Juvenility and Serial Vegetative Propagation of Norway Spruce Clones (Picea abies Karst.)

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Summary

Effects associated with progressive maturation of clones are of greatest concern in clonal tree improvement programs. Serial propagation has been in use at the Lower Saxony Forest Research Institute since 1968 to arrest maturation in Norway spruce clones. By 1980 cuttings were established in the nursery that had been serially propagated from one to five cycles. This material was measured in fall 1983 for several characteristics thought to be indicative of maturation state. Serial propagation appears to have at least considerably slowed, and perhaps arrested, maturation processes in Norway spruce. From a practical point of view, there does not seem to be any restriction for repropagation at least up to the fifth cycle.

Key words: *Picea abies*, vegetative propagation, juvenility, maturation.

Zusammenfassung

Jugendlichkeit und Serienvermehrung von Fichten-Klonen *(Picea abies* Karst.) Die mit der zunehmenden Reifung von Klonen verbundenen Veränderungen haben entscheidende Auswirkungen auf Klon-Züchtungsprogramme. Serienvermehrung ist in der Abteilung Forstpflanzenzüchtung der Niedersächsischen Forstlichen Versuchsanstalt seit 1968 verwendet worden, um die mit zunehmendem Alter einhergehenden physiologischen und morphologischen Veränderungen von Fichtenklonen zu verhindern. 1980 wurden in Escherode Stecklinge verschult, die über einen bis zu 5 Vermehrungszyklen vermehrt worden waren. An diesem Material wurden im Herbst 1983 zahlreiche Merkmale erhoben, von denen anzunehmen war, daß sie eine Veränderung im Reifungszustand widerspiegeln würden. Die Ergebnisse zeigen, daß die Serienvermehrung von Fichte die physiologischen und morphologischen Veränderungen, die mit zunehmendem Alter einhergehen, zumindest erheblich verzögert, wenn nicht sogar ganz unterbrochen hat. Für die Vermehrungspraxis scheinen zumindest bis zum fünften Vermehrungszyklus keine wesentlichen Beschränkungen zu bestehen.

Introduction

Many advantages have been recognized for the use of vegetative propagules in forest genetics research and in production of improved planting stock (Fielding 1964; Thulin and Faulds 1968; Burdon and Shelbourne 1974; Libby 1974, 1977; Burdon 1982). Problems associated with the vegetative propagation of older trees have led to the initiation of clonal tree improvement programs using juvenile material. Large-scale programs relying on early selection and propagation of clones from provenance and progeny trials have been initiated for Norway spruce *(Picea abies* Karst.) in several European countries (Kleinschmit *et al.* 1973; Kleinschmit and Schmidt 1977; Lepistö 1977; Roulund 1977; Werner 1977; Bentzer 1981; Monchaux 1982). The greatest concern in these programs and others is the effects associated with progressive maturation of clones.

The increasing state of maturation of the donor plant affects several characteristics of importance in vegetative propagation. Studies of several species have shown that percent rooting, speed of rooting, root length and number, and subsequent survival and growth after rooting all decrease with increasing age of the ramet (Thulin and Faulds 1968; Libby *et al.* 1972; Black 1973; Girourd 1974; Kiang *et al.* 1974; Shelbourne and Thulin 1974; Roulund 1975). In addition, the transition from plagiotropic to orthotropic growth takes longer (Kleinschmit 1961; Black 1973; Roulund 1975, 1979), and variation within clones rises (Kleinschmit 1977). Other characteristics affected by maturation state include bark and wood properties (Nicholls *et al.* 1976; Lewark 1979, 1981; Olesen 1982), branching characteristics (Libby and Hood 1976; Lewark 1981), flowering (Fielding 1970; Zimmerman 1972; Bolstad and Libby 1982), leaf anatomy (Schaffalitzky 1959; Libby and Hood 1976), and resistance to diseases and browsing (Søegaard 1959; Fielding 1970; Toda 1974; Heybroek and Visser 1976; Libby and Hood 1976).

The maintenance of juvenility is important in clonal tree improvement programs. Unless maturation can be arrested, clones selected early in a program may no longer be easily propagated or may have changed their properties by the time information from clonal tests becomes available. Related to this problem is the problem of early testing. The longer one must wait for accurate clonal information, the greater the concern over progressive maturation effects. Earlier selections, however, carry a greater risk of not maintaining their superiority to the end of the rotation. Two methods are possible to escape this problem: 1. using tested material which is repropagated by generative means and then cloned, or 2. attempting to arrest maturation.

