

GENETIC VARIATION IN EARLY GROWTH AND STEM FORM OF *GREVILLEA ROBUSTA* IN A PROVENANCE-FAMILY TRIAL IN SOUTH-EASTERN QUEENSLAND, AUSTRALIA

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ABSTRACT

A provenance-family trial testing a total of 115 open-pollinated families from 23 provenances across much of the natural range of *Grevillea robusta* was established at Neerdie in coastal south-eastern Queensland, Australia. Fifty-two months after planting, mean height was 7.39 m and mean diameter at breast height (dbh) was 8.02 cm. It is difficult to sample natural provenances of this species because of small effective population sizes. However, there were significant differences between provenances in tree height, stem axis persistence and stem straightness. Of provenances represented by five or more families in the trial, the most vigorous was Duck Creek from New South Wales (mean height 7.57 m and dbh 8.63 m), while the slowest-growing was Rappville, New South Wales (height 6.43 m and dbh 6.97 m). This accorded with the good ranking of Duck Creek in provenance trials elsewhere. Assuming a coefficient of relationship of 0.3 among individuals within families, within-provenance individual-tree heritabilities for height and dbh were very high for height and for dbh at 52 months (0.87 and 0.61 respectively), but only 0.11 for axis persistence and non-significant for stem straightness. The breeding system of *G. robusta* (obligate outcrossing) may also contribute to the high heritabilities in growth traits by reducing within-family variance. The genetic correlation between height and dbh at 52 months age was high (+0.89) while those between axis persistence and height (+0.18) and axis persistence and dbh (+0.19) were much lower. The results indicate the potential for substantial genetic gain in vigour of *G. robusta* through tree improvement programs.

Key words: *Grevillea robusta*, provenance, family, heritability, growth, genetic improvement

INTRODUCTION

Grevillea robusta A. Cunn. ex R.Br., commonly known as silky oak, is endemic to eastern Australia, with a natural range extending from 25°50' S to 30°10' S, and from just above sea level near the eastern coast, to a maximum of 1100 m at the western extreme of its range some 160 km inland. Across this geographic range mean annual temperatures vary from 13 to 21 °C and annual precipitation ranges from 720 to 1710 mm (HARWOOD 1989). The species is found in two main habitats, firstly riverine areas on moist alluvial soils and secondly at low densities in Araucarian vine forests which are generally restricted to basalt-derived soils of medium to high fertility, although stands of vine thicket carrying *G. robusta* also occur on fine-grained sedimentary parent material. Local populations are usually disjunct, separated by several kilometres from their neighbours, and small, with fewer than 100 reproductively mature individuals per population (HARWOOD *et al.* 1997). The large range of environments, reinforced by the marked local and regional disjunction of the

species, suggests the likelihood of strong genetic differentiation through natural selection for adaptation to local conditions. However, a survey of isozyme variation in 23 natural populations did not reveal strong regional patterns in genetic diversity or allelic frequency (HARWOOD *et al.* 1997).

Grevillea robusta has become well established in subtropical and tropical highland environments around the world over the last century (HARWOOD 1989). It is economically important in many countries, particularly in Africa and south Asia. Its first main use was as a shade tree for tea and coffee plantations, and it is now widely planted as a boundary tree and among crops on small farms. The branches are pruned to regulate shading and competition with adjacent crops, and are used for firewood and poles, with leaves used for mulch. The tree recovers well after heavy pollarding and pruning and the main trunk of the tree may be harvested as a small sawlog from age 12–25 years.

The breeding system in natural populations was found to be highly outcrossing from isozyme studies of progeny arrays (HARWOOD *et al.* 1992). Observations

and experimental studies in a planted stand in western Kenya (KALINGANIRE *et al.* 1996; KALINGANIRE *et al.* 2000) confirmed that the species is fully outcrossing and self-incompatible. Nectivorous birds are the principal pollinating agents (BROUGH 1933).

