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Early Assessment of First Year Height Data from Five Acacia mearnsii (black wattle) Sub-populations in South Africa using REML/BLUP

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Abstract

Recent research has shown, Acacia mearnsii (black wattle) to be a source of high quality pulp. This led to a change in the emphasis in the breeding programme at the Institute for Commercial Forestry Research, from improving bark yield and quality, to improving timber yield and quality while maintaining an acceptable bark quality. A Multiple Population Breeding Strategy was implemented to cater for these changes. Five sub-populations were established across different sites in KwaZulu-Natal and were determined by origin of seed. Each sub-population was established as a progeny trial with a seedling seed orchard adjacent to it. The management of the seed orchards will be determined according to the performance of the families within the progeny trials. This paper reports on the first year height measurements taken from the five sub-populations. The intention of this paper is not to base any selections from this data but rather to establish a set of analyses using REML/BLUP which will be used for future data analysis. This will also allow for future assessment of age-age correlations for the various traits being assessed and provide an appropriate decision-making tool, for selecting individuals for future generations.

Key words: Acacia mearnsii, black wattle, BLUP, height measurements, REML, sub-populations.

Introduction

Acacia mearnsii (black wattle) was reportedly first introduced to South Africa in 1864. About ten years later the first wattle plantations were established, primarily for firewood, shelterbelts and shade for livestock (SHERRY, 1971). Early tanning tests carried out in South Africa, in 1884, indicated that the bark from black wattle was rich in vegetable tannins that could be used in the leather tanning industry. This led to widespread planting of black wattle with the greatest success in KwaZulu-Natal (JARMAIN and LLOYD JONES, 1982). The black wattle industry in South Africa, peaked in the

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1960s when approximately 300000 ha were planted to black wattle. Today this figure stands at about 130000 ha (SAWGU, 2001), and this reduction in area can be attributed largely to changes in international markets for vegetable tanning extract (DOBSON and FEELY, 2002). Demand for black wattle timber and bark, however, is again on the increase. The area planted to black wattle will almost certainly not increase to previous figures as land available to plantation forestry in South Africa is limited, even if some eucalypt or pine plantations are converted to black wattle. Future demands will place more emphasis on increasing productivity from the available land area especially in the case of black wattle as it is also seen as an alien invader of indigenous vegetation. These demands have brought about the need to review the current breeding strategy and implement a new strategy.

In 1931, OSBORN described the variation in growth characteristics of black wattle trees grown from open pollinated seed. These early observations laid the foundation for a formalised breeding programme established at the Wattle Research Institute (WRI), now the Institute for Commercial Forestry Research (ICFR).

Unlike most forestry species, black wattle was generally cultivated for its bark with timber production being a secondary consideration (SHERRY, 1971). The aims of the wattle improvement project at the ICFR were therefore to improve the quality and quantity of black wattle bark yields, with one of the main breeding criteria being selecting disease-free trees. This programme would then supply the wattle industry with improved seed. Progeny testing was identified in the 1940s as a mechanism whereby trees selected on morphological and chemical characteristics would be further tested by the behaviour of their progeny. The intention was to vegetatively propagate trees whose progeny showed outstanding characteristics. The clones would then be intermixed in isolated plantations and cross-pollination between these selected clones should produce superior strains (WRI, 1949). In theory this was a sound basis for a breeding strategy, but unfortunately the difficulty in vegetative propagation restricted its success. The difficulty in propagating selected trees ultimately led the researchers to concentrate on a selection and one-parent progeny testing breeding system in order to identify superior material for inclusion in production seed orchards (PSOs) (DUNLOP, 2002).

The recent increase in the use of black wattle timber in local and international pulp mills has changed the emphasis in the breeding programme at the ICFR, from improving bark yield and quality, to improving timber yield and quality while maintaining an acceptable bark quality. A Multiple Population Breeding Strategy was developed to take into account these changes (DUNLOP et al., 2003). This breeding strategy also has the ability to extend the range of the species into colder areas, assess the gain that has already been made, exploit the potential of the improved genetic material already produced and exploit the potential of selections from new provenances. The strategy will allow for the modification of selection criteria and to ensure flexibility in the face of changes in future demands from the industry (DUNLOP et al., 2003).

