

# EFFECT OF GENETIC GAIN IN DIAMETER AND WOOD DENSITY ON ADVANCED GENERATION BREEDING STRATEGY OF *ACACIA MANGIUM* IN INDONESIA

Sunarti S<sup>1</sup>, \*, Nirsatmanto A<sup>1</sup>, Brawner J<sup>2</sup>, Setyaji T<sup>1</sup>, Kartikaningtyas D<sup>1</sup>, Handayani BR<sup>1</sup>, Surip<sup>1</sup> & Hidayati F<sup>3</sup>

<sup>1</sup>Center for Forest Biotechnology and Tree Improvement, Yogyakarta, 55582, Indonesia

<sup>2</sup>University of Florida, Department of Plant Pathology, University of Florida, Gainesville, Florida, 32611, USA

<sup>3</sup>Gadjah Mada University, Faculty of Forestry, Gadjah Mada University, Yogyakarta, 55281, Indonesia

\*nartinirz@biotifor.or.id

Submitted February 2021; accepted May 2021

Breeding of *Acacia mangium* in Indonesia was initially focused on selection for improving growth and stem form. Changes in wood density which resulted from selection for improved growth was impacted by adverse correlation between the both traits. This study aimed to quantify genetic gain in the diameter and wood density from two *A. mangium* breeding generations and to use this information in developing breeding strategy to improve both traits simultaneously. Materials were obtained from 4.5-year-old trees in a progeny trial consisting of families from first (F-1) and second (F-2) generations along with infused families (F-0) as control. Genetic gain was calculated as the percent increase in diameter and wood density from F-1 and F-2 over the control. Diameter and wood density from F-1 and F-2 were higher than F-0. Genetic gains for diameter increased from 3.7% in F-1 to 7.0% in F-2. Conversely, gain for wood density decreased from 1.9% in F-1 to 0.3% in F-2. Correlations between diameter and wood density varied from weak to moderate along the stem sections. The results imply a combined approach incorporating selection for diameter and wood density in mixed-breeding generations will provide simultaneous improvement in both traits.

Keywords: Correlation, growth, progeny trial, selection, wood properties

## INTRODUCTION

*Acacia mangium* is a tropical *Acacia* species that is widely planted in Indonesia and the wet tropics. *Acacia mangium* is valued as a plantation species due to its fast growth and utility as a raw material for both sawn timber and the pulp and paper industry (Tsai 1988, Wong et al. 1988). Significant efforts have been made to improve breeding populations and silvicultural practices to increase productivity and resource utilisation (Harwood 2011, Hardiyanto & Nambiar 2014, Harwood et al. 2015, Nirsatmanto & Sunarti 2019). Growth and wood quality are targets for improvement as they determine the quality and quantity of raw materials produced for industrial use.

Wood density is one of the important wood characteristics which is commonly regarded as a key trait in determining wood quality as it strongly correlates with other wood properties and end products (Zobel & Buijtenen 1989, Bon et al. 2020). Selection is the main activity

in a breeding programme for improving targeted traits, such as wood density. However, adverse genetic correlation (i.e. negative correlation) between growth and wood density has led to difficulties in improving both traits. For example, selection for growth in *Eucalyptus camaldulensis* (Kien et al. 2010) and *Pinus radiata* (Kennedy et al. 2014) have caused reduction in wood density.

Early tree breeding programme of *A. mangium* in Indonesia was focused on selection for growth and form traits (Nirsatmanto & Kurinobu 2002). Under this programme, changes in wood density were achieved indirectly since selection for improved growth and form was the primary focus. The negative correlation provided a challenge to improving wood density in *A. mangium* breeding so that selection for wood density and growth may be achieved simultaneously. Although the current breeding of *A. mangium* in Indonesia

is entering its successive third-generation cycle (Nirsatmanto 2016), reports on genetic improvement in wood density are quite rare. Quantifying changes in wood density following past selection for growth and form traits is crucial to understand how *A. mangium* breeding programme in Indonesia should move forward.

The objectives of this study were to (1) quantify genetic gain in diameter and wood density from two successive breeding generations of *A. mangium*, and (2) use this information to develop breeding strategy to improve both traits simultaneously. The results of study will be a useful point of reference in evaluating past breeding programmes of *A. mangium* with respect to improving wood quality and productivity, using non-destructive assessments of wood density.

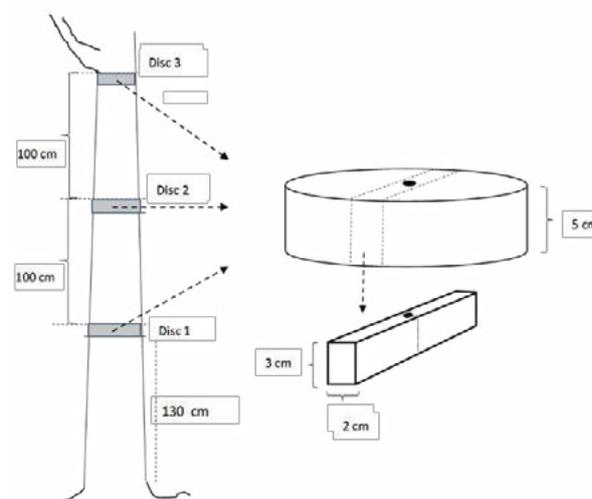
## MATERIALS AND METHODS

### Stand and sample trees

The assessment was conducted in a third-generation progeny trial of *A. mangium* which was established in Central Java, Indonesia (7° 32' S, 110° 41' E) at an elevation of 141 m above sea level. The soil type is Vertisol and mean annual rainfall, maximum and minimum temperatures at the site are 1850 mm, 33.23 and 21.21°C respectively. The stand consisted of 65 open-pollinated families that were derived from three sources: (1) 27 plus tree selected from the second-generation progeny trials, (2) 17 plus trees from first-generation progeny trials, and (3) 21 plus trees from the natural populations as infused families. These three plus-tree populations are hereafter referred to as F-2, F-1 and F-0 respectively. The families were planted in a progeny trial that was established in a randomised complete block design with six replications containing a four tree-row plots of each family at a spacing of 4 m × 2 m. Two successive thinnings were carried out to remove the poorest two trees in each plot at age 2 years, and the poorer tree of the remaining two trees in each plot at age 4.5 years to convert the stand to a seedling seed orchard.

