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## 'Crop' and 'Isolation' Ideotypes: Evidence for Progeny Differences in Nursery-grown *Picea sitchensis*

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### Summary

Ten open-pollinated progenies and two provenance standards (Masset and Hoquiam) of *Picea sitchensis* were grown in a nursery for 4 years in two experiments: (1) as widely-spaced trees (140 cm spacing) so that the trees never came into contact, and (2) in large pure progeny or provenance plots at 14 cm spacing so that there was intense inter-tree competition, which decreased 4-year heights by 26% and mean tree diameters by 60% compared with the widely-spaced trees.

The ten progenies had been evaluated earlier in forest trials at several sites relative to Masset provenance at about

2 m spacing. Many of the progenies that had been ranked as superior in height at age 4—6 after planting in those forest trials, also grew significantly taller and greater in diameter than the provenance standards in this study, but only in experiment (1) as widely-spaced trees. When grown in closed stands in experiment (2) none of the superior progenies were significantly greater than the provenance standards in mean height and diameter per tree, nor in basal area, total above-ground or stem dry weight per unit ground area (means 17.8 and 7.6 t/ha, respectively).

It is suggested that most tree progeny tests favour the selection of genotypes with the attributes of 'isolation' ideotypes, which grow rapidly as widely-spaced individuals, and 'competition' ideotypes which grow large in progeny mixture at their neighbours' expense. Selected genotypes may have few of the attributes of 'crop' ideotypes, which

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contribute to high biomass and volume production per hectare in closed stands. Consequently, genetic gains in volume yield per hectare estimated from many progeny tests may be greater than true gains over a rotation during which there is inter-tree competition. More studies are needed to determine how serious this problem might be, and to determine whether 'crop' ideotypic attributes can be recognised on individual trees.

**Key words:** *Picea sitchensis*, ideotype, competition, genotype  $\times$  environment interaction, biomass.

### Zusammenfassung

Zehn frei abgeblühte Nachkommenschaften und zwei Standard-Herkünfte (Masset und Hoquiam) von *Picea sitchensis* wurden in einer Baumschule in zwei Versuchen vier Jahre lang angezogen: 1.) mit großem Pflanzenabstand (140 cm), so daß die Bäume sich nie berührten und 2.) in großen reinen Nachkommenschafts- oder Herkunftspartzellen mit 14 cm Abstand, so daß ein Konkurrenzwettkampf auftrat, der die Vier-Jahreshöhen um 26% und den mittleren Durchmesser um 60% gegenüber den weitständigen Pflanzen verminderte.

Die 10 Nachkommenschaften waren bereits früher in forstlichen Versuchen an verschiedenen Standorten in Relation zur Herkunft Masset bei einem Abstand von ca. 2 m ausgewertet worden. Viele der Nachkommenschaften belegten in bezug auf die Vier- bis Sechs-Jahreshöhen der Rangfolge nach vordere Plätze, wuchsen signifikant schneller und hatten auch einen signifikant größeren Durchmesser als die Standard-Herkünfte in diesem Versuch, aber nur im ersten Versuch auf großem Standraum. Im zweiten Versuch war keine der besten Nachkommenschaften in Höhenwachstum oder Durchmesser signifikant besser als die Standard-Herkunft, auch nicht im Basalbereich, im totalen Sproßgewicht oder dem Stammtrockengewicht auf gleicher Fläche (entsprechend 17,8 bzw. 7,6 t/ha).

Es wird deutlich, daß die meisten Waldbaum-Nachkommenschaftsprüfungen die Selektion von Genotypen mit den Merkmalen eines „Isolations“-Ideotypen, der als weitständiges Individuum schnell wächst, sowie eines „Wettbewerbs“-Ideotypen, der in Nachkommenschaftsmischungen auf Kosten seiner Nachbarn schnell wächst, begünstigen. Selektierte Genotypen mögen wenige Merkmale eines „Ertrags“-Ideotypen haben, der zu hoher Biomasse- und Volumenproduktion per Hektar in dichten Beständen beitragen würde.

Folglich würden genetische Gewinne im Volumenertrag je Hektar als Schätzwerte vieler Nachkommenschaftsprüfungen größer sein, als der wahre Gewinn während des Umtriebs, da während dieser Zeit zwischen Bäumen ein Konkurrenzwettkampf besteht.