The rest of this paper outlines the data collection, analysis using Restricted Maximum Likelihood (REML) and Best Linear Unbiased Prediction (BLUP) and interpretation of the results from individual tree height measurements taken 12 months after planting. Although these data were collected after only one year it is intended to measure and analyse these trials annually and ultimately use the results to calculate age-age correlations, changes in heritabilities over time and determine the earliest age at which selections can be confidently made. By using the combination of REML and BLUP analyses it is envisaged that the accuracy of identifying truly superior individuals will be greater than the simple ranking techniques used in the past. This in turn will allow for across site comparisons of families and individuals being tested.

Materials and Methods

Trial composition and design

Using the seed available at the ICFR, from historical and current selections as well as from controlled crosses, the breeding population was assembled in five sub-populations constituted as follows (DUNLOP et al., 2003):

1. Advanced generation crosses derived from controlled pollinations. This population is made up of 26 full-sib families with no known relatedness between any of the parents used in the crosses. These families have already undergone some testing in the breeding programme and were selected for good vigour and disease resistance

2. Open pollinated seed from backward selected parents in the breeding programme. These 34 families originated from a set of parents (not included in sub-population 1) that were not vegetatively propagated and were therefore excluded from any further breeding due to their inability to be vegetatively propagated, not due to poor performance

3. Cold/frost-hardy Australian and local seedlots. Previous provenance tests identified two Australian provenances, Lake George and Mittagong, as being more frost tolerant than the other provenances tested (HAGEDORN, 1993). Recent selections, made in the Drakensberg area

Table 1. – Details of the five sites chosen for the establishment of the five sub-populations (amended from DUNLOP et al., 2003).

Sub-population	Location	Longitude	Latitude	Mean annual rainfall (mm)	Mean annual temperature (°C)	Altitude (m)
1	Enon	30°14'E	29°48'S	1054	15,7	1360
2	Bloemendal	30°28'E	29°32'S	897	17,9	850
3	Liff	30°24'E	29°16'S	1134	16,1	1290
4	Bloemendal	30°28'E	29°32'S	897	17,9	850
5	Mistley	30°39'E	29°11'S	708	18,6	740

of KwaZulu-Natal, tested on a very frost prone and cold site, also identified seedlots that have the ability to withstand frost and cold temperatures. This sub-population constitutes a total of 30 families selected from Lake George, Mittagong and the Drakensberg seedlots

4. Unimproved high production Australian provenances. This sub-population consists of 33 families selected on the basis of results from provenance trials for high production and disease resistance and

5. Piet Retief landrace. Eighty-two half-sib families selected in the Piet Retief area for health and volume constitute this population.

The trials were established at five sites according to *Table 1*. In the interim a more intensive study of the individual sites will be conducted, which will include soil typing and the measurement of mean minimum and maximum temperatures throughout the year.

Each sub-population was planted as two adjacent randomised complete block experiments, one with five replications of five-tree line plots and the other with 25 replications of single-tree plots. The five-tree line plot experiment will serve as a progeny test and the main selection base for the founders for the next generation, and the single-tree plot experiment will serve as a progeny test in the early stages and as a seedling seed orchard when it has been thinned to the best individuals of the best families. By having two different trial designs at each site will also allow one to test the impact of each design for selection and variance estimation. Each sub-population progeny test includes nine commercial and genetic checks as entries. To keep the sub-populations unrelated for future crosses, the commercial and genetic checks are not included in the single-tree plot BSOs. The checks are detailed below:

1. A seedlot collected in South Africa in 1960 representing the base population, before any breeding activities (treatment coded as 86);

2. Three seedlots representing mass selected populations. Not all black wattle plantations in South Africa are established by planting seedlings. Some growers opt to allow natural regeneration to occur after clear felling. Seed was collected from three such situations where repeated natural regeneration and subsequent mass selection on the same site has been the management practice (treatments coded as 83–85);

3. Four different full-sib controlled crosses, to provide precise, across site, comparisons (treatments coded as 88–91); and

4. Currently available improved material (a bulk seedlot from a current production seedling orchard) (treatments coded as 87).

Data collection and analysis

The heights of the individual trees in all of the subpopulations were measured 12 months after planting. The data were analysed using the REML method for variance component estimation and the BLUP procedure for breeding value prediction and genetic selection. The Selegen-REML/BLUP software (RESENDE, 2002a) was used for all the analyses.

