

Genetics, breeding and deployment of Melaleuca and Norway spruce

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Cover: Melaleuca plantation in Vietnam (left) and Norway spruce plantation in Sweden (right)

(Left photo: Harry Wu;

Right photo: Thi Hai Hong Nguyen)

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Abstract

Additive effects of genes are cumulative over generations and are the main source of genetic variation exploited by most plant breeding programs. However, the relative importance of additive and non-additive genetic effects is critical information required to properly evaluate the potential for genetic gain from various breeding programs and deployment options used in the genetic improvement of forest trees.

Melaleuca cajuputi is a moderately fast-growing tree species considered as a multipurpose species in Australia and South-East Asia. Breeding programs of *M. cajuputi* have been conducted for three decades. In Vietnam, genetic improvement of subsp. *cumingiana* aims to enhance tree growth for wood production. Genetic analysis of growth, stem form, modulus of elasticity (MOE), bark thickness and bark ratio was examined from 80 half-sib family progeny trial. Narrow-sense heritability ranged from zero to 0.27. MOE had positive genetic correlations with growth. Selection based on volume and MOE showed genetic gains of 31% in volume and 6% in MOE. The optimal early selection age for growth based on DBH alone was four years. A second breeding objective for *M. cajuputi* subsp. *cajuputi* aims to improve oil yield and 1,8-cineole content. Data collected from single trial including 39 full-sib families from 12 parents was analyzed. Narrow-sense heritability were 0.10–0.13 for growth, 0.50 for oil yield and 0.21 for 1,8-cineole content. Genetic relationships among growth, oil concentration and 1,8-cineole content were almost independent. The most optimal selection scenario improved 2.18% in 1,8-cineole content and 27.36% in leaf oil yield.

Genetic improvement of Norway spruce (*Picea abies*) has been carried out for over six decades in Sweden. A large clonal testing program was launched during the mid-1970s. This study evaluated genetic variations for growth and wood quality traits (i.e. Resi, Pilo, AV, MOE and GA) from the six full-sib and two half-sib clonal trials in order to study benefits and risk of implementing clonal forestry. Additive genetic variation accounted for majority of the total genetic variation associated with DBH and wood traits whereas non-additive genetic variation appeared to be more important for height at early ages. Predicted genetic gain was the highest for clonal deployment, followed by full-sib family deployment and open-pollinated deployment. Consequently, clonal forestry could lift genetic gain about 11–31% more for wood traits and 22–120% more for DBH over full-sib family forestry. About 30–40 clones for each family could obtain the maximum clonal genetic gain in clonal testing and selection.

Keywords: clonal forestry, pilodyn, resistograph, acoustic velocity, MOE, grain angle, essential oil, 1,8-cineol, genetic gain.

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Dedication

To my parents, brothers, husband and kids.

Peace comes from within. Do not seek it without.

- Buddha -

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List of publications

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

- I Nguyen Thi Hai Hong, Ryota Konda, Kieu Tuan Dat, Tran Thanh Cao, Phung Van Khang, Tran Tin Hau, Harry Wu. 2019. Genetic improvement for wood production in *Melaleuca cajuputi*. *Journal of Tropical Forest Science* 31(2):?-?.
- II Thi Hai Hong Nguyen, Anto Rimbawanto, Prastyono, Noor K. Kartikawati, Harry Wu. 2019. Genetic improvement for essential oil yield and quality in *Melaleuca cajuputi*. *Industry Crops and Production* (submitted).
- III Thi Hai Hong Nguyen, Zhi-Qiang Chen, Anders Fries, Mats Berlin, Henrik Hallingbäck, Harry Wu. 2019. Estimates of additive, dominance and epistatic genetic variances for growth and wood traits in two Norway spruce clonal trials (manuscript).
- IV Zhi-Qiang Chen, Thi Hai Hong Nguyen, Andreas Helmersson, Mateusz Liziniewicz, Bo Karlsson, Henrik Hallingbäck, Anders Fries, Mats Berlin, Harry Wu. 2019. Estimating genetic parameters and genetic gain for growth and wood quality traits from six Norway spruce clonal trials (manuscript).

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The contribution of Thi Hai Hong Nguyen to the papers included in this thesis was as follows:

- I. Involved in the experimental design and establishment, data collection, data analysis and interpretation, writing the manuscript.
- II. Performed the data analysis and interpretation, writing the manuscript.
- III. Involved in the data collection, data analysis and interpretation, writing the manuscript.
- IV. Involved in the data collection, data analysis, interpretation, and writing.

1 Introduction

1.1 Melaleuca

Melaleuca cajuputi belongs to Myrtaceae family and is a species of considerable variation in nature. Based on differences in morphology, chemical content and geographic distribution, three subspecies are derived such as subsp. *cajuputi*, *cumingiana* and *platyphylla* (Craven and Barlow, 1997) (Figure 1). They are distributed in Australia, Papua New Guinea and South-East Asia (Brophy et al., 2013, Doran and Gunn, 1994). This is a multi-purpose tree as it can be used for fuelwood, piles and frame poles in construction, leaves are used for essential oil distillation, flowers attract honey bees (Doran and Turnbull, 1997, Quat and Cuong, 2005), timber is used for pulp and paper, fiber and particle board, producing quality charcoal and potentially sawn timber (Trung, 2008). *M. cajuputi* plantation can be harvested on 6 – 7 year rotation for wood products (Trung, 2008, Nuyim, 2001) and four years for leaf oil distillation (PlantUse, 2016). The species is adapted to tropical environments with high salinity and high aluminium levels (Brinkman and Xuan, 1991), tolerant of fire and drought (Tran et al., 2013), flooding and low pH (Nuyim, 2001, Osaki et al., 1998, Yamanoshita et al., 1999), seasonal inundation and acid-sulphate soils, which are difficult for tree plantation establishment (Chuong et al., 1996, Doran and Turnbull, 1997).

M. cajuputi subsp. *cumingiana* was evaluated previously as a top priority tree species in reforestation efforts in the Mekong delta of Vietnam (Doran, 1999, Kha et al., 1999, Pinyusarek and Doran, 1999) and also widely planted (Kim et al., 2005). Its essential oil concentration was low (Kim et al., 2005, Thach and Hong, 2012) and breeding program has mainly targeted wood production in Vietnam (Thiet et al., 2017). A breeding program aimed at improving tree growth for wood production commenced in Vietnam in 2006. Previously, *M. cajuputi* has been targeted for production of solid timber and its mechanical

properties of wood were tested (Ban, 2002, Junji, 1999). Anatomical characteristics and wood properties of *M. leucadendron* (a synonym of *M. cajuputi* (Williams, 2011)) were determined at the among-tree variation level (Wahyudi et al., 2014). However, basic information about genetic variation in wood properties of *M. cajuputi* has not been reported. Therefore, evaluating genetic variation in growth and wood quality traits of *M. cajuputi* subsp. *cumingiana*, estimating heritability, genetic and phenotypic correlations between the traits were necessary. The expected response from combined index selection based on genetic parameters for growth and wood quality traits is discussed in relation to the breeding strategy to improve wood production.

