Pilot integrated breeding value prediction in Swedish *Pinus sylvestris* shows high potential gain.

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ABSTRACT

Data for health, growth and knottiness at two ages were integrated for breeding value prediction across 12 control-pollinated first generation and 3 second generation control and open-pollinated trials of the Skogforsk T11 *Pinus sylvestris* population. The prediction used genetic linkages at the parental and latitudinal level and genetic correlations between traits, site types and measurement ages. Spatial analysis reduced error variance by 10% for health, 15% for height and 5% for DBH and data were adjusted accordingly. The best descriptor of genotype by environment interaction for early health and growth was the actual early health and sites were stratified accordingly, although there was residual unexplained genotype by environment interaction. Latitudinal differences for health decreased with increasing site health, as did additive genetic and error variances. Latitudinal origin was positively related to health, but negatively related to growth, whereas the within group genetic correlation between health and growth was positive (0.6). Breeding values were predicted for 14 genetic groups (representing species, latitude of origin and selection history), and 80,000 genotypes across 3 generations for 16 selection criteria representing 4 traits (health, height, DBH and spike knots), two ages classes (approximately 11 and 30 years old), and three site types for health and growth. The data were scaled to a common unit additive variance, with a separate error variance to account for differences in heritability observed between sites and traits. Stand harvest volume (/unit area) was predicted by assuming that with increased site health the correlation with health decreased and that with tree size increased. Latitudinal trends for health and growth complied with broader analyses. The average of selections made at a young age from the first generation trials was only 10-20% of the predicted stand volume of selections identified from this analysis. This difference reflects less integrated use of data and pedigree, poorer estimation of environmental trends within trials, and the availability only of early measurements. Best selections predominantly now came from trials with later age measurements derived from parents of superior latitudinal origin. The pilot project utilised a robust framework to integrate data, pedigree and knowledge of the species which can be readily expanded to a larger population.

KEY WORDS

Pinus sylvestris, Sweden, breeding value prediction, TREEPLAN.

INTRODUCTION

Evaluation of genetic material lies at the heart of selection of new parents for mating, and thus genetic progress. Integrated prediction of breeding values using all available pedigree and data has become a popular method for evaluating genetic material in tree breeding programs over the last decade (Jarvis *et al.* 1995). These methods have been adapted from animal breeding where they were adopted to deal with large imbalance in genetic composition

between herds and across time and to allow simultaneous prediction of value for all animals (parents and offspring) for a breed (Kennedy & Sorensen 1988) in the context of the Mixed Model Equations (MME) and BLUP (Best Linear Unbiased Prediction) (Mrode 1998). Central to this is the use of the numerator relationship to account for all known relationships between animals (Henderson 1976), including genetic groups (provenances) (Westell *et al.* 1988). Substantial increases in rates of genetic gain in animals have been reported through the adoption of integrated analyses, especially once profit indices are defined to allow proper weighting of traits in multi-trait selection (Banks et al 2001).

Until recently many breeding programs have used BLP (Best Linear Prediction) to estimate breeding values (White & Hodge 1989), even though this method assumes that fixed effects are known. This is problematic when dealing with trials with differences in genetic composition, especially across time. White and Hodge (1989) argue that in many forestry situations fixed effects can be adequately estimated so the computational complexity of BLUP can be avoided. Certainly in many situations the problems that led to the development of BLUP for animal breeding – highly unbalanced data making it difficult to estimate sub-class means, genetic trend due to multiple generations of data, and more data on better animals due to culling – are not present in base generation tree breeding programs with large balanced trials. For animal breeding, prediction of breeding values requires the use of large data sets because of the lack of structure and experiments in the breeding populations. This has not been the case for trees.

Increasingly, however, breeding value prediction in forestry trials is moving closer to the animal breeding model. Programs are moving into advanced generations where simple trial means are no longer unbiased estimates of site effects, and relatedness and selection need to be taken into account in variance component estimation and breeding value prediction. Trial designs are now more complex than the simple randomised complete block designs of the past with cyclic and computer-generated designs (Nguyen & Williams 1993) using incomplete blocks within replicates and models using recovery of inter-block information (Williams & Matheson 1994). The computational limitations of the past are being removed with the general increase in processing speed and the development of software for variance component estimation and solving of the mixed model equations. These changes are gradually seeing an increase in the use of the mixed model equations and the numerator relationship matrix in the prediction of breeding values (Apiolaza & Garrick 2001; Araújo *et al.* 1997; Fernandez *et al.* 1998; Jarvis *et al.* 1995; Soria *et al.* 1998; Wei & Borralho 2000).

In their comparison of BLP and BLUP, White and Hodge (1989) urged that the assumptions used in the application of BLUP to animal breeding be examined for their appropriateness when the method is used in tree breeding. Specifically they raise the issues of heterogenous variances, estimation of population effects, dealing with inbreeding and coancenstry, the effect of selection and computational feasibility. Similarly, Borralho (1995) argued that the problems due to uncertain pedigree in open-pollinated material, spatial auto-correlation, and heterogenous variances amongst classes of fixed effects all required attention.

BLUP has been adapted for use in trees by a number of organisations with a variety of programs and a (presumably) a variety of ways of dealing with some of the issues in adapting these methods to trees. Reporting of the use of BLUP with the Numerator Relationship Matrix for routine prediction of individual tree breeding values in large programs has not been widespread in the published literature. These models are being used more and more for large scale evaluations, however these tend to be for proprietary use, rather than for publication. ASReml (Gilmour *et al.* 1999) is being used in a number of programs: New Zealand *Pinus radiata* (L. Apiolaza *pers. comm.*), U.S.A. *Pseudotsuga menziesii* (C. Dean *pers. comm.*), and Chilean (R. Sanhueza and J. Brawner *pers. comm.*) and Portuguese (N. Borralho *pers. comm*.) *Eucalyptus globulus*. It has been mainly used on a univariate basis, as has SAS for *Pinus taeda* (B. Li *pers. comm.*). Multivariate analysis has been carried out using PEST (Groeneveld 1990) in Australia for *E. globulus* (Jarvis *et al.* 1995), *Araucaria cunninghamii* and a number of *Pinus spp*. and hybrids (M. Dieters *pers. comm.*), TREEPLAN (Kerr *et al.* 2001) for *Pinus radiata*, *E. globulus* and *E. nitens* (Dutkowski *et al.* 2006b), and BioCat (De Beer *et al.* 2001) for *Pinus radiata* in Chile. Dutkowski (2006b) reported on the benefits of data and pedigree integration found in a number of tree breeding programs.

The goals of the tree improvement program for Scots Pine (*Pinus sylvestris*) in northern Sweden are to improve vitality (cold hardiness and health), growth, stem form and wood quality. The northern program manages 13 of the 24 Swedish breeding populations of Scots pine. The extensive testing of about 4,000 founder plus-trees is almost completed. The 60-70 best trees from each breeding population are being crossed to produce a new generation of progeny. Crossing has begun in 8 of the 13 breeding populations, with progeny to be established in trials for forward selection or in clonal archives for later progeny testing. Clonal testing of these progenies are considered as an option and is presenly evaluated. Seed orchards are currently being replaced with superior genetic material.

The T11 breeding population was chosen for a pilot study as it exhibits many of the issues that White and Hodge (1989) and Borralho (1995) raise in terms of integrated analyses. A variety of related traits have been measured and these display heterogeneity of variances. The base material comes from different latitude origins and provenance effects are known to be important in performance ((Eiche & Andersson 1974)). The base population trials are of control pollinated origin, so the use of a numerator relationship matrix is advantageous. There is poor genetic linkage between trials and a variety of cross types have been used. There is a large degree of environmental heterogeneity within trials (Ericsson 1997). This population was thus an ideal candidate to assess whether the sorts of gains reported by Dutkowski (2006b) for other species could be attained in Swedish *P. sylvestris* populations as it could be regarded as a microcosm of all Swedish populations. This pilot study was carried out to help in deciding whether a full evaluation across all populations was justified. The TREEPLAN® system (Kerr *et al.* 2001) and its associated data management system were used for the pilot study.

MATERIAL, METHODS AND RESULTS

Producing breeding values by integrating all pedigree, measurement and genetic architecture information is a lengthly process, with a number of distinct stages. Methods and results are thus presented for each stage in turn.

Pedigree Definition

The population (TPOP 11) is based on 97 founder parents (50 plus-trees selected for orchard 411, and 47 for orchard 18/410). Cross-pollination (matings) was done separately for the two orchards, using mainly partial diallel designs. In orchards 411, 199, and 18/410, 153 full sib crosses were made.

