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# Analysis of Mendelian inheritance and genetic linkage in microsatellite loci of *Eucalyptus urophylla* S.T. Blake

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**ABSTRACT**. *Eucalyptus urophylla* is an important species in the Brazilian forest sector due to its rapid growth rates and resistance to disease. The aim of this study was to verify Mendelian inheritance, genetic linkage, and genotypic disequilibrium for 15 microsatellite loci, with the goal of producing a robust set of genetic markers. Mendelian inheritance and genetic linkage analyses were carried out using genotypes from maternal trees, and their open-pollinated seeds and genotypic disequilibrium were assessed using adult trees. By comparing heterozygous maternal genotypes and their seeds, we found no significant deviations from the expected 1:1 Mendelian segregation and the expected 1:1:1:1 segregation hypothesis for pairwise loci. For adult trees, we did not find strong evidence of genotypic imbalance for pairwise loci. Our results indicated that the analyzed set of

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microsatellite loci could be used to carry out analyses of genetic diversity, mating system, and parentage in *E. urophylla*.

**Key words:** Eucalypt; Genetic markers; Population genetics; Seed orchards; Tree breeding

# INTRODUCTION

The impact of classic quantitative genetics on Brazil's high productivity levels in *Eucalyptus* planted forests is indisputable. However, in the last 25 years, possibilities for further progress have arisen due to technological advancements in molecular markers, sequencing methods, and genetic engineering (Harfouche et al., 2014; Barabaschi et al., 2016). Single sequence repeats (SSR) have been used since 1996 as an auxiliary tool to inform genetic improvement and conservation plans (Byrne et al., 1996), providing essential information on levels of genetic diversity within and among populations, inbreeding, effective population size, breeding system, and gene flow. Among the species cultivated in tropical climate regions, *Eucalyptus urophylla* is planted commercially as a pure species or as a hybrid, mainly with *E. grandis* (Hodge and Dvorak, 2015). The wood can be used in civil construction and pulp and cellulose production (Carvalho et al., 1998). The species is also resistant to diseases such as eucalyptus rust (*Puccinia psidii*), wilt (*Ceratocystis fimbriata*), and cancers (*Chrysoporthe cubensis* and *Coniothyrium zuluense*) (Carvalho et al., 1998).

SSR markers have been used extensively due to their codominant inheritance and high locus polymorphism (Grattapaglia et al., 2012; Randall et al., 2015). However, it is critical to confirm if SSR loci employed in population genetic analyses are in fact genetic markers. These markers cannot suffer from segregation distortions and genetic association between loci, as this would negate the principle of random association between alleles of different loci and generate redundant information. Thus, we assess the Mendelian inheritance, genetic linkage, and genotypic disequilibrium for 15 SSR loci of *E. urophylla* to develop a robust set of genetic markers for genetic diversity, inbreeding, and parentage analyses.

# **MATERIAL AND METHODS**

Two seed orchards of *E. urophylla* (SO1, SO2) and a progeny test (PT) were used for the analyses. The study populations are installed in the Teaching, Research and Outreach Farm (FEPE), Ilha Solteira Faculty of Engineering (FEIS/UNESP), in the municipality of Selvíria, Mato Grosso do Sul State, Brazil. For DNA analysis, we sampled leaves from 79 and 298 adult trees in SO1 and SO2, respectively. In PT, we sampled 605 seedlings (denominated seeds) from 23 mother trees. The extraction and purification of the DNA were performed based on the CTAB method (Doyle and Doyle, 1987) and amplification was performed using PCR (polymerase chain reaction), with minor modifications to the protocol (see Faria et al., 2011). For the genotyping of individuals, we used EMBRA microsatellite markers (Brondani et al., 1998, 2006): 15 SSR loci for SO2 and PT; and 13 common SSR loci for SO1. The genetic characterization was performed in multiplex systems, with multi-fluorescence detection, in an ABI 3100XL automatic capillary sequencer. Raw genotypic data (electropherograms) were exported from the sequencer using the Genotyper software (Applied Biosystems) and adjusted to unity using the TANDEM software (Matschiner and Salzburger, 2009). Molecular analyses were performed at the Hereditas/Genomax Laboratory in Brasília, Brazil.

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To investigate the Mendelian inheritance of the SSR loci, we compared maternal heterozygous mother tree genotypes with their seeds, using the method described by Gillet and Hattemer (1989). The assumptions of the method are that the loci have regular segregation and their alleles follow Mendelian inheritance patterns, which are based on the following conditions: i) regular meiotic segregation during ovule production; ii) random fertilization of ovules by each type of pollen; iii) absence of differential selective viability in the progenies prior to the investigation by genetic markers; iv) a co-dominant relationship between alleles. The method further requires that all progeny of a tree possess a maternal allele. In cases of a heterozygous mother tree (e.g.,  $A_i A_j$ ,  $i \neq j$ ), the following are required: a) each one within progeny must have one allele of the maternal tree,  $A_i$  or  $A_j$ ; b) the number of heterozygous progeny  $A_i A_j (n_{ij})$  must be equal to the sum of the number of homozygous progeny  $A_i A_i (n_{ik})$  and  $A_j A_j (n_{ij})$ :  $n_{ij} = n_{ii} + n_{jj}$ ; and c) the number of heterozygous progeny  $A_i A_k (n_{ik})$  must be equal to the number of heterozygous progeny  $A_i A_k (n_{ik})$  must be equal to the number of heterozygous progeny  $A_i A_k (n_{ik})$ , or  $n_{ik} = n_{jk}$ , in other words,  $k \neq i, j$ . The observed segregation of each progeny from a heterozygous maternal tree for a given locus was statistically compared to that expected for the segregation hypothesis of 1:1, using the *G*-test (Sokal and Rohlf, 1981):

$$G = 2\left[n_{ij}\ln\left(\frac{n_{ij}}{E(n1)}\right) + (n_{ii} + n_{ij})\ln\left(\frac{(n_{ii} + n_{jj})}{E(n1)}\right)\right]$$
(Equation 1)

where ln is the natural logarithm, E(n1) is the expected number of offspring genotypes  $A_i A_j$  $(n_{ij})$  and  $A_i A_i + A_j A_i (n_{ij} + n_{ij})$ :  $E(n1) = 0.5(n_{ij} + n_{ij} + n_{ij})$ , or:

$$G = 2 \left[ n_{ik} \ln\left(\frac{n_{ik}}{E(n2)}\right) + n_{jk} \ln\left(\frac{n_{jk}}{E(n2)}\right) \right]$$
 (Equation 2)

where E(n2) is the expected number of genotypes for alleles  $A_i A_k(n_{ik})$  and  $A_j A_k(n_{jk})$ :  $E(n2) = 0.5(n_{ik} + n_{jk})$ . To avoid false positives, the *G*-test was determined only when n1 and n2 were  $\ge 15$ . Deviation from the *G*-test between the observed and expected segregation was determined as statistically significant using the Bonferroni correction for multiple comparisons (95%,  $\alpha = 0.05$ ).

To determine if the loci were genetically linked, we tested pairs of loci using genetic information from mother trees that were doubly heterozygous for two loci  $(A_i A_j, B_i B_m)$ . The segregation was recorded in their progeny. In this case, the null hypothesis  $(H_0)$  was a normal Mendelian segregation of 1:1:1:1. The normal segregation hypothesis between pairs of loci was accepted or rejected based on a maximum likelihood *G*-test (Sokal and Rohlf, 1981) performed for each progeny:

$$G = 2\left[n_{il}\ln\left(\frac{n_{il}}{E(n)}\right) + n_{im}\ln\left(\frac{n_{im}}{E(n)}\right) + n_{jl}\ln\left(\frac{n_{jl}}{E(n)}\right) + n_{jm}\ln\left(\frac{n_{jm}}{E(n)}\right)\right]$$
(Equation 3)

where  $n_{ip}$ ,  $n_{im}$ ,  $n_{jl}$ , and  $n_{jm}$  are the observed numbers of phenotypes  $A_i B_l$ ,  $A_i B_m$ ,  $A_j B_l$ , and  $A_j B_m$ , respectively, and E(n) is the expected number of each genotype  $A_i B_l$ ,  $A_i B_m$ ,  $A_j B_l$ , and  $A_j B_m$ , calculated by  $E(n) = 0.25(n_{il} + n_{im} + n_{jl} + n_{jm})$ . Again, we applied the Bonferroni correction for multiple comparisons (95%,  $\alpha = 0.05$ ) to avoid false positives.

The genotypic disequilibrium test between pairwise loci was only performed for adult samples. Estimates of gene frequencies based on open-pollinated progeny arrays are biased because each progeny has at least one maternal allele, resulting in genotypic disequilibrium. This

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analysis was carried out using the FSTAT 2.9.3.2 software (Goudet, 2002). The probabilities of the significance test were obtained by permutation of alleles among individuals, associated with a Bonferroni correction for multiple comparisons (95%,  $\alpha = 0.05$ ).

