D. V. Shaw

Trait mean depression for second-generation inbred strawberry populations with and without parent selection

Abstract Strawberry genotypes selected for superior fruit yield or chosen at random from first-generation self, full-sib, and half-sib populations were crossed to provide second-generation inbred progenies and composite cross-fertilized control populations. Mean yields for inbred offspring from crosses among selected parents exceeded those from the offspring of unselected parents by 87%, 23%, and 37% for self, full-sib, and half-sib populations, respectively; yields for offspring from unrelated crosses among selected parents were 54% larger than those for crosses among unselected parents. Selection for yield also resulted in significant correlated response for fruit number and plant diameter. Mean yields for second-generation half-sib and full-sib offspring from selected parents were greater than those for offspring from the unselected but noninbred control population. This suggests that selection can be a powerful force in counteracting most of the inbreeding depression expected in cross-fertilized strawberry breeding programs. Selection treatment × inbreeding rate interactions were non-significant for all traits; thus, selection among partially inbred offspring did not have a large effect on the rate of genetic progress. Differential realized selection intensity among individuals with differing levels of homozygosity accumulated due to inbreeding is suggested as the most likely explanation for the absence of association between pedigree inbreeding coefficients and cross performance detected previously in strawberry.

Key words *Fragaria ananassa* · Inbreeding depression · Inbreeding rate · Selection response

D. V. Shaw (✉)
Pomology Department, University of California, Davis, CA 95616, USA

Introduction

Forced inbreeding of naturally cross-fertilized plants often results in severe trait mean depression (Hallauer and Sears 1973; Cornelius and Dudley 1974; Wilcox 1983; Sniezko and Zobel 1998; Woods and Heaman 1989). In domestic strawberry (*Fragaria × ananassa*), fruit yield is among the traits most affected by inbreeding and can be reduced by as much as 80% after two generations of self-fertilization (Jones and Singleton 1940; Marrow and Darrow 1952; Aalders and Craig 1968; Spangelo et al. 1971; Niemirowicz-Szczytt 1989). However, although inbreeding is of general concern to cross-fertilized plant improvement programs, the magnitude of trait mean depression depends on the rate at which homozygosity accumulates (Ehiobu et al. 1989) and the strength of selection pressure counteracting this depression, conscious or inadvertent, at each generation interval (Falconer 1981, Huang et al. 1995). The interaction between selection and inbreeding can be complex, and models that accommodate both factors have been developed only for breeding systems that utilize discrete generations (Wray et al. 1990; Verrier et al. 1990).

Recent experiments with strawberry have demonstrated significant and occasionally severe trait mean depression for populations of inbred offspring constructed from matings among current-generation relatives; fruit yields were depressed significantly even when rather modest rates of inbreeding were applied (Shaw 1995). The magnitude of mean depression observed for first-generation selfs in these studies was consistent with results obtained from other studies where inbreeding was conducted through selfing alone (Jones and Singleton 1940; Morrow and Darrow 1952; Aalders and Craig 1968; Spangelo et al. 1971). However, in companion studies, no relationship was detected between trait means and pedigree inbreeding coefficients (F), where coancestry had accumulated

over several cycles of breeding and selection (Shaw 1995). Although the rate of increase in pedigree inbreeding coefficients may have consequences for long-term selection response (Robertson 1961; Bulmer 1981), the most immediate concern is their relationship to homozygosity and consequent limits to short-term selection response. This study was conducted to evaluate the potential for strong directional selection to compensate for trait mean depression at differing rates of inbreeding.

Materials and methods

Ten randomly chosen genotypes and 10 genotypes selected for high yield were retained from first-generation self, full-sib, and half-sib progenies and used as parents in the present study. Selection was based on individual (phenotypic) values for fruit yield obtained from trials described previously (Shaw 1995); standardized selection differentials were i = 1.69, 1.54, and 1.43 for the selection genotypes retained from self, full-sib, and half-sib populations, respectively.

