Evidence of an Unbalanced Mating Pattern in a Seed Orchard Composed of Two Larch Species

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Summary

Mating patterns of a larch seed orchard composed of one clone of *Larix sibirica* and 6 clones of *L. decidua*, were investigated using allozymes as genetic markers. The studied orchard was designed to produce interspecific hybrid seeds. It was found that the orchard constitutes a population with a mating system that is far from panmixis. Studying outcrossing rates of individual clones by the *mixed-mating model*, some of the symptoms of non-random mating could be detected. They ranged between 0.096 for the Siberian larch clone, and 0.952 to 1.019 for the European larch clones. However, the most profound insight into the mating patterns was possible through the use of the *mating model* methods. Detailed *mating model* analyses revealed that the Siberian larch pollinated almost 93% of all sampled ovules, while the remaining European larches only 7%, with some clones contributing less than 0.2% of all pollen gametes. The effectiveness of Siberian larch as a pollinator could be explained by its high flowering abundance and earlier flowering phenology, as well as by the specific design of the orchard, where a half of the grafts were of Siberian larch. The *neighborhood model* (variant of the *mating model*) applied in this study indicated that fecundity of males and their distance to maternal trees significantly influenced male mating success. The *mating model* studies allowed also for an in-depth analysis of hybridization patterns. Its level for European larches functioning as females averaged on 93.9%, while only 10.5% Siberian larch seeds were hybrids, which has significant implications for forest tree improvement programs. The advantages of applying the *mating model* approach in the studies of mating systems of forest trees, mainly seed orchards, are briefly discussed.

Key words: *Larix decidua*, *Larix sibirica*, allozymes, mating system, hybridization, mixed-mating model, neighborhood, paternity analyses, mating success, seed orchard.

FDC: 165.41; 181.521; 232.311.3; 174.7 *Larix decidua*; 174.7 *Larix sibirica*; (480).

Introduction

The last decades significantly benefited from progress in developing mating system estimation procedures in conifers (NEALE and ADAMS, 1985; RITLAND and EL-KASSABY, 1985; ADAMS and BIRKES, 1989) and many studies of mating systems have been done in natural and seed orchard populations (see for references: MUONA, 1990; ADAMS and BIRKES, 1991; MITTON, 1992; WHEELER and JECH, 1992). The analyses of mating patterns in seed orchards have theoretical as well as great practical importance. Knowledge of these patterns makes it possible to evaluate the genetic compositions of seed orchard crops and factors influencing their quality, including levels of inbreeding, variation in male fertility, patterns of pollen dispersal and amounts of background pollination. Thus, good estimates of mating system parameters are necessary for the proper management of existing orchards, as well as for planning breeding programs and designing seed orchards in the future (MUONA, 1990).

The most widely used procedure for estimating plant mating systems is application of the *mixed-mating model* to genotypic arrays of mother plant offspring (FYFE and BAILEY, 1951; BROWN and ALLARD, 1970; NEALE and ADAMS, 1985; RITLAND and EL-KASSABY, 1985). This model makes several assumptions, one or several of which are usually violated (BROWN et al., 1985; MITTON, 1992). The postulates are almost never met in small populations composed of few genotypes, mainly because of large differences in male fecundity or self-fertility.

Isozymes as genetic markers are ideally suited for *paternity* and *mating model* methods recently developed for mating system analyses of plant populations (SCHOEN and STEWART, 1986; DEVLIN et al., 1988; ROEDER et al., 1989; ADAMS et al., 1992; BURCZYK et al., 1996; BURCZYK and PRAT, 1997) and interest in such studies greatly increased (BROYLES and WYATT, 1990; MEAGHER, 1991; DEVLIN et al., 1992; SMOURS and MEAGHER, 1994). This type of analyses appear to be very useful in predominantly outcrossing species, including most coniferous trees (HAMRICK and SCHINABEL, 1985). The traditional *mixed-mating model* partitions mating events into 2 types – selfing or random outcrossing. Its application in coniferous populations explained very little, since their selfing accounted usually for less than 10% of successful fertilizations (MUONA, 1990; ADAMS and BIRKES, 1991), however patterns of outcrossing remained generally unknown. Outcross mating patterns can be investigated using *paternity methods* (DEVLIN et al., 1988). Once pollen parents of a large sample of offspring have been inferred, mating patterns can be directly determined (WHEELER et al., 1993). However, in order to obtain precise estimates exclusion probabilities (probabilities of being able to exclude potential males on the basis of genetic incompatibility alone) need to be high and the population must be isolated from external pollen sources (DEVLIN et al., 1988; ADAMS and BIRKES, 1989).

