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Estimation of Genetic and Non-Genetic Parameters for Rooting Traits in Hybrid Larch

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Summary

Two experiments were established in 1992 and repeated in 1993 to study genetic and non-genetic effects on rootability of hybrid larch cuttings. Cuttings from 80 clones of 8 full-sib families were rooted in the first experiment. In the second one, 3 primary ramets from each of 24 clones were used as the source of cuttings. Rooting percentage, stem increment length and in part of the experiments, some more detailed rooting traits were assessed. Both strong clonal and less significant family effects were found on the rootability of cuttings. Importance of genetic control was proved by a high broad-sense heritability based on clone means. A non-genetic effect or 'C-effect' could be an important source of bias in genetic parameter estimation. Low genetic correlations were found between rooting percentage and shoot increment. However stem increment was well correlated with some detailed root system traits.

Key words: Hybrid larch, Larix, vegetative propagation, cutting, genetic parameter, non-genetic effect.

FDC: 165.441; 165.72; 165.7; 181.51; 174.7 Larix.

Introduction

Rooting of cuttings, *i.e.* development of adventitious roots and subsequent development of the aboveground shoot, is a process which can influence subsequent growth of propagules in the nursery and in the forest. Rootability in a broader sense is the ability to develop a new root system and restitute complete and functional new plants. Besides growth traits, rootability is very often an important selection criteria in creation of clonal varieties. Many different factors play an important role in the rooting process (Radosta, 1989). These factors can be divided into 2 broad groups: genetically inherited and nongenetic ones.

Among the genetic factors, clonal variation in rooting has been reported by a number of authors (e.g. Kleinschmit, 1974; Morgenstern et al., 1984; Spethmann, 1986; Bentzer, 1988). Less information has been published about the effect of family. For Picea abies, Skrøppa and Dietrichson (1986) and for Pinus taeda, Foster (1990) reported significant variation in rooting percentage due to a family effect. The second author cited papers giving different findings.

Non-genetic factors influencing rooting of cuttings are represented most frequently by the so-called 'C-effects' (Libby and Jund, 1962). According to Burdon and Sheibourne (1974), 'C-effects' can be divided into maternal effects specific to the individual cutting due to its position (e.g. type, size), and maternal effects caused by the different environmental preconditioning and age of the respective ortet. 'C-effects' are considered a source of possible bias in clonal estimation (Libby and Jund, 1962) so that identification of the non-genetic variation in genetic estimation for rooting of cuttings has been investigated by several researchers.

Wilcox and Farmer (1968) first found for rooting traits in eastern cottonwood significant 'C-effects' estimated from primary ramet effects. Foster et al. (1984) estimated in an experiment with western hemlock that variance in rooting ability due to 'C-effects' represented approximatively one third of the total clonal variance. In another experiment using primary ramets as stock plants for a secondary propagation cycle, they found that nongenetic effects although still significant, were reduced to 2 % up to 6 % of total variation. Farmer et al. (1988, 1989, 1992) also reported low or non-significant 'C-effects' for rooting traits, when cuttings were taken from primary ramets grown in the same environmental conditions.

Within a programme of clonal testing of hybrid larch (*Larix x eurolepis*) in France, 2 experiments were set up in spring 1992 and 1993 to investigate genetic parameters of that clonal population when vegetatively propagated by stem cuttings.

Experiment 1 was designed to estimate genotypic parameters of rooting traits while experiment 2 was set up with the aim to detect possible non-genetic effects which might bias the previous results. Our intention was to examine any common environmental effects of clones connected with the use of individual primary ramets as stock plants.

Materials and Methods

For experiment 1, 8 full-sib families of hybrid larch (*Larix decidua x L. kaempferi*) were used in 1992. They were represented by 10 clones each, randomly chosen without any consideration of their rootability. In 1993, only 54 clones out of the 80 were propagated.

In experiment 2, a subset of 24 clones was chosen from the 80 clones of experiment 1. Their choice depended upon the availability of 3 equally developed primary ramets per clone in the clone bank, which could be used as separate stock plants. The same material was tested in 1992 and 1993.

