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Bio-economic Modelling as a Method for Determining Economic Weights for Optimal Multiple-Trait Tree Selection

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Abstract

A bio-economic model provides a framework for simultaneously considering breeding, management, and production decisions. Such a model should result in optimal breeding (and silvicultural) objectives if main goals of a production system are well defined. Historically estimation of economic weights for breeding-objective traits has been based on partial regressions and profit functions relating only to certain parts of the production system. A bio-economic model includes effects of growth rate, branching, form, and wood quality on all production system components and on overall profitability of an integrated production system. However, long rotation cycles in forestry make determination of relative economic values for the breeding-objective traits particularly difficult. When modelling complex systems under uncertainty about future production goals, there are necessary trade offs between the complexity of the model and the use of simplifying assumptions.

Key words: tree improvement, breeding objective, bio-economic modelling, production system analysis.

Introduction

Breeding Objectives and Multiple Trait Selection

The first step in the design of a breeding program is to set its objectives. Correctly set breeding objectives will

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determine how much improvement in different tree characteristics is needed to maximise production system efficiency (GODARD, 1998). Virtually any type of selection in tree improvement involves multiple traits due to the existence of correlations among traits. BAKER, 1986 and more recently LYNCH and WALSH, 1999 provided comprehensive reviews of multiple trait selection techniques, including tandem selection (selection of one trait per generation), independent-culling levels (selection where truncation levels are set for phenotypic values of each trait), and index selection. Index selection is generally more efficient than the other two selection methods, and is now being widely used in tree breeding (LYNCH and WALSH, 1999).

Index selection allows simultaneous improvement of several traits by giving each candidate tree an aggregate index value. A selection index (I) is a linear function of phenotypic (measured) values for n traits (p_i), each of which is weighted by a coefficient (b_i), such that the index value relates the phenotype to the genotypic worth of that tree. The genotypic worth (H) is composed of n breeding values (g_i) weighted by their relative economic values (w_i) per unit change:

$$I = b_1 p_1 + b_2 p_2 \dots bn\ pn \qquad [1]$$

$$H = w_1 g_1 + w_2 g_2 + w_n g_n \qquad [2]$$

The vector of index weights ($\boldsymbol{b}$) is obtained as partial regression coefficients of genotypic worth on phenotypic values (HAZEL, 1943; SCHNEEBERGER *et al.,* 1992), as:

$$\boldsymbol{b} = \boldsymbol{P}^{-1}\boldsymbol{Gw} \qquad [3]$$

where $\boldsymbol{P}$ is the matrix of phenotypic variances and covariances among traits; $\boldsymbol{G}$ is the genetic variance-covariance matrix; and $\boldsymbol{w}$ is the vector of economic weights.

If objective traits can be measured simultaneously and their economic weights, heritability, and genetic correlations are perfectly known, spreading selection intensity over several traits gives a greater aggregate selection-intensity than the independent culling levels for single traits. However, the benefit needs to be weighed up against variations in marginal costs of assessment for additional traits, and uncertainty about various parameters. Certainty about economic weights is especially important if there are adverse genetic correlations (trade-offs) among traits. Thus, the list of breeding-objective traits is usually kept fairly short (BURDON, 2004; VERRYN, 2007).

Economic weights ($\boldsymbol{w}$) are defined as partial linear regression coefficients (i.e. effects of change in one trait at a time, while all other traits are held constant). However, profit response may not be linear over the entire trait range. Linear selection indices also do not take account for non-linear interdependencies among traits, but marginal economic worth for one trait may be dependent on the value(s) for one or more other traits. Although, low trait heritabilities and, to a lesser extent, genetic segregation would diminish the non-linearities, non-linear profit function causes difficulty because the economic value of a trait is not constant, but rather changes as the trait mean changes (e.g. BURDON, 1990). There are two types of selection indices for the "non-lin-

ear situation", and they are non-linear selection indices and linear ones.

Non-linear selection indices restrict the response of some traits to either zero or some other predetermined value while maximizing other traits (KEMPTHORNE and NORDSKOG, 1959; TALLIS, 1962). A similar and widely used index is called "desired gain index" (PESEK and BAKER, 1969; HARVILLE, 1975; YAMADA, 1995). However, GIBSON and KENNEDY (1990) argued that for every restricted index there is a set of implied economic weights. GODARAD (1983) pointed out that if component traits are inherited additively, genetic progress is always better if based on a linear index. Economic weights for linear selection indices with non-linear profit functions can be derived by the method of ITOH and YAMADA (1988), or approximated by using partial derivatives of the profit function, evaluated at the mean before selection.

Most forest tree-breeding programmes do not have formally defined breeding objectives. Various reasons for this include: complexity of the forest processing industry; difficulties in determining the relationships between selection traits and end-uses; and long rotation ages that create uncertainty about end-use (APIOLAZA and GREAVES, 2001). Decision maker's problem in tree improvement is to determine correct economic weights and to set the breeding objectives that maximise profit of the production system. Economic weights and breeding objectives that are determined scientifically, and that are accepted and implemented in practice, require a full cooperation between scientists and industry managers. The objective of this paper is to:

1) Review methodology for estimation of economic weight in forest tree breeding;
2) Describe the components and specification of bio-economic models in forestry;
3) Discuss modelling of complex systems under uncertainty about future production goals, selection index formulation, and risk mitigation through diversified breeding and deployment.

