Performance of Pinus elliottii, Pinus caribaea, *their F_1, F_2 and backcross hybrids and* Pinus taeda *to 10 years in the Mesopotamia region, Argentina*

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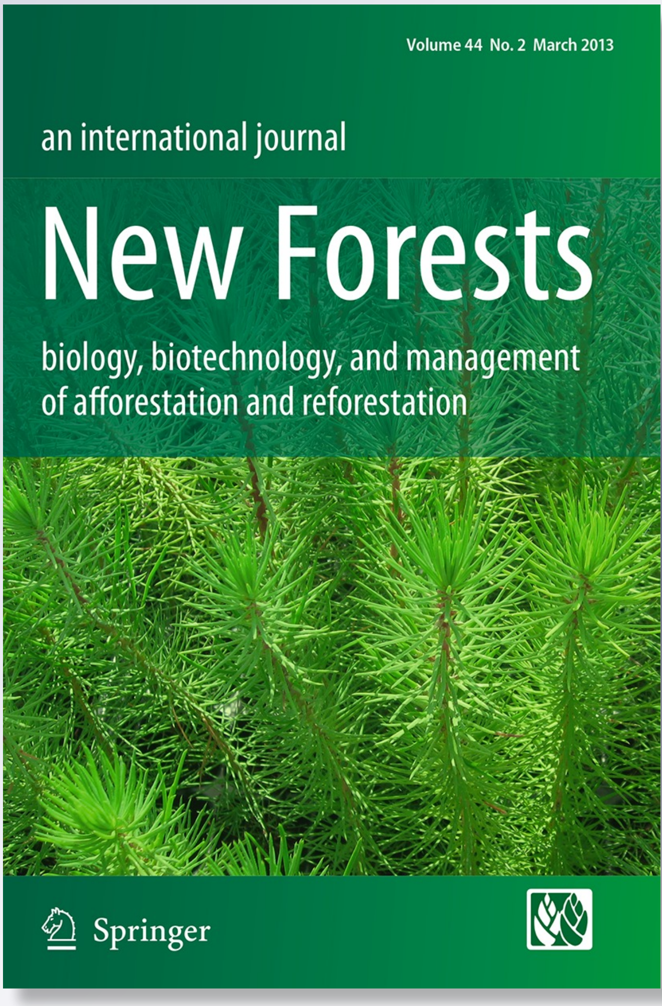

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Performance of *Pinus elliottii*, *Pinus caribaea*, their F_1, F_2 and backcross hybrids and *Pinus taeda* to 10 years in the Mesopotamia region, Argentina

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Abstract Performances of *Pinus* taxa were studied to 10 years of age in two trials in each of Misiones and Entre Ríos provinces across the Mesopotamia region of Argentina. Taxa comprised 22 populations from sources in Argentina, Australia, Brazil and Zimbabwe including *Pinus elliottii* var. *elliottii* (PEE), *Pinus caribaea* var. *hondurensis* (PCH), their four, inter-specific hybrids (F_1, F_2 and backcrosses from F_1 to PCH and to PEE—all as broadly based bulks); other PEE and *Pinus taeda* (PT) comprised narrower or unspecified bulks. Variable numbers of taxa were missing at each site. Mean survival across sites at age 10 years ranged 53.2–91.3% averaging 74.2%. Analysis of variance of plot means indicated population effect was statistically significant ($p < 0.05$) for all or most growth and quality traits at all sites. However, significant differences from the nominated check seedlot at the Entre Ríos sites (PEE, Australia) were extremely rare, while quite common at the northern, Misiones sites (check seedlot a PT population). In the Misiones trials, F_1, F_2 and both backcross hybrids showed better stem straightness than PEE and PT from Argentina, generally with statistically significant differences ($p < 0.05$). PT showed lowest forking scores (desirable). Taxon × environment interaction was statistically significant ($p < 0.01$) for growth traits only ($p > 0.05$). However, this interaction contributed an average of only 34.1% of the taxon variance suggesting a lack of practical importance. Taxa most suitable for deployment in the Mesopotamia region, Argentina are suggested.

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Introduction

In Argentina, more than 60% of the areas planted with fast-growing forest trees are pines with around 680,000 hectares established. More than 90% of this estate of pines is located in the provinces of Misiones and Corrientes, within the Mesopotamia region. In this area, *Pinus taeda* L. (PT, 60%) and *Pinus elliottii* var. *elliottii* Engelm (PEE, 20%) are the preferred species while *Pinus caribaea* var. *hondurensis* (Sénécl) Barrett et Golfari (PCH), *Pinus caribaea* var. *caribaea* (Sénécl) Barrett et Golfari (PCC) and *Pinus caribaea* var. *bahamensis* (Sénécl) Barrett et Golfari (PCB) are planted to a minor extent. In recent years, the area planted with the F_1 and F_2 hybrids between PEE and PCH has increased due to their often superior performance in field tests, reaching about 21,000 hectares.

Early introductions of the F_1 hybrid of PEE and PCH (referred to here as F_1) from the then Queensland Forestry Research Institute (QFRI) have clearly demonstrated marked superiority of the hybrids to valid controls in many tropical and subtropical countries (Nikles 1995, 1996, 2000), e.g. excellent growth and quality properties in Zimbabwe (Gwaze 1999), Florida, USA (Rockwood and Nikles 2000), China (Zheng 2000) as well as in Queensland, Australia (e.g. Powell and Nikles 1996; Dieters and Brawner 2007). This hybrid superiority appears to be derived from a complementary recombination of desirable traits from the two parental species: growth rate and good branching from PCH combined with wind-firmness, adaptability to wet sites, high wood-density and stem straightness of PEE (Dieters et al. 1995; Dieters and Brawner 2007). Powell and Nikles (1996) showed that the F_1 hybrid has displayed a consistently better straightness and wind-firmness compared to the PCH parent species on swampy and some well-drained sites. Based on studies of wood basic density of PEE, PCH and F_1 hybrid in subtropical Queensland, the basic density of F_1 is usually intermediate or equal to that of PEE depending on site and location (Rockwood et al. 1991). Harding and Copley (2000) and Harding et al. (2000) reviewed and reported studies of wood properties and sawing characteristics of PEE, PCH and F_1 hybrids grown in south east Queensland at various ages from 10 to 32 years. They concluded that, in practical terms, the hybrid had better wood properties than the parental species. A full report of wood studies on PEE, PCH and the hybrid is given in Harding (2008). Kain (2003) reported a study of variation in growth and wood properties in two progeny trials (a subset of the four trials of Powell and Nikles 1996) in south east Queensland at 11 years of age based on four North Carolina II mating designs: 6 × 6-parent designs in PEE and PCH, a 12 × 12-parent design using the same set of PEE and PCH parents giving 144 F_1 hybrid families, and a 6 × 6-parent design of unrelated F_1 parents giving 36 F_2 hybrid families. The PEE population exhibited relatively low stem volume and high wood density, while PCH and PEE × PCH F_1 showed the opposite. The F_1 and F_2 hybrids had similar population mean values and within-population variation in most traits.

In Queensland, establishment of plantations of introduced *Pinus* species in the south-eastern coastal lowlands began in the 1930s using PEE and PT; the latter species proved less adaptable and was phased out there in the early 1950s (though continued in cooler, sub-coastal areas). As plantations were extended to other regions there was dynamic development and deployment of various *Pinus* taxa in the State based on results of taxa-region and taxa-site studies. In the past, PEE was deployed extensively in the south-east

Queensland region especially (i.e., from 25°45′ to 26°30′S), but is being replaced following harvesting by hybrids: at first in the 1980s by F_2 hybrid seedlings and F_1 hybrid, mainly as bulked families, then selected families, later (from 2000) by selected clones, and more recently by F_2 hybrid seedlings of superior families. In the central Queensland region (i.e., from 22°34′ to 22°53′S) the most important taxa are PCH in the moist and dry sites, and F_1 in the poorly-drained sites. The main taxon currently planted in the coastal north Queensland region (i.e., from 16°42′ to 18°46′S) is PCH. The total areas of all hybrids, PCH and PEE established in Queensland at June 2010 are 69.381, 49.935 and 16.340 ha respectively, the relatively small area of PEE remaining currently reflecting its phasing out from a peak of 67,660 ha in 1984 in favour of PCH and hybrids.

