Genetic Improvement of Shape Stability in Norway Spruce and Scots Pine Sawn Timber

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Cover: This old Scots pine tree is located in the nature reserve at Pelarsalen, Sweden. It was hit by lightning and the right-handed grain under bark thus became visible to the eye through the cracks. (Photo: H. Hallingbäck)

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Abstract

Poor shape stability of sawn softwood timber, causes substantial economic losses for sawmills and the building industry. Sawn timber twist is regarded to be the most severe deformation and has been shown to be controlled by intrinsic wood properties like wood shrinkage and spiral grain angle. The aim of the studies this thesis is based upon was to investigate the possibility to improve sawn timber shape stability, by genetic selection of genotypes of Norway spruce (*Picea abies* L. Karst.) and Scots pine (*Pinus sylvestris* L.) with a favourable spiral grain angle.

Genetic parameters were estimated for the spiral grain angle in the mature wood of trees in four progeny trials (age 27–36 years) and two clonal trials (age 19 years) of Norway spruce. In addition, in a 36-year-old Scots pine progeny trial, the grain angle was measured and shape stability traits of the boards sawn from sampled trees were assessed.

The estimates of genetic standard deviation (0.7°–0.9°) and heritability (0.29–0.42) in the mature wood of both species suggested that grain angle could be altered by genetic selection. The grain angle measured in single annual rings of Scots pine showed substantial phenotypic correlations (0.54–0.70) with the twist of small sawn timber dried to a 12% moisture content. As an example, twist could potentially be reduced by 0.3°–0.7° by selecting 20% of the parents displaying the lowest grain angle, thereby appreciably decreasing the percentage of excessively twisted boards. Grain angle under bark exhibited non-significant genetic correlations, close to zero, with growth traits, stem form, and branch traits in both species, and with pilodyn penetration in Norway spruce, suggesting that genetic selection for this trait would not generate any appreciable response in the other traits.

The results of the studies imply that the grain angle measured under bark is utilisable in terms of genetic parameter estimation and for predicting the twist propensity of small sawn timber. This suggests that there is potential to improve sawn timber shape stability by genetic selection for a lower grain angle under bark and thus reducing the twist of sawn timber.

Keywords: forest genetics, genetic variation, heritability, *Picea abies*, *Pinus sylvestris*, sawn timber, spiral grain, twist, warp, wood properties

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Contents

List of Publications

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

I   Hallingbäck, H.R., Jansson, G. & Hannrup, B. (2008). Genetic parameters for grain angle in 28-year-old Norway spruce progeny trials and their parent seed orchard. *Annals of Forest Science* 65(3), 301p1–301p8.

II Hallingbäck, H.R., Jansson, G. & Hannrup, B. (2010). Genetic correlations between spiral grain and growth and quality traits in *Picea abies*. *Canadian Journal of Forest Research* 40, 173–183.

III Högberg, K-A., Persson B., Hallingbäck, H.R. & Jansson, G. Relationships between early assessments of stem and branch properties and sawn timber traits in a Scots pine progeny trial. Submitted.

IV Hallingbäck, H.R., Jansson G., Hannrup, B. & Fries, A., Which annual rings to assess grain angles in breeding of Scots pine for improved shape stability of sawn timber? Submitted.

With the kind permission of the publishers, papers **I** (http://www.afs-journal.org/) and **II** (http://pubs.nrc-cnrc.gc.ca/rp-ps/journalDetail.jsp?lang=eng&jcode=cjfr) have been reprinted.

1   Introduction

1.1   Sawn wood shape stability

Sawn wood is a renewable material that is inexpensive and has a very high strength to weight ratio. However, it is an anisotropic material (i.e. its properties are directionally dependent) and it is affected by changes in environmental conditions, especially moisture levels. Hence, it may be deformed (warp) during drying, or afterwards due to fluctuations in humidity. This is potentially damaging, since wooden studs and boards must be straight to be useable for construction, and must remain straight as long as they are in service. Wood that is particularly susceptible to such deformation (e.g. bow, crook, twist and cup, as illustrated in Figure 1) is said to have poor shape stability.

   Wood shape stability traits are very important for many applications of long pieces or sheets of sawn wood, e.g. joinery, glulam, veneers, and timber used in building construction. Of all Swedish sawn softwood, 60–70% is directly or indirectly used in building construction, and up to 30% of this sawn timber has to be discarded due to excessive warp (Woxblom, 1999; Grundberg and Esping, 2003). Consequently, inadequate shape stability of
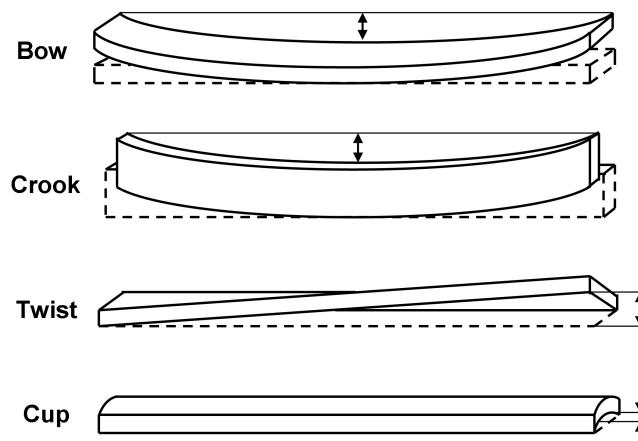

Figure 1. Illustration of the shape stability defects bow, crook, twist and cup (adapted from Johansson *et al.*, 1994).

sawn and dried wood has been a major source of discontent among users of long wood pieces in recent years, and has contributed to a mistrust of wood as a building construction material in both Sweden (Johansson *et al.*, 1994; Woxblom, 1999) and abroad (Eastin *et al.*, 2001; Cown, 2005). The potential price premium for guaranteed straight studs and boards has been estimated to be 20–40 €/m^3 (Grundberg and Esping, 2003).

Sawing and drying methods may influence the development of warp, but intrinsic wood traits like the anisotropic wood shrinkage, microfibril angle, and spiral grain have been shown to have considerable influence over sawn timber shape stability (Dinwoodie, 2000). These traits can be controlled to some extent by silvicultural measures or genetic selection, thus indirectly affecting the shape stability of sawn timber (MacDonald and Hubert, 2002; MacLaren, 2002).

This thesis, and the studies it is based upon, address the possibility to genetically improve shape stability of sawn timber obtained from Norway spruce (*Picea abies* L. Karst.) and Scots pine (*Pinus sylvestris* L.) trees. The genetic variation for spiral grain was a major focus of the studies, since it has been shown to have a strong influence on twist development in sawn boards (Stevens and Johnston, 1960; Harris, 1989). Hence, the genetic variation for spiral grain was estimated, and the relationship between non-destructive spiral grain assessments and warp in sawn timber was evaluated to determine the scope to improve sawn timber shape stability by genetic selection.

1.2   Spiral grain and its relationship to shape stability

Spiral grain is a wood formation phenomenon in which the grain (the orientation of tracheid cells) is consistently inclined relative to the stem axis, thus forming a structure that gradually spirals upwards along the stem (Figure 2). This inclination is systematic in large parts of the stem because newly formed tracheids develop the same orientation as the cambial cell from which they were formed during cell division. Spiral grain is visible only on the wood surface, and cannot usually be detected from observations of the bark. It is frequently quantified as the angle between the grain direction and the stem axis, the grain angle; left-handed grain is indicated by positive values while right-handed grain is indicated by negative values.

