The important long-term C effects are likely to be those associated with maturation or topophysis, as discussed by ROULUND (1975) and OLESEN (1978). Otherwise, C effects may be important only in short-term clonal tests, resulting in biased estimates of genetic variation in rooting and juvenile traits as found by WILCOX and FARMER (1968) and FOSTER *et al.* (1984).

The clones used in this study were originally propagated from 14 to 15-year-old trees, and so were physiologically 'mature' even in the first generation. By the end of the second generation they were 24—25 years old from seed. However, there was little evidence for progressive maturation over the two 5-year generations. In both generations, the clones rooted similarly, established orthotropic growth within the first two years, and grew to the same height at the lowland site. It seems likely, therefore, that progressive maturation was arrested by repropagation as described in a 12-year study of *Picea abies* KARST. by CLAIR *et al.* (1985) and reviewed by FRANCLET (1983).

Acknowledgement

We are grateful to Mr. R. I. SMITH for help in the design and analysis of the experiments.

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The Effect of Damage on Components of Variance for Fifth-Year Height in Norway Spruce

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(Received 27th May 1986)

Abstract

Height of Norway spruce *(Picea abies* (L.) KARST) rooted cuttings was analyzed after five growing seasons in the field. Variance due to clone, location, location × clone and replication sources were significant when all cuttings were included in the analysis. Only clone and replication sources were significant when damaged cuttings were omitted, suggesting that location and location × clone variation was associated with damage. Both individual and clone-mean heritabilities are larger when damaged cuttings are omitted, indicating that any loss in precision due to reduction in observation number (caused by omission of damaged cuttings) is more than offset by elimination of the variation introduced by damage. The consequences of omitting damaged plants from analyses are discussed with reference to selective gains.

Key words: clonal testing, mass selection, rooted cuttings, norway spruce.

Zusammenfassung

Die Höhe von bewurzelten *Picea abies* (L.) KARST.-Stecklingen wurde nach 5 Vegetationsperioden im Freiland analysiert. Wenn alle Stecklinge in die Varianzanalyse mit einbezogen wurden, ergaben Klone, Standorte, Standort × Klon-Interaktion sowie die Wiederholungen signifikante Variationsursachen. Wurden die beschädigten Stecklinge weggelassen, waren nur noch die Unterschiede zwischen den Klonen und den Wiederholungen signifikant, was nahelegt, daß die Standorte und die Standort × Klon-Interaktion mit den Schäden in Verbindung stehen. Sowohl die individuellen, als auch die Heritabilitäten der Klonmittelwerte sind größer, wenn man die beschädigten Stecklinge wegläßt, was anzeigt, daß jeder Verlust an Genauigkeit als Folge der geringen Beobachtungszahlen (verursacht durch das Weglassen beschädigter Stecklinge) größer ist, als ein Ausgleich durch die Vermeidung von Variation durch Schäden. Die Konsequenzen des Wegfalles beschädigter Pflanzen aus Analysen werden im Hinblick auf Selektionsgewinne diskutiert.

Introduction

Clonal testing of forest trees can be a rapid and effective method for screening large numbers of candidates during the initial stages of a genetic improvement program. The efficient capture of genetic variation via mass selection and subsequent vegetative propagation depends on the genetic variability present in the candidate population, the efficiency of test procedures, and the level of confounding introduced by environmental and genetic × environmental interaction sources of variance. In this paper we present results from clonal tests of Norway spruce (*Picea abies* (L.) KARST) in southern Sweden that allow evaluation of testing and selection methods. Further, we examine in detail the distribution of damage to test plants in years prior to measurement and the consequences of such damages for factors that affect selection.

Studies of variation in height of Norway spruce cuttings (SHELBOURNE 1974, KLEINSCHMIT 1983) indicate that substantial

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proportion of the total variance results from genetic differences among clones. A similar study using seedlings (Wellendorf 1982) demonstrated that both additive and non-additive sources of genetic variance are important for one-year height in Norway spruce. Although the source of our candidate population differs from the above cited studies, such results suggest that genetic variation will not be a limiting factor for selective gain in our program.

The proportion of variance attributable to location × clone interaction depends both on origin of the candidate material and on variability among test locations. Keinschmit (1983) reported clone × site interaction variances for Norway spruce cuttings trials that range from 8—50% of the total variance. Shelbourne (1974) also suggested the presence of large location × clone interactions for spruce cuttings, although his estimates were confounded with other environmental parameters. When genotype × environment effects are large, selection for a single set of clones adapted to all test locations may be ineffective. In this case, clonal tests may serve a second function in determining target zones for operational propagation (Burdon, 1971).

