POPLAR BREEDING STRATEGIES BETWEEN CONVENTIONAL METHODS AND NEW TECHNIQUES

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INTRODUCTION

"Poplars can be bred to order" is a famous expression of the North-American breeder E.J. SCHREINER (1949). Is that really so? To a large extent I agree on this optimistic view of what breeding can achieve. One can look at the range of products that are derived from poplars and have an idea of how flexible poplars are in meeting human expectations. We are used, especially in Spain and Italy to production systems aimed at the production of high quality logs for the plywood industry; on the opposite end we find the emerging sector of biomass plantations for the production of energy: very low quality demands, but a high production per hectare needed to make the wood attractive as alternative fuel. In between, we find particle board, paper, matches, packages, furniture and, in less developed countries, timber for construction, firewood, even animal feed.

Poplars are very special trees, domesticated by farmers millennia ago (FAO, 1980). They followed migration routes to and from Europe and Asia, they were brought from North-America to Europe by explorers and from Europe to all over the world by European settlers, confusing common folks and puzzling botanists. One example will serve for all: the fastigiated cultivar *P. nigra* 'Italica', is known in English as "Lombardy poplar" and in South America as "Alamo criollo", although it is neither argentinian, nor from Lombardy, not even Italian, but probably brought by the Romans from the Middle East and distributed everywhere over the centuries.

This special link of poplars with agriculture still distinguishes poplars from almost any other tree that is grown for its wood. Fast growth, multiple use of wood and easy vegetative propagation were the main reasons for the unique role of poplars as a farmer's tree and was a key factor in the rapid scale-up of plantations with the onset of modern industry. Farmers already knew how to propagate it, cultivate it, use it and research and development found a fertile ground where innovation was welcomed.

Modern breeding techniques found other special features of poplars that made the work of breeders easier and more efficient. Short time to maturity made generation turnover faster than with most forest trees; widespread interspecific crossability permitted the exploration of a huge number of hybrids.

Easy vegetative propagation by means of stem cuttings, already appreciated by the farmers, added an extra bonus to the work of breeders permitting the unlimited reproduction of the very best individuals.

The remarkable progress of breeding work in the twentieth century is largely based on interspecific hybridization and clonal propagation. In the last quarter of the century, however, population breeding, although slower in its progress was perceived as a must for sustained progress and many large scale breeding programmes were established. The last decade witnessed the explosion of new tools based on the achievements of molecular biology. The impact that these techniques will have on the commercial use of poplars is still the object of guesses and speculations, but nobody can deny the tremendous effect that molecular biology has on the advancement of scientific knowledge and that, at least as a side-effect, will further contribute to the genetic improvement of poplars.

It is my intention, here, to focus on some key aspects of poplar improvement, to put traditional methods and new tools in a common perspective and provide some simple criteria for the establishment of breeding programmes making efficient use of always limited resources (Figure 1).

Definition of an ideotype

Too many a breeding effort has started without a clear definition of an ideotype. An ideotype is a picture of the kind of tree we want to obtain with regard to the environmental constraints of the cultivation sites, the industrial quality requirements, the economical and technological context in which we operate. The picture should enumerate the desirable features of the tree (DICKMANN *et al*., 1992), possibly with an associated weigh proportional to the economic worth of each one; ideally, each trait should be accompanied by the monetary value of each unit of change along a scale of variation.

The definition of the ideotype is not a task that the breeder should be left alone to accomplish. Rather, it deserves the cooperation of many specialists and, in particular, of the end users of the product.

From the list of traits of economic importance the breeder can pick those that can be improved by genetic means, that is those traits that display genetic, inheritable, variation. Of course not every trait can be improved genetically, nor can progress be equal on all fronts, nor are there "best" breeding strategies for all purposes.

However, the ideotype sets a framework that is invaluable for the work of the breeder as it reduces the chances of following routes that prove to be dead ends with waste of energy and resources. Wood density will serve as an example: it has been demonstrated that mechanical resistance of wood is linearly and positively correlated to wood density; the higher the density the higher the resistance. As wood density is relatively easy to determine, shows a good degree of correlation between juvenile and mature wood and can thus be rated at an early age, a lot of effort was put in the genetic improvement of wood density, especially in North America. However, if considered in the context of the Italian and the Spanish poplar culture this would make no sense at all. In both countries the most rewarding product is plywood; but poplar plywood is almost never used with structural function and therefore its mechanical characteristics have negligible importance, much less than, say, whiteness, absence of tension wood, ease of peeling in thin layers; any effort at increasing wood density would be useless and even detrimental.

