BREEDING FOR WOOD QUALITY — A PERSPECTIVE FOR THE FUTURE*

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ABSTRACT

A challenge for tree breeders and wood quality researchers of today is to respond appropriately to a complex environment demanding more productivity, higher quality, and a quicker adaptation of their crops to rapid changes. This is mirrored in the typical modern commodity trends of the need for increasing quality, decreasing costs, and of increasing rate of change of the markets, surrounding technologies, and the environment.

The result of such demands is that tree breeders are faced with a growing "shopping list" of traits for which to breed, and in a shorter time period. This is a perilous situation, because, as the list of selection criteria increases, so too does the size of the breeding effort increase, or alternatively, the breeder may have to reduce the level of improvement in the traits. This problem is accentuated in the clonal situation, where the market expects all criteria to be met in a single genotype.

In a recent study, with the selection target of only four traits, one tree met all criteria in a trial of 475. In another exercise, zero trees were found to be in the top 20% for all four selection traits in 773 trees. Further to these traits, there was a need to select for rooting ability and resistance to various diseases. This highlights the need to model and understand the impact of multi-trait selection on clonal breeding strategies.

Future breeding developments are likely to: (1) limit selection traits to those anticipated to be required regardless of changing needs, and weight them in consideration of the associated risks of changing needs; (2) design strategies and adopt technologies which will enable more effective selection of multiple traits; and (3) adopt strategies which will allow effective response to the rapidly changing market, technological, and natural environments.

Challenges for wood specialists in response to the above scenarios may be to: (1) identify a few "generic" traits, likely to robustly address a spectrum of possible needs of the future; (2) provide cost-effective early screening

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techniques (biotechnology may compete here); and (3) develop technologies which will enable effective deployment (e.g., matching the predicted phenotype to the site). The objective is to match the realised phenotype (as a result of genetic and environmental influences) to the processing needs.

Keywords: Tree breeding; trends; wood quality; multi-trait selection; forestry

INTRODUCTION

Given the modern, rapidly changing environment, the question may be posed: "Why invest in tree breeding? By the time the product is planted and grown to maturity, technology, the markets, and the natural environment will have changed so much that our efforts will have been futile". Further to this question, if it makes sense to genetically improve our tree crops, which, of the dozens of characteristics for which to breed, will still be in demand at the time of deployment (planting) and at the later time of harvesting?

Plantation forestry is a long-term business, relative to many other industries. Tree breeding for a particular generation of commercial forests will typically be initiated at the equivalent of one and a half to two generations' time prior to establishment of the improved varieties.

The forestry sector finds itself in a rapidly changing natural environment. It has been estimated that the atmosphere will warm by as much as 5.8ºC during the current century (Beerling & Berner 2007), and with this comes the challenge to adapt the genetic base of the plantations accordingly (Wang *et al*. 1994). It was shown that for loblolly pine (*Pinus taeda* L.) and Norway spruce (*Picea abies* (L.) H.Karst.), models predict height growth about 5 to 10% below that expected for a genetically adapted seed source, if the average yearly temperature increases by 4°C (Schmidtling 1993). Climate change will also create new pest and disease regimes, and the tree breeder needs to develop the suitable genetic resource to survive these new scenarios.

Most industries are faced with the challenge of adapting to the fast-moving man-made environment of markets and of new technologies. Forestry is also exposed to such dynamics, and the rate of change in the man-made environment can be even quicker than that experienced in the natural sphere.

There is a need for "rapid response to change" in the forestry sector in general and, in particular, in the development of tree breeding and deployment technologies and strategies (Verryn & Hettasch 2002). "Time-to-market" (TTM) is a measure used in other industries (Wikipedia contributors 2007), and it should become central to the tree breeder's way of thought. If the tree breeder cannot respond quickly enough, it may well be argued that there is no point in responding at all.

One of the areas of rapid change is that of wood processing. As processing technologies advance, and the processors change their expectations regarding the quality and uniformity of the wood properties, so too does the tree breeder's need to re-assess the list of priorities with respect to breeding for wood quality. For example, in the past, wood processors tended to demand absolutely straight logs for sawntimber. Any deviation from straight logs would translate into lost timber production. In modern times, the sawing and drying technologies have advanced to the point where stem straightness may not be as important any more (Verryn & Hettasch 2006). In addition, there is a move to the use of smaller logs — for example, in South Africa, small pine logs (such as those with small-end diameter as small as 10 cm, from plantation thinnings), which were previously sent to pulp mills, are now being used for solid wood products. In the pulp and paper industry, issues such as that of limiting the environmental impact of the processing, of transport costs, and of the productivity of the mills, may require appropriate changes in the characteristics of the wood resource. There is, for example, a premium paid for species of superior wood density and pulp yield, such as *E. globulus* Labill. (Group Editor 1995; Haggblom 2004).

The tree breeder is faced with a growing "information overload" with regard to what is required of the genetic resource (e.g., up to 10 traits in a *P. radiata* D.Don programme (Jayawickrama & Carson 2000)), and there is a need to react to such demands at an ever-increasing speed. Some options available to tree breeders to respond to these challenges, and the potential consequences of choices made, are discussed here.

