Development of Economic Forest Tree Breeding Objectives

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Cover: The oaks of Visingsö, planted in the early 19th century to ensure supplies of raw material for naval shipbuilding. The navy, however, declined the offer to use the oaks when they were ready for harvest in the 1970s, and many of them are now used to make whisky barrels.
(photo: H. Lundberg & T. Warner)

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Abstract

The overall objective of this thesis was to suggest a framework for developing forest tree breeding objectives with particular emphasis on boreal conditions and, as components of this framework, to define breeding objectives and calculate economic weights based on two case studies of Scots pine in northern Sweden.

The framework was designed to take into account boreal conditions, with long rotations, heterogeneous raw materials and a diverse production system. It is suggested that the forest products industry should be divided into subsectors, each representing a particular industrial segment. For each subsector the production system studied should consist of a vertically integrated structure, with the aim of maximising profit, and in which all costs are considered variable. In addition, appropriate objective traits should be applicable over a wide range of site conditions, silvicultural regimes and industrial subsectors.

The first case study examined how to calculate the economic weight of tree survival relative to volume production, taking patchiness into account. For this purpose a new model was developed and then applied to field data in order to obtain relative economic weights for a set of Scots pine breeding populations in northern Sweden. The relative economic weight of survival varied markedly between the studied breeding populations, increasing more than three-fold with decreasing survival and increasing patchiness.

The second case study defined a breeding objective for a vertically integrated company in northern Sweden, which cultivates forests and supplies its own sawmill. Results showed that a compound growth indicator (height and diameter) was a very important selection criterion, while a wood density indicator was of moderate value and vitality and straightness indicators were of negligible value.

The framework can be adapted to determine economic weights appropriate for a boreal forest sector with a diverse production system and can also act as a platform to assist strategic breeding decisions when there is uncertainty within the system. Within the framework, analyses may combine several different scenarios, for which subsectors can be allocated different sizes that represent their future relative importance based on predicted supply and demand.

Keywords: Forest tree breeding, Multi-trait selection, Bio-economic model, Economic weights, Boreal conditions, Scots pine.

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Prediction is very hard, especially about the future.

Niels Bohr (1885-1962)

Contents

List of Publications

This thesis is based on the work contained in the following papers, referred to by bold Roman numerals in the text:

I Berlin, M., Jansson, G., Lönnstedt, L., Danell, Ö. & Ericsson, T. A framework for developing forest tree breeding objectives with emphasis on boreal conditions (Submitted).

II Berlin, M., Danell, Ö., Jansson, G., Andersson, B., Elfving, B. & Ericsson, T. (2009). A model to estimate economic weight of survival relative to volume production taking patchiness into account. *Scandinavian Journal of Forest Research* 24(4), 278-287.

III Berlin, M., Jansson, G., Danell, Ö., Andersson, B., Elfving, B. & Ericsson, T. (2009). Economic weight of tree survival relative to volume production in tree breeding: A case study with *Pinus sylvestris* in northern Sweden. *Scandinavian Journal of Forest Research* 24(4), 288-297.

IV Berlin, M., Lönnstedt, L., Jansson, G., Danell, Ö. & Ericsson, T. Developing a Scots pine breeding objective: A case study involving a Swedish sawmill (Submitted).

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1 Introduction

In most forest tree breeding programmes, multiple traits are taken into account when selecting the best individuals. Therefore, predicted breeding values for the different traits must somehow be assessed relative to one another. In such cases, it is common to use an index, where the important traits are standardised to the same scale by assigning them economic weights then summed to give the index value (Hazel, 1943; Schneeberger et al., 1992).

The economic weight of a trait describes the value of a change in that trait and is calculated on the basis of information about the biological and economic system in which the gains from breeding are to be realised. Economic weights can be expressed in either biological or monetary terms, but the latter is mostly used (e.g. Weller, 1994). Although economic weights are important for genetic selection, knowledge about them is still limited in the forest tree breeding sector. Apiolaza and Greaves (2001) suggested that possible explanations for this are: (i) the complexity of the forest production system; (ii) difficulties in determining the relationship between wood properties and final product quantity and quality; and (iii) uncertainty about the future use of trees due to long rotation times. Therefore, formally defined forest tree breeding objectives have, so far, been derived only for production systems involving fast growing species (e.g. eucalyptus and radiata pine, which have rotations of 10 to 25 years) and have often focused on a single industry or product. In comparison, boreal forestry and the associated forest products industry are characterised by long rotations (often rotations last between 50 years to over a century), a heterogeneous raw material and a diverse production system.

A breeding programme may include many breeding populations, each comprising a set of individuals that contain the population's genetic variation. This variation is the basis of breeding and is exploited by selecting the individuals that perform best. These are then crossed to generate a new generation that performs better than the last. However, there is a general trade-off between genetic gain and genetic diversity. Since higher selection intensity means reduced genetic diversity and variation, the short term aim of high genetic gain in the next generation must be balanced against the long term sustainability of the genetic base for breeding. Therefore, modern breeding programmes have elaborate systems for controlling inbreeding and preserving genetic variation to ensure that substantial genetic gain can be achieved over numerous generations (e.g. Lindgren and Mullin, 1997).

