

Autumn foliage color variation among inbred jack pine families

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Summary

Observations made in the autumn, 1977 on seventy-one 2-0 jack pine families representing 4 progeny groups — S_2 , $S_1 \times S_1$ -mix, S_1 O.P. and S_0 O.P. — in a nursery near Rhinelander, Wisconsin showed that change in foliage color from green to purple started the second week of October after temperatures had dropped to below freezing on at least 4 days. However, any causal relationship of temperature to autumn foliage coloration could not be determined. Color change was most rapid in late October and early November and was complete by November 11.

Variation in amount of foliage colored was noted among progeny groups during the course of change but was especially pronounced among families within progeny groups. Most variation occurred among S_2 families but variation within families was smallest in the S_2 group. Thus, inbreeding and increased homozygosity results in larger inter- but smaller intra-family variation. This is consistent with genetic theory but not previously clearly demonstrated in forest trees. Crosses among S_1 genotypes result in "heterosis" and full recovery from inbreeding depression.

Correlations between progeny groups were significant in some comparisons but showed an inconsistent pattern, possibly because of the wide variation among families within groups.

No relation between tree height and coloration was found either among or within families. Lack of frost damage or winter injury in the trees studied prevented an evaluation of an earlier postulated relation between amount of purple coloration of foliage and hardiness.

Genotypic variation in potential autumn foliage coloration in young jack pine is clearly demonstrated by the study results. However because the autumn coloration characteristics of the parent trees for the seedlings in this study are unknown, definitive information on the mode of inheritance must await evaluation of current, controlled-pollinated progeny tests of the known coloration phenotypes determined in this study.

Key words: *Pinus banksiana*, selfing, inbreeding, genotypic variation, inbreeding depression, heterosis

Zusammenfassung

An 71 2-0 *Pinus banksiana* Familien, vertreten durch die vier Nachkommenschaftsgruppen S_2 , $S_1 \times S_1$ gemischt, S_1 O.P. und S_0 O.P., wurden in einer Forstbaumschule in der Nähe von Rhinelander, Wisconsin, im Herbst 1977 Beobachtungen zur Änderung der Nadelfarbe durchgeführt. Nachdem die Temperatur mindestens an 4 Tagen unter den Gefrierpunkt gefallen war, begann in der zweiten Oktoberwoche die Änderung der Nadelfarbe von grün nach purpur. Ein kausaler Zusammenhang zwischen Temperatur und Nadelfärbung konnte allerdings nicht nachgewiesen werden. Die Farbänderung geschah am schnellsten Ende Oktober/Anfang November und war am 11. November abgeschlossen.

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Zwischen Nachkommenschaftsgruppen wurde eine Variation der Anzahl der gefärbten Nadeln beobachtet, besonders ausgeprägt war die Variation innerhalb Nachkommenschaftsgruppen. Die größte Variabilität wurde zwischen S_2 -Familien gefunden, innerhalb dieser Familien war die Variabilität am geringsten. Inzucht und erhöhte Homozygotie ergeben somit größere Variabilität zwischen, hingegen kleinere innerhalb Familien. Dies stimmt mit der genetischen Theorie überein, wurde aber für Waldbäume bisher nicht klar bewiesen. Kreuzungen zwischen S_1 Genotypen ergeben „Heterosis“ und völlige Aufhebung der Inzuchtdepression.

Korrelation zwischen Nachkommenschaftsgruppen waren signifikant, zeigten jedoch in einigen Fällen Widersprüche, möglicherweise wegen der großen Variation zwischen Familien in Gruppen.

Beziehungen zwischen Baumhöhe und Nadelfärbung wurden weder zwischen noch in Familien gefunden. Wegen fehlender Frost- und Winterschäden an den untersuchten Bäumen konnte eine früher postulierte Beziehung zwischen dem Ausmaß der Purpurfärbung und der Frosthärte nicht berechnet werden.

Die Untersuchungen demonstrieren deutlich eine genotypische Variation der Nadelverfärbung im Herbst. Da jedoch die Herbstverfärbung der Elterbäume der untersuchten Sämlinge nicht bekannt ist, können Aussagen über den Vererbungsmodus erst nach Auswertung gegenwärtig laufender kontrollierter Kreuzungen zwischen bekannten Färbungsphänotypen gemacht werden.

