

Horticulture

Ecology and Agriculture



Wendel Mason

Horticulture: Ecology and Agriculture

About the Book

Horticulture is the growth of plants for self-sustenance as well for as commercial purposes. Horticultural practices dominate the practical aspect of agriculture and horticultural theory too, plays an important aspect in agronomic studies. This book will provide interesting topics for research which interested readers can take up. This book studies, analysis and upholds the pillars of horticulture and its utmost significance in modern times. It attempts to understand the multiple branches that fall under the discipline of horticulture and now such concepts have practical applications primarily with respect to ecology and agriculture. It will help the readers in keeping pace with the rapid changes in this field. Those with an interest in the horticulture field would find this book helpful.

About the Editor

Wendel Mason is an associate professor in the Department of Agricultural Science and teaches courses on organic farming and horticulture to undergraduate and graduate students. He holds a doctoral degree in agricultural science. He also serves as a visiting professor in several colleges across United States. Mason has published over 22 scientific papers in international journals and conference volumes. He has been the recipient of "Distinguished Teaching Service" award.

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Edited by Wendel Mason

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Horticulture: Ecology and Agriculture

PREFACE

Horticulture is the growth of plants for self-sustenance as well for as commercial purposes. Horticultural practices dominate the practical aspect of agriculture and horticultural theory too, plays an important aspect in agronomic studies. This book will provide interesting topics for research which interested readers can take up. This book studies, analysis and upholds the pillars of horticulture and its utmost significance in modern times. It attempts to understand the multiple branches that fall under the discipline of horticulture and now such concepts have practical applications primarily with respect to ecology and agriculture. It will help the readers in keeping pace with the rapid changes in this field. Those with an interest in the horticulture field would find this book helpful.

Various studies have approached the subject by analyzing it with a single perspective, but the present book provides diverse methodologies and techniques to address this field. This book contains theories and applications needed for understanding the subject from different perspectives. The aim is to keep the readers informed about the progress in the field; therefore, the contributions were carefully examined to compile novel researches by specialists from across the globe.

Indeed, the job of the editor is the most crucial and challenging in compiling all chapters into a single book. In the end, I would extend my sincere thanks to the chapter authors for their profound work. I am also thankful for the support provided by my family and colleagues during the compilation of this book.

Editor

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Breeding without Breeding: Is a Complete Pedigree Necessary for Efficient Breeding?

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Abstract

Complete pedigree information is a prerequisite for modern breeding and the ranking of parents and offspring for selection and deployment decisions. DNA fingerprinting and pedigree reconstruction can substitute for artificial matings, by allowing parentage delineation of naturally produced offspring. Here, we report on the efficacy of a breeding concept called “Breeding without Breeding” (BwB) that circumvents artificial matings, focusing instead on a subset of randomly sampled, maternally known but paternally unknown offspring to delineate their paternal parentage. We then generate the information needed to rank those offspring and their paternal parents, using a combination of complete (full-sib: FS) and incomplete (half-sib: HS) analyses of the constructed pedigrees. Using a random sample of wind-pollinated offspring from 15 females (seed donors), growing in a 41-parent western larch population, BwB is evaluated and compared to two commonly used testing methods that rely on either incomplete (maternal half-sib, open-pollinated: OP) or complete (FS) pedigree designs. BwB produced results superior to those from the incomplete design and virtually identical to those from the complete pedigree methods. The combined use of complete and incomplete pedigree information permitted evaluating all parents, both maternal and paternal, as well as all offspring, a result that could not have been accomplished with either the OP or FS methods alone. We also discuss the optimum experimental setting, in terms of the proportion of fingerprinted offspring, the size of the assembled maternal and paternal half-sib families, the role of external gene flow, and selfing, as well as the number of parents that could be realistically tested with BwB.

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Introduction

Plant breeding, including tree improvement, typically follows the classical recurrent selection scheme, which is characterized by systematic and repetitive cycles of breeding, testing, and selection [1], [2]. These programs deal with multiple populations (e.g., base, breeding, and deployment) and large numbers of parents and offspring, planted over multiple sites and years, and requiring extensive monitoring and maintenance. Selection of elite genotypes for either further breeding and/or inclusion in production populations is commonly performed based on their breeding values, determined from the intra-class correlation among relatives produced from elaborate mating designs [3]. As breeding programs advance, the number of parents' increases and their genealogy overlaps, and mating designs become more elaborate and the time required for their completion become real breeding programs' limiting factors [4]. To alleviate the efforts associated with generating offspring with complete pedigree information, specifically for early generation testing, forest geneticists have adopted simplified protocols, ranging from those not requiring a pedigree (e.g., bulk samples from natural populations known as

provenance testing [5] to those with incomplete pedigrees (e.g., open-pollinated [6] or polycross mating [7]). Data analyses with incomplete pedigrees often require invoking and/or accepting untestable assumptions related to the genetic constitution of the tested families and the numbers of male parents involved in their formation, as well as their proportionate contributions. Since these assumptions are not inordinately realistic in practice, the resulting genetic parameters and their associated inferences are often biased, ultimately leading to various degrees of inaccuracy and inefficiency [8]–[10].