In the *modeling approach* a theoretical mating model, designed to account for the distribution of genotypes in offspring (or pollen gametes in conifers), is applied to genotypic arrays of actual offspring and the mating parameters are estimated using various statistical procedures (e.g. maximum-likelihood). Reports to date indicate that these methods, including the *neighborhood model* (ADAMS and BIRKES, 1989, 1991), may be powerful tools when investigating different aspects of mating systems in forest trees (SCHOEN and STEWART, 1986; ADAMS, 1992; BURCZYK et al., 1996; BURCZYK and PRAT, 1997).

Our knowledge on mating behavior in seed orchards is still insufficient. Establishment of advanced generation seed orchards may involve the use of very few highly selected clones (ZOBEL and TALBERT, 1984) and the knowledge of mating
patterns in such orchards seems to be very important for their proper management. Although there are many papers describing outcrossing levels in multiclonal orchards, the investigations in seed orchards established with a few clones only are lacking (MÜLLER-Starck and GREGORIUS, 1988). Hybrid orchards may also play an important role in advanced breeding programs. They are especially promising for larch (PAQUES, 1989) and results of some studies of mating patterns in hybrid larch seed orchards have recently been reported (BERGMANN and RÜTZ, 1987; HACKER and BERGMANN, 1991; ENNOS and QIAN, 1994; LEWANDOWSKI et al., 1994). Presence of individuals from 2 species increases the potential for complexity in mating patterns due to the presence of restricted and perhaps directional hybridization. The assumption of random mating in such cases is probably totally unwarranted. A question then arises as to the best approach for evaluating mating patterns in orchards of this type.

The aim of this study was to investigate mating patterns in a larch orchard composed of one clone of Larix sibirica and a few clones of Larix decidua. It was hoped that Larix sibirica would act as the seed parent, since only hybrid seed (or selfs) would be found in this case. The interesting aspects of this orchard are the small numbers of clones and the absence of background pollination (no larch trees growing in surrounding stands) which can confound results of mating system analyses. In this paper using isozymes as genetic markers we studied the mating patterns based on various statistical procedures.

### Materials and Methods

The Nahkamäki seed orchard is located in Central Finland (62°13′N, 25°24′E). The orchard is surrounded by a Norway spruce (Picea abies (L.) Karst.) forest and no larch trees are found within a distance of several kilometers from the orchard. The orchard consists of 7 clones: 1 clone of Siberian larch (Larix sibirica Ledeb.) (E1037 Raivola; initially originating from Arkhangelsk Province, Russia), and 6 clones of European larch (Larix decidua Mill.) (E1127 – from Switzerland; E1136 – from Scotland; E1138 – from Germany; E1139 – from France; E1149 and E1150 – from Austria). All the scions of the clones were collected from stands growing in the Punkaharju Research Station in Finland. In 1962, about 400 grafts were planted in an area of 1 ha at a 5 m x 5 meters spacing. One half of the grafts consisted of the Siberian larch and the other half of the European larch clones. The grafts of Siberian larch were distributed in the orchard in a systematic chequerboard pattern, while European larch clones were distributed randomly among the Siberian larch grafts. In Autumn 1991, at the time of seed collection, there were 118 grafts of Siberian larch and 98 of European larch (ranging from 7 to 22 ramets per clone) still alive in the orchard.

Cones were collected from 5 ramets of clones E1037, E1127, E1138 and E1139; 4 ramets from clone E1150, and only 1 ramet from clone E1149. About 20 seeds per graft were analyzed electrophoretically, with the total sample size being 507 seeds. The percentage of full seeds was determined by x-ray analysis. Genotypes of all clones in the orchard were determined based on megagametophytes of sampled seed, except clone E1136 due to the lack of seed. Based on flowering data, we assumed that clone E1136 did not produce pollen, or if any, its contribution was not significant compared to the others. Consequently, this clone was excluded as a potential father in the mating system analyses. Because of small number of seeds (20) sampled from clone E1149, it was not possible to obtain individual mating system parameters for this clone. However, the seeds of clone E1149 were included for calculating pooled estimates.