Consequently, a breeding programme is made up of several important steps and trade-offs. This thesis focuses on the development of economic forest tree breeding objectives with particular emphasis on boreal conditions. A framework was developed to account for and adapt to such conditions and then used to define economic breeding objectives for Scots pine in northern Sweden. The results obtained and the general implications for Swedish tree breeding programmes are presented below.

1.1 Boreal conditions and forestry

The taiga or boreal forest is the world's largest terrestrial biome, dominated by conifers such as larch, spruce, fir and pine species. Boreal forests occur in the northern hemisphere, covering large areas of the northern parts of Europe, North America and Asia. In Fennoscandia, Norway spruce and Scots pine are the most prominent species. The boreal climate is harsh, with long cold winters and short growing seasons (often lasting less than 6 months).

Boreal conditions and forestry are defined according to **I**, as being characterised by: (i) long rotations (50+ yrs) with one or several intermediate thinnings; (ii) a heterogeneous raw material with a different set of characteristics depending on when trees are harvested and which end use or part of the tree is being considered; (iii) a forest products industry consisting of several diverse industrial segments utilizing and competing for different subsets of the raw material; (iv) great uncertainty about future industrial use of wood due to the long rotations; and (v) forest tree breeding programmes that, as a result of multiple uses and uncertainty, supply specific parts of the boreal forest sector containing diverse production systems (e.g. at the national level) with appropriate genetically improved material.

1.2 Methods used in multi-trait genetic selection

A basic paradigm in quantitative genetic theory is the infinitesimal model (Fisher, 1918), which is based on the assumption that the genetic expression of a trait is governed by many independent genes, each making a small contribution, and that these contributions are cumulative. Although the biological background of genetic trait expression is more complex than this, this model has proven to be a very robust tool for breeding purposes and most of the methods described below are based on it.

A basic issue that has large implications for multi-trait selection is the presence of genetic correlation between traits. Traits may be genetically correlated because: (i) the same gene(s) affect several different traits (*pleiotropy*); (ii) genes affecting different traits in close physical proximity on the chromosomes are inherited together (*linkage*); and (iii) the definition of different traits are partly overlapping and express the same underlying biological processes. If two traits are negatively correlated, selection for one will have an adverse effect on the other.

A number of different methods have been suggested to handle multi-trait genetic selection. Hierarchically they can be divided into index or non-index methods. With reference to how traits are valued economically, index methods can also be divided into objective and non-objective methods (e.g. Groen, 1989) and, finally, the objective methods can be divided into data evaluation and bio-economic models (Figure 1). These methods are briefly reviewed below.

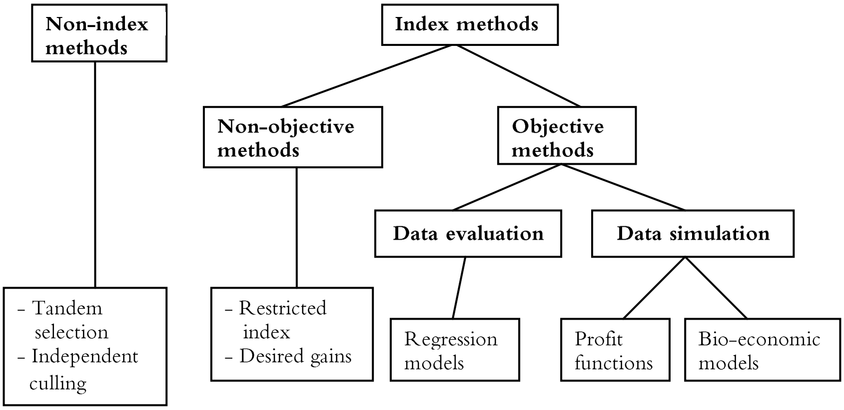

Figure 1. Overview of the different methods used in multi-trait genetic selection

Two classical non-index methods used for multi-trait selection are tandem selection and independent culling. Tandem selection involves selection for several traits, one at a time, over several generations, whereas independent culling involves establishing levels of merit for each trait and simultaneously culling the individuals that do not achieve the specified level (Hazel and Lush, 1942). In index methods a weighted sum of the traits are formed and used for simultaneous selection. Index methods have been found to have greater efficiency in terms of genetic gain compared to non-index methods (e.g. Hazel and Lush, 1942; Finney, 1962; Young, 1961).

In index methods each trait is multiplied by a weight, which describes its economic importance in a defined bio-economic system. Non-objective methods calculate economic weights for which the rate of genetic change in one or more of the traits is in some way pre-determined (Gibson and Dekkers, 2003). Economic weights are assigned to traits indirectly by considering desired or restricted levels of genetic gain with respect to different traits (e.g. Kempthorne and Nordskog, 1959; Brascamp, 1984). Such methods have mainly been advocated when it is considered difficult to model the economic production system accurately or when one or more traits exhibit non-linear relationship with the economic value. An example from animal breeding is the size of hen's eggs, which may have an intermediate optimum (e.g. Kempthorne and Nordskog, 1959). However, Gibson and Kennedy (1990) demonstrated the inefficiency of desired gains methods compared to objective methods and concluded that non-objective methods should be avoided for economic genetic selection.

