Available online at www.sciencedirect.com
ScienceDirect
Forest Ecology and Management 242 (2007) 598–605
Forest Ecology and Management
www.elsevier.com/locate/foreco

Assessing the potential of *Pinus herrerae* as a plantation species for the subtropics

W.S. Dvorak [a,*], Eric Kietzka [✠], G.R. Hodge [a], A. Nel [b], G.A. dos Santos [c], C. Gantz [d]

[a] North Carolina State University, Grinnells Laboratory, P.O. Box 7626, Raleigh, NC 27695, USA
[b] Sappi Forest Research, P.O. Box 473, Howick 3290, South Africa
[c] Klabin PR, Telemaco Borba, PR, Brazil
[d] CMPC Forestry, Los Angeles, Chile

Received 7 December 2006; received in revised form 24 January 2007; accepted 25 January 2007

This manuscript is dedicated to our colleague, Eric Kietzka, who died suddenly in March 2006.

Abstract

Pinus herrerae Martínez is a little known hard pine that occurs in the western mountain ranges of Mexico between 16° and 28°N latitude and 1800 m and 2400 m altitude. Seed collections were made from 12 of the 14 populations that were identified through explorations and seedlings were established in either species, species/provenance, provenance/progeny trials or arboreta plantings in Brazil, Chile, Colombia and South Africa. Productivity of *P. herrerae* in 13 field trials ranged from 3 to 24 m^3/ha/year (overbark), assessed at between 8 and 13 years. *P. herrerae* from temperate areas in Mexico is best adapted to cool dry areas in South Africa where minimum nighttime winter temperatures range −5 °C to 7 °C. Provenances of *P. herrerae* from subtropical regions in Mexico grew well in areas of similar climate in Brazil, Colombia, and South Africa where frosts seldom occurs. *P. herrerae* exhibited good stem form in most trials but growth of temperate sources was not comparable to that of *P. patula*, *P. radiata* or *P. taeda*, even when differences due to levels of genetic improvement were considered. The subtropical source of *P. herrerae* from Oaxaca (Juquila) grew as well as average unimproved sources of *P. tecunumanii* from Chiapas, Mexico when planted on appropriate sites in trials in Brazil, Colombia, and South Africa. Within provenance heritability (h^2) for height and diameter of *P. herrerae* ranged from 0.08 to 0.14 in South Africa and from 0.44 to 0.46 in Brazil in two orthogonal trials. Heritability values for forking were 0.10 and 0.06 at each location, respectively. The ecological niche for *P. herrerae* as an exotic plantation species appears to climatically fall between (and often overlap with) areas that are currently being commercially planted to subtemperate species like *P. greggii* var. *australis* and the subtropical species *P. tecunumanii*.

Keywords: Climatic zones; Provenances; Genetic parameters

1. Introduction

Pinus herrerae Martínez (syn. *P. herrerai*) is a medium to very large pine species that is native to western Mexico. It occurs in the Sierra Madre Oriental and Sierra Madre del Sur from the States of Chihuahua (28°N) to Oaxaca (16°N) in a series of disjunct, and often isolated populations in temperate to subtropical climatic zones (Fig. 1). The species is most commonly found between 1800 m and 2400 m altitude and grows in either pure stands or intermixed with an assortment of other pines and oaks (Dvorak et al., 2000). *P. herrerae* occurs in areas with 850–1300 mm of annual precipitation on well-drained soils. Some populations located in the more temperate climatic zones of Durango and Chihuahua are presumably adapted to winter nighttime temperatures that drop below freezing. Even though *P. herrerae* was first described nearly 70 years ago, the limits of its geographic distribution in the western mountains of Mexico are still poorly defined (Perry, 1991). Local uses for the tree include construction timber, resin production and charcoal (Martínez, 1945).

Because of its straight stem form and apparent good growth in natural stands, *P. herrerae* has attracted the attention of tree breeders and foresters over the last 20 years as a possible plantation species for the subtropic/temperate climatic zones in

* Corresponding author.
E-mail address: dvorak@unity.ncsu.edu (W.S. Dvorak).
✠ Deceased, formerly with Mondi Business Paper Ltd., Pietermaritzburg, South Africa.

