

Geographic Variation in Eastern White Pine

Two-Year Results of Testing Range-Wide Collections in Maryland¹⁾

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1. Introduction

Eastern white pine (*Pinus strobus* L.) is one of the most important forest trees in the eastern United States and southeastern Canada. In suited habitats, it is also one of the most planted species for timber production. About one million seedlings of eastern white pine are planted annually in Maryland alone. Therefore, selection of the best seed sources for planting is of economic interest.

The results of the first provenance test of eastern white pine conducted near Petersham, Massachusetts, suggested that local seedlings (from Massachusetts) grew best, followed in order by sources from New Hampshire, New York, Ontario, Michigan, Minnesota and Virginia (PAULEY et al., 1955).

The first range-wide study of *P. strobus* was organized in 1955 by the Forest Service of the U.S. Department of Agriculture. It included 31 provenances from natural stands. While at the New Jersey state nursery (Washington Crossing, N. J.), 21 provenances showed significant differences in height, duration of growth, and per cent of growth completed by May 18 (SANTAMOUR, 1960). These traits were strongly correlated with latitudes and lengths of growing season at the place of origin.

The U.S. Forest Service experiments were established on various sites and yield valuable information. Six year results from two plantations in Michigan showed significant between-provenance differences in mortality, height, foliage color, and lammass-shoot formation (WRIGHT et al., 1963). Among 15 provenances tested, those from Minnesota and Nova Scotia showed the highest mortality and the smallest heights. The Tennessee and Georgia provenances were tallest, followed by sources from Pennsylvania, southern Ontario, Massachusetts, and New York. The bluest foliage was found among the provenances from Georgia and southern Ontario, and the highest per cent of lammass shoots in progenies from Ontario (Algoma District) and northern Minnesota. Experiments in the southern Appalachian (North Carolina, Georgia and Virginia) showed significant differences in three-year survival and heights (SLUDER, 1963). In all plantations the provenance from Georgia showed the best height growth. The same source showed the best survival in North Carolina and the second best in Virginia, but it ranked only fourth in Georgia. Height measurements were also reported of eight-year old trees of 16 provenances tested in Illinois, Iowa, Ohio (two plantations), Kentucky and Indiana (FUNK, 1964). The Tennessee and Georgia provenances grew most rapidly. However, there was a number of provenances that showed as good (not significantly different) growth rates: in Illinois and Indiana — the North Carolina, Ohio and Pennsylvania sources; in Iowa — a Pennsylvania source; in Ohio (Athens) and Kentucky — a North Carolina source, and in Ohio (Wooster) — seven other

sources. Quite similar rank of heights was found among 14 provenances tested in Pennsylvania (GERHOLD and SCHREINER, 1964). The Georgia and Tennessee provenances had the largest heights, followed by some more-northern sources (southern Ontario, Pennsylvania and New York).

Leader shoots of eastern white pine studied by STROH, 1963, showed a racial variation in bark thickness, depth of inside and outside cortical resin ducts, diameter, and length. Some of these traits appeared correlated with the feeding extent of adult white pine weevil (*Pissodes strobi* PECK). FOWLER and DWIGHT, 1964, found that seeds from the southern regions required longer period of stratification than those from the northern range.

A small preliminary provenance study was initiated in Maryland with five sources of eastern white pine in 1962. At the age of two years, the best growth was found in a source from South Carolina (GENYS, 1965).

From this previous work we can conclude that eastern white pine is a variable species and that local sources may not grow best. However, much remains to be learned — the details of the geographic and local variation patterns, and possible resistance to insect and disease pests.

The present study was undertaken to supply seed source information applicable to Maryland, some details of the geographic variation pattern and relationship among traits. To do this, it was desirable to include more intensive range sampling than in previous provenance studies. This report is based on a two-year study of 119 provenances in the nursery. More intensive studies will be continued in the field plantings in ten different states in the United States and in Australia, Germany and New Zealand.

2. Materials and Methods

Seed collection for this experiment was started in the fall of 1961. A hundred prospective cooperators were asked to send seed from six well separated trees per stand from their nearest native white pine forest. By November 1962, the total collection consisted of 119 seed-lots, including some sources from individual trees. The collection areas are shown in figure 1. Each seed-sample was designated by a Maryland (MdF) number, and the origin data were recorded in a permanent mimeographed record. Four series of seed-lots were sent for studies in Pennsylvania, Australia, Germany, India and New Zealand. The seed-lots classified for the studies in Maryland were stored at a temperature of 35° F.