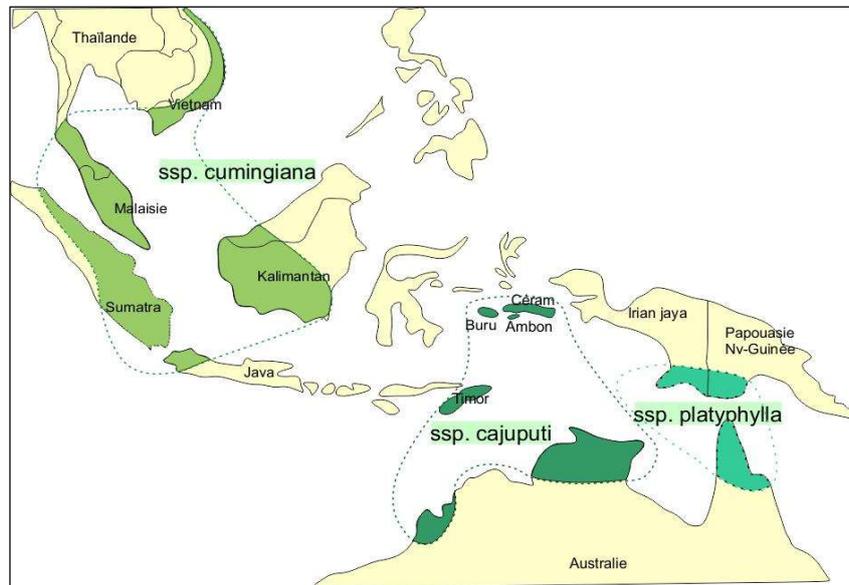


Figure 1. Distribution of the sub-species of *Melaleuca cajuputi* (Wikimedia, 2018)

In contrast, *M. cajuputi* subsp. *cajuputi* plantations are the main source of cajuput oil industry as a part of forestry activities aimed to produce non-timber forest products and an income stream for people living around the forest area in Indonesia (Baskorowati et al., 2012). Essential oil with strong aroma has widely used for medicinal application (Barbosa et al., 2013). However, this oil mostly, but not always, contains substantial amount of 1,8-cineole (3 – 60 %) and oil yield ranging from 0.4 to 1.2 % (fresh weight, w/w) (Doran, 1999). The economic value of this oil is directly related to the level of metabolite terpene (Barbosa et al., 2013); oil with concentration of 1,8-cineole above 55 % is considered as best quality while concentration below 55 % is considered as standard oil (Sakasegawa et al., 2003). Breeding program of *M. cajuputi* subsp. *cajuputi* aimed to improve the oil yield and 1,8-cineole content was therefore

targeted. High genetic variation of offspring originated from parent trees in the seed orchard with mainly outcrossing in parent trees were reported (Kartikawati et al., 2013). Genetic gains of 10 % and 21 % were predicted for the content of 1,8-cineole and oil yield respectively, in the half-sib family progeny trial (Susanto et al., 2003). To further improve the oil yield and 1,8-cineole content, the full-sib progeny trial was established in 2004 at Paliyan, Yogyakarta and full-sib family variation of seed production and viability was assessed (Baskorowati et al., 2012). Thus, examining genetic variation in growth, essential oil quantity and quality, and estimating heritability, genetic relationships and potential genetic gains were essential to design optimal breeding strategy for cajuput oil production.

1.2 Norway spruce

Norway spruce (*Picea abies* (L.) Karst.) is one of the most important conifer species in Europe, both economically and ecologically (Högberg et al., 2013). The versatility of the wood and its large geographic distribution makes it a widely used tree species in the European forest industry (Steffenrem et al., 2016). In Sweden, genetic improvement has been carried out on this species from the 1930s and has mainly focused on improving growth and adaptive traits (Karlsson and Rosvall, 1993) and a large clonal testing program was launched, including more than 18,400 clones during the mid-1970s. Tree breeding programs have traditionally focused on climatic adaptation and volume production (Steffenrem et al., 2007). Recently, wood quality traits have been incorporated into the selective breeding programs (Chen et al., 2015, Chen et al., 2017, Högberg et al., 2013, Wu, 2018). In addition, knowledge about how wood quality traits correlate genetically with each other and with growth rate is scarce and sometimes contradicting (Steffenrem et al., 2007).

Additive genetic effects of genes are cumulative over generations and are the main source of genetic variation exploited by most plant breeding programs. However, non-additive genetic effects including dominance (i.e. interactions between alleles at a locus) and particularly, epistasis (i.e. interactions of alleles between loci) could play a central role in heterosis, polymorphism, and evolution (Phillips, 2008, Yu et al., 1997). The levels of the additive and non-additive genetic variance in traits important for breeding programs have a great impact on the determination of optimal breeding strategies (White et al., 2007). To estimate fully all three variance components and associated heritability in the narrow-sense (only additive genetic variance) and in broad sense (all genetic variance), genetic trials including family and clonal identification are required (Wu, 2018). Estimates of genetic gain from clonally replicated trials in conifers

were initially started in 1980s (Wu, 2018). But only few reliable estimates for the non-additive variation were reported (Baltunis et al., 2007a, Baltunis et al., 2009, Isik et al., 2005, Mullin and Park, 1992, Weng et al., 2008) in which growth traits were focused rather than wood quality traits. Hence, assessing the relative importance of additive, dominance and epistatic genetic effects, estimating heritability, genetic correlations among traits, and predicting genetic gain from clonal deployment as compared with deployment of full-sib family and half-sib family deployment were necessary to Norway spruce breeding and deployment program. In a recent review of deploying clonal forestry of Norway spruce in Sweden, there was a special call to estimate non-additive genetic variance for growth and wood quality traits in order to assess the benefits and risks of Norway spruce clonal forestry (Wu, 2018, Rosvall et al., 2019).

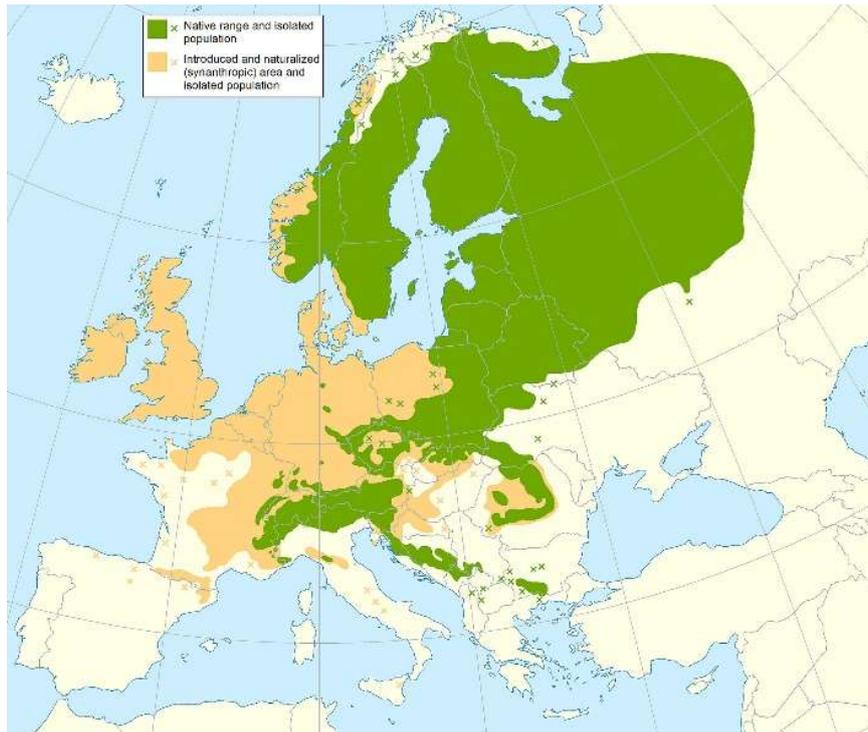


Figure 2. Distribution of Norway spruce (Caudullo et al., 2017)

1.3 Non-destructive evaluation methods for wood traits

Knowledge of wood properties is important for decision-making and production management in the wood processing industries (Lorensani et al., 2017). In recent years, non-destructive evaluation methods have been widely

used to inspect the properties of wood and wood products. Non-destructive evaluation of materials is, by definition, the science of identifying the physical and mechanical properties of a material without altering its end-use capabilities and then making decisions regarding its appropriate application (Ross, 2015). Such evaluations rely on non-destructive testing technologies to supply accurate information relative to the properties, performance, or condition of the material in question (Ross and Engineer, 1994). Predictions of technological wood properties from non-destructive methods on standing tree at early ages accelerates the processes of selection and genetic improvement of a species and improves forest management that aims to produce high quality timber (Sánchez et al., 2017). Among non-destructive testing methods, time-of-flight stress wave technique (Fakopp and Hitman), Pilodyn penetration depth (Pilodyn), micro-drilling resistance (Resistograph) and wedge grain angle gauge have become widely used to improve wood properties of living trees for future forest tree breeding programme because of their reliable, rapid, portable, cost-effective and easily used performance (Chiu et al., 2013, Isik and Li, 2003, Fundova et al., 2018, Hayatgheibi et al., 2017, Jayawickrama, 2001, Hallingbäck et al., 2008, Chen et al., 2015).