The individual sub-populations were analysed by using the progeny trial data and BSO data separately and then combined to establish interaction results. Such analyses provided the rankings of the families and individuals within and across families. It should be mentioned here that interpretation of heritability estimates, generated from the BSO and progeny trials, should be done with caution as the differences in variances could

Varian	ce components generated by REML	Genetic values of the individuals predicted by BLUP					
Va Vabf	Additive genetic variance Additive genetic variance		by blor				
Vplot	Environmental variance among plots						
Ve	Residual variance within plots	GV	Predicted (BLUP) additive genetic value of the tree summed with the general mean				
Vp	Individual phenotypic variance	Gain	Estimated genetic gain with selection with the trees above that specific line				
h ² a s(h ² a)	Individual narrow sense heritability Standard deviation of h ² a	MIP	Mean of the improved population				
c ² plot	Proportion of phenotypic variance due to plot effects	EPS	Effective populations size or unrelated number of individuals selected above that specific line				
h ² fm	Heritability of family means		r				
Acfm	Accuracy of family selection						
h ² aw	Within family heritability						
GM	General trial mean						
c ⁻ int	Proportion of phenotypic						
	interaction effects						
Rgloc	Genetic correlation across trials						

Table 2. – List of variance components generated by REML and genetic values of the individuals predicted by BLUP.

Table 3. – Mean family height (m) results (BLUP's) from the top ten families from the five progeny trials and five BSOs, ranked according to the progeny trial results. If not included in the top ten families the means for the commercial and genetic check families (shaded) are also presented.

Sub-population 1			Sub-population 2			Sub-population 3			Sub	-population	4	Sub-population 5		
Family	Progeny trial	BSO	Family	Progeny trial	BSO	Family	Progeny trial	BSO	Family	Progeny trial	BSO	Family	Progeny trial	BSO
220	3.69	3.41	90	4.10		427	1.85	2.01	123	5.05	5.12	48	3.98	3.19
90	3.65		316	4.08	#	85	1.80		133	5.01	5.24	69	3.94	3.20
226	3.62	3.09	83	4.07		419	1.79	2.01	129	4.98	4.86	85	3.93	
85	3.60		322	4.03	#	83	1.73		125	4.89	4.80	49	3.93	3.18
222	3.60	3.39	326	3.95	#	415	1.71	2.01	120	4.85	4.91	17	3.92	3.19
214	3.59	3.37	331	3.92	3.51	418	1.70	2.01	102	4.84	4.94	1	3.91	3.22
206	3.56	*	321	3.88	3.50	86	1.69		124	4.81	4.95	80	3.90	3.14
256	3.56	3.44	329	3.81	3.51	422	1.68	2.01	110	4.68	4.66	47	3.90	3.19
209	3.54	3.21	332	3.80	3.51	84	1.67		118	4.64	4.84	32	3.90	3.17
219	3.53	3.32	84	3.78		91	1.65		90	4.64		58	3.90	3.22
89	3.51		91	3.66		90	1.62		91	4.62		91	3.87	
84	3.49		88	3.64		89	1.58		89	4.58		84	3.86	
88	3.47		89	3.59		88	1.55		88	4.57		90	3.85	
83	3.45		85	3.57		87	1.54		84	4.49		87	3.79	
91	3.42		87	3.54					87	4.47		83	3.78	
86	3.42		86	3.28					83	4.46		89	3.76	
87	3.33								85	4.43		88	3.76	
									86	3.99		86	3.76	

Table 4. - Estimates of the variance components generated by REML for height in the five sub-populations.

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Estimates	Sub-population 1			Sub-population 2			Sub-population 3			Sub-population 4			Sub-population 5		
	Progeny	BSO	Interaction												
Va	0.04589	0.08472	0.02928	0.32444	0.00242		0.06651	0.00032		0.44635	0.38768	0.40742	0.06156	0.05489	0.06058
Vabf	0.02295	0.04236	0.01464	0.08113	0.00061		0.01663	0.00008		0.11159	0.09692	0.10186	0.01539	0.01372	0.01514
Vplot	0.12601	-	0.08970	0.22785	-		0.05172	-		0.01253	-	0.00892	0.08480	-	0.07922
Ve	0.51145	0.65771	0.60482	0.18188	0.69578		0.19044	0.32546		0.16395	0.29909	0.21734	0.29565	0.33147	0.31256
h ² a	0.06949	0.12102	0.04046	0.44191	0.00347		0.21547	0.00099		0.71664	0.56450	0.62845	0.13928	0.14209	0.13367
s(h ² a)	0.02596	0.04016	0.01520	0.12364	0.01454		0.08409	0.00649		0.14779	0.14112	0.09905	0.04606	0.04924	0.03230
c ² plot	0.19081	-	0.12393	0.31034	-		0.16755	-		0.02012	-	0.01375	0.19186	-	0.17479
c2int	-	-	0.02023									0.02254			0.00190
h ² fm	0.33445	0.61689	0.40330	0.56448	0.02123		0.45451	0.00620		0.85638	0.82145	0.91899	0.33441	0.47937	0.82955
Acfm	0.57832	0.78542	0.63506	0.75132	0.14572		0.67417	0.07874		0.92541	0.90634	0.95864	0.57828	0.69236	0.91080
h ² aw	0.04487	0.06441	0.02421	0.57225	0.00260		0.20756	0.00075		0.67125	0.49294	0.58436	0.13508	0.11050	0.12693
Rgloc	-	-	0.50000									0.87450			0.94607
Trait average	3.49385	3.24474	3.29172	3.66615	3.50977		1.61175	2.00689		4.43791	4.64284	4.60443	3.80549	3.11335	3.22939

