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New Perspectives in Forest Tree Breeding

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IT IS GENERALLY ASSUMED that agricultural plant-breeding concepts and procedures must be adopted in breeding forest trees. These concepts and procedures are, of course, adapted to the materials and conditions of agriculture, which, in numerous respects, are fundamentally different from those of silviculture. As they are incapable of quickly producing practical benefits from tree-breeding work, the assumption has given rise to much skepticism regarding the practicability of breeding forest trees, and it has also delayed progress in tree breeding by causing resources to be expended on inefficient methods. In applying genetic principles to the improvement of silviculture, it is essential at the outset to recognize that the most effective procedure will be that which is best adapted to the materials and conditions of silviculture. Therefore, if proper perspective is to be gained, the problem of breeding forest trees must be viewed against a silvicultural background. Such perspective gives rise to new concepts which suggest a unique procedure capable of producing practical benefits very quickly. The concepts and the essentials of the procedure derived from them are briefly presented herewith.

In agriculture a high degree of genetic uniformity is deemed to be essential in the original stand of a crop. The general assumption that this basic premise is also axiomatic in silviculture leads to the following conclusions: (1) performance testing cannot be combined with crop production but must be conducted as a separate breeding operation; (2) if propagation is to be by seed, true breeding forms are required as parents; hence, (3) the progeny of a hybrid cannot be used; and therefore, (4) an area stocked with a hybrid must be replanted upon harvesting the hybrid.

These conclusions are logical, but the basic premise is not valid because the eventual loss of 90 per cent or more of an original stand, which would be ruinous in agriculture, is natural and beneficial in silviculture, which depends on close spacing to insure good stem form and on the gradual elimination of most of the stand through competition to accommodate growth in size. Thus, it is evident that genetic uniformity is not required in silviculture; in fact, it is seldom, if ever, encountered. Moreover, because of the impracticability of protecting forests from diseases and insects, it would be extremely hazardous in silviculture.

The fact that genetic uniformity is not required greatly simplifies and shortens tree-breeding procedure. For example, if increased rate of growth is the objective, performance testing can be safely combined with crop production by interplanting a promising new or selected population with the commonly used stock. In such a planting, the former will occupy every second or third or fourth, etc., row, depending on spacing and other considerations. Then, if it is adapted to the site and decisively superior to its competitor in rate of growth, it will gradually suppress and eliminate the latter, as well as some of its own weaker or less favored members, and it will occupy the site at maturity. In such an event, practical benefits will begin to accrue as soon as the stock is planted. If, however, the common stock is superior, it will occupy the site at maturity and nothing will be lost through failure of the new form. Finally, if the two forms are equal in vigor and adaptability, the final stand will consist of both, and the yield will be unaffected. Regardless of the outcome, a test will have been made without loss in productivity of the land. This method of testing also (1) provides a convenient means of testing materials on a large scale under forest conditions and (2) makes the most economical use of a superior stock, since fewer of its members will be sacrificed to accomplish the purposes of close spacing than would be the case if they were planted en masse.

The interplanting method of testing performance makes it possible to obtain practical benefits quickly from tree breeding provided superior trees can be produced rapidly in large quantities. Superior trees can be produced through selection or hybridization;

[1] Maintained by the Forest Service in cooperation with the University of California.

