GENETIC PARAMETER ESTIMATES AND GENETIC GAINS FOR *EUCALYPTUS GRANDIS* AND *E. DUNNII* IN ARGENTINA

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ABSTRACT

Genetic parameters (heritabilities and genotype × environment interaction) and breeding values for volume (VOL) and stem straightness (FORM) were estimated from the analyses of 203 open-pollinated (OP) families planted in six test locations of *Eucalyptus grandis* and 76 OP families planted in six tests of *E. dunnii*. All tests were established in the Mesopotamia region of Argentina and age of measurement ranged from 3 to 15 years old. Tests of both species contained checklots from the local land race of Argentina, but the large majority of families originated from native provenances in Australia.

For *E. grandis*, pooled-site heritabilities were in the range commonly observed for growth and form traits: $h^2 = 0.16$ and 0.17 for VOL and FORM, respectively. For *E. dunnii*, heritabilities were slightly smaller (0.10 and 0.14). In both species, there was more family × location interaction for VOL than FORM as indicated by the higher type B genetic correlations for the latter trait: $r_{B_g} = 0.58$ and 0.63 for VOL in *E. grandis* and *E. dunnii*, respectively, while $r_{B_g} = 0.74$ and 0.73 for FORM.

Best linear unbiased prediction (BLUP) was used to predict breeding values for VOL and FORM for all parents and living trees in all tests. Then, a selection index combining data from both traits into a single value for each tree was developed for use in making selections. Using the index to make forward selections of the top 1.3 % of the trees resulted in predicted genetic gains of 22 % for VOL and 14 % for FORM in *E. grandis* and 18 % for VOL and 12 % for FORM in *E. dunnii*. These selection indices are being used by the INTA tree improvement program for both species to choose selections for commercial seed orchards and for advanced-generation breeding populations.

Keywords: Tree improvement, selection index, heritability, genotype × environment interaction.

INTRODUCTION

The major forest region in Argentina, called Mesopotamia, consists of the provinces of Entre Ríos, Corrientes and Misiones, with more than 800,000 hectares of plantations of subtropical pines and eucalypts (Figure 1). In this area, planting has accelerated greatly in recent years due to availability of low cost, highly-productive lands for forestry and because of new policies and economic measures promoting forest management. These measures favor long-term investment in the development of forest plantations.

Eucalyptus grandis (Hill) ex Maiden was introduced into Argentina in the 1930's, and is the main plantation species of eucalypts being preferred for sawn timber, poles and pulp. To date, 200,000 hectares of *E. grandis* have been planted across a wide range of sites with average growth rates between 25 and 50 $m^3 \cdot ha^{-1} yr^{-1}$ on a 10-year rotation depending on site

quality (CARPINETI *et al.* 1995). The first provenance trials of *E. grandis* were planted between 1980 and 1983 by INTA (National Institute for Agricultural Technology) and CIEF (Forestry Research and Experimentation Center) in eight test locations within Mesopotamia. There were significant differences among provenances for growth and quality traits like stem straightness, and most Australian provenances were superior in growth to the local land race (MARCÓ 991). Provenance by environment interactions were relatively small or absent for all traits.

E. dunnii was introduced into Argentina in the late 1970's where it is now a viable alternative for planting on some sites because, in comparison to *E. grandis*, it is more frost hardy and combines good growth and stem straightness with wood suitable for pulp. Limited local information shows inferior sawing and sawn timber properties compared to *E. grandis*. Small areas of *E. dunnii* have been planted in the provinces of Santa Fé,

Figure 1. Portion of South America showing Uruguay, southern Brazil and Paraguay and northern Argentina. All 12 test locations were located in the Mesopotamia region of Argentina consisting of the provinces of Misiones, Corrientes and Entre Ríos. The locations of six test locations of *Eucalyptus grandis* are numbered 1 to 6 and six test locations of *E. dunnii* are numbered 7 to 12.

Buenos Aires, Entre Ríos and Misiones. Most of the provenance trials of *E. dunnii* in Argentina were established by INTA and CIEF just after its first introduction in 1979 (MARADEI 1987). Unlike *E. grandis* where genetic variation in growth among provenances was important, there appears to be little variation in growth among provenances of *E. dunnii* (MARCÓ & LÓPEZ, 1995).

Given the increasing investment in plantation forestry in Argentina and the importance of *E. grandis* and *E. dunnii* as plantation species, INTA began a tree improvement program for both species. We adopted a breeding strategy designed to concentrate limited resources of staff and budget by combining seed source trials, breeding population, progeny testing and commercial seed production into a single population containing open-pollinated families planted in a single series of field tests. Breeding strategies based exclusively on open-pollinated families have been justified on both theoretical grounds (COTTERILL 1986, BARNES 1986) and logistical ease (GRIFFIN 1982). A similar OP breeding strategy has produced excellent genetic gains through four generation of breeding *E. grandis* in Florida (FRANKLIN 1986, WHITE & ROCKWOOD 1993), and is in use in several tree improvement programs in the world (DVORAK & DONAHUE 1992; CANNON & SHELBOURNE 1993; AMPIE & RAVENSBECK 1994;

BARNES *et al.* 1995; OSORIO *et al.* 1995).