Matings were performed among the genotypes within each selection treatment to generate second-generation self, full-sib, and half-sib progenies. Not all parent genotypes contributed to successful matings, but 5–11 second-generation inbred progenies from 5–10 parents were available for each selection treatment and inbreeding rate combination. Also, unrelated crosses were performed among a subset of the first-generation inbreds to form a composite non-inbred control population for each selection treatment. These non-inbred control population included 8 and 7 crosses among 16 and 14 of the parents that were used to generate the second-generation inbred progenies, for unselected and selected sets, respectively. These crosses are expected to have inbreeding coefficients (F) equal to zero, but their among-cross variances may not be representative of randomly mated populations of the same genetic composition.

Twenty seedlings (occasionally fewer) from each of the 63 inbred and composite non-inbred progenies described above were established in field trials on September 14, 1994, at the Wolfskill Experimental Orchard, near Davis, California and cultured as described previously (Shaw 1995). A randomized complete block design was used, with a single plot of 10 seedings from each cross in each of two blocks. Data for growth and productivity traits were collected for individual plants throughout the season following plantation establishment. Plant cross-sectional diameters were obtained on April 4 to describe vegetative growth from planting to mid-spring (Shaw 1993). Weekly yields, fruit numbers, and a commercial appearance scores (Shaw et al. 1989) were recorded for each plant for 8 consecutive weeks, beginning the third week of April and ending in late June of the year following planting. Fruit size was calculated by dividing weekly yields by corresponding fruit numbers; both seasonal fruit sizes and appearance scores were expressed as weighted averages, with weighting performed using weekly yield values.

ANOVAs were conducted using blocks, selection treatments, inbreeding rate, selection treatment × inbreeding rate interaction, and progenies nested in inbreeding rate as sources of variation and SAS procedure GLM (SAS 1988). Inbreeding rates and progenies in selection treatments were treated as random effects; all other sources were considered as fixed effects (Table 1).

Results and discussion

Trait means for second-generation self, full-sib, and half-sib progenies from both the selected and unselected parental sets were uniformly lower than for the progenies of unrelated crosses among samples of the corresponding parents (Table 2). Trait mean depression increased with increasing F, and the trends were similar to those reported earlier for first-generation inbreds (Shaw 1995): a modest depression was found for spring plant diameter, fruit size, and fruit appearance (15–24% reduction for second-generation selfs), and a larger depression was observed for fruit number and yield (36–56% reduction for second-generation selfs). Trait mean depression in yield for second-generation selfed offspring from unselected parents was 56%, and only slightly larger than the 45% mean depression in yield reported previously for first-generation selfs from the same population (Shaw 1995). Linear response of inbreeding depression with F was detected previously (Shaw 1995), and a somewhat larger rate of depression was expected in the second generation than that actually observed. This result may indicate that the relationship between trait mean depression and F becomes increasingly nonlinear at higher inbreeding rates (Crow and Kimura 1970). However, an equally likely alternative is that some inadvertent or natural selection against inbred offspring selection has occurred in this experiment (Huang et al. 1995). Yields here were based only on flowering genotypes A slightly larger number of the second-generation inbred offspring failed to flower (6 of 69 vs. 5 of 133 seedlings for selfs and crosses, respectively), and the rate of depression for second-generation selfed progenies may be a slight underestimate.

Offspring from selected genotypes for self, full-sib, and half-sib populations had 87, 23, and 37% greater yields, respectively, than the corresponding offspring of unselected parents; yields for offspring from unrelated crosses among a sample of the selected parents were 54% larger than for crosses among unselected parents (Table 2). Second-generation full-sib and half-sib offspring from selected parents had 5.3% and 25.9% greater yields, respectively, than the offspring of the unselected but non-inbred control population, demonstrating that selection can be a powerful force in

Table 1 Expected mean squares for five traits with two selection treatments and four rates of inbreeding (AF)

Source	df	Expected mean squares
Block (B)	1	$\sigma^2 + 502.4\ \sigma^2_B$
Selection treatment (S)	1	$\sigma^2 + 13.0\ \sigma^2_{C/SR} + 386.3\ \sigma^2_S$
Inbreeding rate (R)	3	$\sigma^2 + 13.9\ \sigma^2_{C/SR} + 212.3\ \sigma^2_R$
S × R	3	$\sigma^2 + 14.0\ \sigma^2_{C/SR} + 105.4\ \sigma^2_{S \times R}$
Cross/(S × R)	55	$\sigma^2 + 16.5\ \sigma^2_{C/SR}$
Error	1027	σ^2