Most conifer species display spiral grain to some extent, but a high grain angle has been shown to induce twisting of sawn timber from several conifer species (Harris, 1989 and references therein). The grain angle has also been observed to be correlated with twist after drying in Norway spruce (Danborg, 1994a; Forsberg, 1999; Forsberg and Warensjö, 2001; Johansson *et al.*, 2001; Kliger, 2001) and Scots pine (Warensjö and Rune, 2004). The reported
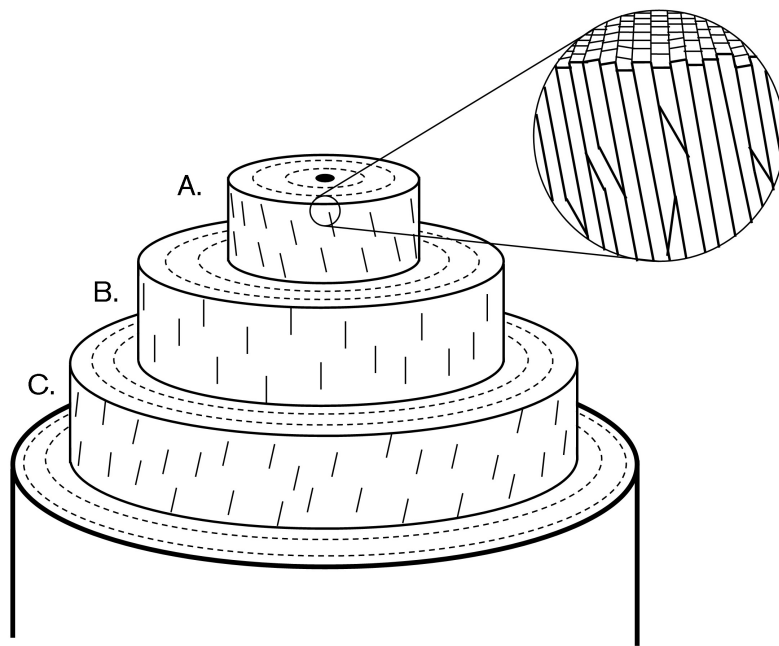
Figure 2. Schematic illustration of grain orientations in annual rings of different age in a conifer stem. (A) Left-handed (positive) spiral grain, (B) straight grain, and (C) right-handed (negative) spiral grain. A magnified image of the systematic inclination of tracheid cells is also shown.

correlations have varied considerably (0.48–0.78 for Norway spruce and 0.36–0.67 for Scots pine) due to differences in the methods used to dry wood and assess twist and grain angle. Furthermore, severe spiral grain has been observed to reduce the stiffness (modulus of elasticity, MOE) and strength (modulus of rupture, MOR) of sawn timber by several authors (e.g. Dinwoodie, 2000).

1.2.1 Within-tree grain angle pattern

The variation in the systematic grain angle within the stem is also an important consideration, because it strongly influences the location and extent of wood with high tendencies to twist in the stem. The age of the vascular cambium (manifested in the number of annual rings from pith) is an important factor in this respect, because the inclination of the tracheids depends heavily on its age. Hence, the direction and magnitude of the grain angle gradually change as the radius of the growing tree increases.

Typically, young conifer trees display a left-handed grain angle under the bark. The grain angle under bark then peaks, and gradually decreases as the tree matures, often resulting in a right-handed grain angle under bark when the tree is old (Harris, 1989). As indicated in Figure 2, an old conifer tree simultaneously comprises left-handed spiral grain in the core close to the pith (the juvenile wood) and right-handed spiral grain in the outer wood close to bark (mature wood). Juvenile and mature wood properties are very different, apart from their differences in spiral grain, because several wood traits (e.g. density) also exhibit patterns that are dependent on cambial age (e.g. Bendtsen, 1978). In Norway spruce and Scots pine, the transition from juvenile wood to mature wood is gradual and the boundary is not easy to define, but in this thesis the wood of the innermost 10 annual rings will be considered to be juvenile, while the wood beyond 20 annual rings from pith will be considered mature (Figure 3).

In Norway spruce, the normal grain angle decreases roughly linearly with the number of annual rings from pith (Figure 3, Säll, 2002; Gjerdrum et al., 2002) and can thus be described by linear models. The relationship between grain angle and age in Scots pine is less well known, but previous observations have indicated that the grain angle in juvenile and mature Scots pine wood is left-handed and right-handed respectively, and thus similar to the pattern observed in Norway spruce (Kaasa, 1976; Harris, 1989). As a comparison, the grain angle is highly left-handed in juvenile wood of radiata pine (*Pinus radiata* D. Don), while in mature wood it appears to decrease asymptotically with further increases in cambial age (unlike Norway spruce) to slightly left-handed or right-handed (Cown et al., 1991; Tian
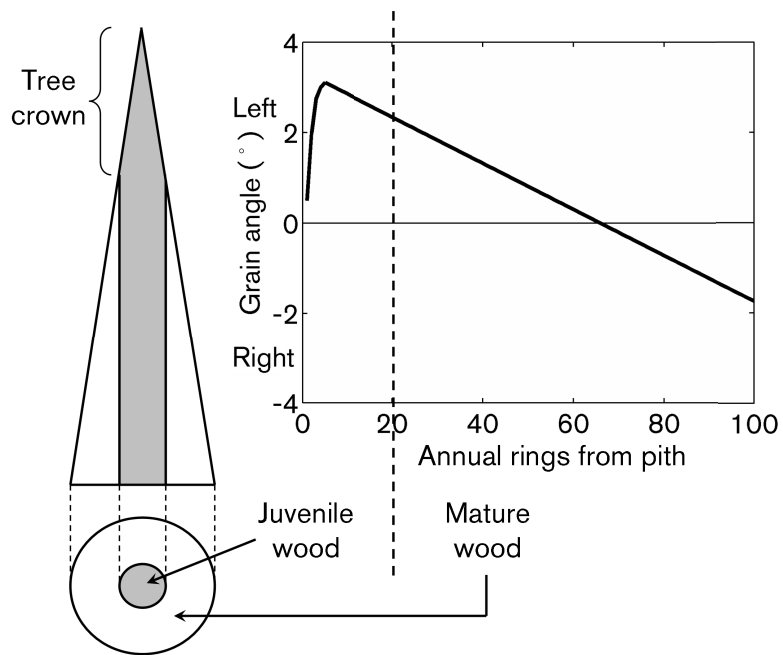
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Figure 3. Schematic illustration of the location of juvenile wood and mature wood in a conifer stem, and graph showing changes in average radial grain with number of annual rings from pith in Norway spruce (from Säll, 2002), exemplifying the differences between juvenile and mature wood.

et al., 1995).

In several conifer species, the grain angle has been shown to be fairly consistent around the circumference of the tree. In Norway spruce, the grain angle measured at different circumferential positions within the same annual ring has been found to be strongly correlated ($r = 0.87$; Danborg, 1994b), and in Sitka spruce (*Picea sitchensis* (Bong.) Carr.) Hansen and Roulund (1998b) found that the effect of the circumferential position on grain angle was small and non-significant.

Many wood traits exhibit gradients with respect to the vertical as well as the radial position in the stem. Some models of wood categorisation even associate the terms juvenile and mature with the physiological age of the leader shoot of the tree, and thus with the vertical position rather than the radial position in the stem (Burdon *et al.*, 2004). Knowledge is limited regarding the dependency of the grain angle on the vertical position, but authors who have investigated the relationship have drawn differing conclusions for different species. In Norway spruce, Säll (2002) found the radial grain angle to be maximal at a greater cambial age, and the subsequent rate of decline to be greater, in stem sections taken from higher in the stem than at breast height, but the effects were small. Furthermore, Hansen and Roulund (1998a) found the grain angle at different heights to be highly correlated (> 0.5) in Sitka spruce trees and Norway spruce (by reexamination of the data from Danborg, 1994b) and similar patterns have been observed in radiata pine (Cown *et al.*, 1991). Hansen and Roulund concluded that the grain angle variation due to the vertical position in the stem was less important than the variation due to radial distance from pith in both Norway spruce and Sitka spruce.

1.2.2 Models for predicting twist

The grain angle is not the sole contributor to the development of twist in boards. Stevens and Johnston (1960) proposed the following model based on the twisting of cylindrical wood shells to describe the main contributors to twist:

$$\alpha = \frac{2ls\theta}{r(1+s)} \tag{1}$$

where α is the sawn board twist in degrees, l is the length of the sawn board in metres, θ is the grain angle of the wood at the centre of the board, r is the radial distance from pith to the centre of the sawn board, and s is its tangential shrinkage after drying. Twist is thus linked inversely to the radial distance from pith ($1/r$ is sometimes referred to as the annual ring curvature), implying that the effect of a given grain angle on board twist is likely

to be strong in boards sawn from juvenile wood close to pith but weaker in boards sawn further away. Consequently, the right-handed grain angle often observed in mature wood of older trees is not as detrimental to shape stability as the left-handed grain angle observed in juvenile wood, because the distance from pith to the mature wood is much greater. Having confirmed this aspect of model 1, and applying knowledge of the grain angle pattern in Norway spruce, Danborg (1994a), Woxblom (1999) and Johansson et al. (2001) concluded that studs and boards sawn from the central part of a log are likely to have inadequate shape stability properties for building construction purposes.