Three F1 progeny tests were established for each orchard series, with about 45,000 seedlings planted and tested. Control lots of northern provenances and *P. contorta* were planted in many of the trials. The trials were measured at ages 10 and 30 years and F1 selections were used as parents to make a total of 111 F2 full sib families and some open-pollinated families. F2 progeny were planted in three field trials with about 2,300 trees in each, making a total of 6,900 individuals.

Sixty three genetic groups were defined to allow appropriate accounting for species and latitudinal differences, and for groups of males in the second generation to allow for open pollination (Table 1). For breeding value prediction, the subrace level (

Table 1) was used to delineate Westell genetic groups (Westell *et al.* 1988), with subdivisions below that only used for validation purposes. The subraces were defined based on latitudinal groups as it is thought that finer scale delineation is not possible due to the homogenising effect of pollen flow swamping any more local differentiation (Figure 1). Groups representing pollen clouds in seed orchards and trials were created and allocated to unselected latitudinal subraces.

Dummy families were defined to allocate plus-trees to their group. Control pollinated families for F1 generation trials were created to reflect the families that existed in trials. Other families representing bulk seed lots and controls were also created. Trees in F1 trials that had become parents of families in the F2 trials were identified. All new CP and OP families in the F2 trials were then created with the male parents of the OP families reflecting their origin.

The number of families per trial and the number of parents represented in each trial (Table 2) was quite different, with often little overlap between trial series. Control pollinated families dominated in the trials, but in each trial there were also other family types represented (Table

3). Although there were plus-trees selected in all F1 trials, only selection in the more recent five acted as parents for the F2 family trials (

Table 4).

Table 1: Groups defined to cover species, native provenances, open pollinated seed and others

Material	*Species/ sub-species*	*Race*	*Sub-Race*	*Locality*	*Population*	*N Gps*
F1 CP parents	*P sylvestris*/ Sweden	North Sweden	Lat XX Selected	Stand plus-tree	Stand code	132
CP Control parents	*P sylvestris*/ Sweden	North Sweden	Lat XX Selected	Control collection	"X"+Stand name	4
Seed Orchards	*P sylvestris*/ Sweden	North Sweden	Lat XX Selected	Seed orchard	Seed Orchard Number	4
Seed Orchard Pollen	*P sylvestris*/ Sweden	North Sweden	Lat XX Unselected	Seed orchard	Seed Orchard Number+Pollen	4
Trial Pollen	*P sylvestris*/ Sweden	North Sweden	Lat XX Unselected	Trial	Trial Number+Pollen	2
Routine seedlots	*P sylvestris*/ Sweden	North Sweden	Lat XX Unselected	Stand Seed	Stand code	18
Unknown	Unknown	Unknown	Unknown			1
Pinus contorta control lots	*P. contorta*	*P. contorta*	*P. contorta*	Lat XX	Stand Number	5

Table 2: Families (lower triangle) and parents in CP families (upper triangle) in common between trials

Trial		F256	F257	F258	F260	F261	F277	F279	F280	F281	F282	F283	F285	F521	F522	F523
F256	55	22	22	12	12	12	21	8	8	8	6	6	6	4	4	4
F257	51	52	23	13	13	13	22	8	8	8	7	7	7	4	4	4
F258	7	8	178	42	42	42	14	12	12	12	8	8	8	4	4	4
F260	7	8	178	187	44	44	16	14	14	14	10	10	10	4	4	4
F261	7	8	175	184	184	44	16	14	14	14	10	10	10	4	4	4
F277	54	51	8	9	9	79	26	12	12	12	9	9	9	3	3	3
F279	6	6	7	8	8	9	211	54	54	54	13	13	12	3	3	3
F280	6	6	7	8	8	9	209	209	54	54	13	13	12	3	3	3
F281	6	6	7	8	8	9	210	209	210	54	13	13	12	3	3	3
F282	2	3	4	5	5	4	6	6	6	169	56	56	55	4	4	4
F283	2	3	4	5	5	4	6	6	6	163	163	56	55	4	4	4
F285	2	3	4	5	5	4	6	6	6	162	162	162	55	4	4	4
F521	6	6	5	5	5	5	6	6	6	3	3	3	162	106	106	106
F522	6	6	5	5	5	5	6	6	6	3	3	3	161	161	106	106
F523	6	6	5	5	5	5	6	6	6	3	3	3	161	161	161	106
	F256	*F257*	*F258*	*F260*	*F261*	*F277*	*F279*	*F280*	*F281*	*F282*	*F283*	*F285*	*F521*	*F522*	*F523*	

Table 3: Family types by trial.

CrossType	F256	F257	F258	F260	F261	F277	F279	F280	F281	F282	F283	F285	F521	F522	F523
Pinus contorta							3	3	3	3	3	3			
Stand Seed Bulk	5	5	5	5	5	5	5	5	5	5	5	5	12	12	12
Seed Orchard Bulk						1	1	1	1	2	2	2			
CP Control	2	2	2	2	2	1	1	1	1	3	3	3	3	3	3
F1 CP	48	45	171	180	177	52	201	199	200	156	150	149			
F2 OP SO						20									
F2 OP Trial													45	45	45
F2 CP													102	101	101

Table 4: Origin of second generation parents.

Trial	*CP*	*OP*
F279	2	
F280	35	31
F281	38	
F283	9	
F285	16	14

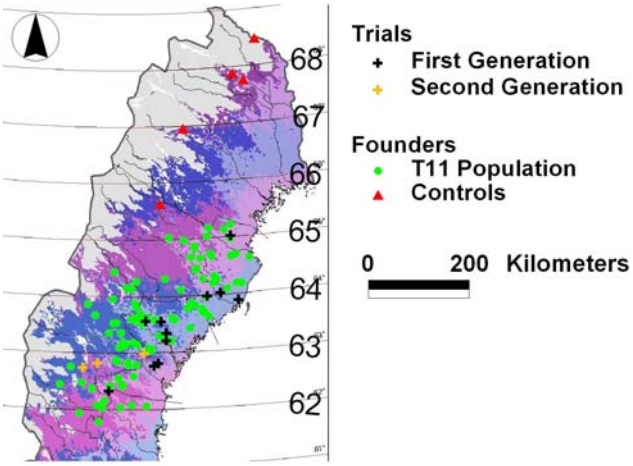


Figure 1: Location of base population plus trees sampled trials in northern Sweden

Trials and Data

Spatial coordinates were allocated to all trees in all trials. Contiguous trials F277 and F279 were treated as a single trial to allow spatial analysis to support the pedigree linkage between trial series. Most trials were single tree plot completely randomised designs where blocks were contiguous blocks of trees grouped for analysis based on blocks of trees grouped for analysis based on post hoc blocking (Ericsson 1997). Early trials F256 to F258 were randomised complete block designs with 2 tree x 2 row plots.

Table 5: Trials with site information and data means for latitude 64/5.

Trial	Gen	Year	Lat	Long	Alt (m)	Temp Sum (°-day)	n	Health 10 (0-3)	Height 10 (m)	Spike Knots 10 (% or √n)	Health 30 (%)	Height 30 (m)	DBH 30 (cm)	Spike Knots 30 (%)
F256	1	1970	63.57	16.82	180	984	2200	2.9	2.3	6%				
F257	1	1970	63.22	17.62	200	938	2200	2.6	2.5					
F258	1	1970	62.33	15.37	450	783	7480	2.4	2.2	7%	64%	10.0	12.5	12%
F260	1	1971	62.82	17.28	365	824	7381	1.6	1.8		49%	9.8	16.6	38%
F261	1	1971	63.55	17.42	320	817	7235	1.9	2.0		58%	10.4	15.9	38%
F277&9	1	1972	63.35	17.63	330	822	11536	1.6	2.2		45%	9.4	16.1	19%
F280	1	1973	64.03	19.85	200	940	8270	2.1	2.1		68%	9.6	14.3	17%
F281	1	1973	62.77	17.12	300	882	8353	2.0*	2.2		92%	9.7	13.7	18%
F282	1	1974	65.02	20.43	260	829	6717	1.5	1.6	26%				
F283	1	1974	63.98	19.32	240	909	5844	2.3	2.3	23%				
F285	1	1974	63.88	20.55	10	1056	6435	1.6	2.4	31%				
F521	2	1992	63.00	16.72	285	880	2283	2.4	4.4	0.42				
F522	2	1992	62.83	14.92	395	799	2178	2.1	2.7	0.73				
F523	2	1992	62.75	14.37	455	753	2178	2.7	2.3	1.08				

* Adjusted to 2.6 after adjustment for early transient rust infection.