The seeds were subjected to standard horizontal starch gel electrophoresis, with methods similar to those described by Conkle et al. (1982), and Cheliak and Pitel (1984). We tried to analyze several enzyme systems, however only 4 systems revealed polymorphism, enabling precise genetic interpretation at 4 loci. Genotypes of megagametophyte and embryo seed tissues were determined based on 4 loci: fluorescent esterase (E.C. 3.1.1.1; locus Fest-2), malate dehydrogenase (E.C. 1.1.1.37; locus Mdh-3), shikimic acid dehydrogenase (E.C. 1.1.1.25; locus Shdh), and phosphoglucomutase (E.C. 2.7.5.1; locus Pgm-1). Pollen (paternal) contribution to each embryo was determined by assaying the haploid megagametophyte and the diploid embryo.

### Statistical procedures

Mating patterns were investigated using the 3 general methods: mixed-mating model, mating model and neighborhood model approach. First, we used a standard mixed-mating model for estimating outcrossing rates (versus selfing). The model accounts for haploid genotypes in pollen gametes, assuming all matings due either to self-fertilizations (with probability s) or random outcrossing (t = 1-s). To estimate t, the model was applied to the observed pollen gamete data using maximum-likelihood procedures developed for conifers (Ritland and El-Kassaby, 1985). Outcrossing rates were calculated for the population as a whole (population-wide estimate), as well as for individual clones. Progeny arrays from ramets of the same clone were pooled together to analyze inter-clonal variation in outcrossing rate.

#### Mating model

The mating model was developed following Roeder et al. (1989) and modified for conifer data. The model assumes that a pollen gamete successful in fertilizing a viable offspring come from one of the individuals acting as male parents. In the model applied, the probability of observing a multilocus genotype $g_j$ in pollen gametes of the sampled offspring is:

$$ P(g_j | F_i) = \sum_j \phi_j P(g_j | F_i) $$

where $P(g_j | F_i)$ is the transition probability for the $j$-th (out of $r$) male to contribute to genotype $g_j$. It defines the proportion of a multilocus haploid genotype $g_j$ among all possible gamete types produced by a male tree, and it depends on segregation likelihoods. It ranges from 0, when a gamete $g_j$ may not be produced by a parent, to 1, when all gametes produced by a parent have multilocus genotype $g_j$ (parental tree homozygous for all loci). The $\phi_j$ parameter indicates mating success of the $j$-th male (male fertility). The number of potential outcross males is restricted to the number of different clones. If the model is applied to the offspring sampled from an individual mother tree, its paternal contribution to the offspring indicates the proportion of self fertilization.

Individual fertilities ($\phi_j$) were estimated by fitting the model to multilocus pollen gametic arrays in the offspring of individual clones (offspring pooled across ramets of the same clone) and the entire offspring sample using maximum likelihood (ML) methods (RAO, 1973) following the EM-algorithm (Roeder et al., 1989). Consecutive approximations of estimated parameters were calculated using the formula:

$$ \phi_j' = \frac{1}{N} \left( \sum_{i=1}^{S} \frac{P(g_j | F_{ij})}{P(g_j)} \right) \cdot \phi_j $$

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Successive values of $\theta_j^*$ were incorporated into equation 1 in order to calculate new $P(g_j)$ probabilities for every iteration. Iterations continued until all parameters converged to specified criteria (here, differences between consecutive estimates less than 0.001).

Individual fertilities calculated from the mating model were compared to those inferred basing on fractional paternity assignment (Devlin et al., 1988). Paternity of each offspring is assigned fractionally to non-excluded males (based on genetic compatibility) in proportion to their transition probabilities. In contrast to other paternity methods, paternity is assigned to all progeny, but some progeny will not be assigned a single male parent (Adams, 1992). Once pollen parents of a sample of offspring have been inferred, mating patterns can be directly determined.

Standard errors of individual fertility estimates, calculated basing on mating model and fractional paternity assignment, were approximated using the bootstrap method with resampling of progeny arrays (Efron, 1979). This was done following 500 simulations (“bootstraps”).