Introduction

The pink, red, and purple colors of tree foliage in late summer and autumn result from reactions between various sugars and anthocyanidins (KRAMER and KOZLOWSKI, 1979). As temperatures decline and photoperiod decreases chlorophyll production stops and, in some species, anthocyanin production increases, particularly in foliage containing large amounts of carbohydrates. The resulting color change is usually to red but as the pH increases the foliage becomes purple. In species not producing anthocyanin, the yellow and orange carotene and xanthophyll pigments show as the chlorophyll disintegrates (KRAMER and KOZLOWSKI, 1979).

Color changes to various intensities of purple or purplish bronze occur in numerous conifer species seedlings but are especially evident in northerly latitude pines (STOECKELER and RUDOLF, 1956). Observations made on seedlings of 29 Minnesota, Wisconsin and Michigan provenances of jack pine (*Pinus banksiana* LAMB.) through 3 years of age in a nursery near Rhinelander, Wisconsin showed that autumn coloration varied significantly among provenances. The most intense purple was found in the northernmost provenances. First-year seedlings showed the earliest, most intense, and most complete color changes, and these progressively decreased in 2- and 3-year-old seedlings. Color change was correlated with average January temperature of the seed origin but not with length of the frost-free period (STOECKELER and RUDOLF, 1956). YEATMAN (1966) noted similar color changes in 3 latitudinal groups of jack pine seedlings grown at New Haven, Connecticut.

In a range-wide study of jack pine in a Michigan nursery, CANAVERA and WRIGHT (1973) also reported that north-

ern provenances turned purple whereas southern provenances remained green. Similarly in 2-year-old trees of 11 provenances from the range-wide collection tested in Hokkaido, Japan, the northerly provenances were most purple in mid-October but the most southerly provenances remained green (CHIBA and NAGATA, 1970).

Progenies from 60 stands in the northern half of Michigan's Lower Peninsula grown in the Michigan nursery showed less overall coloration and much less variation among provenances than was evident in the range-wide collection (CANAVERA, 1975). Coloration differences among half-sib progenies were significant and about 11 percent of the total variance was attributable to seed parent within stand.

No information has been available on genotypic variation in potential autumn coloration as expressed in inbred or outcrossed progenies of individual jack pine trees. Reported here are observations on autumn coloration variation among such progenies.

Materials and Methods

The jack pine seed for S_0 trees was collected in 1950 from a single stand in the Chippewa National Forest in north central Minnesota (RUDOLPH, 1966a, 1966b). The

seedlings were raised near Rhinelander, Wisconsin and field planted in east central Wisconsin in 1954.

Self-pollinations to produce the S_1 generation were made in 1962 and 1963. Information on the S_1 generation has been previously reported (RUDOLPH, 1966a, 1967). Self-pollinations on the S_1 trees to produce the S_2 generation were made in 1974. At the same time, crosses on the S_1 female parents using a mixture of pollen from 29 S_1 trees were made. Open-pollinated seed was also collected from the S_1 and S_0 trees. Seventeen S_2 , 16 $S_1 \times S_1$ -mix, 20 S_1 open-pollinated and 18 S_0 open-pollinated families were available. Results of the controlled pollinations and information on early seedling development and flowering of these families has been reported earlier (RUDOLPH, 1976, 1979).

Ten-week-old seedlings were transplanted from a greenhouse into nursery beds in late June and early July, 1976. Spacing between plants was 25 × 25 cm in 4-tree plots. Ten replications per family were included where enough seedlings were available.

Autumn coloration observations were made in 1977, at the end of the second growing season. On October 20, 1977, coloration was scored as the mean estimated percent of purple foliage and the number of colored trees per 4-tree plot. On October 26 and November 11, 1977, estimated per-

Table 1. — Average coloration of trees in S_1 self (S_2), $S_1 \times S_1$ -mix, S_1 open-pollinated, and S_0 open-pollinated progenies on October 20, 1977, based on plot means.