# RESULTS

No deviation from 1:1 Mendelian segregation was detected for 13 of the 15 microsatellite loci (86.6%) analyzed for progenies of heterozygous maternal trees (Table 1). Significant deviations were identified in two cases: EMBRA2 (18.29) for tree 95 and EMBRA63 (12.67) for trees 10 and 155. Of the 733 *G*-tests carried out for pairwise loci, only 26 (3.5%) were significantly different than expected under the hypothesis of 1:1:1:1 independent Mendelian segregation (Table 2). As

								21	1 2				
Mother	$n_1$	$n_{ii}: n_{ii} + n_{ii}$	$G_1$	$n_2$	$n_{ik}$ : $n_{ik}$	$G_2$	Mother	n <sub>1</sub>	$n_{ii}: n_{ii} + n_{ii}$	$G_1$	<i>n</i> <sub>2</sub>	$n_{ik}$ : $n_{ik}$	$G_2$
EMBRA2		9 10		-	j.:	-	EMBRA12		9 9		-		-
10, 21, 86	66	26:40	2.99	10	5:5	NE	10, 212	18	11:7	0.90	41	14:27	4.19
20, 45	40	18:22	0.04	20	15:5	5.25	20	11	6:5	NE	19	11:8	0.48
55	21	14:7	2.38	6	6:0	NE 18.20*	45	18	10:8	0.22	12	7:5	NE
95	17	4:5	0.53	23	21:2	18.29* NE	55 86 95 458 2473	50	24:26	0.48	43	2:6	0.58
116	23	13:10	0.39	7	3:4	NE	101	26	16:10	1.40	4	0:4	NE
155	10	5:5	NE	20	14:6	3.29	104	7	5:2	NE	18	13:5	3.68
212, 2612	38	13:25	3.86	20	14:6	3.29	116	18	10:8	0.22	12	3:9	NE
214	11	2:9	NE	19	14:5	4.44	118	11	8:3	NE	17	4:13	5.02
EMBRA3	20	0:11	0.20	6	2:4	NE	155, 2612	25	18:7	5.01	31	14:17	0.29
10.86.155	12	5.11	NE	67	46:21	9.56	533	11	8:3	NE	19	6:13	2.64
20, 2612	18	9:9	0	41	19:22	0.22	EMBRA28		0.5			0.15	2.04
21, 513	9	0:9	NE	47	23:24	0.02	1	19	9:10	0.05	6	5:1	NE
45	6	1:5	NE	24	15:9	1.52	10	12	6:6	NE	18	4:14	5.88
55	4	2:2	NE	23	16:7	3.62	21	2	1:1	NE	24	8:16	2.72
95	3	1:2	NE 0.(2	27	19:8	4.61	45	19	12:7	1.33	11	2:9	NE 0.20
104, 236	20	3.8	0.62 NE	19	10:0	4.72	101	22	15:7	2.08	23	7:1	0.39 NE
EMBRA10		5.0	116		10.7	0.05	104	7	3:4	NE	18	11:7	0.90
533	19	9:10	0.05	11	5:6	NE	116	11	6:5	NE	19	8:11	0.48
2612	6	4:2	NE	22	11:11	0	155	17	5:12	2.97	13	8:5	NE
EMBRA11							212	2	0:2	NE	28	17:11	1.30
10	12	5:7	NE	18	9:9	0	214	10	0:10	NE	20	12:8	0.80
45 86	35	22:13	2.34	15	8.7	0.07	236	13	2:4	NE	16	9.8	0.06
55	16	11:5	2.34	15	2:9	NE	458	9	4:5	NE	21	13:8	1.20
EMBRA38							EMBRA157						
21	7	0:7	NE	19	11:8	0.48	2612	18	4:14	5.88	9	4:5	NE
45	22	11:11	0	8	5:3	NE	EMBRA204	10					NE
55, 65, 95, 101, 104	95	47:46	0.01	3/	18:21	0.23	10	18	6:12	2.04	12	7:5	NE 1.21
116 241	42	23:19	0.38	18	7:11	0.36	20, 2612	50	4:1	3.40 NE	21	12:18	0.05
155	23	9:14	1.10	7	5:2	NE	45	23	7:16	3.62	7	4:3	NE
212	2	0:2	NE	27	10:17	1.84	95, 212	11	6:5	NE	48	17:31	4.14
214	18	5:13	3.68	10	5:5	NE	116	11	8:3	NE	19	6:13	2.64
EMBRA63							118	18	10:8	0.22	12	12:0	NE
10, 155	35	11:24	4.95	25	4:21	12.67* NE	155	19	7:12	1.33	11	6:5	NE 6.28
55	21	7:14	2.38	6	2:4	NE	458	50	2:4	0.11	24	9:15	1.52
95.241	46	27:19	1.40	14	10:4	NE	EMBRA210						100
104	6	1:5	NE	19	11:8	0.48	21	8	5:3	NE	19	8:11	0.48
2612	21	8:13	1.20	7	2:5	NE	45	18	12:6	2.04	13	7:6	NE
EMBRA128	10	AL 37	2.00				55	7	5:2	NE	20	9:11	0.20
1, 116, 214	5/	21:56	3.99 NE	27	0:15	0.04	95	5	3:2	NE	23	8:15	2.16
21	16	4.12	4.19	10	4.6	NE.	118	19	10:9	0.05	11	4.7	2.98 NE
118	11	3:8	NE	19	4:15	6.78	155	14	7:7	NE	16	9:7	0.25
212	23	5:18	7.80	7	4:3	NE	212	13	10:3	NE	15	6:9	0.60
EMBRA157							214	18	9:9	0	12	12:0	NE
20, 45, 118, 212	72	23:49	9.60	47	23:24	0.02	533	20	12:8	0.80	10	4:6	NE
21, 116	49	4:13	5.02	2	2:5	NE							
95	6	3:3	NE	24	17:7	4.30							
458	11	1:10	NE	19	8:11	0.48							
EMBRA219							EMBRA681						
1, 101	45	24:21	0.20	11	8:3	NE	10	11	2:9	NE	19	12:7	1.33
20 21 55 116 155 2612	13	4:9	NE 8 20	75	7:10	0.53	45	19	13:6	2.64 NE	19	3:8	NE 0.22
45	30	12:5	2.97	13	4.9	NE.	118	15	8.7	0.07	15	12:3	5.78
95	13	7:6	NE	17	6:11	1.49	155	20	12:8	0.80	10	1:9	NE
118	15	7:8	0.07	15	6:9	0.60	212	15	8:7	0.07	14	9:5	NE
214	12	4:8	NE	18	9:9	0	533	15	7:8	0.07	14	8:6	NE
236	15	8:7	0.07	8	4:4	NE	2612	9	3:6	NE	19	10:9	0.05
459	16	6:14	1.00	8	2:3	NE							
EMBRA333	10	0.10	1.01	1.4	11.5	1915	+				1	1	
1	20	14:6	3.29	5	3:2	NE	1		1		l	1	
10	22	6:16	4.72	8	3:5	NE						1	
21	15	7:8	0.07	14	6:8	NE							
45, 2612	29	11:18	1.71	29	17:12	0.87						<u> </u>	
101	23	16:7	3.62 NE	20	5:2	NE						1	
155	19	2:9	0.05	20	11:0	NE	+	t			l	+	
214	7	0:7	NE	23	13:10	0.39						1	
241	22	9:13	0.73	8	2:6	NE							
53+000000000000000000000000000000000000	24	10:14	0.67	6	0:6	NE							

Table 1. Mendelian inheritance tests	s for 15 microsatel	lite loci in Euca	lyptus urophylla.
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 $n_1$  and  $n_2$  are the sample size;  $G_1$  and  $G_2$  are the maximum likelihood G statistics for the hypothesis of  $n_{ij}n_{ij}+n_{ij}$  and  $n_{ik}n_{jk}$ , respectively, for one degree of freedom. \*Significance after Bonferroni correction for  $\alpha = 0.05$  ( $\chi^2 = 10.83$ ). NE is not estimated due to a sample size of less than 15 progeny.