**Neighborhood model**

In order to determine potential factors influencing the individual male mating success (male fertilities) we applied the neighborhood model (Adams and Birkes, 1989). In this model, an arbitrarily specified area around a mother tree (from which seeds are sampled) is designated its neighborhood. The neighborhood size in this study was established as 30 meters in radius, which included, on average, about 45 flowering trees (potential outcrossing pollen parents) around each mother-tree graft. This model partitions effective matings into tree groups: selfing, outcrossing within the neighborhood, and outcrossing with males outside the neighborhood (gene flow) (Adams and Birkes, 1989, 1991; Adams, 1992). However, because in this study there was no larch trees growing around the orchard, and because no detectable pollen contamination from non-orchard sources was found, we assumed that all matings occurred within the orchard. On the other hand, the neighborhood size of 30 m in radius included generally all clones growing in the orchard. This made it impossible to separate outcrossing events with males located within a designated neighborhood, from outcrossings with trees located outside the neighborhood though still in the orchard. Taking into account the above considerations, we did not estimate the proportion of pollen migrant from outside the neighborhood.

Specific objectives of the neighborhood model analyses were to determine proportion of selfing ($s$), the effect of fecundity ($\gamma$) of male trees and of the distance ($\beta$) of males to the mother trees, on their mating success. For this purpose, progeny arrays were structured by sampled ramets and all flowering ramets, included within a neighborhood, were considered as potential fathers. In the model applied, the probability of observing multilocus genotype $g_i$ in the pollen gametes of offspring from the mother tree was

$$P(g_i) = sP(g_i|M) + (1-s) \sum_{j=1}^{c} \phi_j P(g_i|F_j)$$

where $s$ is the probability of selfing, $P(g_i|M)$ is the transition probability that the mother tree (or other ramets of this clone) produces gametes with genotype $g_c$ and $P(g_i|F_j)$ is the transition probability for the $j$-th (out of $r$) outcross male in the neighborhood (excluding grafts of maternal clone) to contribute to genotype $g_i$.

In this model, the mating success of each outcross male in the neighborhood ($\phi_j$) is assumed to be influenced by one or more factors in the order of an exponential function. In this study, we chose the pollen fecundity of the male and the distance of the male from the maternal tree as factors expected to influence mating success of individual males. Thus, the model (containing the two selected factors) was defined as:

$$\phi_j = e^{\beta d_j + \gamma f_j}$$

where $d_j$ and $f_j$ indicate respectively the distance and the pollen fecundity of the $j$-th male in the neighborhood. $\beta$ and $\gamma$ are the respective parameters describing the effect of particular factors. Pollen fecundity scores were expressed as number of male strobili per tree and were averaged among ramets of a clone, thus for every ramet of a particular clone the same fecundity score was assigned. Unfortunately, pollen fecundity data from 1990 (flowering season resulting in 1991 seed crop) was not available, but we did have data available for 1984. Field observations carried out in spring 1991 generally confirmed the clonal pollen fecundity rank as observed in 1984.

The three parameters ($s$, $\beta$, $\gamma$) were estimated by fitting the neighborhood model to the multilocus pollen gametic arrays in the offspring of individual mother trees using ML methods based on numerical procedures, that involved Fisher’s method of scoring (Newton’s method) (Rao, 1973). Parameters were estimated for individual clones (offspring pooled across ramets of the same clone) as well as jointly for a combined sample over all mothers. This was done using the NEIGHBOR computer program (Burczyk et al., 1993). Details on statistical procedures employed in the NEIGHBOR program were reported elsewhere (Burczyk et al., 1996). The significance of the mating system parameters were tested by the log-likelihood ratio test (Rao, 1973) or by analyzing limits of their confidence intervals.

**Results**

Mixed-mating model outcrossing rate

The population multilocus outcrossing rate ($t_{ml}$) was estimated to be 0.956, and was not significantly different from $t = 1.0$. Individual clonal outcrossing rates ($t_{cl}$) were calculated when pollen gene frequencies ($p$) were allowed to vary among clones (joint $t_{ml}$ and $p$ estimation) (Ritland and El-Kassaby, 1985). The outcrossing estimate calculated for Siberian larch was extremely low, accounting for only 9.6% of outcrossing. The highest value was observed for clone E1150, and it was 1.019 (Table 1). The estimate for clone E1138 did not converge.