The availability of affordable, highly informative DNA markers, coupled with the development of sophisticated pedigree reconstruction methods, has enhanced their utility in converting incomplete pedigree trials into (effectively) complete trials, thus eliminating the pitfalls associated with the invocation of unfulfilled assumptions [11]. Lambeth *et al.* [11] initiative of converting the polycross mating design's incomplete pedigree to complete made proper quantitative genetic analyses possible and the method was repeatedly evaluated for several species [12]–[16]. El-Kassaby *et al.* [13] and El-Kassaby and Lstibůrek [17] capitalized on the restricted maximum likelihood-based “animal model” [18] capa-

bility of analysing unbalanced and incomplete pedigree data, along with pedigree reconstruction (tantamount to paternity assignment), to introduce the concept of “Breeding without Breeding (BwB).” The basic idea of BwB is to combine the use of offspring with incomplete pedigree information (an entire open-pollinated test) with a subset of offspring with complete pedigree information, to construct both parental and offspring breeding values, thus incorporating backwards, forwards, and combined selection into an efficient breeding framework [13], [17]. Most of the DNA fingerprinting effort is dedicated to a subset of the offspring from a small number of known maternal parents (seed donors) to generate information about the entire population (maternal and paternal parents, as well as offspring) after reassembling paternal half-sib families from the pedigree reconstruction of the fingerprinted subset. Pedigree reconstruction permits connecting the entire parental population (sampled or not) through their shared offspring thus allowing the implementation of classical quantitative genetics analyses [18].

Here we experimentally demonstrate the utility, the increased precision of genetic parameters estimation, and increased accuracy of predicted breeding values, hence the effectiveness of the “Breeding without Breeding” concept, using open-pollinated offspring from 15 of 41 parents in a western larch (*Larix occidentalis* Nutt.) “breeding population.” We compared the performance of the combined incomplete (half-sib: HS) + complete (full-sib: FS) analysis to that of both the incomplete and complete pedigree designs. Finally, we illustrate the optimum experimental efforts needed for the successful implementation of BwB and discuss the role of factors such as external gene flow, expansion of the test population (i.e., the number of tested parents), and the size of half- or full-sib family needed for accurate genetic parameter determination.

Results

Pedigree Reconstruction/Mating Design Assembly

The partial pedigree reconstruction allowed direct estimation of gene flow, selfing rate, male reproductive success, and the number and/or size of maternal and paternal half-sib families on the individual as well as the population level (Figure 1). With 95% confidence, 1,419 out of 1,538 (92.3%) fingerprinted offspring were assigned to male parents within the orchard (Figure 1). The remaining 119 paternally unassigned offspring were identified as the product of introgression from an adjacent orchard, suggesting a pollen immigration rate of 7.7%. In addition, a total of 113 individual offspring resulted from selfing (average: 7.4%), ranging from 0.0 to 26.8% among seed donors, reflecting the 15 maternal parents propensity variation to selfing. This variability could be caused by maternal parents’ pollen shed and receptivity period synchrony differences.

Pedigree reconstruction resulted in the formation of 349 full-sib families, nested within the 15 maternal and 38 paternal half-sib families, respectively, indicating that three out of the orchard’s potential 41 male parents did not participate in pollination, at least of these 15 maternal parents, most likely due to their recent introduction to the seed orchard population (pers. observation). The 15 maternal half-sib families had an average size of 283.9 (range: 222–397) and the 38 paternal half-sib families had an average size of 37.3 (range: 1–193 among the 38 recovered paternal sibships), the latter evidently reflecting male fecundity variation within the orchard. There was an apparently high correlation between the difficult to assess male reproductive investment (male strobili production) and male reproductive success (determined by paternity analysis [19] ($r=0.87$; $P<0.001$).

