Dissertationes Forestales 86

Effects of genetic entry and spacing on growth and wood properties in Norway spruce

Ane Zubizarreta Gerendiain
Faculty of Forest Sciences
University of Joensuu

Academic dissertation

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Author: Ane Zubizarreta Gerendiain

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Thesis Supervisors:
Dr. Heli Peltola (main supervisor)
Faculty of Forest Sciences, University of Joensuu, Finland

Dr. Pertti Pulkkinen
Metla, Finnish Forest Research Institute, Vantaa Research Unit, Finland

Pre-examiners:
Dr. Harri Mäkinen
Metla, Finnish Forest Research Institute, Vantaa Research Unit, Finland
Dr. Björn Hannrup
Skogforsk, Forestry Research Institute of Sweden, Uppsala, Sweden

Opponent:
Prof. Barry Gardiner
Forest Research, Northern Research Station, Roslin, Scotland

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ABSTRACT

In recent decades, in forest breeding programmes in Finland, growth has been used as a selection trait of primary importance in Norway spruce (*Picea abies* (L.) Karst.), whereas wood properties have been taken as secondary traits. However, interest in considering wood density and fibre traits in different genetic entries for future regeneration material has increased recently. In this context, this study aimed to analyse how genetic entry and spacing affected the growth, yield, wood density traits and fibre properties in Norway spruce (Papers I-V). Moreover, phenotypic correlations between different traits were analysed. In addition, effects of competition by neighbours on different traits were studied based on a competition index (Paper V). The harvested materials included both normal and narrow crowned (*Picea abies* f. *pendula*) genetic entries. The age of sample trees ranged between 28-30 years for normal crowned clones, representing different origins (Papers I, II, V), and between 14-19 for narrow crowned genetic entries (Papers III-IV). All the materials were harvested from four trials located in Southern Finland on agricultural and medium/fertile forest soils, with spacing ranging from 1 m x 1 m to 2 m x 2.5 m.

Wood density traits and fibre properties showed, in general, lower phenotypic variations than the growth and yield traits (Papers I-V). In addition, the phenotypic variations between narrow and normal crowned genetic entries differed when grown in different spacing (Papers III-IV). Between individual clones of normal crowned Norway spruce (Imatra and Kangasniemi trials), differences were found in most of the studied traits, unlike between origins (Papers I-II and V). Moreover, growth and yield traits of narrow crowned genetic entries were less sensitive to spacing than the normal crowned ones and thus, more productive with narrow spacing (Loppi trial), while in wider spacing (Karkkila trial) the result was opposite (Papers III-IV). On average, the phenotypic correlations between growth and wood density traits were in general negative, and from moderate to strong. However, individual genetic entries with weak or no correlation could still be found. Moreover, all the phenotypic correlations among the wood density traits and among the fibre properties were positive ($p<0.05$), and moderate to strong, indicating that selection for one trait simultaneously affects the others (Papers I-V). On average, the diameter of trees decreased and wood density increased with increasing competition, which explained part of the variation observed among the clones for growth and yield traits (Paper V).

As a conclusion, selection for wood density alone reduces in general stem volume and stem mass, whereas selection for fibre properties alone reduces wood density. However, opposite to general trend, for example, clone C43 in normal crowned Norway spruce had in this study simultaneously high stem volume, relatively high wood density and long fibres, for example. The marked differences observed among different genetic entries, as well as lack of clear differences among the origins also revealed that ranking regarding different traits should be based on individual clones (or families) rather than origin/provenances.

Keywords: tree height, breast height diameter, stem volume, ring width, wood density, fibre length, fibre width, coarseness, narrow crown, phenotypic correlation, competition.

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Joensuu, 19th March 2009

Ane Zubizarreta Gerendiain

LIST OF ORIGINAL ARTICLES

This thesis is a summary of the following papers, which are referred into the text by the Roman numerals I-V. The papers are reproduced with the kind permission of the publishers.

I. Zubizarreta Gerendiain, A., Peltola, H., Pulkkinen, P., Jaatinen, R., Pappinen, A., Kellomäki, S. 2007. Differences in growth and wood property traits in cloned Norway spruce (*Picea abies*). Can. J. For. Res. 37:2600-2611. doi:10.1139/X07-220

II. Zubizarreta Gerendiain, A., Peltola, H., Pulkkinen, P., Jaatinen, R., Pappinen, A. 2008. Differences in fibre properties in cloned Norway spruce (*Picea abies*). Can. J. For. Res. 38:1071-1082. doi:10.1139/X07-113

III. Zubizarreta Gerendiain, A., Peltola, H., Pulkkinen, P., Ikonen, V-P., Jaatinen, R. 2008. Differences in growth and wood properties between narrow and normal crowned types of Norway spruce grown at narrow spacing in Southern Finland. Silva Fennica 42(3):423-437.

IV. Zubizarreta Gerendiain, A., Peltola, H., Pulkkinen, P. 2009. Growth and wood property traits in narrow crowned Norway spruce (*Picea abies* f. *pendula*) clones grown in Southern Finland. Silva Fennica 43(3). In press.

V. Zubizarreta Gerendiain, A., Peltola, H., Pulkkinen, P., Kellomäki, S. 2009. Effects of genetic entry and competition by neighbouring trees on growth and wood properties of cloned Norway spruce (*Picea abies*). Annals of Forest Science. In press.

Ane Zubizarreta Gerendiain had main responsibility in regard to the entire work done in Papers I-V. However, the co-authors of separate Papers (I-V) have helped to improve the work by commenting the manuscripts.

CONTENTS

1 INTRODUCTION

1.1 General background

The increase in wood demand for pulp and paper, and timber products in addition to the progress of the forest industries have increased the pressure in forestry to consider not only the wood quantity, but also the quality of raw material. It is known that silvicultural management affects the growth and yield and the consequent stem and wood properties of different tree species (and genetic entries) through the interactions between biological processes (i.e. height and radial growth of the stem and crown development) and environmental conditions (e.g. temperature, precipitation, availability of nutrients and light) (Figure 1). Correspondingly, stem and wood properties of trees (e.g. stem volume, variation of wood density and fibre properties in various wood assortments) affect their suitability as a raw material both for mechanical wood processing and pulp and paper production. In this sense, the properties of final products and sustainability of the production processes (e.g. energy use) may differ depending on the used raw material characteristics. Even relatively small changes in the wood properties may be very significant for the forest industry (Tyrväinen 1995). Therefore, it is important to have an integrated picture of how different factors (e.g. genetic entry, environmental conditions and silvicultural management) and their interactions affect wood properties.

Nowadays, Norway spruce (*Picea abies* (L.) Karst.) is one of the most common tree species in Europe and is widely grown outside its natural range. In northern and southern Europe, the expansion of Norway spruce is, however, limited by the extreme climatic conditions, unlike in western and central Europe, where it is widespread outside its natural range (Spiecker et al. 2004). In Finland and as well as in other Northern countries, where Norway spruce is growing inside its own natural habitat, it is both economically and ecologically one of the most important coniferous species, especially in regard to pulp and paper products. It is considered to be, for instance, one of the most valuable raw materials for mechanical pulping, because of its low content of extractives and light colour (Tyrväinen 1995).

However, under the climatic conditions typical for Finland, short growing season and low summer temperatures are currently the main factors limiting the growth of Norway spruce. Furthermore, the availability of light within a stand modifies the allocation of growth over the stem and other organs, whereas a lack of water and/or nutrients reduces the overall growth (Panshin and de Zeeuw 1980, Zobel and van Buijtenen 1989). Correspondingly, the changes observed in the growth and wood formation may differ in different environmental conditions and managements systems since these properties result from a complex relation between the cell divisions and the relative amount of different cell types, as well as their proportions (e.g. Herman et al. 1998, Saranpää et al. 2000, Pereira et al. 2003, Jaakkola et al. 2005a, 2005b).

In the long-term breeding programmes carried out in Nordic countries, stem volume growth has typically been considered as the selection trait of primary importance for Norway spruce, whereas wood properties, such as wood density and fibre characteristics, have been considered as secondary traits (e.g. Karlsson and Rosvall 1993). Nonetheless, this perspective has been changing, since the increase of the growth rate is known to also affect the raw material properties (Figure 1). Faced with this concern, tree breeders have realised that wood quantity and quality should not be treated as independent factors anymore (e.g. Zhang et al. 1996, Rozenberg and Cahalan 1997). In fact, the use of tree breeding to select genetic entries with desired wood quality indicators could be particularly attractive, since properties such as wood density and fibre morphology are usually moderately to highly inherited (Boyle et al. 1987, Zobel and Jett 1995, Hylen 1999). Furthermore, they show moderate genetic age-age correlations between juvenile and mature wood, indicating that tree selection could be successful even in reasonably young trees (Petty et al. 1990, Blouin et al. 1994, Hannrup and Ekberg 1998, Hannrup et al. 1998, Zamudio 2002).

In recent decades in forest management in Northern countries, in order to get high stem volumes as fast as possible, attempts have been made to shorten the rotation length. For example, in Norway spruce larger initial spacing as well as heavy thinning has been used to increase the growth rate of trees. Silvicultural management such as thinning affects the growth and formation of wood properties of trees within tree stands, both by accelerating the growth rate of the trees left in the stand after thinning and through the selective removal of trees (from dominant to suppressed trees) in harvesting (Pape 1999a, 1999b). Similarly, fertilisation can be used to increase the growth and development of trees (e.g. in Norway spruce) since nutrient availability is affecting directly the tree physiology and growth processes in different organs such as stem, foliage and roots throughout the growing season (Fober 2007). In response to such intensified management, trees grow faster, but could also have increasing proportion of juvenile wood, which is undesirable in sawn timber products as well as in pulp yield and paper products.

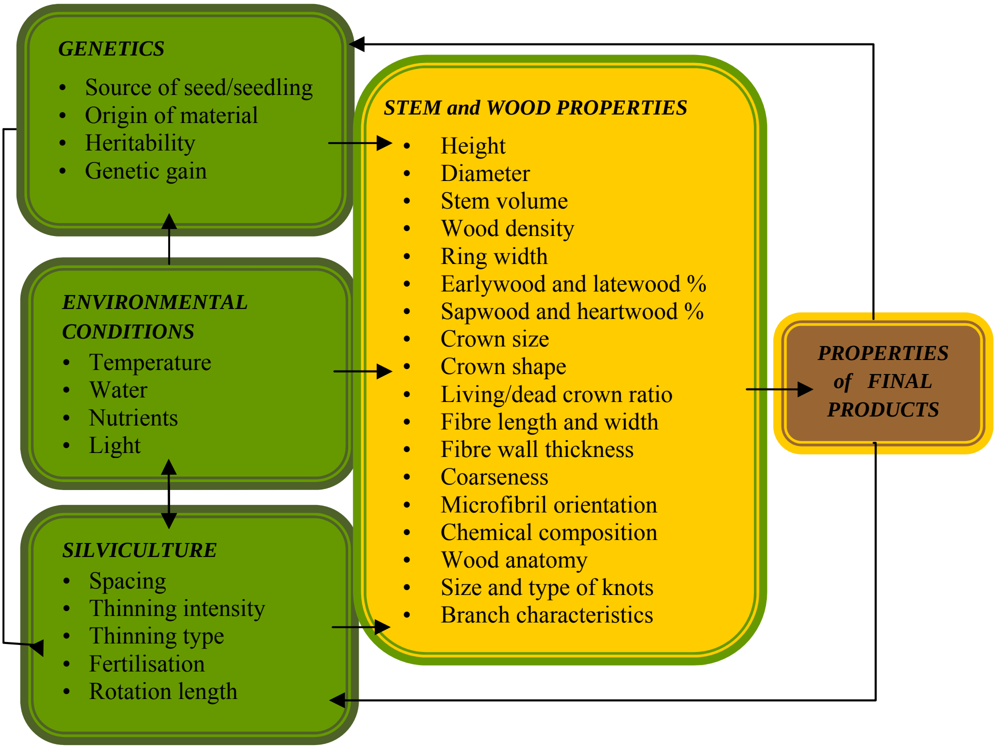


Figure 1. Interaction of different factors affecting the final wood products.

