

Growth potential and genetic parameters of four Mesoamerican pines planted in the Southern Hemisphere

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Summary results are reported from a total of 319 provenance/progeny tests of *Pinus tecunumanii*, *P. maximinoi*, *P. patula* and *P. greggii* that were established on sites in Brazil, Colombia and South Africa. Tests were measured for the growth traits height, diameter at breast height (DBH) and volume at ages 3, 5 and 8 years. At a particular age, correlations among height, DBH and volume were very high (from 0.80 to 0.99) at both the provenance and additive genetic levels, and the three growth traits also had similar heritabilities. Volume at age 3 was highly correlated with age 8 volume (around 0.80), and correlations of age 5 volume with age 8 volume were near 0.95. Low-elevation *P. tecunumanii* had very high between-country correlations both at the provenance and genetic level (around 0.80 to 1.00). Between-country genetic correlations for most other species were around 0.60. Two of the four species, *P. tecunumanii* and *P. maximinoi*, grew substantially faster than the commercial controls planted with the progeny tests (i.e. genetically improved *P. taeda* in Brazil, and improved *P. patula* in Colombia and South Africa). *Pinus greggii* var. *australis* also demonstrated commercial potential on sites in southern Brazil and South Africa. For all species, the best provenance produced 10–20% more volume than the population mean. In all species, additive genetic variation was substantial, and additional genetic gain could be made by family and within-family selection in an intensive tree-breeding effort.

Keywords: genetic correlation, genetic variation, heritability, tree breeding

Introduction

Some of the first steps in any genetic improvement program for plantation forest trees are species selection, and provenance and progeny testing. Even when a long-running plantation program is based on a well-adapted species, a new or alternate species may offer sizeable improvements for important economic traits such as adaptability, growth, wood quality, and disease resistance. Testing species across a wide array of environments can help identify specific sites and environmental conditions in which a 'new' species might be a better commercial option. Over the last 30 years, private forest industry in the Southern Hemisphere has concentrated its efforts on collecting and testing a broad base of genetic material from native populations of *P. patula*, *P. greggii*, *P. maximinoi*, *P. tecunumanii* and other forest species in Mesoamerica through membership in Camcore (International Tree Breeding and Conservation Program) at North Carolina State University. The purpose of these seed collections was to establish field trials either to infuse new genetic material into existing breeding programs (as with *P. patula*), or to search for 'new' species that could outgrow existing commercial ones (as with, for example, *P. greggii*, *P. maximinoi* and *P. tecunumanii*).

These four pine species are adapted to specific environmental niches that make them important for plantation forestry in the Southern Hemisphere. *Pinus patula* is a temperate/subtropical species native to cloud-forest environments in eastern and southern Mexico. It is found on predominantly well-drained soils in its native environment

at altitudes from 1 490 to 3 100 m and with between 1 000 and 2 500 mm of annual precipitation (Dvorak et al. 2000c). Its growth and wood quality is excellent (Poynton 1977, Kanzler et al. 2003, Stanger 2003) when placed on suitable sites as an exotic, and it exhibits good cold tolerance. It is the major commercial pine species in southern and eastern Africa and in the highlands of Colombia, but in Latin America, especially, it is gradually being replaced by the faster-growing *P. tecunumanii* and *P. maximinoi*. In addition, a limiting factor for its continued broad use in South Africa is its susceptibility to serious diseases resulting from infection by the pitch canker fungus (*Fusarium circinatum*) (Hodge and Dvorak 2000, Mitchell et al. 2011).

Pinus greggii is closely related to *P. patula* (Dvorak et al. 2000d). It occurs as two distinct varieties in the mountains of eastern Mexico, namely *P. greggii* var. *australis* and var. *greggii*. The two varieties are geographically separated by 360 km in their native range. *Pinus greggii* var. *australis* is found in subtropical environments in central Mexico and occurs on well-drained soils at slightly lower altitudes (1 360–2 350 m) than *P. patula*. *Pinus greggii* var. *australis* differs from *P. patula* in that it exhibits poorer stem and branch form. It sometimes occurs on dry sites with less than 1 000 mm of annual precipitation. *Pinus greggii* var. *greggii* occurs in a temperate climate in northern Mexico on predominantly shallow calcareous soils. It grows more slowly than var. *australis*. The variety is especially well-adapted to dry sites with 600–700 mm of annual precipitation and is

one of the most cold-hardy of the Mexican pines (Aldrete et al. 2008, Hodge et al. 2012).

Pinus tecunumanii is a tropical/subtropical species that occurs in southern Mexico and throughout the highlands of Central America (Dvorak et al. 2000b). There are two subpopulations of the species in Mesoamerica known as high elevation (HE) *P. tecunumanii* that occur above 1 500 m altitude and low elevation (LE) *P. tecunumanii* that occur below 1 500 m altitude; the subpopulations can be separated by subtle morphological differences and molecular analysis (Dvorak 1986, Dvorak et al. 2009). The HE sources occupy cloud-forest environments. Both subpopulations generally are found on fertile soils on mountain plateaus or valleys in areas with annual rainfall between 1 000 and 2 500 mm. Several populations of HE *P. tecunumanii* exhibit some degree of cold hardiness, whereas LE populations do not (see Hodge et al. 2012). As mentioned before, *P. tecunumanii* is replacing *P. patula* in the more tropical areas of Colombia and seems well suited to the plateau regions of northern Mozambique (Camcore 2010).

Pinus maximinoi is one of the most common species in tropical Mesoamerica (Dvorak et al. 2000a). Its altitudinal range is approximately 600 to 2 400 m in its native range and occurs in regions with 900 to 2 200 mm of annual precipitation. It is often found sympatrically with *P. tecunumanii* in cloud-forest environments on fertile alfisols, but it also occupies drier and shallow ultisols with *P. oocarpa*. The species is planted on a pilot scale in Brazil and Colombia but its fast growth is attracting more users (Kietzka 1988) and, in addition, it has good tolerance to the pitch canker fungus (Hodge and Dvorak 2000). *Pinus maximinoi* has little tolerance to subfreezing temperature (Hodge et al. 2012).

Camcore members in southern Africa and Latin America have established and measured 319 field trials of these four species over the last 30 years. The trials offer the most complete geographic coverage of any international trial series of tropical/subtropical pines, and include a number of provenances from Mesoamerica never before field-tested. In this paper, we summarise the results of these trials to quantify the growth potential of the species and to estimate genetic parameters, heritability and genotype×environment interaction to assess the potential response to selection and future development. We demonstrate that several of the 'new' species and provenances have much greater potential than some of the commercial species being used in plantation forestry today.

Materials and methods

Plant material and genetic tests

Camcore began seed collections of *P. tecunumanii* in 1981 and has sampled more than 800 families from 26 HE provenances (>1 500 m elevation) and 19 LE provenances (<1 500 m elevation) in Chiapas, Mexico, Belize, El Salvador, Guatemala, Honduras, and Nicaragua (Table 1). Although HE and LE *P. tecunumanii* are not technically 'varieties' in a taxonomic sense, for purposes of convenience they will be referred to as varieties in this manuscript.

Collections of *P. maximinoi* began in 1984 and more than 300 families from 26 provenances have been sampled in Guatemala, Honduras, Nicaragua, and Mexico (Table 2).

Collections of *P. patula* began in 1986 and more than 500 families from 22 provenances were sampled in Mexico (Table 3).

Collections of *P. greggii* began in 1988 and more than 300 families from eight provenances of var. *greggii* and seven provenances of var. *australis* were sampled in Mexico (Table 4).

For all species, the seed collections were intended to cover the entire species range. Typically, in every provenance, seeds were collected from 10 to 50 mother trees, with the selected trees standing at least 100 m apart. All seeds from the collections were kept separate by mother tree, were distributed to Camcore members in Argentina, Brazil, Chile, Colombia, Venezuela, and South Africa, and were used to establish provenance/progeny tests and conservation banks. Only a few tests were established in Argentina, and these tests were analysed and grouped with the tests in Brazil, since the geographic climate and environments are similar.

The provenance/progeny tests generally contained a subset of four to seven provenances and/or sources, with each provenance being represented by eight to 15 families. The trial design was the same at all locations, a randomised complete block design, with provenances randomised in each replication, and families randomised within the provenance subblocks. There were nine replications and six trees per family planted in row-plots. Spacing was approximately 3 m × 3 m in all tests. Test measurements were scheduled at ages 3, 5, and 8 years. Measurements were not available at all ages for all tests. Growth traits height in metres and diameter at breast height (DBH; at 1.3 m, in centimetres) were taken and a volume index for juvenile trees calculated as follows:

$$\text{Volume} = 0.00003 (\text{DBH}^2 * \text{height})$$

The form traits stem straightness and branch diameter were assessed using a three-point scale, but will not be discussed at length in this manuscript. Frequency of forking, fox-tailing and broken tops were also assessed, and will be discussed for species where problems were evident.

Table 5 lists the number of tests of each species in each country, along with summary statistics for the latitude, longitude, elevation and precipitation where tests were established (full details of the number of tests of each species, numbers of provenances, families, and trees, and ages of measurements are listed in Appendix 1). Briefly, measurements were available for a total of 133 provenance/progeny tests of *P. tecunumanii*, 43 tests of *P. maximinoi*, 83 tests of *P. patula*, and 62 tests of *P. greggii*. For each species, calculations of growth and survival means for each test, and across all tests for a given country were done using SAS® (SAS Institute 2002). The primary commercial pine species in Brazil is *P. taeda*, in Colombia and South Africa is *P. patula*, and in Chile is *P. radiata*, and checklots of the commercial species were often included in the provenance/progeny tests. In order to evaluate the potential of the Mesoamerican species as commercial species, their mean growth was compared to the growth of commercial checklots.

Table 1: Details¹ for provenances of *Pinus tecunumanii*

Code	Provenance	State/ department	Country	Latitude	Longitude	Elevation (m)		Precipitation (mm)	Volume gain (%) ²		
						Min.	Max.		BRZ	COL	SAF
High-elevation <i>Pinus tecunumanii</i>											
1	Km 33	Guatemala	Guatemala	14°35' N	90°22' W	2 000	2 200	1 543	-10.0	-3.4	-5.4
2	Km 47	Guatemala	Guatemala	14°35' N	90°25' W	2 000	2 200	1 543	-10.8	-1.0	-5.4
3	La Soledad	Jalapa	Guatemala	14°30' N	90°24' W	2 390	2 465	1 543	2.9	2.2	1.7
4	Pachoc	Totonicapán	Guatemala	14°52' N	91°16' W	2 000	2 500	1 350	2.9	-0.2	1.3
5	San Jerónimo	Baja Verapaz	Guatemala	15°03' N	90°18' W	1 620	1 850	1 200	11.1	11.6	7.0
6	San Lorenzo	Zacapa	Guatemala	15°05' N	89°40' W	1 900	2 100	1 700	-5.3	0.7	-2.5
7	San Vicente	Baja Verapaz	Guatemala	15°05' N	90°07' W	1 690	2 200	1 700	-6.8	0.1	-3.2
8	Celaque	Lempira	Honduras	14°33' N	88°40' W	1 540	2 030	1 273	0.3	-1.0	-0.1
9	Las Trancas	La Paz	Honduras	14°07' N	87°49' W	2 075	2 185	1 579	-0.2	-5.9	-1.2
10	Chanal	Chiapas	Mexico	16°42' N	92°23' W	2 010	2 350	1 238	-0.1	-7.5	-1.2
11	Chempil	Chiapas	Mexico	16°45' N	92°25' W	2 020	2 220	1 146	13.0	6.3	7.2
12	El Carrizal	Chiapas	Mexico	15°24' N	92°18' W	2 130	2 280	2 000	-0.7	-4.4	-1.1
13	Jitotol	Chiapas	Mexico	17°02' N	92°51' W	1 660	1 750	1 701	8.4	4.9	4.7
15	Las Piedrecitas	Chiapas	Mexico	16°42' N	92°35' W	2 360	2 500	1 252	-10.4	-1.5	-5.3
16	Montebello	Chiapas	Mexico	16°06' N	91°45' W	1 660	1 750	1 909	23.3	11.4	12.7
17	Napite	Chiapas	Mexico	16°34' N	92°19' W	2 070	2 350	1 350	6.1	-1.8	2.6
18	Rancho Nuevo	Chiapas	Mexico	16°41' N	92°35' W	2 280	2 340	1 238	-8.5	1.8	-3.9
19	Chiul	El Quiché	Guatemala	15°20' N	91°04' W	2 440	2 680	1 996	1.4	4.1	1.2
20	San José	Chiapas	Mexico	16°42' N	92°41' W	2 245	2 400	1 252	-2.4	-7.6	-2.3
21	Cabricán	Quetzaltenango	Guatemala	15°35' N	91°38' W	2 510	2 670	1 010	-12.2	-7.1	-7.0
22	San Miguel	San Marcos	Guatemala	15°16' N	91°45' W	2 280	2 370	2 127	0.6	-0.6	0.1
24	La Piedad	El Progreso	Guatemala	15°02' N	90°02' W	2 080	2 230	2 592	0.1	2.1	0.3
25	El Pinalón	El Progreso	Guatemala	14°59' N	89°55' W	2 100	2 770	2 592	0.0	1.9	0.2
27	El Ingenio	Jalapa	Guatemala	14°43' N	90°02' W	1 850	1 920	1 400	2.6	3.9	1.7
28	Río Chiquito	Chalatenango	El Salvador	14°22' N	89°08' W	1 950	2 280	1 629	-5.7	-3.8	-3.4
29	Montecristo	Santa Ana	El Salvador	14°24' N	89°24' W	1 700	1 850	1 997	0.4	-5.2	-0.7
Low-elevation <i>Pinus tecunumanii</i>											
1	Jocón	Yoro	Honduras	15°16' N	86°53' W	775	1 000	1 166	-8.3	-16.7	-12.5
2	San Esteban	Olancho	Honduras	15°15' N	85°38' W	600	1 200	1 071	3.2	6.3	4.7
3	San Francisco	Olancho	Honduras	14°57' N	86°07' W	900	1 590	1 491	2.5	9.6	5.8
4	Villa Santa	El Paraíso	Honduras	14°12' N	86°17' W	800	1 000	1 302	8.7	12.4	10.9
5	Culmí	Olancho	Honduras	15°08' N	85°36' W	400	950	1 491	3.2	3.7	3.6
6	Los Planes	Comayagua	Honduras	14°48' N	87°53' W	1 100	1 650	2 287	-0.1	-0.3	-0.2
7	Cerro Cusuco	Cortés	Honduras	15°30' N	88°13' W	1 350	1 630	2 287	-6.2	-12.4	-9.3
8	Gualaco	Olancho	Honduras	15°03' N	86°08' W	600	800	1 491	1.6	5.2	3.3
9	Campamento	Olancho	Honduras	14°39' N	86°43' W	900	1 100	1 484	1.1	-2.9	-0.6
10	La Esperanza	Intibucá	Honduras	14°16' N	88°13' W	1 720	1 850	1 363	3.3	1.7	2.8
11	Esquipulas del Norte	Olancho	Honduras	15°15' N	86°30' W	980	1 020	1 067	-13.0	-17.0	-15.5
12	Locomapa	Yoro	Honduras	15°30' N	87°20' W	1 200	1 500	1 167	-8.7	-15.6	-12.3
13	Yucul	Matagalpa	Nicaragua	12°56' N	85°46' W	910	1 170	1 394	7.9	14.8	11.4
14	San Rafael del Norte	Jinotega	Nicaragua	13°14' N	86°07' W	1 080	1 330	1 362	2.9	7.4	5.1
16	Las Camelias	Nueva Segovia	Nicaragua	13°46' N	86°18' W	950	1 060	1 500	4.1	6.8	5.5
17	Apante	Matagalpa	Nicaragua	12°54' N	85°56' W	920	1 040	1 394	4.3	10.7	7.4
18	La Rinconada	Matagalpa	Nicaragua	12°42' N	86°11' W	920	980	900	-0.9	0.4	-0.5
19	Mountain Pine Ridge	Cayo	Belize	16°53' N	88°54' W	560	790	1 558	-1.0	-4.8	-2.7
20	San Pastor Pine Ridge	Cayo	Belize	16°40' N	88°57' W	600	800	1 558	-4.6	-9.5	-7.0

¹ Variables include latitude, longitude, minimum and maximum elevation, annual precipitation

² BRZ, COL, and SAF are the predicted provenance effect for volume gain (%) in Brazil, Colombia, and South Africa, respectively