Measurements were not balanced across trials. Assessment occurred at around age 10 years for all trials and 30 for six F1 trials, with early measurements for height and health (0-3 scale), and late measurement for health (survival), Height and DBH. Spike knots (0/1) were assessed in five F1 trials at the early age and six at the late age. A count of spike whorls was carried out at the early age in the F2 trials and these data were subject to a square-root transformation. Growth was not measured on multi-stemmed trees.

Site means were calculated based on the weighted average of the selected trees from the latitude 64 and 65 groups as these were represented in all trials (Table 5). Trial F281 was found to have a much lower early health score than late health due to early attack of *Mnesampela melampsora* (Pine Twist Rust) and its site mean was adjusted using the general relationship between early and late health. Site means were variable for health and spike knots, but fairly uniform for growth, except for the tall trees at F521. Early health, although on a 4 point scale (0-3), was predominantly a binary trait, with few observations in intermediate classes. The trials cover only a small proportion of the planting range of the species (Figure 1), so genotype by environment interaction is unlikely to be large. The major cause of early mortality was apparently animal damage, not harshness due to cold, which is a primary concern in breeding in northern Sweden (Ref?).

Spatial analysis and data adjustment

Analysis was carried out for all traits on all sites to derive the best statistical environmental model and to estimate group effects. The approach to spatial analysis of Dutkowski *et al*.(2002) was used where spatially auto-correlated residuals are added to the model. The spatial model (Sp) was compared with the standard (Design) model for each trial. The spatial model fitted for the early randomised complete block design trials,

$$\mathbf{y} = \mathbf{B}\mathbf{X}_B + \mathbf{G}\mathbf{X}_G + \mathbf{P}\mathbf{Z}_P + \mathbf{U}\mathbf{Z}_U + \mathbf{S} + \mathbf{e} + \mathbf{e}_{Bulk} + \mathbf{e}_{Unknown}$$

where $\mathbf{y}$ is the data vector, $\mathbf{B}$ is the vector of fixed block effects with its design matrix $\mathbf{X}_b$, $\mathbf{G}$ is the vector of fixed genetic group effect with its design matrix $\mathbf{X}_G$, $\mathbf{P}$ is the vector of random plot effects with its design matrix $\mathbf{Z}_P$, $\mathbf{U}$ is the vector of random additive genetic effects with its design matrix $\mathbf{Z}_U$, $\mathbf{S}$ is the vector of spatial effects estimated using a two-dimensional separable autoregressive model in rows and columns (Dutkowski *et al.* 2002), $\mathbf{e}$ is the vector of random errors, and $\mathbf{e}_{Bulk}$ and $\mathbf{e}_{Unknown}$ are vectors of extra random errors associated with bulk and unknown seedlots. The extra error variances for bulk and unknown seedlots were included to account for any deviation from the zero relatedness assumed in the relationship matrix to avoid bias in estimates of additive and error variances. For the design model, the $\mathbf{S}$ term was not fitted. For the completely randomised designs, block was treated as a random effect to enable recovery of inter-block information (Yates 1939; Yates 1940), no plot term was fitted. For trials with *Pinus contorta* bulk seedlots a separate error variance was fitted to allow for departures from the assumption that the trees were unrelated . The additive genetic effects and group effects were estimated using a genetics group model with the additive relationship matrix ($\mathbf{A}$) modified to incorporate these group effects. The analyses were carried out using ASReml (Gilmour *et al.* 2001)

Growth and health at both early and late ages responded in almost every case to spatial analysis with increased likelihood, but spike knots responded only rarely (**Error! Not a valid bookmark self-reference.**). This is consistent with the pattern found by Dutkowski *et al.* (2006a) for a variety of traits. There seems to be a higher proportion of very large likelihood increases than that study found for comparable trial sizes and degree of variation explained by the design features (replicates or post-blocking blocks) - usually less than 10% for these traits. The additive variance showed no consistent trend between models (not shown), and the design feature variances were usually much reduced where the spatial model was significantly better (not shown), consistent with the work of Dutkowski *et al.* (2006a). The decreases in independent error variance were generally larger than those found by Dutkowski *et al.* (2006a), but the ratio of spatial to independent error variance was lower, as were the autocorrelations, especially for early height (not shown). The latter two are indicative of small scale spatial variation being the dominant pattern and is consistent with field observations. Fitting within block measurement plots and rows and columns in the manner of Fu (1998) lead

to large likelihood increases over the design model and confirms the dominance of small scale trend (not shown). It would seem that northern Swedish trial sites are relatively environmentally heterogenous but that heterogeneity has a spatial structure that makes it suitable for spatial analysis.

Table 6: Change in Log Likelihood and independent error variance ratio from design to spatial models

	Change in Log Likelihood*							Ratio error variance Spatial/Design						
Trial	Health 10	Height 10	Spike Knots 10	Health 30	Height 30	DBH 30	Spike Knots 30	Health 10	Height 10	Spike Knots 10	Health 30	Height 30	DBH 30	Spike Knots 30
F256	1.1	99.2	-					98.2	58.7	-				
F257	-	57.0						-	86.8					
F258	39.0	119.2	-	59.0	133.0	-	10.9	92.7	84.5	-	91.3	85.9	-	96.9
F260	262.2	101.6		158.3	56.3	21.3	-	83.1	80.3		85.4	84.1	92.8	-
F261	129.9	11.2		114.2	33.1	39.6	-	90.7	89.4		91.4	93.7	98.4	-
F277&9	119.3	60.5		120.7	12.1	47.5	-	94.0	92.9		94.0	92.3	94.3	-
F280	254.2	231.6		195.1	151.8	68.4	14.3	85.2	73.1		88.2	81.8	88.3	96.8
F281	63.8	293.7		33.5	297.0	75.2	-	94.7	82.9		96.0	82.5	92.1	-
F282	8.8	248.1	-					93.1	59.9	-				
F283	23.0	152.7	-					100.0	73.9	-				
F285	214.5	99.7	-					85.1	78.4	-				
F521	-	78.4	-					-	79.0	-				
F522	-	48.8	-					-	84.8	-				
F523	-	133.7	32.1					-	63.5	92.5				

* - indicates that the spatial model did not converge or was not significantly better on a likelihood ratio test with 3df.

Where the spatial model was significantly better on a 1 tailed Likelihood Ratio Test (LRT with 3df), the data were adjusted for the estimated spatial surface and the adjusted data were used in subsequent analyses. Trial F260 showed the largest LogL increase for early health, and it can be clearly seen that the design poorly models the spatial distribution of the data compared to the spatial model. The adjusted data for this basically binary trait gives the greatest adjustment for trees next to the border between healthy and unhealthy tree, as would be expected. It creates a variable that has a wider range and is more continuously distributed and thus more amenable to analysis.

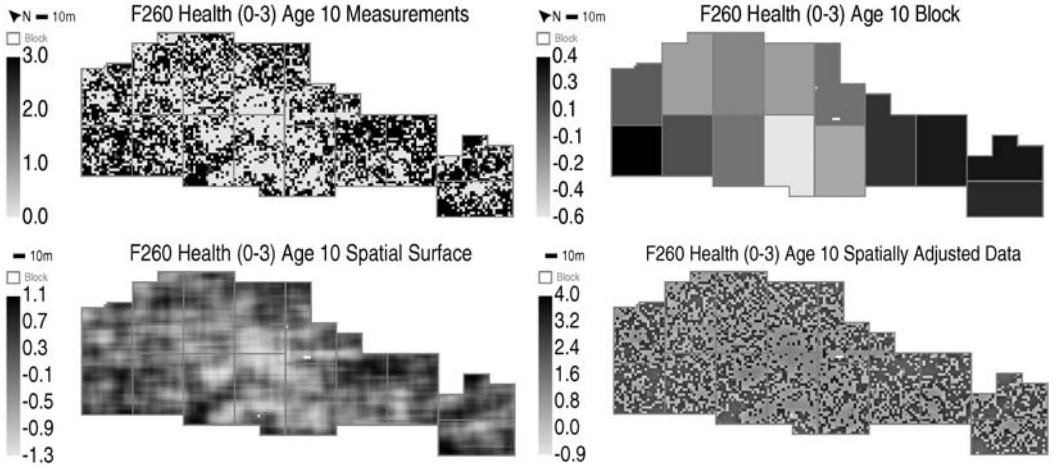


Figure 2: Data, design model surface, spatial model surface, and spatial adjusted data for early health in trial F260

Group Means and Variances

Despite the imprecision of the latitude groups means it could be seen that on harsher sites (lower early health of latitude 65 material), the lower latitude material was less healthy (Figure 3a). While on milder sites the differences were small, this may be an artefact of the analysis, as the variances all decreased as Health approached the boundary value of 3. These trends are consistent with the southerly transfer of seed recommended for site establishment. These results suggest that on mild sites, perhaps the health benefits of such a transfer may not be high. Conversely, the lower latitude seed sources seemed to grow faster than the higher latitude sources (Figure 3b), again consistent with other trials. The site means for early health and height based on the weighted average of the selected latitude 64 and 65 groups were not strongly related to breeding zone (REF), altitude, or temperature sum, or to each other.