Before sowing, a random sample of each seed lot was used to determine the seed weights and the per cent of filled seeds by a cutting test. Seed weight was based on a sample of 50 sound seeds.

The provenance test was conducted at the State Forest Tree Nursery in Harmans, Maryland, five miles south of Baltimore. This location is in plant hardiness zone 7 (average annual minimum temperatures range from 0° to 10° F). The length of frost-free period varies from 180 to 210 days

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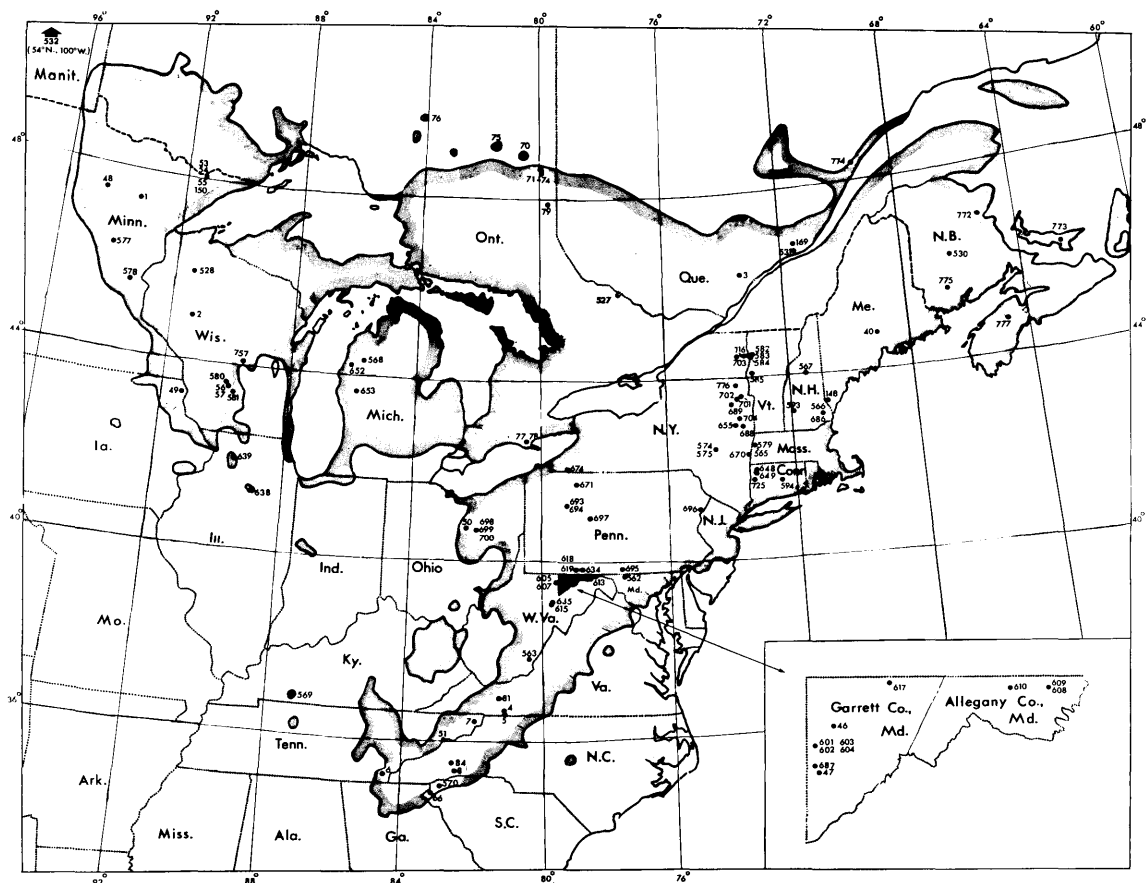


Figure 1. — Natural distribution of eastern white pine (*P. strobus*) in eastern United States and southeastern Canada and provenances included in this experiment (numbered dots). Range map was drawn using outline by E. L. LITTLE, 1959 (U. S. Forest Service).

and the dates of the first frost in autumn range from October 30th to November 10th.