Additionally, tree's position in a stand (dominant versus suppressed trees) will determine the availability of growing space (light) within a stand, which affects the utilisation of soil nutrients and water resources as well. This has consequent effects on the growth processes and crown development, but also on the distribution of growth and wood properties along the stem (Zobel and van Buijtenen, 1989). Thus, it is also important to consider the position of the tree in the stand as well as the response of the trees to the neighbouring tree competitors. In several previous studies some species or even genetic entries within the tree species have already demonstrated different responses to varying competition conditions (Biging and Dobbertin 1992, Mäkinen 1996, 1997, Jayawickrama et al. 1998). In these studies, the effects of neighbouring competition on tree growth have usually been considered based on the use of competition indices (CI) (e.g. Hegyi 1974, Pukkala 1989, Biging and Dobbertin 1995, Mäkinen 1996, 1997). Their use is generally based on the assumption that a tree's competitive ability with regards to all resources can be indicated by an expression of, for example, the number of competitors, as well as the size, hierarchy, distance and spatial distribution of neighbouring trees. In principle, there exist many types of CIs, but as a general rule, despite of the used index, the competition is higher when the target tree has more neighbouring trees, and those neighbour trees are bigger and closer to the measured tree (Tomé and Burkhart 1989, Biging and Dobbertin 1992, 1995). However, these CIs do not explicitly indicate the mechanism of neighbouring interference.

1.2 Relationships between different wood properties

Usually, the growth, yield and wood properties (e.g. wood density) have been studied as variables independent from each other even if some of these properties may have a significant relationship among them. In this sense, the improvement of one trait may affect the others, thus, selection based on one trait could simultaneously affect other properties. For example, wood density can be used as an indicator of fibre morphology, since many studies showed that the latter one has a strong effect on the wood density (Zhang and Morgenstern 1995, Hylen 1997, Pot et al. 2002, Saranpää 2003).

Among all the wood properties, wood density is perhaps one of the most studied single variables. It could be used as a physical gross measurement for different wood properties as it is closely related to the characteristics revealing the end use value of wood such as strength, stiffness, hardness and papermaking attributes (Tyrväinen 1995, Sirviö and Kärenlampi 2001). Furthermore, it is a commonly used wood quality indicator because it is, at the same time, related to other wood properties, such as mechanical strength of wood and shrinkage, as well as pulp yield and paper properties (Panshin and de Zeeuw 1980, Harris 1993, Tyrväinen 1995). Thus, it is an important variable for the prediction of solid wood quality and the evaluation of pulp products. As a consequence, many investigations have already been carried out to study the wood density in different species and genetic entries, using different silvicultural managements (e.g. Persson et al. 1995, Herman et al. 1998, Zhang 1998, Mäkinen et al. 2002a).

However, wood density cannot be considered alone as the only selection trait because it is generally negatively correlated to growth and yield traits; i.e. selection for overall wood density alone would, in many circumstances, produce a reduction in stem volume (Herman et al. 1998, Pape 1999a, 1999b, Wilhelmsson et al. 2002). It is also usually expected that a rapid growth rate results in lower wood density, as a result of wider ring widths, this being the case especially for relative young trees (Larson 1969, Lindström 1996, Jaakkola et al.

2005b). Nonetheless, even if many previous studies have reported about this inverse relationship between wood density and growth, some exceptions have also been observed. As a matter of fact, various previous investigations have even observed a non-existent or positive correlation between tree growth/ring width and wood density in some coniferous tree species (Zhang and Morgenstern 1995, Bujold et al. 1996, Zhang et al. 1996, Wang et al. 2000).

These contradictory results may, however, be partly due to the fact that the wood density has many sources of variation, i.e. there exists variation between trees, within trees and within annual rings in a single tree. On one hand, wood density is strongly genetically controlled and the genetic variation of density is large between individual trees (Saranpää 2003). On the other hand, as a general rule, in softwoods like Norway spruce, the wood density changes within a tree from pith to bark and along the tree height as affected by the ageing of the cambium (Wilhelmsson et al 2002). Early stages of the cambium produce the juvenile wood, which generally has high variability, while older cambium produces the mature wood, which is more even (Sirviö and Kärenlampi 2001, Zamudio et al. 2002, Jyske et al. 2008). In addition, wood density will vary within each annual growth ring so that earlywood has commonly thin cell walls and wide lumen, resulting in a lower wood density, whereas latewood has thicker cell walls and narrow lumen, and thus, higher wood density (Zobel and Buijtenen 1989, Lindström 1996, Mäkinen et al. 2008). In general, the within tree variation in wood density (e.g. from pith to bark) is larger than the average variation between trees in the same tree species, while the variations within each ring are the major source of variation (Jyske et al. 2008).

In addition to wood density, fibre characteristics (i.e. fibre length, fibre width, cell wall thickness and coarseness) are also major causes for the variations observed in the quantity and quality of pulp (Zobel and van Buijtenen 1989, Ekensted et al. 2003). However, similar to wood density, fibre properties vary within single trees, between trees and between different genetic entries and tree species (Atmer and Thornqvist 1982, Molteberg and Høibø 2006). Primarily, the growth rate of a tree is one of the important factors affecting the characteristics of the fibre. It is usually held that by increasing the growth rate (e.g. by increasing availability of nutrients), fibre width increases opposite to fibre length. The latter reaction is especially the case when considering fibre length at same distance from pith to bark (Lindström 1997, Dutilleul et al. 1998, Herman et al. 1998, Sirviö and Kärenlampi 2001). Nevertheless, contradictory results have also been observed on the effects of growth rate on fibre dimensions (Bergqvist et al. 2000).

Moreover, fibre characteristics are also related to cambium maturation, since fibre length increases rapidly and non-linearly during the juvenile growth phase of the tree and more gradually in the mature growth phase (e.g. Dinwoodie 1961, Olesen, 1977 and 1982, Saranpää 1994). In addition, in several previous studies it has been observed that fibre properties are influenced by genetic entry because there exists from moderate to high genetic control for several fibre properties (Wheeler et al. 1965, Barnes et al. 1983, Boyle et al. 1987). Nonetheless apart from the fibre quantity and fibre dimensions, modern pulp and paper industry also currently emphasise the uniformity of the raw material (Ranua 2002). This is because uniform fibre population would considerably reduce, for example, energy consumption required in the production of final products and thus, would make the paper production system more sustainable.

1.3 Differences in growth, yield and wood properties between genetic entries

In general, wood properties such as wood density and fibre characteristics are in Norway spruce, as well as in other coniferous species, mainly influenced by genetic entry, ageing of the cambium and growth rate as affected by growing conditions (Blouin et al. 1994, Zhang and Morgenstern 1995, Zhang et al. 1996, Lindström 1997, Hylen 1999). For this reason, it is expected that it would be possible to select some genetic entries which, if applying proper management, would provide both a high stem volume and a relatively high wood density, or in which increase of the growth rate will have little impact on wood density, for example. In fact, this has already been found in some coniferous species such as black spruce (*Picea mariana* (Mill.)) (Zhang and Morgenstern 1995, Zhang et al. 1996), Scots pine (*Pinus sylvestris* (L.)) (Mörling 2002), lodgepole pine (*Pinus contorta* Douglas ex Loudon) (Wang et al. 2000) and Norway spruce (Bujold et al. 1996). In addition, the identification of appropriate genetic entries for future regeneration materials would be crucial, especially for Norway spruce, but also for other tree species in Finland and elsewhere due to the expected impacts of climate change on tree growth and dynamics. Under warmer climate, for example, the currently used genetic entries in forest regeneration for Norway spruce in Finland may suffer, at least to some degree due to drought, especially on less fertile sites currently occupied by Norway spruce in Southern Finland (Kellomäki et al. 2005). Therefore, the adaptation of current silvicultural management to consider such risks may be required. For instance, the use of more southern Norway spruce provenances, which might be more adapted to warmer climate may provide a suitable combination for stem growth and wood properties (Persson and Persson 1997).

In fact, some previous investigations have found differences, for example, in growth and wood properties among provenances in species such as loblolly pine (*Pinus taeda* L.) (Jayawickrama et al. 1997, 1998) and Scots pine (Ståhl 1998), as well as in Norway spruce (Bujold et al. 1996, Persson and Persson 1997, Skrøppa et al. 1999). These studies linking the growth rate and wood density with the origin of the material (Skrøppa and Magnussen 1993, Ekberg et al. 1994; Skrøppa et al. 1999) have suggested that the northern provenances have usually had the largest proportion of latewood and the highest wood density, but lower growth on average. However, there exist contradictory results in this respect (see e.g. Worrall 1975).

In Finland, genetic entries with special characteristics, such as narrow crowned Norway spruce (*Picea abies* f. *pendula*), which was discovered in Mäntsälä, southern Finland in the 1950s, could in the future also offer suitable regeneration material for practical forestry and raw material, e.g. for pulp and paper production. This narrow crowned Norway spruce is, in fact, a rare mutant of normal crowned Norway spruce and characterised by thin and hanging branches, producing less shade to the neighbouring trees than normal crowned Norway spruce at same size and spacing. As being less sensitive to narrow spacing than the normal crowned Norway spruce, it may also be grown in dense stands even without any thinning and with short rotations. This would provide significantly higher annual stem yield (total stem volume and dry mass, but higher harvest index as well) and larger quantity of raw material for pulp and paper production per occupied ground area than, for example, normal crowned Norway spruce (Pöykkö and Pulkkinen 1990, Pulkkinen 1991a, 1991b). Moreover, the use of relatively short rotation could also avoid the problems due to the decaying fungus *Heterobasidium annosum*, which is a common problem in older Norway spruce stands in Southern Finland (Swedjemark et al. 1997, Venäläinen et al. 2001).

However, it should be considered that the total stem wood production may be smaller in narrow crowned Norway spruce than that of the normal crowned one if planted, for example, at the typical spacing used for this species in practical forestry, such as stand density range of 1600-2000 seedlings/ha (Pulkkinen and Pöykkö 1990, Pulkkinen 1991a, 1991b). The use of narrow crowned Norway spruce trees in practical forestry should also be based on vegetative propagation, since the progenies of open pollinated pendulous trees consist of only 18-50% pendulous seedlings and the inheritance of the pendulous crown form is predominantly controlled by a single dominant gene which is modified by a number of minor genes (Lepistö 1985, Pulkkinen and Tigerstedt, 1992). In this sense, it would be necessary to find a cost efficient planting density, which at the same time provides the desired quantity and properties of wood.

On the other hand, side-by-side with narrow crowned Norway spruce it should also be considered the suitability of different normal crowned Norway spruce genetic entries (and especially clonal material). This would allow to identify their competitiveness in respect to their growth, yield and wood properties compared to narrow crowned ones to use as a future regeneration material. For example, in Sweden it has been observed that the use of genetically selected material in Norway spruce could increase the stem volume growth by 18-27 % compared to the currently used material in forest regeneration (Rosvall et al. 2004). In Finland, similar findings are not yet available. Thus, a future challenge of forestry in Finland and elsewhere is to determine the appropriate tree species and genetic entries, but also their site-specific management (e.g. spacing, thinning, rotation length), which will economically provide a large quantity of uniform and suitable raw material for different products and processes by forest industry. For this purpose, an integrated picture of the suitability of any genetic entry for a raw material is required (for example for pulp and paper and sawn products), including identification of processes affecting the yield and wood traits. This could make it finally possible to produce, for example, large quantities of uniform fibres per unit area even without performing any thinning in as short time as possible with selected genetic entries (Haapanen et al. 2002).

1.4 Aims of the study

The aim of this PhD thesis was to study how the genetic entry and spacing affected the growth (e.g. earlywood and latewood width, ring width), yield (e.g. height, diameter, stem volume) and wood density traits (earlywood and latewood densities, overall wood density) and fibre properties (fibre length and width, fibre wall thickness, coarseness) in Norway spruce grown in four different field trials established on agricultural soils and medium/fertile forest soils in southern Finland. More specifically, this work had the following objectives:

- to find out if a high growth rate was not necessarily associated with low wood density in any of the studied genetic entries (and/or origins) in normal and narrow crowned Norway spruce grown at different spacing (Papers I, III-V).

- to identify how the fibre properties were affected by the growth rate of the studied genetic entries (and/or origins) in normal and narrow crowned Norway spruce grown at different spacing (Papers II-V)

- to investigate the phenotypic relationships between different growth, yield and wood density traits and fibre properties for different genetic entries (and/or origins) in both normal and narrow crowned Norway spruce (Papers I-V).

- to analyse differences in growth and yield, wood density traits and fibre properties between normal and narrow crowned Norway spruce grown with different spacing (Papers III- IV).

- to study how the competition of neighbouring trees affects the growth and yield traits as well as wood properties of target trees in interaction with different genetic entries (and/or origins) in normal crowned Norway spruce (Paper V).

