chore region, rather than the secondary constriction, contains the nucleolar organization region in addition to the microtubule attachment site. Plant species with unusually long kinetochore regions believed to contain the microtubule attachment site and nucleolar organizer region have been previously reported (Hunziker, 1961; Khoshoo and Ahuja, 1963; Kurita, 1953, 1960; LaCour, 1950; Sato, 1942). Meiosis of *Cryptomeria* populations with and without secondary constrictions will have to be studied to ascertain the position of the nucleolus organizer region.

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Clonal selection in Larix laricina. I. Effects of age, clone and season on rooting of cuttings

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(Received 30th September 1983)

Summary

Experiments were conducted with 50 clones of tamarack (*Larix laricina* [Du Roi] K. Koch) of 4 age classes ranging from 3 to 10 years, from which cuttings were taken and struck at 4 dates between May and August. The rooting medium was a mixture of peat and vermiculite kept in styro-blocks, and the cuttings were treated with a rooting hormone and irrigated by intermittent mist. Cuttings when struck were characterized by a distinct phenological state. Assessments after 3 months included rooting percent, percent of cuttings with major roots (more than 3 cm long), number of major roots per cutting, length of the longest root, and shoot phenology. Analysis of variance indicated

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significant differences among clones, dates and ages as well as the interactions. The broad-sense heritabilities for rooting percent ranged from 0.27 to 0.40 for the different dates. Mean values of rooting ranged from 48 to 77 percent at the 4 dates, with best rooting from the 22 July set, which was characterized by lignification of the current-years shoot at the base and a developing bud. In practice, a July rooting date is too late for overwintering of the stock outside and an earlier (e.g. May) rooting would be preferable to avoid overwintering of the cuttings in heated greenhouses.

Key words: early selection, vegetative propagation, stem straightness, growth, shoot phenology.

Zusammenfassung

Versuche zur Stecklingsbewurzelung von *Larix laricina* werden beschrieben. Das Versuchsmaterial bestand aus insgesamt 50 Klonen in 4 Altersstufen zwischen 3 und 10 Jahren, die an 4 verschiedenen Terminen zwischen Mai und August gesteckt wurden. Als Substrat diente eine Mischung von Torf und Vermikulite in Styroblocks. Die Stecklinge wurden mit einem Wuchsstoff behandelt und automatisch besprüht. An jedem Termin des Steckens befanden sich die Stecklinge in einem bestimmten phänologischen Zustand. Nach 3 Monaten wurden die folgenden Merkmale erfaßt: % der bewurzelten Stecklinge, % der Stecklinge mit langen Wurzeln (> 3 cm), Zahl der langen Wurzeln pro Steckling, Länge der längsten Wurzeln, und Phänologie des Triebes.

Die Varianzanalyse ergab signifikante Unterschiede zwischen Klonen, Terminen, Altersstufen sowie auch für die Wechselwirkungen. Die Heritabilität im weiteren Sinne (H^2) für das Bewurzelungsprozent schwankte zwischen 48% und 77% für die 4 Termine. Die beste Bewurzelung wurde am 22. Juli erzielt; zu jenem Zeitpunkt sind die Stecklinge an der Basis leicht verholzt und eine Knospe entwickelt sich. In der Praxis wäre jedoch ein Juli-Datum als Stecktermin nicht optimal, da dieser eine Überwinterung im Gewächshaus erfordert, so daß ein früherer Termin (etwa Mai) vorzuziehen wäre.

Introduction

Larix laricina (Du Roi) K. Koch, tamarack, is distributed in North America from the Atlantic Coast to Alaska and from the Mackenzie Delta and Hudson Bay to the Lake States and Pennsylvania (Fowells 1965). It is a pioneer species found on many sites after cutting or fire, but its frequency is highest in wet sites such as swamps and bogs. Here it persists as a result of less competition than on upland sites, and an exceptional tolerance of high soil moisture and low temperature.

Tamarack may flower as early as at six years of age but seed production is often low and irregular and good seed years are infrequent. The cones open immediately after maturity so that all seed is lost within a few days. Cone and seed insects also contribute to its low seed production (Fowells 1965).