These 80 clones are part of a larger collection of some 400 clones whose ortets were selected in 2 progeny trials in the INRA Forest Tree Improvement Station nursery at 2 years of age. Two hundred and five of the 400 clones were also propagated in operational rooting trials. For each of the 8 families used in this study, total height at 2 years of the 10 clones covered the whole range of intrafamily variability in the nursery. All the clones — the ortets of which were sown in the spring 1980 or 1981 — were repropagated by cuttings between 1986 and 1987 and planted one year later in a hedged clone bank in the INRA nursery (Orléans, Loiret). Each clone is represented by at maximum 3 ramets of the same age.

Between April 5 and 10, 1992 and 1993 (during the flushing period), 8 cm to 10 cm long cuttings were collected from the 3 primary ramets. Cuttings from the 3 primary ramets were combined in experiment 1, but were kept separate by ramet in experiment 2. Basal tips of cuttings were then dipped in talc powder with IBA (0.1%) and inserted into a peat-sand-bark (40:30:30 by volume) rooting medium. They were rooted under greenhouse conditions with an intermittent mist without bottom heat and additional light. Alternating fungicides (Alliette, Benlate) were sprayed as necessary. A 15N/10P/15K liquid fertilizer (1 g/l) was applied once a week during 7 weeks starting by the end of June.

In 1992, clones were tested in a randomized complete block design, with 7 replications and linear plots of 12 cuttings per clone (or primary ramet) and per replication. As a result of the 1992 experiments, only 4 replications were used for the 1993 experiments with plots of 21 cuttings (3 \times 7). A 5 cm spacing was used. In total, more than 10000 and 8500 cuttings were used for the 2 experiments respectively in 1992 and 1993.

Cuttings were lifted by the end of September 1992 and mid-October 1993 for observation and measurement.

Observations and measurements

Presence or absence of roots, root system quality and length of the current year stem increment were recorded for each cutting. The root system quality was assessed according to a 2 score-scale: 0 = poor rooting quality (1 or 2 primary roots, usually short); 1 = good rooting quality. The percentage of rooted cuttings (coded %R), the frequency of well-rooted cuttings (%WR) and the mean 1992 (1993)-stem increment (SI) were finally determined at the plot level and used for analysis.

To evaluate the efficiency of measurement of stem increment length as a short-cut for assessment of rooting quality, a detailed study of the root system was conducted in 1992 including: the length of the longest root, number and total length of all primary roots, average root length and dry weight of all roots. These parameters were then correlated with the length of the 1992-stem increment. A sample of 117 rooted cuttings (4 clones) were examined for this correlation analysis.

Statistical analysis

Analysis of variance was performed on plot means. The following model was used to test differences among families and clones in experiment 1:

$$Y_{ijkl} = \mu + B_i + F_j + C_{k(j)} + \varepsilon_{ijkl}$$
 Model 1 (M1)

where

 B_i = effect of block i;

 F_j = effect of family j;

 $C_{k(j)}$ = effect of clone k nested in family j:

 $\varepsilon_{ijkl} = error.$

In Experiment 2, the model was as follows:

$$Y_{ijkl} = \mu + B_i + C_j + R_{k(j)} + \varepsilon_{ijkl}$$
 Model 2 (M2)

where

 B_i = as defined above;

 C_j = effect of clone j;

 $R_{k(j)}$ = effect of primary ramet k nested in clone j;

 $\varepsilon_{ijkl} = error.$

To detect the influence of 'C-effects' on genetic parameters, a third model was used in which primary ramet source was confounded with clone source (Model 3, M3).

All sources of variation were considered as random. Variance components were estimated using Henderson III's method with Amance computer programs (Bachacou et al., 1981).