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be a result of trial design differences rather than true genetic differences between families.

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The following mixed linear modes were applied according to RESENDE (2002b) (Appendix).

All the sub-populations, except sub-population 1 are constituted of half-sib progenies. Sub-population 1 consists of full-sib progenies and so in the estimation/prediction process the fraction (1/4) of the dominance variance was assumed as zero. The interaction analyses for sub-populations 2 and 3 were not carried out because there was no genetic variation (heritability estimates were equal to zero) for BSO tests concerning these two sub-populations. Without variation in one trial (i.e the BSO) there is no reason to study the interaction between the BSO and progeny trials.

Results

1

The analysis of the data using REML and BLUP gave rise to a number of parameters that are described in *Table 2*, and the abbreviations listed will be used in the rest of this paper. Due to space restraints not all the parameters will be presented or discussed in this paper.

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The mean family height measurements from the top 10 families from the progeny trial and BSO from each sub-population are given in *Table 3. Table 4* presents the variance components generated by REML for the five sub-populations as well as any interaction components that may arise when the progeny trial and BSO parts of the sub-populations are analysed together. The mean height measurements of the nine genetic controls and check families across the five sites are shown in *Figure 1* and in *Table 6* as relative performance of the trial mean. The BLUP technique was then used to identify the best individuals within each sub-population are presented in *Table 5*.

Discussions and Conclusions

Sub-population 1

There is low genetic variability for future selection in this population as evidenced by heritability coefficients $(h^2a = 0.040 \text{ to } 0.121)$ obtained for the three scenarios

Sub-population	Ranking	Block	Family	Tree	GV	Gain	MIP	EPS
1	1	25	220	1	3.51	0.21	3.51	1.00
	2	5	220	4	3.50	0.21	3.50	1.33
	3	2	220	5	3.50	0.21	3.50	1.50
	4	15	220	1	3.49	0.21	3.50	1.60
	5	1	220	1	3.49	0.21	3.50	1.67
	6	5	220	1	3.49	0.20	3.50	1.71
	7	2	220	1	3.49	0.20	3.50	1.75
	8	1	220	5	3.49	0.20	3.49	1.78
	9	8	220	1	3.49	0.20	3.49	1.80
	10	30	220	1	3.49	0.20	3.49	1.82
2	1	1	310	4	4.80	1.13	4.80	1.00
	2	1	310	2	4.74	1.10	4.77	1.60
	3	2	331	2	4.70	1.08	4.75	2.48
	4	4	322	2	4.68	1.06	4.73	3.49
	5	1	83	1	4.59	1.03	4.70	4.49
	6	2	83	5	4.59	1.01	4.68	5.08
	7	4	90	5	4.56	1.00	4.66	6.07
	8	1	316	1	4.55	0.98	4.65	7.06
	9	5	83	1	4.52	0.97	4.64	7.25
	10	5	314	5	4.52	0.96	4.62	8.23
3	1	4	427	1	2.07	0.46	2.07	1.00
	2	4	419	4	2.06	0.45	2.06	2.00
	3	1	85	1	2.05	0.45	2.06	3.00
	4	4	427	4	2.01	0.43	2.05	3.49
	5	5	427	5	2.00	0.43	2.04	3.66
	6	2	85	3	1.99	0.42	2.03	4.36
	7	2	422	4	1.99	0.41	2.02	5.31
	8	5	427	3	1.98	0.41	2.02	5.33
	9	2	427	3	1.97	0.40	2.01	5.26
	10	5	419	5	1.96	0.40	2.01	5.97
4	1	18	123	1	6.05	1.45	6.05	1.00
	2	34	133	4	5.95	1.40	6.00	2.00
	3	32	120	1	5.84	1.34	5.95	3.00
	4	32	133	2	5.84	1.32	5.92	3.49
	5	27	123	1	5.83	1.30	5.90	4.11
	6	2	133	1	5.83	1.29	5.89	4.36
	7	34	123	2	5.83	1.28	5.88	4.74
	8	24	129	1	5.82	1.27	5.88	5.65
	9	14	133	1	5.82	1.27	5.87	5.76
	10	6	133	1	5.81	1.26	5.86	5.74
5	1	31	17	2	3.77	0.54	3.77	1.00
	2	17	l	1	3.61	0.46	3.69	2.00
	3	35	69	5	3.55	0.41	3.64	3.00
	4	14	48	1	3.53	0.39	3.62	4.00
	5	7	2	1	3.53	0.37	3.60	5.00
	6	1	46	1	3.53	0.36	3.59	6.00
	7	12	48	1	3.53	0.35	3.58	6.50
	8	24	44	1	3.53	0.34	3.57	7.50
	9	22	62	1	3.52	0.34	3.57	8.50
	10	25	69	1	3.51	0.33	3.56	9.05