Table 2 Means and standard deviations (in parentheses) for five traits, for sets of bi-parental progenies generated using four rates of inbreeding (ΔF)

Inbreeding rate[a]	N	Selection[b] treatment	Traits				
			Spring diameter (cm)	Yield (g/plant)	Appearance score	Fruit size (g/fruit)	Fruit number
Crosses (ΔF = 0)	128	0	28.3 (4.8)	482.4 (273.5)	2.33 (0.56)	21.8 (7.0)	24.6 (16.8)
	132	+	31.3 (4.9)	743.2 (307.3)	2.21 (0.40)	18.9 (4.3)	41.1 (18.5)
Half-sibs (ΔF = 0.125)	189	0	28.2 (4.1)	444.0 (281.0)	2.20 (0.41)	20.6 (6.4)	22.8 (16.2)
	128	+	32.2 (4.9)	607.2 (404.1)	2.08 (0.38)	20.3 (5.8)	31.3 (21.5)
Full-sibs (ΔF = 0.250)	152	0	27.3 (4.8)	413.5 (232.5)	2.21 (0.41)	19.7 (5.3)	22.3 (13.7)
	103	+	27.8 (3.4)	508.1 (280.8)	2.17 (0.52)	20.7 (6.6)	28.1 (19.1)
Selfs (ΔF = 0.500)	63	0	24.0 (6.4)	210.1 (181.4)	1.82 (0.41)	16.6 (5.1)	12.8 (10.4)
	133	+	24.5 (5.4)	392.7 (271.1)	1.86 (0.42)	16.2 (5.7)	26.1 (17.9)

[a] Pedigree inbreeding coefficients for second-generation half-sibs, full-sibs and selfs are 0.219, 0.375, and 0.75; unrelated crosses among first-generation inbreds have F = 0
[b] 0 and + indicate no selection, on selection for yield with i = 1.43, 1.54, and 1.69 for half-sib, full-sib, and self matings; crosses were performed among the same parents, but such that offspring were not inbred

Table 3 Mean squares and variance components (as a percentage of the phenotypic variance) for five traits, for sets of bi-parental progenies generated using four levels of inbreeding and two selection regimes

Source	Spring diameter	Yield[a]	Appearance score	Fruit size	Fruit number[a]
Block	1,758.9**	4,222.5**	0.16	21.3	97.3**
Selection treatment (S)	755.5*	6,839.3**	1.09	88.7	247.5**
Inbreeding Level (R)	1,062.9**	3,112.6**	5.65**	406.1*	62.3**
S×R	188.6	344.6	0.23	180.1	16.9
Cross/S×R	184.9**	269.5**	0.55**	200.1**	12.0**
Error	11.9	69.0	0.18	25.0	2.4

* and ** indicate statistical significance at the 0.05 and 0.01 probability levels, respectively
[a] Mean square for yield and fruit number have been multiplied by 10^{-3} and 10^{-2}, respectively to shorten the table

counteracting most of the inbreeding depression expected in cross-fertilized strawberry breeding programs. Selection of parents for yield also increased fruit number (26–103%) and plant diameter (2–14%) at all inbreeding levels, indicating a correlated response to selection (Table 2). ANOVAs verified the significance of the selection treatment differences for these traits (Table 3). Selection for yield had no apparent indirect effect on fruit size or appearance score (Table 2), and selection treatment effects for these traits were non-significant in ANOVAs (Table 3).

Selection treatment × inbreeding rate interactions were non-significant for all traits (Table 3). Inbreeding exposes recessive homozygotes in greater frequencies and can increase the rate of change in favorable allele frequency due to selection (Falconer 1981), thus speed-ing the rate of genetic progress. However, although selection compensated for inbreeding depression in yield at all rates, the absence of selection treatment × inbreeding rate interactions suggests that the magnitude of selection response was not increased by selection within increasingly inbred populations. An important caution here is that the absence of differences in selection response among progenies of differing F may be an artifact of the current population structure. Selections from first-generation selfs, full-sibs, and half-sibs were used to generate second-generation progenies with like rates of inbreeding. Thus, selections expected to give the higher rates of selection response were used to produce progenies with the highest increments of inbreeding, and trait means in these experiments are confounded with cumulative homo-

zygosity. The rate of genetic change for differing rates of inbreeding must ultimately be tested using the offspring of unrelated crosses among the selection at each level of homozygosity.