Methodology Review

Methods for estimation of economic weights

Based on plant and animal breeding literature methods for economic weight estimation are divided into four categories: a) partial regressions b) profit functions c) bio-economic modelling (production system analysis) and d) selection based on profit (sidesteps economic weight derivation). The bio-economic method (c) is currently preferred, and involves modelling a production system. The models range from simple to highly complex sets of technical input/output relationships based on production system knowledge. Such models combine genetics with knowledge of wood science and economics. Production system models are developed by management specialists, but economists may incorporate optimisation based on tree characteristics (growth, form, branching or wood quality) to maximise profit (i.e. system analysis and operations research).

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Method of Partial Regressions

Historically, partial regression was the method of choice used to estimate economic weights for developing selection indices, used, for example, by BRIDGWATER and STONECYPHER (1979), and TALBERT (1984) for Loblolly pine in south-eastern USA. For example, COTTERILL and JACKSON (1985) used the partial regression approach of estimating economic weights for radiata pine in Australia. The method required estimates of net profit of trees at the end of rotation. Economic weights for sectional area (w_{SA}), straightness (w_{SS}), and branching (w_{BQ}) were estimated by partial regression of phenotypic values (p) of early-age measurements on the subsequent estimates of the profit (Pr) per tree at harvesting:

$$Pr = c + w_{SA}\, p_{SA} + w_{SS}\, p_{SS} + w_{BQ}\, p_{BQ} \qquad [4]$$

The regression coefficients estimate the dollar amount by which net profit changes when the phenotypic value of a trait increased by one unit of measurement, the other traits remaining constant (i.e. the change is free of effects of other traits). More recently, BEAUREGARD *et al.* (2002) used multiple regressions to determine how key log characteristics are influencing the intrinsic value of various radiata pine products (*e.g.* structural and appearance grade lumber).

Partial regression is the method implied by the above definition of genotypic worth H in selection index derivation. Economic values derived in this way may well be the most easily understood and acceptable by breeders and industry managers. However, the major concern about using this method is that the estimated regression coefficients, which should represent the value of genetic change, may be biased by environmental covariance between the traits (COTTERILL and DEAN, 1990). Furthermore, market prices that ought to reflect true benefit, may have serious imperfections, which are mostly due to lack of information (i.e. market signals) (AMER, 1994). An example on inadequate market signals is current log pricing in Australia that is based on log volume and completely disregards wood quality. In such a case, this method reflects only the current (fashionable) price trends which are highly inconsistent over time and therefore synonym "Hedonic Pricing Technique" (*e.g.* MUNN and PALMQUIST, 1997).

Method of Profit Functions

Profit equations have been extensively used for evaluating genetic differences in animal breeding (BRASCAMP *et al.,* 1985; SMITH *et al.,* 1986; WELLER, 1994). In forestry, this method was first used by BORRALHO *et al.* (1993) for developing breeding objectives for kraft pulp production of a *Eucalyptus globulus* plantation. A simple profit equation relating the cost savings per tone of pulp produced with stem volume, wood density, and pulp yield was developed:

$$Pr = In - \left[\frac{WC}{VOL}\left(c_{PE} + c_{PM}\right) + WC\left(c_H + c_T + c_M\right) \right] \qquad [5]$$

where Pr and In represent profit and income at market price ($/t of pulp produced); c_{PE} and c_{PM} are plantation establishment and maintenance costs ($/ha); c_H, c_T, c_M are harvesting, transport and mill costs, respectively
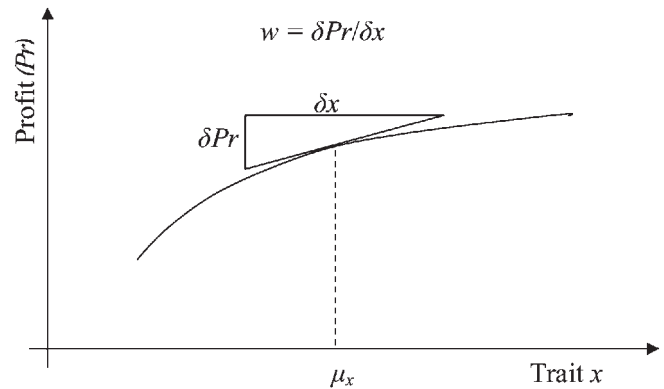

Figure 1. – Economic weight (w) calculated as the partial derivative of the profit function around current population mean current μ_x.

($/m^3$ wood); VOL is the average volume growth of (m^3 wood under bark per ha); and WC is wood consumption of the pulp mill expressed as the volume of wood required to produce a tonne (dry) of pulp. WC (m^3/t) can be estimated as the inverse of the product of wood density (DEN kg dry wood/m^3) and pulp yield ($PULP$, kg dry pulp/kg dry wood), $WC = 1000/(DEN \times PULP)$. The economic importance of each trait was calculated for different management scenarios with widely different cost structures.

Profit equations integrate a production system by expressing profit as function of a series of variables which include different traits as well as costs and incomes. Economic weights for each trait are then calculated as the partial derivative of the profit equation (*Figure 1*) with respect to a unit change in the trait concerned (MOAV and HILL, 1966). The main advantage of this method is that, because of its mathematical basis, it facilitates theoretical derivations of economic values under various circumstances (i.e. basis and perspectives, WELLER, 1994). However, estimation of marginal profit can be quite complex under certain circumstances and depends on both traits under selection and the market constraints. A disadvantage is that simple profit equations describing the relationship between genetic change and enterprise profit may be adequate for simple production systems (or production system segments), but more complex systems are better described by production system modelling. Furthermore, taking partial derivative of profit function does not address single-trait non-linearity, and it does not address marginal economic worth of traits being conditional upon values of other traits (AMER, 1994).

Bio-economic Modelling

POZONI and NEWMAN (1989) developed a general procedure to define breeding objectives and derive economic weights for different tree traits, which includes:
- specification of breeding, production and marketing systems;
- identification of sources of income and expense;
- determination of biological traits influencing income and expense; and
- derivation of economic weights for objective traits.

