Evaluation of Simple Methods for Estimating Broad-Sense Heritability in Stands of Randomly Planted Genotypes

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ABSTRACT

Inexpensive estimates of broad-sense heritability (BSH) may be valuable in plant breeding. This research evaluated two methods for estimating BSH with data from stands of equidistantly spaced genotypes. Both methods depend on the assumption that genetic and environmental contributions to plot variance (plot = group of contiguous plants) change at different rates as plot size changes if genetic variation is distributed randomly. For the method proposed by V.J. Shrikhande, variances among plot means are computed and least-squares regression used to estimate environmental and genetic variances and the change in a plot variance with changes in plot size. The other method involves the same approach, but uses a two-parameter model suggested by G.H. Freeman but not previously used to estimate BSH. Both methods produce biased BSH estimates since genotypic and genotypic × environmental components of variation are inseparable. Our objectives were to: (i) develop software to calculate variances for the methods, and (ii) compare BSH estimates generated using these methods with each other and with those from analysis of variance (ANOVA) of data from families grown in the same environment. Data were from a perennial herb, *Sphaeralcea emoryi* Torr. grown in Tucson, AZ. Shrikhande's method produced parameter estimates with large variances and BSH estimates that averaged 3.6 times larger than those from Freeman's method. Only BSH estimates from Freeman's method agreed well with those from ANOVA for most traits. Freeman's method may be useful for rapidly and inexpensively generating BSH estimates in a variety of situations, especially when traditional genetic analysis are difficult.

Generating estimates of heritability in plants typically involves the evaluation of progenies or clones of known genetic relationship from populations of interest (Namkoong, 1979; Nyquist, 1991). In most crop plants, this usually requires controlled matings and the establishment and evaluation of progenies in field trials. In many situations, it may be difficult to produce the needed genotypes, or to justify the time and expense required to generate highly accurate estimates. It would be useful to have methods that could be used to estimate heritability using data from standard evaluation trials where samples of genotypes produced from open pollination are grown.

Forest geneticists developed a method for generating estimates of broad-sense heritability using data from plantings where the distance between neighboring individual plants in contiguous rows is equal to that between plants within a row (''equidistant spacing'') (Shrikhande, 1957; Nyquist, 1991). This approach is based on the assumption that both random and systematic environmental variation within a planting containing a single genotype follows an inverse logarithmic function of the number of individual plants within a plot (x), where a plot is a group of contiguous plants (Smith, 1936). Given a measure of environmental variation on an individual basis (V_1), Smith (1936) showed that the pattern of environmental variation on a plot mean basis (V_x) in such a planting could be represented by the regression coefficient b (termed the heterogeneity coefficient) of the function (Smith's Law):

$$V_x = \frac{V_1}{x^b} \quad [1]$$

In a planting where environmental variation changes abruptly, phenotypic correlations between neighboring plants and mean plot variance would decrease rapidly as plot size increases and b approaches zero. More consistent environmental effects would be associated with a more gradual decline in plot variance and b values approaching one.

In the case where genetic variation is present and it is distributed randomly within a planting, Shrikhande (1957) suggested that genetic variation among plots within a planting would follow a direct inverse function of plot size and could change at a rate different than environmental variation as plot size changed. Therefore, Shrikhande (1957) expressed phenotypic variance on a plot mean basis for plots of x individuals (V_x) as:

$$V_x = \frac{V_g}{x} + \frac{V_e}{x^b} \quad [2]$$

where V_g and V_e represent estimates of genetic and environmental variances, respectively. To generate estimates of broad-sense heritability ($BSH = V_g/[V_g + V_e]$) by Shrikhande's method, means for traits of interest are calculated for all plots of size $x = 1$ to n (with n typically equal to a maximum of half the total number of plants in the stand) from a planting with equidistant spacing among plants. The variance between these plot means is then calculated for each plot size. The parameters V_g, V_e, and b can be estimated iteratively by Eq. 2 and least-squares procedures (Namkoong and Squillace, 1970). This technique for estimating BSH is referred to here as "Shrikhande's method." Since genotypic and genotypic × environmental components of variation cannot be separated by this technique, these BSH estimates may be biased upward and therefore should be seen as maximum estimates for heritability (Nyquist, 1991).

