Ann. For. Sci. 64 (2007) 691–698
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DOI: 10.1051/forest:2007049

Available online at:
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Original article

Productivity of *Pinus elliottii*, *P. caribaea* and their F_1 and F_2 hybrids to 15 years in Queensland, Australia

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(Received 29 October 2006; accepted 30 March 2007)

Abstract – Growth data are presented to 15 years of age from a genetic study involving factorial matings within and between *P. elliottii* var. *elliottii* and *P. caribaea* var. *hondurensis*, planted across three sites in southeast Queensland. Specific volume equations developed using the centroid method for each taxon/site combination as well as a generic (i.e. conical) volume equation, were used to estimate the mean annual increment (MAI) at 10 and 15 years of age. MAI estimated using the conical volume equation were downwardly biased by 18% in *P. elliottii* but the bias was less than 2% in *P. caribaea* var. *hondurensis*, and yielded different rankings of taxa at each site compared to the taxon/site specific volume equations. At all three sites, *P. caribaea* var. *hondurensis* and the F_1 and F_2 hybrids significantly exceeded the productivity of *P. elliottii*; however, differences between *P. caribaea* var. *hondurensis* and hybrid pine were generally small. Assuming a realistic contribution of the three site-types to the population of deployment environments, average MAIs for southeast Queensland were estimated as: 17.6, 23.0, 23.7 and 23.5 m^3 ha^{-1} y^{-1} for PEE, PCH, F_1 and F_2 respectively.

hybrid superiority / mean annual increment / volume equations / centroid method / genetic gain

Résumé – Productivité de *Pinus elliottii*, *Pinus caribaea* et de leurs hybrides F_1 et F_2 à 15 ans au Queensland (Australie). Des données de croissance jusqu'à l'âge de 15 ans ont été produites par des essais comparatifs de croisements factoriels intra et inter-spécifiques de *Pinus elliottii* var. *elloittii et Pinus caribaea* var. *hondurensis,* plantés dans trois sites au sud est du Queensland. Des équations dendrométriques spécifiques développées par la méthode centroïde pour chaque combinaison taxon/site ainsi qu'une équation générique (conique) de volume ont été utilisées pour estimer l'accroissement moyen annuel (AMA) à 10 et 15 ans. AMA estimé par l'équation conique de volume était affecté par un biais négatif de 18 % pour *Pinus elliottii.* Ce biais restait inférieur à 2 % chez *Pinus caribaea* var. *hondurensis*. Il en est résulté des différences dans les classements des taxons dans chaque site par rapport à la méthode basée sur des équations spécifiques à chaque combinaison taxon /site. Dans les trois sites, *Pinus caribaea* var *hondurensis* et les hybrides F_1 et F_2 ont présenté une productivité supérieure à *Pinus elliottii* ; cependant les différences entre *Pinus caribaea* var. *hondurensis* et les hybrides étaient généralement faibles. En utilisant une fréquence relative des trois types de sites sur l'aire de plantation de ces pins, la moyenne d'accroissement moyen annuel pour le sud est du Queensland a été respectivement estimée à : 17,6, 23,0, 23,7 et 23,5 m^3 $ha^{-1}an^{-1}$ pour PEE, PCH, F_1 et F_2.

vigueur hybride / accroissement moyen annuel / équations dendrométriques / méthode centroïde / gain génétique

1. INTRODUCTION

Genetic improvement of *Pinus* species for deployment in near-coastal environments of southern and central Queensland has led to the testing and development of a range of inter-specific hybrid combinations involving *Pinus elliottii* Engelm. var. *elliottii* (referred to here as PEE). The hybrid between *P. elliottii* and *P. caribaea* Morlet var. *hondurensis* (Sénéclauze) W.H. Barrett and Golfari (PCH) has repeatedly performed well in field trials, and is now used almost exclusively for plantation establishment in central and southeast Queensland [1]. The overall performance of this hybrid combination (PEE × PCH, or simply 'hybrid pine') results in substantial advantages over both parental species, while not necessarily being superior to either parental species in any one trait across a range of sites. This hybrid superiority [6] appears to be derived from a complementary recombination of traits from the two parental species – growth rate from PCH combined with wind-firmness, adaptability to wet sites, high wood-density and stem straightness of PEE.

This paper examines the productivity of the hybrid pine in comparison to the parental species to 15 years after planting, using data from a large genetic study involving factorial matings within and between the two parental species (PEE and PCH) and both the F_1 and F_2 hybrids[1]. This study has some unique advantages for the purposes of this paper: the same 12 PEE and PCH parents were used to generate progeny of PEE, PCH and the F_1 hybrid; mating designs are complete factorials so each parent contributes equally to the different taxa;

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[1] The meaning of terms 'F_1' and 'F_2' hybrid as used here reflects the common usage of these terms in the forestry literature – i.e. the pure species are mated to form the F_1, and then selected (but unrelated) F_1 individuals are mated to form the F_2.