In this controlled comparison, roughly equal selection intensities were applied in retaining the parents from different categories of first-generation inbreds. However, in the breeding population heterogeneous for inbreeding coefficients, selection based on phenotypic expression will result in differential realized selection intensity among individuals with different levels of homozygosity accumulated due to inbreeding. Highly significant variation ($P<0.01$) was detected among crosses within selection treatment and inbreeding rate combinations for all traits (Table 3), indicating considerable opportunity for selection response regardless of inbreeding level. Variability in the intensity of selection among and within crosses of variable inbreeding origin is a likely explanation for the absence of association between pedigree inbreeding coefficients and cross performance in strawberry breeding populations (Shaw 1995).

References

Aalders LE, Craig DL (1968) General and specific combining ability in seven inbred strawberry lines. Can J Genet Cytol 10:1–6

Bulmer MG (1985) The mathematical theory of quantitative genetics. Clarendon Press, Oxford

Cornelius PL, Dudley JW (1974) Effects of inbreeding by selfing and full-sib mating in a maize population. Crop Sci 14:815–819

Crow JF, Kimura M (1970) An introduction to population genetic theory. Harper and Row, New York

Ehiobu NG, Goddard ME, Taylor JF (1989) Effect of rate of inbreeding on inbreeding depression in *Dorsophila melanogaster*. Theor Appl Genet 77:123–127

Falconer DS (1981) Introduction to quantitative genetics. Longman Press, New York

Hallauer AR, Sears JH (1973) Changes in quantitative traits associated with inbreeding in a synthetic variety of maize. Crop Sci 13:327–330

Huang H, Harding J, Byrne T, Famula T (1995) Effects of inbreeding on cut flower yield in gerbera. Euphytica 81:157–161

Jones DF, Singleton WR (1940) The improvement of naturally cross-pollinated plants by selection in self-fertilized lines: III. Investigations with vegetatively propagated fruits. Conn Agric Exp Bull 435:329–347

Morrow EB, Darrow GM (1952) The effect of limited inbreeding in strawberries. Proc Am Soc Hortic Sci 59:269–276

Niemirowicz-Szczytt K (1989) Preliminary studies on inbreeding in strawberry. Acta Horti 265:97–104

Robertson A (1961) Inbreeding in artificial selection programs. Genet Res 2:189–194

SAS Institute (1988) SAS/STAT users guide, release 6.03 edition SAS Institute, Cary, N.C.

Shaw DV (1993) Genetic correlations between vegetative growth traits and productivity at different within- season intervals for strawberries (*Fragaria × ananassa*). Theor Appl Genet 85:1001–1009

Shaw DV (1995) Comparison of ancestral and current-generation inbreeding in an experimental strawberry breeding population. Theor Appl Genet 90:237–241

Shaw DV, Bringhurst RS, Voth V (1989) Genetic parameters estimated for an advanced-cycle strawberry breeding population at two locations. J Am Soc Hortic Sci 114:823–827

Sniezko RA, Zobel BJ (1998) Seedling height and diameter variation of various degrees of inbred and outcross progenies of loblolly pins. Silvae Genet 37:50–60

Spangelo LPS, Hsu CS, Fejer SO, Watkins R (1971) Inbred line × tester analysis and the potential of inbreeding in strawberry breeding. Can J Genet Cytol 13:460–469

Verrier E, Colleau JJ, Fouley JL (1990) Predicting cumulated response to directional selection in finite panmictic populations. Theor Appl Genet 79:833–840

Wilcox MD (1983) Inbreeding depression and genetic variances estimated from self and cross pollinated families of *Pinus radiata*. Silvae Genet 32:89–96

Woods JH, Heaman JC (1989) Effects of different inbreeding levels on filled seed production in Douglas-fir. Can J For Res 19:54–59

Wray NR, Wooliams JA, Thompson R (1990) Methods for predicting rates of inbreeding in selected populations. Theor Appl Genet 80:503–512