Sources of Variation in Plant Reproductive Success and Implications for Concepts of Sexual Selection

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American Naturalist
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SOURCES OF VARIATION IN PLANT REPRODUCTIVE SUCCESS AND IMPLICATIONS FOR CONCEPTS OF SEXUAL SELECTION

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Submitted October 26, 1987: Revised May 20, 1988; Accepted September 14, 1988

The events that occur during sexual reproduction in angiosperms can be divided into three sequential stages: (1) pollination, the import and export of male gametes to and from flowers by abiotic or biotic pollination agents; (2) fertilization, the germination of pollen and the growth of male gametophytes through the pistil to reach the ovules; and (3) seed maturation, the growth of fertilized ovules and fruits until seeds are produced.

After each of these stages, the proportional genetic representation of an individual in the total population is likely to deviate from that in the preceding stage, in part from stochastic events, but also because determinist factors favor certain matings over others. For example, parental phenotypic traits such as floral structure can influence pollination success directly through the mechanics of pollen release, transfer, and capture and indirectly through effects on pollinator behavior (Waser 1983). Similarly, phenotypes of male gametophytes can influence the probability that they fertilize ovules, via physiological interactions with the pistil (Heslop-Harrison 1975; Knox 1984) and perhaps with each other. Finally, phenotypes of embryos and of endosperm tissue, to which both parents contribute genetically, can influence the probability that embryos mature into seeds (Brink and Cooper 1947; Guth and Weller 1986).

A change in the frequency of phenotypes present during any part of the life cycle constitutes a phenotypic selection differential (Falconer 1981; Lande 1982). The extent to which the selection differential depends on the effect of additive gene action determines the levels of heritable variation in traits that, in turn, influence an individual plant’s genetic representation in offspring. Thus, provided that phenotypic traits are not sufficiently negatively correlated with other fitness components, the change in phenotypic frequency can result in potential evolutionary change.

In plants, selection during reproduction has traditionally been treated as fecun-
dity selection, a part of natural selection. Recently, there has been a growing
tendency to invoke sexual selection, a process by which phenotypic variation in
reproductive success occurs because of competition within one sex (usually
males) for access to matings and/or because of the choice by one sex (usually
females) of mating partners (Willson 1979; Bertin and Stephenson 1983; Stephen-
son and Bertin 1983; Willson and Burley 1983; Charlesworth et al. 1987; Queller
1987). It is unclear, however, to what extent sexual selection is a useful concept
for plants (for a critical review of the literature on this topic, see Charlesworth et
al. 1987) and how to apply operational definitions derived for animals (Arnold and
Wade 1984). Nor is it clear how to distinguish competition among members of the
same sex from mate choice. Thus, the use of sexual-selection terminology and
concepts may actually obscure our understanding of processes affecting plant
reproduction.

We develop a heuristic classification of the biological processes likely to deter-
mine the relative reproductive contribution of a given maternal or paternal plant.
To identify causes of differential success, we use analysis of variance (ANOVA), an
experimental approach associated with standard statistical methods. Where ap-
propriate, we outline other analytic and experimental tools. We then use recent
empirical studies to illustrate how such an approach might be applied to identify
nonrandom transmission during the three sequential stages of plant reproduction
outlined above. Our literature review is selective and based on experimental
design, since more-comprehensive treatments of nonrandom plant reproductive
success already exist (Stephenson and Bertin 1983; Willson and Burley 1983). In
addition, we focus on natural rather than agricultural populations. Finally, we
consider the difficulties in applying terms such as mate choice, intrasexual com-
testation, and sexual selection to the phenomena revealed by our experimental
approach. In so doing, we emphasize some advantages and disadvantages of
studying these phenomena in plants and suggest some avenues worthy of future
research.

A FRAMEWORK FOR DETERMINING DIFFERENTIAL REPRODUCTIVE SUCCESS

Sources of Variation in Success

Individual variation in transmitting genes through each stage of the reproduc-
tive process can be partitioned into three basic components: average performance
differences among males (or male functions of hermaphrodites), average perform-
ance differences among females (or female functions), and performance differ-
ences among crosses as a result of interactions between male and female partners.
Relative magnitudes of these variance components should depend on a variety of
intersexual and intrasexual processes. The key to detecting these processes lies in
manipulating the opportunity for intersexual and intrasexual interaction and
measuring the consequences for variation in reproductive success.

The Basic Experimental and Analytic Model

An appropriate experimental design for detecting variation in reproductive
success should measure variance components for different treatment levels of
interaction among members of the same and different sexes, with replication
Fig. 1.—Experimental design: two "types" (A and B phenotypes, genotypes, or lines) are crossed in a diallel design repeated for different density and identity treatments. Male treatment 1 places one male of one type with each female; male treatment 2 places two males of one type with each female; male treatment 3 places one male of each of two types with each female. Female treatments parallel male treatments. Each diallel could be expanded to include more than two types. The protocol can, in principle, be applied to any of the three stages of reproduction.

across male and female types (either genotypes or phenotypes). This objective can be achieved with a reciprocal or factorial cross in which a plant is used as a focal male and/or as a focal female in combinations with other plants. Such designs include complete and partial diallel and factorial crosses (Comstock and Robertson 1952; Griffing 1956b; Kempthorne and Curnow 1961; Cockerham and Weir 1977) that allow the assessment of male, female, and treatment main effects and interactions by factorial ANOVA's or by other means (see below).

