scribe the effects of life cycle stage on meristematic potential. Molisch (1922) used the term *topophysis* to explain the differences observed by Vochting when cuttings from terminal shoots were compared with those from first and second order laterals. A third term, *periphysis*, has been used to refer to the effects of the environment in pre-conditioning tissue (Hallé et al., 1978).

Although each of these had specific meanings to the authors, over the years use of the terms has become confused. Olesen (1978) made a major contribution by drawing attention to the confusion that existed in the literature over the terms *cyclophysis* and *topophysis*. He proposed two definitions to clarify the distinction between these two terms: "Cyclophysis: the process of maturation of the apical meristems. Topophysis: the phenomenon that scions, buddings and cuttings for some time after grafting, budding or rooting maintain the branch-like growth habit they had as shoots on the ortet."

We fully support the definition proposed by Olesen for *cyclophysis*, but we feel that his definition of *topophysis* requires estatement for the following reasons.

1. *Topophysis* should not be confined to phenomena in detached shoots as suggested by the definition. The developmental processes that give rise to topophytic effects take place in the intact plant, but are demonstrated by their persistence in detached parts.

2. Since the term *topophysis* refers to the nature of the plant in relation to position (Gr. *topos*: place; *physis*: nature), it should not necessarily be confined to growth habit characteristics. In conformity with the definition of *cyclophysis, topophysis* should refer to any morphological, anatomical and physiological differences that result from positional influences, and that are maintained in detached shoots.

3. Position requires precise definition. Reference to branch-like growth habit is too vague, and does not adequately separate cyclophytic and topophytic effects, since branch habit may be modified during maturation of the tree (see branch angle differences between trees of different maturation levels, Bolstad and Libby (1982)). Since the study by Vöchting, which prompted introduction of the term *topophysis* by Molisch, was based upon cuttings from first

and second order laterals, it would appear to be appropriate to define position as being the rank order of shoots.

To overcome these objections, we propose that the following definition of *topophysis* should be used in the future.

*Topophysis:* a state resulting from differentiation in developmental and physiological potential of apical meristems among branch hierarchical orders, independent of the processes of maturation of terminal meristems.

Results of a study that support the concept of topophytic differences based upon branch hierarchical position are reported elsewhere (Power, Dodd and Libby, 1985). From these results, and from previous unpublished observations, the authors conclude that the development of shoots (whether it is rooting, stem form, or shoot growth) after detachment from the tree, varies according to the maturation level of the shoot, and also with the branch order position from which the cutting was taken. The results further indicate that within the ortet, the processes of cyclophysis and topophysis interact, such that with increasing maturation of the ortet the degree of differentiation among branch order positions becomes more pronounced.

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# C Effects and Second Generation Clone Performance in Picea sitchensis and Pinus contorta

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### Summary

Clonal variation in 5-year heights was partitioned into genetic and C effects by two-generation cloning, where the first generation was grown in two contrasting environments.

Four clones of each of 5 provenances of *Picea sitchensis* and *Pinus contorta* were propagated from 14 to 15-year-old trees and grown for 5 years at an upland and a lowland site. Second-generation clones were then grown for 5 years at the lowland site. There was no evidence for C effects on 5-year heights in the second generation attributable to the upland and lowland environments of the first generation mother trees.

The second-generation clones grew equally as well as the first generation clones, suggesting that maturation was arrested by repropagation.

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It is concluded that C effects are important only in short-term tests on juvenile traits, or when they are associated with differences in maturity.

*Key words: Picea sitchensis, Pinus contorta,* clones, variation, C-effects, maturation.

## Zusammenfassung

Die Variation der Höhen im Alter 5 wurde bei zwei Klon-Generationen in genetische und C-Effekte aufgeteilt, wobei die erste Generation an zwei unterschiedlichen Standorten aufgezogen wurde.

