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INVITED SPECIAL PAPER

Assessment of pollen viability in hand-pollination experiments: a review[1]

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Pollen viability is known to decline, sometimes rapidly, with age and exposure to environmental stresses. Because of the potential impact of nongenetic factors on the ability of pollen to fertilize ovules, researchers conducting hand-pollinations should attempt to control the freshness or viability of pollen used. We surveyed hand-pollination experiments published in seven major journals from 1980 until mid-1994, collecting data on the purpose of the experiment, the degree of care taken to ensure pollen viability, and the degree of care taken to ensure stigmatic receptivity. Fewer than one-third of the papers reported any consideration of pollen freshness or viability, whereas over one-half made some mention of stigmatic receptivity. Pollen freshness or age was mentioned more frequently for some types of experiments than for others. Experiments attempting to compare performance of different donors are especially susceptible to error when donor pollen is not treated equally or otherwise controlled for viability. We discuss strengths and weaknesses of tests to measure pollen viability, and experimental protocols to reduce differences in pollen condition across donors.

Darwin's concern with the effects of cross- and self-fertilization in plants led him to conduct many controlled pollinations in which he collected pollen from particular donors and transferred it to the stigmas of recipients (1876, 1877). Controlled pollinations remain a mainstay of many investigations today. The questions are diverse, but many still involve comparing the performance of pollen donors. Classical issues, such as inbreeding effects and the functioning of incompatibility systems, are still of interest, but the recent emphasis on the important role of male function in floral evolution has brought new questions with it: sexual selection and "female choice," resource vs. pollen limitation of seed set, gametophytic selection, etc. We lump all of these issues under the heading of "evolutionary ecology." As documented by Kearns and Inouye (1993), publishing activity in pollination biology is soaring, and many of the recent surge of papers use controlled hand-pollination. Although mostly done in the field or in greenhouses with only modest control of the climate, this work is founded on the assumption that differences in the performance of different pollen donors are genetic in origin.

There has also been progress in the study of pollen grain physiology. The issue of pollen viability has received attention, and it is now apparent that there is great variability among species in the effective life spans of pollen grains (see, for example, Table 5.2 in Stanley and Linskens [1974] or Tables 4.1 and 4.2 in Shivanna and Johri [1985]). Storage conditions, especially temperature and relative humidity, can have strong effects on the competence of pollen (Johri and Vasil, 1961; Stanley and Linskens, 1974; Shivanna, Linskens, and Cresti, 1991a). Workers in this field have devised various tests for pollen viability and vigor, and have used them to demonstrate repeatedly that the performance of pollen has an important environmental component (Shivanna, Linskens, and Cresti, 1991b). Unfortunately, from the standpoint of evolutionary ecology, much of this work has been concerned with optimizing long-term storage conditions rather than determining pollen survivorship under field conditions.

Given the widely appreciated conceptual framework of classical quantitative genetics, in which genetic and environmental effects are explicitly distinguished, and variance partitioned between them, one would expect that the evolutionary ecologists would be keenly interested in evaluating and controlling the viability and vigor of the pollen samples whose genetic properties they wish to test. Our impression, however, was that they were not. To test this impression, we chose several journals that frequently publish research that we would categorize as evolutionary ecology by the criteria above. We searched all volumes for the past 15 yr for all papers that used hand-pollinations. Each paper was categorized by the purpose of the pollinations and by the degree of care that was taken to assess the condition of the pollen used. We also noted the degree of care taken to ensure stigmatic receptivity. Lack of stigmatic receptivity is less likely to be conflated with donor identity than is pollen inviability, but pollination of unreceptive stigmas could still lead to erroneous conclusions. The purpose of the review was to determine the extent to which authors documented care taken to ensure pollen viability and stigmatic receptivity in hand-pollination experiments.

METHODS

We chose seven journals that frequently publish papers concerning evolutionary ecological work in pollination biology: *American Journal of Botany, Biotropica, Canadian Journal of Botany, Ecology, Evolution, Oecologia,*

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TABLE 1. Purposes of hand-pollinations, degree of care taken to ensure pollen viability, and degree of care taken to ensure stigmatic receptivity. Lowercase letters are used to represent purpose and care in Tables 2, 3 and Fig. 1.