Of the 552 remaining trees after the first thinning, 270 trees were removed in the second thinning and 186 trees were sampled for wood

density. Wood samples were taken from trees with a diameter at breast height (DBH) within one standard deviation of the mean that had at least a 5-m bole length. Diseased trees were not sampled. Before felling, an indirect assessment of density was taken using the pilodyn wood tester on the northern, southern, western and eastern sides of the stem at breast height. The sampled trees were then felled and three knot-free discs with a width of 5 cm were taken at 1 m intervals from breast height up, which are hereafter referred to as Section-1, Section-2 and Section-3 (Figure 1). The diameter was measured for each disc using diameter tape and the discs were immediately stored in sealed plastic bags for transfer to the laboratory for measurement of fresh weight.



**Figure 1** Preparation of wood samples from three sections along the stem

### Wood samples and wood density assessments

Bark was removed from sections and cut into samples measuring 3 cm thick and 2 cm wide and oriented along the north–south axis so that each sample was 3 cm × 2 cm × diameter (Figure 1). The green weight of each sample was measured using electronic balance, and the volume of green wood was determined using the water displacement method. Samples were then oven dried at 103 ± 2 °C for three days until constant weight was achieved. Wood density was determined as the oven dry matter weight (kg) per unit volume of green wood (m<sup>3</sup>).

### Statistical analysis

SAS software package was used for analyses of variance (ANOVA) to determine the significant of differences in wood density and diameter using individual sample tree data ( $y_{ijkl}$ ) with completely randomised design. The statistical model included the following factors: population, generation and family within generation. The linear model used for the ANOVA is provided in equation 1.

$$y_{ijkl} = \mu + P_i + G_j + F/G_{jk} + e_{ijkl} \quad (1)$$

where,  $\mu$  is the overall mean,  $P_i$  is the  $i$ th population effect,  $G_j$  the  $j$ th generation effect,  $F/G_{jk}$  is the  $k$ th family effect in  $j$ th generation, and  $e_{ijkl}$  is the experimental error associated with  $y_{ijkl}$  observation. In this analysis, the population factor differentiated the improved population (i.e. combination of F-1 and F-2) from the unimproved population (F-0). The generation factor represented the F-0, F-1 and F-2 populations comprising 21, 17 and 27 families respectively.

Genetic gain was calculated as the difference between each of the improved population (F-1 and F-2), and the unimproved population (F-0). Least-square means for each population were estimated from the linear model (equation 1). The percentage of relative gain was calculated

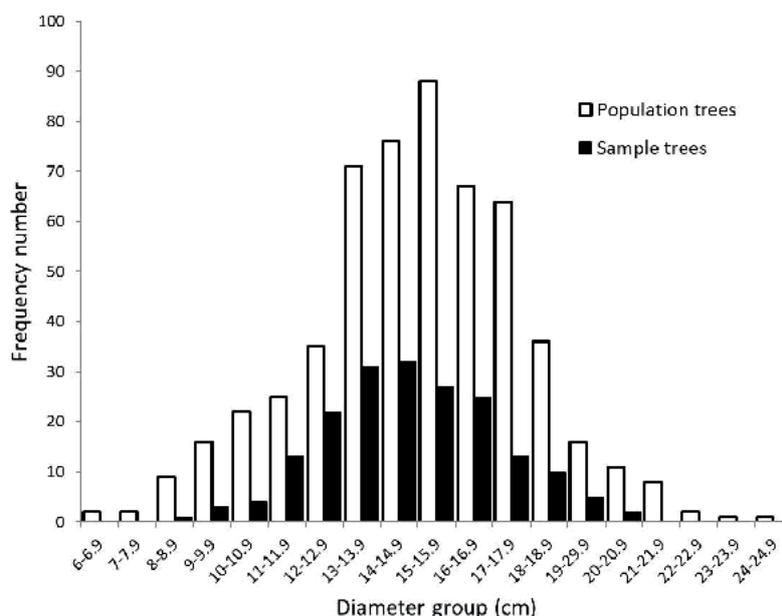
relative to the mean value of each measured trait (diameter and density) of the control (F-0). The four pilodyn observations from each tree were averaged and treated as a single observation. Pearson’s correlation coefficients were used to determine the significance of relationships between diameter, wood density and pilodyn assessments.

## RESULTS AND DISCUSSION

### Descriptive statistics

Means values of DBH ( $\pm$  standard deviations) of the trees before second thinning at 4.5 years of age were  $14.5 \pm 3.1$  cm,  $14.9 \pm 2.7$  cm,  $15.4 \pm 2.6$  cm for F-0, F-1 and F-2 respectively (results not shown). Diameter distribution of the 186 sampled trees within the 552 standing trees prior to the second thinning showed that more than 80% of the sample trees were within one standard deviation of the mean DBH of all trees in the stand (Figure 2). This indicated that the trees from which samples were collected were a representative sample that was suitable to examine the levels of genetic improvement achieved in the *A. mangium* breeding programme.

