

VARIATION IN FLOWERING AND REPRODUCTIVE SUCCESS IN A DANISH *PICEA ABIES* (KARST.) SEED ORCHARD

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ABSTRACT

Number of male and female strobili were counted in a Norway spruce seed orchard in 1993, a year of good flowering. Cones were collected and processed individually for each of the 100 clones in the seed orchard and correlations between number of strobili, cone yield and seed yield were calculated. The number of female strobili could only partly predict the seed yield ($r = 0.72$). Better correlation was found between cone yield and seed yield ($r = 0.91$) of individual clones. The variance effective population number of the seed crop was estimated to be relatively high based on both strobili, cone and seed assessments. Only minor genetic drift have thus taken place during the 1993 seed production in the seed orchard. The inbreeding due to finite number of clones was also estimated to be of minor importance compared to the natural level of selfing in the species. The status number was found to be 70% of the number of clones in the clonal seed orchard. The results are in good concordance with results from similar studies, although the variance effective population and status number were above the level generally found in comparative seed orchards.

Key words: Effective population number, status number, flower assessment, reproduction energy, reproductive success, *Picea abies*.

INTRODUCTION

A clonal seed orchard consists of replicated clones (genotypes). Studies of flowering in coniferous seed orchards over the last three decades have shown large genotypic variation in reproductive energy (VARNELL *et al.* 1967, ERIKSSON *et al.* 1973, JONSSON *et al.* 1976, GRIFFIN 1982, O'REILLY *et al.* 1982, SCHMIDTLING 1983, MÜLLER-STARCK & ZIEHE 1984, BRYAM *et al.* 1986, SCHOEN *et al.* 1986, EL-KASSABY *et al.* 1989, REYNOLDS & EL-KASSABY 1990, EL-KASSABY & REYNOLDS 1990, CHAISURISRI & EL-KASSABY 1993, SAVOLAINEN *et al.* 1993, EL-KASSABY & COOK 1994, KJÆR 1996, SIEGISMUND *et al.* 1996, BURCZYK & CHALUPKA 1997). Unequal flowering causes over-representation of abundantly flowering genotypes and reduces the effective population number, i.e. genetic drift and increase in inbreeding coefficient take place more rapidly than would be predicted from the census number of clones used in the orchard. Implications of imbalanced seed production for domestication has been discussed by SEDGLEY & GRIFFIN (1989).

The differences in gamete contribution from the individual clones can be estimated based on assessment of flowering and seed production, or based on biochemical markers. The female reproductive energy

(abundance of female strobili) is quick and cheap to assess compared to direct evaluation of female reproductive success in terms of seed yield, and much cheaper than surveys based on biochemical markers. The objective of the present study was therefore to compare observations of clonal variation in male and female flower intensity with subsequent seed production, and to estimate the corresponding impact on effective population numbers in a seed crop from a Danish Norway spruce (*Picea abies*) clonal seed orchard.

MATERIAL AND METHODS

The Seed Orchard

Norway spruce (*Picea abies* (L) Karst.) is exotic to Denmark. It was first introduced to Denmark in the 1760's (LARSEN & WELLENORF 1997), and has been used on a large scale in the Danish forestry since the turn of the century. Domestication in terms of tree improvement activities was initiated in the 1950's

This study analyses the 1993 seed harvest in the Norway spruce clonal seed orchard FP240. The seed orchard was established in 1980–87 as a joint venture between the Arboretum, Tree Improvement Station

(The National Forest and Nature Agency), The Forest Seed Centre of the Danish Land Development Service, and the Hoffmannsgave Estate, Denmark. The purpose of the orchard is production of genetically improved seeds for forest plantations. The orchard includes 100 clones, which have mainly been selected for high wood density (WELLENDORF 1988). Ninety-five of the clones were selected in Danish stands, which are expected to be first to third generation in Denmark of west continental origin (probably imports from Germany). The remaining five clones were selected in southern Sweden in stands of west continental origin (PLANT DIRECTORATE 1995). The area of the seed orchard is 6 ha and a total of 3956 ramets were present in the seed orchard in 1993. The ramets are almost balanced with 36–42 ramets per clone (average 39.6 with a standard deviation of 2.6). However, the clonal average height of the ramets varied from 1.1 m to 5.7 m (average = 4.0, standard deviation = 0.8m). The ramets have not been top pruned.