Progeny no.	S_1 Selfed (S_2)	$S_1 \times S_1$ -mix	S_1 O.P.	S_0 O.P.
	Coloration	Coloration	Coloration	Coloration
	(%)	(%)	(%)	(%)
N 2	1/	16.7	11.5	12.8
N 12	4.8	-	14.4	20.8
N 23	15.2	-	20.5	19.0
N 36	45.5	37.5	32.1	-
N 46-1	8.5	10.5	8.1	10.3
N 46-2	10.0	-	15.0	5.8
N 53	-	28.1	21.2	21.0
N 82	1.7	10.8	11.1	9.4
S 42	17.5	11.9	14.8	41.7
S 75	0.0	9.8	7.2	6.2
S 91	14.4	9.9	13.2	11.7
S 100	-	42.0	-	29.0
P 14	90.0	-	-	50.2
P 43	-	-	14.2	19.4
P 49	15.7	16.1	19.4	15.2
P 62	0.0	-	4.1	26.7
P 87	-	9.9	3.5	12.0
P 88-1	34.2	27.0	15.8	-
P 88-2	10.0	7.2	5.2	-
P 90	0.0	22.0	7.9	10.0
P 91	0.0	15.0	3.9	26.7
P 92	12.5	19.8	7.5	-
MEAN	16.5	18.4**	12.5	19.3
S.E.	±5.32	±2.52	±1.56	±2.75

1) No trees available

** Significantly different from S_1 O. P. at 1% level

cent of purple foliage was scored on an individual tree basis. Maximum, minimum, and mean daily temperatures in the nursery were recorded from September 27 through November 13, 1977, that is, before and throughout the period of color change.

Results and Discussion

Color change from green to purple began early in the second week of October, 1977. On the first scoring date, October 20, average percent of foliage colored among the 4 progeny groups ranged from about 13 percent in the S_1 O.P., to 19 percent in the S_0 O.P. (Table 1). The only significant difference between progeny groups was the $S_1 \times S_1$ -mix progenies had more purple color than the S_1 O.P. progenies. Individual progenies averaged 17 percent, but the range was from 0 to 90 percent. The S_2 families showed the greatest variation. Three families showed no coloration then but one had 90 percent purple foliage. These scores cannot be compared to CANAVERA and WRIGHT's (1973) or CANAVERA's (1975) data because those studies cite no scoring dates. However, on the same date in 1953 in the same nursery, STOECKELER and RUDOLF (1956) found that very

similar Minnesota provenances had more than half purple foliage compared to 13 to 19 percent in the present study. Temperature records for the autumn of 1953 show that the first freeze (-3°C) in the nursery was on October 26. In 1977 a freeze (-2°C) occurred on October 2 and 9 days with below freezing temperatures were recorded before October 20. If cold temperatures are related to autumn color change, there should have been more intensive purple coloration in 1977 than in 1953 but the opposite was true. One possible explanation is that the seedlings in the present study were started in the greenhouse and were more than twice as tall at the end of the second year as STOECKELER and RUDOLF's (1956) 2-0 seedlings that were grown from seed sown directly in the nursery. The larger seedlings in this study responded as older seedlings would have, i.e., with less color change, as noted in studies cited above. Also, September of 1953 was colder, with 9 days with minimum temperatures below 4.5°C . Thus, color change probably started much earlier in 1953 than in 1977 and would have been more intense by October 20.

Fifty-six to 68 percent of the trees in the four progeny groups had some purple foliage color on October 20 (Table

Table 2. — Proportion of trees colored in S_1 self (S_2), $S_1 \times S_1$ -mix, S_1 open-pollinated, and S_0 open-pollinated progenies on October 20, 1977.