Objective methods are based on models where one or a set of equations are used to represent the behaviour of an economic production system (*sensu* Groen, 1989). Economic weights are calculated by analysing how marginal changes in the objective traits affect the modelled system (e.g. Groen, 1989; Ponzoni and Newman, 1989). The first of the two types of objective methods is data evaluation, which uses economic field data to estimate multiple regressions that predict the economic results of changes in objective traits (e.g. Goddard, 1998). The regression coefficients may then be interpreted as economic weights. The second approach accounts for sources of income and cost directly and can be divided into profit (or efficiency) functions and bio-economic models. Profit functions are single equation models, whereas bio-economic models contain a complex set of equations describing the relationship between trait values and production results. The latter are more flexible, can represent more complex realities and provide numerous opportunities to vary biological, technological and economic components. They can also handle detailed and complex (e.g. non-linear) relationships between objective traits and production components and variables (e.g. Koots and Gibson, 1998; Ivkovic et al., 2006a). Since the forest production system is complex in this respect, bio-economic models have many features desired in a forest tree breeding context and, therefore this was the approach adopted in the studies upon which this thesis is based.

1.3 Ranking of genotypes using a multi-trait index

When using objective methods to calculate economic weights, a formalised breeding objective must be developed to rank and select the best individuals for the next generation. The breeding objective (H), is the sum of the breeding values of the objective traits ($\boldsymbol{g}$) multiplied by their economic weights ($\boldsymbol{v}$):

$$H = \boldsymbol{g}'\boldsymbol{v}$$

Objective traits are, preferably, those that directly influence income and cost in the production system, while economic weights describe the relative economic importance of the objective traits (e.g. Weller, 1994). Consequently, in order to develop a breeding objective we need knowledge of the objective traits as well as how changing them affects the bio-economic production system.

Objective traits may be expressed throughout the rotation, at thinning and at final harvesting; some are only expressed after industrial processing. Thus, objective traits are often not expressed until late in the rotations and they may be difficult and expensive to measure. Therefore, to optimize gain per unit time, tree breeders often use traits that are measurable early in rotation and are genetically correlated with the objective traits. In contrast to the objective traits, these are sometimes called selection criteria or measurement traits. Genetic multi-trait selection may then be performed by using a selection index (I) (Hazel, 1943) as:

$$I = \boldsymbol{b}'\boldsymbol{x},$$

where $\boldsymbol{x}$ is a vector of phenotypic values of the selection criteria, pre-adjusted for systematic environmental effects, and $\boldsymbol{b}$ is a vector of selection index coefficients, which are obtained as:

$$\boldsymbol{b} = \boldsymbol{P}^{-1}\boldsymbol{G}_{\boldsymbol{os}}\boldsymbol{v},$$

where $\boldsymbol{P}$ is the phenotypic (co)variance matrix of the selection criteria, $\boldsymbol{G_{os}}$ is the genetic (co)variance matrix between the objective traits and the selection criteria and $\boldsymbol{v}$ is the vector of economic weights.

However, the use of pre-adjusted phenotypic values to obtain selection indices has been succeeded by the best linear unbiased prediction (BLUP) (Henderson, 1973). Using a BLUP procedure allows for i.a. simultaneous estimation of genetic and environmental effects taking all genetic information into account, thus allowing comparisons between genetic groups and generations. With an individual tree model, where breeding values are predicted from only a single record of each individual per selection criterion, the breeding values of the objective traits can be obtained from (e.g. Schneeberger et al., 1992):

$$\boldsymbol{\hat{g}} = \boldsymbol{G_{os}G_{ss}^{-1}\hat{u}},$$

where $\boldsymbol{\hat{g}}$ is a vector of predicted breeding values of objective traits, $\boldsymbol{G_{ss}}$ is the genetic (co)variance matrix between the selection criteria and $\boldsymbol{\hat{u}}$ is a vector of BLUP for breeding values of the selection criteria. The selection index is then:

$$I = \boldsymbol{\hat{g}'v}$$

Thus, genetic selection cannot be performed without having estimates of the genetic parameters (genetic and phenotypic variances and covariances) (Figure 2). In general, tree breeders have a much better knowledge of selection criteria than of objective traits including their economic weights. In this thesis I focus on the development of economic breeding objectives, which results in the identification of objective traits and the calculation of economic weights.