0378-1127/$ – see front matter
doi:10.1016/j.foreco.2007.01.076

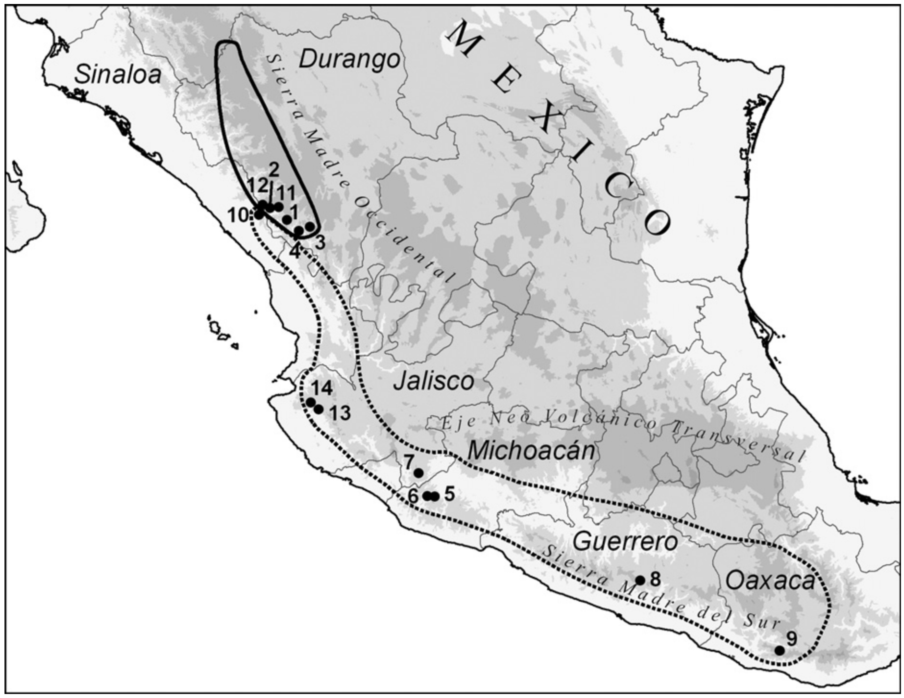

Fig. 1. Location of the *Pinus herrerae* provenances that were visited in western Mexico. Those in Durango and Sinaloa occur in the Sierra Madre Oriental and those from Jalisco south are in the Sierra Madre del Sur. Provenances encircled in a dashed line experience predominantly subtropical climate; those encircled in a solid line, more temperate climate. See text for details (map key found in Table 1).

other areas of the world. Camcore (International Tree Conservation & Domestication), North Carolina State University, began mother tree seed collection of the species in Mexico in the mid-1980s to better quantify the potential of *P. herrerae* as a plantation species. Field trials were established in South America and Southern Africa. The testing of the species at the provenance and family level was the first effort of its kind for *P. herrerae*.

This paper reports on the adaptability and productivity of *P. herrerae* in different field trials in Brazil, Chile, Colombia and South Africa established by Camcore members. Genetic variation in provenance and family performance is examined. Recommendations about where future plantings of the species should be located are made based on initial experiences from field trials as well as FloraMap™ software that predicts optimum placement of plant species using climatic data from confirmed collection sites in natural stands. The advantages and disadvantages of commercial use of *P. herrerae* are discussed.

2. Materials and methods

2.1. Provenance collections

Fourteen different populations of *P. herrerae* were identified during Camcore field visits to western Mexico between 1985 and 2000 (Table 1). Eleven of the populations of the species were well known by Mexican forest biologists prior to the collection efforts and had been referenced in the literature for years (Eguiluz-Piedra, 1978). Two of the provenances, Palo Blanco (Guerrero) and Juquila (Oaxaca), were confirmed to be rare atypical four needle forms of *P. herrerae* through molecular marker assessment subsequent to making the seed collections (Dvorak et al., 2001). Monte Grande, Jalisco was a new sighting of the species. In total, seeds were collected from 317 mother trees in 12 of the 14 populations (Table 1). Trees were selected based on phenotype and abundance of cones. Generally a mature tree produces only about 750 seeds (5 g).

Because of the large distance between collection sites and the propensity of the species to have poor seed years, provenance sampling and trial establishment by Camcore members was separated by several years. The first provenance/progeny trial series to be established in the mid-1990s included the provenances La Puerta, Pino Gordo, El Llano and Guajolota from Durango. These trials were established in Brazil, Chile and South Africa. The second series of trials included Dos Aguas, La Nieve and Sierra Lalo from Michoacán and Jalisco and were planted from the late 1990s to the early 2000s in Brazil and South Africa. The third series of trials include La Lobera, Santa Lucía, Los Negros, and Palo Blanco and will be established by Camcore members in 2008.

The lone Oaxacan source, Juquila, which was originally classified as *P. tecunumanii* by Camcore and Farjon and Styles (1997), was included in a number of trials of high altitude *P. tecunumanii* established in Brazil, Colombia, and South Africa (see Hodge and Dvorak, 1999). Because of its taxonomic misclassification and placement in the *P. tecunumanii* trials, its performance cannot be directly compared with other provenances of *P. herrerae* but is reported here to demonstrate its growth potential.

Table 1
Location of provenances of *Pinus herrerae* visited and sampled by Camcore in western Mexico between 1985 and 2000 (amended from Dvorak et al., 2000)

Map key	Provenance	State	Latitude	Longitude	Elevation range	Rainfall (mm/year)	No. of trees
1	La Puerta	Durango	23°24′N	105°23′W	2000–2450	927	40
2	Pino Gordo	Durango	23°36′N	105°40′W	2200–2300	927	40
3	El Llano	Durango	23° 17′N	105°00′W	2400–2450	927	40
4	Guajolota	Durango	23° 13′N	105°11′W	2050–2150	927	40
5	Dos Aguas	Michoacán	18° 49′N	102°56′W	2150–2250	1090	30
6	La Nieve	Michoacán	18° 49′N	103°03′W	2050–2150	1100	20
7	Sierra Lalo	Jalisco	19° 12′N	103°12′W	2000–2200	980	35
8	Palo Blanco	Guerrero	17° 25′N	99°31′W	2170–2350	1220	15
9	Juquila	Oaxaca	16°15′N	97°13′W	2090–2260	1325	21
10	La Lobera	Sinaloa	23° 29′N	105°51′W	1594–2025	1000	15
11	Santa Lucía	Durango	23° 37′N	105°31′W	1985–2000	1000	10
12	Los Negros	Durango	23° 39′N	105°47′W	1744–2000	1000	11
13	Monte Grande	Jalisco	20° 15′N	104°51′W	2180–2190	1098	0[a]
14	Sierra de Cuale	Jalisco	20° 22′N	104°59′W	2410–2430	1115	0[a]

[a] Visited but not collected.

