THE ROLE OF TREE IMPROVEMENT IN THE NORTHEAST: A GENETICIST'S POINT OF VIEW

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TREE IMPROVEMENT has a restricted meaning for a geneticist. It means simply that whatever is to be improved will be improved by genetic manipulation of a population--usually, but not necessarily, by selection and breeding. Tree improvement may be defined in other ways, but this is the only definition relevant for a tree breeder.

In principle, any genome can be restructured. That is why there are public demands to restrict some kinds of genetic research. In practice, directed manipulation of DNA in higher organisms is not feasible. This is especially true of trees. How long this situation will persist is unknown. In a cynical moment, the President of the National Academy of Sciences remarked that an optimist was one who thought the future uncertain. A scientist who persists in science has to be an optimist in this sense; but for the next 10 years I foresee no dramatic change in tree-improvement technology. Practical genetic manipulation requires indirect approaches, principally, intervention in natural mating processes.

So genetic tree improvement for most species depends on sexual reproduction, though improved material need not be produced or distributed in the form of seed. It follows, then, that the importance of tree-improvement programs in the Northeast critically depends on the amount of plantable commercial forest land in this region. To illustrate why, consider the oversimplified case where product value is proportional to volume. A 15-percent genetic gain (in volume) will result in a 15-percent increase in product value if the entire acreage can be planted to the improved material. But if only 10 percent of the acreage can be converted, the gain in value is only 1.5 percent.

Unfortunately, it seems there is no useful estimate of the acreage of potentially plantable forest land by states or ownership classes in the Northeast. A ballon reproductive biology provide the basis for estimating space, time, and structural requirements of breeding programs for different species.

The natural mating system of a species profoundly affects its genetic structure. Since the breeder's objective is to assemble a population with a gene pool that maximizes the expression of desired characters without seriously impairing its capability to adequately respond to a normal range of environmental disturbances, where a species stands in the mating system continuum will determine how the plant breeder designs his program. And the breeding plan is a major determinant of the eventual cost of the program.

Considerable research is usually required to evaluate the genetic structure of a population, and it usually begins with a determination of the natural level of selfing. But there are a number of biological indicators that suggest the probable location of a species on the mating system continuum. And this is all the breeder needs to know to design his breeding program. Some of these biological characters are shown in Table 1, a summary of some reproductive and genetic characteristics of 15 Northeastern species (U.S. Forest Service 1974) that might be considered as candidates for tree-improvement programs. These species include eastern white pine (Wright 1970); red pine (Fowler and Lester 1970); pitch pine (Ledig and Fryer 1974); paper birch (Hutnik and Cunningham 1961); yellow birch (U.S. Forest Service 1974); sugar maple (Kriebel and Gabriel 1961); red maple (Hutnik and Yawney 1961); cottonwood (Schreiner 1971); white spruce (Nienstadet and Teich 1972); red and black spruce, eastern larch, trembling aspen, white ash, and northern red oak (U.S. Forest Service 1974).

The purpose of this summary is not to identify species that are easy or difficult to work with from a breeder's standpoint, but to provide a basis for appraising the probable cost of tree-improvement programs for various species.

Before leaving species choice I will offer an opinion on the number of species that should be included in a beginning program: one is best; two--possibly; three or more--don't do it. John Wright offered the same advice years ago, and the successful cooperative programs have tended to follow it. Without discussing the pros and cons of multispecies programs, I will simply observe that while it is always possible to add new species to a successful program, if it is necessary to drop one species because of a curtailment of funds or for some other reason, the time, effort, and money expended on that species is a dead loss to the multispecies program.

Selection of characters for improvement.--The choice of characters for improvement will be constrained by program and product objectives. Nevertheless such constraints will usually leave a number of characteristics for evaluation by the opportunity-analysis team. The forest geneticist can contribute importantly to selection of a near optimum set by knowing the heritabilities of each character considered, or having sufficient information to make a shrewd guess as to what they might be. Heritability information is important in this context because it provides a basis for estimating gain over a range of selection intensities. Since gain is on the benefit side of the ledger, and since costs and gains increase (but not equally) when selection efforts are increased, there is an opportunity for tradeoffs.

When the characters are considered in sets, the geneticist may be able to provide genetic correlation information or at least an assessment of the likelihood of genetic correlation. If two characters are highly correlated, selection for one also selects for the other to a high degree. Conversely, if traits are independent, the selection effort to find their chance combination must be enormously greater; in addition, the probability of the transmission of combined independently inherited traits to progeny will be reduced. Clearly, another set of opportunities for tradeoffs exists when characters are considered in combination.

