

Developing a Scots Pine Breeding Objective: a Case Study Involving a Swedish Sawmill

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The aim of this study was to develop a Scots pine (*Pinus sylvestris* L.) breeding objective for a vertically integrated sawmill in northern Sweden. The production system was defined as comprising the sawmill and the forests supplying it. Volume per hectare, wood density, survival and straightness were used as objective traits and the related selection criteria were measurements, collected at young tree age, of height, diameter, pilodyn penetration, vitality and straightness. A bio-economic model was used to calculate economic weights for the objective traits identified. We also investigated the efficiency of different selection indices based on these economic weights, in combination with available data on genetic parameters. Furthermore, we studied the effect of different discount rates on the calculated economic weights. The results showed that, compared to the full index (which included all selection criteria), omitting either vitality or straightness had a negligible effect, reducing predicted profit gain per hectare by less than one per cent. Height or diameter each had a greater effect, with a loss of predicted profit gain per hectare of up to 6%. Excluding pilodyn penetration from the selection index caused the largest reduction in predicted profit gain per hectare, amounting to over 10%. However, when both height and diameter were removed the predicted profit gain per hectare dropped to one-third of that based on the full index. Finally, ranking and genetic selection for the developed breeding objective was insensitive to changes in the discount rate.

Keywords economic weights, bio-economic model, tree breeding, multi-trait selection, *Pinus sylvestris*

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1 Introduction

The Swedish forest industry accounts for 11% of the exports and 3% of the gross domestic production (GDP) of Sweden (Skogsindustrin en faktasamling... 2007). Scots pine and Norway spruce are the two most important commercial tree species, with the former accounting for 38% of the 3000 million m³ of standing volume in Sweden (Statistical Yearbook of... 2008). Scots pine breeding programmes, therefore, have the potential to improve the raw material and produce significant economic and financial gains. Skogforsk (the Forestry Research Institute of Sweden) manages forest tree breeding programmes in Sweden which, for Scots pine, consists of 24 breeding populations with different adaption profiles intended to be representative of environmental conditions across the whole country (Danell 1991). Each breeding population consists of about 50 parents per generation and aims at general purpose objectives. For efficient multi-trait breeding, the objective of the breeding programme needs to be formally defined (e.g. Woolaston and Jarvis 1995). For selection purposes, the formalized breeding (or selection) objective (H) is the sum of the breeding values of the objective traits (\mathbf{g}) multiplied by their economic weights (\mathbf{v}) (Hazel 1943). Objective traits are defined as genetically determined biological traits that have an economic effect on the system under study, and economic weights describe their relative economic importance (e.g. Weller 1994).

To develop a breeding objective, the economic production system, in which gains from breeding are to be realized, must be defined (e.g. Groen 1989). The production system can vary in complexity depending on its extent and scope and the time frame considered (e.g. Groen 1989, Berlin 2009). In forest tree breeding contexts, attempts to define such a breeding objective have predominantly been undertaken for species with short-rotations, for example Eucalyptus (e.g. Borralho et al. 1993), radiata pine (e.g. Apiolaza and Garrick 2001, Ivkovic et al. 2006) and loblolly pine (Lowe et al. 1999). The extent of the production system in these studies ranged from a single company and product to vertically and horizontally integrated companies including pulp mills and

sawmills. However, the Swedish Scots pine breeding programme requires much longer rotations, and must provide genetic material suitable for the entire Swedish forest sector. Considering these conditions, Berlin (2009) suggested a framework for developing forest tree breeding objectives with particular emphasis on boreal conditions. He argued that using many delimited subsectors, each consisting of a particular industrial segment, would be an attractive option when developing a model for a defined part of the boreal forest sector (e.g. a nation), containing diverse production systems. Such subsectors should represent vertically integrated company structures in which all product flows are taken into account.

Objective traits may be expressed throughout the rotation, at thinning and final harvesting. Some are only expressed after industrial processing, making them difficult and expensive to measure and tree breeders often use so-called selection criteria instead. Selection criteria are traits that are mostly measured on standing trees early in the rotation in order to maximize genetic gain per unit of time (e.g. Haapanen 2001, Jansson et al. 2003 for Scots pine) by allowing for a shorter generation turn-over. The selection criteria also need to exhibit high genetic correlations with the objective traits.

The preferred method for genetic evaluation of the candidates for selection is the best linear unbiased prediction (BLUP), from which genetic and environmental effects are estimated simultaneously. In such cases, a multi-trait selection index (I), can be calculated as the sum of the predicted breeding values of the selection criteria for each individual ($\hat{\mathbf{u}}$) multiplied by their index coefficients (\mathbf{b}). These index coefficients may be predicted as follows (e.g. Schneeberger et al. 1992):

$$\mathbf{b} = \mathbf{G}_{ss}^{-1} \mathbf{G}_{s0} \mathbf{v} \quad (1)$$

where \mathbf{G}_{s0} is the genetic (co)variance matrix between the objective traits and selection criteria, \mathbf{G}_{ss} is the genetic (co)variance matrix between the selection criteria and \mathbf{v} the economic weights, as described above.