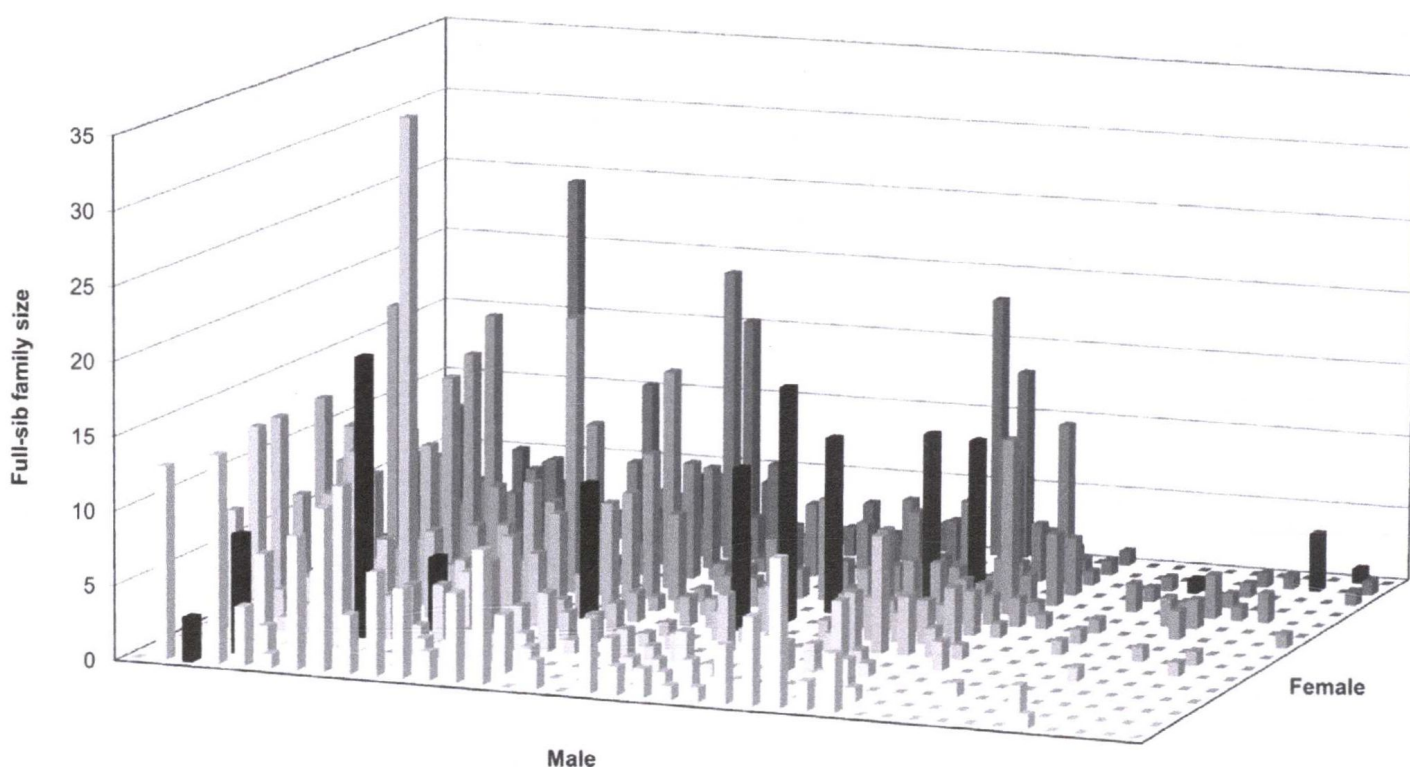


Figure 1. Pedigree reconstruction results showing the formation of full-sib families nested within the maternal and paternal half-sib families (black bars represent selfing).

Table 1. Forth-year height variance components and narrow sense heritability values (h^2_{ns}) and their standard errors for the half-sib (HS), combined half-sib+full-sib (HS+FS) and full-sib (FS) models.

Source of variation	Variance component		
	Incomplete pedigree		Complete pedigree
	HS	HS+FS	FS
Additive	156.8±80.0	69.3±26.9	55.93±25.42
Plot	48.7±11.2	80.7±17.2	101.95±23.93
Error	266.4±60.5	332.4±20.1	315.99±19.52
Total	471.9	482.5	473.9
h^2_{ns}	0.33±0.16	0.14±0.05	0.12±0.05

The reconstructed pedigree formed a structured mating design, which we used to generate quantitative genetic parameters for the complete pedigree model (FS), and was used in concert with the non-fingerprinted individuals within each of the 15 HS families to form a combined pedigree model, consisting of half- and full-sib families (HS+FS) (see below). A minimum paternal half-sib family size threshold of six individuals was established for inclusion in quantitative genetic analyses. Seven male parents did not meet this threshold, but two were retained, because they were also represented as seed-donors, thus far exceeding the established minimum family size threshold.