Assessment of strobili and seed yield

Number of male and female strobili were estimated on 737 ramets in four unbalanced blocks in the seed orchard in May 1993. The representation in this sample ranges from 14 to 0 ramets per clone, but was above 5 for the majority of clones (average = 7.4, standard deviation 2.5). A single clone was not represented in the sample and was therefore treated as being “average” in all further analysis of strobili number. The number of female and male strobili were scored in classes on a logarithmic scale, because counting all single strobili would be very time consuming on abundantly flowering ramets. The scoring scale suggested by WELLENDORF (unpublished) was used (1: no strobili, 2: 1–3 strobili, 3: 4–15 strobili, 4: 16–60 strobili, 5: 61–250 strobili, 6: 251–1000, 7: 1000<). The height was measured on all 4170 ramets in the seed orchard. The sample size was selected so that the flower assessment could be made in one day.

Cones were kept separate by clone during the following harvest and processing. The volume of cones (hl/clone) was measured for each clone prior to the processing. Seed yield (kg/clone) was measured for each clone after processing and cleaning. The 1000 seed weight and germination percent (after 4 weeks) were analysed independently for each clone according to ISTA norms. The 1993 seed crop in FP240 was approximately 700 kg after cleaning, which corresponds to a very good seed year.

Statistical analysis of clonal variation in flowering intensity

The flower intensity based on the log-score showed an acceptable fit to a normal distribution. The data were analysed for male and female strobili separately assuming effects of genotypes (clones) to be random. The height of the ramets were included as a co-variate in order to remove variation due to differences in the size of the ramets.

$$Y_{sij} = \mu_s + G_{si} + \gamma_s H_{ij} + \varepsilon_{sij} \quad [1]$$

s = Male, female, i = 1, ..., 100 (clone), j = 1, ..., 14 (replication of clone)

where Y_{female} is the observed score for female strobili, Y_{male} is the observed score for male strobili, μ_s is the overall mean, G_{si} is the clonal effect, which is assumed independent and normally distributed ($G \sim N(0, s_{G_s}^2)$). γ_s is the linear effect of the height (H_{ij}) of the ramets used as co-variate. ε_{ij} were assumed to be independent and normally distributed ($\varepsilon_{ij} \sim N(0, \sigma_\varepsilon^2)$). Effects of clones and height were tested separately against the full model, i.e. not in successive tests.

Genetic components of variance and covariance were estimated from the analyses of variance and covariance based on model (A). Genetic correlation between female and male strobili score was estimated from genetic components of variance according to BECKER (1985). The genetic coefficient of variation was calculated for male and female strobili scores as the square root of the genetic variance component divided by the overall mean score.

Estimation of relative number of strobili, cone yield, seed yield, and number of viable seeds

The logarithmic scores of strobili were converted into actual number of strobili. Linear and quadratic regression between number of strobili and height was applied in order to establish the relationship between height and expected number of strobili.

$$E(\text{Number of Strobili}_{sij}) = m_s + G_{si} + \gamma_s H_{ij} + \gamma_s' H_{ij}^2 \quad [2]$$

A simple linear model was accepted for female strobili, but a quadratic term was necessary for male strobili. The parameters in model (B) were estimated from linear regression, and the model then used for estimation of the number of male and female strobili for all non-assessed ramets. The expected relative number of male (p_i) and female (f_i) strobili during the 1993 flowering were then calculated for each clone as the percentage of the total

number of male and female strobili in the seed orchard. These estimates represent phenotypic rather than genotypic values, because a fairly large part of the variation between the clones are due to environmental heterogeneity (the values are not multiplied with clonal heritability). The values reflects differences between clones as they are expected to have been in the given year. However, it should be noted that the applied technique may overestimate the true clonal differences in flowering, because the results from a minor part of the seed orchard is used to extrapolate to the full seed orchard (environmental variance may be overestimated).

The relative contribution of cones, seed in kg, total number of seed, and number of viable seed was derived directly from the observation from the clone by clone seed harvest, seed processing and seed testing. These data were therefore based on the seed collection from all ramets in the clonal seed orchard.