Je vier Klone von 5 Provenienzen von *Picea sitchensis* und *Pinus contorta* wurden von 14—15 Jahre alten Bäumen vermehrt und für 5 Jahre auf einem Hoch- und einem Tieflagenstandort aufgezogen. Die Klone der zweiten Generation wurden dann auf einen Tieflagenstandort gepflanzt. Es gab keine Anzeichen für C-Effekte bei der Höhe im Alter 5 der zweiten Generation, die den Effekten der Hoch- bzw. Tieflagenstandorte der Mutterbäume der ersten Generation zuzuschreiben gewesen wären.

Die Klone der zweiten Generation wuchsen genauso gut wie die der ersten Generation, was andeutet, daß eine Klonalterung durch die Vermehrung aufgehalten wurde.

Es wird gefolgert, daß C-Effekte nur in kurzfristigen Tests auf Jugendmerkmale wichtig sind, oder wenn sie mit Entwicklungsunterschieden verbunden sind.

## Introduction

It is well-known that clonal variation in growth traits can be very large in many tree species, offering the prospect of making substantial short-term genetic gains in growth rate. However, it is equally well-known that some of the variation among clones can be non-genetic. Non-genetic variation can occur among whole clones because the ortets (mother trees) grow in different environments, or are in different stages of maturation, so that the vegetative propagules taken from them are in different physiological or morphological states. If these non-genetic, so-called C effects, are confounded with genetic differences, any estimates of genetic variation, heritability (or repeatability) and genetic gain will be biased upwards. C effects can also contribute to poor relationships between the performances of first and second generation[1] clones (i.e. cuttings taken from cuttings) (Shelbourne and Thulin, 1974).

The definition of a C effect used here is that given by Burdon and Shelbourne (1974), namely: a maternal effect common to all ramets of a clone, such as that produced by the nutrient status, size, vigour or age of an ortet or mother tree. We do not include the maternal effects that are peculiar to individual propagules, such as those produced by differences in cutting size, position on the ortet, or presence or absence of flowers. The latter maternal effects add to the variance within clones, but not among clones, and do not therefore bias estimates of genetic gain upwards (Foster et al., 1984).

Clonal variation can be partitioned into genetic and C effects by two-generation cloning, that is, by growing the first generation of clones in different environments and then using them as mother trees for the second generation (Libby and Jund, 1962). There seem to be only three reports of this procedure having been followed in forest tree species.

First, Wilcox and Farmer (1968) found that C effects accounted for 9—11% of the total clonal variation (and were

one-third the size of the genetic component of variation) in two rooting characteristics of *Populus deltoides* Bartr.. They concluded that C effects were large enough to cause important bias in short term clonal experiments, but that they may have little effect after a period of several years. Second, Foster et al. (1984) found that C effects accounted for only 2—6% of the total clonal variation in five rooting characteristics of *Tsuga heterophylla* (Raf.) Sarg.. Such small effects may be important when selecting for rooting ability, but they are unlikely to influence selection for height or volume measured after several years in the field. Third, Bolstad and Libby (1982) reported long-term C effects in *Pinus radiata* D. Don, produced by taking cuttings of the same clones from either hedge-grown or tree-grown clonal mothers. The hedge-grown mother trees produced clones with relatively large crowns and large stem volumes, which Bolstad and Libby attributed to their more juvenile condition. Thus, apart from the last report, the general conclusion has been that C effects, caused by the environment of the mother trees, make a relatively small contribution to total variation compared with genetic effects.

In this paper, we report a long-term study which supports this conclusion. C effects were determined using two-generation cloning of *Picea sitchensis* (Bong.) Carr. (Sitka spruce) and *Pinus contorta* Dougl. (lodgepole pine). The first generation was grown for 5 years at two contrasting field sites (upland and lowland) in Scotland. This generation provided the cuttings for the second generation which was grown for 5 years at the lowland site. Cahalan (1981) reported large clonal heritabilities (repeatabilities) for 5-year heights in the first generation, when genetic differences were confounded with any C effects. In this paper, we show that the upland and lowland environments produced negligible C effects on 5-year heights in the second generation.