1. Purpose of hand pollination
   a. Supplemental for resource vs. pollen limitation of seed set
   b. Comparisons among donors, including self vs. outcross and distance comparisons
   c. Tests of compatibility (e.g,. breeding system)
   d. Attempts to determine timing of receptivity
   e. Stigma clogging or ovule discounting
   f. Pollen competition (high vs. low levels); pollination intensity (effect of pollen grain numbers on seed production)
   g. Hybridization studies
   h. Effects of various treatments on pollen viability (storage time, floral age, etc.)
   i. Comparisons between male and hermaphroditic flowers
   j. As control (for effects of watering, removal of floral part, etc.)
   k. Impact of pollination on duration of female phase
2. Care stated to ensure pollen viability
   a. Nothing said about pollen freshness or age
   b. Something said about using fresh pollen, or pollen from fresh or newly opened flowers
   c. Nothing said about freshness per se but attempt to use donors in equal age/condition
   d. Specific mention of controlling pollen age by either time or by a microphenological indicator, e.g., a certain stage of anthesis
   e. Some pollen tested
   f. Each aliquot of pollen tested individually
   r. Viability test done as response variable for experiment (pooled with category a)
   u. Viability test done, but unrelated to hand pollination (pooled with category a)
3. Care stated to ensure stigmatic receptivity
   a. Nothing said about stigmatic receptivity
   b. Pollinations using flowers of a particular age, or at a particular time of day
   c. Subjective assessment of stigmatic receptivity, including visual cues
   d. Test of receptivity

and *Oikos*. We scanned titles in Tables of Contents, and also examined appropriate key words or index entries. The survey covers the period from 1980 to 1994, with the final issue examined being the most recent available at the SUNY Stony Brook library in mid-July 1994 (June 1994 for *American Journal of Botany, Ecology* and *Oikos*; May 1994 for *Oecologia*; March 1994 for *Biotropica,* and December 1993 for *Canadian Journal of Botany* and *Evolution*).

We included all articles for which a response variable directly depended upon the results of hand-pollinations. By necessity, this included a number of papers, especially in the earlier years, that were strictly descriptive attempts to define breeding systems or interspecific compatibility. We excluded papers where hand-pollinations were done in order to generate and compare progeny, unless the progeny number itself was a response variable. For example, inbreeding depression studies were included if the number of seeds resulting from self- and outcross-pollinations was reported, but excluded if only the number of aborted seeds, or their germination percentages were given, since these variables presume successful fertilization.

We classified each paper according to the purpose that the hand-pollination served (Table 1). Numerous papers included hand-pollinations done to fulfill several purposes; we included all applicable purposes in these cases. We also assigned each paper a code representing the level of care taken to control pollen viability (Table 1). When the experiment included an actual test of viability, we recorded which type of test was used. Finally, we read both Methods sections and species descriptions to look for indications that the authors were aware of the timing of stigmatic receptivity. We once again assigned a code and recorded the type of test, if one was given. We used a computer spreadsheet to sort the journal entries by category and to perform cross-classifications. SYSTAT 5.2 (Wilkinson, 1992) was used to perform statistical analyses.

RESULTS

We found 283 articles that met our criteria for inclusion (Appendix 1). A list of the codes assigned to each paper is available by request from the authors. The majority of the papers concerned resource vs. pollen limitation of seed set (90 papers), comparisons of donors (72 papers), or breeding system investigations (124 papers). Four other topics were taken up with moderate frequency: stigma clogging (19), pollen competition (18), stigmatic receptivity timing (16), and hybridization studies (14). The remaining four topics were represented by only a few papers each.

The majority of authors (70%) did not mention pollen freshness or age (Fig. 1; Table 2). In ≈ 14% of cases, the authors said something about using fresh pollen, or pollen from newly opened flowers. About 6% specified that they attempted to use donors of equal age or condition. Fewer than that made a specific mention of controlling pollen age by either time or a microphenological indicator, or performed a test to measure the viability of donors. A number of authors did test pollen viability, but not in relation to the hand-pollination experiment, or as a response variable for the experiment itself (5% each).

Tests of pollen viability can be divided into three categories: germination tests, tests of pollen metabolism, and traditional stains to indicate presence of cytoplasm. Some authors used more than one indicator, so the number of tests done exceeds the number of studies. Germination tests, either in vivo, in vitro, or semi-vivo, were used in 17 studies. The fluorochromatic procedure, in which fluorescein illuminates cells with active esterase and intact membranes, was used in 14 studies. Lactophenol-aniline blue, which stains nonabortive but not abortive pollen, was also used in 14 studies. The remaining six studies used miscellaneous stains or tests of enzymatic activity.