Shrikhande's method has been used to estimate BSH

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Abbreviations: BSH, broad-sense heritability.

in experiments with various species of long-lived perennial plants (Sakai and Hatakeyama, 1963; Armitage and Burrows, 1966). However, BSH estimates from this method have not been compared with estimates made by any other techniques. Namkoong and Squillace (1970) found that this method may involve large sampling errors. These authors also concluded that Shrikhande's method was "useful and dependable" as long as b was not near one and environmental variation closely followed Smith's Law. Nevertheless, they did not compare estimates with those generated from more traditional techniques. In a simulation study, Usanis (1972) showed that Shrikhande's model may be unreliable in particular circumstances, especially when environmental variation occurs either as random patches or in the form of gradients.

Apparently independent of Shrikhande, Freeman (1963) adapted Smith's Law to provide an estimate of V_e. In this treatment, α is defined as the proportion of the variance calculated for plots containing one plant (V_1) that is due to the environment (i.e., V_e):

$$V_x = \frac{V_1\alpha}{x^b} + \frac{V_1(1 - \alpha)}{x} \quad [3]$$

While Freeman (1963) did not describe this as such, $1 - \alpha$ represents an estimate of the proportion of the phenotypic variance that is due to nonenvironmental effects and is equivalent to BSH. Since this relationship involves the estimation of only two parameters (α and b), compared with three with Shrikhande's method (V_g, V_e, and b), it may be a simpler problem for nonlinear estimation. Moreover, because it does not depend on independent estimation of V_g and V_e, it may be more reliable when autocorrelation between these parameters is high. Under these circumstances, covariance estimates between parameter estimates will be high. Positive autocorrelation will produce high variances for the estimated parameters and less precise BSH estimates.

The basic method outlined by Shrikhande has not been widely investigated in spite of its economy. This may be at least partially due to the computational difficulties associated with estimating variances for means from a series of plot sizes. The availability of a simple method for calculating these variances and the application of Freeman's method may permit rapid and more accurate estimation of BSH from data from plantings of equidistantly spaced individual plants. Our objectives in this research were to: (i) create a computer program to calculate variances needed to execute both the Shrikhande and Freeman estimation methods, and (ii) compare BSH estimates generated by these methods in a population derived from random mating with each other and with those from analysis of variance (ANOVA) of individual plants from families grown in the same environment. The second objective was accomplished with a population of *Sphaeralcea emoryi* Torr. Using the same parental plants, we grew progenies derived from random mating and full-sib families of *S. emoryi* in contiguous plots at Tucson, AZ. Data on various agronomic traits were collected and BSH estimates were generated by the three methods.

MATERIALS AND METHODS

Plant Materials and Field Experiments

The genus *Sphaeralcea* contains primarily short-lived suffrutescent perennial herbs native to arid regions in the western USA and northern Mexico (Kearney, 1935). They may successfully colonize a variety of habitats and represent a valuable source of forage in many disturbed desert sites (Pendery and Rumbaugh, 1993). Our experiments utilized a population of *S. emoryi* from an frequently disturbed site at Tucson, AZ. Open-pollinated seeds were collected in April 1992 from 100 plants growing at this site. An equal number of seeds from each plant were bulked and this sample was used as the basic source population (AZSE-11) in this research.

Controlled hand pollinations were made in the greenhouse with 46 randomly selected plants from the source population in a nested seed parent/pollen parent/progeny design (North Carolina Design I, Comstock and Robinson, 1948). Either two or three seed parents (33 total) were crossed with vacuum emasculation to each pollen parent (13 total) to produce 30 full-sib families. The same 46 parental plants were randomly intercrossed by hand with samples of bulk pollen from all plants in the population without emasculation and the resulting seed bulked (equal amounts per seed parent) to form an intercross population. On the basis of analysis of mating behavior of *Sphaeralcea laxa* Woot. & Standl., all parents were assumed to be noninbred and to have limited self fertility (Hubbard et al., 1993).