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*******	G	Mother	G	Mothar	G	Mothar	G	Mathar	G
EMBRA2xEMBR	A28	EMBRA2xEN	/BRA11	EMBRA2x	EMBRA63	EMBRA28x	EMBRA3	EMBRA28	xEMBRA10
10	12.04	55	2.96	2612	5.61	214	0.58	55	0.80
21	3.97	86	1.46	EMBRA2x	EMBRA12	236	1.26	86	0.95
45	5.26	104	9.28	10	2.87	241	5.33	101	2.31
55	0.25	116	3.70	20	3.58	458	0.24	104	8.73
86	3.19	155	6.67	21	2.46	2473	1.27	116	0.05
104	13.72	212	2.19	45	2.02	EMBRA28x	EMBRA11	155	2.95
116	2.04	2612	4.27	55	6.15	1	2.82	212	1.07
155	6.43	EMBRA2xEN	ABRA10	86	2.60	10	11.05	214	23.68*
212	3.05	10	10.90	95	20.79*	21	1.8/	236	9.23
Z14	4.69	20	7.50	104	10.58	45	3.82	241	4.34
10	0.57	21	3.07	110	7.49	86	0.30	438	0.67
20	2.60	45	2.70	212	/.40	101	1.30	EMDD 4 29	VEMDD A62
20	2.09	86	5.60	212	5.99	101	3.31	10	31.82*
45	1.30	104	5.19	2612	1.79	116	3.00	21	4 23
55	8.02	155	7.09	EMBRA28	xEMBRA3	155	4 53	45	3.61
86	6.62	212	1 94	1	1.37	212	1.76	55	6.34
95	21.19*	214	NE	10	11.57	214	0.58	101	0.95
104	16.94*	2612	1.51	21	5.20	236	9.74	104	4.34
116	1.19	EMBRA2xEM	/BRA63	45	3.89	241	4.36	155	15.37
155	7.77	10	19.51*	55	3.32	458	4.06	241	4.38
2612	1.98	21	5.54	86	2.89	2473	0.12	2473	5.27
EMBRA2xEMBRA	A11	45	4.89	101	1.11	EMBRA28x	EMBRA10	EMBRA28	xEMBRA12
10	0.49	55	9.26	104	2.85	1	2.42	10	7.74
20	3.78	95	20.39*	116	1.53	10	11.97	21	6.28
21	2.43	104	5.36	155	5.44	21	7.59	45	3.38
45	1.17	155	10.62	212	1.62	45	3.03	55	1.96
Mother	G	Mother	G	Mother	G	Mother	G	Mother	G
EMBRA28xEMBF	RA12	EMBRA3xEN	ABRA11	EMBRA3x	EMBRA63	EMBRA3xE	MBRA157	EMBRA11	xEMBRA10
86	0.20	86	1.48	45	6.57	21	3.18	55	2.97
101	0.49	104	10.39	55	5.56	45	2.16	65	0.88
104	2.61	116	2.40	95	7.34	65	0.6/	86	3.25
116	0.57	155	17.28*	104	3.28	95	7.46	101	5.08
212	1.02	230	15.57	155	2.02	226	2.00	104	3.33
212	4.13	2612	5.44	24/3	3.25	230	7.90	212	2.47
214	6.06	EMDD A 2vEN	J.44	EMDD A 2v	EMDD A 12	2473	2.57	212	15.08
458	2.87	LINDRAJALI	0.73	10	4 27	EMBR A 3xE	MBR A 204	230	2.11
2473	0.29	10	5.88	20	0.28	10	3 49	458	3.98
EMBRA28xEMBR	RA157	20	8.10	20	2.22	20	10.22	533	0.18
20	4.07	21	6.25	45	1.03	21	5.85	2612	1.79
45	3.01	45	6.95	55	5.27	45	4.59	EMBRA11	xEMBRA63
116	3.52	55	6.46	65	0.73	55	4.56	10	18.32*
212	4.58	65	0.45	86	4.72	86	9.77	21	8.69
236	5.15	86	5.94	95	8.26	95	8.17	45	4.79
458	2.70	104	2.60	104	5.89	116	1.43	55	11.37
2473	1.07	155	8.57	116	1.34	155	5.83	101	3.54
EMBRA3xEMBR/	A11	236	10.65	155	4.91	533	3.57	104	4.54
10	4.58	533	3.79	236	3.17	2612	5.20	118	1.65
20	0.07	2473	1.26	533	5.56	EMBRA11x	EMBRA10	155	12.79
21	7.03	2612	0.80	2473	0.29	143	6 0 8	0.1.1	1.00
45	2.92		(DD 4 CA	2.12	0.27	10	0.70	241	4.60
- 55	4.47	EMBRA3XEN	/BRA63	2612	1.12	20	6.88	241 2612	4.60 3.52
0.5	0.08	EMBRA3XEM 10	ABRA63 18.98*	2612 EMBRA3xF	1.12 EMBRA157	20	6.88 6.79	241 2612 EMBRA11	4.60 3.52 xEMBRA12
Mother	0.08	EMBRA3XEN 10 21 Mother	ABRA63 18.98* 7.61	2612 EMBRA3xI 20 Mother	1.12 EMBRA157 4.20	20 21 45 Mather	6.88 6.79 2.64	241 2612 EMBRA11 10	4.60 3.52 xEMBRA12 13.37
Mother EMBRA11xEMBE	0.08 G	10 21 Mother EMBRA11xEN	MBRA63 18.98* 7.61 G 4BRA157	2612 EMBRA3xI 20 Mother EMBRA11x	1.12 EMBRA157 4.20 G EMBRA219	20 21 45 Mother EMBRA10x	6.88 6.79 2.64 <i>G</i> EMBR 412	241 2612 EMBRA11 10 Mother EMBRA10	4.60 3.52 xEMBRA12 13.37 <i>G</i> (EMBR A 204
Mother EMBRA11xEMBF 20	0.08 G RA12 0.38	EMBRA3XEN 10 21 Mother EMBRA11XEN 458	MBRA63 18.98* 7.61 G 4BRA157 2.61	2612 EMBRA3xi 20 Mother EMBRA11x 116	1.12 EMBRA157 4.20 G EMBRA219 4.63	20 21 45 Mother EMBRA10xl	6.88 6.79 2.64 G EMBRA12 1.35	241 2612 EMBRA11 10 Mother EMBRA10x 45	4.60 3.52 xEMBRA12 13.37 <i>G</i> EMBRA204 3.00
Mother EMBRA11xEMBR 20 21	0.08 G RA12 0.38 4.83	EMBRA3XEN 10 21 Mother EMBRA11xEN 458 2612	MBRA63 18.98* 7.61 G MBRA157 2.61 0.53	2612 EMBRA3xl 20 Mother EMBRA11x 116 118	1.12 EMBRA157 G EMBRA219 4.63 6.34	20 21 45 Mother EMBRA10xl 86 101	6.88 6.79 2.64 <i>G</i> EMBRA12 1.35 2.13	241 2612 EMBRA11 10 Mother EMBRA10 45 55	4.60 3.52 xEMBRA12 13.37 G EMBRA204 3.00 2.75
Mother EMBRA11xEMBR 20 21 45	0.08 G A12 0.38 4.83 0.81	EMBRA3XEN 10 21 Mother EMBRA11XEN 458 2612 EMBRA11XEN	MBRA63 18.98* 7.61 <i>G</i> MBRA157 2.61 0.53 4BRA204	2612 EMBRA3xJ 20 Mother EMBRA11x 116 118 155	1.12 EMBRA157 4.20 G EMBRA219 4.63 6.34 0.88	20 21 45 Mother EMBRA10x1 86 101 104	6.88 6.79 2.64 <i>G</i> EMBRA12 1.35 2.13 1.83	241 2612 EMBRA11 10 Mother EMBRA10 45 55 86	4.60 3.52 xEMBRA12 13.37 G EMBRA204 3.00 2.75 9.11
Mother           EMBRA11xEMBF           20           21           45           55	0.08 G AA12 0.38 4.83 0.81 3.33	EMBRA3XEN 10 21 Mother EMBRA11xEN 458 2612 EMBRA11xEN 10	MBRA63 18.98* 7.61 G MBRA157 2.61 0.53 MBRA204 1.96	2612 EMBRA3xl 20 Mother EMBRA11x 116 118 155 236	1.12 EMBRA157 G EMBRA219 4.63 6.34 0.88 10.04	20 21 45 Mother EMBRA10xl 86 101 104 155	6.88 6.79 2.64 G EMBRA12 1.35 2.13 1.83 3.49	241 2612 EMBRA11 10 Mother EMBRA102 45 55 86 155	4.60 3.52 xEMBRA12 13.37 <i>G</i> EMBRA204 3.00 2.75 9.11 1.73
Mother           EMBRA11xEMBF           20           21           45           55           65	0.08 G A12 0.38 4.83 0.81 3.33 0.62	EMBRA3XEN 10 21 Mother EMBRA11XEN 458 2612 EMBRA11XEN 10 20	MBRA63 18.98* 7.61 G MBRA157 2.61 0.53 4BRA204 1.96 1.00	2612 EMBRA3xl 20 Mother EMBRA11x 116 118 155 236 241	1.12 EMBRA157 4.20 G EMBRA219 4.63 6.34 0.88 10.04 0.69	20 21 45 Mother EMBRA10x1 86 101 104 155 212	6.88 6.79 2.64 G EMBRA12 1.35 2.13 1.83 3.49 5.04	241 2612 EMBRA11 10 Mother EMBRA100 45 55 86 155 212	4.60 3.52 xEMBRA12 13.37 <i>G</i> :EMBRA204 3.00 2.75 9.11 1.73 3.87
Mother           EMBRA11xEMBF           20           21           45           55           65           86	0.08 G A12 0.38 4.83 0.81 3.33 0.62 3.82	EMBRA3XEN 10 21 Mother EMBRA11XEN 458 2612 EMBRA11XEN 10 20 21	MBRA63 18.98* 7.61 G MBRA157 2.61 0.53 ABRA204 1.96 1.00 2.83	2612 EMBRA3xl 20 Mother EMBRA11x 116 118 155 236 241 458	1.12           EMBRA157           4.20           G           EMBRA219           4.63           6.34           0.88           10.04           0.69           11.61	20 21 45 Mother EMBRA10xl 86 101 104 155 212 214	6.88 6.79 2.64 G EMBRA12 1.35 2.13 1.83 3.49 5.04 NE	241 2612 EMBRA11 10 Mother EMBRA100 45 55 86 155 212 212 214	4.60 3.52 xEMBRA12 13.37 <i>G</i> EEMBRA204 3.00 2.75 9.11 1.73 3.87 3.6.71*
Mother           EMBRA11xEMBF           20           21           45           55           65           86           101	0.08 G A12 0.38 4.83 0.81 3.33 0.62 3.82 2.87	EMBRA3xE8 10 21 Mother EMBRA11xEN 458 2612 EMBRA11xEN 10 20 21 45	MBRA63 18.98* 7.61 <i>G</i> MBRA157 2.61 0.53 ABRA204 1.96 1.00 2.83 1.79	2612 EMBRA3xJ 20 Mother EMBRA11x 116 118 155 236 241 458 2612	1.12           EMBRA157           4.20           G           EMBRA219           4.63           6.34           0.88           10.04           0.69           11.61           5.32	10           20           21           45           Mother           EMBRA10x           86           101           104           155           212           214           236	6.88 6.79 2.64 <i>G</i> EMBRA12 1.35 2.13 1.83 3.49 5.04 NE 17.39*	241 2612 EMBRA11 10 Mother EMBRA102 45 86 155 212 214 458	4.60 3.52 xEMBRA12 13.37 <i>G</i> EMBRA204 3.00 2.75 9.11 1.73 3.87 3.671* 4.86
Mother           EMBRA11xEMBF           20           21           45           55           65           86           101           104	0.08 G A12 0.38 4.83 0.81 3.33 0.62 3.82 2.87 1.36	EMBRA3XEB 10 21 Mother EMBRA11XEN 458 2012 20 20 21 45 55	MBRA63 18.98* 7.61 <i>G</i> 4BRA157 2.61 0.53 4BRA204 1.96 1.00 2.83 1.79 2.03	2612 EMBRA3xl 20 Mother EMBRA11x 116 118 155 236 241 458 2612 EMBRA10x	0.22           EMBRA157           4.20           G           EMBRA219           4.63           6.34           0.88           10.04           0.69           11.61           5.32           EMBRA63	20 21 45 Mother EMBRA10xl 86 101 155 212 214 236 458	6.88 6.79 2.64 G EMBRA12 1.35 2.13 1.83 3.49 5.04 NE 17.39* 8.66	241 2612 EMBRA11 10 EMBRA10 45 55 86 155 212 214 458 533	4.60 3.52 EKBRA12 13.37 G EKBRA204 3.00 2.75 9.11 1.73 3.87 3.671* 4.86 2.43
Mother           EMBRA11xEMBF           20           21           45           55           65           86           101           104           116	0.08 G A12 0.38 4.83 0.81 3.33 0.62 3.82 2.87 1.36 1.5.08	EMBRA3xEA 10 21 Mother EMBRA11xEN 458 2612 EMBRA11xEN 10 20 21 45 55 86 86	dBRA63           18.98*           7.61           G           dBRA157           2.61           0.53           dBRA204           1.96           1.79           2.03           6.09	2612 EMBRA3xJ 20 Mother EMBRA11x 116 118 155 236 241 458 2612 EMBRA10 10	4.20 4.20 G EMBRA219 4.63 6.34 0.88 10.04 0.69 11.61 5.32 cEMBRA63 30.24*	10           20           21           45           Mother           EMBRA10xl           86           101           155           212           214           236           458           533	6.88 6.79 2.64 G EMBRA12 1.35 2.13 1.83 3.49 5.04 NE 17.39* 8.66 1.72	241 2612 EMBRA11 10 Mother EMBRA10 45 55 86 155 212 214 458 533 2612 2612	4.60 3.52 EMBRA12 13.37 <i>G</i> EMBRA204 3.00 2.75 9.11 1.73 3.87 3.671* 4.86 2.43 0.80
