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THE JUVENILE CHARACTERS OF TREES AND SHRUBS

TREES and shrubs during their life cycle pass through the stages of embryonic differentiation, juvenile development, maturity and old age. They do not produce flowers while in the juvenile stage, and even after attaining sexual maturity they may pass through a period of adolescence before settling down to reproduction. Maturity, accompanied by heavy fruiting, usually results in the spreading posture of middle age. Trees and shrubs do, however, continue reproduction into old age and often fruit heavily as they near the end of their life span.

The juvenile stage often differs from the mature form in morphological as well as physiological characters. An outstanding example is the English Ivy, *Hedera helix*. The seedlings have lobed leaves on a trailing stem with aerial roots and produce no flowers, while the adult form has a more compact erect form of branching, no aerial roots, entire leaves and produces flowers. Cuttings from the juvenile form produce juvenile forms while cuttings from the adult form produce compact bush-like forms. In Pecan seedlings the leaves are entire, while the adult form has compound leaves. In some varieties of ornamental apples the seedlings have tri-lobed leaves as juveniles, but entire leaves at maturity.

In some species juvenile forms may persist throughout the life of the tree. The outstanding examples are the Retinisporas, the juvenile forms of *Chamaecyparis* and *Thuja*. These permanent juvenile forms are so unlike the typical forms that they were classed under a new genus, *Retinispora*, by the early botanists. Because of their feathery foliage they are highly prized as ornamentals. Most of the juvenile forms are dwarfs, but *Chamaecyparis pisifera squarrosa* is nearly as large as the normal species. The juvenile form is propagated by grafting or by cuttings. The adult and juvenile branchlets, taken from adjacent trees which were planted in the Arnold Arboretum more than 60 years ago, are shown in figures 1 and 2.

The juvenile forms of *Chamaecyparis* and *Thuja* are readily propagated by cuttings, whereas the adult forms are more difficult to root. Occasionally a normal

tree will revert to the juvenile form and these juvenile branches root more readily than do cuttings from the adult tree. Transitions of the juvenile to the adult form in some branches commonly occur in many Retinisporas as the tree becomes older, but in *C. pisifera squarrosa* the juvenile form is maintained completely, even in trees more than 60 years old. The juvenile varieties rarely set seed.

Permanent juvenile forms are also found in *Picea*. In 1904 Professor J. G. Jack of the Arnold Arboretum staff collected seedlings of *Picea glauca* near Banff in Alberta, Canada. These were planted in the Arnold Arboretum and one of them proved to be a dwarf type and was given the varietal name *conica*. It was propagated vegetatively and widely distributed as an ornamental. Eight of these trees were planted in the Arnold Arboretum collection of dwarf conifers in 1922. They are now beautiful compact trees less than 10 feet tall and have never produced cones. Branchlets of the normal *Picea glauca* and of the dwarf variety *conica* are shown in figures 3 and 4.

The juvenile forms of certain shrubs have more attractive foliage and growth habits than do the adult specimens. An excellent example is found in the Chinese Lilac, *Syringa laciniata*. The young seedlings have compact lobed leaves closely spaced on the branch, while the mature shrub has more widely spaced, partially lobed or entire leaves, as is shown in figures 5 and 6.

We have tried to maintain the juvenile form of *Syringa laciniata* by selection of seedlings and by grafting juvenile forms on other rootstocks, but without success. If permanent juvenile forms were obtained it is probable that they would not flower, but a permanent juvenile form of this lilac would be of value for its ornamental foliage.

The 'Arnold Dwarf' Forsythia possesses several juvenile traits. The slender drooping branches root easily in contact with the soil and it is late in flowering. The original seedling did not flower until it was eight years old and cuttings, even from flowering specimens, are slow to flower.

Trees propagated from buds or scions of young seedling trees are slower to produce fruit than those propagated from mature fruiting trees. In our experiments the genetic variability of seedlings was controlled by using apomictic seedlings of a Sargent apple hybrid. Trees from buds of branches of the fruiting hybrids fruited in four years, while trees from buds of the young apomictic seedlings did not fruit until six years old. The earlier flowering of the bud progeny of mature branches is attributed to a flowering hormone which is present in the fruiting branches but which is not present in the young apomictic seedling. Apparently the hormone is transmitted through the bud, but not through the seed of the mature tree.

The long juvenile period in tree seedlings is a great handicap in breeding fruit and ornamental trees. According to Knight, pear seedlings do not usually fruit until twelve to eighteen years old, and apple seedlings seldom fruit before five to twelve years. Knight did not believe that there was any method of shortening

the juvenile stage. In 1806 he wrote as follows: "When young trees have sprung from the seed, a certain period must elapse before they become capable of bearing fruit, and this period, I believe, cannot be shortened by any means."

