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Estimation of relationship coefficients among progeny derived from wind-pollinated orchard seeds

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Abstract Statistical analyses of trees produced from wind-pollinated seeds to determine levels of additive variance need to be adjusted to compensate for the relationships among the progeny. The assumption that the coefficient of relationship among the progeny is 0.25 will lead to inaccurate estimation of the additive variance if the relationships among the progeny are not entirely half-sib. Foreign pollen intrusion into the orchard pollen cloud, selfing, and reproductive phenology variation (i.e., mating proportion differences) among the parent trees may lead to varying proportions of self, self-half, half-sib, and full-sib relationships among the progeny. The variance of the coefficient of relationship from 0.25 for two coniferous seed orchards subjected to simulated selfing and foreign pollen problems illustrate the need for caaution when estimation techniques are employed.

Key words Foreign pollen · Reproductive phenology · Loblolly pine · Western redcedar

Introduction

Genetic variance estimates for several forest tree species have been determined using methods ranging from those that do not require raising progeny (Toda 1958) to those that rely on elaborate mating designs for progeny production (Namkoong 1979). Wind-pollinated families have often been used for progeny testing due to relatively low expense and availability of seed (see El-Kassaby et al. 1987a; Sorensen and White 1988 for review). Wind-pollinated families are also used for first-generation mass selection schemes and are preferred by many tree breeders for ranking families and for selection after controlled pollination of unscreened parents (Zobel et al. 1972).

Genetic relatedness among members of wind-pollinated families is sometimes presumed to be mathematically equivalent to the covariance among half-sibs, which is equal to one-quarter of the additive variance (Stonecypher et al. 1964), and to have a coefficient of relationship (ρ) of 0.25 (Wright 1922). This assumption is valid when parents are non-inbred and unrelated and maternal parents are being pollinated by a high effective number of paternal parents (Namkoong 1966; Squillace 1974). The presence of family structures (Linhart et al. 1981; Brunel and Rodolphe 1985; El-Kassaby et al. 1987b), limited pollen dispersal (Muller 1976; Shen et al. 1981; Erickson and Adams 1989), assortative mating caused by phenological similarities (El-Kassaby et al. 1988; Erickson and Adams 1990), aand genetic differences among individuals in their selfing ability, even in the presence of strong inbreeding depression (Shaw and Allard 1982; Ritland and El-Kassaby 1985; El-Kassaby et al. 1986, 1993; Perry and Knowles 1990), in natural and experimental populations, usually causes wind-pollinated families to contain selfed, self-half, half-sib, and full-sib relations (Fig. 1) and, as a consequence, $\rho > 0.25$. In these instances, the use of $\rho = 0.25$ will result in overestimation of the additive genetic variance (Namkoong 1966; Squillace 1974).

Estimates of outcrossing (t) and inbreeding ($s = t - 1$) proportions have been reported for many coniferous tree species in natural and experimental populations when allozyme markers were used (Mitton 1991). These estimates vary from $t = 1$ for lodgepole pine (*Pinus contorta* Dougl. ex Loud.) (Epperson and Allard 1984) to $t = 0.32$ for western redcedar (*Thuja plicata* Donn ex D. Don) (El-Kassaby 1993). Cheliak et al. (1985) estimated $t = 0.98$ for a natural stand of white spruce (*Picea glauca*

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(Moench) Voss) and considered 0.25 to be an unrealistic value for ρ. He proposed $\rho = 0.37$. Similarly, $\rho = 0.33$ was used by Sorensen and White (1988) and Vargas-Hernandez (1990) for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). Surles et al. (1990) estimated values of ρ for open-pollinated *Gleditsia triacanthos* L. and *Robinia pseudoacacia* L. families to be in the ranges of 0.29–0.55 and 0.20–0.43, respectively.

Variance estimation from seeds produced in an experimental population (e.g., a seed orchard) will also be affected by family structure and inbreeding. The reproductive phenology of the orchard trees and foreign pollen intrusion into the orchard pollen cloud will affect the mating probabilities of the individual clones and the orchard gametic proportions as a whole (Askew 1986; Askew and Blush 1990; El-Kassaby and Askew 1991; Friedman and Adams 1985). Corrections for ρ may be warranted for these artificial populations if the variance component estimation is to be based on the progeny derived from their seed crops.