Tamarack has never been utilized on a large scale although studies indicate that it is suitable for both pulp and lumber (Mullins and McKnight 1981). Because of its rapid growth on upland sites, there are expectations that it has great potential to rapidly close gaps in wood supply that begin to appear in many areas of eastern North America (MacGillivray 1969, Corriveau and Vallée 1981). To be effective, however, silvicultural programs depend upon reliable sources of seed supply and planting stock improved by selection and breeding.

In the Maritime Provinces of Canada these problems and opportunities have been recognized longer than elsewhere and research with the whole genus *Larix* has been active for about 20 years (MacGillivray 1969, Fowler 1979). This paper describes an experiment that investigates the rooting of cuttings as one of the basic techniques to overcome seed shortages and to give more flexibility to breeding programs.

Review of Literature

The literature dealing with the genetics and vegetative propagation of *Larix laricina* is limited. Several researchers have been concerned with geographic variation and found that the clinal variation pattern typical of many wide-ranging species is also found in this species, and even where stands are isolated, the gene pool is highly variable and unsegmented (Rehfeldt 1970, Cech *et al.* 1977, Riemenschneider and Jeffers 1980). A study of population structure based on a disconnected-diallel mating scheme (Park and Fowler 1982) demonstrated increasing levels of vigor when trees were pollinated by males from successively greater distances in a natural stand. Variance components for specific combining ability were much larger than for general combining ability. The authors concluded that vegetative propagation and clonal selection may have an important rôle to play in the breeding of this species, to capture both additive and non-additive components of variance.

Several of the basic problems in the rooting of cuttings of the genus *Larix* were investigated by Chandler (1960). Propagation under mist is promising and rooting of green softwood cuttings in summer is more successful than rooting of dormant cuttings in winter. During the month of June, when shoots are growing most rapidly, rooting is least successful. Working with hybrid larch *(Larix × eurolepis* Henry), John (1979) found that if cuttings are to be rooted between August and September, early August gives best rooting. He also pointed out that normal orthotropic growth may be difficult to obtain if the parental trees are more than four years old.

Other workers were more concerned with the rooting environment. From his results with *Larix leptolepis* (Sieb. et Zucc.) Rehder, Wunder (1974) inferred that it is not the very high humidity environment that induces best rooting, but rather a certain moisture stress. Fung (1978), working with cuttings from young seedlings of *L. laricina* that were only eight weeks old, found that 1:1 by volume mixtures of peat and vermiculite or peat and sand were equally effective. Instead of installing mist systems, he worked with plastic mini-greenhouses inside of larger greenhouses that possessed effective means of temperature control. The plastic flaps were only opened once or twice a day for watering and to check the temperature. Temperature levels ranged from 18—27° C and natural daylight was sufficient for rooting even in winter. It is clear that Fung worked with plant material of optimum age which was easier to root than materials chosen in most other circumstances.

Objectives

In a selection program for tamarack, stem form and height growth are the principal traits to be improved (Simpson 1982). Stem form variation can probably be recognized at an early age when expected rooting success is high, but variation in height growth observed in natural stands is usually not a good indicator of inherited growth capacity. If selection is done in young stands and plantations, and cuttings are rooted and grown in tests, this approach would take advantage of the rootability of young material as well as the efficiency of clonal tests (LIBBY 1974).

Although it is known that green rather than dormant cuttings root best in the genus *Larix* (CHANDLER 1960), the best time during the growing season and the expected rooting success at different ages still need to be determined.

Therefore, the objective of the experiments to be discussed here was to determine the effect of age and season on the rooting of cuttings of this species.

Methods

In early May, 1981, 10 seedlings or saplings (ortets) were selected in each of 4 age classes (3—4, 5—6, 7—8, 9—10) at Acadia Forest Experiment Station near Fredericton. Selection was on the basis of phenotypic superiority of stem straightness and height growth. Tree ages were estimated by counting bud scars. Ten cuttings were then collected at random from the crown of each ortet on each date, with the exception that the youngest age class yielded only enough cuttings for 2 dates so that 10 more ortets had to be selected for the last 2 dates. All ortets were growing in natural stands - i.e. usually in clearings or along power lines.