It is assumed that there is a priori knowledge of the genetic parameters associated with the selection criteria and objective traits, but in reality the relevant knowledge is continuously being built up

from genetic analyses of test data. Since selection criteria are generally measured in genetic test trials, any estimate of \mathbf{G}_{ss} is often based on substantial amounts of accumulated knowledge. However, less data is available about covariances between selection criteria and objective traits (\mathbf{G}_{so}), and economic weights (\mathbf{v}). For \mathbf{G}_{so} good estimates of age–age correlations are vital, since selection criteria are assessed early and objective traits may be expressed throughout the rotation. In order to calculate \mathbf{v} , appropriate models of the economic production systems must be developed.

The aim of this study was to develop a Scots pine breeding objective for a vertically integrated sawmill in northern Sweden, placing particular emphasis on economic weights. A bio-economic model was used to calculate the economic weights of the objective traits identified. We also investigated the efficiency of different selection indices, using available knowledge about genetic parameters. Furthermore, sensitivity analyses were performed with respect to different discount rates when calculating economic weights.

2 Material and Methods

2.1 Approach

The raw material from boreal forests is very heterogeneous and has a different set of critical characteristics depending on the stage of the rotation when trees are harvested and the part of the tree. In addition, subsequent industrial processes and products are also very diverse. To model an integrated production system with special focus on the production of solid wood products, we used a bio-economic approach to calculate economic weights (cf. Koots and Gibson 1998). The process of developing a formalized breeding objective can be divided into four steps (e.g. Groen 1989, Ponzoni and Newman 1989): 1) definition of the production conditions; 2) identification of the sources and flows of income and costs; 3) identification of biological traits (i.e. the breeding objective traits) that affect efficiency of production; 4) calculation of the economic weight of each objective trait. Herein, we follow the development of a breeding objective via these four steps.

2.2 Definition of Production Conditions

The production conditions define the economic system that makes use of any improvements derived from forest tree breeding; they can be divided into the definitions of: 1) efficiency of production and its function; and 2) production system level and size (sensu Groen 1989).

In this case study we used monetary terms to define efficiency of production (cf. Borralho et al. 1993, Greaves et al. 1997a, Lowe et al. 1999, Apolaza and Garrick 2001, Ivkovic et al. 2006). One sawmill and the forests supplying it, both owned by a Swedish forest products company (SCA), was used to represent a hypothetical vertically integrated company. SCA produces tissue, printing paper, packaging and solid wood products and owns around 2.6 million hectares of forest land in northern Sweden. The sawmill used in this study (Bollsta) is SCA's largest, with an annual production capacity of 450 000 m³ of solid wood products. The harvested forest within the integrated company yields both saw timber, supplying Bollsta, and pulp wood, which is mainly used in SCA's own pulp and paper mills. Since no data relating to the pulping process were available and almost all of the sawmill chips from Bollsta were sold to an adjacent independent pulp and paper mill, we decided not to include pulping in the production system studied. Incomes, therefore, arose from producing solid wood products and selling pulp wood and sawmill chips.

We assumed that the integrated company in our case study aims to maximize its returns given a fixed amount of forest land. Thus, the results were expressed in Swedish crowns (SEK*) per hectare and all costs were considered variable except those associated with forest land.

2.3 Identification of Incomes and Costs

The production system in this case study was vertically integrated. Therefore, both managing forests as well as industrial processing contributed to flows of income and costs. For managing forests, data were provided to represent an average stand

* 100 SEK (svenska kronor) = € 9.69 (2009-10-22)

Table 1. Time of expression of biological flows and economic data over a stand rotation.

	Establishment (t_0)	Pre-commercial thinning (t_1)	1st thinning (t_2)	2nd thinning (t_3)	Final harvesting (t_4)
Time (yrs)	0	10	37	52	85
Stand density (st ha ⁻¹) ^a	2200	2000	1200	800	–
VOL (m ³ ha ⁻¹) ^b	–	–	55	75	400
SAWPROP (%) ^c	–	–	30	65	75
1-SAWPROP (%) ^d	–	–	70	35	25
Silvicultural cost ^e	$C_{ES(t_0)}$	$C_{HA(t_1)}$	$C_{HA(t_2)}$	$C_{HA(t_3)}$	$C_{HA(t_4)}$
Transportation cost ^f	–	–	$C_{TR(t_2)}$	$C_{TR(t_3)}$	$C_{TR(t_4)}$
DEN _{SAW} (kg m ⁻³) ^g	–	–	μ	μ	$\mu + 10$
DEN _{PULP} (kg m ⁻³) ^h	–	–	$\mu - 15$	$\mu - 15$	$\mu - 20$
DEN _{CHIP} (kg m ⁻³) ⁱ	–	–	$\mu + 10$	$\mu + 20$	$\mu + 30$

^a Stand density (stems per hectare) after the activity

^b Harvested volume

^c Proportion saw timber of harvested volume

^d Proportion pulp wood of harvested volume

^e Cost of establishing a new stand, thinning and final harvesting in SEK ha⁻¹

^f Transportation costs in SEK ton⁻¹

^g Wood density of saw timber, $\mu = 400$ (kg m⁻³)

^h Wood density of pulp wood, $\mu = 400$ (kg m⁻³)

ⁱ Wood density of saw mill chips, $\mu = 400$ (kg m⁻³)

under the current silvicultural regime adopted by SCA in the study region. This silvicultural regime consisted of one pre-commercial thinning, followed by two commercial thinnings and a final harvest. Costs, therefore, arose at the time of stand establishment and during all thinning and harvesting operations (Table 1).