The significance of differences varied among the treatments, and only three of nine parameters were significantly different



**Figure 2** Distribution of diameter at breast height of 186 selected sample trees within the 552 trees from 65 families included in the trial

( $p < 0.05$ ); significant differences between populations for diameters of Section-1 and Section-2, and between generations for the Section-2 (Table 1). Differences between families were insignificant across all three sections, probably due to experimental error given the number of sample trees (186 trees) for the ANOVA was small. In other studies, significant differences among families of *A. mangium* for DBH were found when 1265 trees ( $p < 0.01$ ) were sampled at 3 years of age (Nirsatmanto 2016) and 278 trees ( $p < 0.05$ ) at 6 years of age (Hidayati et al. 2019).

For wood density, the population ( $p < 0.01$ ) and generation ( $p < 0.05$ ) factors were different in Section-3 (Table 2). These were due to the low wood density of the F-0 (Table 3). No other parameters were different at a 5% significance level. Families were not significantly different for all sections and for the average across sections.

### Mean values and genetic gain

The differences and relative variation in diameter (cm) and wood density ( $\text{kg m}^{-3}$ ) for three sections are provided in Figure 3. Sample trees from F-2 had the largest diameter, followed by F-1 and then F-0.

Diameter decreased with higher sections at similar rates with a taper of approximately 13%. For wood density, trees from F-1 and F-2 had higher values than F-0. The wood density showed a nonlinear inflection across the three sections: Section-1 showed the highest value, followed by the lowest value in Section-2 and a subsequent increase in Section-3. Similar observations have been reported in other species, such as in *Eucalyptus nitens* (Raymond & Muneri 2001), *Quercus petraea* and *Toona sinensis* (Wassenberg et al. 2014). In contrast, Chowdhury et al. (2005) reported that density consistently decreased with increasing stem height for *A. mangium* in Bangladesh when older trees were sampled ( $> 10$  years).

Mean values and genetic gain for diameter and wood density are presented in Table 3. Although the differences among treatments were insignificant (Tables 1 and 2), diameter growth and wood density of trees from F-1 and F-2 were greater than F-0 across all sections. DBH values were  $15.5 \pm 2.8$  cm for F-1,  $16.0 \pm 2.2$  cm for F-2 and  $14.9 \pm 2.7$  cm for F-0. As expected, the gain in diameter in F-2 was greater (7.0%) than that in F-1 (3.7%). Differences decreased in samples collected from further up the stem. For F-1, improvements were slightly lower than the 1-year-old second-generation seedling

**Table 1** Degrees of freedom (df) and mean square values for factors included in the analysis of diameter from three sections of 4.5-year-old *Acacia mangium*

Source of variance	df	Mean square		
		Section-1	Section-2	Section-3
Population	1	29.805*	18.344*	10.476 <sup>ns</sup>
Generation	2	18.576 <sup>ns</sup>	13.066*	7.179 <sup>ns</sup>
Family/generation	62	6.546 <sup>ns</sup>	3.865 <sup>ns</sup>	4.392 <sup>ns</sup>

\* = significant at 5% level, <sup>ns</sup> = not significant

**Table 2** Degrees of freedom (df) and mean square values for factors included in the analysis of wood density from three sections of 4.5-year-old *Acacia mangium*

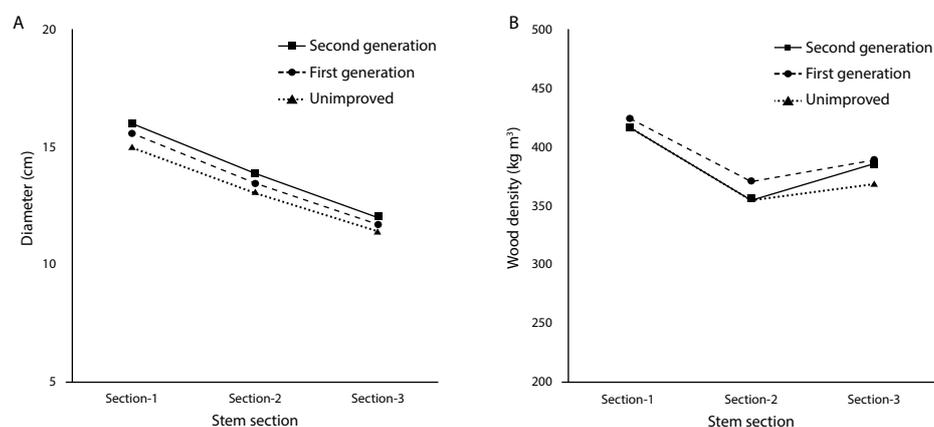
Source of variance	df	Mean square			
		Section-1	Section-2	Section-3	Average
Population	1	590.393 <sup>ns</sup>	2389.894 <sup>ns</sup>	14821.212 <sup>**</sup>	4304.463 <sup>ns</sup>
Generation	2	1083.052 <sup>ns</sup>	4290.561 <sup>ns</sup>	7822.796*	3357.880 <sup>ns</sup>
Family/generation	62	2030.577 <sup>ns</sup>	2051.374 <sup>ns</sup>	1978.692 <sup>ns</sup>	1283.730 <sup>ns</sup>

\*\* = significant at 1% level, \* = significant at 5% level, <sup>ns</sup> = not significant