Mother           EMBRA11xEMBF           20           21           45           55           65           86           101           104           116           118           145	0.08 G AA12 0.38 0.81 3.33 0.62 3.82 2.87 1.36 15.08 10.56	EMBRA3XEB 10 21 Mother EMBRA11XEN 458 2612 EMBRA11XEN 10 20 21 45 55 86 116	IBRA63           18.98*           7.61           G           BBRA157           2.61           0.53           BBA204           1.96           1.00           2.83           1.79           2.03           6.09           5.34	2612 EMBRA3x1 20 Mother EMBRA11x 116 118 236 241 458 2612 EMBRA10x 10 10	1.12           EMBRA157           4.20           G           EMBRA219           4.63           0.88           10.04           0.69           11.61           5.32           EEMBRA63           30.24*           8.80	10           20           21           45           Mother           EMBRA10xl           86           101           104           155           212           214           236           533           2473	6.88 6.79 2.64 G EMBRA12 1.35 2.13 1.83 3.49 5.04 NE 17.39* 8.66 1.72 1.80	241 2612 EMBRA11 10 Mother EMBRA10 45 55 86 155 212 214 458 533 2612 EMBRA10	4.60 3.52 XEMBRA12 13.37 <i>G</i> EEMBRA204 3.00 2.75 9.11 1.73 3.87 3.671* 4.86 2.43 0.80 EEMBRA219
Mother           EMBRA11xEMBF           20           21           45           55           65           86           101           104           116           118           125	0.08 G A12 0.38 4.83 0.81 3.33 0.62 2.87 1.36 15.08 10.56 4.43 4.25	EMBRA3XE3 10 21 Mother EMBRA11xE4 2612 EMBRA11xE4 10 20 21 45 55 86 116 118	dBRA63           18.98*           7.61           G           dBRA157           2.61           0.53           dBRA204           1.96           1.79           2.03           6.09           5.34           7.17	2612 EMBRA3x1 20 Mother EMBRA11x 116 118 155 236 241 458 2612 EMBRA10x 10 21 21	L.2           EMBRA17           EMBRA157           4.20           G           EMBRA219           4.63           6.34           0.88           10.04           0.69           11.61           5.32           EMBRA63           30.24*           8.80           8.03	10           20           21           45           Mother           EMBRA10xl           86           101           104           155           212           214           236           458           533           2473           2612	6.88 6.79 2.64 <i>G</i> EMBRA12 1.35 2.13 1.83 3.49 5.04 NE 17.39* 8.66 1.72 1.80 4.93 MDD 4.77	241 2612 EMBRA10 45 55 212 214 458 533 2612 214 458 533 2612 214 214 214 214 214 214 214 2	4.60 3.52 xEMBRA12 13.37 <i>G</i> EMBRA204 3.00 2.75 9.11 1.73 3.87 3.671* 4.86 2.43 0.80 EMBRA219 1.22 0.07
Mother           EMBRA11xEMBF           20           21           45           55           65           86           101           104           116           118           1355           212           226	0.08 <i>G</i> 4.412 0.38 4.83 0.81 0.81 0.81 0.81 0.62 2.87 1.36 15.08 10.56 4.43 4.85 10.56	EMBRA3XEP 10 21 Mother EMBRA11XEN 458 2612 EMBRA11XEN 10 20 21 45 55 86 116 118 155 212 212 212 21 21 21 21 21 21	ABRA63           18.98*           7.61           G           MBRA157           2.61           0.53           MBRA204           1.96           1.00           2.83           1.79           2.03           6.09           5.34           7.17           2.28           7.5	2612 EMBRA3x1 20 Mother EMBRA11x 116 118 155 236 241 EMBRA10s 241 458 2612 EMBRA10s 10 0 21 45 55 10 <sup>1</sup>	EMBRA157           EMBRA157           4.20           G           EMBRA219           EMBRA219           6.34           0.88           10.04           5.32           ECMBRA63           30.24*           8.03           5.32	10           20           21           45           Mother           EMBRA10x           101           104           155           212           214           236           458           533           2473           2612           EMBRA10xE	6.88 6.79 2.64 <i>G</i> 2.13 2.13 1.83 3.49 5.04 NE 17.39* 8.66 1.72 1.80 4.93 MBRA157	241 2612 EMBRA11 10 Mother EMBRA10 45 55 86 155 212 214 458 533 2612 EMBRA10 1 10 10 20 20 20 20 20 20 20 20 20 2	4.60 3.52 xEMBRA12 13.37 <i>G</i> 2.75 9.11 1.73 3.87 4.86 2.43 0.80 EMBRA219 1.22 9.87 1.22 9.87
Mother           EMBRA11xEMBR           20           21           45           55           65           86           101           104           116           118           155           212           236           459	0.08 <i>G</i> 0.38 4.83 0.81 0.62 2.87 1.36 15.08 10.56 4.43 4.85 10.07 4.85	EMBRA3XE3 10 21 Mother EMBRA11xE3 2612 EMBRA11xE3 10 20 21 45 55 86 116 118 155 212 459	ABRA63           18.98*           7.61           G           MBRA157           2.61           0.53           ABRA204           1.96           1.00           2.83           1.79           2.03           6.09           5.34           7.17           2.28           7.16           2.52	2612 EMBRA3x1 20 Mother EMBRA11x 116 118 135 236 241 458 2612 EMBRA10 10 21 45 55	L         L           EMBRA157         4.20           G         EMBRA219           EMBRA219         6.34           0.69         11.61           5.32         \$20.24*           8.80         \$5.32           3.04         \$5.32           9.98         \$5.32	10           20           21           45           Mother           EMBRA10x1           86           101           104           155           212           214           236           458           533           2473           2612           EMBRA10x1           20           21	6.88 6.79 2.64 <i>G</i> BBRA12 1.35 2.13 1.83 3.49 5.04 NE 17.39* 8.66 1.72 1.80 4.93 MBRA157 4.23 2.8	241 2612 EMBRA10 45 55 86 155 212 214 458 533 2612 EMBRA10 1 10 20 31	4.60 3.52 xEMBRA12 13.37 G 3.00 2.75 9.11 1.73 3.671* 4.86 2.43 0.80 EMBRA219 1.22 9.87 11.29 4.65
Mother           EMBRA11xEMBF           20           21           45           55           65           86           101           104           116           118           155           212           236           458           533	0.08 <i>G</i> 10.38 4.83 0.81 0.81 0.62 2.87 1.36 15.08 10.56 4.43 4.83 10.56 10.56 10.77 4.85 10.77 1.97	EMBRA3XER 10 21 Mother EMBRA11XEN 458 2612 EMBRA11XEN 10 20 21 45 55 86 116 118 155 212 458 533	ABRA63           18.98*           7.61           G           MBRA157           2.61           0.53           ABRA204           1.96           1.79           2.03           6.09           5.34           7.16           2.52           1.26	2612 EMBRA3x1 20 Mother EMBRA11x 116 118 155 236 241 EMBRA10x 2612 EMBRA10 10 21 45 55 101 104 155	12           EMBRA157           4.20           G           EMBRA219           6.34           0.68           10.04           0.69           11.61           5.32           3.024*           8.03           5.32           3.04           0.88           19.15*	10           20           21           45           Mother           EMBRA10x.           86           101           212           214           236           458           533           2473           2612           EMBRA10xE           20           21           458	6.88 6.79 2.64 <i>G</i> 2.13 1.35 2.13 1.83 3.49 5.04 NE 1.7.39* 8.66 1.72 1.80 4.93 (MBRA12 4.93 (MBRA157 4.23 3.28 1.57	241 2612 EMBRA11 10 EMBRA16 45 55 212 214 458 66 155 212 214 458 533 2612 EMBRA10 1 10 20 21 45	4.60 3.52 xEMBRA12 13.37 <i>G</i> 2.75 9.11 1.73 3.87 3.671* 4.86 2.43 0.80 EMBRA219 1.22 9.87 1.29 4.65 9.38
Mother           EMBRA11xEMBB           20           21           35           65           86           101           104           116           118           155           212           236           458           333           7612	0.08 <i>G</i> 2A12 0.38 4.83 0.81 3.33 0.62 3.82 2.87 1.36 10.56 4.43 4.85 10.07 4.85 1.87 2.61	EMBRA3XEP 10 21 Mother EMBRA11XEN 458 2612 20 21 45 55 86 116 118 155 212 45 533 2612	ABRA63           18.98*           7.61           6           WBRA157           2.61           0.53           HBRA204           1.96           1.00           2.83           7.17           2.03           6.09           5.34           7.17           2.28           7.16           2.52           1.26           0.84	2612 EMBRA3x1 20 Mother EMBRA11x 116 118 236 241 458 2612 EMBRA10x 10 21 45 55 101 104 155 241	Line           EMBRA157           4 20           G           EMBRA219           4.63           0.88           10.04           0.69           11.61           5.32           ECMBRA63           8.80           8.30           5.32           3.04           0.88           19.15*	10           20           21           45           Mother           EMBRA10x           86           101           104           155           212           214           236           533           2612           20           21           45           65	6.88 6.79 2.64 <i>G</i> EMBRA12 1.35 2.13 1.83 3.49 5.04 NE 17.39* 8.66 1.72 1.80 MBRA157 4.23 3.28 1.57 0.98	241 2612 EMBRA10 45 55 212 214 458 533 2612 EMBRA10 1 10 20 21 45 55	4.60 3.52 xEMBRA12 13.37 EEMBRA204 3.00 2.75 9.11 1.73 3.671* 4.86 2.43 0.80 0.80 EEMBRA219 1.22 9.87 11.29 4.65 9.38 3.26