Estimation of Quantitative Genetic Parameters

Following the classical individual-tree additive model, three analyses were conducted. The first is for the 15 open-pollinated families (HS) with sample size of $N=5,796$ individuals (i.e., incomplete pedigree). The second is also for the same 15 HS families ($N=5,796$) but after the inclusion of the male parent for 1,419 individuals (i.e., a combination of half- and full-sib families (HS+FS) and also represents an incomplete pedigree). While the third representing full pedigree ($N=1,419$) and was solely based on full-sib families formed by the pedigree reconstruction (FS) (Figure 1; Table 1). Relative to the combined HS+FS model, the HS model grossly overestimated the additive genetic variance (156.8 vs. 69.3), which more than doubled the height heritability estimate (0.33 vs. 0.14) (Table 1). The precision of the additive genetic variance (80.0 vs. 26.9) and heritability (0.16 vs. 0.05) estimates for these two models produced higher standard error for the HS as compared to the combined HS+FS model (Table 1). Additionally, the inclusion of more genetic information in the combined HS+FS model (i.e., those from FS families) increased the sensitivity of the analysis, as subtle plot-to-plot variation was detected, resulting in a more realistic assessment of the residual error term (Table 1). Parental breeding values' comparisons was limited to only the 15 maternal parents in the HS analysis with their corresponding 15 estimates from the HS+FS analysis and produced non-significant product-moment ($r=0.44$ (CI: $-0.099, 0.775$); $p=0.105$, Figure 2) and rank ($\rho=0.44$ (CI: $-0.099, 0.775$); $p=0.105$) correlations. The corresponding comparison of HS with HS+FS breeding values for the offspring yielded significant product-moment ($r=0.69$ (CI: 0.672, 0.700); $p=0.0001$, Figure 3) and rank ($\rho=0.67$ (CI: 0.656, 0.686); $p=0.0001$) correlations. Both results

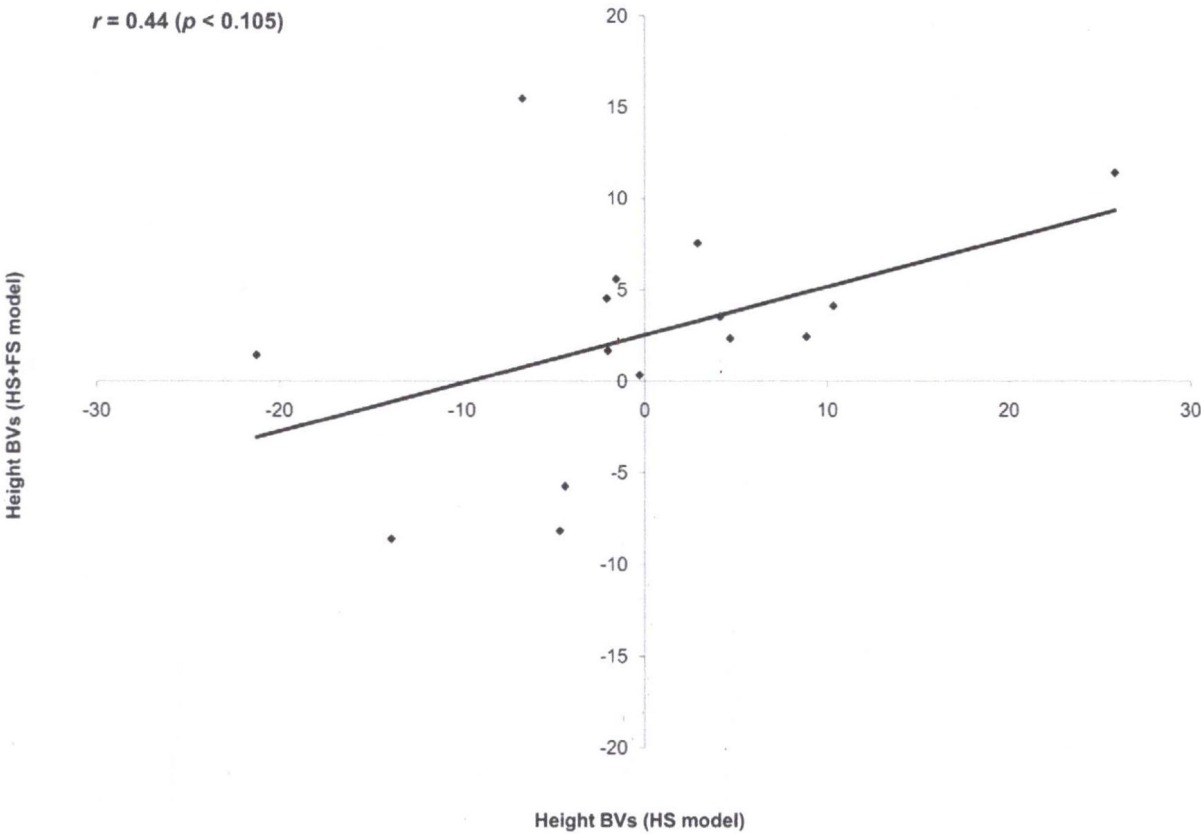


Figure 2. Scatter plot of predicted breeding values for parents from the two incomplete pedigree models (HS and combined FS+HS). Pearson correlation (r) is in the left corner of the graph.

