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Genetic Variation and Tree Improvement of Konishii fir (*Cunninghamia lanceolata* (Lamb.) Hook. var. *konishii*) in Taiwan

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Abstract

We analyzed a 21-year old progeny test of Konishii fir (*Cunninghamia lanceolata* (Lamb.) Hook. var. *konishii*) involving 75 families. Tree height and diameter at breast height (DBH) were periodically recorded. At age 21, average height, DBH, and volume were 15.2 m, 20.2 cm, and 278 dm^3, respectively. At this age, family accounted for 9, 12, and 11% of the total variance in height, DBH and volume, respectively. Also at age 21, individual tree heritability was 0.35, 0.49, and 0.45 for height, DBH and volume, respectively, and family heritability was 0.53, 0.69, and 0.66 for the three respective characteristics. The age trend for all genetic parameters was more stable for DBH than for height and volume. Family (backward) selection for DBH at age 21 resulted in a 9.6% gain and indirectly 5.1 and 21.0% gains for height and volume, respectively, compared to 5.2 and 20.1% gains for height and volume, respectively, when selection for these characteristics is done directly. DBH

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is an effective proxy trait for selection in growth. DBH is also less susceptible than height to typhoon damage, which frequently afflicts tree plantations in Taiwan. Therefore, DBH should be considered as the primary trait for selection for Konishii fir in Taiwan. Konishii fir is a genetically variable species despite its limited geographic range, and is fast growing which makes it a viable candidate species for tree improvement.

Key words: Konishii fir, genetic variation, tree improvement, Taiwan.

Introduction

Taiwan is a subtropical island (*Figure 1*) with a total land area of approximately 36,000 square kilometers. About 35 % of the island is above 1,000 m with over 50 mountains above 3,000 m in elevation. This mountainous topography greatly increases the complexity of the local climate and creates diverse habitats resulting in a rich forest flora with over 4,000 woody species of both angiosperms and gymnosperms (CHANG et al., 1979; HSU et al., 2004). Forests dominate the vegetative landscape of the island. Frequent typhoons bring large amounts of rain and strong winds, which play an important role in ecosystem renewal as well as being a destructive disturbance to forests. These geo-climatic and bio-ecological constraints pose difficult challenges for forest management, including operational tree improvement.

Figure 1. – Map showing the location of the samples and the range of Konishii fir (the shaded area) in Taiwan.

Konsihii fir (*Cunninghamia lanceolata* (Lamb.) Hook. var. *konishii*) is one of the most commonly planted timber species in Taiwan. Its taxonomical status as a species has been debated. Molecular evidence indicates that Konishii fir is phenetically linked to China fir (*Cunninghamia lanceolata*) and is not sufficiently differentiated to be an independent species (LIN et al., 1998; LU et al., 1999; HWANG et al., 2003; CHUNG et al., 2004). Also, there is no evidence that effective reproductive isolation has evolved (YANG and CHUNG, 1999). However, they are different morphologically (LIU et al., 1988). Taiwan Strait, which was formed approximately 3.5 million years ago (LIU, 1972; TSUKADA, 1967), lies between Taiwan and Mainland China and has made gene migration from continental China to Taiwan impossible. This long period of isolation may have facilitated the morphological divergence, but not in supposedly neutral genemarkers. Taxonomically, it is now generally accepted that China fir is the ancestor species of Konishii fir, and the latter is a subspecies endemic to Taiwan (LIU et al., 1988; LU et al., 1999). Konishii fir is also called Luanta fir, after the Luanta Mountain in central Taiwan where it was first found. Its natural distribution is limited to central Taiwan (latitude 23°30' and 24°30' above 1,000 m, *Figure 1*).

The tree improvement program in Taiwan started in the early 1970s. A series of provenance and genetic tests and seed orchards were established for conifer timber species including Konishii fir. The program did not thrive, partly due to the small land base and partly due to the large number of potential target species (over a dozen including broadleaf species) that were available for improvement in terms of desirable wood properties for high-value products such as furniture, panel, veneer, etc. Also, the rapid change in industrial structure and socio-economic factors in Taiwan has reduced wood manufacturing, once a core economic contributor, to a less significant industry. However, the tests and seed orchards have been well maintained and were periodically measured (CHUNG et al., 2009).

