

method of screening trees for spiral grain, the correlations in *Table 5* indicate that a single reading at the seventh ring will be almost as effective a selection criterion as would the mean of rings 3, 5, 7 and 9. A single measurement of spiral grain is desirable due to the time and cost incurred in obtaining additional readings.

In this study, heritability estimates for spiral grain considering spirality direction are higher than those for absolute spiral grain (*Table 3*). We suggest that this is because some real differences between families may be masked when sign is ignored. The standard deviations of the absolute spiral grain values are less, as expected due to elimination of the variation caused by changes in spirality direction between trees.

Investigation of the degree of genetic control over mature wood values of spiral grain in *P. caribaea* var. *hondurensis* should be given high priority as trials reach sufficient age (15 to 20 years) to allow sampling of representative mature wood. COWN *et al.* (1981) recorded some very high spiral grain values, in excess of 10 degrees, in the mature wood (more than ten growth rings from the pith) of Fijian *P. caribaea* var. *hondurensis* which could significantly affect its utilisation potential for sawn products.

Further work is also required to investigate the best approaches to collection, analysis and interpretation of spiral grain results for *P. caribaea* var. *hondurensis*. It is beyond the scope of this study to reliably define such methods but these will be examined in additional studies now in progress.

Acknowledgements

The work reported here is part of the research program of the Queensland Forest Service. We thank the Conservator of Forests for permission to publish these results, and many staff of the Tree Breeding and Wood Structure Sections of the Service for their work in establishing, maintaining and sampling the trials, and processing the samples and data. We thank Dr. D. G. NIKLES for initiating the field trial and encouraging this study and Dr. L. EISEMANN for preliminary analysis of the data. Drs. C. A. RAYMOND and K. G. ELDRIDGE provided constructive comment on the paper which is gratefully acknowledged.

References

ALLEN, P. J.: Estimation of genetic parameters for wood properties in Slash pine in south east Queensland. Research Note No. 41, Department of Forestry, Queensland. 14p + appendices (1985). —