However, model 1 has several limitations because it ignores the effects of longitudinal shrinkage, and it assumes that the grain angle is constant throughout the board. In attempts to obtain better predictions of board twist, several investigators have used different approaches to develop improved, extended models, and different sawn timber materials to validate them, including Norway spruce materials (Ormarsson, 1999; Ekevad, 2005; Bäckström and Johansson, 2006) and radiata pine (Booker, 2005). All of these authors found that the radial grain angle trends influenced the development of twist, in addition to the grain angle and the distance from pith per se.

The results of some of these studies suggested that a stem with a consistently high left-handed grain angle (> 4°) from pith to bark, would result in unacceptably twisted boards, irrespective of the radial position in the log from which they were sawn (Ormarsson, 1999; Bäckström and Johansson, 2006). Säll (2002) reported that a small proportion of Norway spruce individuals consistently displayed such left-grained patterns, thus deviating considerably from the grain angle trends shown in Figure 3. In a study of Norway spruce grain angle and sawn timber, Kliger (2001) also found a few rotation-aged trees with a grain angle under bark exceeding 3°, indicating that these trees were left-grained. The proportion of such trees was just 11%, but they accounted for 86% of cases of excessive twist observed in the sawn and dried boards, thus supporting the model predictions.

In conclusion, the relationship between spiral grain and the development of twist in sawn boards is highly complex, being affected by diverse factors both individually and perhaps even interactively, including: the grain angle, the radial distance from pith, shrinkage (tangential and longitudinal), and the radial grain angle trends.

1.2.3 Biological function of spiral grain

Numerous hypotheses have been formulated regarding the biological function of spiral grain. Since the sap predominantly flows from the root to the crown in a direction parallel to the long axis of the tracheids, it has been suggested that spiral grain formation may enable trees to distribute the sap uniformly to all parts of the crown, even when the supply of water and mineral resources is unevenly distributed among the roots (e.g. Kubler, 1991 and references therein).

Other authors have linked the formation of spiral grain to the stem resistance against wind. Branches on the southern side of the stem are often longer than those on the northern side (in the northern hemisphere), thus resulting in an assymetrical tree crown. Hence, Skatter and Kucera (1998) argued that trees displaying typical grain angle trends of European conifers (as illustrated in Figure 3) may be more resistant to the strong torsional forces exerted on such asymmetrical tree crowns by the prevailing westerly winds.

Włoch *et al.* (2002) observed that the occurrence of inclined tracheids (i.e. spiral grain) in the wood of Scots pine was associated with a non-symmetric deposition of the cell wall during cell division in the cambium. Other authors have observed that newly formed cambial cells adopt orientations parallel with the flow of the plant hormone auxin, suggesting that the development of spiral grain is both governed by, and participates in, the physiological regulation and development of the tree (Zagorska-Marek and Little, 1986; Kramer, 2006).

The cellular processes involved in spiral grain development and the biological functions of spiral grain are still poorly understood, but the findings indicate that spiral grain has some sort of biological role. Conifer trees with completely straight grain from pith to bark might therefore have unexpectedly poor fitness.

1.3 Tree breeding and genetics of spiral grain

Norway spruce and Scots pine are important tree species for sawn timber production in Sweden and several other European countries. In Sweden, tree breeding programmes for these species have been established since the late 1940s. The traits that have been favoured in genetic selection of Norway spruce and Scots pine to date are high growth rates, adaptation to and hardiness to adverse environmental conditions, and stem properties like straightness, small branch sizes and large branch angles (Karlsson and Rosvall, 1993; Wilhelmsson and Andersson, 1993). Wood properties including spiral grain

have not been included in Swedish tree breeding, mainly because destructive, laborious methods are often required to measure them and their relevance for the economic value of the end-products is not clear and difficult to estimate.

1.3.1   Grain angle measurement methods

In order to assess the radial grain angle pattern of trees comprehensively, and acquire robust estimates of associated genetic parameters from stem sections, the trees have to be felled, large numbers of sections have to be cut, and laborious, time-consuming measurements have to be taken. Hence, genetic improvement of the trait would be greatly facilitated by the availability of a rapid, non-destructive measurement technique. Some attempts have been made to assess the within-tree grain angle patternd non-destructively, by computed tomography (Sepúlveda, 2001), laser scattering (Sarén *et al.*, 2006) and X-ray diffractometry (Buksnowitz *et al.*, 2008), but these techniques are still underdeveloped and too imprecise to measure the radial grain angle pattern in increment cores and require too much unwieldy machinery to be applied effectively in the field.

However, assessments of the grain angle in a few annual rings under the bark can be acquired quickly and non-destructively in either of two ways. In one approach, the bark on a small part of the tree can be removed and the grain angle of the underlying wood can be assessed by scribing the exposed cambium (e.g. Harris, 1989). Alternatively, a small wedge can be pushed into the outermost annual rings of the wood. As it is pushed in it is forced to align parallel to the tracheid cells, so the grain angle can be simply quantified by measuring the inclination angle between the orientation of the wedge and that of the stem axis (Chalmers University of Technology, Sweden). These methods have been successfully used to estimate genetic parameters for the grain angle under bark in radiata pine and Sitka spruce, as well as in Norway spruce and Scots pine (Hansen and Roulund, 1997; Sorensson *et al.*, 1997; Costa e Silva *et al.*, 2000; Hannrup *et al.*, 2003).

1.3.2   Grain angle genetic variation

Published studies on grain angle genetic variation and heritability of Norway spruce have focused on six genetic materials (defined here as sets of trees with common parents or clones) distributed in 11 field trials (Table 1). There is only one published study on the grain angle genetic variation of a Scots pine material distributed on two field trials. With only one exception, estimates of the heritability and genetic variation have ranged from 0.29 to 0.47 and 0.6° to 1.1°, respectively. Moreover, the heritability for grain angle was higher, in 10 out of these 13 trials, than the correspond-

Table 1. Estimates of genetic variation and heritability for spiral grain in genetic materials (sets of trees with common parents or clones) of (A) Norway spruce and (B) Scots pine. The number and type of field trials, the number of genetic entries, measurement method, cambial age investigated, arithmetic mean grain angle, heritability ($\hat{h}^2$), and genetic standard deviation ($\hat{\sigma}_G$) for each investigated genetic material are given, and references.

Trials	No of gen. entr.	Method	Cambial age (yrs)	Mean (°)	$\hat{h}^2$	$\hat{\sigma}_G$ (°)	Reference
A. Norway spruce							
1fs,1op	15–50[1]	ub	10–12	2.6–2.7	0.38–0.47	1.0–1.1	Costa e Silva et al., 2000
2op	37	ub	10–12	1.4–2.5	0.29–0.36	1.0	Costa e Silva et al., 2000
2cl	30–43[1]	s	3–15	2.4–2.6	0.42	1.0–1.1	Hannrup et al., 2002
2cl	49	ub	5–7	2.1–2.6	0.30–0.38	0.6–0.7	Hannrup et al., 2003
1fs	15	s[2]	3–30	1.9	0.04	0.3	Hannrup et al., 2004
2hs	13	ub	16–23[3]	1.2–2.4	0.29–0.44	0.7–0.9	Steffenrem et al., 2009
B. Scots pine							
2op	25	ub	10–12	1.4–2.0	0.40–0.49	1.0	Hannrup et al., 2003

Note: Methods: ub = under bark on standing trees, s = destructively on stem sections. Trials: cl = clonal, op = open pollinated, hs = half sib crosses, fs = full sib crosses. Studies in which less than ten genetic entries were examined are not included.

[1] The genetic material was only partially common to the sites.

[2] Assessment height in the tree varied considerably due to severe infections of root rot (*Heterobasidion spp.*).

[3] The given range is an educated guess based on reported field age and growth data.

ing heritabilities estimated for growth traits (height and diameter at breast height). Genetic variation and heritabilities of considerable magnitudes for grain angle have also been observed in several studies of Sitka spruce (e.g Hansen and Roulund, 1998a), maritime pine (*Pinus pinaster*) (Gaspar *et al.*, 2008) and radiata pine (e.g. Jayawickrama, 2001).