For these reasons, INTA started two large series of tests (one for *E. grandis* and one for *E. dunnii*) that had several functions for each species: (1) Serve as the first-generation breeding population and provide a broad genetic base; (2) Quantify seed source differences and estimate genetic parameters across a wide range of sites; (3) Produce commercial seed for operational reforestation; and (4) Serve as a place to make second-generation selections well-adapted to plantation conditions in Mesopotamia Argentina. In 1989 OP seed was collected from 203 trees of *E. grandis* (160 individuals from 11 provenances in Australia and 43 individuals from local collections) and 76 families of *E. dunnii* representing four Australian provenances and one local one. During 1991 and 1992, a series of combined provenance/progeny trials were established within reforested areas in Mesopotamia Argentina (Figure 1).

For both species, the objectives of this paper are to use the data for stem volume and straightness to: (1) Compare performance of Australian provenances and the local land race; (2) Quantify heritabilities and genotype × environment interaction; (3) Predict breeding values for all parents and each seedling planted; (4) Create selection indices combining volume and straightness; and (5) Estimate genetic gains from various scenarios of index selection.

MATERIALS AND METHODS

Plant materials and test designs for *Eucalyptus grandis*

In 1989, OP seed was collected from 188 trees originating from 13 seed sources: (1) 106 families from five natural provenances in New South Wales (NSW), Australia; (2) 54 families from six natural provenances in southeastern Queensland (QLD), Australia; and (3) 28 families from two local land race sources from Concordia, Entre Ríos, Argentina. For the 11 Australian provenances, the 160 mother trees were growing in native stands, and OP seed was collected from between 7 and 25 mother trees per provenance (average = 14.5 families per provenance). For the two sources from the Argentine land race: (1) 20 OP families were collections from selected trees in plantations near Concordia chosen to be superior for stem straightness and volume; and (2) Eight OP families were from mother trees growing in a clonal seed orchard originating from the local land race.

During 1991 and 1992, a total of 188 OP families from the 13 sources mentioned above were established in trials at 4 locations ranging from latitude 24° to 31°S

Table 1. For *Eucalyptus grandis,* descriptive data for each of the six test locations (tests 1 to 6 in Figure 1), test means for survival, height, volume and stem straightness, and results from the single site analyses of variance for volume (VOL) and stem straightness (FORM). NS = not significant at *P* = 0.10.

	Test 1	Test 2	Test 3	Test 4	Test 5	Test 6
Latitude (°S)	31°45′	24°26′	28°02′	25°45′	31°22′	31°22′
Longitude (°W)	58°15′	59°02′	56°03′	54°40′	58°07′	58°07′
Elevation (m)	40	66	105	154	40	40
Age (yrs)	5	5	5	3	16	16
Survival (%)	95	91	62	81	78	77
Height (HT) (m)	15.8	16.7	19.1	20.2	29.2	30.8
Volume (VOL) (m³)	0.107	0.130	0.258	0.214	0.561	0.647
Straightness (FORM) (Scale 1–4)	2.41	3.04	2.28	2.43	2.88	3.02
Significance levels for VOL						
Seed source	0.001	NS	NS	0.004	NS	0.024
Family (source)	0.001	0.001	0.001	0.001	NS	NS
Parameter estimates for VOL						
Single-site heritability (h_b^2)	0.253	0.355	0.235	0.234	0.048	0.109
Phenotypic variance (σ_T^2)	0.178	0.427	1.202	0.926	6.718	8.659
Significance levels for FORM						
Seed source	NS	0.026	0.001	0.001	0.033	NS
Family (source)	0.001	0.001	0.001	0.001	0.011	0.021
Parameter estimates for FORM						
Single-site heritability (h_b^2)	0.108	0.348	0.196	0.309	0.212	0.413
Phenotypic variance (σ_T^2)	0.434	0.668	0.430	0.534	1.1015	0.879

and from altitude 40 m to 150 m within reforested areas in Mesopotamia Argentina (Tests 1 to 4 in Figure 1 and Table 1). A randomized completed block design (RCB) and plots of single trees planted on a 3m square spacing was used. The number of half-sib families in each trial varied from 120 to 188 and there were 17 to 20 blocks per site.

Two additional tests containing 31 OP families of material from the local land race were planted in Concordia in 1982 (Tests 5 and 6 in Figure 1 and Table 1). The two seed sources were: (1) 16 of the 20 families selected in the local land race included in the 1991 /1992 series (which serve to connect the two series of tests); and (2) 15 OP families from randomly chosen trees in the same stands as the 16 selected trees. The experimental design used was RCB with 3 blocks and 5 trees/plot in a row for test 5, and 5 blocks and 9 trees/plot in square for test 6.