BARNES, R. D., GIBSON, G. L. and BARDEY, M. A.: Variation and genotype-environment interaction in international provenance trials of *Pinus caribaea* var. *hondurensis* and implications for population improvement strategy. Paper for IUFRO Symposium and workshop on genetic improvement and productivity of fast-growing tree species. Aguas de Sao Pedro, Brazil. 20p (1980). — COTTERILL, P. P.: On estimating heritabilities according to practical applications. *Silvae Genetica* 36: 46–48 (1987). — COTTERILL, P. P. and CAMERON, J. N.: Multiple population breeding of Radiata Pine for growth and wood density. In: R. D. BARNES and G. L. GIBSON (Eds.). "Provenance and genetic improvement strategies in tropical forest trees". Commonwealth Forestry Institute, Oxford, and Zimbabwe Forestry Commission, Harare. 499p (1984). — COTTERILL, P. P. and DEAN, C. A.: Successful tree breeding with index selection. CSIRO, Melbourne (1990). — COWN, D. J., McCONCHIE, D. C., and YOUNG, G. D.: Wood properties of *Pinus caribaea* var. *hondurensis* grown in Fiji. New Zealand For. Service, FRI, Rotorua, Wood Quality Report No. 39 (unpublished), 73p (1981). — DEAN, C. A., COTTERILL, P. P. and EISEMANN, R. L.: Genetic parameters and gains expected from selection in *Pinus caribaea* var. *hondurensis* in northern Queensland, Australia. *Silvae Genetica* 35: 229–236 (1986). — HARRIS, J. M.: Nondestructive assessment of spiral grain in standing trees. *N. Z. J. For. Sci.* 14: 395–399 (1984). — HARRIS, J. M.: Spiral grain and wave phenomena in wood formation. Springer-Verlag, Berlin. 214p (1989). — HARVEY, W. R.: Least-squares analysis of data with unequal subclass numbers. U. S. D. A. Agric. Res. Serv. Publ. No. ARS 20–8. 157p (1960). — HAZEL, L. N., BAKER, M. L. and REINMILLER, C. F.: Genetic and environmental correlations between the growth rates of pigs at different ages. *J. Animal Science* 2: 118–128 (1943). — HEINRICH, J. F. and LASSEN, L. E.: Improved techniques for determining the volume of irregularly shaped wood blocks. *Forest Prod. J.* 20: 24 (1970). — KANOWSKI, P. J.: Characterization and interpretation of variation in forest trees: a reappraisal based on a progeny test of *Pinus caribaea* MORELET. Unpub. D.Phil. thesis, Oxford Univ. 221p (1986). — KANOWSKI, P. J. and NIKLES, D. G.: A summary of plans for continuing genetic improvement of *Pinus caribaea* var. *hondurensis* in Queensland, Thailand. 28 November to 2 December. 18p (1988). — MEGRAW, R. A.: Wood quality factors in Loblolly pine. Tappi Press, 88p (1985). — NIKLES, D. G.: Progress in breeding *Pinus caribaea* MORELET in Queensland. In: J. BURLEY and D. G. NIKLES (Eds.). "Selection and breeding to improve some tropical conifers". Commonwealth Forestry Institute, Oxford, UK and Department of Forestry, Queensland, Australia. 2: 245–266 (1973). — Queensland Department of Forestry: Annual report 1988 to 1989. 72p (1989). — SWIGER, L. A., HARVEY, W. R., EVERSON, D. O. and GREGORY, K. E.: The variance of intraclass correlation involving groups with one observation. *Biometrics* 20: 818–826 (1964). — TALLIS, G. M.: Sampling errors of genetic correlation coefficients calculated from analyses of variance and covariance. *Australian J. Statistics* 1: 35–43 (1959). — WOOLASTON, R. R., KANOWSKI, P. J. and NIKLES, D. G.: Genetic parameter estimates for *Pinus caribaea* var. *hondurensis* in coastal Queensland, Australia. *Silvae Genetica* 20: 21–28 (1990). — ZOBEL, B. and TALBERT, J.: Applied forest tree improvement. Wiley, New York. 505p (1984).

Stochastic Dominance as an Aid to Genetic Roguing

By R. A. NEWBOLD and G. H. WEAVER*

Louisiana Tech. University, Ruston, Louisiana, USA

(Received 2nd October 1990)

Abstract

Stochastic dominance can be used as a screening technique to divide data distributions into efficient and inefficient sets. This dichotomous division is useful in deci-

sion making where choices involve keeping or discarding certain alternatives. The procedure takes into account all moments of the distributions and is therefore particularly suited to data which are nonnormally distributed.

Stochastic dominance was used to compare loblolly pine (*Pinus taeda* L.) progeny test results. Based on age-15 volumes, stochastic dominance was judged effective in identifying poor families as early as age 5. Advantages of stochastic dominance are its simplicity and the efficient sets resulting independently of statistical confidence levels.

* The authors are, respectively, Associate Professor, School of Forestry, Louisiana Tech. University, Ruston, Louisiana 71272, USA and Associate Professor, Department of Forestry, Mississippi State University, Mississippi State, Mississippi 39762, USA. This material is from a dissertation submitted by the senior author for the Ph. D. degree.

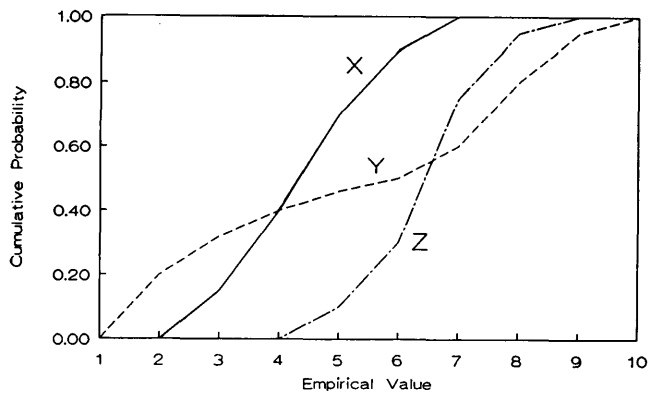


Figure 1. — Example outcome distributions and their stochastic relationships.