In principle, a single experimental model, such as a complete diallel design in each cell of figure 1, can be used to study all three of the previously described reproductive stages. However, details of treatment and statistical analysis depend
<table>
<thead>
<tr>
<th><strong>ANOVA Effect</strong></th>
<th><strong>Pollination Phase</strong></th>
<th><strong>Fertilization Phase</strong></th>
<th><strong>Seed-Maturation Phase</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td>Male</td>
<td>Males differ in pollen deposition.</td>
<td>Males differ in number of ovules fertilized.</td>
<td>Seeds fathered by different males mature differentially.</td>
</tr>
<tr>
<td>Female</td>
<td>Females differ in pollen received.</td>
<td>Females differ in number of ovules fertilized.</td>
<td>Females differ in number of seeds matured.</td>
</tr>
<tr>
<td>Male × Female</td>
<td>Combinations of parents differ in amount of pollen deposition.</td>
<td>Combinations of parents differ in number of successful fertilizations.</td>
<td>Combinations of parents differ in number of seeds matured.</td>
</tr>
<tr>
<td>Treatment (example for males)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1. Single donor, single type</td>
<td>Contrast 1 vs. 2: Pollen deposition varies with density of males.</td>
<td>Contrast 1 vs. 2: Fertilization levels vary with the amount of pollen deposited.</td>
<td>Contrast 1 vs. 2: Number of mature seeds varies with amount of fertilization.</td>
</tr>
<tr>
<td>2. N donors, single type</td>
<td>Contrast 1 vs. 3: Pollen deposition varies with identity and density of males.</td>
<td>Contrast 1 vs. 3: Fertilization levels vary with the amount and diversity of pollen deposited.</td>
<td>Contrast 1 vs. 3: Number of mature seeds varies with amount of fertilization and identity of fathers.</td>
</tr>
<tr>
<td>3. N donors, N types</td>
<td>Contrast 2 vs. 3: Pollen deposition varies with identity of males.</td>
<td>Contrast 2 vs. 3: Fertilization levels vary with the identity of pollen deposited.</td>
<td>Contrast 2 vs. 3: Number of mature seeds varies with identity of fathers.</td>
</tr>
<tr>
<td>Male × Treatment</td>
<td>Deposition by different males varies across density/identity treatments.</td>
<td>Fertilization success for different males varies across treatments.</td>
<td>Maturation of seeds varies for different fathers across treatments.</td>
</tr>
<tr>
<td>Female × Treatment</td>
<td>Reception by female varies with treatment.</td>
<td>Females vary in number of ovules fertilized across different treatments.</td>
<td>Different females mature different numbers of seeds under different treatments.</td>
</tr>
<tr>
<td>Male × Female × Treatment</td>
<td>Combinations of females and males respond differently to treatments.</td>
<td>Combinations of parents fertilize different numbers of ovules under different treatments.</td>
<td>Combinations of parents mature different numbers of seeds under different treatments.</td>
</tr>
</tbody>
</table>

**Note.**—Biological interpretation of male, female, male-by-female interaction and treatment effects detectable by ANOVA using the experimental design shown in figure 1.
on the stage and the response variable being considered. For example, not all
treatments can be applied realistically to all stages, and only certain response
variables can actually be measured. Some response variables represent the overall
effects of adult diploid genomes; others encompass indirect interactions between
parental genomes via haploid gametophytic “samples” of themselves or, in the
case of endosperm, via a (usually) triploid combination of haploid segregation
products. For simplicity, we discuss here the response variables as effects of
diploid adult genomes and consider the complications of ploidy and generation in
the Appendix. Table 1 summarizes major statistical effects that could be revealed
by a factorial anova of the experimental design shown in the figure and outlines
our interpretation of significant effects during the three reproductive stages.

In the pollination stage, interaction among males can be varied by placing
different combinations of male plants together with single females—for example,
in outdoor arrays of potted plants—and examining pollen that reaches the stigmas
as a result of natural pollination (fig. 1). Three useful treatments are (1) one focal
male (or male-phase) plant of type A (genotype or phenotype) presented alone to a
female; (2) several (N) individuals of type A presented together; and (3) one type
A presented together with males of other types, for a total of N individuals. The
appropriate response variable is the number of pollen grains delivered to the
female by the focal male (assuming that the pollen of the types can be distin-
guished by some trait such as pollen-grain size or color). Interaction among
females can be varied in an analogous way, by comparing the amounts of pollen
received by a focal female of type A from a constant number of males (1) when
there is one female of type A; (2) when there are N females of type A; and (3)
when one female of type A is placed together with females of other types, for a
total of N individuals. Such an experimental design can be used to determine how
pollen donation and receipt are affected by the numbers and identities of pollen
donors and recipients.

In the fertilization stage, interaction among males can be varied by placing
different combinations of pollen together on a single stigma of a receptive female
and examining ovule fertilization. Appropriate treatments are (1) a small number
of pollen grains from a focal male of type A placed on the stigma; (2) a larger total
of N grains from type A presented alone; and (3) a small number of grains from
male A presented with those from other males for a total of N grains. Since pollen-
tube growth and fertilization occur within female tissue, male effects on this stage
of reproduction might be better isolated if females can be “disabled,” that is,
rendered more physiologically passive. For example, the stigmatic, stylar, or
ovarian rejection of self-pollen can be reduced by heat shock, carbon dioxide
treatment, or bud pollination (Stout 1938; O’Neill et al. 1984). In some cases,
these same types of manipulations can also remove less complete stylar inhibition
of pollen tubes (Cruzan, pers. comm.).

The appropriate response variable at the fertilization stage is the number of
ovules fertilized by pollen of type A. This can be assessed histologically when
pollen from a single male is applied, but the situation with multiple males is
problematic since it is unlikely that the genotype of a non-fertilizing pollen grain or
that of a newly formed zygote can be determined. A second response variable that
reflects the inverse of fertilization (i.e., the number of pollen tubes that do not achieve fertilization) can often be determined nondestructively by clipping styles off developing fruit 16–48 h after single-male pollinations and examining them for pollen tubes that did not reach ovules (Waser et al. 1987; Cruzan 1989; Lyons, unpubl. data). As with the pollination stage, assessing the identity of multiply applied pollen grains is problematic. There are no analogous female treatments for the fertilization stage, since stigmas of different plants cannot compete for pollen that has already been transferred.

The seed-maturation stage presents further difficulties because it may be difficult to isolate this stage cleanly from fertilization. An ideal manipulation of interaction among males would require placing male gametophytes directly onto different micropyles within an ovary and thus achieving controlled single- and mixed-male fertilizations within a single female. Alternatively, controlled fertilizations might be approximated by determining exactly how stigma pollen loads translate into ovules fertilized, but this approach requires extrapolating results from genotypically pure pollen loads to those with mixed pollen loads. The extrapolation is unwarranted if pollen tubes interact.

When both ways of producing controlled fertilizations are intractable, useful information might still be gained by using as the experimental unit fruits within females, rather than ovules within fruits. Appropriate treatments are (1) gametophytes of a focal male of type A fertilizing some small number of fruits; (2) gametophytes of type A fertilizing a larger total of N fruits; and (3) gametophytes of type A fertilizing some small number of fruits with other males fertilizing the remainder, up to a total of N. Appropriate response variables are numbers of mature seeds or fruits fathered by the focal male. Again, the analogous female treatment makes no biological sense, since ovaries from different female individuals do not interact.