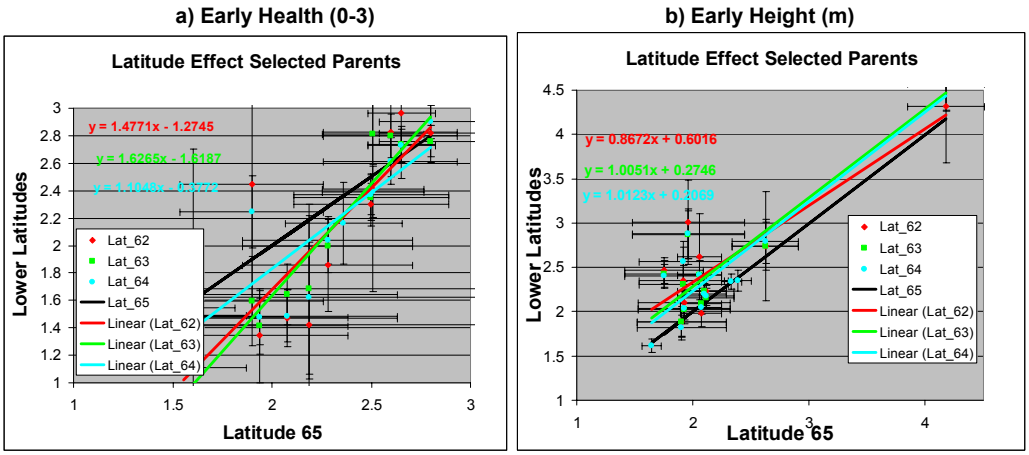


Figure 3: Latitude effect on early health and height relative to latitude 65 (95% CI is shown)

The variances for early and late health declined with increasing site health as full health was approached. F282 had a very high additive variance for early health but with a large standard error (Figure 4a). This is the coldest site in the data set and its high heritability is consistent with that for damage seen on cold sites. Variances for growth were not well related to site averages except for error variance for DBH. However, apart from high early growth at F521, there was not a wide range in site means. Binary early spike knot variances increased with the proportion of spike knots present, however F285 had a very high additive variance for this trait with usually low heritability (<0.1). Late spike knots ($\sqrt{n}$) in second generation trials had a much higher heritability. Of other traits, branch angle score showed both variances decreasing with the mean. Error variance trends were usually stronger – this usually reflects the smaller standard errors associated with error variance estimates. Second generation trials had the same trends as first generation trials although for early height (Figure 4b) they all were on the low side for additive variance and on the high side for error variance, giving them the lowest heritabilities. Subsequent exploration of these trials indicated that the heritability for the control pollinated families (the basis of the figure) was much lower than for the open-pollinated families, while the poor growth of old high latitude control pollinated families was consistent with first generation trials. This suggests that there may be problems with the pedigree for these families which should be investigated using molecular marker systems. The within site additive genetic correlations between early height and health were not related to the site health mean, or to any site environmental variables, in contrast to the recent work of Persson *et al.* (2006) which had a much broader range of site harshness.

Inter-site correlations

The pattern of genotype by environment interaction (inter-site correlations) was explored to try and stratify sites in some meaningful way to provide breeding values for different site types to guide breeding and deployment. Breeding zones are currently defined by a combination of latitude (reflecting the light environment) and temperature sum (reflecting harshness) (REF). There is, however, much variation within the geographic zone due to local variation that is not accounted for by these broad climatic parameters. In TREEPLAN®, genotype by

environment interaction is taken into account by grouping sites into site types with an estimated genetic correlation between site types and an implicit unit genetic correlation between sites within the same site type. Also implicit is the assumption that the partitioning of different sources of genetic variation (group, additive and family/SCA) is constant for a site type.

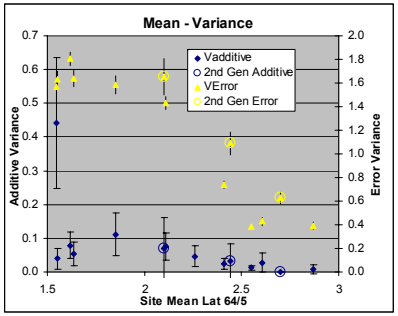
To examine these questions, early health and height data for control pollinated families in first generation trials was used. A design matrix of group effects was directly created for each family to reflect the latitude group contribution (l), and all parents were sequentially encoded to allow a GCA effect (p) using an overlay model in ASReml to substitute for the additive genetic effect, as well as a family effect (f) for SCA. All genetic effects were treated as random effects to allow the use of likelihood statistics (LogL). The base model for early health (Model 0 in Table 7) allowed no genetic correlation between sites, and allowed the ratio of genetic variances to be the different for each site. There was substantial GxE for early health, because constraining the correlations to be unity (Model 1 in Table 7) resulted in a significant reduction in LogL. Estimating a uniform genetic correlation between sites, showed this to be around 0.5 at additive and family level, but one for the groups (Model 2). While the ratios of genetic variances differed substantially between sites, fixing them to be the same across all sites and finding the best ratios by profile likelihood did not significantly lower the likelihood (Model 3). This indicated that the relative genetic control could be assumed to be the same across all sites with a relatively high group effect (0.9) and a low family effect (dominance ratio) (0.1), and these ratios are used for subsequent models. While the genetic correlations are now variable, a single genetic correlation could be assumed across all genetic strata (0.53) and this indicated substantial GxE (Model 4).

The effect of various environmental factors on the genetic correlation was fitted using an auto-regressive mode based on the distance apart on each environmental factor (e): $r_g = \rho^{(e1-e2)}$ (Models 5-10) (similar to the spatial residual model) in order to find the best basis for stratifying sites into different site types. The weighted average of latitude 64 and 65 groups for early health and height was also used as an environmental factor as a bioassay for actual site harshness. Early health proved to be the best environmental indicator of the genetic correlation (Model 9) and as it mirrored the pattern seen for latitude group performance (Figure 3), this seemed a sensible basis for site stratification. However even after the variance ratio between the strata was re-estimated, the best model (11) was still worse than assuming a single correlation between all sites (Model 4). Clearly there were other patterns of inter-site correlations that were not being adequately modelled by the environmental effect alone. Early height followed a similar pattern to early health and again actual early health proved to be the best predictor of inter-site correlations.

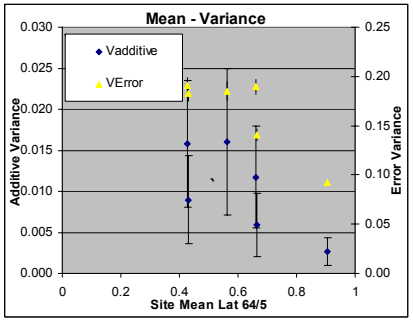
Table 7: Inter-site models for early health

Variances and correlations are followed by their t value (estimate/SE). Variances are for latitude groups (l), parents (p) and families (f).