Weitere Versuche werden benötigt, um zu bestimmen, wie schwerwiegend dieses Problem sein kann, und um zu bestimmen, ob die Merkmale des „Ertrags“-Ideotypen am Einzelbaum erkannt werden können.

### Introduction

The relative performances of tree progenies are usually decided on the basis of mean individual tree heights or stem volumes at ages 4–10 years after planting, using experimental designs in which progenies are mixed together as single trees, rows of 3 to 8 trees, or small plots of 2  $\times$  2 . . . 8  $\times$  8 trees. In those circumstances progeny rankings will depend partly on their relative abilities to grow as widely-spaced individuals and partly on their abilities to compete with neighbouring progenies. In other words, many of the progenies that are classified as superior will be those that rapidly exploit the available space and have a high competitive ability: they will be the ones that become established rapidly, grow tall, probably generate photo-

synthetic surface and root absorptive surface rapidly and thereby make the greatest possible claims on environmental resources of light, water and nutrients even though this may be at the expense of neighbouring progenies.

When DONALD (1968) coined the term 'ideotype' for cereals, he recognised that 'isolation' ideotypes, which give high yields as spaced plants, and 'competition' ideotypes, which give high yields per plant in varietal mixtures, do not necessarily give high yields per hectare in dense monocultures (see DONALD and HAMBLIN 1976). The greatest yields per hectare in closed stands are given by 'crop' ideotypes; these may not be outstanding as individuals, but they produce stands which use environmental resources efficiently to give high yields per unit area of ground. An extensive agronomic literature now exists showing that neither spaced plant performance nor competitive ability are necessarily related to stand yields: large rank differences occur depending on whether genotypes are grown in pots, in mixtures or in pure stands (grasses: KNIGHT 1960, LAZENBY and ROGERS 1960–1965, VAN DIJK and WINKELHORST 1978; soybean: HINSON and HANSON 1962; wheat: SYME 1972, FISCHER and KERTESZ 1976; beans: HAMBLIN and EVANS 1976). There are some well-known instances where competitive ability and stand yield have been inversely related (barley: WEIBE *et al.* 1963, HAMBLIN and DONALD 1974; rice: JENNINGS and DEJESUS 1968, JENNINGS and HERRERA 1968). HAMBLIN and ROWELL (1975) and DONALD and HAMBLIN (1976) discussed the implications of these findings for cereal crop improvement.

The possible implications of the 'crop' ideotype concept for tree improvement may be argued as follows (see also CANNELL 1978, 1979). Because tree breeders need to evaluate large numbers of genotypes over short periods of time with limited resources and on heterogeneous sites, they are bound to test progenies as described above, under conditions which favour progenies with the attributes of 'isolation' and 'competition' ideotypes. It is rarely possible to test every progeny long after canopy closure in large pure stands with adequate border rows (HÜHN 1974). Attributes favouring rapid site capture may be desirable during the years between planting and canopy closure, and a few years after each thinning, but they will be irrelevant during the rest of the rotation. Attributes that enhance individual-tree competitive ability may have some advantages for early sawlog production when we might wish some trees to grow rapidly as individuals at their neighbours' expense, but those attributes will be irrelevant for volume, biomass, pulpwood or fuel production per hectare. Indeed, enhanced competitive ability may depress total volume and biomass yields even in sawlog stands, as long as there is inter-tree competition for some of the time, and we should note that, without pruning, competition is the main agent used to alter diameter frequency distributions and such characters as crown development and bole taper. The fact that forest stands derived from multi-clone seed orchards will be far more heterogeneous than pure stands of the inbred crops referred to above makes no difference to the argument: the existence of any proportion of individuals with any degree of superiority in 'isolation' or 'competitive' traits will still be irrelevant to stand yield improvement after canopy closure, and thinning to leave the biggest trees will make the situation worse. Clearly, the tendency to select for 'isolation' traits will be greatest if selections are made in progeny tests before canopy closure, and the tendency to select for 'competitive' traits will be greatest in long-term progeny tests such as those reported on *Pseudotsuga men-*

*ziesii* (NAMKOONG *et al.* 1972) and *Pinus ponderosa* (NAMKOONG and CONKLE 1976) in which there was a change in progeny ranking and an increase in additive genetic variance around the time when inter-tree and inter-progeny competition began. To conclude the argument, the net effect of evaluating progenies, at any age, on the basis of individual tree performance as described above may be to overestimate the true genetic gain in volume yield obtained when the selected genotypes are grown together in stands over a full rotation.