Another example: matches are made with a technique that is to some extent similar to the production of plywood, that is, both start by peeling the log; but matches are small and the logs can be as short as 1 m. With the trunk spliced into short logs, a curved stem does not pose big problems and a fast growing but very sinuous clone such as the Dutch *P. × canadensis* Monch. 'Dorskamp' is absolutely suitable; whereas it wood be the nightmare of a plywood manufacturer as a lot of wood would be wasted in the process of rounding.

It is a common observation in several industrialized nations that the more quality-demanding uses dictate the choice of cultural models and of breeding goals, even though they take a minor share of production.

Of course, we would need more than one ideotype should we aim at markedly different products with divergent quality requirements. An emerging sector that might see poplars play a central role is that of biomass for energy production. Although not yet convenient from a purely monetary point of view with respect to conventional fuels, it cannot be excluded that either increased incentives or stricter environmental constraints or even an increase in crude oil price will make of short rotation poplar coppices an important source of renewable energy and a new source of income for the farmers. Contrary to plywood, here wood density, positively correlated with calorific power, would be of paramount importance; on the contrary, stem straightness, wood whiteness, the absence of tension wood could all be ignored. Fast growth and resistance to diseases would probably be the only common targets in a breeding effort.

The time framework

A decision on the time framework is essential for the choice of a consistent breeding startegy among available alternatives. Long-term startegies may be combined with short-term results, but short-term strategies cannot provide a steady improvement in time.

The main approaches that will be discussed with regard to the time framework in whiche they operate are:

a) population-based recurrent selection;

b) single-pair matings for the creation of the highest variability followed by clonal selection;

c) clonal selection;

d) gene technology.