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Such derivation of economic weights (or values) must consider all wood flows, all cost and return factors, as well as restrictions on input or output. A well defined breeding objective should include all biological traits of economic importance for a production system. After identification of the traits of economic importance, the development of breeding objectives involves estimation of economic weights of the traits.

For estimation of economic weights a form of systems analysis, "bio-economic" modelling has been widely used in animal breeding programmes (TESS *et al.,* 1983; HIROOKA *et al.,* 1998; KOOTS and GIBSON, 1998a and 1998b; WOLFOVA *et al.,* 2005). A bio-economic model combines biological and economic factors (inputs and outputs) acting within a production system. Using such a model the effects of changes in any of the involved factors on the production system can be investigated. As a result, such a model provides a good tool for estimating the economic value of genetic changes in various traits, but also to investigate the robustness of these values to changes in management and market factors and to optimise the production system.

Derivation of economic weights includes modelling of trait effects on profitability of a production system. Bio-economic modelling uses the partial budgeting of marginal profit change (KLEMPERER, 1996) method to determine net profit that would accrue from a unit increase in each trait. This permits alternatives to be ranked in terms of cost and benefit. For each alternative the time stream of costs and benefits (both in monetary units) are discounted to obtain their present values. For example, in radiata pine in Australia the length of planning horizon is up to 40 years. Comparisons are then made in terms of net present value (income minus cost) or the ratio of income to costs (profitability index). Economic weights expressed in dollars per genetic standard deviation unit are the best indication of the relative potential for economic change in each trait through genetic selection (WELLER, 1994).

Non-linearity of profit can be accommodated within such bio-economic model. For example, for traits expressed as distinct categories (threshold traits) bio-economic models permit that the change of the mean on the underlying scale (normal distribution) can be examined (KOOTS and GIBSON, 1998b; WOLFOVA *et al.,* 2005). Such change on the underlying scale causes changes in proportions falling into different categories (*e.g.* timber grades) and hence economic change (i.e. MoE change vs. timber grade) (GREAVES, 1999; IVKOVIĆ *et al.,* 2006a). When linear selection indices are used they do not take account for non-linear interdependencies among traits. However, such interdependencies can be also incorporated within a bio-economic model, and economic weights adjusted properly for the true value of a trait change (IVKOVIĆ *et al.,* 2006b).

The main issues related to the use of bio-economic models in forestry arise from the complexity of production systems in forestry, uncertainty about production system goals due to long rotation intervals, and acceptability of the model by the breeders and industry managers. Those issues are addressed in the discussion section of this paper.

Selection Based Directly on Profit

Because of long rotation time in forestry there are usually two distinct sets of traits: traits in the index selection traits (measured at an early age) and traits in the objective (measured at harvest age) (FOSTER, 1986; COTTERILL and DEAN, 1988). Traits in the objective may be the same traits as selection traits but measured at mature age, but can also be different from selection traits and usually more closely related to product quality and the profit itself (*e.g.* timber grade recovery). To calculate a selection index it necessary to calculate *genetic juvenile-mature correlations* between selection traits and objective traits (SCHNEEBERGER *et al.,* 1992). However, these correlations are rarely available. For example, a selection trait can be juvenile branch size and genetic correlation may be available between juvenile and mature expression of the same trait. The mature branch size is directly related knot size (or knot area ratio), which in turn has direct effect on timber recovery. Profitability of improvement of mature branch size is then calculated based on phenotypic regressions of timber grade-recovery on knot size, obtained from sawmill performance studies. There are extensive databases and literature on net value of log characteristics at harvest-age (*e.g.* TODOROKI *et al.,* 2002).

There are only a few studies that actually used genetically structured sawmill studies and used timber grade recovery or profit itself as a selection trait. For example, MATHESON *et al.* (1997) used 24-year old trees in a highly-structured genetic experiment (i.e. control-pollinated families), to estimate genetic juvenile-mature correlations between early-selection traits and timber grade recovery. Due to high price of tree evaluation, population sample was limited to 11 full-sib families (families with both parents in common). Selection traits were height, straightness and branch size at age 8, diameter at age 11, and complete chronology of ring width and cell anatomy obtained from increment cores. Traits measured on mature trees at age 24 included structural timber grade and board distortion.

If parents of progenies that were processed in sawmill are selected, the method can effectively sidestep calculation of economic weights and selection indices. Genetic juvenile-mature correlation can also be calculated directly between selection traits and timber grade recovery (or profit itself), but genetically structured processing studies can also provide genetic juvenile-mature correlations between selection traits and various objective traits related to processing (e.g. knot size, wood stiffness). Those genetic juvenile-mature correlations can be used for selecting a different set parents based on the same objective traits. However, because large number of families or clones is required to estimate genetic correlations, such studies tend to be too expensive and are rarely done. The method also does not allow both costs and returns to be accounted and for net profit to be estimated for the mature breeding-objective traits, after grade proportions are obtained. Furthermore, one could rarely have blocks of single-family or monoclonal material, which is needed for projecting single-tree values into whole-crop performance.

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Bio-Economic Models for Forestry Enterprises

Specification of Breeding, Production and Marketing Systems

There have been only a few attempts made to formally develop breeding and deployment objectives for tree breeding (e.g. BORRALHO *et al.,* 1993; GREAVES and BORRALHO, 1996; GREAVES *et al.,* 1997a; CHAMBERS and BORRALHO, 1999; GREAVES, 1999; HARDING *et al.,* 1999; LOWE *et al.,* 1999; APIOLAZA and GARRICK, 2001; WITTOCK *et al.,* 2003; BYRAM *et al.,* 2005; WITTOCK *et al.,* 2006; CATCHPOOLE *et al.,* 2007). Most of those studies involved only one producer, one production system component, or only one segment of the industry, and were based mostly on assumptions. Bio-economic modelling of vertically integrated system for radiata pine structural wood production in Australia, based on data obtained from the industry has been recently done by IVKOVIĆ *et al.,* (2006a).