The first F_1 hybrid pine trial in Argentina was planted in 1981 on a well-drained site of the north-eastern province of Corrientes, as part of a series of collaborative trials sponsored by QFRI (Barrett et al. 1991). This trial included two seedlots of F_1 hybrid, one of PEE (ex clonal seed orchard) all three from QFRI; PEE from a local commercial bulk seedlot of Concordia, Entre Ríos province; and the three varieties of Caribbean pines: PCH, PCC and PCB from commercial bulk seedlots of Agudos, San Pablo, Brazil. The results at age 9 years showed that F_1 hybrid had higher diameter than the local and QFRI PEE seed lots (48.6 and 37.1% respectively). They also observed that the stem straightness of the F_1 hybrid was superior to all 5 populations of the pure species tested. Schenone and Pezzutti (2003), in two progeny trials of F_2 hybrid pines of PEE × PCH planted in both well and poorly-drained sites of the north-eastern province of Corrientes, showed higher values of growth and survival for the F_2 progenies than the check seedlots of PEE from Saint Johns, USA and PT from a seed orchard of 1.5 generation of Marion USA. At both sites, all the F_2 progenies tested were statistically superior to the check seedlots of PEE. In the well-drained soil, the average of the top-ranked three of twenty F_2 progenies outperformed the PEE and PT genotypes by 71.5 and 9.7%, respectively. In the poorly-drained site, the average of the best seven F_2 progenies outranked the PEE and the PT check by 62.7 and 10.3%, respectively. Bunse (2003), at two contrasting sites in the north of Corrientes province, showed that the F_1 progenies from QFRI outperformed the pure check seedlots of PEE from Saint John, USA and PT from a clonal seed orchard of 1.5 generation of Marion, USA. The F_1 families consistently demonstrated an advantage in individual tree volume after 6 years over both pure species (i.e., PEE and PT) on the sandy soil with low fertility and groundwater depth from 1 to 1.5 m (61 and 92%, respectively) and the red, deep, and well drained productive soils (17 and 73%, respectively). On both sites the F_1 hybrid from QFRI showed significantly better stem straightness than the check seedlots of PEE and PT.

Given the adaptability to site, good growth rates and high-quality silvicultural characteristics and wood properties demonstrated locally or elsewhere, F_1 and F_2 hybrids of PEE and PCH have become the favoured taxa for planting in the Mesopotamia region, especially on poor sites such as very dry or wet sites. Consequently in 1995 the Instituto Nacional de Tecnología Agropecuaria (INTA) in collaboration with the then QFRI, Australia and private firms in Argentina and Brazil joined other organizations in researching and developing genetic resources of hybrid pines in Zimbabwe and Brazil and obtained PEE, PCH, F_1 and F_2 hybrids, the backcrosses PEE × F_1 and F_1 × PCH, and PT populations. This new genetic material comprised 22 populations produced in various ways, including open- and controlled- pollinated seeds from seed production areas, seedling and clonal seed orchards. From April 2006 to September 2007, four productivity trials with this genetic material were established across the Entre Ríos and Misiones provinces in the Mesopotamia region (subtropical) of Argentina. The objective of these trials was to evaluate the yield and stability of the 22 populations in this region. In an early assessment of these taxa

(54 months), in the well-drained and productive forest soil site at Puerto Esperanza, Misiones province, the F_1 outperformed the improved local and QFRI PEE (74.3 and 55.5%, respectively), PCH (38.0%) and PT (10.5%) in volume (Pahr et al. 2002). These preliminary results showed that the F_1 hybrid, and derivatives such as the F_2 and the backcrosses, can substantially increase pine productivity in well-drained and productive forest areas of Misiones province, where PT is commonly planted.

The goal of the present research is to study the performance for growth traits, stem straightness (STR), stem forking (FORK), survival (SURV), conical volume per hectare (VOL) and stand conical volume (SVOL) at age 10 years of 22 *Pinus* taxa planted on four sites across the Mesopotamia region of Argentina. The taxa involved PT, PEE, PCC, PCH, F_1 and F_2 hybrids, and F_1 × PCH and PEE × F_1 backcrosses. Additionally, this information will be used to discuss the growth potential of PEE × PCH, F_1 and F_2 hybrids pine and their backcrosses in the Mesopotamia region, Argentina and to compare the performance of these hybrids with improved PEE and PT taxa from different countries across a range of site types.

Materials and methods

Genetic material

In 1995 open- and controlled- pollinated seeds of *Pinus* taxa (PCC, PCH, PEE, four inter-specific populations of the latter two species and PT) were obtained from seed production areas (SPAs), seedling and clonal seed orchards (SSO and CSO, respectively) of INTA (Argentina), Alto Paraná S.A. (Argentina), Paul Forestal S.R.L. (Argentina), Duraflora S.A. (Brazil), the then QFRI (Australia), Instituto de Pesquisas e Estudos Florestais (IPEF, Brazil), and Forest Research Centre (FRC, Zimbabwe). The 6 seedlots from Australia are part of a series of collaborative trials between QFRI and INTA in Argentina and comprised bulked seed subsets of the same 6 taxa as planted in the 4-location study of Powell and Nikles (1996). The composition and origins of the 22 *Pinus* taxa included in the study are given in Table 1. Not all seed lots were represented at all sites. Each test contained at establishment from 14 to 18 taxa (Table 1).

Trial description and data assessment

A total of four productivity trials of *Pinus* taxa were established by INTA in four locations in the provinces of Misiones and Entre Ríos in the Mesopotamia region of Argentina and measured for this study. The general locations of the trial sites are shown in Fig. 1. The sites were identified as Concordia dry soil (Concordia dry), Concordia wet soil (Concordia wet), Cerro Azul and Puerto Esperanza (Pto. Esperanza). The tests were planted between April 1996 and September 1997. The field experimental design was the same at all locations, a randomized complete block design with 4 replicates. In each trial, each taxon was planted in square measure-plots of 9 trees (3 × 3), that were surrounded by a two-tree isolation of the same taxon (i.e., gross plots of 5 × 5 = 25 tree). That is, two buffer rows surrounded 9-tree interior measurement plots. At all sites the spacing was 3 m × 3 m. Ant attack and weed competition during early establishment caused a very low survival rate in block 2 at the Concordia dry site. Consequently, the data from block 2 at this site were eliminated and results presented in this study are based on only three replicates. No artificial thinning had been undertaken up to the time of the 10-year measures and assessments. Additional details of the four trials and the site characteristics are summarized in Table 2.

Table 1 Details seed suppliers, methods of seed production and composition of the taxa seedlots evaluated by site

Code	Taxon[a]	Supplier[b]	Method of seed production[c]	Original and/or Argentinean sources of Taxon	Number of families	Sites[d]			
						1	2	3	4
1	PT	Alto Paraná S.A.	OP from CSO	Marion, Florida (USA)/Libertad, Misiones (Argentina)	na	x	x	x	x
2	PEE	INTA	OP from CSO	Cuartel Río Victoria, San Vicente, Misiones (Argentina)	2	x	x	x	x
3	PEE	INTA	OP of high-gum-yield from SSO	Concordia, Entre Ríos (Argentina)	7	x	x	x	x
4	PT	INTA	OP from SPA	Nassau, Florida (USA)/Concordia, Entre Ríos (Argentina)	na	x	x	x	x
6	PEE	INTA	OP from CSO	Cerro Azul, Misiones (Argentina)	na	x	x	x	x
22	PT	INTA	OP from CSO	Cerro Azul, Misiones (Argentina)				x	
23	PT	A. Larguía	OP from SPA	Livingstone Parish, La (USA)/Mato Quemado, Misiones (Argentina)	na			x	
7	$BC_{(H)}$	QFRI	CP families	(Queensland, Australia)	16	x	x	x	x
8	$BC_{(E)}$	QFRI	ditto	ditto	20	x	x	x	x
9	F2	QFRI	ditto	ditto	19	x	x	x	x
10	F1	QFRI	ditto	ditto	19	x	x	x	x
11	PEE	QFRI	ditto	ditto	16	x	x	x	x
12	PCH	QFRI	ditto	ditto	30	x	x	x	x
13	PEE	Duraflora S.A.	OP from CSO	Agudos, Sao Paulo (Brazil)	na			x	
14	PCH	Duraflora S.A.	OP from SPA	Agudos, Sao Paulo and Esplanada, Bahia (Brazil)	na	0		x	
15	PCH	Duraflora S.A	OP from CSO	Agudos, Sao Paulo and Esplanada, Bahia (Brazil)	na	0		x	
16	PCC	Duraflora S.A	OP from SPA	Agudos, Sao Paulo (Brazil)	na	0		x	
29	PT	IPEF	OP from CSO	Anhembi, Sao Paulo (Brazil)	na		x		x
17	PT	Paul Forestal SRL	OP from 2.0 CSO	Georgia (USA).	na	x		x	
21	PEE	Paul Forestal SRL	OP from 1.5 CSO	Saint Johns, Florida (USA)	na	x			

