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Realized Genetic Gains from Slash Pine Tree Improvement

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Summary

Realized genetic gains of slash pine (*Pinus elliottii* ENGLEM. var. *elliottii*), were estimated for tree volume and rust resistance using data from 2051 controlled-pollinated (CP) families grown in 175 CP tests. All CP families were divided into 5 groups for volume (groups V1 to V5) and 5 groups for rust (groups R1 to R5). For each variable the 5 groups represent the expected performance range from best to worst of the CP families based on parental breeding values (BVs) predicted by best linear prediction (BLP) from an independent data set of 367 open-pollinated (OP) progeny tests.

Using simple linear regression, realized genetic gains were estimated by comparison among these groups and also by comparison of improved materials to unimproved materials (called CHECK) included in most tests. On a region-wide basis, the ranking of realized gain ratios (in percent above unimproved material) for volume and rust of the 5 groups corresponded exactly to the order predicted by *a priori* classification based on the BLP predicted BVs. For example, for volume the realized gain increased linearly for the 5 volume groups.

Regression analyses were used to examine how age and site characteristics (e.g., site index, rust hazard) and their interactions with the 2 types of genetic groupings (V1 to V5, R1 to R5) affected genetic gains in the 2 traits, volume and rust. Age was almost never significant for volume or rust suggesting that the percentage gain above unimproved material is constant over the range of ages 5 to 11. The results also suggest that superior families for tree volume express increased gain in volume (on a % basis) compared to the unimproved material on better quality sites, and that genetic differences among genetic groups are greater on better sites (SIclass 3, 4 and 5) relative to poorer sites (SIclass 1 and 2). Also, genetically superior families for rust resistance have more tree volume on the high hazard sites, and on these sites the most resistant families also had the highest volume gains relative to the CHECK.

Key words: Realized genetic gain, best linear prediction, breeding value.

FDC: 165.4; 165.3; 56; 443; 174.7 *Pinus elliottii*).

Introduction

Tree improvement programs produce genetic gains in specific traits of interest, and even small genetic gains can have enourmous economic returns in a large scale tree improvement program (WEIR, 1973). It is the genetic progress achieved which justifies the costs incurred in the selection and breeding of superior phenotypes (PORTERFIELD, 1975; ROW and DUTROW, 1975). Thus, estimates of realized genetic gains are an important means of evaluating the performance of a tree improvement program (HODGE *et al.*, 1989). However, precise estimates of realized genetic gain are difficult to obtain, and are infrequently found in the tree improvement literature.

Generally, realized gains from a selection or breeding program are determined by a comparison of performance of improved materials with unimproved materials (ZOBEL and TALBERT, 1984; LA FARGE, 1993). Two different genetic test designs can be used to assess the performance of the improved and unimproved materials: 1) Row or single-tree plots, and 2) large block plots (LOWERTS, 1986). Large block plots of improved and unimproved materials provide unbiased estimates of realized genetic gain for growth traits on a per unit area basis (LOWERTS, 1986); however, large block plots suffer from large block (replication) sizes which contribute to low statistical precision. Therefore, a large number of experimental locations are needed to determine statistically significant differences (TANKERSLEY *et al.,* 1983). There are many statistical and logistical advantages of using row or single-tree plots; however, they can provide biased estimates of realized gain for growth traits if dominant phenotypes gain early competitive advantage (WRIGHT, 1975; CANNELL, 1982). Studies on estimating realized genetic gains suggest that the net effect of predicting performance of selected genotypes over a full rotation on the basis of individual tree performance, using traits such as height growth, and stem volumes at certain ages, may result in an overestimate of the true genetic gain (CANNELL, 1982).

In general, very few realized gain studies have been published for southern pines (LOWERTS, 1987), and of those published studies, estimates often are from a small number of parents and genetic tests. This may be due to the experimental complexities and the long time required for the growth of the tree. Most published studies are estimates of realized gains from first-generation mass selection (not from later stages of a breeding program), and have reported genetic gains of increased total volume, better and more uniform quality of timber production and increased disease resistance (GODDARD *et al.,* 1975; LOWERTS, 1986; HODGE *et al.,* 1989, 1990; LA FARGE, 1993). One study done by TANKERSLEY *et al.* (1983) comparing "improved" (unrogued clonal seed orchard) and "unimproved" (commercial checklot) in 15-year-old plantations of slash pine in 10 locations in Georgia suggests no significant differences for tree volume and rust resistance characteristics. However, the analytical method used to estimate realized gain in their study was insensitive and only able to detect differences greater than 10 % in volume and 23 % in rust infection.

As stated earlier, a large amount of data representing many tests and locations is needed in order to get useful and reliable genetic gain estimates. Also, none of the previously reported studies have investigated impacts of site characteristics (such as site index) on realized gains. This study, therefore, utilizes data from 175 genetic tests of slash pine measured for volume and rust resistance from ages 4 to 20 in the Cooperative Forest Genetics Research Program (CFGRP) to quantify and investigate the nature of realized gains.

The specific objectives of this paper were: (1) To quantify realized gains for tree volume and rust resistance of improved and unimproved mixed-family lots compared to commercial checklots; (2) To quantify realized gains of slash pine for tree volume and rust resistance of CP families of varying genetic quality based on their parental performance in independent OP tests; and (3) To determine whether characteristics (such as age, site index class and rust hazard of the site) influence realized gain in volume and rust resistance.