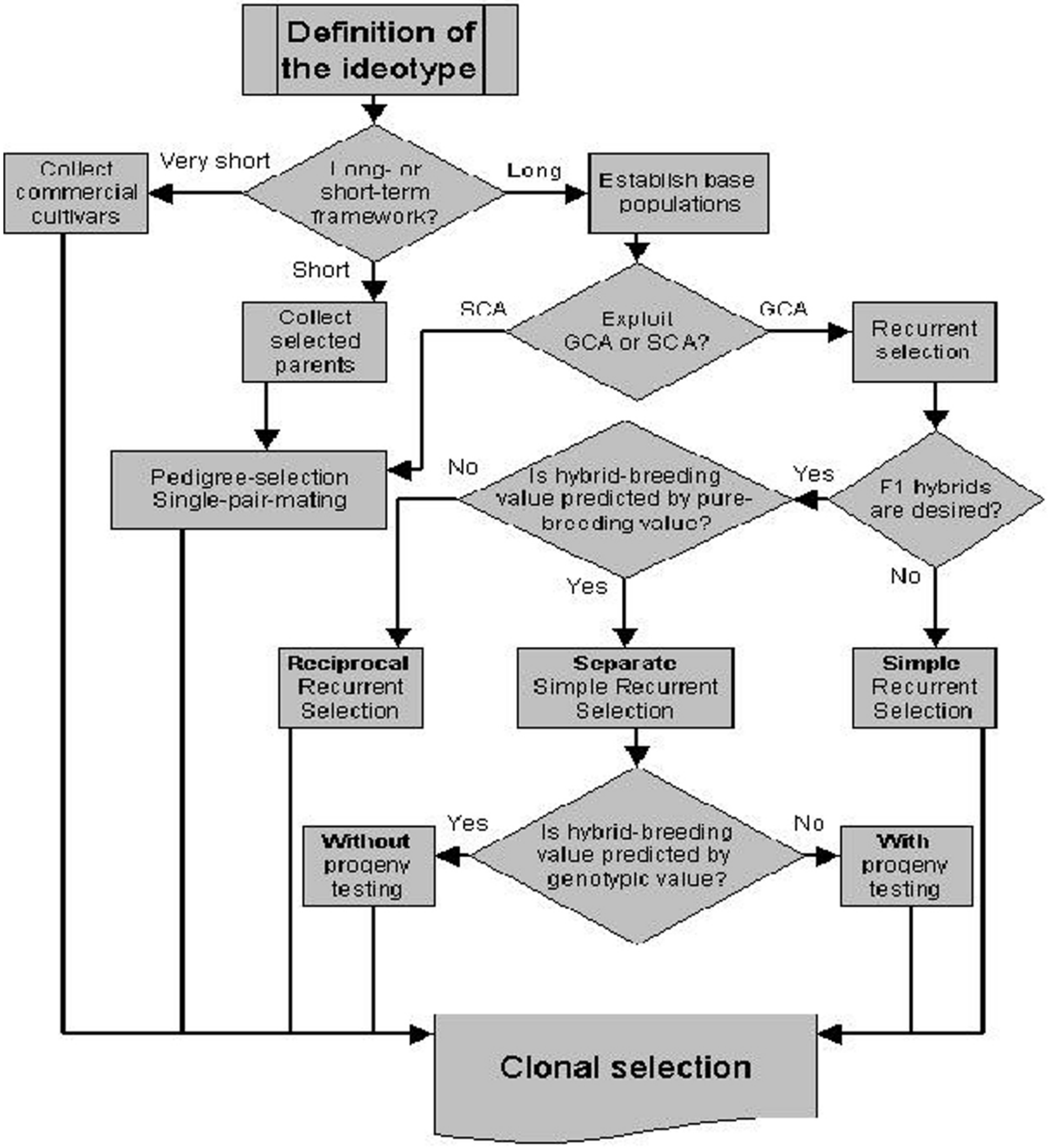

Figure 1 – A decision tree for the development of a breeding strategy with poplars as a function of the time framework and breeding goals.

Clonal selection

Whatever the strategy, clonal selection invariably represents the method to produce commercially viable cultvars starting form a broad range of individuals. Operative aspects and methods will be discussed in greater detail later on. Here I wish to point at clonal selection in its crudest and most straightforward way as a fully justified strategy when results are expected as soon as possible. Cultivars that are already commercially available throughout the world or that are in an advanced stage of selection at breeding Institutions can be gathered, raised in common garden experiments in a range of environments and the most suitable selected for use.

Common sense should give preference to cultivars coming from similar latitudes or climates, although poplars are known for their broad adaptability to different situations. For example, *P.* × *canadensis* 'Triplo', selected in Northern Italy, at 45-45°N latitude, performs well in Curitiba, Paraná, near the tropic line.

This approach has been used widely in the past by nations that imported clones instead of or before setting up breeding plans of their own and worked well in many instances. The main advantage is that it exploits all the work already done in the place of origin. Some characteristics may be important that were not given consideration in the original process of selection, such as resistance to some diseases that were not present, but many traits of general interest were certainly evaluated; rooting ability, growth rate, architectural features, wood quality, resistance to wind, etc.

Recently, Chile has adopted this approach to guarantee short-term results in a new breeding programme that also incorporates other longer-term strategies (Francisco Zamudio, pers. comm.).

Single-pair matings followed by clonal selection

The next step towards longer-term objectives is the creation of the most genetically diverse "population" with which to feed a selection process. Suitable species should be singled out again on the basis of closeness to the ideotype and geographic-climatic similarity of the place of origin. Selected clones, plus trees, unselected trees should be used in this order of preference. If more than one species is used, interspecific hybridization is recommended; hybrid vigour, although rarely demonstrated by valid statistical means, is supposed to be a common feature among poplars. The superiority of F_1 hybrids is probably due to complementation of genes carried at different loci by the parent species, rather than to overdominance, but nevertheless, hybrids are usually more successful than their parents.

The number of parents need not be large. Ten or even less (if selected) parents of a couple of species could be enough. These are to be crossed with the objective of creating the widest possible families, huge numbers of individuals to feed a selection process. The highest variability with the smallest number of crosses is obtained by single-pair matings, that is crosses in which a single male is used for a single female, although other types of crosses could be used as well.

All the individuals created form a wealth of genetic diversity, a huge number of genetically different individuals, a very large sample of the infinite ways in which the genes of the parents can be shuffled by sexual reproduction. Each of them will be screened to evaluate how close it comes to the ideotype.

With respect to the comparison of already selected clones this approach has the advantage of the much higher number of genotypes that enter the selection process; the disadvantage is that none of them has been tested before. Although a judicious choice of parents may produce a progeny of overall desirable characteristics, it is ultimately chance that will produce "the" superior mix of genes that will make a successful clone.

However, it has been frequently observed that, probably due to the high heterozygosity observed among poplars, within each single family there is more variability than among different families. Therefore, the size of families, more than their number, is a prerequisite for a successful commercial breeding effort.

Population-based recurrent selection

If long-term results are wanted, possibly for many generations to come, shuffling the cards (genes) and waiting for the lucky hand (genotype) is not a winning strategy. Population-based recurrent selection is aimed at increasing the frequency of favourable alleles in a population. In its simplest form, recurrent selection consists of repeated cycles of crossing the best parents and selecting, within their offspring, the individuals to be used as parents for the next generation.