Progeny no.	S_1 Selfed (S_2)	$S_1 \times S_1$ -mix	S_1 O.P.	S_0 O.P.
	Trees colored	Trees colored	Trees colored	Trees colored
	(%)	(%)	(%)	(%)
N 2	1/	77.5	63.3	57.5
N 12	54.2	-	67.5	62.5
N 23	72.5	-	75.0	77.5
N 36	86.6	70.0	90.0	-
N 46-1	50.0	65.0	55.0	45.8
N 46-2	100.0	-	100.0	42.5
N 53	-	87.5	85.0	83.3
N 82	8.3	60.0	25.0	50.0
S 42	70.7	77.7	57.3	91.7
S 75	0.0	60.0	27.0	50.0
S 91	68.7	68.8	71.6	60.8
S 100	-	100.0	-	82.5
P 14	100.0	-	-	97.5
P 43	-	-	62.5	70.0
P 49	75.0	62.5	80.0	62.5
P 62	0.0	-	20.0	73.2
P 87	-	50.0	45.0	65.0
P 88-1	90.0	85.0	60.0	-
P 88-2	100.0	37.4	40.0	-
P 90	0.0	53.6	66.7	47.5
P 91	0.0	50.0	60.7	75.0
P 92	71.6	75.0	100.0	-
MEAN	55.7	67.5	62.6	66.4
S.E.	± 9.12	± 3.90	± 5.01	± 3.70

1) No trees available

Table 3. — Average coloration of trees in S_1 self (S_2), $S_1 \times S_1$ -mix, S_1 open-pollinated, and S_0 open-pollinated progenies on October 26, 1977, based on individual tree scores.

Progeny no.	S_1 Selfed(S_2)		$S_1 \times S_1$ -mix		S_1 O.P.		S_0 O.P.	
	Color- ation (%)	Std. Dev. (\pm)	Color- ation (%)	Std. Dev. (\pm)	Color- ation (%)	Std. Dev. (\pm)	Color- ation (%)	Std. Dev. (\pm)
N 2	<u>1/</u>	-	41.4	27.9	37.0	24.9	39.5	32.0
N 12	18.5	14.3	-	-	38.0	27.3	55.2	30.1
N 23	43.6	27.2	-	-	49.0	28.1	56.6	23.8
N 36	70.9	29.1	59.1	29.7	58.2	25.6	-	-
N 46-1	28.2	18.6	33.8	26.9	26.1	21.9	28.9	30.2
N 46-2	24.2	17.0	-	-	50.0	<u>2/</u>	25.1	24.9
N 53	-	-	61.9	23.2	59.8	18.4	55.5	24.6
N 82	19.0	25.5	40.2	30.1	21.2	20.6	35.2	26.7
S 42	47.8	23.7	52.6	24.5	44.4	26.2	63.8	28.4
S 75	10.0	8.2	39.9	23.8	28.0	28.0	32.2	25.0
S 91	50.3	29.2	42.7	28.5	50.2	21.8	42.4	26.5
S 100	-	-	77.2	11.7	-	-	61.0	27.9
P 14	95.6	2.2	-	-	-	-	78.2	11.4
P 43	-	-	-	-	44.9	22.8	53.2	23.6
P 49	50.4	30.0	42.4	30.4	55.5	25.9	43.1	32.3
P 62	2.7	5.1	-	-	17.4	23.2	46.8	28.9
P 87	-	-	39.2	25.7	20.8	15.7	53.2	27.8
P 88-1	73.2	19.2	65.5	25.3	48.6	31.2	-	-
P 88-2	25.0	<u>2/</u>	31.7	29.5	38.2	27.7	-	-
P 90	10.0	<u>2/</u>	47.4	36.7	31.7	23.5	36.8	29.6
P 91	8.8	9.5	40.6	36.2	22.5	20.3	54.9	30.7
P 92	46.2	22.6	55.8	27.0	58.3	12.6	-	-
MEAN	36.7	18.8	48.2 ^{3/}	27.3	40.0	23.4	47.9 ^{4/}	26.9
S.E.	± 6.16		± 3.05		± 3.03		± 3.13	

- 1) No trees available
- 2) Only one tree
- 3) Differs from S_1 O. P. at 5% level
- 4) Differs from S_2 at 5% level

2). S_2 families showed the greatest variation: 3 families had no purple coloration while in another 3 all trees showed some purple. Average S_2 families also had fewer trees with purple foliage but they were not significantly different from the other 3 groups, possibly due to the wide variation among S_2 families. All families in the other 3 progeny groups had trees with some purple foliage, but the October 20 color scoring did not permit meaningful determination of variation within families.