Stigmatic receptivity was mentioned in ≈ 55% of the papers (Table 3). In the majority of these, the authors made some subjective assessment of receptivity, sometimes inserting the adjective "receptive" without stating how the receptivity was assessed, or in other cases describing a morphological change that they associated with receptivity. Less often, some time period was specified during which the stigmas were considered to be receptive. In ≈ 8% of studies, authors performed some kind of test to determine that stigmas were indeed receptive. The most common tests were hand-pollinations, with either pollen

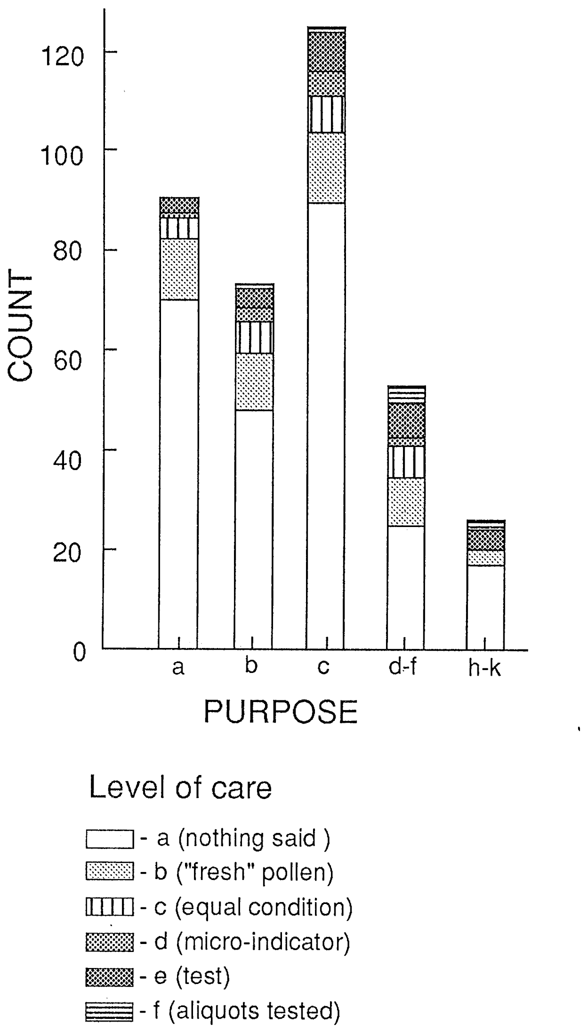

Fig. 1. Number of papers demonstrating various levels of care to ensure pollen viability, grouped according to purpose of the hand pollination. For interpretation of purposes and fuller explanation of levels of care, see Table 1.

tubes or fruit set used as indicators. Chemical tests of enzymatic activity (esterase or peroxidase) were also used.

The degree of concern about pollen viability was not independent of the purpose of the experiment (Fig. 1; likelihood ratio $\chi^2 = 18.5$, $P < 0.05$). Papers concerning pollen competition, stigma clogging, or the timing of stigmatic receptivity tended to be the most careful, with about half of the papers reporting attention to pollen freshness. Papers making comparisons among donors showed less care; about one-third included something about controlling for pollen age. Papers on limitation of fruit set or plant breeding systems had the smallest proportion showing care; only about one-quarter made any mention of pollen freshness or age.

A chronological view shows that the degree of care to ensure pollen viability has remained constant since 1980 (Fig. 2). A possible exception is the first portion of 1994, for which the majority of papers consider pollen freshness or age.

TABLE 2. Purpose of hand pollination cross-classified with care stated to control pollen viability. The total equals more than the number of papers surveyed, since many studies included more than one purpose. See Table 1 for interpretation of codes.

	Care stated						
Purpose	a	b	c	d	e	f	Totals
a	70	12	4	1	3	0	90
b	47	11	6	3	4	1	72
c	89	14	7	5	8	1	124
d	8	3	2	0	2	1	16
e	8	4	3	1	1	2	19
f	9	3	1	1	4	0	18
g	9	2	0	0	2	1	14
hijk	8	1	0	0	2	1	12
Totals	248	50	23	11	26	7	365

DISCUSSION

The majority of papers indicated no concern that pollen used was viable. Perhaps the extent to which authors described care to ensure pollen freshness was associated with the level of detail in the Methods section overall. It is likely that there were many scientists who, through their awareness of the biology of their study organism, were sure that stigmas were receptive but did not mention so in the Methods section. Similarly, it is likely that many authors who did not state it explicitly were careful to ensure that pollen used in hand-pollinations was fresh, and in the case of comparisons among donors, that the pollen of both types was treated equally. In fact, there is evidence that either authors who were more careful about pollen viability were also more careful about stigmatic receptivity, or that some authors simply wrote more complete methods sections than others: there is a highly significant association between mention of pollen freshness and awareness of stigmatic receptivity (Table 3; likelihood-ratio $\chi^2 = 32.6$, $P < 0.001$). Whether this indicates an association of attention to protocol in the execution or description is impossible to tell.