All seedlings for all tests of *E. grandis* were raised at INTA Concordia Research Station nursery and planted in sites prepared under full cultivation. Sites were representative of the eucalypt-growing region of Mesopotamia Argentina and the field tests were well maintained.

In total across all 6 tests of *E. grandis*, there were 203 OP families from 14 seed sources. There were

11,217 trees measured between ages 3 and 5 years (tests 1 to 4 planted in 1991/92) and 15 years (tests 5 and 6 planted in 1982). Measurements included survival, total height, diameter at breast height, and stem straightness (FORM) assessed on a 1 to 4 scale with 1 indicating best and 4 worst.

Plant materials and test designs for *Eucalyptus dunnii*

In 1989, OP seed was collected from 75 families originating from five seed sources. Sixty-three families originated from four original provenances in NSW, Australia, with the mother trees growing in native stands of *E. dunnii*. From the local seed source, 12 mother trees were selected to be superior for stem straightness and volume in plantations of *E. dunnii* located near Oliveros, Santa Fé, Argentina. Seeds for these plantations were originally introduced from the Australian provenance known as Moleton, NSW.

During 1991 and 1992, a series of trials of *E. dunnii* were established by INTA at 6 locations ranging from latitude 25° to 34° S and from altitude 20 m to 300 m (Tests 7 to 12 in Figure 1 and Table 2). The experimental design at each site employed an RCB design and plots of single trees planted on a 3 m square spacing.

Table 2. For *Eucalyptus dunnii*, descriptive data for each of the six test locations (tests 7 to 12 in Figure 1), test means for survival, height, volume and stem straightness, and results from the single site analyses of variance for volume (VOL) and stem straightness (FORM). NS = not significant at $P = 0.10$.

	Test 7	Test 8	Test 9	Test 10	Test 11	Test 12
Latitude (°S)	34°12'	32°33'	31°45'	27°39'	26°06'	25°55'
Longitude (°W)	58°58'	58°26'	58°15'	55°26'	54°28'	54°20'
Elevation (m)	20	35	40	283	176	180
Age (yrs)	5	7	6	5	3	6
Survival (%)	66.2	94.5	95.9	74.8	76.0	71.6
Height (HT) (m)	18.0	14.5	18.1	17.6	17.4	25.1
Volume (VOL) (m³)	0.239	0.107	0.183	0.176	0.155	0.389
Straightness (FORM) (Scale 1–4)	2.64	2.86	2.52	3.15	2.37	3.28
Significance levels for VOL						
Seed source	NS	0.016	0.009	0.073	0.021	NS
Family (source)	0.005	0.001	0.001	0.042	0.001	NS
Parameter estimates for VOL						
Heritability (h_b^2)	0.247	0.124	0.146	0.074	0.260	0.000
Phenotypic variance (σ_T^2)	0.011	0.002	0.004	0.008	0.005	0.037
Significance levels for FORM						
Seed source	NS	0.033	NS	NS	NS	0.057
Family (source)	0.011	0.001	0.001	0.021	0.001	NS
Parameter estimates for FORM						
Heritability (h_b^2)	0.267	0.235	0.184	0.106	0.239	0.000
Phenotypic variance (σ_T^2)	0.756	0.796	1.112	0.782	0.627	0.785

The number of half-sib families in trial varied from 40 to 75 with 15 to 20 blocks per site.

All seedlings of *E. dunnii* were also raised at INTA Concordia Research Station nursery and planted in sites prepared under full cultivation. Sites were representative of the eucalypt-growing region of Mesopotamia Argentina and the field tests were well maintained. In total across all 6 tests of *E. dunnii*, there were 75 OP families and 6,817 trees were measured between ages 3 and 7 years for survival, total height, diameter at breast height and stem straightness (FORM) assessed on a 1 to 4 scale with 1 indicating best and 4 worst.

Data preparation, statistical analyses and genetic parameter estimation

For each tree of both species, the height and diameter measurements were used to calculate tree volumes using the equation developed by GLADE & FRIEDL (1988):

Ln (Volume) = –9.9617 + 1.8234 * Ln (diameter/10) + 1.0698 * Ln (height/10)

where diameter was measured in cm, height in m and volume (VOL) calculated in m³.

Next, means, maxima, minima and standard devia-

tions were calculated by test, block, family and seed source for all measurement traits. Also, graphs of height against diameter were plotted for each block. Dwarf trees believed caused by selfing and trees that were outliers and suspected to be errors in measurements were identified and deleted from the data (MAGNUSSEN 1993; WHITE 1996). In total, less than 1 % of all measurements were deleted.

For all analyses pooling data across test sites, height, diameter and volume data were standardized by dividing the individual tree values by the phenotypic standard deviation of the block. This standardization removes scale effects that cause spurious genotype × environment interaction due to large differences in phenotypic variances among all tests (HODGE et al. 1996; WHITE 1996). Tree values for FORM were not standardized because phenotypic variances were similar across test locations.

