APPROPRIATE TECHNOLOGY IN TREE BREEDING: GAIN WITH LESS PAIN

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Abstract.-- Appropriate technology principles can be applied to tree breeding strategies, incorporating needs of forest managers and silviculturists. The strategy of multiple populations with mass selection can be used to maintain genetic variability while obtaining gain from selection, at a low cost. The effectiveness of mass selection in plantations is reviewed. Increased local control is part of appropriate technology, and changes in roles of geneticists and other forestry workers are described. Appropriate technology can be applied with success to tree breeding in developed countries.

Additional keywords: multiple populations, mass selection, breeding strategies, gene conservation.

INTRODUCTION

The use of appropriate technology in tree breeding programs was discussed by Steiner (1986). As he stated, characteristics of such approaches involve close cooperation between silviculturists, geneticists, and nursery managers, using appropriate technology for a given species (rather than applying some standard tree breeding practices everywhere), and making investments proportional to the expected returns.

In a broader sense, as described by Darrow et al. (1981), appropriate technology includes tools and techniques that:
1) require only small amounts of capital;
2) emphasize the use of locally available materials, in order to lower costs and reduce supply problems;
3) are relatively labor-intensive but more productive than many traditional technologies;
4) are small enough in scale to be affordable to individual families or small groups of families;
5) can be understood, controlled and maintained by villagers whenever possible, without a high level of special training;
6) can be produced in villages or small metal working shops;
7) suppose that people can and will work together to bring improvements to communities;
8) offer opportunities for local people to be involved in the modification and innovation process;
9) are flexible, can be adapted to different places and changing circumstances;
10) can be used in productive ways without doing harm to the environment. The villagers of appropriate technology literature fill a similar role to the field forestry workers of developed countries.

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The possible ways that appropriate technology ideas can influence tree breeding programs are many. In this paper, I will describe one such approach to incorporating appropriate technology into an ongoing tree breeding program.

STARTING WITH AN UNDERVIEW: LOCAL NEEDS

> "Priorities should be arrived at less by overview than by an underview, grounded in the reality of the rural situation. Starting with rural people, their worldview, their problems and opportunities, will give a different perspective. To be able to capture that perspective requires a revolution in professional values and working styles... it requires humility and a readiness to innovate which may not come easily in many research establishments." (Chambers 1978)

One of the basic principles of appropriate technology is that of local control. Local foresters and silviculturists have the best knowledge of what they do and do not need, what will and will not work, and what levels of management are planned for specific forest sites. When problems are considered on a local basis, each area and organization has its own strengths to build on, its own unique set of problems, and its own culture or management philosophy. An appropriate technology must fit the culture rather than attempt to change the culture to fit the technology. Through the history of tree breeding, the implicit model has that of agriculture, with the implicit goals those of industrial forestry. Since forestry is extensive land management, compared to agriculture, and since forest ecosystems are both not easy to replace in a short period of time, and of critical importance to humans for other reasons than timber production, it may well be that the agricultural paradigm is not appropriate for multiple-use management. It may well be that a more extensive or naturalistic approach to management and conservation of forest tree gene resources is appropriate.

The following example is the application of the above principles of appropriate technology to the national forests in south-central Oregon. South-central Oregon is characterized by high elevations, a dry and cold climate, forest sites with moderate to low productivity, and management philosopy and economics which tend toward extensive, or naturalistic, forest management. Since natural regeneration is used as much as possible, seed needs in any given zone can be low. Also, silviculturists prefer to maintain species mixes which occur on any given site. Due to inadequacy of natural regeneration, and the desire to promote, for reasons of diversity, species that otherwise might not regenerate, there is always some level of planting. In some respects, the situation may be similar to areas or species of the north central or northeastern states. The following views are those of managers and silviculturists in south-central Oregon.

The first concern of management is that tree improvement programs be flexible to change. By the time the product of tree improvement is brought to market (20-40 years) at the first commercial thinning, conditions of all kinds can change. In south-central Oregon national forests, stumpage rates have changed drastically within the last ten years, land has been added to and deleted from the timber base, practices have changed from natural to artificial and back to natural regeneration. The mountain pine beetle and the western spruce budworm have changed the amount and timing of seed needs, as well as the production of seed. Finally, the utilization of wood sold has changed. Both large and small timber companies in this area have changed their investment levels in forestry from moderate to very low. It is clear that change is a fact of life, both in the physical, biological, and management sense. Management literature suggests that the pace of change is accelerating, and that the successful organization of the future will have to be able to deal successfully with change.