Comments on the Experimental Design

We have already noted that a factorial ANOVA, with male and female identities as main effects (table 1), is a straightforward means for analyzing a reciprocal cross. Additional information can also be obtained by using the quadratic diallel models of Cockerham and Weir (1977, especially their models b and c; see also Hinkelmann 1977; Antonovics and Schmitt 1986; Simms and Rausher 1987; Lyons, MS). The quadratic models yield four estimates of variance components involving male, female, and interaction effects: (1) overall performance variation of individuals (encompassed in “nuclear general” or “general combining ability” effects); (2) variation in performance of individuals as males versus females (“reciprocal general” or “extranuclear” effects); (3) variation among crosses in mean performance of specific parental combinations (“nuclear specific” or “specific combining ability” effects); and (4) variation in performance of specific combinations when sex roles of parents are reversed (“reciprocal specific” effects). Although diallel designs are excellent for estimating general and specific combining abilities and for further decomposition of variance into additive, dominant, and epistatic sources (Griffing 1956a), the interpretations may not be appropriate unless the response variables are measured in diploid individuals (e.g., fertilization may
depend on interactions between a haploid male and diploid female and thus does not fit easily into these models).

Both ways of subdividing variance may lead to useful insights. Factorial designs discriminate main effects attributable to each sex, whereas quadratic analysis of diallel designs identifies reciprocal general effects, which may indicate gender specialization, and reciprocal specific effects, which suggest maternal genetic or environmental contributions. Further analyses are needed to identify and document such phenomena as gender specialization (as discussed in Robbins and Travis 1986) and the functional nature of male-by-female interaction (e.g., male-by-female interaction resulting from self-incompatibility).

Despite the advantages of a diallel crossing design, examination of the figure reveals a logistic difficulty with this approach: a full analysis for any reproductive stage requires nine treatments (3 per male × 3 per female), each of which must be replicated across female and male phenotypes or genotypes. When only two types are used (as in the figure), 25 separate experimental units are necessary for a full analysis without replication. The necessary number increases dramatically with more types: for 3 types, 49; for 4 types, 81. Thus, it is unrealistic with a complete diallel to sample large numbers of parental types. Large, complete crossing designs may also be more likely to yield incomplete or unbalanced data, making a least-squares statistical analysis difficult and perhaps requiring a computer-intensive maximum-likelihood approach such as that developed by Shaw (1987).

A possible solution to both difficulties is to use several small diallels instead of a single large one or to use a partial diallel in which each plant is mated with only a subset of others (Comstock and Robinson 1952; Simms and Rausher 1987; Lyons, MS). Using incomplete diallels allows sampling of more parental plants, which should yield more-precise estimates of maternal and paternal main effects. The trade-off is likely to be less power in estimating maternal-by-paternal interaction effects. The best design would appear to depend on the aims of the particular study.

In such crossing designs, the treatments may not be independent if they are performed on plant structures that are not physiologically independent. For example, fates of seeds within a fruit may not represent independent data points; pseudoreplication (Hurlbert 1984) can result, especially if the flower was the unit of treatment. Likewise, if one female receives pollen of different males, placed singly on different flowers, the response variable—the number of fruits matured—may not be independent for different males, since the exact combination of males may influence maternal resource allocation to fruits. There are two ways around this problem, one experimental and one statistical. Experimentally, independence within a plant might be assessed by techniques such as those used by Lee and Bazzaz (1986) in order to determine how selective thinning of certain fruits affects development of the remaining fruits. Alternatively, different numbers and combinations of fathers might be used on different ramets of cloned females, allowing both replication of crosses and comparison of full-sib fruits that were matured with different combinations of other fruits. Statistically, nonindependence of fruits may be treated by using a profile MANOVA, a repeated-measures multiple analysis of variance (Simms and Burdick 1988; Lyons, MS), which does not
require assumptions about the independence or correlation structure of data. However, more work is necessary to produce tractable experimental designs for applying a profile ANOVA to various factorial and diallel crossing schemes.

**Interpretation of Analytic Results**

Results of ANOVA’s can be expressed in terms of relative and absolute magnitudes of the variance components. The number of possible analytic outcomes is large (table 1). In some cases the underlying biology may become clear by inspection.

Our experimental framework can distinguish a number of different inter- and intrasexual interactions. Assume that the fertilization phase of reproduction is studied in a hermaphroditic plant with no seed abortion. Assume, as well, that previous work on this species has demonstrated that “disabling” females greatly reduces variation in the pollen-tube growth of different males. A reciprocal diallel cross is conducted (in which males are placed singly on normal and “disabled” females). In the first case study, the variation in paternity is ascribable to a main male effect (table 2A, col. 1). This result may be due to (1) male effects in the absence of male-male interactions (hereafter, noncompetitive male effects) or (2) female determination of male performance. Comparison of results from normal versus “disabled” females should help to disentangle these two effects; a diminution of male effect after disablement would suggest that female determination does influence male performance. If male effects were still significant, even on “disabled” females, pollen grains would be likely to vary in vigor.

To compare a male’s performance alone with performance when combined with different sets of other males, a second set of experiments can be conducted imposing our male treatments on “disabled” females (recall the figure). If there are no significant gender-by-male-treatment effects and a main male effect remains (contrast table 2A, cols. 2 vs. 1), we again conclude that noncompetitive male effects determine the result. When male-by-male-treatment effects are significant (contrast table 2A, cols. 3 vs. 1), we conclude that male phenotypes respond differently to the presence or absence of other males. Conversely, significant female-by-male-treatment effects (table 2A, cols. 4 vs. 1) indicate that the outcome of male interactions is influenced by the female genotype.

Table 2B, column 1, illustrates a simple diallel cross with a male-by-female interaction, in which different singly applied males are favored when crossed with different females. This interaction could be due to (1) a male trait that determines fertilization success in different styles; (2) a female trait that determines pollen-tube growth by different males; or (3) characteristics of both partners, for example, their genetic similarity or some other form of “complementarity,” rather than those of each partner in isolation (see Price and Waser 1979; Waser and Price 1983; Campbell and Waser 1987; Waser et al. 1987; Snow and Mazer 1988; Lyons, MS).

In order to distinguish among these three possibilities, again we need to impose male treatments on “disabled” females. Male-by-female interactions attributable to a male trait would appear as a significant male-by-male-treatment interaction. In this case the general pattern of the male-by-female interaction remains, but the
### TABLE 2
Possible Outcomes of Applying Male Treatments in Diallel Crosses Using Three Individual Plants (A, B, C)

<table>
<thead>
<tr>
<th><strong>Single or Multiple Donor, Single Type</strong></th>
<th><strong>Multiple Donor, Multiple Type</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Male identity</strong></td>
<td><strong>Male identity</strong></td>
</tr>
<tr>
<td>A</td>
<td>B</td>
</tr>
<tr>
<td>Female identity</td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>2</td>
</tr>
<tr>
<td>B</td>
<td>2</td>
</tr>
<tr>
<td>C</td>
<td>2</td>
</tr>
</tbody>
</table>

Significant effects* M M, no M × TM M, M × TM M, F × TM

**B**

| **Female identity** | | | | | | | | | | | | |
|---------------------|---------------|-----------------|---------------|-----------------|---------------|-----------------|---------------|-----------------|---------------|-----------------|---------------|
| A 2 4 2             | B 2 3 8       | C 4 3 4         |               |                |               |                |               |                |               |                |               |

Significant effects* M × F M × F, M × TM M × F, F × TM

Column 1 2 3 4

**NOTE.**—Values indicate the relative success of different parental combinations during a particular stage of reproduction. Columns represent different possible outcomes under various male treatments.