MULTI-TRAIT SELECTION

Inevitably, there is a need for selection and breeding for more than one characteristic. It can be shown that the most rapid strategy to achieve the best net improvement of a portfolio of economic goals in all the traits of interest in a breeding population, is to concurrently select for all the traits by means of selection index (Falconer 1989; Gjedrem 1971). It has, however, also been shown, that as one increases the number of selection traits, so too is there an inevitable "dilution" of the rate of breeding progress in the traits under selection (Fins *et al*. 1992). These conclusions are population-based, and valid as such. The "dilution" of individual trait breeding progress due to multi-trait selection is justified in index selection on the assumption that the traits have been allocated appropriate economic weights (Hazel *et al*. 1994; Lin 1978). Incorrect economic weights have been shown to cause significant rank changes in some cases, and insignificant changes in others (Beard 1988).

In clonal selection for plantation deployment purposes, we may find it difficult to satisfy all the minimum criteria (or expectations) in a single individual. A selection process with an increased number of traits, and with more stringent criteria, will have a diminished likelihood of successfully identifying such a clone (or clones). To illustrate, using a completely random, probabilistic approach, if P_i is the probability of finding an individual meeting the minim criterion for trait "i" in a population, i.e.,

P_i = (number of individuals meeting the criterion of trait "i" / population size)

Assuming a random association between traits and a genetic correlation of zero between traits, the probability (P_C) of finding a clone satisfying all "r" trait's criteria would be:

$$P_C = P_1 * P_2 * P_3 * \dots P_r$$

Assuming we have five traits, each with a probability of 0.1 (i.e., in the top 10%) that the i^{th} criterion for a production clone would be met in that population, then $P_C = 0.00001$. So, in order to select one suitable clone we would need a population of 100 000, and for five suitable clones, we would need a population of 500 000. The requirement of five traits may be conservative in a eucalypt clonal program, where we may select for growth, stem form, resistance to a disease (or two), wood density (and/or other wood properties), and rooting ability.

In recent studies on data from an experimental population of 475 *Eucalyptus grandis* Maiden trees, with the selection target of only four traits, no tree met the test criterion of being within the top 10% for all traits (Louw 2006). When the selection criteria were relaxed to "commercially acceptable" thresholds of being in the top 15% (diameter at breast height), 20% (stem form), 15% (wood end-splitting), and 30% (wood density) of the population of 475, for each of the four traits (P_C= 0.00135 or 1.35 in 1000), then it was found that one tree met all criteria in the trial. In another trial of 773 *E. grandis* trees, zero trees were found to be in the top 20% for all four selection traits. Further to these four traits, there was a need to select for at least two other traits (rooting ability and disease resistance). This could translate into a probabilistic value of $P_C = 0.00135 * 0.5 * 0.25 = 0.000169$, or 1.69 in 10 000 trees.

TIME, RISK, AND TREE BREEDING

Given the long-term nature of forestry, and particularly tree breeding, there is a case for the inclusion of time scaling in breeding and selection. In general, economic weights of breeding programmes are calculated with present values. However, in the future we may develop more sophisticated economic modelling in forest tree breeding. There may be a need to model economic trends and the impacts on the relative importance of selection traits. For instance, in *E. grandis* breeding we may model that it takes 10 years to develop a new clone for deployment, then an additional 2 years for nursery bulk up, followed by deployment in plantations, and harvest 8 years later. The relative economic importance of a trait after the total period of 20 years to harvest may be significantly different to today's value. In other words, there is an associated risk with this forecast relative value. The long time periods, together with the "rapid change" environment, make the risk of large forecast errors potentially high.

Normally, economic weights of selection indices (and Best Linear Unbiased Prediction or BLUP) are considered absolute values, with no margin for error. It is suggested that, in forestry, where there are variable degrees of certainty in our predictions of economic worth of the different traits at time of harvest, the economic weights should be risk-adjusted. For instance, it may be argued that there is a high degree of certainty that a trait, such as the rate of tree growth, is likely to carry a significant economic value in years to come; however, there is less certainty that the pulping technology will require similar wood properties to the present. The BLUP equation may be expanded to include a risk adjustment factor, R, for the economic weight vector, a:

$$\hat{w} = Ra'C'V^{-1}(y - X\beta),$$

where:

- $X\beta$ = the Generalised Least Square Mean estimate, with X, the design matrix relating y to the fixed effects
- $\hat{w}$ = the vector of predicted genetic worth
- y = the vector of observed value of individuals
- V = the phenotypic (co)variance matrix
- C = the genotypic (co)variance matrix between the observation and the predicted traits
- R = the economic weight risk adjustment square matrix
- a = the (predicted) economic weight vector.

IMPLICATIONS FOR TREE BREEDING

The selection of clones for nursery production purposes in the above examples illustrates the impact which additional traits, together with their selection intensities, have on the size and potential efficiency of a breeding programme. Assuming that the tree breeder has a limited budget, he or she will be faced with the challenge of trying to meet minimum requirements for some characteristics, whilst breeding for the broad portfolio of traits and managing the risk of changing needs. There are many possible strategies to address this challenge, of which the following are a few:

(1) Limit the number of selection traits, especially for production purposes. The breeder may do well to carefully interrogate the real value and relevance of the traits in future years, given changes in technology, the markets, and the environment.