Broad-sense heritability equal to

$$H^{2}_{G} = \sigma^{2}_{G}/\sigma^{2}_{Pc} = (\sigma^{2}_{A} + \sigma^{2}_{NA})/\sigma^{2}_{Pc}$$

where

 σ^2_{Λ} = additive variance and;

 $\sigma^2_{\rm NA} = \text{non-additive variance};$

 $\sigma^2_{
m PC}~=~{
m phenotypic}$ variance of clone mean

was computed on clone means for each trait in experiment 1 as

$$H_{C}^{2} = (\sigma_{F}^{2} + \sigma_{C}^{2})/(\sigma_{F}^{2} + \sigma_{C}^{2} + \sigma_{w}^{2}/k_{c})$$

where σ^2_F , σ^2_C , $\sigma^2_w =$ variance component due to family, clone within family and error and $k_c =$ expected mean square coefficient of clone within family.

In experiment 2, H²_G was estimated by

$$H_{G}^{2} = \sigma_{C}^{2}/(\sigma_{C}^{2} + k_{r}.\sigma_{R}^{2}/k_{c} + \sigma_{w}^{2}/k_{c})$$

where $\sigma^2_{\rm C}$, $\sigma^2_{\rm R}$, $\sigma^2_{\rm w}=$ variance component due to clone, primary ramet within clone and error and $k_{\rm r}$, $k_{\rm c}=$ expected mean square coefficient of primary ramet and clone; MS = mean square.

Standard errors of variance components as well as of heritability were computed following Namkoong (1979).

Expected gains were then estimated by

$$\Delta_G = i. H^2_G. \sigma_{Pc}$$

and expressed as a percentage of clone means.

Results and Discussion

Rooting of cuttings

The average rooting percentage in experiments 1 and 2 was 41.5 % and 39.4 % respectively in 1992 and 1993. Within rooted cuttings, 69.4 % in 1992 and 79.0 % in 1993 of them were assessed as 'well rooted'. The average stem increment during the rooting period was 8.8 cm long in 1992 but a bit less in 1993: 6.0 cm. As many different factors influence rootability of cuttings, the general results

Table 1. - Rooting and current year-stem increment characteristics (Experiment I).

		1992		1993			
	%R	%WR	SI	%R	%WR	SI	
	(%)	(%)	(cm)	(%)	(%)	(cm)	
Clonal mean	41.5	69.4	8.8	39.4	79.0	60.1	
Phenotypic standard deviation	16.1	14.1	2.1	15.4	19.8	15.6	
Range of clone means	3.6-73.8	0.0-98.7	2.5-12.6	0.0-83.7	0.0-100.0	1.1-8.7	

Table 2. - ANOVA for rooting traits (%R and %WR) and length of current year stem increment (SI) (Experiment 1).

		1992				1993								
		%	R	%V	VR	S	I		%	R	%\	WR	5	SI
Sources	D.F.	M.S.	F	M.S.	F	M.S.	F	D.F.	M.S.	F	M.S.	F	M.S.	F
Blocks Families Clones Error	6 7 72 731	0.268 0.909 0.189 0.037	6.089*** 4.815*** 5.104***	0.825 0.536 0.163 0.087	9.459*** 3.288** 1.872***	22.454 164.279 32.966 12.148	1.848 ^{ns} 4.983*** 2.714**	3 5 48 351	0.114 0.835 0.313 0.024	4.761** 2.662* 13.099***	0.713 0.104 0.136 0.040	18.039*** 0.768ns 3.432***	1906.254 3306.493 1345.775 244.235	7.805*** 2.457* 5.510***

^{*, **, *** =} significant at $\alpha = 0.05$, 0.01 and 0.001

Table 3. — Estimated variance components (standard errors) and their relative percentage of total variance ($\% = \sigma^2_{TD}$) (Experiment 1)).