Correction of heights for broken top trees

For both *P. maximinoi* and HE *P. tecunumanii*, about 10% of the tests had significant frequencies of broken tops (>15%) in 5-year and 8-year data. Rather than discard observations for trees with broken tops, an estimated height was calculated for trees with broken tops and with extremely small height/DBH ratios. For each test, a simple linear regression of log height – inverse DBH equation

(Matney and Sullivan 1982) was fit for 5-year and 8-year data using only non-broken top trees as follows:

$$\ln(\text{height}) = a + b \text{ DBH}^{-1}$$

The test-specific equations fit the non-broken top trees very well (average $R^2 = 0.86$), and thus should make reliable predictions of height for trees with broken tops. Volume was

Table 2: Details¹ for provenances of *Pinus maximinoii*

Code	Provenance	State/department	Country	Latitude	Longitude	Elevation (m)		Precipitation (mm)	Volume gain (%) ²		
						Min.	Max.		BRZ	COL	SAF
1	Cobán	Alta Verapaz	Guatemala	15°28' N	90°24' W	1 300	1 440	2 075	0.4	-1.1	4.9
2	San Jerónimo	Baja Verapaz	Guatemala	15°03' N	90°15' W	1 280	1 860	970	-0.5	1.4	6.6
3	San Juan Sacatepéquez	Guatemala	Guatemala	14°41' N	90°38' W	1 580	2 000	1 138	-2.0	-5.8	5.0
4	Dulce Nombre de Copán	Copán	Honduras	14°50' N	88°51' W	1 100	1 300	1 386	0.9	5.6	2.2
5	Marcala	La Paz	Honduras	14°10' N	88°01' W	1 600	1 800	1 670	0.0	2.1	-1.7
6	Tapiquil	Yoro	Honduras	15°10' N	86°50' W	1 500	1 769	1 069	2.5	-3.9	-10.0
7	Tatumbula	Fco. Morazán	Honduras	14°02' N	87°07' W	1 400	1 600	1 153	-0.4	9.9	0.2
8	Altamirano	Chiapas	Mexico	16°43' N	92°02' W	1 280	1 350	1 644	-0.4	0.7	3.4
9	San Jerónimo CH	Chiapas	Mexico	17°03' N	92°08' W	940	1 020	1 417	-1.4	2.4	8.4
10	Ciénega de León	Chiapas	Mexico	16°41' N	94°00' W	1 050	1 240	1 078	0.6	-5.8	-5.7
11	Coapilla	Chiapas	Mexico	17°08' N	93°10' W	1 360	1 510	1 350	0.0	-9.9	-7.1
12	La Cañada	Chiapas	Mexico	16°49' N	92°09' W	1 270	1 360	1 576	-1.1	5.7	8.2
13	Monte Cristo	Chiapas	Mexico	15°44' N	92°33' W	750	900	2 000	-0.8	-6.5	1.1
14	Valle de Angeles	Fco. Morazán	Honduras	14°10' N	87°02' W	1 200	1 600	1 118	0.9	-1.8	-7.5
15	San Juan Copala	Chiapas	Mexico	17°10' N	97°58' W	1 370	1 560	1 350	-1.5	1.1	4.4
16	San Jerónimo OA	Oaxaca	Mexico	16°10' N	97°00' W	1 220	1 480	1 350	-1.2	-1.9	-2.3
17	Candelaria	Oaxaca	Mexico	16°00' N	96°31' W	1 370	1 480	1 117	-1.8	0.9	4.4
18	Las Compuertas	Guerrero	Mexico	17°10' N	99°59' W	1 050	1 200	1 400	0.5	-0.3	-1.4
19	El Portillo	Ocotepaque	Honduras	14°28' N	89°01' W	1 400	1 600	1 325	1.7	-3.4	-9.4
20	Yuscarán	El Paraíso	Honduras	13°50' N	86°55' W	1 500	1 700	1 300	4.0	-2.1	-10.0
22	La Lagunilla	Jalapa	Guatemala	14°42' N	89°57' W	1 540	1 860	1 017	0.0	2.1	0.9
23	San Lorenzo	Zacapa	Guatemala	15°05' N	89°40' W	1 900	2 100	1 500	-0.2	-1.7	0.1
24	San José Bayuncún	Nueva Segovia	Nicaragua	13°45' N	86°20' W	980	1 240	1 184	0.9	9.9	3.1
25	San Francisco Murra	Nueva Segovia	Nicaragua	13°45' N	86°00' W	930	1 130	1 410	-0.7	-0.1	0.9
26	Datanlí	Jinotega	Nicaragua	13°07' N	85°54' W	980	1 200	1 213	-0.3	2.7	1.4

¹ Variables include latitude, longitude, minimum and maximum elevation, annual precipitation

² BRZ, COL, and SAF are the predicted provenance effect for volume gain (%) in Brazil, Colombia, and South Africa, respectively

Table 3: Details¹ for provenances of *Pinus patula*

Code	Provenance	State/department	Country	Latitude	Longitude	Elevation (m)		Precipitation (mm)	Volume gain (%) ²		
						Min.	Max.		BRZ	COL	SAF
1	Potrero de Monroy	Veracruz	Mexico	20°24' N	98°25' W	2 320	2 480	1 350	11.0	-11.5	9.8
2	Ingenio del Rosario	Veracruz	Mexico	19°31' N	97°06' W	2 770	2 870	1 346	-1.2	-10.8	-2.0
3	Corralitla	Veracruz	Mexico	18°38' N	97°06' W	2 000	2 230	2 500	5.0	15.1	6.2
4	El Manzanal	Oaxaca	Mexico	16°06' N	96°33' W	2 350	2 660	1 348	-6.4	8.1	-7.0
5	El Tlacuache	Oaxaca	Mexico	16°44' N	97°09' W	2 300	2 620	2 000	-8.4	3.9	-9.4
6	Ixtlán	Oaxaca	Mexico	17°24' N	96°27' W	2 600	2 870	1 750	-4.9	1.6	-5.6
7	Santa María Papalo	Oaxaca	Mexico	17°49' N	96°48' W	2 270	2 720	1 100	-2.1	9.3	-2.1
8	Conrado Castillo	Tamaulipas	Mexico	23°56' N	99°28' W	1 500	2 060	1 012	0.3	-49.4	-5.9
9	Cuajimoloyas	Oaxaca	Mexico	17°10' N	96°21' W	2 450	2 770	1 135	-1.6	-10.8	-7.0
10	Tlacotal	Tlaxcala	Mexico	19°40' N	98°05' W	2 750	2 915	1 097	-11.6	-23.4	-9.1
11	Pinal de Amoles	Querétaro	Mexico	21°07' N	99°41' W	2 380	2 550	1 350	-7.1	-4.5	5.2
12	Zacualtipán	Hidalgo	Mexico	20°39' N	98°40' W	1 980	2 200	2 047	13.9	3.6	5.5
13	Llano de las Carmonas	Puebla	Mexico	19°48' N	97°54' W	2 530	2 880	1 097	1.1	-7.1	0.7
14	Carrizal de Bravo	Guerrero	Mexico	17°34' N	99°53' W	1 980	2 440	1 209	-0.3	0.0	-0.5
15	El Cielo	Tamaulipas	Mexico	23°04' N	99°14' W	1 600	1 730	1 200	9.0	-3.5	1.6
16	La Encarnación	Hidalgo	Mexico	20°53' N	99°13' W	2 400	2 650	1 200	-5.1	8.0	5.4
17	La Cruz	Hidalgo	Mexico	20°17' N	98°18' W	2 300	2 450	1 869	6.0	24.6	5.7
18	Cumbre de Muridores	Hidalgo	Mexico	20°19' N	98°21' W	2 380	2 480	1 869	-2.4	17.1	4.1
19	Cruz Blanca	Veracruz	Mexico	19°39' N	97°09' W	2 450	2 550	1 347	8.0	13.5	6.4
20	Calchualco	Veracruz	Mexico	19°07' N	97°06' W	2 350	2 400	2 020	0.9	-2.8	0.6
22	Sierra Huayacocotla	Veracruz	Mexico	20°29' N	98°28' W	1 840	2 860	1 405	2.8	3.1	0.7
23	Acaxochitlán	Hidalgo	Mexico	20°09' N	98°10' W	2 460	2 490	1 857	-7.0	15.9	-3.6

¹ Variables include latitude, longitude, minimum and maximum elevation, annual precipitation

² BRZ, COL, and SAF are the predicted provenance effect for volume gain (%) in Brazil, Colombia, and South Africa, respectively

Table 4: Details¹ for provenances of the northern and southern varieties of *Pinus greggii*

Code	Provenance	State/department	Country	Latitude	Longitude	Elevation (m)		Precipitation (mm)	Volume gain (%) ²		
						Min.	Max.		BRZ	COL	SAF
<i>P. greggii</i> var. <i>greggii</i> (northern variety)											
4	Las Placetas	Nuevo León	Mexico	24°55' N	100°11' W	2 370	2 520	750			-0.2
5	Los Lirios	Coahuila	Mexico	25°22' N	100°29' W	2 300	2 400	650			1.5
6	Jamé	Coahuila	Mexico	25°21' N	100°37' W	2 500	2 590	650			-2.6
7	Cerro El Potosí	Nuevo León	Mexico	24°54' N	100°12' W	2 430	2 500	750			-14.6
8	Ojo de Agua	Nuevo León	Mexico	24°53' N	100°13' W	2 115	2 400	750			-8.8
9	La Tapona	Nuevo León	Mexico	24°37' N	100°10' W	2 090	2 350	650			23.7
14	Loma el Oregano	Coahuila	Mexico	25°22' N	100°54' W	2 270	2 430	600			-7.2
15	Sierra el Tarrillal	Coahuila/Nuevo León	Mexico	25°26' N	100°30' W	1 960	2 540	650			8.3
<i>P. greggii</i> var. <i>australis</i> (southern variety)											
1	El Madroño	Querétaro	Mexico	21°16' N	99°10' W	1 500	1 660	1 100	0.0		1.3
2	Laguna Atezca	Hidalgo	Mexico	20°49' N	98°46' W	1 250	1 420	1 642	14.0		-1.8
3	Laguna Seca	Hidalgo	Mexico	21°02' N	99°10' W	1 750	1 900	820	-14.1		-2.7
10	Valle Verde	Querétaro	Mexico	21°29' N	99°10' W	1 150	1 250	1 400	14.2		12.5
11	San Joaquín	Querétaro	Mexico	20°56' N	99°34' W	2 130	2 350	1 109	-27.3		-8.5
12	Jalamelco	Hidalgo	Mexico	20°48' N	98°42' W	1 800	1 880	1 642	6.2		2.2
13	Carrizal Chico	Veracruz	Mexico	20°26' N	98°20' W	1 360	1 770	1 855	7.0		-3.1

¹ Variables include latitude, longitude, minimum and maximum elevation, annual precipitation

² BRZ, COL, and SAF are the predicted provenance effect for volume gain (%) in Brazil, Colombia, and South Africa, respectively

Table 5: Summary statistics for latitude, elevation, and precipitation for provenance/progeny tests of *P. tecunumanii*, *P. maximinoi*, *P. patula* and *P. greggii* established in various countries

Variety ¹	Country	Tests	Latitude			Elevation (m)			Precipitation (mm)		
			Median	Min.	Max.	Median	Min.	Max.	Median	Min.	Max.
<i>P. tecunumanii</i>											
HE	Argentina	1	26°02' S	26°02' S	26°02' S	195	195	195	1965	1 965	1 965
HE	Brazil	22	19°56' S	15°32' S	27°32' S	780	614	1 190	1490	1 081	1 800
HE	Colombia	19	2°20' N	2°16' N	5°21' N	2 142	1 747	2 704	2166	2 011	2 512
HE	South Africa	30	25°04' S	23°00' S	31°14' S	1 150	45	1 590	1254	858	1 953
LE	Argentina	1	26°02' S	26°02' S	26°02' S	195	195	195	1965	1 965	1 965
LE	Brazil	26	24°07' S	18°38' S	24°25' S	780	25	1 080	1490	1 081	2 077
LE	Colombia	17	4°00' N	2°31' N	4°43' N	1 758	1 545	2 526	2167	1 207	2 661
LE	South Africa	17	26°10' S	24°58' S	32°10' S	930	45	1 530	1175	900	1 316
<i>P. maximinoi</i>											
	Argentina	1	26°02' S	26°02' S	26°02' S	195	195	195	1965	1 965	1 965
	Brazil	13	18°38' S	16°30' S	24°25' S	810	625	855	1400	986	1 561
	Colombia	13	2°35' N	2°16' N	5°27' N	1 854	1 626	2 630	2207	1 333	3 177
	South Africa	16	25°14' S	24°55' S	28°24' S	980	69	1 080	1201	1 194	1 316
<i>P. patula</i>											
	Brazil	30	26°00' S	23°59' S	27°45' S	850	760	1 140	1473	1 271	1 873
	Chile	3	35°52' S	35°19' S	38°36' S	130	93	205	1183	837	1 437
	Colombia	13	2°35' N	2°18' N	5°23' N	2 542	1 788	2 897	2270	1 608	2 653
	South Africa	37	26°12' S	24°55' S	31°02' S	1 350	980	1 730	921	757	1 953
<i>P. greggii</i>											
<i>greggii</i>	Chile	4	35°52' S	35°19' S	38°36' S	130	93	205	1183	837	1 437
<i>greggii</i>	South Africa	20	29°34' S	24°58' S	31°27' S	1 500	960	1 800	823	712	1 316
<i>australis</i>	Brazil	16	25°09' S	24°02' S	27°31' S	820	710	1 110	1473	1 394	1 769
<i>australis</i>	Chile	4	35°52' S	35°19' S	38°36' S	130	93	205	1183	837	1 437
<i>australis</i>	South Africa	16	26°57' S	25°10' S	31°27' S	1 500	952	1 782	846	712	1 194

¹ *Pinus tecunumanii* has two elevation sources (HE = high-elevation provenances and LE = low-elevation provenances), and *Pinus greggii* has two varieties (the northern var. *greggii* and the southern var. *australis*)

then calculated for broken-top trees using the estimated height and the observed DBH.

Standardisation of data

Forest tree growth traits often display a strong relationship

between the mean of the trait and its phenotypic and genetic variances, such that field tests with bigger trees will have larger phenotypic and genetic variances than field tests with smaller trees (even if the tests are of the same age). To deal with this situation of heterogeneous

variances (sometimes called scale effects), White et al. (2007) recommend data standardisation prior to ANOVA, variance component analysis, or multiple-site mixed model analysis. The goal is primarily to homogenise variances that will be pooled together in the linear model, and to eliminate 'spurious' genotype \times environment interaction (Eisen and Saxon 1963, Burdon 1977, Hill 1984). For the analyses in the current paper, standardisation was performed as follows: the phenotypic coefficient of variation was calculated for each replication for each growth trait, and a mean coefficient of variation (CV_y) was calculated for each species–country–trait combination. Phenotypic observations were then standardised in each replication to a mean = 100, and standard deviation = 100 CV_y using PROC STANDARD in SAS®. Effectively, this is equivalent to dividing all observations by the phenotypic SD, as recommended by White et al. (2007), followed by adding a constant (100%) and multiplying by a constant (100 CV_y). The advantage of this standardisation is that the population mean for the growth trait can be interpreted as 100%, and the associated variances and standard deviations are the same size relative to mean as in the raw data, thus all variance components and predicted breeding values can be directly interpreted in terms of percent gain (above or below 100%) without any further need for back-transformation or rescaling.

Species–country variance components and genetic parameters

All variance component analyses were done using ASREML (Gilmour et al. 2006). Several variance component analyses were conducted for each species (and variety/source) and for each country where the species was tested.

- (1) Single-trait analyses for the three growth traits (height, DBH, and volume index) at each age of measurement (3, 5 and 8 years) were done.
- (2) Multiple-trait analyses for the three growth traits at a single-age of measurement were used to estimate genetic parameters for each trait, and genetic correlations among traits.
- (3) Multiple-trait analyses for volume at three different ages (3, 5 and 8 years) were done to estimate age–age genetic correlations, and final genetic parameter estimates for volume.

The variance-covariance parameter estimates from the single-trait analyses were provided to the ASREML program as starting values for the initial iteration of the multiple-trait analyses in steps 2 and 3.