Forest plantation industry is generally segmented (i.e. international and national industry, breeding co-operative, individual firm, plantation and sawmill) and market signals in perfectly competitive markets should transfer benefits back to the point in the production system where the genetic improvement occurs. In an analysis at the national level the goal may be to increase the efficiency of production, while the goal of a particular analysis may be to increase the grower's profit. Even at the level of a regional breeding program, the goal will be different if the breeding enterprise is commercial or co-operative. Customised economic weights (selection indices) can be applied to maximise profitability at different levels and niche markets for material of particular technical properties (DEKKERS and GIBSON, 1998; APIOLAZA and GARRICK, 2001; IVKOVIĆ *et al.,* 2006a). However, due to operational constraints, objective specificity is more likely to be dealt at deployment stage rather than in breeding (POWELL *et al.,* 2004).

Identification of Sources of Income and Expense

As an example of forestry production system we use radiata pine (*Pinus radiata* D. Don.) plantation and processing in Australia. Radiata pine is the dominant softwood grown on more than 750,000 ha in Australia, targeting largely structural timber markets. *Table 1* contains the wood flows, costs and incomes per hectare for an average integrated production system at the base level and after improvements in four breeding objective traits: mean annual increment, branch size, stem straightness and wood stiffness (see IVKOVIĆ *et al.,* 2006a for more details). The radiata pine production system can be roughly partitioned into the following operations: plantation establishment, maintenance and silviculture, wood harvesting and transportation, and wood processing. The value of the end-product is typically determined by log or timber grades.

Each production system component has its associated cost or income. The cost of tree breeding and related research was not explicitly modelled in this example. It was considered to be a part of the royalties industry pays to co-operative for planting material (i.e. included in the cost of planting material). Tree breeding and

research activities in Australia are largely a co-operative effort, between industry and various research organisations, coordinated by The Southern Tree Breeding Association (MCRAE, 2005).

Determining how Biological Tree Traits Influence Income and Expense

In general, all traits that directly contribute to profit should be included in the breeding objective. In practice, however, for wood quality traits cost of trait measurement and evaluation (usually destructive) can be a limitation (SORRENSON *et al.,* 1997). Possibilities for genetic manipulation are also critical and traits that have little or no genetic variation do not need to be included (GODARD, 1998). For development of breeding objectives for radiata pine in New Zealand SHELBOURNE *et al.,* (1997) identified a number of important traits related to tree growth and form, solid wood (appearance and structural) products, poles, veneer, and pulp (kraft and mechanical) and paper.

To determine the relationship between biological tree traits and profitability of forestry enterprises, it is necessary to establish which elements of production and marketing systems of forestry enterprises are affected by certain biological traits. Recently, in Australia and New Zealand, the main focus is on wood quality and to identify traits (branching, form, and wood properties) that influence the outturn of different structural timber grades. It is important to establish technical and economic relationships between wood properties and final products so that breeding efforts could be directed towards the genetic improvement of those characteristics that strongly influence mechanical properties, appearance and stability of timber (e.g. IVKOVIĆ *et al.,* 2006a; CATCHPOOLE *et al.,* 2007). The technical details of the estimation of effects of various traits on pine production system are described elsewhere (e.g. GREAVES, 1999; HARDING *et al.,* 1999; IVKOVIĆ *et al.,* 2007), but some examples and models are described here.

Traits affecting plantation establishment and volume yield

Adaptability of plant material (i.e. frost and drought tolerance, pest and disease resistance) to different planting sites significantly influences the profitability of a production system in plantation establishment and maintenance stages. Growth rate, tree form, merchantable volume per hectare and overall enterprise profitability are related to adaptability (e.g. KLEMPERER, 1996; CHAMBERS and BORRALHO, 1997; BAHTI, 2000).

Growth rate is usually measured as *Mean Annual Increment* (MAI) per hectare. Improvement of growth rate can allow for shortening of rotation length, thus effectively reducing annual land and maintenance costs. Available growth and yield tables and other growth models usually do not include effect of genetics which can accelerate forest stand growth. Generally genetic gain in growth rate was modelled as a boost in site index, although CARSON *et al.* (1999) found a big boost in the basal-area function. Accounting for increased growth rates due to genetically improved material in growth models can be done by utilisation of so called "genetic

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Table 1. – Summary of the wood flows, costs and incomes per hectare for a radiata pine integrated production system in Australia (IVKOVIĆ *et al.,* 2006a). The values are in Australian dollara at the base level and after improvements in four breeding objective traits: mean annual increment (MAI), sweep (SWE), branch size (BRS) and modulus of elasticity (MoE).