Table I. Additional site, experiment and establishment details for three trials used in the study.

	Beerwah Site	Toolara Site	Tuan Site
Experiment	Ex674/2DTBS	Ex674/2CTBS	Ex674/2BTBS
Latitude (° S)	26° 52’	26° 05’	25° 38’
Longitude (° E)	152° 58’	152° 50’	152° 50’
Altitude (m asl)	30	60	14
Rainfall (mm/y ave.)	1665	1370	1340
Site and soil type	Well-drained; yellow earth	Well-drained; red-yellow podozlic	Poorly-drained; lateritic – gleyed podzolic
Planting date	May–June 1987	April 1987	April–May 1987
Number replicates	12	12	16
Planting spacing (r × t)	4.0 × 2.7 m	4.5 × 2.4 m	4.5 × 2.4 m
Initial stocking (sph)	926	926	926

each taxon is planted in large plots (112-tree plots); and the study was planted across three contrasting sites in southeast Queensland. As a consequence of the mating design used, the observed taxa differences reflect the effects of interspecific hybridization free of bias that may have been caused by using a variable set of parents to produce each taxon. The large taxon-plots make it possible to estimate the productivity (per unit area) of each taxon without concern for edge effects due to competition between taxa.

The F_2 hybrids, however, share no direct genetic linkage to the parents used to generate the PEE, PCH and F_1 taxa. Nevertheless, all parents (PEE, PCH and F_1 parents) used to generate the four taxa were, at that time, considered to be representative of the breeding populations. This can be demonstrated by examination of breeding values obtained from the analysis of over 100 000 PEE progeny, 300 000 PCH progeny, and 120 000 hybrid progeny – the average predicted breeding values for height at 10 years of age are –0.03, –0.20, and 0.00 of the 12 PEE, 12 PCH, and 12 F_1 parents respectively, where breeding values are expressed as Z-scores (average of zero and standard deviation of one). Consequently, it can be seen that the sample of parents used were near-average in terms of growth potential.

Therefore this study allows a direct comparison of the four taxa that have been most widely planted in southeast Queensland during the past 20 years; allowing investigation of differences in volume production of the four taxa to 15 years of age (i.e. over half the projected rotation length of 25–28 years) in replicated experiments, with common parents used to produce the PEE, PCH and F_1 progeny. Differences in productivity are commonly examined in genetic evaluation trials by applying either generic volume equations (e.g. [5, 7, 10, 16, 17, 21, 25, 26]) or an index of volume such as conical volume (e.g. [12, 15, 16]). Reasons for this include: the ranking of the genetic entries (provenances, families, clones, etc.) is often more important than estimating the true volume; and reliable volume equations are either not suitable for small trees, not available for new species/taxa that are included in genetic studies, or genetic selection and breeding has changed tree form such that standard volume equations are no longer relevant. Further, in genetic studies it is often not possible to destructively sample trees to develop volume equations because the trees are required for later-age measurements and breeding. Only rarely have differences in tree form been considered when estimating volume [24] in tree improvement studies. Due to differences between PCH, PEE and their hybrid in bark-thickness and taper it was expected that a generic volume equations would not be sufficiently reliable to accurately estimate the yield potential of the parental species and hybrid taxa. As well, differences between the test locations may also lead to changes in tree form. Therefore, existing (generic) volume equations were not considered to be adequate, and individual volume equations were generated for each of the four taxa, at each site, in order to most reliably estimate volume (inside bark) from measurements of tree diameter (outside bark) at breast height and tree height.

2. METHODS AND MATERIALS

2.1. Field trials

The field trials used for this study were planted in 1987 on three sites in southeast Queensland (located near Beerwah, Toolara and Tuan, Tab. I). Twelve parents of PEE and PCH were inter-mated to produce a 6 × 6 factorial of each parental species (i.e. 36 full-sib families of each parental species), and a 12 × 12 factorial of the F_1 hybrid (i.e. 144 full-sib hybrid families). Twelve unrelated F_1 individuals of similar genetic quality, but unrelated to the PEE and PCH parents, were also mated to form a 6 × 6 factorial of the F_2 hybrid. PEE is normally used as the female parent when producing the F_1 hybrid with PCH, because PEE flowers approximately 2 months later than PCH and grafted ramets of PEE tend to be smaller (i.e. slower growing) and more prolific seed producers than in PCH. Consequently, it is biologically easier to use PEE as the female parent in this hybrid. Further, there is no evidence of significant maternal or reciprocal effects in this hybrid.