Wood density is the most important wood property for both solid and fiber products in both conifers and hardwoods because of its strong relationship to both yield and quality as well as its large variance and high heritability (Zobel and Jett, 1995). Wood density is indirectly measured by pilodyn penetration, with increased pilodyn penetration indicating decreased wood density (Whitlock et al., 2003). Pilodyn penetration is used to measure penetration depth of a spring-loaded blunt pin that is shot into the wood with an exact force. Its records give strong genetic correlations with wood density in some conifer species (Chen et al., 2015, Högberg et al., 2013, Isik and Li, 2003, Gao et al., 2012). However, the penetration depth is limited to the outer wood and, hence, no information is provided about the rest of a tree's profile (Fundova et al., 2018). In addition, bark thickness might affect the estimates. Besides, resistance micro-drilling tool, also called Resistograph, is used to measure the relative resistance (drilling torque) as a rotation drill bit is driven into the wood from bark to bark at a constant speed (Gao et al., 2012). It produces the whole stem's profile which provides not only resistance value but also diameter and bark thickness (Downes et al., 2018). Strong genetic correlations between wood density and mean resistograph value have been reported (Bouffier et al., 2008, Fundova et al., 2018, Isik and Li, 2003). Resistograph could be therefore a reliable and effective tool for wood density assessment of live trees in tree improvement programs.

Modulus of elasticity (MOE) is a property that describes the wood stiffness. A high value of MOE indicates that the wood has a high resistance to

deformation (Hassan et al., 2013). Fakopp Microsecond Timer and Hitman ST300 are tools used to measure indirectly wood stiffness through acoustic velocity. Strong genetic correlation between MOE estimated by acoustic velocity alone or together with pilodyn, and MOE determined by SilviScan were reported on Norway spruce (Chen et al., 2015) and other conifer species (Hayatgheibi et al., 2017, Hong et al., 2014).

Grain angle (i.e. spiral grain) is one wood property of primary interest for solid wood products because of its influence on timber strength and stability (Hallingbäck et al., 2008). The investigation of this characteristic of wood is a challenge due to the complexity of the measurement procedures (Zobel and Jett, 1995). However, a wedge grain angle gauge is easily used as non-destructive tool to measure grain angle of standing trees (Hannrup et al., 2003, Fries et al., 2014). Significant genetic variation and considerable heritability have been observed for grain angles in Scots pine (Hannrup et al., 2003) and Norway spruce (Hallingbäck et al., 2008). Grain angle had small or non-significant genetic correlations with most other important breeding traits (Hannrup et al., 2003), suggest that breeding for reduced grain angles is a promising strategy for the improvement of sawn timber shape stability.

2 Objectives

The overall objectives of the studies were to estimate genetic parameters for growth, wood quality, essential oil traits and genetic relationship among them which aimed to effectively develop optimal breeding programs for essential oil and timber production of *Melaleuca* and study optimal deployment program for wood production of Norway spruce. The following specific questions were addressed:

- 1) How large is the heritability of growth and wood quality traits important for timber products, what are their genetic relationships and genetic improvement potential for wood production in *M. cajuputi* subsp. *cumingiana* (Paper I)?
- 2) How can essential oil yield and oil quality be incorporated into selective breeding programs of *M. cajuputi* subsp. *cajuputi* and how much genetic gain will be obtained for these traits using selection indices for optimal cajuput oil production (Paper II)?
- 3) How is the relative importance of additive, dominant and epistatic genetic effects on growth and wood quality traits, and how much genetic gain will be produced from deployment of the top 5 % of clones compared with deployment of full-sib and open-pollinated family forestry from two full-sib clonal progenies of Norway spruce (paper III)?
- 4) How are genetic parameters estimated for different traits and different ages in four control-pollinated and two open-pollinated clonal trials of Norway spruce, and how family size affects genetic gain in a deployment population (paper IV)?

3 Materials and Methods

3.1 Materials and field trials

3.1.1 Melaleuca

Detailed descriptions about the two field trials of *Melaleuca* are given in Table 1. The open-pollinated (as half-sib family) trial of *M. cajuputi* subsp. *cumingiana* comprised 80 families collected from individual plus trees with fast growth, good stem form (straightness and narrow crown), fruiting and no visible insect or disease damage in the Mekong delta, Vietnam. The entire trial was thinned at age 4 years, to retain the best two trees in each family plot. Felled trees were either dead, or had other deficiencies (slow growth, broken stems or attacked by stem borer) (in the paper I).

The partial diallel mating design was applied for the full-sib family trial of *M. cajuputi* subsp. *cajuputi*. The trial comprised 39 families as crossing combinations from 12 parents, which were selected from plus trees, based on their high 1,8-cineole (56.9 – 63.1 %) and oil content (1.3 – 4.6 %) obtained by steam distillation (in the paper II).

Table 1. Details for the two field trials of *Melaleuca* in Vietnam and Indonesia

| Details | <i>M. cajuputi</i> subsp. <i>cumingiana</i> | <i>M. cajuputi</i> subsp. <i>cajuputi</i> |
|---|---|---|
| Location | Thanh Hoa, Long An, Vietnam | Playen, Gunungkidul, Yogyakarta, Indonesia |
| Planted date | July 2009 | December 2004 |
| Latitude | 10°35' N | 7°58'00.59" S |
| Longitude | 106°11' E | 110°30'23.71" |
| Altitude (m) | 12 | 150 |
| Mean annual rainfall (mm) | 1325 - 1670 | 2157 |
| Mean annual temperature (°C) | 27.3 | 27 |
| Soil type | seasonally inundated acid sulphate (pH ~ 2.9–3.7) | red and black grumosol limestone (pH ~ 6.5 – 7.5) |
| Number of families | 80 | 39 (12 parents) |
| Number of replicates | 51 | 8 |
| Number of trees each family per replicate | 4 | 6 |
| Spacing (m x m) | 1.0 x 1.5 | 1.5 x 3.0 |
| Experimental design | random complete block | random incomplete block |
| Type of material | Half-sib | Full-sib |

3.1.2 Norway spruce

A large number of clones were tested in single-tree plot experiments on eight trials. The sparse partial diallel mating designs were applied for the full-sib clonal trials. Rooted cuttings were used to plant in all full-sib and half-sib clonal trials. Detailed descriptions about the eight field trials of Norway spruce including soil type and climate condition are given in Table 2.

Among studied trials, the two full-sib clonal trials (S209 and S241) were established in 1991 and comprised 1015 clones from 167 full-sib families crossed between 58 parents including 36 females and 37 males. Each family from these two trials has an average of 6.2 clones (1 – 16 clones), each clone has 1 -10 ramets (average 3.2 ramets) (the paper III).