	Base	Effect of 10% Trait Improvement[1]			
		MAI	SWE	BRS	MoE
Wood Flows (m³/ha)					
total harvested volume	736	810	736	736	736
WTC[2] and/or pulplog	178	194	171	168	178
preservation wood	25	28	25	25	25
sawlog	513	564	522	532	513
- small sawlog <20 cm SED[3]	61	69	64	65	61
- prime sawlog 20-45 cm SED	432	473	438	445	432
- large log >45 cm SED	20	22	20	21	20
green sawn timber	238	267	246	248	238
dry structural timber	133	148	138	139	142
- MGP 15[4]	3	3	3	3	12
- MGP 12	31	34	32	33	50
- MGP 10	77	86	79	81	68
- F8&F5	23	25	24	22	11
other sawn products	41	48	43	44	38
sawmill residue (chip)	136	151	138	141	136
Costs ($/ha)					
establishment costs	1912	1912	1912	1912	1912
ann. maintenance costs	1472	1472	1472	1472	1472
harvest costs	2073	2337	2069	2021	2073
transport costs	1201	1346	1199	1201	1201
wood procurement costs	236	269	241	246	236
green mill costs	2972	3350	3037	3109	2972
dry mill costs	3254	3682	3365	3391	3254
Total NPV[5] costs ($/ha)	*13121*	*14368*	*13295*	*13351*	*13121*
ΔNPV costs ($/ha)		*1247*	*174*	*230*	*0*
ΔNPV costs %		*9.5*	*1.3*	*1.8*	*0.0*
Income ($/ha)					
total stumpage	9191	10280	9219	9296	9191
WTC and/or pulplog	2663	2916	2534	2448	2169
preservation	549	627	549	549	549
sawlog	6355	7170	6443	6545	6355
- small sawlog <20 cm SED	584	645	608	606	584
- prime sawlog 20-45 cm SED	5451	6192	5515	5601	5451
- large log >45 cm SED	320	333	320	338	320
sawn timber	11930	13423	12328	12510	13004
- MGP 15	204	226	210	250	1016
- MGP 12	2467	2747	2548	2604	4189
- MGP 10	6005	6720	6210	6300	5341
- F8&F5	1133	1266	1175	1106	525
other sawn products	144	158	148	133	89
sawmill residue chip	2968	3406	3041	3134	2968
Total NPV income ($/ha)	*17561*	*19873*	*18079*	*18292*	*18793*
ΔNPV income ($/ha)		*2312*	*517*	*731*	*1232*
ΔNPV income %		*13.2*	*2.9*	*4.2*	*7.0*

[1] Mean Annual Increment (present mean 22.6 m³/ha/y); Sweep (present mean 10.3 mm/m); Branch Size (present MaxBRS mean 5.8 cm); Modulus of Elasticity (present mean 11.2 GPa);
[2] Whole Tree Chip;
[3] Small-end Diameter;
[4] Machine Graded Pine;
[5] Net Present Value at 6% discount rate.

multipliers" (HAMILTON and REHFELDT, 1994). In tree improvement there is also the problem of projecting individual-tree early age measurements to harvest-age whole-crop performance (DUTKOWSKI *et al.,* 2006).

However, increased growth rate does not necessarily translate into financial gain, because in radiata pine growth rate generally has a negative correlation wood quality (COWN, 1992; KUMAR, 2004). For example, currently, some mills in Australia may pay a premium for logs of a particular age class, of a minimum threshold green density or for logs from a particular area or site class (JAMES, 2001). The future influence of carbon cred-

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its on value of growth rate would depend on particular financial scenario. The economic weights of traits which determine dry weight of biomass and therefore carbon content (i.e. volume and wood density) are expected to increase relative to other traits (JAAKKO PÖYRY, 2000, NSW DPI, 2005; JAYAWICKRAMA, 2001; WHITTOCK et al., 2007). At the same time economic value of carbon content, due to a non-linearity of dry-weight function in respect to component traits, may favour stabilising selection for volume and wood density (*Fig. 2*).

Traits Affecting Harvesting and Transportation

The cost of log harvesting and transportation can influence forest profitability greatly. Harvesting and transportation costs vary with *log size* and *green density.* Branching habit has an effect on harvesting costs (large branches can increase harvesting cost up to 5%), while stem *straightness* affects both harvesting and transportation costs (IVKOVIĆ et al., 2006a). The developments in harvesting technology are likely to reduce relative significance of form and branching.

Traits Affecting Processing and End-Product Quality

Volume Recovery depends on log shape, which can be described by its small-end *diameter*, taper (ratio small-end diameter/large-end diameter) and sweep (BEAUREGARD et al., 1997). The general rule of thumb is that each 0.1 increase in the sweep deviation/small-end diameter ratio leads to a 5% decrease in timber recovery (COWN et al., 1984; TODOROKI, 1996). Nevertheless, log scanning and optimisation and automation of sawmilling technology can increase the sawn timber recovery (e.g. TODOROKI and RONNQVIST, 2002).

Mechanical performance is of high importance for structural lumber which is now routinely machine-stress-graded. The genetic relationship between wood density and stiffness (modulus of elasticity, MoE) or strength (modulus of rupture, MoR) was shown to be strong in radiata pine clear samples (KUMAR et al., 2002). Nevertheless, the relationship is influenced by the position (radial and longitudinal) of the specimen within a stem (COWN et al., 1999). There is good correlation between the mechanical performance of green and dry clear wood samples (BOOKER, 1997).

Besides wood density, microfibril angle (MFA) also has a major influence on mechanical performance of clear samples. Those two traits combined are reliable predictors of MoR and MoE (DONALDSON, 1995; COWN et al., 1999; IVKOVIĆ et al., 2008). Lower wood density and higher MFA are likely to be the causes of low stiffness and strength in inner (juvenile) wood of radiata pine. The importance of *juvenile stiffness* has to be stressed, especially from the perspective of shortening rotations and possibility for early selection.