Interest in tree improvement was rekindled in recent years out of concerns over the impacts of global warming (HSU and CHEN, 2002; QUAN et al., 2009) and also the dwindling forest resources in neighboring countries in Southeast Asia, a major timber source for Taiwan in the past decades. Analyses of the growth data from these progeny tests, which are now close to rotation age, can provide the basic information on genetic variability, heritability, selection regime, and potential gain for assessing the short and long term viability for tree improvement.

Konishii fir is a fast growing timber species with a dominant central stem. It can sustain over one centimeter of annual diameter growth and produce 300 m^3 of merchantable volume per hectare at age 30 (LIU et al., 1979). The diameter growth of the trees from the Konishii provenance test was in decline. Consequently, CHUNG et al. (2009) used growth curve analyses as a tool for assisting with decisions about what age to make selections. In this report, we analyze the data focusing on genetic parameter estimates to recommend approaches for the genetic improvement of Konishii fir.
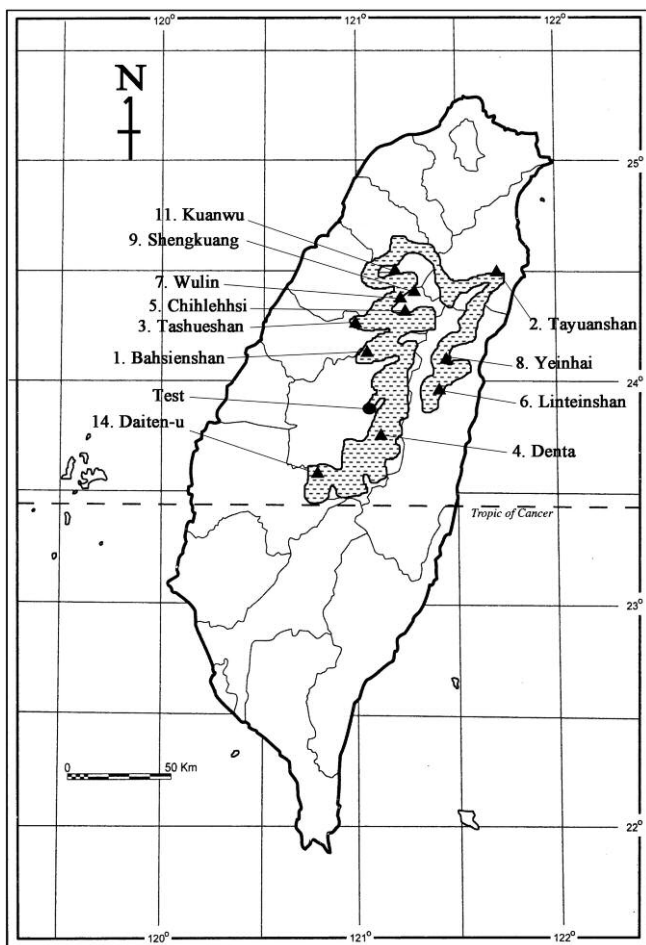
Table 1. – Measurement schedule.

Year/ month	Plantation age (yrs)	Height	Diameter		Year/ month	Plantation age (yrs)	Height	Diameter
73/08	0.5	✓			80/01	7.0	✓	✓
74/12	2.0	✓			81/01	8.0	✓	✓
75/06	2.5	✓	✓		87/01	14.0		✓
76/01	3.0	✓			94/01[a]	21.0	✓	✓
77/01	4.0	✓			97/01	24.0	✓	✓
78/01	5.0	✓	✓		99/01	26.0	✓	✓
78/12	6.0	✓	✓					

✓ Measured.
[a] Individual tree identities were not recorded.

Materials and Methods

The Test Plantation

Four provenance tests were established, three of which were abandoned because of low initial survival. The test reported here was planted in January 1973 in central Taiwan at an elevation of 1,044 m. Ninety-five families from 12 provenances of Konishii fir (*Figure 1*) and one China fir source were tested in a randomized complete block design with five blocks. Each family was planted in a 10-seedling row plot at 2×2 m spacing (CHUNG et al., 2009). The planting stock was $1+1$ bare-root seedlings. The test was spaced in 1989 after 16 growing seasons and about one-third of the trees were removed to reduce inter-tree competition. The seeds were from natural stands except the China fir seed. For the 'purity' of genetic parameter estimates, we excluded the China fir source (20 families) from our analysis, leaving growth data from 75 Konishii fir families to analyze.