Each of the three trials used a randomised complete block design, with families nested within taxon. In each trial, each taxon was represented by two trees of each full-sib family in each block, planted in measure-plots of 72 trees that were surrounded by a single tree (or row) isolation of the same taxon (i.e. gross plots of 8 rows × 14 trees = 112 trees). The PEE, PCH and F_2 taxa were represented by a single 112-tree measure plot in each replicate, while the F_1 hybrid was represented by four contiguous 112-tree plots in each replicate. Ten replicates of the Beerwah site were thinned to half-stocking at 11 years of age to provide wood samples for a study of the genetic control of wood properties [14]. Therefore, results presented are based on only 5 replicates at the Beerwah site, but all replicates at both the Toolara and Tuan sites.

2.2. Data collection

All surviving trees were measured at approximately 10 and 15 years after planting in each of the three trials for diameter outside-bark at breast height (i.e. 1.3 m above ground level, DBH) and total tree height (HT), and stem straightness (ST) on a 6-point scale [4] at 10 years of age.

Following the 15 year measurement of these trials, 360 sample-trees (drawn from across three sites and four taxa) were remeasured in order to determine the volume inside bark (VIB) of each sample tree using the centroid method [23]. Tree volumes obtained using the centroid method where subsequently used to derive volume equations for each taxon, at each site. These volume equations were then used to estimate the individual tree volumes of all surviving trees in each taxon, using existing data on height and diameter at 10 and 15 years of age. As the mean diameter and height at 10 years of age, was within the range of the trees sampled to derive the volume equations, application of the equations to the earlier measure data was considered appropriate. The large (72-tree net) plots were then used as a taxa comparison trial to determine differences in the total volume of wood produced in each taxon.

2.2.1. Sample trees used for derivation of volume equations

The year 15 height data were used to select a stratified random sample of 120 trees per site; 30 trees within the PCH, PEE, F_1 and F_2 hybrid taxa at each site. At each site, 30 sample trees for each taxon were selected to cover the observed height range of each taxon at that site: 10 were selected as being small, 10 were of average height and 10 were taller than average. Any nominated sample tree that was subsequently found to have either a broken top, severe lean or foxtail was replaced with a suitable tree of the same size class. Fifteen trees were measured in each of two randomly selected blocks of each taxon at each site.

2.2.2. Tree volume – centroid method

Tree volume inside bark was estimated using the centroid method [11, 23], which requires height and DBH measurements as well as an additional diameter measurement at the centroid height (HC – third of tree height). Measurements for each tree in the 360-tree sub-sample included: (1) total tree height (HT), (2) diameter outside bark at breast height (DBH), (3) bark-thickness at breast height (BT – three sample points located equidistant around the stem), (4) centroid height (HC), (5) diameter outside bark at centroid height (DC), (6) bark-thickness (average of two measurements on opposite sides of each tree) at centroid height (CBT). All heights were measured to the nearest 0.1 m using a Vertex hypsometer (taking the average of three readings). Diameters were measured over-bark to the nearest 1 mm using a diameter tape. Bark-thickness was measured to the nearest 1 mm with a bark punch.

Use of the centroid method to determine the standing volume of sample trees carries the implied assumption that this is a true and accurate estimate of standing volume. Here we defer to Coble and Waint [3] who concluded that the centroid method provides accurate estimates of the volume of standing trees, and represents a considerable improvement in both efficiency and cost-effectiveness when compared to standard dendrometry techniques for estimating tree volume. Undoubtedly, more accurate measurements of individual volume could be obtained from detailed stem analysis of the sample trees, but this is neither practical nor possible in the context of applied tree improvement programs and so was not considered for this study.

2.3. Data analysis

All statistical analyses were conducted in SAS using either PROC GLM or PROC REG [20]. Initial analyses of height, volume inside bark, bark-thickness (at breast and centroid heights) and taper (measured as change in diameter inside bark between breast height and centroid height, expressed in mm/m) measured in the 360 sample trees at 15 years of age, were conducted to determine if there were significant differences between the sites and taxa for these traits, and to examine the importance of taxon × site interactions. Lack of significant differences between taxa and sites for bark-thickness and taper would indicate that a single volume equation could be developed from the sample tree data.