Pulp wood was sold at the forest, producing income based on market prices. Transportation costs were, therefore, only incurred for sawlogs. Data from the sawmill were collected over a 4-year period and mean values were used in an attempt to mitigate annual variation (see Table 2). The processing cost from the sawmill was a combined value, where all costs were considered to vary (e.g. buildings, machines and wages were varied in relation to the products produced). Income was also generated from sales of sawn wood products, sawmill chips and sawdust at the sawmill site. Dry saw chips and bark were used as a source of energy in the sawmill and internal pricing was considered to represent income. We did not attempt to model any market dynamics and made the simplifying assumption that demand was always satisfied by supply at the assumed market price.

Since costs and income occurred at different points in time (Table 1) they were discounted to a net present value using a real discount rate of 3%.

Table 2. Abbreviations used for product flows and economic data in the model description.

Symbol	Explanation
C_{PR}	Sawmill processing cost ^a
$SAWREC_{BASE}$	Sawmill recovery (%) ^b
$PROP_{rawchip}$	Raw chip proportion (%) ^c
$PROP_{drychip}$	Dry chip proportion (%) ^d
$PROP_{sawdust}$	Sawdust proportion (%) ^e
$PROP_{bark}$	Bark proportion (%) ^f
P_{saw}	Price of sawn products (SEK m ⁻³ s) ^g
$P_{rawchip}$	Price of raw sawmill chips (SEK kg ⁻¹)
$P_{drychip}$	Price of dry sawmill chips (SEK m ⁻³)
$P_{sawdust}$	Price of sawdust (SEK m ⁻³)
P_{bark}	Price of bark (SEK m ⁻³)
P_{pulp}	Price of pulp wood (SEK kg ⁻¹)

^a All costs are distributed relative to production and are consequently considered to be variable. Costs of processing are expressed in SEK m⁻³

^b Proportion of the de-barked log converted into solid wood products

^c Proportion of the de-barked log processed into raw chips sold to pulp mills

^d Proportion of the de-barked log ending up as dry chips (used for energy production in the mill)

^e Proportion of the de-barked log ending up as sawdust (sold to pellets-producer)

^f Amount of bark available after de-barking expressed relative to the de-barked log

^g (m³s) refers to volume of sawn products

2.4 Identification of Objective Traits Affecting Income and Costs

The objective traits chosen in this study were considered to be expressed at harvesting and were: 1) survival (*SUR*); 2) volume per hectare (*VOL*); 3) wood density (*DEN*); and 4) straightness of logs (*STR*). Survival of Scots pine in northern Sweden is often affected by climatic stress and is partly controlled by the growth rhythm, with an exploitable genetic variation (e.g. Persson 2006). Since mortality in Scots pine stands can have a considerable effect on volume production in northern Sweden, it is included in breeding programmes; models that include its effect have been developed (e.g. Berlin et al. 2009). *VOL* and *DEN* together represent biomass production. Besides being a good indicator of the strength properties in solid wood, wood density is also vital in all pulping processes (e.g. Bowyer et al. 2003, Wilhelmsson 2005). The straightness of the logs affects the proportion of sawmill recovery and is therefore of fundamental importance. Branching properties are important for Scots pine sawn timber, affecting both aesthetic and mechanical properties in the sawn boards (e.g. Measuring rules for ... 2008). Traits describing branching properties are also suggested by Berlin (2009) as potentially useful objective traits. Models have been developed to relate branching characteristics to sawn timber properties in Scots pine e.g. by using growth models together with models of taper, live crown and branching (e.g. Ikonen et al. 2003) or by modelling the shape of stem and interior knot structure directly from site, stand and tree characteristics (e.g. Moberg and Nordmark 2006). However, these models are not adapted to include genetic changes in objective traits useful for calculation of economic weights. Thus, branching characteristics were not included as objective traits in this study.

2.5 Bio-Economic Model for Calculation of Economic Weights

The model of the production system is intended to: 1) handle different uses of the raw material (i.e. sawing, selling pulpwood) and account for by-product flows (e.g. sawmill chips); and 2) handle changes in important characteristics (e.g. *VOL*, *DEN*) that depend on the time of harvesting and the part of the log that is being considered (see Table 1). The current bio-economic model and its components are described below, followed by the calculation of the economic weights.

When creating this bio-economic model, we have directly used or adapted many of the basic functions developed by Greaves (1999). The explicit equations for each income and cost item are given in Appendix A and the model equations for income were:

$$R_{tot(t_i)}(VOL_{(t_i)}, DEN_{(t_i)}, STR_{(t_i)}) = VOL_{(t_i)} \cdot (R_{pulp(t_i)} + R_{saw(t_i)} + R_{rawchip(t_i)} + R_{drychip(t_i)} + R_{sawdust(t_i)} + R_{bark(t_i)}) \cdot \left(\frac{1}{(1+r)^{t_i}} \right) \quad (2)$$

and for costs:

$$C_{tot(t_i)}(VOL_{(t_i)}, DEN_{(t_i)}) = (C_{est(t_i)} + C_{harv(t_i)} + VOL_{(t_i)} \cdot (C_{tran(t_i)} + C_{proc(t_i)})) \cdot \left(\frac{1}{(1+r)^{t_i}} \right) \quad (3)$$

where, r is the discount rate, t_i a certain point in time and the income and costs are those presented in Table 3.

