SOME INTERESTING ASPECTS OF FLOWER MORPHOLOGY AND FLOWER ECOLOGY OF VARIOUS FOREST TREES

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Every forest tree breeder who has worked on flower morphology and flower ecology knows that, particularly in hardwood species, the subject is quite complicated. Besides this normal complexity, many exceptions from normal conditions found in a certain species or genus may occur. In a few cases it is incorrect to speak of normal conditions because, as we will see later on, it is not possible to define what is normal.

Silviculturists very seldom observe these conditions because they are less interested in flower morphology and ecology than other aspects of tree growth. Secondly, studies can only be made during a short time in the spring, and thirdly, these studies are difficult to carry out since most flowers are located in the tops of the trees.

It is not my object to present the various types of irregularities. By this I mean, for example, flowers which are normally unisexual but have rudimentary parts of the opposite sex. The frequency of occurrence of such a phenomena is usually less than 1 in a 1000. hat I would like to present this morning are some observations that I have made in the last 4 or 5 years while studying trends in flower evolution. Most of my observations are based on European forest trees--and some species native to this country.

Our forests are predominantly of either conifers or hardwoods. The structure of their flowers are quite different, as everyone knows. During this study only a very few cases of irregularities in coniferous flowers were observed such as androgyn[1] conelets. In checking the literature only relatively few cases are mentioned where exceptions to the rule have occurred. The coniferous flowers seem to be very stable.

In comparison, the situation in our hardwoods is much more complicated. Some species are so variable that it is sometimes difficult to observe their sex or to call a flower male, female, or bisexual. Willows, poplars, green ash and box-elder for instance, are tree species which are normally dioecious; that is, trees on which only one sex is present. It has been known for many years however, that all trees in these genera or species are not fully dioecious. Cases are known where male and female parts appeared in the same flower. Exceptional flowers in which male and female parts occur together are called androgynous. Runquist (1951) was, as far as I know, one of the first to report a Populus tremula (European Aspen) on which the catkins showed both male and female seg ments. Seitz (1952, 1953) and Schlenker (1953) reported a similar condition, and also reported finding catkins that had perfect flowers. Schlenker (1953) re ported five different sex types: (1) Pure female plants; (2) strong female plants, weak androgyn; (3) pure male plants; (4) strong male, weak androgyn; (5) strong androgyn plants.

[1]For terminology see Glossary, p. 75.

Pauly and Mennel (1956) found, among 206 quaking aspen trees, 71.8 percent male or predominantly male, and 28.2 percent female or predominantly female trees; in other words a ratio of about 3 to 1. Of the 148 male trees, 142 had unisexual flowers (96 percent) but 6 (L percent) had bisexual flowers. Of the 58 female or predominantly female trees, 46 had unisexual flowers, but 12 (20.6 percent) had bisexual flowers. This means that in the female, or predominantly female, quaking aspen trees, the percentage of trees with bisexual flowers is higher than in male or predominantly male trees.

Seitz and other investigators believe in a so-called bisexual tendency in some of our poplar species. Seitz goes a step further when he states that at least aspens apparently are at the end of an evolution from monoecy and hermaphroditism to dioecy. Of practical importance is the fact that such trees can be inbred as has been done by Seitz and others. One tree of F. tremuloides with androgynous catkins was discovered last year near Syracuse by Valentine ; he is planning to initiate an inbreeding program next year.

Applying the designations developed by Correns (1912) (G stands for female sex power and A stands for male sex power) we get by phenotypic sex determination the formula AG for the haploid phase and AAGG for the diploid phase. The sex of the trees mentioned above is determined by that sex which expresses itself most powerfully. Since we generally assume that the sex power is not genetically determined but rather influenced by environmental factors, it is understandable that sexuality may vary from year to year or can be changed artifically, as is done successfully in some agricultural plants.

