SCREENING FOR YIELD IN FOREST TREE BREEDING[1]

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SUMMARY

Product quantity and quality have been substantially improved in many previously unselected forest tree populations by one generation of selection. Estimated and realized heritabilities have been appreciable for numerous traits and may well increase under more intensive culture. However, environmental variations are higher than for most agricultural crops and more diverse sites for afforestation are expected in the future. Also, unlike most agricultural crops, trees take several years to mature both sexually and economically. Therefore the changes in ecological and economic desiderata per breeding cycle are large and demand that breeding populations be adaptable for variable futures. These factors require that screening for yield be highly efficient in use of time and materials and hence necessitate the use of multiple trait and indirect selection, use of information on relatives, and tests performed in a wide range of environments. Screening procedures thus commonly involve use of progeny tests with mating and environmental designs which efficiently estimate entry means, genetic and environmental variance-covariance matrices and genotype-environment interactions, and which often also provide materials for recurrent selection. Several component units of yield are assessed at various ages to estimate juvenile-mature performance correlations and the type of genetic control of each. These include anatomical, physiological, morphological and chemical traits which affect either ecological or economic utility.

In addition to efficiency in screening for yield among trees within populations, we believe it to be essential to screen among populations for present and potential future value. Since the option of backcrossing from wild, unimproved stocks into otherwise improved varieties is very costly in forestry, and since many natural populations are being lost, breeding populations of future value must be developed now. Many tree breeding agencies and the Commonwealth Forestry Institute especially, are responsible for the long term development of several tree species and must construct and maintain useful populations for future improvements. At the population level we screen for the same kinds of traits but, with the uncertainty implicit in long range programmes, more emphasis is placed on selecting for variation among populations and for the level of genetic variances within populations.

RESUME

Les espèces des peuplements spontanés ont été sensiblement améliorées quantitativement et qualitativement à la première génération après sélection. On estime que par rapport aux gains possibles d'héritabilité, les caractères fixés sont déjà appréciables et qu'ils augmenteront encore par des traitements plus intensifs. Mais la variabilité des conditions de milieu est plus importante dans les plantations forestières que dans les cultures agricoles, par ailleurs, les emplacements à reboiser risquent de présenter des caractéristiques très diverses à l'avenir. De plus, à la différence de la plupart des espèces cultivées en agriculture, les arbres exigent

1 Paper presented at the meeting on "Screening techniques in plant breeding" held by the Plant Breeding Group of the Association of Applied Biologists in Edinburgh, 3-5 July, 1979.

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plusieurs années pour atteindre leur maturité, pouvoir se reproduire et présenter une valeur économique. Il convient donc de prévoir que les populations améliorées puissent s'adapter aux conditions variables de l'avenir, en recherchant, une gamme suffisamment importante de caractéristiques qui facilitent les adaptations écologiques et économiques. Ces facteurs exigent qu'une sélection très poussée pour obtenir une productivité élevée soit hautement efficiente, quant à la durée et au choix des matériels végétaux. Ce qui nécessite donc l'utilisation de caractères héréditaires multiples, une sélection indirecte, l'usage d'informations sur la parenté et des essais sur un large éventail de types de milieux. Les protocoles de sélection poussée nécessitent, généralement, des tests de descendance prévoyant par fécondation et conditionnement du milieu, l'évaluation effective des possibilités moyennes de sa constitution génétique, l'obtention de matrices de variance et covariance des observations effectuées sur les caractères génétiques et les réactions au milieu, sur les effets de leurs interactions, toutes opérations qui, souvent, fournissent les matériaux pour obtenir certains caractères spécifiques par retrosélection.

Plusieurs composantes de rendement sont évaluées à différents âges pour apprécier les corrélations jeunesse-maturité de leur développement et le type de constitution génétique de chacune. Celle-ci comprend les caractères anatomiques, physiologiques, morphologiques et chimiques spécifiques qui affectent son adaptation écologique ou son intérêt économique.