To simplify the current model, costs of establishment and harvesting were fixed, since we assumed that a change in *VOL* would not lead to a change in the silvicultural regime. This means that the same number of seedlings would be planted and the slight increase in tree size would not affect costs of harvesting. Volume affected all other incomes and costs in a multiplicative way (Eq. 2 and Eq. 3), reflecting its basic and crucial importance. As a further simplification, it was assumed that changes in straightness did not affect the proportion of logs classified as saw

Table 3. Income and costs in the studied production system and the objective traits affecting each source of income and cost.

Income/cost at time t_i for:	Symbol	Objective traits that have an effect
Pulp wood	$R_{pulp(t_i)}$	$VOL_{(t_i)}, SUR_{(t_i)}, DEN_{(t_i)}$
Sawn products	$R_{saw(t_i)}$	$VOL_{(t_i)}, SUR_{(t_i)}, STR_{(t_i)}$
Raw sawmill chips	$R_{rawchip(t_i)}$	$VOL_{(t_i)}, SUR_{(t_i)}, DEN_{(t_i)}, STR_{(t_i)}$
Dry sawmill chips	$R_{drychip(t_i)}$	$VOL_{(t_i)}, SUR_{(t_i)}, STR_{(t_i)}$
Saw dust	$R_{sawdust(t_i)}$	$VOL_{(t_i)}, SUR_{(t_i)}, STR_{(t_i)}$
Bark	$R_{bark(t_i)}$	$VOL_{(t_i)}, SUR_{(t_i)}$
Establishment	$C_{est(t_i)}$	–
Harvesting	$C_{harv(t_i)}$	–
Transports	$C_{tran(t_i)}$	$VOL_{(t_i)}, SUR_{(t_i)}, DEN_{(t_i)}$
Industrial processing	$C_{proc(t_i)}$	$VOL_{(t_i)}, SUR_{(t_i)}$

logs (*SAWPROP*) but affected sawmill recovery (*SAWREC*) in a linear way, as follows (cf. Greaves 1999):

$$SAWREC(STR_{(t_i)}) = SAWREC_{BASE} + (STR_{(t_i)} - STR_{BASE}) \cdot \Delta SAWREC \tag{4}$$

where $SAWREC_{BASE}$ is the average recovery of logs with average straightness (STR_{BASE}) and $\Delta SAWREC$ is the change in recovery resulting from a change in straightness. The value of $\Delta SAWREC$ was adapted from Greaves (1999), and other values in Eq. 4 were obtained from SCA and the Bollsta sawmill.

Wood density was considered to affect transportation costs; since the maximum allowed weight of truck transports in Sweden is 60 tonnes they are limited by the weight rather than the volume of the load. Furthermore, *DEN* affected income from pulp wood and sawmill chips, which are both sold to the pulping industry. Although *DEN* has been found to be strongly related to the stiffness and strength of solid wood products, the effects of *DEN* on product value for solid wood products were not available in this case study. However, the Bollsta sawmill produces more products intended for joinery, furniture, floors and panels than for use as structural timber, reducing the importance of *DEN* in this case study.

The total result (P_{tot}) for an entire rotation with n extractions of trees from the stand (thinnings and final harvesting) and m objective traits was given by:

$$P_{tot}(X_1, \dots, X_m) = \tag{5}$$

$$\sum_{i=1}^n (R_{tot(t_i)}(X_1, \dots, X_m) - C_{tot(t_i)}(X_1, \dots, X_m))$$

The economic weight of a trait (v_{x_j}) was then given by:

$$v_{x_j} = \tag{6}$$

$$\frac{P_{tot}(X_1, \dots, X_j + \frac{\Delta X_j}{2}, \dots, X_m) - P_{tot}(X_1, \dots, X_j - \frac{\Delta X_j}{2}, \dots, X_m)}{\Delta X_j}$$

where X_j is the baseline (mean) value of the trait (j) under consideration and ΔX_j is the change in that trait. In order to relate the size of the trait change to the potential for genetic change, the coefficient of additive genetic variation (CV_A , the additive genetic standard deviation (σ_A) in relation to its mean value) was chosen to represent ΔX_j . This is a linear approximation of a likely non-linear system and as a result genetic gain estimates may be inflated (e.g. Greaves et al. 1997b). Therefore, to mitigate effects of any non-linearities, the economic weight was calculated by applying the change (ΔX_j) around the baseline value, as in Eq. 6.

Finally, the economic weight of *SUR* was expressed in terms of volume production equivalents (Berlin et al. 2009). Based on a series of five field trials representative of the region in which the raw material for the study sawmill grows, the estimated average level of survival was set to 70% and, accordingly, the economic weight of survival relative to volume production was:

Table 4. Additive genetic (σ_A^2) and phenotypic (σ_P^2) variances used and the genetic (above the diagonal) and phenotypic (below the diagonal) correlations for the selection criteria assumed to be representative of the studied region.