2 MATERIALS AND METHODS

2.1 Experimental data

Norway spruce sample trees harvested in the present study were taken from four unique field trials established during the 1970-90s in southern Finland (Figure 2). These trials, maintained by the Finnish Forest Research Institute (FFRI), have now reached the age, which allows the assessment of many growth and wood quality traits, but also partly the competition effects on these traits. The sample material harvested represented genetic entries grown both on forest (Papers IV-V) and agricultural (Papers I- III) soils typical for Norway spruce with initial spacing ranging from dense to currently used planting densities in Finnish forestry. The materials harvested for this work represented mainly normal crowned Norway spruce clones with different climate regions typical for Finnish conditions (Papers I-II), but also provenance hybrids of crosses between Finnish and foreign trees (Paper V) (Table 1). Additionally, narrow crowned genetic entries of Norway spruce were harvested for this work (Table 1) (Papers II-III).

The first study material analysed (Papers I-II) came from a trial established on agricultural soil for normal crowned type of Norway spruce in 1974 at Imatra, south-eastern Finland (28^{o}48’E, 61^{o}08’N) (Figure 2). In spring 2004, 20 clones with southern and central Finnish origin were randomly harvested from the trial. The clones in this trial were grown at normal spacing of 2 m x 2.5 m for Norway spruce (Table 1). Altogether 198 sample trees were harvested (i.e. 9-10 replicates from each clone) and, at the time of harvesting, tree height and diameter at both breast height and at 6 meters high for each sample trees were measured (Papers I-II).

The second study material analysed in this work (Paper V) was also harvested from a normal crowned Norway spruce field trial, which was established on a medium fertile forest site, *Myrtillus* type (according to Cajander 1926) in 1979 in Kangasniemi, southern Finland (61°59’3N, 26°38’54E) (Table 1, Figure 2). In autumn 2007, 10 clones with Finnish provenance (FxF) representing different breeding regions in Finland were harvested. In addition, 2 Russian provenances clones (RxR), and 8 hybrid provenance clones representing crosses between Finnish father trees and mothers from Germany (FxG), Switzerland (FxS), Latvia (FxL), Ukraine (FxU) and Estonia (FxE) were chosen. The studied genetic entries were grown with a spacing of 2 m x 2 m. Altogether, 99 sample trees were harvested from this trial (i.e. 4-5 samples per each genetic entry) and their heights and diameters at breast height and at 6 m high measured. Unlike in the first trial, the average diameter of the crown of the target tree, as well as its nearest surrounding neighbours were measured in order to study the effects of competition of neighbouring trees on different traits of target trees in interaction with different genetic entries and/or origins.

In order to study the effects of spacing on the differences between narrow and normal crowned Norway spruce (Papers III-IV), materials from two additional trials were harvested, i.e. from one trial established in Loppi (60°38'N, 24°13'E) in 1991 (Paper III) and from another trial established in Karkkila (60°32′N, 24°12′E) in 1988 (Paper IV) (Table 1, Figure 1). The spacing of the Loppi trial was 1 m x 1 m and it was located on agricultural soil. As a comparison, the spacing of Karkkila trial was 1.5 m x 2 m and it was located on a fertile forest soil (i.e. *Myrtillus* - *Oxalis-Myrtillus* type according to Cajander 1926).

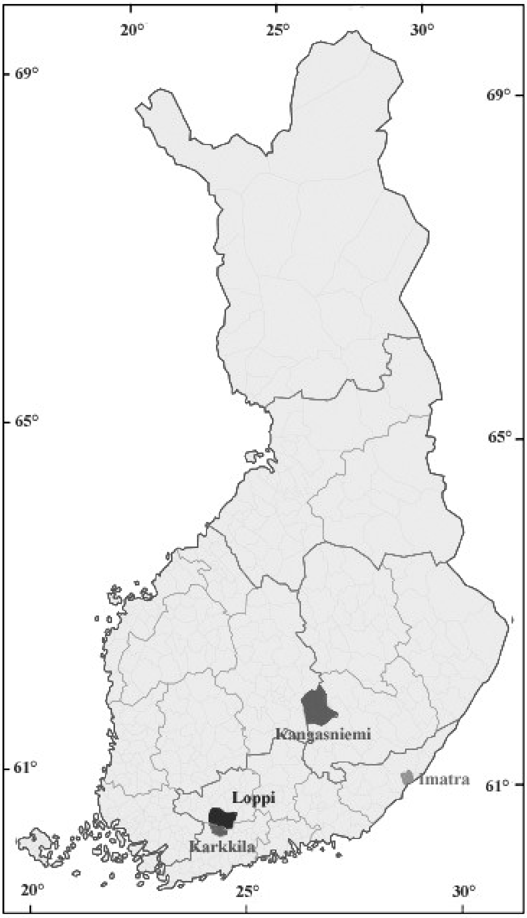


Figure 2. Location of the experimental trials used in this study.

Table 1. Number (N) of harvested genetic entries (GE) and sample trees from the different experimental trials.

Paper	Trial Location	Spacing m x m	Age	N of genetic entries Normal	Narrow	Total	Trees /GE	Total trees
I-II	Imatra*	2 x 2.5	30	20	0	20	8-10	198[1]
III	Loppi*	1 x 1	14	6	9	15	4-6	75
IV	Karkkila**	1.5 x 2	19	3	13	16	6	96
V	Kangasniemi**	2 x 2	28	20	0	20	4-5	99

[1] 183 trees for paper II

*Agricultural soil, **Medium fertile to fertile forest soil

During the winter 2005-2006, 15 genetic entries were randomly chosen and harvested from Loppi trial. The harvested material included 9 genetically narrow crowned Norway spruce (*Picea abies* f. *pendula*) full-sib families and six genetic entries with normal crowned Norway spruce. Altogether, 75 sample trees were harvested from this trial. The corresponding material harvested from the Karkkila trial during 2007 included 16 randomly chosen genetic entries, 13 of which were narrow crowned Norway spruce clones with the remaining three genetic entries representing normal crowned Norway spruce. In total, 96 trees were harvested from this trial. For each sample tree, tree height and diameter at breast height was measured (Papers III-IV). The narrow crowned Norway spruce material (Papers III-IV) for both trials originated from controlled crosses between narrow crowned spruces from Mäntsälä stand (60°40’N, 25°15’E) with narrow crowned spruces from the same stand or with normal crowned spruces originating from southern or central Finland (latitudes 60°45’N-64°58’N). The additional normal crowned Norway spruce genetic entries used in comparison originated from seeds collected from commercial forest stands located in southern Finland (latitudes 60°40’N-63°22’N) (Papers III-IV).

Regardless of the trial (Papers I-II, IV and V), and the harvested material, the age of the mother trees of the clones varied from 2 to 4 years at the time of cloning and this range was not expected to affect the results (Rautanen 1995). Furthermore, no thinning was carried out up to the time of the harvesting in any of the studied field trials (Papers I-V). After the field measurements, the trees were first cut and thereafter a sample disc taken at 1-1.3 meter height for each sample for the laboratory analyses (at the Faculty of Forest Sciences, University of Joensuu), regarding annual growth, wood density traits and fibre properties (Papers I-V).

2.2 Measurements

2.2.1 X-ray densitometry measurements

The intra-ring wood densities were measured using an ITRAX X-ray microdensitometer (Cox Analytical Systems, Göteborg, Sweden) located at the University of Joensuu, Faculty of Forest Sciences (Figure 3) (Papers I-V). For that purpose, first of all, a rectangular wood specimen of size 5 mm x 5 mm representing two opposing radii (from pith to bark) were cut out of each sample disc (taken at 1-1.3 m above ground) using a twin-bladed circular saw.

Figure 3. Layout for the ITRAX X-ray microdensitometer (left) and density profile obtained with ITRAX X-ray microdensitometer (right).

Thereafter, these wood specimens were kept for a few weeks under fixed conditions until they had reached a moisture content of 12% (air dry). Thereafter the sample specimens were scanned with ITRAX, which works with an automatic collimator alignment (Bergsten et al. 2001) at a geometrical resolution of 40 measurements per mm. In the present work, the standard X-ray intensity (30 kV, 35 mA) for X-ray measurements was used, with an exposure time of 20 ms based on previous works by e.g. Kilpeläinen et al. (2005) and Peltola et al. (2007).

Subsequently, the obtained X-ray radiographic images were analysed with the Density software (Bergsten et al. 2001) to determine the intra-ring density profiles for each sample from pith to bark (Figure 3). Furthermore, with the help of Excel macros, ring width (mm), earlywood and latewood widths (mm) and proportions (%), mean wood density (g/cm^3), minimum and maximum wood densities (g/cm^3) and earlywood and latewood densities (g/cm^3) were determined. Similar to previous works (Peltola et al. 2007, Helama et al. 2008), the mean of the maximum and minimum intra-ring densities were used as the threshold for earlywood and latewood in each ring, i.e. the values above and below this threshold represented the latewood and earlywood, respectively.

2.2.2 Fibre property measurements

An L&W Fiber Tester (AB Lorentzen & Wettre, Kista, Sweden), located at the Faculty of Forest Sciences, University of Joensuu, was used for the analyses of the intra-ring fibre properties (Figure 4) (Papers II-V). In all studies, similar procedure was followed; matchstick-sized wood specimens were first chipped away for every two annual ring pairs from pith to bark from the same stem discs as used for the X-ray analysis in each sample tree. Subsequently, these chipped samples were macerated in a boiling 1:1 (v/v) mixture of acetic acid and hydrogen peroxide. The fibre measurements by the L&W Fiber Tester are based on image analysis and thus, as the highly diluted suspension flows between two glass plates, this limits the possibility of the fibres moving in one direction, but allows them to move freely in the other two directions. As a result, the two-dimensional images permit the measurement of fibre size and deformations separately. The use of the L&W Fiber Tester makes it possible to observe a large number of fibres for each sample (i.e. up to tens of thousands of fibres) in a few minutes, and provide, in addition to fibre length (FL, mm) and fibre width (FW, µm) mean values, the distributions of fibre properties classified in different fibre length classes (e.g. <0.2 mm, 0.2-0.5 mm, 0.5-1.0 mm etc).

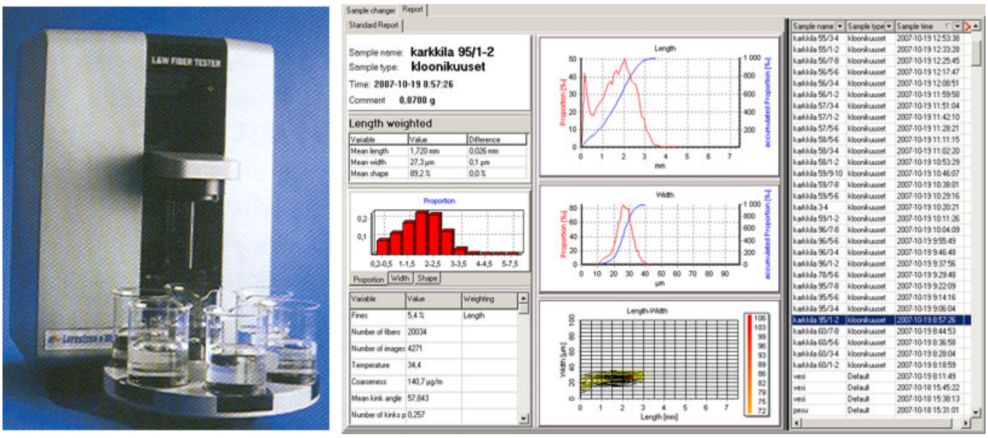
Based on the dry weight of each sample and total length of fibres measured in that sample, fibre coarseness (C, fibre mass per unit fibre length of sample, µg/m) was calculated (see Karlsson 2006). Correspondingly, an average of fibre wall thickness (FWT) per sample was defined based on fibre measurements as follows:

$$\mathrm{FWT} = \frac{\mathrm{FW}}{2} - \sqrt{\frac{\mathrm{FW}^2}{4} - \frac{\mathrm{C}}{\pi * \mathrm{R}}} \qquad (1)$$

where FW is the average fibre width (µm) measured by the fibre tester, C the average coarseness of the sample (µg/m) and R is the expected fibre wall density (for Norway spruce 1.5 g/cm^3, see Kollman and Cõte 1968).