Several promising methods have been developed to arrest maturation and possibly even induce rejuvenation including cultural treatments of the donor plant, repeated regrafting, tissue culture, hedging, and serial propagation. The two methods most frequently discussed and used for large scale propagation are hedging and serial propagation. Juvenility appears to be related in part to the distance of the plant parts from the roots (Fortainer and Jonkers 1976; Wareing and Frydman 1976; Paton *et al.* 1981), and both these techniques decrease this distance. Hedging involves the repeated pruning of the donar plant, and has been shown to provide cuttings of an apparently lower maturation state then those from non-hedged plants (Libby *et al.* 1971; Black 1973; Libby and Hood 1976; Bolstad and Libby 1982; Copes 1983). It has been suggested that different maturation states may be set and maintained, depending on the height of the hedge (Bolstad and Libby 1982). Hedging also provides a convenient way to produce and harvest many cuttings from a small area. Despite promising results, it is not known how long hedging will maintain clones in a juvenile state.

Serial propagation involves the repeated propagation of cuttings from other recently rooted cuttings. Results from earlier studies indicate that serial propagation may be effective in slowing maturation, but whether it completely arrests maturation is uncertain. Kleinschmit and Schmidt (1977) reported earlier results for Norway spruce clones that indicate no decline in rooting ability in secondary and tertiary cuttings as compared to primary cuttings, but secondary cuttings took somewhat longer to make the physiological change from branch habit to orthotropic growth. Morgan *et al.* (1980) found that secondary live oak cuttings taken from the 2-year-old primary cuttings of a 2-year-old seedling had significantly higher rooting than primary cuttings from the same seedling at 4 years of age. Pawsey (1971) noted that grafts using scion from Monterey pine clones serially propagated for four and five cycles grew in a more juvenile manner than grafts from material propagated in earlier cycles.

These studies indicate that serial propagation may indeed be slowing maturation. Delisle (1954), however, found a marked decrease in rooting ability with each repropagation of eastern white pine serially propagated every four years for five cycles. Fielding (1970) noted that female flowers were present on 2-1/2-year-old secondary cuttings propagated from 3-year-old primary cuttings, which in turn were propagated from 4-year-old Monterey pine seedlings. However, no female flowers were present on 2-1/2-year-old primary cuttings from 3-year-old seedlings, or on 2-1/2-year-old seedlings .The results of Delisle and Fielding are somewhat less encouraging for the use of serial propagation to slow maturation.

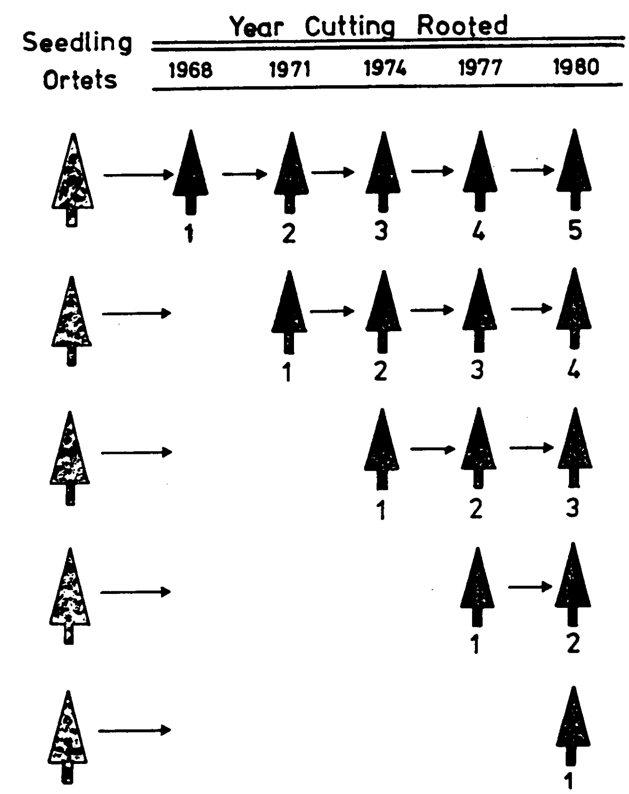

Figure 1. — Serial propagation of study material. Seedling ortets were 4 years of age. Cuttings were grown for 3 years before repropagation. The number below each cutting indicates the number of propagation cycles. Cuttings used in this study were rooted in 1980 and measured in autumn 1983.

Table 1. — One-way, hierarchical analysis of variance using individual tree values.

