Modeling Forage Legume Polycross Pollen-Parent Gamete Contributions to Progeny Based on Empirical Measurements with Implications for Effective Polycross Size

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Fig. 1 Plot of standardized pollen-parent frequency position sorted (least to most) (x-axis) with pollen-parent gamete contribution to progeny frequency deviation from a uniform frequency distribution (y-axis)

Random mating is a fundamental assumption in quantitative genetic theory and assumes pollen-parents contribute uniform gamete numbers to the progeny generation; polycross-size-expected-inbreeding rests on this assumption. This study empirically determined polycross pollen-parent gamete frequency contribution to the progeny generation and developed a model for these frequencies that depends on polycross pollen-parent number. Ten isolated forage legume polycrosses were evaluated ranging from 9 to 94 polycross pollen-parents, in three species [alfalfa (only outcross progeny considered), kura and red clover], pollinated with bumble or leafcutter bees. The Pioneer, Alforex, and KU09B polycrosses included clonally replicated parents. Parents and 321 to 1704 progeny per polycross were genotyped and paternity tested (seed-parent Individual was known). pollen-parent frequency contributions to the progeny generation were calculated for

each polycross. Pollen-parent frequencies and polycross size were standardized so comparisons between different sized polycrosses could be made. In no polycross was a uniform pollen-parent contribution to progeny observed (Fig.), indicating that a standard assumption of random mating is never observed. Weibull distributions fit best with observed pollen-parent frequencies, specifically an inverse Weibull cumulative distribution function fit the standardized combined across polycross pollen-parent frequencies with an of $R^2 = 0.953$ (Fig.). A model [1] was developed to predict pollen-parent frequency distribution of gamete contribution to the progeny generation given the number of pollen-parents in a polycross.

[1]
$$Pf_i^* = \frac{\frac{1}{N} \left[-1 + 1.1237(-\ln(1 - \frac{Pp_i}{N+1}))^{\frac{1}{1.495}} \right] + \frac{1}{N}}{\sum_{i=1}^{N} Pf_i}$$
 [2] $Pf_i = \frac{1}{N} \left[-1 + 1.1237(-\ln(1 - \frac{Pp_i}{N+1}))^{\frac{1}{1.495}} \right] + \frac{1}{N}$ where,

N = Number of possible pollen-parents

 Pf_i = Frequency of progeny having the i^{th} pollen-parent (Formula [2])

 $Pp_i = i^{\text{th}}$ pollen-parent sequence position in array of possible pollen-parents (N) ordered from least frequent (Pf_b Min.) to most frequent (Pf_b Max.) pollen-parent of polycross progeny

$$Pf_i^* =$$
adjusted Pf_i such that $\sum_{i=1}^N Pf_i^* = 1$

This model [1] was then applied to the simple situation of a polycross with uniform seed-parent gamete contribution to progeny (i.e., equally bulked seed-parent halfsib seed) and the modeled expected pollenparent gamete contribution to progeny. Effective polycross size was reduced in a linear fashion ($N_{Effective} = 0.9N_{Actual} + 0.485$, $r^2 = 1$), resulting in a 7-10% effective polycross size reduction for polycross sizes ranging from 15 to 100. Further implications of an inverse Weibull cumulative distribution function pollen-parent gamete contribution frequency distribution to the progeny generation should be examined in the context of other known perturbations to classic random-mating such as distance dependency and fecundity.