In the following pictures[2] I will show catkins of European paper birch in which one section of the catkin became male and the other female. As far as the behavior of these catkins is concerned, it is of interest to note that if the male part is greater than the female part the whole catkin reacts as a male, which means that it looses its turgor pressure and is thrown off early by the tree. If the female part is greater it will react as a female and remain on the tree until the seeds are ripened.

The situation, at least in some dioecious tree species, is not as simple as it seems to be, since androgyn flowers occur more often than we think. Therefore, from the scientific point of view it is not completely correct to call all aspen or other poplar species dioecious. Autotriploid aspen may be due to a parent tree with androgyn flowers and resultant inbreeding. Unreduced pollen grains would be another possibility.

The genus Fraxinus as a whole is called polygamous, that is, generally speaking, many different sex conditions occur. Let us consider first one particular species: F. excelsior (European ash). By studying the flowering conditions we will obsevehe f o lowing: (1) all male; (2) all female; (3) male and female flowers; (4) perfect flowers; (5) perfect plus male flowers; (6) perfect plus female flowers. According to Rohmeder (1952) who investigated 494 trees in the vicinity of Munich the following percentages were found: 39 percent male; 4 percent female; 1 percent separated male and female flowers; 41 percent perfect flowers; 11 percent perfect and male flowers; 4 percent perfect and female flowers.

[2]Reference is to slides used in the presentation of this paper. Editor.

Considering these results we must say that most of the trees, at least near Munich, are hermaphrodite or male; pure female trees are rare. In other words the male sex is predominant. The situation of the entire genus *Fraxinus* is similar to the condition of F. excelsior. Referring to Rehder (1956), in the 30 species he mentioned, the followingsex conditions occur: species with perfect flowers; species with male or female flowers; or species which are polygamous. Since in the majority of cases in *Fraxinus* the trees are polygamous, the male sex seems to be predominant.[3]

In addition to the sex conditions in the genus I would like to mention that some species are wind-pollinated and others are insect-pollinated. However, we occasionally see insects on the wind-pollinated trees as for example on F. excelsior as the male flowers still produce nectar. On the other hand there are a few species which are entirely pollinated by insects such as *F. ornus*, a shrub species from southern Europe.

Considering all the facts, we believe the genus Fraxinus is in the process of evolution. Based on F. excelsior this process of evolution is proceeding in this manner: (1) from hermaphroditism to unisexual flowers; (2) from monoecy to dioecy; (3) from insect-pollinated to wind-pollinated trees. Since the genus tends to be overwhelmingly male it is interesting to note that F. ornus, although still insect-pollinated, produces tremendous amounts of pollen, which leads to the conclusion that this species is in the process of evolving from insect to wind-pollination, a stage which has already been reached by most of the other species in the genus. This has the following practical aspects:

1. When selecting trees of the genus Fraxinus for breeding purposes (seed orchards, etc.,) we have to determine their sex conditions very carefully so that both sexes are available for hybridization.
2. Sex dimorphism is also present. It expresses itself in that the male trees in general grow faster than all other trees not purely male. (Generally speaking female flower production and subsequent seed produc tion draws more heavily on food reserves of the tree than does pollen production.)
3. Thinning a stand of ash will take out most of the smaller trees which are female or hermaphroditic trees, leaving mostly male trees. From the silvicultural point of view this would lower the reproductive power of the stand.

According to Rehder (1956) there are about 115 different maple species in the world, most of them shrubs or bushes. Anyone who has studied the flowering conditions of any maple may be confused by the variety of forms that the flowers take, and by the many varying sex conditions which can exist. Concerning the sex condition in the genus as a whole we find stated the following:

1. Monoecious tree species (unisexual flowers on the same tree).
2. Dioecious tree species (unisexual flowers on different trees).

[3] Besides *Fraxinus excelsior* I studied the sex conditions of F. *ornus* and F. *angustifolia*.

3. Andro-monoecious tree species (staminate and bisexual flowers on the same tree).
4. Andro-dioecious tree species (staminate and bisexual flowers on different trees).
5. Andro-polygamous tree species (staminate and bisexual flowers are either on one tree or on different individuals within the species).