Source	df	Expected mean squares
Propagation cycle, P	4	$\sigma^2_E + n\sigma^2_{C/P} + nc\sigma^2_P$
Clones within cycles, C (P)	365	$\sigma^2_E + n\sigma^2_{C/P}$
Trees within clones, T (C(P))	7,068	σ^2_E

Table 2. — Randomized block analysis of variance for propagation cycles two through five using clonal means.

Source	df	Expected mean squares
Propagation cycle, P	3	$\sigma^2_E + n\sigma^2_{BxP} + nr\sigma^2_P$
Block, B	2	$\sigma^2_E + n\sigma_{xB\ p} + np\,\sigma^2_B$
Block x cycles, BxP	6	$\sigma^2_E + n\sigma^2_{BxP}$
Clones within blocks x cycles, C (BxP)	471	σ^2_E

The following study was undertaken to compare different numbers of cycles of repeated repropagation for progressive maturation effects in Norway spruce clones. This paper reports the initial results from 4-year-old cuttings in the nursery propagated for one to five cycles.

Material and Methods

The material used in this study is part of the Norway spruce clonal tree improvement program of the Lower Saxony Forest Research Institute in West Germany. Propagation procedures and the breeding scheme of this program have been described earlier in Kleinschmit *et al.* (1973), Kleinschmit (1974), and Kleinschmit and Schmidt (1977).

Primary ramets propagated from 4-year-old seedlings selected in the nursery were rooted every 3 years beginning in 1968, and then repropagated on a 3-year cycle *(Figure 1)*. By 1980 cuttings were established in the nursery that had been serially propagated from one to five cycles. All except the fifth propagation material originated from the same provenance. The fifth cycle material included some clones originating from other provenances due to restricted material available in 1968. Trees were measured in fall 1983 after four growing seasons in the nursery for several characteristics thought to be indicative of maturation state. The characteristics measured include height, root collar diameter, branch length, tropism, habitus, and form. Branch length was measured as the longest branch in the top whorl. Tropism, habitus, and form are measures of the growth form of the plant. Tropism is a measure of vertical growth form with a score of one representing orthotropic growth and a score of five representing plagiotropic growth. Habitus is a measure of symmetry when looking down on the plant from above. A score of one indicates branches and buds extending in all directions, whereas a score of five indicates branches and buds extending bilaterally. Form is a subjective assessment of the overall shape of the plant. A score of one represents good form and a score of five, bad form. Percent rooted for each clone was also noted.

The experimental design was a randomized block design with clones nested within propagation cycles and trees nested within clones. A variable number of clones per propagation cycle and trees per clone existed due to the nature of the propagation program. The study was replicated three times, except for the first cycle, which was only replicated twice since only a few trees per clone were available. Due to the unbalanced nature of the study, two separate analyses were done. First, all five cycles were analyzed as a one-way, hierarchal analysis of variance using trees from the first two blocks, but not considering block effects *(Table 1)*. Second, cycles two through five were analyzed as a randomized block design with clones nested within cycle *(Table 2)*. Clones nested within cycle was the error term used to test cycles in the second analysis since significant block × cycles interaction did not exist for any of the six traits. Thus the two analyses would have given similar results except that the exclusion of the first propagation cycle increased the variance associated with phases since the means of the first cycle were often close to the means of the fifth cycle and the overall means. Only the results from the one-way, hierarchal analysis of variance are presented since it is not biased by exclusion of the first propagation cycle.

Due to the discrete nature of scoring for tropism, habitus, and form, a square-root transformation was used in order to normalize the results. Analysis of variance of the transformed data was used to check for significance, while variance components were estimated without a transformation.

Since height was thought to be correlated with several variables, an analysis of covariance was completed using height as the independent variable. The results differ substantially only with respect to root collar diameter. A smaller example was taken for further analysis in which clones were chosen such that the mean height for each cycle would be near the overall mean height. The objective of this sample was to look at other characters within a narrow range of heights and eliminate some of the correlative influences associated with height. The additional characters examined included the fresh and dry weights of roots, leader and branches, and the number of branches of first and second order. Ten clones within each propagation cycle were chosen and three plants per clone measured. The analysis used a one-way, hierarchical analysis of variance.