Pour être efficiente, la sélection, entreprise pour obtenir des rendements élevés, ne doit pas se limiter à des individus choisis dans certaines populations, mais doit porter essentiellement sur la sélection parmi les populations de caractères ayant une valeur actuelle ou potentielle pour les années à venir. Comme les techniques d'amélioration par croisement en retour d'hybrides sauvages, avec l'un de leurs parents sont très coûteuses chez les arbres forestiers et comme beaucoup de populations de la forêt spontanée n'existent plus, on devrait développer, dès maintenant des populations améliorées possédent une valeur d'avenir. De nombreuses organisations spécialisées dans l'amélioration des arbres et le C.F.I. en particulier, travaillent au développement à long terme de plusiers espèces d'arbres et s'attachent à créer et maintenir des populations utilisables dans de futures opérations d'amélioration des peuplements. Au niveau d'une population, la sélection porte sur les mêmes genres de caractères spécifiques, mais en raison de l'incertitude qui est implicite dans les programmes à long terme, on s'attache plutôt à sélectionner en vue d'apprécier la variation parmi les populations et de mesurer le niveau de variances génétiques dans ces populations.

RESUMEN

Se han mejorado mucho la cantidad y la calidad de productos de poblaciones previamente no seleccionadas de árboles forestales a través de una generación de selección. Los heredables estimados y obtenidos han sido sensibles para numerosas características y podrían ser incrementados bajo una cultivación más intensiva. Sin embargo, las variaciones ambientales son más grandes que para la majoría de cosechas agrícolas y se espera encontrar sitios más diversos para reforestación en el futuro. Además, a diferencia de la mayoría de cosechas agrícolas, los árboles necesitan varios años para madurarse, tanto sexualmente como económicamente. Por consiguiente, los cambios en 'desiderata' ecológicas y económicas durante un ciclo de cría son grandes y demandan que las poblaciones sean adaptables a futuros variables. Estos factores requieren que la tamización para rendimiento sea muy eficiente en el uso de tiempo y materiales y por lo tanto exigen el uso de múltiples características y selección indirecta, el uso de información sobre parientes y pruebas realizadas en una amplia gama de ambientes. Así, los procedimientos de tamización invuelven frecuentamente el uso de pruebas de progenie con reproducción y diseños ambientales que evaluan eficientamente los medios de ingreso, los matrices de variación-covariación genéticos y ambientales y las interacciones genetipicos-ambientales, y que frecuentamente dan materiales para una selección recurrente. Algunas unidades componentes de rendimiento estan evaluadas a varias edades para estimar las correlaciones entre el comportamiento juvenil-maduro y el tipo de control genético de cada uno. Estas incluyen características anatómicas, fisiológicas, morfológicas y químicas que influyen en la utilidad ecológica o económica.

Además de eficiencia en la tamización para rendimiento entre árboles adentro de poblaciones, creamos que es indispensable tamizar entre poblaciones para valores actuales y futuros-potenciales. Como la opción de cruzar por atrás desde existencias salvajes no mejoradas a variedades por lo demás mejoradas es muy costoso en silviculture y como se estan perdiendo muchas poblaciones naturales, las poblaciones criadoras de un futuro valor deben estar desarrolladas ahora. Varias agencias de cría de árboles y sombre todo el Instituto Forestal de la Mancomunidad son los responsables para el desarrollo a largo plazo de algunas especies árboreas y deben establecer y mantener poblaciones útiles para futuros mejoramientos. Al nivel de poblacion tamizamos para los mismos tipos de características pero con la incertidumbre inherente a los programas de largo alcance se pone más énfasis en seleccionar para variación entre poblaciones y para el nivel de las variaciones genéticas adentro de las poblaciones.

Introduction

Like most other cross-pollinated crops when first brought under controlled breeding, forest tree species exhibit appreciable amounts of genetic variation in plantation conditions. Not only do features of the anatomy and morphology of trees show large heritable components, but traits affecting growth rate, fibre yield, photosynthetic efficiency and pest resistance are known to be under genetic control. These traits have been used in screening for yield, and breeding populations have been constructed for recurrent selection programmes. Genetic and economic laws operate no differently for trees than for peas, and we shall review the common first generation efforts which affirm these likenesses. However, we wish to draw attention to some differences between forest trees and other crops which are caused by the larger magnitude of environmental and economic variations to which trees must be suited, and the longer time required to breed trees. These differences have quantitative effects on screening and breeding procedures and also force consideration of population gene management which is qualitatively different from most crop breeding programmes.