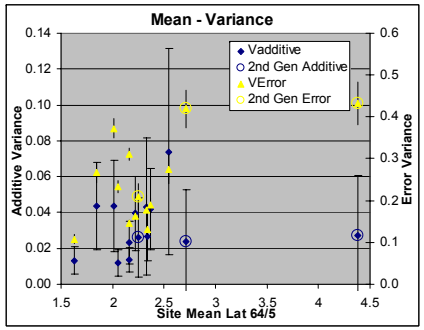
Model	*Description*	*ΔLogL*	σ^2_l/σ^2_p	σ^2_f/σ^2_p	r_l	r_p or ρ_p	r_f
0	No corr	0	Free	Free	0	0	0
1	No gxe	-15.6	Free	Free	1	1	1
2	Multiple corr	39.02	Free	Free	0.99 (B)	0.54 (7.7)	0.52 (1.4)
3	Multiple corr, fixed ratio	30.68	0.9	0.11	0.89 (5.5)	0.50 (7.2)	1.00 (1.7)
4	Single corr, fixed ratio	29.3	0.9	0.11	0.53(8.26)		
5	Altitude (m/100)	9.4	0.9	0.11	0.305 (4.4)		
6	Breeding Zone	11.02	0.9	0.11	0.745 (15.2)		
7	Latitude	10.65	0.9	0.11	0.438 (5.9)		
8	Temp Sum (°-day/100)	12.79	0.9	0.11	0.269 (3.8)		
9	Early Height (m *10)	11.23	0.9	0.11	0.56 (8.1)		
10	Early Health (0-3 *10)	20.6	0.9	0.11	0.857 (32)		
11	Early Health (0-3 *10)	20.8	0.6	0.12	0.857 (32)		



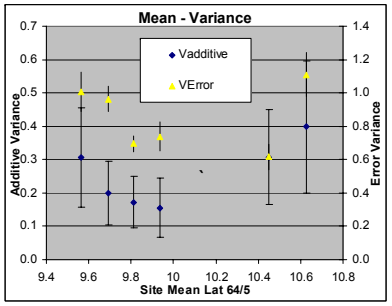
(a) Early Health (0-3)



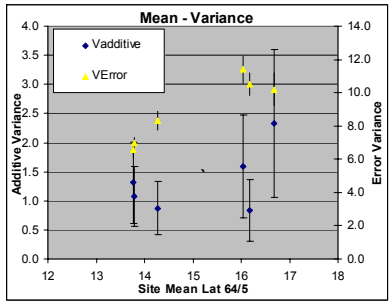
(b) Late Health (0/1)



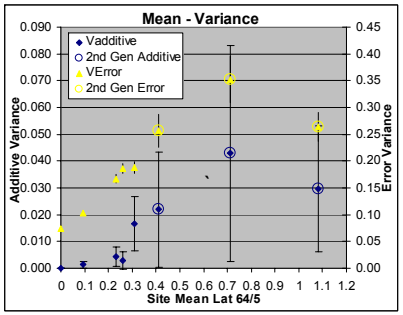
(c) Early Height (m)



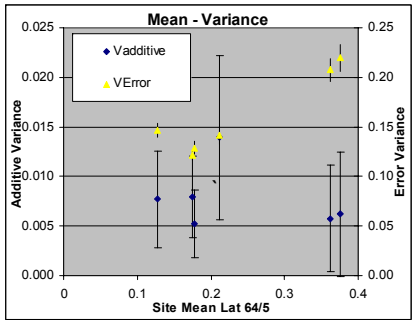
(d) Late Height (m)



(e) Late DBH (cm)



(f) Early Spike Knots (Gen 1:0/1, Gen 2 √n)



(g) Late Spike Knots (0/1)

Figure 4 Variance-Mean Relationships with 95% CI

Dividing the sites into three site types based on units of 0.5 early health score (4=1.5-1.99, 5 =2-2.49, 6 = 2.5-3) enabled direct estimation of within and between site type correlations. The full model (12,**Error! Not a valid bookmark self-reference.**) was better than the single correlation model (4, Table 7), but the within site type correlation declined as Health increased. This might be expected if increasing health meant that health on different sites was no longer correlated, and a banded correlation model (13) that forced the within site-type correlations to be the same across all site types was significantly worse. Constraining the within site-class correlation to be unity was significantly worse, confirming that substantial within-class GxE still existed.

Table 8: Early Health class genetic correlations (and their t-values)

Site Type	*Model*	*12*	*ΔLogL*	*37.5*	*Model*	*13*	*ΔLogL*	*31.9*	*Model*	*14*	*ΔLogL*	*10.5*
4	0.78	(11)	(6.8)	(3.5)	0.64	(8.1)	(6.8)	(3.4)	1	F	(5.8)	(1.1)
5	0.54	0.24	(0.9)	(4.2)	0.51	0.64	(8.1)	(6.8)	0.52	1	F	(5.8)
6	0.40	0.47	-0.09	(0.3)	0.41	0.51	0.64	(8.1)	0.30	0.52	1	F
	4	5	6		4	5	6		4	5	6	

Examination of GxE for early spike knots was not possible as there were insufficient families in common in the first generation trials where spike knots was present. For the late spike knots, the pattern of GxE was best explained by altitude (ΔLogL above no corr 27.3), but actual Early Health was not far behind (23.7). In contrast to the early health and height, this model was similar to the single correlation model (r_g=0.74, ΔLogL =23.9), which indicated that there was a high within health class correlation. As the predicted inter-class correlations were relatively high (r_g=0.81 and 0.65), and as the information was weak, it was decided not to subdivide spike knots into site types.

Preliminary bivariate early health-height analysis results indicated that taking both error and genetic correlations into account is necessary for proper estimation of variances and correlations (not shown), hence a bi-variate across site model was used to examine the within and between class inter-trait and inter-site type correlations. Due to model convergence problems in ASReml, and because prior analysis showed that the different genetic strata had similar correlations, and little family variance was present, only a parental model was used to examine the correlations. Trial F256 was excluded as it had been shown to behave strangely (not shown). The base model (Model 15 in Table 10) assumed no site typing and no GxE model with a unit correlation between site types and a correlation of 0.56 between health and height. Assuming uniform GxE model (Model 16) was much better, with similar inter-site correlations for Health (0.65) and Height (0.57), and a lower inter-trait correlation (0.37). Structuring the inter-site and trait correlations to be a function of site type using a banded correlation model (Model 17) was even better and showed declining correlations with differences in site-class. Again, however, forcing the within site-type correlations to be one resulted in a poorer model (Model 17). While these classes can be used, clearly there is still substantial intra-site type GxE that is not accounted for.

Selection criteria definition and correlation

Selection criteria are groups of measured traits across sites for which breeding values are to be estimated. The data are standardised across a range of sites in TREEPLAN® to have a unit additive variance, implied unit within selection criterion correlation, but a different error variance for each site. Testing has shown that this is an appropriate model (Dutkowski *et al.* 2006b). The definition of selection criteria depends on appropriate data being collected and models of inter-site, inter-trait and inter-age genetic correlations being created to allow estimation of genetic correlations between all selection criteria.

Table 9: Inter-site type correlations

Health				*Height*				*DBH*			
4	1	0.48	0.3	4	1	0.55	0.32	4	1	0.55	0.32
5	0.48	1	0.48	5	0.55	1	0.55	5	0.55	1	0.55
6	0.3	0.48	1	6	0.32	0.55	1	6	0.32	0.55	1

	4	5	6		4	5	6		4	5	6

Table 10: Inter-trait and inter-site type correlations without F256 (t value).

Model	*Trait*	*Class*	*Health*			*Height*			
15	Health	4	1	F	F	F	(7.6)	(7.6)	(7.6)
		5	1	1	F	F	(7.6)	(7.6)	(7.6)
ΔLogL		6	1	1	1	F	(7.6)	(7.6)	(7.6)
	Height	4	0.56	0.56	0.56	1	F	F	F
0		5	0.56	0.56	0.56	1	1	F	F
		6	0.56	0.56	0.56	1	1	1	F
16	Health	4	0.65	(11)	(11)	(11)	(5.8)	(5.8)	(5.8)
		5	0.65	0.65	(11)	(11)	(5.8)	(5.8)	(5.8)
ΔLogL		6	0.65	0.65	0.65	(11)	(5.8)	(5.8)	(5.8)
	Height	4	0.37	0.37	0.37	0.57	(10)	(10)	(10)
233		5	0.37	0.37	0.37	0.57	0.57	(10)	(10)
		6	0.37	0.37	0.37	0.57	0.57	0.57	(10)
17	Health	4	0.82	(17.0)	(6.1)	(2.1)	(12.1)	(3.0)	(0.1)
		5	0.49	0.82	(17.0)	(6.1)	(3.0)	(12.1)	(3.0)
ΔLogL		6	0.29	0.49	0.82	(17.0)	(0.1)	(3.0)	(12.1)
	Height	4	0.60	0.22	0.02	0.74	(16.2)	(6.9)	(1.8)
286		5	0.22	0.60	0.22	0.48	0.74	(16.2)	(6.9)
		6	0.02	0.22	0.60	0.23	0.48	0.74	(16.2)
	Health	4	1.00	F	(5.7)	(2.0)	(15.1)	(3.4)	(0.3)
18		5	0.48	1.00	F	(5.7)	(3.4)	(15.1)	(3.4)
		6	0.30	0.48	1.00	F	(0.3)	(3.4)	(15.1)
LogL	Height	4	0.69	0.27	0.04	1.00	F	(7.9)	(2.4)
		5	0.27	0.69	0.27	0.55	1.00	F	(7.9)
199		6	0.04	0.27	0.69	0.32	0.55	1.00	F
			4	5	6	4	5	6	

Site types were defined based on the inter-site analysis. The health and growth correlations (Table 9) were based on Model 18, and there were assumed to be no Spike Knots site types. The inter-trait correlations (Table 11) were defined from the weighted average of the bivariate estimates, except for the health-height correlation, which was used from the multi-trait-multi-site analysis (Table 10). The same health-height correlation was used at both ages. The inter-age correlations were similarly derived (Table 12), but as only two ages had been measured, correlation modelling was not possible. The full correlation matrix for all of selection was built up from information available about its component parts (

Table 13: Correlations of harvest stand Volume (per unit area) with health and growth selection criteria according to target site type.