Results and Discussion

Height

Height growth is expected to decrease with increasing maturation state of the donor plant (Roulund 1975). Results from the larger sample showed a decreasing trend in height from the second to the fourth propagation cycle, but the fifth cycle was nearly as tall as the first (Figure 2). The analysis of variance for the larger sample indicated a significant difference between cycles (p < .25), but cycles accounted for only 1,4 percent of the total variation (Table 3). Although little variation existed between cycles, slightly decreasing heights from the second to the fourth cycle may be indicative of an increasing maturation state. The increasing height of plants that have undergone five propagation cycles may have resulted from selection among clones between cycles. Before each repropagation, a decreasing percentage of clones were excluded from the program based on growth performance in clonal field trials. Thus decreases in height growth due to maturation may have been offset by increases due to selection between propagation cycles. This problem will be avoided in future studies by repropagating a standard set of clones each cycle.

No trends with propagation cycle were evident in the smaller sample *(Figure 2)*, and differences in heights between propagation cycles were not significant *(Table 3)*. This was expected since clones from each cycle were chosen to be around the overall mean. The mean of the smaller sample was actually somewhat greater than the mean of the larger sample, but the deviation of the mean of each cycle from the overall mean appeared to be random.

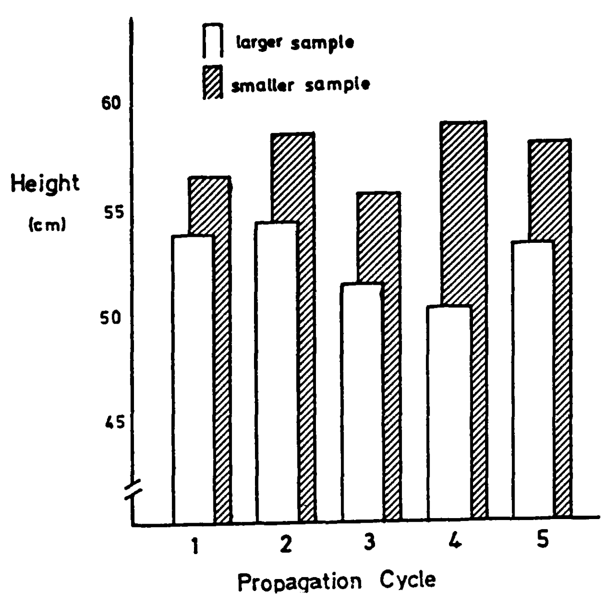

Figure 2. — Mean heights of Norway spruce clones propagated from one to five cycles.

Table 3. — Analysis of variance for height growth.

Larger sample

Source	df	MS	F	%
P	4	3508.8	2.95*	1.4
C (P)	365	1191.4	9.84***	30.2
T(C(P))	7068	121.1		68.4

Smaller Sample

Source	df	MS	F	%
P	4	57.73	0.59	0
C(P)	45	97.31	2.02**	25.4
T(C(P))	100	48.09		74.6

P < .10 *
P < .01 **
P < .001***

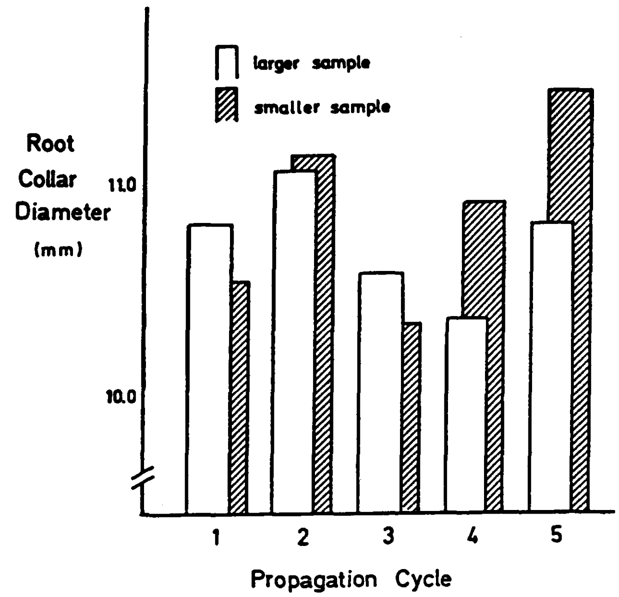

Figure 3. — Mean root collar diameter of Norway spruce clones propagated from one to five cycles.

Table 4. — Analysis of variance for root collar diameter.

Larger sample

Source	df	MS	F	%
P	4	81.55	3.41**	o.8
C(P)	365	23.9o	3.93***	12.7
T(C(P))	7,o68	6.o8		86.5

Larger sample with covariance analysis using height as the independent variable.