Mother           EMBRA11xEMBB           20           21           45           55           65           86           101           104           116           118           155           212           236           458           533           2612           EMBRA11xEMBE	0.08 G KA12 0.38 4.83 0.81 0.81 0.62 3.82 2.87 1.36 15.08 10.56 4.43 4.85 10.07 4.85 1.87 2.61 X157	EMBRA3XEP 10 21 Mother EMBRA11xEP 2612 EMBRA11xEP 10 21 45 55 86 116 118 155 212 458 2612 21 45 55 86 116 118 155 212 458 2612 21 21 21 21 21 21 21 21 21	ABRA63           18.98*           7.61           G           MBRA157           2.61           0.53           HBRA204           1.96           1.79           2.03           6.09           5.34           7.16           2.52           1.26           0.84           MBRA219	2612 EMBRA3x1 20 Mother EMBRA1x 116 118 155 236 241 458 2612 EMBRA10 10 21 45 55 55 101 104 155 241 241 2473	L         L           EMBRA157         4.20           G         G           EMBRA219         4.63           0.88         0.04           10.04         0.69           11.61         5.32           CEMBRA28         8.00           5.32         3.04           0.88         19.15*           6.93         2.23	10           20           21           45           Mother           EMBRA10x           86           101           155           212           214           236           458           533           2473           2612           EMBRA10xE           20           21           65           212	6.88 6.79 2.64 <i>G</i> EMBRA12 1.35 2.13 1.83 3.49 5.04 NE 17.39* 8.66 1.72 1.80 4.93 MBRA157 4.23 3.28 1.57 0.98 5.39	241 2612 EMBRA10 45 55 212 214 458 65 212 214 458 533 2612 EMBRA10 10 10 20 21 45 55 65	4.60 3.52 xEMBRA12 13.37 <i>G</i> 2.75 9.11 1.73 3.87 3.671* 4.86 2.43 0.80 EMBRA219 1.22 9.87 1.29 4.65 9.38 3.26 6.17
Mother           EMBRA11xEMBB         20           201         21           45         55           65         86           101         104           116         118           155         212           236         458           533         2612           20612         20612	0.08 <i>G</i> (A12 0.38 4.83 0.81 3.33 0.62 2.87 1.36 15.08 10.07 4.85 1.87 2.61 XA157 0.73	EMBRA3XEP 10 21 Mother EMBRA11XEP 458 2612 EMBRA11XEP 10 20 21 45 55 86 116 118 155 212 458 533 2612 EMBRA11XEP 10 0 118 118 118 118 118 118 1	ABRA63           18.98*           7.61           G           G           0.53           HBRA157           2.61           0.53           HBRA204           1.96           1.79           2.03           6.09           5.34           7.16           2.52           1.26           0.84           4BRA219           2.37	2612 EMBRA3x1 20 Mother EMBRA11x 116 118 155 236 241 458 2612 EMBRA10x 10 21 45 55 101 104 155 101 104 155 241 2473 2612	L12           EMBRA157           4.20           G           EMBRA219           6.34           0.634           0.04           0.53           0.04           5.32           EMBRA219           3.024*           8.80           5.32           3.04           0.88           19.15*           6.93           2.15	10           20           21           45           Mother           EMBRA10x           86           101           104           212           214           236           533           2473           2612           21           45           665           212           236	6.8 6.8 6.79 2.64 G EMBRA12 1.35 1.83 3.49 5.04 NE 17.39* 8.66 1.72 1.80 4.93 MBRA157 4.23 3.28 1.57 0.98 5.39 22.45*	241 2612 EMBRA11 10 EMBRA10 45 55 86 155 212 214 458 533 2612 EMBRA10 1 10 20 21 45 55 65 65 86	4.60 3.52 xEMBRA12 13.37 <i>G</i> 2.75 9.11 1.73 3.671* 4.86 4.86 0.80 1.22 9.87 1.129 4.65 9.38 6.12 1.97
Mother           EMBRA11xEMBB           20           21           45           55           65           86           101           104           116           118           212           236           458           533           2612           EMBRA11xEMBB           201           212           232           EMBRA11xEMBB           201	0.08 <i>G</i> A12 0.38 4.83 0.81 3.33 0.62 3.82 2.87 1.36 15.08 10.56 4.43 4.85 10.56 4.43 4.85 1.05 1.05 4.85 1.07 0.73 7.87	EMBRA3XEP 10 21 Mother EMBRA11xEP 2612 EMBRA11xEP 10 21 45 55 86 116 118 155 212 458 53 2612 EMBRA11xEP 10 20 21 20 21 20 20 20 20 20 20 20 20 20 20	dBRA63           18.98*           7.61           G           4BRA157           0.53           dBRA204           1.96           1.00           2.83           1.79           2.03           6.09           5.34           7.17           2.28           7.16           2.52           1.26           0.84           4BRA219           2.37	2612 EMBRA3x1 20 Mother EMBRA11x 116 118 236 241 458 2612 EMBRA10 10 21 45 55 101 104 155 241 241 241 241 241 241 241 241 241 241	0.12           EMBRA157           4.20           G           EMBRA219           4.63           0.88           10.04           0.69           11.61           5.32           cEMBRA63           30.24*           8.80           5.32           3.04           0.88           19.15*           6.93           2.23           2.15           EMBRA12	10           20           21           45           Mother           EMBRA10x           86           101           104           155           212           214           236           458           533           2473           2612           20           21           236           458	6.88 6.79 2.64 <i>G</i> EMBRA12 1.35 2.13 1.83 3.49 5.04 NE 17.39* 8.66 1.72 1.80 4.93 3.49 1.72 1.80 4.93 3.28 1.57 0.98 5.39 2.245* 1.57 0.98 5.39 2.245* 1.57 1.56 1.57 1	241 2612 EMBRA10 45 55 86 155 212 214 458 533 2612 214 458 533 2612 100 20 21 45 55 65 86 101	4.60 3.52 xEMBRA12 13.37 <i>G</i> 3.00 2.75 9.11 1.73 3.87 3.671* 4.86 2.43 0.80 EMBRA219 11.22 9.87 11.29 9.87 11.29 4.65 6.12 1.97 9.37
Mother           EMBRA11xEMBB           20           21           45           55           66           86           101           104           116           118           155           226           23612           2012           2012           2012           21           45	0.08 <i>G</i> 20.38 4.83 0.81 0.81 3.33 0.62 2.87 1.36 15.08 10.56 4.43 4.85 10.07 4.85 10.07 4.85 1.87 2.61 2.61 2.61	EMBRA3XEP 10 21 Mother EMBRA11XEN 458 2612 EMBRA11XEN 10 20 21 45 55 86 116 118 155 212 458 2612 EMBRA11XEN 10 21 21 21 21 21 21 21 21 21 21	dBRA63           18.98*           7.61           G           WBRA157           2.61           0.53           dBRA204           1.96           1.79           2.03           6.09           5.34           7.16           2.52           1.26           0.84           4BRA219           2.58           6.99	2612 EMBRA3x1 20 Mother EMBRA11x 116 118 155 236 241 458 2612 EMBRA10 10 21 45 55 101 104 155 241 155 241 2473 2473 2612 EMBRA10 10	L12           EMBRA157           4.20           G           EMBRA219           6.34           0.63           0.69           11.61           11.61           11.61           30.24*           8.80           5.32           EMBRA219           6.33           0.69           10.04           0.69           2.3           0.4*           0.88           19.15*           6.33           2.15           EMBRA12	10           20           21           45           Mother           EMBRA10x           86           101           155           212           214           236           458           533           2473           2612           20           21           65           212           214           236           458           533           2612           20           212           213           65           212           236           458           236           236           236           236           2473	$\begin{array}{c} 6.528\\ 6.528\\ 6.79\\ 2.64\\ \hline G\\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\$	241 2612 EMBRA11 10 Mother EMBRA10 45 55 212 214 458 533 2612 EMBRA10 1 20 21 455 55 65 65 86 101 10 20	4.60 3.52 xEMBRA12 13.37 <i>G</i> 2.75 9.11 1.73 3.87 3.671* 4.86 2.43 0.80 EMBRA219 1.22 9.87 1.129 4.65 6.12 1.97 9.37 4.56