This paper examines the impacts of reproductive phenology, foreign pollen, and orchard size on the value of ρ in wind-pollinated orchard seed crops.

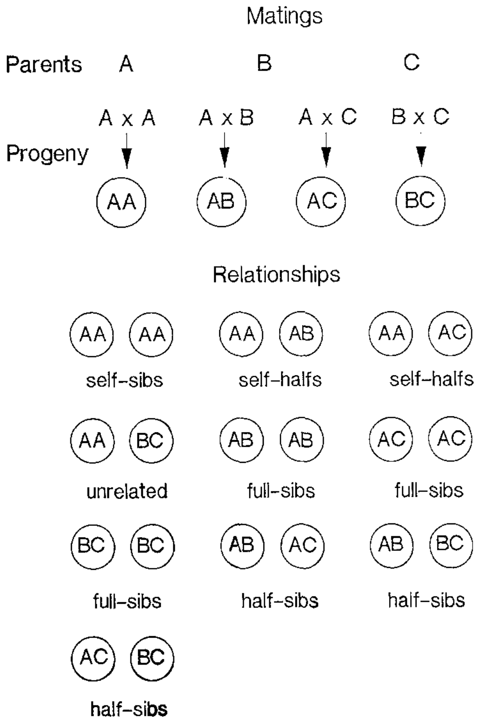


Fig. 1 Possible relationships among orchard progeny

Methodology

Accurate estimation of ρ using progeny produced from seed collected from individual trees requires an estimate or measurement of the family structure of the progeny. Wind-pollinated seeds from a single tree share a common maternal parent, but the paternal parentage is not easily assessed. Allozyme studies can be used to estimate selfing levels and contributions from paternal sources of known allozyme patterns such as might be found in seed orchard situations (Cheliak 1984) and natural populations (Neale 1984). The assignment of paternal contributions from trees of unknown allozyme patterns such as those from foreign pollen sources in seed orchards requires further estimation or assumptions. We used information gathered from two seed orchards to mathematically simulate the impact of reproductive phenology, selfing rate, foreign pollen, and orchard size (i.e., number of parents) on the value of ρ and subsequent estimation of the amount of additive genetic variance.

Reproductive phenology effects were quantified using phenological overlap values (Askew and Blush 1990). Overlap values are based on the synchronization of pollen release and flower receptivity and are calculated for all pairs of orchard clones. The overlap values are then used as estimates of the relative mating proportions of the clone pairs.

Lobolly pine (*Pinus taeda* L.) seed orchard

The mature, first-generation, 15-clone coastal loblolly pine seed orchard near Charleston, South Carolina described by Askew and Blush (1990) was used as a representative of southern pine seed orchards. The phenological overlap values demonstrated that the flowering was not synchronous among the clones and that there was a great deal of variation in the estimated mating proportions of the clone pairs.

Western redcedar seed orchard

The Fletcher Challenge Canada Ltd western redcedar seed orchard also provided data for this study. The orchard is composed of vegetatively propagated rooted cuttings of 100 trees selected from natural stands on sites ranging in elevation from 2 m to 200 m on Vancouver Island and in wetern Briish Columbia, latitude 48′18′ to 50′43′ and longitude 122′01′ to 127′00′. Origins of selected trees were sufficiently distant from each other to allow an assumption of non-relatedness among the orchard's clones. The reproductive phenology of each clone was monitored throughout the 1989 pollination season and has been characterized as being narrow and lacking variation among clones (El-Kassaby 1991). In the present study, the mating probabilities have been estimated as described by Askew and Blush (1990) for a sample of 15 clones. In addition, the level of outcrossing rate has been estimated to be 0.32 ± 0.001 using a sample of 28 clones (El-Kassaby et al. 1993). The orchard is well isolated from contamination sources with the nearest neighboring western redcedar trees being scattered single trees approximately 2 km from the orchard. A lack of inbreeding depression has been documented in western redcedar (Owens et al. 1990), which results in successful production of viable seeds by selfing. Estimates of unadjusted variance components for 2-year height were obtained from a common progeny test that was established from wind-pollinated seed collected from 96 clones from this seed orchard (J. Russell, B. C. Ministry of Forests, March 1991).