For each species, genetic parameters were estimated for volume (VOL) and stem straightness (FORM) separately in a three-stage process: (1) Single-site analyses were conducted using only data from a single test; (2) All possible 15 pairs of tests (1 with 2, 1 with 3, etc.) were analyzed jointly in pooled analyses to investigate patterns of genotype × environment interactions; and (3) All data from all tests of the species were

combined in a single analyses.

In all three stages, a mixed linear model was employed through Proc Mixed of SAS (SAS INSTITUTE 1996). Proc Mixed uses REML (restricted maximum likelihood) techniques to estimate variance components for all random effects and estimates least square means for fixed effects through GLS (generalized least squares). Tests of significance were conducted in Proc Mixed for fixed effects and in Proc GLM with the Satterthwaite option for random effects. Stages two and three of the analyses involved pooling data across two sites (stage 2) or several sites (stage 3). The linear model included fixed effects for test, block, seed source, and the test × seed source interaction, and random effects for family, family × test, family × block, and within-plot (with all family effects being nested within seed source). The first stage of the analysis used data only from a single site and employed a linear model as described only with all terms involving test being deleted form the model.

For the single site analyses of each species, unstandardized data were used and two genetic parameters were calculated for each trait of VOL and FORM:

$$h_b^2 = 3\sigma_F^2 / \sigma_T^2$$

$$\sigma_T^2 = \sigma_F^2 + \sigma_{FB}^2 + \sigma_W^2$$

where h_b^2 is the single-site heritability, σ_F^2 is the variance due to family within seed source effects, σ_T^2 is the total phenotypic variance, σ_{FB}^2 is the variance due to family by block interactions and σ_W^2 is the within-plot variance. Note that σ_W^2 was estimated only for two tests (5 and 6), but not for the other 10 tests established in single tree plots. The coefficient 3 instead of 4 was used for the numerator of the heritability equation to reflect possible inbreeding and full-sib relatives in open-pollinated families (SQUILLACE 1974; SORENSEN & WHITE 1988; HODGE *et al.* 1996). Single site heritabilities are upwardly biased due to test × family interaction confounded with family variance in the numerator (COMSTOCK & MOLL 1963, WHITE & HODGE 1992).

From stages 2 and 3 of the analyses (pairs of tests and pooled across all tests of the same species, respectively), we estimated two more genetic parameters, heritability (h^2) and type B correlation (r_{Bg}) as:

$$h^2 = 3\sigma_f^2 / \sigma_T^2$$

$$r_{Bg} = \sigma_f^2 / (\sigma_f^2 + \sigma_{fe}^2)$$

where h^2 is the unbiased pooled-site heritability, σ_f^2 is the variance due to family within seed source effects, σ_{fe}^2 is the variance due to family by environment interaction, σ_{fb}^2 is the variance due to family by block interac-

tion and $\sigma_T^2 = \sigma_f^2 + \sigma_{fe}^2 + \sigma_{fb}^2$. The type B genetic correlation measures the amount of genotype × environment interaction between each pair of sites or across all sites since the numerator, σ_f^2, includes only those family effects that are consistent and stable across sites, while σ_{fe}^2 is the amount of variance caused by family × test location interaction (YAMADA 1962). When $r_{Bg} = 1$, the family rankings are identical across sites, while r_{Bg0} implies no correspondence between ranking on the two sites.

Breeding value prediction and selection index formation

Breeding values were predicted by best linear unbiased prediction (BLUP) (WHITE & HODGE 1989; MRODE 1996). All analyses used the computer program MTDFREML (BOLDMAN *et al.* 1993) and used individual tree data across tests for a single variable of each species. That is, standardized volumes were combined together in a single analysis for each species and the straightness measurements were combined together in a second analysis for each species. A tree or individual model was employed which predicts two types of breeding values simultaneously (MRODE 1996): (1) Parental breeding values for all mother trees; and (2) Tree-level breeding values for every tree planted in the genetic tests. These two types of breeding values are on the same scale and, therefore, completely comparable. The linear model used for BLUP analysis included test, block and seed source as fixed effects with tree and family × test interaction as random effects. The family effect normally included in the linear models used in forestry is not included in tree-level linear models for BLUP analysis because the BLUP computer program automatically predicts breeding values for all parents and progeny included in the pedigree file.

Each of the BLUP analyses for *E. grandis* (one for VOL and one for FORM) produced fixed effects estimates for 14 *E. grandis* seed sources and predicted breeding values for 203 parents and each tree of *E. grandis*. The BLUP analyses for *E. dunnii* produced fixed effects estimates for five seed sources and predicted breeding values for 75 parents and each tree of *E. dunnii*. The seed source effects were then added to the breeding values so that all breeding values within a seed source average to the least square mean of that source.