Table 5. – BLUP estimates for the genetic value (GV) of the top 10 individuals from each sub-population for first year height.

namely the progeny trial, BSO and interaction (*Table 4*). These coefficients are lower than those obtained for subpopulations 4 and 5 but higher than those values obtained from the BSOs in sub-populations 2 and 3. This overall low heritability in this sub-population can be explained partially by the fact that the population is at an advanced generation of selection and/ or due to the fact the trials are only one year old. It can be noticed that there is some genetic variability for percentage survival. The survival rate was 87.64%, which is lower than that for sub-population 4 (94.31%) and higher than that for sub-population 5 (77.90%). This shows the benefit of past selection on survival of sub-population 1.

The genetic correlation (rgloc) between performance in the progeny test and in the BSO is of moderate magnitude (0.500). This indicates the considerable value of genotype x environment interaction (c^2 int, when compared with h^2a), with c^2 int indicating the proportion of the variation due to GxE. This results in a slightly different ranking of the families in the progeny trial compared to the BSO. In this case, five families are common among the best 10 families in each trial (*Table 3*).

The best selection strategy within this sub-population would be using the ranking from the joint analysis of both (progeny and BSO) tests. This did not provide the highest heritability coefficient for family selection ($h^2 fm = 0.403$) (*Table 4*), but it eliminates the overestimation of genetic values due to genotype x environment interaction.

There is low genetic variability for selection within families in the population as shown by the within family heritability coefficients ($h^2aw = 0.024$) (*Table 4*). This is expected as the progenies in this trial are full-sibs.

The average height in this sub-population (trait average : 3.245 to 3.494 m) is lower than that for sub-populations 2 (trait average : 3.510 to 3.666 m) and 4 (trait average : 4.438 to 4.643 m) and the progeny trial in sub-population 5 (trait average : 3.805 m). It is, however, higher than sub-population 3 (trait average : 1.612 to



Figure 1. – Mean family height measurements of the nine commercial and genetic check families, across the five sites.

2.007 m) and the BSO and interaction analysis of subpopulation 5 (trait average : 3.113 and 3.230 m, respectively). This can be due to environmental site effects, genetic population effects and/or both.

Although not presented in this paper, among the best 20 individuals overall, 9 come from the BSO and 11 from the progeny trial. Noticeably it was found that all the top 20 individuals come from the same family 220. This is due to the near zero within family heritability ($h^2aw = 0.024$), which leads only to between family selection (high heritability of family means, contrasting with very low within family heritability). Therefore, some restriction on maximum number of individuals selected per family should be practised. This aims at increasing the effective population size of the selected population, which is desirable for long-term selection as explained below for sub-population 2. This too, will prevent the occurrence of inbreeding depression in the planting generation.

Sub-population 2

At this early age (one year), there is enough genetic variability for future selection in the progeny trial only, as shown by the heritability coefficients ($h^2a = 0.442$). The BSO did not show genetic variability ($h^2a = 0.003$). It can be noticed that there is some genetic variability for percentage survival in this sub-population with the survival rate being 90.88% with survival genetic values ranging from 83 to 94%.

The heritability coefficients for family selection (h^2 fm) was high, i.e. 0.564 and provides a selection accuracy or precision value of 0.751 (75%) (Acfm). There is also enough genetic variability for selection within families in this trial as shown by the within family heritability coefficient (h^2 aw = 0.572).