When F_1 hybrids among two species are desired, recurrent selection can take other forms:

a) Simple recurrent selection (SRS) of the two parent species and hybridization of the best parents of each generations; hybrids can then enter a clonal selection process (Figure 2a).

b) Reciprocal recurrent selection (RRS) in which parents of each species are progeny-tested by means of hybrid progenies; that is, males of the species A are crossed with females of species B and males of species B with females of species A. The best "parents of hybrids" are then crossed within the same species in order to obtain a recombination of genes and start a new cycle. The "very best" parents of hybrids can be crossed on a wide scale for mass production of hybrids that will enter clonal selection.

c) Intermediate between a) and b) is the case when RRS is made impossible by a one-way compatibility as in the *P. deltoides* Marsh. x *P. nigra* L. cross that is viable only when *P. deltoides* is used as female. This gives rise to a "Semi-reciprocal recurrent selection" (SRRS) that consists of a RSR for the compatible genders and SRS for the incompatible ones (BISOFFI, 1989).

When is RRS a better choice than SRS? In those cases in which the "hybrid-breeding" value of parents cannot be predicted by their genotypic values. Even moderately positive correlations would recommend SRS if one thinks of other advantages in breeding two species separately:

a) One complete cycle of SRS is made of one generation, instead of two of RRS;
b) Genotypic selection can be very intensive without the risk of a dangerous reduction of population size; for example, if one selects 40 parents out of 300 in a progeny trial, the selection intensity is 1.6 family phenotypic standard deviations; by selecting 40 individuals out of 20000, selection intensity is 3.2 individual phenotypic standard deviations. Considering that both phenotypic variances and heritabilities are higher at the individual than at the family level, the difference in genetic gain is even more striking and can certainly compensate for an imperfect prediction of breeding values by genotypic values.
c) Different traits can be improved in the two species.
d) Generations need not keep the same pace. Species with a shorter time to maturity can have a faster generation turnover than species with a longer juvenile phase.

Multiple-population breeding

Multiple-population breeding (KANG & NIENSTAEDT, 1987) brings the above advantages to the extreme consequences; the breeding population, be it made of one or more species, is split into subsets, each of which is exposed to an independent process of recurrent selection (Figure 2b). Subdivision into sub-populations may be based on traits to be improved, with each subset aimed at the improvement of a single trait, or at different environments, or both. The advantages are manifold:

a) aiming at one character only in a population improves selection efficiency;

b) genetic diversity is maintained, and even increased, globally, by the independence of sub-populations (GULLBERG, 1987);

c) specific combinations of traits can be obtained at any moment by crossing individuals belonging to the relevant subsets;

d) there is more protection against future shifts in priorities in the relative importance of traits; for example, one could breed for high wood density in one group and low wood density in another, and pick parents from either group according to the materials desired;

e) overall flexibility is increased; every breeder knows how difficult and demanding the maintenance of a large breeding population is, with respect to the management of smaller groups of individuals;

f) cooperative breeding between different institutions is also easier; g) different strategies (e.g. exploitation of inbreeding, use of F_1s as parents, etc.) can be explored.

Methods employed in clonal selection

Clonal selection is the final stage of all breeding programmes with poplars. It starts with an abundance of genetically diverse individuals and ends with a small number of commercial cultivars. No new genetic combination is created in the process; therefore, the success of clonal selection lies in the quality of the materials it starts with and in the efficiency of their evaluation.

The ideotype should be again the guiding reference for the choice of traits to be considered, keeping in mind that the degree of improvement of each of them is, generally speaking, in inverse proportion to their number (NAMKOONG *et al.*, 1971). In general, the common denominator of clonal selection programmes, as of breeding work, is the increase of production by means of high growth rates and reduced losses. Growth rate and resistance to adverse factors are thus the most important targets of breeding and selection (THIELGES, 1985).