Trait	Unit	σ_A^2	σ_P^2	Correlations				
				<i>HTH</i> ₁₅	<i>DIA</i> ₁₅	<i>VIT</i> ₁₅	<i>PIL</i> ₁₅	<i>STR</i> ₁₅
<i>HTH</i> ₁₅	(m)	0.16	0.8		0.8	-0.15	0	0
<i>DIA</i> ₁₅	(cm)	0.16	0.8	0.8		-0.15	0.3	0
<i>VIT</i> ₁₅	(0,...,3)	0.08	1.6	-0.15	-0.15		0	0
<i>PIL</i> ₁₅	(mm)	4	13	0	0.3	0		0
<i>STR</i> ₁₅	[0,...,9]	0.16	1.07	0	0	0	0	

$$v_{SUR} = 0.12 \cdot v_{VOL} \tag{7}$$

assuming that the breeding values for survival were predicted using a continuous liability scale, as described in Berlin et al. (2009).

2.6 Selection Criteria and Efficiency of Selection Index

Based on the objective traits, the selection criteria must be chosen. To optimize gain from breeding per unit of time, traits are measured early in the rotations and we assumed that measurements were made when the trees were 15 years old. Height (*HTH*₁₅) and diameter (*DIA*₁₅) were used as indicators of *VOL*. Vitality (*VIT*₁₅) and straightness (*STR*₁₅) were assessed using ordinal scales, ranging from dead to fully vital (0–3) and from crooked to straight (0–9); these were also included as selection criteria. All selection criteria therefore refer to measurements at tree age 15. Finally, pilodyn penetration (*PIL*₁₅) was used as an measure of wood density.

Selection index coefficients were calculated according to Eq. 1 and the correlation between the selection index and the breeding objective (i.e. the accuracy of the selection index) was approximated as follows (cf. Schneeberger et al. 1992):

$$\tilde{r}_{HI} = \frac{\sqrt{s_I^2}}{\sqrt{\sigma_H^2}} = \sqrt{\frac{\mathbf{b}'(\text{var}(\hat{\mathbf{u}}))\mathbf{b}}{\mathbf{v}'\mathbf{G}_{00}\mathbf{v}}} \tag{8}$$

where s_I^2 is the approximate variance of the selection index, σ_H^2 is the variance of the breeding objective, \mathbf{G}_{00} is the genetic (co)variance matrix of the objective traits, \mathbf{b} is the vector of selection index coefficients as in Eq. 1 and \mathbf{v}

is the vector of economic weights. In addition $\text{var}(\hat{\mathbf{u}}) = \mathbf{B}'\mathbf{P}_{ss}\mathbf{B}$, where $\mathbf{B} = \mathbf{P}'_{ss}\mathbf{G}_{ss}$ and \mathbf{P}_{ss} and \mathbf{G}_{ss} are the phenotypic and genetic (co)variance matrix of the selection criteria, respectively. The $\text{var}(\hat{\mathbf{u}})$ was approximated assuming that breeding values are predicted solely using information retrieved from the individual itself with one record per selection criterion (cf. Schneeberger et al. 1992, Wei and Borralho 1999).

The correlation between the selection index and the breeding objective (\tilde{r}_{HI}) was used to calculate the predicted gain (i.e. profit gain per hectare) from an assumed individual or mass genetic selection given by:

$$\Delta H = i \cdot \tilde{r}_{HI} \cdot \sigma_H \tag{9}$$

where ΔH is the gain from genetic selection of parental trees and i is the selection intensity. Here we assumed i to be 2.665 standard deviations, which corresponds to individual or mass selection of the best 1% of trees as parents within a large population (e.g. Falconer and Mackay 1996). We omitted some of the selection criteria, so that the loss, in monetary terms, of excluding them could be calculated (cf. Wei and Borralho 1999).

Our estimates of \mathbf{G}_{ss} and \mathbf{P}_{ss} were based on both published studies (e.g. Haapanen et al. 1997, Hannrup and Ekberg 1998, Persson 2006) and own results from genetic field trial analyses (unpublished) (see Table 4). Regarding the negative genetic correlations between *VIT*₁₅ or *SUR* and other traits, the between-site survival ability concept as described in Persson (2006) is implied.

The genetic correlations between the selection criteria and objective traits are not well known and are mostly based on age–age correlations

(e.g. Lambeth 1980), since very few studies of Scots pine include actual measurements of the objective traits, due to the long rotation time for the species. Therefore, our estimate of \mathbf{G}_{s0} (see Table 5) was based on approximations from studies of age–age correlations (e.g. Haapanen 2001, Jansson et al. 2003) where available, and educated guesses elsewhere.

The genetic (co)variance matrix of the objective traits, \mathbf{G}_{00} , is arguably the most difficult component to produce good estimates for. In this case, therefore, the variances and correlations used (Table 6) were based on results in the literature relating to other species (e.g. Wei and Borralho 1999).