Of all the Acer species mentioned by Rehder (1956), 8 can be monoecious, 7 are usually dioecious, 8 can be dioecious, only 1 can be andro-monoecious, 5 are andro-dioecious, 5 can be andro-dioecious, 31 are usually andro-polygamous and 4 can be andro-polygamous.

In the two most important European maple species, Acer *plantanoides* and *A. pseudoplatanus*, the male flowers are actually male, no complete pistils visible. The female flower, however, has both pistil and stamens; therefore, from the morphological point of view it is a perfect flower, but not from the physiological point of view. The stamens remain short and the pollen is not disseminated because the sacs remain closed. If we wish to split hairs we might call the male flower perfect because a rudimentory pistil is present in the bottom of the corolla. This would indicate that at one time this flower was also perfect.

The process of blooming is also very complicated. Yale and functional female flowers in the panicle open at different times, beginning usually with a male flowering period followed by a female flowering period and ending again with a male flowering period. This sequence minimizes the possibility of inbreeding.

Both A. plantanoides and A. *pseudop*latanus are insect-pollinated. A. platanoides flowers early, sometimes as early as the middle of April; A. pseudoplatanus flowers 3 to 4 weeks later, when conditions for insect-pollination are much better. This results in A. *pseudoplatanus* being very common in European mixed hardwood stands, whereas A. *platanoides* makes up only 5 to 15 percent of the total maple reproduction.

Returning to what I mentioned before of evolutionary tendencies, in maple the development trend seems to be in this direction: from monoecy to andro-monoecy, to andro-polygamy, to andro-dioecy, finally to dioecy; or more simply that most of our maple species are still evolving. The general trend as far as the genus is concerned seems to be from monoecy to dioecy if we exclude the various intermediate stages. The trend is also from bisexual flowers to unisexual flowers, a line of development which I have discussed in the genus *Fraxinus*, specifically in F. excelsior. A similar trend also exists in Populus as was pointed out in the beginning. Let me conclude by making the following more or less general points:

1. Host of our coniferous species are very stable, at least as far as flower morphology and flower ecology are concerned. Irregularities are seldom found; and we may assume, considering their age, that they have reached the ultimate in their development.
2. In contrast to our conifers, many of our hardwood genera are highly unstable in both flower morphology and ecology. There are certain species within some genera and entire genera which appear to be stable, but which upon more intensive examination are found to be not so stable; for example certain poplars and willows.

3. Examples of highly unstable genera are Acer, Fraxinus, and Ulmus. The genera Betula, Alnus, Populus, Quercus and Fagus seem to be somewhat more stable.
4. From the point of evolution it is interesting to observe in the genera Fraxinus, Acer, and Populus, a tendency from monoecy to dioecy, and from bisexuality to unisexuality.
5. A point of ecological evolution seems to be the tendency for insect-pollinated trees to become wind-pollinated, which is found in certain species of Fraxinus and Ulmus.
6. In all species mentioned above the male sex is predominately expressed.
7. Some of the practical considerations of these statements are as follows:

   a. In selection, the sex conditions of all trees of the genera mentioned must be carefully studied if they are to be used in breeding work. This concerns in particular exotic species of which not too much is known; and deviations from what is told in dendrology text books can be expected.
   b. Silviculturists should become more interested in flower morphology and ecology since therein may lie some causes for the lack of natural reproduction in a given stand.
   c. Since autotriploid poplar material can be the result of androgyn flowers, more intensive study of poplar flowering should be of interest, if we seek autotriploid material.
   d. There may be relations between flower morphology, ecology, and hybridization technique, which would result in better, faster, and easier crossing or inbreeding procedures.
   e. Since the genus Populus can be assumed as one with a bisexual tendency, should be able to change the sex conditions of its trees. As far I know, nobody has done such experiments; they should be started immediately.