It is known that the ranking of breeding values predicted from one trial, and thus one environment, may not always be valid in other environments, due to genotype-by-environment interactions (G×E). To estimate the magnitude of the effects of such potential interactions on grain angle, genetic correlations between the grain angle measured in the same genetic material in different trials have been estimated. All published estimates of genetic correlations for the grain angle across sites in Norway spruce have been above or equal to 0.87 (Costa e Silva *et al.*, 2000; Hannrup *et al.*, 2003, 2004; Steffenrem *et al.*, 2009), and above or equal to 0.74 for Scots pine (Hannrup *et al.*, 2003), implying that the breeding values predicted from grain angle data in one trial should generally have a high degree of validity in other environments. Thus, the relatively high heritability and small G×E-interactions suggested that reliable breeding values for the grain angle in juvenile wood of Norway spruce and Scots pine could be predicted from data acquired from material at just one or a few sites.

In one of the few published studies available of the genetic variation for the grain angle pattern in Norway spruce stem sections, Hannrup *et al.* (2002) observed genetic variation related to the coefficient of grain angle decline by increasing cambial age (GAta), indicating that the radial grain angle trend could be considered as a heritable trait *per se*. This observation raised the possibilities that the grain angle in mature wood and continuously left-grained patterns might also be heritable. It could however not be merely assumed that genotypes with a high breeding value for left-handed grain angle in the juvenile wood would be continuously left-grained from pith to bark at rotation age, especially since the extent of genetic variation for the grain angle in mature wood was not well known. Thus, there was a need for robust estimates of genetic parameters for grain angle in mature Norway spruce and Scots pine wood.

The majority of investigations listed in Table 1 were also confined to the study of grain angle in a few annual rings of mostly juvenile wood in trees with highly variable stem diameters. Consequently, the radial distance from pith was not taken into account, and the grain angle trend could not be determined from single assessments of the grain angle under bark. Since both of these factors had been shown to be important (Cown *et al.*, 1996; Woxblom, 1999; Ekevad, 2005; Bäckström and Johansson, 2006), the rel-

evance of assessments of the grain angle under bark in young trees for the twisting of sawn timber was questioned. Consequently, estimates of the correlation between the grain angle of single annual rings and shape stability traits were needed to estimate the correlated responses in sawn timber shape stability traits that could be generated from genetic selection for lower grain angle assessed under bark.

1.3.3 The genetic relationship between grain angle and other traits

Genetic selection to achieve a desired change in one trait may inadvertently cause alterations in another trait if they are genetically correlated. On the other hand, genetic improvement of several traits might also be facilitated by favourable genetic correlations between the traits. Therefore, the genetic relationship between traits is an important aspect of genetic improvement and tree breeding.

Most of the few published estimates of genetic correlations between grain angle and other traits have been close to zero (Table 2), although Costa e Silva *et al.* (2000) found a somewhat positive, and thus unfavourable, genetic correlation between grain angle and diameter at breast height (DBH) in Norway spruce. Genetic correlations between DBH and grain angle of

Table 2. Previous estimates of genetic correlations between grain angle and height, diameter (DBH), number of branches (BR), branch angle (BA), stem straightness (STR), pilodyn penetration (PIL), wood density (DEN), microfibril angle (MFA) and modulus of elasticity (MOE) in Norway spruce and Scots pine materials, and references.

Trait	N. spruce				S. pine
	Costa e Silva et al 2000	Hannrup et al. 2003	Hannrup[1] et al. 2004	Steffenrem et al. 2009	Hannrup et al. 2003
Height	-	-0.1 to 0.0	-0.3 to -0.2	0.1 to 0.2	-0.3 to 0.0
DBH	0.3 to 0.5	0.1 to 0.2	0.0 to 0.1	-0.1	-0.2 to 0.1
BR	-	-	-	-	0.1 to 0.5
BA	-	-	-	-	0.2 to **0.6**
STR	-	-	-	-	0.0 to 0.4
PIL	0.2 to 0.3	-	-	-	-
DEN	-	-	0.0 to 0.1	**0.6**[2]	-
MFA	-	-	-0.4 to 0.1	-	-
MOE	-	-	-0.4 to -0.1	-	-

Note: Estimates that were significantly different from zero ($p < 0.05$) are indicated in bold. Studies in which less than 10 genetic entries were examined are not included.
[1] The measurements of grain angle, DEN, MFA and MOE, were averaged over the values of annual rings 3–15.
[2] Based on area-weighted averages of density measurements in all available annual rings.

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varying magnitudes, but with a mean of 0.35 (weakly unfavourable), have been compiled from the results of several studies of radiata pine (Wu *et al.*, 2008 and references therein). In Sitka spruce, genetic correlations between the grain angle and DBH have been found to be close to zero or slightly negative at a low cambial age (5–10 years), while in an older trial (cambial age, 18 years), the corresponding genetic correlation was found to be positive (0.45) (Hansen and Roulund, 1997, 1998a; Hansen, 1999).

Steffenrem *et al.* (2009) observed a surprisingly positive (unfavourable) genetic correlation between grain angle under bark at about 20 annual rings from pith and wood density. This has not been observed in other studies of Norway spruce, but the observation agrees with a corresponding correlation estimated in wood approximately 12 annual rings from the pith in maritime pine (Gaspar *et al.*, 2008).

Genetic correlations are difficult to interpret because their estimates usually have very large standard errors (due to the limited number of genetic entries available in a trial). Consequently, estimates of genetic correlations in several genetic materials are often needed to interpret the genetic relationship. It is therefore notable that there were no published studies available about the genetic correlations between grain angle and stem straightness, branch diameter or branch angle in Norway spruce. Moreover, the few published genetic correlations between grain angle and other traits in Norway spruce and Scots pine were far too few for a comprehensive understanding of the genetic relationships among the traits. Therefore, more estimates of genetic correlations between grain angle and other traits targeted in tree breeding were required.

2 Aims

The overall purpose of the studies this thesis is based upon was to investigate the possibility to improve the shape stability of sawn timber from Norway spruce and Scots pine, by genetic selection of genotypes with a favourable grain angle. The following specific questions were addressed:

1. How large is the genetic variation for grain angle in mature wood of Norway spruce (**I**) and Scots pine (**III**), and how large genetic responses in grain angle could be made?

2. How strong is the relationship between the current non-destructive grain angle measurements made on one occasion and the shape stability of small sawn timber (**III**), and hence how strong responses in shape stability of small sawn timber can be induced by selection for lower grain angle, as assessed in a single annual ring (**IV**)?

3. Is the grain angle genetically correlated with other important traits in Norway spruce and Scots pine (**II & III**)?

4. How high are the genetic correlations for grain angle in mature wood of Norway spruce across different sites (**I**)?

5. What annual ring or distance from pith is best for obtaining measurements of grain angle that are relevant to the shape stability of small Scots pine sawn timber (**IV**)?

3 Materials and methods

3.1 Materials and field trials

Three genetic materials comprising (A) three Norway spruce full-sib progeny trials and their parent seed orchard, (B) two Norway spruce clone trials, and (C) one Scots pine progeny trial were examined in the studies underlying this thesis (Figure 4 & Table 3). The Norway spruce trials were located in the southernmost part of Sweden, while the Scots pine trial (Ramsberg) was located in the southern-central part of Sweden. The trees of the Norway spruce and Scots pine full-sib progeny trials (materials A and C) were likely to have completed the transition from juvenile to mature wood formation since their cambial ages under bark were in the ranges 22–25 and 28–30 years years, respectively.
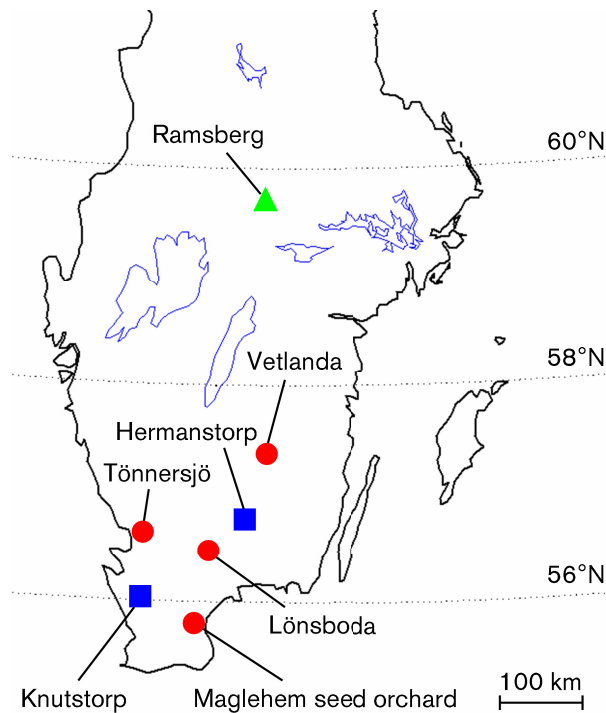

Figure 4. Locations of the studied field trials of material A, the Norway spruce progeny trials and their parent seed orchard (●); material B, the Norway spruce clonal trials (■); and material C, the Scots pine progeny trial at Ramsberg (▲).