Source	df	MS	F	%
P	4	1o.68	o.73	o.2
C(P)	365	14.55	5.34***	17.8
regression	1	2373o.9o	87o7.64***	
T(C(P))	7,o67	2.73		82.o

Smaller Sample

Source	df	MS	F	%
P	4	5.91	1.63	2.4
C(P)	45	3.63	1.27	8.o
T(C(P))	1oo	2.86		89.6

P < .1o *
P < .o1 **
P < .oo1 ***

Root collar diameter

Root collar diameter was correlated with height (r = 0.74) and therefore trends in both traits were similar (*Figure 3*). Root collar diameter decreased from the second to the fourth propagation cycle, then increased in the fifth cycle to the level found for the first cycle. Significant differences were found for propagation cycles (p < .01), but cycles only accounted for 0.8 percent of the total variation (*Table 4*).

Because of the strong correlation between root collar diameter and height, the analysis of covariance using height as the independent variable differed from the analysis of variance (*Table 4*). Differences between cycles were no longer significant and cycles only accounted for 0.2 percent of the variation. No trends existed in the adjusted means for propagation cycles. Root collar diameter of trees in the smaller sample did not differ significantly among phases, nor among clones (*Table 4*). The correlative influence of height on root collar diameter was not completely eliminated, but conclusions from the covariance analysis were the same.

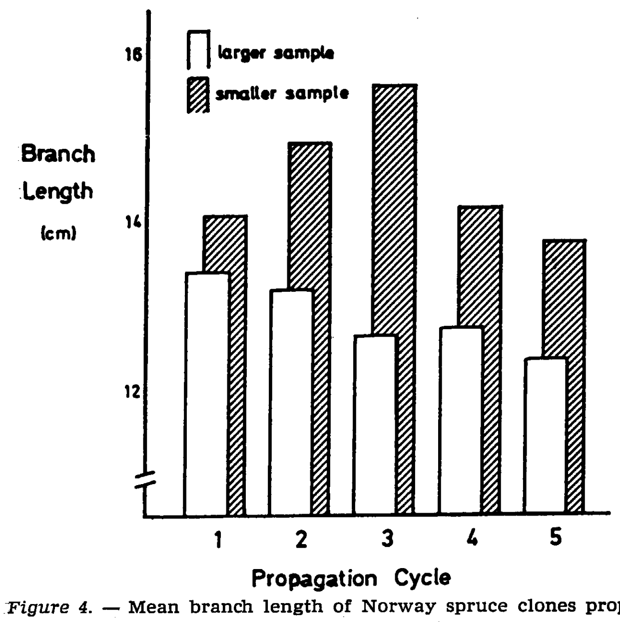

Figure 4. — Mean branch length of Norway spruce clones propagated from one to five cycles.

Table 5. — Analysis of variance for branch length.

Larger samples

Source	df	MS	F	%
P	4	256.62	3.59**	1.4
C(P)	365	71.46	7.25***	23.4
T(C(P))	7.o68	9.86		75.2

Smaller sample

Source	df	MS	F	%
P	4	17.66	1.27	3.8
C(P)	45	13.95	2.67***	34.4
T(C(P))	1oo	5.22		61.8

P < .1o *
P < .o1 **
P < .oo1 ***

Branch length

Branch length among trees in the larger sample decreased slightly from the first to the fifth propagation cycle (*Figure 4*). This may be indicative of decreasing vigor with increasing propagation cycle. Although a significant difference was found between cycles (p < .01), cycles, again, accounted for very little of the total variation, only 1.4 percent (*Table 5*). The smaller sample does not follow the same trend, and the analysis of variance indicated no significant cycle differences.

Tropism, habitus and form

Scores for tropism, habitus and form are expected to increase with increasing maturation state of the donor plant, indicating a worsening of form and a tendency of the plant to be more branch-like (Roulund 1975). Tropism, habitus and form were favourable among cuttings from all five propagation cycles (*Figure 5*). Significant differences between cycles existed within the larger sample (*Table 6*; p < .001) with a slight increase in scores between the first and fourth cycles. However, the scores were so low that any differences were biologically insignificant. Moreover, propagation cycle accounted for only 1.0, 1.0 and 1.4 percent of the total variation in tropism, habitus and form, respectively. The analysis of variance for the smaller sample indicated no significant differences between cycles.

Dry weight of roots, leader and branches

The fresh and dry weights of roots, leader and branches were measured only in the smaller sample. Since fresh and dry weights were highly correlated (r ≧ 0.97), only the results from dry weights are presented. Differences between cuttings and seedlings indicate that leader weight may be expected to decrease relative to branch weight with increasing maturation state (Kleinschmit 1978). No significant differences were found between propagation cycles in the dry weights of roots, leader, or branches (*Table 7*), and no trends were evident (*Figure 6*). Therefore, no evidence for maturation could be found.