Mathematical development

Progeny from individual tree seeds may contain proportions of self, self-half, half-sib, and full-sib relationships (Fig. 1). Estimation of the variance components within each relationship group follows the work of Squillace (1974) and Cockerham and Weir (1984).

Given:

$\theta_{x,y}$ = coancestry of progeny x and y;

$\delta_{x,y}$ = the double identity probability;

$\gamma_{x,y}$ = the four-gene identity; then

$$\sigma_{x,y} = 2\theta_{x,y}\sigma_A^2 + \delta_{x,y}\sigma_D^2 - 2\gamma_{x,y}\sigma_D^2$$

$\sigma_{x,y}$ is the covariance of individuals x and y where parents of x and y are unrelated and non-inbred. σ_A^2 is the additive variance component, and σ_D^2 is the dominance variance component.

Four covariances are important for this discussion:

1) Covariance among selfs:

$$\theta_{x,y}=\frac{1}{2};\quad \delta_{x,y}=\frac{1}{2};\quad \gamma_{x,y}=\frac{1}{8};$$

$$\sigma_{x,y}=\sigma_A^2+\frac{1}{2}\sigma_D^2-\frac{1}{4}\sigma_D^2$$

$$=\sigma_A^2+\frac{1}{4}\sigma_D^2$$

2) Covariance among self-halfs:

$$\theta_{x,y}=\frac{1}{4};\quad \delta_{x,y}=0;\quad \gamma_{x,y}=0;$$

$$\sigma_{x,y}=\frac{1}{2}\sigma_A^2$$

3) Covariance among half-sibs:

$$\theta_{x,y}=\frac{1}{8};\quad \delta_{x,y}=0:\quad \gamma_{x,y}=0;$$

$$\sigma_{x,y}=\frac{1}{4}\sigma_A^2$$

4) Covariance among full-sibs:

$$\theta_{x,y}=\frac{1}{4};\quad \delta_{x,y}=\frac{1}{4};\quad \gamma_{x,y}=0;$$

$$\sigma_{x,y}=\frac{1}{2}\sigma_A^2+\frac{1}{4}\sigma_D^2$$

The coefficient of relationship (Wright 1992), ρ, between individuals x and y is:

$$\rho_{x,y}=\frac{2\theta_{x,y}}{\sqrt{(1+F_x)(1+F_y)}}$$

where F_x and F_y are the inbreeding coefficients of individuals x and y, respectively. The coefficients of relationship among individuals in the four relationship groups are then:

Selfs: $F_x=F_y=0.5$; $\rho_{x,y}=0.667$;
Self-halfs: $F_x=0.5, F_y=0$; $\rho_{x,y}=0.408$;
Half-sibs: $F_x=F_y=0$; $\rho_{x,y}=0.250$;
Full-sibs: $F_x=F_y=0$; $\rho_{x,y}=0.500$.

Analyses of variance for traits measured on trees within these specific relationship types can be used to extract a variance component that is equivalent to $\rho\sigma_A^2$. That variance component would then be multiplied by $\hat{\alpha}=1/\rho$ to obtain an estimate of the degree of additive variance for the particular trait in question.

Open-pollinated seedlots collected from orchards generally contain a mixture of relationships. For the purposes of this study, we assumed mating probabilities to be proportionaal to the phenological overlap values for all clone pairs in both orchards. Expected relationship proportions among the seed of each seed parent were calculated dividing the pairwise phenological overlap values for each pollen parent by the sum of the pairwise phenological overlap values for all pollen parents.

After the mating probabilities were calculated, the proportion of matings expected in each relationship type were calculated for each seed tree. Selfs, self-half, half-sib, and full-sib matings were possible (see example below). Estimates of ρ were calculated for each seed parent as weighted averages of the coefficients of each relationship type using the relationship proportions as weights.

Example of relationship proportions:

> if seed tree A received 33% of its pollen from each of A, B, and C the following relationships would exist among the progeny: 11% selfs (AA), 44% self-halfs (AA/AB and AA/AC), 22% half-sibs (AB/AC), and 22% full-sibs (AB/AB and AC/AC).

Estimates of ($\hat{\alpha}$) were calculated using mathematically simulated scenarios with specified levels of foreign pollen intrusion, selfing, and orchard size.