Dates and physiological condition were as follows:

(1) 23 May; needles began to flush but shoot extension had not yet begun; most of the cutting consisted of the previous year's wood;

(2) 3 July; cutting consisted of current year's growth, which was succulent;

(3) 23 July; most cuttings lignified at the base, some partially succulent; buds beginning to develop;

(4) 14 August; cuttings lignified and buds set.

On each date, 10 cuttings were removed from each ortet, placed in a plastic bag containing wet sphagnum moss and then held in cold storage for 1 to 2 days until they were struck. The cuttings were prepared by trimming to approximately 8 cm in length, stripping the needles from the basal 4 cm, and dipping the base in water and then a rooting powder (Seradix 3; 3-indolebutyric acid, 0.08%). The rooting medium consisted of a 1:1 mixture of sphagnum peat and vermiculite in styroblock-20 containers.

The experiment was designed such that for each date, the 10 cuttings from a particular ortet were set in 2 rows (plots) of 5 cuttings each which were distributed in a completely randomized experiment.

Difficulties were experienced with the original location chosen for the experiments and therefore the sets for different dates had to be moved to two different greenhouses. These were irrigated by mist propagation systems but humidity and temperature could not be held as uniform as was planned. However, the physiological state of the cuttings at the four dates was so strikingly different that this state was assumed to be more influential than environmental differences. This is supported by the literature on seasonal effects. Fungicides were applied at weekly intervals and fertilizers added beginning one month after the striking date.

The cuttings were assessed three months after striking following removal from the styroblocks. The characters assessed were:

1. *rooting percent*, based on the 5-tree plots, and transformed by arcsin before analysis (STEEL and TORRIE 1980);
2. *percent of cuttings with major roots* (longer than 3 cm) based on the 5-tree plots and transformed by arcsin;
3. *number of major roots* (> 3 cm) per individual cutting, transformed by $\sqrt{x + 0.5}$;
4. *length of the longest root*, based on individual cuttings and transformed by $\sqrt{x + 0.5}$;
5. *shoot phenology based on individual cuttings:* 0, dead; 1, all buds dormant; 2, partially active (2—3 buds burst, needle extension beginning); 3, active (most buds burst, shoot extension in progress).

The data were analysed statistically, first by calculation of means, standard deviations, coëfficients of variation, and subjected to Bartlett's test for homogeneity (STEEL and TORRIE 1980) before transformation. Correlations between the clonal means were calculated for each date separately.

The analyses of variance including all dates were carried out according to the following model:

$$Y_{ijkl} = \mu + D_i + A_j + C_{jk} + DA_{ij} + DC_{ijk} + e_{ijkl}$$

where: Y_{ijkl} = the l^th observation of the k^th clone in the j^th age class on the i^th date;

μ = the overall mean;

D_i = effect of dates (fixed effect), $i = 1 \ldots . 4$;

A_j = effect of ages (fixed effect), $j = 1 \ldots . 4$;

C_{jk} = effect of clones nested within ages (random effect), $k = 1, \ldots . 20$ (or $k = 1, \ldots . , 10$ for age classes with 10 clones);

DA_{ij} = effect of the interaction of dates and ages (fixed effect);

DC_{ijk} = effect of interactions of dates and clones (random effect);

e_{ijkl} = random error, $l = 1, \ldots . , 10$ (number of individual cuttings per clone, or $l = 1, 2$ (number of plots per clone for % variables).

A second series of analyses was carried out to provide for the calculation of variance components and broad-sense heritabilities. This was done separately for each date, firstly, because of the differences in propagation environments for each date, and secondly, because in practice it is likely that a particular batch of cuttings would be taken on the same date for propagation purposes. The model for this analysis was as follows:

$$Y_{ijk} = \mu + A_i + C_{ij} + e_{ijk},$$

where: Y_{ijk} = the k^th observation of the j^th clone in the i^th age class;

μ = the overall mean;

A_i = effect of ages (fixed effect), $i = 1, \ldots . , 4$;

C_{ij} = clones within ages (random effect), $j = 1, \ldots . , 20$;

e_{ijk} = random error, $k = 1, 2$ (plot means) or $k = 1, \ldots . , 10$ (individual cuttings).