The negative influence of spiral grain (SG) on mechanical properties of juvenile wood is also significant. Higher grain angle reduces the strength because wood is much stronger along the grain than across it. This holds in general for "cross grain" in structural lumber and boards (COWN et al., 1996a; TSEHAYE and WALKER, 1996; COWN et al., 1999). However, evaluation of density, MFA and SG is difficult and new acoustic tools are used for standing tree and log stiffness evaluation (CARTER, 2007). Therefore acoustic velocity or resonance may become a selection trait, although MoE will remain a breeding objective trait, which translates directly to timber stress grades (IVKOVIĆ et al., 2006a)

In addition to traits related to strength of clear samples, edge knots in lumber are considered as primary determinants of its strength in loblolly pine (RAJESHWAR
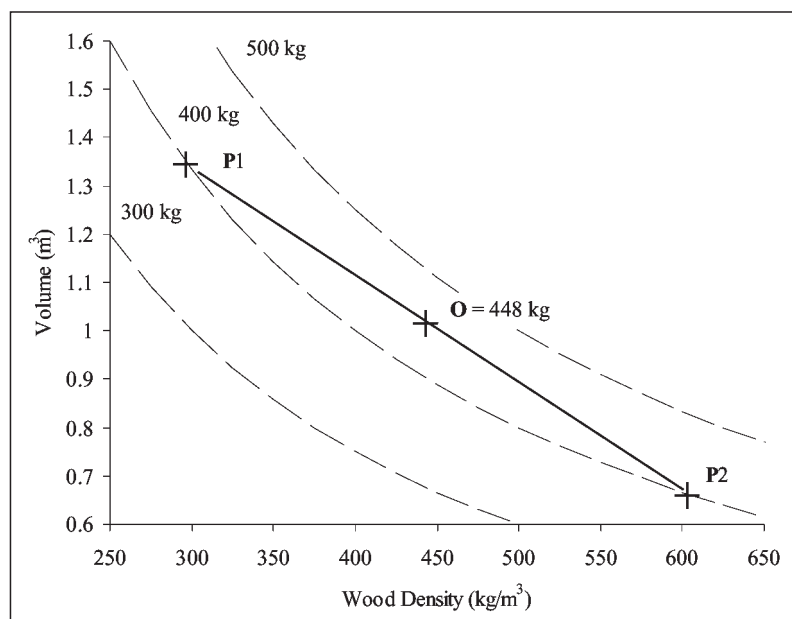

Figure 2. – Dry-weight function (Volume × Wood Density) isoclines showing the values of two parents (P) and their offspring (O). Offspring has an intermediate (mid- parental) value for both volume and wood density, but it has higher dry weight than either of the two parents.

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et al., 1997). Accuracy of prediction of MoR using MoE was shown to be independent of lumber density, but was improved by including in the regression knot area and sometimes position (GRANT *et al.,* 1984). However, in another study by BIER (1986), the average bending strength and stiffness of the timber were dependent on the basic density of the log, and the lower fifth-percentile strength may be more dependent on knot characteristics.

Caution is recommended when using results on sawmill grade outturn because prediction of average board grade per log based on sonic velocity was more reliable then prediction of actual grade proportions. Different logs can produce same average grade but can have different board grade proportions and different values because of non-linear prices for timber grades (IVKOVIĆ *et al.,* 2007). Similarly, variation of wood quality within and among trees is a major issue for wood products manufacturing. Despite narrowing of the genetic base of radiata pine planting materials (i.e. family and clonal deployment), timber from plantations are still highly variable (RIDOUTT, 1997). There is variation even between ramets of the same clone (SORENSSON, 2001), but most of the variability in wood properties resides within individual trees. A lesser proportion or better quality of highly variable *juvenile wood* would mean less steep gradients for physical and mechanical properties of wood (COWN, 1992; GAPARE *et al.,* 2006; WU *et al.,* 2007).

Timber Appearance and Clear-wood Proportion

For certain timber grades, mechanical properties are secondary to appearance. Timber appearance is determined by the size, number and quality of knots, and presence of other defects such as internal checking, resin pockets (bleeding), and needle traces. Wood defects were shown to be a significant cause of sawn timber degrade, with a strong economic impact (MILLER, 2001). The term "clearwood" is defined as defect-free solid wood material of any length. An analysis of the wood product markets showed a constant demand for clear wood products (HORGAN, 1991). A high proportion of clear wood can be achieved by an appropriate pruning regime. In unpruned trees, the proportion of clearwood is related to *internode length* (multiple or single nodes). CARSON (1988) reports grade recovery and profitability of long-internode and multinodal radiata pine trees grown in a direct sawlog regime.

Stability of Sawn Products

Dimensional stability of lumber is a major concern for building material and furniture. Shrinkage, twists, bow, crook and warping of lumber all cause dimensional instability. The problem is especially pronounced in *juvenile wood*, in which *microfibril angle* and *spiral grain* are larger and a significant amount of *compression wood is present*. Twist is the main cause of instability of radiata pine lumber produced in the fast grown plantations (COWN *et al.,* 1996b). Spiral grain is one of the major factors of this drying degrade. It does not cause longitudinal shrinkage directly, but a portion of tangential shrinkage is transferred in a longitudinal

direction (HASLETT *et al.,* 1991). In fast grown trees with wide rings, *ring curvature* has a similar effect as spiral grain. *Large knots* and associated cross-grain can also cause warping, especially bow and crook (COWN, 1992). If the quality of timber derived from fast-grown plantations does not improve, reconstituted wood or other materials may replace solid timbers (JOHANSSON *et al.,* 1994; COWN and VAN WYK, 2004).

Derivation of Economic Weights for Objective Traits

Based on the production system model (e.g. summary given in *Table 1*) and models of trait effect on various production system components linear economic weights can be calculated by changing value for a trait and observing the change in net present value (NPV) (e.g. IVKOVIĆ *et al.,* 2006a). However, non-linearities are common and trait effects on the NPV are often not linear over a wide range of trait values (IVKOVIĆ *et al.,* 2006b). Furthermore, the value of one objective trait may depend on the value of other traits in the objective. For example, the value of wood stiffness increases at high growth rates (GREAVES *et al.,* 1997b; IVKOVIĆ *et al.,* 2006b). If there is such a non-linear relationship between two main objective traits, their relative economic importance would depend on the base values in the population in which the selections are to be made. Re-optimisation of the production system is needed as the value of individual traits changes from generation to generation of genetic improvement.