Relatively little is known about genetic variation in *G. robusta*. Seed collections from natural provenances are difficult, as the seed is shed from fragile capsules within a day or two of reaching maturity. Two trials in Rwanda on a set of seven provenances from Queensland demonstrated significant differences in early growth (KALINGANIRE & HALL 1993). Systematic collections from a wide range of natural provenances did not become available until 1990. Since then, results of trials testing these provenance have been reported from the Atherton Tablelands of north-east Queensland (SUN *et al.* 1995), northern Tanzania (MALIONDO *et al.* 1998) and north-eastern Argentina (LOPEZ *et al.* 1999). These studies have found significant differences in growth between the provenances tested, not all of which were common to the different trials. Significant differences between provenances in stem straightness were also demonstrated in all three trials in Argentina. To date, no information on variation in growth and stem form at the level of individual families has been published.

This paper reports growth and stem form of a *G.*

robusta provenance-family trial at Neerdie in coastal south-eastern Queensland. Estimates of provenance performance, heritabilities and genetic correlations are presented. The results obtained are compared with other published studies, and the implications for genetic improvement of *G. robusta* are considered.

METHODS AND MATERIALS

A total of 115 open-pollinated family seedlots of *G. robusta* from 27 different seed collections identified with CSIRO provenance seedlot numbers were available for field testing. Several of the CSIRO seedlots represented duplicate collections in different years from within the one local geographic area (less than 5 km in extent), so for the purpose of analysis these duplicate collections were grouped, giving a total of 23 geographically distinct provenances as shown in Table 1.

The trial was conducted at Neerdie (152°47'S, 25°59' E, 60 m asl) in the subtropical coastal lowlands of south-eastern Queensland. The nearby meteorological station at Toolara Forest Station, 5 km to the east, has a mean annual temperature of 20 °C, and a mean annual rainfall of 1328 mm with summer maximum rainfall (BUREAU OF METEOROLOGY 1988). The soil was a dermosol (ISBELL 1996), a soil type which

Table 1. Locations of *Grevillea robusta* provenances tested.

CSIRO Seedlot No.	Provenance name	Latitude (S)	Longitude (E)	Altitude (m)	No. of families
17957	Imbil	26° 29'	152° 37'	100	3
18614	Linville	26° 49'	152° 16'	140	1
17779	20 km NW Kilcoy	26° 50'	152° 30'	170	2
17778	Crows Nest	27° 16'	152° 04'	600	1
17952	Wivenhoe	27° 19'	152° 40'	70	2
17953	Samford	27° 20'	152° 50'	60	3
17700	Upper Beechmont	28° 08'	153° 11'	550	1
18971	Emu Vale	28° 14'	152° 17'	550	6
18616	Rathdowney	28° 15'	152° 51'	100	7
17699	Albert River	28° 16'	153° 16'	280	6
18967	Oxley River	28° 21'	153° 12'	80	6
17613, 18615, 18968*	Woodenbong	28° 26'	152° 45–47'	200	9
17612	Nimbin	28° 38'	153° 13'	50	2
17614	Duck Creek	28° 43'	152° 33'	200	5
17616, 18617*	Paddys Flat	28° 44'	152° 26'	180	4
17615	Bottle Creek	28° 48'	152° 39'	200	3
17617	Mummulgum	28° 50'	152° 49'	100	5
17618	Rappeville	29° 07'	152° 58'	40	5
17620	Mann River	29° 24'	152° 29'	60	12
18969	Cangai Creek	29° 33'	152° 29'	60	10
17619	Fine Flower	29° 33'	152° 40'	60	3
17621	McPhersons Cree	29° 48'	152° 54'	40	4
17622, 18970*	Boyd River	29° 52'	152° 27–30'	200	15

* Two or three CSIRO seed collections from the same locality, designated as the same provenance

supports natural stands of *G. robusta* nearby. The previous land use had been improved pasture for beef cattle production, so soil fertility levels were considered adequate and no fertilizer was applied at establishment.