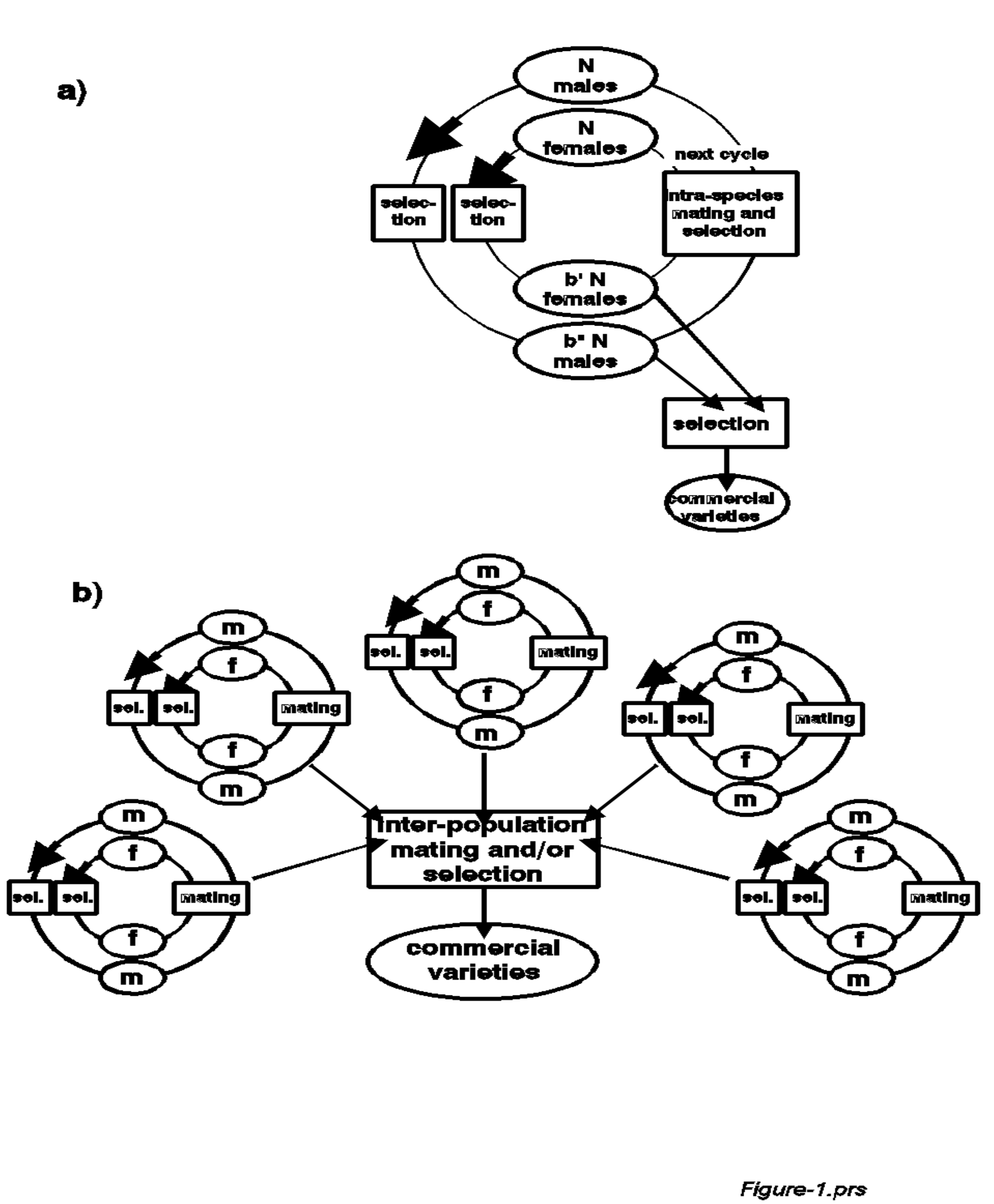

Figure 2 – a) Simple Recurrent Selection and b) Multiple Population Breeding Strategy with poplars (BISOFFI & GULLBERG, 1996)

As trees, poplars are demanding in space and time. Therefore, the adoption of optimal methods of selection are even more crucial than with other agricultural crops. Clonal selection is a typically stepwise process of evaluation; at each stage different traits are considered and a decreasing number of individuals are "promoted" to the next level for further testing. It is quite usual to start with traits that are either stable across ages (strongly correlated juvenile and mature expressions) or with traits that bear economic relevance in juvenile material (e.g. "branchiness" of nursery stock). The nursery is the typical starting point as it requires limited space per plants.