If selection was based on results from the progeny test, using a selection pressure of 2%, selection of the best 20 individuals could provide a genetic gain of 0.86 or 23.5% enhancing the population mean to 4.53 m (MIP-mean of the improved population). These best 20 individuals are associated to an effective population size (EPS) of 12.93, i.e. equivalent to approximately 13 unrelated individuals. The maintenance of an adequate EPS is essential for reaching the selection limit of the population after selecting for several generations. This adequate EPS should be at least 30 (COMSTOCK, 1996). Therefore a greater number of individuals should be selected for the long-term breeding, but for the shortterm breeding, namely for the seed production population, this EPS is adequate for preventing inbreeding depression.

Sub-population 3

There is enough genetic variability for future selection in the progeny trial only, shown by the heritability coefficients ($h^2a = 0.215$). The BSO tests did not show genetic variability ($h^2a = 0.001$). It can be noticed that there is some genetic variability for percentage survival in this sub-population with the survival rate being 74.46% with survival genetic values ranging from 76 to 81%.

The heritability coefficients for family selection (h^2 fm) was high, i.e. 0.455 and provides a selection accuracy or precision values of 0.674 (67%) (Acfm). There is also enough genetic variability for selection within families in this trial as shown by the within family heritability coefficient (h^2 aw = 0.208).

The relatively low mean height in this sub-population (trait average : 1.612 to 2.007 m) could be due to environmental site effects, genetic population effects or both. It is likely that it is a combination of both as this sub-population was selected for frost resistance and not for productivity, and the site experienced a very cold winter in 2003.

If selection was based on results from progeny test, using a selection pressure of 2%, selection of the best 20 individuals could provide a genetic gain of 0.36 or 22.4% enhancing the population mean to 1.97 m (MIP-mean of the improved population). These best 20 individuals are associated to an effective population size (EPS) of 7.11, i.e. equivalent to approximately seven unrelated individuals. For practical breeding this number should be higher.

Sub-population 4

There is enough genetic variability for future selection in this sub-population, in both the progeny trial and BSO, with the possibility of using the combined data as well. The heritability coefficients (h^2a) is high in all three cases (0.628 for combined analysis). These high heritability coefficients are due to the origin of the families being unselected Australian material. It can be noticed that there is some genetic variability for percentage survival in this sub-population with the survival rate being 94.31% with survival genetic values ranging from 87 to 97%.

Genetic correlation (rgloc) between the performance of the families in the progeny trial and in the BSO was high (0.875), as expected. This is reinforced by the low value of the genotype x environment interaction (c^{2} int = 0.023) and similar ranking of families in both tests.

The best selection strategy would be the selection by using the ranking from joint analysis of both (progeny and BSO) tests. This provided the highest heritability coefficients for family selection ($h^2 fm = 0.919$) and provides a selection accuracy or precision value of 0.959 (96%) (Acfm). Among the best 20 individuals overall, 13 come from the BSO trial and seven from the progeny trial. This revealed the importance of vegetative propagation as a means to capture these seven individuals into a clonal seed orchard or into the BSO. Selection of the best 20 individuals can provide a genetic gain of 1.20 or 26% enhancing the population mean to 5.80 m (MIP-mean of the improved population). These best 20 individuals are associated to an effective population size (EPS) of 8.96, i.e. equivalent to approximately nine unrelated individuals.

There is also enough genetic variability for selection within families as indicated by the within family heritability coefficients ($h^2aw = 0.584$).

Sub-population 5

There is reasonable genetic variability for future selection in this sub-population, in both the progeny trial and BSO, with the possibility of using the combined data as well. The heritability coefficient (h^2a) ranges from 0.134 to 0.142 in all three cases. This sub-population is a South African local population and explains the lower heritability coefficients when compared to sub-population 4 $(h^2a : 0.628 \text{ to } 0.717)$. It can be noticed that there is some genetic variability for percentage survival in this sub-population with the survival rate being 77.90% with survival genetic values ranging from 71 to 82%.

Genetic correlation (rgloc) between the performance of the families in the progeny trial and in the BSO was high (0.946), as expected. This is reinforced by the low value of the genotype x environment interaction (c^{2} int = 0.002) and similar ranking of families in both tests.