1.4 Development of economic forest tree breeding objectives

Most of the methodology regarding formally defining breeding objectives and calculating economic weights has been developed in the context of animal breeding, but it is also applicable to forest tree breeding. To develop a formally defined breeding objective and calculate economic weights, a study of the system that utilises the output from breeding is required. The first step in such a study is to define the production conditions, i.e. the conditions that determine the organisation and the efficiency of production (Groen, 1989). Thereafter the subsequent process can be divided into three further steps, following Ponzoni and Newman (1989): (i) identification of the sources and flows of income and cost; (ii) identification of the biological traits (i.e. the breeding objective traits) that affect efficiency of production; and (iii) calculation of the economic weight of each objective trait. This process results in the development of a formalised breeding objective once the objective traits have been identified and their economic weights calculated (Figure 2).

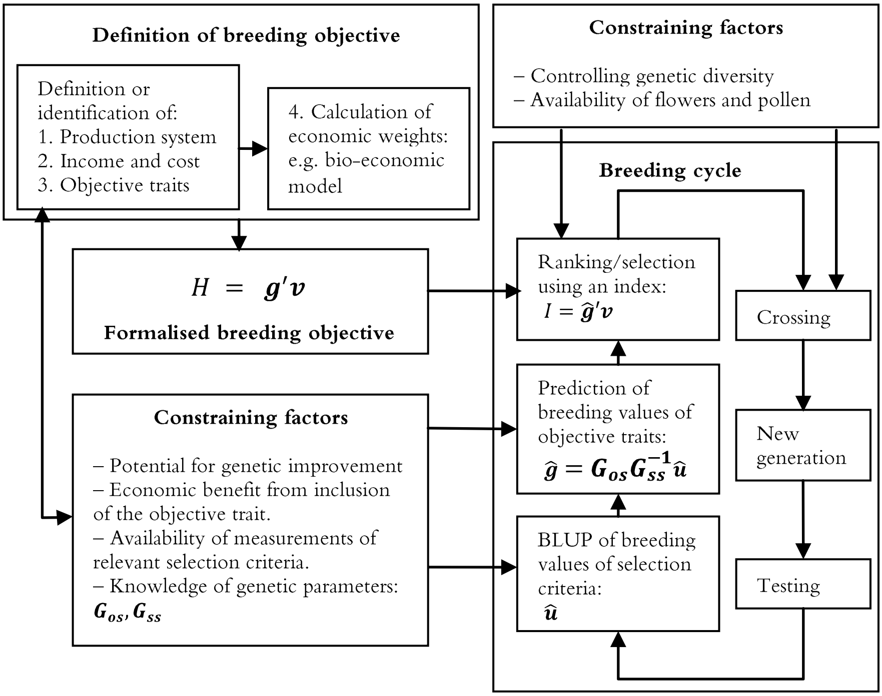

Figure 2. An overview of how the definition of a breeding objective is affected by, and connects to, different parts of a breeding program. The symbols are explained in the text.

The definition of production conditions can be divided into several steps, the most important of which are defining the extent and limits of the economic system and selecting a definition of its efficiency or profit. In forest tree breeding contexts the economic system could extend, for example, to the stand, the company, the forest industry sector, the nation or competing sectors (e.g. Borralho et al., 1993). However, attempts to develop bio-economic models in forestry have mostly been limited to the company level, since complexity quickly increases if industrial sectors or an entire nation is studied (e.g. Apiolaza and Greaves, 2001). In many studies a vertically integrated company, including both cultivation and processing of the trees, has been considered to be preferable (e.g. Apiolaza and Garrick, 2001; Greaves, 1999), even though forest owners may have different breeding objectives than pulp mill and sawmill owners (e.g. Ivkovic et al., 2006a; Wei and Borralho, 1999).

Efficiency of production may be defined in biological or economic terms, so that economic weights do not necessarily correspond to monetary units (e.g. Groen, 1989). In forest tree breeding contexts the biological definition has been used to calculate the economic weight of tree survival relative to volume production (e.g. Chambers and Borralho, 1997; **II**; **III**) but the economic definition is generally preferred (e.g. Apiolaza and Garrick, 2001; Borralho et al., 1993; Chambers, 2000; Greaves et al., 1997; Ivkovic et al., 2006a Lowe et al., 1999; Wei and Borralho, 1999). For the latter, defining efficiency and the limits of the production system are related issues. The efficiency function has been defined on the basis of minimising the cost per unit product (e.g. Borralho et al., 1993; Greaves et al., 1997; Lowe et al., 1999) or on maximising the profit (e.g. Apiolaza and Garrick, 2001; Ivkovic et al., 2006a). Since these definitions may affect the relative economic weights there are numerous studies that address the assumptions and effects of different definitions of efficiency and production system size (e.g. Amer et al., 1994; Brascamp et al., 1985; Goddard, 1998; Smith et al., 1986). Goddard (1998) suggested that an appropriate approach is to use profit maximisation, in which, all costs are attributed to the variables that determine them in the long run. Depending on the time frame, costs considered fixed in industrial structures today (e.g. cost of land and buildings) may be considered variable in the long run due to the long-term and industry-wide nature of genetic improvement (e.g. Amer and Fox, 1992; Goddard, 1998; Smith et al., 1986).