The linear model for all of the analyses was as follows:

$$y_{ijklm} = \mu + E_i + B(E)_{ij} + P_k + PE_{ik} + F(P)_{kl} + F(P)E_{ikl} + e_{ijklm}$$

where y_{ijklm} = phenotypic observation for the $ijklm$ th tree, μ = overall mean, E_i = fixed effect of the i th test, $B(E)_{ij}$ = fixed effect of the j th block nested in the i th test, P_k = random effect of the k th provenance, $E[P_k] = 0$, $\text{Var}[P_k] = \sigma_{\text{prov}}^2$, PE_{ik} = random interaction of the k th provenance and the i th test, $E[PE_{ik}] = 0$, $\text{Var}[PE_{ik}] = \sigma_{\text{pe}}^2$, $F(P)_{kl}$ = random effect across sites of the l th family in the k th provenance, $E[F(P)_{kl}] = 0$, $\text{Var}[F(P)_{kl}] = \sigma_{\text{f}}^2$, $F(P)E_{ikl}$ = random interaction of the l th family in the k th provenance and the i th

test, $E[F(P)E_{ikl}] = 0$, $\text{Var}[F(P)E_{ikl}] = \sigma_{\text{fe}}^2$, e_{ijklm} = random error term associated with the $ijklm$ th tree, $E[e_{ijklm}] = 0$, and $\text{Var}[e_{ijklm}] = \sigma_{\text{e}}^2$.

Phenotypic variance within-provenance (σ_{phen}^2) was estimated as:

$$\hat{\sigma}_{\text{phen}}^2 = \hat{\sigma}_{\text{f}}^2 + \hat{\sigma}_{\text{fe}}^2 + \hat{\sigma}_{\text{e}}^2.$$

Narrow-sense heritability within provenance (h^2) was estimated as:

$$h^2 = \hat{\sigma}_{\text{f}}^2 / \hat{\sigma}_{\text{phen}}^2$$

The covariance among open-pollinated families would typically be higher than one-quarter of additive genetic variance; this could result from inbreeding and/or from a small number of effective male pollinators leading to the presence of some percentage of full-sibs with the open-pollinated family (Squillace 1974). Thus a coefficient of 3 instead of 4 was multiplied by the family variance in the calculation of heritability. This has been found to give better agreement between parameter estimates from open-pollinated and control-pollinated data sets for the same genetic material (Dieters et al. 1995).

The amount of provenance variation was estimated as:

$$P^2 = \hat{\sigma}_{\text{prov}}^2 / \hat{\sigma}_{\text{phen}}^2$$

This allows a direct comparison of provenance variation (P^2) and additive genetic variation (h^2). Standard errors of P^2 and h^2 were estimated using the standard errors of $\hat{\sigma}_{\text{prov}}^2$ and $\hat{\sigma}_{\text{f}}^2$, respectively, as calculated by ASREML, and treating $\hat{\sigma}_{\text{phen}}^2$ as a constant according to Dickerson's approximation (Dickerson 1969).

Type B genetic (r_{Bg}) and provenance (r_{Bprov}) correlations were estimated as:

$$r_{\text{Bg}} = \hat{\sigma}_{\text{f}}^2 / (\hat{\sigma}_{\text{f}}^2 + \hat{\sigma}_{\text{fe}}^2)$$

$$r_{\text{Bprov}} = \hat{\sigma}_{\text{p}}^2 / (\hat{\sigma}_{\text{p}}^2 + \hat{\sigma}_{\text{pe}}^2)$$

Type B correlations measure the genetic or provenance correlation between the same trait expressed on two different sites (Burdon 1977). Assuming homogeneous variances, the Type B correlation will measure the type of genotype \times environment interaction that is due to rank changes across environments. It is this type of interaction that is of most interest to tree breeders selecting provenances or families that will perform well across the range of sites. Type B correlations over multiple sites range between zero and one; an $r_{\text{B}} \approx 1$ indicates a near-perfect correlation between performance in different environments or, in other words, an absence of genotype (or provenance) \times environment interaction.

Standard errors of r_{Bg} were estimated using the standard errors of $\hat{\sigma}_{\text{f}}^2$ and $\hat{\sigma}_{\text{fe}}^2$ and $\text{Cov}(\hat{\sigma}_{\text{f}}^2, \hat{\sigma}_{\text{fe}}^2)$ from ASREML and a first-order approximation of a Taylor-expansion series (Lee and Forthofer 2006), and SE of r_{Bprov} estimated in a similar manner.

A genetic coefficient of variation (GCV) was calculated as:

$$\text{GCV} = 100 * \hat{\sigma}_{\text{f}} / \bar{x}$$

where \bar{x} = the trait mean. The GCV expresses the additive genetic standard deviation in terms of percent, and gives a breeder an estimate of how much genetic improvement could be made in a trait.

Finally, ASREML was used calculate trait correlations (height–DBH, height–volume, and DBH–volume) and age–age correlations for volume (VOL3–VOL5, VOL3–VOL8, and VOL5–VOL8) at the genetic and provenance levels. The ASREML program is well suited for multiple trait analyses, and allows the user to specify each data point as a particular trait, and also to specify the structure or form of the variance-covariance (or correlation) matrix for each random effect in the linear model. Thus for each random effect, ASREML can calculate the variance component for each trait and correlations among the traits, along with associated standard errors (Gilmour et al. 2006).

Across-country variance components and provenance BLUPs

When the species-country analyses were completed, an across-country analysis was done for each species using the variable VOL58, defined as volume at age 8 years when available, and volume at age 5 years as a proxy when not available. Since both VOL5 and VOL8 were standardised, they have the same mean and results showed that they have essentially the same genetic parameters and a genetic correlation $r_g(\text{VOL5–VOL8}) \approx 1.00$.

ASREML was used to conduct the multiple-trait analyses, with VOL58 in each country being treated as a distinct trait. Fixed and random effects in the models were the same as defined above. Country-country correlations at the genetic and provenance level (and standard errors) were estimated directly from the ASREML output. These analyses were also used to produce best linear unbiased predictions (BLUPs) of provenance effects for VOL58 for each country.

Climatic distribution modeling

The plant distribution model MaxEnt (Elith et al. 2011) was run for all four species using a worldwide climatic data base available from BIOCLIM (<http://www.worldclim.org/bioclim>). Our goal was to determine if the locations of the Camcore trials actually sampled the highest probability climatic matches between native environments and field trial locations, and also was used to locate new geographic regions that might support additional plantings.

Results

Growth results

Mean survival, height, DBH, and volume per tree for each species in each country are presented in Table 6. Survival rates were generally good, with average survival of 81% across all species–country combinations. For a particular species–country combination, average survival rates ranged from 67.2% (*P. maximinoi* in Brazil) to 87.7% (LE *P. tecunumanii* in Brazil), and this variation should be borne in mind when interpreting growth rates. In general, the two varieties of *P. tecunumanii* and *P. maximinoi* demonstrated relatively similar growth rates across all countries, with the highest growth rates in Colombia, slightly less in Brazil, and slightly less again in South Africa.

For example, *P. maximinoi* had mean height at 8 years of 17.4, 15.7, and 13.7 m and mean DBH of 21.4, 19.6, and 18.3 cm in Colombia, Brazil, and South Africa, respectively. The patterns for the two varieties of *P. tecunumanii* were the same, but with smaller differences.

Growth rates for *P. patula* and *P. greggii* were substantially less than those of *P. tecunumanii* and *P. maximinoi* in all cases. In Colombia, South Africa, and Brazil, mean height of *P. patula* at 8 years was 12.3, 11.9, and 10.9 m, respectively, and mean DBH was 18.8, 18.0 and 17.5 cm. *Pinus greggii* var. *australis* was tested in both South Africa and Brazil, and had similar growth rates, but did better in Brazil (height = 11.9 m, DBH = 18.9 cm) than in South Africa (height = 11.0 m, mean DBH = 17.5 cm).

Pinus patula, *P. greggii* var. *australis*, and *P. greggii* var. *greggii* were also tested in Chile. The species were not as well adapted there, which was seen both in somewhat lower survival (typically 65–75%) and substantially lower growth rates (heights of around 6.5–8.5 m at 8 years).

Comparisons with commercial species

In Brazil, both varieties of the unimproved *P. tecunumanii* and *P. maximinoi* showed substantial gain over improved *P. taeda* (Table 7). *Pinus maximinoi* showed the highest gain potential, with nearly 130% volume gain over *P. taeda* at age 8 years. Low-elevation *P. tecunumanii* had nearly 80% gain, and HE *P. tecunumanii* had 15.8% gain, over *P. taeda* at 8 years. Height, DBH and volume gains were apparent as early as 3 years.

The more temperate species, *P. patula* and *P. greggii* var. *australis*, grew well in Brazil, but mean species growth was not superior to *P. taeda*, with around 30% less volume at 8 years than improved *P. taeda*.

In Colombia, where the commercial species is *P. patula*, the unimproved *P. tecunumanii* and *P. maximinoi* showed substantial growth superiority. Eight-year volume gains over improved *P. patula* were 32.7% for HE *P. tecunumanii*, 21.3% for LE *P. tecunumanii*, and 38.6% for *P. maximinoi*. For LE *P. tecunumanii* and *P. maximinoi*, gains in height, DBH, and volume were apparent at 3 years. For HE *P. tecunumanii*, the pattern was not the same, as essentially no gains in growth were observed at 3 years, whereas volume gain at 5 years was 8.7%, and 32.7% at 8 years.

As in Colombia, the primary commercial pine species in South Africa is *P. patula*, and the comparison of *P. patula* with unimproved *P. tecunumanii* and *P. maximinoi* showed similar results. High-elevation *P. tecunumanii* had 16.8% advantage in volume compared to improved *P. patula* at 8 years, LE *P. tecunumanii* had 25.9% advantage in volume, and *P. maximinoi* had 42.2% volume advantage.

In South Africa, *P. greggii* var. *greggii* had less than half the volume of *P. patula* at 8 years. Although the unimproved *P. greggii* var. *australis* also grew more slowly than *P. patula*, it demonstrated much more potential as a commercial species. At 8 years, *P. greggii* var. *australis* averaged about 17.5% less volume growth than improved *P. patula*.

In both Colombia and South Africa, improved varieties of *P. patula* were included as checklots in the Camcore *P. patula* provenance/progeny trials. In both countries, the unimproved provenances grew about 8–9% less than the improved commercial variety. This corresponds reasonably

Table 6: Growth and survival in progeny tests of *P. tecunumanii*, *P. maximinoi*, *P. patula* and *P. greggii* averaged across all available progeny tests in various countries

Variety ¹	Country	Age 3				Age 5				Age 8						
		Tests	Survival (%)	Height (m)	DBH (cm)	Volume (m ³)	Tests	Survival (%)	Height (m)	DBH (cm)	Volume (m ³)	Tests	Survival (%)	Height (m)	DBH (cm)	Volume (m ³)
<i>P. tecunumanii</i>																
HE	Argentina				–	–	1	83.3	9.7	15.4	0.0804	1	78.6	13.9	18.7	0.1707
HE	Brazil	19	91.2	4.5	6.8	0.0085	18	89.8	8.2	12.5	0.0473	13	87.2	14.8	18.6	0.1769
HE	Colombia	17	90.2	5.8	9.1	0.0202	19	87.8	9.4	15.3	0.0791	19	85.1	14.9	21.2	0.2235
HE	South Africa	24	78.3	4.2	5.6	0.0058	28	76.2	8.3	12.4	0.0445	28	73.3	13.4	18.5	0.1496
LE	Argentina	0	68.6	5.4	–	–	1	71.9	9.9	15.2	0.0795	1	67.8	14.7	18.9	0.1791
LE	Brazil	23	88.3	5.0	7.3	0.0111	20	87.5	8.7	13.0	0.0530	14	87.7	15.1	18.6	0.1823
LE	Colombia	15	86.3	6.6	10.2	0.0241	17	84.6	10.2	15.6	0.0865	15	79.3	15.7	19.9	0.2080
LE	South Africa	14	79.8	4.4	6.4	0.0081	13	76.0	8.7	12.8	0.0485	14	79.4	13.0	17.8	0.1354
<i>P. maximinoi</i>																
	Argentina				–	–	1	74.7	9.0	15.1	0.0684	1	71.1	15.7	20.0	0.2043
	Brazil	11	76.0	5.6	7.5	0.0118	8	70.4	10.3	14.6	0.0776	7	67.2	15.7	19.6	0.2246
	Colombia	13	90.4	6.0	7.9	0.0140	10	87.1	11.2	15.5	0.0917	10	82.6	17.4	21.4	0.2668
	South Africa	13	73.7	5.2	6.2	0.0079	15	71.5	9.7	13.0	0.0548	15	68.9	13.7	18.3	0.1543
<i>P. patula</i>																
	Brazil	24	93.1	4.4	5.7	0.0056	26	90.7	7.7	12.9	0.0457	24	86.1	10.9	17.5	0.1175
	Colombia	12	83.9	4.5	6.8	0.0082	13	84.7	7.5	13.3	0.0471	13	83.0	12.3	18.8	0.1533
	South Africa	35	82.9	3.9	5.0	0.0044	36	81.4	7.1	11.5	0.0328	38	79.9	11.9	18.0	0.1269
	Chile	1	62.7	2.4	1.5	0.0002	3	67.5	4.9	6.8	0.0085	3	68.0	8.6	13.3	0.0576
<i>P. greggii</i>																
greggii	South Africa	9	84.7	2.5	4.2	0.0024	20	85.1	5.0	8.9	0.0138	21	82.3	8.4	14.4	0.0582
greggii	Chile	1	80.7	1.8	1.9	0.0003	4	80.2	4.2	6.2	0.0063	5	81.7	6.6	10.2	0.0271
australis	Argentina	2	81.9	5.9	8.8	0.0175	0	–	–	–	–	0	–	–	–	–
australis	Brazil	13	92.6	4.5	6.5	0.0074	14	90.6	7.4	12.8	0.0423	14	86.4	11.9	18.9	0.1490
australis	South Africa	8	88.9	4.0	6.4	0.0073	16	85.7	6.8	11.5	0.0307	16	84.0	11.0	17.5	0.1118
australis	Chile	1	72.7	2.2	2.3	0.0006	4	74.5	5.1	7.7	0.0121	5	77.5	7.9	12.3	0.0469

¹ *P. tecunumanii* has two elevation sources (HE = high elevation provenances, and LE = low elevation provenances), and *Pinus greggii* has two varieties (the northern var. *greggii* and the southern var. *australis*).

Table 7: Growth of genetically improved commercial species in Brazil, Colombia, South Africa, and Chile compared to genetically unimproved alternate species *P. tecunumanii*, *P. maximinoi*, *P. patula* and *P. greggii*. Values for growth traits are units of percentage above or below commercial species

Species	Variety ¹	Age 3			Age 5			Age 8		
		Height	DBH	Volume	Height	DBH	Volume	Height	DBH	Volume
Brazil (commercial variety = improved <i>P. taeda</i>)										
<i>P. tecunumanii</i>	HE	+19.8	+8.2	+55.7	+17.3	+7.5	+43.2	+10.3	-0.6	+15.8
<i>P. tecunumanii</i>	LE	+53.3	+71.8	+110.0	+33.7	+29.8	+148.9	+21.0	+18.4	+79.9
<i>P. maximinoi</i>		+46.5	+78.3	+65.8	+31.8	+21.0	+126.9	+24.8	+27.0	+129.5
<i>P. patula</i>		+1.3	-21.3	-31.8	-3.3	-14.6	-23.3	-10.3	-19.4	-35.6
<i>P. greggii</i>	S	+9.6	-1.6	+14.2	+1.5	-12.0	-14.5	-4.3	-17.7	-29.4
Colombia (commercial variety = improved <i>P. patula</i>)										
<i>P. tecunumanii</i>	HE	-1.0	-5.2	+0.8	-0.1	-0.9	+8.7	+4.3	+6.9	+32.7
<i>P. tecunumanii</i>	LE	+3.7	3.2	+18.0	+1.7	+1.0	+13.3	+5.8	+3.1	+21.3
<i>P. maximinoi</i>		+11.3	3.4	+18.8	+7.1	+6.3	+19.5	+8.0	+12.7	+38.6
<i>P. patula</i>		-8.1	-9.2	-16.1	-8.3	-6.4	-12.6	-7.5	-4.7	-9.7
South Africa (commercial variety = improved <i>P. patula</i>)										
<i>P. tecunumanii</i>	HE	0.0	7.3	+9.7	+1.1	+7.1	+15.9	+1.2	+7.1	+16.8
<i>P. tecunumanii</i>	LE	+2.6	3.3	+20.4	+3.1	+5.8	+21.5	+4.4	+6.1	+25.9
<i>P. maximinoi</i>		+9.7	8.1	+38.6	+10.1	+7.0	+31.8	+7.5	+12.2	+42.2
<i>P. patula</i>		-3.3	-6.2	-13.2	-4.6	-4.6	-12.0	-3.1	-3.1	-8.6
<i>P. greggii</i>	<i>greggii</i>	-29.3	-35.5	-65.8	-30.3	-28.0	-61.8	-31.7	-29.9	-63.8
<i>P. greggii</i>	<i>australis</i>	-2.6	-3.6	-7.1	-5.2	-6.1	-15.4	-6.4	-6.9	-17.5
Chile (commercial variety = improved <i>P. radiata</i>)										
<i>P. patula</i>		-42.7	-	-	-38.5	-52.3	-82.4	-35.6	-42.5	-75.4
<i>P. greggii</i>	<i>greggii</i>	-33.3	-46.7	-	-42.3	-50.9	-84.3	-45.1	-48.5	-83.5
<i>P. greggii</i>	<i>australis</i>	-13.9	-27.3	-	-27.9	-38.2	-69.4	-31.9	-37.1	-70.1

¹ *Pinus tecunumanii* has two elevation sources (HE = high-elevation provenances and LE = low-elevation provenances), and *Pinus greggii* has two varieties (the northern var. *greggii* and the southern var. *australis*)

well with published estimates of genetic gain from one cycle of selection and breeding of 10% in *P. elliotii* (Hodge et al. 1989) and 13% in *P. radiata* (Carson et al. 1999). The stem form of the improved material was generally better than the unimproved introductions.