Table 3. Species, genetic design and name of trials, number of genetic entries (gen. entr.), field age (years), and studied traits with references in which further details can be found for each genetic material.

	Material A	Material B	Material C
General description			
Species	N. spruce	N. spruce	S. pine
Trial genetic design	full-sib[1]	clonal	full-sib
Trial names	Vetlanda	Hermanstorp	Ramsberg
	Tönnersjö	Knutstorp	
	Lönsboda		
No. of gen. entr.	36	30–43	25
Field age	27–28	19	36
Measured traits in field trials, abbreviations and papers			
Grain angle (GAub)[2]	**I,II**	-	**III,IV**
Grain angle (GAs)[2]	-	**II**	**IV**
Diameter (DBH)	**I,II**	-	**III**
Radial growth (RGs)[2]	-	**II**	**IV**
Height (H)	**II**	-	**III**
Branch diameter (BD)	**II**	-	**III**
Branch number (BR)	**II**	-	**III**
Stem straightness (STR)	**II**	-	**III**
Pilodyn (PIL)	**II**	-	-
Internodal twigs (TW)	**II**	-	-
Ramicorns (RAM)	**II**	-	-
Measured traits on sawn timber, abbreviations and papers			
Bow	-	-	**III,IV**
Crook	-	-	**III,IV**
Twist	-	-	**III,IV**

[1] The 48-year-old parent clonal seed orchard Maglehem (30 clones) was also included in Material A (only GAub and DBH were assessed, **I**).
[2] Measurement method: ub - under bark on standing trees at breast height, s - destructively on individual rings in stem sections.

Figure 5. The non-destructive indicator (Chalmers University of Technology, Sweden) for grain angle measurements under bark (GAub).

3.2   Studied traits and measurement methods

Data regarding the grain angle and other traits were obtained from non-destructive assessments of standing trees in the field, assessments on stem sections, and assessments on sawn timber (Table 3). Non-destructive grain angle measurements (materials A and C) were performed by pushing a small metal wedge through the bark of the standing tree, and an indicating needle with a freely rotatable weight was attached to the bottom edge of the wedge (Figure 5).

The destructive grain angle assessments were obtained from stem sections cut from felled trees (materials B and C). Stem sections were sawn into radial bark-to-bark profiles and the grain angle was assessed using the scribe test method in combination with a precision protractor (Figure 6, Tian *et al.*, 1995; Säll, 2002). By analysing the grain angle in a given annual ring jointly with the accumulated radial growth from the pith to that ring (RGs), the grain angle at a specific distance from pith (GAd, **II, IV**) and the radial grain angle rate of change (GAtd, **II**) could be calculated. For com-
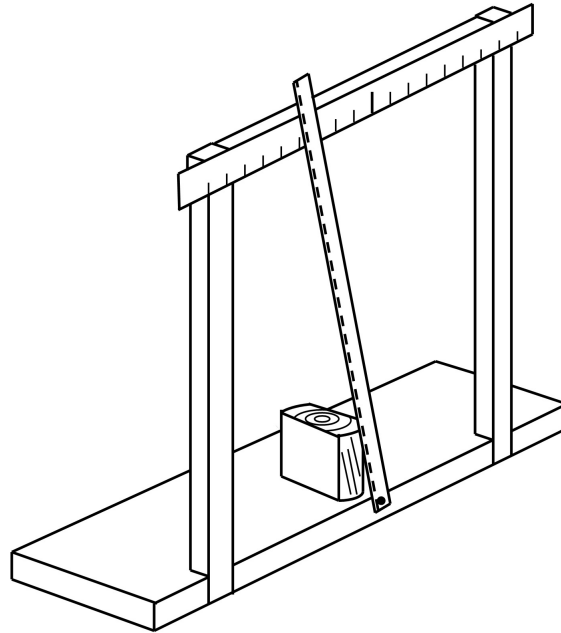
Figure 6. Protractor for destructive grain angle measurements of radial profiles sawn from stem sections (GAs).

parative purposes, the radial grain angle trend with increasing cambial age (GAta, **II**) was also estimated.

3.3 Sawn timber trait assessment

At the Scots pine progeny trial in Ramsberg (material C) non-destructive measurements were performed for all trees in the trial, but 162 sample trees were felled (**III, IV**) and stem sections were taken from the top of the bottom logs. The bottom logs were then sawn into boards which were dried to a moisture content (MC) of approximately 12 %, and subsequently assessed for a number of sawn timber traits. In order to study the relationship between the grain angle assessments and shape stability traits, bow, crook and twist were measured in the topmost 2 m of the boards (see Figure 1 for illustrations of these deformations). The assessment strategy and the positions of the measurements are illustrated in Figure 7.

Field age 16 years   Field age 36 years   Stem sections

100 mm

GAs & RGs (IV)

50 or 32 mm

2000 mm

3300 mm

1300 mm

Bow, Crook & Twist, (III, IV)

...and other traits (III)

Early assessment of field traits (III)

GAub (III, IV)

Bottom logs   Sawn timber
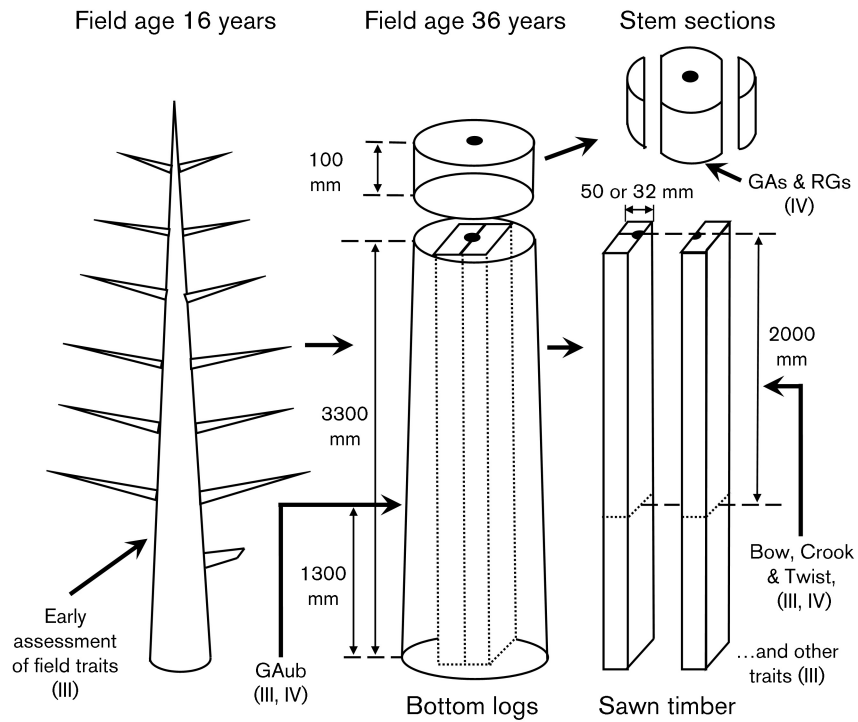
Figure 7. Decomposition strategy, sawing pattern and positions of assessments of the grain angle under bark (GAub), grain angle in stem section (GAs), radial growth in stem section (RGs) and shape stability traits (Bow, Crook and Twist) for the sawn timber samples from the Ramsberg Scots pine field trial (Material C, **III, IV**). The papers describing analyses of each trait are indicated by the Roman numerals, and the pith by black spots.