but heretofore selection has generally been regarded as the more promising method. Large-scale production of hybrids through controlled pollination has been suggested by several authors, but the general opinion regarding its difficulties, which is based largely on experience with angiosperms, has not justified optimism, and consequently the impracticability of the method has been tacitly or expressly assumed. This assumption is not necessarily valid, inasmuch as many of the most important timber-tree species are gymnosperms. Between the angiosperms and the gymnosperms there are fundamental differences in factors that affect crossability and fertility and hence the ease with which hybrids and their progenies can be produced in abundance. For example, double fertilization, which in effect may be a barrier to crossability (D. C. Cooper and R. A. Brink: *Science,* 1942, **95**, 75), is not encountered in the conifers. Moreover, chromosome mutation, which has been a prominent causative factor in the evolution of the angiosperms, appears to have been relatively unimportant in the evolution of the conifers, inasmuch as cytological investigations have shown that there is little or no variation among coniferous species in number, morphology, and behavior of their chromosomes (K. and H. J. Sax. *J. Arnold Arboretum,* 1933, **14**, 356). Hence, speciation in coniferous genera may be attributed mostly to gene mutation. From this it has been suggested that many species of a genus may not differ enough to prevent interspecific hybridization and relatively high fertility in the hybrids. In short, crossability among the angiosperms may be limited by genic and genomic differences between species, as well as by double fertilization, whereas among the conifers it may be limited for the most part mainly by genic differences between species.

Some years ago, in considering these and other differences between gymnosperms and angiosperms, it occurred to me that many fertile, coniferous hybrids could be produced readily and in large quantities through controlled pollination. This hypothesis had some support in the occurrence of natural hybrids, several of which were known to be fertile, whereas none were known to be sterile. Tests conducted at the Institute of Forest Genetics, Placerville, California, have since shown that the hypothesis is entirely tenable. For example, the number of sound seed obtainable per 1,000 pollination bags,[2] as judged by results of smaller tests, from 16 interspecific crosses in *Pinus* ranged from 5,100 to 238,500. From each of 10 of the crosses sufficient sound seed was obtained per 1,000 bags to produce enough seedlings (after deducting 40 per cent for failure to germinate, mortality, culling, etc.) to stock more than 100 acres when interplanted to every sixth row, or at the rate of 200 seedlings per acre in a spacing 6 feet by 6 feet. Progenies of several of these hybrids are already under observation in the nursery. These results are only indicative of the possibilities. Most of the crosses were made between single individuals of the parental species. Increased yields may be expected from including in a cross numerous individuals of the parental species and from improving techniques. Lower costs may be expected to result from economies incidental to large-scale operations.

The foregoing considerations, together with others to be presented later, indicate that certainly among the conifers, and possibly among the angiospermous trees as well, numerous interspecific hybrids can be produced in large quantities at reasonable cost through controlled pollinations. Both genetic theory and experimental results indicate that many of the hybrids will have a much greater rate of growth than one or the other of the parental species and that some of them will be more vigorous than both parents. They can therefore be used to increase timber production within the distribution range of the weaker, if not of both, parental species. The interplanting method of testing performance makes it possible to take advantage of their potentialities immediately and at a lower cost than if it were necessary to plant pure stands of improved varieties.

We are now in a position to consider breeding procedure. Since genetic uniformity is not required in silviculture, hybridization on a large scale, followed by the production of an enormous F_2 population from natural interbreeding among the hybrids, recommends itself as a highly practicable and effective procedure. Its essentials are as follows: Two species are crossed on a small scale to ascertain crossability. If hybrids are obtained, their vigor and form are tested by pitting them against the parental species in small nursery tests for two or three years. If the hybrids prove to be readily obtainable and of sufficient promise, they are then produced in quantity and interplanted with the common stock on the area to be reforested.

Assuming that the hybrid population proves to be adapted to the site, superior to its competitor in rate of growth, and satisfactory in other respects, the next step is to decide what to do about the succeeding crop. This will depend upon the hybrid's fertility, the growth rate of the more vigorous members of its progeny, and the ability of the latter to establish itself naturally. These questions can be resolved considerably in advance of harvesting by means of investigations of seed production and of ability of the F_2 generation to establish itself and by testing the vigor

[2] The seed-production phase of a thousand-bag breeding job on large trees requires from 30 to 45 man-days, depending on travel required and other circumstances.

of the latter in small experiments in the nursery and in plantations. If the results of such investigations are favorable, restocking of the area is left to the F_2 population. This population, which will exhibit great genetic diversity, will then be subjected to natural selection and, better still, resources permitting, to artificial selection also, since the great flexibility of silvicultural art makes such selection readily applicable. If the results are unfavorable, the area is replanted with the F_1 hybrid or, perhaps, a backcross of one of the parental species and the hybrid.