Finally, in Chile, the commercial species *P. radiata* demonstrated substantial growth superiority over both *P. greggii* and *P. patula*, which had 70% to 84% less volume than *P. radiata* at 8 years. The more tropical species, *P. tecunumanii* and *P. maximinoi*, were not tested in progeny trials in Chile, as they were not expected to have sufficient cold and frost tolerance to survive.

Growth trait correlations – one country, one age

Genetic parameter analyses were performed for each species in each country at each age, primarily to examine the provenance and genetic correlations between the three different growth traits – height, DBH, and volume. These correlations are fully detailed in Appendix 2, and Table 8 presents a summary of these correlations at the species level (averaged across ages and countries), at the country level (averaged across ages and species), and for each of the three ages (averaged across species and countries). As one might expect, there were very strong correlations among height, DBH, and volume regardless of what species–country–age combination or level was examined (Table 8). Mean provenance correlations for a given age (across species and countries) ranged from 0.82 to 0.94 for r_{prov} (height, DBH) and 0.97 to 0.99 for r_{prov} (DBH, volume). Mean genetic correlations for a given age ranged from

0.79 to 0.85 for r_g (height, DBH), and from 0.97 to 0.98 for r_g (DBH, volume). Provenance correlations were almost always slightly higher than genetic correlations, and height–DBH correlations were typically lower than height–vol and DBH–volume correlations.

In general, for any particular species–country–age analysis, all three growth traits typically gave very similar genetic parameter estimates for provenance variation (P^2), type B provenance correlation (r_{Bprov}), heritability (h^2), and type B genetic correlations (r_{Bg}) (for full details, see Appendix 2). In most cases, h^2 for height was slightly higher than for DBH, and h^2 for volume was intermediate. Across all species–country–age combinations, the mean h^2 for height, DBH, and volume was 0.15, 0.13 and 0.14, respectively, and the mean r_{Bg} was 0.63, 0.65 and 0.64, respectively. For the provenance-level parameters, across all species–country–age combinations the mean P^2 was 0.07, 0.04 and 0.05 for height, DBH and volume, respectively, and mean r_{Bprov} was 0.69, 0.71 and 0.73, respectively. The only genetic parameters that did vary by growth trait were total phenotypic variance and the GCV. Typically, GCV for height was around 5 to 8%, for DBH was around 7 to 10%, and for volume was around 15 to 25%. These match very well with mean GCV values of 11% for height, 9% for DBH, and 23% for volume reported by Cornelius (1994) in a summary of 67 publications on various *Pinus* species.

It was clear from these results that further analyses based on multiple ages would give similar results regardless of which of the three growth traits was used. All

Table 8: Average genetic and provenance correlations among growth traits (height, DBH, and volume) for *P. tecunumanii*, *P. maximinoi*, *P. patula* and *P. greggii* tested at three ages in four different countries. Error values are the SE

Species/country/age ¹	Provenance correlations			Genetic correlations			h^2
	r_{prov} (ht,DBH)	r_{prov} (height, volume)	r_{prov} (DBH, volume)	r_g (height, DBH)	r_g (height, volume)	r_g (DBH, volume)	
Species¹ (averaged across ages and countries)							
<i>P. tecunumanii</i> HE	0.93 ± 0.09	0.97 ± 0.04	0.99 ± 0.01	0.85 ± 0.05	0.89 ± 0.04	0.98 ± 0.01	0.11 ± 0.02
<i>P. tecunumanii</i> LE	0.95 ± 0.06	0.97 ± 0.03	0.99 ± 0.01	0.83 ± 0.06	0.91 ± 0.04	0.97 ± 0.02	0.14 ± 0.04
<i>P. maximinoi</i>	0.80 ± 0.13	0.88 ± 0.08	0.99 ± 0.02	0.75 ± 0.20	0.83 ± 0.13	0.97 ± 0.01	0.16 ± 0.06
<i>P. patula</i>	0.90 ± 0.09	0.94 ± 0.05	0.99 ± 0.01	0.81 ± 0.05	0.89 ± 0.03	0.98 ± 0.01	0.13 ± 0.03
<i>P. greggii</i> var. <i>greggii</i>	0.79 ± 0.25	0.92 ± 0.09	0.97 ± 0.05	0.91 ± 0.09	0.93 ± 0.04	0.97 ± 0.02	0.18 ± 0.08
<i>P. greggii</i> var. <i>australis</i>	0.97 ± 0.05	0.98 ± 0.04	0.98 ± 0.04	0.83 ± 0.08	0.88 ± 0.04	0.98 ± 0.01	0.13 ± 0.06
Country (averaged across ages and species)							
Brazil	0.96 ± 0.06	0.96 ± 0.05	0.98 ± 0.03	0.83 ± 0.07	0.88 ± 0.04	0.98 ± 0.01	0.13 ± 0.06
Chile	0.88 ± 0.22	0.98 ± 0.05	0.97 ± 0.05	0.93 ± 0.09	0.95 ± 0.04	0.97 ± 0.03	0.11 ± 0.05
Colombia	0.92 ± 0.10	0.96 ± 0.05	0.99 ± 0.01	0.76 ± 0.17	0.85 ± 0.11	0.98 ± 0.01	0.15 ± 0.04
South Africa	0.85 ± 0.15	0.93 ± 0.08	0.98 ± 0.02	0.84 ± 0.06	0.90 ± 0.04	0.98 ± 0.01	0.15 ± 0.06
Age (averaged across species and countries)							
3	0.94 ± 0.09	0.97 ± 0.05	0.99 ± 0.01	0.85 ± 0.08	0.91 ± 0.04	0.97 ± 0.02	0.13 ± 0.05
5	0.92 ± 0.09	0.95 ± 0.06	0.99 ± 0.02	0.83 ± 0.09	0.89 ± 0.07	0.98 ± 0.01	0.14 ± 0.05
8	0.82 ± 0.17	0.93 ± 0.08	0.97 ± 0.03	0.79 ± 0.14	0.86 ± 0.09	0.98 ± 0.01	0.14 ± 0.06

¹ *Pinus tecunumanii* has two elevation sources (HE = high-elevation provenances and LE = low-elevation provenances), and *Pinus greggii* has two varieties (the northern var. *greggii* and the southern var. *australis*)

subsequent analyses were performed using volume at ages 3, 5, and 8 years.

Volume genetic parameters – one country, multiple ages

Genetic parameter analyses were done for each species for a single country and age 3-, 5-, and 8-year volume growth. Appendix 3 presents detailed parameter estimates for each species and country, and Table 9 presents a summary of parameter estimates for each species (averaged across all countries), and overall averages (across all species and all countries).

Provenance and genetic correlations among different ages for volume growth were quite high. Mean provenance correlations (across species and countries) were $r_{prov}(3,5) = 0.93$, $r_{prov}(3,8) = 0.83$, and $r_{prov}(5,8) = 0.94$ (Table 9). Mean genetic correlations were $r_g(3,5) = 0.92$, $r_g(3,8) = 0.80$, and $r_g(5,8) = 0.96$ (Table 9).

Genetic parameters for the different ages were remarkably similar (Table 9). Heritability tended to increase with age, although the increase was small: mean $h^2 = 0.13$ at 3 years, 0.14 at 5 years, and 0.15 at 8 years. Conversely, there was a tendency for provenance variation to decrease slightly with age, from $P^2 = 0.06$ at 3 years, $P^2 = 0.05$ at 5 years, and $P^2 = 0.04$ at 8 years. One curious result was with *P. maximinoi*: in South Africa and Colombia, volume at 5 years and 8 years had small, but detectable, levels of provenance variation ($P^2 = 0.02$ – 0.03), but in Brazil, provenance variation was essentially non-existent ($P^2 = 0.00$).

For all species, there was a moderate level of genotype×environment interaction, both at the provenance and the genetic level. Mean r_{Bprov} ranged from 0.71 to 0.74 for ages 3, 5, and 8 years, whereas mean r_{Bg} ranged from 0.65 to 0.71. The GCV for age 3-, 5-, and 8-year volumes were also very similar across ages and ranged from 19 to 21%.

Genetic parameters for the different species were also

quite similar (Table 9). There appeared to be no meaningful differences for any of the parameter estimates, with one exception. *Pinus maximinoi* showed less provenance variation than the other three species; *P. maximinoi* had a range of $P^2 = 0.03$ at 3 years to $P^2 = 0.01$ at 8 years compared to the mean P^2 of 0.06 for the other species (Table 9). Possibly this lack of provenance variation is because populations in Mesoamerica are more inbred than species such as *P. tecunumanii* (Matheson et al. 1989, Dvorak et al. 2002).

Volume growth correlations – between countries

Across-country analyses (or equivalently, multiple-country analyses) for volume growth were performed both to examine between-country provenance and genetic correlations, and to predict provenance effects. Volume at 8 years was used as the primary analysis variable, with volume at 5 years as a proxy when 8-year data was not available. This was because the standardised 5-year and 8-year data had essentially the same genetic parameters and variance structure (Table 9, Appendix 3). Analyses were restricted to tests in Brazil, Colombia and South Africa, with Chile excluded as there were too few tests to generate precise estimates of between-country correlations.

Low-elevation *P. tecunumanii* had quite high provenance and genetic correlations across all three country pairs (Brazil–Colombia, Brazil–South Africa and Colombia–South Africa) (Table 10). The weakest correlations (although still rather high) were observed for Brazil–Colombia, with $r_{prov} = 0.82$, and $r_g = 0.76$. For Brazil–South Africa and Colombia–South Africa, the correlations were $r_{prov} = 0.97$ and 1.00, and $r_g = 0.92$ and 0.85, respectively. High-elevation *P. tecunumanii* had similar correlations for Brazil–South Africa ($r_{prov} = 1.00$, $r_g = 0.83$), and Colombia–South Africa ($r_{prov} = 0.64$, $r_g = 0.77$), but the correlations for Brazil–Colombia were markedly lower ($r_{prov} = 0.49$, $r_g = 0.46$).

Table 9: Average age–age genetic correlations (above diagonals) and provenance correlations (below diagonals) and other genetic parameters for volume growth at ages 3, 5, and 8 years (vol3, vol5 and vol8, respectively) for *P. tecunumanii*, *P. maximinoi*, *P. patula* and *P. greggii* in four countries. Error values are the SE

Species/trait ¹	Age–age correlations				P ²	r _{Bprov}	h ²	r _{Bg}	GCV	V _{phen}
	With vol3	With vol5	With vol8	With vol8						
Trait (averaged across species and countries)										
vol3		0.92 ± 0.04	0.80 ± 0.09		0.06 ± 0.03	0.71 ± 0.15	0.13 ± 0.04	0.65 ± 0.11	21.2	3 655.5
vol5	0.93 ± 0.06		0.96 ± 0.02		0.05 ± 0.04	0.74 ± 0.12	0.14 ± 0.04	0.66 ± 0.12	18.7	2 584.8
vol8	0.83 ± 0.15	0.94 ± 0.07			0.04 ± 0.03	0.72 ± 0.20	0.15 ± 0.05	0.71 ± 0.10	19.0	2 438.4
Species and trait (averaged across countries)										
<i>P. tecunumanii</i> HE	vol3	0.92 ± 0.02	0.81 ± 0.06		0.04 ± 0.02	0.73 ± 0.16	0.11 ± 0.03	0.63 ± 0.04	19.3	3 526.6
<i>P. tecunumanii</i> HE	vol5	0.89 ± 0.03	0.97 ± 0.01		0.03 ± 0.01	0.70 ± 0.03	0.12 ± 0.01	0.67 ± 0.05	16.2	2 151.5
<i>P. tecunumanii</i> HE	vol8	0.78 ± 0.22	0.96 ± 0.07		0.02 ± 0.01	0.76 ± 0.12	0.12 ± 0.02	0.69 ± 0.06	16.3	2 244.9
<i>P. tecunumanii</i> LE	vol3	0.94 ± 0.01	0.87 ± 0.01		0.07 ± 0.02	0.74 ± 0.12	0.12 ± 0.04	0.64 ± 0.22	19.0	3 102.7
<i>P. tecunumanii</i> LE	vol5	0.97 ± 0.03	0.97 ± 0.01		0.06 ± 0.02	0.78 ± 0.19	0.14 ± 0.04	0.70 ± 0.21	17.4	2 110.3
<i>P. tecunumanii</i> LE	vol8	0.98 ± 0.02	1.00 ± 0.00		0.04 ± 0.01	0.77 ± 0.29	0.14 ± 0.04	0.69 ± 0.22	17.3	2 233.3
<i>P. maximinoi</i>	vol3	0.88 ± 0.02	0.82 ± 0.01		0.03 ± 0.01	0.66 ± 0.05	0.13 ± 0.05	0.63 ± 0.12	20.6	3 700.7
<i>P. maximinoi</i>	vol5	0.88 ± 0.16	0.98 ± 0.02		0.02 ± 0.02	0.77 ± 0.18	0.15 ± 0.04	0.72 ± 0.14	19.7	2 575.5
<i>P. maximinoi</i>	vol8	0.82 ± 0.26	0.97 ± 0.04		0.01 ± 0.01	0.66 ± 0.42	0.16 ± 0.03	0.75 ± 0.07	20.2	2 662.9
<i>P. patula</i>	vol3	0.95 ± 0.04	0.95 ± 0.04		0.06 ± 0.05	0.64 ± 0.23	0.10 ± 0.01	0.56 ± 0.05	20.7	4 050.9
<i>P. patula</i>	vol5	0.97 ± 0.03	0.80 ± 0.11		0.06 ± 0.06	0.69 ± 0.09	0.13 ± 0.03	0.68 ± 0.05	20.0	3 243.2
<i>P. patula</i>	vol8	0.89 ± 0.06	0.95 ± 0.04		0.05 ± 0.05	0.76 ± 0.12	0.15 ± 0.02	0.76 ± 0.10	20.2	2 875.7
<i>P. greggii</i> var. <i>greggii</i>	vol3	0.93 ± 0.00	0.84 ± 0.03		0.10 ± 0.00	0.94 ± 0.00	0.22 ± 0.00	0.72 ± 0.00	34.7	4 879.1
<i>P. greggii</i> var. <i>greggii</i>	vol5	0.83 ± 0.00	0.96 ± 0.00		0.08 ± 0.03	0.81 ± 0.06	0.19 ± 0.08	0.57 ± 0.17	20.3	2 384.4
<i>P. greggii</i> var. <i>greggii</i>	vol8	0.83 ± 0.00	0.90 ± 0.12		0.06 ± 0.02	0.72 ± 0.07	0.23 ± 0.09	0.68 ± 0.01	20.6	1 948.6
<i>P. greggii</i> var. <i>australis</i>	vol3	0.86 ± 0.06	0.68 ± 0.12		0.08 ± 0.00	0.64 ± 0.14	0.14 ± 0.02	0.74 ± 0.02	22.0	3 405.7
<i>P. greggii</i> var. <i>australis</i>	vol5	0.94 ± 0.07	0.95 ± 0.04		0.07 ± 0.02	0.71 ± 0.15	0.13 ± 0.05	0.63 ± 0.11	18.0	2 764.6
<i>P. greggii</i> var. <i>australis</i>	vol8	0.69 ± 0.01	0.89 ± 0.06		0.05 ± 0.04	0.68 ± 0.22	0.15 ± 0.04	0.69 ± 0.10	19.2	2 499.0

¹ *P. tecunumanii* has two elevation sources (HE = high-elevation provenances and LE = low-elevation provenances), and *Pinus greggii* has two varieties (the northern var. *greggii* and the southern var. *australis*)

In general, the correlations for *P. patula* were lower than those for *P. tecunumanii*, but the pattern was similar. The highest correlations were observed for Brazil–South Africa ($r_{\text{prov}} = 0.69$, $r_g = 0.68$), lower for Colombia–South Africa ($r_{\text{prov}} = 0.46$, $r_g = 0.63$), and lowest for Brazil–Colombia ($r_{\text{prov}} = 0.28$, $r_g = 0.60$).