Table 1 continued

Code	Taxon[a]	Supplier[b]	Method of seed production[c]	Original and/or Argentinean sources of Taxon	Number of families	Sites[d]			
						1	2	3	4
30	PT	FRC	OP from CSO	(Zimbabwe)	6		x		x
31	PEE	FRC	OP from CSO	(Zimbabwe)	6		x		x

[a] PEE = *Pinus elliottii* var. *elliottii*; PT = *Pinus taeda*; PCH = *Pinus caribaea* var. *hondurensis*; PCC = *Pinus caribaea* var. *caribaea*; F_1 = PEE × PCH; F_2 = (PEE × PCH) × (PEE × PCH); $BC_{(H)}$ = F_1 × PCH; $BC_{(E)}$ = PEE × F_1

[b] *INTA* Instituto Nacional de Tecnología Agropecuaria (Argentina), *QFRI* Queensland Forestry Research Institute (Australia), *IPEF* Instituto de Pesquisas e Estudos Florestais (Brazil), *FRC* Forest Research Centre (Zimbabwe)

[c] *OP* open-pollinated, *CP* controlled-pollinated, *CSO* clonal seed orchard; *SSO* seedling seed orchard; *SPA* seed production area

[d] 1 = Concordia dry, 2 = Concordia wet, 3 = Cerro Azul, and 4 = Pto. Esperanza; x = Taxon originally included in the trials; 0 = Taxon not measured

na = data not available

Fig. 1 Approximate location of the four trials in Argentina

All surviving trees in the measure plots were assessed at 10 years after planting for growth traits, stem straightness, stem forking, and survival, and tree conical volume and stand conical volume were calculated for each of the four trials. Over bark diameter at breast height (1.3 m, DBH) were measured in centimeters (cm) and total height (TH) was measured in meters (m). The tree stem straightness (STR) was measured in cm for each single-stemmed (i.e. not forking) tree. Assessment of STR consisted of measuring the maximum deviation from the stem and a virtual vertical line passing through the base of the stem to 3 m high, thus lower values indicate better straightness. The crown form of each tree was scored as forking (FORK) on a scale of 1–4 according to its position in the stem: 1 = Nil, 2 = High, 3 = Medium, and 4 = Low. Lowest values for means of STR and FORK are the most desired. Survival (SURV) was determined based on the 10-year assessment in each measurement plot for each site. Individual-tree conical volume over bark (CVOL) in m^3 was calculated using the formula

$$CVOL = 1/3 \times \pi/4 \times DBH^2 \times TH$$

where DBH^2 is the diameter over bark at breast height squared (m^2) and TH the total height (m). Then, this formula was used to estimate the conical volume per hectare (VOL = CVOL × Trees ha^{-1}; m^3 ha^{-1}), assuming 3 m × 3 m spacing (i.e., 1111 tree ha^{-1}). Stand

Table 2 Details of the locations and characteristics of trial sites, the establishment and the management for each of the four trials planted in Argentina from 1996 to 1997

Site characteristics	Concordia dry	Concordia wet	Cerro Azul	Pto. Esperanza
Locality	Concordia	Concordia	Cerro Azul	Pto. Esperanza
Province	Entre Ríos	Entre Ríos	Misiones	Misiones
Latitude (South)	31°21′	31°22′	27°39′	26°10′
Longitude (West)	58°06′	58°06′	55°26′	54°35′
Altitude (m)	47,5	47,5	283	200
Soil	Entisol (Dry)	Entisol (Wet)	Ultisol	Ultisol
Av. annual rainfall (mm)	1,275	1,275	1,950	2,000
Av. annual temp. (°C)	18.5	18.5	20.8	22
Abs. min. temp. (°C)	−5.1	−5.1	−3.9	−3.0
Abs. max. temp. (°C)	41.3	41.3	41.4	39
Frost events	Early frost	Late frost	–	Late frost[b]
	−5.1°	−4.6° C		
	Winter 1996	Winter 1999		Winter 2000
Planting date	April 1996	Sept 1997	Sept 1996	May 1997
Measurement date	Dec 2006	Dec 2006	Oct 2006	Sept 2006
Design[a]	RCB	RCB	RCB	RCB
Number of seedlots	16	14	18	14
Number of replicates	4	4	4	4
Number of trees per plot	25	25	25	25
Maximum number of trees measured per plot	9	9	9	9
Spacing (m × m)	3 × 3	3 × 3	3 × 3	3 × 3
Survival at 10 years (%)	53.24	67.86	84.41	91.27

[a] *RCB* randomized complete block; [b]The absolute minimum temperature was not recorded

conical volume (SVOL) was also analyzed because it accounts for differences in adaptation that are reflected by both survival and growth. SVOL was calculated by multiplying the conical volume per hectare (VOL) by the survival of the 9-tree plots (SVOL = VOL × SURV, m^3 ha^{-1}).

Statistical analyses

Analyses of variance were performed on all traits measured or assessed or calculated for each site using the GLM procedure in SAS (SAS Institute Inc. 2002). All analyses were conducted on a plot means basis (i.e., the average of all trees from a given taxon within each replication). Plot means were considered appropriate for analyses because their use enabled improved normality of data for all traits, as mentioned in Jansson and Danell (1993), and this made it possible to estimate the volume per hectare. However, data for survival rate (SURV) were non-normally distributed. This problem was likely due to low or high survival in one replicate relative to the others within a site. Survival rate from plot means could not be normalised by natural logarithmic and arccosine transformation and were thus excluded from the analyses of variance.

To estimate least-square means for taxa, and to test the significance of taxa differences, the following linear model was used for each individual site:

$$y_{jk} = \mu + B_j + T_k + e_{jk} \qquad ([1])$$

where y_{ij} is the plot means of each dependent variable of the kth taxon in the jth replicate, μ is the overall mean, B_j is the fixed effect of the jth replicate, T_k is the fixed effect of the kth taxon and e_{jk} is the random residual error term.

Testing the statistical significance of the differences between any taxon and the nominated check seedlot was undertaken with the Dunnett Test for individual site analysis. At pairs of sites the check seedlot was different. The PEE from QFRI (taxon 11) was chosen as the check seedlot at the Concordia dry and wet trials based on the edaphic conditions of these sites (wet and dry and less productive forest soil) and for its known genetic linkage with the F_1 and F_2 QFRI hybrids. Meanwhile, the PT from a CSO of Libertad, Misiones (taxon 1) was used as the check seedlot at Cerro Azul and Pto. Esperanza because of its geographical origin (i.e. Marion, Florida, USA) and its good performance where it is widely planted in the dark red, clay, deep, well-drained and productive forest soils of Misiones province. The taxon differences between the F_1 and F_2 and the average of the PEE and PT taxa across all sites were tested using the "ESTIMATE" statement of the GLM procedure in SAS (2002).

To examine the significance of taxon × environment (T × E) interaction effect, the following linear model was fitted for the across-site analyses:

$$y_{ijk} = S_i + B_{j(i)} + T_k + ST_{ik} + e_{ijk} \qquad ([2])$$

where y_{ijk} is the plot means of each dependent variable of the kth taxon in the jth replicate at the ith site, S_j is the fixed effect of the ith site, $B_{j(i)}$ is the fixed effect for the jth replicate within the ith site, T_k is the fixed effect of the kth taxon, ST_{ik} is the fixed interaction between the ith site and kth taxon and e_{ijk} is the random residual error term. Prior to across-site analyses, homogeneity of residual variances was checked. The residual variances are relatively homogeneous in the trials evaluated for all the variable analyzed (data not shown). The range in residual variance for forking was greater than for other traits, but smaller than a ten times range considered acceptable by Patterson and Silvey (1980).