<table>
<thead>
<tr>
<th>Clone</th>
<th>$t_{cl}$ (SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>E1037</td>
<td>0.096 (0.007)</td>
</tr>
<tr>
<td>E1127</td>
<td>0.952 (0.040)</td>
</tr>
<tr>
<td>E1139</td>
<td>0.982 (0.033)</td>
</tr>
<tr>
<td>E1150</td>
<td>1.019 (0.125)</td>
</tr>
</tbody>
</table>

| mean $t_{cl}$ | 0.762 |

Estimates for clone E1138 did not converge.
Mating model

Mating model provided estimates of male fertilities of clones realized among the offspring (seeds) of individual clones functioning as mothers (Table 2). The largest contribution was achieved by Siberian larch clone, and the estimate for the pooled sample accounted for more than 92.5% of all successful fertilizations. Among European larches only E1138 fertilized more than 5% (6.28%), with others generally much below 1%. A similar pattern was observed, when the progeny of individual maternal clones was considered. When the paternal contributions of individual clones into the offspring of every clone were estimated we could simply determine individual selfing rates. They ranged from 0 for the clone E1150 to 0.895 for E1138 (Siberian larch) (Table 2).

Table 2. – The estimates of paternal contribution (male fertilities) of individual clones into the progeny of individual clones functioning as mothers, based on mating model (a) and fractional paternity assignment (b) approaches.

(a) mating model approach:

<table>
<thead>
<tr>
<th>Clone</th>
<th>Paternal contribution</th>
<th>log. likelihood</th>
</tr>
</thead>
<tbody>
<tr>
<td>E1037</td>
<td>0.8950</td>
<td>-159.5079</td>
</tr>
<tr>
<td>E1127</td>
<td>0.9538</td>
<td>-160.7599</td>
</tr>
<tr>
<td>E1138</td>
<td>0.9638</td>
<td>-147.8900</td>
</tr>
<tr>
<td>E1150</td>
<td>0.9854</td>
<td>-114.9601</td>
</tr>
</tbody>
</table>

(b) fractional paternity approach:

Sampled | Paternal contribution | log. likelihood |
---------|-----------------------|----------------|
| E1037   | 0.6764                | -119.1526      |
| E1127   | 0.7042                | -104.4747      |
| E1138   | 0.6640                | -105.3293      |
| E1150   | 0.7390                | -100.8411      |

The mating pattern generated in the table 2, was analyzed in a $f \times m$ contingency table (where $f$ and $m$ were the numbers of functional females and males, respectively) by means of a G-test, to test for any incorporated heterogeneity (SOKAL et al., 1981). Contribution of fathers was significantly different ($P < 0.001$) from the expectation of even contribution (null hypothesis $\theta = 1/\gamma$, where $r$ is the number of potential fathers). However, the proportions of male contributions was not heterogeneous across sampled females. One of the clones (E1138) sired females in significantly ($P = 0.004$) different proportions, than the rest of the clones (heterogeneous mating success). While most clones contributed more or less similar proportions of male gametes to every female, the clone E1138 differed in that contribution. Relative contributions of E1138 to the progeny of females E1037 and E1139 were higher than to the other clones.

The estimates of individual fertilities inferred based on fractional paternity assignment were lower for the Siberian larch clone and greater for the clones of European larch compared to the mating model estimates (Table 2). DEVLIN et al. (1988) found, that if substantial differences in fertilities exist in the mating population then the fractional paternity method gives the fertility estimates biased toward the null hypothesis (equal fertilities). The bias may exist additionally due to relatively low exclusion probabilities observed in this study (mean 0.55), which were determined empirically (ROEDER et al., 1989; ADAMS, 1992). For each individual sampled mother tree the haploid genotype of a pollen gamete was generated randomly basing on diploid genotype of a randomly chosen potential father. The exclusion probability was calculated as the proportion of males which are excluded for each generated pollen gamete and it was averaged over all generated gametes following 10000 simulations per sampled mother tree (ROEDER et al., 1989).

Neighborhood model

The neighborhood model, applied to all maternal trees analyzed jointly, demonstrated that all mating system parameters ($s$, $\beta$, $\gamma$) were significant in explaining mating patterns occurring within neighborhoods (Table 3). Seling ($s$) accounted for 0.150 (outcrossing, assuming $t = 1$-s, was 0.850). An estimate of selfing of individual clones was obtained only for the Siberian clone (E1037), and was similar to selfing inferred from the outcrossing rate ($s = 1-t$) calculated basing on the mixed-mating model (0.940 vs. 0.904). Selfing estimates were not possible to obtain for the other clones, as the model including this parameter did not converge, but probably $s$ is actually close to 0. Thus we excluded seling from the model, estimating only the remaining parameters. However, for clone E1150 only the $\gamma$ parameter was estimable. Distance effect appeared to be significant only for the pooled sample ($\beta = 0.2132$; $P = 0.038$), but not for individual clones (Table 3). The negative value indicates that mating success decreased with distance increase. In contrast, fecundity effect was significant ($P < 0.0001$) for the pooled sample and for all except the Siberian larch clone. The positive $\gamma$ estimates show that the more fecund trees contributed more pollen to the progeny.