As observed in the single-country analyses, *P. maximinoi* had substantially lower levels of provenance variation for 8-year volume than the other species. This was also the case in the across-country analysis, with P^2 just slightly above 0.0 in Brazil, and $P^2 = 0.02$ in both Colombia and South Africa (see Appendix 3). Thus, in the across-country analysis, r_{prov} is not defined for Brazil–Colombia and Brazil–South Africa. The low provenance correlation ($r_{\text{prov}} = 0.39$) for Colombia–South Africa is relatively unimportant because there is little provenance variation for *P. maximinoi* in these countries. In contrast, the genetic correlations were all moderately high and ranged from $r_g = 0.67$ to 0.93.

For *P. greggii*, the country pair Brazil–South Africa gave the only set of correlation estimates for this data set, with $r_{\text{prov}} = 0.62$, and $r_g = 0.84$. Across all other species and country pairs, the mean r_{prov} was 0.67, and mean r_g was 0.74, which were very similar to the *P. greggii* estimates.

Provenance BLUPs

Best linear unbiased predictions were made for G_{prov} (provenance effect for volume, expressed in units of percentage gain above the unimproved population mean). Predictions of G_{prov} were made for Brazil, Colombia and South Africa for each species, and are listed in Tables 1–4.

Low-elevation *P. tecunumanii*

Given the high across-country provenance correlations for LE *P. tecunumanii*, G_{prov} values for Brazil, Colombia, and South Africa were very similar. Top-performing provenances in all three countries were southern sources Villa Santa (Honduras), Yucul and Apante (Nicaragua), and bottom-ranking provenances in all three countries were northern sources Jocón, Locomapa, and Esquipulas del Norte. There was a statistically significant correlation between latitude of origin and G_{prov} in all countries (e.g. for Colombia, $r = -0.61$, $p < 0.0055$), with more southerly provenances showing better growth. Provenances from high latitudes in Belize, namely Mountain Pine Ridge (MPR) and San Pastor Ridge, did quite poorly in Brazil, Colombia and South Africa. The MPR source especially has the propensity to produce foxtail trees that eventually leads to main stem breakage. The Apante, Nicaragua source is seldom mentioned in the literature along with the other three well-known Nicaraguan

provenances (Yucul, Las Camilias, and San Rafael del Norte), but performed quite well in these trials (Table 1). Apante is located only 17 km from Yucul and at some time in the past these two might have been part of one contiguous natural pine forest that followed the 1 000 m altitudinal contour in the region.

There was also a statistically significant correlation between longitude of origin and G_{prov} for Colombia and South Africa (e.g. for Colombia, $r = -0.56$, $p < 0.0125$), with more westerly provenances showing better growth. The range from the best to the worst provenance was smallest in Brazil (+8.7% for Villa Santa to -13.0% for Esquipulas del Norte) and largest in Colombia (+14.8% for Yucul to -17% for Esquipulas del Norte).

The provenance La Esperanza (Honduras) was tested with the LE populations, but technically should have been tested with the HE populations as it sits at 1 720 to 1 850 m elevation (Table 1). The HE populations ranged from around 1 500 m to 2 700 m elevation (Table 1). La Esperanza had $G_{\text{prov}} = 3.3$, 1.7 and 2.8% in Brazil, Colombia, and South Africa, respectively, essentially at the population mean. Although La Esperanza would represent the 'low end' of the HE populations, this does illustrate that there is a substantial overlap of LE and HE *P. tecunumanii* growth potential.

High-elevation *Pinus tecunumanii*

For HE *P. tecunumanii*, the top three provenances in all three countries were the same: San Jeronimo (Guatemala), Montebello, and Chempil. The provenance correlation between Brazil–South Africa was $r_{\text{prov}} = 1.00$, so this makes sense, but for Colombia–South Africa r_{prov} was 0.64, and Brazil–Colombia r_{prov} was only 0.49 (Table 10). The range in G_{prov} for Brazil was +23.3% (Montebello) to -12.2% (Cabricán). For South Africa, the provenances ranked essentially the same as Brazil, but the variation was lower, from +12.8% for Montebello to -6.9% for Cabricán.

Most of the disagreement in provenance rankings between Colombia and the other countries was in the middle- and lower-ranking provenances. There was a moderate but significant correlation between elevation of origin and G_{prov} for all three countries (e.g. for Brazil, $r = -0.47$, $p < 0.0155$), with lower-elevation sources showing better growth. The *P. tecunumanii* provenances sampled at altitudes between 1 600 and 1 800 m generally grew better than sources from locations above 2 000 m elevation. Presumably, this trend is due in part to the fact that sources above 2 000 m altitude have a shorter growing season than those from warmer climates at 1 600 to 1 800 m elevation. The five provenances from the San

Table 10: Between-country genetic and provenance correlations for age 8 volume growth for *P. tecunumanii*, *P. maximinoi*, *P. patula* and *P. greggii*. Error values are the SE. na = correlations and/or SEs could not be calculated

Species	Brazil–Colombia		Brazil–South Africa		Colombia–South Africa	
	r_{prov}	r_g	r_{prov}	r_g	r_{prov}	r_g
<i>P. tecunumanii</i> HE	0.49 ± 0.24	0.46 ± 0.14	1.00 (na)	0.83 ± 0.07	0.64 ± 0.20	0.77 ± 0.11
<i>P. tecunumanii</i> LE	0.82 ± 0.23	0.76 ± 0.09	0.97 ± 0.15	0.92 ± 0.08	1.00 (na)	0.85 ± 0.07
<i>P. maximinoi</i>	na	0.73 ± 0.11	na	0.93 ± 0.08	0.39 ± 0.34	0.67 ± 0.08
<i>P. patula</i>	0.28 ± 0.29	0.60 ± 0.07	0.69 ± 0.16	0.68 ± 0.05	0.46 ± 0.23	0.63 ± 0.06
<i>P. greggii</i> var. <i>australis</i>			0.62 ± 0.32	0.84 ± 0.06		

Cristobal de las Casa plateau, Chiapas (Chanal, Chempil, Las Piedrecitas, Rancho Nuevo and San José), which is located above 2 000 m altitude, all performed average to below average with the exception of the Chempil provenance. Chempil grew well above the average in all three countries. Phenotypically, there was nothing noteworthy about the Chempil source compared to the other four locations, except that the provenance was under severe pressure from farmers growing annual crops of maize. The Rancho Nuevo source is the most cold-hardy of the *P. tecunumanii* HE populations (Dvorak et al. 2000b, Hodge et al. 2012) but had poor growth performance.

Pinus maximinoi

For *P. maximinoi*, G_{prov} values were low, reflecting little provenance variation. In Brazil, G_{prov} ranged from +4% to -2%. In Colombia, the top-performing provenances were San José Bayuncún and Tatumbra, both with $G_{prov} = +9.9\%$, and the worst-performing provenance was Coapilla at -9.9%. In South Africa, the top-performing provenances were San Jerónimo from Chiapas, Mexico (+8.4%), La Cañada (+8.2%), and San Jerónimo, Guatemala (+6.6%), and the worst-performing provenances were Tapiquil and Yuscarán (both -10.0%). There were no correlations with any of the provenance origin data (latitude, longitude, elevation or precipitation) and the G_{prov} for *P. maximinoi* in any of the three countries.

Pinus patula

For *P. patula*, there was not a great deal of agreement among the G_{prov} values due to relatively low provenance correlations across country, with r_{prov} values of 0.28, 0.46, and 0.69 (Table 10). Potrero de Monroy performed quite well in both Brazil (+11%) and South Africa (-9.8%), ranking in the top two, but grew poorly in Colombia (-11.5%). There was a significant relationship between elevation and G_{prov} in Brazil ($r = -0.53$, $p < 0.0098$), with lower-elevation sources showing better growth. The top three provenances in Colombia (La Cruz, Cumbre de Muridores, and Acaxochitlán) were all average performers in Brazil and South Africa. In Colombia, there was a significant correlation between precipitation and G_{prov} ($r = 0.55$, $p < 0.0082$), with higher-precipitation sources tending to have better growth. Conrado Castillo, the most northern provenance, performed extremely poorly in Colombia ($G_{prov} = -49.4\%$). Although it was not outstanding, Conrado Castillo did grow better in Brazil ($G_{prov} = +0.3\%$) and South Africa ($G_{prov} = -5.9\%$). Of interest is that Conrado Castillo appears to have extremely high-density wood in South Africa, perhaps making it valuable to breeders for that trait (Stanger 2003).

Pinus greggii

For *P. greggii* var. *australis*, the two top provenances in Brazil were Valle Verde (+14.2%) and Laguna Atezca (+14.0%). These two were the lowest-elevation provenances in the collection. The highest-elevation provenance (San Joaquín) had the lowest G_{prov} in Brazil (-27.3%). The correlation between elevation of origin and G_{prov} in Brazil was $r = -0.89$ ($p < 0.0069$). In South Africa, the correlation between elevation of origin and G_{prov} was also high, but was just below statistical significance ($r = -0.73$, $p < 0.0625$).

The top provenance (Valle Verde, +12.5%) and bottom provenance (San Joaquín, -8.5%) were the same in South Africa as in Brazil.

Finally, for *P. greggii* var. *greggii*, the La Tapona provenance was by far the best performer in South Africa with $G_{prov} = +23.7\%$. La Tapona is the most southern source of var. *greggii*, and the second-lowest elevation. The Sierra el Tarrillal provenance, the lowest-elevation source, had the second-largest volume gain with $G_{prov} = +8.3\%$. Some of the other northern sources came from very small genetic bases. For example, the Cerro El Potosi source was made up of the only four mature trees that could be found on the mountain. Genetic diversity levels in *P. greggii* var. *greggii*, as measured in isozyme studies, are the lowest of the species/varieties tested in the field trials (Ramírez Herrera et al. 1997).

Discussion

Genetic parameters and provenance variation

One surprising result of this study was the consistency of the genetic parameter estimates across all species, countries and ages. The measurement ages in this study were 3, 5, and 8 years, and mean heights at those ages ranged from around 5 m to 15 m. For volume growth across this age range, standard parameter estimates of $h^2 = 0.15$, $r_{Bg} = 0.65$, $P^2 = 0.05$, and $r_{Bprov} = 0.70$, and GCV = 20% would probably serve extremely well. In the absence of good data for other species, it seems reasonable to expect that these parameters could be used for simulations and breeding strategy development, for example.

For two of the species in this study, *P. tecunumanii* and *P. maximinoi*, previous analyses reported in the literature (based on a large subset of data used in the current study) showed an increase in heritability of growth traits with increasing age. For *P. tecunumanii* volume, Hodge and Dvorak (1999) reported an increase in single-site heritability (h^2_b) from $h^2_b = 0.12$ at 3 years to around $h^2_b = 0.16$ at 8 years. For *P. maximinoi* DBH, Gapare et al. (2001) reported an increase in single-site heritability from $h^2_b = 0.13$ at 3 years to around $h^2_b = 0.21$ at 8 years). Single-site heritability estimates are slightly larger than across-site heritability estimates (h^2 , as reported in the current study), because of the presence of genotype×environment interaction variance in the numerator (Comstock and Moll 1963, Burdon 1977, Eisen and Saxton 1983). In the current study, there were slight increases in volume heritability with increasing age, but they were rather small, from $h^2 = 0.13$ at 3 years to around $h^2 = 0.15$ at 8 years (averaged across all species, Table 9).

The mean age 5–age 8 genetic correlation was never lower than 0.95 for any species or country (Table 8). The mean age 3–age 8 correlation was 0.80, and was at a minimum of 0.68 only for *P. greggii* var. *australis*. Indirect selection efficiency is a function of heritability and genetic correlation (Falconer and Mackay 1996, White and Hodge 1991). For these species, heritability at 3, 5, and 8 years is very similar, and genetic correlation between 5 years and 8 years is near unity. This strongly suggests that selection at 5 years, or perhaps 4 years, would be optimal in terms of genetic gain per unit time. Pulpwood rotations for most

of these species would be around 17 years in Colombia and 20 years in South Africa. Selection at 4–5 years would be about one-quarter to one-third of the rotation age. Selection at one-quarter to one-third of the rotation age has been found to be near optimum for species such as *P. taeda* (at age 8 for a 25-year rotation) (McKeand 1988, Gwaze and Bridgwater 2002), and for long-rotation species such as *Pseudotsuga menziesii* (from age 13 to 17 for a 60-year rotation) (Magnusson and Yanchuk 1993, Johnson et al. 1997).

The between-country genetic (r_g) and provenance correlations (r_{prov}) tended to show a similar pattern for *P. tecunumanii*, *P. maximinoi* and *P. patula*: (Brazil–South Africa) > (Colombia–South Africa) > (Brazil–Colombia). Clearly, there are many environmental factors that could be important, but one that almost certainly has an impact is precipitation. The test sites in Colombia typically experience about 2 200 mm of rainfall with a uniform distribution throughout the year. In contrast, the sites in Brazil and South Africa have much lower rainfalls (around 1 450 mm, and from 1 000 to 1 200 mm, respectively), with distinct wet and dry seasons. In addition, low-latitude sites in Colombia would experience very uniform temperatures throughout the year, whereas most sites in southern Brazil and South Africa would have distinct summers and winters.

Potential for genetic gain

For almost every species–country combination, there was important provenance variation for volume growth. Generally, the best provenance was 10–20% better than the species mean, and there was a 20–35% range from the best to worst provenance (Tables 1–4). In addition to gains from provenance selection, there are substantial opportunities for genetic improvement by selecting good families and individual trees. The GCV expresses the additive genetic standard deviation (within provenance) in terms of percent, and generally was around 16–20% at age 8 years for these four species (Table 9). In other words, the trees in the population that have breeding values one genetic standard deviation above the mean will show 15–20% more volume growth than the provenance mean (Cornelius 1994). If it is possible to identify the very best trees in the population that are two genetic standard deviations above the mean, this would represent 30–40% additional gain above the provenance mean. Clearly, there are tremendous opportunities to make genetic gain, and investments in testing, selection, and breeding will pay off handsomely.

Growth and yield

Provenance/progeny tests are designed to compare and rank genetic entries such as families. They are often planted in single-tree plots or row-plots, as in this case. Furthermore, the data is often available only through around one-third of rotation age, 8 years in this case. As such, the data were not intended to be used to project growth and yield as in a formal mensurational or silvicultural study, but nevertheless the data may have some value at least to obtain an estimate of MAI through 8 years. Assuming a spacing of 3 m × 3 m (1 111 stems ha⁻¹), and multiplying by individual tree volume and species survival (Table 6), unimproved *P. patula* is estimated to be growing at around

17.7 m³ year⁻¹ in Colombia and 14.0 m³ y⁻¹ in South Africa. These figures match up reasonably well with published figures of 20 m³ y⁻¹ in Colombia (Ladrach 1986) and 15–20 m³ y⁻¹ in South Africa (Lamprecht 1990), presumably based on plantations with adapted or genetically improved material. Following the same approach, one can calculate MAI = 30.6 m³ y⁻¹ for unimproved *P. maximinoi* in Colombia, 21.0 m³ y⁻¹ in Brazil, and 14.8 m³ y⁻¹ in South Africa. For unimproved LE *P. tecunumanii*, estimated MAI is 22.9 m³ y⁻¹ in Colombia, 22.2 m³ y⁻¹ in Brazil, and 14.9 m³ y⁻¹ in South Africa.

Both *P. tecunumanii* and *P. maximinoi* showed substantially better growth than the commercial species *P. taeda* in Brazil and *P. patula* in Colombia and South Africa (Table 7). The gain figures in these studies could be biased by the planting of the two species (the control versus the target species) in row-plots next to each other in the provenance/progeny tests. For example, a ‘fast-starting’ tropical species that grows very rapidly during the first 2–3 years might capture a site and gain a competitive advantage over a ‘slow-starting’ control species. These growth differences might not be completely maintained if the species comparison was made using large species block plantings. Nevertheless, the differences are large enough, especially considering that the alternate species are genetically unimproved, to suggest that significant growth gains will be made by switching species on sites where it is possible to grow *P. tecunumanii* or *P. maximinoi*.