Although heritability estimates are available for a number of characters (Campbell 1964; Hattemer 1963), judgment is required in their use, especially for program appraisal. Heritability estimates are a function of the test environment that generated them. Also, there has accumulated persuasive evidence that genetic variance (hence, heritability) changes with age (Namkoong and Conkle 1976). Consequently, the geneticist's familiarity with the program and his interpretation of how to use available genetic information in forming judgments are crucial to this phase of opportunity evaluation.

Current and prospective technology for genetic improvement of trees.--It is a common misunderstanding of forest managers and administrators that tree breeding simply consists of selecting super trees in natural stands, grafting them into orchards, and, after progeny testing, removing trees whose progeny grew poorly. In their opinion, the procedures for each step are pretty well standardized.

The clonal seed orchard approach (and it is only that, an approach for the production of first-generation improved seed) is far more complex than the process of selecting, grafting, and progeny testing described previously. There are also alternative approaches. At one time, the relative merits of alternative breeding schemes for producing first-generation improved material were vigorously debated. Today, forest geneticists appreciate better what we knew even then, namely, that the efficiency of a system is not necessarily proportional to its genetic merit. There are no clonal seed orchards of cottonwood, for example, because the improved material is not seed but cuttings; at the other extreme, there are few, if any, clonal seed orchards of oak, because as a group they are difficult to graft.

In addition to evaluating alternative breeding programs for the opportunity-analysis team, the forest geneticist can also indicate the most cost-sensitive components, and possibly procedures to minimize their expense without compromising effectiveness. First-generation selection and progeny testing are common components of most breeding plants. If it were possible to identify desired genotypes accurately, progeny testing would not be necessary. It is not possible to do so; consequently, the success and cost-effectiveness of the program depend on the effectiveness of first-generation selection (Porterfield 1974). Progeny tests require considerably more space than the populations that produce the test material. There is uncertainty about how long they must be maintained to yield results, but we do know the longer they run, the more expensive they become.

Currently, the operational principles of selection are to locate candidates expressing desired characters to the highest degree, and to attempt to maximize selection efficiency by considering in some fashion how the environmental situation affects character expression in the candidate tree. Since genes control the developmental processes that result in character expression, it follows that selection for processes rather than their end results should significantly improve selection efficiency, and suggest more sensitive and less costly progeny test procedures.

There are, to my knowledge, several opportunities for forest geneticists to select indirectly or directly for the process rather than the character. Shigometer readings, for example, have been related to tree vigor when phloem probes are used (Wargo and Skutt 1975). This instrument measures conductance, in this case, ionic strength in the phloem stream. Sap sweetness (sucrose concentration) may be realted to the number of elements in the rays of sugar maple (R. Gregory, personal communication). Variation in the photosynthetic rate in loblolly pine and other species is under strong genetic control, and it is related to dry weight accumulation (Ledig 1974).

Improved selection technology promises significant reductions in cost; it may also radically alter progeny , test procedures. To the extent that conventional progeny test space and time requirements are reduced, a substantial reduction in the cost of tree-breeding programs will have been achieved. Progeny testing for photosynthetic efficiency, for example, would seem to require a greenhouse-laboratory complex resulting in evaluations after 1 to 2 years rather than the conventional 10- to 15-year progeny test for vigor in different environmental situations.

I began by noting that technical difficulties associated with organized plant tissue were such that the likelihood of genetic engineering in plants, particularly trees, in the near future is vanishingly small. (But fusion of plant cell protoplasts has already been achieved!) (Carlson et al. 1972); in the case of trees, there is another kind of obstacle--the slow pace of cytogenetics research.

The NEW guidelines for DNA recombination research specifically prohibit "shotgun" experiments. Whatever restrictions are imposed eventually on genetics research, this stipulation is likely to stick--as it should. This means the experimenter must know the experimental genome and be able to state how he is going to change it. Geneticists and breeders have a fairly comprehensive cytogenetic knowledge of many organisms, including agricultural species--but not trees. Karyotype analysis of a few commercially important species and some polyploidy surveys are the extent of the information on forest trees.

Tree-improvement programs, by emphasizing the creation of superior populations to produce improved material, require plant breeders well trained in population genetics. But the accumulation of a pool of desirable genes in a foundation population has a fantastic quality, no matter how well designed the breeding program: the breeder knows neither the location nor the function of the genes he assembles in his superior population.

Cytogenetics and supporting research in molecular biology do not attract support because they are too fundamental and because potential breeding-program applications are not obvious. But these attitudes almost guarantee that tree-improvement programs will be locked into conventional, though ever more sophisticated,, plant-breeding programs.

Cytogenetics research, however, like process research (and at a certain point they become one) can also radically alter approaches to plant breeding. Again, it is a matter of operating much closer to the genome rather than the character level, with consequent advantages in reducing the time and space requirements for selection and progeny testing. Genetic screening has become a common phase; we understand it and its utility for fruit flies, agriculturally important plants, animals, and even humans, but not for forest trees.