	1992					1993						
•	•	%R	%WR		S	I	%R		%WR		SI	
Variance component	Est.	σ^2_T	Est.	$%\sigma^{2}_{T}$	Est.	$%\sigma^{2}_{T}$	Est.	$%\sigma^{2}_{T}$	Est.	$% \sigma^{2}_{T}$	Est.	$%\sigma^{2}_{T}$
σ_{B}^{2}	0.002 (0.001)	3.3	0.006 (0.003)	6.1	0.089	0.6	0.001 (0.001)	1.3	0.007 (0.005)	12.0	18.164 (13.178)	4.0
σ_F^2	0.007 (0.004)	10.8	0.003 (0.002)	3.3	1.223 (0.767)	7.9	0.006 (0.007)	8.8	0.000 (0.001)	0.0	23.919 (28.809)	5.3
σ^2_{C}	0.015 (0.003)	25.3	0.008 (0.005)	7.4	2.116 (0.555)	13.6	0.040 (0.009)	56.2	0.014 (0.004)	23.4	163.729 (40.513)	36.4
σ_{w}^{2}	0.037 (0.002)	60.6	0.087 (0.042)	83.2	12.148 (0.635)	77.9	0.024 (0.071)	33.7	0.040 (0.003)	64.6	244.235 (19.308)	54.3

in rooting can not be directly compared with results of other authors dealing with vegetative propagation of larch (John, 1979; Jacques and Nanson, 1989; Mason, 1989). However, rooting percentages in this study are comparable in 1992 and 1993 and consistent with our results from previous years' experiments with the same material and in the range of published results (Morgenstern et al. 1984).

A wide clonal variation existed for all traits (*Table 1*). The rooting percentage per clone ranged from 3.6 % to 73.8 % in 1992 and from 0 % to 83.7 % in 1993 and the proportion of well rooted cuttings per clone varied from 0 % to 100 %. A high clonal variation for rooting traits is reported for many species such as Norway spruce (Kleinschmit and Schmidt, 1977), eastern larch (Morgenstern et al., 1984), loblolly pine (Foster, 1990), western hemlock (Pounders and Foster, 1992) and poplar (Farmer et al., 1989).

Choice of clones

Based on rooting success, the random sample of clones used in experiment 1 did not differ appreciably from the wider population. A Kolmogorov-Smirnov test (Dagnelie, 1975) confirmed that result (DN = 0.172 with an approximate significance level = 0.067). The set of 80 clones can thus be considered as representative of the original clone collection.

Genetic effects

Highly significant differences between clones within family were observed for rooting traits and stem increment in experiment 1 (Table 2). Significant differences were found too between families but probability levels were lower in 1993 than in 1992 and for %WR compared to %R or SI. Block effect was significant for rooting characteristics (%R, %WR) but non-significant for stem increment length in 1992 (SI). Allocation of variance components (Table 3) confirmed the family and above all clonal influence on all assessed traits. The total genetic contribution to total variation accounted for more than 36 % for the percentage of rooting (%R), 22 % for SI and 11 % for %WR in 1992. In 1993, these values were even higher with respectively 65 %, 42 % and 23 % for %R, SI and %WR. For all traits, total genetic effects were superior to block effects. Clonal variation was always predominant over family variation. For rooting percentage, it accounted for 25.3 % (65 % in 1993) of total variation which was more than twice (6 times in 1993) the variation owing to the family effect. The family component of variation was particularly negligible for the quality of the root system (%WR) over the 2 years.

The importance of clonal effects on the rooting of hybrid larch agrees with the results of other authors for

Table 4. — ANOVA for rooting traits (%R and %WR) and length of current year stem increment (SI) (Experiment 2).

1992						1993					
		%R	%WR	SI		%R	%WR	SI			
Sources	D.F.	M.S. F	M.S. F	M.S. F	D.F.	M.S. F	M.S. F	M.S. F			
Blocks Clones Ramets Error	6 23 47 403	0.172 5.754*** 0.304 1.917* 0.159 5.306*** 0.030	0 10g 2 001 TTT	11.947 1.116 ^{ns} 55.472 3.113*** 17.817 1.664** 10.704	3 23 48 213	0.109 4.156** 0.435 12.252*** 0.035 1.354(*) 0.026	0.455 12.847*** 0.079 2.883** 0.027 0.769ns 0.035	1839.565 8.262*** 1812.481 5.480*** 330.752 1.846**			

 $(*, *, **, *** = significant at \alpha = 0.06, 0.05, 0.01 and 0.001$

Table 5. — Estimated variance components (standard errors) and their relative percentage of total variance ($\%\sigma^2_{T}$) (Experiment 2).