However, these arguments are based largely on analogies with field crops. To the author's knowledge no work has been published in which tree progenies have been evaluated both on a mean tree basis as spaced plants and on the basis of yields per hectare in single-progeny closed stands of at least 10 × 10 trees. Several decades of conventional progeny testing have shown that inherent differences exist within species in spaced plant performance, and inherent differences in competitive ability have been reported within *Pinus elliotii* (SNYDER and ALLEN 1971), *Pinus taeda* (ADAMS *et al.* 1973) and *Populus trichocarpa* (TAUER 1975). But there is little evidence for inherent differences in pure stand performance.

WEARSTLER (1980) grew 17 open-pollinated families of *Pinus taeda* in large pure blocks at three spacings (3, 7 and 10 cm) in a nursery, and found family differences in rate of stand closure, but no differences in maximum average plant size at given densities; he concluded that "spatial limitations on individual growth rates resulted in the elimination of significant family variation in height and diameter". CAMPBELL and WILSON (1973) found no appreciable genotype × spacing interactions among 30 full-sib families of *Pseudotsuga menziesii* grown for 3 years in a nursery (2.5 to 17.8 cm spacings), but their study did not include spaced plants, and was based on 7-tree row plots which, like most progeny tests, favour competitive families rather than 'crop' ideotypes.

The nursery experiments reported here were designed to determine whether tree progenies could be ranked differently depending upon whether they were tested as widely-spaced individuals or in pure stands with within-progeny competition. They should be regarded as pilot studies, a first step taken to see whether the arguments and analogies discussed above apply to trees, and to see whether there might be a problem for tree breeders that warrants further examination in more expensive long-term forest experiments.

In this study progenies of *Picea sitchensis* were used that had already been evaluated to age 4–6 after planting in forest progeny tests. These were grown again from the same seed lots and planted in two separate tests in a nursery. In one, a wide spacing was chosen so that the trees never came into contact, presumed to favour progenies with the attributes of 'isolation' ideotypes, with the expectation that the ranking at age 4 would be similar to that in the forest progeny tests. In the other, each progeny was grown in a pure stand of 10 × 10 trees (inside 2–3 border rows) at very close spacings so that there was inter-tree competition, presumed to favour progenies with the attributes of 'crop' ideotypes.

#### Materials and Methods

Twelve populations of *Picea sitchensis* (BONG.) CARR were studied, classified as follows:

(a) Two provenance standards: Masset, Queen Charlotte

Islands, B.C., Canada, and Hoquiam, Washington State, U.S.A.

(b) Seven open-pollinated progenies of candidate plus trees selected in Scotland (at Borgie, Eilanreach etc.) progeny tested at 4–8 forest sites in upland Britain (but not all at the same sites) and found to be significantly (10–30%) taller than Masset provenance at most sites 4–6 years after planting: 1903 and 1913 Borgie, 333 and 339 Eilanreach, 726 Inverliever, 321 South Strome, 494 Cairn Edward; these are denoted S1, S2 . . . S7, respectively (S = superior at forest sites).

(c) Three open-pollinated progenies with poorer performance at age 4–6: 720 Inverliever tested at 8 sites and 1888 Borgie tested at 6 sites, both poorer than Masset, and K Rose Isle, a below-average member of a 6 × 6 diallel (SAMUEL *et al.* 1972) tested at three sites. Progenies 720, 1888 and K are denoted I1, I2 and I3 (I = inferior at forest sites).