Materials and Methods

Plant Material and Genetic Tests

From 1954 to 1963, the CFGRP selected over 2500 superior slash pines from across the species' range. Subsequent to selection, clones were grafted into seed orchards and all of them were progeny tested with orchard OP seed, beginning from 1960. Data from over 300 of these OP progeny tests were used to predict parental BVs of original selections for tree volume at 15 years and fusiform rust resistance (WHITE and HODGE, 1988).

In addition to OP progeny tests, the CFGRP established 2 separate series of full-sib tests. The first series was established during 1966 to 1973, and is comprised of 78 tests in a factorial crossing scheme; each test contains from 6 to 86 full-sib families (mean = 30) created by crossing some of the mass selected parents (from the population of over 2500 first-generation selections). The second series, established during 1975 to 1989, is comprised of 187 tests and utilizes either potentially-superior first-generation parents chosen from very early OP progeny test data mated in diallels or factorial mating designs (DIETERS, 1994).

A randomized complete block design was used for all tests in both series, and each full-sib family was represented either in a single row plot or non-contiguous plot with 5 to 10 trees in each block with 3 to 10 blocks per test. Trees in these tests were measured between ages 4 and 20 years. The measured traits were height, diameter at breast height (DBH) (4.5 ft above ground), and rust incidence. Rust incidence was evaluated by eye and scored 0 for no rust and 100 for trees infected with at least one rust gall. Inside bark tree volume (bole) was calculated using the volume equations provided by GODDARD and STRICKLAND (1968) for DBH ≤ 7 inch and ROCKWOOD (1981) for DBH > 7 inch.

In 1994 measurements from 175 tests were available for analysis. These 175 CP tests included 669 slash pine parents, which had been used to create 2051 full-sib families. In each test, a subset of these families were planted along with various commercial, improved, and unimproved checklots that were used in calculating and comparing realized gains. The BVs of each parent used to create the CP slash pine families in these tests had been previously predicted from an independent set of 367 OP slash pine tests. For the purpose of analysis, age measurements were grouped into 3 age classes centered at ages 5, 8, and 11 with 144, 120, and 120 measured tests, respectively (some tests were measured at more than 1 age). The mean percentage of rust infection in a test varied from 0% to 100%. Tests with rust infection of ≤ 10% were not used to examine realized gains for rust since low levels of infection do not provide reliable information on rust resistance (WHITE and HODGE, 1989). Therefore, 79, 86, and 84 tests at age 5, 8, and 11, were used in the analysis of rust resistance.

Checklots and Groupings of Families in Controlled-Pollinated Tests

The genetic gains in this study were determined by the comparison of performance of improved materials versus unimproved materials. All the 175 CP tests included some kind of checks which were: (1) commercial checks (CC); (2) a University of Florida checklot (UC); (3) a bulk mix of families (1001); and (4) a second bulk mix (1002). The CC are various woods-run, unimproved checks planted by the individual cooperators in progeny tests established on their land. The UC is seed collected from a single unimproved stand in southeast Georgia and has been used by the CFGRP as a standard check across most progeny tests to compare with family performances. The checks 1001 and 1002 were bulk mixes included in many of the CP tests. The mixes were constructed in the mid 1960's based on early OP progeny test results, and were intended to represent "improved" and "unimproved" materials, respectively. The "improved" check, 1001, is a bulk mix of OP seed from 22 families collected in 1.0 and 1.5 generation rogued orchards. The "unimproved" check, 1002, is a bulk mix of OP seed from 20 families from an unrogued 1.0 generation orchard (Horticulture Unit at Gainesville, Florida).

The UC and CC are both thought to represent unimproved slash pine as it existed before domestication, and these 2 checks were compared to examine if they were of similar genetic quality. The UC and CC consistently performed similarly, in terms of genetic gains, against each other and against other genetic entries and were never more than 2.7 % different for volume and 7 % different in rust resistance. All statistical analyses done using SAS® (SAS® Institute Inc., 1988) indicated that these 2 types of checklots were not statistically different across the 155 total observations (51, 43, and 61 tests at age 5, 8, and 11, respectively) in which they occurred together. Since there was little apparent difference, and since both types were samples of unimproved material prior to improvement activities, these checks were pooled together and treated as one throughout the remainder of the study. Hereafter, this pooled checklot of unimproved material is called CHECK.

The BVs for tree volume and rust resistance of the 669 parents used to create the full-sib families had been previously predicted with Best Linear Prediction (BLP) using data from OP row-plot progeny tests (WHITE and HODGE, 1988). These BVs predicted from independent OP data sets were used to calculate an expected value for each of the three OP checklots (CHECK, 1001 and 1002). Based on OP data, CHECK has a mean BV volume = –0.38 (where the mean of all first-generation selections has BV = 0) and mean BV R50 = 50 (the amount of rust to be expected on a site with a rust hazard of 50 %, i.e. an area where unimproved material will incur 50 % infection). The 1001 bulk mix had mean BV volume = 0.32; mean BV R50 = 35. The 1002 bulk mix had mean BV volume = 0.01; mean BV R50 = 50. On this basis, the expected genetic quality for tree volume is 1001 > 1002 > CHECK. For rust, low values are more improved (indicating less infection), thus 1001 is expected to be better than both 1002 and CHECK.

The independently-predicted BVs were also used to calculate an expected genetic value for each full-sib family as the mid-parent of the two parental BVs. All families were then divided into 5 groups according to the expected BV for volume (groups V1 to V5) and into 5 groups according to BV for rust (groups R1 to R5). For each variable the 5 groups represent the expected performance range from best to worst based on the independent ranks calculated from OP progeny tests (*Table 1*).