Damages that occur at random to tested trees increase the within-clone component of variance, decrease the precision of each estimated clone mean, and consequently decrease the gains obtainable via selection. When each tested clone is represented by several copies (ramets) the option exists for excluding damaged plants from the analysis without removing the clone from the program (and thus reducing selection intensity). We estimate parameters relevant to clonal selection both including and excluding cuttings damaged at early ages and discuss the relative merits of each alternative.

Materials and Methods

The Norway spruce clones used for our study are a subset of the population established in clonal tests by Hilleshög Forestry AB. Geographic origins and source information are detailed in *Table 1*. Most of the clones originated from Czechoslovakian provenances approved for planting in southern Sweden by government regulatory agencies. The few clones collected from Swedish provenances are probably not of Swedish origin. Estimates of genetic parameters for our candidate population will include the effects of both within- and between-provenance genetic variation.

Table 1. — Source information for clones tested in Rössjöholm and Knutstorp filed trials.

Provenance	Latitude	Longitude	Elevation (m)	Number Included
Kosice	48°48'	20°40'	700	10
Zilina	49° 28'	18° 53'	600	8
Zakamenne	49° 27'	19° 15'	700	8
Rusnaka	49° 24'	19° 15'	860	5
Norra Skåne	56° 25'	14° 0'	125	5
Rössjöholm	56° 25'	14° 0'	125	8
Banska Bystrika	48° 33'	19° 30'	850	6
Ceirny-Balog	48° 46'	19° 40'	730	33
Krasno	49° 21'	18° 55'	600	2
Kram	48° 46'	19° 34'	550	10
Bollebygd	57° 39'	12° 35'	---	10
Alingsås	57° 55'	12° 32'	---	5
Namestovo	49° 26'	19° 28'	850	3

Candidate clones were originally selected from bare-root nurseries at three and four years of age. This initial culling was based primarily on height and approximately 1 plant in 3,000 was retained. Cuttings were collected from the selected nursery plants and rooted in the spring of 1976. Rooted cuttings were transplanted to a bare-root nursery in the fall of 1976. Measurements were taken in 1978 on at least five ramets per clone for date of bud burst and bud set, and for second-year nursery height. A further culling was made prior to outplanting, with priority given to selection of clones with bud burst and bud set adaptable to the southern Swedish climate (Eriksson *et al.* 1976); approximatelly 1 of 12 clones were retained at this second stage of selection.

Cuttings from 113 selected clones were outplanted in spring of 1979. The test consisted of an unbalanced incomplete block design with two locations in southern Sweden: Knurtstorp (latitude 56°00', longitude 13°04', elevation 75 m), and Rössjöholm (latitude 56°20', longitude 13°04', elevation 175 m). Each clone was represented by a single ramet in each of five blocks at both locations. Cuttings were scored after three, four, and five growing seasons for height and damage; only fifth-year height was analyzed in our study.

Damages were originally segregated by both source (animal, insect, frost, etc.) and severity. Preliminary investigations (Shaw unpublished) indicated that damage source was relatively unimportant and that severity ratings could be simplified into three classes: undamaged plants, moderately damaged plants and severely damaged plants. Further, such investigations indicated that the effects of damages scored after three and four growing seasons were reflected as a height reduction at age five. We reacted to these observations by classifying each cutting based on the worst damage rating acquired over the three measurement years. For example, a plant scored as severely damaged in year three, but undamaged in years four and five was classified as severely damaged. In fact, there is substantial auto-correlation for damage rating over years i.e., damage categories usually contain the same cuttings over the three measurement years.

The form of the analysis of variance for our trials is given in *Table 2*. All analyses were performed using SAS procedure GLM and components of variance were estimated using linear functions of the expected mean squares given in *Table 2*.

Broad sense clone and clone-mean heritabilities were calculated as follows:

$$H^2 = \frac{\sigma^2_c}{\sigma^2_c + \sigma^2_{1c} + \sigma^2} \qquad (1)$$

$$H^2_{\bar{x}} = \frac{\sigma^2_c}{\sigma^2_c + \sigma^2_{1c}/1 + \sigma^2/1r} \qquad (2)$$

Where, 1 = number of locations
r = number of replications
σ^2_c = variance among clones
σ^2_{1c} = variance due to clone x location interaction
σ^2 = error variance
H^2 = broad sense heritability
$H^2_{\bar{x}}$ =broad sense heritability on a clone-mean basis

Table 2. — Form of the analysis of variance for fifth-year height.