BLUP-predicted breeding values are already predicted genetic gain values (MRODE 1996), and the final step in breeding value prediction was to convert each predicted value into a percentage gain prediction. For VOL, the breeding values obtained using standard-

ized data were converted to percentage gain (VOL-GAIN) as follows: (1) Each breeding value prediction was multiplied by the mean phenotypic standard deviation of all tests; (2) The resulting value was divided by the mean volume of all tests; and (3) The value was multiplied by 100. Since FORM breeding values were predicted from unstandardized data, only the final two steps were required to obtain FORMGAIN values in percent.

Since the goal of selection in the INTA breeding programs is to improve both volume and stem straightness in both species, a selection index was created to combine data from both VOLGAIN and FORMGAIN into a single criterion that can be conveniently used for making selections. In the absence of information about the relative economic importance of the two traits in each species, a Monte Carlo process (COTTERILL & DEAN 1990) was used to develop the index. The Monte Carlo process is a trial-and-error procedure in which many different index weights are tried until one is found that produces desirable gain in both traits.

RESULTS AND DISCUSSION

Seed source differences

For *E. grandis*, single site analyses showed that seed sources were significantly different ($P = 0.05$) in three of the six sites for VOL and four of the six sites for FORM (Table 1). In the combined analyses, seed source effects were highly significant for FORM (P = 0.01) and significant at $P = 0.07$ for VOL (Table 3). Seed source × test location interaction was highly significant for both traits. Examination of the means showed rank changes involved in the interaction, but these were not large compared to seed source main effects. For example, the two best seed sources ranked at the top for VOL in all six tests.

Least square means of the seed source effects from the combined analysis across sites indicated the following (Table 4): (1) The worst seed source for both VOL and FORM was seed source 1 consisting of OP families from unselected, random trees in the local land race (–7.5 % and –9.9 % below the mean for VOL and FORM, respectively); (2) Selection for fast-growing and well-formed trees of *E. grandis* from the same stands in the local land race was effective, because seed

Table 3. Significance levels and parameter estimates for volume (VOL) and stem straightness (FORM) from the pooled analyses combining data across sites. For *E. grandis*, pooled analyses were conducted with data from all six tests (tests 1 to 6) and only the four tests established in 1991/1992 in single tree plots (tests 1 to 4). For *E. dunnii*, three types of pooled analyses were conducted: all six tests (tests 7 to 12), five tests (tests 7 to 11) and four tests (tests 7 to 10) progressively omitting the poorest tests.

Species, trait and tests analyzed		Significance levels				Parameter estimates	
		Seed source	Source × test	Family (source)	Family × test	Heritability (h^2)	Type B genetic correlation (r_{Bg})
Eucalyptus grandis							
Volume	Test 1–6	0.073	0.001	0.001	0.001	0.140	0.575
	Test 1–4	NS	0.001	0.001	0.001	0.156	0.577
Form	Test 1–6	0.001	0.001	0.001	0.001	0.172	0.735
	Test 1–4	0.001	0.001	0.001	0.001	0.162	0.686
Eucalyptus dunnii							
Volume	Test 7–12	0.003	0.015	0.052	0.001	0.026	0.179
	Test 7–11	0.004	0.050	0.015	0.001	0.067	0.380
	Test 7–10	0.017	0.049	0.001	0.001	0.095	0.628
Form	Test 7–12	NS	NS	0.013	0.001	0.077	0.489
	Test 7–11	NS	NS	0.001	0.001	0.127	0.624
	Test 7–10	NS	NS	0.001	0.001	0.141	0.726

Table 4. For *E. grandis*, least square means for seed source effects (expressed as a percentage above or below the overall average) and relative rankings for volume and stem straightness. Both traits are expressed as percentage genetic gains above or below the mean so positive values are good for both variables. Seed sources 1 to 3 originated from the local land race in Argentina, while sources 4 to 8 and 9 to 14 were from New South Wales and Queensland in Australia, respectively. The number of OP families representing each seed source is shown in parenthesis.

Seed source (number of families)	Volume		Stem straightness	
	(%)	Rank	(%)	Rank
1. Random Collections (ARG) (15)	–7.50	14	–9.91	14
2. Local Selections (ARG) (20)	0.56	6	–0.13	7
3. Local Seed Orchard (ARG) (8)	–0.47	9	6.45	2
4. Bachelor & W. Wank (NSW) (25)	3.72	4	–4.04	11
5. Kendall (NSW) (12)	6.18	2	0.99	6
6. Landsdowne (NSW) (23)	–2.05	11	–2.33	10
7. Middle Brother (NSW) (21)	–5.22	12	–5.30	13
8. Wallingat (NSW) (25)	0.49	7	–4.51	12
9. Beerwah & Mt. Mee (QLD) (11)	0.99	5	–1.14	9
10. Gympie & Woondum (QLD) (9)	0.33	8	10.28	1
11. Bellthorpe (QLD) (8)	–1.08	10	–0.36	8
12. Kenilworth (QLD) (7)	4.49	3	1.33	5
13. Kin Kin (QLD) (12)	–7.49	13	3.18	4
14. Ring Tail (QLD) (7)	7.04	1	5.46	3
Overall mean	0.00	7	0.00	7

Table 5. For *Eucalyptus dunnii*, least square means for seed source effects (expressed as a percentage above or below the overall average) and relative rankings for volume and stem straightness. Both traits are expressed as percentage genetic gain above the mean, so positive values are good for both variables. Seed sources 1 – 4 originated from New South Wales in Australia, while number 5 contains selections made in the local land race in Argentina. The number of OP families representing each seed source is shown in parenthesis.