Phenotypic correlations were calculated between all these variables. However, only 79 clones (represented by more than 5 ramets per clone in the flower assessment sample) were included in calculation of correlation between strobili numbers and cone/seed contribution.

Effective population number

The concept of effective population number was introduced by WRIGHT (1931) in order to quantify the effects of deviation of natural populations from idealised panmictic breeding situations. These deviations influence inbreeding and genetic drift (which are both important in the seed orchard situation) in different ways (cf. e.g. CROW & KIMURA 1970). It is therefore important to distinguish between influence on inbreeding and influence on genetic drift.

The inbreeding effective population number $N_e^{(i)}$ relates to the increase in the inbreeding coefficient (F). In the clonal seed orchard situation where clones are unrelated, inbreeding is only generated by selfing. $N_e^{(i)}$ is therefore sensitive to sexual asymmetry; low or negative correlation between male and female flowering obviously reduces the probability of selfing. Following MUONA & HARJU (1989), the amount of selfing can be estimated as $P = (f_i p_i)$, for $i=1...100$, where f_i and p_i are the relative female and male contribution of clone i . This estimate includes selfing due to breeding between ramets of the same clones in the seed orchard. Additional inbreeding is to be expected within the crown of individual ramets, because Norway spruce in general follow a mixed mating system, with outcrossing rates (t) estimated to be 0.83-1.00 (MOUNA 1990, FINKELDAY 1995). This can be taken into account by adding the "natural" level of selfing ($1-t$), i.e. $P = (1-t) + t (f_i p_i)$ (KJÆR 1996). Postzygotic self-incompatibility is well known in gymnosperms (SEDGLEY & GRIFFINS, 1989).

Selection against inbred progenies can take place during embryo development, poly-embryo competition, seed maturation, germination and early stage seedling survival/competition, which will reduce the percentage of surviving selfings. MUONA *et al.* (1987) find that selfed progeny apparently are eliminated in successive developmental stages of *Pinus sylvestris* seedlings. SHAW & ALLARD (1982) found a lower percentage of selfed progenies than should be expected from the constitution of the pollen cloud in a study of *Pseudotsuga menziesii*. A similar result is found by YAZDANI & LINDGREN (1991) based on controlled pollinations in *Pinus sylvestris*. They found only 35% inbred progenies of what should be expected from the amount selfing pollen in the pollennix. The estimate $S(f_i p_i)$ should therefore be reduced with the relative fitness w of selfed zygotes compared to outcrossed zygotes in order to obtain a realistic estimate of the amount of selfing due to crosses between ramets of the same clones, i.e.:

$$P = (1-t) + w t (f_i p_i).$$

No specific estimates of w and t were available for the present study. However, for the purpose of calculating a rough estimate of the inbreeding effective population number we assumed the following values: $t = 0.95$ (based on FINKELDAY (1995) - who estimated t in plantation conditions of non seed orchard origin - and $w = 1/3$ (based on YAZDANI & LINDGREN'S (1991) study on *Pinus sylvestris*). $N_e^{(i)}$ could then be estimated as

$$N_e^{(i)} = 1/P \approx 1/((1-t) + 1/3 t (f_i p_i)) = 1/(0.05+0.32 (f_i p_i)), \text{ for } i=1...100$$

It is seen that the inbreeding effective population number estimated in this manner have a maximum of $N_e^{(i) \text{ max}} = 1/0.05 = 20$, independent of the number of clones in the seed orchard and independent of their relative contribution of male and female gametes. One can say that $N_e^{(i) \text{ max}}$ is the expected inbreeding effective population number in large population of abundantly flowering, unrelated trees. A natural reference level can also be the situation where all clones contribute equally and sexual symmetric ($f_i = p_i = 1/N_c = 1/100$), which correspond to $N_e^{(i)} = 18.8$.

The variance effective population number $N_e^{(v)}$ relates to the genetic drift from the population of seed orchard clones to their progeny. This measure is therefore sensitive to the number of progenies collected per clone (i.e. sample size). A large number of seeds are normally collected from clonal seed orchards, and KJÆR (1996) therefore recommends that $N_e^{(v)}$ are calculated as

$$N_e^{(v)} (\text{infinite}) = \frac{N_{i-1} - 1/2}{\text{for } i=1, \dots, 100 \quad N_{i-1} S_i^2 - 1}$$

N_{L-1} is the number of clones (i.e. 100 in the present study), and r_i the average of male (p_i) and female (f_i) contribution ($r_i = \frac{1}{2}(f_i + p_i)$). All calculations above assume that the gametes unite at random in time and space, except that a fixed amount of selfing is expected in the calculation of inbreeding effective population number.