2.3 Data Analysis

For each sample tree, stem volume (V, m^3) was calculated with the measured tree height and diameters at 1.3 m and 6 meters (Papers I-V) based on the stem volume functions developed by Laasasenaho (1982) for Norway spruce. In addition, using the intra-ring measurements from pith to bark, weighted averages for overall wood density (WD), earlywood density (EWD), latewood density (LWD), fibre length (FL), fibre width (FW), fibre wall thickness (FWT) and coarseness (C) were calculated by weighting each value with its corresponding ring width. For further statistical analyses mean widths of the annual ring (RW), earlywood (EWW) and latewood (LWW), and latewood width percentage (LWW%) were also calculated.



Sample name: **karkkila 95/1-2**
Sample type: **kloonikuuset**
Time: **2007-10-19 8:57:26**
Comment **0,0700 g**

Length weighted

Variable	Value	Difference
Mean length	1,720 mm	0,026 mm
Mean width	27,3 µm	0,1 µm
Mean shape	89,2 %	0,0 %

Variable	Value	Weighting
Fines	5,4 %	Length
Number of fibers	20034	
Number of images	4271	
Temperature	34,4	
Coarseness	140,7 µg/m	
Mean kink angle	57,843	
Number of kinks p	0,257	

Sample name	Sample type	Sample time
karkkila 55/3-4	kloonikuuset	2007-10-19 12:53:38
karkkila 55/1-2	kloonikuuset	2007-10-19 12:33:28
karkkila 56/7-8	kloonikuuset	2007-10-19 12:25:45
karkkila 56/5-6	kloonikuuset	2007-10-19 12:17:47
karkkila 56/3-4	kloonikuuset	2007-10-19 12:08:51
karkkila 56/1-2	kloonikuuset	2007-10-19 11:59:58
karkkila 57/3-4	kloonikuuset	2007-10-19 11:51:04
karkkila 57/1-2	kloonikuuset	2007-10-19 11:42:10
karkkila 57/5-6	kloonikuuset	2007-10-19 11:28:21
karkkila 58/5-6	kloonikuuset	2007-10-19 11:11:15
karkkila 58/3-4	kloonikuuset	2007-10-19 11:02:20
karkkila 58/1-2	kloonikuuset	2007-10-19 10:53:29
karkkila 59/9-10	kloonikuuset	2007-10-19 10:46:07
karkkila 59/7-8	kloonikuuset	2007-10-19 10:38:01
karkkila 59/5-6	kloonikuuset	2007-10-19 10:29:16
karkkila 3-4	kloonikuuset	2007-10-19 10:20:21
karkkila 59/1-2	kloonikuuset	2007-10-19 10:11:26
karkkila 96/7-8	kloonikuuset	2007-10-19 10:04:09
karkkila 96/5-6	kloonikuuset	2007-10-19 9:55:49
karkkila 96/3-4	kloonikuuset	2007-10-19 9:46:48
karkkila 96/1-2	kloonikuuset	2007-10-19 9:37:56
karkkila 78/5-6	kloonikuuset	2007-10-19 9:29:48
karkkila 95/7-8	kloonikuuset	2007-10-19 9:22:09
karkkila 95/5-6	kloonikuuset	2007-10-19 9:14:16
karkkila 95/3-4	kloonikuuset	2007-10-19 9:06:04
karkkila 95/1-2	kloonikuuset	2007-10-19 8:57:26
karkkila 60/7-8	kloonikuuset	2007-10-19 8:44:53
karkkila 60/5-6	kloonikuuset	2007-10-19 8:36:58
karkkila 60/3-4	kloonikuuset	2007-10-19 8:28:04
karkkila 60/1-2	kloonikuuset	2007-10-19 8:18:59
vesi	Default	2007-10-19 8:11:49
vesi	Default	2007-10-18 15:45:22
vesi	Default	2007-10-18 15:38:13
pesu	Default	2007-10-18 15:31:01

Figure 4. Layout for the L&W Fiber Tester (AB Lorentzen & Wettre, Kista, Sweden) and the fibre information table.

SPSS statistical program package (SPSS for Windows, version 13.0 and 15.0, SPSS, Chicago, IL) was used for statistical analyses. Analysis of variance procedure applying the General Linear Model (GLM) was performed for the growth and yield traits (diameter, height, stem volume, EWW, LWW, LWW% and RW), wood density traits (WD, EWD, LWD) and fibre properties (FL, FW, FWT and C) to identify any differences among the studied genetic entries, origins and crown types (Papers I-V). The block effect was included as random factor for statistical analyses only for materials harvested in Kangasniemi trial (Paper V) since it was not a significant variable in the other trials. In addition, in order to identify the differences among the clones concerning the studied traits, Tukey's pairwise test was used ($p<0.05$) (Papers I-II). On the other hand, GLM procedure was used for the analysis of the differences in terms of crown type, nesting the genetic entries in each crown type (Papers III-IV).

The phenotypic coefficient of variation (CV_p) for each genetic entry and/or origin was also calculated by normalising the standard deviation (σ) by the mean (μ) of the property (i.e. $CV_p = \sigma*100/\mu$) (Papers I-V). Furthermore, the phenotypic correlations (r_p) between properties were computed using the Pearson's correlation method (Eq. 2);

$$r_p = \sigma_{p1p2} / \sigma_{p1}\, \sigma_{p2} \tag{2}$$

where σ_{p1p2} is the phenotypic covariance between properties 1 and 2, while σ_{p1} and σ_{p2} are the phenotypic standard deviation for properties 1 and properties 2, respectively (Papers I-V). In this work, the relatively small number of genetic entries available in each study did not support the calculation of genetic correlations (see e.g. Hannrup et al. 2000). On the other hand, previously Haapanen and Pöykkö (1993) suggested that genetic and phenotypic correlations appeared to be considerably analogous, especially if the latter ones were computed on the genetic entry-mean level (see e.g. Zhang and Morgenstern 1995, Skrøppa et al. 1999). However, since the genetic correlations estimate the degree of relationship between two traits due to genetic causes and the phenotypic correlations measure the closeness of the relationship between two observed traits (combining genetic and environmental causes), these correlations would not be fully comparable to each other (see e.g. Hannrup et al. 2000).

In addition, to determine if there existed interaction between clone and competition of neighbouring trees (Paper V), a competition index (CI) for different clones was calculated. For this purpose, a distance dependent CI developed by Schütz (1989) (Eq. 3) was applied;

$$CI_{\mathrm{Schütz}} = \sum_{i=1}^{n} 0.5 - \frac{d_{ij} - (cr_j + cr_i)}{(cr_j + cr_i)} + 0.65\frac{h_i - h_j}{d_{ij}} \tag{3}$$

where *j* is the competitor tree and *i* the target tree, *n* is the number of neighbours, d_{ij} (meters) is the horizontal distance between the target tree and its competitor, *h* (m) is the trees height and *cr* (meters) is the mean crown radius. The sum over all the competitors is giving the CI. However, a neighbouring tree was only considered in this approach as a competitor if the calculated value was greater than zero. The calculated CI was used as a covariate in the GLM, when analysing differences between clones for breast height diameter, tree height, ring width and overall wood density, which were expected to be affected most by the competition between neighbours.

3 RESULTS

3.1 Variation in growth, yield and wood properties

In general, among all the analysed traits, wood density traits and fibre properties (particularly fibre width and fibre wall thickness) showed, on average, the lowest phenotypic variation regardless of the study material (Papers I-V). Among all the harvested materials (and trial), the coefficient of phenotypic variation (CV_p) for the different wood density traits ranged from 1.6% to 11.7%, while corresponding range was from 2.9 % to 16.9% for the fibre properties (Tables 2-5). On the contrary, the studied growth and yield traits showed, in general, much higher phenotypic variation; ranging between 7.7% and 36.9% for the growth traits and between 6.8% and 84.9% for the yield traits (Tables 2-5). Nevertheless, among the normal crowned clones harvested from the Imatra trial (Papers I-II), and to some degree also among the clones and origins harvested from the Kangasniemi trial (Paper V), the variation observed for these traits was lower compared to the material harvested from the other trials, which included both narrow and normal crowned genetic entries. This was the case especially for the growth and yield traits, but also, in certain respects for the wood density traits and fibre properties (Tables 2-3).

Table 2. Statistics for the average of the 20 normal crowned Norway spruce clones harvested from the Imatra trial (spacing 2 m x 2.5 m), in terms of diameter (DBH, mm), height (H, m), stem volume (V, m^3), earlywood and latewood width (EWW, LWW, mm), ring width (RW, mm), earlywood and latewood densities (EWD, LWD, g/cm^3), overall wood density (WD, g/cm^3), fibre length (FL, mm), fibre width (FW, µm), coarseness (C, µg/m) and fibre wall thickness (FWT, µm) (Papers I-II). Significance of F-ratio with p<0.05 is given in bold.

Trait	Statistics for the 20 clones			
	Mean	CV_p	F-ratio	Sig.
DBH	140.2	8.1	**4.94**	**0.00**
H	12.88	6.8	**11.31**	**0.00**
V	0.097	19.0	**5.54**	**0.00**
EWW	2.46	9.2	**5.01**	**0.00**
LWW	0.67	11.8	**3.28**	**0.00**
RW	3.13	7.7	**4.25**	**0.00**
EWD	0.331	5.3	**19.73**	**0.00**
LWD	0.596	4.8	**15.04**	**0.00**
WD	0.388	5.6	**15.31**	**0.00**
FL	1.94	8.1	**11.24**	**0.00**
FW	28.7	2.9	**5.78**	**0.00**
C	159.6	5.5	**4.49**	**0.00**
FWT	1.23	3.4	**3.43**	**0.00**

Table 3. Statistics for the origins (left hand side) and the 20 clones (right hand side) harvested from the Kangasniemi trial (spacing of 2 m x 2 m), for growth, yield, and wood density traits and fibre properties (Paper V). Significance of F-ratio with p<0.05 is given in bold.

Trait[1]	Statistics for the origins				Statistics for the 20 clones			
	Mean	CV_p	F-ratio	Sig.	Mean	CV_p	F-ratio	Sig.
DBH	107.3	6.7	0.68	0.67	111.4	18.0	1.87	**0.03**
H	10.50	5.8	0.75	0.61	10.61	14.8	1.77	**0.04**
V	0.058	14.6	0.77	0.60	0.064	38.5	2.19	**0.01**
EWW	1.79	11.9	1.71	0.13	1.84	18.1	2.36	**0.00**
LWW	0.60	8.7	1.34	0.25	0.61	11.2	2.07	**0.01**
RW	2.39	9.5	1.42	0.22	2.44	15.4	2.32	**0.01**
EWD	0.341	2.8	1.81	0.11	0.341	4.7	4.52	**0.00**
LWD	0.600	3.2	4.25	**0.00**	0.596	4.5	3.60	**0.00**
WD	0.408	3.4	3.07	**0.01**	0.407	5.3	3.78	**0.00**
FL	1.94	5.0	1.49	0.19	1.94	6.2	1.87	**0.03**
FW	27.9	3.4	1.61	0.15	27.8	3.9	1.92	**0.02**
FWT	1.24	3.8	2.45	**0.03**	1.23	4.4	1.98	**0.02**
C	156	6.3	2.01	0.07	154	6.9	1.66	0.06

[1] see table 2 for the explanation and units of the traits.

Concerning the differences between narrow and normal crowned Norway spruce, the phenotypic variation was observed to be, on average, smaller in narrow crowned families (excluding for WD and LWD) than in normal crowned genetic entries, when the spacing was 1 m x 1 m (Table 4), in the Loppi trial (Paper III). For instance, in the narrow crowned families the phenotypic variation for growth and yield traits ranged between 17.2% and 45.9% while for normal crowned genetic entries the corresponding values were almost double that, ranging between 27.6 % and 81.5% (Table 4) (Paper III). On the contrary, in the Karkkila trial, with a spacing of 2 m x 1.5 m, the phenotypic variation was similar in normal and narrow crowned genetic entries for all other traits except the yield traits, in which narrow crowned clones showed higher values than normal crowned genetic entries, this was especially the case for stem volume (84.9%) (Table 5).