In a vertically integrated production system, both forest cultivation and industrial processing will generate income and incur costs. These economic flows occur at different points in time, so a discount rate is commonly used to transform economic flows to a net present value. In published attempts to define forest tree breeding objectives formally, the discount rate has ranged between 5% and 10% (**I**, Table 1). In comparison, the discount rates used in boreal forestry analyses have predominately been considerably lower, around 3-4% (e.g. Row et al., 1981; Wibe, 1981). There is an ongoing debate among economists and researchers in other fields about the appropriate rate to use when examining long-term investments (e.g. Baumol, 1968; Bird and Mitchell, 1980; Gibson and Wilton, 1998; Klemperer et al., 1994; Marglin, 1963; Smith, 1978; Weitzman, 2001). This unresolved question complicates boreal forest tree breeding, with its long rotations, since the size of the discount rate could affect the relative economic weights when objective traits are expressed differently during rotation (cf. Greaves et al., 1997).

The most common objective traits discussed in published attempts to develop formal forest tree breeding objectives are traits related to tree growth, stem form, wood density and pulp yield (**I**, Table 2). It has been recommended that, ideally, objective traits should be all that directly affect income and cost (e.g. Gjedrem, 1972; Ponzoni and Newman, 1989; Shelbourne et al., 1997; Woolaston and Jarvis, 1995). In practice, the decision about which objective traits to include is also affected by the potential for genetic improvement, uncertainty about the future economic importance of traits, the difficulty of deriving a robust selection index from a large number of objective traits and the cost of including each trait (e.g. labour, equipment and time) compared to its potential gain (Cotterill and Dean, 1990; Gibson and Wilton, 1998; Harris, 1970; Hayes and Hill, 1981; Smith, 1983). Bourdon (1998) suggested that underlying biological traits should be used; these describing the genetic potential of different traits rather than trait expression in a particular environment. With this approach, objective traits would be generally applicable to a range of environments (e.g. different silvicultural regimes and industrial uses). One example is growth ability, which is a continuously expressed realisation the of genetic potential that influences harvested volume according to site conditions and silvicultural regimes. There are clear advantages in using underlying biological traits but it is difficult to measure the genetic potential of underlying biological traits directly, and models would have to be further developed to establish relationships between these traits and economic flows.

When defining formal breeding objectives, both profit functions and bio-economic models, which describe the relationships between objective traits and economic flows, have been used to calculate economic weights. Such relationships have varied in their complexity depending on the level of detail of the production system they represent (cf. Borralho et al., 1993; Ivkovic et al., 2006a). Economic weights have been calculated relative to a baseline of trait means by: (i) partially differentiating a profit function with respect to the trait in question (e.g. Borralho et al., 1993; Lowe et al., 1999);

and (ii) studying the change in output of the bio-economic model as a consequence of a marginal change in the genetic input of objective traits (e.g. Apiolaza and Garrick, 2001; Greaves, 1999; Greaves et al., 1997; Ivkovic et al., 2006a; Wei and Borralho, 1999). However, changes in one trait may affect other traits and relationships between traits and economic flows may be non-linear (e.g. Greaves et al., 1997; Ivkovic et al., 2006b). In fact, on the basis of the formal economic theory of production (Amer and Fox, 1992), all factors of production (e.g. different inputs, outputs and costs) may be considered as variables to be optimized before and after a genetic change. However, due to practical difficulties the latter have seldom been used in a breeding context (Goddard, 1998).

Furthermore, economic weights are calculated from data based on present industrial conditions, but the genetic improvements will be realised in a future production system. As the time frame considered increases, there is increasing uncertainty about the future industrial use of any wood produced and thus there is also uncertainty about the validity of the calculated economic weights. It has been suggested that this problem could be addressed by the development of several breeding populations with different objectives (e.g. Namkoong, 1988; Smith, 1985) or by merging several different objectives into one generic breeding objective by weighting the objectives according to the expected relative importance of industry sectors (Apiolaza and Garrick, 2001). Therefore, assumptions about future industrial conditions and the probabilities of different scenarios are an integral part of the development of breeding objectives, especially if the breeding efforts are aimed at supplying a diverse production system and the rotations are long.

1.5 Scots pine breeding in Sweden

Swedish forest tree breeding has been pursued in an organised fashion since the 1940s and the two most important commercial forest tree species are Norway spruce and Scots pine. The founder populations of Scots pine in Sweden consists of: (i) a first selection of around 1300 plus-trees (trees with outstanding phenotypic performance) selected from natural stands during the 1950s and early 1960s; and (ii) a second selection of about 4700 plus-trees during the 1980s, primarily incorporated to increase the genetic base for breeding (Wilhelmsson and Andersson, 1993). On average, genetic gain in the Scots pine breeding population is estimated to 10% in growth per generation. The tested and selected founders are now being crossed to form the second generation within the breeding programme. However, the production population (i.e. seed orchards) give a higher genetic gain than the breeding populations, since only the best trees are selected from several different breeding populations, creating higher selection intensity. Thus, currently, Scots pine seed orchards have a genetic gain of 10-25% (cf. Rosvall et al., 2001).