However, the proportion of authors who indicated awareness of the importance of stigmatic receptivity (55%) was far greater than the proportion who commented on pollen viability ($G = 32.6$; $P < 0.001$). For all purposes listed here but the study of limitation of fruit set, failure to ensure pollen viability will more drastically alter results than failure to ensure stigmatic receptivity; yet viability

TABLE 3. The amount of care stated to ensure pollen viability cross-categorized with the care stated to ensure stigmatic receptivity. Three studies used more than one method to ensure stigmatic receptivity. For interpretation of codes, see Table 1.

Care stated to ensure stigmatic receptivity	Care stated to ensure pollen viability						
	a	b	c	d	e	f	Totals
a	112	9	4	0	4	0	129
b	21	10	7	5	3	1	47
c	57	17	5	5	3	1	88
d	11	3	1	0	5	2	22
Totals	201	39	17	10	15	4	286

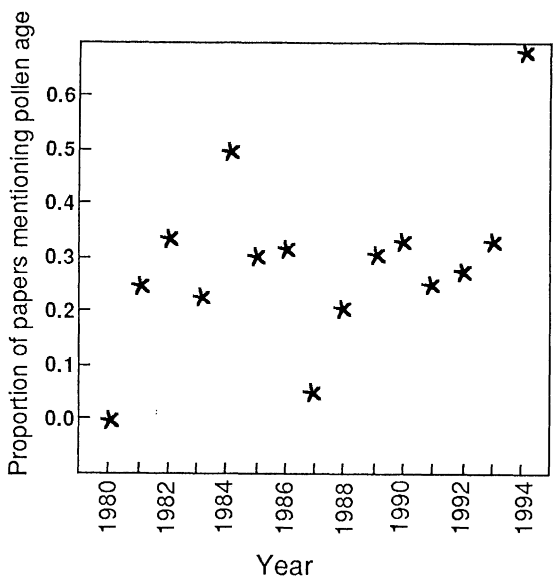

Fig. 2. Proportion of papers in each year mentioning care to ensure pollen viability.

is mentioned less often. The low reporting rate of such procedures may reveal a lack of consciousness by the authors and their reading public that failure to control pollen viability may jeopardize the reliability of their results.

How delicate *are* pollen grains? Most studies of pollen life involve laboratory conditions, usually at low temperatures. Under field conditions, it is likely that many taxa have grains that are durable enough to allow experimenters to ignore viability losses over the period of an experiment. However, some studies done under laboratory conditions give cause for concern. For example, Hoekstra and Bruinsma (1975a) examined pollen germinability at 30 C and high (97%) humidity. The half-life of pollen of six species of Asteraceae (with trinucleate pollen) ranged from 1.7 to 3.7 hr ($\bar{X}$ = 2.45 hr). Under these conditions, binucleate pollen lasted longer ($\bar{X}$ for four species = 19.9 hr, range 5–35 hr) but even these half-lives could compromise certain experimental designs. The influence of relative humidity was critical. By lowering relative humidity to 60%, the viability of Asteraceae pollen could be extended to several days (Hoekstra and Bruinsma, 1975b). Working at the opposite end of the humidity scale, Shivanna and Heslop-Harrison (1981) showed that *Secale cereale* pollen held at 5%–10% relative humidity irreversibly lost all germinability within 1 hr. *Iris pseudacorus* lost germinability even more rapidly, although in this species germinability could be partially restored by following the desiccation period with exposure to moist air.

Generally speaking, graminaceous pollen seems especially vulnerable to low humidity, while the pollen of composites and many other species does best at low humidity. There are exceptions, however (see Linskens and Stanley, 1974, pp. 56–57). Overall, pollen physiologists have avoided typical field conditions with uncanny precision, but we may conclude that for some taxa, some (perhaps extreme) field conditions are likely to limit pollen life to a few days or even hours. This possibility needs further study, but for the present we feel that investigators should be conservative.