At the Imatra trial (Papers I-II), differences were found among the 20 clones (p<0.05) for all the studied traits (Table 2). For instance, C308 had both the highest stem volume and diameter growth, being 38% and 13% (Figure 5a) higher than the average for all the clones, respectively. In contrast, C332 had the lowest growth, with only 56.1% of the average stem volume and 79% of the average diameter for all the clones (Figure 5a). Similar to the growth and yield traits, statistically significant differences between the clones were found for different wood density traits and fibre properties (Table 2). For instance, clone C364, originating from south-eastern Finland, showed the highest overall wood density (WD, 9.5% higher than the average for the clones), while clone C314 originating from southern Finland had the lowest (88% of the average WD) (Figure 5b). In addition, in relation to the fibre properties, clone C328 had the largest fibres, i.e. the fibre length and width were 16% and 5.4% above the average for all the clones respectively, while clone C3151 had the shortest fibres (88% of the average) and clone C48 the narrowest ones (96%) (Figure 5c).In this sense, similar to the growth and yield traits, the ranking for the clones in regards to the different wood density traits as well as fibre properties, varied substantially depending on the considered trait. In addition, even if differences were found among the 20 clones in all the studied traits, no systematic differences were observed concerning the geographical origin of these clones.

Table 4. Mean and coefficient of variation (CV_p) for growth, yield, wood density and fibre traits for normal and narrow crowned genetic entries from the Loppi trial (spacing of 1 m x 1 m, Paper III). Different letters imply differences ($p<0.05$) among narrow and normal crowned means.

Trait[1]	Narrow crown		Normal crown	
	Mean	CV_p	Mean	CV_p
DBH	62.2^a	20.2	48.1^b	42.4
H	7.04^a	17.7	5.24^b	33.2
V	0.013^a	45.9	0.008^b	81.5
EWW	2.14^a	18.3	1.56^b	45.1
LWW	0.65^a	24.3	0.59^a	27.6
RW	2.79^a	17.2	2.15^b	36.9
EWD	0.327^a	7.8	0.349^b	11.7
LWD	0.549^a	5.5	0.560^a	4.9
WD	0.379^a	7.6	0.409^b	1.6
FL	1.60^a	8.5	1.45^b	16.9
FW	25.8^a	4.2	24.2^b	7.3
C	133^a	5.2	121^b	7.4
FWT	1.14^a	7.4	1.10^b	8.2

[1] see table 2 for the explanation of the traits.

Table 5. Mean and coefficient of variation (CV_p) for growth, yield, wood density and fibre traits for normal and narrow crowned genetic entries from Karkkila trial (spacing 2 m x 1.5 m, Paper IV). Different letters imply differences ($p<0.05$) among narrow and normal crowned means.

Trait[1]	Narrow crown		Normal crown	
	Mean	CV_p	Mean	CV_p
DBH	57.2^a	23.6	72.8^b	17.1
H	6.01^a	32.7	8.01^b	25.8
V	0.012^a	84.9	0.022^b	59.8
EWW	2.51^a	23.5	2.81^a	25.4
LWW	0.57^a	20.9	0.59^a	16.1
RW	3.08^a	20.7	3.39^a	21.6
EWD	0.340^a	7.9	0.320^a	7.7
LWD	0.585^a	6.0	0.575^a	6.6
WD	0.386^a	8.0	0.366^a	8.4
FL	1.56^a	12.4	1.62^a	12.9
FW	25.2^a	5.8	26.4^a	6.3
C	122^a	10.8	133^b	11.2
FWT	1.07^a	5.9	1.12^b	5.4

[1] see table 2 for the explanation of the traits.

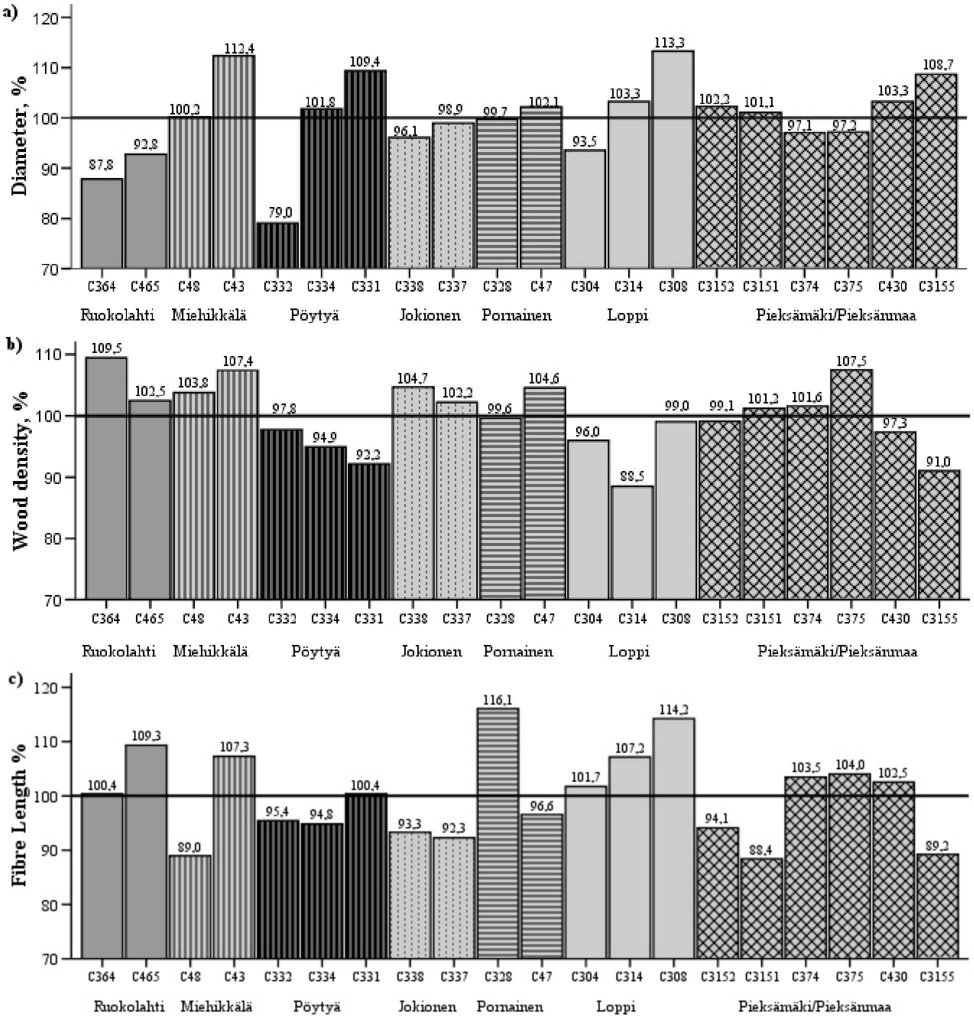


Figure 5. Relative differences in % for diameter, overall wood density and fibre length between clones (grouped by origins) for normal crowned Norway spruce harvested from the Imatra trial (spacing of 2 m x 2.5 m, see Papers I-II). Averages observed over all clones (100%) are marked as a line.

In general, similar results were obtained for the material harvested from the Kangasniemi trial with spacing of 2 m x 2 m (see Paper V), where among the studied 20 clones, statistically significant differences were observed for all the studied traits, except for coarseness ($p<0.05$) (Table 3). Among the individual clones, F430 with Finnish (FxF) origin had the largest diameter (34% above the average for the clones), while clone G384, originating from Finnish-German cross (FxG), showed the poorest diameter growth (69% of the average for the clones) (Figure 6a). In terms of overall wood density, Russian clone

R330 (RxR) had 11% higher WD than the average for all the clones while clone G384 from a Finnish German cross (FxG) showed the lowest WD, being 92% of the average for all the clones (Figure 6b). On the other hand, regarding fibre length, clone G478 (FxG) had the longest fibres (9% higher than the average), while clone G384, also with a German father (FxG), showed the shortest fibres (87% of the average) (Figure 6c).

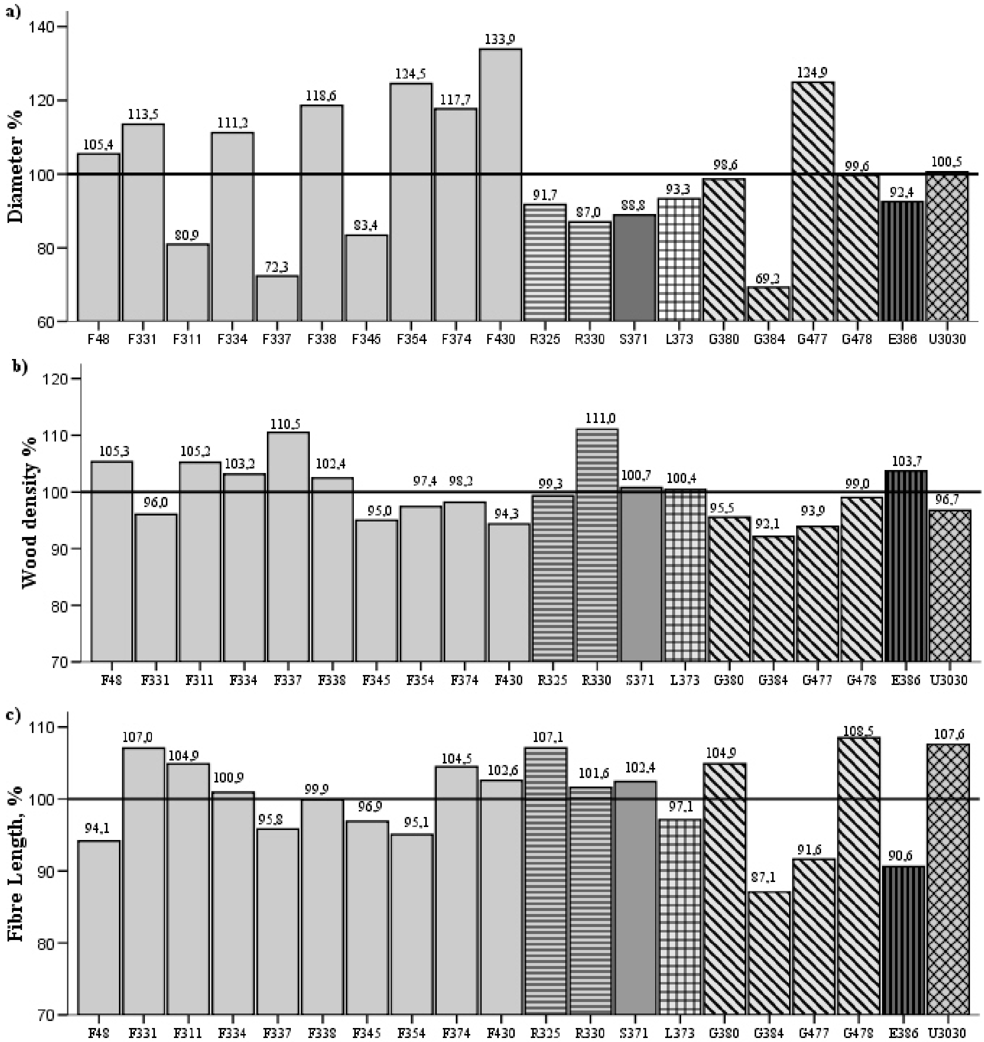


Figure 6. Relative differences in % for breast height diameter, overall wood density and fibre length between different clones (grouped by origins) for normal crowned Norway spruce harvested from the Kangasniemi trial (spacing of 2 m x 2 m, see Paper V). Average observed over all clones (100%) is marked as a line.

Regarding origins, only LWD, WD and FWT were significantly different, but no differences were observed regarding the other traits in the Kangasniemi trial (Table 3). In respect to yield traits, on average, Finnish origin (FxF) had the largest diameter and stem volume, being 10% and 24% larger than the average, while the Swiss origin (FxS) had, at the same time, both the lowest diameter growth (92% of the average) and the largest height growth (110 % of the average). Regarding other traits, WD ranged for the different origins between 0.43 g/cm^3 for the Russian origin (RxR) and 0.39 g/cm^3 for clones of Finnish-German cross (FxG), with those differences being significant ($p<0.05$) (Table 3).

When comparing narrow and normal crowned genetic entries, dissimilarities between the materials harvested from both trials were found (Papers III-IV). At the Loppi trial with narrow spacing (Paper III), the results regarding the yield traits showed that the narrow crowned families had, on average, significantly higher height (34% higher), diameter (30%) and stem volume (66%) than the normal crowned genetic entries ($p<0.05$) (Table 4, Figure 7a). In addition, narrow crowned families had, on average, significantly larger EWW (37% higher) and RW (30% higher) than the normal crowned genetic entries ($p<0.05$), whereas the LWW was 11% higher ($p>0.05$). On the contrary, in the Karkkila trial (Paper IV), with wider spacing than in the Loppi trial, the normal crowned genetic entries had a higher growth than the narrow crowned clones (Table 5). In particular, on average, normal crowned genetic entries had 94% higher stem volume than narrow crowed clones, and 33% and 27% larger diameter and height, respectively ($p<0.05$) (Figure 7b). Nevertheless, even if normal crown, on average, also showed 10% wider annual rings, those differences were not significant ($p>0.05$) for any of the growth traits (Table 5).