* Significant effects are male (M), female (F), male treatment (TM), and interaction (×). Male-treatment effects in columns 2–4 refer to comparisons with the results of single-type treatments in column 1. For example, column 4 in A indicates a significant main male effect and a significant interaction effect between female identity and single-type vs. multiple-type male treatments.

The magnitude of the interaction varies among the interacting males (i.e., down the columns in table 2B, diallel 2 vs. 1). Likewise, when a female trait is responsible for the interaction, there would be a significant female-by-male-treatment effect. Again, the pattern of male-by-female interaction remains, but the magnitude varies across females (i.e., across rows in table 2B, diallel 3 vs. 1). If a female trait determines the outcome of the interaction, we would expect the significance of the female-by-male-treatment interaction to be much lower for “disabled” females than for normal females.

It may be possible to attribute male-by-female interactions to characteristics of both partners. For example, if significant male-by-female interactions were due to self-incompatibility, there would be a strong effect (e.g., low or zero fertilization) on the leading diagonal in table 2B, column 1. With information on the relatedness of individuals (e.g., from distance between plants), males and females could be arranged along the axes in table 2 to explore directly trends in reproductive success associated with male-by-female interactions (Waser and Price 1983; J. Nason, pers. comm.; Cruzan and Thomson, pers. comm.).
APPLICATION OF THE MODEL

General Remarks

A complete empirical accounting of the sources of nonrandomness in genetic transmission requires, first, a separation of reproduction into pollination, fertilization, and seed-maturation phases and, second, an examination of effects on males, females, male-by-female interactions, various density and identity treatments, and higher-order interactions (table 1). We know of no study that approaches this ideal. We have therefore selected examples from the literature to illustrate how the experimental model just outlined might be used to study causes of differential mating success and to indicate difficulties in applying the model. We have chosen studies that exhibit some design elements consistent with those we advocate or that illustrate the sort of outcome our analysis is expected to produce. In some cases our interpretation of results differs from that of the authors.

Pollination Stage

As the first stage in the reproductive process, pollination is the easiest stage to isolate and to study independently of other stages. This is especially true when the amount of pollen removed from or received by a flower, rather than the number of seeds produced, can be quantified as the response variable. The use of species with variation in pollen traits such as grain size or color would facilitate the identification of pollen genotypes.

It has been demonstrated that variation among females in pollen receipt or paternity depends on flower color in Phlox pilosa (Levin and Kerster 1967), Delphinium nelsonii (Waser and Price, unpubl. data), and Raphanus raphanistrum (Stanton 1987), on the presence of pollen in the anthers of recipient flowers in Ipomopsis aggregata (Price and Waser 1982) and Erythronium grandiflorum (Thomson et al. 1986), and on nectar reward in Diervilla lonicera (Thomson and Plowright 1980; see also Galen and Plowright 1985). Receipt of self-pollen depends on plant size in Mertensia ciliata (Geber 1985).

Few studies have documented an effect of floral traits on both male and female components of pollination success, that is, on pollen dissemination and receipt. Success in both disseminating and receiving fluorescent dye, a pollen analogue, depends on the length of the pistillate phase, stylar exsertion, and corolla width in I. aggregata (Campbell 1989) and on floral morph in distyous Palicourea lasiorrachis (Feinsinger and Busby 1987).

A few studies provide evidence for male-by-female interaction. Assortative (or disassortative) pollination is based on flower morph in many distyous species (Barrett 1978, 1979; Feinsinger and Busby 1987), on floral morphology and stylar exsertion in I. aggregata (Waser and Price 1985; Campbell 1989), on temporal rather than morphological differences in protandrous or protogynous walnuts (Gleeson 1982), on floral color in Phlox pilosa (Levin and Kerster 1967), and on plant stature in Lythrum salicaria (Levin and Kerster 1973).

Our experimental protocol also includes the effects of number or density of pollen donors; Silander and Primack (1978) found that visitation rate and pollen
deposition are correlated and that pollinator visitation rate per flower varies about twofold between sparse and dense stands of *Oenothera fruticosa*.

Much more common than studies of pollen movement are those that estimate success in terms of pollinator visitation patterns (see Waser 1983). However, because visitation is not necessarily analogous to our response variable, pollen movement, these studies are not discussed further here.

**Fertilization Stage**

As noted above, it is logistically difficult to separate events that occur in the fertilization stage from those in the seed-maturation stage. Given the difficulties of genotyping pollen tubes and nondestructively studying pollen-tube growth and resulting fertilization, most studies begin with a manipulation of stigma pollen load and end by measuring fruit or seed set. Results often are promoted as evidence for vaguely defined “male competition,” “female choice,” or both, even though fertilization and seed development clearly are confounded.

Where separation of these two phases has been possible, there is evidence of male, female, and male-by-female interaction effects on fertilization. A number of studies have demonstrated differences between males in pollen-tube growth rate in vitro (see, e.g., Bookman 1984; Mazer 1987). Significant male effects on ovule fertilization have been reported for *Leavenworthia crassa* (Lyons, MS) and *Raphanus sativus* (Marshall and Ellstrand 1986). The results of the latter study must be interpreted with caution, however, because *R. sativus*, unlike *L. crassa*, has high levels of cryptic seed abortion (Nakamura and Stanton 1987).

Malti and Shivanna (1985) reported that stigmatic leachates of *Crotolaria rotusa* markedly increase variation in pollen-tube growth rates in vitro and interpreted this as part of a mechanism for female control over fertilization. Strong female effects on ovule fertilization rates were found in *R. raphanistrum* (Mazer et al. 1986) and in *L. crassa* (Lyons, MS). In the latter species, male-by-female interaction effects on ovule fertilization were significant in only two of six diallels (Lyons, MS). In addition, no significant nuclear specific or reciprocal specific effects were evident during this stage of reproduction. In contrast, Hill and Lord (1986), on examining *R. raphanistrum* ovules with pollen tubes in their micropylles, found that fertilization was affected by the interaction of female identity, male identity, and ovule position within the ovary.

Several studies have reported density effects on fertilization dynamics after pollination. For example, differences among males in the ability to engender pod formation in *Asclepias speciosa* became more pronounced when pollen of multiple rather than single males was applied to each umbel, a result Bookman (1984) interpreted in terms of “pollen competition” rather than differential fruit abortion. However, this interpretation cannot be accepted unreservedly because treatment effects were confounded across populations, seasonal timing, and pollination intensity.