Source of Variation	df	Expected Mean Square
Locations (L)	l -1	$\sigma^2 + c\,\sigma^2_{R/L} + r\,\sigma^2_{LC} + rc\sigma^2_L$
Clones (C)	c-1	$\sigma^2 + r\sigma^2_{LC} + rl\,\sigma^2_C$
L x C	(l-1)(c-1)	$\sigma^2 + r\,\sigma^2_{LC}$
Replications (R)/L	l(r-1)	$\sigma^2 + c\,\sigma^2_{R/L}$
error	l(c-1)(r-1)	σ^2

l = number of locations

c = number of clones

r = number of replications

σ^2_L = variance among locations

σ^2_C = variance among clones

σ^2_{LC} = variance due to clone x location interaction

$\sigma^2_{R/L}$ = variance among replications within locations

σ^2 = variance within replications

Table 3. — Estimated parameter values for fifth-year height, for cases including three levels of damage.

	Damage case		
Parameter	all surviving trees	severely damaged trees omitted	all damaged trees omitted
n	1018	889	616
$\bar{x}$	166.79	177.36	187.85
σ_p	53.03	47.14	41.52
$\sigma_{p_{\bar{x}}}$	27.57	27.86	27.87

n = total number of cuttings observed

$\bar{x}$ = phenotype mean height in cm

σ_p = individual phenotypic standard deviation

$\sigma_{p_{\bar{x}}}$ = clone mean phenotypic standard deviation

Table 4. — Analysis of variance for fifth-year height for cases including three levels of damage.

	all surviving trees		severely damaged trees omitted		all damaged trees omitted	
Source	df	MS	df	MS	df	MS
Location[†] (L)	1	27699.77[††]	1	200.86	1	1606.73
Clones (C)	112	6687.43**	112	5472.86**	111	3828.16**
L x C	110	2942.94**	109	2128.77**	98	1315.60
Replication/L	16	7247.47**	16	5805.67**	16	3788.29**
error	776	2222.76	647	1586.97	387	1153.13

[†] location effects are tested with a synthetic F-test (Cochran 1951).

[††], * and ** indicate significance at the 0.10, 0.05 and 0.01 probability levels.

Table 5. — Variance components*, broad sense heritability on an individual basis (H^2), and broad sense heritability on a clone-mean basis ($H^2_{\bar{x}}$) for data sets of fith-year height including three levels of damaged plants.

	All surviving trees		Severely damaged trees omitted		All damaged trees omitted	
Parameter	Value	% of Total	Value	% of Total	Value	% of Total
σ^2_L	90.60	3	0.00	0	0.00	0
σ^2_C	425.51	14	488.39	21	508.61	28
σ^2_{LC}	163.68	6	146.43	6	62.49	3
$\sigma^2_{R/L}$	101.51	3	101.90	5	104.57	6
σ^2	2222.76	74	1586.97	68	1153.13	63
H^2	0.15		0.22		0.29	
$H^2_{\bar{x}}$	0.56		0.63		0.66	

*Variance components defined in Table 2.

Results

Fifth-year height averaged 167 cm over both test locations (*Table* 3). The Rössjöholm site yielded slightly better growth than Knutsstorp (173 cm vs. 160 cm) and had fewer cuttings scored as damaged (40% vs. 51%). In fact, the above difference in fifth-year height can be explained entirely by concomitant differences in damage. Average fifth year height for undamaged cuttings differ by only one centimeter across locations.

For analysis, the data are presented as three cases that progressively exclude damaged trees: (1) all surviving trees, (2) omission of severely damaged trees, and (3) all damaged trees omitted (*Table* 3). The total number of observations decreases as the two classes of damaged cuttings are progressively excluded. The average number of ramets per clone for both locations decreases from 9 (of 10 planted) for all surviving trees to 5.5 for undamaged trees only. Despite the reduction in usable observations only one clone was eliminated as a result of all of its ramets being scored as at least moderately damaged in at least one year. As expected, omission of damaged plants acts to increase the mean fifth-year height and to decrease the phenotypic standard deviation (*Table* 3). The phenotypic standard deviation of clone means remains unchanged as damaged plants are omitted from the analysis.