In the week preceding October 26 average purple coloration increased rapidly to between 37 and 48 percent in the 4 progeny groups (Table 3), an average of about 43 percent, up 26 percent from the October 20 scoring. STOECKELER and RUDOLF (1956) reported a similar (25 percent) increase in color, also in 2-0 trees, but during a two-week period following October 20, 1953 in the same nursery. Therefore, though color change started later in 1977 than in 1953, the rate of change was faster in late October 1977. Yearly differences in color change rate are undoubtedly related to cold temperature patterns. Temperatures in

September, 1953 were lower than in 1977 but October temperatures were higher.

Significantly more coloration was present on October 26 in the $S_1 \times S_1$ -mix than in the S_1 O.P. progenies and in the S_0 O.P. than in the S_2 progenies (Table 3). The difference in coloration between S_2 and $S_1 \times S_1$ -mix progenies was not significant possibly because of the wide variation among S_2 progenies. The S_2 progenies continued to have the least coloration but the largest standard error, i.e., the widest variation among progenies. Scoring of the coloration on an individual tree basis on this date permitted determination of variance for each family (Table 3). Great variation was found within as well as among families in the progeny groups. The greatest inter-family variation occurred in the S_2 group with a standard error of the mean twice that in the other groups. However, the S_2 group also showed the smallest average intra-family variance (standard deviation). In theory, this is what should be expected as a result of inbreeding but has not been clearly demonstrated in forest trees. The above results show that, in a given

population, inbreeding increased homozygosity resulting in increased inter-family color variation but decreased intra-family variation.

The four progeny groups had an average of 55 percent purple foliage on November 11, an increase of about 12 percent since October 26 (Table 4). This was again somewhat lower than that noted in 2-0 jack pine by STOECKELER and RUDOLF (1956) on November 4, 1953. Differences among the 4 progeny groups were no longer significant. However, the standard error for the S_2 families was again more than twice that of the other 3 progeny groups. Variation among families within the 4 groups was still striking ranging, for example, from 10 to 98 percent among S_2 families. Color variation within families on November 11 was less than on October 26 as evident in the lower standard deviations (Table 4). This suggests that genotypic differences exist in onset of coloration and in rate of coloration (phenology) as well, and that genotypic variation is less evident in the final winter color than any other stage. Also, whereas inbreeding and increased homozygosity apparently delay the

coloration onset and result in a slower rate of coloration and larger inter-family and smaller intra-family variation, crosses between S_1 genotypes result in "heterosis" which restores all of these characteristics to the "normal" ancestor outcrossed condition. Furthermore, positive transgressive heterosis appears likely in some $S_1 \times S_1$ combinations making immediate genetic gains possible by crossing selected inbred genotypes.

No measurable additional color occurred after November 11, 1977, and by November 27 the seedlings were snow-covered.

Correlations between progeny groups in coloration were significant for some comparisons for the 3 observation dates (Table 5). The strongest relation was between S_1 O.P. and S_2 progenies. However, the correlations are not consistent, probably because of the wide color variation among families within progeny groups and in the rates and patterns of color change.

The color variation noted by STOECKELER and RUDOLF (1956) and CANAVERA and WRIGHT (1973) showed the same relation

Table 4. — Average coloration of trees in S_1 self (S_2), $S_1 \times S_1$ -mix, S_1 open pollinated, and S_0 open-pollinated progenies on November 11, 1977, based on individual tree scores.