	1992					1993					
37	%R	%WF	s s	I	%	R	%	WR	SI		
Variance component	Est. $%\sigma^2$	T Est. %	σ ² _T Est.	$%\sigma^{2}_{T}$	Est.	%σ ² 1	Est.	$%\sigma^{2}_{T}$	Est.	$%\sigma^{2}_{T}$	
σ^2_B	0.002 3.6 (0.001)	0.009 9	0.018		0.001	1.8	0.006 (0.004)	13.5	23.895 (17.196)	5.9	
σ ² c	0.007 12.5 (0.004)	.	7.5 1.884 (0.806)	13.8	0.033	52.9	0.004 (0.002)	9.7	129.382 (45.183)	32.0	
σ_R^2	0.019 32.7 (0.005)	(0.002)	0.0 \big(1.054) (0.545)		0.002 (0.002)	3.7	0.000 (0.002)	0.0	28.434 (18.349)	7.0	
σ_{w}^{2}	0.030 51.2 (0.002)	0.073 82 (0.005)	2.6 10.704 (0.752)		0.026 (0.003)	41.6	0.035 (0.004)	76.8	222.644 (22.154)	55.1	

larch (e.g. Morgenstern et al., 1984; Farmer et al., 1992; Pâques, 1992) or other conifers (e. g. Foster, 1978; Pounders and Foster, 1992).

The family effect on rootability is more controversial. Foster (1990) reported nonsignificant variance due to the male x female interaction in loblolly pine and cited other papers confirming very low or negligible family variation in rooting (Foster, 1978; Sorensen and Campbell, 1980). By contrast, Greenwood and Nussbaum (1981) with loblolly pine and Skrøppa and Dietrichson (1986) with Norway spruce obtained a significant family effect in rooting of cuttings. Foster (1990) suggested there may be different genetic mechanisms governing rooting ability in respective populations.

'C-effects'

Primary ramets proved to be a significant source of variation for rooting percentage and length of stem increment in 1992 (Table 4). For rooting percentage, this kind of 'C-effect' was a very important variation component, nearly three times more than the clonal portion of total variance (Table 5). In contrast with the high 'C-effect' component of variation for total rooting percentage, no similar effect was observed for %WR (Table 5). This trait was probably mostly influenced by the rooting environment as can be seen from the error and block effects.

In 1993, a similar trend was detected: significant differences between primary ramets were observed for SI but not for %WR as in 1992. For rooting percentage (%R), the primary ramet effect was close to be significant at $\alpha = 0.05$. But probability levels and contribution of primary ramets to total variation were much lower than in 1992.

In contrast to 1992, results from our 1993 experiment on 'C-effect' on rooting of hybrid larch are comparable to the findings of other authors. FARMER et al. (1992) obtained

negligible (11 % of total variance less replication variance) or even no primary ramet effect on rooting percentage of tamarack (*Larix laricina*). Primary ramets within clones constituted a significant source of variation for rooting of western hemlock (Foster *et al.*, 1984) but it remained a minor source of variation (6 % of total variation) as it represented the fifth of the clone variance component.

But according to the years, it is clear that 'C'-effects could be a major source of variation or a negligible one for rooting percentage; it has always been negligible for rooting quality but consistently high for the first year development of the stem.

A different environmental pre-conditioning of stock plants (primary ramets) prior to re-propagation is a possible partial explanation for such differences in the relative importance of 'C-effect'. In Farmer et al. (1992) and Foster et al. (1984)'s studies, primary ramets were potted and grown in comparatively uniform environmental conditions while in our study, they were directly outplanted in the nursery and raised in less uniform conditions. The microsite effect could be important. The age of primary ramets at time of secondary propagation differed too; they were 2.5-year old in Farmer et al.'s study, 4-year old in Foster et al.'s one and between 7- and 8-year old in our experiment.