2.7 Sensitivity Analysis

When developing the breeding objective in this study we used a baseline real discount rate of 3% and performed sensitivity analyses by studying the economic weights at five different discount rates (1%, 2%, 3%, 4% and 5%). To investigate the sensitivity of genetic selection response from a varying discount rate we also studied the correlation amongst the breeding objectives for different discount rates (r_{H_k, H_l}) and the correlation amongst the corresponding selection indexes (r_{I_k, I_l}) as (James 1982):

$$r_{H_k, H_l} = \frac{\mathbf{v}'_k \mathbf{G}_{00} \mathbf{v}_l}{\sqrt{(\mathbf{v}'_k \mathbf{G}_{00} \mathbf{v}_k)(\mathbf{v}'_l \mathbf{G}_{00} \mathbf{v}_l)}} \tag{10}$$

and

$$r_{I_k, I_l} = \frac{\mathbf{b}'_k \mathbf{G}_{ss} \mathbf{b}_l}{\sqrt{(\mathbf{b}'_k \mathbf{G}_{ss} \mathbf{b}_k)(\mathbf{b}'_l \mathbf{G}_{ss} \mathbf{b}_l)}} \tag{11}$$

where \mathbf{v}_k and \mathbf{v}_l is the vector of economic weights and \mathbf{b}_k and \mathbf{b}_l is the vector of selection index coefficients for discount rate k and l respectively.

Table 5. Genetic correlations between selection criteria and objective traits used in the calculation of selection index coefficients.

Trait	<i>VOL</i>	<i>SUR</i>	<i>DEN</i>	<i>STR</i>
<i>HTH</i> ₁₅	0.8	−0.1	0	0
<i>DIA</i> ₁₅	0.8	0	−0.2	0
<i>VIT</i> ₁₅	−0.1	0.7	0	0
<i>PIL</i> ₁₅	0	0	−0.5	0
<i>STR</i> ₁₅	0	0	0	0.5

Table 6. Additive genetic variances (σ_A^2) and genetic correlations used for the objective traits assumed to be representative of the studied region.

Trait	unit	σ_A^2	<i>SUR</i>	Correlations <i>DEN</i>	<i>STR</i>
<i>VOL</i>	(m ³ /ha)	1600	−0.1	−0.13	0
<i>SUR</i>	(σ_i) ^a	0.01		0	0
<i>DEN</i>	(kg/m ³)	1600			0
<i>STR</i>	(mm/m)	0.09			

^a Expressed at an underlying scale as described in Berlin et al. (2009).

3 Results

Based on the model calculations, the breeding objective for the production system under consideration was:

$$H = 4.46 \cdot g_{SUR} + 37.2 \cdot g_{VOL} + 17.92 \cdot g_{DEN} + 251.5 \cdot g_{STR} \tag{12}$$

where g_i is the breeding value for the i :th objective trait ($i = SUR, VOL, DEN, STR$). All economic weights were expressed in SEK per unit of each objective trait. It was also assumed that the breeding values would be given in the form of deviations from their population means. The above calculated economic weights can also be expressed on a genetic scale to take the exploitable genetic variation of each objective trait into account. By multiplying the economic weight of each trait by its additive genetic standard deviation, the economic weights on a genetic scale for *SUR*, *VOL*, *DEN* and *STR* were 236.5, 1971, 716.7 and 75.4 SEK respectively. By using Eq. 1 the corresponding selection index became:

$$S = 1485 \cdot \hat{u}_{HTH_{15}} + 1887 \cdot \hat{u}_{DIA_{15}} + 190.6 \cdot \hat{u}_{VIT_{15}} - 292.4 \cdot \hat{u}_{PIL_{15}} + 94.3 \cdot \hat{u}_{STR_{15}} \quad (13)$$

where \hat{u}_j is the predicted breeding value for the j :th selection criterion ($j = HTH_{15}, DIA_{15}, VIT_{15}, PIL_{15}, STR_{15}$).

Results showed that omitting VIT_{15} and STR_{15} reduced predicted profit gain per hectare by less than one per cent (Table 7). The exclusion of one growth variable (HTH_{15} or DIA_{15}) had a greater effect; omitting DIA_{15} decreased the predicted profit gain per hectare by almost 6%. The single selection criterion with the largest marginal effect on predicted profit gain per hectare was PIL_{15} . Excluding PIL_{15} decreased the predicted profit gain per hectare almost by 10%. However, if both variables describing growth (HTH_{15} and DIA_{15}) were omitted only a third of the predicted profit gain per hectare compared to the full index remained.

Table 7. Accuracy of the selection index (\tilde{r}_H) and predicted increase in profit per hectare (ΔH) given a selection intensity of $i \approx 2.665$ for parents, with different sets of selection criteria included. The discount rate was set to 3%.

Selection index	\tilde{r}_H	ΔH (%) ^a
Full index ^b	0.386	100
HTH_{15} excluded	0.377	97.8
DIA_{15} excluded	0.364	94.4
VIT_{15} excluded	0.384	99.5
PIL_{15} excluded	0.344	89.3
STR_{15} excluded	0.385	99.9
HTH_{15} and DIA_{15} excluded	0.129	33.4

^a Relative selection gain (predicted profit gain per hectare) in H compared to the full index
^b All selection criteria ($HTH_{15}, DIA_{15}, VIT_{15}, PIL_{15}, STR_{15}$) are included in the selection index.

