

REPRODUCTIVE BIOLOGY AS A FACTOR IN GENETIC IMPROVEMENT OF URBAN TREES

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In a recent paper (Barker 1986), I concluded that "Selecting (additional) non-fruiting individuals, getting clones of these produced, and planting them instead of fruit-bearing trees of the same species may be the best long-term solution to the problem of fruit litter of urban trees." This paper reports new information about the reproductive biology of various tree species as further insight into potential opportunities for selecting trees for urban uses that produce none or only a meager amount of fruit. Although species-specific, the information assumes similarities in other species.

American Sweetgum (Liquidambar styraciflua).

One of the assets of American sweetgum, a popular monoecious species, is its fall coloration. On the other hand, for the homeowner, its fruit are a dreaded nuisance. These are prickly, leathery spheres, slightly smaller than golf balls. Although the individual spheres are known as fruits, each of them is actually a multiple of fruits, normally originating from a stalked head of female flowers of an inflorescence. Additionally, a terminal segment of an inflorescence typically has several sessile heads of male flowers which abscise as a unit after pollen release.

An occasional sweetgum tree will also have atypical fruit of sessile, clustered spheres. Such fruit develop from inflorescences having female

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flowers, exclusively, in both the sessile and the stalked heads of flowers. These sessile fruit persist on the tree for several years, much longer than stalked fruit. Clusters of sessile fruit may be found on trees as small as 5-gallon stock sold by nurseries. Despite the uniqueness of such a reproductive anomaly, the inevitable buildup and unattractiveness of fruit in the crown makes this tree particularly unsuited for landscape use.

Conversely, some inflorescences on a tree may have male flowers exclusively and, therefore, no fruit. Obviously, such a tree would be a likely candidate for cloning as a non-fruiting selection of American sweetgum, provided, of course, the trait is stable.

A novel American sweetgum known as Liquidambar styraciflua 'Rotundiloba' (Santamour and McArdle 1984) may be fruitless for still another reason. This naturally occurring anomaly, with rounded instead of pointed leaf lobes, was found in a stand of mixed hardwoods near Cameron, North Carolina, more than 50 years ago (Barker 1986). Six ramets of this phenotype, each about 20 years old, are growing at a tree test site in San Jose, California, maintained by the Saratoga Horticultural Foundation. In spring 1988, these trees had only rudimentary inflorescences. On some trees these rudimentary inflorescences had either predominantly male flowers or male and female flowers, intermixed. On one tree the inflorescences had female flowers exclusively. Because no fruit had been previously observed on trees of this phenotype, the inflorescences were presumed to have aborted before fruit development.

In summary, American sweetgum may have any of the following types of reproductive organs:

1. Normal inflorescences (stalked heads of female flowers and sessile heads of male flowers)
2. Anomalous inflorescences
 - a. Female flowers only

- b. Male flowers only
- c. Rudimentary inflorescences
 - (1) Female flowers only
 - (2) Male flowers only
 - (3) Female and male flowers intermixed.

The potential, therefore, for developing non-fruiting American sweetgum trees is through (1) selection of trees with male flowers exclusively, (2) selection of trees with rudimentary inflorescences that fail to develop fruit, and (3) selection of trees resulting from controlled crosses, using pollen from rudimentary inflorescences, provided it is viable.

Regardless of the method of selection, the stability of reproductive traits would need to be determined. Contrary to our common understanding, individual trees of a particular species may be unstable as to their reproductive biology, as has been shown for numerous species, including the dioecious ginkgo (Ginkgo biloba) (Santamour et al. 1983) and the monoecious canyon maple (Acer grandidentatum) (Barker et al. 1982).

Canyon Maple (Acer grandidentatum).

Canyon maple, a species closely related to sugar maple (Acer saccharum), typically has inflorescences that contain both male and female flowers. Yet, in a study of 24 native, mature trees in Utah during two consecutive flowering years, only about half of them showed normal monoecy. About one fourth of the trees were androecious, with male flowers only, and therefore fruitless. On the other hand, sex expression was flexible in the other one fourth of the trees. They had male flowers 1 year and both male and female flowers (and fruit) the other year.