Number of first and second order branches

Differences between seedlings and cuttings indicate that cuttings of comparable height have less first order branches and more second order branches(Kleinschmit and Schmidt 1977, Kleinschmit 1978). Significant differences were found between propagation cycles in the number of branches of first and second order (*Table 8*; p < 0.1 and p < .05, respectively). In addition, cycles accounted for 11.0 and 11.2 percent of the total variation in number of first and

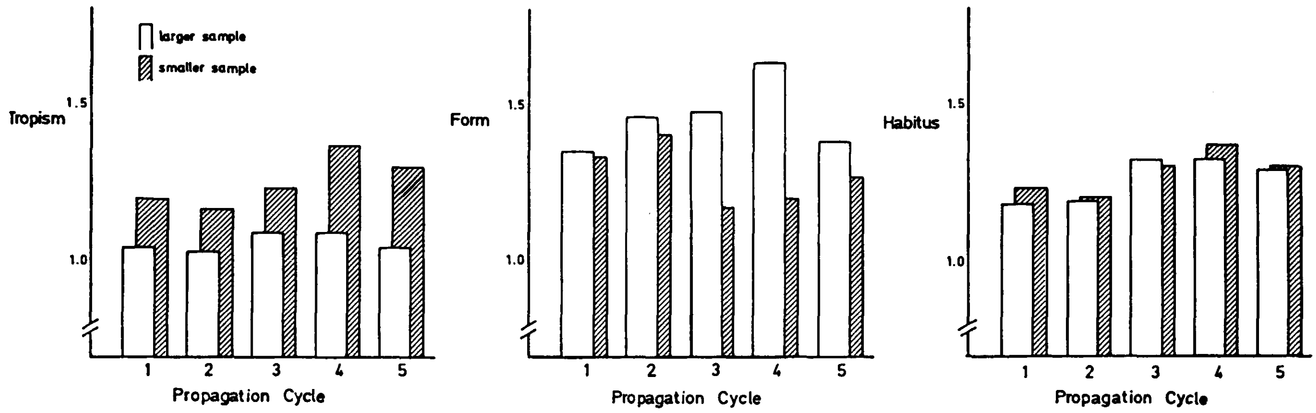

Figure 5. — Mean scores for tropism, habitus, and form of Norway spruce clones propagated from one to five cycles.

second order branches, respectively. This is considerably more than the percent of the total variation found between cycles in the other traits. However, trends were not evident that indicate cuttings propagated five cycles had less first order branches and more second order branches than cuttings propagated fewer cycles *(Figure 7)*.

Percent rooted

The percent of cuttings rooted was high for all five propagation cycles, between 70 and 80 percent *(Figure 8)*. Rooting percentage decreased somewhat from the first to third propagation cycle, but then increased again in the fourth and fifth cycles. No effect of propagation cycle on rooting percentage is evident and cuttings appear to con-

Table 6. — Analysis of variance for tropism, habitus and form.

Larger sample

		tropism			habitus			form		
Source	df	MS	F	%	MS	F	%	MS	F	%
P	4	o.75o	8.56***	1.1	1.o4o	1o.12***	1.9	1.943	8.67**	1.4
C(P)	365	o.o18	1.97***	4.6	o.1o3	3.o7***	9.1	o.226	2.51***	6.9
T(C(P))	7.o68	o.oo9		94.3	o.o33		89.o	o.o3o		91.7

Smaller sample

		tropism			habitus			form		
Source	df	MS	F	%	MS	F	%	MS	F	%
P	4	o.o42	o.86	o	o.o19	o.28	0	o.o34	o.45	0
C(P)	45	o.o49	2.36*	36.7	o.o7o	2.65***	31.3	o.o76	1.16	7.1
T(C(P))	1oo	o.o21		63.3	o.o26		68.7	o.o66		92.9

P < .1o *
P < .o1 **
P < .oo1 ***

Table 7. — Analysis of variance for dry weight of roots, leader, and branches.

Source	df	MS	F	%
		dry weight-roots		
P	4	39.22	1.55	2.1
C(P)	45	25.37	1.34*	1o.o
T(C(P))	1oo	18.94		87.9
		dry weight-leader		
		MS	F	%
		22.22	o.82	0
		27.18	1.41*	12.1
		19.24		87.9
		dry weight-branches		
		MS	F	%
		2oo.35	1.28	1.1
		156.6o	1.36*	1o.7
		114.79		88.2

P < .1o *
P < .o1 **
P < .oo1 ***

Table 8. — Analysis of variance for number of first and second order branches.