The necessity of site-specific volume equations for each taxon was further investigated using a generalized linear model that included terms for test-location and taxon, as well as covariates for D^2H (the product of DBH squared and height), taper (measured as the change in diameter inside bark between breast height and centroid height, expressed in mm/m), and bark-thickness (the average bark-thickness measured at breast height) plus all interactions This was undertaken to investigate causes for the observed variation in the estimated volume inside bark (VIB). This also allowed for testing whether or not the relationship between the covariates (i.e. growth as measured by D^2H, taper and bark-thickness) and volume (as estimated using the centroid method) were consistent across taxa and sites, therefore indicating whether equations should be pooled across taxa or sites.

Volume equations for each taxon at each site were then developed relating DBH and height to total volume inside bark, starting with the following general regression model: i.e. $VIB = b_1 + b_2D^2 + b_3H + b_4D^2H$, where VIB = volume inside bark (m^3), D = diameter outside bark at breast height (i.e. DBH in m), and H = total tree height (m), D^2 = DBH squared (m^2), and $D^2H = D^2 \times H$ (m^3). Regression equations of this form are commonly used in Queensland to predict tree volume [13, 22]. Any non-significant terms were progressively dropped from the regression models, in order to identify the simplest possible volume equation for each site and taxon where all terms in the model were significant (based on *t*-tests), with high R^2 values, low mean square error (MSE) and low coefficient of variation (CV).

Measurements of height and diameter from all surviving trees at 10 and 15 years of age in the trials at Beerwah, Toolara and Tuan were used to calculate individual tree volumes inside bark (VIB) using the most appropriate volume equation. Individual tree volumes in each plot were summed, and then divided by the plot area and the exact age at the time of measurement, to obtain an estimate of the mean annual increment (MAI, in $m^3\ ha^{-1}\ y^{-1}$). To examine the potential bias that would arise from the use of a non-specific/generic volume equation, conical volume (i.e. $CVol = 1/3 \times \pi/4 \times DBH^2 \times$ height, m^3) of each tree was also estimated for all taxa at each site, and then used to calculate MAI as above. Analysis of variance was then used to determine the significance of differences between taxa for: (1) volume production per hectare (i.e. MAI for VIB and CVol), (2) stem straightness (ST), 3) double leaders (DL), and (3) survival at 15 y (SURV15). All analyses were conducted on a plot-mean basis.

Table II. Average tree height (HT), volume inside bark (VIB), bark-thickness at breast height (BT), bark-thickness at centroid height (CBT), and stem taper between breast height and centroid height at 15 years of age, in *P. elliottii* var. *elliottii* (PEE), *P. caribaea* var. *hondurensis* (PCH) and their F_1 and F_2 hybrids across three sites in southeast Queensland. Estimates from 360 trees sampled for estimation of volume by the centroid method.

Site	Taxon	HT (m)	VIB (m^3)	BT (mm)	CBT (mm)	Taper (mm/m)
Beerwah	PEE	19.4 ± 0.21	0.330 ± 0.015	11.5 ± 0.23	8.6 ± 0.29	0.58 ± 0.04
	PCH	22.0 ± 0.25	0.441 ± 0.021	19.4 ± 0.55	12.2 ± 0.49	0.75 ± 0.04
	F_1 hybrid	21.4 ± 0.33	0.460 ± 0.032	14.6 ± 0.43	9.2 ± 0.39	0.57 ± 0.03
	F_2 hybrid	21.0 ± 0.31	0.417 ± 0.031	14.3 ± 0.57	9.0 ± 0.41	0.67 ± 0.04
Toolara	PEE	18.6 ± 0.29	0.278 ± 0.020	15.7 ± 0.49	10.3 ± 0.40	0.54 ± 0.04
	PCH	22.0 ± 0.31	0.460 ± 0.030	21.0 ± 0.66	13.6 ± 0.48	0.77 ± 0.04
	F_1 hybrid	20.5 ± 0.32	0.416 ± 0.030	19.0 ± 0.50	12.4 ± 0.39	0.73 ± 0.05
	F_2 hybrid	21.3 ± 0.25	0.403 ± 0.021	17.8 ± 0.65	12.0 ± 0.33	0.67 ± 0.04
Tuan	PEE	18.1 ± 0.28	0.263 ± 0.020	15.6 ± 0.54	11.1 ± 0.36	0.62 ± 0.04
	PCH	19.7 ± 0.30	0.360 ± 0.026	18.2 ± 0.66	12.9 ± 0.58	1.12 ± 0.06
	F_1 hybrid	19.7 ± 0.34	0.409 ± 0.033	16.2 ± 0.65	11.2 ± 0.49	0.86 ± 0.03
	F_2 hybrid	19.4 ± 0.31	0.316 ± 0.026	16.4 ± 0.62	11.4 ± 0.42	0.88 ± 0.06

3. RESULTS

Analysis of the data collected on the 360 sample trees detected significant ($p < 0.05$) taxon × site interaction for all traits except volume inside bark, indicating the performance of taxa was not consistent across sites. Nevertheless there was little re-ranking of taxa across sites for the traits measured. The ranking of taxa for VIB was PCH > F_1 > F_2 > PEE except at the poorly drained Tuan site, where the F_1 produced a greater volume/tree than PCH (Tab. II).