The status number (LINDGREN *et al.*, 1997, LINDGREN & MULLIN, 1997) was used in the present study to assess the more general build up of coancestry in the seed orchard progeny. The status number (N_s) was estimated as,

$$N_s = 1/r_i^2, \text{ for } i = 1 \dots 100$$

following LINDGREN & MULLIN (1997). It can be shown that N_s in this situation equals the variance effective population number in a situation, where the seed orchard offspring consists of only 100 trees (stable population size, KJÆR (1996)). Examples of specific interpretation of the different measures of effective population numbers in the seed orchard situation is given in Table 1. It is obvious from the above discussion, that the effective population number refer to seed orchard progeny, i.e. the seed crop, rather than to the actual seed orchard as such.

The female contribution was, as mentioned earlier, estimated at different stages: (i) female strobili (number/clone), (ii) cones (hl/clone), (iii) seed (kg/clone), (iv) number of seeds (seeds/clone) and (v) viable seeds (number of viable seed per clone). Male contribution could only be estimated from the observation of male strobili. Sepa-

rate estimates of the effective population numbers were therefore calculated for each of the five female evaluation stages applying the same male strobili data in all calculations.

RESULTS

The genetic differences in flowering between the 100 clones were small, although significant for male strobili (Table 2). Actual contribution of female strobili from individual clones ranged from 0.2 % to 4.3% (standard deviation = 0.7%) and of male strobili from 0.1% to 3.8% (standard deviation = 0.6%). The genetic correlation between male and female strobili score was found to be positive, $r_g = 0.38$, but it must be noted that female strobili score was not significant on a 5% level.

The various estimates of female contribution are presented in Figure 1. The clones are arranged according to contribution of viable seed in this figure, and it is clear that seed contribution in either term (kg, number or total number of seeds, or number of viable seed) are highly correlated. This is true even though the weight of 1000 seed varied between clones from 5.3–11.3 g (average = 7.6 g, standard deviation = 1.2 g), and the germination percent from 88–100% (average 97%, standard deviation = 2.7%). Figure 1 also reveals a high degree of covariation between female strobili, cone yield and seed yield, although some clones “break the correlation”, i.e. change rank when evaluated on female strobili or cone yield rather

Table 1. Effective population numbers in a clonal seed orchard crop.

Type	General meaning	Example of specific interpretation in clonal seed orchard crop
Inbreeding effective population number, $N_e^{(i)}$	The size of an ideal Mendelian population which give the same increase in inbreeding coefficient as experienced in the observed population	The number of equally fertile clones in an ideal, random mating clonal seed orchard that is expected to produce the same amount of selfed progenies - as is expected in the present seed orchard crop.
Variance effective population number, $N_e^{(v)}$ (<i>infinite</i>)	The size of an ideal Mendelian population which give the same expected change in gene frequencies as experienced in the observed population	The number of equally fertile clones in an ideal, random mating clonal seed orchard that is expected to give the same change in gene frequencies between the seed orchard clones and the progeny <i>due to genetic drift</i> - as is expected between the present seed orchard clones at the seed orchard progeny due to <i>unequal clonal contribution of gamets</i>
Status number, N_s	The number of non-inbred and unrelated genotypes which (including self-coancestry) has the same average coancestry as the studied population	The number of equally fertile clones in an ideal, random mating clonal seed orchard that - following random mating in the seed orchard progeny - gives raise to the same amount of inbreeding as expected following random mating in the present seed orchard progeny

Source: based on KJÆR (1996) and LINDGREN & MULLIN (1997)

Table 2. Analysis of variance in flower scores. Means squares (MS), F-tests (F), Degrees of freedom, genetic coefficient of variation (CV(g),%) and level of significance (P>F)