Site Type	*Health-Volume*	*Growth-Volume*
1	0.917	0.083
2	0.750	0.250
3	0.583	0.417
4	0.417	0.583
5	0.250	0.750
6	0.083	0.917

Breeding value predictions

The individual site models and data and pedigree were stored in an integrated data management system. Individual site data were allocated to each of the selection criteria and their variance components, and those of the breeding objective traits, were also entered into the data base. The TREEPLAN® software was then run, extracting the information from the database, and returning it to the database, after adjusting the breeding values to a common baseline of selected parents from latitude 65/5.

Table 14). Early and Late refer to the age of measurement, and the numeric suffix for Health and growth traits reflects the early health class based on 0.5 width class units of early health of selected families for Latitude 64/5.

Table 11: Inter-trait correlations

DBH	1	0.62	0.38	0.34
Health	0.62	1	0.69	0.48
Height	0.38	0.69	1	0.35
Spike_Knot	0.34	0.48	0.35	1
	DBH	***Health***	***Height***	***Spike_Knot***

Table 12: Inter-age correlations

DBH	0.71
Health	0.95
Height	0.71
Spike_Knot	0.55

Once the selection criteria correlations were defined, then these were used to re-estimate the variances and non-genetic correlation for CP crosses for each site which had these Selection Criteria represented. This is to ensure that the variances and correlations that are used for each site match the integrated model. SCA was left out of the model as it had been shown to be small enough to be ignored. No design feature correlations were allowed for model simplicity, to enable model convergence, and because the spatial adjustment would have accounted for much within site medium to large scale environmental correlation. The heritability of the second generation sites was consistently low and a minimum heritability value of 0.05 had to be assumed for a number of traits.

Indicative Breeding Objective Traits

While selection criteria is the term used in animal breeding, it is somewhat misleading as selection should be based on an economic breeding objective index (Ponzoni & Newman 1989). . Such indices are defined in terms of breeding objective traits, those which actually have an economic value. In tree breeding most economic models are framed in terms of breeding objective traits at harvest age at the stand level (Borralho *et al.* 1993), which are rarely measured. Breeding objective trait breeding values are predicted from the selection criteria breeding value using the method of Schneeberger *et al.* (1992). As no economic model was available, but breeding values for a variety of traits at different ages needed to be integrated, indicative Breeding Objective Traits were defined. These reflected stand harvest volume (per unit area) for site types 4, 5 and 6, and for spike knots, on a unit additive standard deviation scale. We assumed a sliding linear scale of correlations between health and growth selection criteria and harvest stand Volume for the site type. Using all possible site types (based on 0.5 unit health score increases) shows that as the health of the site type increased, then the putative correlation with survival decreased, but that with individual tree growth increased (Table 13).

An overall correlation table was thus developed (

Table 13: Correlations of harvest stand Volume (per unit area) with health and growth selection criteria according to target site type.

Site Type	*Health-Volume*	*Growth-Volume*
1	0.917	0.083
2	0.750	0.250
3	0.583	0.417
4	0.417	0.583

5	0.250	0.750
6	0.083	0.917

Breeding value predictions

The individual site models and data and pedigree were stored in an integrated data management system. Individual site data were allocated to each of the selection criteria and their variance components, and those of the breeding objective traits, were also entered into the data base. The TREEPLAN® software was then run, extracting the information from the database, and returning it to the database, after adjusting the breeding values to a common baseline of selected parents from latitude 65/5.

Table 14, lower part). The overall correlations developed with this approach were very low, but are sufficient at this stage to demonstrate the concepts. Stand Volume is better correlated with health and growth selection criteria in the same site type, than in other site classes. The strength of this correlation changes with the target site type, with Health being more important for site type 4 (moderate survival), than for site type 6 (high survival), and vice-versa for growth. Later age measurements have a higher correlation than early measurements.

Table 13: Correlations of harvest stand Volume (per unit area) with health and growth selection criteria according to target site type.

Site Type	*Health-Volume*	*Growth-Volume*
1	0.917	0.083
2	0.750	0.250
3	0.583	0.417
4	0.417	0.583
5	0.250	0.750
6	0.083	0.917

Breeding value predictions

The individual site models and data and pedigree were stored in an integrated data management system. Individual site data were allocated to each of the selection criteria and their variance components, and those of the breeding objective traits, were also entered into the data base. The TREEPLAN® software was then run, extracting the information from the database, and returning it to the database, after adjusting the breeding values to a common baseline of selected parents from latitude 65/5.

Table 14: Selection Criteria and Breeding Objective trait correlation matrix

	Early_Health_4	Late_Health_4	Early_Health_5	Late_Health_5	Early_Health_6	Late_Health_6	Early_Height_4	Late_Height_4	Early_Height_5	Late_Height_5	Early_Height_6	Late_Height_6	Late_DBH_4	Late_DBH_5	Late_DBH_6	Early_Spike_Knot	Late_Spike_Knot
Early_Health_4	1.00	0.91	0.48	0.44	0.30	0.27	0.69	0.56	0.33	0.27	0.21	0.17	0.50	0.24	0.15	0.48	0.35
Late_Health_4	0.91	1.00	0.44	0.48	0.27	0.30	0.56	0.69	0.27	0.33	0.17	0.21	0.62	0.30	0.19	0.35	0.48
Early_Health_5	0.48	0.44	1.00	0.91	0.48	0.44	0.33	0.27	0.69	0.56	0.33	0.27	0.24	0.50	0.24	0.48	0.35
Late_Health_5	0.44	0.48	0.91	1.00	0.44	0.48	0.27	0.33	0.56	0.69	0.27	0.33	0.30	0.62	0.30	0.35	0.48
Early_Health_6	0.30	0.27	0.48	0.44	1.00	0.91	0.21	0.17	0.33	0.27	0.69	0.56	0.15	0.24	0.50	0.48	0.35
Late_Health_6	0.27	0.30	0.44	0.48	0.91	1.00	0.17	0.21	0.27	0.33	0.56	0.69	0.19	0.30	0.62	0.35	0.48
Early_Height_4	0.69	0.56	0.33	0.27	0.21	0.17	1.00	0.71	0.48	0.34	0.30	0.21	0.27	0.13	0.08	0.35	0.22
Late_Height_4	0.56	0.69	0.27	0.33	0.17	0.21	0.71	1.00	0.34	0.48	0.21	0.30	0.38	0.18	0.11	0.22	0.35
Early_Height_5	0.33	0.27	0.69	0.56	0.33	0.27	0.48	0.34	1.00	0.71	0.48	0.34	0.13	0.27	0.13	0.35	0.22
Late_Height_5	0.27	0.33	0.56	0.69	0.27	0.33	0.34	0.48	0.71	1.00	0.34	0.48	0.18	0.38	0.18	0.22	0.35
Early_Height_6	0.21	0.17	0.33	0.27	0.69	0.56	0.30	0.21	0.48	0.34	1.00	0.71	0.08	0.13	0.27	0.35	0.22
Late_Height_6	0.17	0.21	0.27	0.33	0.56	0.69	0.21	0.30	0.34	0.48	0.71	1.00	0.11	0.18	0.38	0.22	0.35
Late_DBH_4	0.50	0.62	0.24	0.30	0.15	0.19	0.27	0.38	0.13	0.18	0.08	0.11	1.00	0.48	0.30	0.21	0.34
Late_DBH_5	0.24	0.30	0.50	0.62	0.24	0.30	0.13	0.18	0.27	0.38	0.13	0.18	0.48	1.00	0.48	0.21	0.34
Late_DBH_6	0.15	0.19	0.24	0.30	0.50	0.62	0.08	0.11	0.13	0.18	0.27	0.38	0.30	0.48	1.00	0.21	0.34
Early_Spike_Knot	0.48	0.35	0.48	0.35	0.48	0.35	0.35	0.22	0.35	0.22	0.35	0.22	0.21	0.21	0.21	1.00	0.55
Late_Spike_Knot	0.35	0.48	0.35	0.48	0.35	0.48	0.22	0.35	0.22	0.35	0.22	0.35	0.34	0.34	0.34	0.55	1.00
Volume_4	0.35	0.38	0.17	0.18	0.10	0.11	0.30	0.41	0.14	0.20	0.09	0.12	0.41	0.20	0.12	0.11	0.19
Volume_5	0.10	0.11	0.21	0.23	0.10	0.11	0.18	0.26	0.38	0.53	0.18	0.26	0.26	0.53	0.26	0.11	0.19
Volume_6	0.02	0.02	0.03	0.04	0.07	0.08	0.14	0.20	0.22	0.31	0.46	0.65	0.20	0.31	0.65	0.11	0.19
Spike_Knots	0.40	0.42	0.40	0.44	0.40	0.44	0.18	0.25	0.18	0.26	0.19	0.25	0.24	0.24	0.24	0.30	0.55