Bark-thickness (measured at either breast height or centroid height) and stem taper both followed the same general trend: PEE had the thinnest bark and smallest taper, PCH the thickest bark and greatest taper, and the F_1 and F_2 hybrids were intermediate between the two parental species for both traits (Tab. II). When averaged across samples from all three sites, the parental species and hybrids were significantly different from one another in both bark-thickness at breast height (14, 17, 16 and 18 mm in PEE, F_1, F_2 and PCH respectively), and taper (0.57, 0.72, 0.74 and 0.88 mm/m in PEE, F_1, F_2 and PCH respectively). Differences in both bark-thickness and taper between the F_1 and F_2 hybrids were non-significant as determined by Tukey's Studentized Range test.

These trends are reflected in the relationship of VIB to diameter and height (as measured by D^2H) (Fig. 1) all linear regressions of D^2H on VIB having R^2 values exceeding 0.98, with zero intercepts, and slopes of 0.32, 0.23, 0.30 and 0.29 for PEE, PCH and F_1 and F_2 respectively. These slopes indicate that a PEE tree will have greater volume under bark than a hybrid tree of the same diameter and height, while a PCH tree of this size would have the least wood volume. The difference between the F_1 and F_2 inside bark volume at a given DBH was not significant while PEE and PCH were dissimilar to all other taxa.

When D^2H, taper and bark-thickness were used as covariates in the across site analyses of volume (VIB), analyses indicated significant differences between the main effects of taxon and sites as well as D^2H and bark thickness ($p < 0.0001$) when used as covariates on volume; however, the main effect for taper was not significant ($p = 0.11$) when used as a covariate. Neither taper nor bark thickness showed any significant interaction with sites ($p = 0.0019$) or taxa ($p < 0.0001$), suggesting that a given change in taper or bark thickness has the same impact on the estimated volume, across all taxa and sites. However, the covariate D^2H showed significant two-way interactions with both taxa and site, indicating that the impact of stem form (i.e. the ratio of diameter to height) on volume was not consistent across sites and taxa therefore confirming the need for separate volume equations for each site and taxon in this study.

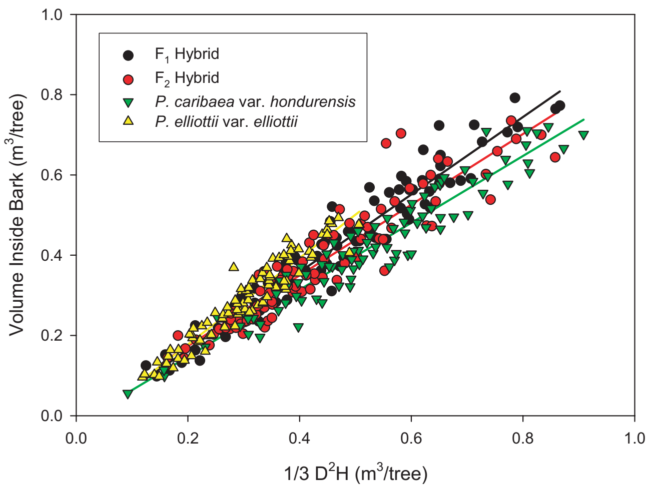

Figure 1. Relationship between volume inside bark (estimated by the centroid method) and one third of (diameter at breast height)^2 × total tree height at 15 years of age, for *P.elliottii* var. *elliottii*, *P. caribaea* var. *hondurensis* and their F_1 and F_2 hybrids, from a stratified random sample of 30 trees per taxon on each of three sites in southeast Queensland. (Note: Regression equations and R^2 values for 'all sites' listed in Tab. III.)

Consequently, separate volume equations were developed for each taxon at each of the three sites. In all cases the most appropriate model proved to be a simple function of D^2H

Table III. The best fitting volume equations for each taxon at each site, and across sites, were all of the form VIB = b D^2H, where D = diameter at breast height (m) and H = total tree height (m).