Heritability and genotypic gains

Broad-sense heritabilities on clone means are given in $table\ 6$ for rooting and stem increment traits in experiments 1 (M 1) and 2 (M2 and M3). Total genetic variance was used in the numerator as explained previously. Genotypic gains were then estimated using a selection intensity of 10 %.

In experiment 1, for the whole population of 80 clones structured into families (M1), clonal selection appeared to be particularly efficient for rooting traits. Rooting per-

Table 5. — Compared estimated broad-sense heritabilities and expected genotypic gains for models M1 M2 and M3 (see text).

		1992			1993	
	%R	%WR	SI	%R	%WR	SI
Genotypi	c variance (σ ²	$_G$ in % σ^2_T)				
Ml	36.1	10.7	21.5	65.0	23.4	41.7
M3 M2	22.5 12.5	7.1 7.5	16.1 13.8	53.9 56.5	8.5 9.7	33.9 32.0
Phenotyp	ic standard de	viation of clone m	ean (σ_{Pc})			
M1	16.1	14.1	2.14	22.1	14.2	1.50
M2,M3	12.3	9.9	1.67	19.0	8.3	1.26
Broad-se	nse heritability	(H^2_G) and stand	ard deviation			
Ml	0.854 (0.033)	0.555 (0.087)	0.730 (0.061)	0.933 (0.014)	0.709 (0.059)	0.838 (0.036)
М3	0.857 (0.043)	0.631 (0.112)	0.794 (0.062)	0.936 (0.019)	0.569 (0.128)	0.865 (0.040)
M2	0.478 (0.188)	0.675 (0.117)	0.679 (0.116)	0.918 (0.016)	0.653 (0.119)	0.818 (0.064)
Genotypi	c gain (ΔG) an	d ΔG (in % of cla	ne mean)			
M1	24.1 58.0%	13.8 19.9%	2.74 31.0%	36.3 92.0%	17.7 22.4%	2.20 36.6%
М3	18.6 36.6%	10.9 15.3%	2.32 23.9%	31.3 79.3%	8.3 10.5%	1.91 31.8%
M2	10.3 20.4%	11.7 11.4%	1.99 20.5%	30.7 77.8%	9.5 12.0%	1.81 30.0%

centage was highly heritable at the clone level (over 0.85) and a high genotypic gain of more than 24 % in rooting is expected through clonal selection due both to a high level of heritability and an important clonal variability. For the percentage of 'well rooted cuttings' (%WR), the level of heritability and clone variability is less important but the estimated gain remains non negligible as 13.8% in 1992 and 17.7 % in 1993 additional 'well rooted cuttings' per clone are expected. Clonal heritability was still important for stem increment length (SI).

These levels of genotypic heritability for rooting ability were about 2 to 3 times higher than those reported by Morgenstern et al. (1984) for rooting percentage with Larix laricina (between 0.27 and 0.40 according to date of propagation). However similar levels were found for other species such as western hemlock by Foster et al. (1984) (0.87) and by Pounders and Foster (1992) (0.72). However, as suggested by Foster (1990) and Pounders and Foster (1992), these values must be considered as a maximum and are probably overestimated when derived from experiments confounding clone x environmental effects, such as different dates or sites of propagation. Overestimation can be as high as 30 %. If this is confirmed, our results would be overestimated too, but in any case, still substantial gains in rooting can be expected.

Compared to those from model M1, genotypic parameters and gains in experiment 2 (model M3, *Table 6*) were very similar in size but estimated with a lower statistical precision since the number of clones (24) under test in ex-

periment 2 was a sub-sample of the population tested in experiment 1 (80 clones).