Stratified seeds were sown in paper pots of peat:sand:loam in April 1977, germinated under lights in a heated glasshouse, moved outside in July 1977 and planted in October 1977 in clay loam, pH 5.8, in a nursery at the Bush Estate, Penicuik (55° 51' N, 198 m). In May 1978 the trees were given a liquid feed of NPK and dead plants were replaced; the trees were irrigated in June 1978, regularly hand-weeded and in March 1979 the plots received 300 kg/ha Enmag (20% P<sub>2</sub>O<sub>5</sub>, 11% K<sub>2</sub>O, 9% Mg).

Each of the 12 populations (2 provenances and 10 progenies) was planted in two experiments, (1) in closed stands at 14 cm spacing (51 trees/m<sup>2</sup>) and (2) as widely-spaced trees at 1.4 m spacing. There were two replicate blocks per experiment, with 10 × 10 trees per sample plot in the closed stands, and 4 × 4 trees per plot in the widely-spaced experiment, with guard rows as shown in *Figure 1*. Environmental differences between blocks and experiments were minimized by planting them together in an area of the nursery which had been rotovated annually and left fallow for 5 years prior to planting, and also by applying uniform fertilizer and irrigation treatments as described above.

Tree heights were measured after establishment in November 1978, providing initial values for covariate analysis. Final assessments were made during the winter of 1980/81, four growing seasons after germination, before there was more than 5% competition-driven mortality in the closed stands, and while the guard rows in these stands still provided protection from serious edge bias (the guard areas were 42 cm deep, and sample trees averaged 67 cm in height at sampling; *Fig. 1*). All experimental trees were measured for height, previous year's height and basal diameter over and under bark. Above-ground oven-dry weights were determined on 8 trees (out of 16) per population in both blocks in the widely-spaced experiment, and 20 trees (out of 95–100 living trees) per population in one of the two blocks of the closed stand experiment, with check samples from the other block. In all instances the sample trees were chosen to span the complete size range. Stem sections were taken at the bases of sample trees and used to determine basal areas in 1980 and 1979. Under-bark diameters in 1979 were then estimated from linear regressions of 1980 under-bark diameter on 1980 basal area.

Allometric regression equations of the form

$$\log_e y = a + b (\log_e D^2 H)$$

where  $y$  = tree dry weight,  $D$  = under-bark diameter,  $H$  = height,  $b$  = allometric coefficient and  $a$  = constant

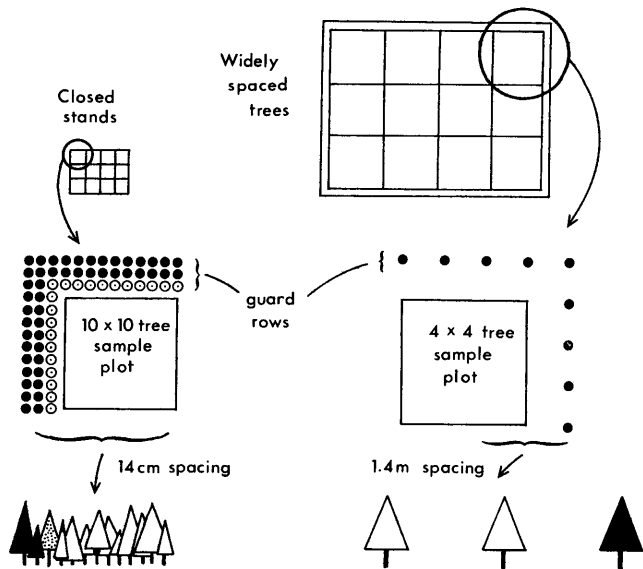


Figure 1. — Experimental layout of 12 populations of *Picea sitchensis* in one replicate block of miniature closed stands and one block of widely-spaced trees. ● guard trees of Queen Charlotte Islands provenance, ○ guard trees of the same genetic constitution as the sample plot. The trees drawn at the base of the figure are approximately to scale.

(OGAWA and KIRA 1977) were calculated for total above-ground (stems, branches and needles) and stem dry weights per tree, separately for each population in each of the two experiments, using trees sampled from both of the widely-spaced blocks (i.e. 16 sample trees per regression, compared with 20 sample trees for each closed stand regression). The regression equations were significantly different between populations, and check samples taken from the second closed stand block confirmed that treatment differences were consistent between blocks. Twenty-two of the 24 equations calculated for the closed stand experiment (total above-ground and stem weights for 12 populations) had  $r^2$  values exceeding 0.9, and 19 of those calculated for the widely-spaced experiment had  $r^2$  values exceeding 0.8; none accounted for less than 65% of the variation.