Limitations include conflicting outcomes in the lower tails of the distributions and a lack of formal sensitivity analysis.

Key words: stochastic dominance, efficiency, progeny, roguing.

Introduction

Stochastic dominance (SD) is a decision tool used to identify an efficient set of alternatives when choices must be made. The efficient set is one which excludes possible choices whose outcome distributions are dominated by at least one other distribution under consideration. The stochastic dominance test involves a pairwise comparison of ordered distributions to determine if one or a few choices will provide the highest returns across the range of data, and throughout the cumulative probability range 0.0 to 1.0. Possible relationships are demonstrated in figure 1.

In this example, reading across any probability level from 0.0 to 1.0, values of alternative Z would always be preferred to corresponding values of alternative X, however Z would only be preferred to alternative Y in the lower tail of the probability distribution. Different degrees of dominance are recognized. First degree stochastic dominance (FSD) requires that the distributions not cross indicating that one is preferred throughout (e. g. Z dominates X by FSD but does not dominate Y by FSD). FSD may not narrow the field of choice much if clearcut differences are not apparent.

To narrow the efficient set, second degree stochastic dominance (SSD) can be used. Although this test is not as strong as the first degree test, it is useful and compares areas under the probability distributions. Note that moving up the probabilities to some maximum range, the area under Z is always less than the area under Y because the overall distribution lies further to the right. Therefore, when taken as a whole, Z expresses second degree dominance over both X and Y. If a choice of one alternative was made, alternative Z would be chosen, but if we could keep two, both Y and Z would be kept because one is stronger in the lower tail and the other is stronger in the upper tail of the probability distribution. Alternative X can be eliminated from consideration because Z outperforms it throughout. In the absence of Z, a clear choice could not be made between X and Y. This problem results because two distributions which cross below the 50 percentile usually exchange advantage at some point. Exceptions to this general rule occur in the case of second degree efficiency where the lead is temporary and the area does not offset the difference

between the alternatives to that point, or where the area between the curves *above* their intersection is less than the area between the curves *below* their intersection.

The mathematical basis for proving dominance of one distribution by another was first presented by QUIRK and SAPOSNIK (1962), and further developed by HADAR and RUSSELL (1969). Stochastic dominance (SD) has since been used for comparing alternatives in areas of finance and agricultural economics (PORTER and GAUMNITZ, 1972; PORTER, 1974; POPE and ZIEMER, 1984; DANOK et al., 1980; COCHRAN et al., 1982; KING and OAMEK, 1983; HARRIS and MAPP, 1986; and KLEMME, 1985) and can be applied in many circumstances where empirical testing or managerial opinion indicates that prospects follow probability distributions, rather than consensus values. SD helps eliminate undesirable alternatives, and applies to normal and non-normal distributions.

Stochastic Dominance As a Tool in Genetic Roguing

Family selection from progeny tests offers an area where decisions must be made which affect the future pool of genetic resources. Roguing (removal) of undesirable families is a particularly productive aspect of tree improvement and especially if it can be accomplished at an early age. SD procedures can provide a definitive rejection criterion for breeding stock and seed orchards while retaining families which hold some promise.

Stochastic dominance is an appropriate technique for evaluating choices where higher moments of the distributions may have important consequences. In progeny testing, strengths in any portion of the distribution may become dominant factors in the growth exhibited over time. Rapid growth of a few individual seedlings may not reflect much in an overall family mean, but may be an indicator of a favorable trait about to be expressed.

A 15-year-old loblolly pine (*Pinus taeda* L.) progeny test was evaluated to assess stochastic dominance as a tool in progeny test selection. The test consisted of 12 families of loblolly pine including a commercial check. Each family was represented by 36 trees in each of 6 replications to provide 216 trees per family. Test plots were planted in a randomized complete block design.