Progeny no.	S_1 Selfed (S_2)		$S_1 \times S_1$ -mix		S_1 O.P.		S_0 O.P.	
	Color-ation (%)	Std. Dev. (\pm)	Color-ation (%)	Std. Dev. (\pm)	Color-ation (%)	Std. Dev. (\pm)	Color-ation (%)	Std. Dev. (\pm)
Ni 2	1/	-	48.5	24.0	49.4	24.0	45.2	27.9
N 12	39.0	22.2	-	-	50.0	24.4	64.9	27.6
N 23	69.4	17.3	-	-	59.6	23.2	65.1	19.9
N 36	76.3	24.0	67.3	26.2	65.6	21.5	-	-
N 46-1	39.2	20.9	47.5	23.9	43.0	23.9	38.4	27.5
N 46-2	47.9	19.0	-	-	70.0	2/	39.8	25.7
N 53	-	-	74.4	15.8	76.2	11.1	65.1	21.4
N 82	29.8	23.2	50.5	27.9	37.0	23.9	42.8	25.2
S 42	38.5	16.4	59.9	27.0	53.9	23.6	65.8	16.2
S 75	27.5	16.6	54.1	25.4	42.4	29.7	43.6	24.2
S 91	65.0	18.5	58.2	23.6	62.6	18.6	59.7	21.6
S 100	-	-	85.6	13.0	-	-	76.7	17.4
P 14	98.1	4.5	-	-	-	-	79.8	13.1
P 43	-	-	-	-	47.7	21.6	60.8	22.3
P 49	64.6	20.8	49.5	25.3	63.2	21.1	56.4	28.9
P 62	21.9	31.4	-	-	36.5	26.4	49.9	23.7
P 87	-	-	53.5	21.8	47.8	21.7	63.8	20.2
P 88-1	85.4	9.7	73.4	18.9	60.9	27.3	-	-
P 88-2	85.0	2/	47.7	25.9	53.2	26.3	-	-
P 90	10.0	2/	58.4	30.9	44.8	22.8	43.9	28.3
P 91	16.2	6.8	51.9	24.9	40.5	23.1	60.6	28.5
P 92	58.3	23.6	67.1	22.7	78.3	29.0	-	-
MEAN	51.3	18.3	59.2	23.6	54.1	23.3	56.8	23.3
S.E.	± 6.21		± 2.74		± 2.71		± 2.86	

1) No trees available

2) Only one tree

Table 5. — Correlation between progeny groups in coloration characteristics on three dates.

	<u>S₁ Selfed(S₂)</u>	<u>S₁ x S₁-mix</u>	<u>S₁ O.P.</u>	<u>S₀ O.P.</u>
<u>MEAN PERCENT COLORATION ON OCTOBER 20, 1977</u>				
S ₁ Selfed(S ₂)	1.000	0.749**	0.811**	0.696**
S ₁ x S ₁ -mix		1.000	0.756**	0.368
S ₁ O.P.			1.000	0.108
S ₀ O.P.				1.000
<u>PERCENT OF TREES COLORED ON OCTOBER 20, 1977</u>				
S ₁ Selfed(S ₂)	1.000	0.342	0.606*	0.299
S ₁ x S ₁ -mix		1.000	0.499	0.563
S ₁ O.P.			1.000	0.047
S ₀ O.P.				1.000
<u>MEAN PERCENT COLORATION ON OCTOBER 26, 1977</u>				
S ₁ Selfed (S ₂)	1.000	0.722**	0.818**	0.611*
S ₁ x S ₁ -mix		1.000	0.689**	0.667*
S ₁ O.P.			1.000	0.188
S ₀ O.P.				1.000
<u>MEAN PERCENT COLORATION ON NOVEMBER 11, 1977</u>				
S ₁ Selfed (S ₂)	1.000	0.470	0.722**	0.616*
S ₁ x S ₁ -mix		1.000	0.713**	0.726**
S ₁ O.P.			1.000	0.333
S ₀ O.P.				1.000

* Significant at 5% level

** Significant at 1% level

to latitude as did tree height, i.e., the slower growing northern provenances also were more purple. In the present study, no relation between tree height and coloration was evident among or within families. CANAVERA and WRIGHT (1973) suggest that selection in northern provenances may have favored hardy, slow-growing color-changing types but that in southern provenances faster growing, less hardy, and less color-changing types were more prevalent. Although these relationships may occur among provenances, similar relations among families within the one provenance in this study were not evident. Possible differences in hardiness among families with varying amounts of coloration could not be evaluated in the 2-year-old jack pine in the present study because no frost or winter injury occurred in any of the trees. Should such a relationship exist, the great amount of inter- and intra-family color variation should make selection for hardiness feasible.

Abstract

Change in foliage color from green to purple was evaluated on 3 dates in autumn, 1977, on families of 2-0 jack pine representing S₂, S₁ x S₁-mix, S₁ O.P. and S₀ O.P. progenies. Color change started in the second week of October and ended by November 11. Inbreeding resulted in larger inter- but smaller intra-family color variation. Crosses among S₁ genotypes restored original foliage coloration patterns. Genotypic variation in potential autumn foliage coloration in young jack pine is clearly demonstrated by the results.