The analyses made use of a computer program, RUMMAGE (SCOTT *et al.* 1980) and other statistical packages (ANONYMUS: SAS Institute 1979).

The expected mean squares of both analyses are shown in *Table 1*. The imbalance in the data resulted in unequal expected mean square coefficients for combined analyses and, therefore, approximate F-tests. Variance components were estimated from the analyses of variance for separate dates and broad-sense heritabilities (H^2) calculated:

$$H^2 = \frac{\sigma_C^2}{\sigma_C^2 + \sigma_E^2}$$

where σ_C^2 and σ_E^2 are variance components for clones and within clones, respectively.

Table 1. — The two analyses of variance.

Source	DF[1]	Expected MS with Coefficients[2]	F-test[3]
a) Dates combined (example: rooting percent, based on plot means)			
Dates(D)	3	$\sigma_E^2 + 1.92\ \sigma_{DC}^2 + 0.33\ \sigma_C^2 + 80.00\ \phi_D^2$	MS(D)/MS(DC)
Ages (A)	3	$\sigma_E^2 + 0.25\ \sigma_{DC}^2 + 7.00\ \sigma_C^2 + 80.00\ \phi_A^2$	MS(A)/MS(C)
Clones in A (C)	46	$\sigma_E^2 + 0.42\ \sigma_{DC}^2 + 0.43\ \phi_{DA}^2 + 6.33\ \sigma_C^2$	MS(C)/MS(E)
D x A (DA)	8	$\sigma_E^2 + 2.00\ \sigma_{DC}^2 + 20.00\ \phi_{DA}^2$	MS(DA)/MS(DC)
D x C (DC)	99	$\sigma_E^2 + 2.00\ \sigma_{DC}^2$	MS(DC)/MS(E)
Error (E)	160	σ_E	
b) Dates separately (example: number of major roots, based on individual cuttings).			
Ages (A)	3	$\sigma_E^2 + 10\sigma_C^2 + 100\phi_A^2$	MS(A)/MS(C)
Clones in Ages (C)	36	$\sigma_E^2 + 10\sigma_C^2$	MS(C)/MS(E)
Within clones (E)	60	σ_E^2	

[1] Some degrees of freedom have been lost due to imbalance of the data.

[2] σ^2_C, σ^2_{DC} or σ^2_E, variance due to random effect of C, DC, or E; Φ^2_D, Φ^2_A or Φ^2_{DA}, variance due to fixed effects of D, A or DA.

[3] The F-tests are approximate as a result of unequal expected MS coefficients.

Table 2. — Mean values of rooting characters measured on cuttings collected at four dates from four age classes of ortets. The first two characters are based on plot means, the ~~last~~ two on individual cuttings.

Date of Cutting Collection	Age Class, years									
	3-4	5-6	7-8	9-10	$\bar{x}$	3-4	5-6	7-8	9-10	$\bar{x}$
	(1) Rooting Percent					(2) Percent with major roots				
23 May	68	63	33	28	48	44	42	12	11	27
3 July	66	65	75	52	65	17	24	28	10	20
22 July	90	85	62	70	77	48	52	28	22	38
14 Aug	52	55	46	38	48	9	14	8	2	8
$\bar{x}$	69	67	54	47	59	30	33	19	11	23
	(3) No. of major roots per cutting					(4) Length of longest root, cm				
23 May	1.26	1.21	0.33	0.24	0.76	2.4	2.6	0.9	0.9	1.7
3 July	0.27	0.28	0.44	0.13	0.28	1.5	1.8	1.9	0.9	1.5
22 July	0.99	1.04	0.36	0.33	0.68	2.9	3.3	1.8	1.6	2.4
14 Aug	0.10	0.18	0.08	0.02	0.10	0.9	1.2	0.7	0.5	0.8
$\bar{x}$	0.66	0.68	0.30	0.18	0.46	1.9	2.2	1.3	1.0	1.6

Results

Means

Mean values for rooting percent, percent of cuttings with major roots, number of major roots per cutting and length of the longest root are given in *Table 2*. It is apparent that three of the four characters indicated the best response for 22 July; only the number of roots was slightly higher for the May striking date. For all characters there was a strong decline following treatment in August.