Progenies from the Design I families and randomly drawn seeds from the intercross population were sown in the greenhouse in September 1992. The resulting seedlings were transplanted into directly contiguous field plantings in the same irrigation basin at the Tucson Plant Materials Center at Tucson, AZ, in November 1992. Plants were placed on 0.75-m centers in rows separated by 0.75 m. In the Design I planting, five progenies per family were planted together in a row (plot) within each of three replications, which were constructed in a randomized complete block design with families as treatments. This planting covered an area of 7.5 by 33.75 m. A total of 300 plants from the intercross population were randomly transplanted to produce a second 10×30 matrix (area: 7.5 by 22.5 m) of equidistantly spaced plants. Both plantings were 10 rows wide were surrounded by unmeasured border plants, and were not irrigated after establishment. Prior observation of plant growth had suggested that similar patterns of environmental variation could be expected at the site where the two plantings were located (B. Munda and M. Pater, 1992, personal communication).

Beginning in March 1993, data were collected on each individual in both plantings. Traits considered relevant for the use of this species in rangeland revegetation (Pendery and Rumbaugh, 1993) and evaluated were as follow: plant height and width; length of pedicels, scored by a 1-to-3 scale with 1 = <2 cm and 3 = >4 cm, and length of the longest primary shoot; reproductive maturity, scored midway and late in the growing season by a 1-to-5 scale with 0 = no flowers and 5 = mature seed shed; biomass, scored by a 1-to-10 scale with 0 = little biomass to 10 = maximal biomass; and plant habit, scored by a 1-to-4 scale with 1 = upright and 4 = decumbent. All analyses were conducted with untransformed data except those for plant habit. This variable was Box-Cox transformed (Sokal and Rohlf, 1981) to improve its fit to normality.

Parameter Estimation

A program (PLANTVAR) was written in the C language to calculate variances for mean values from plots of size x and used a data matrix taken from a stand of equidistantly spaced plants. This program was compiled for use on DOS-based computers. (Copies of the program along with detailed instructions for its use can be requested from the senior author.) Input required are the number of columns and rows in the matrix (planting) as the first line followed by the data matrix for a given variable. The specific plot sizes and dimensions to be used are stipulated within a two-column "rule" file. For example, for a plot size of $x = 16$, the dimensions column in the rule file could include 1×16, 2×8, and/or 4×4. Each line of the output from PLANTVAR includes the plot size (x) and variance among means for each plot size (V_x). The accuracy of PLANTVAR was confirmed by randomly generated 5×5 matrices where variances among plot means were calculated by hand.

By means of input data sets containing x and V_x produced by PLANTVAR for each trait, least-squares estimates were made for the parameters α and b of Freeman's model (Eq. 3) by the unweighted Marquardt iteration method in PROC NLIN in SAS (SAS Inst., 1989). Iterations that included α and b in increments of 0.01 generally produced small residual sums of squares after relatively little calculation time. Confidence limits (90%) were calculated with the standard errors associated with each parameter generated by PROC NLIN assuming that the underlying distribution of each parameter was normal. Estimates of V_g, V_e, and b were also made for all traits in both species by the same iteration method, but with the three-parameter model (Eq. 2) defined by Shrikhande (1957) as described by Namkoong and Squillace (1970).

For at least the Shrikhande method, errors associated with the least-squares estimates for parameters are quite sensitive to the number of different plot sizes, their dimensions, and the largest plot size used (Usanis, 1972). Repeated estimates were therefore made with both the Freeman and Shrikhande methods with a wide variety of plot sizes and dimensions in order to minimize these errors. Included as a default were maximum plot sizes (x) from 2 to one-half the total number of plants in the matrix (Namkoong and Squillace, 1970). For $x < 10$, all possible square and rectangular plots were included. With $10 \leq x < 20$, $1 \times x$ plots were excluded, and with $x \geq 20$, $1 \times x$ and $2 \times x$ plots were excluded. Fit to the model using variances associated with a given set of plot sizes and dimensions was determined by analyzing the size of the standard error for each estimated parameter. Best fit was associated with the smallest sum of standard errors for all parameters with standard errors represented as a proportion of the estimated parameter before summation.