Concerning wood density traits of the material harvested from the Loppi trial (Paper III), differences were observed between narrow crowned families and normal crowned genetic entries ($p<0.05$) for the overall wood density and earlywood density, unlike in latewood density (Table 4, Figure 7c). In this case, values for normal crowned genetic entries used in comparison were higher; 6% higher EWD and 8% higher WD. In contrast, in the Karkkila trial (Paper IV), even if, on average, the narrow crowned clones showed higher wood density than normal crowned genetic entries used in comparison, those differences were not significant for any of the three wood density traits ($p>0.05$, see Table 5, Figure 7d).

Additionally, and concerning the fibre properties, contradictory results were also found in both the Loppi and the Karkkila trials. In the Loppi trial (Paper III), there were significant differences regarding average fibre properties, having the narrow crowned families on average, 11% longer and 7% wider fibres, but also 4% thicker cell walls and 10% higher coarseness ($p<0.05$, see Table 4, Figure 7e). Conversely, in the Karkkila trial (Paper IV), normal crowned genetic entries showed longer and wider fibres than narrow crowned clones, with higher coarseness and fibre wall thickness values but, only the differences in the last two traits were significant, unlike for FL and FW ($p<0.05$) (Table 5, Figure 7f).

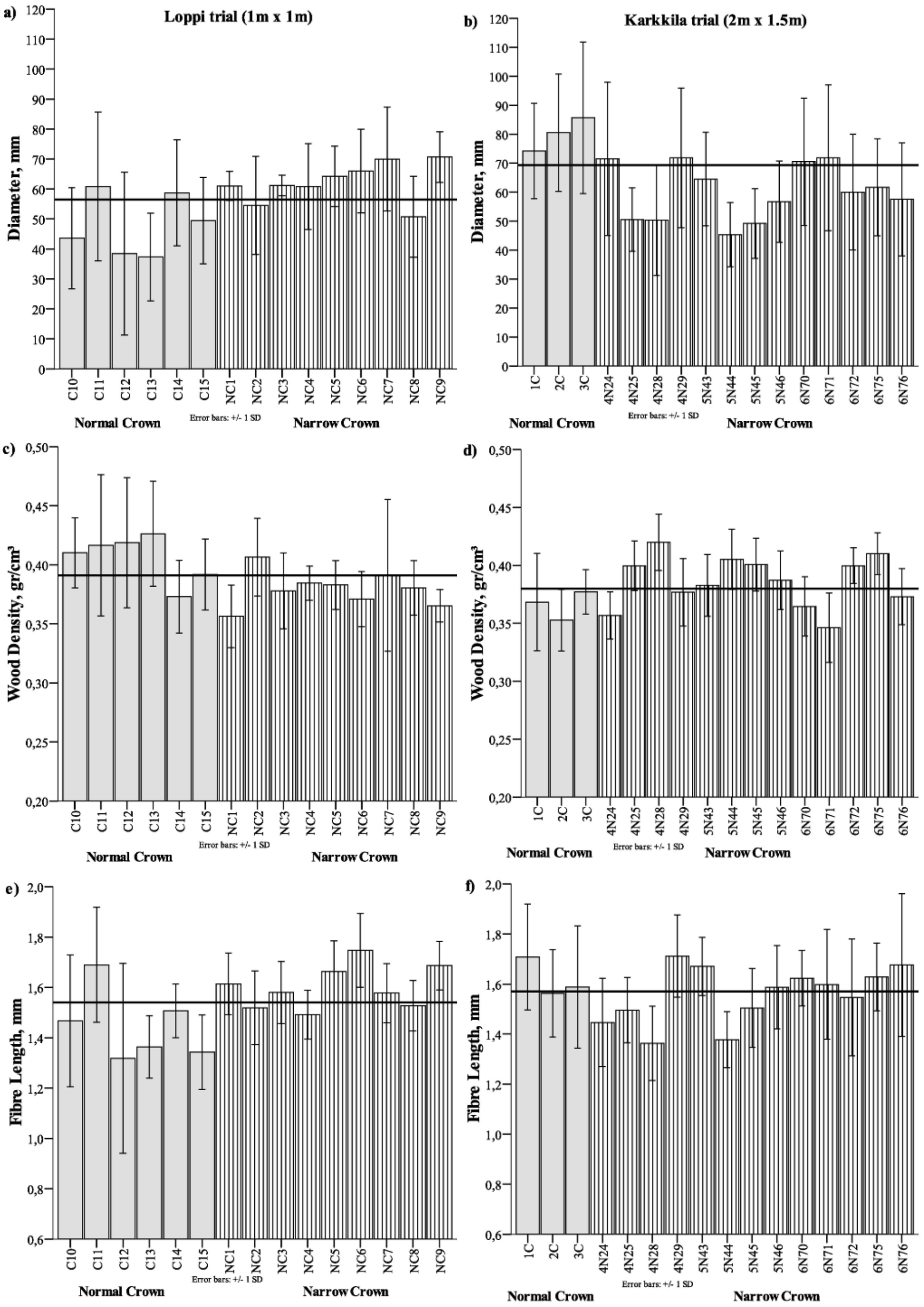


Figure 7. Averages for diameter at breast height, overall wood density and fibre length for narrow crowned (striped) and normal crowned (solid) genetic entries harvested from the Loppi trial with 1 m x 1 m spacing (left hand side) and from the Karkkila trial with 2 m x 1.5 m spacing (right hand side). Average for all the genetic entries for each trial marked with a solid line.

3.2 Phenotypic correlations among different traits

For all the harvested materials (Papers I-V), the phenotypic correlations (r_p) among the different yield traits (diameter, height and stem volume) were strong and positive ($p<0.05$), ranging between 0.69 and 0.96 (Table 6, Table 7). Nonetheless, stem volume is, by definition correlated with diameter and height, since it is calculated based on those two variables. Similarly, in general, the correlation among earlywood width and ring width and between those and yield traits were regardless of the harvested material (Papers I-V) positive and ranged from moderate to strong ($0.56< r_p <0.99$, $p<0.05$). On the other hand, even if the latewood width showed positive phenotypic correlations with all other growth and yield traits, in general, it was weaker and in some cases not significant.

Regardless of the harvested material (Papers I-V), the overall wood density and its components (EWD, LWD and WD) showed, on average, from moderate to strong positive phenotypic correlations among them ($0.41< r_p <0.97$, $p<0.05$), excluding LWD and EWD correlation at the Loppi trial for normal crowned spruce (being positive but weak, and statistically not significant) (see Paper III: Table 6). In contrast, the correlations between growth and yield traits (excluding LWW) and WD/EWD were, in general, negative and ranged from moderate to high ($p<0.05$) (Papers I-V) (Table 6, Table 7). Nonetheless, at the Imatra trial (Papers I-II), there were some exceptions among the 20 individual normal crowned clones, in which the correlation between overall wood density and growth traits were either not existent or even positive (see Paper I: Table 6). In addition, those correlations were higher for normal crowned Norway spruce compared to narrow crowned ones harvested at the Loppi trial (see paper III: Table 6), while at the Karkkila trial they were similar for both crown types (see Paper IV: Table 6). On the contrary, LWD neither followed any general pattern nor correlated well with growth traits or yield traits, regardless of the material harvested from the different trials or crown type (Papers I-V) (Table 6-7).

Table 6. Phenotypic correlation between different traits for normal crowned Norway spruce harvested from the Kangasniemi (upper right) and Imatra trials (lower left). Significance with $p<0.05$ is given in bold.

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	Trait[1]	Kangasniemi trial												
		DBH	H	V	EWW	LWW	RW	EWD	LWD	WD	FL	FW	C	FWT
Imatra trial	DBH		**0.85**	**0.96**	**0.85**	**0.69**	**0.86**	**-0.47**	-0.16	**-0.54**	**0.35**	**0.62**	**0.39**	0.11
	H	**0.69**		**0.81**	**0.65**	**0.54**	**0.67**	**-0.36**	0.08	**-0.39**	**0.53**	**0.70**	**0.58**	**0.36**
	V	**0.95**	**0.79**		**0.81**	**0.64**	**0.83**	**-0.43**	**-0.21**	**-0.52**	**0.25**	**0.55**	**0.33**	0.07
	EWW	**0.85**	**0.56**	**0.79**		**0.64**	**0.99**	**-0.55**	**-0.33**	**-0.71**	0.13	**0.46**	0.15	-0.15
	LWW	**0.35**	**0.33**	**0.39**	0.12		**0.74**	**-0.31**	-0.18	**-0.24**	0.19	**0.38**	**0.23**	0.06
	RW	**0.88**	**0.62**	**0.84**	**0.93**	**0.47**		**-0.54**	**-0.32**	**-0.67**	0.15	**0.47**	0.17	-0.12
	EWD	**-0.34**	**-0.27**	**-0.32**	**-0.37**	0.04	**-0.31**		**0.53**	**0.89**	**-0.25**	-0.12	-0.01	0.09
	LWD	-0.14	-0.04	-0.10	**-0.15**	0.03	-0.12	**0.60**		**0.69**	**0.43**	**0.32**	**0.53**	**0.60**
	WD	**-0.33**	**-0.20**	**-0.28**	**-0.47**	**0.36**	**-0.29**	**0.89**	**0.71**		-0.06	-0.12	0.12	**0.31**
	FL	**0.22**	**0.23**	**0.23**	**0.29**	0.00	**0.26**	**-0.18**	0.01	-0.07		**0.72**	**0.79**	**0.70**
	FW	**0.23**	**0.25**	**0.24**	**0.24**	0.05	**0.24**	-0.12	0.09	-0.04	**0.64**		**0.87**	**0.55**
	C	**0.22**	**0.23**	**0.23**	**0.22**	-0.01	**0.19**	**-0.15**	0.10	0.11	**0.60**	**0.83**		**0.89**
	FWT	**0.16**	**0.16**	**0.16**	0.15	-0.07	0.10	-0.14	0.08	**0.20**	**0.43**	**0.50**	**0.90**	

[1] see table 2 for the explanation of the traits.

Table 7. Phenotypic correlation between different traits for narrow crowned Norway spruce harvested from the Karkkila (upper right) and Loppi trials (lower left). Significance with $p<0.05$ is given in bold.

	Trait[1]	Karkkila trial												
		DBH	**H**	**V**	**EWW**	**LWW**	**RW**	**EWD**	**LWD**	**WD**	**FL**	**FW**	**FWT**	**C**
Loppi trial	DBH		**0.94**	**0.95**	**0.86**	**0.50**	**0.89**	**-0.55**	-0.09	**-0.54**	**0.67**	**0.82**	**0.48**	**0.71**
	H	**0.85**		**0.90**	**0.76**	**0.48**	**0.80**	**-0.48**	0.00	**-0.45**	**0.70**	**0.83**	**0.57**	**0.77**
	V	**0.95**	**0.85**		**0.80**	**0.56**	**0.84**	**-0.44**	-0.08	**-0.42**	**0.56**	**0.76**	**0.46**	**0.67**
	EWW	**0.91**	**0.78**	**0.86**		**0.30**	**0.98**	**-0.59**	-0.10	**-0.65**	**0.52**	**0.71**	**0.31**	**0.57**
	LWW	**0.43**	**0.34**	**0.42**	**0.41**		**0.47**	-0.14	-0.19	0.01	0.13	**0.32**	0.10	**0.24**
	RW	**0.88**	**0.75**	**0.84**	**0.95**	**0.67**		**-0.57**	-0.13	**-0.60**	**0.51**	**0.72**	**0.31**	**0.57**
	EWD	**-0.33**	**-0.37**	**-0.33**	-0.26	**0.30**	-0.11		**0.59**	**0.96**	**-0.43**	**-0.51**	**-0.26**	**-0.42**
	LWD	-0.25	-0.28	**-0.29**	-0.28	-0.14	-0.27	**0.64**		**0.61**	0.02	-0.06	0.14	0.04
	WD	**-0.40**	**-0.43**	**-0.38**	**-0.39**	**0.32**	-0.21	**0.97**	**0.69**		**-0.43**	**-0.51**	-0.22	**-0.40**
	FL	**0.38**	**0.34**	**0.38**	**0.32**	-0.03	0.25	-0.10	0.11	-0.12		**0.81**	**0.74**	**0.84**
	FW	**0.48**	**0.35**	**0.40**	**0.44**	0.08	**0.39**	-0.08	0.07	-0.13	**0.74**		**0.71**	**0.93**
	FWT	-0.06	-0.06	-0.02	-0.12	-0.23	-0.17	0.17	**0.33**	0.17	**0.65**	**0.57**		**0.91**
	C	0.22	0.16	0.21	0.17	-0.10	0.11	0.06	0.23	0.04	**0.78**	**0.87**	**0.90**	

[1] see table 2 for the explanation of the traits.