Data

Diameter at 1.3 m (DBH, cm) was measured 9 times and total height (HT, m) was measured 12 times (*Table 1*). Individual tree identity (tree position in the family plot) was not recorded at the age 21 measurement. The number of trees that were measured in each plot varied at different ages. At the ages when only partial measurements were taken, about five trees (usually the same trees) in each plot were measured. The last measurement was done in 1999 at age 26, which is very close to the harvest age of about 30 years (KUO, 1995). A severe typhoon in 1996 caused considerable damage to the test plantation, which mainly affected height (CHUNG et al., 2009). The final measurement before the typhoon was in 1994 at age 21, which served as the target age in our calculations of genetic response to selection. However, the trees were already exhibiting asymptotic growth before the typhoon, most evident in DBH (CHUNG et al., 2009). In this report we focus the analyses on the growth before the typhoon.

Individual tree volumes (VOL, dm³) were estimated using the following equation (FENG and JENG, 1992):

$$\text{VOL} = 0.0000702 \times (\text{DBH}^{1.8942224}) \times (\text{HT}^{0.8869654}).$$

Estimates of variance components and genetic parameters

Growth traits at different ages were analyzed according to the following model:

Table 2. – Expected mean squares for the variance components assuming all the effects are random.

Source	Expected mean squares[a]
Block	$\sigma^2 + k_1\sigma^2_{fb} + k_2\sigma^2_b$
Family	$\sigma^2 + k_3\sigma^2_{fb} + k_4\sigma^2_f$
Block × Family	$\sigma^2 + k_5\sigma^2_{fb}$
Residual	σ^2

[a] The k coefficients are from procedure GLMs estimate function IV.

$$Y_{ijk} = \mu + B_i + F_j + BF_{ij} + \varepsilon_{ijk}$$

where Y_{ijk} is HT, DBH, or VOL of tree k from the jth family planted in the ith block, μ is the overall mean, B is the random block effect, F is the random family effect, BF is their interaction and ε is the error term. The expected mean squares (EMS) for the model terms are given in *Table 2*.

We did not include provenance effect because provenance variation is not correlated with its geographic origin and accounts for small amount of the total variance in our previous analyses (CHUNG et al., 2009). In other words, provenance variation is not geographically structured and thus not adaptive in nature (LIN et al., 1998). We, therefore, treated the 75 families as representative samples of the species in our analyses.

We employed the SAS procedure MIXED with the REML method to estimate the variance components (VCs) and predict the family means. Procedure MIXED does not allow the estimates of the VCs to be negative and produces best linear unbiased predictions (LITTELL et al., 1996). Variance component estimation also does not require the data to be strictly normally distributed (SEARLE, 1971). We also subjected the same data to an analysis of variance using procedure GLM in SAS with estimate function IV based on the same linear model described above. The error VCs were identical to those obtained from procedure MIXED, the VCs for the block and family interaction were almost identical, and the VCs for the main factors were slightly different. We reported the VC estimates from procedure MIXED and used the component coefficients (*Table 2*) from procedure GLM to derive the heritabilities and genetic gains.

Individual tree heritability (h^2_i) and family heritability (h^2_f) were estimated using the following equations (NYQUIST, 1991):

$$h^2_i = 4 \times \sigma^2_f / (\sigma^2 + \sigma^2_b + \sigma^2_{fb} + \sigma^2_f)$$

$$h^2_f = \sigma^2_f / (\sigma^2 + k_3 (\sigma^2_{fb} + \sigma^2_b) + k_4 \sigma^2_f) / k_4$$
$$= \sigma^2_f / ((\sigma^2 / k_4) + (\sigma^2_b + \sigma^2_{fb}) / (k_4 / k_3) + \sigma^2_f) \; (\textit{Table 2})$$

The inclusion of σ^2_b in calculating family heritability is debatable (NYQUIST, 1991). Site variation in different locations in the mountainous terrain is largely random, which makes it ineffective to stratify the land base into manageable and meaningful strata according to site factors. Test sites in different locations from the site that we analyzed will most likely encounter the same type of variation represented by the blocks within the site, though perhaps with differing magnitudes. We included both σ^2_b and σ^2_{fb} mainly to compensate for the lack of site replication in our study. Including σ^2_b only slightly affected the heritability estimates (e.g. age 21 individual-tree heritability for DBH with and without the σ^2_b were, respectively, 0.492 and 0.501).