Discussion and Conclusions

The objective of radiata pine silviculture is often defined as "to produce high-quality medium-sized logs with small in-grown knots and even-grown uniform rings". Relatively high initial stocking and multiple thinning practices are used to achieve even-grown rings, straightness and good branch control throughout the rotation (LEWIS and FERGUSON, 1993). However, the objective has not been formalised and quantified, especially with regards to the trade-off between volume growth and wood quality. One of the main benefits of the in-depth analysis is to better understand how improvement in different biological traits affects the overall economics of the production system. Bio-economic modelling can be used to define silvicultural objective as well as breeding objective.

A bio-economic model can also serve for evaluations of return on investment in forestry research (CUBBAGE, 1990). Since tree breeding is a long-term activity, systems analysis has been used to guide and evaluate tree improvement programs (e.g. PORTERFIELD, 1976; IVKOVICH and KOSHY, 2001; DANUSEVICIUS and LINDGREN, 2005, DIAZ-BALTEIRO and ROMERO, 2008). Production system modeling allows for sensitivity analyses to be used to determine which are the main factors affecting the production system profitability. If costs in monetary units can be assigned to different uncertainties and risks, risk analyses can be performed and a comparison made of the discounted sum of risk costs and other costs with the discounted sum of benefits that are predicted to result from a decision. However, it is often difficult to

assign exact monetary value to each uncertainty or risk (IVKOVIĆ *et al.,* 2006B).

Analysis of Complex Production Systems

In general, uncertainty specific to using economic weights in forestry are mainly related to complexity of production systems and length of rotation. Such uncertainty was the reason that a number of authors opted for other methods than explicit economic weights for deriving selection index weights (*e.g.* desired gain approach, PESEK and BAKER, 1969; Monte Carlo simulation, DEAN *et al.,* 1988; equal proportion of improvement, WU and YING, 1997). When modelling any system there is a necessary trade off between the complexity of the model and the use of simplifying assumptions. With increased model complexity may also be difficult to see how specific model components interact to produce results. On the other hand, invalid generalisations and simplifications and use of arbitrary assumptions are also undesirable.

An approach would be to evaluate effects on economic response when all model parameters have error probability densities (VOSE, 1996; IVKOVIĆ *et al.,* 2006b). Bio-economic models can also examine the "propagation" of errors in a production system model (DAQUITAINE *et al.,* 1999). Propagation of errors occurs in complex models when a sequence of models is used and the output of one model is the input to another model. Such analyses have the objective of controlling the spread of errors in order to improve predictive quality and accuracy of the models and determine which results are sensible to what model components. Increasing the accuracy of a bio-economic model (and of economic weights) is relatively cheap, in comparison with increasing the accuracy of genetic parameters and records on new parents and new traits. If desired accuracy cannot be obtained for a complex model, then a simpler but more accurate model may be preferred.

Uncertainty about Production System Goals
(Significance Time Frame)

Bio-economic modelling should result in more realistic silvicultural and breeding objectives if goals of a production system are clearly defined. Long generation intervals characteristic of forest trees make determination of relative economic values for the traits included in breeding objective particularly difficult. Extensive economic analyses and partial regression techniques have been applied, but the results may not be valid by the time progeny of selected trees are ready for harvesting (COTTERILL and JACKSON, 1984; BORRALHO *et al.,* 1993; AUBRY, 1998). At the same time, the application of selection indices requires estimates of genetic parameters, but errors of these estimates may also be high.

Although future changes from management and technological progress may be even more difficult to predict than improvements from genetic selection, the effects on production of economic values also can be evaluated in sensitivity analyses. For example, fixed costs do not affect economic values in the short term and are therefore ignored in the economic values derived in the base situation. However, in the long term fixed costs should

be included as variables (AMER, 1994). Another long term consideration is that the derivation of economic weights must consider future conditions rather than current economic and market conditions, because of the length of the plantation rotation. Modelling of future demands, prices and potential change in technologies is complicated by inherent uncertainties in markets, but is required for proper estimation of economic values.

Economic weights also need to account for re-optimisation of the production system input and output levels in response to genetic changes. MCARTHUR (1987) redefined an economic weight as: "the amount by which net benefit of the optimal (management) policy may be expected to increase for a unit of improvement in that trait". If a trait influences output quality rather than quantity, this can be reflected in the model by considering an alternative market for improved output in which the output price is higher. Such re-optimisation was first applied using mathematical programming by LADD and GIBSON (1978). GODARD (1983) presented an algebraic argument that re-optimisation of management is of trivial importance, though this is true only for (infinitely) small genetic changes. BRASCAMP *et al.* (1985) also questioned the extent to which re-optimisation of output levels is useful because in the long run, with widespread adoption of genetic improvement, increases in output would be offset by reduction in the output price and profit in the long run would be zero (e.g. DICKERSON, 1970; BRASCAMP *et al.,* 1985; SMITH *et al.,* 1986; WELLER, 1994). AMER (1994) criticized the theory of estimation of economic values in animal breeding literature, because it conflicts with the rational and empirical basis of economic theory. Genetic changes from tree improvement programs have been appreciable even in single generation. Bio-economic modelling showed that the re-optimisation can be important when evaluating economic importance of genetic changes (GREAVES *et al.,* 1997a; IVKOVIĆ *et al.,* 2006b).