Estimation of BSH with data from full-sib families followed procedures described by Nyquist (1991). Estimates of variance components (Table 1) were generated by the restricted maximum-likelihood method of PROC VARCOMP in SAS (SAS Inst., 1989). Assuming no maternal effects (Mitchell-Olds and Bergelson, 1990), BSH was estimated by:

$$BSH = \frac{4\ \sigma_F^2}{\sigma_F^2 + \sigma_M^2 + \sigma_\varepsilon^2 + \sigma_W^2 + \sigma_R^2} \qquad [4]$$

where σ_F^2, σ_M^2, σ_ε^2, σ_w^2, and σ_R^2 refer to variance components for seed parents within pollen parents, pollen parents, experimental error, individual plants within plots, and replications, respectively. The variance component for replications was included as part of the phenotypic variance since all replications together would represent the area for which the environmental variance is calculated by the Shrikhande and Freeman methods. Normal-approximation delete-one jackknife estimates of 90% confidence limits for BSH values from ANOVA were calculated following the procedures of Knapp et al. (1989).

Table 1. Analysis of variance for individuals from full-sib families of *Sphaeralcea emoryi* mated using a Design I scheme (seed parents nested within pollen parents). These were grown and evaluated using a randomized complete block design in a single environment with multiple plants per family within a plot in each replication.

Source of variation	df†	Expected mean squares‡
Replications	$r - 1$	$\sigma_w^2 + n\sigma_\varepsilon^2 + r(\Sigma f)\sigma_R^2$
Pollen parents	$m - 1$	$\sigma_w^2 + n\sigma_\varepsilon^2 + r\sigma_F^2 + rf\sigma_M^2$
Seed parents within pollen parents	$\Sigma_{i=1}^{m} (f_i - 1)$	$\sigma_w^2 + n\sigma_\varepsilon^2 + r\sigma_F^2$
Experimental error	$(r - 1)(\Sigma f_i - 1)$	$\sigma_w^2 + n\sigma_\varepsilon^2$
Individuals within plots	$r(\Sigma f_i)(m - 1)$	σ_w^2

† r, m, f_i, and n refer to number of replications, pollen parents, seed parents, and number of plants per family and replication, respectively.
‡ σ_R^2, σ_M^2, σ_F^2, σ_ε^2, and σ_w^2 refer to variance components for replications, pollen parents, seed parents within pollen parents, experimental error, and individual plants within plots respectively.

RESULTS

Heterogeneity coefficients estimated by Freeman's method ranged from 0.49 to 0.88 for the traits measured in the intercross population (Table 2). By Freeman's method, the smallest standard errors as a proportion of the parameters were associated with estimates made with a maximum plot size of 36 and with the 16 smallest plot sizes (x = 1–6, 8–10, 12, 15, 16, 20, 25, 30, and 36) constructed with the default plot dimensions. With Shrikhande's method, a maximum plot size of 30 (15 smallest plot sizes) and the default plot dimensions produced the smallest proportional standard errors for the estimated parameters. These plot sizes were used in generating all parameter estimates with each method.

Excluding pedicel length score, for which Freeman's method estimated BSH equal to zero, BSH estimates with Shrikhande's method averaged about 3.6 times larger than those generated by Freeman's method (Table 2). In no case did the Shrikhande BSH estimate fall within the 90% confidence interval for the Freeman estimate. Estimates for V_g and V_e generated by Shrikhande's method were closely correlated with each other in all cases ($r > 0.96$), and this was reflected in generally large standard errors for the estimated parameters (mean SE = 208% of the parameter). Using Freeman's method, correlation between α and b was in the range of r = 0.20–0.30 and standard errors associated with the estimated parameters were much smaller (mean SE = 40% of the parameter).