Variances due to clone and replication sources are significant regardless of damage case (*Table* 4). However, both sources become a substantially larger proportion of the total variance in cases that omit damaged plants from analysis (*Table* 5). Variance due to locations and due to location × clone interaction are not a large proportion of the total (three to six percent. *Table* 5), but are significant when all trees are included in the analysis. Conversely, both locations and location × clones sources of variance become non-significant, and decrease as a proportion of the total variance, as damaged trees are omitted from the analysis.

Both clone and clone-mean broad sense heritabilities increase for cases that omit damaged trees, compared to the case in which all trees are analyzed (*Table* 5). The change in clonal heritability was suggested by previous observation on phenotypic standard deviations, and indicates that a reduction of environmental variance results from the omission of damaged cuttings. The increase in clone-mean heritability indicates that the reduction in number of observations (ramets) per clone in equation (2), r, is more than offset by reductions in the location × clone interaction and the error component of variance.

Discussion

Our analyses indicate that both location and location × clone effects contribute little to the variation in fifth-year height observed in our trials. General conclusions cannot be drawn from the above results, as our two sites were separated by only 40 km and were visually quite similar. However, our results are encouraging in that our intuitive concept of site similarity seems biologically justified. Also, our results support the conclusion of SHELBOURNE (1974); clones are reasonably well characterized by measurements on few ramets.

Omission of cuttings damaged during any phase of field testing from further analyses is strongly supported by our results Justification for such an omission is obtained from the substantial reduction in location, location × clone and error components of variance, and from the increases in clone and clone-mean heritability that result from analyzing only undamaged cuttings. Resultant clone-mean heritability is the ultimate criterion for deciding whether to include or omit damaged plants, as it is linearly related to genetic gain. For our trials, omission of all damaged cuttings results in an 18% improvement in clone-mean heritability (and thus for gain) over the case in which all cuttings are included. The above recommendation should not be accepted uncritically for all trials, as clone-mean heritability depends both on the variance introduced by damaged plants and on the number of observations (ramets) per clone remaining after omission of damaged cuttings. When damage introduces little variation, or is so widespread as to eliminate most of the available observations, omission may not be justified. Further, when damage is genetically correlated with the trait of interest (i.e. frost damage and height), elimination of damaged trees may bias selection.

As indicated above, the observed reduction in the location × clone component of variance due to omission of damaged cuttings creates a dilemma: the biological factors that cause such an interaction appear to be associated with damage. If location × clone component of variance due to omission of damaged cuttings creates a dilemma: the biological factors that cause such an interaction appear to be associated with damage. If location × clone variation is caused by rank changes across locations, omission of damaged cuttings may bias selections. For our case, analysis of fifth-year height transformed to a log (10) scale gave essentially the same results as for untransformed values, with the important exception that interaction variance was no longer associated with damage classification. This result suggests that location × clone interactions result from changes in variance or scale across locations, rather than changes in rank.

Regardless of the source of the interactions in our study, interaction variance is a small proportion of the total; and omission of damaged cuttings is probably justified. Our results indicate opportunities for improvement of clonal selection methods and demonstrate the value of early damage assessment as a tool in Norway spruce clonal selection programs.

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Inheritance and Gain in a Half-Diallel Cross Among Loblolly Pines Selected for Resistance to Fusiform Rust

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(Received 16th June 1986)

Summary

Ten seed orchard clones of loblolly pine (*Pinus taeda* L.) were selected for resistance to fusiform rust based on progeny test performance. These 10 clones were crossed in a half-diallel and the resulting progenies planted in an area of high rust hazard. Inheritance and genetic gains were estimated at age 10. In the field test, a standard check lot and a seed orchard bulk check lot each averaged 1.5% rust-free. The 45 progenies in the half-diallel averaged 15.8% rust-free. Five of the 10 clones had good breeding values for rust resistance. The 10 crosses among these five clones averaged 35.8% rust-free. Family heritability of rust-free percentage was 0.69. The two stages of selection done—selecting 10 clones then the best five of them—produced a genetic gain in rust-free percentage of 28.1. Gains in other traits were not large but greater gains in them should occur when individuals within families are selected. Selection and breeding should be quite effective in developing fusiform-rust resistance in loblolly pine.

Key words: Pinus taeda, Cronartium quercuum f. sp. *fusiforme*, breeding.

Zusammenfassung

Zehn Samenplantagen-Klone von *Pinus taeda* L. wurden auf der Grundlage ihrer Leistung in einer Nachkommenschaftsprüfung als resistent gegen *Cronartium quercuum*

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