Seeds were sown directly into 90 cm³ root trainers in December 1994, using a potting mix of 1/3 peat and 2/3 vermiculite, incorporating 2.5 kg·m⁻³ of Osmocote slow-release complete fertilizer, and raised in a nursery at Gympie to an average stem height of 25 cm before planting out in March 1995. The field trial used a latinized row-column design produced using the software package Alpha+ (WILLIAMS & TALBOT 1994). Each of the six replicates incorporated 115 plots set out in five rows and 23 columns, providing incomplete blocking in two dimensions. The six replicates were contiguous, and the design was latinized, so that no seedlot occurred twice in any one long column of 30 seedlots. There were three trees per plot, with spacing of 2.1 m between trees along columns, and 4 m between columns, giving total dimensions of 189 × 92 m. The trial was surrounded by a single external perimeter row of surplus *G. robusta* planting stock at the same spacing. The site was deep ripped and ploughed prior to planting. Woven polypropylene weed mat squares (0.9 m²) were placed around each tree immediately after planting and weed free conditions were maintained for 12 months. Subsequent to this, the interrows were periodically slashed to control grasses, vines and woody weeds. During 1997 the climbing weed Siratro (*Macroptilium atropurpreum*) invaded the site and damaged the form and height growth of 20 of the trees before weeding could be completed. These trees were excluded from the statistical analysis.

Measurements and/or assessments of the trial were conducted at 16, 26 and 52 months after planting. Tree height was measured to the nearest 0.1 m using height poles, and stem diameter at 1.3 m (dbh) was measured with a diameter tape to the nearest 0.1 cm. Stem form and other traits including axis persistence, stem straightness, branch angle of major branches, presence/absence of ramicornes, presence of flowering/fruitleting and overall tree health were visually assessed in July 1999. Of the assessed traits, only axis persistence and stem straightness are reported here as they alone displayed significant differences among provenances and/or families. Axis persistence was scored as follows: 1 = stem forks at ground level, 2 = stem forks in first ¼ of tree height, 3 = stem forks in second ¼ of tree height, 4 = stem forks in third ¼ of tree height, 5 = stem forks in fourth ¼ of tree height and 6 = stem remains unforked for entire tree height, with forking defined as having occurred when a second leader was greater than half the diameter of the main leader. Stem straightness was scored on a subjective 4-

point scale from 1 (least straight) to 4 (straightest), only for those trees with an axis persistence score of 4 or greater.

Most of the statistical analysis was carried out using the statistical software package Genstat 5.4 (PAYNE *et al.* 1987). Data sets were first screened for outlying individual-tree and plot values, and checks were made that residual error distributions from analysis of variance were normally distributed around zero. A very small number of trees which were clear outliers (no more than 5 trees for any one of the variates) were removed from the data sets prior to final analysis. A non-orthogonal fixed effects analysis of plot means, using the *fit* command in Genstat, tested a model incorporating replicate, column, replicate.row, replicate.column and family. This analysis showed that the incomplete blocking factors replicate.row and replicate.column accounted for a significant part of overall variation, and reduced the residual mean square, for all measures of height and dbh. For the traits of axis persistence and stem straightness, replicate.column was significant but replicate.row was not. Latinised long columns did not contribute to reducing the residual mean squares, so this blocking factor was dropped from the model. The next step was to run a mixed model on plot means using the *reml* command in Genstat, with replicates and provenances as fixed effects, and families, replicate.row and replicate.column as random effects, except that for variates axis persistence and stem straightness, the term replicate.row, being non-significant, was omitted from the model. This analysis provided best linear unbiased estimates of provenance means for each variate (WILLIAMS & MATHESON 1994). The statistical significance of differences among provenances was determined using Wald-statistics (PAYNE *et al.* 1987).

Within-provenance, individual-tree heritabilities h^2 , genetic correlations between traits and their standard errors, were calculated from mixed-model analysis carried out at the individual-tree stratum using the software program ASReml (GILMOUR *et al.* 1998). These calculations were done using a model with provenance and replicate set as fixed effects, and families and replicate.row and replicate.column as random effects. Heritabilities were also re-calculated with the incomplete blocking factors dropped from the model.

Heritabilities were derived from variance components as follows:

$$h^2 = \frac{\sigma_f^2/r}{\sigma_f^2 + \sigma_e^2}$$

where r is the coefficient of relationship among individuals within families, and σ_f^2 and σ_e^2 are the family and error variance components respectively. The coefficient of relationship, r , was set at 0.3, rather than the 0.25 applying to half-sib families, to account for there being a limited number of male parents contributing to open-pollinated *G. robusta* families, given the small effective population size in most natural provenances (HARWOOD *et al.* 1997). The error variance did not include the variances associated with incomplete blocks, because it was assumed that there would be adjustment of individual tree values for any field trend across incomplete blocks (as well as replicates), when ranking trees for selection. Phenotypic correlations between traits were calculated at the individual-tree stratum using the *correlate* command in GENSTAT.