Several methods exist for coping with multi-trait selection:

a) Index selection (SMITH, 1936; HAZEL & LUSH, 1942; BAKER, 1986), is theoretically the most efficient method provided one can base it on reliable estimates of the variance-covariance structure for the traits considered and an appropriate ideotype, with economic values attached to variations of each is available. These conditions are seldom met in practice and this makes index selection a rarely applied method in the real world.

b) Tandem selection, improvement of one trait at a time, is not usually considered applicable to plants with long reproductive cycles.

c) Independent culling levels (HAZEL & LUSH, 1942) is most frequently used in the selection of poplars as it naturally matches the "common sense" criterion of gradually increasing the number of propagules of a decreasing number of individuals. From a theoretical point of view, especially for positively correlated selective traits, the efficiency of independent culling levels comes close to that of index selection (MUIR & XU, 1991; NAMKOONG, 1970; SMITH & QUAAS, 1982).

d) Principal Component Analysis can provide a solution to the problem that, although a sequence of tests, the evaluation taking place at each stage necessarily considers a number of traits (GODSHALK & TIMOTHY, 1988). PCA proves useful in reducing complexity of multi-dimensional data sets and by diverting selection criteria from individual traits to their combination in independent components.

Juvenile selection

Selection cycles can be reduced through the prediction of the future behaviour of trees based on observations made at a previous age (age-age correlation or juvenile-mature correlation): if predictions are reliable, then decisions about the value of the material available can be accelerated accordingly. Statistical correlation is the concept involved; causal relationships are not necessarily looked for. The basic question is: considering that the behaviour of mature trees is only imperfectly related to juvenile performance, how much information can be sacrificed in order to save time?

In the context of juvenile selection there are essentially two types of variables: in the first case the observed level of a variable at age T includes any value attained at age $t<T$, in the second case it does not. The first case is typical of size-related variables: the second one refers to all the other cases, such as resistance to diseases, wood quality, chemical contents and so on. The reason for separating the discussion of the two cases lies in the peculiar mathematical nature of the correlation coefficient in the first case, which must be properly understood for a correct application (KANG, 1991; KRÉMER, 1992; LAMBETH, 1980).

Wood characteristics were frequently studied in poplars and interesting degrees of correlation (both genetic and and genotypic) have been found between very early ages (nursery stage) and commercial maturity (NEPVEU *et al*., 1978; PICHOT, 1993; SCARAMUZZI, 1973; SCARAMUZZI & FERRARI, 1982).

Much effort has also been devoted to the development of early tests of susceptibility to diseases and to the evaluation of their reliability. However, due to obvious difficulties in the quantitative expression of observations in this field, the degree of correlation is seldom translated into figures. The reliability is often high when the organs affected by the disease are renewed every year (e.g. leaves), so that age and size of the tree are of secondary importance, and when the behaviour of the disease agent is relatively neutral with respect to those microclimatic factors that vary with the size of the trees. Juvenile selection is very efficient for *Marssonina brunnea* (Ell. et Ev.) P. Magn. (ANSELMI *et al*., 1975) and *Xanthomonas populi* (RIDÉ) Ridé et Ridé (RIDÉ & RIDÉ, 1978; DE KAM & HEISTERKAMP, 1987), dubious for *Melampsora larici-populina* Kleb. (PICHOT, 1993). A better control of the environmental factors in the juvenile evaluation, especially *inoculum* pressure, certainly improves the efficiency of early tests; this is the case of lab tests that have been developed for *Melampsora* species (PINON *et al*., 1987).

High age-age correlations have been found also for crown architecture (MUHLE LARSEN, 1967) and phenological traits (PICHOT, 1993).

As for incremental traits the cumulative nature of the commonly used size variables determines particular aspects of age-age correlations: that is, correlation between age t and $T>t$ is made of two components, the first one being proportional to the variance of size at the juvenile age alone, and the second to the covariance between juvenile size and subsequent increments. As the size at age T incorporates the size at age t, positive covariance is the rule. It could be demonstrated that, if annual increments were normally and independently distributed,

$$r_{T,t} = \frac{t\sigma^2 + 0}{\sqrt{t\sigma^2 \cdot T\sigma^2}} = \sqrt{\frac{t}{T}}$$

Given the above assumptions, $r_{T,t}$ for a given T increases continuously with age even though annual increments are totally random and do not reflect any genetic effects.

Therefore, the interpretation of correlations for incremental traits should be considered cautiously. Nevertheless, if one wants to know at which age in a field experiment one gets a focused picture of the final results, age-age correlations are indeed useful (PADRÓ & ORENSANZ, 1994). Genotypic correlations $r_{T,t}$ > 0.9 are found for $\frac{1}{4}T < t < \frac{1}{2}T$. Test plantations expected to be concluded in a rotation of, say ten years, can be assessed at age three to five. A fertile environment can considerably improve age-age correlations by accelerating juvenile growth.