These equations were used to estimate the dry weights of unsampled trees and of sampled trees one year previously, assuming that the allometric coefficients between tree weights and  $D^2H$  were the same in 1979 as in 1980. A duplicate set of allometric regression equations was then calculated as above, but with  $y$  = annual increment in total above-ground or stem dry weight during 1979–1980 (4th year after germination). In all instances, when transforming dry weight values from logarithmic to arithmetic units, the transformed value  $y'$ , was taken as  $y' = \exp(u + \sigma^2/2)$  where  $u$  = observed dry weight in logarithmic units and  $\sigma^2$  = sample variance. Omission of this correction would have resulted in slight underestimates of dry weight values (BASKERVILLE 1972).

Analyses of variance were carried out separately for the closed stand and widely spaced experiments (12 populations, 2 replicate blocks) with and without heights in 1978 as an adjustment covariate.

## Results

### Heights

During their third and fourth growing seasons (i.e. the two seasons before harvest) the widely-spaced trees, which never came within 0.5 m of each other (see Fig. 1), grew

on average from 25 cm to 52 cm to 90 cm tall, whereas the trees in closed stands, which closed canopy in their third year, grew on average from 21 cm to 46 cm to 67 cm tall. That is, inter-tree competition decreased final tree heights by an average of 26%.

At age 4 the height rankings of populations grown as widely-spaced trees was broadly similar to that found in forest progeny trials (with the exception of I1) with or without covariance adjustment on initial heights. Thus, all seven superior progenies (S1 . . . S7 in Fig. 2) which were significantly taller than Masset 4–6 years after planting in most forest trials, were taller than Masset in this experiment, and also taller than both Hoquiam and inferior progenies I2 and I3 (Fig. 2). However, progeny I1 performed much better in these nursery trials than in forest trials.

When the populations were grown in closed stands none of the 'superior' progenies (as determined in forest trials) grew significantly taller than Masset provenance or inferior progenies I2 and I3 with or without covariance adjustment; indeed the tallest progeny was I1. There was no significant correlation between population rankings as widely-spaced trees and in closed stands.

### Stem diameters and basal areas

At age 4, the mean over- and under-bark basal stem diameters of widely-spaced trees were 24 mm and 19 mm, and of closely-spaced trees, 9.5 mm and 7.5 mm, respectively. Basal areas over- and underbark averaged the equivalent of 38 and 24  $m^2/ha$  in the closely-spaced plots. Thus, the latter had basal areas comparable to those of mature forest stands, and inter-tree competition decreased mean diameters and basal areas per tree by about 60% and 85%, respectively.

Whereas all of the seven superior progenies were taller as widely-spaced trees than Masset, Hoquiam, I2 and I3 (significantly so, taking the means), only S2, S3 and S5 were greater in basal stem diameter or basal area per tree (Fig. 3). Again, in closed stands none of the seven superior progenies were significantly greater in mean diameter or basal area per tree (or basal area per unit ground area) than the provenance standards nor I2 and I3, and only I1

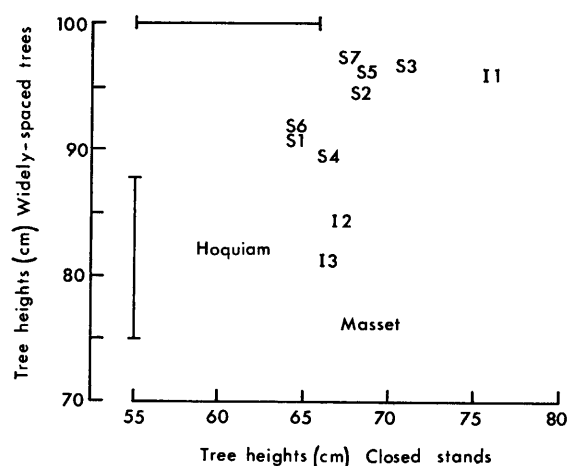


Figure 2. — Mean heights of 12 populations of *Picea sitchensis* (Masset and Hoquiam provenances, and 10 progenies) at age 4 when grown in a nursery as either widely-spaced trees or in closed stands. Values have been adjusted by covariance on initial heights. S denotes a progeny with superior height at age 4–6 in replicated forest trials relative to Masset; I denotes a progeny with inferior height at age 4–6 in forest trials. The vertical and horizontal bars denote least significant differences at  $P = 0.05$ .