**Seed-Maturation Stage**

The final stage of reproduction may not be independent of earlier stages. One type of evidence for such integration is that the fate of ovules is consistent across
successive reproductive stages according to the ovule’s position within the developing ovary. Such parallel position effects were observed for fertilization, abortion, and seed weight in *Leavenworthia crassa* (Lyons and Antonovics, MS) and for paternity and seed weight in *Raphanus sativus* (Marshall and Ellstrand 1988). If a plant typically matures (or aborts) more seeds in the basal ovules of fruits and if ovules in these positions are differentially fertilized by pollen tubes, the maturation of seeds sired by different males will be a function of both the fertilization and seed-maturation phases. These genotypic effects often remain confounded in the absence of controlled pollination of specific ovules or a knowledge of the genotype of aborted ovules. Studies in which pollination is not varied and females are manipulated (e.g., stressed) after fertilization have pinpointed seed maturation as the stage that produces differences in seed number and overall quality, without differences in genotype. For example, Stephenson and Winsor (1986) have noted that in *Lotus corniculatus* natural fruit abortion results in fruits with more seeds and fitter offspring than does experimentally induced random abortion.

The large horticultural and anecdotal literature on fruit and seed abortion, one facet of the seed-maturation stage (review in Stephenson 1981), is dominated by studies that consider broad maternal effects on fruit set, seed set, and/or seed weight and may include both genetic and environmental components (Roach and Wulff 1987). Relatively few studies document male, female, and male-by-female interaction effects on abortion. In *Phaseolus vulgaris*, application of pollen from closely related plants yielded significantly nonrandom effects for seed abortion within fruits (Nakamura 1988). The position effects disappeared when pollen of less closely related males was used, suggesting that patterns of abortion were affected by characteristics of the males or, more likely, of both parents. Reciprocal crosses with *R. raphanistrum* (Mazer et al. 1986; Mazer 1987) and with *L. crassa* (Lyons, MS) yielded similar results; seed weight and seed set were strongly influenced by maternal, but not paternal, main effects, and evidence for male-by-female interactions was limited.

A number of studies have examined the effects of multiple pollen donors on seed maturation, a treatment that approximates our density treatment. Some have documented little or no effect (e.g., Bertin 1986; Cruzan 1989); others have shown that multiple donors can lead to higher seed set (e.g., Schemske and Pautler 1984; Lyons, unpubl. data; Waser and Price, unpubl. data). Vander Kloet and Tosh (1984) found that the consequence of pollen-donor number depends on the identity of the female plant. This result is somewhat analogous to our female-by-male-treatment effect (table 2B, col. 2), in which the female genotype mediates the outcome of male competitive treatment.

Most studies of seed maturation with multiple pollen donors have measured only seed number or size, since assessing paternity is time-consuming and costly (Meagher 1986). Marshall and Ellstrand (1985) have demonstrated, however, that application of multiple pollen donors does not necessarily result in multiple paternity. In a companion study, Marshall and Ellstrand (1986) showed that fruit set, seed set, and seed weight in *R. sativus* are influenced by both male parentage and the number of donors per stigma and that variation in male success increases with the application of mixed-pollen loads. In this study, as with all of those cited
above, experimental-design problems weaken the authors' inferential power and limit the generality of their findings. For example, cryptic abortion may obscure contrasting fertilization and/or seed-maturation patterns, self-incompatibility differences could confound results, the relative success of multiple crosses within each female may be interrelated, and the few individuals included in the crossing design may not be representative of the entire population.

DISCUSSION

Our brief literature review provides ample evidence for nonrandom transmission of genes through various stages of plant reproduction. Although the studies reviewed include some elements of the experimental and analytic protocol that we propose for determining the causes of nonrandom transmission, none has systematically applied as complete a design. We propose that the first steps in understanding selection during reproduction are to identify the sources of nonrandomness and then to determine the mechanisms responsible. Our purpose is to offer a way of more clearly identifying whether one gender or an interaction between genders acts to yield nonrandomness during each phase of reproduction.

In this regard, the virtues of our experimental protocol are twofold. First, in order to attribute variation in reproductive success to one gender, the process of reproduction is divided into different phases in which the genders can be manipulated and in which we know how the fundamental biology of the genders differs. Second, sources of variation in reproductive success are identified by systematically repeating a reciprocal-crossing design with treatments that alter the intensity with which males and/or females can interact.

We constructed our experimental design to elucidate the phenomena of selection (natural or sexual) that occur during the course of the experiment. We recognize, however, that the concepts of natural selection and sexual selection are used both to interpret current processes that yield nonrandom survival or reproduction and to infer whether specific traits are an outcome of such processes that worked in the past. We hope that by careful experimentation we can better infer the former—that is, the process of current selection—and at the same time eliminate other potential processes either by experimental design or by examination of results.

Given the complex experimental protocol, it became clear in discussion among the five authors that even when selection is identified and the source of nonrandomness isolated, biological interpretation of the results is difficult, and there remains substantial disagreement about the proper interpretation of a given experimental outcome. In particular, assessing which outcomes might be appropriately interpreted as sexual selection is a difficult matter, especially when the selection criteria, the underlying evolutionary assumptions, and the experimental constraints contributing to that assessment are not explicitly stated.

In what follows, we first discuss some difficulties in identifying sources of nonrandom reproductive success; we then consider the problem of inferring what constitutes sexual selection; and finally, we arrive at some general conclusions.
Difficulties in Identifying Causes of Nonrandom Transmission

In many ways angiosperms provide excellent material for the experimental study of selection acting on sexual reproduction. First, most are hermaphroditic and thus easily used in reciprocal crosses to identify maternal and paternal effects precisely. Second, genotypes often can be cloned, allowing genetically identical crosses to be repeated. Third, events that occur during the pollination stage are amenable to experimental manipulation, as evidenced by many modern pollination studies (e.g., Jones and Little 1983; Real 1983). Fourth, events that occur during the fertilization and seed-maturation stages are accessible to histological examination (Guth and Weller 1986; Lyons 1986; Waser et al. 1987), which often can be done nondestructively. For example, in some species, clipping styles 1–2 days after pollination allows examination of postpollination events without damaging the ovary and developing seeds.

However, plants present some experimental difficulties for the study of nonrandom transmission. Determining the appropriate experimental male treatments can be problematic. Recent evidence of multiple paternity in natural populations (Ellstrand 1984; Meagher 1986) indicates that we know little of the timing, quantity, and source of pollen donation from reference populations. This information is needed to establish meaningful experimental pollination regimens.