Table 1. – Groups of full-sib families for tree volume (vol) and rust resistance (rust) based on their expected genetic value calculated from mid-parental breeding values predicted from OP progeny tests. For vol, the parental breeding values are in units of cubic feet at 15 years with mean = 0. For rust, the parental breeding values represent expected rust incidence in a site in which unimproved material gets 50% rust. Number of tests indicate the number of full-sib test locations containing families of each genetic quality group.

Group	Level	Number of tests			Breeding value range	Mean
		Age 5	Age 8	Age 11		
V1	worst	45	39	48	vol ≤ -0.75	-0.92
V2	poor	106	95	108	-0.75 ≤ vol ≤ -0.25	-0.45
V3	average	144	120	120	-0.25 ≤ vol ≤ 0.25	0.03
V4	good	138	115	117	0.25 ≤ vol ≤ 0.75	0.45
V5	best	89	74	70	vol ≥ 0.75	0.96
R1	best	59	63	47	rust < 20	13
R2	good	79	86	78	20 ≤ rust < 40	32
R3	average	75	81	81	40 ≤ rust < 60	48
R4	poor	33	35	58	60 ≤ rust < 80	65
R5	worst	5	4	19	rust ≥ 80	83

Estimation of Region-Wide Realized Gains

The unit of observation for all analyses of realized gains was the mean of a given type of genetic entry in a given progeny test location. This was calculated in 2 steps. First a least square mean (LSmean) of each full-sib family and check was calculated in each test. LSmeans were used in order to take account of unequal representation of families in blocks. Second, the mean of the LSmeans for each type of genetic entry was calculated (CHECK, 1001, 1002, V1, V2, … V5, R1, R2, … R5). Thus, in general there was one value for each type of genetic entry in each test, although some types of genetic entries were not represented in some tests.

To estimate realized genetic gain across all tests, 2 kinds of approaches were used: (1) Ratio (hereafter called ratio approach), and (2) Separate variable regression (hereafter called regression approach). In each approach, each test in the data set described above provided at most one observation to estimate the realized gain for a particular type of genetic entry. In both approaches, all realized gains were estimated relative to the CHECK (the pooled UC and CC checks believed to be representative of unimproved slash pine). In the ratio approach, the ratio of the genetic entry divided by the CHECK was calculated in each test. For example, if in a given test, $VOL_{V5}/VOL_{CHECK} = 1.25$, this indicates that the V5 group had 25 % more volume than the unimproved check. These ratios were then averaged across all tests to estimate realized gains for each type of genetic entry (such as the V5 group). Average ratios were calculated for both tree volume and rust resistance.

In the regression approach, a linear regression for each type of genetic entry was fit using the following model:

$$X_{ENTRY} = b\ X_{CHECK}.$$

For all regression analyses, the regression approach was first investigated with an intercept, and intercept terms were never significantly different from zero. Therefore, all models were forced through the origin. Since the regression line is fit through the origin, the slope coefficient b estimates the average ratio of performance of the genetic entry versus the unimproved check across all tests. If b = 1.25 for volume of the V5 group, this indicates 25 % improvement for volume of this group. Similar regressions were fit for all VX groups (V1 … V5), RX groups (R1, … R5), 1001, and 1002 all against the CHECK as the regressor variable.

The 2 approaches (ratio and regression) were used to examine the same questions, but provided different weights to different data points. The regression approach provides more weight on higher values of the independent variable (X_{CHECK}) because the regression is fit through the origin (and hence values nearer the origin cannot strongly influence the slope). In contrast, the ratio approach gives equal weight to all observations. In this paper both ratio and regression approaches were used, and the results of the two approaches are slightly different. Final results are always the average of the 2 approaches (ratio and regression).

Influence of Age and Site Characteristics on Realized Gains

Influence of age and site characteristics on realized gains was investigated using only the 5 volume and 5 rust groups. The 1001 and 1002 checks were not used because they were bulk mixtures of many families that might buffer some influences and bacause the 5 groups for each trait were linear relative to predicted BVs.

One of the site characteristics investigated in this study was site index, which was estimated for each test following the approach used by DIETERS (1994). The mean height of the largest 43.5 % trees ranked by diameters was used to estimate dominant height (BAILEY and BROOKS, 1994), and then the formulae developed by PIENAAR *et al.* (1990) was utilized to estimate site index using the dominant height. DIETERS (1994) found that data less than 8 years of age over-estimated site index, but data older than 8 provided site index estimates not significantly different from those obtained with 8-year data. Therefore, the estimated site index was adjusted to that estimated from 8-year data, when necessary (DIETERS, 1994).

Using this approach, each test was assigned to 1 of 5 site index classes (siclass 1 to 5, 1 = poor, 5 = good) using this 8-year adjusted site index (SI) (SI predicted at a base age of 25 years): SIclass 1, SI < 62 ft; SIclass 2, 62 ≤ SI < 68; SIclass 3, 68 ≤ SI < 73; SIclass 4, 73 ≤ SI < 78; SIclass 5, SI ≥ 78.

The influences of age on realized gains were investigated using 3 defined age classes of 5, 8 and 11 years. To investigate impact of rust hazard levels, each test was assigned to 1 of 5 rust hazard (rushaz) levels (rushaz 1 to 5 with 1 indicating low rust and 5 indicating high rust) on the basis of rust incidence observed in the CHECK (ruschk); rushaz 1, 10 ≤ ruschk < 20 %; rushaz 2, 20 ≤ ruschk < 40; rushaz 3, 40 ≤ ruschk < 60; rushaz 4, 60 ≤ ruschk < 80; rushaz 5, ruschk ≥ 80.