We calculated genetic correlations and genetic responses to selection only at the family level because individual tree identities were missing at age 21 (the target age of selection). Also the focus of our analysis is to evaluate the family (backward) selection for the operational tree improvement of the species (see Discussion). Age-age genetic correlations of family means for both between- and within-traits are calculated with the following equation:

$$R_{xy} = cov(xy) / (\sigma_x \sigma_y),$$

where, cov(xy) is the covariance between early (x) and target (y) age of the same trait or different traits, and σ_x and σ_y the square root of their family components.

The family selection calculations for genetic gains are based on the following equations:

$$G = i \times h^2_f \times (\sigma^2 / k_4 + (\sigma^2_b + \sigma^2_{fb}) / (k_4 / k_3) + \sigma^2_f)^{1/2}$$ for direct selections at the different age individually (NAMKOONG et al., 1966), and

$$G_{xy} = i \times (h^2_x \times h^2_y \times \sigma^2_{p(y)})^{1/2} \times R_{xy}$$ for selections at younger ages with target growth traits at age 21 (LAM-

Table 3. – Variance components (VC × 100), also presented as intra-class correlations (% of total variance), and individual (h_i) and family (h_f) heritability for total height at different ages.

	Plantation Age (years)					
	Variance Component (%)					
Source	4.0	5.0	6.0	7.0	8.0	21.0
Block	26 (19)	24 (10)	34 (10)	25 (7)	26 (5)	12 (1)[a]
Family	28 (21)	33 (14)	55 (16)	53 (15)	79 (16)	127 (9)
Block × Family	40 (29)	25 (11)	32 (9)	31 (9)	55 (11)	257 (18)
Error	44 (31)	154 (65)	222 (65)	236 (68)	337 (68)	1045 (72)
Error Df	709	2332	2285	2247	2198	1189
	Heritability					
h_i	0.821	0.556	0.643	0.617	0.638	0.352
h_f	0.629	0.692	0.731	0.738	0.744	0.534

[a] The variance component is not statistically significant at the 0.05 level, otherwise it is significant.

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BETH, 1980) or indirect selections between traits at the same age, where i = 0.956 assuming a selection intensity of retaining 30 out of the 75 parent trees in the seed orchard (the clonal seed orchard was established in 1971, two years before the progeny test) (NAMKOONG and SNYDER, 1969); h^2_x and h^2_y are the family heritabilities at the age when the selection was made and at the target age, respectively. For indirect between-trait selection at the same age, they are family heritabilities for trait x and y, respectively; $\sigma^2_{p(y)}$ is the phenotypic variance of the target trait as defined in h^2_f and R_{xy} the family correlation as described above.

We employed the above analytical approach considering its relevance to the situation in operational tree improvement in Taiwan (see Discussion) and constraints of the data, an operational mode of analysis (SEARLE, 1971; NYQUIST, 1991).

Results

Variance components and heritability estimates for HT, DBH and VOL are shown in *Tables 3* to *5* (we did not report the results before age 4 for better between-trait comparisons in age trend); all the effects were sta-

Table 4. – Variance components (VC × 100), also presented as intra-class correlations (% of total variance), and individual (h_i) and family (h_f) heritability for DBH at different ages.

Plantation Age (years)						
Variance Component (%)[a]						
Source	5.0	6.0	7.0	8.0	14.0	21.0
Block	28 (4)	70 (5)	42 (3)	23 (1)	76 (2)	86 (2)
Family	77 (10)	160 (12)	197 (13)	256 (14)	420 (14)	592 (12)
Block × Family	92 (11)	80 (6)	86 (6)	89 (5)	70 (2)	201 (4)
Error	597 (75)	986 (76)	1218 (79)	1494 (80)	2533 (82)	3932 (82)
Error Df	2273	2272	2246	2196	2096	1198
Heritability						
h_i	0.387	0.495	0.512	0.550	0.542	0.492
h_f	0.632	0.718	0.749	0.780	0.783	0.687

[a] All variance components are significant at the 0.05 level.

Table 5. – Variance components (VC), also presented as intra-class correlations (% of total variance), and individual-tree (h_i) and family (h_f) heritability for total volume (dm³) at different ages.

Plantation age (years)					
Variance component (%)[a]					
Source	5.0	6.0	7.0	8.0	21.0
Block	6 (5)	34 (7)	35 (4)	57 (3)	835 (2)
Family	10 (8)	48 (10)	95 (11)	237 (12)	5406 (11)
Block × Family	16 (13)	33 (7)	55 (7)	111 (6)	2844 (6)
Error	89 (74)	352 (75)	654 (78)	1536 (79)	38543 (81)
Error Df	2273	2272	2246	2196	1188
Heritability					
h_i	0.322	0.412	0.453	0.488	0.454
h_f	0.573	0.660	0.711	0.739	0.659

[a] All variance components are significant at the 0.05 level.