The second concern is the concern over capital investment occurring at the beginning of the investment period. To establish a seed orchard which will produce large quantities of seed in 15 years, which will then yield products 20-40 years from then (a total of 35-55 years) is perceived as potentially risky compared to other investments, in, for example, precommercial thinning, fertilization, or release. On the other hand, when capital is limited, not establishing a seed orchard is not seen as being as risky as not doing precommercial thinning. Not having a seed orchard means seed has to be collected elsewhere, but not doing precommercial thinning means risking stand stagnation or insect attack. Thus, large investments up front in tree improvement not favored by many managers.

The third concern is that time is fully utilized. Currently many species require 15-25 years to flower on a production basis. Of course, technology exists to speed up flowering, but in most species/zones, these investments are not cost-effective. Moreover, in long-rotation, relatively slowly growing species, it takes at least 10 years before people would feel comfortable with selection, even if accelerated breeding techniques were available.

As Paul Cotterill (1986) detailed, genetic gain achieved and gain per unit time are two separate measures of efficacy of a program- due to the additional time taken to complete a complicated crossing design, it can have a lower gain per unit time than a simpler approach. But besides considering gain per unit time, costs and their distribution are also critical to any analysis of efficiency. The ideal situation would be to wait until just prior to seed collection to make selections. At that point in time, the breeder would have a better idea of 1) the planting environments which will be used, 2) what traits are desirable for the different environments, 3) how much seed is needed. All this information could then be used in an economic analysis to establish what level of investment in selection, pollination, and cone and seed insect control could be justified.

The fourth concern is that the seed provided meets the needs of silviculturists. These needs, in south-central Oregon, are that the seed must be dependable, adapted, variable, and superior. First in importance is that the seed be currently available, for whatever species the silviculturist chooses to plant. Sometimes tree breeders have chosen to focus their efforts on widely planted species, which is important, but have left silviculturists to scrounge for other species they plant. The role of tree improvement and genetics, at least in some organizations, is to provide genetic technical assistance in obtaining seed for each species and zone that silviculturists need. When silviculturists mix species in plantations, it may be that a relatively low level of gain in all planted species may lead to an overall net value greater than a high level of gain in one and none in the other species.

Again, these types of questions can be addressed in zone-specific economic analyses.

Dependability of seed, in most of the species of south-central Oregon, requires some type of seed production area, in which trees can be thinned to open the crowns to light, fertilizer treatments can be applied and insect and animal damage control measures can be used to ensure successful seed production. If the seed production area is thinned to wide spacing on gently sloping ground, the use of equipment can lower costs compared to collecting from unmanaged areas. Thus seed production areas may have economic advantages even when genetic improvement is not expected.

In addition to dependability, the seedlings must be adapted to the site. Generally, western silviculturists are conservative about seed movement, and there is controversy about zoning among geneticists as well. Silviculturists tend to regard geneticists as the technical experts on zoning decisions, while sometimes developing special areas or collections which recognize differences the zones do not. The feeling on the ground is that in some theoretical world there may be sources that are better adapted and faster growing than the locals, but 1) we can't afford to put in the long term tests or wait to find out, 2) if we don't, we're taking risks, so 3) let's work with the locals. The challenge to tree breeders, then, is to develop many local populations cheaply.

In addition to adaptation, variation is also important in sources for reforestation. Silviculturists feel that there is a great deal of variation in the woods, and planning to plant the offspring of 50-200 clones in a standard type of breeding program across a 100,000 acre zone (which may currently have at least 50 trees per acre, for a total of 5,000,000 genotypes) may entail some risk. In fact, most would prefer to try to keep about the same variation that currently exists in stands or increase the variation.

Finally, silviculturists would prefer some level of genetic superiority in the planting stock, given that the seed is first dependable, adapted, and variable. But to the silviculturist, genetic superiority is desirable, but not necessary; while, to the geneticist, genetic superiority has tended to be the focus of attention with variability, adaptation, and dependability also considered. Yet the focus of geneticists in genetic superiority has tended to be long-term improvements in yield, while superiority to the silviculturist sometimes takes the form of improvements in ease of plantation establishment. For example, early growth in a plantation environment has a value for each application of animal or brush control which is saved. Again, savings in the short term may be of greater value than increases of volume in the long term, and can be compared in an economic analysis. Other considerations are those outside the timber management objectives, for example, one timber company enjoys the public relations aspects of using improved stock which requires fewer herbicide applications. One characteristic of appropriate technology is that it is used in the context of the whole forest/land management enterprise, and is integrated into that whole.