The four full-sib clonal trials (S387, S388, S389 and S390) were established in 2007 and comprised 1430 clones from 32 families crossed between 49 parents including 30 females and 22 males. Each family in the four trials has an average of 44.7 clones (18 – 64 clones). Besides, the two half-sib clonal trials (S237 and S239) were planted in 1996 and consisted of 2244 clones from 138 half-sib families. Average of clones for each half-sib family was 16.9 (paper IV).

Table 2. Details for the eight clonal field trials of Norway spruce in southern and central Sweden

| Details | S209 ^a | S237 ^b | S241 ^a | S239 ^b | S387 ^b | S388 ^b | S389 ^b | S390 ^b |
|------------------------------|-------------------|-------------------|-------------------|-------------------|-------------------|-------------------|-------------------|-------------------|
| Location | Lugnet, Bålsta | | Rådahöjden | Grangärde | Tagels gård | Skåne Fagerhult | Rössjöholm | Knutstorp |
| Planting date | 1991 | 1996 | 1991 | 1996 | 2007 | 2007 | 2007 | 2007 |
| Latitude (north) | 59.38 | | 60.00 | 60.28 | 57.16 | 56.4 | 56.3 | 56.02 |
| Longitude (west) | 17.31 | | 13.31 | 15.12 | 14.4 | 13.47 | 13.13 | 13.09 |
| Altitude (m) | 10 | | 210 | 300 | 220 | 112/135 | 105 | 115 |
| Mean annual rainfall (mm) | 593.7 | | 849 | 811 | 832.6 | 958.3 | 1002.7 | 1044.4 |
| Mean annual temperature (°C) | 7.3 | | 5 | 5 | 6.8 | 7.7 | 8.1 | 8.4 |
| Soil type | Sedimentary clay | | Sandy till | Podzol | Podzol | Podzol | Podzol | Podzol |
| Number of clones | 548 | 2243 | 1015 | 804 | 1428 | 1424 | 1412 | 1409 |
| Number of families | 74 | 148 | 167 | 118 | 32 | 32 | 32 | 32 |
| Number of ramets/clone | 1.9 | 4.1 | 3.4 | 5 | 3.6 | 3.5 | 3.4 | 3.2 |
| Type of material | Full-sib | Half-sib | Half-sib | Half-sib | Full-sib | Full-sib | Full-sib | Full-sib |

^a the field trials for the paper III; ^b the field trials for the paper IV

3.1.3 Essential oil

Leaf samples for oil analysis including essential oil (mg/g leaf dry weight) and 1,8-cineole content (percentage of 1,8-cineole in leaf oil) were randomly collected from two of six individuals of each plot at three of the eight replicates in 2008. Oil extraction was done following the method described by Baker et al. (2000). Essential oils were then analysed in ethanol extracts by gas chromatography using Shimadzu GC-17A. Estimation of oil concentration was ratio to leaf dry weight (mg/g LDW). The relative amount of 1,8-cineole was calculated as percentage of leaf oil (in the paper II).

3.1.4 Wood traits

Wood density was indirectly measured by pilodyn and resistograph. Pilodyn penetration depth (Pilo) was measured using a Pilodyn 6J Forest (PROCEQ, Zurich, Switzerland) with a 2.0 mm diameter pin. While measuring, the bark was not removed. The measurement was conducted at approximate 1.3 m above the ground for each tree and on the same side for all trees (paper III & IV).

Micro-drill resistograph IML-RESI PD300 (Instrumenta Mechanic Labor, Germany) was used for estimating wood density of standing trees. Each profile was checked immediately after drilling on the tool's screen. Then, resistance traces were transferred from the resistograph to the PD Tools Pro software and exported as text files. Custom software available as a web URL <https://forestquality.shinyapps.io/ResiProcessor/> was used to process the resistance traces and extract the over-bark diameter and bark thickness, together with the mean resistance (Resi) value of the under bark portion of the trace (Downes et al., 2018) (the paper III & IV).

Acoustic velocity (AV) was determined using the Hitman ST300 tool (Fiber-gen, Christchurch; New Zealand) (the paper III & IV) and Fakopp (the paper I). Two probes were inserted into a tree stem, separated vertically at a distance of 0.7 - 1.3 m and orientated at an angle of 45° to the stem with the tips facing each other. The acoustic velocity were calculated:

$$AV (ms^{-1}) = \frac{s}{t} \quad (1)$$

where s is the distance between probes and t is the transit time.

Modulus of elasticity (MOE) was evaluated as an indirect measure of wood stiffness in standing trees according to the following equations (Johnson and Gartner, 2006, Chen et al., 2015):

$$MOE (GPa) = AV^2\rho \quad (2)$$

$$\text{MOE (GPa)} = \frac{1}{\rho_{\text{pilo}}} \times 10,000 \times AV^2 \quad (3)$$

where ρ is the green density of the material (kgm^{-3}).

Grain angle (GA) was measured at 1.3 m height using the wedge grain angle gauge (Fries et al., 2014, Hannrup et al., 2003). Measurements from two opposite sides (northwest and southeast) of the stem were taken and the mean was used as the phenotypic GA value thus eliminating measurement errors due to leaning stems (the paper III).

3.2 Statistical analysis

3.2.1 General model

Variance and covariance components for all phenotypic traits were estimated by the mixed-model equation:

$$y = Xb + Zu + e \quad (4)$$

where, y is the vector of each individual tree observation, b is the vector of fixed effect, u is the vector of random effect and e is the vector of residuals. X and Z are the incidence matrices of fixed effect (b) and random effect (u), respectively.

3.2.2 Variances and heritability

The phenotypic variance among individual trees for a given trait (σ_p^2) was estimated as (White et al., 2007b):

$$\sigma_p^2 = \sigma_G^2 + \sigma_{G \times E}^2 + \sigma_E^2 \quad (5)$$

where σ_G^2 is the total genetic variance, $\sigma_{G \times E}^2$ is the variance of genotype by environment interaction, and σ_E^2 is the variance among trees caused by environmental effects. The total genetic variance includes the additive (σ_A^2), dominance (σ_D^2) and epistatis (σ_I^2) variances.

For each trait, heritability of narrow-sense (h^2), broad-sense (H^2) and clonal mean (H_c^2) were estimated as follows:

$$h^2 = \frac{\sigma_A^2}{\sigma_p^2} \quad (6)$$

$$H^2 = \frac{\sigma_G^2}{\sigma_p^2} \quad (7)$$

$$H_c^2 = \frac{\sigma_G^2}{\sigma_c^2} \quad (8)$$

3.2.3 Relationship between traits, genetic gains and optimal family size

The correlations between two traits were calculated from variances and covariance using the mixed model equation, and the following formula were used for calculation (Fins et al., 2013):

$$r_{(x,y)} = \frac{Cov_{(x,y)}}{\sigma_x \sigma_y} \quad (9)$$

where $Cov_{(x,y)}$ is covariance component between traits x and y , σ_x and σ_y are standard deviations of traits x and y .

Expected genetic gain (ΔG) was estimated under selection intensity (i) as follows (Baltunis et al., 2009):

$$\Delta G_{h^2} = ih^2\sigma_p \quad (10)$$

$$\Delta G_{H^2} = iH^2\sigma_p \quad (11)$$

$$\Delta G_{H_c^2} = iH_c^2\sigma_c \quad (12)$$

In the paper III and IV, three deployment strategies considered were (1) open-pollinated family deployment (HS), individual mass selection and grafted seed orchard and deployment with their seedlings; (2) full-sib family deployment (FS), mass selection of the best individuals and cloning, deployment with rooted cuttings; and (3) clonal deployment (Clone), selection based on clonal means and clonal deployment with rooted cuttings.