		1^{o} branches			2^{o} branches		
Source	df	MS	F	%	MS	F	%
P	4	6o1.8	4.14**	11.o	8832.7	3.o7 *	11.2
C(P)	45	145.3	1.3o	8.2	2876.6	3.14 **	37.o
T(C(P))	1oo	111.5		8o.8	916.7		51.8

P < .1o *
P < .o1 **
P < .oo1 ***

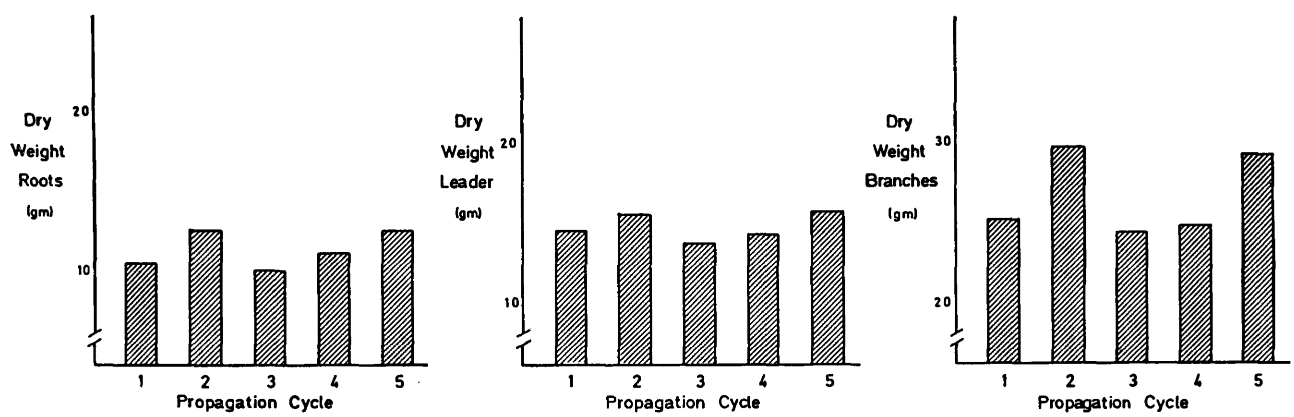

Figure 6. — Mean dry weight of roots, leader, and branches of Norway spruce clones propagated from one to five cycles (smaller sample only).

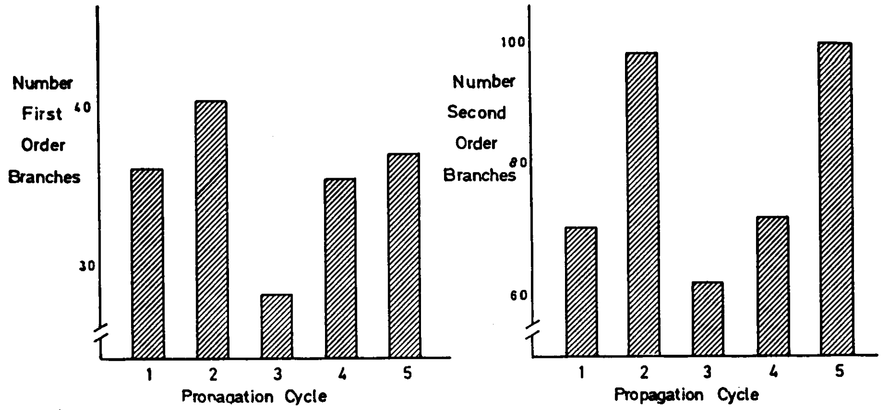

Figure 7. — Mean number of branches of first and second order for Norway spruce clones propagated from one to five cycles (smaller sample only).

tinue to root easily, at least through five propagation cycles.

Conclusions

Serial propagation appears to have at least considerably slowed, and perhaps arrested, maturation processes in Norway spruce. From a practical point of view, there doesn't seem to be any restriction for repropagation at least up to the fifth cycle, which corresponds to an age of the original ortet of 16 years. At this age clonal performance can be judged quite well and further changes in rank are minor (Kleinschmit *et al.* 1978). This study will be followed to higher propagation cycles to see if observed tendencies become significant. Further analysis will use a standard set of clones to be propagated each cycle in order to eliminate bias due to selection. In addition, the material used in this study will be followed in the field to see if tendencies observed at 4 years become significant at later ages. It would be of advantage to be able to directly mass propagate superior trees, and to directly rejuvenate clones that may have matured in spite of serial propagation. Several techniques of rejuvenation are now being developed. These include serial propagation (Fielding 1964; Black 1973; Dormling and Kellerstam 1981), severe pruning of mature ortets (Black 1973; Franclet 1979; Dormling and Kellerstam 1981; Copes 1983), repeated regrafting (Franclet 1981), and growth of mature ortets under various cultural treatments (Franclet 1979; Dormling and Kellerstam 1981).