**Table 3** Value of minimum, maximum, coefficient of variance, mean ( $\pm$  SD), and genetic gain (%) for diameter and wood density in three sections at 4.5-year-old for 186 sample trees from two generations and the unimproved *Acacia mangium*

Parameter	Diameter (cm)			Wood density (kg m <sup>-3</sup> )			
	Section-1	Section-2	Section-3	Section-1	Section-2	Section-3	Average
Unimproved (N = 59)							
Minimum	7.1	6.7	5.5	224	128	239	232
Maximum	22.2	19.0	17.5	498	499	472	484
CV (%)	18.5	16.8	20.2	12.6	14.0	11.6	9.6
Mean	14.9 $\pm$ 2.7	13.0 $\pm$ 2.2	11.3 $\pm$ 2.3	417 $\pm$ 53.1	354 $\pm$ 50.1	368 $\pm$ 43.1	380 $\pm$ 36.6
First-generation (N = 48)							
Minimum	10.03	9.5	8.0	352	268	265	295
Maximum	22.2	18.5	16.9	514	453	508	482
CV (%)	18.0	15.2	18.0	9.6	10.7	12.8	9.1
Mean	15.5 $\pm$ 2.8	13.4 $\pm$ 2.0	11.6 $\pm$ 2.1	425 $\pm$ 41.2	371 $\pm$ 39.9	391 $\pm$ 50.5	396 $\pm$ 36.5
Gain (%)	3.7	2.7	2.5	1.9	4.7	6.1	4.2
Second-generation (N = 79)							
Minimum	12.3	10.8	8.0	304	225	242	263
Maximum	23.0	18.0	16.0	566	499	466	480
CV (%)	13.9	12.7	15.5	10.0	11.9	11.3	8.5
Mean	16.0 2.2	13.9 1.7	11.9 1.8	419 42.1	357 42.8	386 43.9	387 33.0
Gain (%)	7.0	6.7	5.7	0.3	0.6	4.7	1.8
Grand mean	15.5 $\pm$ 2.6	13.5 $\pm$ 2.0	11.7 $\pm$ 2.2	420 $\pm$ 45.4	360 $\pm$ 44.7	382 $\pm$ 46.1	387 $\pm$ 35.3

CV = coefficient of variance, N = number of sample trees; genetic gain was calculated as percentage increase of improved trees from the two generation breeding over unimproved



**Figure 3** Trend of diameter (A) and wood density (B) across the three sections demonstrated in Figure 1

seed orchard of *A. mangium* established in Kalimantan (5%) but similar to the 4-year-old (Nirsatmanto et al. 2013).

Mean values of wood density at breast height were 425  $\pm$  41.2, 419  $\pm$  42.1 and 417  $\pm$  53.1 kg m<sup>-3</sup> for F-1, F-2 and F-0 respectively (Table

3). The densities across the three sections were 396  $\pm$  36.5, 387  $\pm$  33.0 and 380  $\pm$  36.6 kg m<sup>-3</sup> for F-1, F-2 and F-0 respectively. These average wood densities were lower than those reported for *A. mangium* grown at several sites in Indonesia and Bangladesh (500–600 kg m<sup>-3</sup>,

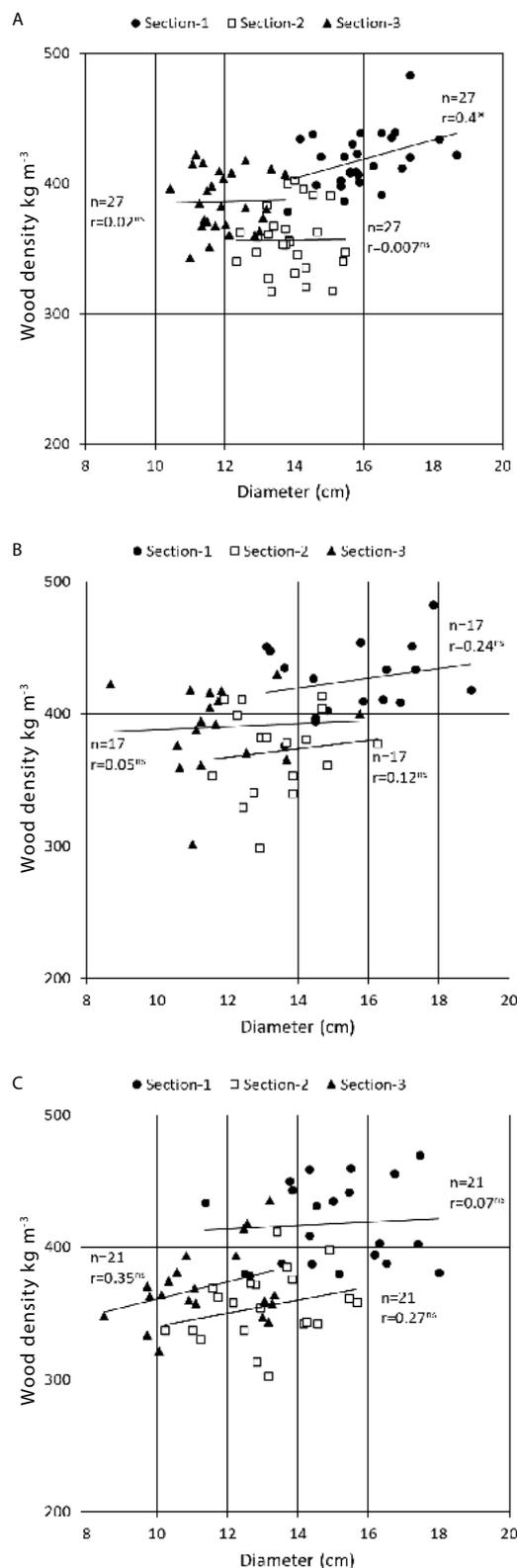
Chowdhury et al. 2005, Nugroho et al. 2012). The higher values in the latter were likely caused by the age of trees in the study, i.e. between 10 and 20 years.