Acceptability of Economic Weights and Selection Indices

Economic values can be estimated based on future market demands, however, industry managers and breeders tend to judge the suitability of economic values (and selection indexes) in relation to present economic circumstances, perhaps modified by their perception of future trends in consumer demands. Economic incentives that are provided through the current pricing system may not promote optimum selection decisions (*e.g.* log pricing based only on size without premium for wood quality). On the other hand, an index based on future market trends may not reflect the producer's perception and such an index therefore may be difficult to implement. A realistic pricing system should reflect the true value of the product, and should be flexible enough to accommodate changes in the market values. Customised indexes should allow producers to develop selection indices based on economic circumstances that are specific to an individual enterprise.

To improve acceptability of economic weights and selection indices, DEKKERS and GIBSON (1998) proposed that economic weights be used in conjunction with desired gain indices. The method is looking at the gain

rather than at the economic weights *per se*. Scientific principles of economic weight estimation are used to ensure that the outcome best meets the perceptions and needs of the users, while remaining as close as possible to the technical economic optimum. Other methods of presenting and delivering selection indexes, such as index expression, index formulation, focusing on the response to selection rather than on index weightings, construction of component indices and the use of direct accounting for costs of constraints rather than rescaling methods, can all help in improving the acceptance of an index. Development and implementation of selection criteria also involve consideration of the selective mating decisions. Strategies that focus on the use of a linear index for the selection of parents followed by selective mating of selected parents have been widely implemented (KINGHORN *et al.,* 2002).

Risk Mitigation through Breed Differentiation and Targeted Deployment

The complexity of factors influencing forestry production systems, the development of new technologies, and the ever-changing market conditions often cause tree breeders to choose conservative strategies for selection. They are reluctant to clearly declare the breeding objectives of their tree improvement programs (KING *et al.,* 1988; NAMKOONG *et al.,* 1988; MAGNUSSEN, 1990). In this situation of high uncertainty, when economic weights are practically unpredictable, optimisation has been suggested to find a mini-max solution, which maximizes minimum gain regardless of which value criteria applies at harvesting time (NAMKOONG *et al.,* 1988; BARNES, 1994; IVKOVICH and KOSHY, 2002; BYRAM *et al.,* 2005; DIAZ-BALTEIRO, 2008). However, this is a highly conservative option, which may result in loss in potential gain.

This problem, however, can be avoided to some extent, if a multiple-population strategy is adopted, and a different breeding objective is given to each of several breeding and deployment populations. Such an approach has been the key ingredient of recently proposed strategies for breeding and deployment of pines in New Zealand, USA, and Australia (KIBELLWHITE, 1997; JAYAWICKRAMA and CARSON, 2000; SORENSSON *et al.,* 2001; POWELL *et al.,* 2004; BYRAM *et al.,* 2005). The multiple-index selection technique, described by NAMKOONG (1976), can then be employed. The breeding or, more often, deployment population can be divided into several smaller ones and within each population a different selection index can be applied. By doing so, specific current objectives, but also a whole array of possible future alternatives, can be covered (HARWOOD, 1999). "Clonal-Portfolio" concept proposed by BURDON (2004) is one example of such approach.

Acknowledgements

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Response to Selfing in Seed Set, Seedling Establishment and Nursery Growth Based on Controlled Crosses of *Abies nordmanniana* Clones

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Abstract

Nordmann fir (*Abies nordmanniana*) is used for production of high value Christmas trees in short rotation. Potentially all trees are intended to be sold – no thinnings are normally applied. A high proportion of saleable trees per ha is the main key to secure economic return to the growers. Consumers demand a symmetric and rather uniform tree and, dependent on local traditions, it should be more or less dense and narrow. In Denmark, breeding of Nordmann fir and establishment of seed orchards focus on seed supply and improved Christmas tree quality – aiming at adaption and a rather uniform ideotype Christmas tree. Benefits from employing rather few clones, to maximise gain and uniformity, may potentially be counteracted by increased selfing. The objective of this study was to quantify the effect of selfing on percentage of filled seed and nursery establishment of seedlings. Inbreeding depression was seen for filled seeds (40%), growth traits (5–17%), plus mortality and axial damage (5–12 percent units). Many selfed seedlings survive and develop into marketable seedlings, although with a depression in numbers of 23–37%, or 9–12 percent units. Nursery sorting procedures can only partially reduce the number of inbred seedlings in Nordmann fir. The large variation among clones in the response to selfing indicates that knowledge of the behaviour of selfed progeny from specific clones in 'small number seed orchards' is of practical interest. Trade-offs between increased gain by selection of few clones and a penalty paid for increased inbreeding need further studies during a full Christmas tree rotation.

Key words: Seed orchard, selfing, filled seeds, inbreeding depression, nursery practice, Christmas tree.

Introduction

Nordmann fir (*Abies nordmanniana* (Stev.) Spach) is the most important Christmas tree species (in numbers sold) in Europe, and has been shown an increasing interest in North America too. In Denmark, breeding activities have been carried out since 1992 (NIELSEN, 2000, 2008) and seed orchards are now entering the stage where they produce commercial quantities of seed (DITLEVSEN, 2007, pers. comm.).

Nordmann fir is an exotic tree species to Denmark and is used as a short rotation crop harvested after 10 years, often on farm land. Because of the short rotation there is no need for keeping high genetic variation within the seed production populations (clonal seed orchards) to secure long term stability in the stands coming out of the seed. Furthermore, the small size of the Christmas trees means that thinning is normally not done in the production stands and that every tree in the stand potentially is the final saleable product. Therefore, any cause that delays the attainment of the end product or diminishes the quality is of major inter-

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