Additionally, in plants (and many animals), mating is not easily defined operationally as a discrete temporal event but is instead a complex set of interrelated events. The existence of intermediate stages, between the start of mating and progeny maturation, is often obvious in plants (more so than in animals) by the presence of aborted fruits and seeds.

A more vexing difficulty is separating male from female effects because much of the mating process occurs within the female. After pollination, there are manifold opportunities for physiological interaction between male gametophytes. This is usually referred to as “pollen competition.” We use the term competition in the broadest sense, as a blanket term that does not define in any way how the presence or absence of another male produces changes in male performance (in the sense of Harper 1961, 1977, p. 151). Despite widespread reference to “pollen competition,” much more work is needed to provide this term with a detailed functional definition. Not only might male gametophytes interact with each other, but also opportunities occur for interactions between male gametophytes and the female sporophyte, a phenomenon usually referred to as “female choice” (Heslop-Harrison 1975; Raff and Knox 1982; Knox 1984; Malti and Shivanna 1985). However, the extent to which pollen-tube growth is a trait of the pollen, of the field of competitors, of the style, or of some combination of all of these is unknown. It should prove useful in measuring the female effect on differential fertilization to compare paternal success on “disabled” females incapable of “preference” with paternal success on untreated females.

Distinguishing between male and female traits in plants in general can be difficult, especially if male and female reproductive success are phenotypically and/or genetically coupled, as in hermaphroditic flowers. Varying a characteristic such as nectar production or flower size is likely to affect both male and female
pollination success simultaneously. It is also particularly difficult to assign gender roles in plants because plants do not exhibit behavior during mating. For example, since the pollination stage relies on external pollinating agents, plants may have little control over pollen dispersal (Waser and Price 1983). There are no obvious behavioral cues (analogous to approach or rejection behaviors in animals) that might be used to assign to females or males the active role in promoting intermale differences in pollen donation. Thus, it is difficult to ascribe distinct and active behaviors to male and female sexual functions (contra Janzen 1977) that correspond to male and female behavior during animal mating.

Certainly with plants it is more difficult to study female "preference" independent of male behavior than it might be in animals, where female discrimination can be evaluated by presenting male pheromones to females, independent of the males themselves (Boake 1986). Again, comparing maternal effects in a set of "disabling" experiments may prove informative.

Despite these practical difficulties, the most serious hurdles lie in interpreting experimental outcomes.

Difficulties in Applying the Concept of Sexual Selection in Plants

Darwin's (1871) original separation of sexual from natural selection centered on access to matings or copulations in animals. At present, rigorous functional and operational definitions are needed, preferably in mathematical or statistical terms, for studying all aspects of nonrandom transmission in plants as well as in animals. Arnold and Wade (1984) made a good beginning by dividing animal reproduction into sequential stages, as we have with plants, and equating sexual selection with an elevated variance in overall reproductive success attributable to variation in mating success (for cautions, see Hubbell and Johnson 1987). Charlesworth et al. (1987) provided both a general definition of sexual selection in plants, which may be difficult to use experimentally, and a list of phenomena distinct from sexual selection (see below).

In modern usage, "mate choice" implies intersexual interaction, "competition" implies intrasexual interaction, and variance in success that can be attributed to intra- or intersexual interactions is necessary (but not sufficient) for "sexual selection" (Bertin and Stephenson 1983; Koenig and Albano 1986). For any of these interactions to foster evolution by sexual selection, there must be heritable variation in the male traits on which selection acts, and selection must also act on the expression of the male's trait, not on a trait of his progeny.

Although few would argue that these statements demarcate the bounds of sexual selection, they leave large areas open for interpretation: (1) identifying selection in the form of main and/or interaction effects and assigning causation to one or the other gender, (2) identifying male plant traits on which selection might act, and (3) separating the action of selection on a male's genotype from that on his progeny's genotype.

Identifying male-by-female interactions.—The issue that generates the widest range of interpretation of sexual selection in plants is identifying the source of nonrandom transmission and assigning its causation to a particular gender or interaction between the genders. Our approach provides an interpretation of se-
lection as a statistical result (e.g., a significant male-by-male-treatment effect) and allows the interaction to be attributed to one gender or the other. It seems unreasonable to discuss sexual selection if there are no significant effects at all (i.e., if between-cross variance is not significantly greater than error variance). Similarly, without significant male-by-male-treatment effects or female-by-male-treatment effects (i.e., if reproduction is unaffected by the opportunity for interaction among members of one sex), it seems unreasonable to invoke intra- or intersexual interactions as important determinants of reproductive success.

Other factors figure in the interpretation of results, especially when such strong statistical inference is not possible. First, scientists vary in their willingness to invoke arguments of past selective events to explain results (see below). Second, different resolutions of experimental difficulties may lead to different interpretations. Nonrandom paternity of a seed crop might be attributed to differential male competitive effects if seed abortion were not detectable, but to female choice if seed abortion were detectable and nonrandom. Finally, the state of knowledge about a physiological mechanism can influence interpretation; for example, if more is known about styril biochemistry than pollen-tube growth, a dominant role might be assigned to the female.

This type of interpretive divergence is likely in experiments in which the opportunity for interaction has not been varied. If variance in paternity is explained mostly by the combination of male and female identity in a reciprocal diallel cross (i.e., the factorial ANOVA yields significant female-by-male interaction effects; table 2B, col. 1), there are at least two interpretations. In the first, the results are considered relatively uninformative because the interaction reflects (1) variance in a male trait that determines fertilization success in different females, (2) variance in a female trait that determines pollen-tube growth by different males, or (3) some combination of the two.

In a second interpretation, assumptions about past selective forces are used and a physiological role of the style is invoked. If one accepts the evolutionary argument that natural selection cannot lead to male gametophytes that "commit suicide" (i.e., relinquish a strong attempt at fertilization once committed to a given pistil; see Charnov 1979), this interaction is labeled as a form of female choice. It has also been called "discordant choice" because the identity of successful males differs across females (Waser et al. 1987). Arguments for female choice from a different kind of experiment, in which males are presented one at a time on separate flowers at separate times, rely on another set of assumptions. Because males are not presented together, there is no simultaneous choice but rather only the opportunity for sequential choice. For sequential choice to occur, one must suppose that selection has acted in the past to yield a preference scale or threshold that females can use in the absence of direct simultaneous comparison. Male-by-female interaction alone, even if it reflects a form of female choice, may not contribute to variance in reproductive success of either sex, that is, to sexual selection (Waser et al. 1987; see also Schwarmeyer et al. 1987).