Table 3. – The estimates of seling rate ($s$), distance ($\beta$ and fecundity ($\gamma$) effect calculated using the neighborhood model (standard errors in parentheses).

<table>
<thead>
<tr>
<th>Clone</th>
<th>$s$</th>
<th>$\beta$</th>
<th>$\gamma$</th>
<th>log. Likelihood</th>
</tr>
</thead>
<tbody>
<tr>
<td>E1037</td>
<td>0.9399$^a$</td>
<td>0.0591</td>
<td>-0.0063</td>
<td>-162.5258</td>
</tr>
<tr>
<td>E1127</td>
<td>–</td>
<td>-0.0096</td>
<td>0.0007$^a$</td>
<td>-160.8849</td>
</tr>
<tr>
<td>E1138</td>
<td>–</td>
<td>-0.0129</td>
<td>0.0008$^a$</td>
<td>-149.7738</td>
</tr>
<tr>
<td>E1139</td>
<td>–</td>
<td>-0.2901</td>
<td>0.0003$^a$</td>
<td>-170.1384</td>
</tr>
<tr>
<td>E1150</td>
<td>–</td>
<td>–</td>
<td>0.0009$^a$</td>
<td>-115.4923</td>
</tr>
</tbody>
</table>

a) parameter significant at $P < 0.05$ level

Discussion

The mating system of larch species has already been studied in recent years. In tamarack (Larix laricina) the mean outcrossing rate in 5 populations was equal to 0.730 (KNOWLES et al., 1987), which is one of the lowest values reported for conifers (MUONA, 1990; ADAMS and BIRKES, 1991). The outcrossing rates observed for European larch appeared to be
higher, both in natural stands \((t = 0.943; \text{LEWANDOWSKI et al., 1991})\), and in seed orchards \((t = 0.929; \text{BURCZYK et al., 1991})\), \((t = 0.852; \text{PAULE and GOMORY, 1992})\).

Outcrossing rates of individual clones, calculated on the basis of a mixed-mating model (Table 1), were similar to those inferred from the mating model analysis \((t = 1-\gamma; \text{Table 2})\). While the values estimated for clones of European larch were close to unity (no significant difference from \(t_{\infty} = 1\) (Table 1)), the estimate obtained for the Siberian larch clone was extremely low \((0.096)\). This means that over 90% of successful fertilizations were due to selfing. Such a high level of self-fertilization was never reported for conifers, unless it resulted from controlled self-pollination. In our case no Siberian larch pollen was available to the grafts other than from the studied clone. It should be noted that the percentage of full seed of the Siberian clone was only about 6.34%, and was much lower than the respective values for the clones of European larch \((13.3\% \text{ to } 31\%\), with a mean of 24%)\).

In a detailed analysis of the contribution of European larch into the seed of clones of European larch, with a mean of 93.9%. In contrast, European larches pollinated together only 10.5% of Siberian larch ovules, the individual contributions ranging between zero \((E1127 \text{ and E1149})\) and 8.35% \((E1138)\). Thus, the hybridization pattern seems to be unidirectional. The percentage of hybrids among seeds of European larch, detected for the same investigated material using the rare marker alleles approach \((\text{LEWANDOWSKI et al., 1994})\) was similar to the values reported in this study. However, that method did not allow for a detailed analysis of the contribution of European larches into the progeny of the Siberian larch clone. Hybridization of \textit{Larix} species was often observed \((\text{BERGMANN and RUETZ, 1987; HACKER and BERGMANN, 1991; ENNOS and QIAN, 1994})\), and generally high percentages of hybrid seed were found, ranging between 10% and 85%, depending mainly on the seed orchard design \((\text{number of clones of hybridizing species})\) and the species acting as the seed parent. However, all those studies used single-locus, or rare marker alleles methods.