Foreign pollen impacts were simulated by specifying a proportion of the seed crop to be considered as pollinated by foreign sources while maintaining the original reproductive phenology and no selfing. We assumed a foreign pollen pool with an effective size sufficient to make the proportion of full-sib relationships among the foreign pollen-produced progeny negligible. Eleven simulations were conducted with the contamination levels ranging from 0 to 1 in 0.1 increments.

Selfing effets were simulated by specifying a selfing proportion while maintaining the original reproductive phenology with no foreign pollen. Calculated phenological overlap values were used to determine mating-type proportions among the outcrossed seed.

The impact of orchard size was examined by simulating orchards ranging in size from 2 to 15 clones with complete reproductive phenology synchronization, no foreign pollen, and no selfing.

$\hat{\alpha}$ was calcuated for each of the simulations and compared to $\hat{\alpha}=4$, the standard value when the "half-sib only" relationship exists among the progeny.

Results

Loblolly pine orchard

Reproductive phenology

In the absence of selfing and foreign pollen contamination, half-sibs accounted for 88.7–92.3% of the pairwise progeny relationships with full-sib relationships accounting for the remaining percentage. As $\hat{\alpha}$ ranged from 3.593–3.713 among the individual trees, $\hat{\alpha}=4$ would be a 7.7–11% overestimation of α for these orchard trees. The average $\hat{\alpha}$ from the 15 individual seed trees was 3.7. Calculations were repeated after the reproductive phenology indices for all clone pairings were equalized. This would correspond to uniform gamete contributions among the orchard pollen parents. The average difference between uniform phenology (e.g., El-Kassaby and Askew 1991) and natural phenology (e.g., Erickson and Adams 1989) estimates for $\hat{\alpha}$ (3.733 versus 3.698) was small.

Due to low variability in $\hat{\alpha}$ among seed parents and the small difference attributable to reproductive phenology, $\hat{\alpha}=3.7$ was used in simulations of selfing and foreign pollen impacts.

Selfing

Selfing levels ranging from 0% to 100% were examined in the absence of foreign pollen. As reported in the previous section, when selfing was 0, $\hat{\alpha}$ was 3.7. $\hat{\alpha}$ declined as the selfing level increased, reaching a value of 1.5 when selfing reached 100% (Fig. 2).

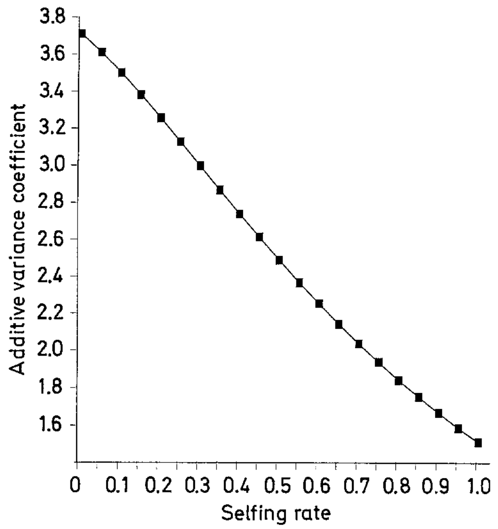


Fig. 2 Impact of selfing on the average additive variance coefficient for a 15-clone loblolly pine seed orchard

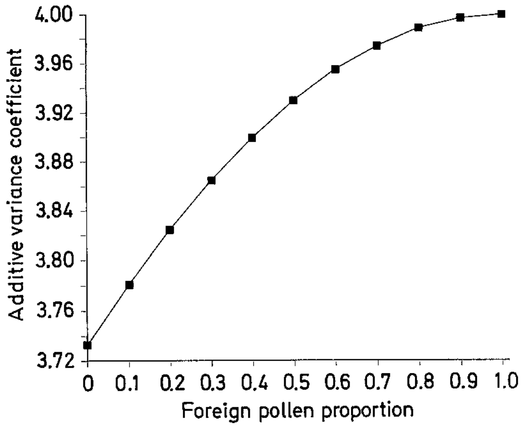


Fig. 3 Impact of foreign pollen on the average additive variance coefficient for a 15-clone loblolly pine seed orchard

Foreign pollen

Specified proportions of foreign pollen ranged from 0 to 1. $\hat{\alpha}$ was 3.73 with no foreign pollen and attained a maximum value of 4 when 100% of the pollen was of foreign origin (Fig. 3). $\hat{\alpha}$ was 3.87 for the loblolly pine orchard in the absence of selfing when the foreign pollen percentage was set at 36% to simulate the findings of Friedman and Adams (1985).