The selection criteria group effects show that for early health, there is a trend of increasing health with latitude for Site Type 4 (Figure 6). Selected and unselected groups seem to generally perform similarly. These trends are less clear for site type 5 and for site type 6 there are only small differences between groups. This is consistent with Figure 3– as the site health increases, the advantage of cold hardy northern genotypes decreases. This contrasts with historic records that indicate animal damage is the primary cause of mortality of most sites except F282, suggesting resistance to the two agents may be related.

There is some suggestion of better growth of low latitude groups on healthy sites, but this is less clear. For the Volume traits, the low latitude groups seem to be best for all site types, with a trend clear for latitudes 62-65 for the mild sites. The correlations used for these site types all favour growth over health (Table 13), and the group effects seem to reflect this. The overall higher heritability of early growth (average 0.12) over early health (0.05) may also contribute. Early spike knots seems to show no trends, but late spike knots and overall Spike Knots seems to show more spike knots with higher latitudes.

The distribution of health breeding values gets narrower with increasing site health, consistent with the group trends. There is also a slight trend towards lower heritability with increasing site health (not shown) which may contribute to this narrower distribution. The decreasing additive variance for health with average health does not however contribute to the trend as all the data is standardised to the additive variance. This standardisation does, however, lead to a narrower distribution of predicted breeding values for low heritability sites. While the distribution of growth breeding values shows no variability trend with site type, the distribution of Volume_4 breeding values certainly is narrower than the other site types. This is presumably due to the contrary group effects for health and growth cancelling each other out for this trait which has a more even correlation with both trait types. The Volume breeding values clearly show that health and height breeding values from the same site type are more important, and that height becomes more important for milder sites (Figure 5). The breeding values from trials on each site type do not show a wider distribution for trials on that site type, which could have been expected. The Volume breeding values are related across site types, but the relationship decreases as the site type get further apart (Figure 5). Despite the relationships, there is clearly potential to select for specific site types. Volume is not (or only weakly) related to Spike Knots, so gain in both can be made if the relative economic value of

each is known. Live trees have higher health breeding values than dead trees, although this is not discernibly the case for growth (not show).

The averages of the first generation selections and the second generation trial trees are consistently higher (unfortunately more knotty) than the average of the base population trees, although the difference is not great (

Table 16). The best trees, irrespective of generation, are many times better than the first generation selections. The best 5% of trees for each trait are not uniformly spread across trials (Table 15). Some of the base population trees are still very good – their values are more dispersed as they have more information contributing to them. F277&9, F280, and F281 have a high proportion of selections for Volume - all have later measurements and have been progeny tested.

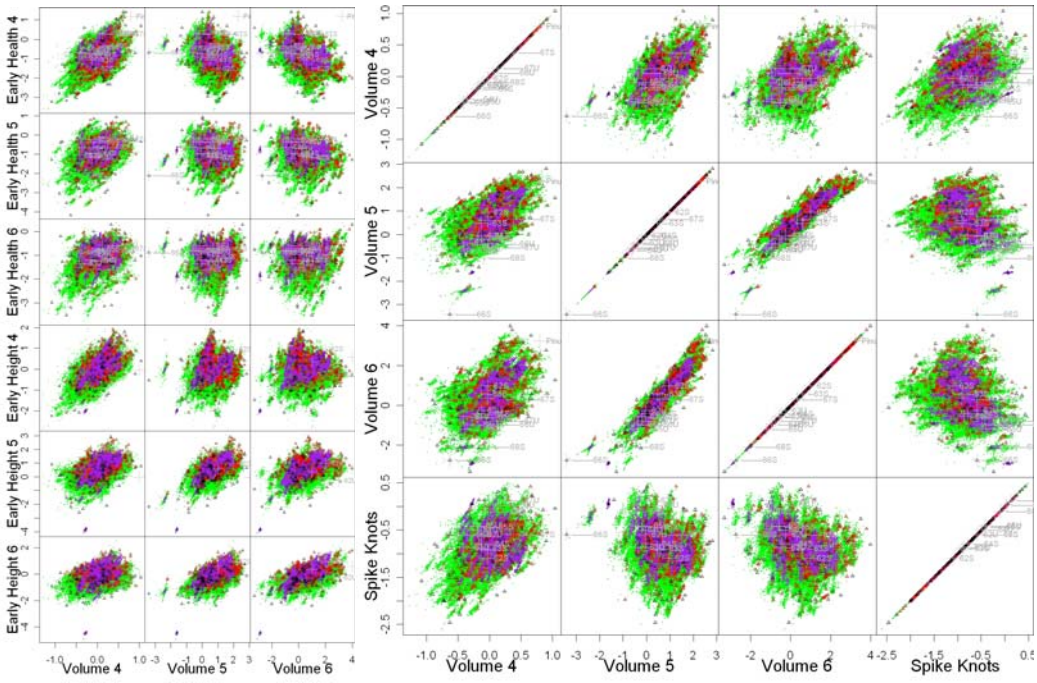


Figure 5: Selection Criteria and Breeding Objective Trait breeding values

Groups, Base Trees, First Generation, First Generation Selected, Second Generation

Table 15: Top 5% for Volume as % of live trees in trial

Trial	*Gen*	*Site Type*	*Last Msmt Age (yrs)*	*n Genotype*	*n Alive*	*Volume 4*	*Volume 5*	*Volume 6*
Base				136		8.1%	8.1%	8.1%
F256	1	6	10	2200	2111	5.1%	3.6%	1.7%
F257	1	6	10	2068	1967	5.0%	3.4%	1.5%
F258	1	5	31	7108	5639	4.6%	6.5%	1.5%
F260	1	4	30	7377	2648	6.4%	4.2%	0.8%
F261	1	4	30	6308	3284	6.5%	4.2%	1.2%
F277&9	1	4	28	11411	4781	8.8%	7.3%	8.2%
F280	1	5	28	8147	4986	6.1%	10.3%	12.7%
F281	1	6	28	8230	7293	5.7%	9.6%	12.6%
F282	1	4	10	6585	3714	2.3%	0.0%	0.0%
F283	1	5	10	5707	4336	1.0%	0.0%	0.0%
F285	1	4	10	6294	3323	1.4%	0.0%	0.0%
F521	2	5	12	2083	1805	4.7%	3.5%	5.6%
F522	2	5	12	2124	1558	4.6%	3.2%	5.6%
F523	2	6	12	2150	2001	5.0%	3.0%	6.1%

Table 16: Gain from univariate selection for best living trees for growth Breeding Objective Traits

Population	*Volume 4*	*Volume 5*	*Volume 6*
Base	-0.12	0.27	0.62
1st Gen selections	-0.01	0.54	0.84
Top 10000	0.41	1.61	1.71
Top 5000	0.51	1.89	2.12
Top 2000	0.62	2.14	2.59
Top 1000	0.70	2.27	2.89
Top 500	0.76	2.36	3.10
Top 200	0.81	2.45	3.28
Top 100	0.83	2.51	3.38

DISCUSSION

This study clearly demonstrates the benefits of integrated breeding value prediction using a framework adapted from animal breeding. Multivariate analysis using the mixed model equations and records from relatives (Henderson & Quaas 1976) has enabled us to account for different sources of genetic material, measured traits, ages of measurement and site types. Spatial analysis, data standardisation and heritability heterogeneity have enabled the application of these methods to a heterogenous set of forestry trials. The covariances between all observations due to relatedness, related traits and shared environments have been accounted for. Most of the concerns raised by White and Hodge (1989) and Borralho (1995) have been addressed. Projections to harvest age that integrate the breeding values of measured traits have been used, greatly simplifying selection and ensuring that the most has been made of all the data that has been collected. This is a powerful framework for breeding value prediction.