The directional hybridization pattern should be taken into account when the progeny of the studied orchard will be genetically tested and used for reforestation, as well in the future planning of breeding programs based on hybrid seed orchards.

Acknowledgments

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References


Buchbesprechungen


Red spruce (Picea rubens SARG.) stands show symptoms of decline throughout their natural range in the Appalachian Mountains of the eastern United States since the 1960's. While the above ground symptoms of declining trees were very well documented, little information exists on the status of the root system, especially of the non-woody fine roots. The very exact and detailed investigations give useful comparisons between crown deterioration and root vitality on basis of morphological and physiological indices on apparently healthy and declining red spruce trees at 2 sites in Vermont (1221 m elevation) and New York (1483 m elevation). The changes in the crown (various growth, stem, twig and needle characteristics) and in the root system are reported very precisely, and are discussed at the whole tree level. An appendix contains statistical models for the variables as well as figures for the annual radial and basal area increments of red spruce trees in three healthy classes. The studies are a significant contribution to the forest decline syndrome.

B. R. Stephans (Grosshandelsd)


B. R. STEPHAN (Grosshansdorf)


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schaftstheoretische und -historische Fragen werden im Zusam-
menhang mit Interdisziplinarität behandelt. Der Schwerpunkt


Das vorliegende Lehrbuch 'Molekularle Entwicklungsbiologie' richtet sich an Studenten der Botanik im Hauptstudium sowie an Pflanzen- und Entwicklungsphysiologen. Es stellt einen ersten Versuch dar, das Gesamtgebiet der pflanzlichen Entwicklungsbiologie in mehreren Hauptthemen zu behandeln. Für das Vorhaben haben sich 5 Hochschullehrer aus 5 Universitäten in Deutschland zusammengefunden, die in unterschiedlichen Forschungsgebieten dieses Faches tätig sind. In insgesamt 7 Kapiteln versuchen sie, Grundlagen der Entwicklung sowie angewandte Aspekte wie den Einfluß von Phytohormonen und Interaktion von Pflanzen mit anderen Lebewesen zu behandeln. Die einzelnen Kapitel sind jeweils übersichtlich in Vorspann, Basiswissen, Definition und Zusammenwissen gegliedert und erleichtern somit dem Studenten die Erlernten des behandelten Stoffes der einzelnen Kapitel. In den ersten 5 Kapiteln werden neueste Ergebnisse zu allbekannten Themen dargestellt, die in vielen pflanzenphysiologischen Lehrbüchern bereits einen festen Platz haben. Ein besonders interessantes Thema der molekularen Entwicklungbiologie, auf dem besonders in den letzten Jahren intensiv gearbeitet wurde, ist die Erforschung der molekularen Grundlagen der Blütenentwicklung. In dem Buch sind diese leider sehr kom-
pakt und dadurch für einen Laien schwer nachvollziehbar in nur einem Unterkapitel berücksichtigt worden. Unverständlich bleibt der Umstand, warum scheinbar keiner der Wissenschaftler zum MAX-PLANCK-Institut für Züchtungsforschung in Köln, die maßgeblich mit an der Entschlüsselung von Entwicklungs-
gen gen geforscht haben, an der didaktischen Gestaltung dieses Unterkapitels mitgewirkt hat. Insgesamt gesehen jedoch stellt dieses Lehrbuch eine wertvolle Hilfe für jeden Studenten dar, das faszinierende Thema der pflanzlichen Entwicklungsbio-
gie selbständig zu erarbeiten. Neben den zahlreichen Abbildun-
gen und Tabellen finden sich zahlreiche sogenannte Boxen, die über neueste Forschungsergebnisse und Methoden informiere-
ren. Somit ist das Buch, das den vielsagenden Untertitel 'Vom Gen zur Pflanze' trägt, jedem Interessierten sehr zu empfehlen.