Genetic gain in wood density in the upper sections were 6.1% for F-1 and 4.7% for F-2, while the gain across the three sections was 4.2 and 1.8% for F-1 and F-2 respectively (Table 3). In contrast to the increased gain for DBH between the two successive generations, gains for wood density at breast height (Section-1) decreased from F-1 (1.9%) to F-2 (0.3%). Section F-1 exhibited a linear increase in gains from Section-1 to Section-3. While for the F-2, the gains were small between Section-1 and Section-2, but increased in Section-3. The greatest wood density variation between the populations and generations was found higher up the stem, as evidenced by the significant differences in Section-3 (Table 2).

The changes in genetic gains for wood density from F-1 to F-2 showed that reduction in wood density resulted from selection for growth improvement. A 90% relative increase for DBH from F-1 to F-2 was associated with reduction in wood density of 84 and 57% for breast height section and average across sections respectively (Table 3). A similar decrease was observed by Yulianto (2005) where a 41% gain estimate for volume in *A. mangium* breeding was associated with a decrease in wood density of 2%. Studies on other species presented similar results, where selection for diameter resulted in reduction in wood density of 1.2 to 3.1% in *E. camaldulensis* (Kien et al. 2010), 2.9 to 3.9% in Scots pine (Fries 2012) and 1.2% in black spruce (Zhang & Morgenstern 1995).

**Correlations**

The correlation between diameter and wood density was positive and varied from weak ( $r = 0.007$ ) to moderate ( $r = 0.40$ ) (Figure 4). The correlation was weaker in upper sections in the F-1 and F-2 generations and was stronger in F-0. Correlation increased with each generation in Section-1, but decreased in Sections-2 and 3. Changes in the trend

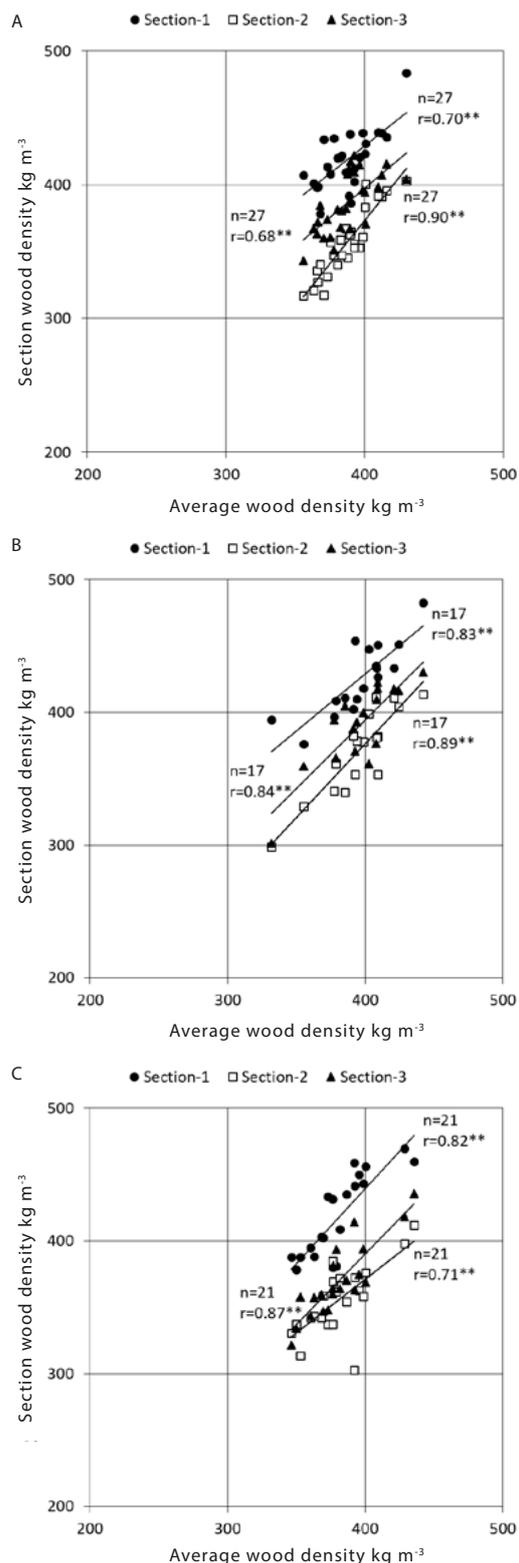


**Figure 4** Trends in correlations between diameter and wood density in three sections; second generation (A), first generation (B), unimproved (C)