ONE APPROACH: MULTIPLE POPULATIONS WITH MASS SELECTION

"In general, it seems we can all appreciate the first principle of 'appropriate' language: jargon should be used only when absolutely necessary, and should be both reasonably obvious in meaning and retain a sense of humor and human scale." (Darrow and Pam, 1976)

To meet the many objectives necessary in tree breeding, multiple populations, as described by Namkoong (1981, 1984), Barnes (1984) and Kang (1980) are essential. But to carry forward many populations at low cost, mass selection is also an important tool.

Mass selection, also known as individual selection or phenotypic selection, has been defined in both agriculture and forestry textbooks (Mayo, 1980; Wright, 1976; Zobel and Talbert, 1984) as a form of selection in which individual plants are selected and the next generation propagated from the aggregate of their seeds. This procedure can also be called phenotypic or individual selection. The term mass selection will be used here in an inclusive way to refer to phenotypic selection coupled with some form of crossing- which can range all the way from open-pollination with surrounding unselected trees to polycrosses with known groups of male parents. The key is that identity control by individual or family is not maintained. The utility of the mass selection approach lies in the wide range of alternatives that exist; from the simplest, "eyeballing" the best looking trees and collecting open-pollinated seed from them, to using a multitrait (individual) index, using biochemical genetic techniques to assign them to unrelated groups, and polycrossing with other highly selected individuals. Thus, a vast continuum of alternatives exist, with the decision on level of investment deferred until the selections are ready to produce seed.

Many traits of value in forest trees have been shown to be amenable to mass selection. Gains from mass selection were estimated by Stonecypher *et al*. (1973) for eight traits, including growth, wood quality, and disease resistance traits in loblolly pine (*Pinus taeda*, L.). Gains at selection intensity 2.2 ranged from 3% for crown shape to 35% for rust score in heavily infected stands. Height yielded 12% gain and volume 21% gain based on 7 year data (mean 16 feet). Also in loblolly pine, individual heritabilities of some traits were calculated in Matziris and Zobel (1973): tracheid length .97, moisture content .80, specific gravity .47, volume .28, bark thickness .28, straightness .66, crown form .31. These heritabilities are all of the size for which substantial gains can be expected from mass selection.

While a great deal of the literature is on conifers, hardwoods can also be successfully improved by mass selection. Heritabilities for hardwoods are reviewed in Robison's paper in these proceedings. La Farge and Lewis (1987) calculated individual tree heritabilities for northern red oak (*Quercus rubra*, L.) of .20-.23 for height, .14 for dbh, .15 for straightness, .13 for forking, .11-.13 for d h, .31-38 for survival, and .16-.19 for insect defoliation. The net result of individual selection (approximately 1/^ of the individuals were selected) for seven traits combined was 8-10% for d h and 6% for height, with 3% increase in straightness, and 4-5% decrease in insect defoliation.

It may be argued that progeny tests, and seed orchards, from which the above estimates are derived, are managed differently than reforestation plantations, so that therefore gains could be substantially lower. Certainly reforestation plantations have a wide array of survival and growth. Still, Shelbourne (pers. comm.) reported 5-10% increases in volume from open-pollinated plantation selections in Monterey pine (*Pinus radiata*, D. Don), compared to 13-18% increases from seed orchard stock (the seed orchards are estimated to have 50% pollen contamination). Other evidence for the efficacy of selection in operational plantations is that of Webb and Barber (1965), in slash pine, (*Pinus elliottii*, Englm) who obtained very strong offspring-parent regressions for height when trees in plantations were control-pollinated (r's equal to .88 and .97). The fact that these relationships were not observed for open-pollinated progenies suggests that factors in the mating system may be responsible for failures to achieve gain.

As shown in Stonecypher *et. al.* above, fusiform rust resistance in loblolly pine was found to be particularly amenable to mass selection at high rust infection rates. Sohn (1978) proposed establishing seed orchards through recurrent rust free selections in high rust hazard areas as the best alternative to meet the challenge of pathogenic variability in the fungus while maintaining a moderate gain. Sohn and Goddard (1979) predicted gains up to 20% from intensive mass selection in infected stands. They predicted the highest gain from sites with 70% infection.