All gains were expressed as the percentage gain over the mean of the trait:

$$\% \Delta G = \frac{\Delta G}{\bar{y}_x} \times 100 \quad (13)$$

where \bar{y}_x is the population mean for trait x .

The correlated responses were calculated as:

$$CR_y = ih_x h_y r_{G(x,y)} \sigma_{P_y} \quad (14)$$

In order to estimate optimal family size (number of clones within a family) for clonal trial, a subset of trees (5, 10, 15, 20, 25, 30, 35, 40, 50, 55, and 60) from each of 32 full-sib families were selected in this study. Two selection strategies were implemented: (1) selecting 10 clones without limitation of relationships among the selected clones; and (2) selecting the best single clone from each of 10 families, based on the suggestion from the review (Rosvall et al, 2019), to manage risk for a single clonal stand in Sweden. Thus, 22 selection scenarios with each of 10 repeats. Genetic gain (%) is developed

$$\Delta G = \frac{\sum p_i GV_i}{\bar{y}} * 100 \quad (15)$$

where p_i is the fractional contribution to the clonal mixture by the i^{th} clone; GV_i is the i^{th} clonal genetic value ($GV = Z_1 a + Z_2 f + Z_3 c$).

3.2.4 Index selection

Breeding selection was based on selection indices constructed for improvement of single and multiple traits and with or without gain restriction among traits (Falconer and Mackay, 1996).

$$I = b_1P_1 + b_2P_2 + \dots + b_mP_m \quad (16)$$

where P_1 to P_m are phenotypic measurements of m characters on which selection is to be based, and b_1 to b_m are the corresponding weighting factors to be determined.

The index coefficients were obtained from

$$b = P^{-1}x G x a \quad (17)$$

where P and G are the phenotypic and additive genetic variance–covariance matrices for selected traits, and a is vector of weighting coefficients assigned as reciprocals of the phenotypic standard deviations for each of objective traits (equal economic values are assigned to one standard deviation for change in each character) (paper I & II).

For restricted selection index, equation 17 could be modified as (Mrode, 2005)

$$b^* = \begin{bmatrix} P^* & G^* \\ G^* & 0 \end{bmatrix}^{-1} \times \begin{bmatrix} G^{**} \\ 0 \end{bmatrix} \times a \quad (18)$$

where P^* is the phenotypic variance–covariance matrix for selection traits, G^* is the additive genetic variance–covariance matrix between selected traits and traits excluding restricted traits, G^{**} is the additive genetic variance–covariance matrix between selected traits excluding restricted traits, 0 is the zero vector.

The expected genetic gain of each individual trait was calculated as:

$$\Delta G_x = \frac{i}{\sigma_I} (b_x A_x + b_y A_{xy}) \quad (19)$$

where ΔG_x is the expected genetic gain in trait x , i is the selection intensity, σ_I is the phenotypic standard deviation of the index, A_x is the additive genetic variance of trait x , A_{xy} is the additive genetic covariance of trait x and y , b_x and b_y are the index coefficients of trait x and y (paper I & II).

Statistical analyses were done using ASReml 4.0 (Gilmour et al., 2014) and ASReml-R 4.0 was used to conduct the simulation (Butler et al., 2017).

4 Results and discussion

4.1 Melaleuca

4.1.1 Variations and inheritances of studied traits

Additive, dominant genetic and phenotypic coefficients of variation, estimated narrow-sense and broad-sense heritability of studied traits are given in Table 3. The general trend of additive genetic coefficients of variation for growth was an increase over time while phenotypic coefficients of variation decreased in subsp. *cumingana*. Coefficients of variation for DBH were usually higher than height. This was similar to subsp. *cajuputi*. However, dominant genetic coefficients of variation for growth and phenotypic coefficients of variation for DBH had decreasing trends whereas additive genetic coefficients of variation for growth and phenotypic coefficients of variation for height changed negligibly with age in subsp. *cajuputi*. This subsp. *cajuputi* had higher additive genetic and phenotypic coefficients of variation for growth traits than subsp. *cumingana*. MOE and 1,8-cineol content had low additive genetic and phenotypic coefficients of variation as compared to other traits in this study.

The trends for narrow-sense heritability for DBH and height growth of *M. cajuputi* subsp. *cumingana* increased with ages. The increased heritability for growth after the thinning at age 4 showed significant effect of selective thinning which caused considerable reduction of phenotypic variation but slight change in additive genetic variation. Effect of selective thinning on heritability were reported in *E. urophylla* (Kien et al., 2009), *P. radiata* (Wu et al., 2007), *Pinus sylvestris* (Hannrup et al., 1998). Selective thinning produced higher heritability than the unthinned progeny trial. Commercial thinning inflates heritability estimates of growth (DBH), but has less impact on heritability of wood quality traits (Wu et al., 2007).

The previous studies of mechanical properties of *Melaleuca* wood used destructive methods (Wahyudi et al., 2014, Ban, 2002, Junji, 1999). In this study, non-destructive evaluation of mechanical property of wood (i.e. wood stiffness) was conducted. The narrow-sense heritability for MOE of subsp. *cumigiana* at age seven was moderate, similar to the estimates in *Eucalyptus nitens* (Blackburn et al., 2014), but lower compared with the estimates of 10-year-old *E. globulus* (Hamilton et al., 2017) and eight-year-old *E. urophylla* (Wu et al., 2013) and higher than 24-year-old Norway spruce (Chen et al. 2015).

Bark thickness of the tree or log is important in forest inventory and has a major effect on the amount of usable wood (Kleinn, 2007). The narrow-sense heritability of bark thickness and bark ratio in this study were 0.23 and 0.21, similar to the report in *Eucalyptus globulus* (Whitlock et al., 2003) but higher than those in *Eucalyptus grandis* and *Eucalyptus urophylla* (Retief and Stanger, 2009) and lower than those in *Pinus patula* (Ladrach and Lambeth, 1991) and *Hevea brasiliensis* (Gonçalves, 2005).

In general, the observed traits of *M. cajuputi* subsp. *cajuputi* in this study had low to high narrow-sense heritability (0.10 - 0.50). Narrow-sense heritability of 0.50 for essential oil concentration in subsp. *cajuputi* was higher than the estimate of 0.40 while 1,8-cineole content (0.21) was considerably lower than the value of 0.54 reported for the same species in the previous study (Susanto et al., 2003). The higher narrow-sense heritability of 0.67 for essential oil concentration was reported on *M. alternifolia* (Butcher et al., 1996). However, these estimates were comparable to the summary on some *Eucalyptus* species that narrow-sense heritability for oil concentration ranged from 0.11 to 0.54 while 1,8-cineole content had the estimate range of 0.27 to 0.61 (Doran, 2003). Half-sib family mean heritability of subsp. *cajuputi* in this study was higher than the value reported for 1,8-cineole content in *M. alternifolia* (Butcher et al., 1996) and *Eucalyptus camadulensis* (Doran and Matheson, 1994) but lower than those in *Eucalyptus kochii* (Barton et al., 1991). In addition, broad-sense heritability of subsp. *cajuputi* were high for oil yield (0.85) and moderate for 1,8-cineol content (0.46). Although these estimates cannot be directly compared due to their differences (e.g. number of selected trees per family, number of family in each trial, etc.), they indicate that there is strong genetic control of oil concentration and 1,8-cineole content.