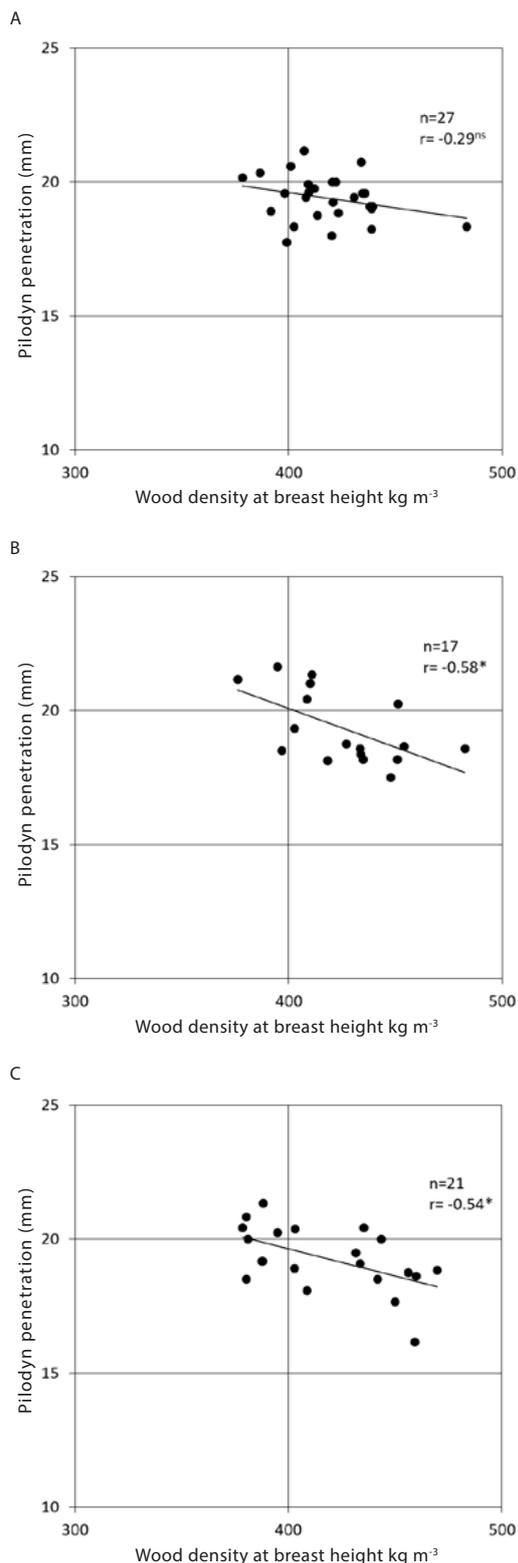
of correlation between generations and sections suggested that imposing selection on growth and form traits in past breeding for F-1 and F-2 caused variation in wood density between trees and within trees. A moderate positive and significant correlation ( $p < 0.05$ ) was found between DBH and wood density in Section-1 of F-2, which proved that selection simultaneously increased DBH and wood density in *A. mangium*.

Average wood density across sections and in the respective sections was significant and highly correlated, but there was a slightly different trend between generations (Figure 5). The correlation in F-2 was considerably higher for Section-2 ( $r = 0.90$ ) than for the other two sections. With respect to growth improvement, the high correlation in Section-2 of F-2 seemed to be independent of improvements in DBH because of the weak correlation between diameter and wood density in this section ( $r = 0.007$ ) (Figure 4). This indicated that although the mean value of density across generation decreased from Section-1 to Section-2 by 59 and 38  $\text{kg m}^{-3}$  to Section-3, assessment of wood density in the upper parts of stem (above breast height) seemed to be necessary in determining more accurately the whole wood density of the tree, particularly for the improved population. Using only wood samples collected at breast height could lead to overestimation of average wood density by more than 7%. Studies in spruce, birch and pines also revealed that average wood density based only on the measured density of sample disc at breast height resulted overestimates of the overall wood density (Repola 2006).

The correlation between wood density and pilodyn penetration varied among the populations, namely  $r = -0.29, -0.59$  and  $-0.54$  in F-2, F-1 and F-0 respectively (Figure 6). This may reflect past selection for growth altering wood structure which has led to pilodyn penetration being less predictive of wood density in *A. mangium*. Differences in genetic backgrounds of the populations seemed to influence the change of correlation strength between pilodyn and density.



**Figure 5** Trends in correlations between average wood density across three sections; second generation (A), first generation (B), unimproved (C)



**Figure 6** Trends in correlations between wood density at breast height and pilodyn penetration; second generation (A), first generation (B), unimproved (C)

## Further breeding strategy

### Selection criteria

The improvement for DBH was verified in this study with smaller increase in wood density between F-1 and F-2. The reduction in gain estimates appeared to have continued in successive generations when the selection criteria for DBH remained unchanged. Incorporating wood density as a selection criterion is necessary to ensure reduction in wood quality associated with selection for growth is managed for future *A. mangium* breeding strategy.

In this study, we simulated the incorporation of wood density as an additional selection criterion in our advanced generation breeding programme for *A. mangium* with the intention of increasing genetic diversity by selection from all generations of the breeding population. The concept of ‘recycled’ genetic resources (Nirsatmanto 2016) was evaluated by incorporating families that had been removed in previous generations into further successive generation breeding. This concept could be used to explore the impacts of increasing the diversity of genetic material and capturing some improvements in wood properties that might have been neglected in early generations that were selected only for growth. The breeding population would proceed using overlapping generations (White et al. 2007) that included selections derived from F-2, F-1 and F-0 generations. Both traits will be used to select advanced generation breeding populations. Relatedness between the families was carefully considered to avoid the negative impact of inbreeding in the breeding population.