SUMMARY

At this point many will feel that I have strayed so far from the subject--the role of tree improvement in the Northeast from a geneticist's viewpoint--that it is not worth the effort to return to it, or that I never intended to address the issue. The last statement is at least partially true because the role of tree improvement in the Northeast is part of a much larger question--the role of Northeastern forests for wood production (Manthy 1977).

But all of us must believe in the importance of wood production from the Northeast. On that basis, and trying to keep in mind R. Maynard Hutchins's comment that "the narrower the field in which a man must tell the truth the wider the area in which he is free to lie",[3] I have attempted to provide a general framework that would lead to tree-improvement investment decisions.

First, by making a crude estimate of the plantable forest land in the Northeast, I concluded that there is sufficient plantable land to support substantial tree improvement. But each situation requires its own appraisal. For preliminary planning, relevant information is available and it should be possible to assemble it quickly.

It would be naive to assume that an opportunity-appraisal analysis would actually be conducted as outlined in this paper. My point is that the geneticist can make a contribution in matters of species choice, selection of characters for improvement, and alternative technologies to achieve improvement goals.

The discussion of alternative technologies led to remarks on the potential of relatively new research--which I called process research--to reduce the cost of some components of breeding systems. And I concluded with a plea for more cytogenetics research on forest trees, because recent developments at the molecular level clearly foreshadow the need for far better information on the genetic structure of tree species than exists now.

I deliberately refrained from speculating on how a tree-improvement opportunity analysis for the Northeast might appear. There are too many circumstances; and tree-improvement programs require substantial investments (depending on the species, it is possible, however, to achieve modest levels of genetic gain with minimum investment or essentially a one-shot effort). So I will leave unanswered the implied question in the title of this paper. However the Northeast is the most densely forested region in the U.S.; it produces the poorest quality wood, and at a rate slower than most other forest regions. This situation, if nothing else, should be a considerable challenge to the skills of forest managers and scientists.

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FOOTNOTES

[1] Maine, New Hampshire, Vermont, Massachusetts, Rhode Island, Connecticut, New York, New Jersey, Pennsylvania and Delaware.

[2] Northeast Electronics Corporation, Concord, New Hampshire. The use of trade, firm, or corporation names in this publication is for the information and convenience of the reader. Such use does not constitute endorsement or approval by the forest service of the U.S. Department of Agriculture of any product or service to the exclusion of others that may be suitable.

[3] From "Science, scientists, and policy", a speech delivered in 1967 at a conference sponsored by the Center for the Study of Democratic Institutions, and the Civil Service Commission.

Table 1.--Biologic Characteristics, Relevant to Tree-Improvement Programs, of Some Northeastern Species

Species	Seeds				Pollen			Asexual propagation			Breeding characteristics			
	Collection unit	Seeds/unit	Storage	Periodicity	Quantity	Storage	Vector	Grafts	Buds	Cuttings	Natural regen. Asex/Sex	Floral[a] morphology	Incompatibility Cross	Incompatibility Self
			Years			Days								
Eastern white pine	Cone	20-40	10	3-10	+++	365	Wind	++	0	-	0	M	0	+++
Red pine	Cone	20±	30	3-7	++	365	Wind	+	0	-	0	M	0	+
Pitch pine	Cone	74±	11±	4-9	+++	912	Wind	++	0	+	+	M	0	+
Eastern larch	Cone	?	4	3-6	+	365	Wind	?	?	-	0	M	?	?
White spruce	Cone	34±	5	2-6	+	365	Wind	++	?	+	0	M	0	++
Red spruce	Cone	?	5	3-8	?	?	Wind	?	?	?	0	M	?	?
Black spruce	Cone	?	5	4±	?	?	Wind	?	?	?	+	M	?	?
Cottonwood	Catkin	800	0.5-1	1	++	30±	Wind	?	+	+++	+	D	0	oo
Trembling aspen	Catkin	3000	1	4-5	++	?	Wind	?	+	-	+++	D	0	oo
Paper birch	Catkin	?	2	2	-	20-48	Wind	?	?	+	+	M	?[b]	?
Yellow birch	Catkin	?	?	2	-	30±	Wind	?	?	+	+	M	?[b]	?
White ash	Inflor	20±	7	3-5	?	300	Wind?	?	+	?	+	D	?[b]	oo
Sugar maple	Inflor	60±	1-2	3-7	--	16	Insect	+	+	+	++	H-	-	++[c]
Red maple	Inflor	6	3	3-4	--	18	?	?	+	+	+++	H	?	?
Northern red oak	Fruit cluster	2-5	<1	3-5	+	?	Wind	-	?	+	+	M	?	?

[a] M - Monoecius; D - Dioecious; H - Hermaphrodite;

[b] Polyploidy known or suspected;

[c] Dichogamous.