The influences of age and site characteristics were examined using four types of analyses which examined how these test characteristics and their interaction with the 2 types of genetic groupings (V1 to V5, R1 to R5) affected genetic gains in the 2 traits, volume and rust. In other words, one analysis examined how realized genetic gains in volume were affected by the test characteristics and their interactions with the volume groups V1 to V5 (the V/V analysis). A second analysis examined realized genetic gains in volume as affected by the test characteristics and interactions with the rust genetic groups R1 to R5 (V/R analysis). The third analysis examined realized gains in rust affected by test characteristics and interaction with the rust genetic groups R1 to R5 (R/R analysis), and the fourth examined gains in rust affected by test characteristics and interaction with volume genetic groups V1 to V5 (R/V analysis).

For each of the 4 analyses, both the ratio and regression approaches were conducted with groups (R1 to R5 or V1 to V5), ages (5, 8, and 11), site index classes (1, … 5) and rust hazard levels (1, … 5) used as independent class variables (regressors) in the analysis. For the ratio analysis, the unit of observation (independent variable) was gain ratio of a given group (genetic entry) to the CHECK in a given test. A full linear model with all effects and 2- and 3-way interactions was first fit (for details see DHAKAL, 1995).

The regression (or covariance) approach was also employed for each of the 4 analyses (V/V, V/R, R/R, R/V) with the volume or rust of a given genetic entry in a given test as the independent variable (for details see DHAKAL, 1995). In the regression approach, the goal was to determine whether a different slope (and hence a different ratio) is needed for each group and all of the other factors in the model. If a factor is significant in the regression or ratio approach it implies that realized gains are impacted by that factor.

After fitting the above full models for both the ratio and regression approaches to a given analysis (such as the V/V analysis), the following steps were employed to determine the final model: (1) All statistically-significant 2-way interactions and 3-way interactions were examined graphically to determine the biological importance; (2) The influence of main-effects and interactions were examined for consistency in direction and magnitude across the 2 approaches (ratio and regression); (3) Many types of reduced models were fit and examined graphically; and (4) A final model was chosen in which all effects in the model were statistically significant (at α = 0.05), biologically interpretable, and consistent across both approaches.

Results and Discussion

Regionwide Gains for Tree Volume and Rust Resistance

The rankings of realized gains for volume of the genetic entries correspond exactly to the order predicted by the *a priori* classification based on the predicted genetic quality from the BLP predicted BVs from the OP data. The V1 group, the designated worst volume group on the basis of the BVs (*Table 1*), had the poorest tree volume, performing slightly worse than the unimproved CHECK (ratio = 0.97 in Figure 1 indicates that V1 had 97 % of the volume of the check average over the ratio and regression methods). All other genetic entries (V2, V3, V4, V5, 1001 and 1002) had significantly (p = 0.05) higher tree volume than the CHECK in the 2 different approaches (ratio and regression). The V2, V3 and V4 groups performed increasingly better relative to the unimproved CHECK, and the V5 group (containing the best CP families based on parental OP breeding values), produced over 22 % more volume than the unimproved CHECK (ratio = 1.22, *Figure 1*). In addition, the 1001 bulk check produced slightly more volume than the 1002 check (approximately 18 % gain versus 16 % gain above unimproved) the same order predicted by their rankings based on OP breeding values.

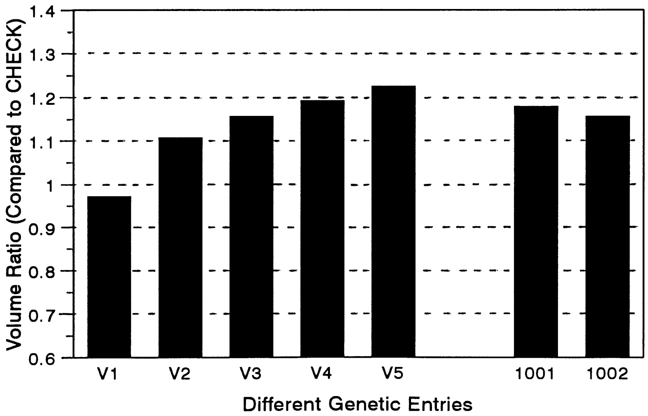

Figure 1. – Volume ratios compared to CHECK of different genetic entries, estimated by ratio and regression approaches. The value presented is the average of the 2 approaches for each entry. In both the ratio and regression approaches all genetic entries (except V1) were significantly different than 1 indicating statistically-significant gain above CHECK.

Although the realized gain ratios presented for volume in *figure 1* (and for rust in *Figure 2*) are averages of the ratio and regression approaches, the 2 methods produced very similar estimates and trends. Using the ratio approach, it was possible to partition the sums of squares among volume groups into components due to a linear and quadratic relationship with mean OP breeding value for each group. The linear term accounted for 90 % of the group sums of squares, indicating a nearly linear increase in realized gain with increasing volume BV. Thus, the CP families predicted to perform better based on the BLP-predicted BVs of the parents in OP progeny tests actually did grow faster in nearly linear fashion with predicted performance.