When genetic parameters estimates from model 2 (M2) -distinguishing clonal and primary ramets sources are compared with those from model 3 (M3) — where clonal and 'C-effect' sources are confounded, a systematic overestimation of genetic parameters is noted for all traits except for %WR when 'C-effect' source is confounded with clone effects (Table 4). In 1992, estimates of heritabilities were biased upward by 37.9 % for rooting percentage (%R) and by 11.5 % for stem increment (SI). As a result, genotypic gains from clonal selection were inflated as well and passed for example for increase of rooting percentage from 10.3 % to 18.6 %. For the quality of the root system (%R), 'C-effects' related to primary ramets source of variation, were negligible and did not modify either clone variance or heritability and thus the level of expected gain. For stem increment, gain was only slightly reduced. As expected from previous results, in 1993, overestimation of heritabilities was in the range of their standard deviation and therefore, it should not be considered. Genotypic gains were comparable.

Use of primary ramets and subsequent secondary cloning obviously permits more precise estimates of genetic parameters and gains as suggested by Foster *et al.* (1984). As simulated in *table* 7, precise estimates of parameters could be gained as efficiently from reduced experimental designs with 3 to 4 blocks instead of 7. This result justified the change of the experimental design in 1993.

Table 7. — Estimated genetic parameters for rooting percentage for alternative experimental designs (Experiment 2).

	Number of ramets x blocks		σ_{Pc}	н ² _G	ΔG	ΔG (% clone mean)
3	х	7	12.3	0.478	10.3	20.4%
3	x	5	12.5	0.465	10.2	20.1%
3	x	3	13.0	0.429	9.8	19.3%
3	x	2	13.6	0.390	9.3	18.5%
1	x	7	17.5	0.237	7.3	14.4%

Correlations between traits

No significant correlations were found between rooting percentage (%R) and other traits, including quality of the root system (%WR).%R and %WR ($r_{\rm p}=0.20~{\rm ns}$ and $r_{\rm G}=0.27$) are apparently not under the same degree of genetic control and both rooting traits should be considered independently in rooting ability estimation. Stem increment length during the propagation phase (SI) was significantly and positively correlated with the root system quality parameter (%WR): $r_{\rm p}=0.32$ ** and $r_{\rm G}=0.40$, while weakly and non-significantly correlated with the rooting percentage ($r_{\rm p}=0.18~{\rm ns};~r_{\rm G}=0.24$).

Spearman rank correlation was also computed between rooting percentages observed in 1992 and in a previous experiment of 1984 (Cornu, personal communication), for 205 clones common to both propagation dates. The correlation coefficient was positive but nonsignificant ($r_S = 0.15$ ns). No fitting in rooting percentages for 2 different stages of clones — namely 2-year old seedlings in 1984 and 7-year old primary ramets in 1992, indicates high sensitivity of rooting process to at least one another non-genetic effect: cyclophysis. Similar low correlations between clonal rooting percentages over propagation cycles were found in Norway spruce by Kleinschmit (personal communication). If confirmed, this result might seriously affect the efficiency of clonal selection for rooting potential.

Correlation analysis for several rooting traits on 4 clones indicated that stem increment (SI) measurement was a valuable method for assessing root system quality. Indeed, it was well correlated in this study namely with total dry weight of roots ($\mathbf{r}=0.67^{****}$), moderately with the length of the longest root (0.37^{****}) and the total length of all primary roots (0.35^{****}) but weakly with the average root length (0.19^{**}), which depended too on number of roots per cutting (0.29^{***}). Thus stem increment length was considered in this study a proper trait for description of both the aboveground part of the cutting but also of the newly developed root system. Morgenstern et al. (1984) noted as well that shoot phenology observed three months after striking was a good indicator of rooting success, making unnecessary root examination.

Conclusion

The prospective success of clonal forestry depends on effective techniques of vegetative propagation and these techniques are influenced both by genetic and by nongenetic factors. Within genetic ones, the effect of the respective clones on rooting percentage and stem increment of rooting cutting proved to be the most important for hybrid larch. Possible genetic gain considering a 10%-selection intensity — compatible with our aims to create multiclonal varieties of 40 clones selected from our 400

clones collection — could yield a significant increase of rooting percentage in the selected clonal collection. However, selection on rooting ability should finally be applied only if clonal rooting potential proved to be stable over propagation cycles and if it does not alter further growth traits of the selected clonal population.