Genotype × Environment Interactions (GEI)

Cultivars are tested in a necessarily finite set of environments but can be employed in virtually an infinite number of situations once released for commercial use. Statistically speaking, GEI is always present in clonal trials, as the response of individual clones to variations of the environment, for whatever reason, is never perfectly linear. However, the main problem for the breeder is not so much to understand the genetic causes, as to decide on how to deal with it once it has been detected.

GEI diminishes the ability of the breeder to generalize the results of his experiments and complicate his decisions about selection strategies: shall he give preference to stable clones with good average performance over a range of environments or to clones that display excellent performance in specific environments.

There is not a clear-cut answer to this dilemma (BURDON & SHELBOURNE, 1977) and fine statistical methods have been proposed to give insight into the nature and causes of GEI. However, a rule-of-thumb is to give preference to adaptive clones unless one knoe what are the characteristics of the environment that affect the behaviour of each clone. Until such knowledge is built up adaptive clones are the "best bet" for use in previously untested environments.

Molecular techniques

Most of the traits of economic value are polygenic and the effect of the single components are confused by the blurring effect of the environment. Sophisticated statistical tools (BAKER, 1986; FALCONER, 1989; MATHER & JINKS, 1982; NAMKOONG, 1979; NARAIN, 1990) play a central role in the improvement of tree species, but do not remove the main drawback of tree improvement, that is, the long time necessary for results to be applicable on a commercial scale.

A special kind of indirect selection that may shorten breeding cycles is that based on genetic markers, characters that are easy, fast and cheap to identify and that can be used as clues for the detection of other characters to which they are associated but that cannot be observed directly or need big investments in terms of time and money.

RFLP, RAPD, AFLP, STS, etc. are akronyms that have become of common use in genetics with the boom of molecular methods. Individuals can be compared for differences in their DNA, rather than (or in addition to) differences in the expression of genes and a multitude of applications of molecular tools in poplar breeding have been envisaged and proved viable.

A genomic map is the central organizing concept of almost all activities in the field of genetic analysis as it allows the integration of results from separate studies of the same species or genus (STETTLER, 1993). Dense genomic maps have been developed starting from several poplar pedigrees (BRADSHAW *et al*., 1994) and are being integrated. Poplars are at an advantage among trees for the small size of their genome as compared, for instance, with some conifers.

The first successes in the molecular analysis of poplars have been obtained within the framework of disease resistance (LEFÈVRE *et al*., 1994; VILLAR *et al*., 1996), with molecular markers identified at small distance from major genes for resistance/susceptibility and "Marker assisted selection" (MAS) has been sometimes proposed as a modern alternative to conventional evaluation of phenotypic expression of traits.

However, when it comes to tree species, MAS does not promise dramatic results, at least, not proportional to the high investments in research that molecular techniques require (CHELIAK & ROGERS, 1990; NEALE *et al*., 1992). Breeding populations are often near linkage equilibrium and in such a condition, it is impossible to predict if a useful gene and a marker are in linkage (cis) or in repulsion (trans) in any single member of the population.

There is also the risk of relying too much on the action of individual genes (e.g. for vertical resistance) instead of sets of alleles with additive effect (e.g. for horizontal resistance). The majority of characters that are of economical importance for forest trees are under polygenic control (even though with a number of major genes (BRADSHAW & STETTLER, 1995)) and would need multiple sets of markers.

Quantitative trait loci (QTL) can be singled out by comparing the phenotypic performance of subgroups in a segregating population and looking for matching segregation patterns in molecular markers but it is questionable if the effort is worth the investment, especially if one considers the potential gain still to be expected from conventional methods. In no case, as molecular biologists themselves acknowledge, can molecular tools replace traditional breeding methods and strategies. Breeding work will still require many crosses, careful selection and good luck; molecular genetics may only make the process more deterministic and reduce chance components (YOUNG, 1992).

The freedom of marker-assisted selection from any real or feared negative environmental impact that makes other innovative techniques suspicious in the eyes of the public, e.g. genetic engineering, will be an additional factor of success.

Gene technology

Given the ease of in vitro manipulation of most poplar species and their susceptibility to *Agrobacterium tumefaciens*, the most common gene vector in the genetic transformation of plants, gene technology is a viable option for poplars. Indeed, genetically modified poplars have been obtained as early as 1987 (FILLATTI *et. al*., 1988; RIEMENSCHNEIDER & HAISSIG, 1991) and in many labs around the world in the last decade.