Additionally, even if in general, and regardless of the material harvested from different trials, the phenotypic correlation between wood density traits and growth and yield traits were negative, some clones or families that had, at the same time, high diameter growth and relatively high overall wood density could be found. Moreover, there were some clones growing both at the Imatra (Paper I) and Kangasniemi trials (Paper V) that showed in both environmental conditions higher stem volume and/or diameter and overall wood density than the average over the whole material harvested from these trials (e.g. clone V48, see Paper I: Figure 3, and clone F48, see Paper V: Figure 1).

Concerning the fibre properties such as fibre length (FL), fibre width (FW), coarseness (C) and fibre wall thickness (FWT), the phenotypic correlations observed between them, regardless of the material harvested from different trials and in both, narrow crowned as well as in the normal crowned genetic entries were, on average, positive and ranged from moderate to strong depending on the fibre properties considered ($0.43< r_p <0.97$, $p<0.05$). In addition, for the material harvested from the Imatra trial, all fibre properties had a weak but significant positive correlation with tree diameter, height and stem volume ($0.16< r_p <0.25$, $p<0.05$) (Table 6). As a comparison, for the material harvested from the Kangasniemi trial, these correlations were also positive, but stronger with FL, FW and C ($0.25< r_p <0.70$, $p<0.05$ (Table 6). When comparing both crown types (Paper III-IV), it was found that normal crown genetic entries harvested from the Loppi trial had moderate to strong positive correlation between all fibre properties and growth and yield traits ($p<0.05$), unlike narrow crowned families, where these correlations were significant only for FL and FW, but not for FWT and C (see Paper III: Table 6). On the contrary, for the material harvested from the Karkkila trial, fibre properties showed statistically significant ($p<0.05$) and from moderate to high positive correlation with all growth and yield traits in narrow crowned clones (excluding correlation between FWT and LWW) (Table 7), but not clear correlation in normal crowned genetic entries (see Paper IV: Table 6)

3.3 Effects of competition by neighbours on different traits of target trees

For the material harvested from the Kangasniemi trial (Paper V), it was observed that when the competition by the neighbouring trees increased (higher values of competition index), the diameter and height of the target trees decreased in general. On the contrary, with higher values of CI, the overall wood density was also higher (Figure 8). Furthermore, when the competition index was included as a covariate in the statistical analysis for the prediction of breast height diameter, tree height and ring width, the covariate was significant, and could improve the prediction of those variables, i.e. the mean square error for the models was reduced (see Table 8). On the contrary, CI could not be used as a covariate to explain the overall wood density.

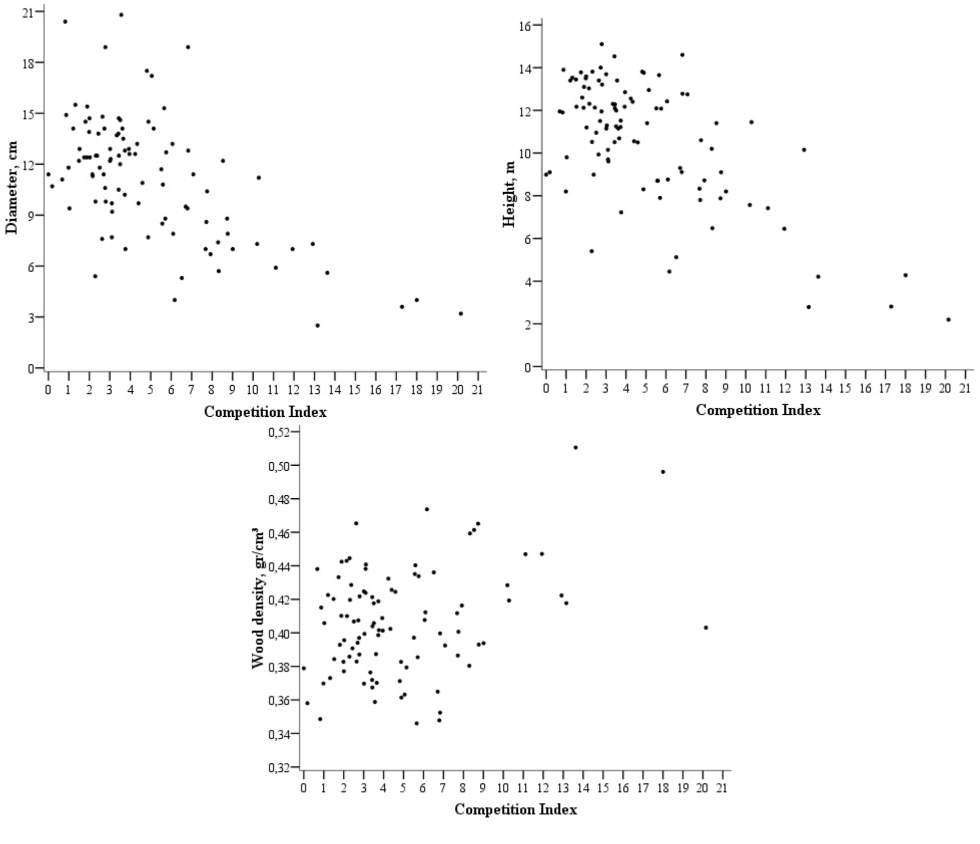

Figure 8. Relations between competition index (Schutz, 1989) and breast height diameter, height and overall wood density over all the clonal material harvested from the Kangasniemi trial (spacing of 2 m x 2 m).

Table 8. Mean square error (MSE), F-ratio and significance for the models including competition index (CI) and clone (left hand side) or only clone as explanatory variables. Significance of F-ratio with $p<0.05$ is given in bold.

Trait	Including clone and CI					Including only clone		
		Clone		CI			Clone	
	MSE	F-ratio	Sig.	F-ratio	Sig.	MSE	F-ratio	Sig.
Diameter	7.34	1.72	**0.05**	35.70	**0.00**	10.70	1.87	**0.03**
Height	3.52	2.01	**0.02**	74.52	**0.00**	7.01	1.77	**0.04**
Ring Width	0.22	2.25	**0.01**	29.62	**0.00**	0.30	2.32	**0.01**

4 DISCUSSION AND CONCLUSIONS

4.1 Evaluation of the effects of genetic entry, spacing and competition by neighbours on growth, yield and wood properties

This work studied how the genetic entry (and/or origin) affected the different growth and yield, wood density traits and fibre properties in Norway spruce based on materials harvested from four different field trials established in southern Finland in the 1970s to 1990s (Papers I-V). On one hand, the materials harvested from the Loppi (Paper III) and Karkkila (Paper IV) trials offered the possibility to compare the effects of spacing on different traits between normal and narrow crowned Norway spruce. On the other hand, differences among normal crowned Norway spruce clones harvested from the Imatra (Papers I and II) and Kangasniemi trials (Paper V) could also be studied. In addition, the data collected from the Kangasniemi trial made it possible to study how the competition of neighbouring trees affected different traits of the target trees in normal crowned Norway spruce (Paper V). Related to this work, the phenotypic correlations among different traits (Papers I-V) were calculated. However, the genetic correlations could not be calculated because of the relatively small number of genetic entries harvested from each trial (maximum of 20) resulted in the computation of high error values for these estimates; this was the case even for the material harvested from Imatra trial. For this purpose, significantly higher amount of genetic entries than that harvested for this work would have been needed (Haapanen, personal communication), which was not possible for the present study.

The yield (diameter, height, stem volume) and growth traits (earlywood, latewood and ring width) showed in this work, on average, higher phenotypic variation than wood density traits (earlywood, latewood and overall wood density) and fibre properties (fibre length and width, coarseness and fibre wall thickness) regardless of the genetic entry, crown characteristics, site and/or spacing (Papers I-V). These results are in agreement with previous findings for Norway spruce, for example by Hylen (1997), who also found that phenotypic variation was much higher in diameter, height and latewood proportion than in any of the studied wood density traits. Moreover, Hannrup et al. (2004) observed similar results for Slovakian provenance clones of Norway spruce, with the phenotypic variation for stem volume and diameter being considerably higher than that for fibre wall thickness and fibre length. In the same study, the variations of the wood density traits were lower than those of yield and fibre properties. Similar observations have also been reported in other species such as Scots pine (Hannrup et al. 2001) and black spruce (Zhang and Morgenstern 1995, Zhang 1998). In regards to previous research (e.g. Zhang 1998), these results could imply that the high variability in traits such as growth and yield are under poor genetic control, and therefore, they are more affected by environmental and competition factors among the trees. On the contrary, the properties with lower variation, such as wood density traits and fibre properties are more strongly genetically controlled, and less affected by silvicultural management. This implies that tree growth could possibly be considerably increased by silvicultural management, while wood density and fibre properties would not be affected as much as growth since they have stronger genetic intrinsic control for the response (Jyske 2008).

In this work, at the Loppi (Paper III) and Karkkila (Paper IV) trials, narrow and normal crowned genetic entries had considerably higher variation in the growth and yield traits than in the other trials. Nonetheless, when comparing narrow and normal crowned genetic entries harvested from the Loppi trial, where the spacing was 1 m x 1 m, narrow crowned genetic entries had, on average, substantially smaller phenotypic variation than normal crowned ones for many of the traits. On the contrary, for the material harvested from the Karkkila trial, where the spacing was 1.5 m x 2 m, the phenotypic variation was similar in both crown types for wood density traits and fibre properties, but larger, to some degree, for narrow crowned Norway spruce genetic entries in respect to the yield traits. Thus, the phenotypic variability of the two crown types varied when grown in different spacing, which could be related to the different ability of the two crown types to adapt to the neighbouring competition conditions and to fully utilise the increase in growing space.

Previous studies have shown that the variability in wood properties in Norway spruce is affected mainly by factors such as genetic entry, heritability, cambial maturation and growth rate as controlled by environment and silvicultural management (Zobel and van Buijtenen 1989, Lindström 1996, Hylen 1999, Sirviö and Kärenlampi 2001, Hannrup et al. 2004). In this respect, the present study showed that the genetic entries had an important role regarding the differences among the studied traits. In the normal crowned individual clones harvested from the Imatra (Papers I and II) and Kangasniemi trials (Paper V), differences were found among the studied clones for all the traits (excluding coarseness at the Kangasniemi trial), meaning that there were clones showing different characteristics. As a matter of fact, some of the clones showed similar response in both trials, even if they had different soil types and spacing (e.g. V48 and C48). In this respect, clones with the desired properties and high stability over sites would also be preferred in practise since they would, to a certain degree, maintain those characteristics among the different environmental and management conditions.

On the contrary, when referring to the same clones but grouping by origins, only few traits showed significant differences. Opposed to the results of the present study, for example, Fottland and Skrøppa (1989) found differences in height growth of Norway spruce between provenances. Some previous investigations have showed that the southern provenances, when planted in more northern regions, have had higher growth compared to the northern ones due to their longer growing periods (Skrøppa and Magnussen 1993, Skrøppa et al. 1999). Furthermore, in several previous investigations in Norway spruce, unlike in the present study, differences among provenances for all studied wood density traits were observed, with, in general, the northern provenances having higher wood density than the southern ones (Persson and Persson 1997, Skrøppa et al. 1999). The different results obtained in the present study (Paper V) compared to previous ones could be explained by the fact that in many cases the differences related to the seed source are relatively small compared to individual tree or family variation (Zobel and Jett 1995). In addition, more detailed information than that available for the present study for the latitude and altitude of the origins of the parent trees would be needed for better understanding of the results related to the origins (see Paper V).