## Materials and Methods

The experiments were conducted using 4 clones of each of 5 provenances of *P. sitchensis* and *P. contorta*. The provenances spanned the range of each species and were, for
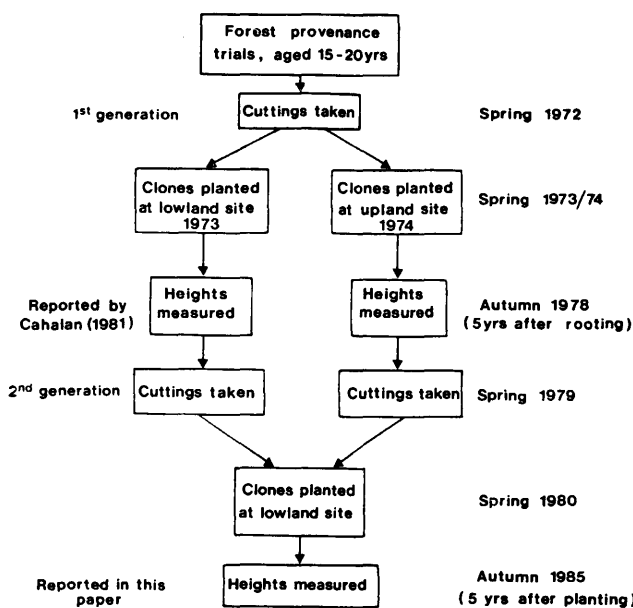


*Figure 1.* — The experimental programme used to produce first and second-generation clones of *Picea sitchensis* and *Pinus contorta.*

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[1] The term 'generation' has no breeding connotation; it is used in this paper in preference to 'stages of serial propagation'.

*P. sitchensis:* Cordova, Alaska (61⁰ N), Sitka, Alaska (57⁰ N), Skidegate, Queen Charlotte Islands (53⁰ N), San Juan, Vancouver Island (49⁰ N) and North Bend, Oregon (43⁰ N); and for *P. contorta:* Skagway, Alaska (59⁰ N), Queen Charlotte Islands (54⁰ N), Anahim Lake, B. C. (52⁰ N), Ladysmith, Vancouver Island (49⁰ N) and North Bend, Oregon (43⁰ N).

The timetable of the two-generation experimental programme is given in *Figure 1.*

### First-generation clones

The original cuttings were taken in February 1972. The mother trees of *P. sitchensis* were chosen at random from within a 15-year-old frost damaged provenance trial at Wark, Northumberland. The mother trees of *P. contorta* were trees of average height, within each provenance, in a 14-year-old provenance trial at Selm Muir, Lanarkshire. The cuttings were rooted on a mist propagation bench, the percentage rooted cuttings was recorded at intervals until July 1972, and the rooted cuttings were then potted up and hardened off outside.

In April 1973, the clones were planted in mineral soil at a *lowland site* at Roslin, Midlothian (56⁰ N, 150 m). In spring 1974, a duplicate set of clones (rooted at the same time) that had been grown outside in containers was planted in peaty-gley soil on a north-facing slope at an *upland site* at Cloich, Tweeddale (56⁰ N, 310 m). At both sites, a split-plot randomized block design was used, with provenance main plots, clone sub-plots and 3 (lowland site) or 4 (upland site) ramets per plot at 1.0 m spacing. CAHALAN (1981) reported the heights, basal diameters, branch numbers, and other characters measured in 1978 at the end of the fifth growing season.

### Second-generation clones

In February-March 1979, 3—4 cuttings were taken from mid-level on each tree of each first-generation clone at both the lowland and upland sites. The cuttings were rooted as before.

In March-April 1980, these second-generation clones were planted in a mineral soil at a lowland site (Glencorse, Midlothian, 185 m) about 5 km from Roslin, where the first-generation clones had been planted.