3.4 Statistical analysis

To estimate genetic and phenotypic parameters and correlations, statistical analyses were undertaken using both univariate and multivariate mixed linear models. Restricted maximum likelihood values of variance and covariance components were estimated using ASReml (Gilmour *et al.*, 2006). Log-likelihood ratio tests were used to determine whether correlations were significantly different from zero and standard errors of the variance components, genetic parameters and correlations were estimated by ASReml using the Taylor series expansion.

4 Results and discussion

Parameters for both Norway spruce and Scots pine are presented and discussed, assuming that some of the results can be compared and some conclusions drawn across the species. From the studies this thesis is based upon and previous literature, there are evident similarities between Norway spruce and Scots pine that support this assumption with respect to the genetic variation of grain angle (Hannrup *et al.*, 2003, **I, III**), the relationship between grain angle and board twist (e.g. Forsberg and Warensjö, 2001; Johansson and Kliger, 2002; Warensjö and Rune, 2004), and to some extent the within-tree spiral grain pattern (Kaasa, 1976; Harris, 1989, **IV**).

4.1 Genetic parameters for grain angle in mature wood

The grain angle genetic variation was in the range 0.7° to 0.9°, the heritabilities were in the range 0.29 to 0.42 in mature wood (cambial age 20–30 years) of Norway spruce and Scots pine materials (Table 4), and the prediction accuracy of grain angle breeding values obtained for these materials was in the range 0.83 to 0.90 (**I, III**). The results thus indicate that the heritability and genetic variation of grain angle in mature wood is very similar to that of juvenile wood (reported by Costa e Silva *et al.*, 2000; Hannrup *et al.*, 2002, 2003) and wood in the juvenile-mature transition stage (Steffenrem *et al.*, 2009). The genetic standard deviation for grain angle does not appear to depend on the cambial age of the wood at breast height (at least not below a cambial age of 30 years) and the results suggest that the occurrence of Norway spruce with a continuous left-handed grain angle pattern might be

Table 4. Genetic variation and heritability for grain angle under bark measured in mature wood estimated in the papers **I-IV**. Number of parents, cambial age range at breast height, arithmetic mean, the phenotypic standard deviation ($\hat{\sigma}_P$), the additive genetic standard deviation ($\hat{\sigma}_A$), and the individual narrow sense heritability ($\hat{h}^2$) for each investigated trial.

Trial	No of parents	Cambial age (yrs)	Mean (°)	$\hat{\sigma}_P$ (°)	$\hat{\sigma}_A$ (°)	$\hat{h}^2$
Material A. Norway spruce (I, II)						
Vetlanda	36	22–25	2.1	1.4 (0.1)	0.9 (0.3)	0.37 (0.09)
Tönnersjö	36	22–25	1.5	1.2 (0.1)	0.7 (0.2)	0.32 (0.09)
Lönsboda	36	22–25	1.5	1.3 (0.1)	0.8 (0.3)	0.42 (0.11)
Material C. Scots pine (III, IV)						
Ramsberg	25	28–30	-0.1	1.5 (0.1)	0.8 (0.3)	0.29 (0.11)

Note: Standard errors are given in parentheses.

Table 5. Phenotypic correlations estimated between grain angle under bark at cambial age 28–30 years (GAub), grain angle in annual ring 10 (GAs10) and shape stability traits (Bow, Crook and Twist) of the sawn boards dried to a moisture content of 12%.

	Bow	Crook	Twist
GAub	-0.06 (0.08)	0.12 (0.08)	**0.54 (0.06)**
GAs10	-0.09 (0.08)	**0.19 (0.08)**	**0.70 (0.04)**

Note: Standard errors are given in parentheses. Estimates significantly different from zero ($p < 0.05$) are indicated in bold. Details can be found in papers (**III** and **IV**)

under genetic control (**I, III**).

4.2   Grain angle and shape stability

4.2.1   Phenotypic correlations between grain angle and shape stability

The results presented in paper **III** showed that the phenotypic correlation between grain angle measured under bark and twist of Scots pine sawn boards was fairly strong (0.54, Table 5). This estimate agrees with the correlation previously reported for Scots pine (Warensjö and Rune, 2004), even though the grain angle in their study was assessed on debarked logs and the boards they examined were dried hanging from the kiln ceiling without any restraint, while in paper **III** the grain angle was assessed in living trees and the boards were dried in stacks. Thus, an assessment of grain angle under bark (two measurements on opposite sides of the stem) in each tree on a single occasion showed promising relevance to the development of twist in centrally sawn boards of Scots pine even though the assessment was limited to a few annual rings (cambial age range, 28 to 30 years at an average DBH of 168 mm).

However, the 10th annual ring assessed in stem sections exhibited an even higher phenotypic correlation (Table 5) with twist ($\hat{r}_P$=0.70), similar to the phenotypic correlations estimated between the grain angle measured on Norway spruce logs and twist (e.g. Forsberg and Warensjö, 2001). It was also similar to corresponding correlations between clonal means of grain angle and twist in the hybrid *P. elliottii* Engelm. x *P. caribaea* Morelet var. *hondurensis* Barrett & Golfari (Harding *et al.*, 2008). The impact of phenotypic selection for a lower grain angle in the existing material is illustrated in Figure 8. The average twist could be reduced by 1° (Figure 8b) and the
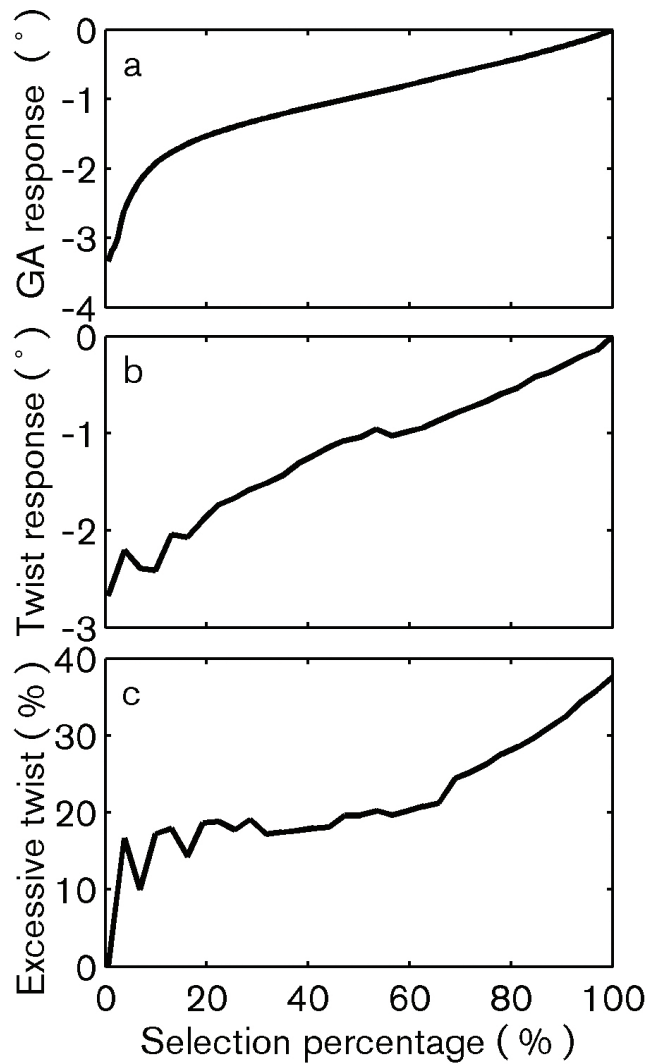
Figure 8. Responses of phenotypic selections in the existing material of the trees with the lowest grain angle in one annual ring (GA). Response in (a) grain angle, (b) twist (from a mean of 2.7° at no selection), and (c) percentage ratio of boards with excessive twist (according to the limits described by Johansson *et al.*, 1994) are shown.

proportion of excessively twisted boards (with respect to Johansson *et al.*, 1994) could be halved (Figure 8c) by selecting the 50% of the logs exhibiting the lowest grain angle in the 10th annual ring.

The grain angle of the 10th annual ring also displayed a significant ($p < 0.05$) but weak correlation with crook (Table 5), implying that improvement by selection for lower grain angle would also be possible, although not very effective, for this trait.