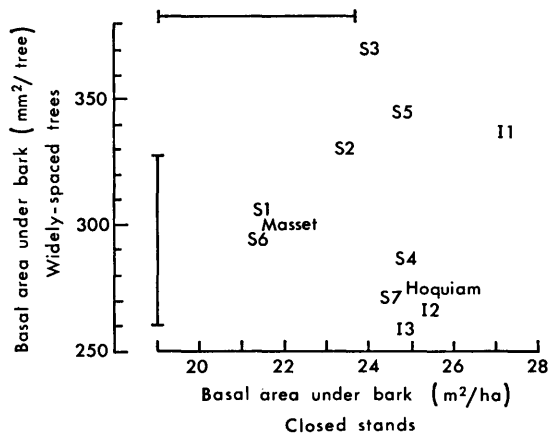


Figure 3. — Mean basal areas of 12 populations of *Picea sitchensis*. See legend to Figure 2.

was significantly greater than Masset. Again there was no significant rank correlation between the diameter growth of populations grown as widely-spaced trees and in closed stands.

#### Tree weights

The mean total above-ground dry weight of widely-spaced trees was 363 g/tree, of which 91 g/tree was stem (wood and bark). It was estimated that total and stem dry weights increased by 262 g/tree and 71 g/tree, respectively, during the year before harvest (4th growing season); that is, about 75% of the final dry weight was accumulated during the previous season. The mean total above-ground dry weight of the closed stands was 17.8 t/ha, of which 7.6 t/ha was stem (there were 48–51 trees/m<sup>2</sup>). Mean net total and stem dry weight increments during the previous season were estimated to be 11.5 t/ha and 4.5 t/ha, respectively (excluding a small amount of needle fall) that is, about 60% of the final dry weights. Because so much of the final dry weight had been produced in the fourth year, population rankings in dry weight increment during that year were similar to those in final dry weight and need not be reported separately. The mean proportion of stem to total dry weight was 43% in closed stands (39% of the net increment in the previous year) compared with 25% on the widely-spaced trees (27% of net increment the previous year).

Progenies S2, S3, S5 and I1, that were both relatively tall and large in mean diameter as widely-spaced trees, were inevitably large in total above-ground dry weight, because dry weights were closely correlated with D<sup>2</sup>H. However, only 21–26% of the total dry weights of progenies S2, S3 and I1 consisted of stem, compared with 31% on S5, so that only the latter was significantly greater than Masset, Hoquiam, I1 and I2 in stem dry weight per tree (Fig. 4).

In closed stands progeny I1 which had grown more in height and basal area than the other progenies, also produced more total and stem dry matter per unit ground area. But none of the superior progenies was in any way superior in total or stem dry weight production in closed stands.

#### Discussion

Although the experiments reported here were done on juvenile trees in nursery conditions and with only two replicate blocks per experiment, they provided evidence supporting the views that (a) progenies can be ranked very

differently when evaluated in pure stands rather than as isolated trees, and/or (b) some progeny differences in individual tree performance might be eliminated after stand closure in pure stands, as WEARSTLER (1980) found for *Pinus taeda*. Equally disturbing, but no less surprising, was the fact that progeny rankings depended upon whether the criterion was height, basal area, total above-ground or stem dry weight.