Height measurements were taken at the time of planting and at ages one through four. Measurements at ages 5, 10, and 15 included both total height and diameter at breast height on all trees over 4.5 feet tall. The 5-year data were compared with the 15-year data to determine which families would eventually be selected for seed production and advanced-generation breeding.

The cubic foot volume of trees at age 15 was the parameter used for selection in this analysis to show how SD can be used to advantage, and as parameter of interest to producers of timber crops. A KOLMOGOROV-SMIRNOV goodness-of-fit test was used to test the null hypothesis that all family values came from normal distributions. Based on age-5 cubic foot volumes, the normality hypothesis was rejected in all but one family at the 0.05 level of confidence. Based on age-15 cubic foot volumes, the null hypothesis was rejected in only three of the 12 families indicating that with time the distributions approached the normal. Early selection from test distributions that exhibit non-normality should benefit from a procedure uninfluenced by skewness and kurtosis. These results suggested that an alternative basis for family selection was warranted.

Table 1. — Analysis of Variance and Mean Separation Tests for Tree Volume of Progeny at Age 5.

SOURCE	DF	SS	MS	F-VALUE	PR>F
BLOCK	5	4.17	0.834	52.41	0.0001
FAMILY	11	2.27	0.206	12.98	0.0001
ERROR	1800	28.62	0.016		
TOTAL	1816	35.06			

AGE 5 MEAN = 0.170

FAMILY	N	MEAN (FT ³)	DUNCAN GROUPING
SH-13	161	.237	A
CR4xBL5	174	.217	AB
SH-7	133	.205	BC
SH-3	152	.188	BCD
SH-11	166	.178	CDE
SH-8	137	.158	DEF
SH-2	178	.147	EF
SH-5	163	.147	EF
CEF	169	.142	F
SH-10	156	.139	F
SH-4	119	.136	F
SH-9	109	.126	F

Table 2. — Analysis of Variance and Mean Separation Tests for Tree Volume of Progeny at Age 15.

SOURCE	DF	SS	MS	F-VALUE	PR>F
BLOCK	5	1642	328.4	26.09	0.0001
FAMILY	11	1439	130.8	10.39	0.0001
ERROR	1741	21917	12.6		
TOTAL	1757	24998			

AGE 15 MEAN = 6.905

FAMILY	N	MEAN (FT ³)	DUNCAN GROUPING
SH-7	127	8.72	A
SH-13	148	7.84	B
CR4xBL5	169	7.70	BC
SH-4	114	7.38	BCD
SH-8	135	7.18	BCD
SH-9	110	6.98	BCDE
SH-3	146	6.96	BCDE
SH-5	163	6.81	CDEF
SH-11	156	6.71	DEF
SH-10	150	6.23	EF
CEF	163	5.94	FG
SH-2	177	5.16	G

DUNCAN'S New Multiple Range Test (RAY, 1982) of ranked family means for age 5 volumes (Table 1) is only moderately helpful in revealing which families could be rogued. Mean separation tests rest on the assumption of symmetrical distributions. Based on the KOLMOGOROV-SMIRNOV test, this assumption for this test data is questionable.

A case could be made for keeping only two families (significance group A), but age five may be too early to rogue 83% of the families. The top four families are in the first two groups, while the top five families would retain all families above the overall test mean of 0.170 cubic feet. Table 2 shows the ANOVA test for cubic foot volume at age 15. The best two families at age five moved to the 2nd and 3rd positions while SH-3 dropped from 4th to 7th ranking. The big change was in families SH-4 and SH-9, moving from 11th and 12th positions at age five to 4th and 6th positions at age 15. If the roguing decision had been made at age five, both of these families would have certainly been lost. SH-8 was below the test mean at age five, but was above the mean at age 15.