For pairs of non-zero BSH estimates, those made by Freeman's method were on average 23% smaller than estimates generated by ANOVA (Table 2). However, all BSH estimates made with Freeman's method fell within the 90% confidence interval for the ANOVA-based estimate for these traits and the mean absolute value ($\pm$ SE) of the differences between the two estimates was 0.18 ± 0.04. With Shrikhande's method, BSH estimates for the same traits were always greater (mean = 152% larger) than the ANOVA-based estimates. Shrikhande BSH estimates for only two traits

Table 2. Analysis of agronomic traits in *Sphaeralcea emoryi* at Tucson, AZ, in order of decreasing heterogeneity coefficient. Measured heterogeneity coefficients and heritability estimates and confidence limits generated using ANOVA and Freeman's and Shrikhande's iterative methods.

Trait	Evaluation protocol, month (1993)	Heterogeneity coefficient†	Broad-sense heritability estimation method		
			N.C. Design I-variance components‡	Freeman	Shrikhande
Plant height	Natural maximum height (cm), Sept.	0.88	0.464 (0.067–0.862)	0.090 (0–0.206)§	0.482
Pedicel length score	1 = <2 cm, 2 = 2–3 cm, 3 = >4 cm, May	0.85	0.317 (0.012–0.623)	0 (0–0.032)	0.501
Plant width	Natural maximum width (cm), Sept.	0.84	0.246 (0.017–0.475)	0.110 (0–0.214)	0.755
Late-spring maturity score	0 = no flowers → 5 = seed shed, May	0.82	0.208 (0.011–0.404)	0.220 (0.153–0.287)	0.818
Biomass score	0 = little → 10 = maximal, Nov.	0.69	0.202 (0–0.544)	0.330 (0.232–0.428)	0.784
Mid-spring maturity score	0 = no flowers → 5 = seed shed, Apr.	0.66	0.179 (0–0.296)	0.110 (0.059–0.161)	0.318
Shoot length	Longest primary stem, base → apex (cm), Sept.	0.63	0.513 (0.133–0.925)	0.340 (0.262–0.418)	0.760
Plant habit score	1 = upright → 4 = decumbent, Apr.	0.58	0 (0–0.045)	0.258 (0.227–0.289)	0.503

† Heterogeneity coefficient as estimated by Freeman's method. Differences between these values and heterogeneity coefficients estimated using Shrikhande's method (not shown) were always <5% of the Freeman estimate.

‡ Broad-sense heritability (biased) estimated by $4\sigma_P^2/(\sigma_P^2 + \sigma_M^2 + \sigma_\varepsilon^2 + \sigma_w^2 + \sigma_R^2)$ where σ_P^2, σ_M^2, σ_ε^2, σ_w^2, and σ_R^2 are variance component estimates for pollen parents, seed parents within pollen parents, experimental error, plants within plots, and replications, respectively (Table 1) (Nyquist, 1991), assuming no maternal effects. Normal-approximation 90% jackknife confidence limits based on untransformed point estimates are in parentheses (Knapp et al., 1989).

§ 90% confidence interval assuming underlying distribution is normal.

fell within the confidence intervals for the estimates from ANOVA and the mean difference between the two estimates for all traits was 0.35 ± 0.08.

The theory underlying the Shrikhande and Freeman methods (Shrikhande, 1957) indicates that separation of V_g and V_e is not possible when the phenotypes of neighboring plants are highly positively correlated with each other, i.e., when the heterogeneity coefficient approaches one. In our experiments, the proportional difference between the Shrikhande and Freeman BSH estimates tended to decline along with the decline in the heterogeneity coefficient (Table 2). The largest proportional difference between the Freeman and ANOVA-based BSH estimates was seen for plant height, which had the highest heterogeneity coefficient, and was less for other traits that had lower heterogeneity coefficients.