J. C. Louden, however, believed that seedlings could be induced to fruit earlier if grafted onto fruiting trees. This method, still widely used by horticulturists and foresters, was described by Louden in 1842 as follows: "A seedling apple, if grafted the second year on the extremities of a full-grown apple tree, or even on the stock or young tree of five or six year's growth, will show flowers the third or fourth year; whereas, had it remained on its own root, it would probably not have come into flower for ten or twenty years."

The grafting of young seedlings on the branches of mature fruiting trees might be expected to induce earlier fruiting since the fruiting hormone of the mature tree might be expected to pass into the seedling scion and hasten fruiting. Although this is a common technique among tree breeders there is no conclusive published evidence to support the idea that this method will promote earlier fruiting. Several forest tree breeders have stated that seedling conifers grafted on branches of mature trees will produce cones in several years, but the evidence has not yet been published.

The controversy still continues. Kemmer of Germany is the leading advocate of shortening the juvenile stage by checking the growth of the seedling. This he does by root-pruning, girdling, or grafting the seedling apple on dwarfing rootstocks. Another German experimental horticulturist, Fritsche, found little if any shortening of the juvenile stage by checking the growth of the young seedling. In our experiments with ornamental apples we have been able to curtail the growth of the seedlings by tying knots in the stems, but the treatment does not induce earlier flowering.

There is evidence that the juvenile form of English Ivy produces a substance that will induce juvenility in the adult type. A juvenile scion grafted on an adult type induced the adult plant to develop some juvenile leaves. Frank and Renner in Germany grew juvenile and adult forms together in a nutrient solution and some of the adult shoots reverted to the juvenile stage. More recently, Robbins of the New York Botanical Garden induced juvenile shoots on adult plants of English Ivy by treating the mature plant with gibberellic acid. Whether the gibberellic acid acts directly or indirectly as a juvenile inducing agent is not known.

It has long been known that cuttings taken from young seedlings root more readily than do cuttings from the tops of mature trees. This behavior was first described by the German botanist Goebel in 1900. An extensive test made by Gardner at the University of Maryland in 1929 showed that cuttings from one-year-old seedlings of apples, pears, cherries, elms, locusts, pines and spruce rooted easily but that rooting ability declined rapidly with the age of the seedling. Cuttings from mature trees rooted with difficulty. Similar results have been found by other horticulturists.

DESCRIPTION OF FIGURES ON PLATE I

Figure 1. *Chamaecyparis pisifera*, the Sawara False Cypress.
Branchlets from a tree planted in the Arnold Arboretum in 1891, showing the foliage of the normal mature tree. This tree produces abundant seeds.

Figure 2. *Chamaecyparis pisifera squarrosa*, the juvenile form of *C. pisifera*.
Branchlets from a tree planted in the Arnold Arboretum in 1894, showing the juvenile foliage. The tree, although about the same age and nearly as large as the normal species, has rarely, if ever, produced seeds.

Figure 3. *Picea glauca*, the White Spruce.
Branchlet from a tree planted in the Arnold Arboretum in 1874.

Figure 4. *Picea glauca conica*, a dwarf form of White Spruce.
Branchlet from a tree planted in the Arnold Arboretum in 1922. These trees have never produced cones.

Figure 5. *Syringa laciniata.*
A terminal branch of a three-year-old seedling showing the mature, partially lobed or entire leaves.

Figure 6. *Syringa laciniata.*
A branch from the base of the same seedling, showing the typical juvenile leaves.

Figure 7. *Malus* hybrid.
Leaves from the upper branches of a mature fruiting tree. The leaves are entire or only slightly lobed. The young seedlings had tri-lobed leaves.

Figure 8. *Malus* hybrid.
Leaves from a sucker shoot which developed from the base of the same tree. These tri-lobed leaves are of the juvenile type, showing that the juvenile trait is retained at the base of the tree.