2.2. Trial design, statistical analysis and measurements

The seed collected from different populations in Mexico were used to establish 16 Camcore *P. herrerae* tests in four different trial types on members' land: (a) species trials, (b) species/provenance trials, (c) provenance/progeny trials and (d) small arboreta plantings (Table 2).

The Camcore provenance/progeny tests were established in a compact family design where open-pollinated families are nested within provenances in each block and replicated nine times. The species and species/provenance trials were generally established in randomized complete blocks with four replications and 36 trees (6 × 6 tree blocks). The arboreta plantings were groups of at least 100 trees planted at normal commercial spacing.

The Camcore provenance/progeny trials were assessed for survival, total height and diameter at breast height and forking at 3, 5, and 8 years. Forking was measured as 0 = no forks and 1 = forked. Volume for juvenile pine trees were calculated using a formula derived by Ladrach and Mazuera (1978):

$$V = 0.00003d^2h$$

The species trials PST038T, 039T and 040T was established on three sites by Sappi with the extra seedlings of *P. herrerae* from Camcore test 380701D and assessed for survival, height, and diameter, at 11 years of age (Nel and van der Hoef, 2006). Volume was calculated using the formula shown above. Stem and crown form was also assessed in these trials using a 1 (poor) to 3 (good) scale. The Camcore species/provenance trial established by CMPC Forestal at San Juan, Chile was analyzed at 10 years of age for height, diameter, and stem form (Schenone and Rothen, 2005). Provenance mean height and diameter results from this assessment were used to calculate mean individual tree volumes using the above formula. The other species/provenance trials and arboreta were assessed over

Table 2
Field trials of *P. herrerae* established by Camcore members over a 15-year period

Test	Company	Locations/Country	Provenances	*N*	Trial Type	Latitude	Altitude (m)	Rainfall (mm/year)	Measurements (years)
992101A	Arauco	Los Rios, Chile	3, 4	60	Species/prov 4 reps	37°30′S	150	1437	13
994101C	CMPC Forestry	San Juan, Chile	3, 4	265	Species/prov 4 reps	37°22′S	150	1375	8
992701A	Rigesa	Paredao, SC, Brazil	1, 3, 4	53	Species 4 reps	26°05′S	780	1645	8
382603C	Klabin	Imbauzinho, PR, Brazil	1, 5–7	153	Prov/progeny 9 reps	24°15′S	710	1490	3
382601A	Klabin	Anta Brava, PR, Brazil	1–4	2000	Prov/progeny 9 reps	24°07′S	750	1469	3, 5, and 8
381702B	Pisa	Jaguariava, PR, Brazil	1–4	1148	Prov/progeny 9 reps	24°24′S	790	1834	3
380701D	Sappi	Helvetia, South Africa	1–4	1495	Prov/progeny 5 reps	25°32′S	1700	770	3, 5, and 8
PST038T	Sappi	Glenthorpe, South Africa	Mix of 1–4 ex 38071D	136	Species/4 reps	25°47′S	962	835	11
PST039T	Sappi	Ndubazi, South Africa	Mix of 1–4 ex 38071D	136	Species/4 reps	25°49′S	1178	1031	11
PST040T	Sappi	Uitkyk, South Africa	Mix of 1–4 ex 38071D	136	Species/4 reps	25°21′S	1502	788	11
130232D	SCC	P. Negras, Colombia	9	500	Prov/progeny 9 reps	2°15′N	2490	2500	3, 5, and 8
131033B1	KLF	Tweefontein, South Africa	9	367	Prov/progeny 9 reps	25°04′S	1250	1053	3, 5, and 8
131032B1	KLF	Entabeni, South Africa	9	344	Prov/progeny 9 reps	23°00′S	1270	1810	3, 5, & 8
130732C1	Sappi	Mooiplaas, South Africa	9	390	Prov/progeny 9 reps	31°14′S	943	1200	3, 5, & 8
131832C3	Mondi	Ncula Est., South Africa	9	361	Prov/progeny 9 reps	30°12′S	1200	900	3, 8
381801CB	Mondi	Mt. Home, South Africa	1–4	512	Species/prov unreplicated	29°34′S	1181	1047	13

various ages and height and diameter from the oldest measurement were used to calculate volume in the same manner as described above (Table 2).