A relatively large proportional difference between BSH estimates from Freeman's method and ANOVA was observed for plant habit score. The low ANOVA-based estimate for BSH (0) was observed most likely because data for this trait were strongly negatively skewed and were not normally distributed even following Box-Cox transformation ($\lambda = 1.065$; Shapiro-Wilk statistic [W] = 0.769; $P < W = 0.01$). Comparison of either Shrikhande or Freeman BSH estimates with ANOVA-based estimates of BSH for this trait are therefore of little practical value.

DISCUSSION

The Shrikhande and Freeman methods for estimating BSH depend on the data following Smith's Law. The absence of heterogeneity coefficients >1.0 indicates this as well as the lack of significant interplant competition or local environmental variation within the planting (Namkoong and Squillace, 1970). Together, these observations establish that the primary assumptions underlying the Shrikhande and Freeman methods were met in these experiments.

Estimates of BSH generated by the Freeman and Shrikhande methods were consistently different from each other. Nevertheless, Freeman's method produced BSH estimates that agreed well with ANOVA-based estimates when heterogeneity coefficients were <0.85. Shrikhande's method produced BSH estimates that were generally significantly larger than BSH estimates from ANOVA.

These findings demonstrate the potential utility of the Freeman procedure under the assumption that BSH estimates from ANOVA accurately represent true BSH. It is not possible to establish acceptable upper thresholds for heterogeneity coefficients for BSH estimates made by the Shrikhande or Freeman methods. However, such estimates will certainly be inaccurate when the heterogeneity coefficient is near one (Namkoong and Squillace, 1970). Our experiments demonstrate this; the proportional differences and absolute values between the ANOVA and Freeman BSH estimates were considerably larger for traits with heterogeneity coefficients >0.84 than for traits with lower coefficients. Shrikhande's method was less precise as BSH estimates produced by it were based on parameters with large standard errors. Shrikhande estimates were also less accurate as they deviated significantly from BSH estimates from ANOVA. This was especially true for traits with lower heterogeneity coefficients where this method would again be expected to provide more accurate BSH estimates.

Estimation of BSH by the Freeman or Shrikhande methods requires careful selection of the plot sizes and dimensions to use in calculating variances of plot means. Using a trial-and-error approach, Namkoong and Squillace (1970) concluded that at least nine plot sizes should be used with Shrikhande's method to estimate V_g, V_e, and b with minimal smallest errors associated with the estimates. A wide variety of plot sizes and planting configurations are possible in actual applications. In our research, at least 15 plot sizes were needed to minimize these errors. This was possible with the default plot configurations, suggesting that V_x estimates were relatively insensitive to this factor. Similar iterative approaches to those described here will be needed to determine the optimum plot size set and plot configurations for estimation purposes in a given experiment. This would be especially important for very large data matrices where the choice of plot size sets and configurations are also large and could considerably complicate the use of this estimation method.

Given adequate consideration of its limitations, the procedure described here for estimating BSH on the basis of the research of Freeman (1963), which has not been used previously to estimate BSH, may be useful in a variety of applications in crop breeding and genetics. Most evident would be its use to provide economical estimates of BSH for use in planning breeding programs when estimates of the components of genetic variance are not available and biased BSH estimates are acceptable. This approach may be especially valuable in situations where breeding experience or genetic information is limited, as in breeding new crops (Janick and Simon, 1993), or other crops where traditional methods of genetic analysis are difficult. This procedure may also be useful with many perennial forage crops where mass selection is commonly practiced (Cameron, 1983; Casler, 1992), or in cases where generating unbiased estimates of BSH by traditional methods is prohibitively expensive. Freeman's method could be used with data from observation or selection plantings where individual plants are equidistantly spaced as was the case in the experiments described here. Alternatively, it may be possible to use data from plantings where interplant spacing is not necessarily uniform as might be the case in a farmer's field. For example, in a row crop where intrarow plant spacing is 0.25 m and rows are 0.5 m apart, data taken from alternate plants within each row could form a matrix with approximately equidistant spacing among individuals. This application could also be particularly useful in genetic resources conservation activities where methods for rapidly and inexpensively assessing genetic variation for useful traits are often needed (Frankel et al., 1995). Moreover, the existence of the PLANTVAR program may simplify efforts to quantify soil heterogeneity or to determine optimum plot size in a variety of experimental situations (Gomez and Gomez, 1984).