Non-genetic effects represented in this study by different microsite and environmental conditions of donor plants (primary ramets) were the main source of variation in rooting percentage in 1992; but their importance proved to be variable from year to year as they appeared negligible in 1993. Allowing for 'C-effect' sources seems however essential to obtain precise evaluation of clones and estimation of genetic parameters and gains, especially when primary ramet-donor plants are not pre-conditioned under uniform controlled conditions as in clone banks. Moreover, hybrid larch clones seem to be particularly sensitive to different sources of 'C-effects' such as cyclophysis (Morgenstern, et al., 1984; Greenwood et al., 1989; Pâques and Cornu, 1991) or interaction with other common environmental effects, e.g., season of rooting (Morgenstern et al., 1984).

Rooting traits play an important role not only in the economy of large-scale nursery production, but they can influence further field performance of rooted cuttings (Pâques and Cornu, 1991). Rooted cuttings from the reported experiments were lined out in the nursery and will be assessed for growth and stem form in following years.

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Designs for Genetic Field Experiments with Permutated Neighbourhoods for Genotypes and Planned Systematic Thinnings to Eliminate Competition

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Summary

A modified experimental design with single tree plots was elaborated. This design allows the conduct of observations and measurements of trees over a period of 40 to 50 years in Temperate zone conditions. It is possible to perform systematic thinnings, without changing the design orthogonality, but only reducing the number of replications in the experiment. A permutation of genotype neighbourhoods is maintained throughout. A special design with 2 systematic thinnings and 4 complete replications (blocks) is proposed which can be applied for g genotypes where $g=4\ p$ and $p\geq 4$. In the paper an experimental design for g=20 genotypes is described as an example.

Key words: Quantitative forest genetics, seed orchard designs, modification single tree plot designs, systematic thinnings, replications, field test design for genotypes.

FDC: 165.3; 165.4.

Introduction

The spatial distribution of trees within seed orchards commonly hinders an appropriate assessment of clones or progenies used. This resulted primarily from the fact that at the moment of orchard establishment the number of trees per clone or progeny differed greatly because of technical difficulties connected with the effectiveness of grafting or poor cropping of seed. Secondly, within seed orchards, is not possible to eliminate soil variability because trees of the same genotypes are not distributed in all blocks. Those difficulties still increased after exe-

cution of the 1st systematic thinning. Thirdly systematic seed orchard designs have the same composition of genotypes in neighbourhoods, which may cause bias.

Thus in order to assess the usefulness of clones or progenies used in seed orchards it was necessary to conduct parallel testing experiments. On their basis selection of elite clones for the establishment of 2nd generation orchards is conducted.

There exists a mode of distribution of single-trees, set out by LIBBY and COCKERHAM (1980), into random noncontiguous plots in interlocking field layouts. Individual sub-blocks contain trees from all investigated genotypes planned for removal in the 1st and in the 2nd cutting respectively and to be left until the end of the experiment. A testing experiment or seed orchard set out in such a way allows correct evaluation of genotypes during a period longer than that in experiments arranged in a completely randomized block design with single-tree plots, because it is possible to remove competition between trees through systematic thinnings. Sub-blocks, being in fact specifically designed complete blocks distributed over the whole experimental area, do not exclude soil variability because they contain its full range (LIBBY and COCKERHAM 1980).

An experimental design for 36 genotypes (progenies) allowing 3 systematic cuttings and soil variability evaluation through replicate blocks was elaborated at the Forest Research Institute (Burzynski, 1992a). It was also presented on 17 th September 1992 at the IUFRO-AFOCEL Congress in Carcans (Burzynski, 1992b). It was used to lay out a Douglas fir seed orchard planted in the spring of 1991. This experiment includes a series of trials with 36 geno-

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