The two species were planted in neighbouring experiments. Each experiment had a split-split-plot randomized



*Figure 2.* — Mean heights (m) of first and second-generation clones of *Picea sitchensis* and *Pinus contorta* 5 years after planting. Closed circles: first generation planted at an upland site. Open circles: first generation planted at a lowland site.
Lines mark 1:1 relationships, showing a close correspondence between the heights of first and second generation clones where both were growing at the lowland site.

block design, with 3 blocks, provenance main plots (5), split for clones within provenance (4), split for source of the cuttings (upland or lowland site). There were 3 trees per sub-sub-plot at 0.5 m spacing, with 1.0 m between plots.

Tree heights were measured in November 1985, at the end of the fifth growing season.

### Analyses of data

The form of the analyses of variance of second-generation clone heights is given in *Table 1.* Analyses were based on sub-sub-plot means (of 3 trees) and all sources of variation were assumed to be random. There were 3 missing values for *P. contorta* and 6 missing values for *P. sitchensis.*

Components of variance were calculated by equating observed mean squares with the expected mean squares given in *Table 1* and solving the resulting equations. The C effects variance was taken to be $V_s$, that attributable to the source of the first-generation mother clones (upland or lowland).

Assuming that the clones were a random sample of all clones within each provenance, the repeatability of clone means within provenances, $h^2_c$, was calculated as:

$$h^2_c = \frac{V_c}{(V_e + sV_{cb} + bV_{sc} + bsV_c)/bs}$$

where the symbols are as defined in *Table 1.*

### Results

#### First and second generation heights

The percentage rooting varied between clones in the range 10—60%. All clones grew orthotrophically 2 years after field planting. However 5 year heights were not relat-

*Table 1.* — Form of the analysis of variance of heights of second generation clones of *Picea sitchensis* and *Pinus contorta.*

| Source of Variation | Degrees of freedom | Expected mean squares |
|---|---|---|
| Blocks | b - 1 | $V_e + sV_{cb} + csV_{pb} + pcsV_b$ |
| Provenances | p - 1 | $V_e + sV_{cb} + csV_{pb} + bcV_{sp} + bcsV_p$ |
| Provs x Blocks | (b-1)(p-1) | $V_e + sV_{cb} + csV_{pb}$ |
| Clones within Provs | p (c-1) | $V_e + sV_{cb} + bV_{sc} + bsV_c$ |
| Clones x Blocks | (b-1)p(c-1) | $V_e + sV_{cb}$ |
| Sources of Clones | s-1 | $V_e + bV_{sc} + bcV_{sp} + bpcV_s$ |
| Sources x Provs | (p-1)(s-1) | $V_e + bV_{sc} + bcV_{sp}$ |
| Sources x Clones | p(c-1)(s-1) | $V_e + bV_{sc}$ |
| Residual | (b-1)pc(s-1) | $V_e$ |

b = blocks (3), p = provenances (5), c = clones within provenances (4), s = source of clones (upland or lowland).
$V_e, V_{sc}, V_{sp}, V_s, V_{cb}, V_c, V_{pb}, V_p$ and $V_b$ are variances due to sub-sub-plots, source × clone, source × provenance, source, clone × block, clone, provenance × block, provenance, and block, respectively.
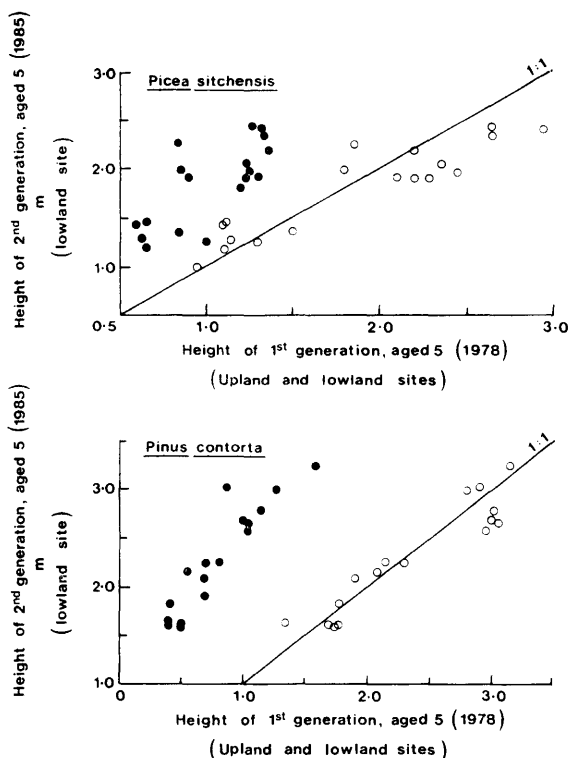
ed to rates or percentage rooting in either generation (r < 0.2), and there was no consistent difference in rooting between cuttings taken from the lowland and upland sites.