Correlations

Correlation coefficients for all five characters are shown in *Table 3*. Since the trends for all four dates were similar, only the 22 July correlations are presented. The correlation coefficients are all positive and significant at the 1% level, demonstrating that once rooting is initiated, trends are similar in all characters.

Table 3. — Correlation coefficients among all characters from cuttings struck on 22 July, calculated using 40 clone means [1].

Variable	x_1	x_2	x_3	x_4	x_5
x_1 Rooting percent	1.00	+.49	+.44	+.75	+.85
x_2 Percent with major roots		1.00	+.88	+.87	+.61
x_3 No. of major roots per cutting			1.00	+.88	+.55
x_4 Length of the longest root				1.00	+.79
x_5 Shoot phenology					1.00

[1] All coefficients are significant at 1% level (38 d.f.).

Analyses of Variance

The analyses of variance from all dates combined are summarized in *Table 4*. All of the main effects (dates, ages, clones) were significantly different at the 1% level. The interactions were marked by lesser statistical significance in the analyses using plot means: date × age was significant in all cases at least at the 5% level; date × clone was barely significant in two cases at the 5% level. Changes in rank of the clones therefore have taken place, but these were more pronounced for dates × ages than for dates × clones.

Variance Components and Heritabilities

The separate analyses for the four dates have yielded the variance components given in *Table 5*. All clonal effects were significant and age effects were also significant except on 3 July and 14 August. On these dates, rooting percentages were the lowest. On the best date for rooting, 22 July, the within-clone variability (σ_E^2) was relatively large in relation to clonal variability (σ_E^2) so that the values

Table 4. — Analyses of variance for all dates combined.

Source	Rooting Percent			Percent with Major Roots		Number of Major Roots per Cutting			Length of longest Root per Cutting	
	DF	MS	F[1]	MS	F	DF	MS	F	MS	F
Dates (D)	3	9,964	16.1**	9,757	22.6**	3	5.71	17.8**	17.54	24.0**
Ages (A)	3	5,757	4.7**	5,665	5.9**	3	3.67	5.9**	13.43	7.9**
Clones within Ages (C)	46	1,217	3.1**	954	3.4**	46	0.62	6.2**	1.70	6.5**
D x A	8	1,555	2.5*	953	2.2**	8	1.10	3.4**	2.15	2.9**
D x C	99	618	1.6*	431	1.5*	109	0.32	3.2**	0.73	2.8**
Error	160	388		283		1,430	0.10		0.26	

[1] Significance levels: *, 5%; **, 1%.

Table 5. — Variance components and broad-sense heritabilities (H^2) for separate dates.

Date	Rooting Percent			Percent with Major Roots			Number of Major Roots/Cutting			Length of Longest Root/Cutting		
	σ^2_C	σ^2_E	H^2	σ^2_C	σ^2_E	H^2	σ^2_C	σ^2_E	H^2	σ^2_C	σ^2_E	H^2
23 May	262	485	.35	250	407	.38	.079	.173	.31	.141	.346	.29
3 July	206	375	.35	145	293	.33	.010	.069	.13	.070	.243	.22
22 July	95	262	.27	145	269	.35	.030	.151	.17	.045	.322	.12
14 August	286	430	.40	84	147	.36	.004	.023	.15	.047	.164	.22

for broad-sense heritability (H^2) tended to be smaller than for other dates. Of primary interest is the heritability of rooting percent which ranges from 0.27 on 22 July to 0.40 on 14 August. If calculated from the combined analyses, it amounts to 0.18 because of the inclusion of more variance components in the denominator. The former method of calculation is more realistic than the latter inasmuch as, in practice, the best date for rooting would be used in an operational program.

Discussion

In a clonal selection program for any species, reliable techniques of vegetative propagation must be available before the program can be properly planned. Furthermore, a viable clonal selection method would also require the assurance that cuttings or grafts develop normally in subsequent years; clonal tests would not yield adequate data if they were biased by topophytic or cyclophytic effects. In this study we are only concerned with the first aspect, namely the development of reliable rooting techniques. We have concentrated on the effects of clone, age and season.