Mother           EMBRA11xEMBB           20           21           35           65           86           101           104           115           212           236           458           533           2612           EMBRA11xEMBF           201           2458           533           5612           EMBRA11xEMBF           201           55	0.08 <i>G</i> 2A12 0.38 4.83 0.81 3.33 0.62 3.82 15.08 10.56 10.56 4.43 4.85 10.07 4.85 1.87 2.61 2.87 7.87 1.26 0.90	EMBRA3XEB 10 21 Mother EMBRA11XED 458 2612 20 21 45 55 86 116 118 155 212 458 533 2612 EMBRA11XED 10 20 21 45 21 21 45 55 21 21 21 45 86 118 118 118 125 21 21 21 21 21 21 21 21 21 21	MBRA63           18.98*           7.61           6           WBRA157           2.61           0.53           MBRA204           1.96           1.79           2.83           1.79           2.03           6.09           5.34           7.16           2.28           7.16           2.52           1.26           0.84           4BRA219           2.37           2.58           6.99           3.00	2612 EMBRA3x1 20 Mother EMBRA11x 116 118 155 236 241 458 2612 EMBRA10x 10 21 45 55 101 104 155 241 2473 2612 EMBRA10x 104 215 241 2612 EMBRA10x 104 2612 2612 2612 EMBRA10x 2612 2612 2612 2612 2612 2612 2612 261	Line           EMBRA157           4 20           G           EMBRA219           6 34           0.08           10.04           0.69           11.61           5 32           EEMBRA63           3.04           8.80           9.15*           6.93           2.15           EEMBRA12           6.34	10           20           21           45           Mother           EMBRA10x           86           101           104           155           212           214           236           458           533           2473           2612           21           45           65           212           236           458           2473           2612	6.88 6.79 2.64 <i>G</i> EMBRA12 1.35 2.13 1.83 3.49 5.04 NE 17.39* 8.66 1.72 1.80 4.93 4.93 MBRA157 4.23 3.28 1.57 0.98 5.39 2.245* 1.66 0.57 0.83	241 2612 EMBRA10 45 55 86 155 212 214 458 533 2012 EMBRA10 10 20 21 45 55 65 86 100 155 100 21 21 21 21 21 21 21 21 21 21	4.60 3.52 xEMBRA12 13.37 E-BBRA204 3.00 2.75 9.11 1.73 3.87 3.671* 4.86 2.43 3.87 3.671* 4.86 2.43 0.80 E-BBRA219 11.22 9.87 11.29 9.38 3.26 6.12 1.97 9.33 4.65 9.33 3.26 6.12 1.97 9.33 4.55 2.330*
Mother           EMBRA11xEMBB           20           21           45           55           65           86           101           104           116           118           212           236           458           533           2612           20           21           45           65           116	0.08 <i>G</i> KA12 0.38 4.83 0.81 3.33 0.62 3.82 2.87 1.36 15.08 10.56 4.43 4.85 10.07 4.85 1.87 2.61 KA157 0.73 7.87 1.26 0.90 3.08	EMBRA3XEP 10 21 Mother EMBRA11xEP 2612 EMBRA11xEP 10 21 45 55 86 116 118 155 212 458 333 2612 EMBRA11xEP 10 21 458 55 86 116 118 155 212 458 533 2612 20 20 21 21 21 20 21 21 21 21 21 21 21 21 21 21	HBRA63           18.98*           7.61           G           MBRA157           2.61           0.53           HBRA204           1.96           1.79           2.03           6.09           5.34           7.16           2.52           1.26           0.84           4BRA219           2.37           2.58           6.99           3.00           2.99	2612 EMBRA3x1 20 Mother EMBRA11x 116 115 236 241 EMBRA10x 10 21 45 55 101 104 155 241 2473 2612 EMBRA10x 105 104 155 241 2473 2612 EMBRA10x 10 241 2473 2612	EMBRA12           EMBRA137           4           G           EMBRA219           EMBRA219           10.04           0.88           10.04           0.69           11.61           5.32           KEMBRA63           30.24*           8.80           8.03           5.32           3.04           0.88           19.15*           6.93           2.23           2.15           cEMBRA12           6.34           6.01           3.89	10           20           21           45           Mother           EMBRA10x           86           101           212           212           214           215           212           214           215           216           458           20           21           20           21           20           21           45           65           212           236           458           212           236           458           212           236           458           2473           2473           2612           EMBRA10xE	6.88 6.79 2.64 <i>G</i> BBRA12 1.35 2.13 1.83 3.49 5.04 NE 17.39* 8.66 1.72 4.23 3.28 1.57 0.98 5.39 22.45* 1.66 0.57 0.83 MBRA204	241 2612 EMBRA10 45 55 212 214 45 53 212 214 458 533 2612 EMBRA10 1 10 20 21 458 55 212 214 214 214 215 212 212 212 212 212 212 212	4.60 3.52 xEMBRA12 13.37 <i>G</i> 2.75 9.11 1.73 3.87 3.671* 4.86 2.43 0.80 EMBRA219 1.22 9.87 1.129 4.65 9.38 3.26 6.12 1.97 9.37 9
Mother           EMBRA11xEMBB           20           21           45           55           65           86           101           104           116           115           20612           20612           20612           20612           65           65           61           116           118           116           118	0.08 <i>G</i> (A12 0.38 4.83 0.81 3.33 0.62 2.87 1.36 15.08 10.07 4.85 1.87 2.61 XA157 7.87 7.87 1.26 0.90 3.08 2.69	EMBRA3XEB 10 21 Mother EMBRA11XED 458 2612 EMBRA11XED 10 20 21 45 55 86 118 155 212 458 533 2612 EMBRA11XED 10 20 21 21 21 25 55 53 2612 21 21 21 25 55 55 55 55 55 55 55 55 55	ABRA63           18.98*           7.61           G           G           0.53           ABRA157           2.61           0.53           HBRA204           1.96           1.00           2.83           6.09           5.34           7.16           2.52           1.26           0.84           4BRA219           2.58           6.99           3.00           2.99           2.16	2612 EMBRA3x1 20 Mother EMBRA11x 116 118 155 236 241 458 2612 EMBRA10x 10 21 45 55 101 104 155 241 2473 2612 EMBRA10x 105 241 2473 2612 EMBRA10x 104 155 241 2473 2612 EMBRA10x 104 155 241 2473 2612 EMBRA10x 104 155 241 2473 2612 EMBRA10x 105 155 241 245	0.12           EMBRA157           4.20           G           EMBRA219           6.34           0.88           10.04           0.69           11.61           5.32           EMBRA63           3.024*           8.80           8.03           5.32           2.33.04           0.88           19.15*           6.93           2.215           cEMBRA12           6.34           6.01           3.89           0.84	10           20           21           45           Mother           EMBRA10x           86           101           104           155           212           214           236           458           533           2473           2612           20           21           45           65           212           236           458           210           45           21           65           212           236           458           2473           2612           236           458           2473           2612           EMBRA10xE           2612           EMBRA10xE           10	6.8 6.79 2.64 <i>G</i> EMBRA12 1.35 2.13 1.83 3.49 5.04 NE 17.39* 8.66 1.72 1.80 4.93 MBRA157 4.23 3.28 1.57 4.23 3.28 1.57 0.98 5.39 5.	241 2612 EMBRA10 45 55 86 155 212 214 458 533 2612 EMBRA10 15 214 20 21 45 55 86 101 155 214 20 21 21 21 21 21 21 21 21 21 21	4.60 3.52 xEMBRA12 13.37 EMBRA204 EMBRA204 2.75 9.11 1.73 3.87 3.87 4.86 2.43 0.80 EMBRA219 1.22 9.87 11.29 9.87 11.29 9.87 11.29 9.38 3.26 6.12 1.97 4.55 5.56
Mother           EMBRA11xEMBB           20           21           45           55           65           86           101           104           116           118           212           236           458           533           2612           EMBRA11xEMBB           201           45           65           116           117           118           212           213           214           215           216           2116           118           212	0.08 <i>G</i> KA12 0.38 4.83 0.81 3.33 0.62 2.87 1.36 15.08 10.56 4.43 4.85 10.05 4.43 4.85 10.07 4.85 1.07 4.87 2.61 XA157 0.73 7.87 1.26 0.90 3.08 2.69 5.65	EMBRASEE 10 21 Mother EMBRA11xE 2612 EMBRA11xE 10 20 21 45 55 86 116 118 155 212 458 533 2612 EMBRA11xE 10 20 20 20 21 45 55 86 86	ABRA63           18.98*           7.61           G           WBRA157           2.61           0.53           MBRA204           1.96           1.00           2.83           1.79           2.03           6.09           5.34           7.16           2.52           1.26           0.84           MBRA219           2.37           2.58           6.99           3.00           2.16           0.13	2612 EMBRA3xl 20 Mother EMBRA11x 116 118 236 241 458 2612 EMBRA10 10 21 45 55 101 104 155 241 2473 2473 2473 2473 2473 2473 2472 20 20 21 45 55	0.12           EMBRA157           4 20           G           EMBRA219           4 63           0.88           10.04           0.88           10.04           5.32           xEMBRA63           30.24*           8.80           5.32           3.04           0.88           19.15*           6.93           2.23           2.15           EMBRA12           6.01           3.89           0.84           1.19	10           20           21           45           Mother           EMBRA10x           86           101           104           155           212           214           236           458           231           2612           20           21           458           2473           2612           236           458           2473           2612           EMBRA10xE           2612           2612           2612           2612           20	$\begin{array}{c} 6.88\\ 6.79\\ 2.64\\ \hline\\ G\\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ $	241 2612 EMBRA10 45 55 86 155 212 214 458 65 86 100 100 20 21 45 55 212 214 458 86 86 100 100 201 21 214 214 214 214 214 214 214	$\begin{array}{r} 4.60\\ 3.52\\ \times EMBRA 12\\ 13.37\\ \overline{G}\\ 0.25$