Seed source (number of families)	Volume		Stem straightness	
	(%)	Rank	(%)	Rank
1. Boomi Creek & Unumgar (12)	–5.97	5	1.78	3
2. Death Horse & Acacia Creek (33)	5.83	1	–3.61	5
3. Oaky Creek (9)	0.80	3	3.16	1
4. South Yabra (9)	–5.56	4	–3.12	4
5. Oliveros, Santa Fe (12)	4.95	2	1.80	2

sources 2 and 3 were superior to seed source 1 for both traits; (3) The range in means for the 11 Australian provenances was approximately 15 % for both traits; and (4) When considering both traits, the two most desirable provenances were from Ring Tail in Queensland and Kendall in New South Wales.

It is important to note that only Australian provenances from southeastern Queensland and northeastern New South Wales were included in this study. These provenances had performed well in previous tests in Argentina (unpublished data, senior author). This may explain why there were not larger differences among the seed sources represented in these progeny tests as can be found in other studies of *E. grandis* (ROEDER 1980;

DARROW & ROEDER 1983; MATHESON & MULLIN 1987; BURGESS 1988; MARCÓ 1991). However, provenance patterns in *E. grandis* are often difficult to interpret with differences among local provenances being as large as those among distant provenances (ELDRIDGE *et al.* 1993). In this study, the best and the worst provenance for VOL are from southeastern Queensland (Ring Tail and Kin Kin in Table 4).

For *E. dunnii*, single site analyses showed that seed sources were significantly different (*P* = 0.05) in four of the six sites for VOL and two of the six sites for FORM (Table 2). In contrast to *E. grandis*, the combined analysis for FORM indicated no significant differences among seed sources of *E. dunnii* (Table 3).

The *E. dunnii* combined analysis for VOL indicated that seed source effects were significant and so was seed source × test location interaction. Most of the rank changes occurred among middle and lower ranking seed sources. The top source for VOL (source number 3 from Death Horse and Acacia Creek in New South Wales) ranked best at all six sites (Table 5). The range among the seed sources for VOL was approximately 11 % which is slightly larger than previously reported (MARCÓ 1995). For both species in this study, the ranges of family and individual tree breeding values were much larger than the range among seed source means, as described later.

Family differences and genetic parameter estimates

For *E. grandis*, family differences were highly significant in tests 1 to 4 for both VOL and FORM, but not significant for VOL and less significant for FORM in tests 5 and 6 (Table 1). For VOL, this pattern of significance levels was mirrored by that of the single-site heritabilities which averaged 0.27 for tests 1 to 4, but were 0.048 and 0.109 for tests 5 and 6, respectively. For tests 1 to 4, these values compare favorably with those from other species (CORNELIUS 1994). Tests 5 and 6 are older trials established in row or block plot designs with fewer blocks than tests 1 to 4. There was no clear pattern of single-site heritabilities for FORM, which averaged 0.264 over all six tests.

Based on the single-site analyses, we conducted combined analysis both with all six tests and with only tests 1 to 4 (excluding tests 5 and 6). Family and family × test location interaction were highly significant for both VOL and FORM in both analyses (Table 3). Deletion of tests 5 and 6 did not materially alter either heritability or type B genetic correlations for either trait. Further, analyses of all 15 pairs of tests (results not shown) did not reveal any pattern associated with tests 5 and 6 (i.e., the type B correlations involving test 5 or 6 with other tests were not lower than other pairs of tests). For these reasons, all six test locations were used in all further analyses of genetic parameter estimation and breeding value prediction.

The pooled-site heritabilities for *E. grandis* were 0.14 for VOL and 0.17 for FORM (Table 3). These heritabilities are in the range normally observed for growth and form traits for tree species (Cornelius 1994). The type B genetic correlation from the combined analyses was only 0.58 for VOL, while it was higher (0.74) for FORM (Table 3). That is, there is more family × environment interaction for volume than stem straightness. In fact, for VOL, this value of 0.58 falls below the value of 0.67 suggested by Shelbourne (1972) as a threshold below which breeders need to be

concerned about genotype × environment interaction in the design of breeding and deployment strategies. Nevertheless, as mentioned above, there was no clear pattern to this interaction revealed by the pairwise analyses of all trials.