First degree stochastic dominance was determined by sorting the array of observation values for each family and calculating values to correspond to each percentile. The first value in the array was the minimum of the range, the last value in the array was the maximum of the range, and the data distribution was fully expressed by the complete percentile array. Comparing respective values

pairwise between families, the stochastic dominance test was applied. Array Z() dominates array X() by the FSD rule if $Z(i) > X(i)$ for all possible i with at least one strong inequality (Figure 1). Any distribution that has an equal or higher value at each and every point dominates the distribution to which it is compared. The FSE set is the set of families whose distributions are undominated by any other family.

Using first degree SD, seven families would have made up the efficient set at age five (SH-3, SH-4, SH-7, SH-8, SH-11, SH-13, and CR4xBL5). These families included the top five, and six of the top seven at age 15 based on family mean volume. The five dominated families were all dominated by family SH-13, and in addition, SH-11, SH-8, and CR4xBL5 dominated at least one of the families.

Inspection of family distributions revealed why some families with low mean volumes remained in the efficient set. Table 3 provides age-5 and age-15 distribution statistics and table 4 illustrates how families SH-11 and SH-4 remained in the efficient set even with low family means, and why SH-2 was eliminated.

Family SH-11 is in the efficient set by virtue of a strong lower tail. The smallest tree in this family had a volume 2½ times as great as the smallest tree in SH-13 (0.005 vs. 0.002 cubic feet) which kept it in the efficient set. This relationship is represented by distributions X and Y in figure 1. The DUNCAN grouping was unchanged from age five to age 15, but the mean ranking fell from 5th to 9th.

Family SH-4 was undominated by virtue of the upper tail of its distribution i.e. the volume of the largest tree. In this instance, the mean volume for the family at age 5 placed it in Duncan group F, but at age 15 it had moved into group BCD—not significantly different from SH-13. This relationship is represented by distributions Y and Z in figure 1.

The third comparison in table 4 involves SH-2 which was not in the efficient set but is provided for the sake of comparison. The range (and all intermediate values) of SH-2 lie below comparable values of SH-13, thus the family was not in the FSE set (represented by distributions

Table 3. — Comparative family distribution statistics at age 5 and age 15.

Family	Age 5				Age 15			
	Range	Median	Mean	Duncan's Group	Range	Median	Mean	Duncan's Group
SH-2	.001-.529	.119	.147	EF	0.32-11.58	4.87	5.16	G
SH-3	.001-.713	.145	.188	BCD	0.87-20.22	6.02	6.96	BCDE
SH-4	.001-.665	.120	.136	F	1.16-17.92	6.28	7.38	BCD
SH-5	.001-.577	.090	.147	EF	0.48-23.49	5.53	6.81	CDEF
SH-7	.001-.735	.156	.205	BC	0.23-20.00	8.19	8.72	A
SH-8	.002-.709	.124	.158	DEF	0.07-18.59	6.70	7.18	BCD
SH-9	.000-.566	.091	.126	F	1.03-27.98	6.04	6.98	BCDE
SH-10	.001-.519	.101	.139	F	1.63-15.88	5.75	6.23	EF
SH-11	.005-.577	.144	.178	CDE	0.74-16.42	6.18	6.71	DEF
SH-13	.002-.613	.216	.237	A	1.49-18.39	7.41	7.84	B
CR4xBL5	.001-.602	.185	.217	AB	1.62-17.25	7.40	7.70	BC
CEF	.001-.577	.122	.142	F	0.47-22.65	5.48	5.94	FG

Table 4. — A statistical comparison of selected family distributions.

Family	Age 5				Age 15			
	Range	Median	Mean	Duncan's Group	Range	Median	Mean	Duncan's Group
SH-13 vs. SH-11	.002-.613	.216	.237	A	1.49-18.39	7.41	7.84	B
SH-11 vs. SH-13	.005-.577	.144	.178	CDE	0.74-16.42	6.18	6.71	DEF
SH-13 vs. SH-4	.002-.613	.216	.237	A	1.49-18.39	7.41	7.84	B
SH-4 vs. SH-13	.001-.665	.120	.136	F	1.16-17.92	6.28	7.38	BCD
SH-13 vs. SH-2	.002-.613	.216	.237	A	1.49-18.39	7.41	7.84	B
SH-2 vs. SH-13	.001-.529	.119	.147	EF	0.32-11.58	4.87	5.16	G

X and Z in figure 1). This family would be rogued at age five by SD criteria and, in fact, did not reflect good growth through age 15.