In western white pine (*Pinus monticola*, Dougl.), phenotypic selection in stands (natural stands, in this case) where western white pine stocking was reduced 80-90% by blister rust was estimated to give an 18% increase in resistance (Hoff, McDonald and Bingham 1976). Mass selection has other advantages for disease and insect resistance, as they noted:

> Mass selection will provide a high degree of genetic diversity and resistance stability because the total array of resistance will be selected--not just those traits man can see; the total genetic diversity of the rust will be used as inoculum-- not just the sample man picks; and all environments can be included in the selection-- not just the few to be used in expensive artificial breeding programs.

The same philosophy could be used for other traits, by finding sites with serious problems, mixing seed, and planting it at close spacing to increase the likelihood that some trees survive. This procedure could be used with insect infestations, animal damage centers, and disease pockets, as well as with droughty, frosty and wet sites. If trees survive under those kind of conditions, tree improvement has visibly solved a real reforestation problem.

Therefore it is clear that mass selection can be effective for many traits of importance in forest trees. The total amount of gain achieved in any one zone or breeding population will not be as great as under, say, combined index selection followed by controlled crossing. Multiple populations with mass selection (MP-MS) is a "shotgun" approach, as opposed to the more elegant "rifle" approach. Each bullet has more force (genetic gain) under the rifle approach, but if you don't know what direction the target is moving, you may be more successful with an array of pellets (breeding populations), each of which has less force (genetic gain). Another point is that the cost per unit gain would almost always be lower under an MP-MS approach; so that economic criteria such as benefit cost ratio might favor MP-MS. Net present value types of analyses might favor identity control options, especially when planting needs and yields are high, and rotations are short. Namkoong (1970) examined the problem of optimally allocating selection intensity in wild stands and progeny testing, and states that due to the differences in cost between field selection and progeny testing, that for most forestry situations progeny testing cannot be justified on the basis of the gain per unit cost. His findings are even more valid when selection in plantations is considered rather than selection in wild stands, since both the costs of selection are lower than in wild stands, and the heritabilities and potential gains are higher.

A significant obstacle to the use of mass selection was concern over inbreeding. Since the parent trees are not identified under this system, it was thought that there would be a tendencey to select most trees from a few families, thereby creating an opportunity for inbreeding, both within the breeding population and the seed production population.

Inbreeding occurring within breeding populations may have certain advantages, however. Wright (1963) considered an organism to be a vast network of interaction systems which ensures that gene substitutions can have very different effects in different combinations. He therefore suggested that plant improvement, as any evolutionary process, requires coupling of a more or less random process to furnish raw material with a selective process. This process consists of " subdivision of a crossbreeding species into small populations, sufficiently isolated to permit differentation under the joint effects of random drift and intragroup selection, but coupled with intergroup selection." If mass selection is done without subdivision, the population is moved to one selective peak, but not necessarily the highest. Further advance requires that the population move down somewhat from the peak it is on, and by some tiral and error process work its way to a higher peak. In 1978, he restated this premise for natural populations:

> "There may often be subdivision of the species into small local popultions that permit wide stochastic variability (but not fixation) at all nearly neutral loci and this favor occasional local crossing of saddles leading to higher selective peaks."

Wright's concept of a combination of genetic drift and mass selection within groups, with selection among groups is a very powerful evolutionary or breeding strategy.

In his book Animal Breeding Plans, J. L. Lush described an "ideal system for the rapid improvement of the whole breed" based on Wright's ideas, with subdivision of the breed into partially isolated subgroups into which individuals from othe subgroups are rarely introduced. This idea was impractical for animal breeders due to one breeder's inability to use the best of the subgroups (owned by another breeder). In the world of trees, with large ownerships and tree improvement cooperatives, this breeding system could be readily employed.

Kang (1980) noted that heterosis could be increased by allowing sampling drift to occur in the subpopulations and subsequently crossing between them for reforestation seed. He also stated that inbreeding has the advantages of increasing heritability, and exposing deleterious alleles to selection.

If inbreeding were thought to be undesirable, in either the seed produced or in the breeding populations, there are both low-tech and high-tech ways to deal with it (Friedman, in preparation). One example is the use of restriction fragment length polymorphisms (RFLP's) or isozymes to analyze the selected trees in a population. These individuals could then be assigned to different subgroups based on their likelihood of relatedness, or different combinations of trees could be used to reduce the value of F in the breeding population. These biochemical techniques could also be used in plantations which already exist and are good sites for selection, but were established with seed of unknown origin or unknown numbers of parents. As more information on isozyme or RFLP variation in forest trees becomes available it is likely that the origins of seedlots can be discovered retroactively, and the genetic variability can be assessed. By selection in these plantations and using improved seed in the next ten years, it is possible that the economic value of using molecular genetics in this way will be far greater than any use of forest trees derived from genetic engineering, which may not be available for 10-20 years, may then be field tested, and then finally planted for production.