In this experiment progeny performances in isolation were neither positively nor inversely related to performances in closed stands. Progenies that were either superior or inferior as widely-spaced trees could be very similar in closed stands, both in height and diameter per tree and in biomass production per unit area. Progenies S1 to S7 which had been identified as superior relative to Masset provenance on the basis of mean individual tree height at age 4–6 in forest progeny tests, and which also grew relatively tall as widely-spaced trees in this nursery study, were not significantly greater in height, basal area or biomass in closed stands relative to Masset and three inferior progenies. These superior progenies did not, apparently, use environmental resources efficiently in conditions of inter-tree competition. There was no evidence that they were very inefficient either, that is, that selection for performance in isolation would depress current annual increment in biomass or volume per hectare in closed stands. Rather, the evidence was that selection in progeny tests at age 6 might be ineffective at increasing productivity per hectare after stand closure. This finding is in accor-

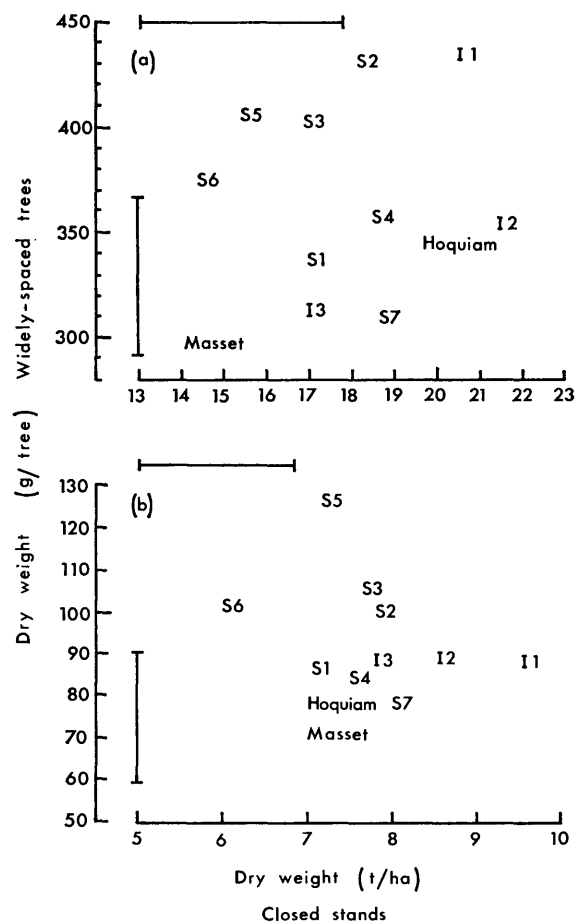


Figure 4. — (a) Total above-ground dry weights (stems, branches and needles) and (b) stem dry weights, of 12 populations of *Picea sitchensis*. See legend to Figure 2.

dance with theory (STERN 1969), with the experience of some field crops (DONALD and HAMBLIN 1976) and with data on some undomesticated herbaceous plants (HARPER 1977).

The important implication for tree breeding is that the normal process of selection on the basis of mean individual tree performance in progeny tests may overestimate genetic gain measured in terms of biomass or volume yield per hectare over a full rotation — with the possible exception of heavily-thinned sawlog stands. Note that this is not the same as saying that juvenile-mature correlations may be weak. Juvenile evaluation in progeny tests may favour juvenile 'isolation' ideotypes, while mature-tree evaluation after canopy closure may favour mature 'competition' ideotypes, unless it can be shown that there is no appreciable inter-progeny competition (HÜHN, 1974): this study suggests that neither may have the attributes of 'crop' ideotypes.

Unfortunately it will rarely be possible or cost-effective to test tree progenies in large, pure, single-progeny blocks on heterogeneous forest sites, in the same way as done in this study, and in field crop studies. It is, therefore, even more important for trees than for field crops to be able to define a set of 'crop' ideotypic traits that can be identified on individual, isolated plants. Several field crop breeders have attempted to do this, for instance the wheat 'crop' ideotype is said to have short, stiff straw, erect leaves and a high harvest index (SYME 1972; FISCHER and KERTESZ 1976; DONALD and HAMBLIN 1976).

It has been suggested that the 'crop' ideotype for some north-temperate conifers will have a long, narrow, pointed crown, short, thin, hanging branches, thin bark and a high shoot/root ratio (see LEDIG 1975; CANNELL 1979; ANON 1980) but this is based more on theory than on evidence. From crop physiological principles it is possible to say what stand characteristics are likely to be desirable: large leaf area indices spread over large vertical distances, rapid and efficient nutrient cycling, low maintenance respiration rates, high photochemical efficiency of shaded foliage and so on (KIRA 1975; JARVIS *et al.* 1976; CANNELL 1979), but it is difficult to identify these characteristics on individual trees. And the situation is further complicated by the fact that trees, like most plants, modify their structure and physiology when subjected to competition, and this phenotypic plasticity is itself probably under genetic control (BRADSHAW 1965).