The best selection strategy would be the selection by using the ranking from joint analysis of both (progeny and BSO) tests. This provided the highest heritability coefficients for family selection (h^2 fm = 0.830) and provides a selection accuracy or precision values of 0.911 (91%) (Acfm). Among the best 20 individuals overall, 15 come from the BSO trial and five from the progeny trial. The genetic gain with selection of the best 20 individuals could provide a genetic gain of 0.30 or 9.3% enhancing the population mean to 3.53 m (MIP-mean of the improved population). These best 20 individuals are associated to an effective population size (EPS) of 14.69, i.e. equivalent to approximately 15 unrelated individuals.

There is also sufficient genetic variability for selection within families in both populations as evidenced by the within heritability coefficients (h^2aw) .

The heritability figures obtained over the five sub-populations, in the present work, varied from 0.04 to 0.72, according to degree of improvement of the populations and site qualities. Similar heritability estimates for growth in black wattle were obtained by RESENDE et al. (1992 and 1998) when comparing a local Brazilian population ($h^2a = 0.11$ and 0.33, respectively) with Australian populations grown in Brazil ($h^2a = 0.31$ to 0.36). BI et al. (1991) recorded heritability estimates of 0.29 and 0.37 for Australian black wattle populations grown in China. This suggest that the results reported in this paper are coherent with that published in the literature.

From Figure 1 and Table 6, it can be seen that there are remarkable differences in the performances of the commercial and genetic check families across the five different sites. The concept of relative performance used in Table 6 is a measure of adaptability of the genetic materials to sites and follows BURDON (1998). The relative performance (RP) in relation to the trial mean varied from 95% to 104% in site 1; from 89% to 112% in site 2; from 96% to 112% in site 3; from 90% to 105% in site 4; from 99% to 103% in site 5 (Table 6). Clearly the third sub-population site is the most unfavourable as the overall heights of the trees in the trial were all shorter than at the other sites and the control families performed the worst at this site. Site 5 did not provide great differences between checks, and will be monitored more thoroughly in later analyses. There is some degree of genotype x environment interaction and this too will be investigated more thoroughly with more specific statistical tests. Control family 90 performs, on average, best across all the sites, and in particular on the more moderate sites (it ranked first on sites 1 and 2 and second on site 4) but it is not suited to the cold site of subpopulation 3 (Table 6). This family is an advanced generation controlled cross from the existing breeding programme. Family 85 is the second best performer overall, being ranked first on sites 3 and 5 and second on site 1. The third best performer across all sites was family 83, which ranked second on sites 2 and 3. The fourth best performer was family 84. Family 91 showed specific adaptability to site 4 on which it ranked first. The worst performer was family 86 as expected being from unselected material. Family 87 was almost as bad as family 86 (Table 6).

Concluding Remarks

This is the first time that a series of trials of this nature has been planted as part of a breeding strategy for black wattle in South Africa. These early results show great potential for genetic gain in future. One may argue that first year height measurements are not an appropriate parameter to base any selections. This is, however, not the intention. The rigorous analysis that took place while analysing these data was done for a number of reasons:

1. Set up a suite of analyses that can be routinely performed on these data as the trials are measured annually;

Table 6. – Relative performance (in percentage of the trial mean) of the genetic check material within and across sites. Numbers within the brackets refers to the ranking.

Genetic Checks	Site 1	Site 2	Site 3	Site 4	Site 5	Overall
83	99 (6)	111 (2)	107 (2)	100(7)	99 (6)	103 (3)
84	100 (4)	103 (3)	104 (4)	101 (5)	101 (3)	102 (4)
85	103 (2)	97 (7)	112 (1)	100 (8)	103 (1)	103 (2)
86	98 (8)	89 (9)	105 (3)	90 (9)	99 (9)	96 (9)
87	95 (9)	96 (8)	96 (9)	101 (6)	99 (5)	97 (8)
88	99(5)	99 (5)	96 (8)	103 (4)	99 (8)	99 (7)
89	100 (3)	98 (6)	98 (7)	103 (3)	99 (7)	100 (6)
90	104 (1)	112(1)	100 (6)	104 (2)	101 (4)	104 (1)
91	98 (7)	100 (4)	102 (5)	105 (1)	102 (2)	105 (5)
Mean	3.49	3.62	1.61	4.44	3.81	3.40

2. Obtain results that will be useful in future to assess age-age correlations for the various traits assessed;

3. Track the changes in heritabilities and other genetic parameters over time, in an attempt to identify the earliest age at which selections can be made; and

4. To have an appropriate decision-making tool, to use to select individuals for future generations.

The lack of potential improvement from the advanced generation sub-populations suggests that the continual infusion of new, unrelated material into the breeding population is very important. This is emphasised by the potential genetic gain shown in sub-population 4 (made up of the unimproved Australian material).