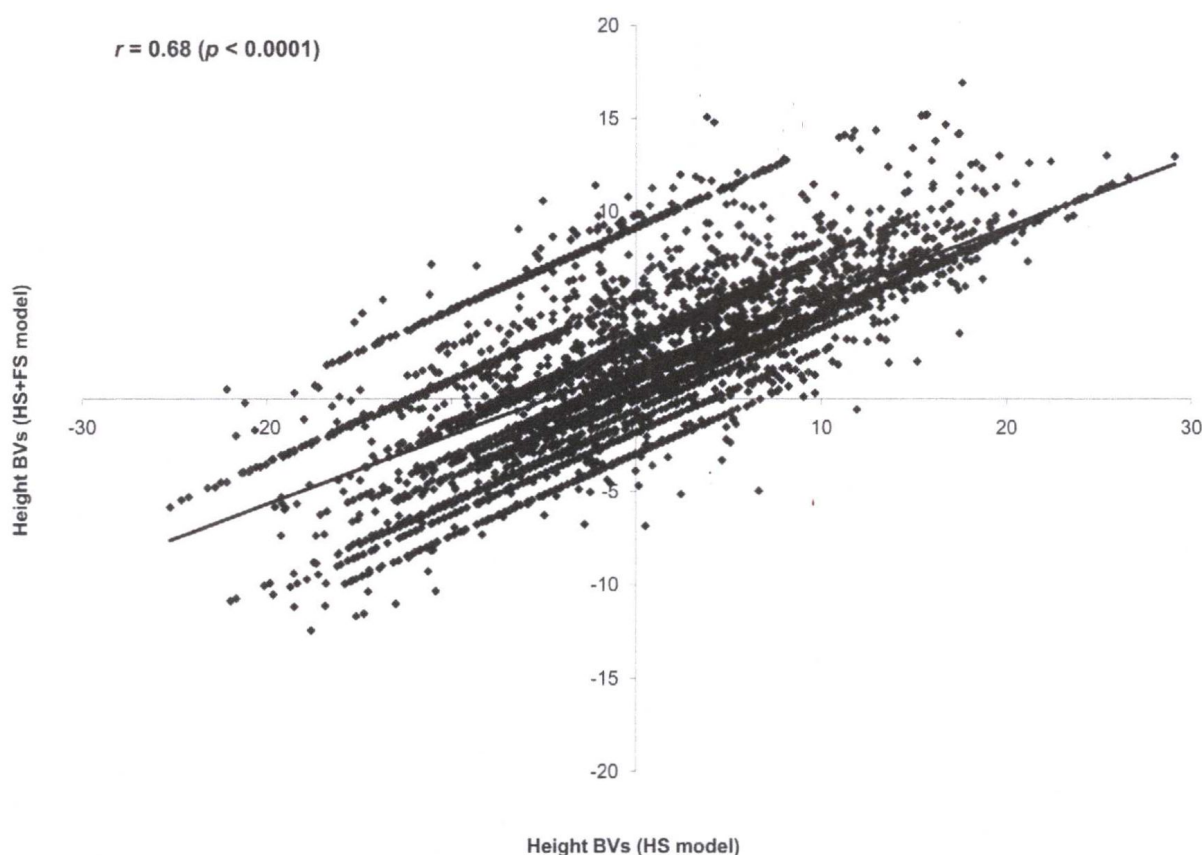


Figure 3. Scatter plot of predicted breeding values for offspring from the two incomplete pedigree models (HS and combined HS+FS). Pearson correlation (r) is in the left corner of the graph (note the greater extent of variation between the two models).

clearly demonstrate the reduced utility of the HS model's estimates for forward selection, relative to the results from the HS+FS treatment as indicated by both product-moment and rank correlations. Finally, the average accuracy of predicted breeding values, calculated from the combined HS+FS model was higher for parents (0.81) and offspring (0.55), than their corresponding values (0.56 and 0.45, respectively), calculated from HS model.

The full (FS) and combined HS+FS pedigree models produced comparable additive and heritability estimates, with similar precision (Table 1). Predictions of parental breeding values extracted from both models were comparable and highly correlated (product-moment ($r = 0.96$ (CI: 0.928, 0.982); $p = 0.0001$, Figure 4) and rank ($\rho = 0.94$ (CI: 0.875, 0.968); $p = 0.0001$) correlations). The same was true for offspring breeding values (product-moment ($r = 0.97$ (CI: 0.971, 0.976); $p = 0.0001$, Figure 5) and rank ($\rho = 0.97$ (CI: 0.967, 0.973); $p = 0.0001$) correlations). The results from the combined HS+FS pedigree approach are robust and reliable. Moreover, the average accuracy of breeding values from parents and offspring calculated from the FS model (0.78 and 0.69, respectively) were very similar to those estimated from the combined HS+FS model (0.76 and 0.64, respectively). It is interesting to note that predicted parental breeding values were produced for the entire parental population (i.e., all seed and pollen donors), even when only 15 maternal parents were used and these estimates were based on the entire population ($N = 5,796$) for the combined HS+FS model as opposed to $N = 1,419$ for the FS model.