The most significant observation is that SH-4 reflected good growth within a very narrow portion of the age-5 distribution, yet the potential shown in the upper tail proved to be an expressed trait at age 15. This family would not have been retained based on volume growth using analysis of variance alone.

The value lost when a potentially productive family is discarded not only includes the cost of locating, grading, breeding, and progeny testing to that point in time, but also the discounted value of its contribution in the next generation. Variability in programs precludes a general statement on estimated value lost, but stochastic dominance is efficient in locating choices that are strong in any portion of their distribution. Any part of this distribution may become a strong attribute in the final analysis given adequate time for it to be expressed, however, it seems unlikely that a strong lower tail would ever be of any great value, and in this study, family SH-11 did not respond in the succeeding ten year period.

Height was not an efficient variable to use for selecting families strong in volume production at age 15. Based on heights at age five, three of the seven selections at age 15 fell below the overall test mean. These three represented 15-year rankings of 4th, 5th, and 6th. With SD the problem was even more severe with only two of seven being retained in the efficient set, discarding rankings 1st, 4th, 5th, 6th, and 7th. Using only the mean heights, family SH-11 was again retained; with SD it was not.

Second degree stochastic dominance (SSD) was also applied to the progeny test data. At age 5, only 2 families expressed SSD-- SH-13 and SH-11. Family SH-13 had the greatest cumulative volume, but SH-11 dominated at the lower end of the distribution. Thus, SH-13 was the best in the upper tail while SH-11 excelled in the lower tail. Using SSD for genetic selection may be too restrictive to meet the goals of a broad genetic base. The very attribute by which it expresses advantage over FSD, that of reducing the efficient set to one or a few choices, may be overly restrictive for genetic selection. Also, in the absence of perfect correlation between alternatives, diversification should be considered where combinations may be more efficient than regarding each family as a mutually exclusive choice (McCARL et al., 1987).

Conclusions and Recommendations

Efforts to reduce the time required to make genetic selections are well grounded and will no doubt pay dividends in the coming years. The correct criteria for selection and the proper technique to separate families into those kept for advanced generations and those discarded will be fundamental to the success of early selection.

Stochastic dominance tests for FSE sets based on age-5 data resulted in selection of families that remained strong through the 15-year volume measurements. SD is more objective than are ANOVA tests and in this test retained one family that was slow to start but was a strong producer at age 15. This was particularly encouraging realizing the time and expense involved in locating and testing superior tree selections and the chance of discarding a good selection too early.

Stochastic dominance testing will directly address the issue of which families should be rogued. Rather than reserving the "best 10 to 12 families", or keeping some percentage of those tested, SD can aid in specifying those families which have exhibited good characteristics based on their entire outcome distribution. Some years, when the interfamily differences are clearly evident, few families may be retained, but in other years when distributions fail to express dominance, many will be retained for re-assessment at a later age.

The need to maintain good sampling procedures, especially experimental design, is a prerequisite for accurate comparisons. If measurements of field tests are not comparable or are compromised in some way, then the decisions based on those measurements cannot be reliable either. Work needs to proceed in identifying those variables important for accurate early selection-indicators of growth characteristics, importance of test survival, effect of vegetative competition, and others.

Stochastic dominance does have its limitations. As with other mathematical tests, the data or predicted outcomes are assumed to be an accurate representation of the actual situation. Aside from that assumption, the problem of distributions crossing in the lower tail and precluding dominance is one of the most obvious detractors. If the distributions of two alternatives cross at any point in the lower tail such that the best alternative is reversed with some probability, dominance can never be expressed regardless of how high the best alternative goes or how low the worst one remains. Another limitation of SD when compared to simplex-based models is that there is no sensitivity analysis other than inspection that would indicate the narrowness or the robustness of the efficient set.