Pinus greggii var. *australis* grew reasonably well in Brazil, with an estimated MAI of 17.9 m³ y⁻¹. Although this was substantially less than improved *P. taeda*, selection of the best provenances and the best families within a provenance would make *P. greggii* var. *australis* quite comparable to *P. taeda*. In South Africa, var. *australis* had an estimated MAI of 13.0 m³ y⁻¹, which is less than *P. patula* but well within the range where selection would make it a viable alternate species.

Commercial outlook

Pinus tecunumanii

Pinus tecunumanii has good growth potential as a pure species in the highlands of Colombia between 1 750 and 2 000 m elevation where it is now being planted on a commercial scale. It is also being planted commercially in northern Mozambique above 1 000 m altitude. Based on our field tests, *P. tecunumanii* will outperform *P. taeda* in the warmer subtropical regions of Paraná and São Paulo states in southern Brazil and should be tried on a larger scale there to improve not only growth but wood properties (Camcore 2008a). The *P. patula* × *P. tecunumanii* hybrid is being established on a commercial scale in plantations in subtropical regions of Mpumalanga province, South Africa.

The species also appears well suited to the more tropical plateau regions of Minas Gerais, Goiás and Mato Grosso del Sur of Mato Grosso where the forest plantation area is expected to increase over the next decade. On some of these new locations, fertiliser application will help maximise its growth. It also has potential in the eastern highlands of Zimbabwe (1 200 to 1 500 m elevation) and the highland areas of East Africa (western Kenya at 1 800 to 2 000 m

elevation, north-eastern Tanzania at 1 600 m elevation and northern Uganda at 1 000 m elevation) based on the results of old genetic trials and pilot plantings. These conclusions are also generally consistent with results of predicted species distribution using the MaxEnt climatic model (Camcore unpublished data). In addition, MaxEnt also predicts that *P. tecunumanii* is well suited for the Andean region from Ecuador to south-western Bolivia (Camcore unpublished data).

Our results indicate that the performance of LE *P. tecunumanii* provenances was very consistent across Brazil, Colombia and South Africa. The top-performing HE provenances were similar in all three countries, which indicates that the interchange of genetic material among breeding programs in the different countries would be beneficial and useful to broaden genetic bases.

In the first generation of breeding, Camcore asked its members to keep HE and LE subpopulations separate. In the second cycle of breeding, many organisations are merging the two groups as growth differences are relatively small, and original adaptability gains from provenance selection within the two groups were presumably captured in the first generation. The one exception that favours continued separation of the two subpopulations is when breeding for specialty traits such as pitch canker resistance. The LE sources are generally much more resistant to the disease in the seedling stage than HE sources (Hodge and Dvorak 2007, 1999), even though there is great within-provenance variability in HE provenances at the family level (Mitchell et al. 2012).

Several factors could limit commercial gains in productivity of pure *P. tecunumanii*. The species has a propensity for stem breakage that often discourages plantation growers. However, we believe that the stem breakage problem is manageable; first, by selecting against this trait in the provenance/progeny tests, and second, by using good silviculture that includes proper site placement (Dvorak et al. 1993). Another challenge is that the species generally produces only a small amount of seeds when planted as an exotic, and most commercial programs will have to develop the capability to mass-produce seedlings by vegetative propagation. Flower production can be increased with gibberellin applications (Isaza 2008). A third challenge is that when *P. tecunumanii* does produce flowers, it has the propensity to hybridise naturally with *P. patula* in environments where the latter is the predominant plantation species, a situation that is common in southern Africa and Colombia. The results of this large infusion of random, unselected natural *P. patula* pollen into *P. tecunumanii* orchards are progeny that are highly variable in productivity and morphology. It forces breeders to ask the question on how important is it to maintain pure species lines in traditional breeding and conservation programs. To circumvent contamination problems, controlled crosses using the best *P. tecunumanii* parents may be necessary. Alternatively, crossing *P. tecunumanii* with other species to produce hybrids is becoming more technically feasible and economically important, especially in Colombia and South Africa where breeding expertise is well in place (Kanzler et al. 2012). Most Camcore *P. tecunumanii* programs are in their second cycle of genetic improvement.

Pinus maximinoi

Pinus maximinoi has shown good potential across multiple sites in the tropics and subtropics and should be developed into a major commercial pine species. It is currently being grown commercially in Colombia (2–4° N) between 1 800 and 2 200 m altitude, in Mozambique (14° S) between 1 200 to 1 400 m, and in southern Brazil (24° S) (Paraná and São Paulo states) on a pilot scale at 800 to 850 m elevation. It would be well suited for most of south-eastern and south-central Brazil (Minas Gerais, Mato Grosso del Sur, and Mato Grosso states). In Africa, it could be planted commercially in the same areas as described for *P. tecunumanii*: the warmer areas of Mpumalanga, South Africa, the eastern highland of Zimbabwe at 1 100 to 1 600 m, the plateau regions of Malawi at 1 400 to 2 000 m, the São Hill district of central Tanzania at 1 600 m and in western Kenya above 1 800 m altitude.

Despite its potential, *P. maximinoi* offers some important challenges to tree breeders. First, like *P. tecunumanii*, it is a shy seed producer. Vegetative propagation programs would need to be developed to produce sufficient plants commercially. Second, it shows a high degree of graft incompatibility caused by the scion outgrowing the rootstock (Dvorak et al. 2000a). Alternative methods of propagation to create seed orchards would need to be developed such as air layering, ring barking and tissue culture. Third, the species often produces large branches and breeding to reduce branch diameter will be important in the future. Fourth, it produces a high number of foxtails when planted at too low an altitude in the tropics. The percentage of foxtails can be lessened by selecting against this trait and by planting *P. maximinoi* at higher elevations and latitudes, but out of any frost zones. Fifth, because of its frost susceptibility, planting the species in areas with periodic cold spells during the dry season or winter months carries some risks.

Second-generation trials have been established by Camcore members to improve growth and stem quality. Similar to *P. tecunumanii*, *P. maximinoi* responds to applications of gibberellins to promote flower production (Isaza 2008). As mentioned before, the potential planting ranges of *P. tecunumanii* and *P. maximinoi* will overlap. Generally, *P. maximinoi* will do better at higher altitudes (where frosts are not common) and on deeper, more fertile soils than *P. tecunumanii*.

Pinus patula

Pinus patula will continue to be an important species at high elevations in the Andean countries of South America and in southern and eastern Africa. Long-term breeding programs for pitch canker resistance will need to be developed and continued since the disease can be found now in pine nurseries in both continents (Mitchell et al. 2011). The *P. patula* × *P. tecunumanii* hybrid will continue to gradually replace pure *P. patula* in some areas because of its improved tolerance to the disease. In southern Brazil, small stands of good-quality *P. patula* can be found in the plateau region of Santa Catarina state at 750 to 1 000 m elevation. The attraction for growing the species is to have an alternative to *P. taeda* and to produce wood of higher quality. However, *P. patula* at this latitude will realise its maximum

growth potential on sites above 1 000 m elevation and only a small area of land reaches this altitude in Santa Catarina state. The MaxEnt climatic model predicts that the best match for *P. patula* actually lies further north in Brazil in the Serra da Montiqueira of Minas Gerais, Rio de Janeiro and São Paulo states that climb well above 2 000 m elevation in some locations. Some *P. patula* has successfully been grown in these areas, but development of large plantation areas is limited by logistics and environmental and social concerns.

Breeding of *P. patula* is in its third cycle in Colombia and South Africa. The challenge is how to incorporate the Camcore unimproved material into advanced-generation breeding programs. Some of the Camcore selections in progeny tests were comparable in growth to local second-generation controls but slightly poorer in terms of stem form. Second-generation trials of Camcore *P. patula* are being established in both South America and Africa to close the generational gap and facilitate infusion of genetic material with local programs.

Pinus greggii var. *greggii*

Based on our international trial series, *Pinus greggii* var. *greggii* has commercial potential only in the high elevations (>1 700 m) of the Drakensberg in the north-eastern Cape region of South Africa, in areas too cold or too dry for *P. patula*. There, the growth of var. *greggii* is poorer than *P. patula* but survival is often better. Currently, the variety is being planted below 1 700 m in some areas of South Africa because of its good stem form and consistent, regular branching pattern but other species or varieties, such as improved *P. greggii* var. *australis*, would be better suited.

Our trial results showed that northern populations of the species survived well in the highlands of Colombia and coastal and inland Chile but died out over several years after planting in Paraná and Santa Catarina, Brazil, presumably because the climate was too humid and the trees could not be established at sufficiently high elevations. In Chile, var. *greggii* grew much more slowly than *P. radiata*, and in Colombia, var. *greggii* could not compete well with the subtropical/tropical pines. The variety *greggii* is found to be highly susceptible to Diplodia shoot blight (*Sphaeropsis sapinea*) wherever it is planted in warm, humid conditions (e.g. Auer and Grigoletti 1997).

Even though the MaxEnt climatic model indicates this variety could be planted along the entire Andean chain from Venezuela to approximately Concepción, Chile, as well as the Cape region of South Africa, we believe that, commercially, the future of var. *greggii* is only on cool, dry sites located at high elevations in subtropical/temperate regions in environments that are very harsh.

From a genetic standpoint, the challenge with this variety is maintaining a large enough base to continue breeding efforts. The La Tapon source is much better than the other provenances, but special care was taken in the Camcore breeding efforts to include selections from poor sources in the second generation of testing to maintain an adequate breeding base.

Pinus greggii var. *australis*

Commercially, the optimal use of this variety is in a climatic niche between *P. maximinoi*/*P. tecunumanii* and *P. patula*

in regions that experience warm summers and cold winters, and uniform or well-defined seasonal precipitation patterns. The variety gives users the opportunity to plant trees in dry areas that experience subfreezing temperatures in winters. In some ways, it is an alternate species to *P. elliotii*, which is now planted on the harsher sites in South Africa. In many of the trials in southern South Africa, growth was respectable with occasional outstanding trees. Initially, when planted the variety looks poor (multiple stems and foxtails) but the quality improves with age. In Chile, var. *australis* grows reasonably well but cannot capture the site like *P. radiata*. In central Santa Catarina, Brazil, and northern (Corrientes) Argentina, var. *australis* outcompetes *P. taeda* in the first five years but gradually falls behind with age. Possibly these differences could be minimised if var. *greggii* is planted on the poorest soils. Similar to var. *greggii*, var. *australis* is attacked by Diplodia shoot blight but the most productive populations seem to outgrow the disease and survive (Camcore unpublished data).

Pinus greggii var. *australis* has more potential as a plantation species than var. *greggii* and will outgrow the northern variety on all but the coldest sites. It appears to have potential as an alternative species to *P. taeda* on some sites in southern South America, and Camcore members in that region have established first-generation seed orchards. MaxEnt analysis suggests that the species could be planted over a wider range of sites than covered by our international trial series. However, for this variety to reach its commercial potential, breeders must move var. *australis* through the second cycle and possibly onto a third cycle of improvement. Traits such as growth and stem form can easily be improved and second-generation progeny tests are well underway in several countries. Breeding efforts will be facilitated by the early flowering of both varieties. However, as with *P. tecunumanii*, breeders in southern Africa and Colombia will need to develop strategies to keep pure lines of *P. greggii* in place, since it will naturally hybridise with *P. patula*.

Both varieties of *P. greggii* are susceptible to the pitch canker fungus, but var. *australis* is more tolerant than *P. patula*, and var. *greggii* is less tolerant than *P. patula* (Camcore 2008b). The future of both varieties of the species might be as parents in hybrid crosses that promote drought and cold resistance. Hybrids between *P. patula* and *P. greggii* show good hybrid vigor in South Africa (Kanzler et al. 2012), and *P. greggii* var. *australis* × *P. tecunumanii* hybrids also appear promising in that country. Crosses between *P. taeda* and *P. greggii* var. *australis* have also been made and might be of value in southern South America.

Summary

The testing and development of these four species represents a mammoth effort by the forestry industry over the last 30 years. Collectively, millions of dollars have been spent to collect, test, breed and conserve populations of *P. patula*, *P. tecunumanii*, *P. maximinoi* and *P. greggii* by the Camcore membership. The payback are new selections that are better adapted, grow faster, have better wood properties and, in some cases, have better disease resistance. The key to continued development is

finding ways to reduce the length of the breeding cycle to make more genetic gains per unit time, while at the same time having sufficient genetic material in well-designed conservation plantings to use in times of rapid environmental or market change.

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Appendix 1: Numbers of tests, provenances, and families of *P. tecunumanii*, *P. maximinoi*, *P. patula* and *P. greggii* included in progeny tests in various countries

Variety ¹	Country	Age 3			Age 5			Age 8			All ages combined			
		Tests	Provs	Fams	Tests	Provs	Fams	Tests	Provs	Fams	Tests	Provs	Fams	Trees
<i>P. tecunumanii</i>														
HE	Argentina	0	0	0	1	2	11	1	2	11	1	2	11	134
HE	Brazil	19	25	261	18	26	301	13	22	193	22	26	311	24 329
HE	Colombia	17	28	353	19	28	362	19	28	362	19	28	362	21 494
HE	South Africa	24	28	425	28	28	438	28	28	428	30	28	439	40 262
LE	Argentina	0	0	0	1	3	17	1	3	17	1	3	17	273
LE	Brazil	23	19	354	20	19	346	14	13	249	26	19	355	38 028
LE	Colombia	15	17	357	17	17	363	15	15	295	17	17	364	23 830
LE	South Africa	14	16	250	13	18	275	14	14	217	17	18	282	22 513
<i>P. maximinoi</i>														
	Argentina	0	0	0	1	5	32	1	5	32	1	5	32	675
	Brazil	11	20	309	8	21	301	7	21	293	13	21	349	21 801
	Colombia	13	19	326	10	18	306	10	18	306	13	19	326	24 677
	South Africa	13	20	293	15	24	313	15	24	313	16	24	313	27 285
<i>P. patula</i>														
	Brazil	24	21	422	26	20	440	24	20	440	30	21	461	61 241
	Chile	1	8	58	3	11	157	3	11	157	3	11	157	7 138
	Colombia	12	26	487	13	26	502	13	26	502	13	26	502	31 436
	South Africa	35	26	513	36	27	510	38	27	521	37	27	521	78 937
<i>P. greggii</i>														
<i>greggii</i>	Chile	1	5	34	4	7	75	5	8	98	4	7	75	4 526
<i>greggii</i>	South Africa	9	8	127	20	8	144	21	8	145	20	8	144	16 669
<i>australis</i>	Brazil	13	7	158	14	7	144	14	7	134	16	7	158	18 699
<i>australis</i>	Chile	1	3	22	4	7	91	5	7	109	4	7	91	4 391
<i>australis</i>	South Africa	8	7	123	16	7	127	16	7	127	16	7	127	14 169

¹ *Pinus tecunumanii* has two elevation sources (HE = high-elevation provenances and LE = low-elevation provenances), and *Pinus greggii* has two varieties (the northern var. *greggii* and the southern var. *australis*)

Appendix 2: Genetic correlations (above diagonal) and provenance correlations (below diagonal) among growth traits (height, DBH, and volume) and other genetic parameters for *P. tecunumanii* HE, *P. tecunumanii* LE, *P. maximinoi*, *P. patula*, *P. greggii* var. *greggii* (N) and *P. greggii* var. *australis* (S) at different ages and in four countries. Error values are the SE. na = SE of a genetic or provenance correlation could not be calculated as the estimate was bounded at the theoretical limit of zero or one