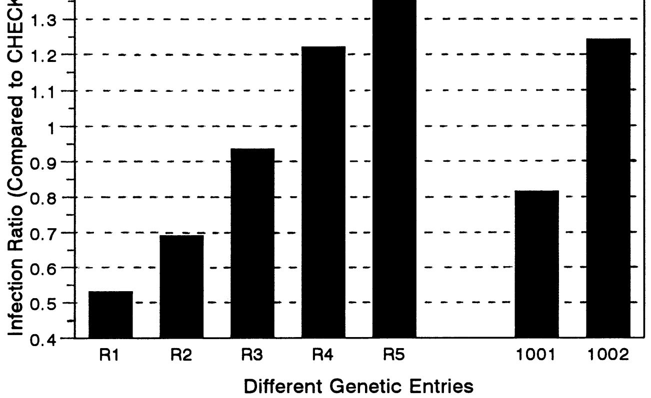

Figure 2. – Infection ratio of fusiform rust of different genetic entries, estimated by ratio and regression approaches. The value presented is the average of the two approaches for each entry. Note that for rust infection, a ratio greater than 1.0 indicates the genetic group had higher rust incidence than the CHECK.

The trends in realized gain ratios for rust were similar to those for volume (*Figure 2*). The realized gain ratio for rust infection for the R1 group (the most resistant group according to the OP breeding value predictions) incurred approximately half the rust incidence incurred by the unimproved checks (ratio = 0.53, *Figure 2*). The R2 group had a higher ratio than R1 (ratio = 0.69), followed by the R3 group which averaged approximately the same amount of infection as the unimproved CHECK (ratio = 0.94). The most susceptible group, R5, did in fact have the poorest realized gain ratio (ratio = 1.37) indicating that if the unimproved checks incurred 50 % infection, the R5 families would incur approximately 70 % infection (1.37 x 50). Also as expected, the 1001 check showed significantly more resistance than the 1002 check, (ratio = 0.81 versus 1.24, respectively). Using the analysis of variance (ANOVA), the partitioning of the sums of squares among rust groups indicated that the linear trend with mean BV for rust accounted for over 96 % of the sums of squares. Thus, as in volume, there is a nearly perfect linear relationship between expected group performance based on OP breeding values and actual realized gains of the 5 groups.

Influence of Age and Site Characteristics on Volume Gains

Volume Gains for Volume Groups

The intent of this analysis was to examine the impact of site and age characteristics on realized gains in volume and to ascertain whether some volume groups (V1, ... V5) responded differently to these characteristics. The final model for this analysis included effects for the volume groups (V1 to V5), SIclass, and group • SIclass interaction (*Figure 3*). These factors significantly and consistently (in both the ratio and regression approaches) impacted the realized gains ratios for volume. The final model for this analysis did not include site rust hazard (rushaz) or age class nor their associated interactions. Rust hazard effects were not included in the final model because: (1) The main effects for rushaz class were not consistent across the regression and ratio approaches; and (2) The interactions with other effects were uninterpretable biologically and graphically. Age class was not included in the final model, but there may be some marginally significant effect on realized gain ratios for tree volume expressed as percentage gains above CHECK as in this study. In some of the models examined, age significantly impacted realized gain ratios for volume, but this varied depending on what other main effects and interactions were in the model, and on which analytical approach (ratio versus regression) was used. When significant, the realized gain ratio for tree volume was approximately 2 % to 3 % lower at age 11 than at ages 5 and 8. Thus, when expressed as percentage gain above unimproved material extrapolation of tree volume gain to the rotation age may need to be reduced from the percentages reported here.

The final model for volume gain ratio (*Figure 3*) indicates the following. First, there is increased volume gain (when expressed as a ratio to CHECK) on sites of better quality (note tendency of SIclasses 1 and 2 to exhibit 5 % to 10 % less gain than better sites). Secondly, on every site the volume groups ranked in the order predicted by their OP breeding values (V5 > V4 > V3 > V2 > V1 as indicated by upwardly sloping lines for all SIclasses). The only exception to this was the V1 group in SIclass 1 which had only 17 observations. Finally, genetic differences appear to be greater on better sites (3, 4 and 5) relative to poorer sites (1 and 2). Note that for SIclass 1 and 2, the curves are relatively flat, indicating smaller differences in realized gain across volume groups. The curves for SIclass 3, 4 and 5 are steeper indicating progressively larger percentage realized gains with increasing genetic quality on better sites.