Table 3. The additive (CV_A), dominant (CV_D) genetic and phenotypic (CV_P) coefficients of variation, and estimated narrow-sense (h^2) and broad-sense (H^2) heritability and their standard errors of *M. cajuputi* subsp. *cumingiana* in the half-sib family trial and *M. cajuputi* subsp. *cajuputi* in the full-sib family trial.

| Variable | CV_A (%) | CV_D (%) | CV_P (%) | h^2 | H^2 |
|--|------------|------------|------------|-----------|-----------|
| <i>M. cajuputi</i> subsp. <i>cumingiana</i> | | | | | |
| H ₁ | 0.01 | | 17.16 | 0.00±0.00 | |
| H ₂ | 3.12 | | 14.70 | 0.05±0.03 | |
| H ₄ | 5.66 | | 22.08 | 0.07±0.03 | |
| H ₄ (after thinning) | 4.95 | | 12.55 | 0.16±0.05 | |
| H ₅ | 4.52 | | 11.91 | 0.14±0.05 | |
| H ₇ | 6.13 | | 11.94 | 0.27±0.07 | |
| DBH ₁ | 2.20 | | 31.68 | 0.00±0.02 | |
| DBH ₂ | 0.01 | | 23.48 | 0.00±0.00 | |
| DBH ₄ | 7.54 | | 23.34 | 0.10±0.03 | |
| DBH ₄ (after thinning) | 7.91 | | 18.79 | 0.18±0.05 | |
| DBH ₅ | 7.94 | | 19.28 | 0.17±0.05 | |
| DBH ₇ | 10.14 | | 20.19 | 0.25±0.06 | |
| Volume | 25.13 | | 49.56 | 0.26±0.06 | |
| Stem form | 11.75 | | 31.99 | 0.13±0.04 | |
| Acoustic velocity | 2.73 | | 5.90 | 0.21±0.06 | |
| MOE | 5.49 | | 11.62 | 0.21±0.06 | |
| Bark ratio | 10.44 | | 21.97 | 0.23±0.06 | |
| Bark thickness | 11.37 | | 24.54 | 0.21±0.06 | |
| <i>M. cajuputi</i> subsp. <i>cajuputi</i> | | | | | |
| H ₁ | 9.61 | 7.98 | 27.14 | 0.13±0.08 | 0.21±0.09 |
| H ₂ | 9.43 | 0.02 | 27.31 | 0.12±0.07 | 0.12±0.07 |
| D ₁ | 13.86 | 16.39 | 43.00 | 0.10±0.08 | 0.25±0.11 |
| D ₂ | 12.70 | 7.99 | 36.83 | 0.12±0.08 | 0.17±0.10 |
| Oil content | 20.00 | 16.68 | 28.29 | 0.50±0.24 | 0.85±0.27 |
| 1,8-cineole content | 6.42 | 6.99 | 13.98 | 0.21±0.17 | 0.46±0.25 |

H_n: total height at age n; DBH: diameter at breast height, D: diameter at 30 cm above ground level

4.1.2 Genetic correlations between studied traits and age-age correlations

In genetic studies, it is necessary to distinguish two causes of correlation between characters, genetic and environmental (Falconer and Mackay, 1996). The genetic correlations between traits can be used to predict the effectiveness of indirect selections on a correlated trait with the primary goal of improving a trait under the direct selection (Isik et al., 2017). In the paper I, genetic correlations between all studied traits except for bark ratio of *M. cajuputi* subsp. *cumigiana* were positive and favourable. The genetic correlations between all studied traits and the bark ratio of *M. cajuputi* subsp. *cumigiana* were negative, but favourable. This suggests that selection for one of these traits should result in a simultaneous positive response in other traits. The results of this study are comparable to different studies of trees in a manner that diameter, height and volume are strongly inter-correlated (Butcher et al., 1996, White et al., 2007, Retief and Stanger, 2009, Whittcock et al., 2003, Gonçalves, 2005). In addition, age-age genetic correlations for DBH and height of subsp. *cumigiana* were strong between age 7 and earlier ages except for age 1 and 2 (Figure 4 in the paper I). DBH had strong correlation relative to height at all ages except for only age 1 (Figure 3 in the paper I). Therefore, early selection for growth of subsp. *cumigiana* at age 4 based on DBH alone could be sufficient and reduce costs of multiple early measurements.

Positive moderate genetic correlations between MOE and growth in subsp. *cumigiana* were similar to *Eucalyptus nitens* and *E. globulus* (Hamilton et al., 2017, Blackburn et al., 2014), but with exception in *Eucalyptus urophylla* (Wu et al., 2013). This positive correlation is in contrast to most studies in conifer species where high or moderate negative genetic correlations were observed between growth and wood quality traits, such as *Pinus radiata* (Wu et al., 2008), *Pseudotsuga menziesii* (Johnson and Gartner, 2006) and *Picea abies* (Chen et al. 2015). The results of this study indicated that it was possible to select trees for larger stem and higher MOE in Melaleuca.

In the paper II, the genetic correlations between growth, oil concentration and 1,8-cineole content (-0.08 to 0.08) of *M. cajuputi* subsp. *cajuputi* were found almost independent, and selection for one is unlikely to affect the other significantly. These results were similar to the values reported for the same species (-0.18 to 0.10) (Susanto et al., 2003). The genetic association between growth and leaf oil yield was also very weak in *M. alternifolia* (Butcher et al., 1996) and disappeared with maturity in *Eucalyptus polybractea* (Kainer et al., 2015). Many MEP pathway genes were correlated with total oil yield but not correlated with cineole in *M. alternifolia* (Webb et al., 2013). These indicated

that selection for essential oil concentration would have no or negligible effect on 1,8-cineole content.

4.1.3 Response for different selection scenarios

The six different selection scenarios and their expected response for studied traits in *M. cajuputi* subsp. *cumigiana* are presented in Table 4 of the paper I. The choice of a breeding selection scenario is dependent on the breeding objective and purpose. The positive genetic correlation among growth, stem form, MOE and adverse correlation between these traits and bark ratio are a considerable advantage for simultaneous improvement of multiple traits in an advanced breeding program. For example, selection for timber production based on volume and MOE showed genetic gains of 31% in volume, 6% in MOE which was higher than the gain obtained from selection based on volume alone (1% in MOE) or DBH alone (4% in MOE).

Several factors affect the economic value of cajuput oil production. The independent relationships between growth, oil concentration and 1,8-cineole content indicate potential for simultaneous improvement of multiple traits in an advanced breeding program of *M. cajuputi* subsp. *cajuputi*. The optimal way to increase economic values is using the index selection approach if economic weights are known from breeding objective study or market research (Ivković et al., 2006). Both oil yield and 1,8-cineole content traits could be improved simultaneously and the increased income reached maximum (~ 29 %) when the economic weights for oil content ranging from 0.3 to 4 relative to 1 for 1,8-cineole content. The optimal selection scenario for combined leaf oil concentration and 1,8-cineole content was the half weight of oil concentration relative to 1,8-cineole content. This will improved 2.18 % for 1,8-cineole content and 27.36% for leaf oil concentration, respectively with a maximum of economic value of 29.84 (Paper II).

4.2 Norway spruce

4.2.1 Partitioning of genetic variances and genetic parameters

Single site and across site estimates of variance components and genetic parameters for growth and wood traits, obtained from the analysis of six full-sib and two half-sib clonal progeny trials, are presented in Table 2 of the paper III and Table 2a & 2b of the paper IV. Partitioning of genetic variance for growth and wood traits indicated that both additive and non-additive genetic variances

were important sources of total genetic variances. However, considerable differences of partitioned genetic components of variances were observed between different ages, traits and trials in Norway spruce.