The meaning of yield

Yield is usually measured in terms of volume or dry matter production on a per tree or per hectare basis, averaged over time in years. In the economics of forest management, however, the value of an increment in quantity or quality of such measures of yield is a very complicated function of various physical elements of yield and other factors such as land values, and is further complicated by the need to integrate these over variable time intervals as different products are harvested. While forest products usually have a lower economic yield per hectare per year than most agricultural crops, in many countries outside Britain the larger land area suitable for forestry offsets this to the extent that forest products often form a leading element in their national productivity. Increases in unit productivity can then have major economic effects such as in British Columbia where an increase of 10 per cent in plantation survival and a 10 per cent increase in individual tree growth rate will bring millions of acres of brush land into forest production. In the Republic of Korea similar increases would convert lands in marginal agriculture to more profitable grazing-forestry uses. A similar improvement could facilitate the change of marginal agriculture to forestry in Britain (C.A.S., 1976). Since land values are affected, yield on a per tree or per hectare basis does not translate directly into economic productivity and the total effects of breeding are much greater than can be directly perceived.

One effect of these evaluations of yield is that tree breeding programmes must include relatively large geographic areas. To the extent feasible, planting zones are restricted for any one population's range of adaptation, but relatively few populations or species must still fulfil wide environmental requirements within the aegis of single breeding programmes. Some national tree breeding programmes, especially in tropical areas, cover exceedingly wide ranges of conditions often going from sites on sterile coastal sands, through tropical evergreen forest areas to savannas and moist montane plateau grasslands. Such variations clearly require broad adaptabilities to one or more of these conditions and a sub-division of breeding and management efforts into large segments.

Breeding objectives sometimes concentrate on survival rather than growth on harsh sites where erosion control, amenity, sanitation, or watershed values are high; mere survival as on mine spoil banks, on grazed or eroded hillsides, or on barren hilltops, is a valid single measure of yield.

Wood protection, however, is generally a further economic objective and, on better sites, it is usually the primary product. Most effort has focused on individual stem quality and growth rate but these are not exactly equivalent to rates of production per hectare; we have not yet used breeding to improve competitive performances. It is hoped that individual performance will correlate well with stand performance and per hectare yield; most testing does take some account of planting density and competitive quality.

Unfortunately, screening for value even on this basis is complicated. Stem volume is important but deviations from cylindrical stem form and branching habit can be factors of more significance affecting value. Where fibre yield is the objective of forestry, then wood density is as important as volume, but average wood density may not be as important as fibre type in determining value. Fibre length, fibre wall thickness, chemical extractives, and other heritable features of wood anatomy affect value not only by their average parameters but also by their relative uniformity within trees which is also a heritable trait.

Growth is also affected by resistance to insects and disease and recovery following attacks, and by climatic and edaphic response functions which involve not only average responses, but also include growth during, and recovery rates following short and long period stresses.

Trees are grown over long rotations during which there is variation due to climatic and biotic factors as well as site changes, and averages and variances of performances both affect final value.

Finally, it must be mentioned that the relationships among these traits in determining value are not linear, frequently not monotonic, and the effect of one trait is often dependent on the levels of several other traits as well.

Since yield is so multi-faceted and complicated a function, and since most component traits have been shown to be heritable, the management problem has been to determine which traits should be included in breeding programmes and in screening for yield.

Initial screening programmes

In this first generation of breeding forest trees the traits listed in screening criteria include:

a) height, diameter, stem volume, bark thickness
b) stem form, branch habit, crown shape
c) wood density, fibre dimensions, grain angle
d) resin composition
e) resistance to damage by various biotic and physical agencies

Height and volume growth have low correlations between natural stand performance and growth under managed plantations and progeny testing in plantations is often needed to improve those traits. Under plantation conditions almost all have been shown to be at least moderately heritable, and some, such as stem form, branching habit and disease resistance, more highly heritable than expected.

Since most components of yield have proved to be heritable but difficult to evaluate, breeders tend to make an intuitive combination of field and laboratory assessments of multiple traits. No careful relative weighting of trait values is made; instead, initial screenings are usually made with a large set of independent culling levels, and a secondary screening made by subjectively combining the economically significant traits. Heaviest weighting seems to have fallen on volume and dry matter growth rates and stem form. These methods, while not very sophisticated nor maximally efficient, can be expected to improve yields and they require minimal information for the breeder to screen reasonably well.

The use of selection indices has been extremely limited because of several factors. Not only are the required covariance matrices poorly estimated, but the economic weights are also difficult to assess and are only approximately linear. In addition, the choice of traits to be included or excluded in any such indices has required a precognizance beyond our capacities.