Untreated seeds were sown on November 19, 1962. Enough sound seed was used to produce 20 seedlings per square foot. Ninety-nine seed lots were sown in a 4-times replicated experiment in which the plots were 2-foot rows spaced six inches apart. In addition to the replicated experiment, a series of 4' × 4' broadcast sown plots were grown to supply stock for the establishment of a series of field tests in Maryland, Illinois, Maine, Michigan, New York, Pennsylvania, South Carolina, Tennessee, Virginia and West Virginia. Twenty provenances of the total experiment were not represented in the replicated experiment but were available for height measurements in single plots. One-year heights were available also from tests in Pennsylvania, Australia and Germany.

The seedlings were kept unfertilized, weed-free and watered as needed. The traits studied, coded by (11) to (23), were:

- (11) Speed of germination (scored on April 23, 1963).
- (12) Speed of shedding seed coats (scored on May 10, 1963).
- (13) Number of cotyledons (based on counts of five randomly chosen seedlings per plot).
- (14) Day of year when 50 per cent of the 1-year seedlings had terminal buds.
- (15) One-year heights (based on measuring the largest seedling in each quarter plot).
- (16) One-year height at Mont Alto, Pennsylvania, was measured by J. A. WINIESKI in October 1963.

(17) One-year height at Canberra, Australia, was measured by Dr. L. D. PRYOR in May 1963.

(18) One-year height at Schmalenbeck, Germany, was measured by Dr. K. STERN in autumn 1963.

(19) Two-year height of the largest seedling in each quarter plot was measured in autumn 1964.

(20) Two-year diameter (based on measuring the lowest portion of stem on three largest sample trees dug from each plot during the planting season in 1965).

(21) The per cent of trees adding secondary growth was counted in autumn 1964.

(22) Color was scored in July, 1964. Grades of 1 (yellowish green) to 3 (bluish green) were used.

(23) Needle-length was determined from three needles of each of three largest trees per plot.

The plot means were punched on IBM cards. Analysis of variance and analysis of correlation were performed by the Service Bureau Corporation (Wheaton, Md.) with electronic computers. The basic analysis of variance for 99 replicated seedlots had the following degrees of freedom: 98 for seedlots, 3 for blocks, 294 for interaction and 395 for total. Least significant differences among seedlots were determined by using the results of the analysis of variance and the DUNCAN'S multiple range test (DUNCAN, 1956). Correlations were calculated using seedlot means as items.

For better interpretation, the seedlots were grouped by climatic regions, using the maps of plant hardiness zones and isotherms of mean length of frost-free periods in the eastern United States and Canada (U. S. D. A., 1960; BOUCHNER *et al.*, 1956).

Table 2. — Correlations among characters in eastern white pines (*P. strobus*) of different origin. Two asterisks indicate correlation coefficients (*r*) that are significant at the 1 per cent level.

Code numbers:	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)	(15)	(16)	(17)	(18)	(19)	(20)	(21)	(22)
Correlation analysis conducted between the corresponding data of the factors on the right (y_1) and the factors below (y_2)	Latitude	Longitude	Elevation	Age of mother trees	Weight of seed	Speed of germination	Speed of seed-coats shed	Number of cotyledons	Day of year, terminal buds formed	One-year height	One-year height in Pennsylvania	One-year height in Australia	One-year height in Germany	Two-year height	Two-year diameter	Trees with secondary growth	Color intensity toward blue
(10) Weight of seed	-.34**	-.06	-.04	-.58**													
(11) Speed of germination	.26	-.13	-.49**	-.03	-.01												
(12) Speed of seed-coat shedding	.04	-.06	-.41**	-.13	.18	.39**											
(13) Number of cotyledons	.26	-.37	.12	-.56	.24	.37	-.75**										
(14) Date, terminal buds formed	-.77**	-.01	.30**	-.29	.18	-.25	-.01	-.34									
(15) One-year height	-.63**	.11	.26	-.49**	.55**	-.15	.27**	.01	.59**								
(16) One-year height in Penna.	-.15	.06	-.24	-.18	.35**	.03	.38**	-.19	.20	.48**							
(17) One-year height in Australia	-.55**	.15	.32	-.25	.20	-.36	-.01	.01	.47**	.65**	.47**						
(18) One-year height in Germany	-.31	.08	-.05	-.17	.51**	-.07	.13	.38	.29	.73**	.24	.56**					
(19) Two-year height	-.65**	-.02	.13	-.42**	.45**	-.16	.28**	.22	.56**	.86**	.41**	.37**	.59**				
(20) Two-year diameter	-.58**	-.01	.12	-.42**	.40**	-.08	.17	.04	.65**	.69**	.31	.42**	.50**	.79**			
(21) Trees with secondary growth	-.38**	-.03	.11	-.12	.15	-.08	.14	-.14	.41**	.50**	.40**	.49**	.33**	.46**	.46**		
(22) Color	-.05	.14	-.03	-.27**	.30**	-.10	-.02	.00	.17	.22	.18	.16	.07	.31**	.31**	.00	
(23) Needle-length	-.65**	.12	.27	-.38**	.22	-.23	.03	.10	.65**	.61**	.09	.61**	.46**	.54**	.70**	.34**	.30**