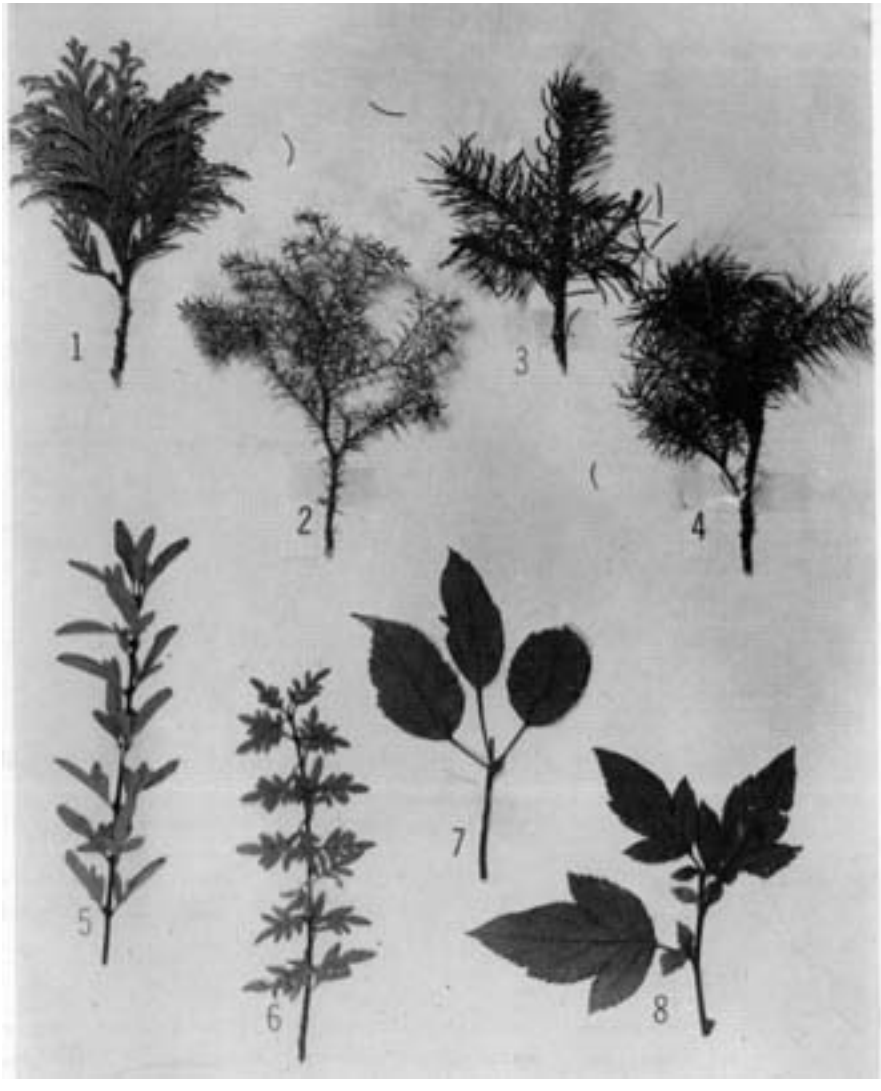

PLATE I
Some juvenile foliage forms.

It has also long been known that the base of the tree remains in the juvenile stage even in a mature tree. Nearly one hundred and fifty years ago Thomas Andrew Knight in England took scions from basal suckers and from the fruiting branches of an old seedling pear tree and grafted them on pear seedlings. The scions from the basal shoots produced trees which were more thorny and fruited later than those from scions from fruiting branches.

An outstanding example has been described in a recent letter from F. E. Gardner as follows: "We have in Florida many old seedling orange trees, some over a hundred years old. Cuttings from the tops of these trees of course root with great difficulty and have long since outgrown any juvenile characters such as thorniness. We frequently get, however, sprouts from adventitious buds appearing from the roots or from low on the trunk. These revert to their juvenile character and are very thorny and will root from cuttings with considerable ease."

The ease of rooting of stump sprouts of the Honey-locust has been described by Stoutemyer and others at the Iowa Experiment Station. Cuttings from stump sprouts rooted readily, but it was very difficult to get any roots from cuttings taken from the terminal branches of the mature tree.

The retention of the juvenile stage at the base of the tree is well shown by the sucker shoots from the base of a Sargent apple hybrid. As a seedling the hybrid has tri-lobed leaves, like the Sargent parent, but as the tree develops to maturity the leaves become entire. If, however, a sucker shoot develops from the base of the mature tree, the leaves are of the juvenile type, as is shown in figures 7 and 8.

The seedling tree can be kept in the juvenile stage by cutting it back to the ground each year. This behavior of young apple seedlings was first described by Fritsche in Germany in 1948 and has been confirmed by Blair and his associates at the Central Experiment Farm in Ottawa.

This technique could be of value in breeding ornamental and fruit trees for propagation by cuttings. The hybrid seedlings could be tested for ornamental or fruit value, and the desired types selected could then be cut back to the ground level and readily propagated by cuttings. On the other hand, budding or grafting with buds or scions from the fruiting hybrid would hasten flowering and fruiting of the progeny.

Ease of propagation, delay in fruiting, and, in some cases, enhanced ornamental characters of leaf and growth habit, are associated with the juvenile stage of trees and shrubs. These relationships are of theoretical interest and of practical value to the horticulturist.

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