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Table 6. – Age-age genetic correlation of family means between early and target age at 21 within and between traits.

Selection Trait	Target Trait		
	HT (age 21.0)	DBH (age 21)	VOL (age 21.0)
HT (age 4.0)	0.66	--	--
HT (age 5.0)	0.68	0.51	0.44
HT (age 6.0)	0.68	0.52	0.43
HT (age 7.0)	0.74	0.58	0.50
HT (age 8.0)	0.74	0.56	0.47
HT (age 21.0)	1.00	0.87	0.81
DBH (age 5.0)	0.77	0.74	0.70
DBH (age 6.0)	0.79	0.81	0.75
DBH (age 7.0)	0.79	0.81	0.77
DBH (age 8.0)	0.82	0.85	0.81
DBH (age 14.0)	--	0.95	--
DBH (age 21.0)	0.87	1.00	1.00
VOL (age 5.0)	--	--	0.76
VOL (age 6.0)	--	--	0.77
VOL (age 7.0)	--	--	0.81
VOL (age 8.0)	--	--	0.85
VOL (age 21.0)	--	--	1.00

tistically significant at probability 0.05 except the effect of block at age 21 (*Table 3*). The family VC for height stabilized at around 15% from age 5 to 8, and then dropped to 9% at age 21. The size of the family-block interaction VC showed a similar trend, becoming stable at about 10% from ages 5 to 8, and then a sharp increase to 18% at age 21. The family-block interaction and error VCs together accounted for about 75% of the total variance for most years. The VCs for DBH (*Table 4*), on the other hand, showed a high degree of stability with age compared to that for height; the family component varied from 10 to 14% of the total variance from age 5 to 21. Both family-block interaction and error components were remarkably stable over the age range, and together accounted for about 85% of the total variation (*Table 4*). Within the same age range, the size of the block effect for height was not only substantially larger but also more variable than that for DBH (1 to 10% vs. 1 to 5% from age 5 to 21) (*Table 3* and *4*). Both the size and stability of the block and family-block interaction VCs suggested that height growth was more sensitive to within-site environments than DBH. The VC age trend for volume (*Table 5*) essentially followed that of DBH. This is expected since DBH is more related to volume (CHUNG et al., 2009). Again, the family-block and error components combined accounted for about 85% of the total variance. With such a high within-plot variance,

individual tree selection for any of the growth traits in this test cannot be expected to be effective.

Individual tree heritability for height (*Table 3*) remained at about 0.6 for most of the years except at age 4, and a sharp drop at age 21 to 0.35; family heritability was relatively stable over time, varying from 0.5 to 0.7. The trend for both individual and family heritability for DBH (*Table 4*) was stable without the sharp drop from age 8 to 21 as seen for height. Heritability stabilized at around 0.5 for individuals and at 0.7 for the families after age 5. Volume heritability showed a similar age trend as DBH, and, after age 5, stabilized at around 0.45 for individual heritability and around 0.7 for family heritability (*Table 5*).

The family genetic correlation (*Table 6*) between early and target ages within traits increased as age approached the target age of 21 years. Correlation coefficients were higher for DBH than for height and volume at the same early ages. Between-trait correlations associated with DBH at the same age combinations were also higher than others, e.g. at age 21, DBH-volume genetic correlations were 1.00, compared to 0.81 for height-volume. Genetic correlations (*Table 6*) clearly indicate that selection on DBH can be highly effective to achieve a genetic gain in growth. Indeed, predicted responses to selection on DBH in either a direct or indi-

Table 7. – Genetic gains (% of target trait in parentheses) at target age 21 from within- and between-trait family selection at early and target ages.