Production Population Selection

We implemented three selection options; namely, forwards, backwards, and combined (combination of backwards and forwards), utilizing either the parental (backwards) and/or offspring

(forwards) "Best Linear Unbiased Predictors" (BLUPs) generated from the HS or the combined HS+FS models. The backwards selection option was applied exclusively to the combined HS+FS model as parental breeding values were determined from both maternal and paternal information. The limited number of maternal parents (15 seed donors) precluded the application of the backwards selection option under the HS model; however, maternal breeding values along with offspring was used in the HS combined selection. Additionally, the limited number of maternal parents minimized the response to selection's differences between the forwards and combined selections resulting in somewhat identical results (Figure 6). Without exception and across the range of effective population size tested, the HS model overestimated the response to selection as compared to that from the combined HS+FS model, reflecting the observed additive genetic variance overestimation (Figure 6). For example, compared to the combined HS+FS model, the HS combined selection overestimated the response to selection by a range of 15 and 25% for effective population size of 10 and 40, respectively (Figure 6). The combined HS+FS model's forward and/or combined selections were superior to their backward with response to selection differences ranging between 7 and 12% for effective population size of 10 and 30, respectively (the paternal HS family size restriction of $n = 6$ limited the effective population size range for backward) (Figure 6). Finally, as expected and for all selection methods and both HS and the combined HS+FS models, the response to selection decreased with increased in effective population size (Figure 6).

Estimating Offspring Optimum Sample Size

Drastic difference in the additive genetic variance magnitude and its standard error was observed with increasing the number of

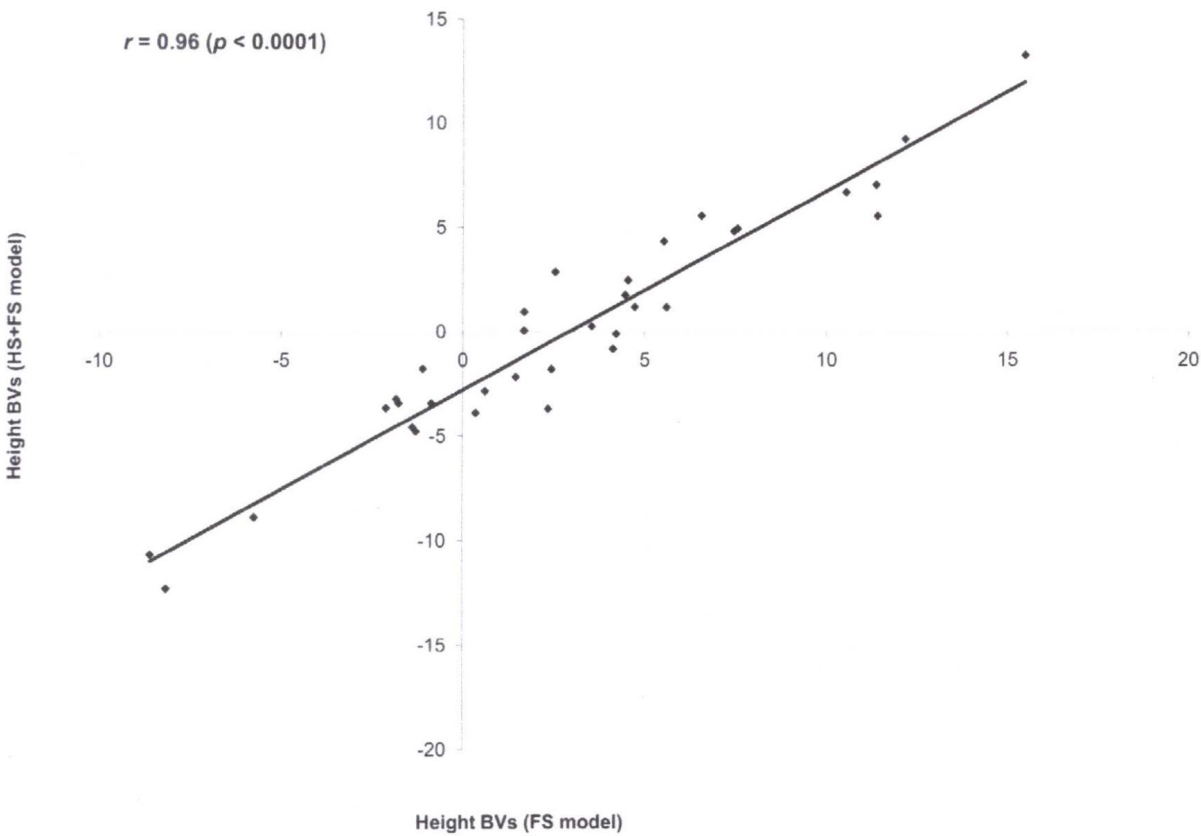


Figure 4. Scatter plot of predicted breeding values for parents from the incomplete (combined HS+FS) and complete (FS) pedigree models. Pearson correlation (r) is in the left corner of the graph.