To estimate the relative magnitudes of variation due to T × E interaction, the 22 populations data set was analyzed using the VARCOM procedure in SAS (2002) for all the traits assessed with mixed model [2], but with all effects random rather than fixed, except for the site effect. This gave variance components for T × E interaction from which their percentage contribution to the total variance due to random effects were calculated. Additionally, the estimated least-square means of each common taxon were ranked for all traits at each site, as well as across the four sites. Then, the mean rank deviation (Matheson and Raymond 1984 in Zas et al. 2004) was calculated as: $RD_i = \frac{1}{n}\sum_j \left|r_{ij} - \bar{r}_{ij}\right|$where r_{ij} is the ranking of the mean of the ith taxon at the site j (j = 1,…, n = 4) and $\bar{r}_{ij}$ is the ranking of each taxon over all sites. The taxa with greatest rank deviations across sites were considered the most interactive taxa. Finally, Spearman correlations were also calculated to compare whether the ranking of estimated least-square means of the common taxa differed among all combinations of pairs of sites. A high correlation (i.e., values close to one) in any pair of sites indicates that taxa perform similarly at both sites.

Results and discussion

Overall phenotypic means

Overall phenotypic means and standard deviations for all traits analysed at each site are presented in Table 3. The overall mean survival rate after 10 years across the four sites ranged from 53.2 to 91.3% with an average of 74.2%. An early frost during establishment in winter 1996 (plants were from 15 to 30 cm tall), the lowest ever recorded on screen at Concordia Research Station (−5.1°C), and a late frost (−4.6°C) during winter 1999, affected the survival of the Concordia dry and wet trials, respectively. As a result of the mortality from these frost events, mean survival in the Concordia dry and wet was 53.2 and 67.9%, respectively. The tropical Caribbean pines (PCH and PCC) were severely affected with 0.0% survival followed by $BC_{(\mathbf{H})}$ backcrosses with 48.2 and 38.9%, for the Concordia dry and wet trials respectively. The Pto. Esperanza trial was less affected by a late frost (without record of absolute minimum temperature) during the winter of 2000.

The Cerro Azul and Pto. Esperanza trials showed the best growth in total height (TH) at age of 10 years due to better soil conditions (mainly deep, well-drained and productive forest soil) and climatic conditions and were followed by the sites Concordia dry and Concordia wet. The same results were obtained for the 9 common taxa to the four sites. However, the Concordia dry site showed the worst growth in stand conical volume (SCVol) caused by the low survival at this site.

The average of stem straightness (STR) deviation was 6.41 cm across the four sites, ranging from 5.4 (best) at Concordia dry site to 8.9 (poorest) at Concordia wet site. The presence of crown defects in relation to their crown position (FORK) ranged from 1.3 to 1.8.

Taxon survival

Although the survival data could not be analyzed, differences among populations were very large within the dry and wet sites at Concordia and some tendencies could be observed (Table 4). Survival rate for all the pure species and hybrids at 10 years were lower (average of 60.1%) at the southern sites: Concordia dry from 0.0% (PT from Argentina and PCH from Brazil) to 92.6% and wet from 0.0% (the only PCH present) to 91.7%; and high (average of 87.5%) at the northern sites: Cerro Azul from 58.3% (PCC from Brazil) to 94.5% and Pto. Esperanza from 78.0% (PCH from Australia) to 97.3%. In the present study, all the PEE and PT taxa had high to relatively high survival at all sites, except for the PT from a SPA of Concordia, Entre Ríos (taxon 4) that had 0.0% survival rate at the Concordia dry trial. The major cause of mortality at Concordia dry site of the PT taxon was largely due to atypical establishment problems, i.e. damage by ants and weed competition, therefore we do not consider this variation in survival due to adaptive traits important for this area of Argentina. One or more PCH taxa had lower survival rates than PEE and PT at all sites except Concordia dry site where, as mentioned, one sample of PT had zero survival rate. Additionally, PCC and one or more PCH taxa had 0.0% survival rate at both the furthest south and the lowest in the landscape sites (i.e., Concordia dry and wet trials) due probably to frost events (see above). The F_1 hybrid from QFRI had moderate to high survival at all sites; its poorest survival was at Concordia wet and dry trials (63.9 and 74.1%, respectively), probably also associated with frost events. The F_2 hybrid had similar survival to the F_1. The F_1 backcross to PCH (i.e., $BC_{(H)}$) had inconsistent survival rates relative to PCH from QFRI, though it seemed better at Concordia wet trial and Pto.

Table 3 Overall phenotypic means (Mean), standard deviations (SD) and ranges for diameter at breast height (DBH), total height (TH), stem straightness (STR), stem forking (FORK), survival (SURV), conical volume per hectare (VOL) and stand conical volume (SVOL) in the four trials (based on plot means) at age of 10 years

Site	Trait	Mean	SD	Range
Concordia dry	DBH (cm)	22.64	1.97	19.56–26.38
	TH (m)	13.21	0.82	11.5–14.71
	STR (cm)	5.21	1.58	2.00–8.33
	FORK (scale 1–4)	1.57	0.37	1.00–2.56
	SURV (%)	53.24	35.28	0.00–100.00
	VOL (m^3/ha)	205.92	43.44	134.05–289.04
	SVOL (m^3/ha)	144.31	44.11	54.95–229.96
Concordia wet	DBH (cm)	21.48	2.27	15.98–27.40
	TH (m)	13.03	1.42	9.83–16.21
	STR (cm)	9.13	3.71	4.33–23.00
	FORK (scale 1–4)	1.49	0.32	1.00–2.11
	SURV (%)	67.86	31.91	0.00–100.00
	VOL (m^3/ha)	184.96	54.05	78.71–359.49
	SVOL (m^3/ha)	145.28	56.55	26.08–279.60
Cerro Azul	DBH (cm)	20.25	2.03	16.39–25.58
	TH (m)	15.92	1.66	12.63–18.73
	STR (cm)	5.31	1.76	2.14–8.80
	FORK (scale 1-4)	1.27	0.27	1.00–2.11
	SURV (%)	84.41	17.06	22.22–100.00
	VOL (m^3/ha)	202.60	55.80	107.17–367.12
	SVOL (m^3/ha)	168.72	52.92	44.26–289.97
Pto. Esperanza	DBH (cm)	21.51	2.95	16.72–27.92
	TH (m)	14.36	2.24	10.43–18.81
	STR (cm)	5.93	1.87	2.67–10.00
	FORK (scale 1-4)	1.64	0.39	1.00–2.44
	SURV (%)	91.36	9.07	56.00–100.00
	VOL (m^3/ha)	212.94	89.84	93.38–432.07
	SVOL (m^3/ha)	192.77	80.54	83.00–432.07

For traits STR and FORK lowest values are the most desired

Esperanza and about equal at the other sites. The F_1 backcross to PEE (i.e., $BC_{(E)}$) seemed to have equal to or better survival rates than $BC_{(H)}$ and mostly about equal to the PEE from QFRI probably reflecting its close genetic affinity to PEE, a relatively cold-tolerant taxon (López-Upton et al. 1999).

In summary, our results are fairly consistent across the sites and taxa in that the F_1 and F_2 hybrids and the $BC_{(E)}$ were more cold tolerant than the two pure Caribbean *Pinus* taxa (i.e., PCH and PCC) and the $BC_{(H)}$, and less tolerant than almost all PEE and PT taxa. These results agree with those reported in eight field tests in the lower Coastal Plain of the south-eastern USA (i.e., northern Florida and southern Georgia; López-Upton et al. 1999). Likewise, Duncan et al. (1996) under controlled greenhouse conditions found that the F_1 hybrid pine was intermediate in survival due to freeze hardiness to the parental species PCH

Table 4 Survival (%) by taxon for the four trials at the age of 10 years

Taxon	Concordia dry	Concordia wet	Cerro Azul	Pto. Esperanza
1- PT, Argentina	77.78	69.45	94.45	91.75
2- PEE, Argentina	70.37	91.67	88.89	91.75
3- PEE, Argentina	62.96	86.11	94.45	91.75
4- PT, Argentina	0.00	69.45	88.89	91.75
6- PEE, Argentina	81.48	75.00	91.67	86.25
7- $BC_{(H)}$, Australia	48.15	38.89	80.56	91.75
8- $BC_{(E)}$, Australia	62.97	69.44	83.34	97.25
9- F_2, Australia	81.48	66.67	75.00	83.50
10- F_1, Australia	74.08	63.89	83.34	91.75
11- PEE, Australia	66.67	66.67	83.34	97.25
12- PCH, Australia	59.26	0.00	80.56	78.00
13- PEE, Brazil	–	–	88.89	–
14- PCH, Brazil	0.00	–	66.67	–
15- PCH, Brazil	0.00	–	83.34	–
16- PCC, Brazil	0.00	–	58.34	–
17- PT, USA	74.08	–	94.45	–
21- PEE, USA	92.59	–	–	–
22- PT, Argentina	–	–	91.67	–
23- PT, Argentina	–	–	91.67	–
29- PT, Brazil	–	91.67	–	94.50
30- PT, Zimbabwe	–	80.56	–	94.50
31- PEE, Zimbabwe	–	80.56	–	97.25
Mean (SD)	53.24 (35.28)	67.86 (31.91)	84.41 (17.06)	91.36 (9.07)
Range	0.00–92.59	0.00–91.67	58.34–94.45	78.00–97.25