2.3. Statistical analysis

Single site analyses were conducted for two of the *P. herrerae* provenance/progeny trials in the first series of tests at 8 years of age using Proc GLM in SAS. These were 382601A and 380701D established by Klabin (Brazil) and Sappi (South Africa). Thirty-three open pollinated families were common to both trials. The linear model for the provenance/progeny tests was

$$y_{ijklm} = \mu_i + B_j + P_k + F(P)_{kl} + Bf(P)_{jkl} + e_{ijklm}$$

where y_{ijklm} is the phenotypic observation for the *ijklm*th tree, μ_i the mean in the *i*th test, B_{ij} the fixed effect of the *j*th block in the *i*th test, P_k the random effect of the *k*th provenance, $E[P_k] = 0$, $\text{var}[P_k] = \sigma^2_{\text{prov}}$, $F(P)_{kl}$ the random effect of the *l*th family in the *k*th provenance, $E[f(P)_{kl}] = 0$, $\text{var}[f(P)_{kl}] = \sigma^2_{F(P)}$, $Bf(P)_{jkl})$ the random effect of the *jkl*th row plot in the *i*th test, i.e., the interaction of the *j*th block and the *l*th family of the *k*th provenance, $E[r_{ijkl}] = 0$, $\text{var}[r_{ikl}] = \sigma^2_r$, e_{ijklm} the random error term associated with the *ijklm*th tree, $E[e_{ijklm}] = 0$, and $\text{var}\,E[e_{ijklm}] = \sigma^2_e$.

Variance components for height, diameter at breast height and forking were estimated using PROC VARCOMP METHOD = REML on SAS (SAS, 1989). Phenotypic variance within-provenance (σ^2_T) was estimated as

$$\sigma^2_T = \sigma^2_{F(P)} + \sigma^2_r + \sigma^2_e$$

Single site (or biased) heritability estimates within provenance (h^2_b) were estimated using the formula:

$$h^2_b = \frac{3\sigma^2_{F(P)}}{\sigma^2_T}$$

The covariance among open-pollinated families can often be higher than one-fourth of additive genetic variance due to inbreeding and/or a small number of effective male pollinators leading the to presence of some percentage of full-sibs with the OP family (Squillace, 1974; Dieters et al., 1995). Thus, a coefficient of three instead of four was multiplied by the family variance in the calculation of heritability. Combined analysis across sites was not conducted on these trials simply because the data represented only two locations and it was obvious by examining the provenance and family means that there were major rank changes among provenances and families across sites. Spearman rank (r_s) correlation for volume on family means was calculated to better quantify the degree of similarity between genetic entries at the two locations. Information from provenance/progeny trials with only 3-year data (382603C and 381702B) was used to mainly strengthen insights on early adaptability and survival.

An amended linear model was used for the analyses of the species and species/provenance trials since provenance and/or family components were not present. Significant differences among provenances in both the provenance/progeny trials and the species/provenance trials were determined using the Waller–Duncan k ratio test.

2.4. FloraMap™ climatic model

FloraMap™ climatic software developed by Jones and Gladkov (1999) at the Center for Tropical Agriculture (CIAT) became available to assist researchers to better match species to site several years after the last of the trials listed in Table 2 were planted. It is designed to use climatic data from known natural stands of a species to predict where additional populations should occur in the region but have not yet been identified. The FloraMap™ software can also be used to predict where a species could be planted as an exotic species based on a climate/site match probability. FloraMap™ was used in this study to determine if the 14 provenances of *P. herrerae* represented different climatic zones in Mexico. A cluster analysis using the unweighted paired group method (UPGMA) was run based on monthly average temperature, monthly diurnal temperature, and average monthly precipitation at the collection sites to detect climatic variation patterns. When significant clusters are found, the program allows a subset of accession points that represent each climatic group to serve as the database for searching for additional (similar) climatic zones. Prediction criteria for finding more *P. herrerae* populations in Mexico and possible planting locations elsewhere in South America or southern Africa were based on at least a 40% probability. Weights of 1.00 for precipitation and 1.22 for temperature were used in the computer runs. Temperature was weighted more heavily than annual precipitation because the apparent propensity of *P. herrerae* to suffer frost damage at some of the Camcore planting sites.

3. Results and discussion

3.1. Climatic ecotypes in Mexico

The FloraMap™ climatic program divided the 14 native *P. herrerae* populations into two broad climatic groups that generally corresponded to whether they occurred in the Sierra Madre Oriental, the northern mountain range in western Mexico, or the Sierra Madre del Sur, the southern mountain range in western Mexico (Fig. 1). Precipitation generally increases from north to south in this area with average annual rainfall amounts slightly below 1000 mm/year in the Sierra Madre Oriental and slightly above 1000 mm/year in the Sierra Madre del Sur where natural populations of *P. herrerae* occur. The main difference between the two climatic zones is that the northern temperate populations experience longer dry seasons (7 months versus 5.5 months) and colder nighttime temperatures during the winter (−7 °C versus approximately −1 °C to +10 °C) than do the more southern subtropical sources. The only exception to the temperate/subtropical division of climatic zones based on mountain ranges was the placement of the La Lobera, Sinaloa population from the Sierra Madre Oriental as an outlier in the Sierra Madre del Sur cluster (see Fig. 1). La Lobera is the population closest to the Pacific coast of those sampled in the Sierra Madre Oriental. It experiences more rainfall and warmer winter temperatures than the five other nearest populations in the same region, and therefore, grouped as an outlier with the subtropical populations that shared more similar climatic characteristics. We have found similar results in examining climatic zones for other pine species in Mexico; their position relative to the warm Pacific Ocean is as significant in the climatic groupings as latitude. The FloraMap™ program was run separately for each climatic cluster when predicting planting sites of *P. herrerae* in other areas of the world, that is, a temperate provenance group (excluding La Lobera) and subtropical provenance group (including La Lobera).