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REFERENCES

Armitage, F.B., and P.M. Burrows. 1966. Preliminary heritability estimates for *Pinus patula* in Rhodesia. Rhodesia Zambia Malawi J. Agric. Res. 4:111–117.

Cameron, D.F. 1983. To breed or not to breed. p. 237–250. *In* J.G. McIvor and R.A. Bray (ed.) Genetic resources of forage plants. CSIRO, Melbourne.

Casler, M.D. 1992. Usefulness of the grid system in phenotypic selection for smooth bromegrass fiber concentration. Euphytica 63: 239–243.

Comstock, R.E., and H.F. Robinson. 1948. The components of genetic variance in populations of biparental progenies and their use in estimating the average degree of dominance. Biometrics 4:254–266.

Frankel, O.H., A.H.D. Brown, and J.J. Burdon. 1995. The conservation of plant biodiversity. Cambridge Univ Press, Cambridge, England.

Freeman, G.H. 1963. The combined effect of environmental and plant variation. Biometrics 19:273–277.

Gomez, K.A., and A.A. Gomez. 1984. Statistical procedures for agricultural research. Wiley-Interscience, New York.

Hubbard, T., D.M. Conta, and S.E. Smith. 1993. Seed production and pollen tube growth following cross and self pollinations in *Sphaeralcea laxa* Woot. & Standl. Southwest. Nat. 38:331–335.

Janick, J., and J.E. Simon. 1993. New crops. John Wiley and Sons, New York.

Kearney, T.H. 1935. The North American species of *Sphaeralcea* subgenus *Eusphaeralcea*. Univ. Calif. Public. Bot. 19:1–128.

Knapp, S.J., W.C. Bridges, and M.-H. Yang. 1989. Nonparametric confidence interval estimators for heritability and expected selection response. Genetics 121:891–898.

Mitchell-Olds, T., and J. Bergelson. 1990. Statistical genetics of an annual plant, *Impatiens capensis*. I. Genetic basis of quantitative variation. Genetics 124:407–415.

Namkoong, G. 1979. Introduction to quantitative genetics in forestry. USDA Tech Bull 1588.

Namkoong, G., and A.E. Squillace. 1970. Problems in estimating genetic variance by Shrikhande's method. Silvae Genet. 19:74–77.

Nyquist, N.E. 1991. Estimation of heritability and prediction of selection response in plant populations. Crit. Rev. Plant Sci. 10:235–322.

Pendery, B.M., and M.D. Rumbaugh. 1993. Globemallows. Rangel. 15:127–130.

Sakai, K., and S. Hatakeyama. 1963. Estimation of genetic parameters in forest trees without raising progeny. Silvae Genet. 12:152–157.

SAS Institute. 1989. SAS/STAT user's guide, Release 6, Fourth Edition. SAS Institute, Inc., Cary, NC.

Shrikhande, V.J. 1957. Some considerations in designing experiments on coconut trees. J. Ind. Soc. Agric. Stat. 9:82–99.

Smith, H.F. 1936. An empirical law describing heterogeneity in the yield of agricultural crops. J. Agric. Sci. (Cambridge) 28:1–23.

Sokal, R.R., and F.J. Rohlf. 1981. Biometry. The principles and practices of statistics in biological research, 2nd ed. W.H. Freeman and Company, New York.

Usanis, R.A. 1972. A simulation study on the estimation of random and systematic variance components in a plantation with randomly planted genotypes. Ph.D. Diss., North Carolina State Univ., Raleigh (Diss. Abst. AAC 7326755).