Refer to Table 1 for full codes for taxa

and PEE for young seedlings. In an early assessment at 41 months in Pto. Esperanza site, Pahr et al. (2002) showed that the PCH and $BC_{(H)}$ were more adversely affected by frost than the other taxa. However, Dieters and Brawner (2007) reporting relative performance of the hybrids, PEE and PCH at three sites: two well- and one poorly-drained in southeast Queensland, Australia, at 15 years of age, found significant differences in survival at only one of the three sites studied (Toolara, the driest site), where the F_1 hybrid showed slightly lower survival (92%) than the PEE, F_2 and PCH taxa (range 96–98%). Gwaze (1999) showed for two sites in Zimbabwe with material also provided by QFRI, similar, high (95%) survival percentages for the F_1 hybrid, PEE and PCH taxa analysed.

Taxon productivity by site

Details of individual and across sites analyses of variance of plot means for growth and assessment traits in the four trials are summarized in Table 5. The analysis of variance of plot means using model 1 indicated that the taxon effect was statistically significant ($p < 0.05$ or $p < 0.01$) for all or most of the six growth and quality traits at all sites. The traits TH, STR, FORK and SVOL did not exhibit such differences in the Concordia wet site, where only DBH and VOL were significant, and for STR in the Concordia dry site.

Table 5 Individual and across site analysis of variance of plot means for assessment traits in the four trials

Site	Degree of freedom	Source of variation	Means squares					
			DBH (cm)	TH (m)	STR (cm)	FORK (scale 1–4)	VOL (m^3/ha)	SVOL (m^3/ha)
Concordia dry	2	Block	4.00[ns]	2.01[**]	2.43[ns]	0.09[ns]	2891.91[*]	1107.26[ns]
	15	Taxon	8.28[**]	1.25[**]	2.65[ns]	0.24[*]	4288.57[**]	3427.13[*]
Concordia wet	3	Block	17.73[**]	13.14[**]	20.91[ns]	0.33[*]	13206.51[**]	20477.36[**]
	13	Taxon	10.92[**]	1.66[ns]	15.17[ns]	0.05[ns]	5073.84[**]	3479.40[ns]
Cerro Azul	3	Block	4.20[ns]	1.56[ns]	2.51[ns]	0.12 [ns]	1319.84[ns]	3280.70[ns]
	17	Taxon	10.86[**]	8.72[**]	8.72[**]	0.06[**]	9820.94[**]	7139.51[**]
Pto. Esperanza	3	Block	2.55[ns]	1.29[ns]	1.38[ns]	0.32[*]	526.83 [ns]	1276.27 [ns]
	13	Genotype	28.02[**]	17.60[**]	10.59[**]	0.27[**]	27486.06[**]	20496.81[**]
Across site	3	Site	47.92[**]	76.45[**]	157.26[**]	1.10[**]	6693.29[**]	29497.80[**]
	11	Block(Site)[a]	7.40[**]	4.73[**]	7.21[ns]	0.23[**]	4631.21[**]	7028.87[**]
	21	Taxon	25.41[**]	12.38[**]	15.13[**]	0.22[**]	20393.42[**]	11916.46[**]
	32	T × E[b]	6.53[**]	3.83[**]	5.47 [ns]	0.10 [ns]	5322.43[**]	6346.79[**]

Significance of the effects are noted by *ns* not statistically significant, i.e. $p > 0.05$; or superscripts * = statistically significant, i.e. $0.01 < p < 0.05$; or superscripts ** = statistically highly significant, i.e. $p < 0.01$. Abbreviations used for the traits were described in the text and in the captions of Tables 3 and 6, 7, 8, 9, 10

[a] Block(Site): Block-within-Site; [b]T × E: taxon × environment interaction

Details of the least square estimates of taxon means for all traits analyzed and significance of differences *from the means of the respective checks* are given in Table 6, 7, 8 and 9 for the Concordia dry and wet, Cerro Azul and Pto. Esperanza sites, respectively. For the six traits analyzed, significant differences from the Pee check (taxon 11—Pee from Australia) were extremely rare at the Concordia sites, but quite common at the northern sites where Pt (taxon 1—PT from Argentina) was the check. The most meaningful single criterion of productivity is likely to be SVOL as it takes account of adaptation of the taxa reflecting both survival and growth. Considering this trait in the three sites that had significant taxon effects (i.e., Concordia dry, Cerro Azul and Pto. Esperanza; Table 5), the F_2 hybrids from QFRI (taxon 9) and the check seedlot of Pt from a CSO of Libertad, Misiones (taxon 1) had the best performances at this Concordia dry site. On the contrary, the $BC_{(H)}$ backcross from QFRI (taxon 7) was the poorest taxon at Concordia dry site though not statistically significantly worse than the check seedlot. The taxon 1 and the F_1 hybrids (taxon 10) had the best performances and Pcc from Duraflora S.A. (taxon 16) and Pee from a CSO of Agudos, Sao Paulo (taxon 13) the worst performances at the Cerro Azul site. Finally, the F_1 hybrids (taxon 10) and $BC_{(H)}$ backcrosses (taxon 7) showed the best performances (first and second ranks, respectively) and Pee from a CSO of San Vicente, Misiones (taxon 2) and the Pee from a CSO of Cerro Azul, Misiones (taxon 6) the poorest performances for the growth volume trait SVOL at Pto. Esperanza site.

The F_1 and F_2 hybrids were not statistically different for the growth traits (DBH, TH and both conical volume parameters) from the nominated controls, i.e., Pee taxon 11 (at both Concordia sites) and Pt taxon 1 (at both northern Misiones provinces sites) checks (Tables 6, 7, 8 and 9). However, the F_1 and F_2 hybrids were statistically superior ($p < 0.05$) to the average of the Pee and Pt taxa tested in this study in volume production (VOL),

Table 6 Least square means estimates for diameter at breast height (DBH), total height (TH), stem straightness (STR), stem forking (FORK), conical volume per hectare (VOL) and stand conical volume (SVOL) in the *Concordia dry site*

Taxon	DBH (cm)	TH (m)	STR (cm)	FORK (scale 1-4)	VOL (m^3/ha)	SVOL (m^3/ha)
1- PT, Argentina	24.01^{ns}	14.24^{ns}	7.00^{ns}	1.15^{ns}	244.24^{ns}	186.27^{ns}
2- PEE, Argentina	21.30^{ns}	12.84^{ns}	5.53^{ns}	1.48^{ns}	174.37^{ns}	118.01^{ns}
3- PEE, Argentina	21.00^{ns}	12.79^{ns}	5.69^{ns}	1.44^{ns}	166.73^{ns}	102.61^{ns}
6- PEE, Argentina	20.35^{ns}	12.22^{ns}	5.80^{ns}	1.56^{ns}	152.74^{ns}	123.39^{ns}
7- BC$_{(H)}$, Australia	23.19^{ns}	12.58^{ns}	3.70^{ns}	1.67^{ns}	207.49^{ns}	98.55^{ns}
8- BC$_{(E)}$, Australia	24.45^{ns}	13.25^{ns}	4.04^{ns}	1.37^{ns}	245.51^{ns}	153.95^{ns}
9- F$_2$, Australia	24.22^{ns}	14.23^{ns}	5.28^{ns}	1.70^{ns}	247.11^{ns}	201.78^{ns}
10- F$_1$, Australia	24.04^{ns}	13.80^{ns}	5.61^{ns}	1.74^{ns}	240.86^{ns}	177.52^{ns}
11- PEE, Australia	**22.58**	**13.26**	**4.38**	**1.22**	**205.33**	**142.02**
12- PCH, Australia	24.70^{ns}	13.51^{ns}	5.17^{ns}	1.85^{ns}	246.36^{ns}	146.19^{ns}
17- PT, USA	20.41^{ns}	12.61^{ns}	3.90^{ns}	1.51^{ns}	159.71^{ns}	115.15^{ns}
21- PEE, USA	21.43^{ns}	13.24^{ns}	5.83^{ns}	2.19**	180.65^{ns}	166.33^{ns}