3.2. Adaptability

The field survival of *P. herrerae* as an exotic species appears to be directly related to the severity of the cold during the winter and the choice of provenances. *P. herrerae* trial 380701D established at Helvetia, South Africa that included the temperate sources of La Puerta Pino, Gordo El Llano and Guajolota from Durango, Mexico has maintained survival of >90% through 8 years. Its survival was equivalent to the *P. patula* control on a site where minimum nighttime temperatures occasionally drop to −7 °C. In contrast, *P. herrerae* trial 382603C planted at Imbauzinho, Brazil, was destroyed at 3 years of age by a sudden cold spell in 2002. The trial included sources from the subtropical climatic zone in Sierra Madre del Sur in Jalisco. Mean survival of the sources from Michoacan was 14% versus 77% for the *P. herrerae* control lot of La Puerta from the temperate climate zone in the Sierra Madre Occidental. The commercial *P. taeda* control had 94% survival. Two other *P. herrerae* trials with provenances from the subtropical climatic zone were also destroyed by frosts that were planted by Mondi Business Paper Ltd. in the Natal Midlands in South Africa in 2000 and 2002. Interestingly, one of the planting of the subtropical provenances that failed was at Mountain Home, Kwazulu-Natal, South Africa (latitude 29°34′S, altitude 1260 m) where the temperate sources of *P. herrerae* were successfully established 9 years earlier.

The temperate sources of *P. herrerae* also exhibited better than average drought tolerance than *P. patula*, *P. leiophylla* and *P. teocote* in the species trials 039T, and 040T on mid- to high-elevation sites and survived as well as *P. elliottii* in trial 038T on a low altitude site in South Africa (Table 3). Average annual rainfall in the region is approximately 900 mm. During the last 5-year period of tree growth in the trials, there have been 2 years when far lower than normal rainfall was experienced in the area. During 2003 and 2005 when the trees were 8 and 10 years old, only 55% (2003) and 73% (2005) of the normal mean annual rainfall was received. The general conclusion from the three species trials is that *P. herrerae* has drought tolerance similar to *P. greggii* var. *australis* and often superior to *P. patula*.

Often the degree of forking in pines can be indicative of whether a species is well adapted to a particular environment.

Table 3
Average survival percent from a 5-year drought in three species trials age 11 years established in South Africa

	PST038T Glenthorpe	PST039T Ndubazi	PST040T Uitkyk
Rainfall (mm)	835	1031	788
P. elliottii	96	74	
P. greggii var. greggii			91
P. greggii var. australis	87	88	90
P. herrerae	94	81	92
P. kesiya	94		
P. leiophylla	78	67	80
P. patula		67	84
P. teocote	80	76	84

Survival is expressed as standing number of live trees in the trials over the total number of tree planted (from Nel and van der Hoef, 2006).

At Helvetia, forking percents were 11% and 16% for *P. patula* and *P. herrerae*, respectively at 8 years of age. In a sister study that included the same genetic material established in Anta Brava, Brazil, the mean forking percents were 19% and 57% for *P. taeda* and *P. herrerae* (Table 4).

3.3. Growth and development

3.3.1. Temperate sources

P. herrerae trees initially grow slowly in height during their juvenile stage compared to *P. patula*, but exhibit impressive diameter increment. At the Helvetia, South Africa trial at 8 years of age, the shoot height/diameter ratio of *P. herrerae* was 6.5% less than *P. patula* (Table 4). In the species/provenance trials in southern Brazil (992701A) and central Chile (992101A and 994101C) the growth performance of *P. herrerae* made up of provenances from the temperate climatic zone in Mexico was not impressive. In Chile, *P. herrerae* ranked far below improved 1st generation *P. radiata*, and unimproved *P. patula* and *P. greggii* var. *australis* with *P. leiophylla* better than *P. herrerae* at San Juan and worse that it at Los Rios (Table 5). At Paredao in southern Brazil, *P. herrerae* ranked significantly below improved *P. taeda*, and unimproved *P. patula*, *P. greggii* and *P. leiophylla* (from central Mexico). In the three sister species trials in South Africa (038T, 039T and 040T), the growth of temperate *P. herrerae* provenances was significantly better than *P. elliottii* and *P. greggii* var *greggii*, was better to about equal to *P. teocote* and *P. leiophylla*, but greatly inferior to *P. greggii* var. *australis* and improved *P. patula*. In the unreplicated conservation bank planting at Mt. Home, South Africa (331801CB), 13-year-old *P. herrerae* exhibited the same productivity as *P. leiophylla* and *P. teocote* but was superior in volume to *P. greggii* var. *greggii* (based on results from the top three provenances of each species). In these species field trials aged 8–13 years and the provenance/progeny trials (38071D and 382601A) assessed in South Africa and Brazil at 8 years of age, the productivity of *P. herrerae* ranged from 3 to 24 m^3/ha/year (overbark) depending on the site and the provenance used (Table 5).