Mother           EMBRA11xEMBB           20           21           45           55           66           86           101           104           116           118           236           2612           201           212           236           458           65           116           118           2012           2012           2014           2015           2016           2017           2018           2019           202           203	0.08 <i>G</i> KA12 0.38 4.83 0.81 3.33 0.62 3.82 2.87 1.36 15.08 10.56 4.43 4.85 10.07 4.85 10.07 4.85 10.73 7.87 2.61 KA157 0.73 7.87 1.26 0.90 3.08 2.69 6.05 16.23	EMBRASKE 10 21 Mother EMBRAILXEN 458 2612 EMBRAILXEN 10 20 21 45 55 86 116 118 155 212 458 2612 EMBRAILXEN 10 20 21 45 55 212 EMBRAILXEN 10 20 21 45 55 86 10 10 20 21 21 21 21 21 21 21 21 21 21	ABRA63           18.98*           7.61           0.7.61           0.61           0.53           WBRA157           2.61           0.53           WBRA204           1.96           1.79           2.03           6.09           5.34           7.16           2.52           1.26           0.84           4BRA219           2.58           6.699           3.00           2.99           2.16           0.13           3.42	2612 EMBRA3x1 20 Mother EMBRA11x 116 118 155 236 241 458 2612 EMBRA10s 10 21 45 55 101 104 155 2473 2473 2473 2473 2473 2473 2473 2473	EMBRA12           EMBRA157           4.20           G           EMBRA219           4.63           0.634           0.634           0.63           0.69           11.61           5.32           EMBRA218           0.04           0.69           10.04           5.32           EMBRA63           3.04           0.88           19.15*           6.93           2.15           EMBRA12           6.34           0.84           1.19           0.91	10           20           21           45           Mother           EMBRA10x           86           101           104           155           212           214           236           533           2473           2612           21           45           65           212           236           458           236           452           236           452           236           453           212           21           458           236           2473           2612           EMBRA10xE           10           20           21	$\begin{array}{c} 6.28\\ 6.79\\ 6.79\\ 2.64\\ \hline G\\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\$	241 2612 EMBRA10 45 55 212 214 458 533 2612 214 458 533 2612 214 458 533 2612 214 458 533 2612 214 458 55 65 65 86 101 155 214 45 202 214 45 202 214 45 202 214 45 202 202 214 45 202 202 202 202 202 202 202 20	4.60 3.52 xEMBRA12 13.37 <i>G</i> 2.75 9.11 1.73 3.87 3.671* 4.86 2.43 0.80 EMBRA219 1.22 9.87 11.29 4.65 6.12 1.97 9.37 4.56 2.3.00* 12.52 5.56 8.80 5.60
Mother           EMBRA11xEMBB           20           21           35           65           86           101           104           115           212           236           458           533           2612           EMBRA11xEMBF           20           21           458           533           2612           211           45           65           1116           118           212           236           Mother	$\begin{array}{c} 0.08\\ \hline G\\ RA12\\ \hline 0.38\\ 4.83\\ 0.81\\ \hline 0.81\\ 3.33\\ 0.62\\ 2.87\\ 1.36\\ 15.08\\ 10.56\\ 4.43\\ 4.85\\ 10.07\\ 1.36\\ 1.36\\ 1.43\\ 4.85\\ 10.07\\ 7.87\\ 1.26\\ 0.73\\ 7.87\\ 1.26\\ 0.90\\ 3.08\\ 2.69\\ 6.05\\ 16.23\\ G\\ \end{array}$	EMBRASEE 10 21 Mother EMBRA11xEN 10 20 21 45 55 86 116 118 155 212 458 53 2612 2612 2612 2612 2612 2612 20 20 20 20 21 45 55 65 65 86 86 10 10 00 00 00 00 00 00 00 00 00 00 00	$\begin{array}{c} {\rm MBRA63} \\ {\rm 18.98^*} \\ {\rm 7.61} \\ {\rm 7.61} \\ {\rm 7.61} \\ {\rm 7.61} \\ {\rm 2.61} \\ {\rm 0.53} \\ {\rm MBRA157} \\ {\rm 1.96} \\ {\rm 1.79} \\ {\rm 2.83} \\ {\rm 7.16} \\ {\rm 2.52} \\ {\rm 1.26} \\ {\rm 0.84} \\ {\rm 4BRA219} \\ {\rm 2.52} \\ {\rm 1.26} \\ {\rm 0.84} \\ {\rm 4BRA219} \\ {\rm 2.52} \\ {\rm 2.58} \\ {\rm 6.99} \\ {\rm 3.00} \\ {\rm 2.99} \\ {\rm 2.16} \\ {\rm 0.13} \\ {\rm 3.42} \\ {\rm G} \\ {\rm G} \end{array}$	2612 EMBRA3x1 20 Mother EMBRA11x 116 118 155 236 241 458 2612 EMBRA10x 10 21 45 55 101 104 155 241 2473 2612 EMBRA10x 104 155 241 2612 EMBRA10x 104 155 2612 EMBRA10x 105 165 65 Mother	Line           EMBRA157           4 20           G           EMBRA219           4 6.3           0.634           0.08           10.04           0.69           11.61           5.32           EEMBRA63           3.04           8.80           8.30           5.32           2.15           EEMBRA12           6.34           0.88           19.15*           0.349           6.01           3.89           0.84           1.19           0.91           6	10           20           21           45           Mother           EMBRA10x           86           101           104           155           212           214           236           458           533           2473           2612           21           45           65           212           236           458           2473           2612           236           65           212           236           458           2473           2612           236           458           2473           2612           236           458           2612           20           21           21           21           21           21           21           21           21           21           21           30	$\begin{array}{c} 6.88\\ 6.79\\ 2.64\\ \hline\\ G\\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ $	241 2612 EMBRA10 45 55 86 155 212 214 458 533 2012 EMBRA10 10 20 21 45 55 86 10 10 20 21 45 55 86 10 212 214 458 86 10 202 214 458 86 86 212 212 214 458 86 202 202 201 202 201 202 202 202	$\begin{array}{c} 4.60\\ 3.52\\ xEMBRA12\\ 13.37\\ G\\ zemBRA204\\ 3.00\\ 2.75\\ 9.11\\ 1.73\\ 3.671*\\ 4.86\\ 2.43\\ 0.80\\ z.43\\ 0.80\\ z.5\\ 0.80\\ z$
Mother           EMBRA11xEMBB           20           21           45           55           65           86           101           104           116           118           212           236           458           533           2612           214           45           65	0.08 <i>G</i> AA12 0.38 4.83 0.81 0.81 3.33 0.62 2.87 1.36 15.08 10.56 10.56 10.56 10.56 10.56 10.56 10.56 10.56 10.56 10.57 1.26 0.90 3.08 2.69 6.05 16.23 <i>G</i> <i>G</i> <i>G</i> <i>G</i> <i>G</i> <i>G</i> <i>G</i> <i>G</i>	EMBRA3XEP 10 21 Mother EMBRA11xEP 458 2612 EMBRA11xEP 10 21 45 55 86 116 118 155 212 EMBRA11xEP 10 21 45 53 212 EMBRA11xEP 10 21 45 55 86 10 20 21 45 55 86 10 Mother EMBRA63xEF EMBRA63xEF	dBRA63           18.98*           7.61           G           WBRA157           2.61           0.53           MBRA204           1.96           1.79           2.03           6.09           5.34           7.16           2.52           1.26           0.84           4BRA219           2.58           6.99           3.00           2.99           2.16           0.13           3.42           G           WBRA12	2612 EMBRA3x1 20 Mother EMBRA11x 116 118 155 236 241 458 2612 EMBRA10x 10 21 45 55 101 104 155 241 2473 2612 EMBRA10x 10 20 21 21 45 55 65 65 65 Mother EMBRA63x	112           EMBRA157           4.20           G           EMBRA219           4.63           0.634           0.69           1.61           1.61           1.63           3.024*           8.80           9.15*           6.34           0.88           19.15*           6.34           6.93           2.15           EMBRA12           6.34           6.01           3.89           0.91           0.91           0.91           0.91           0.91           0.92	10           20           21           45           Mother           EMBRA10x           86           101           212           214           236           458           533           2473           2612           20           21           45           65           212           236           45           62           212           236           45           612           20           212           236           458           2473           2612           236           2473           2612           20           210           20           21           00           20           21           Mother           EMBRA10xE	$\begin{array}{c} 6.58\\ 6.79\\ 6.78\\ 6.79\\ 2.64\\ G\\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ \\ $	241 2612 EMBRA10 45 55 212 214 458 86 155 212 214 458 2612 10 10 20 21 458 55 212 212 214 458 55 212 212 214 458 65 86 101 155 212 212 212 212 212 212 21	$\begin{array}{c} 4.60\\ 3.52\\ xEMBRA12\\ 13.37\\ G\\ 3.00\\ 2.75\\ 9.11\\ 1.73\\ 3.87\\ 3.6.71*\\ 4.86\\ 2.43\\ 0.80\\ EMBRA219\\ 11.22\\ 9.87\\ 11.29\\ 4.65\\ 9.38\\ 3.26\\ 6.12\\ 1.97\\ 9.33\\ 3.26\\ 6.12\\ 1.97\\ 9.33\\ 3.26\\ 6.12\\ 1.97\\ 9.33\\ 3.26\\ 6.12\\ 1.55\\ 6.330*\\ 12.52\\ 5.56\\ 8.80\\ 5.60\\ G\\ EMBRA219\\ \end{array}$