It is not my intention to go into the details of the techniques involved, very well reviewed by LEPLÉ *et al*. (1999). I here wish to put gene technologies in the framework of conventional breeding and discuss its potential application in commercial culture of poplars.

There are two main advantages of genetic transformation with respect to conventional breeding based on sexual reproduction:

a) Genes encoding for specific proteins can be "cut" from virtually any living being, from viruses to higher plants to animals and "pasted" into poplars. Thanks to the universal structure of the nucleic acids, DNA and RNA, foreign sequences can be integrated into the genome and operate much in the same way as in the original organisms. Therefore, the range of genes available for poplars is potentially much larger than what is already present in the genus.

b) Individual genotypes can be modified for one or a small number of well defined traits while preserving the rest of the genome intact. Giving the importance of commercial cultivars in practice, the long selection process that they undergo before commercial release, the broad range of desirable features they must have to be successful, point modification of commercial cultivars could add value to them without disrupting their genome.

Many genes controlling many traits have been tested in poplars: resistance to herbicides, resistance to insect pests, resistance to diseases, modifiers of the lignin synthesis. All with good potential for practical applications and, generally, with a view to increase the profitability of poplar culture while reducing the environmental impact of cultivation.

Poplars that produce the *Bacillus thuringiensis* δ-endotoxin or protease inhibitors would defend themselves from a range of insects without the expensive and environmentally negative use of insecticides.

Low-impact but non-selective herbicides could be used on Poplars modified to tolerate them.

Cultivars with a lower lignin content or a lignin type less demanding in chemicals for its removal could make the production of paper, notably a high source of pollution, less damaging to the environment.

Many more applications are available, and with the potential for an exponential growth of their number given the progress in molecular genetics from the points of view of both the advancement of knowledge and the continuous improvement of laboratory technology. The relatively recent discovery that genes controlling equivalent functions are almost identical over very different systematic groups and that quite often whole clusters of genes are conserved in the same linear arrangement means that knowledge (on DNA sequences) obtained from intensively studied species (such as *Arabidopsis thaliana*) could be rapidly exported to other systematic groups and make the identification of the corresponding genes straightforward.

However, at least in the Western world, genetically modified organisms are meeting with a mounting wave of hostility led by the environmentalist movements that is negatively affecting the public opinion.

As for many similar cases the attitude of the man-in-the-street is more emotional than rational and indeed a deep ignorance of the scientific aspects is evident even in the press treating the subject. The subject itself is a prone to manipulation as it shakes the faith in "Mother Nature" as the sole legitimate ruler of living beings. High standing personalities have accused scientists of "playing God", disregarding the fact that the progress of agriculture throughout the millennia is a long line of successful attempts at overcoming Nature's borders.

Poplars have good arguments on their side: they are used neither for food nor for animal feed; their product, wood or paper, will come in contact with the end users in a biologically inactive state; poplar plants are usually entirely removed from the fields after harvest. However, one cannot exclude that transgenes migrate via pollen or seed to wild relatives (e.g. P.nigra in Europe) with probably negligible, but so far unknown effect on natural populations.

The so-called "precautionary principle", that is withholding the application of any new technology until a proof is reached of the absence of risk, is sacred by the public opinion. Although a logical nonsense, as absence of any risk cannot be assessed at all, this principle prevails upon the more rational principle of balancing pros and cons of the new and the old technologies in the light of scientific evidence.

CONCLUSIONS

RIMENSCHNEIDER *et al*. (in press) give a realistic view of breeding and selection with poplars as "the application of 'best intuition' and brute force empiricism".

To a large extent this will be true for a long time in the future. Despite the development of sophisticated statistical tools for the interpretation of experimental data and of a better understanding of genetic mechanisms by means of molecular approaches, the main problem will always be one of allocation of limited resources.

Paradoxically, advanced techniques that were developed to support population breeding now represent a major threat as they compete for research funds. Conventional breeding, lacking the glamour of frontline research, is at a loss when compared with molecular biology and sometimes conventional breeding is presented in applications as functional to molecular studies rather than the other (and obvious) way around.

A weakpoint of population breeding is the long time it must rely on steady, if not necessarily abundant, funding, a situation that conflicts with the prevailing concept that research should be based on compact, short term, manageable projects of up to three, four years.

The flexibility of a multiple-population breeding strategy, an effort to create cooperative breeding programmes within and across national boundaries and a cooperation with growers' organizations for all the phases of clonal selection is probably the answer for a sustained poplar breeding effort in any part of the World

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