(2) Relax the selection criteria for some less crucial production traits. If, for instance, certain threshold values are non-negotiable, then the selection intensities of other traits may have to be relaxed in order to have sufficient candidate clones. The assumption that all the traits have linear economic benefits in relation to their values, is often not valid, and deviations from the linear assumption need to be taken into account (Greaves *et al*. 1997; Meuwissen & Goddard 1997). The relaxing of selection criteria will most likely result in a loss of genetic gains for that trait.

(3) Breeding and production strategies may need to be tailored for effective multi-trait selection. For instance, certain screening may take place in the nursery with large numbers of candidates, allowing selection of other traits at a later stage. In addition, the sizes of populations and trials need to be designed for the number of traits to be selected, together with their selection intensities.

(4) Design breeding populations and strategies in such a way as to build in the ability to respond to the risk of a sudden change in the selection needs. A new disease, market need, or technology need may require an initial rapid response from the tree breeder. In order to address this, the tree breeder may have a conservation plan for a number of species, or may maintain a rather robust and large breeding population, from which customised sub-populations may be derived.

IMPLICATIONS FOR SELECTION FOR WOOD QUALITY

Some of the numerous wood characteristics which are typically considered for genetic improvement programmes are: wood density, pulp yield (for different processes), lignin types and content, cellulose configuration, fibre length and fibre wall characteristics, colour, internal wood stresses, wood end splitting, interlocking grain, shrinkage, microfibril angle, modus of elasticity, and modus of resonance. In addition, the markets and processing technologies demand different, changing, and sometimes opposing, wood properties. A significant challenge for the wood specialist is, therefore, to guide the tree breeder by identifying the key wood properties which, if improved, will give the grower a significant competitive advantage in the foreseeable future. These traits should be robust enough to be valuable, no matter what the likely changes in processing technologies and market needs. If viable heritabilities are observed for these traits, then they may be included in the breeding programme.

In clonal deployment programmes, it may be necessary to either limit the number of wood property selection traits, or relax threshold values of the traits, or model the non-linear economic weights of traits, in order to ensure that the best selections are obtained within the confined resources of the programme.

Once traits of importance have been identified, and the associated economic weights predicted, there is generally a need from tree breeders to screen large numbers of trees, rapidly, accurately, at a young age, and usually in a non-destructive manner. Successful research in aid of this requirement can result in a more effective breeding programme, and hence greater genetic gains. Globally, there has been significant research (and progress) directed at the need for rapid, (cost)effective, early screening, such as the use of near-infrared spectroscopy (Michell 1995; Michell & Schimleck 1997; Schimleck *et al*. 1996) and sonar (Schafer 2000). In recent years, there has been a growing trend towards applying DNA and proteonic technologies in support of rapid screening. These technologies are gaining in accuracy and gradually becoming more cost-effective.

A strategic research question is: which of the technologies will most effectively address the screening for specific traits in future? For many polygenic traits, screening at a genomic level will require an immense amount of knowledge of the interactions of large numbers of genes with each other and with the environment. There will still be a need to research, and phenotypically screen, a significant number of individuals, in order to collect this information.

Understanding the interaction between the genotype and the environment is increasingly becoming a key modelling element for the management of forests. Resource uniformity, in terms of wood properties, can have significant economic savings. The phenotype of the tree, as with most biological organisms, is in part genetically determined and part environmentally, and there may be an interaction effect. Once the appropriate genotypes are bred, it remains necessary to manage the genotypes in different environments, so as to obtain maximum uniformity and productivity. Various initiatives are investigating these factors and interactions in an effort to obtain maximum benefit for the industry. These include the recent research of the CRC for Forestry, Australia, and that of CSIR, South Africa, with its collaborators (not published). Here logistical mechanisms are put in place with a view to scheduling the harvesting and processing of batches of timber of similar characteristics.

CONCLUSIONS

Modern breeding programmes need to be able to address increasing needs in a rapidly changing environment. This can result in breeding programmes being faced with a large number of selection traits. Conventional breeding strategies tend to be based on the fact that simultaneous selection of any number of traits is, in the long run, more beneficial than tandem selection. This theory is population-based and assumes that there are dependable economic weights attached to the traits.

The inclusion of numerous traits, with strict selection criteria, in clonal programmes can result in the need for very large clonal testing programmes, or alternatively, result in few or no clones being deemed suitable for deployment. In the latter case, it may become necessary to relax the criteria, resulting in lower genetic gains for certain traits.

The rapidly changing environment, market, and technologies can also result in the importance of certain selection traits changing over the time it takes to develop, deploy, and harvest the genetic material. The risk-adjusted economic weights of the different traits, can be included in BLUP models.

It is suggested that the breeder and wood specialists invest in very careful consideration of which traits are of key importance, and will still be of such importance in years to come (target deployment and harvesting time). Misguided inclusion of traits, or erroneous economic weights, can be very costly in terms of realised benefits from a breeding programme.

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