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Random non-contiguous plots in interlocking field layouts

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Summary

Experiments with forest trees are expensive on a per-organism basis. They require large areas, which are generally more environmentally variable than areas used for agricultural research. A proposal is presented to take advantage of the efficiencies of small-plot designs, while minimizing some of their difficulties. Independently-randomized replications are interlocked, with plot members arranged non-contiguously within each block. This design allows small plots that are relatively safe from disqualification due to local causes of mortality or damage.

Such small-plot designs incorporate high levels of genetic dissimilarity between neighboring trees. It is argued that the interactions between such neighboring trees are normal in forest stands and plantations. Lethal competition between neighboring trees can be delayed by systematic thinnings of interlocked replications, with both the cut trees and the remaining plantation fully analysable as balanced and unbiased experiments.

Key words: Competition, Double planting, Hexagonal spacing, Mortality, Nursery organization, Quantitative genetics, Replication, Single-tree plots, Statistical efficiency, Thinning.

Zusammenfassung

Zufallsverteilte zwischengeschaltete Parzellen nichtbenachbarter Versuchsglieder in Feldversuchsplänen

Versuche mit Waldbäumen sind je untersuchte Pflanze teuer. Sie benötigen große Versuchsflächen, die normalerweise größere Umweltvariation aufweisen als Flächen für landwirtschaftliche Versuche. Hier wird ein Vorschlag unterbreitet, der es ermöglicht, die Vorteile der Wirksamkeit (Effektivität) kleiner Parzellen zu nutzen und gleichzeitig einige ihrer Schwierigkeiten zu minimieren. Unabhängig randomisierte Wiederholungen werden zwischengeschaltet mit nichtbenachbarten Parzellen gleicher Versuchsglieder innerhalb eines Blockes. Diese Versuchsanordnung erlaubt kleine Parzellen, die gegen örtlich bedingte Disqualifikation

durch Mortalität oder Schädigung weitgehend gesichert sind.

Versuchspläne mit kleinen Parzellen schließen große genetische Unterschiede zwischen benachbarten Bäumen ein. Es wird argumentiert, daß Interaktionen zwischen solchen benachbarten Bäumen in Naturbeständen und Forsten üblich sind. Tödliche Konkurrenz zwischen benachbarten Bäumen kann durch systematische Durchforstung der zwischengeschalteten Wiederholungen verzögert werden. Dabei bleiben sowohl die herausgenommenen Bäume als auch die verbleibende Pflanzung als balanciertes und fehlerfreies Experiment voll analysierbar.

Résumé

Parcelles unitaires, non contigües et randomisées, dans des dispositifs expérimentaux de terrain avec emboitement.

Les expériences concernant les arbres forestiers sont chères, si ce coût est rapporté à chaque arbre testé. Elles nécessitent de grandes surfaces qui sont en général plus variables sur le plan écologique que celles utilisées pour les plantes agricoles. Le présent article propose d'utiliser les avantages de l'efficacité des dispositifs comportant des parcelles unitaires de petite taille, tout en minimisant les difficultés inhérentes à ceux-ci. Des répétitions randomisées indépendamment sont imbriquées et les éléments d'une parcelle unitaire sont arrangés de façon non contigüe à l'intérieur de chaque bloc. Le dispositif autorise de petites parcelles qui présentent certaines garanties en cas de mortalité ou de dégâts localisés.

De tels dispositifs avec petite parcelle unitaire entraînent le voisinage d'arbres présentant une forte dissemblance génétique. Les auteurs soulignent que de telles interactions entre arbres voisins sont habituelles dans les peuplements et les plantations forestières; la compétition allant jusqu'à la létalité, entre arbres voisins, peut être retardée par éclaircies systématiques des répétitions emboîtées, tout en autorisant l'analyse des données concernant les arbres restant ou enlevés en éclaircie, comme des dispositifs non biaisés et équilibrés.

Introduction

Quantitative genetic experiments are usually initiated to serve one of two purposes. One is investigation of the

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