As expected, the absolute values of the economic weights changed drastically when the discount rate was varied (data not shown) and uncertainty about the appropriate discount rate will hamper attempts to calculate the profitability of breeding programmes. In comparison, the variation of the economic weights in relative terms was much less pronounced over the different discount rates used in the sensitivity analysis, but still over 10% for some of the relative ratios of economic weights (Table 8). However, all correlations amongst breeding objectives and all correlations amongst selection indexes for different discount rates showed negligible difference from 1.0 (data not shown). Thus, in this case, ranking and genetic selection for this breeding objective should not be severely affected by the discount rate. However, it is noteworthy that a discount rate of 5% resulted in the company achieving a negative return.

4 Discussion

To our knowledge, this is a first attempt to develop a formalized breeding objective based on a bio-economic model for Scots pine. The breeding objective developed was based on a case study involving a single sawmill representing one sub-sector of the Swedish forest products industry. This study used currently relevant data from the production system studied, but the long time-spans associated with the growth of boreal forests mean that possible far-reaching and widespread changes in the forest industry sector create great uncertainty about the future industrial uses of the wood. Therefore, the breeding objective described herein cannot be directly generalized to the entire

Table 8. Relative ratios of economic weights at five different discount rates (1%, ..., 5%).

Discount rate (%)	v_{SUR}/v_{VOL}	v_{DEN}/v_{VOL}	v_{STR}/v_{VOL}	v_{SUR}/v_{DEN}	v_{STR}/v_{DEN}	v_{SUR}/v_{STR}
1	0.12	0.501	7.519	0.240	15.152	0.016
2	0.12	0.492	7.194	0.244	14.493	0.017
3	0.12	0.482	6.757	0.249	14.085	0.018
4	0.12	0.471	6.329	0.254	13.514	0.019
5	0.12	0.460	5.917	0.262	12.821	0.020

Swedish breeding programme for Scots pine. Instead this study and its results should be considered to form a partial solution within a broader framework, which will be capable of representing the entire Swedish forest sector and addressing the associated uncertainty (Berlin 2009). In such a framework, a joint analysis of industrial segments, their relative importance, the products and their prices would be necessary, but this is beyond the scope of the current study. However, results from this study could be used as guidelines when performing genetic selection of Scots pine, primarily in the studied region, until more generally applicable models are available. Moreover, due to a scarceness of data and/or knowledge, several simplifying assumptions and limitations had to be imposed in this study. Therefore, this study has also highlighted areas where knowledge is less developed and where research is needed.

In the region where the raw material used in the study sawmill grows, mortality is generally not a major concern. The low importance of VIT_{15} as a selection criterion was therefore reasonable and expected. Including STR_{15} in the selection index had a negligible effect on the gain. This may, to some extent, be explained by the fact that we took all by-products into account and assumed no effect of STR on transportations. However, it is probably more important that Scots pine in northern Sweden has a generally good (i.e. straight) stem form compared to many other conifers in other locations (e.g. loblolly pine). The importance of including growth traits (HTH_{15} , DIA_{15}) as selection criteria is well-known and without the inclusion of any growth indicators, gain from selection would be greatly reduced. However, the importance of PIL_{15} was somewhat surprising. In addition, the effects of including PIL_{15} would probably have been greater, if the production system had included pulp mill processing and the well-established relationship between wood stiffness/strength and density. Thus, the results from this study indicate that DEN may be an important objective trait for Scots pine and we suggest that the feasibility and value of including pilodyn measurements (or other indicators of DEN) in the selection criteria for predicting breeding objectives including DEN should be examined.

The sensitivity analyses showed that the different discount rates had only a marginal effect on

the relative relationships between the economic weights. This is because all objective traits in the current production system were considered to be the same or expressed similarly at the time of all thinning and harvesting operations. However, this study relied on several simplifying assumptions and limitations. If more elaborate and complete models were used it is likely that some objective traits would be expressed differently during the different stages of rotation. Therefore, the use of appropriate discount rates is essential, primarily for evaluation of the profitability of the breeding programme but also for proper genetic selection, when the breeding objectives for Scots pine in Sweden become further developed.

VOL is a composite outcome of growth and environmental components including silvicultural regime and site conditions. Berlin (2009) suggested that appropriate objective traits for boreal conditions should be applicable over a wide range of site conditions, silvicultural regimes and industrial subsectors. Therefore, it could be argued that growth rather than VOL should be chosen as an objective trait, since a change in growth will probably affect the silvicultural regime, either by encouraging the planting of a different number of seedlings or by influencing the timings of thinning and final harvesting. If the silvicultural regime changes due to increased growth, this affects the entire system including the other objective traits (see e.g. the discussion by Amer and Fox (1992) concerning the optimization of a production system). Assuming, for example, that increased growth leads to shorter rotations, the value of the other objective traits (e.g. DEN) will change compared to the baseline situation. Ivkovic et al. (2006) used the mean annual increment in volume per hectare at the end of rotation (MAI) as an objective trait and allowed MAI to vary during the rotation by using a growth and yield model. In addition, a genetic change in growth was treated as a site-quality class change. In contrast, we used VOL as an objective trait with the simplifying assumption that a genetic change in VOL affected all harvests equally, in relative terms. In addition, we assumed a fixed amount of forest land and that a change in tree growth would not alter the silvicultural regime. Therefore, we believe that a growth and yield simulator capable of producing values for all objective traits under different

silvicultural situations, given a genetic change in growth, would be a considerable improvement compared to the model developed in this case study. Such simulators are under development for Scots pine (e.g. Hynynen et al. 2005).