The concepts and derivative procedure presented herein, together with breeding results obtained in recent years at the Institute of Forest Genetics, provide a reasonable basis for stating that forest tree breeding can yield substantial practical benefits even more quickly, perhaps, than they are ordinarily obtained from breeding agricultural plants.

Technical Papers

The Property of Certain Calcium Silicates to Impart Supersaturation of $CaCO_3$ to Carbonatated Water Extractions

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The presently noted property of calcium silicates was observed in recent experiments that were prompted by certain carbonate *versus* silicate studies conducted at the Tennessee Agricultural Experiment Station in 1914–1916 (*4, 7, 8*). Although the efficacy of silicates of calcium as liming materials then was deemed primarily of academic interest, the utilization of such silicates in soil liming became a matter of practical importance when phosphate-reduction furnace operations brought substantial tonnages of slag that carries calcium silicate in the range of 80 to 85 per cent of $CaCO_3$-equivalence. When air-cooled, this slag is visibly crystalline; when quenched, it is a "glassy" material. When incorporated as the "unground" granulated by-product, and also as −20 + 60-mesh siftings, in the rate range between 2 and 40 tons per acre, the quenched slag proved highly beneficial to plant growth. But, when incorporated as −100-mesh screenings at rates beyond 5 tons per acre, the initial infertility resultant from the heavy incorporations of the 100-mesh quenched slag was succeeded ultimately by marked fertility, the rapidity of recovery being inverse to the increase in the rate of incorporation. In contradistinction, the mineral silicate, wollastonite, proved effective upon both the immediate and the subsequent plant growth, regardless of the fineness and the rate of the incorporations. Although the larger fraction of the detrimental input of slag-calcium had been converted from silicate to carbonate during the growth of the initial crop, the repressive effect upon plant growth was protracted. The transition of the heavily slagged soils from a state of virtual sterility to one of fertility was retarded by the periodically determined high alkalinity that prevailed during the persistence of the calcium silicate of the incorporated glassy slag. Progression in the carbonatation of incorporations of quenched slag in parallel with wollastonite and with limestone, all being −100-mesh, therefore was determined by subjecting the treated soils to a succession of analyses to determine $CaCO_3$ content. These analyses established the surprising fact that 40-ton, $CaCO_3$-

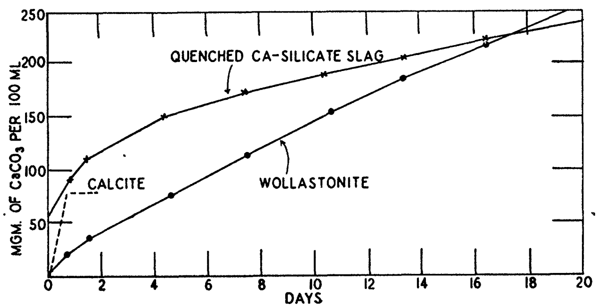

Fig. 1. Formation of calcium bicarbonate through progressive dissolution of certain silicates in carbonatated water (1 atmosphere of CO_2 at 30° C.).

equivalent incorporations of wollastonite remained uncarbonatated in the soil, upon which 9 crops had been grown in succession, although the corresponding incorporations of slag showed $CaCO_3$ cumulations of 30 tons per acre.

Since this protracted resistance of the wollastonite against carbonatation in the several soil systems was opposite to the expectancy pointed by the preceding studies of carbonatated water suspensions of carbonates and silicates (*4–9*), the presently reported carbonatated water digestions of wollastonite, slag, and calcite (and also limestone and precipitated $CaCO_3$) were made in an attempt to clarify the apparent anomaly. The results graphed in Fig. 1