Orchard size

$\hat{\alpha}$ was 2 for a 2-clone orchard and increased to 3.733 for 15 clones on a theoretical asymptotic approach to 4 at infinity (Fig. 4).

Western redcedar orchard

Results for the western redcedar orchard were almost identical to those for the loblolly pine orchard. Response patterns for $\hat{\alpha}$ were the same with respect to selfing and foreign pollen impacts and will not be repeated in detail. In the absence of foreign pollen and with a selfing rate of 0.68, as reported by El-Kassaby et al. 1993, $\hat{\alpha}$ was 2.36.

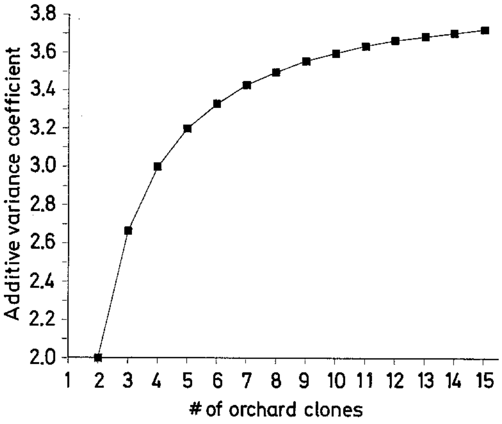


Fig. 4 Impact of orchard size on the average additive variance coefficient for a 15-clone loblolly pine seed orchard

Variance component estimates for 2-year height obtained from the orchard's wind-pollinated progeny:

$\sigma_F^2 = 1125.366$ (among O-P families)

$\sigma_B^2 = 194.131$ (among blocks)

$\sigma_{FB}^2 = 1224.682$ (O-P families × block interaction)

$\sigma_e^2 = 5362.289$ (residual)

Heritability was estimated as:

$$h^2 = \frac{4\hat{\sigma}_F^2}{4\hat{\sigma}_F^2 + \hat{\sigma}_{FB}^2 + \hat{\sigma}_e^2} = \frac{4501.11}{11088.44} = 0.406$$

(J. Russell, unpublished)

assuming only half-sib relationships ($\hat{\alpha} = 4$) among the progeny. Using the reproductive phenology data and the selfing estimate of 0.68, we calculated an adjusted heritability estimate, assuming no dominance variance and $\hat{\alpha} = 2.36$, as:

$$h^2 = \frac{2.36\hat{\sigma}_F^2}{2.36\,\hat{\sigma}_F^2 + \hat{\sigma}_{FB}^2 + \hat{\sigma}_e^2} = \frac{2655.86}{9242.83} = 0.287.$$

Adjusting $\hat{\alpha}$ in the heritability model resulted in a 29% reduction in the heritability estimate.

Discussion

Variation in proportions of foreign pollen, selfing rate, and orchard size all affected the estimation of $\hat{\alpha}$. Deviations from the idealized value of $\hat{\alpha} = 4$ varied for each situation. When the calculated value of $\hat{\alpha}$ is less than the idealized value of 4 the assumption of all half-sib relationships and the use of $\hat{\alpha}=4$ will overestimate the proportion of additive genetic variance. Selfing affected the rate of overestimation in a slightly exponential fashion with increasing levels of selfing (Fig. 5). Low selfing levels resulted in a 7–15% overestimation rate, and selfing levels beyond 30% would result in great overestimation.

Foreign pollen intrusion reduced the overestimation rate by increasing the effective size of the paternal population. As the foreign pollen proportion increased, the overestimation rate exponentially and asymptotically declined toward 0 (Fig. 6). Indeed, wind-pollinated seed orchards dominated by effectively large foreign pollen populations will produce the "idealized" seed crop situation of virtually all half-sib relationships.