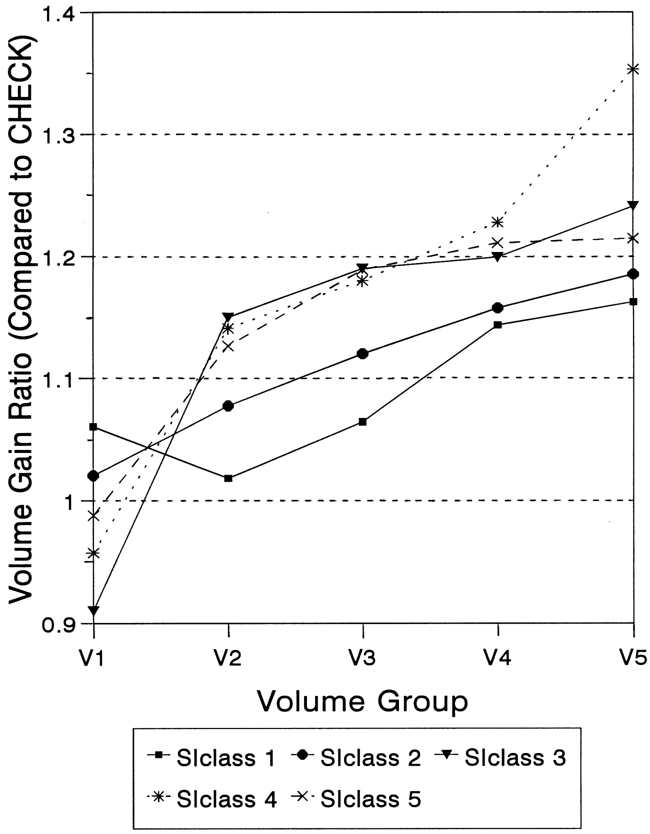

Figure 3. – Volume gain ratios (compared to the unimproved CHECK) of volume groups of full-sib families grouped according to the BLP-predicted breeding values of tree volume (X axis: V1 = worst and V5 = best) and plotted for different site index classes (SIclass1 = poor and 5 = good) of the test locations.

Perhaps genetic differences in tree volume are poorly expressed on very poor sites, and better expressed as site quality improves. Taken together these results imply that the breeding values from the open-pollinated progeny test data accurately predicted genetic rankings across all site qualities, but that more gain (expressed as ratio or %) was evidenced on better sites.

Volume Gains for Rust Groups

The intent of this analysis was to examine the impact of rust resistance (using the genetically-different rust groups as independent class variables) on realized gains for volume. In this analysis neither the main effect of age class nor the 2-way interactions associated with age class, SIclass, and rust group were included in the final model. Age class effects were not significant in either analytical approach (ratio of regression). The 2-way interactions of age class, SIclass and group were found to be unimportant in various models investigated graphically.

The final model for both approaches (ratio and regression) contained rust group, SIclass, rushaz and rushaz • group. In both approaches all the terms were highly significant and biologically consistent across the 2 approaches.

Examination of the estimated realized gains (*Figure 4*) suggests that rust resistance does confer some tree volume advantage, but mainly on high hazard rust locations. This is evident for the most rust resistant groups (R1 and R2) where the rankings show progressively more volume gain with increasing rust hazard of the site. For both of these groups containing resistant families, the gains are only evidenced in rust hazard classes 4 und 5 where the unimproved checklots incurred 60 % to 80 % rust incidence (class 4) or greater than 80 % rust incidence (class 5). In these high hazard areas, the most rust resistant groups of families had volume gain ratios some 10 % to 15 % higher than on lower hazard sites.

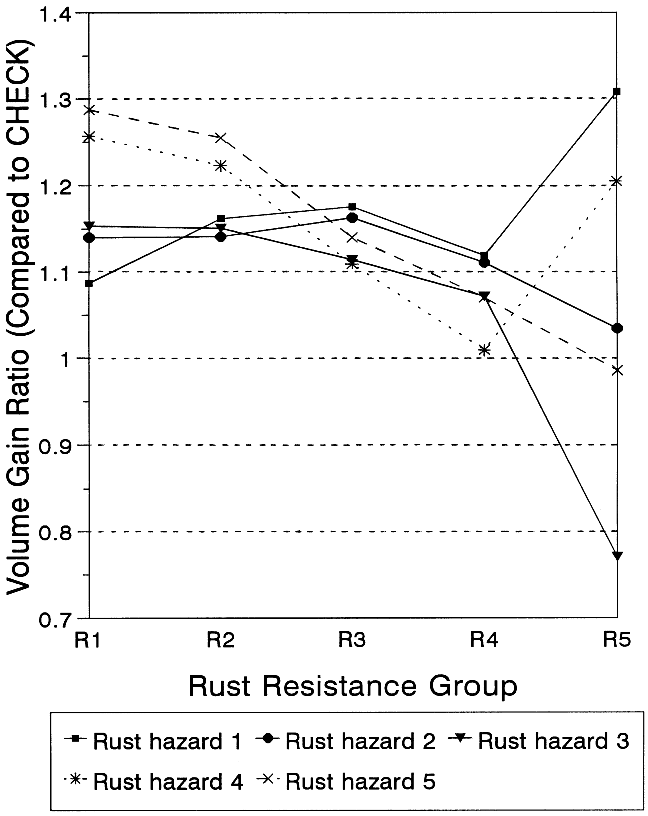

Figure 4. – Volume gain ratios (compared to CHECK) for full-sib families grouped according to the family levels of rust resistance (X axis: R1 = most rust resistant and R5 = most susceptible) and plotted for different levels of rust hazard (rust hazard1 = low rust and 5 = high rust) of the test locations as measured by rust incidence of CHECK.

The same conclusions are supported by noting that for rust susceptible family groups 4 and 5, the rankings of the hazard classes are basically random. Finally, the lines representing low hazard sites (classes 1, 2 and 3) (disregarding the data point of rushaz group 3 for rust group R5 which had only 2 observations) are basically flat while those for high hazard sites (site hazard classes 4 and 5) are generally downward sloping (disregarding the data point of rushaz group 4 for rust group R5 which has only 1 observation) due to the progressively smaller volume gains with the rust susceptible material (in the higher numbered RX groups) on these high hazard sites.

All volume gains are in mean tree volume, not plot volumes, and therefore do not account for gains from better survival. Thus, if mortality due to rust infection were also less in rust resistant groups, even larger volume gains due to rust resistance might be expected.