NEW ROLES FOR SILVICULTURISTS AND FIELD WORKERS

> "Clearly we must keep in mind the fact that craftsmen and farmers commonly have a knack for devising tools. They also have a firm grasp of acceptability, affordability, and usefulness that is sorely needed in institutional research and development programs. The magnitude of the potential contribution by craftsmen and farmers in an innovation process is at least as great as that of the professionals and outsiders." (Darrow et al., 1981)

As field selection receives the importance is deserves in a tree breeding program, the importance of field people doing the selection is also increased. It is possible that in some organizations, such as federal agencies, in which many different resource people walk through stands of trees, that noting outstanding candidates for selection could be incorporated as a part of field work. The locations could be noted, and financial incentives given to the locator of the tree after approval by some quality control group. In fact, Antomologists and pathologists, soil scientists and others have suggested that information on the trees they locate with outstanding, possibly genetic characteristics (e.g., a healthy tree in the center of a root rot pocket) be stored in a central place so that the trees could later be used in research or establishing new breeding populations. Regardless of the specific method of using information, it is clear that educating people who visit the field and providing incentives for them to report outstanding trees will lead to a larger population of selections, representing more of the variability in the field, than approaches currently used.

A NEW ROLE FOR THE GENETICIST

"Appropriate technology efforts should be designed to take advantage of this large and creative group of people and support them, with technical assistance when necessary and with formal and nonformal educational programs, to put such inventive activity on a firmer technical footing and accelerate it." (Brace, 1976)

As can be seen above, field people will be empowered to start breeding populations to address specific problems of local concern. In addition to supporting local efforts and education, there is a great need for new information to support this kind of program. One need is to understand the structure of natural populations, so that efforts can be made to develop breeding populations through time with an understanding of what is successful in nature. Another need is to determine the minimum number of breeding populations per zone. The model could incorporate information on natural stand variation, both among and within stands, pollen and seed distribution parameters, the proportion of the zone to be naturally regenerated, proportion of the species in the planting mix, the difference between initial stocking and stocking at rotation, and the ecological harshness of the site, as well as other population biology or silvicultural parameters. Gene conservation would be thus integrated within the tree breeding/gene management framework.

To increase the efficacy of field selection, we need information on how to assess the relative effectiveness of selection on a given site, perhaps by measuring factors which are correlated. One potential candidate is the phenotypic coefficienct of variation for a given trait. How do different plantation management techniques, for example site preparation techniques, affect selection effectiveness? Information on heritabilities from existing progeny tests could be brought together to yield important insights into factors which increase or decrease selection efficacy. Heuristic or quantitative models could be developed to focus selection on plantations, or parts of plantations, where selection will be most effective.

Information from existing progeny tests could also be used to compare covariances among different traits from different zones within a species, with the objective of learning how many separate experiments to yield variance component estimates are necessary within different species. Geneticists may also develop environmental and growth and yield trials comparing breeding populations with simple, replicated, large plot designs. Since individuals are not tracked, and since fencing is not done, substantially more environments may be tested. More information than in progeny tests could be obtained on mortality, variability, etc. in populations when they are planted and managed according to standard reforestation practices. Growth could be tracked by standard forest inventory or plantation monitoring procedures, which both saves costs and acquaints field workers with characteristics of different breeding populations.

More work need to be done on mapping genetic variability using isozymes and RFLP's, and using them to assess the variability of selections. Finally, both geneticists and local people need to work on cost-effective pollen control methods which can be used in plantations. Under these appropriate strategies, the role of the geneticist is changed, the focus of research is shifted, but the importance of the geneticist is increased, and is increasingly integrated into the whole of forest resource management.

SUMMARY

The concepts of appropriate technology can be applied to problems of tree breeding and gene conservation in developed countries with success. A shift in roles of geneticists, field workers, and other forest biologists is necessary for this to occur:

> "Success should not be judged by the extent to which the community adapts to the new technology, but .. by the extent to which the community becomes more self-reliant and more able to solve its own problems in the future."

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