**Table 2.** Values of maximum likelihood G-test for the hypothesis of independent segregation between pairwise loci (1:1:1:1) for Eucalyptus urophylla.

Continued on next page

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Table 2. C	Continued.								
EMBDA10vEMBD	A 322	2472	4 73	118	11.08	118	2.40	21	5.18
1	2.96	2475	2.19	155	11.58	212	7.99	45	1 74
10	17.32*	EMBRA63xEN	ABRA157	241	5.40	236	13.02	55	2.19
21	6.59	21	8.90	2473	3.32	458	2.28	65	3.37
45	5.34	45	4.60	2612	4.22	2473	0.12	86	0.34
65	2.94	95	8.23	EMBRA63x	EMBRA333	2612	1.74	95	0.20
86	6.40	118	0.83	10	25.43	EMBRA12xF	EMBRA204	101	2.87
101	2.76	2473	5.69	21	9.59	10	0.33	116	2.85
155	9.21	2612	0.80	45	1.26	20	2.01	118	4.53
212	5.15	EMBRA63xEN	ABRA204	101	0.78	21	1.38	155	2.03
214	NE 6.11	10	8.30	241	10.11	45	1.40	214	0.88
533	2.03	45	8.61	241	1.54	86	10.84	458	7.21
2473	1.01	55	5.17	2612	4.46	95	1.40	2473	4.72
2612	3.35	95	7.20	EMBRA63x	EMBRA128	116	3.42	2612	1.48
EMBRA63xEMBR	CA12 21.02*	118	7.45	10	6.69	118	11.78	EMBRA12:	LEMBRA333
21	3.75	2612	0.76	118	13.48	212	8.09	21	1.35
45	5.14	EMBRA63xEN	/IBRA219	EMBRA12x	EMBRA157	214	6.28	45	0.73
55	3.81	10	20.57*	20	1.23	458	5.48	65	5.17
101	2.35	45	6.00	45	0.06	2612	2.71	101	0.74
104	5.96	55	5.83	65	3.05	EMBRA12xE	EMBRA219	116	8.19
118	3.77	95	2.75	95	4.06	10	3.35	155	10.24
Mother EMPRA12vEMPR	G	Mother EMPRA12×EI	G ADD A 29	Mother EMPRA157	G EMDDA222	Mother EMDP A 157v	G EMPRA210	Mother EMPRA204	G VEMDD A 222
212	9.01	212	10.26	21	1.41	95	3.97	212	9.77
214	4.18	214	1.97	45	3.04	116	3.43	214	7.01
533	2.95	236	2.42	65	2.41	118	0.25	533	0.72
24/3	1.54	20	4,01	212	5.48	212 EMBRA204x	10.00 EMBRA219	2612 EMBRA204	0.49 xEMBRA128
EMBRA12xEMBR	RA128	21	2.33	2473	1.02	10	1.23	10	3.21
10	2.08	45	2.37	2612	1.95	20	3.21	21	3.37
21	2.32	95	1.79	EMBRA157:	EMBRA128	21	8.97	86	16.49*
116	2.62	118	4 23	116	1.98	4.5	2.02	118	6.62
118	17.19*	212	9.66	118	12.65	86	5.75	212	7.07
212	3.39	458	2.79	212	5.19	95	3.81	214	16.94*
214 EMBRA12xEMBR	12.83	2612 EMBRA157xE	0.90 MBR 4 219	21 EMBRA157	XEMBRA38 3.25	116	3.95	21 EMBRA204	1 74
21	7.83	20	0.56	45	0.47	155	3.04	45	5.21
45	0.57	21	1.53	65	1.10	214	12.61	55	0.51
55	0.73	45	4.01	95	5.94	458	9.77	86	11.22
86	1.50	95	7.21	118	0.48	EMBRA204x	4.05 EMBRA333	95	2.53
95	0.83	116	3.69	212	3.35	10	6.24	118	4.49
101	1.52	118	6.99	236	16.86*	21	3.15	155	3.23
104	6.68	236	16.03	21 EMBRA1573	2 33	45	4.14	212	6.81 5.84
118	8.16	2473	3.76	45	0.67	116	5.33	EMBRA204	xEMBRA210
155	3.71	2612	4.47	65	4.59	155	10.75	21	8.72
Mother EMPRA204×EMP	G PA210	Mother EMPRA210vE	G MDD A 222	Mother EMBRA210	G VEMDDA29	Mother EMPRA210v	G EMDD A 691	Mother EMPRA222	G VEMDD A 210
45	3.72	45	3.50	101	4.33	118	7.99	45	0.97
55	12.14	65	6.22	116	4.60	155	4.24	65	6.85
86	5.29	86	4.17	118	7.82	2473	4.86	86	2.83
95	3.38 7.97	101	3.25	214	5.80	EMBR 4333x	9.10 FMBR 4128	110	5.26
118	8.56	155	11.38	236	0.23	1	0.30	212	7.84
155	3.53	214	9.03	241	1.57	10	5.04	214	11.37
212	8.48	241	2.50	EMBRA219:	KEMBRA210	21	2.81	533 EMDD 4 222	0.90
533	14.94	2473	4.66	45	3.17	116	2.08	10	5.42
EMBRA204xEMB	RA681	EMBRA219xE	MBRA128	55	10.09	212	2.32	45	0.75
10	1.53	1	1.18	65	6.91	214	12.75	65	7.75
45	2.92	10	5.12	86	3.55	EMBRA333>	LEMBRA38	116	3.49
95	1.14	21	9.14	95	2.87	45	6.35	212	7.80
116	3.46	116	4.71	118	3.65	65	3.60	533	0.38
118	12.25	118	16.13	155	3.18	86	6.00	2473	4.32
155	1.05	214	12.12	214	13.16	101	1.80	2612	6.44
522	1.68	EMBRA219xE	MBRA38 2.56	EMBRA2193	L 40	116	7.35	21 21	5 59
2612	4.66	45	3.25	45	2.09	212	8.26	86	1.88
EMBRA219xEMB	RA333	55	1.74	55	0.65	214	3.84	116	1.87
1	0.20	65	2.12	65	4.36	241	4.30	118	6.59
10	5.89	86	0.39	95	11.98	EMBRA333x	EMBRA210	212	3.72
Mother	5./4 G	95 Mother	1.20 G	110 Mother	5.50 G	21 Mother	1.90 G	∠14 Mother	12.34 G
EMBRA128xEMB	RA210	EMBRA128xE	MBRA681	EMBRA38x	EMBRA210	EMBRA38xH	EMBRA681	EMBRA210	xEMBRA681
21	4.44	118	16.97*	116	13.66	95	12.36	95	9.33
86	3.44	212	1.73	118	3.17	116	0.75	116	6.97
110	8.44	EMBRA38xEN	15KA210	155	1.30	118	5.13	118	2.88
212	2.35	45	0.27	212	10 27	212	4 49	212	1.40
214	15.41	55	0.53	EMBRA38x	EMBRA681	EMBRA210x	EMBRA681	533	0.06
EMBRA128xEMB	RA681	65	5.31	45	0.58	45	0.53		
10	0.34	86	2.38	55	0.52	55	0.90		
110	1.15	95	2.08	65	2,42	05	8.47	1	1

\*Significance after Bonferroni correction for  $\alpha = 0.05$  ( $\chi^2 = 16.27$ ). *G* is the *G*-test at three degrees of freedom.

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the deviations were observed in different families, our results do not provide solid evidence of genetic linkage between the loci (Table 3). Considering the two seed orchards, only 5.8% of the pairwise loci were significant for genotypic disequilibrium. In both orchards, significance was found between the following loci: EMBRA681 x EMBRA2 and EMBRA204 x EMBRA210.

**Table 3.** Genotypic disequilibrium between pairwise microsatellite loci for *Eucalyptus urophylla* adult trees from seed orchard SO1 (lower diagonal) and SO2 (upper diagonal).

	EMB2	EMB28	EMB3	EMB11	EMB10	EMB63	EMB12	EMB157	EMB204	EMB128	EMB38	EMB210	EMB681
EMB2	-	0.01090	0.00363	0.08419	0.37607	0.05406	0.16368	0.33718	0.32885	0.09829	0.31346	0.01068	0.00021*
EMB28	0.55449	-	0.07778	0.13120	0.12308	0.01111	0.00363	0.02308	0.07863	0.01239	0.17073	0.05449	0.13312
EMB3	0.01731	0.00278	-	0.08205	0.00385	0.00983	0.00128	0.00021*	0.00043	0.00812	0.00705	0.00192	0.03547
EMB11	0.66175	0.02970	0.06175	-	0.00406	0.08462	0.00299	0.31880	0.30299	0.14124	0.16453	0.12991	0.00641
EMB10	0.93462	0.48397	0.80321	0.45855	-	0.00556	0.10299	0.49017	0.11432	0.08868	0.00021*	0.02393	0.34979
EMB63	0.03718	0.18974	0.00534	0.27030	0.26538	-	0.27842	0.01987	0.22628	0.69380	0.04359	0.10043	0.08419
EMB12	0.14615	0.66731	0.04487	1.0000	0.08718	0.40342	-	0.00299	0.03376	0.11346	0.06132	0.04850	0.02778
EMB157	0.64017	0.10192	0.00919	0.00620	0.26410	0.06731	0.02885	-	0.02073	0.05000	0.02009	0.00256	0.01239
EMB204	0.01667	0.85128	0.03120	0.36731	0.76154	0.18568	0.85491	0.30855	-	0.13654	0.00171	0.00021*	0.00021*
EMB128	0.13889	0.00620	0.15085	0.03868	0.23974	0.21859	0.33226	0.39487	0.87286	-	0.00021*	0.18483	0.06944
EMB38	0.58932	0.30342	0.04444	0.56731	0.25833	0.88739	0.62115	0.75021	0.31346	0.27286	-	0.05983	0.00150
EMB210	0.06709	0.84167	0.02970	0.33739	0.53462	0.27970	0.83504	0.30726	0.00021*	0.86239	0.26560	-	0.00021*
EMB681	0.00021*	0.04103	0.10021	0.06261	0.04231	0.14530	0.93568	0.13355	0.64316	0.06026	0.71816	0.38590	-

P values represent the probability of genotypic disequilibrium after 1440 permutations of alleles among individuals. Value at which results are deemed significant after Bonferroni correction: \*P = 0.00021 ( $\alpha = 0.05$ ).

#### DISCUSSION

Mendelian 1:1 segregation at the individual locus was confirmed for 13 of the tested SSR loci. Significant deviations were only found in isolated cases of EMBRA2 (tree 95) and EMBRA63 (trees 10 and 155), where we found disproportionate results for segregated maternal alleles in their progenies. Of the 30 seeds collected from mother tree 95 (110/132), 27 received allele 110 (90%); for trees 10 and 155 (168/172), 30 (100%), and 26 (86.7%) of the 30 offspring, respectively, received allele 172. These results suggest the occurrence of segregation deviation caused by pre- or post-zygotic factors. Segregation deviations in a limited number of SSR loci of some families can also be caused by sampling errors, small family size, misinterpretation of allele size, or the presence of null alleles (Danner et al., 2013; Tambarussi et al., 2013). Nevertheless, these limited instances found herein do not indicate that the loci deviate from the expected Mendelian inheritance and we can conclude that the 15 EMBRA SSR markers are genetic markers.

The small numbers of significant *G*-test deviations from independent segregation between pairs of loci (1:1:1:1) indicate that the loci segregate independently. Significant values were observed for different families and occurred more frequently between the following pairs: EMBRA2xEMBRA3, EMBRA2xEMBRA63, and EMBRA204xEMBRA128. The significant linkage may be the result of true genetic linkage or deviations from 1:1 Mendelian segregation (Manoel et al., 2015; Moraes et al., 2015), as observed for EMBRA2 and EMBRA63. The absence of linkage between the loci is important concerning models used in population genetic analyses, which assume random segregation between alleles of different loci.

Considering the two seed orchards, our results do not indicate genotypic disequilibrium. Only 5.8% of the results between pairs of loci were significant, and the majority (78%) was detected in SO2. This is likely due to relatedness that exists between the 79 and 298 adult trees on SO1 and SO2, respectively, and the unbalanced proportion of individuals within families that remained after selective thinning during orchard establishment. In both orchards, significance was found between loci EMBRA681xEMBRA2 and EMBRA204xEMBRA210. The imbalance may be affected by selection, recombination, migration, population reduction,

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genetic drift, and population structure (Kumar et al., 2004). Tarazi et al. (2010) found genotypic disequilibrium between pairwise loci in open-pollinated seeds of *Copaifera langsdorffii*, probably due to the inheritance of maternal alleles. When the family structure was considered in the analysis, with a limited number of seeds per family, a few significant values of genotypic disequilibrium were detected, thus supporting the idea that the inheritance of maternal alleles produces genotypic disequilibrium. In conclusion, our results show that the 15 SSR loci analyzed herein form a robust set of genetic markers, which can be used to assess issues related to genetic diversity, mating system, and parentage analysis, providing more in-depth information that can be used to advance *E. urophylla* breeding programs.

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