These first generation screening efforts with forest trees have been concentrated on the conifers and especially on the pines in temperate countries, and the selected genotypes have been incorporated into simple recurrent selection or mass selection systems. The resultant gains in timber volume have been 10–20 per cent with slightly less in dry matter yields. In the mass selection systems, as typified by Douglas fir breeding in the western United States, initial screenings retained perhaps .01 per cent of the wild trees. Their open-pollinated seeds were collected and seedlings grown with a subsequent retention of 10–50 per cent of these half-sib families and around ten per cent of the individuals in the remaining families. These selected individuals will either be crossed within test plantations or they will be clonally propagated into seed orchards for commercial seed production and the start of the next cycle of breeding for either mass or simple recurrent selection.

The simple recurrent selection system commonly followed with most pine species excludes the use of open-pollinated seeds from the natural forests and instead brings clonally propagated ramets (rooted cuttings or grafts) of selected parents into clonal seed orchards. This selective screening is more intensive in the initial stage (around .001 per cent retained) since costs of subsequent screening stages are high and, on the basis of progeny tests, retain as many as 50–90 per cent of the entries.

In either system, the programme for each species is usually limited to 20–100 selected genotypes for each broad geographic regionl Some concern is now being felt about a breeding population of this small size and additional selections are being made but most plans seem to aim for a comparable effective population size (N_e) in the next generation. Selections are also expected to be refined and N_e can become rather small especially if site subdivisions are made, special traits selected for, or specific combining abilities are to be used.

Screening problems

Three major factors will reduce the effectiveness of screening and breeding in forest trees and pose problems beyond those encountered in most other crops. These are:-

1) the time and material required to test for mature tree performance when juvenile-mature trait correlations are poor or unreliable;
2) the time and material required to complete a breeding cycle from seed to test to selection to breeding to seed;
3) the scale of environmental and economic variations that must be accommodated within a single generation and changes in future generations.

In tree breeding, the length of time required for one breeding cycle is long and carrying costs are high. Therefore, to reduce the time involved in testing, screenings are also made on the basis of correlated traits and on performance of relatives. The correlations between juvenile and mature tree performances are not yet well established; hence selection is usually postponed to half rotation (harvest) age in the United States and up to 90 per cent of rotation age in Japan, thus limited selection to well over 15 years. With use of correlated traits, juvenile selection may reduce the selection age but not to much less than five years since genetic correlations are notoriously liable to change over breeding generations. Screening on the basis of physiological processes which are components of yield may improve predictability but growth in forests is complicated and early attempts to correlate photosynthetic efficiency with growth have been largely unsuccessful (Ledig, 1976).

The time required to mature sexually is now mostly between 7 and 15 years for gymnosperms, but 10-25 years for some such as Sitka spruce which is the most important planted gymnosperm in Britain. Some angiosperms take longer but others such as certain *Eucalyptus* and *Betula* species only require two years. Unlike seed and fruit crop species, seed production is not a useful trait except for producing commercial quantities of seed for planting, and in fact takes energy which might otherwise go into stem growth as in some clones of *Pinus radiata* in Australia. Shorter breeding cycles are not likely to be realized unless special treatments are applied. Thus far, such treatments as root pruning, partial stem girdling, crown topping, branch tying, soil fertilization and hormone sprays have proved to be partially successful in one or another species but very early sexual activity is still elusive.

Progeny or sib testing for selection purposes is usually costly of time, effort, and money since some environmental control is needed on large areas. Also, inexperience in handling large complicated trials in these first generation efforts has limited environmental sampling. Thus, most tests are planted on "typical" sites with replications clustered around accessible areas. Experimental design efficiencies are often sought, for example, in various incomplete block designs. However, each experiment is costly and multiple experimental objectives such as variance component estimation, ranking for general combining ability, provision of material for the next generation of selection and seed production, impose restrictions on design parameters. In addition, plantation security for the duration of a long lived experiment is low and hence balanced block designs within a few sites are used.

Finally, the scale of forestry operations and the low rate of return on land costs relative to most agronomic crops usually require that a single population be adapted to larger environmental variations. The extended time scale also requires that the crop be adapted for end products which may change rapidly compared with the time required to change breeding objectives. Nevertheless, long term breeding is likely to be a more economic means for improving fibre yield than either fertilizer applications or changing the pulping technology at least in the southern pines in the United States (Porterfield, 1973).