In narrow and normal crowned Norway spruce, different results were obtained between the Loppi trial (Paper III), with narrow spacing (of 1 m x 1 m), and the Karkkila trial (Paper IV), with a wider spacing (of 2 m x 1.5 m). Narrow crowned Norway spruce families showed, on average, statistically higher yield traits than normal crowned genetic entries when grown at very narrow spacing. On the contrary, the normal crowned genetic entries showed higher yield than the narrow crowned clones, when grown at a wider spacing (Karkkila trial). Nonetheless, when comparing the findings of the narrow and normal crowned genetic entries in the wider spacing in the Karkkila trial, we should keep in mind that it was a mixed stand; where around 90% of the trees were narrow crowned ones. In this situation, the crown competition between neighbouring trees was, in practice, significantly lower for normal crowned genetic entries, compared to the situation in which the whole plantation would consist of only normal crowned genetic entries (if considering a crown size ratio of normal crowned tree to be about twice that of a narrow crowned one).

In the same way, in previous investigations, the normal crowned genetic entries had larger above ground dry biomass production than narrow crowned ones when grown at wider spacing of 2 m x 2 m (Pulkkinen and Pöykkö 1990, Pulkkinen 1991a, 1991c). These results could be justified by the lower plasticity to the free growing space of the narrow crowned Norway spruce. Thus, it could not be competitive compared to normal crowned Norway spruce in wider spacing such as the typical spacing (about 2.5 m x 2.0 m) used in practical forestry for Norway spruce in Finland nor the one used in the Karkkila trial (where normal and narrow crowned trees were grown as a mixture in a spacing of 2 m x 1.5 m, see Paper IV for further details). On the contrary, as a stand, narrow crowned Norway spruce is more efficient and superior in very narrow spacing compared to normal crowned one. Thus, in future investigations, narrow and normal crowned Norway spruces grown in a wider range of different spacing should be studied in more detail in order to obtain a clearer picture on their possible differences in growth and yield traits and wood properties. Nonetheless, it would also be important to take into account the higher regeneration costs of the narrow crowned Norway spruce, since the plants are produced with a vegetative propagation. Therefore, a future goal should be to define the ideal spacing for different genetic entries to provide desired wood quantity and quality in the most cost-efficient way.

In the present work, the possible effect of the neighbour tree competition was also studied regarding growth, yield and wood properties in normal crowned Norway spruce. For that purpose, a distance dependent index formulated by Schütz (1989), which included crown size, was included in the analysis (Paper V). In line with previous investigations in other species such as Scots pine, white fir (*Abies concolor* (Gord. & Glend.) Lindl), ponderosa pine (*Pinus ponderosa* (Law.) and loblolly pine, significant improvements in the prediction of tree diameter, height and ring width were obtained (Biging and Dobbertin 1992, Mäkinen 1997, Jayawickrama et al. 1998). Nonetheless, the competition index was not statistically applicable as a covariate on the prediction of the overall wood density. In the future the effects of competition on different traits in Norway spruce with different crown types, including narrow crowned Norway spruce, especially after canopy closure, should also be analysed in more detail.

4.2 Evaluation of phenotypic correlations among different traits

In this work, and in agreement with previous studies in different coniferous species (e.g. Zobel and Buijtenen 1989), the phenotypic correlations between different yield (stem volume, height and diameter) and growth traits (earlywood, latewood and ring width) were positive and from moderate to strong. In addition, the lowest phenotypic correlation was observed between LWW and all the other growth and yield traits, which may suggest that while diameter, height, RW and EWW are more dependent on the growth rate, LWW might be a more genetically controlled trait. In regard to the wood density, in the present study, the phenotypic correlations among the different density traits were also positive and ranged from moderate to strong ($p<0.05$, excluding EWD/LWD correlation in normal crowned genetic entries harvested from the Loppi trial), with the correlation between EWD and overall WD being the highest ones.

Similar to the results in the present study, in previous investigations in other species such as in radiata pine (*Pinus radiata* D. Don) (Donaldson et al. 1995) and in black spruce (Zhang and Morgenstern 1995), the EWD had the largest impact on overall wood density. The same strong positive phenotypic or genetic correlations among the different wood density traits were also found in several previous studies in Norway spruce (Hylen 1997, Hannrup et al. 2004) as well as in other species such as Scots pine (e.g. Hannrup et al. 2000) or maritime pine (*Pinus pinaster* Ait.) (Louzada 2003, Gaspar et al. 2008). As suggested by Hylen (2002), this strong correlation between the different density traits could imply that the same set of genes might control the different wood density components Opposite to these findings, Zhang and Morgenstern (1995) found a strong negative correlation between EWD and LWD in black spruce.

Generally, the contradictory findings observed for the correlation among different wood density traits might be explained by the fact that overall wood density is a result of the proportions of earlywood and latewood and the relative density of each (Vargas-Hernandez and Adams 1991). Additionally, in previous studies many different kinds of methodologies have been applied for determining the earlywood and latewood transition point (E/L transition point), which could also affect the results. Such methods, in which E/L transition point has been determined based on intra-ring wood density profiles measured by X-ray densitometry (see e.g. Koubaa et al. 2002), include threshold density, mean of intra-ring min-max densities, two-thirds of intra-ring min-max and maximum derivative method, for example. Despite the fact that wood density varies at the E/L transition point from juvenile to mature wood, the results of previous studies have shown a relatively good agreement between earlywood and latewood features as determined based on different methods and as a comparison to Mork’s definition, which is based on double wall thickness and lumen diameter (see e.g. Koubaa et al. 2002, Helama et al. 2008). Nonetheless, none of the method gives the real E/L transition point (Kumar, 2002). In this work, the approach used to divide the annual rings into early and latewood was based on mean of intra-ring min-max ring density, following the approach used previously with the same X-ray densitometry (e.g. Peltola et al. 2007, Helama et al. 2008). However, as a general remark, and based on the results of the present study, it could be said that when aiming to improve the selection for overall wood density, direct selection by itself would be the most efficient criteria since separate earlywood and latewood density information have little additional value.

Regarding the relationship between growth traits and wood density traits, the findings of this work were, in general, in line with previous ones, which suggest that the increase in growth rate of coniferous species such as in Norway spruce also increases earlywood proportion, but decreases overall wood density (e.g. Lindström 1996, Pape 1999a, 1999b, Wilhelmsson et al. 2002, Ekensted et al. 2003). Nevertheless, in the present work, no clear relation or even positive relation between wood density and growth traits was found in some individual clones (Paper I), thus, this gives the opportunity to increase the growth rate in this clones having little effect on the overall wood density. Moreover, it was observed that the normal crowned Norway spruce showed, in general, higher correlations than narrow crowned ones when planted in narrow spacing, unlike in wider spacing (paper III, IV). In this respect, different management may also have different effects on wood density and growth traits. For example, Jaakkola et al. (2005a) suggested that wood density was only slightly affected in Norway spruce as a result of quite heavy thinning, despite the significant increase in the growth rate and proportion of earlywood. Accordingly, it has been suggested that by proper selection of genetic entries Norway spruce clones with favourable combination of both growth and wood density traits may also be found (Rozenberg and Cahalan, 1997, Hylen 2002), as was the case in other species such as in black spruce (Zhang and Morgenstern 1995, Zhang et al. 1996) and in lodgepole pine (Wang et al. 2000).

Moreover, in the present work it was found that the phenotypic correlations between different fibre properties were in general positive ranging from moderate to high. However, the significant positive relationship found between fibre wall thickness and fibre width as well as coarseness is partly due to the fact that the fibre wall thickness is calculated based on the latter two traits. In a similar way, Mäkinen et al. (2002b) found a positive correlation between fibre length and fibre width, but also between fibre length and fibre wall thickness in Norway spruce. Similarly, Pot et al. (2002) found in Maritime pine a high positive correlation between different fibre morphology traits, including fibre length, fibre width and coarseness. This findings suggest that the same set of genes are likely to be responsible for their control allowing breeders to consider even only one of the traits in order to improve them all. On the other hand, for the correlations between fibre properties and other wood properties the patterns are not so clear since many different results have been observed in previous investigations as in the present one (see e.g. Zobel and van Buijtenen 1989).

On the whole, in this work, with increasing growth rate (D, H, V and EWW), fibre length and width also increased, and those results were supported by other previous studies in Norway spruce (Berqvist et al. 2000, Hannrup et al. 2004), Scots pine (e.g. Hannrup et al. 2000) and loblolly pine (e.g. Loo-Dinkins et al. 1984). Nonetheless, many previous studies show negative relation between growth rate and fibre length in Norway spruce or Scots pine, for example (Lindström 1998, Jaakkola et al. 2007, Kilpeläinen et al. 2007). In addition, studies exist confirming that fibre morphology, and predominantly fibre wall thickness, have an important impact of the overall wood density (Mäkinen et al. 2002a, 2002b). But, in this work these correlations were not clear and only in some of the studies could be observed (although in Paper I and V: positive correlation between WD and FWT was observed).

Lately, in addition to fibre size, fibre length distribution has also been an increasing issue of interest. In general, more uniform material is desired, since such material makes it possible, for instance, to reduce the consumption of the required energy and chemicals in pulp and paper industry (Tyrväinen 1995). In this study, the length distribution of the fibres in the Imatra trial was also analysed (Paper II), and showed differences among the different clones (see Paper II: Figure 1). In this sense, the clones representing, on average, the longest fibres had, at the same time, the most uniform fibre material. Nonetheless, taking into account the increasing importance of the uniformity of the raw material, more detailed investigation regarding fibre length distribution would be needed for further conclusions.

4.3 Conclusions

The main aim of this work was to investigate how growth and yield, as well as wood density traits and fibre properties were affected by genetic entries and spacing in Norway spruce. Previously several studies have discussed growth and yield traits and wood properties in Norway spruce and other conifers, but few of them have considered them at the same time in such detail as was done in this work. Furthermore, no previous corresponding studies have been carried out relating the growth and yield traits and the wood properties in narrow crowned Norway spruce. In this sense, the approach used in this work could enable the identification of genetic entries having simultaneously both, high growth and yield as well as desired wood properties.

In the present study, large differences were observed, on average, among the genetic entries (clones, families) regarding the different traits, unlike between origins. This leads to the conclusion that the selection for a desired trait or a combination of traits would be more successful based on a selection of a specific clone rather than an origin/provenance. For instance, clone C43 (Paper I-II), representing normal crowned Norway spruce, showed a high stem volume and overall wood density and long fibres, and would thus, be interesting alternative for use on forest regeneration and breeding (however, further testing would be needed to support this result based on larger sample size, and different management systems). On the other hand, clones such as C332, with poor growth and low wood density could already be discarded for further breeding programs. Thus, the present investigations have shown that differences could be found among the genetic entries regarding growth as well as wood properties, and therefore, some genetic entries with desired characteristics could be found.

Furthermore, narrow crowned Norway spruce clones could also offer potential alternatives for normal crowned ones as a future regeneration material, since, even if they are not outstanding trees as individuals, they utilise the environmental resources in a more efficient way especially in narrow spacing, as was demonstrated in this work. Consequently, they could be grown in a narrow spacing even without thinning, and with a relatively short rotation considerably reducing, at the same time, the risk of infection by *Heterobasidium* spp. fungi, which mostly affects old Norway spruce stands. A recent study among Finnish forest owners and forest professionals showed that they would be willing to use narrow crowned spruce as a raw material in the future, provided that it would be economically profitable compared to traditional forestry, thus, more information in this respect would be necessary.

In future investigations, the response of growth and yield, wood density traits and fibre properties in both normal and narrow crowned genetic entries in Norway spruce, and to a range of spacing and environmental conditions (climate, site) should still be studied in more detail. It would also be important to study such materials at an older age, in order to include at the same time juvenile and mature wood characteristics for comparison. This is because the sample material analysed in this work presented mainly trees at juvenile phase (typically 10-15 inner rings in Norway spruce), and the properties of juvenile and mature wood would differ from each other. Additionally, the effect of the neighbouring trees on different genetic entries, with different crown characteristics should also be analysed in more detail, as this kind of work would give a better understanding on the effects of competition on different growth, yield and wood property traits. Moreover, in addition to phenotypic correlations, based on a larger number of genetic entries, also genetic correlations should be calculated. This further work suggested could allow the determination of the optimal management (e.g. spacing), which would provide high quantity and quality of raw material in the most cost-efficient way.

Nevertheless, it is important to keep in mind that it will not be possible in the future to measure, in all available trials and genetic entries (with sufficient number of replicates), the many different property traits simultaneously and in such detail as was done in this work, as it would be too laborious and expensive in practice. It seems also clear that tree breeding for wood property traits would not be reasonable without simultaneously considering growth traits and vitality/climatic adaptation as well. This means that the selection should be done based on genetic entries which already have shown higher growth than an average over other genetic entries as was also previously suggested by Pot et al. (2002).

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