The breeding values that have been produced seem to make sense given the information that was used. Within site variations was modelled much better with spatial analysis than with previously used models. Northern seed sources were healthier, especially on harsher sites, while southern seed sources grew better. Correlations between sites types declined as the sites became more different. Sites with later age measurements and offspring yielded more selections. Harvest volume on harsh sites was more related to health than growth. Live trees had better health breeding values than dead trees. Finally, field inspection of the selected trees largely confirmed that the trees that were selected for harvest Volume were good ones.

Gain predictions from this analysis were much greater than that achieved from previous selection in the first generation trials. All of the data and pedigree information was used and integrated. Spatial analysis better coped with within site variation. Heterogenity of variance and heritability was dealt with. Later age measurements and offspring information were used. The size of the potential increase is consistent with the low historic selection efficiency found in other species for multi-trait selection (Dutkowski *et al.* 2006b). For this single trait selection scenario, other unknown historic factors may have come into play in selection decisions that were made, and perhaps the highly heterogenous nature of northern Sweden trial sites has limited the gain that could have been

Even with all of this, the breeding values that have been produced are undoubtedly wrong. BLUP breeding values are only best and unbiased when the variances and covariances are known without error (Henderson 1984). This is never the case, but you can get close with good estimates. In this case, our partitioning of the environments to account for GxE was only partially successful for this set of trials with a restricted environmental range. Historic records indicate that animal damage was the predominant cause of health variation, yet the patterns are consistent with resistance to cold. The problems with heritability estimation in second generation trials indicates that some of the pedigree relationships may not be right. Our knowledge of inter-trait correlations is limited because of the small number of trials and theenvironments in which they occur. Persson *et al.*(2006) indicate that the health-growth correlation varies with site harshness, yet we used a single correlation. Only a rudimentary inter-age correlation model was used. The model for relative contribution of health and growth to harvest volume is probably of the right form, but the correlations used were only guesses. No economic model was available to properly weight growth and knottiness for best economic gain.

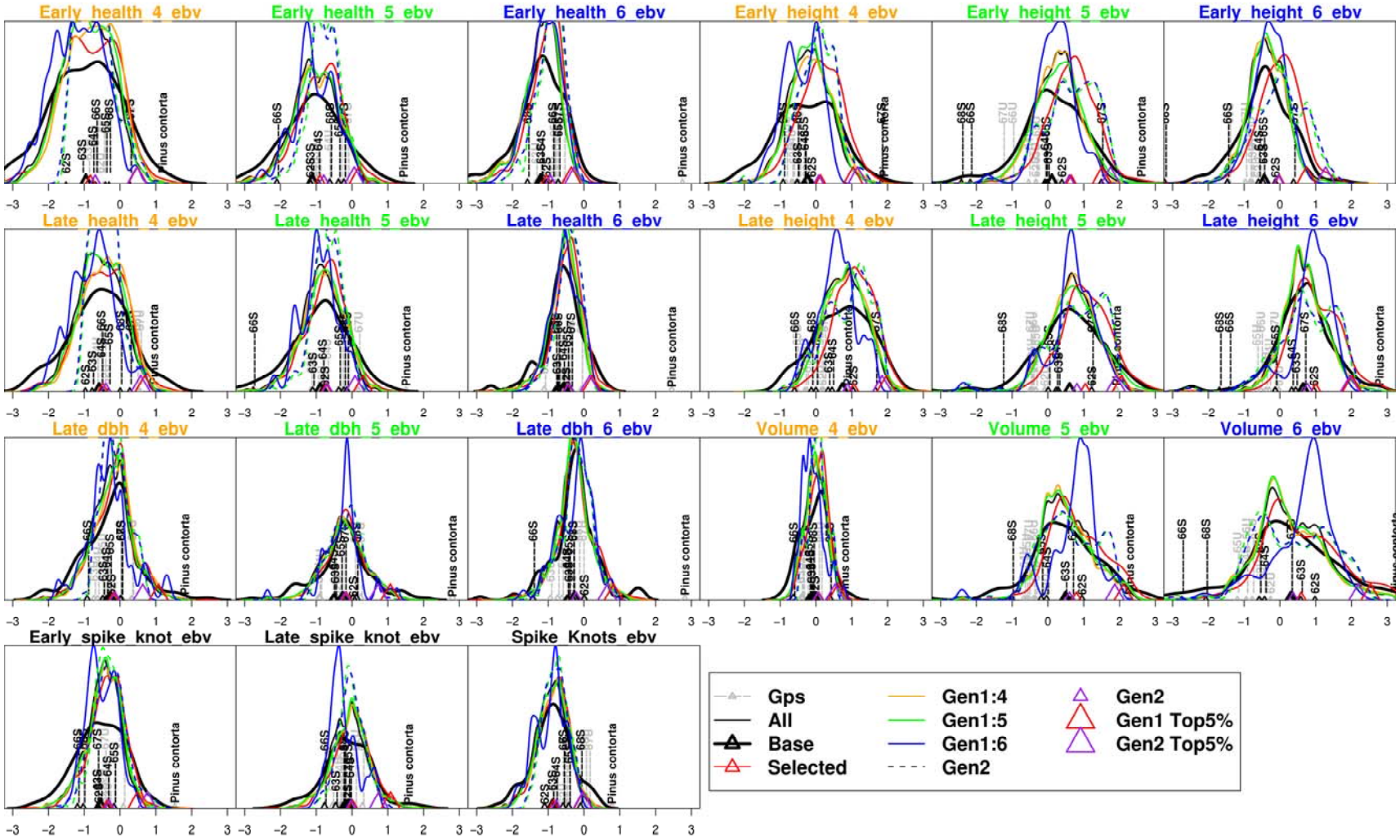


Figure 6: Distribution of breeding values for living trees

Group names: Latitude + S(elected)/U(nselected) and line length related to latitude (Low accuracy high latitude groups are clumped)

Even given these limitations, the framework that we have used enables research that sheds light on any of these limitations to be quickly and effectively used. Better understanding of GxE can be reflected in site type definitions. Longer run measurements will enable better age:age correlation models. Measurement of new traits can lead to new selection criteria once inter-trait correlations are known. Realised gain trials can better model the effects of health and growth on harvest volume. Economic information can be integrated. The analysis can be expanded to all Swedish *P sylvestris* populations in the current framework, albeit with the results of research as outlined above, although this will not be without logistical challenges due to the scale.

Some model changes may be necessary for an integrated analysis of all Swedish *P sylvestris* populations. Currently the software uses a standard set of genotypes as a baseline for all traits, which includes site types. However, currently the baseline for performance that is used in Sweden is the local provenance. Genetic groups are treated as unrelated, however, the groups are not independent as close latitudes are better related than distant latitudes. Seed transfer rules from historic provenance trials could be incorporated into the group estimates, without necessarily incorporating that data directly, if it is unavailable. Unexplained GxE still exists, so a site repeatability could be introduced to cater for site types in which there is a low correlation between performance in different trials. This would have the benefit of increasing the variance of predicted values as more sites are sampled where the repeatability (akin to the inter-site correlations) is low. This will additionally favour parents over offspring as with seedlings the parents can be tested on many sites, but the individual seedling will only be tested on one site. Clonal testing will become more important in such a situation.

CONCLUSION

This pilot study demonstrates the power and flexibility of the framework for integrated analysis that has been adapted from animal breeding, despite any limitations using the current data. All information is integrated and given its appropriate weight due to pedigree relationships, site:site, age:age, trait:trait genetic correlations and environmental correlations. Predicting stand harvest volume for each genotype in all for each site type greatly simplifies selection and will increase the flexibility of the breeding and deployment programs.

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