RESULTS

Provenance means for height, diameter, axis persistence and stem straightness are shown in Table 2. Wald tests confirmed that for differences among provenances in height and diameter at all ages of measurement were highly significant ($P < 0.001$). Differences in axis persistence were also significant at $P < 0.001$, while differences in stem straightness were significant at the $P < 0.05$ level. Many of the provenances were poorly represented in the trial, with fewer than five families tested, so their performance could not be established with confidence.

Of the provenances with five or more families tested, the fastest-growing was Duck Creek, with a mean height of 7.57 m and mean dbh of 8.63 cm at 52 months, while the slowest-growing was Rappville, with height 6.43 m and dbh 6.97 cm. That with the best axis

Table 2. Provenance mean values for height (m), dbh (cm), axis persistence and stem straightness.

Provenance	Families	Height 16 month	Height 26 month	Dbh 26 month	Height 52 month	Dbh 52 month	Axis pers. 52 month	Stem str. 52 month
Imbil	3	2.81	3.87	3.85	7.53	8.88	4.66	2.61
Linville	1	2.76	3.90	3.57	7.62	9.01	5.42	2.77
Kilcoy	2	2.87	3.93	3.67	7.64	8.35	4.64	2.62
Crows Nest	1	2.73	3.93	3.55	7.09	8.21	3.88	2.45
Wivenhoe	2	2.65	3.89	3.46	7.85	7.85	4.08	2.73
Samford	3	2.53	3.63	3.43	7.16	7.93	3.82	2.42
Upper Beechmont	1	2.63	3.95	4.10	7.81	9.12	3.85	2.41
Emu Vale	6	2.75	4.03	3.83	7.65	8.43	4.80	2.51
Rathdowney	7	2.64	3.58	3.24	6.87	7.07	3.65	2.49
Albert River	6	2.83	3.91	3.66	7.53	7.76	4.64	2.57
Oxley River	6	2.73	3.87	3.73	7.50	8.24	4.16	2.50
Woodenbong	9	2.69	3.92	3.77	7.64	8.34	3.90	2.62
Nimbin	2	2.81	3.99	3.53	7.74	7.90	4.98	2.67
Duck Creek	5	2.83	3.91	3.98	7.57	8.63	4.36	2.49
Paddys Flat	4	2.92	4.22	4.03	7.91	8.62	4.91	2.49
Bottle Creek	3	2.87	4.06	3.96	7.98	8.81	5.06	2.66
Mummulgum	5	2.60	3.72	3.62	7.27	8.16	4.45	2.54
Rappville	5	2.69	3.52	3.35	6.43	6.97	4.41	2.44
Mann River	12	2.79	3.97	3.82	7.46	8.17	4.65	2.62
Cangai Creek	10	2.7	3.73	3.32	6.91	7.13	4.23	2.53
Fineflower	3	2.65	3.78	3.61	7.74	8.51	3.27	2.50
McPhersons Creek	4	2.76	3.92	3.75	7.50	8.49	4.93	2.58
Boyd River	15	2.72	3.83	3.41	7.02	7.29	4.42	2.61
		2.74	3.87	3.67	7.39	8.02	4.39	2.56
Standard error of provenance differences:								
average s. e.		0.09	0.14	0.24	0.31	0.49	0.42	0.11
maximum s. e.		0.16	0.25	0.44	0.55	0.87	0.74	0.19
minimum s. e.		0.04	0.07	0.12	0.11	0.23	0.20	0.05
Significance of diff. between provenances (Wald test)		$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.05$

persistence was Emu Vale (mean axis persistence score 4.80) and that with the worst was Woodenbong (3.90). Stem straightness differed little among these better-tested provenances, with Mann River best (mean stem straightness score 2.62) and Rapville worst (2.44).