Taxon	Site	Regression coefficient (b) on D^2H (± s.e.)	Adjusted R^2	Square-root MSE	Coefficient of variation (%)
PEE	Beerwah	0.33894 ± 0.00511	0.99	0.02799	8.5
	Toolara	0.31603 ± 0.00621	0.99	0.03183	11.5
	Tuan	0.30533 ± 0.00568	0.99	0.02880	10.9
	All sites	0.32106 ± 0.00357	0.99	0.03228	11.1
PCH	Beerwah	0.27688 ± 0.00421	0.99	0.03779	8.5
	Toolara	0.27152 ± 0.00408	0.99	0.04008	8.7
	Tuan	0.24901 ± 0.00450	0.99	0.03821	10.6
	All sites	0.26669 ± 0.00271	0.99	0.04281	10.2
F_1 hybrid	Beerwah	0.32625 ± 0.00471	0.99	0.03873	8.4
	Toolara	0.29397 ± 0.00621	0.99	0.04073	9.8
	Tuan	0.29318 ± 0.00378	0.99	0.03134	9.7
	All sites	0.30436 ± 0.00304	0.99	0.04352	10.2
F_2 hybrid	Beerwah	0.31214 ± 0.00762	0.98	0.05954	14.3
	Toolara	0.28994 ± 0.00518	0.99	0.04078	10.1
	Tuan	0.26851 ± 0.00574	0.99	0.04016	12.7
	All sites	0.29172 ± 0.00404	0.98	0.05298	14.0

Table IV. Mean Annual Increment estimated for each taxon and site using specific equations for each taxon and site to estimate volume inside bark, and a generic (conical volume) equation.

Site	Taxon	Conical volume (m^3/ha/y)		Volume inside bark (m^3/ha/y)	
		10 y	15 y	10 y	15 y
Beerwah	PEE	10.2 ± 0.51	14.4 ± 0.55	13.2 ± 0.61	18.6 ± 0.66
	PCH	16.2 ± 0.51	21.4 ± 0.55	17.1 ± 0.61	22.7 ± 0.66
	F_1	16.0 ± 0.25	20.4 ± 0.28	20.0 ± 0.31	25.4 ± 0.33
	F_2	15.8 ± 0.51	21.0 ± 0.63	18.9 ± 0.61	25.1 ± 0.74
Toolara	PEE	9.4 ± 0.27	13.9 ± 0.26	11.3 ± 0.31	16.8 ± 0.29
	PCH	18.2 ± 0.27	24.0 ± 0.26	18.8 ± 0.31	24.9 ± 0.29
	F_1	15.1 ± 0.14	19.5 ± 0.13	16.9 ± 0.15	22.0 ± 0.15
	F_2	14.8 ± 0.27	19.9 ± 0.26	16.3 ± 0.31	22.1 ± 0.29
Tuan	PEE	9.1 ± 0.38	12.1 ± 0.48	10.6 ± 0.41	14.1 ± 0.53
	PCH	14.9 ± 0.38	20.1 ± 0.48	14.2 ± 0.41	19.2 ± 0.53
	F_1	13.0 ± 0.19	16.8 ± 0.24	14.6 ± 0.21	18.8 ± 0.26
	F_2	13.1 ± 0.38	17.2 ± 0.48	13.5 ± 0.41	17.7 ± 0.53

(Tab. III). Inclusion of any additional terms either did not improve fit, or increased both the square root of the error mean square and/or the coefficient of variation. The best models identified by pooling sample-tree data across all sites within each taxon also provided high R^2s and did not adversely impact on the mean square error or the coefficient of variation (Tab. III). Therefore, it might be argued that a single volume equation could be used for each taxon, across the sites. Nevertheless, as the primary aim of this study was to examine the actual volume differences observed in the pure species and hybrids, we believed that it was more appropriate to use the site-based volume equations to compare volume production at each site due to the presumed increase in accuracy.

Analyses of all surviving trees in the three trials indicated highly significant taxon × site interactions ($p < 0.001$) for all traits (MAI, DBH, at HT at 10 and 15 year, and stem straightness, ST). However, analysis of survival at 15 years did not show any interaction between taxon and site, with small but significant differences between taxa across the three sites (95, 92, 93 and 96% survival in PEE, F_1, F_2 and PCH respectively). When each site was examined separately, survival differences were only significant at the Toolara site, where the survival of the F_1 hybrid (92%) was worse than that of the other three taxa (96–98%). Survival at the two remaining sites ranged from 91 to 96%, so all taxa were near full stocking, and it is therefore very unlikely that volume differences have been significantly impacted by differences in survival. Due to the significant site × taxon interactions, results for mean annual increment and straightness were analyzed separately for each site. Differences between taxa in MAI and ST were highly significant ($p < 0.001$) at each site; however, absolute differences in stem straightness between the taxa were relatively small, with PCH averaging 3.0 across the three sites, and the other three taxa being similar and 0.5–1.0 points straighter than PCH.