Refer to Table 1 for code of taxon. The significance of differences *from mean of the check taxon* (11- PEE, Australia) are indicated by *ns* not statistically significant, i.e. $p > 0.05$; or superscripts: * = statistically significant, i.e. $0.01 < p < 0.05$; or ** = statistically highly significant, i.e. $p < 0.01$. The line in the Table with bolded means represents those of the check taxon 11- PEE, Australia

Table 7 Least square means estimates for diameter at breast height (DBH), total height (TH), stem straightness (STR), stem forking (FORK), conical volume per hectare (VOL) and stand conical volume (SVOL) in the *Concordia wet site*

Taxon	DBH (cm)	TH (m)	STR (cm)	FORK (scale 1-4)	VOL (m^3/ha)	SVOL (m^3/ha)
1- PT, Argentina	24.78*	13.89^{ns}	13.84^{ns}	1.53^{ns}	259.74*	190.64^{ns}
2- PEE, Argentina	20.78^{ns}	12.21^{ns}	9.43^{ns}	1.50^{ns}	157.59^{ns}	147.54^{ns}
3- PEE, Argentina	21.05^{ns}	13.11^{ns}	9.00^{ns}	1.72^{ns}	173.33^{ns}	148.36^{ns}
4- PT, Argentina	21.05^{ns}	13.05^{ns}	10.75^{ns}	1.36^{ns}	177.31^{ns}	133.99^{s}
6- PEE, Argentina	20.20^{ns}	12.07^{ns}	8.36^{ns}	1.64^{ns}	152.69^{ns}	119.33^{ns}
7- BC$_{(H)}$, Australia	18.35^{ns}	11.70^{ns}	7.15^{ns}	1.40^{ns}	124.05^{ns}	50.24^{ns}
8- BC$_{(E)}$, Australia	22.42^{ns}	13.42^{ns}	11.98^{ns}	1.39^{ns}	211.46^{ns}	158.25^{ns}
9- F$_2$, Australia	19.16^{ns}	12.95^{ns}	6.19^{ns}	1.48^{ns}	145.73^{ns}	123.83^{ns}
10- F$_1$, Australia	24.07^{ns}	13.78^{ns}	10.25^{ns}	1.42^{ns}	237.14^{ns}	151.22^{ns}
11- PEE, Australia	**20.66**	**12.29**	**6.82**	**1.52**	**160.04**	**139.07**
29- PT, Brazil	21.13^{ns}	13.49^{ns}	7.38^{ns}	1.31^{ns}	183.77^{ns}	168.93^{ns}
30- PT, Zimbabwe	20.87^{ns}	13.10^{ns}	9.41^{ns}	1.39^{ns}	172.83^{ns}	140.38^{ns}
31- PEE, Zimbabwe	21.82^{ns}	12.63^{ns}	9.10 ^{ns}	1.53^{ns}	180.58^{ns}	142.98^{ns}

Refer to Table 1 for code of taxon. The significance of differences *from mean of the check taxon* (11- PEE, Australia) are indicated by ns = not statistically significant, i.e. $p > 0.05$; or superscripts * = statistically significant, i.e. $0.01 < p < 0.05$; or ** = statistically highly significant, i.e. $p < 0.01$. The line in the Table with bolded means represents those of the check taxon 11- PEE, Australia

Table 8 Least square means estimates for diameter at breast height (DBH), total height (TH), stem straightness (STR), stem forking (FORK), conical volume per hectare (VOL) and stand conical volume (SVOL) in the *Cerro Azul site*

Taxon	DBH (cm)	TH (m)	STR (cm)	FORK (scale 1–4)	VOL (m^3/ha)	SVOL (m^3/ha)
1- PT, Argentina	**21.91**	**17.87**	**8.21**	**1.28**	**254.55**	**240.11**
2- PEE, Argentina	18.55^{*}	14.14^{**}	5.85^{ns}	1.22^{ns}	146.16^{**}	130.64^{**}
3- PEE, Argentina	18.09^{**}	14.19^{**}	6.60^{ns}	1.22^{ns}	139.55^{**}	132.31^{**}
4- PT, Argentina	21.21^{ns}	16.63^{ns}	6.52^{ns}	1.11^{ns}	222.93^{ns}	197.08^{ns}
6- PEE, Argentina	17.76^{**}	13.92^{**}	5.21^{**}	1.42^{ns}	131.42^{**}	120.79^{**}
7- $BC_{(H)}$, Australia	20.07^{ns}	16.31^{ns}	3.52^{**}	1.56^{ns}	208.23^{ns}	167.26^{ns}
8- $BC_{(E)}$, Australia	20.37^{ns}	15.88^{*}	2.77^{**}	1.31^{ns}	199.54^{ns}	168.28^{ns}
9- F_2, Australia	20.87^{ns}	17.53^{ns}	3.69^{**}	1.22^{ns}	229.15^{ns}	169.74^{ns}
10- F_1, Australia	22.45^{ns}	17.88^{ns}	2.96^{**}	1.36^{ns}	276.21^{ns}	227.41^{ns}
11- PEE, Australia	18.76^{*}	14.98^{**}	3.70^{**}	1.17^{ns}	160.46^{**}	134.39^{**}
12- PCH, Australia	22.53^{ns}	17.53^{ns}	4.99^{**}	1.17^{ns}	278.65^{ns}	217.13^{ns}
13- PEE, Brazil	18.25^{**}	13.63^{**}	5.31^{**}	1.14^{ns}	136.12^{**}	120.00^{**}
14- PCH, Brazil	21.98^{ns}	16.64^{ns}	6.87^{ns}	1.47^{ns}	243.81^{ns}	152.33^{*}
15- PCH, Brazil	21.72^{ns}	17.45^{ns}	5.83^{*}	1.42^{ns}	251.89^{ns}	210.14^{ns}
16- PCC, Brazil	19.32^{ns}	14.51^{**}	6.33^{ns}	1.22^{ns}	171.51^{**}	97.17^{**}
17- PT, USA	18.31^{**}	14.63^{**}	5.30^{**}	1.17^{ns}	156.61^{**}	148.97^{*}
22- PT, Argentina	21.70^{ns}	16.78^{ns}	6.20^{ns}	1.22^{ns}	234.82^{ns}	215.19^{ns}
23- PT, Argentina	20.68^{ns}	16.03^{ns}	5.73^{*}	1.17^{ns}	205.28^{ns}	188.00^{ns}

Refer to Table 1 for code of taxon. The significance of differences *from mean of the check taxon* (1- PT, Argentina) are indicated by *ns* not statistically significant, i.e. $p > 0.05$; or superscripts * = statistically significant, i.e. $0.01 < p < 0.05$; or ** = statistically highly significant, i.e. $p < 0.01$. The line in the Table with bolded means represents those of the check taxon 1- PT, Argentina

except on the swampy site (Concordia wet site) where only the F_1 has shown better performance than PEE and PT (data not shown).

The F_1 hybrid had higher yield than PEE and PT taxa in previous studies in the coastal lowlands of south-east Queensland, Australia, South Africa, and in the north of Corrientes province, Argentina (Nikles 1991). Powell and Nikles (1996) reporting on a study of PCH, PEE, F_1, F_2, $BC_{(E)}$ and $BC_{(H)}$ taxa across four sites ranging from south-east to central Queensland, Australia that included well- and poorly-drained sites, showed the superior growth of the F_1 over both parent species at age 6 years. Dieters and Brawner 2007, employing a subset of the same trials and taxa as were used in the earlier work of Powell and Nikles (1996), showed that the F_1 and F_2 hybrids were more productive than PEE at age 15 years. This poor performance of PEE was confirmed at the age of 20 years across the same Australian trial sites. In four tests located in southern Florida, USA, Rockwood and Nikles (2000) showed that the F_1 hybrid from QFRI outperformed at 8 years of age both the native PEE (developed for rapid growth in northern Florida, USA) and QFRI PEE taxa. Zheng (2000) at 3 years after planting reported that 3 of the 6 F_1 families imported from Queensland, Australia had larger height than the local improved PEE control, in a trial established in Jiangxi province, China. In Argentina, Barrett et al. (1991) and Bunse (2003) also reported better performance of the (QFRI) F_1 hybrids than the local and QFRI PEE and PT taxa, in three different trials established on sandy and red productive soils in the north-eastern province of Corrientes at the age of 9 and 6 years, respectively.