Source	MS	F	DF	CV(g), %	P > F
Female strobili score					
Clones	2.65	1.24	1e+09	8.8%	0.0693
Covariate: Height	82.25	38.55			0.0001
Male strobili score					
Clones	3.09	1.50	1e+09	6.8%	0.0024
Covariate: Height	303.29	147.53			0.0001

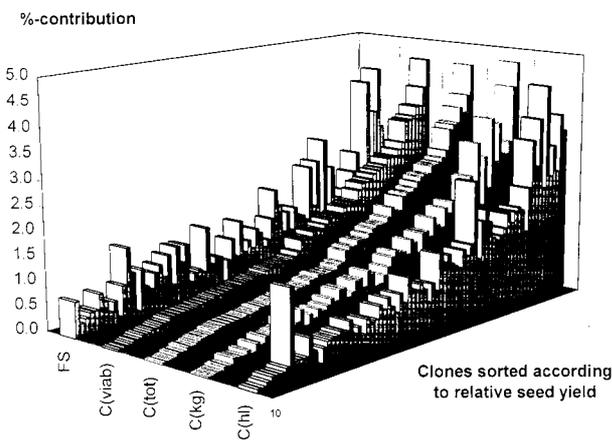


Figure 1. Relative contribution of the clones in terms of female strobili (FS), cones in volume (C(hl)), seed in weight (C(kg)), number of seeds (C(tot)), and number of viable seed (C(viab)). See text for further explanation.

than seed yield. The correlations between the various estimates - plus the seed yield per volume of cones and the germination percent - are presented in table 3. Correlation between cone yield and seed yield were found to be above 0.91, and correlation between seed yield and total number of viable seed was 0.97. The estimates of 1000 seed weight and germination percent for each of the 100 clones have thus not contributed much new information in the present study.

A fraction of the observed differences between clones could in principle be avoided if all clones were represented by exactly the same number of ramets per clone. However, the seed orchard is almost balanced, and the effects of unbalanced number of ramets per clone were therefore of minor importance in the present study (calculations *per graft* (and clone) gave almost exactly the same results as presented above (data not shown)).

Table 3. Phenotypic correlations between male strobili number (MS), female strobili number (FS), cones (C(hl)), seed (C(kg)), number of seed (C(tot)), number of viable seed (C(viab)); seed yield pr cone volume (Q), and germination percent (G%). Levels of significance are printed in italics.

	MS	FS	C (hl)	C (kg)	C (tot)	C (viab)	Q	G%
Msc	1	0.47 <i>0.001</i>	0.71 <i>0.001</i>	0.74 <i>0.001</i>	0.69 <i>0.001</i>	0.700 <i>0.001</i>	0.02 <i>0.879</i>	0.15 <i>0.181</i>
Fsc		1.00	0.72 <i>0.001</i>	0.68 <i>0.001</i>	0.73 <i>0.001</i>	0.72 <i>0.001</i>	0.01 <i>0.925</i>	0.15 <i>0.193</i>
C (hl)			1.00	0.91 <i>0.001</i>	0.92 <i>0.001</i>	0.91 <i>0.001</i>	0.07 <i>0.510</i>	0.17 <i>0.086</i>
C (kg)				1.00	0.97 <i>0.001</i>	0.97 <i>0.001</i>	0.34 <i>0.001</i>	0.22 <i>0.027</i>
C (tot)					1.00	0.99 <i>0.001</i>	0.29 <i>0.004</i>	0.18 <i>0.067</i>
C (viab)						1.00	0.30 <i>0.003</i>	0.21 <i>0.034</i>
Q							1.00	0.15 <i>0.132</i>
G%								1.00

Table 4. Variation in clonal contribution and corresponding effective population number in the seed crop based on male strobili numbers combined with and female strobili numbers (FS), cones (C(hl)), seed (C(kg)), number of seed (C(tot)), number of viable seed (C(viab))

	S	C (hl)	C (kg)	C (tot)	C (viab)
$\sum f_i p_i$	0.01197	0.01311	0.01341	0.01326	0.01326
$\sum r_i^2$	0.01315	0.01387	0.01418	0.01418	0.01420
$N_e^{(v)}$ (infinite)	315.2	256.9	238.1	238.1	236.7
N_s	76.0	72.1	70.5	70.5	70.4
$N_e^{(i)}$	18.6	18.5	18.5	18.5	18.5

Legends. S = strobili number, C(hl) = cones in volume, C(kg) = seed in weight, C(tot) = number of seeds, C(viab) = number of viable seeds. Male contribution (p_i) is estimated from male strobili in all columns. See text for further explanation.