Mean annual increment estimates obtained from the taxon/site specific equations were consistently higher than estimates obtained by using a generic conical volume equation (Tab. IV). MAI of pure slash pine was consistently lower than the other three taxa, while PCH and the hybrids had similar productivity across the three sites.

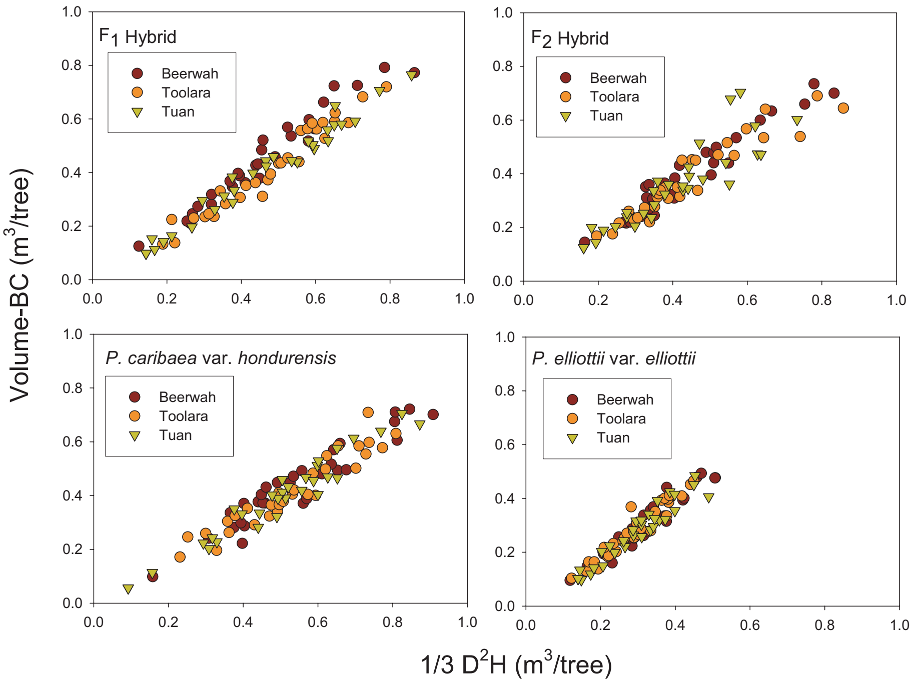

Figure 2. Relationship between volume (inside bark) estimated by centroid method and 1/3 D^2H (i.e. conical volume) at 15 years of age, for *P. elliottii* var. *elliottii* (PEE), *P. caribaea* var. *hondurensis* (PCH) and their F_1 and F_2 hybrids, across three sites in southeast Queensland.

4. DISCUSSION

The results presented clearly demonstrate that the use of a generic (i.e. conical) volume equation is not adequate for making productivity comparisons between parental species and hybrids. Further, the application of the centroid method to quickly generate site and taxon specific volume equations provides a simple and low cost method that can be used to improve the accuracy of such comparisons in genetic studies of forest trees.

Differences between taxa as illustrated in Figure 1 indicate that the relationship between taxa diverges with increasing tree size, suggesting that the inside bark form changes between taxa as trees grow larger. Taxa differences in the relationship between a proxy for growth ($1/3D^2H = 1/3 \times DBH^2 \times$ height, i.e. conical volume) and VIB calculated with the centroid method are apparent and indicate the taxa differ in form as tree size increases. The question more generally: "Is the relationship between measured D^2H and predicted VIB different for these four taxa?" The general linear model showed there were significant differences in volume production between taxa and that D^2H was a very useful covariate in explaining taxa differences in volume, while both bark-thickness and taper were not. Examination of the relationship between VIB and D^2H at each site, within each taxon (Fig. 2) suggests a consistent pattern with trees from the southern-most site (Beerwah) tending to have greater volume (for a given tree size) than the northern-most site (Tuan), with trees from the Toolara site tending to be intermediate. Although this pattern appears to be related to the latitude of the test-location, it may be coincidental. Changes in the size of the coefficients associated with D^2H in the volume equations derived for each taxon/site (Tab. III) also follow a similar latitudinal trend, but changes in the mean bark-thickness and taper of each taxon across the three sites reveal no such trend (Tab. II).