3. Results

The 1- and 2-year data on the performance of different provenances of eastern white pine are listed Table 1. Significant differences among sources were found in speed of germination, speed of shedding seed-coats, date of terminal bud formation, height and diameter of seedlings, tendency to secondary growth, foliage color, and leaf length. Some of these traits were related to geographic factors such as latitude and elevation of the seed collection areas or to mother tree age and seed weight. Some traits were related to each other. The degree of these relationships is expressed by correlation coefficients (*r*) in Table 2.

Seed Weights

Thousand seed weights among different sources ranged from 13.4 to 31.6 grams (Table 1). The extremes were both from Maryland. Seed weight was negatively correlated to the age of mother tree ($r = -.58$), and latitude ($r = -.34$, Table 2). Further correlations were between seed weight as one variable, and 1-year height, 2-year height, diameter and color. Respective coefficients of determination (r^2) were .30, .20, .16 and .09.

Speed of Germination

All seed lots were exposed to natural stratification during the winter of 1962–1963. On April 29, 1963, some provenances showed nearly complete germination whereas others had not started (Table 1). Speed of germination was negatively correlated with elevation ($r = -.49$). In other words, sources from the lowest elevations germinated fastest. FOWLER and DWIGHT (1964) reported that southern provenances require longer stratification periods than do the northern origins. In the present study, southern origins receiving the same amount of stratification germinated slightly slower than northern ones. Correlation between speed of germination and latitude ($r = .26$) was significant at the 5 per cent level.

Speed of Shedding Seed Coats

Speed of seed-coat shedding was related to speed of germination and elevation. This trend of relationships, however, was strongly modified by number of cotyledons. The larger the number of cotyledons, the slower were the seed-coats dropped ($r = -.75$). Speed of seed coat shedding was also correlated with 1- and 2-year heights in Maryland and Pennsylvania nurseries, but these correlations were not strong — $r^2 = .07$ to .14.

Cotyledon Number

Individual seedlings had from 6 to 12 cotyledons. The mean number of cotyledons ranged from 8.1 to 9.8 among 16 provenances studied. Seedlings originating from two extreme locations of the species range, Manitoba and South Carolina, had significantly larger numbers of cotyledons than those from other locations.

Date of Terminal Bud Formation

Date of terminal bud formation in 1-year trees varied by 45 days. Provenance No. 532 (Manitoba) formed buds on the 267th day of the year (= Sept. 24) whereas No. 570 (South Carolina) continued to grow until the 312th day (= Nov. 8). Lateness of bud set was correlated negatively with latitude ($r = -.77$) and positively with elevation, growth rate, needle length and percentage of trees with secondary growth.

It is tempting to postulate a cause — and effect — between lateness of bud set and growth rate. However, such a correlation has not been evident in Scotch pine or Japanese larch provenance tests, nor in the older eastern white pine test reported from Michigan. Indeed, it is better to say that the correlations exist because late-setting buds and several other traits are common to southern seed sources.

Growth Rate

There were 3 to 1 differences in height growth at the end of the first and second growing seasons. The tallest

Table 3. — Variation in two-year heights of eastern white pine (*P. strobus*) from regions of differing minimum temperature and length of growing season.