The clones performed very similarly in the second generation (at the lowland site) to the way they had performed in the first generation at the lowland site.

The overall mean 5-year heights of *P. sitchensis* at the lowland and upland sites in the first generation were 1.87 and 1.00 m respectively, and their mean 5-year height at the lowland site in the second generation was 1.80 m. Equivalent values for *P. contorta* were 2.33 and 0.80 m in the first generation and 2.30 m in the second generation.

The provenances of both species were ranked for height in a similar order in the two generations, namely, for *P. sitchensis* Cordova < Sitka < Skidegate < San Juan < North Bend, and for *P. contorta*, Skagway < Q.C.I. Anahim Lake < Ladysmith < North Bend. Furthermore, the relative heights of the clones within provenances were similar in the two generations, as shown by the close 1:1 correspondence between first and second generation heights in *Figure 2*. The correlations between first and second generation 5-year heights at the lowland site were r = 0.92 for *P. sitchensis* and r = 0.94 for *P. contorta*.

### Sources of variation in the second generation

Mean heights, mean squares, and corresponding estimates of the variance components, are given in *Tables 2, 3* and *4*.

Provenances accounted for 51% and 65 % of the variance in 5-year heights of *P. sitchensis* and *P. contorta*, respectively, while clones within provenances accounted for 18% and 8% *(Table 4)*.

There was no evidence for any consistent C effect on 5-year heights attributable to the upland or lowland environment of the first generation mother trees. Mean heights were virtually the same for the lowland and upland sources[1] of cuttings *(Table 2)*, and source accounted for a negligible percentage of the total variance *(Table 4)*.

However, there were significant source × clone interactions, especially in *P. contorta*. For instance, in Skagway

Table 2. — Mean heights (cm) of second generation clones of *Picea sitchensis* and *Pinus contorta* after five growing seasons. The cuttings were taken from mother trees at either a lowland or an upland site.

| Provenance | Clone | Picea sitchensis Lowland source | Picea sitchensis Upland source | Provenance | Clone | Pinus contorta Lowland source | Pinus contorta Upland source |
|---|---|---|---|---|---|---|---|
| Cordova | A | 142 | 144 | Skagway | A | 195 | 129 |
| | B | 105 | 131 | | B | 173 | 149 |
| | C | 144 | 145 | | C | 167 | 150 |
| | D | 129 | 240 | | D | 197 | 288 |
| Sitka | A | 110 | 87 | Q.C.I. | A | 172 | 148 |
| | B | 138 | 113 | | B | 186 | 178 |
| | C | 125 | 131 | | C | 224 | 191 |
| | D | 144 | 129 | | D | 178 | 200 |
| Skidegate | A | 230 | 223 | Anahim Lake | A | 213 | 215 |
| | B | 218 | 218 | | B | 224 | 226 |
| | C | 201 | 179 | | C | 225 | 223 |
| | D | 182 | 200 | | D | 233 | 271 |
| San Juan | A | 189 | 208 | Ladysmith | A | 293 | 280 |
| | B | 175 | 209 | | B | 303 | 301 |
| | C | 202 | 209 | | C | 276 | 261 |
| | D | 197 | 196 | | D | 276 | 252 |
| North Bend | A | 149 | 210 | North Bend | A | 318 | 279 |
| | B | 253 | 236 | | B | 239 | 273 |
| | C | 234 | 236 | | C | 275 | 280 |
| | D | 227 | 255 | | D | 326 | 321 |
| Means | | 180 | 185 | | | 235 | 231 |

[1] The term 'source' is used in this paper to refer to the upland or lowland environments, not to the provenance.