Species	Var	Country	Age	Trait	Correlation \pm SE			P^2	r_{Bprov}	h^2	r_{Bg}	GCV	V_{phen}
					With height	With DBH	With volume						
tec	HE	Brazil	3	ht		0.92 \pm 0.03	0.91 \pm 0.02	0.05	0.80	0.14	0.60	8.0	450.0
tec	HE	Brazil	3	dbh	1.00 (na)		0.98 \pm 0.01	0.03	0.83	0.12	0.59	10.5	915.4
tec	HE	Brazil	3	vol	1.00 (na)	1.00 (na)		0.04	0.81	0.13	0.60	23.4	4 104.9
tec	HE	Brazil	5	ht		0.87 \pm 0.03	0.86 \pm 0.03	0.03	0.51	0.13	0.72	6.6	342.8
tec	HE	Brazil	5	dbh	1.00 (na)		0.98 \pm 0.01	0.02	0.77	0.12	0.67	7.5	473.0
tec	HE	Brazil	5	vol	1.00 (na)	1.00 (na)		0.03	0.72	0.13	0.65	17.6	2 410.1
tec	HE	Brazil	8	ht		0.79 \pm 0.03	0.83 \pm 0.03	0.04	0.83	0.15	0.78	6.1	247.1
tec	HE	Brazil	8	dbh	0.88 \pm 0.07		0.99 (na)	0.01	0.93	0.11	0.62	7.3	481.4
tec	HE	Brazil	8	vol	0.97 \pm 0.03	0.97 \pm 0.02		0.02	1.00	0.12	0.60	17.3	2 464.4
tec	HE	Colombia	3	ht		0.75 \pm 0.05	0.84 \pm 0.03	0.03	0.50	0.13	0.77	6.4	313.3
tec	HE	Colombia	3	dbh	1.00 (na)		0.97 \pm 0.01	0.04	0.75	0.12	0.80	7.4	467.6
tec	HE	Colombia	3	vol	1.00 (na)	1.00 (na)		0.05	0.69	0.13	0.74	17.8	2 388.2
tec	HE	Colombia	5	ht		0.86 \pm 0.04	0.92 \pm 0.03	0.02	0.46	0.13	0.65	4.3	142.3
tec	HE	Colombia	5	dbh	0.95 \pm 0.10		0.99 \pm 0.01	0.02	0.67	0.11	0.72	7.3	477.7
tec	HE	Colombia	5	vol	0.97 \pm 0.07	1.00 \pm 0.02		0.02	0.65	0.13	0.72	16.0	2 003.6
tec	HE	Colombia	8	ht		0.81 \pm 0.03	0.88 \pm 0.02	0.02	0.31	0.08	0.56	3.3	139.2
tec	HE	Colombia	8	dbh	0.76 \pm 0.11		0.98 \pm 0.00	0.02	0.73	0.08	0.54	6.0	474.9
tec	HE	Colombia	8	vol	0.87 \pm 0.07	0.98 \pm 0.01		0.03	0.89	0.09	0.61	13.5	1 979.3
tec	HE	South Africa	3	ht		0.90 \pm 0.02	0.94 \pm 0.02	0.02	0.61	0.10	0.73	6.1	386.8
tec	HE	South Africa	3	dbh	1.00 (na)		0.98 \pm 0.01	0.01	0.52	0.07	0.65	7.6	825.5
tec	HE	South Africa	3	vol	1.00 (na)	1.00 (na)		0.02	0.62	0.08	0.64	18.0	3 995.9
tec	HE	South Africa	5	ht		0.86 \pm 0.03	0.92 \pm 0.02	0.03	0.61	0.12	0.69	5.4	249.2
tec	HE	South Africa	5	dbh	0.96 \pm 0.04		0.98 \pm 0.00	0.01	0.69	0.09	0.69	5.9	397.1
tec	HE	South Africa	5	vol	0.99 \pm 0.02	0.99 \pm 0.01		0.02	0.66	0.11	0.68	14.8	2 002.7
tec	HE	South Africa	8	ht		0.86 \pm 0.03	0.89 \pm 0.02	0.03	0.68	0.10	0.58	4.4	190.8
tec	HE	South Africa	8	dbh	0.82 \pm 0.09		0.99 \pm 0.00	0.00	0.75	0.11	0.67	6.5	398.8
tec	HE	South Africa	8	vol	0.96 \pm 0.04	1.00 (na)		0.01	0.79	0.12	0.63	15.3	2 008.6
tec	LE	Brazil	3	ht		0.81 \pm 0.05	0.91 \pm 0.02	0.09	0.94	0.10	0.48	6.3	392.3
tec	LE	Brazil	3	dbh	0.98 \pm 0.02		0.94 \pm 0.02	0.04	0.86	0.07	0.35	6.9	722.4
tec	LE	Brazil	3	vol	0.95 \pm 0.04	0.96 \pm 0.03		0.05	0.86	0.08	0.39	16.3	3 206.4
tec	LE	Brazil	5	ht		0.83 \pm 0.05	0.92 \pm 0.03	0.10	0.88	0.11	0.47	5.2	249.0
tec	LE	Brazil	5	dbh	1.00 \pm 0.01		0.97 \pm 0.01	0.06	0.96	0.08	0.42	6.1	477.8
tec	LE	Brazil	5	vol	1.00 \pm 0.01	1.00 (na)		0.08	0.95	0.10	0.45	14.6	2 170.9
tec	LE	Brazil	8	ht		0.71 \pm 0.07	0.82 \pm 0.05	0.03	0.57	0.09	0.43	4.8	250.5
tec	LE	Brazil	8	dbh	1.00 (na)		0.97 \pm 0.01	0.01	0.74	0.08	0.44	6.2	482.6
tec	LE	Brazil	8	vol	1.00 (na)	1.00 (na)		0.01	0.73	0.08	0.41	13.5	2 196.3
tec	LE	Colombia	3	ht		0.92 \pm 0.04	0.94 \pm 0.02	0.11	0.95	0.16	0.65	7.5	354.2
tec	LE	Colombia	3	dbh	0.98 \pm 0.02		0.98 \pm 0.01	0.08	0.90	0.15	0.72	8.2	435.3
tec	LE	Colombia	3	vol	0.99 \pm 0.01	1.00 \pm 0.00		0.11	0.92	0.17	0.71	18.7	2 080.8
tec	LE	Colombia	5	ht		0.86 \pm 0.03	0.91 \pm 0.02	0.05	0.52	0.15	0.68	6.0	248.2
tec	LE	Colombia	5	dbh	0.97 \pm 0.05		0.98 \pm 0.00	0.02	0.52	0.18	0.97	8.8	433.6
tec	LE	Colombia	5	vol	0.99 \pm 0.02	0.99 \pm 0.01		0.04	0.55	0.19	0.92	19.8	2 069.8
tec	LE	Colombia	8	ht		0.87 \pm 0.04	0.92 \pm 0.03	0.19	0.86	0.16	0.73	5.4	187.3
tec	LE	Colombia	8	dbh	0.98 \pm 0.04		0.99 \pm 0.00	0.03	0.65	0.17	0.80	8.6	436.1
tec	LE	Colombia	8	vol	0.99 \pm 0.02	1.00 \pm 0.01		0.07	0.73	0.19	0.81	19.6	2 068.3
tec	LE	South Africa	3	ht		0.82 \pm 0.02	0.94 (na)	0.07	0.85	0.14	0.78	8.8	534.7
tec	LE	South Africa	3	dbh	0.83 \pm 0.07		0.94 (na)	0.06	0.85	0.10	0.72	9.7	979.5
tec	LE	South Africa	3	vol	0.91 \pm 0.05	0.99 (na)		0.06	0.85	0.11	0.75	20.7	3 994.6
tec	LE	South Africa	5	ht		0.83 \pm 0.03	0.91 \pm 0.02	0.04	0.83	0.21	0.94	7.6	274.5
tec	LE	South Africa	5	dbh	0.86 \pm 0.06		0.98 \pm 0.01	0.03	0.91	0.18	0.92	8.7	426.8
tec	LE	South Africa	5	vol	0.92 \pm 0.05	0.99 (na)		0.04	0.88	0.19	0.93	20.2	2 111.9
tec	LE	South Africa	8	ht		0.86 \pm 0.03	0.91 \pm 0.02	0.06	0.88	0.15	0.62	5.3	187.3
tec	LE	South Africa	8	dbh	0.96 \pm 0.03		0.98 \pm 0.00	0.02	0.99	0.17	0.72	8.5	433.2
tec	LE	South Africa	8	vol	0.97 \pm 0.02	1.00 (na)		0.04	0.95	0.17	0.67	19.4	2 146.9
max		Brazil	3	ht		0.69 \pm 0.06	0.82 \pm 0.04	0.00	0.13	0.07	0.35	5.6	431.0
max		Brazil	3	dbh	1.00 (na)		0.96 \pm 0.01	0.02	0.65	0.07	0.39	6.9	661.6
max		Brazil	3	vol	1.00 (na)	1.00 (na)		0.02	0.64	0.08	0.39	16.7	3 643.7

Appendix 2: (cont.)

Species	Var	Country	Age	Trait	Correlation \pm SE			P^2	r_{Bprov}	h^2	r_{Bg}	GCV	V_{phen}
					With height	With DBH	With volume						
max		Brazil	5	ht		0.83 \pm 0.02	0.87 \pm 0.02	0.01	0.49	0.27	0.92	8.2	253.3
max		Brazil	5	dbh	–		0.98 \pm 0.00	0.00	0.24	0.24	0.94	11.1	527.9
max		Brazil	5	vol	–	–		0.00	0.39	0.21	0.96	22.8	2 498.9
max		Brazil	8	ht		0.92 \pm 0.04	0.93 \pm 0.03	0.03	0.82	0.34	0.88	8.2	201.2
max		Brazil	8	dbh	–		0.99 \pm 0.01	0.00	0.11	0.18	0.61	9.6	503.7
max		Brazil	8	vol	–	–		0.00	0.08	0.19	0.69	21.2	2 368.8
max		Colombia	3	ht		0.73 \pm 0.03	0.87 \pm 0.02	0.04	0.67	0.23	0.77	8.4	310.3
max		Colombia	3	dbh	0.70 \pm 0.14		0.95 \pm 0.01	0.03	0.66	0.16	0.75	9.0	513.3
max		Colombia	3	vol	0.87 \pm 0.07	0.96 \pm 0.02		0.04	0.63	0.18	0.76	21.0	2 417.1
max		Colombia	5	ht		0.57 \pm 0.07	0.68 \pm 0.06	0.03	0.87	0.14	0.77	5.2	193.0
max		Colombia	5	dbh	0.85 \pm 0.11		0.98 \pm 0.00	0.03	0.98	0.18	0.83	9.5	520.4
max		Colombia	5	vol	0.90 \pm 0.07	1.00 \pm 0.01		0.04	0.98	0.19	0.83	21.4	2 452.9
max		Colombia	8	ht		0.32 \pm 0.17	0.56 \pm 0.13	0.03	0.70	0.09	0.70	3.8	166.0
max		Colombia	8	dbh	0.86 \pm 0.11		0.96 \pm 0.02	0.01	0.93	0.16	0.79	9.0	525.0
max		Colombia	8	vol	0.91 \pm 0.07	0.99 \pm 0.01		0.02	1.00	0.14	0.74	18.4	2 476.7
max		South Africa	3	ht		0.91 \pm 0.02	0.93 \pm 0.01	0.02	0.46	0.13	0.71	9.1	654.5
max		South Africa	3	dbh	0.87 \pm 0.06		0.97 \pm 0.01	0.04	0.66	0.09	0.67	9.9	1 050.8
max		South Africa	3	vol	0.94 \pm 0.05	1.00 (na)		0.04	0.64	0.09	0.62	21.5	4 996.4
max		South Africa	5	ht		0.85 \pm 0.02	0.92 \pm 0.01	0.01	0.51	0.19	0.77	7.8	316.4
max		South Africa	5	dbh	0.67 \pm 0.16		0.97 \pm 0.00	0.03	0.93	0.12	0.72	7.8	516.4
max		South Africa	5	vol	0.78 \pm 0.12	0.98 \pm 0.01		0.03	0.88	0.12	0.70	18.5	2 740.3
max		South Africa	8	ht		0.90 \pm 0.02	0.92 \pm 0.01	0.01	0.55	0.17	0.87	6.1	221.1
max		South Africa	8	dbh	0.67 \pm 0.16		0.98 \pm 0.00	0.02	0.96	0.13	0.81	8.2	520.0
max		South Africa	8	vol	0.77 \pm 0.12	0.97 \pm 0.02		0.02	0.88	0.12	0.77	18.4	2 762.6
pat		Brazil	3	ht		0.79 \pm 0.03	0.88 \pm 0.02	0.02	0.43	0.12	0.61	6.5	355.5
pat		Brazil	3	dbh	0.86 \pm 0.11		0.98 \pm 0.00	0.02	0.47	0.10	0.55	8.9	828.4
pat		Brazil	3	vol	0.86 \pm 0.11	0.99 \pm 0.01		0.03	0.54	0.11	0.59	21.5	4 154.8
pat		Brazil	5	ht		0.80 \pm 0.03	0.88 \pm 0.02	0.05	0.68	0.12	0.57	6.5	347.8
pat		Brazil	5	dbh	0.88 \pm 0.08		0.98 \pm 0.00	0.03	0.63	0.11	0.63	8.3	614.1
pat		Brazil	5	vol	0.90 \pm 0.06	0.99 \pm 0.01		0.04	0.61	0.13	0.63	19.4	2 953.9
pat		Brazil	8	ht		0.89 \pm 0.02	0.92 \pm 0.01	0.06	0.76	0.15	0.61	7.2	344.9
pat		Brazil	8	dbh	0.90 \pm 0.07		0.99 \pm 0.00	0.03	0.62	0.13	0.69	8.9	612.0
pat		Brazil	8	vol	0.93 \pm 0.05	0.99 \pm 0.01		0.03	0.65	0.15	0.69	20.8	2 947.3
pat		Colombia	3	ht		0.85 \pm 0.04	0.94 \pm 0.02	0.10	0.73	0.20	0.69	9.0	399.8
pat		Colombia	3	dbh	1.00 (na)		0.96 \pm 0.01	0.12	0.85	0.11	0.53	10.0	881.4
pat		Colombia	3	vol	1.00 (na)	1.00 (na)		0.10	0.80	0.12	0.54	21.9	3 906.3
pat		Colombia	5	ht		0.80 \pm 0.05	0.87 \pm 0.03	0.23	0.82	0.20	0.65	8.7	381.8
pat		Colombia	5	dbh	0.98 \pm 0.02		0.98 \pm 0.01	0.15	0.87	0.15	0.66	7.5	368.3
pat		Colombia	5	vol	0.99 \pm 0.01	0.99 \pm 0.01		0.14	0.80	0.16	0.69	25.1	3 876.0
pat		Colombia	8	ht		0.80 \pm 0.05	0.87 \pm 0.03	0.23	0.82	0.20	0.65	8.7	381.8
pat		Colombia	8	dbh	0.98 \pm 0.02		0.98 \pm 0.01	0.15	0.87	0.15	0.66	7.5	368.3
pat		Colombia	8	vol	0.99 \pm 0.01	0.99 \pm 0.01		0.14	0.80	0.16	0.69	25.1	3 875.9
pat		South Africa	3	ht		0.86 \pm 0.02	0.92 \pm 0.01	0.10	0.81	0.14	0.65	7.2	382.8
pat		South Africa	3	dbh	0.94 \pm 0.03		0.98 \pm 0.00	0.05	0.75	0.09	0.57	9.6	1 066.1
pat		South Africa	3	vol	0.96 \pm 0.02	0.99 \pm 0.00		0.05	0.74	0.10	0.57	19.9	4 104.0
pat		South Africa	5	ht		0.78 \pm 0.03	0.86 \pm 0.02	0.12	0.82	0.12	0.66	5.0	212.4
pat		South Africa	5	dbh	0.89 \pm 0.05		0.98 \pm 0.00	0.04	0.74	0.11	0.66	6.4	390.2
pat		South Africa	5	vol	0.96 \pm 0.02	0.99 \pm 0.01		0.07	0.78	0.12	0.66	15.2	1 948.8
pat		South Africa	8	ht		0.74 \pm 0.03	0.84 \pm 0.02	0.09	0.80	0.12	0.64	5.0	212.1
pat		South Africa	8	dbh	0.71 \pm 0.13		0.98 \pm 0.00	0.02	0.66	0.11	0.74	6.7	392.5
pat		South Africa	8	vol	0.90 \pm 0.05	0.95 \pm 0.03		0.03	0.74	0.13	0.72	15.9	1 961.7
greg	S	Brazil	3	ht		0.86 \pm 0.03	0.89 \pm 0.02	0.15	0.98	0.23	0.57	8.1	280.7
greg	S	Brazil	3	dbh	0.99 (na)		0.97 \pm 0.01	0.10	0.90	0.20	0.65	10.6	561.5
greg	S	Brazil	3	vol	0.99 \pm 0.01	0.99 \pm 0.01		0.10	0.92	0.21	0.64	23.7	2 711.2
greg	S	Brazil	5	ht		0.91 \pm 0.03	0.92 \pm 0.02	0.05	0.93	0.19	0.47	7.6	312.0
greg	S	Brazil	5	dbh	0.98 \pm 0.04		0.98 \pm 0.01	0.05	0.86	0.16	0.53	9.9	602.2
greg	S	Brazil	5	vol	0.90 (na)	0.90 (na)		0.05	0.87	0.18	0.62	22.7	2 905.0

Appendix 2: (cont.)