Results of even the experiments we outline may yield controversial interpretations. In one of our hypothetical cases (table 2A, cols. 2 vs. 1), main male effects
were evident in the diallel, but there were no significant male-by-male-treatment effects or female-by-male-treatment effects. We ascribe this result to noncompetitive male effects. Several authors using simple diallel crosses have suggested that it is logical to invoke choice by the style when proportional paternity of a number of males changes as resources for seed maturation or mating opportunities become limited (Bertin 1985). This has been called "concordant" female choice (Waser et al. 1987). This interpretation assumes that there is no variation in male traits that could yield such a result, that some female choice scale has been established in the selective past, and that the choice scale is the same for all females.

Male traits on which selection might act.—In order for sexual selection to result in evolutionary change, there must be a potential for a response to selection, in the form of heritable variation in male traits. The absence of a consensus on what constitutes sexual selection in plants derives from several sources. These include differences in the relative importance of male traits for various experimental approaches, distinctions between male traits subject to fecundity selection rather than to sexual selection, and a lack of information on the heritability of male traits.

Our protocol focuses on the differential success of various genotypes during reproduction, rather than on male or female traits that co-vary with fitness. In this way, it embodies one of the two approaches to the study of sexual selection taken by plant evolutionary biologists. One method, following Darwin's approach and paralleling investigations in animal systems, examines the consequences of particular traits for differential male as opposed to female reproductive success (see review in Charlesworth et al. 1987).

The other approach has been followed by plant biologists who have considered the issue of nonrandom genetic transmission from a tradition of factorial-crossing designs. These designs are suited to an analysis of variance in reproductive success that can be attributed to male and female sources, independent of any particular reproductive trait (Antonovics and Schmitt 1986; Marshall and Ellstrand 1986; Lyons, MS). This method has been valuable for studying the period of reproduction from fertilization to seed set, when traits are not as easily isolated and quantified as are floral traits in the pollination phase. Furthermore, such a trait-independent approach can pinpoint significant effects to a particular phase of reproduction, thus providing the stimulus to study specific physiological mechanisms operating during the period of interaction.

Although our experimental protocol has clearly sprung from the trait-independent tradition, we feel that distinguishing causative traits is useful when applying our design. The pattern of interactions illustrated in table 2 can reveal processes other than sexual selection. For example, a significant gender-by-treatment effect that meets our experimental and statistical criteria for selection may be attributable not to sexual selection but rather to outbreeding depression. Furthermore, with this interpretation, an evolutionary response to selection would not be possible because a trait such as outbreeding depression is not likely to be heritable. Therefore, we agree with Charlesworth et al. (1987) and Waser et
al. (1987) that, whenever possible, sexual selection should be distinguished from such phenomena as inbreeding depression, epistasis, outbreeding depression, and self-incompatibility.

Our protocol can be combined with measurements of male and female traits as they co-vary with fitness, but a major difficulty remains in distinguishing the effects of natural and sexual selection on primary sexual characteristics, especially those of hermaphrodites. Darwin (1871, p. 260; see also Lloyd and Yates 1982) mentioned one such characteristic, protandry, which he speculated might have arisen through male-male competition. Some workers favor extending this logic to explain essentially all floral traits as a result of sexual selection caused by intrasexual competition during pollination (Queller 1987). In our opinion this merely changes nomenclature, replacing fecundity selection with sexual selection, rather than providing some finer and more useful subdivision of selection components.

A prime reason for distinguishing sexual selection as a special subset of, or separate process from, natural selection is the possibility of runaway coevolution brought about by an increased genetic covariance of male adornments with female preferences for those adornments (Lande 1981; Kirkpatrick 1982; Heisler 1985). However, runaway evolution of arbitrary floral characters is unlikely because those characters reflect strong physical and physiological constraints imposed by the biotic or abiotic pollination agents that mediate interactions between the sexes.

Regardless of the type of selection invoked, little is known about the heritability of traits that affect male reproductive success in natural populations. Mazer (1987) found that pollen-donor identity has no significant additive genetic effect on fruit and ovule abortion, fertilization, and seed weight in the wild radish *Raphanus raphanistrum*. Clearly, either heritability estimates or selection experiments are necessary to determine the potential for response to selection acting on traits such as pollen-grain number and size and pollen-tube germination and growth rates.

*Selection acting on male traits, not on offspring traits.*—A final problem in interpreting selection acting on male traits in plants is the lack of general agreement on how to separate the action of selection on a male’s traits from that on traits of a male’s diploid offspring. The difficulty arises because interactions during pollen-tube growth or zygote maturation present an opportunity for selection based not on the parental phenotypes but rather on traits related to offspring fitness (Queller 1987).

Postfertilization events may be caused by genetic attributes of the diploid zygote itself, such as inbreeding or outbreeding depression (in the sense of Price and Waser 1979; Campbell and Waser 1987), rather than by female discrimination related to the male’s haploid contribution. Thus, Queller (1987) and Charlesworth et al. (1987) advocated a view of sexual selection that does not include postfertilization events.

Others do not hold the same criteria and allow that female choice may act on male haploid contributions within a diploid offspring. Arguments for maternal control over offspring fate or fitness (e.g., Lee and Bazzaz 1986; Stephenson and Winsor 1986) are often remarkably parallel to the “good genes” hypothesis for
sexual selection; that is, since fit offspring are more adaptive, maternal control is adaptive and more likely to evolve. However, a correlation between nonrandom paternity or maturation and increased offspring fitness does not constitute evidence for sexual selection. Theoretical results suggest that offspring of sexually selected males need not have higher fitness for sexual selection to proceed (Lande 1981; Kirkpatrick 1982). If higher fitness does occur, the direction of natural and sexual selection may be coincidental. Evolutionary response to this selection will depend on whether the variation is additive or nonadditive. Thus, differential fertilization or ovule maturation that derives from male-by-female interaction or "complementarity," based on nonadditive gene action (Griffing 1956a; Waser et al. 1987), will not lead to evolution via sexual selection.

CONCLUSIONS

Plant biologists will continue to differ, as indeed we have, on whether a particular pattern of nonrandom transmission is considered evidence of sexual selection. Consensus can be encouraged by the use of the experimental designs and manipulations we have outlined and by more explicit discussion of experimental constraints, underlying evolutionary assumptions, and the criteria used for distinguishing natural from sexual selection.

Whether sexual selection occurs in plants is clearly not the only interesting question, nor even the most interesting one. Why examine only sexual selection and ignore the study of other kinds of postfertilization events? Plant reproduction is strikingly different from animal reproduction and may, in fact, be better suited to the experimental study of nonrandom genetic transmission. The mechanisms underlying unequal transmission of genes from one generation to the next, whether or not they embody sexual selection, require investigation. Even our limited literature review hints at the fascinating diversity of effects that may not readily qualify as sexual selection. Given such a rich mine of information waiting to be explored and the advantages of working with plants, we hope that workers will not be overly distracted by the pros and cons of fitting plants into animal-derived models and will concentrate instead on systematically documenting how evolutionary mechanisms work on plant reproduction.