Hardiness Zone, and Average minimum temperature	Length of frost-free periods in days				
	90-or less	90-120	120-150	150-180	180-210
	<i>per cent of average height</i>				
2 —45°F	65	83	—	—	—
3 —35°F	89	91	—	—	—
4 —25°F	—	95	92	—	—
5 —15°F	—	100	106	—	—
6 —5°F	—	—	116	117	—
7 5°F	—	—	100	116	127

trees were from southern and central states with warm winters and long growing seasons (Tables 1 and 3). Thus there was a significant negative correlation between height or diameter and latitude of origin. The tallest provenances were also the ones with the largest seeds ($r = .20$ to $.55$), the longest needles ($r = .09$ to $.61$), late first-year bud formation ($r = .20$ to $.59$), and the most secondary growth during the second year ($r = .33$ to $.50$). It is uncertain whether these correlations indicate cause and effect relationships or reflect the fact that large seeds, long needles, a great amount of secondary growth, and rapid growth are all characteristic of warm-climate provenances.

Negative correlation between age of mother tree and height, and the positive correlation between seed weight and height, may be artefacts. The factual effects of these factors should be studied for individual regions rather than using the range-wide data.

As expected the correlation between 2-year height and 2-year diameter ($r = .79$) was strong, even though the measurements were made on different trees. Diameter-measurements demonstrate the significance of geographic variation in volume production if both components, height and diameter, are taken in consideration.

The correlation between 1- and 2-year heights of the trees grown in Maryland was strong ($r = .86$). The correlations between 2-year height in Maryland and 1-year height of the same provenances grown in Pennsylvania, Germany, and Australia were statistically significant ($r = .37$ to $.59$) but not particularly strong. Taken at face value, such correlations mean that selection practiced in Maryland can be used to indicate what may be the best 50 percent (but not the best 10 percent) of the progenies for use in these other places. At the present time one cannot say whether the weakness of the correlations is due to true site-genotype interaction or to differences in experimental technique.

Secondary Growth

The tendency for secondary growth (starting growth after terminal buds were once formed) significantly varied (Table 1). Some provenances from Minnesota included as few as four per cent of trees starting secondary growth, while some other sources included as many as 50 per cent. This trait was negatively correlated with latitude ($r = -.38$), meaning that secondary growth was somewhat more common among the southern sources than among the northern. It was also correlated positively with growth rate (height and diameter).

Color

The intensity of color toward blue was not correlated to either the latitude, longitude, or elevation. Most bluish color (in July) was found among three out of four sources from Ohio. Other provenances having bluish-green color

Table 4. — Variation in needle-lengths of eastern white pine from regions of differing minimum temperature and length of growing season.

Hardiness zone, and Average minimum temperature	Length of frost-free period in days				
	90-or less	90-120	120-150	150-180	180-210
	<i>average needle-lengths in centimeters</i>				
2 —45°F	5.5	6.3	—	—	—
3 —35°F	6.5	6.6	—	—	—
4 —25°F	—	6.7	6.7	—	—
5 —15°F	—	7.2	7.6	—	—
6 —5°F	—	7.2	7.5	7.5	—
7 5°F	—	—	8.1	9.1	8.8

were from some locations in New York, Pennsylvania, Connecticut and Maryland. It appears that bluish-green color of leaves was more common among the sources from the central range than among those from north or south.

Needle Length

Table 1 shows that needle-lengths among different provenances were very significantly different. A distinct variation was also among some sources from the same region. Provenances No. 532 from Manitoba and No. 55 from Minnesota had the shortest needles (5.5 centimeters), and provenance No. 9 from North Carolina had the longest (10 centimeters). Apparently, the sources from warmer regions had longer needles than those from the northern range (Table 4). Correlation between latitude and needle length was negative ($r = -.65$). Needle length was also correlated to other traits that are typical to southern provenances.

Discussion

Color, number of cotyledons and speed of shedding seed-coats were traits that showed no relationship to latitude. Other characters demonstrated a more or less gradual change from north to south. This latitudinal change was modified by differences in elevation and the lengths of growing season. Apparently, climate was one of the main factors that acted strongly in the natural selection and formation of different geographic strains. In the northern regions, climatic conditions favored trees that had short needles (less exposure to snow break) and stopped growing early in the fall (avoided injuries by the early frosts). On the other hand, the climatic conditions in the south favored trees that germinated slower (germination during the warm fall would be disadvantageous), and continued the growth longer in the fall (utilized long growing season).

