the same tree and put these buds on clonal rootstocks. The branch with the bark inversion should flower earlier than the normal branches, and we might expect buds from the bark inversion branch to produce earlier fruiting trees than those from the normal branch, even though neither branch had ever borne flowers or fruits. These and other experiments in progress should provide more information on the nature of early induction of flowering.

SUMMARY

Buds from a fruiting apomictic ornamental apple tree and buds from its young seedlings were budded on uniform clonal dwarfing stocks in 1951. Of the five trees from the "old" buds, one flowered in 1953 and all flowered in 1954. None of the five trees from the "young" buds have yet produced any flowers. The earlier flowering of the trees from the "old" buds cannot be attributed to the suppression of vegetative growth. The evidence, although not conclusive, supports the assumption that a flower-stimulating substance was transmitted by the buds from the fruiting tree, but not by the apomictic seeds of the fruiting tree.

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