In this study there were no striking differences in crown form between progeny I1 which performed best in closed stands and S6, which performed worst, and the physiological basis of the difference in ranking of progenies as widely-spaced trees and in closed stands is unknown. Progeny I1 (720 Inverliever) was found in other studies to have a more prolonged period of shoot elongation than the other progenies (equal to Hoquiam, suggesting that some of the parent trees at Inverliever were of Washington provenance) and in a seedling progeny × environment study I1 responded very favourably to protection in a nursery and glasshouse. This may explain why I1 grew so much larger relative to other progenies in this nursery test than at forest sites, and why it grew well in the microclimate of closed stands.

In conclusion, I submit that this pilot study has identified a potential problem in tree breeding that justifies further study. More experiments are needed to identify single-tree characters that are correlated with high performance in closed stands. More importantly, more forest experiments should be planted in which progenies (or groups of progenies) that differ in individual-tree performance are

planted in large pure blocks, big enough to be able to subject them to given silvicultural thinning regimes without edge bias. Only then will it be possible to judge whether the suggested bias towards 'isolation' and 'competition' ideotypes in progeny tests has a serious or trivial impact on estimates of genetic gain over a full rotation.

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#### REVIEW:

## Isolation, Culture, and Fusion of Protoplasts: Problems and Prospects\*

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#### Summary

The status of protoplast research in plants, including herbaceous and tree species, is reviewed. Methods for isolation, culture, and fusion of plant protoplasts are discussed. Protoplasts can be isolated and cultured from a wide range of higher plants, both herbaceous and tree species. However, sustained cell divisions leading to callus formation have been achieved only in a limited number of plant species. Plant regeneration from protoplasts is still a rare event and has been reported in some 12 genera, more than half of which belong to the family *Solanaceae*. Protoplast fusion leading to somatic hybrids in intraspecific interspecific, and intergeneric combinations have been reported in a limited number of plant species. Most somatic

hybrids are genetically unstable and exhibit chromosomal and phenotypic variability. The availability of genetic variability in the somatic hybrids, and the fact that protoplasts are efficient experimental system for uptake of cell organelles, microorganisms, and macromolecules, offer far reaching possibilities for genetic modification and improvement of plant species.

**Key words:** Protoplast, isolation, culture, fusion, growth and differentiation, herbaceous and tree species, somatic hybrids, genetic variability, genetic modification, plant improvement.

#### Zusammenfassung

Es wird über den Stand der Protoplastenforschung bei Pflanzen, sowohl bei krautigen Arten als auch bei Baumarten berichtet. Methoden zur Isolierung, Kultur und Fusion von Protoplasten werden diskutiert. Bei einer Vielzahl von krautigen Arten und Baumarten ist die Isolierung und Kultur von Protoplasten möglich. Jedoch ist bei einer geringen Zahl von Arten die Bildung von Kallus, die nach anhaltender Zellteilung entstehen, erreicht worden. Die Regeneration von ganzen Pflanzen aus Protoplasten ist immer noch ein seltenes Ereignis und ist für Arten von 12 Gattungen berichtet worden, mehr als die Hälfte davon gehört zur Familie der *Solanaceae*. Von Protoplastenfusionen, die zu somatischen Hybriden innerhalb und zwischen Arten sowie zwischen Gattungen führen, sind nur in wenigen Arten berichtet worden. Die meisten somatischen Hybriden sind genetisch instabil und zeigen chromosomale und phänotypische Variabilität. Die Verfügbarkeit genetischer Variabilität in somatischen Hybriden und die Tatsache, daß Protoplasten als Versuchssysteme für die Aufnahme von Zellorganellen, Mikroorganismen und Makromolekülen geeignet sind, bieten viele Möglichkeiten für genetische Modifikationen und Verbesserungen von verschiedenen Pflanzenarten.

#### I. Introduction

Recent advances in organ, tissue, cell, and protoplast culture technology have opened up new avenues for con-

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