The longer the period of field experimentation, the more significant will be the results for recommending particular seed sources for practical use. Present data, however, suggest a few guidelines concerning Central Maryland. It appears that seed sources from colder regions with short vegetative periods may fail to fully utilize the opportunities in a more favorable climate of Central Maryland. It may be disadvantageous to use seeds from plant hardiness zones 2, 3 and 4 (that are in the range of the minimum annual temperatures of -20° to -50° F), or from areas that have less than 120 frost-free days. Longer study is needed to learn if the most rapidly growing sources from South Carolina and Tennessee can be used. However, it is quite safe to plant selected provenances from region "p" in Pennsylvania and region "x" in Maryland and Pennsylvania (Table 1). If color quality is of concern to Christmas tree growers, the Ohio sources appear most promising. In addition, these sources may offer a relatively fast growth rate. If short

needles are preferred by horticulturists, the best opportunity for this selection is in the northern (Canadian) areas. This character is particularly distinct (but not measured) among the sources from Nova Scotia- and Prince Edward Islands.

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Summary

Nine characters of eastern white pine (*Pinus strobus* L.) from 99 geographic sources were studied in a replicated experiment at the State Forest Tree Nursery in Harman, Maryland, in 1963-1964. Heights were available also from 20 other sources planted in single plots, and from 1-year tests in Australia, Germany and Pennsylvania.

Seed weights were inversely correlated with latitude, and rapid germination was related to low elevations in the north. The rapidity of seed coat dropping was inversely proportional to the number of cotyledons, that were most numerous among the seedlings from the latitudinal extremes (Manitoba and South Carolina). Date of terminal bud set in 1-year trees varied by 45 days and was inversely correlated with latitude. There was also an inverse correlation between latitude and a tendency to resume secondary growth. Two-year height varied from 7.1 cm. (Prince Ed-

ward Island, Canada) to 21.6 cm. (South Carolina). In general, the fastest growing trees were from regions with long frost-free periods in southern and central states, thus height was negatively correlated with latitude. Two-year height was correlated positively (in decreasing degree) with 1-year height, date of terminal bud set, needle length, tendency for secondary growth, seed weight, and bluish foliage color. Diameter at two years ranged from 3 mm. to 5 mm. and was strongly correlated with height. Bluish-green foliage in summer was most common among seedlings from Ohio and other locations in the central range. Needle-length varied from 5.5 cm. (Manitoba) to 10 cm. (North Carolina) and was inversely correlated with latitude.

The correlations between 2-year heights in Maryland and 1-year heights of the same sources grown in Australia, Germany and Pennsylvania were statistically significant, but not particularly strong ($r = .37$ to $.59$). This may be due to actual site-genotype interaction or to differences in experimental technique.

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Seed Orchard Designs for Sites with a Constant Prevailing Wind

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Most East African softwood planting areas lie in the intertropical convergence zone of the monsoon wind system. Consequently many sites receive light winds which blow remarkably constantly from the East. At Muguga, Kenya, for example, winds from a westerly direction were recorded on 218 afternoons in a total of 3581 afternoons, over a period of ten years, (Fig. 1). Similar constant wind directions have been recorded from other forest stations and elsewhere in East Africa (E. A. Met. Dept., 1964).

Current thought on the design of clonal seed orchards favours the "polycross" design (see, for example, FAULKNER, 1965) in which all clones are arranged in such a way that no ramet is neighbour to a ramet of its own clone and, it is hoped, every clone has an equal chance of pollination by

every other clone in the orchard. The design of polycross orchards is often time consuming and computer programmes developed to construct these laborious designs tend to be slow and expensive of machine time²⁾.

Where polycross designs have been adopted, seed collected in bulk from the seed orchards is often assumed to be of the full polycross mixture with equal contributions of genes from all clones in the orchard. The early seed collected from an orchard is sometimes used in progeny trials in an attempt to obtain an early estimate of genetic gain achieved by the plustree selection programme, but seed from this type of orchard can only be the full polycross mixture if a number of conditions are fulfilled. All clones in the orchard must be equally prolific in the production of seed and pol-

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