Application of the derived volume equations to all the surviving trees in each of the three trials to estimate mean annual increments at 10 and 15 years of age, demonstrated that the use of a generic (conical) volume equation would under estimated MAI for all taxon-site combinations except for PCH at the Tuan site (Tab. IV). At 15 years of age, use of conical volume most severely underestimated the volume in the F_2 and PEE (averaging –17 and –16% respectively); however, the bias was much less for PCH (averaging less than –1%) and intermediate in the F_1 hybrid (–11%). Due to the differential bias between taxa, the use of a generic volume equation would have led to: (i) re-ranking of the taxa at two of the three sites, (ii) major changes in apparent differences between taxa, and (iii) over-estimation of the heterosis associated with hybrids compared to the average of the two parents. To illustrate, using the taxon/site specific volume equations the hybrids (F_1 and F_2) are significantly superior to both parental species at the Beerwah site, but using conical volume the hybrids are not significantly different to the PCH parent, while at the Tuan site the opposite result was observed – non-significant differences between PCH and the hybrids using the taxon/site specific volume equation, but significant differences between the hybrids and PCH if conical volume were used. Use of a generic volume equation to compare different taxa can lead to markedly different conclusions, with unpredictable consequences between sites.

When compared on the basis of MAI estimated using the taxon/site specific volume equations, PEE was always significantly ($p < 0.05$) inferior to the hybrids or PCH on all three sites, the F_1 and F_2 hybrids did not differ significantly in productivity, and PCH was significantly better than the hybrids only at Toolara, but significantly worse than the hybrids at Beerwah, with no significant difference at Tuan (Tab. IV). The lack of significant differences between the F_1 and F_2 hybrids at all three sites indicates non-significant differences in heterosis between these taxa. If heterosis is determined largely by dominance, then the F_2 hybrid would be expected to lose approximately 50% of heterosis observed in the F_1 hybrid [9]. The fact that heterosis is approximately equal in the F_1 and F_2 hybrids may reflect the differences in the genetic origin of these taxa, or that hybrid superiority is largely due to additive and additive × additive epistatic genetic effects [14].

The volume production of PEE was markedly inferior to both PCH and the hybrid pines in all three sites of this study (Tab. IV), as has been demonstrated previously in other field studies (e.g. [2, 18, 19]). The relative productivity of PCH and the pine hybrids observed across the three trial sites in southeast Queensland are thought to reflect water stress due to both site position (i.e. ridge vs. lower slope) and soil type (i.e. well drained vs. poorly drained soils). Additionally, the very high mounds (i.e. beds) which were used to establish the Tuan site are believed to have induced periodic water stress during periods of low rainfall. PCH is known to have reasonable drought tolerance [8], and is believed to be more tolerant of water stress than either pure PEE or its hybrid with PEE in southeast Queensland. Consequently, PCH is likely to be better adapted to sites subject to periodic water stress than the hybrids. As sites-types similar to the Toolara site (used in this study), occupy a relatively small proportion of the total plantation estate in southeast Queensland, and because the use of high-mounding during establishment of second rotation crops on poorly drained sites is now restricted, this suggests that the superiority of the hybrid when deployed across sites in southeast Queensland may be greater than reflected in the results of this study.

Clearly the operational gain captured through the use of hybrid pine in southeast Queensland is highly dependent on the relative proportion of different environment types (i.e. slope position, soil type, management regimes, etc.) in the landscape over which hybrid pine will be deployed. For example, if we assume that the target population of environments over which the hybrid between PEE and PCH may be deployed in southeast Queensland is composed in equal proportions of site-types represented by the three trials in this study, we could use the average performance of the taxa in this study to estimate expected gains in productivity in southeast Queensland – average MAIs of 16.5, 22.3, 21.6, and 22.1 $m^3\ ha^{-1}\ y^{-1}$ for PEE, PCH, F_1 and F_2 respectively at 15 years of age, for near fully stocked stands established with approximately 1000 stems per ha in southeast Queensland. However, it would be more realistic to assume that site-types similar to the Beerwah site predominate the target environments (60%), while site-types similar to the Toolara site are rare (10%), this indicates average MAIs 17.6, 23.0, 23.7 and 23.5 $m^3\ ha^{-1}\ y^{-1}$ for PEE, PCH, F_1 and F_2 respectively should be expected across the forest estate.

Consideration of other traits, such as stem straightness (PCH was significantly inferior to PEE and both hybrids at all three sites in this study), and superior wood quality (Hybrid ⩾ PEE > PCH [14, 18]) and resistance to wind-damage (PEE > hybrid > PCH), also favour the use of hybrid pine over PCH for deployment on most sites in southeast Queensland for production of structural-grade timber.

Acknowledgements: The authors wish to thank Eric Keady (Forestry Plantations Queensland) and Chris Brack (Australian National University) for advice and guidance on the application of the centroid method in this study, and the Queensland Department of Primary Industries – Forestry (now Forestry Plantations Queensland) and Cooperative Research Centre for Sustainable Production Forestry for financial support of this research, provision of data and relevant information used in this study.

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