Selection Trait	Target Trait		
	HT (age 21.0)	DBH (age 21.0)	VOL (age 21.0)
HT (age 4.0)	0.57 (3.7)	--	--
HT (age 5.0)	0.61 (4.0)	0.99 (5.9)	25.67 (9.2)
HT (age 6.0)	0.62 (4.1)	1.02 (5.1)	25.83 (9.3)
HT (age 7.0)	0.69 (4.5)	1.15 (5.7)	30.46 (10.9)
HT (age 8.0)	0.69 (4.5)	1.12 (5.6)	28.26 (10.2)
HT (age 21.0)	0.79 (5.2)	1.48 (7.3)	41.81 (15.0)
DBH (age 5.0)	0.66 (4.4)	1.38 (6.8)	39.07 (14.1)
DBH (age 6.0)	0.72 (4.7)	1.60 (7.9)	44.4 (16.0)
DBH (age 7.0)	0.74 (4.9)	1.63 (8.1)	46.8 (16.8)
DBH (age 8.0)	0.78 (5.1)	1.75 (8.7)	50.35 (18.1)
DBH (age 14.0)	--	1.96 (9.7)	--
DBH (age 21.0)	0.79 (5.1)	1.93 (9.6)	58.40 (21.0)
VOL (age 5.0)	--	--	40.91 (14.7)
VOL (age 6.0)	--	--	44.87 (16.1)
VOL (age 7.0)	--	--	48.76 (17.5)
VOL (age 8.0)	--	--	52.11 (18.7)
VOL (age 21.0)	--	--	57.97 (20.1)

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rect manner were higher than on height or volume (*Table 7*). Selection on DBH at age 21 would result in 21.0% gain in volume and 5.1% in height, compared to a gain of 20.1% from direct selection for the former and 5.2% the latter. On the other hand, selection on height would result in a 15.0% gain in volume and 7.3% gain in DBH, while a direct selection on DBH would produce a 9.6% gain (*Table 7*). Judging from the incremental trend in percentage gain from selecting at early ages (*Table 7*), selection could start after age 8.

Discussion

Konishii fir is fast growing and genetically variable (*Tables 3–5*) despite its limited geographic range (*Figure 1*). Selection for genetic improvement of growth can be expected to be effective. Gain from family selection (i.e. roguing the existing clonal seed orchard) can yield a 20% increase in volume (*Table 7*), which may be optimistic because they were based on a single site. How - ever, with family-structured open pollinated progeny testing, backward selection is expected to be reliable (RUOTSALAINEN and LINDGREN, 1998; HAAPANEN, 2001). The selection of the 30 parental trees is mainly for some immediate gain for plantations, but not large enough to sustain a long-term breeding program (JAYAWICKRAMA and CARLSON, 2000; ERIKSSON et al., 2006). The genetic base needs to be substantially broadened (see below).

The analysis of the variance components and heritability both indicate that DBH is genetically more stable than height over time (*Tables 3* and *4*). COSTA and DUREL (1996) found similar results in maritime pine (*Pinus pinaster*) and GWAZE and BRIDGWATER (2002) in loblolly pine (*Pinus taeda*), and they suggest that the genetic regulation on eco-physiological processes resulting in height growth may be different from those resulting in diameter growth.

CORNELIUS (1994) broadly reviewed individual tree heritability in forest tree species; our estimates at age 21 were higher than his means (0.35, 0.49, and 0.45 vs 0.28, 0.23, and 0.21, respectively, for height, DBH, and volume), but were within the ranges of their normal distributions (approximately 0.1–0.5). More recent reports also showed individual tree heritability is mostly within the range cited in the Cornelius review, e.g. Coastal Douglas-fir (*Pseudotsuga menziesii*) (JOHNSON et al., 1997), maritime pine (KUSNANDAR et al., 1998), and lobololly pine (GWAZE and BRIDGWATER, 2002).

The test trees averaged 15.2 m in height (range: 12.5–17.1 m), 20.2 cm in DBH (14.9–24.3 cm), and 278 dm^3 in volume (148.4–422.4 dm^3) at age 21 (before the typhoon). This growth is comparable to that found in a similar genetic trial located at a higher elevation (1,300 m) involving 18 families (at age 25, the average height was 15.2 m, DBH was 27.7 cm, and volume was 300 dm^3) (SU, 2004), and that of KUO (1995) (at an intermediate site class at age 20, height was 15.7 m, DBH was 28.0 cm, and volume was 530 dm^3), and similar to that of its sister species, China fir (height, DBH, and volume at age 20 were 17.2 m, 20.8 cm and 310 dm^3, respectively) (LIU et al., 1979). The average growth from a single test, though, is probably representative of the

species and its genetic gain estimates at age 21 (*Table 7*) are likely good indicators of gains at a typical harvesting age of 30 years.