The aim of the Swedish long-term Scots pine breeding is to combine: (i) conservation of genetic variation; (ii) preparedness for future climatic changes; and (iii) breeding for general purpose objectives. This is achieved using a meta-population approach, consisting of basically closed and genetically unrelated nucleus breeding populations with different adaptation profiles (Danell, 1991). The breeding programmes for Scots pine comprise 24 breeding populations intended to be representative of environmental conditions across the whole country (Figure 3). Each population has a target area defined by photoperiod and temperature climate and consists of about 50 parents per generation.

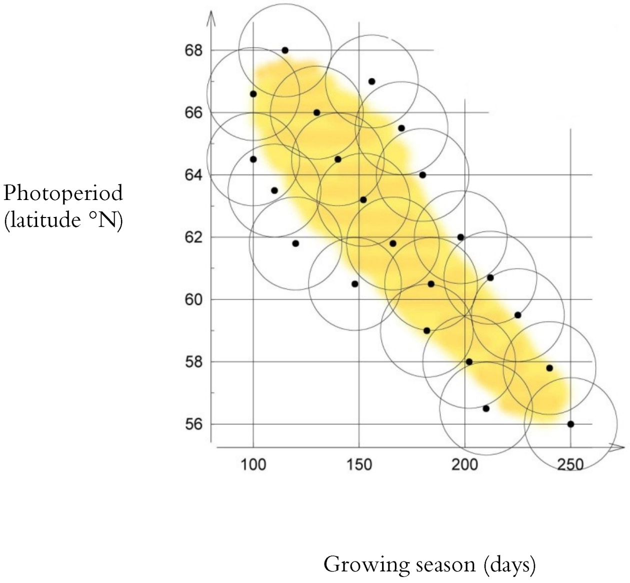

Figure 3. General figure describing the distribution of breeding populations with different adaptation profiles for Scots pine in Sweden (adapted from Danell, 1993). The shaded (yellow) area indicates the current extent of Swedish forest land

For each breeding population some 500-2000 candidate trees are tested in four or five field trials. The geographical locations of the field trials are selected so that they are representative of the specific adaptation profile, or target area, for that breeding population. In addition, field trials are distributed to both harsh and mild locations within each target area. A general objective, valid for all breeding populations, is to improve vitality, growth and wood quality. To meet this general objective, multi-trait selection is performed based on an index. However, the indices used in Swedish Scots pine breeding programmes have, so far, not been based on a formally developed breeding objective, with economic weights of traits calculated by formal economic analysis of gains, as envisaged by Groen (1989) and Ponzoni and Newman (1989).

2 Objectives

The overall aim of this study was to suggest a framework for developing forest tree breeding objectives with particular emphasis on boreal conditions (**I**) and, as components of this framework, to define breeding objectives and calculate economic weights based on case studies of Scots pine in northern Sweden (**II**-**IV**).

3 Main results and discussion

3.1 Framework development

A framework for developing forest tree breeding objectives with particular emphasis on boreal conditions, using bio-economic modelling to calculate economic weights, was developed in **I**. The aim was that the framework should be capable of representing the entire forest sector in a defined country or region. The study started with a literature review of formally defined forest tree breeding objectives. Nearly all studies to date related to fast-growing species with short rotation. Two major differences between these studies and our definition of boreal conditions were identified: (i) the latter are associated with considerably longer time spans causing major uncertainty with respect to future industrial conditions; and (ii) they involve more complex and diverse production systems, consisting of the entire forest products industry in a country or region. To adapt to these conditions a framework consisting of a set of separate modules for different subsectors was suggested (**I**, Figure 2). Each subsector should represent a specific industrial segment with the following suggested general characteristics relevant to boreal conditions (**I**):

- ➢ A vertically integrated production system, including both cultivation and processing of the trees.
- ➢ Efficiency of production is defined as profit maximisation.
- ➢ All costs are considered variable.
- ➢ A low baseline discount rate (≤ 3%) that should be subject to sensitivity analyses.
- ➢ An appropriate set of objective traits, applicable over a wide range of site conditions, silvicultural regimes and industrial subsectors. As far as

possible, these should describe underlying biological traits and general characteristics of the trees associated with basic properties in forest cultivation and of the different industrial processes. In particular, key conceptual objective traits for boreal conditions are suggested to be those that describe: (i) biomass production, including the cultivation phase, which is important for all possible industrial uses; (ii) the basic chemical content of the wood, which is important for pulping and for bio-energy and bio-fuel purposes; (iii) stem form and branch properties, which are mainly important for solid wood products; and (iv) wood properties that can be identified as important for certain industrial uses.

- Descriptions of silvicultural measures, other environmental conditions, industrial processing and objective trait mean values should be subjected to sensitivity analyses.