Species	Var	Country	Age	Trait	Correlation \pm SE			P^2	r_{Bprov}	h^2	r_{Bg}	GCV	V_{phen}
					With height	With DBH	With volume						
greg	S	Brazil	8	ht		0.86 ± 0.02	0.89 ± 0.02	0.15	0.66	0.01	0.10	1.5	280.7
greg	S	Brazil	8	dbh	0.99 ± 0.01		0.97 ± 0.01	0.10	0.61	0.03	0.48	4.3	561.5
greg	S	Brazil	8	vol	0.99 ± 0.01	1.00 ± 0.00		0.10	0.59	0.03	0.42	8.5	2 711.2
greg	S	South Africa	3	ht		0.84 ± 0.04	0.90 ± 0.03	0.07	0.61	0.20	0.42	7.7	292.7
greg	S	South Africa	3	dbh	1.00 (na)		0.99 ± 0.01	0.07	0.64	0.12	0.60	8.7	629.4
greg	S	South Africa	3	vol	1.00 (na)	1.00 (na)		0.10	0.72	0.13	0.52	19.3	2 949.6
greg	S	South Africa	5	ht		0.70 ± 0.07	0.83 ± 0.04	0.07	0.66	0.10	0.57	5.0	236.9
greg	S	South Africa	5	dbh	1.00 (na)		0.98 ± 0.01	0.03	0.52	0.11	0.73	6.7	424.8
greg	S	South Africa	5	vol	1.00 (na)	1.00 (na)		0.05	0.61	0.11	0.68	14.6	1 915.3
greg	S	South Africa	8	ht		0.74 ± 0.07	0.83 ± 0.04	0.06	0.69	0.13	0.68	4.9	184.3
greg	S	South Africa	8	dbh	0.86 ± 0.18		0.98 ± 0.01	0.02	0.54	0.11	0.69	6.3	352.8
greg	S	South Africa	8	vol	0.98 ± 0.06	0.96 ± 0.06		0.03	0.57	0.13	0.72	16.1	1 961.4
greg	N	South Africa	3	ht		0.95 ± 0.02	0.94 ± 0.03	0.08	0.89	0.19	0.51	8.2	364.8
greg	N	South Africa	3	dbh	0.95 ± 0.04		0.97 ± 0.02	0.04	0.98	0.20	0.68	14.7	1 070.9
greg	N	South Africa	3	vol	0.97 ± 0.03	0.99 (na)		0.03	1.00	0.25	0.65	34.7	4 879.1
greg	N	South Africa	5	ht		0.86 ± 0.03	0.91 ± 0.02	0.11	0.88	0.27	0.74	7.7	221.7
greg	N	South Africa	5	dbh	0.83 ± 0.14		0.97 ± 0.01	0.06	0.71	0.22	0.72	9.5	405.0
greg	N	South Africa	5	vol	0.91 ± 0.10	1.00 (na)		0.08	0.79	0.23	0.68	22.2	2 133.4
greg	N	South Africa	8	ht		0.82 ± 0.03	0.88 ± 0.02	0.14	0.85	0.28	0.71	7.9	223.3
greg	N	South Africa	8	dbh	0.42 ± 0.35		0.98 ± 0.00	0.07	0.78	0.30	0.78	10.3	347.9
greg	N	South Africa	8	vol	0.75 ± 0.19	0.91 ± 0.07		0.09	0.80	0.28	0.71	23.1	1 885.2
greg	N	Chile	3	ht		1.00 (na)	0.94 ± 0.06	0.08	0.99	0.05	0.25	5.1	492.9
greg	N	Chile	3	dbh	1.00 (na)		0.94 ± 0.04	0.09	0.51	0.19	0.43	20.7	2 205.3
greg	N	Chile	3	vol	1.00 (na)	1.00 (na)		0.09	0.50	0.17	0.40	40.9	9 759.9
greg	N	Chile	5	ht		1.00 (na)	1.00 (na)	0.09	0.98	0.10	0.54	5.4	297.7
greg	N	Chile	5	dbh	1.00 (na)		1.00 ± 0.01	0.06	0.73	0.04	0.25	5.8	780.8
greg	N	Chile	5	vol	1.00 (na)	1.00 (na)		0.07	0.85	0.05	0.29	14.3	4 251.7
greg	N	Chile	8	ht		0.82 (na)	0.91 ± 0.04	0.03	0.45	0.15	1.00	5.8	224.9
greg	N	Chile	8	dbh	0.56 (na)		0.95 (na)	0.02	0.48	0.16	1.00	9.3	535.4
greg	N	Chile	8	vol	0.90 (na)	0.90 (na)		0.02	0.45	0.15	1.00	21.0	2 861.3
greg	S	Chile	5	ht		0.91 ± 0.03	0.93 ± 0.02	0.00	0.03	0.12	0.04	6.4	338.7
greg	S	Chile	5	dbh	0.97 ± 0.03		0.98 ± 0.01	0.01	0.13	0.07	0.02	7.0	710.0
greg	S	Chile	5	vol	1.00 ± 0.01	0.98 ± 0.02		0.02	0.26	0.10	0.03	19.8	3 815.3
greg	S	Chile	8	ht		–	–	–	–	–	–	–	–
greg	S	Chile	8	dbh	–		–	–	–	–	–	–	–
greg	S	Chile	8	vol	–	–		–	–	–	–	–	–

Appendix 3: Age–age genetic correlations (above diagonals) and provenance correlations (below diagonals) and other genetic parameters for volume growth for *P. tecunumanii* HE, *P. tecunumanii* LE, *P. maximinoi*, *P. patula*, and *P. greggii* var. *greggii* (N) and *P. greggii* var. *australis* (S) in four different countries. Error values are the SE. na = SE of a genetic or provenance correlation could not be calculated as the estimate was bounded at the theoretical limit of zero or one

Var	Country	Trait	Age–age correlations			P^2	r_{Bprov}	h^2	r_{Bg}	GCV	V_{phen}
			With vol3	With vol5	With vol8						
<i>P. tecunumanii</i>											
HE	Brazil	vol3		0.94 ± 0.02	0.86 ± 0.06	0.05 ± 0.00	0.87 ± 0.14	0.13 ± 0.02	0.58 ± 0.10	23.3	4 149.3
HE	Brazil	vol5	0.91 ± 0.06		0.97 ± 0.02	0.03 ± 0.01	0.68 ± 0.20	0.13 ± 0.02	0.63 ± 0.11	17.9	2 433.1
HE	Brazil	vol8	0.91 ± 0.08	1.00 (na)		0.03 ± 0.01	0.65 ± 0.21	0.13 ± 0.02	0.66 ± 0.12	18.6	2 581.4
HE	Colombia	vol3		0.90 ± 0.05	0.74 ± 0.10	0.06 ± 0.01	0.76 ± 0.19	0.12 ± 0.02	0.66 ± 0.18	16.7	2 393.5
HE	Colombia	vol5	0.85 ± 0.08		0.98 ± 0.03	0.03 ± 0.01	0.74 ± 0.25	0.12 ± 0.02	0.67 ± 0.17	15.6	2 012.2
HE	Colombia	vol8	0.52 ± 0.20	0.88 ± 0.07		0.03 ± 0.00	0.89 ± 0.21	0.10 ± 0.02	0.65 ± 0.18	14.4	2 090.7
HE	South Africa	vol3		0.93 ± 0.02	0.82 ± 0.03	0.02 ± 0.00	0.56 ± 0.15	0.08 ± 0.01	0.64 ± 0.08	17.9	4 037.1
HE	South Africa	vol5	0.90 ± 0.06		0.96 ± 0.01	0.02 ± 0.00	0.68 ± 0.14	0.11 ± 0.01	0.72 ± 0.07	15.2	2 009.3
HE	South Africa	vol8	0.90 ± 0.08	0.99 ± 0.02		0.01 ± 0.00	0.74 ± 0.15	0.12 ± 0.01	0.75 ± 0.07	15.8	2 062.6
LE	Brazil	vol3		0.94 ± 0.02	0.86 ± 0.03	0.04 ± 0.01	0.72 ± 0.21	0.08 ± 0.02	0.39 ± 0.07	16.3	3 194.8
LE	Brazil	vol5	0.94 ± 0.07		0.98 ± 0.01	0.06 ± 0.00	0.91 ± 0.13	0.10 ± 0.02	0.46 ± 0.07	14.9	2 185.7
LE	Brazil	vol8	0.96 ± 0.08	1.00 (na)		0.04 ± 0.00	0.93 ± 0.15	0.09 ± 0.02	0.44 ± 0.08	14.4	2 264.4
LE	Colombia	vol3		0.94 ± 0.02	0.87 ± 0.04	0.08 ± 0.02	0.63 ± 0.19	0.16 ± 0.02	0.70 ± 0.11	17.9	2 046.2
LE	Colombia	vol5	0.98 ± 0.03		0.96 ± 0.01	0.04 ± 0.01	0.56 ± 0.20	0.16 ± 0.02	0.79 ± 0.10	18.4	2 103.6
LE	Colombia	vol8	1.00 (na)	1.00 (na)		0.03 ± 0.01	0.43 ± 0.22	0.17 ± 0.02	0.83 ± 0.11	19.2	2 227.0
LE	South Africa	vol3		0.95 ± 0.01	0.88 ± 0.02	0.08 ± 0.01	0.86 ± 0.01	0.13 ± 0.02	0.82 ± 0.01	22.9	4 067.1
LE	South Africa	vol5	1.00 (na)		0.98 ± 0.01	0.07 ± 0.00	0.87 ± 0.01	0.17 ± 0.02	0.85 ± 0.00	18.8	2 041.7
LE	South Africa	vol8	0.97 ± 0.02	1.00 (na)		0.04 ± 0.00	0.95 ± 0.07	0.15 ± 0.02	0.80 ± 0.04	18.4	2 208.6
<i>P. maximinoi</i>											
	Brazil	vol3		0.87 ± 0.06	0.81 ± 0.07	0.02 ± 0.00	0.71 ± 0.28	0.11 ± 0.02	0.52 ± 0.11	19.6	3 671.0
	Brazil	vol5	–		1.00 (na)	0.00 ± 0.00	0.57 ± 0.48	0.15 ± 0.03	0.57 ± 0.12	19.1	2 509.8
	Brazil	vol8	–	–		0.00 ± 0.00	0.17 ± 0.57	0.19 ± 0.03	0.69 ± 0.12	22.4	2 607.0
	Colombia	vol3		0.87 ± 0.03	0.83 ± 0.05	0.04 ± 0.01	0.63 ± 0.19	0.18 ± 0.02	0.76 ± 0.08	21.0	2 418.2
	Colombia	vol5	0.77 ± 0.10		0.97 ± 0.02	0.03 ± 0.00	0.88 ± 0.12	0.19 ± 0.02	0.84 ± 0.10	21.6	2 453.7
	Colombia	vol8	0.63 ± 0.15	0.94 ± 0.03		0.02 ± 0.00	0.91 ± 0.16	0.14 ± 0.02	0.72 ± 0.12	18.7	2 537.2
	South Africa	vol3		0.91 ± 0.02	0.81 ± 0.04	0.03 ± 0.01	0.63 ± 0.15	0.09 ± 0.01	0.61 ± 0.09	21.3	5 012.8
	South Africa	vol5	0.99 ± 0.02		0.96 ± 0.01	0.03 ± 0.00	0.87 ± 0.11	0.12 ± 0.02	0.76 ± 0.08	18.5	2 763.1
	South Africa	vol8	1.00 ± 0.04	1.00 (na)		0.02 ± 0.00	0.89 ± 0.12	0.14 ± 0.02	0.83 ± 0.08	19.6	2 844.5
<i>P. patula</i>											
	Brazil	vol3		0.91 ± 0.02	0.67 ± 0.05	0.01 ± 0.01	0.38 ± 0.17	0.11 ± 0.01	0.60 ± 0.06	21.6	4 150.8
	Brazil	vol5	0.94 ± 0.06		0.90 ± 0.02	0.03 ± 0.01	0.56 ± 0.15	0.13 ± 0.01	0.65 ± 0.05	19.7	2 971.1
	Brazil	vol8	0.83 ± 0.13	0.95 ± 0.04		0.03 ± 0.00	0.64 ± 0.14	0.16 ± 0.02	0.73 ± 0.05	22.2	3 102.9
	Colombia	vol3		0.99 ± 0.03	0.87 ± 0.06	0.11 ± 0.01	0.82 ± 0.15	0.11 ± 0.02	0.51 ± 0.13	20.8	3 903.0
	Colombia	vol5	0.99 ± 0.01		0.98 ± 0.02	0.15 ± 0.02	0.77 ± 0.15	0.15 ± 0.02	0.63 ± 0.12	24.3	3 807.4
	Colombia	vol8	0.91 ± 0.06	0.95 ± 0.03		0.12 ± 0.01	0.76 ± 0.16	0.16 ± 0.02	0.66 ± 0.12	24.8	3 932.4
	South Africa	vol3		0.95 ± 0.01	0.86 ± 0.02	0.05 ± 0.00	0.71 ± 0.09	0.09 ± 0.01	0.57 ± 0.04	19.6	4 098.9
	South Africa	vol5	0.99 ± 0.01		0.97 ± 0.01	0.06 ± 0.00	0.75 ± 0.08	0.13 ± 0.01	0.68 ± 0.04	16.1	1 971.6
	South Africa	vol8	0.94 ± 0.04	0.96 ± 0.02		0.03 ± 0.00	0.71 ± 0.09	0.14 ± 0.01	0.74 ± 0.03	16.7	2 010.8
<i>P. greggii</i>											
S	Brazil	vol3		0.93 ± 0.02	0.81 ± 0.04	0.08 ± 0.01	0.81 ± 0.12	0.16 ± 0.02	0.71 ± 0.07	24.9	3 902.0
S	Brazil	vol5	0.86 ± 0.14		0.97 ± 0.01	0.09 ± 0.01	0.89 ± 0.11	0.20 ± 0.03	0.70 ± 0.07	24.1	2 886.7
S	Brazil	vol8	0.70 ± 0.24	0.97 ± 0.03		0.11 ± 0.00	0.93 ± 0.06	0.21 ± 0.03	0.79 ± 0.06	25.5	3 025.3
S	South Africa	ht3		0.83 ± 0.05	0.61 ± 0.08	0.08 ± 0.02	0.56 ± 0.21	0.13 ± 0.02	0.75 ± 0.08	6.1	286.0
S	South Africa	vol5	0.98 ± 0.05		0.92 ± 0.03	0.05 ± 0.01	0.59 ± 0.21	0.11 ± 0.02	0.67 ± 0.09	14.4	1 943.0
S	South Africa	vol8	0.68 ± 0.30	0.84 ± 0.17		0.02 ± 0.01	0.50 ± 0.27	0.13 ± 0.02	0.71 ± 0.08	16.0	2 018.2
N	South Africa	ht3		0.94 ± 0.02	0.86 ± 0.04	0.10 ± 0.01	0.94 ± 0.06	0.22 ± 0.04	0.72 ± 0.07	8.9	357.8
N	South Africa	vol5	0.93 ± 0.06		0.96 ± 0.01	0.10 ± 0.01	0.84 ± 0.11	0.23 ± 0.04	0.67 ± 0.07	22.3	2 168.9
N	South Africa	vol8	0.83 ± 0.15	0.97 ± 0.04		0.07 ± 0.01	0.76 ± 0.16	0.28 ± 0.04	0.69 ± 0.06	23.3	1 942.3
S	South Africa	vol3		0.83 ± 0.05	0.61 ± 0.08	0.08 ± 0.02	0.56 ± 0.21	0.13 ± 0.02	0.75 ± 0.08	19.0	2 909.3
S	South Africa	vol5	0.98 ± 0.05		0.92 ± 0.03	0.05 ± 0.01	0.59 ± 0.21	0.11 ± 0.02	0.67 ± 0.09	14.4	1 943.0
S	South Africa	vol8	0.68 ± 0.30	0.84 ± 0.17		0.02 ± 0.01	0.50 ± 0.27	0.13 ± 0.02	0.71 ± 0.08	16.0	2 018.2
N	South Africa	vol3		0.94 ± 0.02	0.86 ± 0.04	0.10 ± 0.01	0.94 ± 0.06	0.22 ± 0.04	0.72 ± 0.07	34.7	4 879.1
N	South Africa	vol5	0.93 ± 0.06		0.96 ± 0.01	0.10 ± 0.01	0.84 ± 0.11	0.23 ± 0.04	0.67 ± 0.07	22.3	2 168.9
N	South Africa	vol8	0.83 ± 0.15	0.97 ± 0.04		0.07 ± 0.01	0.76 ± 0.16	0.28 ± 0.04	0.69 ± 0.06	23.3	1 942.3