Why, such flexible sex expression? An answer may be inferred from results of experiments in 1987 and 1988 on California buckeye (Aesculus californica).

California Buckeye (Aesculus californica).

California buckeye, a monoecious species, inhabits the foothills of northern and central California. Unique to this species is its customary defoliation in early July and exceptionally early leafing out in spring. These adaptive traits enable it to survive the rigors of virtually no summer rainfall. The species may be useful in urban areas but, like American sweetgum, its fruit, which are round and slightly larger than golf balls, would be a nuisance.

California buckeye flowers are borne in racemes 6 to 10 inches long. Each raceme has 100 or more male flowers and, near the apex, a few bisexual flowers. The latter are visually recognizable by a single pistil that protrudes prominently beyond the petals. However, the gender of California buckeye flowers is not fixed. In March 1987, when the raceme stalks of this species had elongated to about their ultimate length but the flowers were still in bud stage, I shortened several of the stalks to about one-half their original length. The remaining portion of stalk typically would have only male flowers. When the flowers of these shortened stalks opened, they showed evidence of a qualitative factor influencing gender expression. A few of the flowers near the apex of the shortened stalk that typically would have been male were bisexual, in the same relative location of bisexual flowers in whole inflorescences. Similar response has been observed by Benseler (personal communication) who has extensively studied the reproductive biology of this species (Benseler 1968).

Although not yet tested, this qualitative factor could be the plant hormone, cytokinin, which has been shown to cause cell division in pistillate tissue of typically male flowers of two unrelated plant species (Negi and Olmo 1966, Jong and Bruinsma 1974). Cytokinin is known to be synthesized in the

roots of plants, and this synthesis is suppressed under drought or other adverse environmental conditions (Torrey 1976).

As cytokinin is translocated into the inflorescence stalk and into the individual flowers, perhaps it accumulates primarily in the most distal flowers. A critical concentration of this substance may stimulate cell division in the pistillate tissue, and the flower, which typically would become male, develops bisexually. If this is true and the substance is a finite quantity, there should be an indirect relationship between number of flowers in an inflorescence, as represented by stalk length, and number of bisexual flowers. To test this hypothesis, in spring 1988, I shortened 30 inflorescence stalks to 66 and 33 percent of their original length when they were at the same stage of development as in 1987. The results were dramatic: the shorter the stalk, the greater the frequency of bisexual flowers on it (Fig. 1).

This quantitative relationship may account for the aforementioned production of only female flowers in some inflorescences of Liquidambar styraciflua. Such trees may be capable of synthesizing exceptionally large amounts of cytokinin or other hormones that promote development of pistillate tissue of flowers which otherwise would develop as male.

These findings suggest the need for further research:

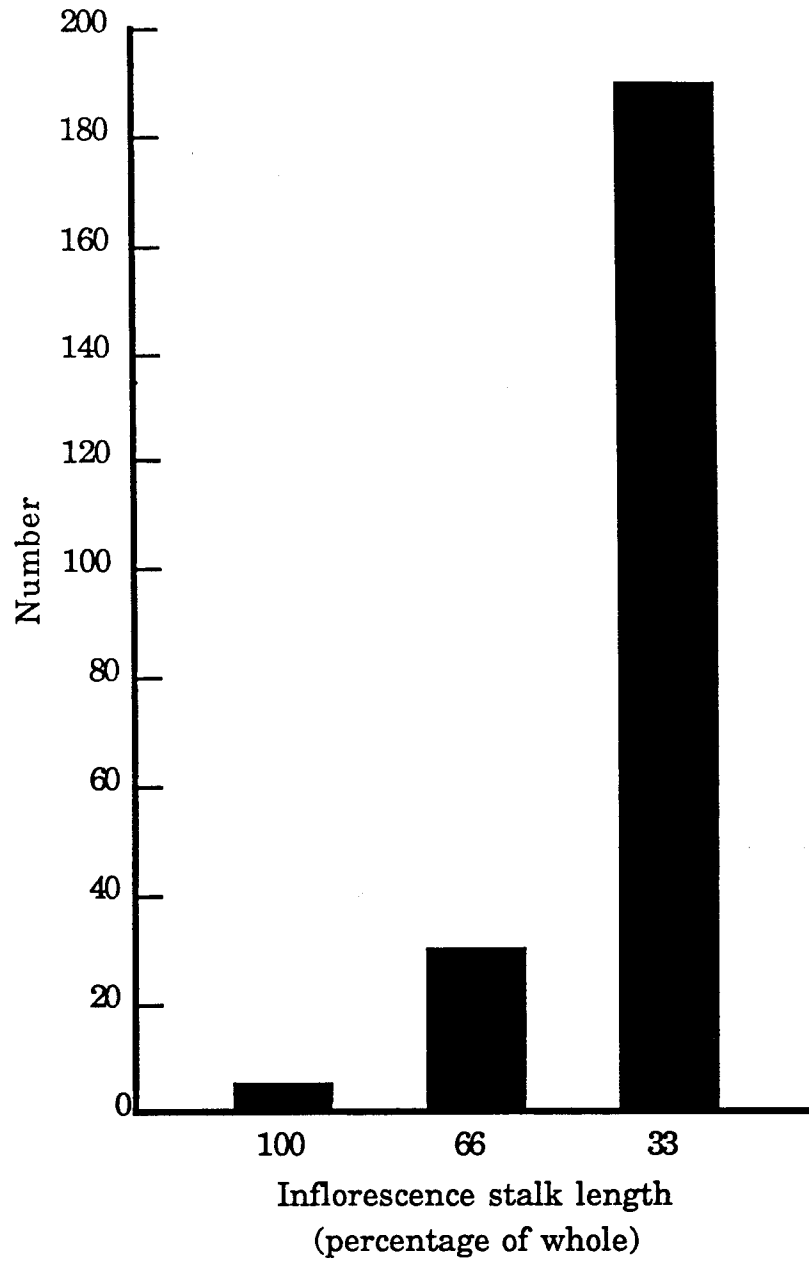
1. Chemical analysis of female-developing and male-developing flowers of California buckeye or any other species with similar reproductive biology, to determine, if possible, what substance or substances may be promoting development of female flowers.
2. Selection of trees found to be deficient in this substance to determine whether any female flowers are produced.

Besides selecting for fruitlessness based on flower anomalies, selection may also be based on absence of flowers or else their scant production, as exemplified in European hornbeam.

European Hornbeam (Carpinus betulus).

So popular is the very narrow upright or fastigate form of European hornbeam, in terms of its nursery production, that the species, itself, has become stereotyped. But in reality, this monoecious species is highly variable in crown character, including fastigate, pyramidal, globular, and spreading forms. Whatever the form, this species could rank among the best for use in cities, save for the flowers and fruit it may produce. Male catkins develop in spring before leaf bud expansion. Female catkins develop along with the opening of the leaves. Some trees have exceptionally heavy yields of catkins of one or both genders, others moderate amounts, and a few, particularly the fastigate forms, meager amounts. Observations from 1983 to 1988 of 50 trees of this species planted in 1965 in Davis, California, have revealed that one tree, notable for its wide-spreading crown, has produced neither male nor female catkins. It is a candidate for introduction as a non-fruiting clone.

In conclusion, individual trees devoid of flowers and/or fruit may exist for any species, awaiting discovery through meticulous, long-term observation of large populations, either in natural stands or along urban streets. Finding, producing, and using such trees may be the best way to reduce the problems of fruit litter in cities.



Caption

Figure 1.--Number of bisexual flowers in 30 inflorescences (5 inflorescences per tree x 6 trees) for each of three stalk lengths of Aesculus californica (California buckeye).

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