Clonal effects are documented by the combined analyses of variance *(Table 4)* as well as separate analyses for individual dates *(Table 5)*. There are significant differences for all characters. In addition, the broad-sense heritabilities derived from clone and within-clone variance were substantial *(Table 5)*, particularly for rooting percent. Large differences among clones in rooting ability even within the same age group have frequently been discovered, e.g. by Roulund (1977). Broad-sense heritabilities of rooting characteristics for other species have often been higher than observed here (Mergen 1960, Wilcox and Farmer 1968, Ying and Bagley 1977) but such differences may result from the design of experiments (number of clones, replicates) rather than intrinsically stronger genetic control.

The age effects, too, were well expressed. As expected, the youngest age classes rooted best. The difference between the 3—4 and 5—6 year age classes was slight (67 vs. 69%, see *Table 2)*, possibly because of the thinner branches of the younger trees which as a rule suffered more from weed competition. The general trend of decreased rooting with increased age of parent donor agrees well with the literature (John 1977, Rauter 1982). That cutting diameter plays a rôle has also been observed by Hansen and Tolsted (1981).

The effects of rooting date (season) were strong and significant *(Tables 2 and 4)*. Cuttings struck on 22 July had the highest rooting percent, the largest percentage with major roots, and the longest roots. Although the second highest rooting percent was obtained on 3 July, the three other characters pointed to a more favourable second date in May. Good rooting of shoots that show lignification at the base during mid-summer has also been reported by Wunder (1974) for *Larix leptolepis* while Calvert and Rauter (1979) found good rooting of *Larix decidua* Mill. from cuttings taken early in July. From his studies of *Picea abies* (L.) Karst., Holzer (1972) concluded that root formation potential may follow seasonal patterns of root growth, which is high in spring before shoot extension and again in July before the second period of growth.

Conclusions

1. *Timing.* Green cuttings struck between May and August require three months to root well. Those that are struck at the optimum time, late in July, cannot be assessed until late October at which time it is too late to transplant them outside. They must be overwintered in heated greenhouses, and therefore an earlier (May) rooting would be less costly.

2. *Assessment procedure.* High correlations between shoot development and rooting indicate that rooted cuttings can be effectively identified from their shoot condition so that root examination is not necessary.

3. *Age effects.* The experiments described here were only concerned with root development in the short term. More long-term consequences, particularly on shoot develop-

ment, still need to be determined. Whether stem straightness in the younger age classes of the wild parents was reliably assessed, and also, to what extent cuttings from the older age classes develop straight stems or suffer from plagiotropic growth, remains to be seen. For these reasons, experimentation will be continued and results will be described in subsequent papers.

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A Control Concept of Gene Conservation

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(Received 29th November 1983)

Summary

A new concept is introduced for the joint management of gene conservation and tree breeding programs. The control of yield in an environmental space is defined as the objective and multiple populations are described as the variable elements in both conservation of natural populations and developing breeding populations. The optimization of the array of populations is then suggested to be soluble by the method of control theory. A management strategy, based on these control concepts is then discussed, and includes the use of *in situ* and *ex situ* programs.

Key words: Multiple Populations, Conservation, Diversity.

Zusammenfassung

Es wird ein neues Konzept zur Verknüpfung der Durchführung von Gen-Erhaltung und Forstpflanzenzüchtungsprogrammen vorgestellt. Die Kontrolle des Ertrages in einer bestimmten Umwelt wird als Zielpunkt betrachtet und multiple Populationen werden als variable Elemente sowohl zur Erhaltung natürlicher Populationen als auch entwickelter Züchtungspopulationen angesehen. Die Optimierung einer Reihe von Populationen wird dann durch die Methoden der Kontrolltheorie lösbar. Eine Management-Strategie, die auf diesen Kontrollkonzepten basiert, schließt die Verwendung von *in situ* und *ex situ* Programmen ein und wird diskutiert.

Introduction

Current interest in gene conservation is largely based on economic, esthetic, or other human uses of the biota and not on any inherent values of non-human organisms themselves. While philosophers debate the moral issues surrounding gene conservation (Regan, 1982), this topic is not treated in this paper. I do, however, include among the objectives of gene conservation, not only immediate economic utility, but also maintaining the evolutionary capacity of species to adapt to changing economic and ecological requirements and the viability of the supporting ecosystems.