We directly used or adapted many of the functions describing relationships between objective trait changes and production system items (e.g. product value, costs, biological flows) from other studies (e.g. Greaves 1999) due to lack of fully elucidated relationships for Scots pine. Although models relating branching characteristics to sawn timber properties in Scots pine exist, they are not adapted to include genetic changes in objective traits useful for calculating economic weights. Thus, branching characteristics were not included as objective traits in this study. However, since the quality and value of Scots pine sawn timber is affected by branching characteristics we believe that they should be included as objective traits when improved models and information is obtainable. Furthermore, effects of *DEN* and *STR* on the quality of boards were also ignored and their importance may, therefore, have been underestimated in this study. In addition, we suggest that an expansion of the production system assumed in this study needs also to include pulp production, in order to deliver a more complete breeding objective. For example traits describing the basic chemical contents of the wood (e.g. cellulose and lignin content) are potentially important traits (Berlin 2009) but could not be included in this breeding objective. We therefore suggest that more studies should be done to determine, for Scots pine in Sweden, relationships between objective traits and aspects of the production system.

In this study there is uncertainty about the genetic parameters necessary for performing selection for the suggested breeding objectives. We used age–age correlations for estimating G_{s0} . For example, age–age correlations of height at a young age and volume at approximately half rotation age (e.g. Jansson 2007) were used to guide our assumed correlation between HTH_{15} and VOL . However, most studies of age–age correlations in Scots pine have examined height and only a few studies have considered other traits, e.g. diameter and density (e.g. Hannrup and Ekberg 1998, Hannrup et al. 2000). Thus,

most of the parameter estimates for G_{s0} and particularly G_{00} were derived from literature on other species and general assumptions. Since the efficiency of a selection index is sensitive to errors in genetic correlations (e.g. Hayes and Hill 1980, Sales and Hill 1976, Gibson and Dekkers 2003), increased knowledge of these parameters is essential. More research and the development and maintenance of long-term genetic field trials are therefore needed to increase our knowledge of genetic parameters.

In summary, a breeding objective for Scots pine in northern Sweden was developed based on a case study involving a single sawmill. This study and its results should be considered as a partial solution of a broader framework, capable of representing the entire Swedish forest sector. Results showed that VIT_{15} and STR_{15} were of negligible value as selection criteria, but that PIL_{15} was of moderate value and that compound growth indicators (HTH_{15} , DIA_{15}) was very important. The discount rate was found to have a very small effect on the relative economic weights. Furthermore, we identified several areas where knowledge is less developed and research is needed. The most important of these were: 1) relationships between objective trait changes and aspects of the production system (to allow for inclusion of more objective traits and a more complete breeding objective); 2) a flexible growth and yield simulator to model growth and other traits better; and 3) the genetic parameters necessary for performing selection for the suggested breeding objectives (G_{s0} , G_{00}).

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Appendix A

Income and cost items in Eq. 2 and Eq. 3 of the bio-economic model. The symbols are as described in Tables 1, 2 and 3 except for $GDEN$, which is described in Eq. A.11.

$$R_{pulp(t_i)} = P_{pulp} \cdot (1 - SAWPROP_{(t_i)}) \cdot GDEN_{pulp(t_i)} \quad (A.1)$$

$$R_{saw(t_i)} = P_{saw} \cdot SAWPROP_{(t_i)} \cdot SAWREC(STR_{(t_i)}) \quad (A.2)$$

$$R_{rawchip(t_i)} = P_{rawchip} \cdot SAWPROP_{(t_i)} \cdot DEN_{rawchip(t_i)} \cdot (1 - SAWREC(STR_{(t_i)})) \cdot PROP_{rawchip} \quad (A.3)$$

$$R_{drychip(t_i)} = P_{drychip} \cdot SAWPROP_{(t_i)} \cdot (1 - SAWREC(STR_{(t_i)})) \cdot PROP_{drychip} \quad (A.4)$$

$$R_{sawdust(t_i)} = P_{sawdust} \cdot SAWPROP_{(t_i)} \cdot (1 - SAWREC(STR_{(t_i)})) \cdot PROP_{sawdust} \quad (A.5)$$

$$R_{bark(t_i)} = P_{bark} \cdot SAWPROP_{(t_i)} \cdot PROP_{bark} \quad (A.6)$$

$$C_{est(t_i)} = C_{ES(t_i)} \quad (A.7)$$

$$C_{harv(t_i)} = C_{HA(t_i)} \quad (A.8)$$

$$C_{tran(t_i)} = C_{TR(t_i)} \cdot SAWPROP_{(t_i)} \cdot GDEN_{saw(t_i)} \quad (A.9)$$

$$C_{proc(t_i)} = C_{PR(t_i)} \cdot SAWPROP_{(t_i)} \quad (A.10)$$

Green density ($GDEN$) is calculated by

$$GDEN_{type} = \left(DEN_{type} + MC \left(1 - \frac{DEN_{type}}{SG} \right) \right), \text{ type} \in [pulp(t_i), saw(t_i)] \quad (A.11)$$

Where the moisture content (MC) is assumed to be 70% and the specific gravity of wood (SG) is assumed to be 1.5 ton/m³ (cf. Greaves 1999)