Additive genetic variation accounted for the majority of the total genetic variation associated with DBH growth (52 – 84 %) whereas non-additive genetic variation contributed low to moderate portion to the total genetic variation (3 – 47 %) in the six full-sib trials. Among them, dominance genetic variation contributed a lower or zero portion to the total genetic variation (0 – 40 %). In general, non-additive genetic variation appeared to be more important for tree height (46 – 72 %) in which epistasis contributed considerably (13 – 55 %) and the relative importance between dominance and epistasis obviously varied with age. However, non-additive genetic variations were high for both height and DBH (64 – 67 %) and there were negligible changes with age in the two half-sib trials. These estimates of dominance variances for growth were close to previous studies on two conifer species, such as black spruce (Mullin and Park, 1994, Mullin and Park, 1992), white spruce (Weng et al., 2008) and hardwood *Eucalyptus globulus* (Costa et al., 2004). In the paper III, non-additive components were greater than additive components for height at early ages but reduced considerable and much lower additive components for DBH as age increases. This was similar to the study of white spruce (Weng et al., 2008). In addition, negative estimates of epistasis were recorded for DBH₂₆ and Resi₂₇ in this study. Similarly, negative epistasis for growth variables were reported on loblolly pine (Baltunis, 2007b, Baltunis et al., 2007a, Isik et al., 2003). Negative epistasis means that the phenotype variance is lower than expected while positive epistasis indicates the higher phenotype variance than expected (Phillips, 2008).

For wood traits (i.e. Pilo, Resi, AV, MOE and GA) including bark thickness, non-additive genetic effects ranged from 0 to 43 % except for Pilo₁₂ (54.5 %) in both full-sib and half-sib clonal trials. The dominance variances ranged from zero to 30 % while epistasis variances were less than 17 % (-8 to 17 %). The estimates of dominant variance (0 %) and epistasis variance (12.2 %) for Pilo₂₆ were close to the report in *Eucalyptus globulus* (Costa et al., 2004). However, dominance and small epistasis genetic variances indicated for AV but those were zero for Pilo and MOE in the recent study on Norway spruce (Chen et al., 2018). The contributions of non-additive genetic effects, especially epistasis could be species-specific, populations, sites and even traits (Tan et al., 2018).

Both narrow-sense and broad-sense heritability are trait-specific, population-specific and greatly influenced by the homogeneity of the test environment (White et al., 2007). The higher broad-sense heritability (H^2) as compared to narrow-sense heritability (h^2) showed that non-additive effects were implied in

this study. The ratio of h^2/H^2 ranged from 0.22 to 0.83 for height and DBH growth traits while they were higher for most wood properties and bark thickness (0.55 to 1.00). These results were comparable to the usual range of the ratio of h^2/H^2 reported from 0.18 to 0.84 for tree growth traits (Wu et al., 2008, White et al., 2007). In previous studies on Norway spruce, the ratio of h^2/H^2 for height varied from 0.35 to 0.84 (Chen et al., 2018, Kroon et al., 2011). Wu (2018) indicated that a valid comparison must use datasets from the same trial with comparable pedigree.

Narrow-sense heritability estimates were low to moderate for growth traits (0.02 – 0.20) and from moderate to high for wood property traits (0.18 – 0.51) in this study. These results were comparable to the conclusion in the recent studies on Norway spruce that narrow-sense heritability ranged 0.07 – 0.40 for growth and 0.15 – 0.53 for wood properties (i.e. AV, Pilo, MOE, GA and wood density) (Chen et al., 2018, Chen et al., 2015, Högberg et al., 2013, Kroon et al., 2011, Steffenrem et al., 2009, Hallingbäck et al., 2008, Hannrup et al., 2004). Early estimates of broad-sense heritability in Norway spruce from clone tests in the fields ranged from 0.17 to 0.40 for height growth at age 1 to 10 years (Hogberg and Karlsson, 1998, Lepistö, 1993, Bentzer et al., 1989, Roulund et al., 1986). In this study, estimates of broad-sense heritability were 0.09 – 0.32 for growth and 0.29 – 0.61 for wood properties. These were comparable to broad-sense heritability of 0.20 – 0.54 for growth and 0.14 – 0.55 for wood traits (i.e. wood density, Pilo, AV, MOE and GA) reported in Norway spruce (Chen et al., 2018, Hannrup et al., 2004, Hallingbäck et al., 2008). Both narrow-sense and broad-sense heritability for growth traits reported in the paper III were higher than those reported in the paper IV.

Clonal mean heritability were from 0.22 to 0.65 for growth and bark thickness, and 0.52 to 0.75 for wood property traits (Table 2 in the paper III and Table 3a in the paper IV). Estimates of clonal mean heritability for growth were always higher in the full-sib clonal trials than in the half-sib clonal trials but there were no considerable differences of those for wood traits. Clonal mean heritability were similar to estimates for DBH and lower than those for height in the same species in previous studies (Lepistö, 1993, Bentzer et al., 1989) and other species, such as white spruce (Weng et al., 2008), black spruce (Mullin and Park, 1994) and loblolly pine (Baltunis et al., 2007a, Isik et al., 2005).

4.2.2 Trait-trait correlations

Total genetic correlations are applicable to clonal forestry as additive genetic correlations are applied to breeding selection. Estimates of total genetic correlations among traits were generally comparable or slightly different from

additive genetic correlations but had lower standard errors (Table 3 in the paper III). Strong genetic correlation among growth traits in this study were similar to those in other with genetic correlations ranging from 0.70 to nearly one (White et al., 2007) and previous studies on Norway spruce (0.48 – 0.95) (Chen et al., 2015, Kroon et al., 2011, Hannrup et al., 2004, Bentzer et al., 1989, Roulund et al., 1986).

Observed genetic relationships between DBH and Resi, Pilo and MOE were slightly lower than those estimated previously on the same species (Chen et al., 2015) and in *Pinus taeda* (Isik and Li, 2003), but comparable to those in other conifer species, such as *Pinus contorta* (Hayatgheibi et al., 2017) and *Pinus sylvestris* (Fundova et al., 2018). The high genetic correlations between Pilo and wood density were reported in Norway spruce (-0.62) (Chen et al., 2015) and Scots pine (-0.59 with bark and -0.74 without bark) (Fundova et al., 2018) using Siviscan. In addition, the very strong genetic correlations between Resi and wood density were indicated in *Pinus taeda* (0.95) (Isik and Li, 2003) and 0.87 – 0.96 in *Pinus sylvestris* (Fundova et al., 2018). In the present study, Resi and Pilo had high genetic correlation (-0.80) and resistograph provided more measurement of DBH and bark thickness. Thus, it has a great potential to reliably assess the relative wood density of standing trees for selection in tree improvement programs.

The genetic correlations between grain angle and all measured other traits except for AV and MOE were very weak. The additive genetic correlation between GA and MOE was -0.21, and close to previous report on Norway spruce (Högberg et al., 2013). Nevertheless, the study of Hallingbäck et al. (2008) showed that total genetic and additive genetic correlations between GA and DBH were moderate, and among them total genetic correlation was slightly higher.

4.2.3 Response for different selection schemes and optimal family size

To maximize genetic gain is one of the most important objectives in tree improvement programs. However, meaningful calculations of gain require obviously reliable estimates of all parameters (Mullin and Park, 1992). In conifer species, an additional genetic gain of 5 to 25% is possible from clone testing and deployment, effectively doubling that achievable from family forestry within the same generation (Wu, 2018). In this study, the top 5 % of clones reached 14 - 17 % genetic gain for DBH, an improvement of 58 - 280 % over open-pollinated deployment in the full-sib trials. Similarly, study on radiata pine reported 24% genetic gain, an improvement of more than 100% over family forestry (Baltunis et al., 2009). Eventual differences on estimated extra gains are mainly due to the

size of population, number of clones within-family tested, accuracy of the progeny testing, ratio of additive to non-additive genetic variances (Wu, 2018).