Heritabilities and genetic and phenotypic correlations are shown in Table 3. Within-provenance, individual-tree heritabilities for height and diameter were moderate to high (0.42–0.76), while that for axis persistence was much lower at 0.11. Examination of the variance components from which the heritabilities were calculated showed that between-plot variance components were small, relative to between-family and within-plot components, for all traits analysed. The heritability for stem straightness was non-significant at 0.02, so this variate was excluded from calculation of genetic and phenotypic correlations. When the trial was analysed as a randomised complete block design, excluding the incomplete blocking factors replicate.row and replicate.column from the statistical model, heritabilities for height and dbh were lower by from 1 to 11 percentage points, but that for axis persistence was the same. Genetic and phenotypic correlations between height and dbh, and age-age correlations for both height and dbh, were high, at least 0.7, except where the first height measurement at 16 months was involved. Correlations between growth traits and axis persistence at 52 months were also positive, but lower.

DISCUSSION

The overall mean tree size attained in our trial, height 7.39 m and dbh 8.02 cm at age 52 months, is a typical early growth rate for *G. robusta* planted in a suitable soil and climate in subtropical latitudes (HARWOOD 1989). Of those provenances that were well-represented, with five or more families in the trial, Duck Creek (CSIRO 17614) displayed the greatest dbh at 52 months. This was also the outstanding provenance across three provenance trials in northern Argentina (LOPEZ *et al.* 1999), and it was above-average in two trials in Tanzania (MALIONDO *et al.* 1998) and two trials in north Queensland, Australia (SUN *et al.* 1995). The Neerdie trial does not test the full natural range of *G. robusta*. Provenances from elevations above 600 m in the north-west of the natural distribution (Bunya Mountains and Porters Gap) were not available for planting. In the Argentine trials, CSIRO 17694 Bunya Mountains displayed below-average growth, and CSIRO 17694 Porters Gap was the slowest-growing provenance. The two provenance trials in north Queensland also showed similar low growth rankings for these two provenances. Apart from the poor performance of the high-elevation provenances, there does not appear to be any consistent geographic trend in provenance performance of *G. robusta*. For those provenances which were reasonably well-represented in the Neerdie trial, with 5 or more families tested, regressions of provenance means on latitude, longitude and

Table 3. Within-provenance individual-tree heritabilities (bold, on diagonal, with standard errors in brackets), within-provenance genetic correlations (above diagonal) and phenotypic correlations (below diagonal) for *G. robusta* in the provenance-family trial at Neerdie. Heritabilities in italics are calculated using a randomised complete block model, ignoring incomplete blocks within replicates.

	Ht 16 months	Ht 26 months	Dbh 26 months	Ht 52 months	Dbh 52 months	Axper 52 months
Ht 16 months	0.45 (0.08) <i>0.42</i> (0.08)	0.85 (0.04)	0.64 (0.08)	0.74 (0.06)	0.62 (0.08)	0.38 (0.17)
Ht 26 months	0.79	0.65 (0.10) <i>0.56</i> (0.09)	0.90 (0.02)	0.88 (0.03)	0.85 (0.04)	0.29 (0.17)
Dbh 26 months	0.73	0.86	0.61 (0.10) <i>0.57</i> (0.09)	0.79 (0.05)	0.92 (0.02)	0.22 (0.18)
Ht 52 months	0.52	0.70	0.65	0.87 (0.12) <i>0.82</i> (0.11)	0.89 (0.03)	0.18 (0.17)
Dbh 52 months	0.56	0.72	0.82	0.80	0.74 (0.11) <i>0.74</i> (0.10)	0.19 (0.09)
Axper 52 months	0.33	0.32	0.40	0.21	0.39	0.11 (0.05) <i>0.12</i> (0.04)

altitude of provenance origin did not reveal any significant geographic trends in growth performance or stem form traits. Substantial differences in height and dbh at 52 months were evident between some nearby provenances, for example Mann River and Cangai Creek, separated by less than 20 km. However, many natural provenances remain unsampled, and the small effective population size of most provenances (typically fewer than 100 reproductively mature trees in a local population: HARWOOD *et al.* (1997)) makes it impossible to obtain seed from the 10–20 well-spaced trees considered necessary to give a representative sample of a provenance (FAO 1995). The moderate to high heritabilities for growth traits (Table 3) reflect substantial variation between families within provenances, so poorly sampled provenance will have means subject to substantial sampling errors.