Different characters may respond variably to rejuvenation treatments. Although better rooting, for example, may be indicative of a more juvenile state, other characters may indicate that only a partial rejuvenation was achieved. Furthermore, partial rejuvenation may be a result of an improved physiological condition of the plant, and not a result of true ontogenetical rejuvenation. Full rejuvenation in the absence of meiosis is uncertain. However at least one example in plants of apparent complete rejuvenation exists using tissue culture techniques. Mullins *et al.* (1979) has induced the juvenile form of an ancient clone of the grapevine following *in vitro* culture of shoot tips. In conifers, plantlets have been produced from older plant material in western red cedar (Coleman and Thorpe 1977), redwood (Franclet 1979) and maritime pine (Franclet *et al.* 1980). An the case of redwood and maritime pine, *in vitro* propagation was proceeded by various cultural treatments of the donor plant, and the expression of juvenile morphology varied according to the pretreatment.

Even if maturation should occur in later propagation cycles and techniques of rejuvenation were not effective, the gain associated with the knowledge of clonal performance would not be lost. Norway spruce begins producing cones at 20 to 30 years. If maturation effects have become significant by this age, little time is lost using clonal information to conduct controlled crosses between proven performers. New clonal varieties can then be propagated from the improved seedlings. Only a few crosses are necessary since large numbers of ramets per clone can be generated quickly using serial propagation. Information from clonal tests includes the sum of additive and non-additive genetic effects. Controlled crosses would result in the loss of favorable genetic interactions resulting from non-additive effects. Other favorable genetic interactions would be generated, but would only become apparent after another round of clonal tests.

Serial propagation has several advantages for use in large-scale vegetative propagation. First, large numbers of ramets per clone can be produced quickly. Rauter (1979) has used short-cycle serial propagation to increase the amount of black spruce planting stock rapidly. Second, new material can be integrated into a clonal program with ease, including new selections, material from breeding work, and recently rejuvenated clones. This enables a possible

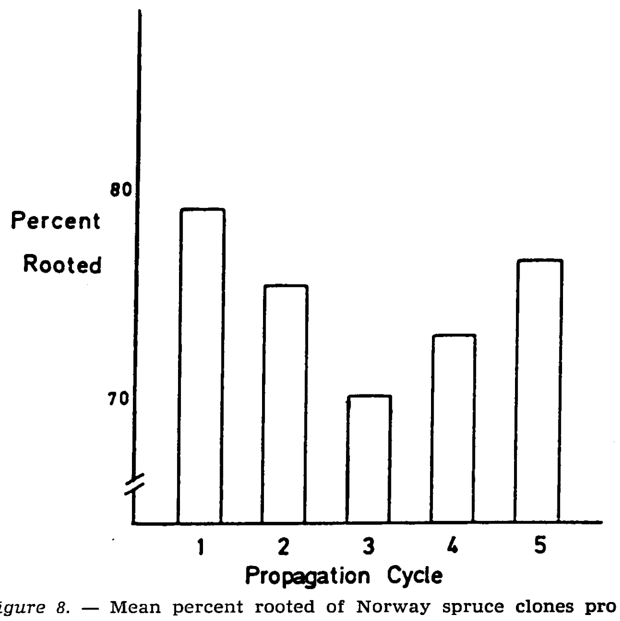

Figure 8. — Mean percent rooted of Norway spruce clones propagated from one to five cycles.

shift in clonal composition in response to new selection goals, or in order to increase genetic diversity. Third, serial propagation permits large initial numbers of clones with subsequent use of large selection differentials. Large numbers of clones can be dropped from further propagation with little loss in investment, because after propagation, all material is used in clonal tests or as planting stock. Hedge orchards, however, must be managed for several years before large numbers of cuttings can be obtained, and when clones are dropped from the program, the investment in managing a hedge that is no longer used is lost. This is of little consequence when working with small numbers of clones, but as the number of clones increases, so does the problem. Finally, serial propagation appears to be an effective technique in Norway spruce to slow, and possibly even arrest, maturation processes.

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