Traits other than the grain angle (Table 3), all displayed phenotypic correlations close to zero with twist (-0.15 to 0.08, **III**). Previous non-genetic studies in Norway spruce sawn timber have also found that other commonly assessed traits measured in the field, on logs or boards (e.g. knot area ratio and density) could not be used to predict the development of twist in sawn timber (Johansson *et al.*, 2001; Johansson and Kliger, 2002). Consequently, assessment of the grain angle under bark appears to be the only non-destructive method to detect twist-prone wood applicable in the field.

4.2.2 Predicted twist response to genetic selection for lower grain angle

Based on the observed grain angle genetic variation and the correlations between grain angle and twist, the potential response in twist due to backward selection (i.e. selection of the best parents based on the performance of their progenies) for a lower grain angle in one annual ring can be illustrated. The sawn material was too limited to allow the estimation of genetic correlations between grain angle and board twist, but it has been found that corresponding genetic and phenotypic correlations between two traits are frequently similar, at least when the magnitude of the phenotypic correlation is high (Roff, 1995).

The genetic correlation between the grain angle and twist was thus assumed to be similar to estimates of the corresponding phenotypic correlations obtained in the studies underlying this thesis and in the literature ($r_A = 0.6$). In accordance with the observations made in these studies, a genetic standard deviation for grain angle of 0.8° and a grain angle breeding value prediction accuracy of 0.85 (**I,III**), were used to predict the potential genetic response in twist due to backward selection for a lower grain angle. The following formula was used:

$$\Delta G_{Tw,GA} = i \cdot r_{TI} \cdot r_A \cdot \sigma_A = i \cdot 0.85 \cdot 0.6 \cdot \sigma_A \qquad (2)$$

where $\Delta G_{Tw,GA}$ is the genetic response of twist in degrees, i is the selection intensity, r_{TI} is the breeding value prediction accuracy for grain angle, r_A is the genetic correlation between grain angle and board twist and σ_A is the genetic standard deviation of twist. Since an estimate of the phenotypic
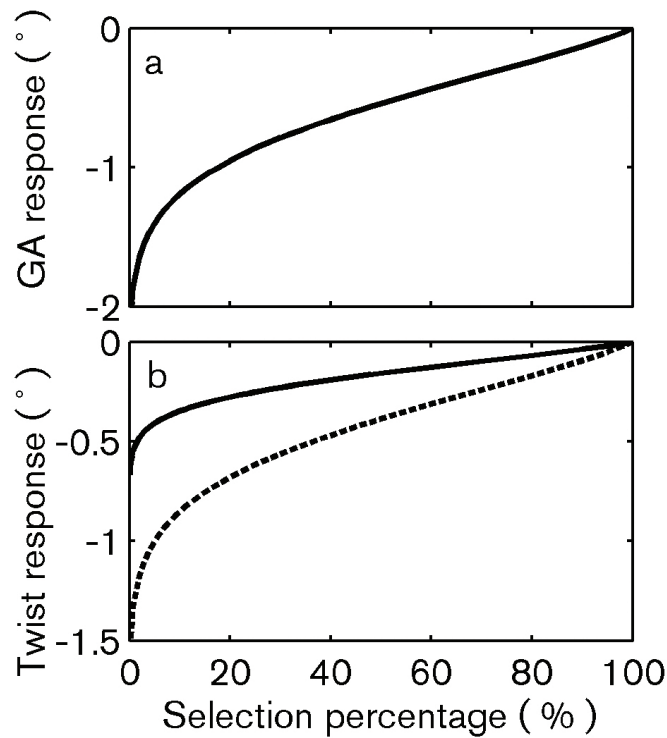
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Figure 9. Predicted genetic responses in (a) grain angle and (b) board twist at a moisture content of 12% within a twist heritability range of 0.05 (solid line) to 0.30 (dashed line) from backward selection in Scots pine for lower grain angle as assessed in one annual ring (GA). Parameters used for the calculations can be found in equations 2 and 3.

standard deviation for twist ($\sigma_P = 1.7°$; **III,IV**) was available, the additive genetic standard deviation of twist could be calculated by using an assumed range of reasonable heritabilities (0.05–0.30) for twist as:

$$\sigma_A = \sqrt{\frac{\sigma_A^2}{\sigma_P^2} \cdot \sigma_P^2} = h_{Tw} \cdot \sigma_P \tag{3}$$

where σ_A and σ_P are the additive genetic and phenotypic standard deviations of twist, respectively, and h_{Tw} is the square root of the heritability for twist.

The results of the predictions (Figure 9) indicated that the board twist and grain angle would decrease non-linearly as the selection proportion decreased. For an assumed selection proportion of 20%, which is within the

range of proportions applied in Swedish conifer breeding, the grain angle was predicted to decrease by 1° and the board twist by 0.3° to 0.7°. At this selection intensity the proportion of excessively twisted boards in the existing sawn timber material was predicted to decrease by 4 to 11% (Table 6). It would be possible to reduce excessive board twist substantially (by 2 to 7%-units) even if the twist heritability was as low as 0.05. The calculations are based on some assumptions that should ideally be validated, but until better estimates of genetic parameters are available, they still give an indication of the possible reductions in twist by genetic selection for a lower grain angle measured in a single annual ring.

It should be noted that the results and predictions are mainly valid for centrally sawn timber with a high proportion of juvenile wood. However, the genetic alteration of juvenile wood grain angle patterns might be the best strategy to reduce overall sawn timber twist, because sawn juvenile wood timber is associated with the most severe shape stability deficiencies (Zobel and Sprague, 1998; Johansson *et al.*, 2001). This was also clearly evident in the examined material since 38% of the boards were unacceptably twisted, which is even higher than the proportion of sawn timber (30%) reported to be unacceptably warped in general (Woxblom, 1999; Grundberg and Esping, 2003). The results and predictions of this thesis suggest that genetic selection for a reduced grain angle is a promising strategy for reducing sawn

Table 6. Predicted responses of grain angle (ΔG_{GA}) and of the proportion of boards (%) with excessive twist (ΔG_{Exc}), from 38% at no selection, at a moisture content of 12%, to backward selection for lower grain angle as assessed in one annual ring in Scots pine. Responses are shown for assumed twist heritabilities (h^2_{Tw}) of 0.05 and 0.30 with a selection proportion (Sel.) ranging from 5% to 100%.

Sel. (%)	ΔG_{GA} (°)	ΔG_{Exc} (%-units)	
		h^2_{Tw}=0.05	h^2_{Tw}=0.30
100	0.0	0	0
50	-0.5	-2	-7
20	-1.0	-4	-11
10	-1.2	-6	-16
5	-1.4	-7	-18

Note: Excessive twist is defined according to Johansson *et al.* (1994)

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timber twist, and currently, it appears to be the only available assessment method that could be practically applied on a large scale in tree breeding for that purpose.

4.3 Genetic correlations between grain angle and other traits

The genetic correlations between grain angle under bark in mature wood and growth traits, as well as other traits, were consistently close to zero and non-significantly ($p \geq 0.05$) different from zero (-0.2 to 0.4), for both Norway spruce and Scots pine (Table 7, **II,III**). The estimates were similar to most of the previous correlations estimated in Norway spruce and Scots pine juvenile wood (Hannrup *et al.*, 2003, 2004; Steffenrem *et al.*, 2009) and

Table 7. Genetic correlations described in papers **I-III**, between grain angle and other traits measured in Material A (Norway spruce progeny trials), B (Norway spruce clonal trials) and C (Scots pine progeny trial).

| Paper | Norway spruce | | Scots pine |
| | Material A | Material B | Material C |
	I & II	**II**	**III**
Correlations with growth traits			
GAub – H	0.0 to 0.4	-	0.0
GAub – DBH	0.1 to 0.4	-	-0.1 to 0.1
GAs – RGs	-	-0.2 to 0.3	-
GAd – H	0.3 to **0.6**	-	-
GAd – RGs	-	0.1 to 0.4	-
GAta – RGs	-	-0.1 to 0.4	-
GAtd – RGs	-	**0.5** to **0.7**	-
Correlations with other traits			
GAub – BD	0.1 to 0.4	-	0.0
GAub – BR	0.1 to 0.4	-	-0.1
GAub – BA	0.0 to 0.1	-	0.0
GAub – STR	0.0 to 0.2	-	0.2
GAub – PIL	0.0 to 0.1	-	-
GAub – TW	-0.1 to 0.3	-	-
GAub – RAM	-0.2 to 0.0	-	-

Note: Estimates that were significantly different from zero ($p < 0.05$) are indicated in bold. GAd - grain angle at a specific distance from pith, GAta - grain angle trend with respect to cambial age ($°\text{yr}^{-1}$), GAtd - grain angle trend with respect to distance from pith ($°\text{mm}^{-1}$). All other abbreviations are explained in Table 3

those reported in other species, e.g. radiata pine (Jayawickrama, 2001). The genetic selection for a lower grain angle under bark thus only appears to confer weak – if any – responses in other traits, and selection for other traits does not appear to generate any appreciable response in grain angle under bark.