Compared to the growth of coniferous species in other regions, Konishii fir is substantially more productive than fast growing temperate conifers, e.g. western larch (*Larix occidentalis*) (top height 6.7 m at age 20 on a site index 20 m site) (BRISCO et al., 2002), and coastal Douglas-fir (top height 11.2 m at total age 20 on a site index 34 m site) (NIGH and MITCHELL, 2003). Konishii fir has height growth that is comparable to southern pines in the United States, e.g. loblolly and longleaf (*Pinus palustris*) pine with top heights of 17.6 m and 17.3 m, respectively, at age 21 on good sites (CAO et al., 1997).

Diameter should be used as the primary trait in selection since selecting on DBH either directly or indirectly can be more effective than selecting on either height or volume (*Table 7*). Diameter growth is also less vulnerable to injuries caused by typhoons, which occur almost yearly in Taiwan and often cause severe damage to plantations. Typhoons, like fires in the temperate forests, are a natural agent that is essential to the renewal of natural ecosystems. Unlike fires, however, they cannot be controlled or prevented. CHUNG et al. (2009) found a very different pattern of growth between height and diameter based on growth curve fitting using a subset of the same data as in this analysis. Diameter growth was well into the asymptotic phase at age 21, whereas height was still increasing at the same age. Therefore, diameter can serve as better indicator of the gain at harvesting age at about 30 years.

Our study, having a single test site, naturally leads to the question of whether a progeny-site environment interaction (i.e., GxE) exists. The practical application of GxE is for breeding zone delineation as means to reduce the within-zone GxE in order to enhance genetic gain in operational tree improvement. For this purpose, the GxE has to be classifiable according to its cause-effect association with site environmental factors and can be efficiently administered (NYQUIST, 1991). HAAPANEN (2001) did one of the most comprehensive analysis of such an interaction involving over 100,000 trees from over 300 families of Scots pine in 26 tests with different planting spacing in different edaphic site conditions in Finland; the results still failed to shed evidence of a cause-effect correlation of genetic parameters with site characters. Cause-effect relationship in GxE is difficult to delineate, except it is related to a broad regional climate (WU and YING, 2004); In Taiwan with its limited land base and a mountainous terrain, such breeding zone delineation can be difficult and costly. From a cost-benefit perspective, multiple breeding zones is not a viable option for any operational tree improvement in Taiwan, even if substantial GxE exists (JAYAWICKRAMA and CARLSON, 2000; HAAPANEN, 2001; DEAN, 2007). However, the above does not suggest multiple tests to provide precision estimates of genetic parameters and gain is not needed.

We did not do an in-depth analysis to determine the optimal age of selection. There is not yet a quantitative method that is applicable in all situations. The LAMBETH

(1980) model is probably the most commonly used model in quantifying the optimal age of selection. However, the model has a built-in bias in favour of selecting at younger ages when gain per unit time is the criterion (CHEN et al., 2003), and the juvenile-mature correlation is based on time rather than biological process of tree growth (MAGNUSSEN, 1989). Using growth curve analysis techniques to determine the optimal age of selection (e.g. MAGNUSSEN, 1989; MAGNUSSEN and PARK, 1991; MAGNUSSEN and KREMER, 1993) is often complex conceptually and mathematically, and therefore, this approach is not commonly used. With Konishii fir, selection can start any time between ages 8 and 14 based on the time trend in age-age correlations (*Table 6*) and projected gains (*Table 7*), particularly if the selection is made on DBH (no further gain in diameter growth after age 14). CHUNG et al. (2009) recommend early selection at around age 10 when the diameter growth is entering into the asymptotic phase.

One immediate concern about selecting for genetic gain in growth is the negative effect of rapid growth on wood density; the market value of Konishii fir is tied to the quality of its wood. Wood density is the indicator trait of quality wood (ZOBEL and VAN BUIJTENEN, 1989). In particular, plantations today may encounter warmer climates and hence grow faster, resulting in less dense wood (STOEHR et al., 2009). Forty-eight out of the 75 families from the same test were assessed for wood density at age 25 by YANG et al. (2001); the average density was 0.36. Out of the 30 families selected, either on DBH, height, or volume, about 27 of them happen to be included in the wood density assessment; their average density was 0.35. We thus expect the production population consisting of these 30 parent trees in the rogued seed orchard will maintain the average wood density of the species. This was one factor that we took into consideration when we opted for a low selection intensity (i = 0.956) in our analyses.