Table 3. — Analyses of variance of heights (m) of second generation clones of *Picea sitchensis* and *Pinus contorta* at age 5.

| Source of variation | Mean squares P. sitchensis | P. contorta |
|---|---|---|
| Blocks | 5.1 | 6.9 |
| Provenances | 405.8*** | 625.2*** |
| Provs x Blocks | 15.2 | 14.8 |
| Clones within Provs | 50.2*** | 41.8*** |
| Clones x Blocks | 13.8 | 7.6 |
| Sources of clones | 8.2 | 4.4 |
| Sources x Provs | 10.9* | 5.1 |
| Sources x Clones | 6.5 | 19.3** |
| Residual | 3.9 | 5.3 |

* P ≤ 0.05, ** P ≤ 0.01, *** P ≤ 0.001.

Table 4. — Estimated variance components of heights (m) of second generation clones of *Picea sitchensis* and *Pinus contorta* at age 5.

| Variance component | P. sitchensis Estimate | P. sitchensis % of total variance | P. contorta Estimate | P. contorta % of total variance |
|---|---|---|---|---|
| $V_p$ Provenances | 16.09 | 50.6 | 26.03 | 65.0 |
| $V_{pb}$ Provs x Blocks | 0.17 | 0.5 | 0.91 | 2.3 |
| $V_c$ Clones within Provs | 5.64 | 17.8 | 3.36 | 8.4 |
| $V_{cb}$ Clones x Blocks | 4.95 | 15.6 | 1.14 | 2.8 |
| $V_s$ Source (C effect) | 0.07 | 0.2 | - 0.01 | 0.0 |
| $V_{sp}$ Sources x Provs | 0.37 | 1.2 | - 1.19+ | - 3.0+ |
| $V_{sc}$ Sources x Clones | 0.87 | 2.7 | 4.68 | 11.7 |
| $V_e$ Residual | 3.86 | 12.1 | 5.30 | 13.2 |

+ A negative variance occurred because clones within provenances interacted with source but provenances (each the means of 4 clones) did not interact with source.

provenance, clone A performed best when grown from cuttings taken from the lowland source, whereas clone D performed best using the upland source *(Table 2)*.

Estimated repeatabilities ($h^2$) of clone means within provenances were 0.67 for *P. sitchensis* and 0.48 for *P. contorta*.

### Discussion

The main finding of this study was that C effects, attributable to the environment of the mother trees, had no effect, on average, on the heights of clones after 5 years growth. From this study, it seems unlikely that C effects of this kind will often be important in masking genotypic values of growth traits measured after several years in the field. Thus, the high repeatabilities of clone means reported for *P. sitchensis* and *P. contorta* at age 5 by CAHALAN (1981) and for *P. sitchensis* at age 6 by ROULUND (1978) - and by several workers on other species - will probably have been overwhelmingly due to genetic differences between clones. It should be stressed that this study was a severe test of long-term C effects, because the first generation mother trees at the lowland site were growing twice as fast as those in the cooler, less fertile conditions at the upland site. It was surprising that this difference in mother tree vigour had no effect on rooting, nor on the long-term performance of the clones. A few individual clones seemed to perform better when propagated from cuttings taken at the lowland site, but strangely, there were also clones that performed better when propagated from cuttings taken at the upland site.

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 snort-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).

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

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B. Bentzer[2])

### 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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