However, sawn timber twist is primarily controlled by the grain angle at specific distances from pith or by the radial grain angle trend with increasing distance from pith (Ekevad, 2005; Bäckström and Johansson, 2006). In this respect, the positive genetic correlations (0.1–0.7) found between growth and the grain angle at specific distance to pith (GAd) and the grain angle trend with increasing distance from pith (GAtd) were unfavourable (Table 7). A likely explanation for these unfavourable correlations is that the proportion of juvenile wood with a high grain angle is likely to be higher in genotypes with fast radial growth. The sawn timber produced from such genotypes would be more likely to twist, especially if genetic gain in growth is realised by earlier final harvests. A genetic selection for a lower grain angle under bark in juvenile wood, could however counteract this effect and would be unlikely to have any substantial impact on the growth traits because the genetic correlations between grain angle under bark *per se* and growth traits were close to zero.

4.4 Genetic correlations for grain angle across trials

Genetic correlations for grain angle across the three Norway spruce progeny trials (Material A) were in the range 0.97 to 1.00, and thus very high (Table 8, **I**), in accordance with observations of the grain angle in more juvenile wood (Costa e Silva *et al.*, 2000; Hannrup *et al.*, 2003, 2004; Steffenrem *et al.*, 2009). This suggests that G×E-interactions for grain angle are generally very weak and that grain angle breeding values predicted from one or a few trials of Norway spruce should be valid for different environments within reasonable ranges. In addition, genetic correlations between grain angle in the progeny trials and the parent seed orchard were in the range

Table 8. Genetic correlations for grain angle under bark across the progeny trials of Material A.

	Tönnersjö	Lönsboda
Vetlanda	1.00 (0.05)	0.99 (0.06)
Tönnersjö	-	0.97 (0.06)

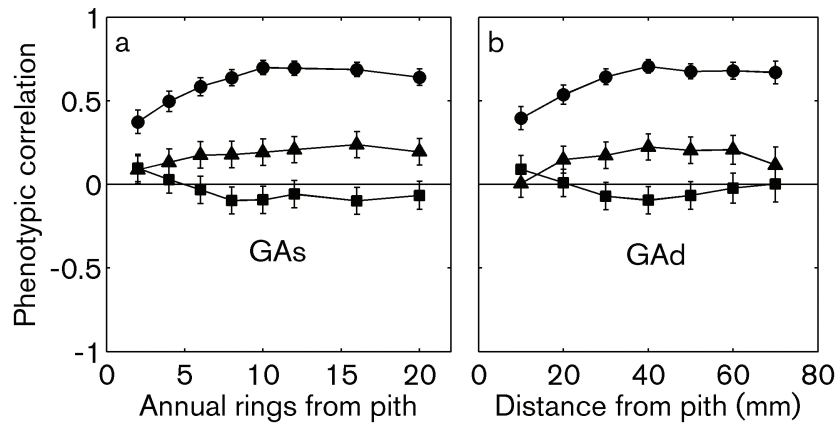Note: Standard errors are given in parentheses.

Figure 10. Phenotypic correlations between shape stability traits and the grain angle measured at (a) specific annual rings numbered from the pith (GAs) or (b) specific distances from the pith (GAd). Correlations with bow, crook and twist are indicated by (■), (▲) and (●) respectively, and standard errors of the correlations by error bars.

0.66 to 0.84 (**I**), indicating that parental genotypes could be ranked with respect to mature wood grain angle even by grain angle assessments in a seed orchard.

4.5 Choice of annual ring to assess grain angle non-destructively

The grain angle assessments in stem sections showed that all annual rings in a wide range of ages (8–20 years old) and distances from pith (30–70 mm) exhibited stronger phenotypic correlations with twist ($\hat{r}_P > 0.60$, Figure 10, **IV**), than the grain angle under bark ($\hat{r}_P = 0.54$, Table 5). This suggests that the phenotypic correlation between grain angle under bark and the twist of centrally sawn boards could have been higher if measurements had been performed on younger or smaller trees than those actually assessed (36-years-old, mean DBH 168 mm).

Assuming that the genetic correlations between the grain angle measured in these rings are similar to the corresponding estimated phenotypic correlations, the potential reductions in twist of small sawn timber (Figure 9 & Table 6) could probably be achieved by the genetic selection for a lower grain angle based on assessments of the grain angle under bark when the trees have grown to a diameter within the range 60–140 mm.

5   Conclusions and implications for tree breeding

Based on the results presented in this thesis, the following conclusions were made:

- The genetic variation ($\sim 0.8°$) and heritability (~ 0.35) of grain angle under bark in mature wood appeared to be as high as in juvenile wood in Norway spruce and Scots pine, indicating that predicting grain angle breeding values and genetic selection for lower grain angle are possible in mature wood as well as juvenile wood.

- The estimated phenotypic correlations between the grain angle assessed in single annual rings (including assessments under bark) and the board twist were high (~ 0.6). This indicated that there is potential to reduce the proportion of excessively twisted Scots pine central boards appreciably, even if the heritability of twist would be assumed to be very low. The studies this thesis is based upon and previous research have indicated a similar potential for twist reductions in Norway spruce. No other trait studied showed correlations of such magnitude with twist. At the moment, the grain angle under bark appears to be the only available assessment method that could be practically applied on a large scale in tree breeding to improve sawn timber shape stability by genetic selection.

- The grain angle at a given distance from pith was observed to be unfavourably genetically correlated to growth traits, implying that selection for growth could potentially generate adverse responses in the overall shape stability of sawn timber. However, grain angle assessed under bark, or in any given annual ring, did not appear to be genetically correlated with any other trait studied, indicating that genetic selection for lower grain angle under bark could be performed independently from that of other traits.

- In Norway spruce, genetic grain angle correlations across trials were close to unity, suggesting that genetic ranking based on mature wood grain angle breeding values obtained from one or a few trials, would be valid in other environments within reasonable ranges.

- The grain angle of all annual rings within the range 30–70 mm from pith exhibited phenotypic correlations with the board twist exceeding 0.6, indicating that the grain angle under bark assessment should be assessed when trees have a diameter in the range 60–140 mm if the

objective is to reduce twist in Scots pine sawn small timber by selection.

6   Future perspectives

Robust estimates of genetic correlations between the grain angle and shape stability traits need to be obtained to fully evaluate the effect of genetic alteration of the grain angle on sawn timber shape stability. Norway spruce should be prioritised, since its sawn timber is primarily used in building construction, where shape stability is essential (Woxblom, 1999; Grundberg and Esping, 2003). Moreover, since Norway spruce clonal tests are available for examination, genetic parameters can be estimated for this species with smaller errors than for Scots pine (for which only progeny tests are currently available), even when the sample number is limited. In a study of five full-sib families of Norway spruce, Steffenrem *et al.* (2007) recorded potential genetic associations between a high grain angle and low wood stiffness and strength. In studies of more diverse materials, it would therefore be advisable to consider other important sawn timber traits such as stiffness and strength.

   Juvenile-mature wood genetic correlations for grain angle also need to be estimated, since they will have implications for the possibility to reduce twist in timber sawn from the mature wood part of the tree. The genetic variation for the grain angle in juvenile as well as mature wood was shown to be substantial, and the genetic correlations of grain angle have been shown to be high within the juvenile core of Norway spruce (Hannrup *et al.*, 2002) and radiata pine (Gapare *et al.*, 2007). Nevertheless, the genetic grain angle correlations between juvenile wood and mature wood are not well known. Hence, obtaining further information regarding these relationships, should not only facilitate attempts to reduce the proportions of sawn timber with unacceptable shape stability, but also increase general knowledge regarding the genetic regulation of the grain angle during tree development.

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