Table 4
Survival, productivity, and forking percent of *P. herrerae* provenances and local improved control lots at 8 years of age in South Africa and Brazil

Provenance/location	*N*	Survival (%)	Ht (m)	DBH (cm)	Vol (m^3)	Fork (%)
Helvetia, South Africa						
Pino Gordo	247	91	12.4	18.1	0.1275 b	15
El Llano	366	94	12.3	18.2	0.1265 b	15
Guajolate	516	96	11.7	17.6	0.1122 c	16
La Puerta	366	94	11.4	17.7	0.1120 c	15
PATULA control	27	90	15.0	19.8	0.1856 a	7
Overall	1495	94	11.9	17.8	0.1102	16
h^2			0.08 ± 0.06	0.14 ± 0.06		0.10 ± 0.04
Anta Brava, PR, Brazil						
Guajolota	476	89	9.5	15.6	0.0826 b	51
Pino Gordo	380	89	9.3	15.8	0.0822 bc	61
La Puerta	502	85	8.9	15.7	0.0787 c	54
El Llano	642	85	8.9	15.0	0.0696 d	61
TAEDA control	54	100	14.3	26.9	0.3201 a	19
Overall	2000	87	9.1	15.5	0.0774	57
h^2			0.46 ± 0.12	0.44 ± 0.11		0.06 ± 0.03

Narrow sense heritability (h^2) is also shown for selected traits. Means and h^2 estimates exclude control lots.

Admittedly, growth rate differences between *P. herrerae* and commercial species like *P. taeda* and *P. radiata* in southern Latin America are somewhat exaggerated because of varied levels of genetic improvement and/or plot configurations for the controls. Nonetheless, a general conclusion is that temperate sources of *P. herrerae* show little potential when grown in areas of high rainfall in southern Latin America. However, *P. herrerae* might serve as legitimate alternate species to *P. greggii* var. *greggii* and *P. patula* in the colder, drier regions of South Africa, like Helvetia where productivity is approximately 15 m^3/ha/year between ages 8 and 15 years.

3.3.2. Subtropical sources

The Juquila source was planted on tropical and subtropical sites better suited for *P. tecunumanii* than *P. patula*. It performed well, like the unimproved *P. tecunumanii* populations, when compared to more temperate and genetically improved *P. patula* in both Colombia and South Africa (Table 5). The Juquila population from the subtropical climatic zone seemed very productive compared to some of the *P. tecunumanii* populations in the trials. However, when the Juquila population was included in a best linear unbiased prediction (BLUP) analysis with all the other *P. tecunumanii* provenances in Camcore trials (25 populations and over 100,000 trees), it ranked about average in Colombia (+2%), and slightly below average in Brazil (−5%) and South Africa (−2%) (Camcore, unpublished results).

3.4. Genetic variation

Little information about provenance performance can be gained from these test series at this stage because the trials that have reached at least 8 years of age are those that include only four populations, all from the same general region in Durango in northern Mexico. The difference in volume between the best and the worst populations in sister provenance/progeny trials in South Africa and Brazil, were 12% and 15%, respectively (Table 3). Generally, we have found differences among provenances for

Table 5
Mean volume (overbark) for *unimproved P. herrerae* (H) vs. *improved* control lots of *P. patula* (P), *P. radiata* (R), *P. taeda* (T) and *P. elliottii* (E) expressed in m^3/ha/year

Test	Company	Locations/country	Provenances	*N*	Age (years)	H	P	R	T	E
992101A	Arauco	Los Rios, Chile	3, 4	60	13	6.3		28.1		
994101C	CMPC Forestry	San Juan, Chile	3, 4	265	8	2.6		9.7		
992701A	Rigesa	Paredao, SC, Brazil	1, 3, 4	53	8	10.2			29.5	
382601A	Klabin	Anta Brava, PR, Brazil	1–4	2000	8	9.4			44.4	
38071D	Sappi	Helvetia, South Africa	1–4	1495	8	15.4	21.2			
130232D	SCC	P. Negras, Colombia	9	500	8	23.6	27.9			
131033B1	KLF	Tweefontein, South Africa	9	367	8	10.5	11.6			
131032B1	KLF	Entabeni, South Africa	9	344	8	13.0	12.5			
130732C1	Sappi	Mooiplas, South Africa	9	390	9	15.2	15.6			
131832C3	Mondi	Ncula Est., South Africa	9	361	9	14.5	15.7			
PST038T	Sappi	Glenthorpe, South Africa	Bulk mix of 1–4	136	11	16.5				13.0
PST039T	Sappi	Ndubazi, South Africa	Bulk mix of 1–4	136	11	9.5	13.4			8.3
PST040T	Sappi	Uitkyk	Bulk mix of 1–4	136	11	11.1	16.1			6.2

several of the Mexican pine species to be on the order of 25–30% when the entire geographic range is sampled (Hodge and Dvorak, 1999, 2001). We expect *P. herrerae* to be no different in this respect when the entire range of populations is analyzed.