The authors believe that this strategy and the analytical techniques employed will best identify the best individuals and families to be used in future breeding populations. Ultimately the benefits of this strategy will be reaped by the growers who choose to use the seed emanating from this breeding programme.

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Appendix

In the individual analyses by trial the linear model applied to the progeny trial data was:

y = Xb + Za + Wc + e, where:

y, b, a, c and e: data vector, block effects (fixed), additive genetic effects (random), plot effects (random) and random error effects, respectively.

X, Z and W: incidence matrices for b, a and c, respectively.

Distributions and variance structures

$$\begin{aligned} v|b, V \sim N(Xb, V) \\ a|A, \ \sigma_A^2 \sim N(0, \ A \ \sigma_a^2) \\ c|\sigma_c^2 \sim N(0, \ I \ \sigma_c^2) \\ e|\sigma_e^2 \sim N(0, \ I \ \sigma_e^2) \end{aligned}$$

 $Cov(a, c') = 0; \quad Cov(a, e') = 0; \quad Cov(c, e') = 0$

$$E\begin{bmatrix} y\\ a\\ c\\ e \end{bmatrix} = \begin{bmatrix} Xb\\ 0\\ 0\\ 0 \end{bmatrix} e Var \begin{bmatrix} y\\ a\\ c\\ e \end{bmatrix} = \begin{bmatrix} V & ZG & WC & R\\ GZ' & G & 0 & 0\\ CW' & 0 & C & 0\\ R & 0 & 0 & R \end{bmatrix},$$
 where:

$$G = A \sigma_A^2$$
$$R = I \sigma_c^2$$
$$C = I \sigma_e^2$$

$$V = ZA \ \sigma_a^2 Z' + WI \ \sigma_c^2 W' + I \ \sigma_e^2 = ZGZ' + WCW' + R$$

Mixed-model equations

$$\begin{bmatrix} X'X & X'Z & X'W \\ Z'X & Z'Z + A^{-1}\lambda_1 & Z'W \\ W'X & W'Z & W'W + I\lambda_2 \end{bmatrix} \begin{bmatrix} \hat{b} \\ \hat{a} \\ \hat{c} \end{bmatrix} = \begin{bmatrix} X'y \\ Z'y \\ W'y \end{bmatrix}, \text{ where:}$$
$$\lambda_1 = \frac{\sigma_e^2}{\sigma_a^2} = \frac{1 - h^2 - c^2}{h^2}; \qquad \lambda_2 = \frac{\sigma_e^2}{\sigma_a^2} = \frac{1 - h^2 - c^2}{c^2}$$

 $h^{2} = \frac{\sigma_{a}^{2}}{\sigma_{a}^{2} + \sigma_{c}^{2} + \sigma_{e}^{2}} = \text{narrow sense individual heritabil-ity in the block;}$

$$c^2 = \sigma_c^2 / (\sigma_a^2 + \sigma_c^2 + \sigma_e^2)$$
 = correlation due to the common environmental effect in the plot;

- σ_a^2 = additive genetic variance;
- σ_c^2 = variance among plots; σ_e^2 = residual variance (environmental within plot + non additive);
- A = additive genetic correlation matrix among individuals under evaluation.

REML estimators for variance components using the EM (Expectation-Maximization) algorithm were:

$$\hat{\sigma}_{e}^{2} = [y'y - \hat{f}'b'y - \hat{a}'Z'y - \hat{c}'W'y]/[N - r(x)]$$

$$\hat{\sigma}_{a}^{2} = [\hat{a}' A^{-1} \hat{a} + \hat{\sigma}_{e}^{2} tr A^{-1} C^{22})/q$$

 $\hat{\sigma}_c^2 = [\hat{c}'c + \hat{\sigma}_e^2 tr C^{33}]/s$, where:

tr = trace operator;

r(x) = rank of the matrix X;

N-r(x) = error degrees of freedom;

q = number of individuals;

s = number of plots;

N = Total number of data.

C22 and C33 come from:

$$C = \begin{bmatrix} C^{11} & C^{12} & C^{13} \\ C^{21} & C^{22} & C^{23} \\ C^{31} & C^{32} & C^{33} \end{bmatrix} = \text{generalised inverse of the coefficient matrix of the mixed model equations.}$$

The same model, excluding the plot effect, was applied to BSO data sets. For the interaction analyses involving the progeny and BSO data sets the family x trial interaction effect was added.