Glossary

Andro-dioecious. Staminate and bisexual flowers on different plants.
Androgynous. Flowers with both staminate and pistillate in the same inflorescence (Androgyn) (for example in the same catkin).
Andro-monoecious. Staminate and bisexual flowers on the same plant.
Andro-pogygamous. Staminate and bisexual flowers whether on the same plant or on different plants.
Autotriploid. An individual having 50 percent more chromosomes than a regular diploid plant of the same species. (3x)
Dioecious. Staminate and pistillate flowers on different plants.
Hermaphrodite flowers. Perfect flowers.
Monoecious. Unisexual flowers of both sexes on the same plant.
Perfect flowers. Flowers having both stamens and pistil; bisexual.
Pistillate flowers. Flowers having a pistil but no stamens.
Polygamous trees. Trees bearing unisexual and bisexual flowers on the same plant.
Staminate flowers. Flowers having stamens but no pistil.

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DISCUSSION

GABRIEL. As you know, we have what is known as tolerant and intolerant species; for example, hemlock vs. loblolly pine. In your opinion, do you think there is any relationship between efficiency in photosynthesis and tolerant and intolerant species? In other words, is there any relationship in photosynthesis and the degree of tolerance in different pine species?

BOURDEAU. One of the basic causes of shade tolerance may be, but not always is, a greater photosynthetic efficiency in weak light. Tolerant species are expected to have a lower compensation point and lower light saturation intensity. There are other points to consider; mutual shading for instance. Individual leaves of intolerant species may very well be quite efficient in weak light but the tree as a whole may not, due to the arrangement of the leaves which shade each other. Another point is that of adaptation to light intensity. Shade grown leaves, of intolerant species, may be as efficient at low light intensity as sun-grown leaves of tolerant species.

GABRIEL. I was referring to species in general. What I was trying to bring out is that the difference between photosynthesis rates has no significance with regard to tolerance and intolerance of these particular species. In other words a tolerant species doesn't indicate that it is photosynthetically more efficient.

BOURDEAU. There is a relationship in many instances.

KRIEBEL. I am not sure I understood you on one or two points. I believe you said that Norway spruce was slower growing than Douglas fir. However, in the east, Rocky Mountain Douglas fir is not nearly as fast growing as Norway spruce. Since this is the Douglas fir which must be grown in this region, could you elaborate a little on the differences observed between Douglas fir and Norway spruce and how much you think environment and heredity might influence it?

BOURDEAU. I did not mean to say that Douglas fir is always faster growing than Norway spruce. The batch of seedlings grown in our nursery under a given set of environmental conditions happened to be faster-growing than the Norway spruce in the same nursery.

KRIEBEL. It is not absolute?

BOURDEAU. No. Both heredity and environment, past and present, determine the photosynthetic efficiency. For instance, red pine seedlings grown in the shade had considerably higher unit rates than seedlings grown in full light.

MARVIN. In your paper you were describing the very interesting section on efficiency. How about the count per unit per dry weight and the chlorophyll content?

BOURDEAU. Determinations of moisture content were always made. Differences in the same direction appeared when photosynthetic rates were expressed on a dry weight basis. As far as chlorophyll content is concerned, there was a correlation between it and unit rates of photosynthesis in the sun and shade grown pine seedlings but this is not always true.

MERGEN. Would it not be desirable to make measurements on seedlings of known ancestry which might be expected to be fast- or slow-growing, before growth differences actually appear?

BOURDEAU. Yes, indeed. I am very much interested in getting as much material as possible on fast-growing or potentially fast-growing seedlings of as many species as possible. For instance, it would be interesting to make some measurements on the Maryland white pine which Mr. Buckingham showed us yesterday.

BUCKINGHAM. How practical is this air-layering? Can I tell Christmas tree growers to use this method?

MERGEN. As in all work which deals with vegetative propagation, one has to familiarize himself with the technique. As a result, one will probably not obtain good results during the first year, but during successive trials the results should be good, especially since younger trees are used. The characteristics which make a Norway spruce tree desirable as a Christmas tree appear at a relatively young age. If a large number of air-layers are applied to a tree, it also acts as a pruning and makes the crown bushier.