Table 9 Least square means estimates for diameter at breast height (DBH), total height (TH), stem straightness (STR), stem forking (FORK), conical volume per hectare (VOL) and stand conical volume (SVOL) in the *Pto. Esperanza site*

Taxon	DBH (cm)	TH (m)	STR (cm)	FORK (scale 1–4)	VOL (m^3/ha)	SVOL (m^3/ha)
1- PT, Argentina	**23.64**	**15.63**	**8.29**	**1.16**	**267.79**	**243.53**
2- PEE, Argentina	17.99^{**}	11.61^{**}	6.61^{ns}	1.49^{ns}	113.08^{**}	103.29^{**}
3- PEE, Argentina	19.43^{**}	13.10^{*}	8.95^{ns}	1.80^{ns}	156.48^{*}	142.96^{*}
4- PT, Argentina	20.60^{ns}	13.38^{*}	7.94^{ns}	1.27^{ns}	171.99^{ns}	156.47^{ns}
6- PEE, Argentina	18.44^{**}	12.04^{**}	6.69^{ns}	1.63^{ns}	122.82^{**}	105.07^{**}
7- $BC_{(H)}$, Australia	25.03^{ns}	16.89^{ns}	3.99^{**}	1.99^{**}	325.23^{ns}	302.15^{ns}
8- $BC_{(E)}$, Australia	22.34^{ns}	14.96^{ns}	3.62^{**}	1.63^{ns}	227.08^{ns}	220.08^{ns}
9- F_2, Australia	23.56^{ns}	17.24^{ns}	4.61^{**}	1.67^{ns}	287.75^{ns}	240.72^{ns}
10- F_1, Australia	26.09^{ns}	17.57^{ns}	4.35^{**}	1.78^{ns}	360.99^{ns}	328.16^{ns}
11- PEE, Australia	19.95*	13.22*	5.68^{*}	1.76^{ns}	164.34^{**}	159.32^{ns}
12- PCH, Australia	24.44^{ns}	16.78^{ns}	5.94^{ns}	1.62^{ns}	313.54^{ns}	251.08^{ns}
29- PT, Brazil	20.04^{*}	12.55**	5.89^{*}	1.44^{ns}	157.70*	148.08^{ns}
30- PT, Zimbabwe	20.82^{ns}	13.60^{ns}	5.50^{*}	1.56^{ns}	179.23^{ns}	169.52^{ns}
31- PEE, Zimbabwe	18.74^{**}	12.43^{**}	4.91^{**}	2.15^{**}	133.13^{**}	128.41^{*}

Refer to Table 1 for code of taxon. The significance of differences *from mean of the check taxon* (1- PT, Argentina) are indicated by ns = not statistically significant, i.e. $p > 0.05$; or superscripts * = statistically significant, i.e. $0.01 < p < 0.05$; or ** = statistically highly significant, i.e. $p < 0.01$. The line in the Table with bolded means represents those of the check taxon 1- PT, Argentina

In the current research, there is slight evidence that F_2 hybrid is particularly intolerant to the swampy Concordia site relative to F_1 hybrid. Although not statistically significant ($p < 0.05$), when we compared the two nearest dry and wet Concordia sites, the F_2 was rather lower than the F_1 hybrid for TH (12.95 vs. 13.78, respectively; Table 7) and lower for SVOL (123.83 vs. 151.22, respectively; Table 7) at the wet Concordia site. At the dry Concordia site, the F_2 hybrid had a higher performance than the F_1 hybrid, being rather higher for TH (14.23 vs. 13.80, respectively; Table 6) and higher for SVOL (201.78 vs. 177.52, respectively; Table 6). In spite of the F_2 families not being directly derived from the F_1 families (although both F_1 and F_2 are represented by large numbers of families and both come from the same broad base of PEE and PCH parents in the respective breeding populations), Dieters and Brawner (2007) showed that the F_1 hybrid significantly outperformed the F_2 hybrid at the age of 15 years for individual tree volume inside bark at the poorly drained site (0.409 vs. 0.316 m^3 respectively). For height F_2 was very marginally and non-significantly lower than F_1 (19.4 vs. 19.7, respectively). For the same southeast Queensland trials at the age of 20 years, there is a very slight indication that F_2 might be less adaptable than F_1 in the swampy Tuan site as regards the average stem volume, but not for the whole stand on a volume per hectare basis. From all the above results, there is no strong, consistent evidence that the F_1 and F_2 hybrid populations have clear differences in adaptability at this Australian swampy site, though it should be noted that the naturally-poor soil drainage at the Tuan site was mitigated during the life of the trial by planting on very high mounds (beds) and for much of the trial life by drought conditions.

The PCH taxon from QFRI (taxon 12) and the F_1 hybrid (taxon 10) were among the best populations for VOL, while the PEE from a CSO of Cerro Azul, Misiones (taxon 6) was one of the poorest performing taxa on all sites. In particular, in the three high-survival sites, taxon 12 ranked first (Cerro Azul), second (Concordia dry) and third (Pto. Esperanza), being surpassed only by the F_2 hybrid in Concordia dry and the F_1 and $BC_{(H)}$ in Pto. Esperanza. Additionally, at these three sites, differences among the most outstanding taxa (12 and 10) and the poorest taxon (6) were statistically significant ($p < 0.01$) for volume (VOL, data not shown). The inferior volume production of PEE compared with PCH is consistent with previous studies (e.g. Gwaze 1999; Dieters and Brawner 2007). However, diverse results in terms of the performance of the PCH when compared with the F_1 hybrids have been reported in literature due to the different environments of the tests. In Queensland, Australia, Powell and Nikles (1996) showed that at age 6 years the PEE × PCH F_1 hybrid had a consistent advantage over both parent species on swampy sites and is generally considered equal to PCH on the better quality well-drained sites. In a trial established in deep sandy soils of Ituzaingo, Corrientes province, Argentina, Barrett et al. (1991) found comparable growth of the F_1 hybrid and the PCH taxa (from Agudos, Brazil) likely due to the low incidence of frost in this site. Dieters and Brawner (2007) showed only small growth differences at age 15 years between F_1, F_2 and PCH at two well- and one poorly-drained sites in southeast Queensland, Australia. However, Gwaze (1999), at two sites in Zimbabwe, reported that the F_1 hybrids were substantially superior (101 and 37%) in volume to the parental PCH, at 5 years of age, although the F_1 hybrids in this study were not compared to their true parents.

Taxon quality by site

In the two trials in Misiones province (i.e., Cerro Azul and Pto. Esperanza) the F_1, F_2, $BC_{(H)}$ and $BC_{(E)}$ taxa from QFRI showed better stem straightness (i.e., small deviation from the vertical) than the PEE and PT taxa from Argentina, generally with statistical difference ($p < 0.05$; data not shown). Meanwhile, in spite of non statistically significant differences, the $BC_{(H)}$ and $BC_{(E)}$ backcross and the $BC_{(H)}$ and F_2 hybrid taxa were the most straight at Concordia dry and wet sites, respectively. The PT from a CSO of Libertad, Misiones (taxon 1) had the highest stem deviation from the vertical in all sites, except for Pto. Esperanza site, where the PT ranked second behind PEE from the SSO of INTA Concordia (taxon 3). On all sites tested in the coastal lowlands of Queensland, Australia, Nikles (1991) reported that the F_1 hybrid was superior in stem straightness to PCH. This was confirmed very convincingly by Powell and Nikles 1996 and Dieters and Brawner 2007 as their studies involved large numbers of comparable suites of hybrid and PCH families across four or three sites. The same results were found for Gwaze (1999) at two sites in Zimbabwe and Bunse (2003) in Argentina. Dieters and Brawner (2007) stated (p. 697) that "PCH was significantly inferior (in straightness) to PEE and both hybrids (i.e., F_1 and F_2) at all three sites in this study", i.e. at age 15 years in southeast Queensland, Australia.