### Scenarios of family selection

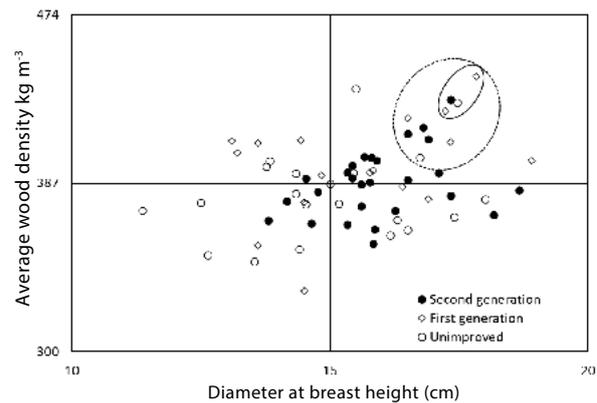
In the third-generation progeny trial of *A. mangium*, the genetic gain estimates from family selection for growth traits has been reported at around 3% for height, 5% for DBH and 1% for stem straightness (Nirsatmanto 2016). However, changes in the wood density have not been reported. As sample trees were collected from

the thinned trees, backward selection using family information provided more accurate selection method in this study.

Scatter plots of the 65 families tested in the progeny trial for both DBH and average wood density are presented in Figure 7. Two selection scenarios were considered in this study. First, an independent culling level in which the truncation for selection was set at above 15 cm for DBH and 387 kg m<sup>-3</sup> for wood density (close to the mean value of each trait). Twenty four of 65 families were selected and provided a gain estimate of 5.7% for DBH and 4.7% for wood density (Table 4). Increasing the truncation level to select the top 10 families increased the differential selection to 9.7% for DBH and 8.1% for wood density, while selection of the top 4 families increased gain estimates to 12.3% for DBH and 11.3% for wood density. Families were selected from each generation, with the 24 selected families representing 50, 29 and 20% families of the F-2, F-1 and F-0 respectively.

The second scenario investigated used tandem selection amongst the 27 families that were derived from F-2 generation. In this scenario, selection was based on the average wood density with the same truncation value as in the first scenario (387 kg m<sup>-3</sup>). The selection differential for wood density was 3.4% which was associated with a small increase of 0.7% in DBH (Table 4). Gain estimates were lower than those obtained from the first scenario. In addition, truncation selection reduced the number of selected families to 14, fewer than the number selected in first scenario (24 families). Twelve out of the 14 selected families were the same as in the first scenario.

Recycling genetic resources (as the first scenario) could increase genetic variation in the third generation and improve wood density while maintaining improvement in growth. It is suggested that the independent culling level is more effective for family selection in such given mixed-generation breeding stand of *A. mangium*. For Norway spruce, despite the negative relationship between growth and density, using carefully selected genotypes and incorporating wood density in the selection



**Figure 7** Clustering of the 65 families based on average wood density across three sections and DBH; smooth lined circle identifies the top four selected families, dashed lined circle identifies the top 10 selected families

strategy enhanced stem volume and maintained wood density (Levkoev et al. 2017).

Incorporating a large variation in wood properties up the stem may be adopted for family selection in the given third generation breeding stand to obtain a representative whole wood density of the trees. For the improved populations (F-2 and F-1), wood density at Section-2 could be considered as an important value in assessing average wood density of the trees due to its considerably stronger and positive correlation (Figure 5).

Non-destructive sampling of trees for wood properties is often required for wood quality assessments in tree breeding programmes. Pilodyn could become an effective tool in assessing the density of all trees in a trial. It is particularly useful in the F-1 and F-0 populations of *A. mangium* due to a moderate correlation between the penetration and density in both populations (Figure 6).

## CONCLUSIONS

The impact of selecting for improved growth, which was used to identify F-1 and F-2 populations, was assessed in a third-generation progeny trial of *A. mangium*. Genetic gains for

diameter were positive and increased from F-1 to F-2 generation. The gain in wood density was also positive, but not as large in the F-2 population relative to the F-1 population. Given a selection criterion that focused on DBH alone, gain in wood density would continue to decrease in advanced generation breeding. Therefore, improving the selection methods used for *A. mangium* breeding was necessary in order to increase wood density while maintaining improvements in growth. This could be achieved by increasing the diversity of the populations and altering the selection strategy to incorporate wood density directly. Families that were eliminated in previous generations based on selection for growth alone may be recycled and integrated into the breeding population for further improvement of wood density. Wood density should be incorporated as one of the selection criteria and independent culling level strategy should be adopted during family selection. Selection based on non-destructive sampling of wood density using pilodyn may be used to improve wood properties, although the pilodyn method had more effect on F-1 and F-0 populations compared with F-2 population. Selection for both growth and wood density are recommended to advance *A. mangium* breeding populations that have been developed for Indonesia.