With these problems, screening and breeding for yield is complicated. Economic value can be improved by changing growth rate, wood anatomy, fibre dimensions, tree survival and resistances, but relative values are unknown even for present markets and will undoubtedly change in future markets with new wood technologies. Adaptability to sites can also be improved by testing widely over multiple site variables to select for generally good performances or for using genotype-environment interactions in subdivided regions. However, sites will differ in the future in unknown ways and the only certainty is that such variations will be wide and uncertain.

In addition, given the present tendencies of tree breeders to restrict population sizes, inbreeding levels will vary from expectations and unacceptably low N_e will occur relatively soon. Then, if major changes in economic or ecological demands occur, and other good qualities in the breeding populations are not to be lost, tree breeders will be faced either with reduced gains or with constantly having to develop new varieties with little cumulative improvement in any trait.

The solution which agronomic crop breeders often use, backcrossing from wild populations to improve established varieties or to inject new genetic variability, will generally not be available to tree breeders. The combined time required for testing and for producing progeny generations will usually be too long for any reasonable programme of backcrossing. The improved varieties which may be suitable for most growth and quality traits but unsuitable for new environmental or economic demands cannot be adapted by such simple genetic injection techniques. Even the classic use of backcrossing to improve disease or pest resistance may be controlled by many genes. Thus, new demands would require that the whole constellation of traits be improved from scratch and hence that little cumulative improvement in even those traits of consistent value would be achieved.

In addition, like many species under human population pressure, the natural stands of the wild progenitor stocks are rapidly disappearing. In particular, the tropical pines and hardwoods are being heavily cut and desirable source stands of trees are being completely lost (Kemp and Burley, 1978).

Thus, while tree breeders do have opportunities and problems similar in kind to other crop breeders, time, space and components of yield differences and their uncertainties create dilemmas for tree breeders in developing varieties for both long term development and for maximising present value.

Population screening

At this time, there is debate on how tree breeding efforts can be developed best for future use. One proposal is to select a single population with wide adaptability under a single breeding plan. The control over data and material is potentially excellent and, as long as large population sizes are maintained, cumulative varietal improvements can be made at least on a conservative basic set of traits, and for wide general adaptability.

An alternative proposal is to allow as many pedigreed populations to develop independently as local demands dictate. If several or all have identical selection criteria for both environmental and economic objectives, then maintaining separate populations and later recombining them would follow the replicate population proposal of Baker and Curnow (1969). If there are multiple and diverse criteria for selection, then separate populations can be maintained. In fact, it may well be that global perspectives require that populations be selected for environments not now frequent enough to justify any one nation's breeding effort. Screening at the population level for a basic set of initial breeding populations for diverse site requirements or economic objectives can then be used in a programme of multiple population breeding for potential future uses. Within each selected population, individuals can be screened according to criteria defined specifically for them and may be as refined or as simple as desired. Some genes will be lost in each of these populations. To minimize the effects of such losses and achieve a global balance in the greater species development, it would be necessary for the international community to confer and cooperatively develop supplemental population breeding programmes to compensate for these local inbalances.

At the Commonwealth Forestry Institute we believe that screening at two levels is a viable option for maximising progress towards immediate breeding goals and for developing longer term recurrent selection programmes for forest tree species. The CFI is a multi-laterally funded agency directed towards assisting any forestry agency in the tropics in its forest development programmes. Nationally, major efforts in breeding have been devoted to screening individual trees for the immediate use of agencies in seed production for afforestation and reforestation. However, since the CFI has been recommended by the FAO Panel of Experts on Forest Gene Resources to assist in the exploration, conservation, and development of the Central American pine species, we are in the unique position to coordinate programmes of tree introduction and improvement at the population level. In particular, *P. caribaea* and *P. oocarpa,* are being extensively developed throughout the tropical world and we have a series of 350 tests of these species in some 50 countries. The individual trees have been selected for very general vigour within their native habitats. Data on the multiplicity of traits previously listed are being accumulated in the extended tests. Screening for some source populations for each participating agency will reduce the total number of independent initial populations used, but subsequent breeding may create many more diverse populations in the next few generations. At this time we are providing the source populations for initial breeding programmes but we are also in a position to advise and assist in screening within populations.

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