In general, the PCH taxa and the backcrosses with PCH (i.e., $BC_{(H)}$) had a marked tendency to fork near the base at the sites that showed statistically significant differences ($p < 0.05$; Table 5). Forking in the PT taxa (taxa 1, 4 and 29) occurred mainly in crowns rather than lower in the stem and were better in this regard than the other taxa studied. However, Barrett et al. (1991) did not find significant differences for forking between the F_1 hybrids and PEE, and the three different varieties of Caribbean pines: PCH, PCC and PCB. Powell and Nikles (1996) showed that the F_1 hybrid had higher frequency of ramicorns and double leaders than PCH, and equalled the worst performing parent PEE confirming the broader experience in Queensland that the forking and branching habits (form) of PEE × PCH hybrid seedling families are intermediate between those from their pure-species parents, e.g. Powell and Nikles 1996; however, the intensively-selected hybrid families and clones that are deployed in Queensland plantations have very good form (Harding et al. 2010).

Analysis across site: taxon × environment interaction

When data from all the sites were combined in an analysis (Model 2), results presented in Table 5 indicated that the taxon × environment (T × E) interaction term was statistically significant ($p < 0.01$) for growth traits (DBH, TH and both conical volume parameters) and not statistically significant ($p > 0.05$) for quality traits (STR and FORK). In the growth traits, the T × E interaction contributed an average of 20.6% of the total variance in the traits analyzed, ranging from 19.2 to 29.9% for diameter and stand conical volume, respectively. Furthermore, the T × E interaction term ranged from slightly more than 50% (i.e., 53.3%) of the taxon variance for SVOL, to only 25.7% of the taxon variance for DBH and VOL. If the 'rule of thumb' proposed by Shelbourne (1972), that the genotype (taxon in our case) by environment interaction component of variance needs to be about twice that of the genotype component to warrant regionalisation of a selective breeding program, applies in the Mesopotamia region then regionalisation appears unnecessary there.

Further investigation of T × E interaction, based on mean rank deviations for the 9 taxa common to the four sites, indicated that the unstable behaviour was being caused mainly by the $BC_{(H)}$ backcross (taxon 7) and F_2 hybrid (taxon 9), the two taxa with the greatest mean rank deviations for growth traits (Table 10). When these two generally-most interactive common taxon (taxa 7 and 9) were individually excluded, the T × E interaction term became not statistically significant for DBH ($p = 0.1837$). On the other hand, the PEE from QFRI (taxon 11) and from a CSO of Cerro Azul, Misiones (taxon 6) showed high stability across all sites (smaller mean rank deviation, Table 10). In contrast, PEE taxon 3 from the Argentine SSO of INTA also exhibited considerable instability for all traits analysed. Powell and Nikles (1996) showed that only the PCH taxon had a significant re-ranking at age 6 years while remaining taxa (i.e., PEE, F_1, F_2, $BC_{(E)}$ and $BC_{(H)}$) had relatively consistent growth performance across the sites. However, Dieters and Brawner (2007), reported statistical significance ($p < 0.001$) for the genotype by environment effect in mean annual increment in volume and straightness, when a subset of the trials and taxa (i.e., PCH,

Table 10 Mean of taxon rank deviations, for diameter at breast height (DBH), total height (TH), stem straightness (STR), stem forking (FORK), conical volume per hectare (VOL) and stand conical volume (SVOL) for the 9 common taxa in the four study sites

Taxon	DBH	TH	STR	FORK	VOL	SVOL
1- PT, Argentina	1.00	1.00	0.38	2.50	1.00	0.75
2- PEE, Argentina	1.00	1.00	0.50	1.25	0.88	1.25
3- PEE, Argentina	1.38	1.13	1.25	2.25	1.38	1.25
6- PEE, Argentina	0.75	0.50	1.25	1.50	0.75	0.88
7- $BC_{(H)}$, Australia	1.88	2.50	0.75	2.38	2.00	2.75
8- $BC_{(E)}$, Australia	1.25	0.75	2.50	1.38	1.25	0.88
9- F_2, Australia	1.88	1.00	1.13	1.75	2.13	1.75
10- F_1, Australia	0.75	0.75	2.00	1.75	1.00	0.75
11- PEE, Australia	0.00	0.75	1.25	2.25	0.38	0.38

The taxa with greatest rank deviations across sites are considered the most interactive taxa

PEE, F_1 and F_2) used by Powell and Nikles (1996) were analyzed at age 15 years. Gwaze (1999) found that the ranking of the F_1 hybrid and parental species were stable across the two sites, particularly for growth traits.

There were significant changes in ranking of estimated least-squares means for the 9 common taxa for stand conical volume (SVOL) mainly associated with Concordia wet site. The Spearman rank correlations were moderate to low i.e. 0.45, 0.53, and 0.17 and not significantly different from zero ($p > 0.05$), for Concordia dry/Concordia wet, Cerro Azul/Concordia wet, and Pto. Esperanza/Concordia wet, respectively, suggesting that the Concordia wet site is distinctly different from the other three sites. These major interactions of the taxa $BC_{(H)}$ backcrosses and F_2 hybrids in Concordia wet site for stand conical volume may result mainly from edaphic factors (i.e., swampy site), rather than large-scale climatic differences. In contrast, the Spearman rank correlations between the estimated least-square means for Cerro Azul/Concordia dry and Pto. Esperanza/Cerro Azul were moderate to strong i.e. 0.72 and 0.85, respectively; these were significant ($p < 0.05$) in both cases.

In summary, the results presented in this paper suggest that taxon by environment interaction in growth traits (DBH, TH and both conical volume measures) are a consequence of a few interactive taxa (7 and 9) that may be particularly susceptible to environmental variation. However, these results are not considered to be a serious problem for breeding programs in the Mesopotamia region given that the taxon × environment interaction contributed an average of only 34.06% of the taxon variance across the four trials evaluated.

As a final comment, the F_1 and F_2 hybrids reported in this study were developed in Australia where the environmental conditions are different from those in the Mesopotamia region. Given the potential of these hybrids in the subtropical areas of the Mesopotamia region of Argentina and that it is important to test the potential of locally produced hybrids, INTA Montecarlo Experimental Station started a short- and long-term tree improvement program based on genetically improved, locally adapted PEE and PCH sources that are fast growing and have good stem straightness (Maria Elena Gauchat, INTA Montecarlo Experimental Station, 2010, *pers. comm.*). Based on that high percentage of F_1 hybrid cutting can be induced to form roots (Hunt et al. 2011), the short-term goal of the improvement program includes the vegetative propagation of the superior F_1 families. Meanwhile, the long-term goal of the program is to provide F_2 seedlings for commercial deployment from selected F_1 hybrid clones arranged in a Clonal Seed Orchard. The first controlled crossing of hybrids between selected trees of PEE (from first-generation progeny trials) and PCH (from origin trials and commercial plantations) were attempted at INTA Montecarlo (Misiones province) in July of 2004. From these controlled pollinated crosses, 66 families were produced and established in two control-pollinated progeny trials in the north of Misiones province in 2007.

Conclusion

The results of our study of four taxa comparison trials indicate that the F_1 hybrid between PEE and PCH, if available commercially, would be a good option, on a combination of traits, for planting in the warmer subtropical areas of the Mesopotamia region of Argentina, where PEE (on poorly-drained soil and low productive forest sites) and PT (on well-drained and productive forest sites) are commonly planted, with the result of a considerable increase in the productivity of these sites. Our results also show that the F_2 outperformed most of the pure species of PEE and PT from Argentina except on the swampy site. These results reinforce the trends that have been found previously in early works in the Mesopotamia region of Argentina. The PT from a CSO of Libertad, Misiones was among the best populations for stand conical volume production on all sites but it never exhibited superior straightness. Consequently, such a taxon would likely require intensive breeding before it would become attractive for commercial deployment.

The results reported also highlighted that, in general, the F_1 and F_2 hybrids also showed better stem straightness than the PEE and PT taxa from Argentina; thus, this desirable trait will improve the sawn timber quality of future commercial pine plantations of these taxa in the Mesopotamia region of Argentina. Additionally, across the range of sites studied, the F_1 hybrids between PEE and PCH were relatively stable for the growth and quality traits. These results suggest that follow-up studies of wood quality of the better hybrids and pure species would be appropriate to provide a better understanding of the possible future role of the alternative *Pinus* taxa studied in relation to the pine wood industry in north-eastern Argentina. Meanwhile, the lumber of fast-growing F_1 and F_2 hybrids is likely appropriate locally for the purpose of higher-value applications such as furniture, interior fitting, etc. They also are appropriate for silvopastoral systems because of favourable crown architecture.

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