SUMMARY

There is growing evidence of nonrandom reproductive success in plants. The potential evolutionary effect of these patterns depends on the extent to which they reflect nonrandom transmission of genes between generations. A recent tendency has been to examine these patterns in the context of sexual selection.

We present an experimental protocol designed to yield more information on nonrandom transmission in general and on sexual selection as a special case. The mainstays of the protocol are twofold. First, reproduction is separated into pollination, fertilization, and seed-maturation phases, in which functional processes associated with the genders are known and in which the genders can be manipulated. Second, sources of variation in reproductive success are identified by
systematically repeating a reciprocal-crossing design with treatments that alter the intensity with which males and/or females can interact. We discuss appropriate experimental and analytic techniques, especially designs for analyses of variance. Our emphasis is primarily on identifying genetic sources of variance.

A selective literature review illustrates how some of our design elements have been applied in the three stages of reproduction.

We discuss some of the statistical and experimental difficulties that plants pose for the study of nonrandom transmission, as well as some of the advantages of working with plants. Even when the difficulties are overcome, there is considerable disagreement about the biological interpretation of results, particularly with regard to sexual selection. Disagreements result from differential reliance on arguments about past selective events, difficulty in identifying heritable male traits on which selection can act, and limits on inference imposed by experimental constraints. Plant biologists will continue to disagree on these matters. We hope that they will not be overly concerned with fitting plants into animal-derived models of sexual selection and will concentrate instead on systematically documenting how evolutionary mechanisms work on plant reproduction via nonrandom genetic transmission.

ACKNOWLEDGMENTS

For discussion of ideas we thank D. R. Campbell, M. B. Cruzan, N. C. Ellstrand, A. M. Montalvo, G. H. Pyke, and M. L. Stanton. R. M. Bush, N. L. Christiansen, Ellstrand, R. R. Nakamura, D. W. Schemske, Stanton, D. E. Stone, M. K. Uyenoyama, B. S. Weir, and three anonymous reviewers provided valuable comments on earlier drafts of the manuscript. This paper is based, in part, on a portion of a dissertation submitted by E.E.L. to Duke University in partial fulfillment of the requirements for the Ph.D. Financial support was provided by National Science Foundation (NSF) Dissertation Improvement grant BSR 84-01153 (to J.A. for E.E.L.), National Institutes of Health training grant 5T32GM-07754 (E.E.L.), NSF grant BSR 83-13522 (N.M.W.), and NSF grant BSR 84-07960 (J.A. and A.F.M.).

APPENDIX

Complications Resulting from Differences in Ploidy and Generation

Throughout this paper we have analyzed reproductive success as if only male and female diploid parental genotypes were involved. Here we address the fact that parental genotypes interact indirectly, via haploid gametophytic “samples” of themselves, or in the case of endosperm, via a (usually) triploid combination of haploid segregation products.

During pollination, diploid-diploid interactions predominate, involving parental floral traits that affect pollen pickup and delivery. At this stage haploid genotypes generally are unimportant, although we can conceive that they might influence pollination success through subtle effects on pollen size or adhesion properties (S. Tonsor, pers. comm.; Cruzan, pers. comm.). Between pollination and fertilization, interactions involve diploid female tissue and diploid paternal gene products carried by male gametophytes (as in sporophytic self-incompatibility), or haploid gametophytic traits expressed when pollen tubes grow through the diploid style. Haploid-haploid interactions predominate during
fertilization, although diploid maternal tissue surrounding ovules may play a role in pollen-tube orientation. Interactions during seed maturation are even more complex; they involve the maternal diploid genome, two haploid genomes forming the zygote, and often three haploid segregation products forming a triploid endosperm (Brink and Cooper 1947; Westoby and Rice 1982).

For most plant populations, we would expect variation among different parents in their reproductive success to be greater than variation among segregation products (haploid samples) from any one parent. However, the considerable discussion in the literature on gametophytic selection acting on haploid pollen tubes (Mulcahy and Mulcahy 1983; Pfahler 1983; Snow 1986) and the potential for kin selection given differences in relatedness within and between fruit and seed tissues (Kress 1981; Queller 1983, 1984) compels us to consider briefly how to study the effects of tissues of different genetic composition. In order to study their consequences for reproductive success experimentally, one must ideally be able to replicate, hold constant, and vary, in turn, each of up to four sets of tissue: maternal, pollen, ovule, and endosperm. In reality, this may prove impossible.

Subsampling of haploid genomes is possible using pollen culture to generate haploid and subsequently di-haploid completely homozygous lines from the products of a meiotic segregation in a single plant (Kasperbauer et al. 1980; Han and Honyoan 1986) (with possible attendant confounding effects of inbreeding depression). In this way, pollen-grain genotypes could be replicated within individuals. The haploid genotypes of individual ovules could also be made identical, but only by generating them from a completely homozygous maternal diploid plant, which would also produce identical endosperm contributions.

It may be possible to minimize maternal diploid effects by using embryo culture to raise post-meiotic ovules fertilized by identical pollen on artificial media (Raghavan and Srivastava 1982; Nakamura 1988; Nakamura and Stanton 1989). For seeds developing within fruits, however, maternal haploid effects cannot be separated from maternal diploid effects or from endosperm genotype effects. Reciprocal crosses yield identical embryos on different mothers, but with both ovule and endosperm genotypes necessarily determined by the maternal diploid genotype in which they grow.

Maternal effects are additionally complex since they may also involve environmental effects and/or differences in organelle transmission to the embryo. If female plants can be replicated or set up in a particular family structure, maternal genetic effects can be distinguished from maternal environmental effects (Falconer 1981; Alexander and Wulff 1985). Cytoplasmic effects can be controlled by performing crosses among the progeny of one female parent, in which case (providing appropriate designs are followed and environmental “carry over” effects are eliminated) any remaining reciprocal effects may be due to maternal diploid nuclear or endosperm genotype.

The ability to manipulate only some of the four types of tissue within a fruit may introduce a bias in interpreting experimental results; since it is only feasible to ascribe differential ovule success to paternally derived haploid contributions, haploid genome effects via the zygote are seen as a consequence of sampling the male parental genome. Hence, the process of ovule abortion is often seen as “female choice” of “male parent” when in fact, if such a choice exists, the diploid mother “chooses” the male and/or female haploid genomes. Rejection of her own haploid segregation products is as feasible as rejection of male haploid genomes.

LITERATURE CITED


VARIATION IN PLANT REPRODUCTIVE SUCCESS