What kinds of errors can intrude if inviable grains are used? In the case of supplemental pollination, the researcher may erroneously conclude that resources, and not pollen, limit seed set in a given population (see Young and Young, 1992). For other purposes, the potential for error is highest where variation in viability is likely to be correlated with experimental treatments. When the performance of donors is being compared, inattention to pollen age or viability is particularly serious when the pollen of one class of donors is more likely to be inviable, due to longer storage or travel times. For comparisons of donors at varying distances from the maternal plant, pollen traveling from the farthest parent may be most likely to suffer from age effects, thus compounding environmental degradation with the experimental treatment. Outcross pollen and interspecific pollen may similarly suffer in comparison with self or intraspecific pollen in breeding system and hybridization studies. The perceived impact of stigma clogging could be exaggerated if stale pollen were used in the delayed pollinations.

How should researchers ensure that environmental effects on pollen performance do not confound treatment effects or otherwise lead to misleading conclusions? A variety of tests have been proposed, well summarized by Kearns and Inouye (1993). Nonvital stains, such as Alexander's stain or aniline blue in lactophenol can distinguish aborted from nonaborted pollen grains, and are therefore useful in determining the degree of sterility in hybrids (Alexander, 1969). They stain dead cells as well as live ones, however, so should not be used in attempts to verify viability (Heslop-Harrison, Heslop-Harrison, and Shivanna, 1984). More effective tests to measure viability include germination assays and tests for enzymatic activity.

Germination tests include in vitro (Stanley and Linskens, 1974), in vivo (Heslop-Harrison, Heslop-Harrison, and Shivanna, 1984), and semi-vivo (Shivanna, Linskens, and Cresti, 1991a, b). In vivo tests can use either pollen-tube growth or seed set as the response variable. In vivo tests are doubtless the most exacting available for determination of pollen viability; however, they are accompanied by obvious drawbacks. If seed set is used as a response variable, a significant delay will ensue before it is possible to determine whether the experiment was carried out successfully, that is, whether the pollen used was indeed viable. If either seed set or pollen tubes are monitored, the test itself occupies time and stigmatic surfaces, potentially limiting sample sizes. In vitro pollen germination circumvents the above drawbacks. Pollen grains are germinated in sucrose solutions on agar or gelatin media (for recipes see Shivanna and Rangaswamy, 1992; Kearns and Inouye, 1993). In vitro tests need to be carefully controlled; many environmental factors such as temperature, concentration of grains, and substrate constituents can affect pollen-tube growth (Brewbaker and Kwak, 1963; Kearns and Inouye, 1993). In addition, pollen of some species is not amenable to germination in vitro. For semi-vivo tests, hand-pollinated styles are placed in germination media. The pollen tubes grow out of the styles into the medium. Semi-vivo tests are suggested as an improvement over in vitro tests because some pollen grains may be too stressed by environmental exposure to grow pollen tubes through a style, yet able to germinate in medium (Shivanna, Linskens, and Cresti, 1991a, b). Of course, semi-vivo tests can introduce complications because they involve pollen–stigma interactions. For example, an aliquot of pollen may fail in a semi-vivo test due to a strong incompatibility reaction; therefore, poor performance in such a test need not indicate low pollen viability. Both in vitro and semi-vivo tests will show better results with some species than with others. Workers using taxa unrelated to those previously studied can expect to invest some time perfecting culture conditions.

A traditional test for enzymatic activity uses colorless tetrazolium salts (Hauser and Morrison, 1964; Stanley and Linskens, 1974). These salts are converted to formazan, a reddish substance, in the presence of dehydrogenase, an enzyme used in cell respiration. For many species, tetrazolium tests are reliable indicators of pollen viability; however, for other species, they may yield false positive scores for viability when compared with results from germination tests (Heslop-Harrison, Heslop-Harrison, and Shivanna, 1984). Therefore, the reliability of the enzymatic procedure needs to be established for each study species. Another drawback of the method is that pollen grains may vary from pale to deep red, making it difficult to establish a consistent cut-off point for viability (Shivanna and Rangaswamy, 1992).

The fluorochromatic reaction test (FCR), introduced by Heslop-Harrison and Heslop-Harrison (1970), also uses enzymatic activity as an indicator. Pollen grains are immersed in a fluorescein diacetate solution, which is hydrolyzed to fluorescein by cytoplasmic esterases in living cells. When the cell membrane is intact, the fluorescein accumulates in the cell, and shines brightly when viewed with a fluorescence microscope. The test therefore confirms two aspects of viability: enzymatic activity and an intact cell membrane. FCR correlates well with in vitro germination for a range of species (Shivanna and Heslop-Harrison, 1981; Heslop-Harrison, Heslop-Harrison, and Shivanna, 1984; La Porta and Roselli, 1991). It is easier and faster than in vitro germination tests. Since FCR measures the potential for germination, rather than germination itself, it may overestimate viability in some cases (Shivanna and Heslop-Harrison, 1981).