Influence of Age and Site Characteristics on Gains in Rust Resistance

Rust Gains for Rust Groups

In the examination of the impact of age, site characteristics and family groups for rust resistance on realized gains in rust incidence, the final model included family groups, rushaz and the group • rushaz interaction. In the final model all terms were significant in both the ratio and regression approaches with consistent trends for both approaches. Other main effects (age and SIclass) and associated interactions were found not to be significant in either approach (ratio nor regression).

From the graphical display of the averaged values from the ratio and regression models (*Figure 5*), several inferences are possible. First, there is a steady increase in the observed incidence ratios (indicating more rust incidence relative to the CHECK and therefore less gain) for the less resistant groups. This trend is true for all rust hazard levels as evidenced by the fact that all lines lope upward. The increasing spread of among the rust hazard lines for the R4 and R5 groupings reflects the statistically significant rust group • rushaz interaction probably resulting from a scale effect due to the fact that rust incidence is measured on a binomial scale.

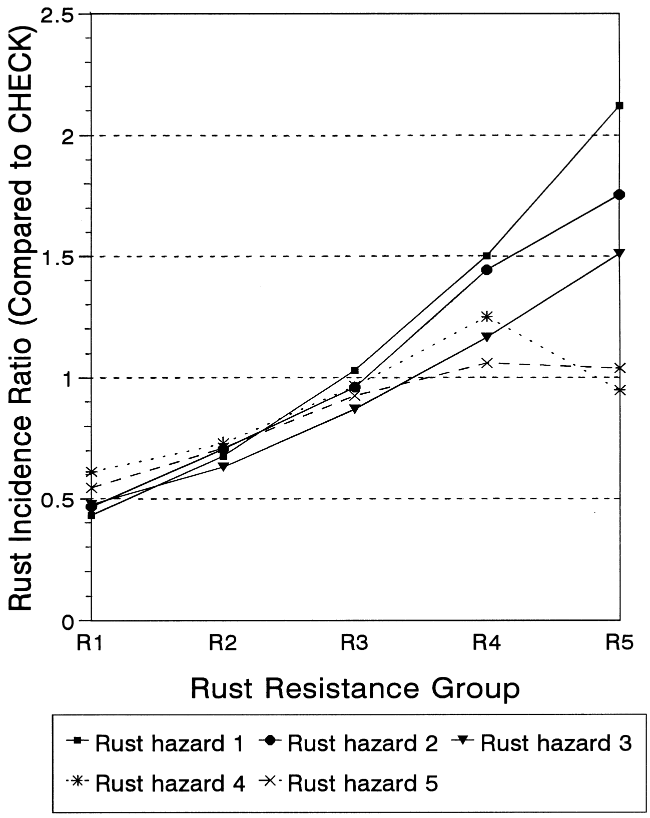

Figure 5. – Rust incidence ratios (compared to unimproved CHECK) plotted against the family groupings of different rust resistance levels (X axis: R1 = most rust resistant, R5 = most rust susceptible) for different values of rust hazard class (rust hazard 1 = low rust and 5 = high rust) of the test location as measured by rust incidence of CHECK.

For example, in sites with high rust hazard (rushaz = 5), commercial checks averaged greater or equal to 80 % rust infection. Even the most susceptible group (group 5) has maximum ratio of $100/80 \approx 1.2$ if all the trees in the group are infected. On lower hazard sites (rushaz 1 and 2), the checks incur only 20 % to 40 % rust so that susceptible families can double this value (incidence ratios of 1.8 to 2.2 for susceptible group R5) without topping out the scale. As with all binomial variables the scale is important, but basically the more rust resistant families were more rust resistant for all site hazards, and neither age of the test nor site quality influence the realized gains observed.

A final analysis was done to examine whether realized gains in rust incidence ratio were affected by families predicted to grow at different rates (the volume groups). Generally, there were few significant terms in either the ratio or regression approach and little consistency across the approaches. Also, main effects or interactions that were significant seemed spurious and not directly related to the *a priori* resistance groups for volume. Thus, while the previous analysis indicated higher volume gains from more rust-resistant families planted in high hazard sites, the converse is not true. In no situation did being a genetically-superior family for tree volume help reduce rust incidence.

General Discussion and Conclusions

The results of this study indicate that families which are genetically superior for tree volume will express increased percentage gain in volume (relative to the CHECK) on better quality sites and the genetic differences appear to be better expressed on better sites (SIclass 3, 4 und 5) relative to poorer sites (SIclass 1 and 2). The maximum range among the 5 volume groups for realized gains occurs on SIclass 4. Perhaps genetic differences in tree volume are poorly expressed on very poor sites, and better expressed as site quality improves; however, beyond a certain site quality, conditions become somewhat "luxurious" and genetic differences again become abscured. An alternative explanation for this observation may reflect genotype by environment (GxE) interaction associated with site quality (HODGE and WHITE, 1992). The best linear prediction process using OP data to predict volume breeding values placed more weight on data from sites of average quality (WHITE and HODGE, 1988), which corresponds most closely to SIclass 4 in this study. Thus, since the OP BVs may apply most appropriately to a "average" site (SIclass 4), and since these BVs were used to partition the volume family groups, it would follow that the maximum range in realized gain would be observed on SIclass 4. The smaller ranges observed among the volume groups on other site classes may occur since the BVs which define the groups are less precise on those sites due to GxE interaction (i.e., a lower Type B genetic correlation, BURDON (1977)).