For *E. dunnii*, family differences were not significant for either VOL or FORM in test 12 and single-site heritabilities were zero for both traits in this test (Table 2). Averaging over the remaining 5 tests (using the values in Table 2 and excluding test 12), the average single-site heritability for VOL and FORM were 0.206 and 0.170, both of which are smaller than the averaged single-site heritabilities for the same traits in *E. grandis*.

The pairwise analyses of all 15 pairs of *E. dunnii* tests revealed that test 11 had consistently smaller type B genetic correlations with other tests. For VOL, the average of the pairwise type B correlations involving test 11 was 0.108, compared values of 0.354, 0.396, 0.404, 0.462 and 0.336 for pairs involving tests 7, 8, 9, 10 and 12, respectively. A similar pattern was observed for FORM: $r_{B_g} = 0.382$ for pairs of tests involving test 11 and 0.687, 0.564, 0.558, 0.648 and 0.252 for pairs involving tests 7, 8, 9, 10 and 12, respectively. The test is located on a site of good soil quality in the northernmost part of Argentina, and has exhibited average survival and excellent growth. There is no apparent reason why this test should exhibit high levels of genotype × environment interaction with the other tests.

Based on the above findings, pooled-site analyses for *E. dunnii* were conducted in three ways (Table 3): (1) Combining data from tests 7 through 12; (2) Combining data from tests 7 through 11, excluding test 12; and (3) Combining data from tests 7 through 10, excluding tests 11 and 12. For both VOL and FORM there is a progressive increase in both heritability and type B genetic correlation as the questionable tests are excluded. When only tests 7 through 10 are combined, the type B genetic correlations for volume and stem straightness are 0.63 and 0.73, which are very similar to the values for *E. grandis* estimated for the same traits across the same geographic region. The heritabilities are also more similar for the two species when tests 11 and 12 are excluded from the combined analyses.

Predicted breeding values, selection indices and genetic gains

For each trait for *E. grandis*, the BLUP analysis predicted a total of 11,420 breeding values: one for each of the 203 parents and for each of the 11,217 living trees in tests 1 to 6. For *E. dunnii*, there were 5,379 predicted breeding values for each trait: one for each of the 75 parents and for each of the 5,304 living trees in tests 7

to 10. While we could not explain the poor quality of test 12 nor the high genotype × environment interaction caused by test 11, these two tests were excluded from the BLUP analyses. The raw breeding value predictions in units of measure were converted into VOLGAIN for volume and FORMGAIN for stem straightness by: (1) Transforming the predicted breeding values into percentage values; and (2) Adding the appropriate least square means for seed source effects from Tables 4 and 5. VOLGAIN and FORMGAIN values average to zero for both species (positive values are favorable) and are predicted genetic gains in the sense that all values have been adjusted for quantity and quality of data (HENDERSON 1972; WHITE & HODGE 1989; MRODE 1996).

The 203 predicted parental breeding values for *E. grandis* ranged from –49 % to 33 % for VOLGAIN and from –36 % to 32 % for FORMGAIN. As predicted genetic gains, the maximum VOLGAIN for *E. grandis* means that the best parent mated with another parent of equal predicted breeding value is expected to produce offspring that grows 33 % faster than the average of the *E. grandis* population in these trials (ignoring specific combining ability). This range of 82 % for VOLGAIN includes the range of approximately 15 % among the *E. grandis* seed sources (from –7.5 % to 7.49 % in Table 4) and indicates that parental or family differences are more important than seed source differences. The 76 predicted parental breeding values for *E. dunnii* ranged from –19 % to 33 % for VOLGAIN and from –37 % to 27 % for FORMGAIN. The smaller ranges observed for both traits in *E. dunnii* compared to *E. grandis* are caused by lower heritabilities and less data. Individual tree breeding values had similar ranges as parental breeding values.

A selection index for each species was developed using a Monte Carlo process involving trying many different combinations of weights on VOLGAIN and FORMGAIN (Figure 2). For each species data from both parental and tree-level breeding values were used to develop an index (i.e., two indices per species), but only the tree-level indices are presented since the results were similar. For each species, 21 different indices (*I*) were calculated for all trees:

$$I = a * VOLGAIN + b * FORMGAIN$$

where *a* and *b* are linear weights on the two traits, *a* + *b* = 1 and the 21 different indices were obtained by starting with *a* = 0 and *b* = 1 and varying *a* and *b* in incremental steps of 0.1. For each calculated index, simulated forward selection of the top 1.3 % of the trees (150 out of 11,217 trees in *E. grandis* and 70 out of 5,304 trees in *E. dunnii*) was conducted subject to the constraint that no more than seven trees were selected
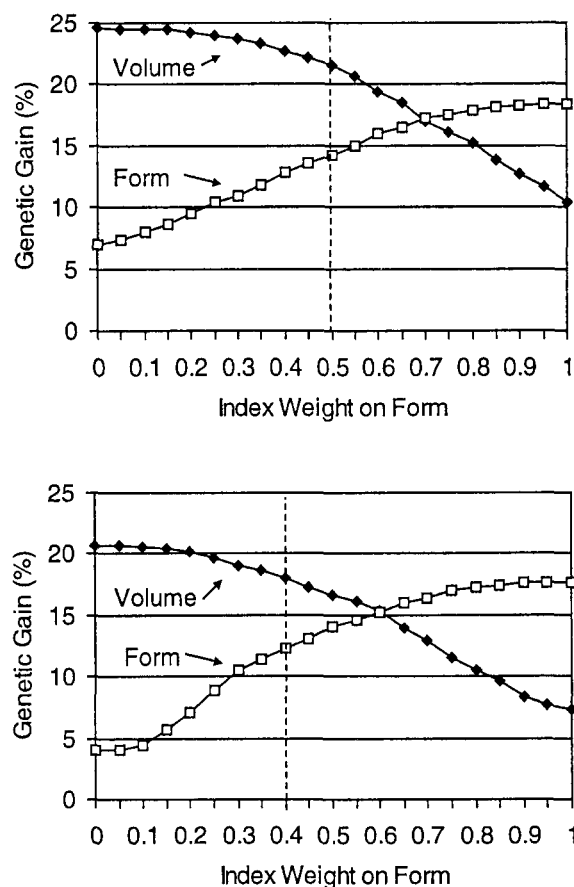

Figure 2. Genetic gains for volume and form from forward selection of the top 1.3 % of the individuals based on different selection indices: (a) Selecting the best 150 out of 11,217 trees of *E. grandis*; and (b) Selecting the best 70 out of 5304 trees of *E. dunnii*. For both species, 21 different selection indices were tried, and a constraint on relatedness specified that no more than 7 trees were selected from a given family.

from the same OP family. This value was chosen to mimic the effects of an intensive forward selection aimed at forming a breeding population. Finally, the genetic gains for each calculated index were obtained as the average VOLGAIN and FORMGAIN of the selected trees. These genetic gains were plotted (Figure 2) to choose an index producing desirable gains in both traits.

When all the weight is placed on VOLGAIN (i.e., a = 1 and b = 0 in the equation above), genetic gain in volume is maximized and stem straightness is ignored in the selection process. Selection of the top 1.3 % of the trees based solely on VOLGAIN results in genetic gains for volume of approximately 25 % and 21 % above the mean of all trees for *E. grandis* and *E. dunnii*, respectively (Figure 2). Gains for stem straightness are

slightly positive (7 % and 4 %) presumably due to a positive genetic correlation between the two traits in both species. When all the weight is placed on FORM-GAIN (i.e., $a = 0$ and $b = 1$), then gain in form is maximized at approximately 18 % for both species.

As final selection indices, we chose: $I = 0.50*\text{VOL-GAIN} + 0.50*\text{FORMGAIN}$ for *E. grandis* and $I = 0.60*\text{VOLGAIN} + 0.40 * \text{FORMGAIN}$ for *E. dunnii* (as indicated by the vertical lines in Figure 2). Use of these indices produces nearly 90 % of the maximum possible genetic gains in volume, while still achieving very acceptable gains in stem straightness. For example, in *E. grandis*, use of the final index to select the top 1.3 % of the individuals results in gains of approximately 22 % for volume and 14 % for stem straightness (compared to maximum gains achievable of 25 and 18 %, respectively, when all weight is placed on a single trait). While it is partially fortuitous that the genetic correlation between the two traits permits desirable gains to be achieved in both traits, the Monte Carlo method is an objective process of determining index weights in the absence of economic information.

CONCLUSIONS

Mass selection was quite effective at identifying fast-growing, well-formed trees within the local land race of *E. grandis* as indicated by comparison of seed sources 1 and 2 (selected and unselected families). However, results also confirm the wisdom of returning to Australia to enrich the genetic base available to the tree improvement program since many of the native provenances were superior to even selected material from the local land race. Substantial genetic gains in the INTA tree improvement programs will be made by having new sources and families from the native range of both species.

Genetic parameter estimates indicate that significant genetic gain can be made in both species for both traits: volume and stem straightness. Both traits should be included in the tree improvement program since both are heritable, of economic importance and appear to have a slight favorable genetic correlation. There is considerable family × location interaction for volume ($r_{Bg} = 0.58$ and 0.63 for *E. grandis* and *E. dunnii*, respectively) and this is more than we would expect for eucalypts. This could be because the test sites range widely across much of northern Argentina with variation in both soils, precipitation and to a lesser extent temperature.

The creation of a selection index that combines data from both volume and stem straightness into a single index seems appropriate to achieve gain in both

traits. The index can be used for making selections for advanced-generation breeding populations and to establish seed orchard or clonal propagation populations. Use of this index is expected to capture approximately 90 % and 80 % of the maximum possible genetic gain achievable when all emphasis is placed on the single traits of volume and stem straightness, respectively. Thus, in this case, use of the index produces highly acceptable gain in both traits of economic importance in the INTA tree improvement program.

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