Empirical evidence in at least one circumstance indicates that FCR scores may be overly conservative, however. In *Erythronium grandiflorum,* pollen exposed in dehisced anthers declines rapidly in FCR score. However, pollen that has aged long enough to have very low FCR scores shows comparatively little decline in germination on artificial medium, and is just as capable of siring seeds as fresh pollen, when fresh and aged are applied simultaneously in mixed pollinations (Thomson et al., 1994). It may be that desiccated grains score low on FCR tests due to low enzymatic activity, but that once they are rehydrated on growth medium or stigmas, their viability is restored. In at least this species, apparent decline in viability due to dehydration is reversible once hydration occurs.

Adequate hydration is necessary in order to test viability in species that can resume enzymatic activity following dehydration. However, artificial rehydration in order to assess viability leads to a conundrum. Speed of rehydration may affect germination rates, and may therefore itself impact pollen competitive ability (Thomson, 1989). Moreover, in some species there is maternally inherited variation in pollen aperture number, with grains with more apertures becoming hydrated and germinating more quickly than grains with low aperture numbers (Dajoz, Till-Bottraud, and Gouyon, 1993). Therefore, some of the genetic basis for pollen performance of interest to researchers may be obscured when pollen is hydrated artificially in order to assess viability. Viability cannot be assessed without hydration, but artificial hydration itself will obscure some of the variation of interest.

A greater awareness of pollen viability in hand-pollination experiments is clearly needed, yet each of the tests described above possesses drawbacks. In vivo fertilization consumes time and material, in vitro fertilization and the tetrazolium test may be technically difficult for some species, and FCR will give misleading results when pollen retains fertilization ability although dehydrated. What kind of approaches could circumvent these problems? A sampling of solutions from the literature reveals two approaches: fastidiously controlling microphenological indicators so that pollen from all donors is in equal condition, and clever applications of viability tests.

A paper by Harder, Cruzan, and Thomson (1993) exemplifies the first approach. They placed undehisced anthers in vials, waited for them to dehisce, and performed pollinations within an hour. Cruzan (1990) controlled anther dehiscence rates by storing undehisced anthers in airtight tubes at 2 C. Anthers would dehisce shortly after the vials were opened. This method allows hand-pollinations between mates that flower asynchronously, however, continued viability following prolonged storage would need to be ascertained for each particular species. Rigney et al. (1993) used partly dehisced anthers, taking only "the most recently exposed pollen from the cleft where the thecal suture was opening." Of course, this procedure assumes that the youngest pollen is the most desirable. In fact, very young pollen may be still immature and not fully functional (Knox, Williams, and Dumas, 1986). Nevertheless, the procedure of Rigney et al. does yield pollen with a precisely controlled exposure history.

As mentioned above, germination tests give a conclusive demonstration of pollen viability. Kephart (1981) chose pollinia from the same *Asclepias* flowers used for hand-pollinations, and placed them in an agar/sucrose solution. Only pollinia producing ten or more pollen tubes were considered germinable, and the pollinations resulting from those flowers could be eliminated from further analysis. An elegant modification of in vivo techniques was used by Fenster and Sork (1988). They first determined that 10 hr was necessary for most, but not all pollen tubes to reach the ovary. Ten hours following hand-pollinations, they removed the styles and then examined stigmas for pollen tubes using aniline blue with a fluorescence microscope. They then excluded from analysis any pistils showing no germination, thereby ensuring both pollen viability and stigmatic receptivity. Both of these methods entail performing extra hand-pollinations to compensate for the inevitable shrinking in sample size, but they share the advantage that the pollen performance can be assessed soon after the pollinations are done.

As these examples illustrate, researchers can reduce environmental differences in pollen viability either by carefully controlling the freshness of pollen used in hand-pollinations, or by monitoring the performance of pollen used. We hope that their example leads other researchers to include descriptions of the measures that they take to ensure equality of pollen condition across donors, or demonstration of sufficient viability in the case of supplemental pollination experiments. We also hope that this review stimulates more workers to assess the longevity of pollen under field conditions. Ideally, there will accumulate information for a broad enough range of taxa that researchers beginning work on a new species will have an idea of the care required to ensure pollen viability.

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APPENDIX 1. Articles included in review.

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