Tree improvement is a proven enterprise for investment; there are many successful programs worldwide, including the coastal Douglas-fir program in British Columbia, Canada (STOEHR et al., 2010), the radiata pine in New Zealand (JAYAWICKRAMA and CARLSON, 2000), and loblolly pine in the southern United States (DOUGHERTY and WRIGHT, 2009). These programs can be useful models for tree improvement in Taiwan. Successful tree improvement has to be a long term proposition which evolves and progresses depending on a large extent on the accumulation of local knowledge and experience (JAYAWICKRAMA and CARLSON, 2000). Tree improvement does not necessarily need a complicated scheme at the start; a simple recurrent selection may be sufficient (ERIKSSON et al., 2006). One advantage of Konishii fir is that the seed orchard is already producing a commercial quantity of seed; an operational tree improvement program can be launched with an immediate, although perhaps modest, gain. Taiwan's tree improvement program has lost three decades. The sooner the program can get back on track, the better.

The main purpose of this research was to provide guidance on making informed decision regarding the operational tree improvement of Konishii fir. We conclude by recommending:

1) The expansion of breeding and selection including China fir. Konishii fir is genetically variable and fast growing which makes it a suitable candidate for operational tree improvement (ERIKSSON et al., 2006). China fir has been planted in Taiwan for centuries and is a land race. No reproductive barrier exists between Konishii and China fir (YANG and CHUNG, 1999). Including China fir broadens the genetic basis and also expands the potential land base for plantations, the latter a major barrier to operational tree improvement in Taiwan. The genetic combination of Konishii-China fir is expected to be productive in the low elevation foothills, where economic crops of fruit trees and vegetables were once planted. These labour intensive crops are no longer profitable.

2) Roguing the clonal seed orchard to retain about 30 parental clones with the best progeny performance for seed production and some immediate genetic gain.

3) Establishing multi-site progeny trials (including China fir) at representative locations to enable efficient assessment of the magnitude of site variation and classifiable progeny-site interactions for the long-term benefits of genetic improvement (HAAPANEN, 2001).

4) Developing a general breeding strategy using realistic approaches that consider both technical and administrative structures and be flexible to allow progressive changes of the program in the long term ((JAYAWICKRAMA and CARLSON, 2000; ERIKSSON et al., 2006).

Taiwan is rich in forest flora. On wood property alone, a number of species could be candidate species for tree improvement. Unfortunately, all the top candidate species seem to have certain undesirable silvicultural or biological characteristics, for example, *Chamaecyparis formosensis*, and *C. obtuse* tend to grow poor stem form and excessive branches in plantations, and *Calocedrus formosana* and *Taiwania cryptomerioides* are reproductively late mature species, cone production starts at about age 30 for the former (CHUNG et al., 2001), and at 45 for the later (LIU and SU, 1983). These undesirable characteristics have hindered efforts to improve these species employing genetic breeding. Again, with limited land base for plantation forests, a multiple-species breeding program is probably not a realistic option, economically.

Acknowledgements

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The effectiveness of phenotypic selection in natural populations: a case study from the Peruvian Amazon

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Abstract

Phenotypic selection is commonly used in agroforestry, both in genetic improvement and as a component of "good practice" in seed collection. In the first case, the aim is to secure genetic gain. In the second case, selection is used to ensure that seed supplies meet given minimum quality standards, or that poor quality sources are avoided. Here we examine the effectiveness of phenotypic selection in natural forest stands of the Amazonian timber and multipurpose tree *Calycophyllum spruceanum* Benth.. We ask (a) whether mother-trees with high estimated annual height and diameter increments had faster growing progeny than mother-trees with low values; (b) whether forked mother-trees tended to have higher proportions of forked progeny than unforked trees; (c) whether spatially isolated mother-trees tend to produce slower growing progeny than mother-trees growing together with conspecifics. In each case, we found no evidence of differences between the respective groups. We offer explanations for these findings and discuss their implications for tree improvement and seed collection.

Key words: Calycophyllum spruceanum, progeny-test, tree domestication, tree improvement, seed collection, tropical rainforest.

Introduction

Phenotypic selection is used commonly in agroforestry, both in genetic improvement programmes (e.g. MESÉN et al., 1994) and as a component of "good practice" in seed collection (e.g. MULAWARMAN et al., 2003). In the first case, the aim is to secure genetic gain. In the second case, selection is used to ensure that seed supplies meet given minimum quality standards, or that poor quality sources are avoided.

Phenotypic selection involves a cost. Therefore, its effectiveness is of interest. CORNELIUS (1994a) established that plus-tree selection for yield can be effective. However, there were indications that selection is less effective in wild stands than in plantations. There are

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