It was also found that a high degree of rust resistance confers a tree volume advantage on the high hazard site locations. In high hazard areas, the most rust resistant groups of families had 10 % to 15 % higher volume gain ratios (compared to unimproved CHECK) than on the low rust hazard sites. Further, on the highest sites, the most resistant family groups had 10 % to 15 % more volume gains (relative to the CHECK) than less resistant family groups. Some authors have suggested there is genetic cost to having disease resistance genes (VANDERPLANK, 1978, p. 133). This study can not provide strong additional evidence supporting this idea; however, on the lowest rust hazard sites (rust hazard 1), the most resistant group (R1) had the lowest volume gain ratio, while the most susceptible group (presumably with the fewest resistance genes) had the highest volume gain ratio.

Compared to the unimproved checklots (CHECK), the 1001 bulk mix of families is approximately 18 % better for volume, and incurs 81 % (ratio = 0.81) of the rust infection. In comparison, the 1002 bulk mix is approximately 16 % better for tree volume, incurs more rust (ratio = 1.25) than the unimproved checklots. The difference in gain between the 1001 and 1002 checks was not as great for volume as it was in rust resistance even though the original intent of these checklots was for the 1001 check to be better than 1002 for both volume and rust resistance. The lack of difference for volume may reflect the fact that the younger age progeny test data and the genetic evaluations used by the CFGRP for volume were not as accurate nor precise as for rust resistance. Heritabilities for volume in slash pine clearly increase with age (HODGE and WHITE, 1992; DIETERS, 1994), while age appears to have no effect on heritability for rust resistance (DIETERS, 1994).

The examination of the impact of site characteristics and the family groups for rust resistance on realized gains in rust incidence indicates that more resistant family groups incur less rust across all site qualities and ages and that the realized gains (expressed as a ratio to the unimproved CHECK) are not impacted by these factors. The only interaction (that of rust resistance group with the rust hazard of the location) is likely due to scale effects. The more resistant groups produced more realized gains in rust incidence (evidenced by smaller infection ratios to the CHECK) across all levels of rust hazard of the test location.

This study suggests that on sites where rust is essentially absent (rushaz 1), families which carry resistance genes may produce slightly less volume. On sites where rust hazard is moderate (rushaz 2 and 3), there is little relationship between rust resistance and tree volume, but on sites where rust hazard is high (rushaz 4 and 5), resistant families produce more volume (on an individual tree basis). Thus, on average across all rust hazard levels there appears to be no strong genetic correlation between volume and rust resistance. This agrees with the alternate analysis of rust infections by the volume genetic groupings: being genetically superior for volume had no impact on rust infection ratios.

Lastly, and most importantly, the *a priori* ranking based on the BLP predicted BVs for different genetic entries corresponded exactly to rankings in realized genetic gain observed both for tree volume and rust resistance. The linearity of gains across different groups also suggests that there is progressively more gain from families with higher OP BVs in volume gain and lower OP BVs in rust resistance. The fact that these groups of CP families ranked exactly as expected based on the independently predicted BVs should give the breeder confidence that the relative performance of individual families will also be accurately predicted by the BVs.

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Genetic Variation in Characters of Importance for Stand Establishment in Sitka Spruce (*Picea sitchensis* (BONG.) CARR.)

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Summary

This paper summarizes the results of 2 series of clonal trials-F206 including 151 clones and F215 including 196 clones. The characters measured are: selection intensity for height growth in the nursery, height, autumn coloration, flushing, leader breaks, April-frost damage, and mortality, all characters of expected importance for stand establishment. Genotype-environment interaction and correlation between characters are studied as well.

Compared to the standard, a direct import from Queen Charlotte Islands, the clones, selected in a danish second generation material, have a superiority in height growth of 23% to 31%, fewer leader damage, 16% to 17%, and less damage due to April-frost, score 1.1 to 2.5, whereas there is hardly no differences in flushing time and only minor differences in mortality, 1 % to 5 % less dead trees.

There is considerable variance among clones for April-frost damage, but the results are only based on one year. If the frost hits later in the spring the differences between the clones will probably be less because they all are closer to the growing season and all will have an active cambium. Severe damage due to April-frost is a rather seldom event in Denmark and one may question the effort to avoid damage by selecting less sensitive clones, unless it is an indirect gain by selecting for late flushing clones to late spring frost exposed sites, where even small differences in time of flushing will make a difference.

There is only a very limited possibility to select for late flushing in spite of high heritability estimates.

Autumn coloration shows no reasonable correlations to field damage and may not be an appropriate measure of autumn hardening.

Selection based on 3 year old cuttings yield about 63% to 77% of the results obtained by direct selection 5 years later in the field. Concerning the ageing-problem of the hedges for cutting production 3 year nursery results seem to be a reasonable basis to start commercial production of selected clones.

Early selection of ortets among 3 or 4 year old seedlings for height growth seems not to be an appropriate way to increase height growth within the danish provenance.

General problems with ageing of propagation material restricts the practical use of the clonal material.

Clonal mean values of ecovalence as a stability measure is estimated for the characters showing genotype-environment interaction. Only a rather limited number, around 15%, of the clones acounts for more than 50 % of the genotype-environment interaction sums of square.

Key words: Sitka spruce, broad sense heritablility, genetic variation, height, flushing, April-frost damage, genotype-environment interaction.

FDC: 165.3; 165.5; 181.221.1; 181.6; 232.11; 422.12; 228.0; 174.7 *Picea sitchensis.*

Introduction

Sitka spruce (*Picea sitchensis* (BONG.) CARR.) is a common used exotic conifer in Denmark, actually, in the recent years the most planted. Traditionally, Sitka spruce is one of the most

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