To be able to use the subsectors in a joint analysis, representing a defined boreal forest sector, they should fulfil two additional criteria: (i) they should range over all existing (sawmills, kraft pulp mills, mechanical pulp mills) and emerging (e.g. bio-fuel, bio-energy) industrial segments; and (ii) the results within each subsector should be generally applicable, which can be achieved, for example, by analyzing several mills in one or more case studies. The framework can, therefore, be used to provide economic weights appropriate for the defined boreal forest sector and also act as a platform to assist strategic breeding decisions under situations where there is uncertainty.

3.2 Economic weights for Scots pine in northern Sweden

Two case studies based on the framework developed were used to define breeding objectives and calculate economic weights for Scots pine in northern Sweden. The first study examined how to calculate the economic weight of tree survival relative to volume production, taking patchiness into account (**II** and **III**). The second study focused on an integrated company in northern Sweden, cultivating forests and supplying its own sawmill (**IV**).

3.2.1 Economic weight of tree survival relative to volume production

In order to obtain economic weights of tree survival relative to volume production a new model was developed (**II)** and then applied to field data from a set of Scots pine breeding populations in northern Sweden (**III**). In these two studies, efficiency of production was defined in biological terms and the economic weight of survival was expressed in volume production equivalents (i.e. relative to volume production). A theoretical simulation of the model developed in **II** showed that both the absolute value of survival and its patchiness affected the projected production per unit area. When survival was higher than 50%, the relative economic weight of survival increased with decreasing survival and an increasing patchiness (**II**, Figure 4). Results from genetic field trials involving five breeding populations of Scots pine in northern Sweden, showed that the economic weight of survival increased up to three-fold with decreasing levels of survival and increasing patchiness of survival (**III**, Table 5). This indicates that survival is an important objective trait at the harshest sites in northern Sweden. However, at milder sites, with moderate to high levels of survival, only a relatively small reduction in volume production was found. This was partly due to the low levels of estimated patchiness, but the main reason was the combination of high initial stand density and thinning regimes for Scots pine. Even if almost half of the trees died, a substantial number of stems per hectare remain. In addition, adaptive thinning, targeting a specific stocking rate at harvest, further reduced the impact of mortality.

A sensitivity analysis showed that the relative economic weight of survival was insensitive to changes in site index and harvesting age, but was clearly affected by different initial stand densities (**II**, Figures 5-7). Results of the sensitivity analysis imply that economic weights for a certain value of site index and harvesting age are also valid for other site indices or harvesting ages. However, changing the initial stand density substantially affected the calculated economic weights, which means that using the appropriate initial stand density is crucial.

For the calculated economic weights to be realistic an accurate description of the target area is needed. Genetic field trials could be used for this purpose but it is important that (i) genetic and environmental effects are not confounded in the model; and (ii) no additional mortality is likely to occur after the time of assessment. The latter is especially important for harsh areas. Since mortality sometimes does not level off until the trees are around 20 years old (Ståhl & Andersson, 1985; Persson & Ståhl, 1993), economic weights calculated for breeding populations based on late (17 or

19 yrs) assessments are more reliable than for those based on early (9 or 11 yrs) assessments (paper **III**, Table 5).

This model produces economic weights of survival relative to volume production, i.e. not in monetary terms. Therefore, they cannot be compared directly to other objective traits in a more complex production system. However, they could easily be converted to monetary values by using this model together with an economic system capable of assigning a monetary value to an economic weight for volume production (**IV**).

3.2.2 Defining a breeding objective for a Scots pine sawmill

A Scots pine breeding objective for a vertically integrated company in northern Sweden, including a sawmill and the forests supplying it, was developed in **IV**. The identified objective traits were survival (SUR), volume per hectare (VOL), wood density (DEN) and straightness of logs (STR); the economic weights for each trait were also calculated (**IV**, eq. 10). A sensitivity analysis showed that the economic weights of the objective traits were not responsive to changes in the discount rate (**IV**, Table 8). This was expected since all objective traits in the studied production system were expressed during the same thinning and harvesting operations.

A selection index was also developed for which the selection criteria were measurements of height (HTH_{15}), diameter (DIA_{15}), pilodyn penetration (PIL_{15}), straightness (STR_{15}) and vitality (VIT_{15}), all measured when the trees were 15 years old (**IV**, eq. (11)). The efficiencies of different selection indices were investigated by omitting selection criteria one at a time and comparing the predicted profit per hectare with the full index, in which all selection criteria were included (**IV**, Table 7). Results showed that omitting either VIT_{15} or STR_{15} had a negligible effect, reducing predicted profit per hectare by less than one per cent. The low importance of VIT_{15} was expected since mortality is not a major concern in the region studied. The limited effect of STR_{15} can probably be mainly explained by the fact that Scots pine in northern Sweden has a naturally straight stem form compared to many other studied species. Omitting either HTH_{15} or diameter DIA_{15} had a greater effect (up to 6%) on the predicted profit per hectare, but the effect of omitting either one was only moderate since these traits are almost complementary indicators of growth. However, when both HTH_{15} and DIA_{15} were omitted, the predicted profit per hectare dropped to only 33% of the full index, illustrating the fundamental importance of growth. It was somewhat unexpected that omitting PIL_{15} from the selection index resulted in a 10% decrease in predicted profit per hectare.