The effective population numbers of the seed crop were estimated, and are presented in Table 4. The inbreeding effective population number $N_e^{(i)}$ was estimated to be approximately 18 for both strobili scores, and male strobili combined with cones or seed yield. This is close to the maximum of 20, which are to be expected in large populations of unrelated, equally flowering trees as discussed above. The selfing due to crossing between ramets of the same clones was thus of minor importance compared to the inbreeding due to the mixed mating system. The variance effective population number $N_e^{(v)}$ (infinite) was estimated to be 315 when evaluated on strobili scores, 257 based on cones and male strobili, and 237–238 when evaluated on male strobili combined with seed yield. The status number varied from 76 (strobili scores) to 70 (viable seed + male strobili).

All population numbers are relative high. A low degree of genetic drift – and inbreeding due to crosses between ramets of the same clone – are thus to be expected from these estimates. The status number was approximately 2/3 of the census number and reflects a low expected degree of coancestry in the gametes pool that forms the seed orchard offspring. The effective population and status number based on female strobili gave a good prediction of estimates based on cone and seed yield. Estimates based on cones gave a very good prediction of the seed based estimates.

DISCUSSION

A fairly low degree of genetic variation in flowering was found between the 100 investigated clones. As a consequence, the effective population numbers were found to be relative high for both inbreeding and drift. The level of relative effective population numbers (i.e. effective population number relative to the number of clones in the seed orchard) found in the present study is higher than reported by SIEGISMUND *et al* (1996) in an *Abies procera* seed orchard and by CHAISURISRI & EL-KASSABY (1993)

in a *Picea sitchensis* seed orchard, although the *Picea sitchensis* study is not fully comparable as the effective population numbers are based on female contribution only. KJÆR (1996) found the relative effective population number to vary according to the size of the seed crop in a *Picea abies* clonal seed orchard. $N_e^{(v)}$ (infinite) was reported to be between 30% and 130% of the number of clones, i.e. lower than found in the present study. KJÆR & BARNER (1997) report the development in relative effective population number in a *Pinus sylvestris* seed orchard with 10 clones, over a 20 years period (based on clonal contribution to cone yield). They found the effective population number to increase from a low level in the first years to stabilise at a relative high level compared to the fact that only 10 clones were included in the CSO: $N_s \approx 8$, (which corresponds to $N_e^{(v)}$ (infinite) ≈ 35) after 15 years. In general, the level of relative effective population number may therefore depend highly on age of the investigated clonal seed orchards.

Flower assessment – as performed in the present study – is a cheap way to estimate the gamete contribution of a large number of trees, but the limitations of flowering based predictions shall be recalled. The fact that Norway spruce follow a mixed mating system was addressed in the present study when calculating inbreeding effective population numbers, but the assumption on outcrossing rate (t) and relative fitness of the selfed zygotes (w) are critical to the result. The assumption that pollen and ovules mates randomly in time and space (questioned by e.g. EL-KASSABY 1989, and MATZIRIS 1994) should also be considered. Observation of the strobili maturation for the individual clones can be used to infer on the impact of genetic variation in phenology (ASKEW 1988), but this will require repeated assessment during the flowering period. The effects of pollen contamination has been discussed by KJÆR (1996) and LINDGREN & MULLIN (1997).

Flower assessment is more reliable for estimation of variance effective population numbers than inbreeding effective population numbers, because of the large influ-