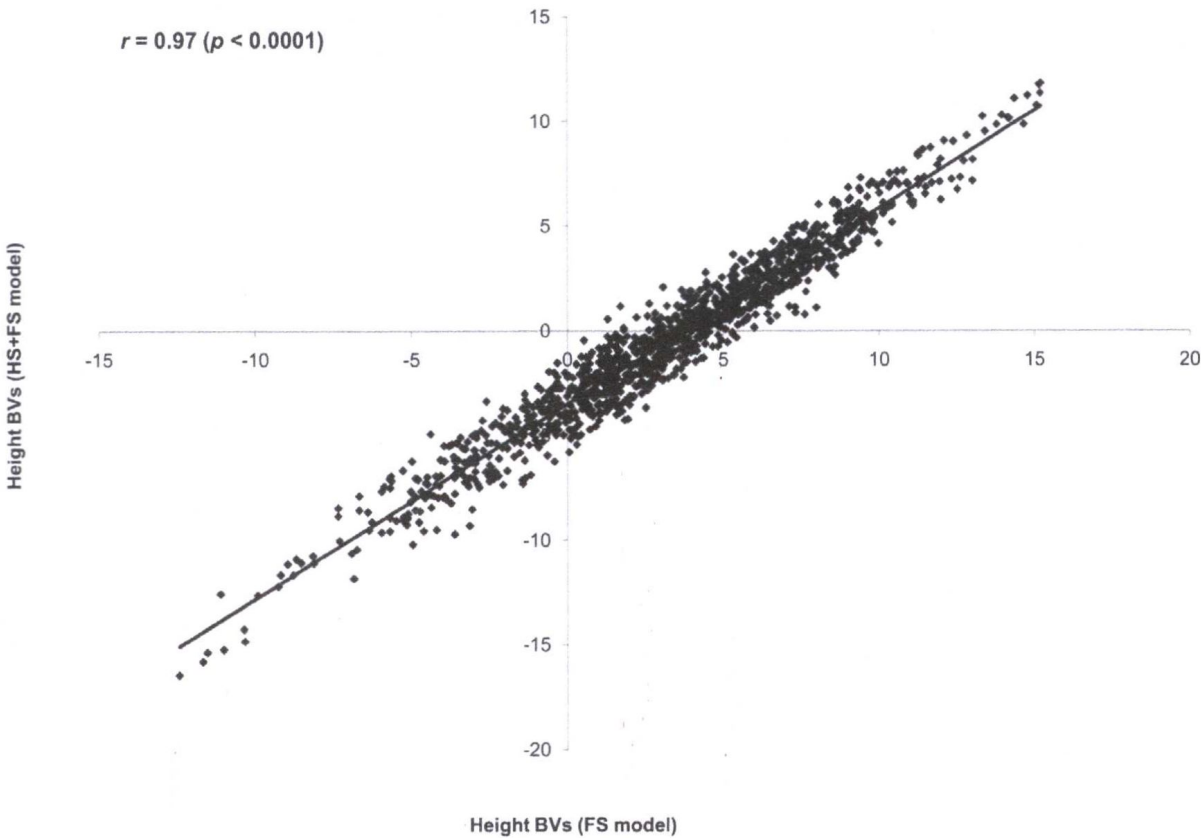


Figure 5. Scatter plot of predicted breeding values for offspring from the incomplete (combined HS+FS) and complete (FS) pedigree models. Pearson correlation (r) is in the left corner of the graph.