## REFERENCES

- BON PV, HARWOOD CE, CHI NQ, THINH HH & KIEN ND. 2020. Comparing wood density, heartwood proportion and bark thickness of diploid and triploid *Acacia* hybrid clones in Vietnam. *Journal of Tropical Forest Science* 32: 206–216. <https://doi.org/10.26525/jtfs32.2.206>
- CHOWDHURY Q, SHAMS I & ALAM M. 2005. Effects of age and height variation on physical properties of mangium (*Acacia mangium* Willd.) wood. *Australian Forestry* 68: 17–19. <https://doi.org/10.1080/00049158.2005.10676221>
- FRIES A. 2012. Genetic parameters, genetic gain and correlated responses in growth, fibre dimensions and wood density in a Scots pine breeding population. *Annals of Forest Science* 69: 783–794. <https://doi.org/10.1007/s13595-012-0202-7>
- HARDIYANTO EB & NAMBIAR EKS. 2014. Productivity of successive rotations of *Acacia mangium* plantations in Sumatra, Indonesia: impacts of harvest and interrotation site management. *New Forests* 45: 557–575. <https://doi.org/10.1007/s11056-014-9418-8>
- HARWOOD C. 2011. Strengthening the tropical *Acacia* plantation value chain: the role of research. *Journal of Tropical Forest Science* 23: 1–3.
- HARWOOD CE, HARDIYANTO EB & YONG WC. 2015. Genetic improvement of tropical acacias: achievements and challenges. *Southern Forests: A Journal of Forest Science* 77: 11–18. <https://doi.org/10.2989/20702620.2014.999302>
- HIDAYATI F, LUKMANDARU G, INDRIOKO S, SUNARTI S & NIRSATMANTO A. 2019. Variation in tree growth characteristics, pilodyn penetration, and stress-wave velocity in 65 families of *Acacia mangium* trees planted in Indonesia. *Journal of the Korean Wood Science and Technology* 47: 633–643. <https://doi.org/10.5658/WOOD.2019.47.5.633>
- KENNEDY SG, YANCHUK AD, STACKPOLE DJ & JEFFERSON PA. 2014. Incorporating non-key traits in selecting the *Pinus radiata* production population. *New Zealand Journal of Forestry Science* 44: 1–9. <https://doi.org/10.1186/s40490-014-0012-9>
- KIEN ND, JANSSON G, HARWOOD CE & ALMQVIST C. 2010. Clonal variation and genotype by environment interactions in growth and wood density in *Eucalyptus camaldulensis* at three contrasting sites in Vietnam. *Silvae Genetica* 59: 17–28. <https://doi.org/10.1515/sg-2010-0003>
- LEVKOEV E, KILPELAINEN A, LOUSTARINEN K ET AL. 2017. Differences in growth and wood density in clones and provenance hybrid clones of Norway spruce. *Canadian Journal of Forest Research* 47: 389–399. <http://dx.doi.org/10.1139/cjfr-2016-0285>
- NIRSATMANTO A. 2016. Recycled genetic resource as an optional strategy in advanced generation breeding for tropical species: a case study in optimizing genetic resource for *Acacia mangium* breeding program. Pp 762–772 in Siregar PDCA et al. (eds) *Proceedings of International Conference of Indonesia Forestry Researchers. III. Forestry Research to Support Sustainable Timber Production and Self-sufficiency in Food, Energy, and Water*. 21–22 October 2016, Bogor.
- NIRSATMANTO A & KURINOBU S. 2002. Trend of within-plot selection practiced in two seedling seed orchards of *Acacia mangium* in Indonesia. *Journal of Forest Research* 7: 49–52. <http://dx.doi.org/10.1007/BF02762598>
- NIRSATMANTO A, SETYAJI T & SURIP. 2013. Trend of realized genetic gain observed in second-generation seedling seed orchards of *Acacia mangium* in South Kalimantan, Indonesia. *Indonesian Journal of Forestry Research* 10: 57–64. <https://doi.org/10.20886/ijfr.2013.10.1.57-64>
- NIRSATMANTO A & SUNARTI S. 2019. Genetics and breeding of tropical acacias for forest products: *Acacia mangium*, *A. auriculiformis* and *A. crassirarpa*. Pp 3–28 in Al-Khayri et al. (eds) *Advances in Plant Breeding Strategies: Industrial and Food Crops*. Springer Nature, Cham. <https://doi.org/10.1007/978-3-030-23265-8>
- NUGROHO WD, MARSOEM SN, YASUE K ET AL. 2012. Radial variations in the anatomical characteristics and density of the wood of *Acacia mangium*

- of five different provenances in Indonesia. *Journal of Wood Science* 58: 185–194. <https://doi.org/10.1007/s10086-011-1236-4>
- RAYMOND CA & MUNERI A. 2001. Nondestructive sampling of *Eucalyptus globulus* and *E. nitens* for wood properties. I. Basic density. *Wood Science and Technology* 35: 27–39. <http://dx.doi.org/10.1007/s002260000078>
- REPOLA J. 2006. Models for vertical wood density of Scots pine, Norway spruce and birch stems, and their application to determine average wood density. *Silva Fennica* 40: 673–685. <https://doi.org/10.14214/sf.322>
- TSAI LM. 1988. Studies on *Acacia mangium* in Kemasul Forest, Malaysia. I. Biomass and productivity. *Journal of Tropical Ecology* 4: 293–302. <https://doi.org/10.1017/S0266467400002856>
- WASSENBERG M, CHIU HS, GUO W & SPIECKER H. 2014. Analysis of wood density profiles of tree stems: incorporating vertical variations to optimize wood sampling strategies for density and biomass estimations. *Trees* 29: 551–561. <https://doi.org/10.1007/s00468-014-1134-7>
- WHITE TL, ADAM WT & NEALE DB. 2007. *Forest Genetics*. CABI, Cambridge.
- WONG WC, HO KS & WONG CN. 1988. *Acacia mangium* from Sabah for plywood and decorative panel manufactures: initial trials. *Journal of Tropical Forest Science* 1: 42–50.
- YULIARTO M. 2005. Genetic gain and breeding strategy in progeny test of *Acacia mangium* at PT. Riau Andalan Pulp and Paper, Riau. Master thesis, Gadjah Mada University, Yogyakarta. (In Indonesian)
- ZHANG SY & MORGENSTERN EK. 1995. Genetic variation and inheritance of wood density in black spruce (*Picea mariana*) and its relationship with growth: implications for tree breeding. *Wood Science and Technology* 30: 63–75. <https://doi.org/10.1007/BF00195269>
- ZOBEL BJ & VAN BUIJTENEN JP. 1989. *Wood Variation: Its Causes and Control*. Springer, Heidelberg. [https://doi.org/10.1007/978-3-642-74069-5\\_1](https://doi.org/10.1007/978-3-642-74069-5_1)