Low Spearman rank correlation ($r_s = 0.12$, $P > 0.54$) was found between the 33 common open-pollinated families in the two trials planted at Anta Brava, Brazil and Helvetia, South Africa. Within-provenance h^2 for height, diameter, and forking are shown in Table 4. Values at Helvetia, a cool and dry site ranged from 0.08 to 0.14, well within the range found for other tropical and subtropical pines (Table 4). Within-provenance h^2 values at Anta Brava, Brazil, a warm and wet location, were much higher for the growth traits than at Helvetia, South Africa ranging from 0.44 to 0.46. Difference in family mean performance between the best and the worst families for growth traits was three times larger at Anita Brava, Brazil than at Helvetia, South Africa. Higher h^2 values in warm climates in Brazil compared to cooler climates in South Africa has been found in other studies of tropical pines (Gapare et al., 2001) and probably are the result of faster tree growth on more uniform sites.

The stem form and branch diameter of *P. herrerae* relative to commercial species varied across site. In South Africa, the general trend was for populations from temperate areas in Mexico to have straighter stem form and lighter crowns at the mid- (1150 m) and high elevation (1500 m) sites than did *P. elliottii*, *P. greggii* var. *greggii*, *P. greggii* var. *australis*, *P. leiophylla* and *P. teocote* (Nel and van der Hoef, 2006). The only species with better stem and crown form was improved *P. patula*. The subtropical population of Juquila had no better stem and branch form than *P. tecunumanii* in South Africa and Colombia, which in turn exhibited more form defects than *P. patula*. In Chile, *P. herrerae* exhibited better stem form and smaller branch diameters than *P. radiata* but not as good as *P. patula* (Schenone and Rothen, 2005). The apparent superiority of *P. herrerae* in stem form might simply be a function of the smaller trees receiving higher straightness scores than the larger radiata pine trees. In Brazil, temperate populations of *P. herrerae* were only slightly more crooked than improved *P. taeda* and *P. elliottii*, but had smaller branch diameters than *P. taeda*. Generally, the stem and branch form of unimproved *P. herrerae* was found to be very acceptable across most sites, with populations from temperate areas exhibiting higher quality form than the subtropical Juquila source.

3.5. Climatic ecotypes in Mexico

FloraMap™ predicts that *P. herrerae* should be relatively common in the Great Cross Range or Volcanic Axis, the mountain range that links the east and west coast of Mexico (see Fig. 1). Eguiluz-Piedra (1985) describes this range as one of the major migration routes of pines from one side of the country to the other. With the exception of western Mexico where the Volcanic Axis and the Sierra Madre del Sur intersect, *P. herrerae* has not been identified in eastern areas of the Great Cross Range. We have found FloraMap™ useful when using to predict species occurrence for other MesoAmerican pines like *P. caribaea* (Dvorak et al., 2005).

FloraMap™ indicates that trees from the northern provenances could be planted in the Cape region and eastern highlands of South Africa, the Pampa and Mendoza regions of Argentina, and very limited areas of Santa Catarina, Brazil. Some of the sites predicted to be the closest climatic matches were those where Camcore trials were located; Tweefontein, Mooiplaas, Uitkyk and Helvetia, South Africa. The Paraedo, Brazil test site is located 30 km from where FloraMap™ predicted an important climatic match.

FloraMap™ indicated that the populations of *P. herrerae* in the subtropical climatic zone could be established in the eastern highlands of South Africa and Zimbabwe, the states of Santa Catarina and Parana, Brazil and most of Uruguay and the coastal areas west of Buenos Aires, Argentina. The FloraMap™ predictions for the subtropical cluster included the Camcore planting sites of Ncula, Tweefontein and Helvetia in South Africa, and Jaguariava, and Paredao in Brazil. In our opinion Ncula, Tweefontein and Jaguariava are well suited to the subtropical populations, but Helvetia and Paredao are better sites for the more temperate populations because of the occurrence of occasionally severe frosts. As predicted by FloraMap™, Juquila did well at both Ncula and Tweefontein. FloraMap™ predicted that Chile would not be a good location for *P. herrerae*, which it was not, but it did not predict that the highlands of Colombia would be a reasonably good location for subtropical sources like Juquila, which it is. Both field experience and FloraMap™ results now show that we originally overestimated the cold hardiness of sources of *P. herrerae* from the subtropical climatic zone.

Based on the results of these studies, it appears that the temperate sources of *P. herrerae* are best suited for climates with a well-defined dry season and occupy an ecological niche between where the more cold hardy *P. patula* and *P. greggii* var. *australis* are planted commercially in southern Africa and where the more subtropical pines like *P. tecunumanii* are best suited. The species' generally good stem form is offset by slower than average productivity, at least in the first 10 years after planting. The subtropical sources appear to fit into climate zones used for high-elevation populations of *P. tecunumanii* in Colombia, South Africa and Brazil. Growing the straight-stemmed *P. herrerae* as alternative to *P. greggii* trees for longer rotation solid wood products in southern Africa might still hold potential on drought-prone sites. Even though *P. herrerae* showed better resistance to *Sphaeropsis sapinea* in Brazil than *P. patula* and *P. greggii* (Dvorak et al., 2000), it was as susceptible to the Pitch Canker Fungus (*Fusarium circinatum*) as the two closed-cone pines in a seedling screening study in the US (Hodge and Dvorak, 2000).

Efforts are now underway by Camcore to more intensively study the wood quality of *P. herrerae*. Wide hybrid crosses with both varieties of *P. greggii, P. elliottii* and *P. taeda* are being attempted in South Africa to determine if progeny express heterosis. Low level breeding and continued *ex situ* conservation efforts are planned for the species.