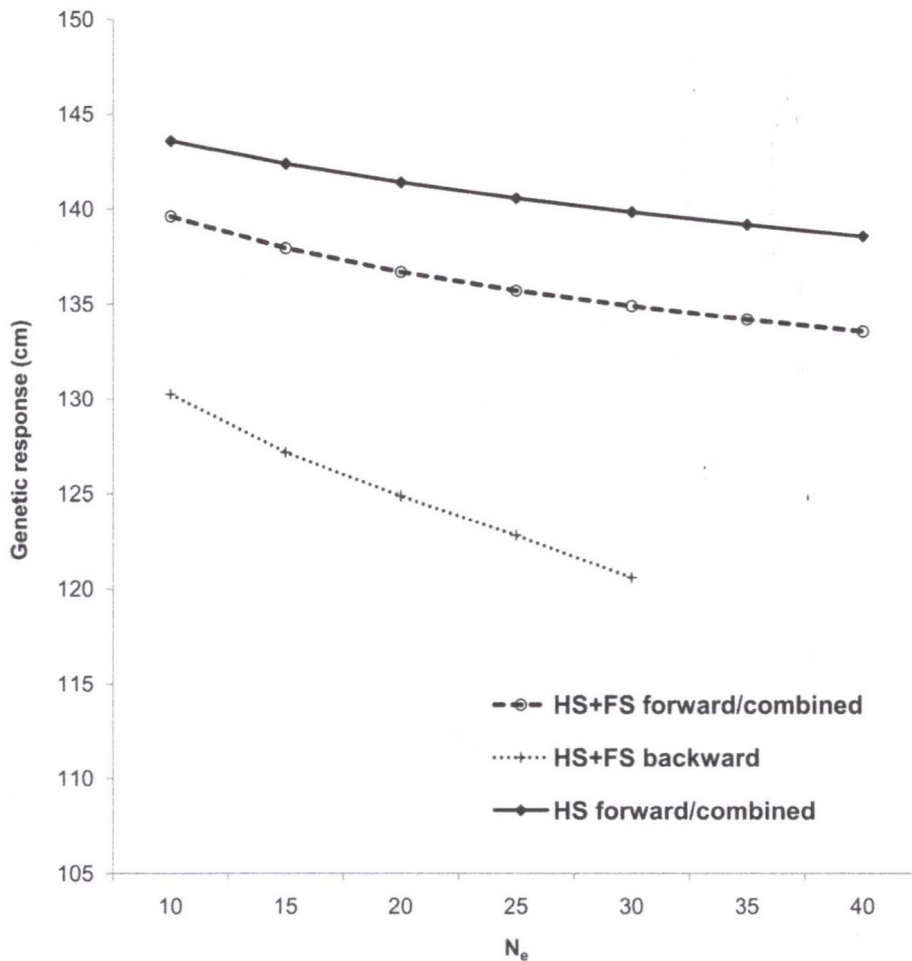


Figure 6. Response to selection comparison between the half-sib (HS) (forward and combined) and combined half- and full-sib (HS+FS) (backward, forward and combined) models assessed across various effective population sizes (10 to 40). (The small number of tested parents resulted in identical results for forward and combined selection methods under the combined HS+FS and HS scenarios).

trees with known paternal information (Figure 7). Increasing the number of trees with known fathers (i.e., those from the pedigree reconstruction) to those already with known mothers improved the direct and/or indirect connectedness among parents and thus permitted their unbiased comparison as well as their genetic parameters' estimation. The observed improvement in the additive genetic variance precision leveled after the inclusion of 600 individuals and no substantial fluctuations were observed beyond this point, indicating that a threshold was reached and the inclusion of any additional offspring would not substantially affect the results (Figure 7). Based on the observed trend and in this particular case, it appears that the inclusion of paternal information for 10% of the evaluated offspring population is adequate to create the direct and/or indirect connectedness among parents is sufficient to achieve the available precision.

Discussion

The concept of marker-assisted estimation of quantitative genetic parameters was introduced by Ritland [20], whereby traits' heritabilities and the magnitude and direction of their genetic correlations are derived from regressing pair-wise phenotypic similarity on their corresponding pair-wise genetic relatedness. This concept is appealing, because of its obvious simplicity, *in situ* nature (i.e., no experiments or mating designs), and most of all its suitability to long-lived organisms such as trees

or wildlife that require long-term experiments or extensive field observations. The distribution of relatedness among the studied individuals is assumption-free, thus it is applicable to natural populations where a vast array of genetic relationships can occur [21], [22]. In situations where offspring are derived from random mating among a set of known parents and more specifically when their number is somewhat limited, the *no a priori* assumption about the expected distribution of genetic relationship becomes inappropriate for a network of full-sibs, half-sibs, and selfs (albeit absence of spatial autocorrelation in relationship coefficients as well as in trait performance in the wild are assumed). It should be stated; however, that the regression approach does not permit the prediction of parents and/or offspring breeding values, thus its application to selection and breeding is somewhat limited.

Conventional tree breeding programs are structured around three main activities: breeding, testing and selection [23]. These activities are long-term endeavours, based on structured pedigree produced from one or a combination of different mating designs [23]; they also require extensive testing in large experimental settings, distributed throughout vast territories [4], and (most important of all), they require sustained organizational and financial commitment. Obviously, simplified breeding schemes that reduce time and cost would be of great value. The generation of complete pedigreed offspring for testing and selection is an obvious target for simplification, fostering incomplete pedigree methods such as open-pollinated family testing [6] and polycross