As with foreign pollen, increasing orchard size also reduced overestimation; conversley, extremely small orchards may have great potential for overestimation (Fig. 7), but increasing the number of clones results in an exponential decrease in the overestimation rate. The decrease is due to an ameliorization of the effects of non-synchronous reproductive phenology by increasing the effective number of parents that reduces the proportional impact of any one parent.

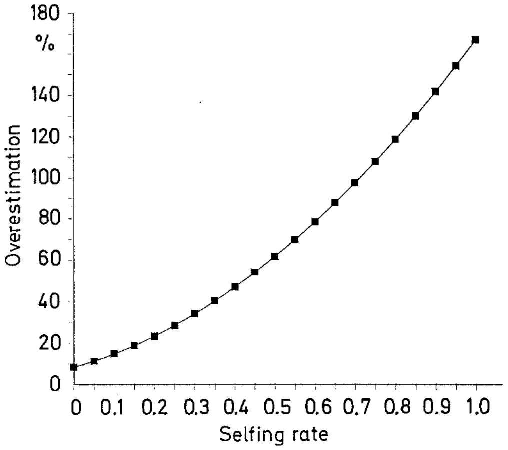
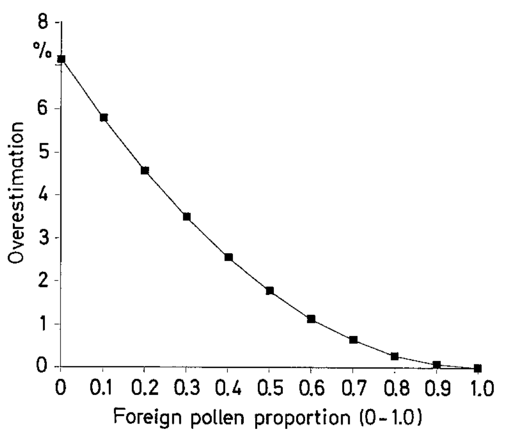


Fig. 5 Impact of selfing on overestimation of the average additive variance coefficient in a 15-clone loblolly pine seed orchard

Fig. 6 Impact of foreign pollen on overestimation of the average additive variance coefficient for a 15-clone loblolly pine seed orchard



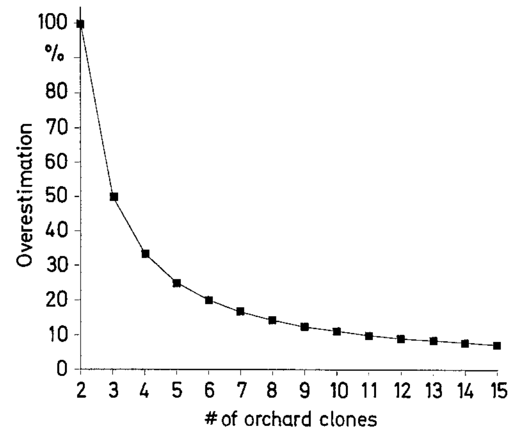


Fig. 7 Impact of orchard size on overestimation of the average additive variance coefficient for a 15-clone loblolly pine seed orchard

Use of wind-pollinated seed for progeny production with the goal of variance estimation requires consideration of the reproductive phenology, selfing rate, foreign pollen proportion, and orchard size. Reliance on an assumption of purely half-sib relationships among the progeny of single seed trees will rarely be accurate. $\hat{\alpha}$ can be greatly reduced by selfing and increased by the presence of foreign pollen. Orchard size will affect the number of potential half-sib and full-sib relationships that will exist among the progeny, and the reproductive phenology of the orchard trees can affect $\hat{\alpha}$ in either a positive or negative manner.

Any testing program that depends on wind-pollinated seed for estimates of genetic variance should carefully evaluate the factors that determine the relationships among the progeny. Natural populations will require an estimate of the selfing rate, at a minimum, and should include some estimate of the paternal population gamete contribution potential.

Finally, careful estimation of the paternal factors must be integrated with the use of proper mathematical estimation procedures. The methods of Cockerham and Weir (1984) provide an excellent model for incorporating paternal factors in the calculation of additive variance estimates. As in all studies that employ assumptions of basic biological factors, slight deviations from the assumption may have severe impacts on the accuracy of the results. In the case of wind-pollinated seed production in forest trees, the assumption of half-sib relationships is rarely true and may often be far from accurate.

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