The genetic resources of *P. herrerae* are threatened in Mexico, especially the subtropical populations. *P. herrerae* trees that reached heights of 55 m at Dos Aguas, Michoacán have all been harvested. The Palo Blanco source has been nearly destroyed by agricultural development and the Juquila source is threatened because of its easy road access. Further explorations for new populations of the species in the Great Cross Range and the Sierra Madre del Sur would be worthwhile, but poor seed yields even in the best fruiting years, make such efforts costly.

Acknowledgements

We would like to thank both Jeff Donahue and José Romero, formerly of Camcore, with their assistance in seed collection. We would also like to thank Mexican foresters, Martin Arizmendi and Manuel Mapula, for their help in explorations and seed collections of *P. herrerae* in Mexico. The assistance of Camcore members Klabin, Rigesa and Pisa (Brazil), Smurfit Colombia (Colombia), Komatiland Forests, Mondi Business Paper Ltd., Sappi (South Africa), Arauco and CMPC Forestry (Chile) in the establishment and measurement of trials was much appreciated. We would especially like to thank Johan Vermaak (Mondi Business Paper Ltd.) and André van der Hoef (Sappi Research) for making additional measurements in field trials to supplement information in the Camcore database for the purpose of manuscript development. The authors would also like to thank Willi Woodbridge (Camcore) for development of the *P. herrerae* range map.

References

Dieters, M.J., White, T.L., Hodge, G.R., 1995. Genetic parameter estimates for volume from full-sib tests of slash pine (*Pinus elliottii*). Can. J. For. Res. 25, 1397–1408.

Dvorak, W.S., Hamrick, J.L., Gutiérrez, E.A., 2005. The origin of Caribbean Pine in the season swamps of the Yucatán. Int. J. Plant Sci. 166 (6), 985–994.

Dvorak, W.S., Kietzka, J.E., Stanger, T.K., Mapula, M., 2000. *Pinus herrerae*. In: Conservation & Testing of Tropical and Subtropical Forest Tree Species by the Camcore Cooperative, College of Natural Resources, North Carolina State University, Raleigh, NC, USA, pp. 86–95.

Dvorak, W.S., Jordan, A.P., Romero, J.L., Hodge, G.R., Furman, B.J., 2001. Quantifying the geographic range of *Pinus patula* var. *longipedunculata* in southern Mexico using morphologic and RAPD marker data. S. Afr. Forest. J. 192, 19–30.

Eguiluz-Piedra, T., 1985. Origin y evolución del genero *Pinus*. Dasanomia Mexicana 3 (6), 5–31.

Eguiluz-Piedra, T., 1978. Ensayo de integracion de los conocimientos sobre el genero *Pinus* en Mexico. M.S. Thesis. Universidad Autonoma Chapingo, p. 623.

Farjon, A., Styles, B.T., 1997. *Pinus* (Pinaceae). Flora Neotropica Monograph 75. Organization for Flora Neotropica & The New York Botanical Garden, p. 291.

Gapare, W.J., Hodge, G.R., Dvorak, W.S., 2001. Genetic parameters and provenance var of *Pinus maximinoi* in Brazil, Colombia, and South Africa. For. Genet. 8 (2), 159–170.

Hodge, G.R., Dvorak, W.S., 2000. Differential responses of Central American and Mexican pines species and *Pinus radiata* to infection by the pitch canker fungus. N. For. 19, 241–258.

Hodge, G.R., Dvorak, W.S., 2001. Genetic parameters and provenance variation of *Pinus caribaea* var. *hondurensis* in 48 international trials. Can. J. For. Res. 31, 496–511.

Hodge, G.R., Dvorak, W.S., 1999. Genetic parameters and provenance variation of *Pinus tecunumanii* in 78 international trials. For. Genet. 6 (3), 157–180.

Jones, P.G., Gladkov, A., 1999. FloraMap^{TM}, Version 1. A Computer Tool for predicting the Distribution of Plants and Other Organisms in the Wild. Centro Internacional de Agricultura Tropical (CIAT), Cali, Colombia.

Ladrach, W.E., Mazuera, H., 1978. Growth and development of the Chupillauta arboretum at 7 years and the Mexican pines in San José at 6.3 years. Cartón de Colombia Research Report 34, p. 4.

Martínez, M., 1945. Las Pinaceas Mexicanas, vol. 1. Instituto de Biologia, Mexico City, Mexico, p. 345.

Nel, A., van der Hoef, A., 2006. Eleven year results from a 6-species trial series planted on three sites in Mpumalanga. Sappi Research Pine Breeding Report 28/06. Sappi Forests Research, Howick, South Africa, p. 6.

Perry Jr., J.P., 1991. The Pines of Mexico and Central America. Timber Press Inc., p. 231.

SAS, 1989, SAS Institute Inc., SAS/STAT User's Guide, Version 6, 4th ed., vol. 2, Cary, NC, 846 pp.

Schenone, R., Rothen, B., 2005, Ensayo de especies y procedencias Camcore, PC9280 San Juan. Internal Report, CMPC Forestal, p. 19.

Squillace, A.E., 1974. Average genetic correlations among offspring from open-pollinated forest trees. Silv. Genet. 23, 149–156.