From similar clone trials in Germany, Denmark, Norway and Finland, genetic gains for tree height were estimated between 10% and 25% at different selection intensity (Bentzer, 1993). When using the best ten percent of tested clones in the paper III, estimated genetic gain for height ranged from 12 to 18 %, which were similar to 13 - 25 % estimated for the same species in Sweden (Karlsson, 1993, Bentzer et al., 1988), and 13 – 19 % in Finland, respectively (Lepistö, 1993).

Genetic gains for wood quality traits including bark thickness except for GA reached from 5 % to 19 % in clonal deployment, relative to 2% - 16 % in full-sib family and open-pollinated deployments in the half-sib and full-sib clonal trials. Clonal forestry indicated an improvement of 11 - 38 % over full-sib family forestry and 16 - 140 % over open-pollinated deployment for the wood property traits if the top 5 % of clones were selected.

In Figure 1 of the paper IV, genetic gains for DBH₁₂ based on the two selection scenarios: 1) selecting the best 10 clones based on genetic values for DBH without pedigree constrain for 12 family sizes (5, 10, 15, 20, 25, 30, 35, 40, 45, 55, and 60 clones per family, respectively) and 2) selecting the single best clone in each of the best 10 families (pedigree constraint) for DBH₁₂. The estimated genetic gain (EGG) used in scenario 1 was higher than that from scenario 2 under all types of family size but showed a similar trend for both scenarios. EGG using scenario 2 increased quickly from 13.7% with 5 clones per family to 18.7% with 25 clones per family and then slightly increase to 19.2% with 40 clones per family, and the gain stabilized after 40 clones per family. Thus, with 30–40 clones per family the realized genetic gain will be maximized after clonal propagation, both with respect to selecting the best ten individual trees without any coancestry restriction and the best single individual from the best ten families.

5 Conclusions and future perspectives

Based on the four studies in this thesis, following conclusions can be drawn with future perspectives:

5.1 Melaleuca

The study on *M. cajuputi* subsp. *cumingiana* indicated that:

- There was increased heritability for growth traits with tree age and as a consequence of selective thinning. Such thinning reduced considerably phenotypic variation but had little effect on genetic variation.
- The age–age genetic correlations for growth traits increased with time and was higher than 0.77 from age 4 with final age 7. Optimal selection age for a 7-year rotation based on DBH was 4 years.
- Positive genetic correlations between growth traits and MOE indicated that simultaneous improvement of growth and stiffness were possible. Negative genetic correlation between tree volume and bark ratio meant that selection for bigger tree would reduce bark to volume ratio, which was favourable for sawn timber production.
- However, restriction of no change on bark thickness can reduce genetic gain for volume. Therefore, selection for volume and MOE simultaneously would be the best strategy for *M. cajuputi* subsp. *cumingiana* breeding selection for sawn timber production.

The results of the study on *M. cajuputi* subsp. *cajuputi* showed that:

- Narrow-sense heritability were low for growth traits, moderate for 1,8-cineole content and high for leaf essential oil concentration.
- There were no genetic relationships between growth, oil concentration and 1,8-cineole content. Selection for one of the traits would therefore have no or negligible effect on the others.

- However, simultaneous improvement of oil concentration and 1,8-cineole in *M. cajuputi* subsp. *cajuputi* breeding program was possible by using index selection. The most optimal selection scenario was genetic responses improved 1,8-cineole content by 2.18 % together with leaf oil concentration 27.36 %.

5.2 Norway spruce

- Both additive and non-additive genetic variances were important sources of total genetic variances. Additive genetic variation accounted for the majority of the total genetic variation for DBH growth and wood traits whereas non-additive genetic variation appeared to be more important for height at early ages. The relative importance of genetic variances for growth varied with age.
- Clonal mean heritability estimates were always the largest in magnitude as compared with broad-sense and narrow-sense heritability for the studied traits. Wood quality traits (i.e. Resi, Pilo, AV, MOE and GA) had generally higher heritability than growth traits.
- Total genetic correlations among observed traits were generally comparable or negligibly different from additive genetic correlations. Wood density measured indirectly by Resi and Pilo, and MOE had moderate unfavourable genetic correlations with DBH but low with height. Genetic relationships between GA and all traits except AV and MOE were very weak.
- Predicted genetic gain of clonal deployment was the highest, followed by full-sib family deployment and open-pollinated deployment. When selecting the top 5 % of clones, clonal forestry indicated an improvement of 11 - 31 % for wood traits and 22 - 120 % for DBH over full-sib family forestry, and 16 - 140 % for wood traits and 58 - 280 % for DBH over open-pollinated deployment.
- The generation of 30–40 clones per full-sib family will assure the maximum realized genetic at future clonal propagation following a selection scenario of either selecting the best ten individuals from the population (no restrictions on coancestry) or selecting the single best individual from the best ten families.

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Popular science summary

Timber and non-timber forest products (i.e. essential oil, honey, bark, secondary compounds) are well known as natural materials used by societies for multiple purposes since long time ago. Effective and sustainable use of natural materials based on forest products is still a challenge for mankind. Therefore, knowledge of hereditary variation of characters in forest trees are necessary for tree improvement and conservation. Tree breeding programs aim to improve the overall value of forest products for the human needs. It is then needed to apply principles of forest genetics, but also reproductive biology, silviculture and economics to the tree population.

Genetic improvement for wood and essential oil production has been carried out on *Melaleuca* for three decades in South-East Asia while breeding program aimed to improve growth and wood properties of Norway spruce was launched during the 1950s. However, knowledge of about how wood quality as well as essential oil traits correlate genetically with each other and with growth is limited. Reliable estimates directing whether using clonal forestry relative to family forestry are also needed to be implemented for using Norway spruce most efficiently.

In this thesis, the genetic parameters have been estimated and the principles of tree breeding have been applied to quantify the genetic variation and to design the optimal way to improve both wood and essential oil quantity and quality. Deployment of tree breeding material is optimised to meet the societal needs of biomaterial for timber production, construction and pulp and paper making as well as essential oil products.

Populärvetenskaplig sammanfattning

Sågvirke, massavirke och övriga skogsprodukter (oljor, extraktivämnen, bark, och andra biprodukter) är välkända naturprodukter som sedan lång tid tillbaka används för många ändamål. Att utnyttja naturprodukter effektivt och uthålligt är fortfarande en utmaning för mänskligheten. För skogsträdsförädling är därför vetenskap om den genetiska variationen hos olika egenskaper i skogsträd nödvändiga för genetisk förädling och bevarande av den genetiska resursen. Förädlingsprogram för skogsträd syftar till att förbättra det totala värdet av skogsprodukten för mänsklighetens behov. Det är då nödvändigt att beakta genetiska aspekter, men även reproduktionsbiologi, skogsskötselåtgärder och ekonomi.

Genetisk förädling för virkesegenskaper och oljeproduktion har bedrivits för *Melaleuca* i tre decennier i sydöstra Asien medan förädlingsprogram syftande till att förbättra tillväxt och vedegenskaper i gran startade under 1950-talet. Kännedom om hur vedkvalité och viktiga oljeprodukter korrelerar genetiskt med varandra och med tillväxt är begränsad. Tillförlitliga data som visar om man bör använda kloner eller sexuellt baserade metoder är också nödvändiga för att kunna använda gran mest effektivt.

I denna avhandling har genetiska parametrar beräknats och principer för skogsträdsförädling har applicerats för att bestämma storleken hos den genetiska variationen och för att designa det bästa sättet att förbättra vedegenskaper och utbyte av oljeprodukter. Dispositionen av förädlingsmaterialet ska optimeras för att bemöta allmänhetens behov av material för virkesproduktion, produktion av pappersmassa och papper liksom viktiga oljeprodukter.

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