The recommendations pertaining to genetic selection based on the results of this study are to: 1) proceed in making selections based on early data (age 5 and older); 2) incorporate SD in the evaluation process as a supplement to analysis of variance procedures; 3) use parameters other than height alone to define the productive potential of the family.

Literature Cited

- COCHRAN, M., LODWIK, W., JONES, A. and ROBINSON, L.: Selection of Apple Scab Pest Management Strategies Under Uncertainty: An Application of Various Stochastic Dominance Techniques. Agricultural Economics Staff Paper 1982-34, Michigan State University (1982). — DANOK, B., McCARL, B. A. and WHITE, T. K.: Machinery selection modeling: incorporation of weather variability. *American Journal of Agricultural Economics* 62: (4) 700-708 (1980). — HADAR, J. and RUSSELL, W. R.: Rules for ordering uncertain prospects. *American Economic Review* 59 (1): 25-34 (1969). — HARRIS, TH., R. and MAPP, H. P.: A stochastic dominance comparison of water-conserving irrigation strategies. *American Journal of Agricultural Economics* 68 (2): 298-305 (1986). — KING, R. P. and OAMEK, G. E.: Risk management by Colorado dryland wheat farmers and the elimination of disaster assistance program. *American Journal of Agricultural Economics* 65 (2): 247-255 (1983). — KLEMME, R. M.: A stochastic dominance comparison of reduced tillage systems in corn and soybean production under risk. *American Journal of Agricultural Economics* 67 (3): 550-557 (1985). — McCARL, A., KNIGHT, Th. O., WILSON, J. R. and HASTIE, J. B.: Stochastic dominance over potential portfolios: caution regarding covariance. *American Journal of Agricultural Economics* 69 (4): 804-812 (1987). — POPE, R. and ZIEMER, R. F.: Stochastic efficiency, normality, and sampling errors in agricultural risk analysis. *American Journal of Agricultural Economics* 66 (1): 31-40 (1984). — PORTER, R. B.: Semivariance

and stochastic dominance: a comparison. *American Economic Review* 64: 200–204 (1974). — PORTER, R. B. and GAUMNITZ, J. E.: Stochastic dominance vs. mean-variance portfolio analysis: an empirical evaluation. *American Economic Review* 62: 348–446 (1972). — QUIRK, P. and SAPOSNIK, R.: Admissibility and meas-

urable utility functions. *Review of Economic Studies* 29: 140–146 (1962). — RAY, A. A. (Editor): *SAS User's Guide: Statistics*, 1982 Edition. SAS Institute Inc., Cary, NC. (1982). — VAN BUITENEN, J. P. and HANOVER, J. W.: Designing for yield. *Journal of Forestry* 84 (3): 28–30 (1986).

Allozyme Variation in Italian Populations of *Picea abies* (L.) Karst.

By R. GIANNINI¹⁾, M. MORGANTE²⁾ and G. G. VENDRAMIN³⁾*)

(Received 28th January 1991)

Summary

Genetic diversity and genetic differentiation of nine Italian populations of Norway spruce (*Picea abies* (L.) KARST.) were studied analyzing allozyme variation at 21 loci. On average, the expected heterozygosity was 0.165, 45.50% of loci were polymorphic, the number of alleles per locus was 1.831 and the effective number of alleles per locus was 1.198. Only 4.2% of the total genetic variation was due to interpopulational differentiation. The mean value of Nei's genetic distance (0.019) confirmed that the variation among populations is low. The characteristics of the relic population of Campolino (the only natural stand located in Italy outside the Alps), such as a quite high gene diversity, the presence of some unique alleles and a peculiar genetic structure at the locus GOT-B, may provide some support to the hypothesis of a post-glacial recolonization of the Italian slope of the Alps in West-East direction, starting from refugial populations in Central Italy.