Other studies including pulp mills and/or solid wood products graded on wood stiffness/strength (e.g. Apiolaza & Garrick, 2001; Borralho et al., 1993; Greaves et al., 1997) have showed the importance of including DEN in the breeding objective. Therefore, the importance of DEN and its related selection criteria would probably increase if pulp mill processing and the importance of wood stiffness and/or strength had been included in our studied production system.

Several areas that are less understood and where research is needed were identified (**IV**). These include: (i) relationships between objective trait changes and economic consequences in the production system (to allow for inclusion of more objective traits and a more complete breeding objective); (ii) a flexible growth and yield simulator to improve the modeling of growth and other traits; and (iii) the genetic parameters necessary for performing selection for suggested breeding objectives.

3.3 Implications for the Scots pine breeding programme

In **I** it is suggested that objective traits should, as far as possible, describe underlying biological traits and describe general characteristics of the trees that are associated with basic properties in forest cultivation and of the different industrial processes. Furthermore, traits related to biomass production are considered to be important for all industrial situations. Therefore, objective traits representing growth, wood density and, in harsh areas, survival are of crucial importance and should be emphasised in the Swedish forest tree breeding programme. However, the suggested emphasis on biomass production does not mean that other traits that have different degrees of importance for different industrial sectors and those whose importance may be more sensitive to future technological development, are unimportant. It means only that their importance is less certain and depends on future industrial uses of wood and possible technological innovations. Their relative importance compared to traits related to biomass production could be evaluated in a joint analysis within the framework, as suggested in **I**.

The economic weights of tree survival relative to volume production calculated in **III** could be directly applied in the Scots pine breeding programme for the studied breeding populations. For the other breeding populations, economic weights can easily be calculated based on the relevant genetic field trials. However, both **II** and **III** showed that small to moderate levels of mortality caused, at most, a 10% production loss. It is therefore important not to put too much emphasis on survival, if not in the harshest areas, in the Scots pine breeding programme, since this would reduce tree growth. This is especially true if growth and survival are assumed to have an antagonistic relationship (e.g. Persson, 2006). The economic weights developed in **II** and **III** optimise volume production and should, therefore, place the appropriate emphasis on survival.

The breeding objective developed in **IV** is not directly applicable to the whole Swedish breeding programme for Scots pine since it is derived from a case study of a single sawmill representing a single subsector of the Swedish forest products industry. However, results from this study could be used as guidelines when performing genetic selection of Scots pine, particularly in the studied region, until more generally applicable models are available.

Wood density has not been included as an objective trait in the Scots pine breeding programme. In **IV** it was shown that PIL_{15} may be an important selection criterion, which in turn indicates the importance of wood density for efficient ranking and selection. This result warrants further analysis to determine whether PIL_{15} or other indicators of wood density should be measured along with other selection criteria in Scots pine field trials.

4 Future perspectives

The major aim of this thesis was to suggest a framework capable of developing breeding objectives relevant for a defined part of the boreal forest sector involving a diverse production system. Some of the most important challenges were identified in **I** and directly encountered in **IV**. It is difficult to rank their importance since they are all vital in developing the framework; most tasks and challenges need to be addressed simultaneously to make significant progress. However, challenges and tasks can be divided into three major categories:

Future studies should include developing models so that the suggested key objective traits could be defined in a way that is generally applicable to as many different industrial situations, site conditions and silvicultural regimes as possible. Growth needs to be defined such that it is compatible with growth and yield models capable of producing values for all objective traits given a genetic change in growth. How branching traits and wood property traits could be included should also be considered. A definition of branching properties relevant within the context of this framework needs further research and improvement before including it as an objective trait.

Furthermore, additional subsectors need to be studied, and there need to be multiple case studies within each subsector. First, the focus should be on sawmills and kraft pulp mills but eventually studies of bio-fuel and bio-energy sectors should be included. Since the suggested objective traits are economically important in a range of industrial conditions, they may not be directly related to income and costs, and extra efforts must be put into determining the relationships between objective traits and economic flows in the different subsectors.

Selection criteria related to the objective traits also need to be identified. This will mean that special attention will need to be paid to objective traits such as wood density and basic chemical content of wood. In addition, the genetic parameters necessary for genetic selection need to be estimated.

During this development process, it is vital that stakeholders within the breeding programme should be involved to provide the necessary inputs (e.g. their perspectives relating to the future use of wood) and to give necessary feedback. In addition, developing the framework is a complex and difficult task which requires multi-disciplinary collaboration involving stakeholders and researchers in areas other than forest genetics (e.g. economists and wood engineers).

Finally, apart from the general framework described in **I**, this work focused on Scots pine breeding. In the Swedish forest tree breeding programme, other commercial tree species (e.g. Norway spruce) are also important. Therefore, the same research and development described for Scots pine also needs to be undertaken for them.

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