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Teil natürlicher Evolutionsprozesse ist die Besiedlung neuer Lebensräume durch gebietsfremde Tierarten (Neozoen). Die zunehmende Mobilität des Menschen sowie die Intensivierung internationaler Handelsbeziehungen haben diesen Prozeß nachhaltig unterstützt. Eingeschleppt oder bewußt ausgebracht, haben sich zahlreiche Tierarten im Laufe der Zeit mehr oder weniger stark ausgebreitet. Zu den bekanntesten Beispie-
len zählen die Kaninchen in Australien und das Rotwild in Neuseeland. Aber auch in Deutschland sind Tierarten (z. B. Waschbar, Bisam, Nutria, Dreiecksmuschel, Amerikanischer Flusskrebs), die man als Neubürger unserer Fauna bezeichnen kann, anzutreffen. Für den Naturschutz, aber auch die Land- und Forstwirtschaft können einige Arten ein ernst zu nehmendes Problem darstellen. Das Auftreten gebietsfremder Tierarten und deren Auswirkungen auf einheimische Arten, Lebensgemeinschaften und Lebensräume sowie mögliche ökonomische Folgen wurden im Mai 1995 während eines Kollo-
quiums in Fellbach bei Stuttgart diskutiert. Die vorgetragenen 21 Beiträge sind im vorliegenden Band in der Reihe Umweltforschung in Baden-Württemberg erschienen. Das Buch ist nicht nur für Zoologen wertvoll, sondern auch für Zoologen, Öko-
logen, Landschaftspflegern, Forstwissenschaftlern, Umwelt-
verbänden und Umweltbehörden neue Erkenntnisse für eine differenzierte Betrachtungsweise der Neozoen-Problematik. Mit zahlreichen Tabellen, Abbildungen, Verbreitungs- bzw. Ausbreitungskarten und umfangreichen Literaturverzeichnis-
sen ist das Buch als Informationsquelle uneingeschränkt zu empfehlen.

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Induced Mutations and Molecular Techniques for Crop Improvement. By International Atomic Energy Agency, Vienna. 1995. 748 pages with 94 figures. Paperback öS 2160,–

This proceedings is based on an International Symposium on the "Use of Induced Mutations and Molecular Techniques for Crop Improvement", which was jointly organized by the Plant Breeding and Genetics Section of the International Atomic Energy Agency (IAEA), and the Food and Agriculture Organization (FAO) of the United Nations, in Vienna, 19 to 23 June, 1995. A somewhat related symposium on “Plant Mutat

ion Breeding for Crop Improvement" was organized by the same organizations in 1990, indicating the commitment of IAEA/FAO to application of mutation breeding to crop improve-
ment. Induced or spontaneous mutations have played a very

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important role in crop improvement. However, all types of mutations are not always useful; many are deleterious and some may even lead to genetic instability. The objective of this symposium was to review the current status of induced mutations in plants and the use of molecular biology techniques in practical crop breeding and improvement. The application of molecular biology techniques has been valuable in elucidating the nature and mechanisms of mutations. Therefore, use of induced mutations, combined with molecular techniques, would be crucial for future genetic improvement of agricultural crops. The symposium was divided into 12 sessions, including one evening session, and there were 2 additional 2 poster sessions. The following topics are included in this volume: 1) Plant breeding: problems and current techniques; 2) Seed quality; 3) Apomixes and F1 hybrids; 4) Plant pathology and disease resistance; 5) Genome architecture, genome manipulation and comparative gene mapping; 6) Methylhydroxylation and gene expression; 7) Molecular markers, Part 1: Application of DNA based marker mutations for improvement of cereals and other sexually reproduced crop species; Part 2: Use of novel DNA fingerprinting techniques for the detection and characterization of genetic variation in vegetatively propagated crops; 8) Stress tolerance; 9) Genetic transformation; 10) Looking into the future: Looking into model plants; 11) Biotechnology in developing countries; and 12) Current application of mutation techniques. In addition, there were 2 poster sessions devoted to: 1) Molecular markers and genetic transformation for crop improvement; and 2) Mutation techniques and biotechnology for crop improvement. There were altogether 46 invited papers and some 66 posters presentations in this symposium. Papers on molecular markers, molecular techniques, genetic engineering and biotechnology were well represented in this symposium. As it turns out, mutations are not only induced by physical and chemical agents, but also by tissue culture (somaclonal variation), and by transgenes (somatoclonal variation). Most of the somaclonal variation may be undesirable for crop improvement. Instability of transgenes in plants following genetic engineering may also pose a certain genetic risk. However, some genotypes produced by tissue culture or genetic engineering may be useful. The utility of a mutation would, invariably, depend on the environment in which it is tested. Therefore, it is important to specify the environmental conditions under which a new crop mutant is grown. This book deals with the prospects of induced mutations and bears on some of the related problems. Altogether, this is a useful volume on the induction of mutations and molecular techniques for crop improvement, and would be of interest to those working in this area.

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