Key words: allozymes, *Picea abies*, genetic diversity, genetic differentiation, recolonization.

Zusammenfassung

Die genetische Diversität und die genetische Differenzierung von neun italienischen Fichtenpopulationen (*Picea abies* (L.) KARST.) wurden anhand von 21 Isoenzym-Genloci untersucht. Im Durchschnitt betrug der erwartete Heterozygotiegrad 0,165 und 45,50% der Loci waren polymorph. Die Anzahl der Allele pro Locus betrug 1,831 und die der effektiven Allelen pro Locus 1,198. Nur 4,2% der gesamten genetischen Variation basierte auf der Differenzierung zwischen Populationen. Der durchschnittliche Wert von Nei's genetischem Abstand (0,019) bestätigte, daß die Variation zwischen den Populationen gering war.

Auf Grund charakteristischer genetischer Eigenschaften der Reliktpopulation von Campolino, außerhalb des Alpengebietes der einzige autochtone Fichtenbestand Italiens, wie z. B. der relativ hohen genetischen Diversität, dem Vorkommen einiger einzigartiger Allele und einer besonderen genetischen Struktur am Locus GOT-B, wird vermutet, daß die Rückwanderung von Refugien in Mittelitalien in West-Ost-Richtung entlang der italienischen Alpenseite stattgefunden hat.

¹⁾ Istituto di Selvicoltura, Università di Firenze, Via San Bonaventura, 13, I-50145 Firenze, Italy.

²⁾ Istituto di Produzione Vegetale, Università di Udine, P. le M. Kolbe, 4, I-33100 Udine, Italy

³⁾ Istituto Miglioramento Genetico Piante Forestali C. N. R., Via San Bonaventura, 13, I-50145 Firenze, Italy

*) Correspondance address

Introduction

Up to now isoenzymatic analyses on Norway spruce have been restricted to populations of Middle-northern Europe and have had following goals: to estimate their level and distribution of genetic variability (BERGMANN, 1973a, 1974a; LUNDKVIST and RUDIN, 1977) and to study their genetic structure related to the spatial distribution of the trees (BRUNEL and RODOLPHE, 1985), to the distribution along altitudinal and latitudinal gradients (BERGMANN, 1978, 1988), and also to sensitivity to atmospheric pollution (BERGMANN and SCHOLZ, 1987). Moreover, some isoenzymatic variants have been useful to establish the processes of recolonization in Europe of Norway spruce in the post-glacial era (BERGMANN, 1984).

Nine Italian populations were electrophoretically investigated. The analysis of the relic population of Campolino seems to be particularly important. This narrow sized and isolated population may be useful in order to verify the hypothesis of a post-glacial migration in West-East direction, starting from refugial populations situated in the plains of Central Italy (FIRBAS, 1949 and 1952; GIACOMINI, 1958).

Materials and Methods

Populations sampled

Nine native Italian populations were sampled: eight are located in the Alps, the ninth, a relic population, is situated in the natural reserve of Campolino nearby the Alpe delle Tre Potenze on the Tuscan Apennine (Figure 1). The population of Campolino is relic (MAGINI *et al.*, 1980; BORGHETTI *et al.*, 1989), narrow sized and completely isolated.

Bulk provenance collections (populations No. 1, 2, 3, 5, 6) and seedlots from individual trees were analyzed to characterize the populations.

Electrophoresis

The allozyme analysis was carried out on the endosperm. About 140–160 endosperms were examined for the bulk provenance collections. For the populations with seeds from single trees the individual genotype was inferred by examining 6 endosperms for each tree. 20, 18, 33 and 40 trees were genotyped for populations No. 4, 7, 8, and 9, respectively.

Horizontal electrophoresis on starch gel was utilized to separate the isozymes at 11 enzyme systems. The systems assayed, their acronyms, the applied gel and electrode buffer systems, the number of gene loci scored and references for the inheritance of the allozymes are given