The within-provenance individual-tree heritabilities for height and dbh estimated in this trial (0.45–0.87) are the first available for *G. robusta*. These heritabilities are much higher than the low to moderate heritabilities generally found for growth traits in open-pollinated progeny trials of other angiosperm genera such as *Eucalyptus* (POTTS & WILTSHIRE 1997). While caution is required in interpreting the heritabilities obtained from a single trial, three factors are believed to be contributing to these high heritabilities for growth traits. The first is the breeding system of *G. robusta*. A coefficient of relationship of 0.3 within open-pollinated *G. robusta* families has been used for the estimation of additive genetic variance and heritabilities. *Grevillea robusta* is bird-pollinated (BROUGH 1933, KALINGANIRE *et al.* 1996). An isozyme study (HARWOOD *et al.* 1992) provided multi-locus estimates of outcrossing rates for two of the natural provenances, Emu Vale ($t = 0.97 \pm 0.03$) and Woodenbong ($t = 0.86 \pm 0.03$). The small degree of inbreeding detected in the Woodenbong provenance in the isozyme study derives from neighbourhood inbreeding associated with mating among relatives, rather than selfing. Controlled pollination studies (KALINGANIRE *et al.* 2000) demonstrated conclusively that the species is an obligate outcrosser with a stigmatic barrier to self-fertilization. The absence of any selfed plants displaying very poor performance may be reducing variance within *G. robusta* families relative to open-pollinated families of genera with a mixed mating system, such as *Eucalyptus*, which include a proportion of selfs (POTTS & WILTSHIRE 1997), thus contributing to the observed higher heritabilities in *G. robusta*. However, because of the small size of natural provenances of *G. robusta* and the geographic separation of individual provenances, there may be very few fathers contributing pollen to the majority of the open-pollinated families. If the coefficient of relationship

were set higher, at say 0.33 (equivalent to equal pollen contributions from each of three male parents to an average family), this would reduce the heritabilities by 10 % from the estimates shown in Table 3.

The second factor contributing to high heritabilities for growth traits is the use of a trial design with two-dimensional incomplete blocking. This reduces the error variance component, by separating out variance associated with differences between the incomplete blocks, which are estimated as random effects (WILLIAMS & MATHESON 1994). The incomplete block variance components are excluded from the estimate of phenotypic variance used in the calculation of heritability since in any selection procedure the rankings of individual trees in the trial would be adjusted for incomplete block effects (as they would for replicate effects, which are also excluded from the error variance). The ratio of additive genetic variance to residual variance and hence the heritability may thereby be increased. This contribution of the incomplete blocking factors increases the heritabilities of some of the growth traits by up to 9 % (height at 26 months), relative to those obtained by analysing the trial as a randomised complete block design (Table 3). If provenance is not declared as a fixed effect in the statistical model used to calculate heritabilities, they increase by up to 20 percentage points over the values shown in Table 3 (data not presented). Such higher values are incorrect, because additive genetic variances would be incorrectly estimated since differences in the pollen pools of the different provenances would not be accounted for (WILLIAMS & MATHESON 1994).

The family plot size of three trees was small, so competition between adjacent plots, suppressing the growth of poorer families and thus inflating the differences between families, is another factor that may have contributed to the observed high heritabilities for growth traits, particularly at age 52 months. However, heritabilities for height and dbh in our trial were already high at age 26 months, before significant competition effects had set in. The low to moderate heritabilities for growth traits typical for other forest tree species have also been estimated mostly from progeny trials using small family plot sizes (single-tree plots or row plots).

Substantial differences between families within provenances underlie the high heritabilities for growth traits. Thus, for example, family mean dbh at 52 months in the six families of the Oxley River provenance ranged from 6.8 cm to 10.2 cm. This variation is in addition to the significant differences between provenances. There is clearly excellent potential for gain in vigour of *G. robusta* plantations through provenance selection and subsequent genetic improvement programs. Significant genetic variation in stem axis

persistence and stem straightness shows there is also some potential for genetic improvement in these traits.

Seed from identified superior natural provenances of *G. robusta* is expensive to collect, and quantities that can be collected are insufficient to meet current demand. Only a few kilograms of seed can be collected annually from some provenances, even if all seed-bearing trees in the provenance are sampled (CSIRO, unpublished records). Genetic improvement programs are therefore justified for this economically important species. The provenance-family trial at Neerdie is being developed into a seedling seed orchard by selective thinning, and it is hoped that it will provide a diverse genetic base of seed for use in breeding programs elsewhere.

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