ence of w and t . The flower assessment could only partly predict the seed yield on the clonal level in the present study, but gave a good prediction of the effective population number compared to estimates based on seed yield. The correlation between cone production and seed yield (the latter requiring a much more costly clonal seed processing) was fairly high, $r = 0.91$. EL-KASSABY & COOK (1994) found a similar result ($r = 0.93$) in a study of *Pseudotsuga menziesii* in British Columbia, but still concluded that the size of cone crop was not a good estimate for seed yield as several clones changed in rank when seed yield rather than cone yield was used for ranking. CHAISURISRI & EL-KASSABY (1993) studied a clonal seed orchard of sitka spruce (*Picea sitchensis*) and found correlations of $r = 0.86$ and 0.81 in two subsequent years. KJÆR *et al.* (1995) found lower correlation between cone yield and seed yield (filled seeds) in a Danish sitka spruce seed orchard of 113 clones ($r = 0.63$). The three studies (EL-KASSABY & COOK 1994, CHAISURISRI & EL-KASSABY 1993, and KJÆR *et al.* 1995) found almost the same effective population numbers based on cone yield and seed yield. The question whether cone yield and/or flower assessment are satisfactory estimates of the total reproductive success will depend on the purpose of the assessment. It would seem as if variance effective population number and status number based on cone yield – or even flower assessment – in general give useful estimates of the impact of unbalanced seed production on genetic diversity.

The results have also implications in the case of seed collection for provenance testing or *ex situ* gene resource conservation. Cones from different trees can be kept separate during collection and mixed in equal proportions prior to processing. This will probably reduce the genetic drift – and keep the coancestry in the progeny gene pool – to a minimum, which can be valuable for both seed source testing and sampling for *ex situ* conservation.

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ERRATA

Belletti, P., Lanteri, S. & Leonardi, S. 1997: Genetic variability among European larch (*Larix decidua* Mill.) populations in Piedmont, North-Western Italy. *Forest Genetics* 4(3):113-121.

Abstract

The third sentence from the end (Principal components analysis) should read:

Non-metric multidimensional scaling showed that the first dimension was significantly correlated with longitude and the second with latitude.

- p. 114, 2nd column, 3rd paragraph, 5th line:
acronyms and Enzyme Commission numbers
p. 114, 2nd column, 4th paragraph, 1st line:
30 µl
p. 115, 1st column, 1st paragraph, 4th line:
by the χ^2 and

p. 115, 1st column, 1st paragraph, 15th line:
were estimated

p. 116, Table 2,
population 10, the allele frequencies should read: .500,
.415, .085, and $H_e = .578$

p. 117, Table 3,
Percentage of polymorphic loci**
expected*

p. 118, 2nd column, 3rd paragraph, 2nd line
The Navette population was seen

p. 118, 2nd column, 3rd paragraph, 9th line
similar; although

p. 118, 2nd column, 3rd paragraph, 15th line
were clearly differentiated.....

P. 120, 1st column, 1st paragraph, 8th line:
BELLETTI & LANTERI 1996

Kjær, E. D. & Wellendorf, H., 1997: Variation in flowering and reproductive success in a Danish *Picea abies* (Karst.) seed orchard. *Forest Genetics* 4(4):181-188.

p. 182, 2nd column, 2nd paragraph, 4th line:
instead of s^2_{sg} should be σ^2_{sg}

p. 183, 1st column, 5th paragraph, 8th line:
instead $P = (f_i p_i)$ should be $P = \Sigma (f_i p_i)$

p. 183, 1st column, 5th paragraph, 17th line
the equation should read

$$P = (1-t) + t \Sigma (f_i p_i)$$

p. 183, 2nd column, 1st paragraph, 15th line
instead of $S(f_i p_i)$ should be $\Sigma(f_i p_i)$

p. 183, 2nd column, 1st equation should read:

$$P = (1-t) + w t \Sigma (f_i p_i)$$

p. 183, 2nd column, 2nd equation should read:

$$N_e^{(i)} = 1/P \approx 1/(\Sigma (1-t) + 1/3 t \Sigma(f_i p_i)) = 1/(0.05+0.32 \Sigma(f_i p_i)), \text{ for } i=1...100$$

p. 183, 2nd column, 3rd equation should read:

$$N_e^{(v)}(\text{infinite}) = \frac{N_{r-1}-1/2}{N_{i-1}\Sigma r_i^2-1}, \text{ for } i = 1, \dots, 100$$

p. 184, 1st column, 1st equation should read:

$$N_s = 1/ \Sigma r_i^2, \text{ for } i = 1...100$$

p. 187, 2nd column, 17 line from bottom:
KJÆR, E. D., GRAUDAL, L. & MYRTHUE, Å. K. 1995:

p. 187, 2nd column, 6th line from bottom:
Forest Genetics 4(2):69-76.