

Exceptionally Low Seed Set in *Dedeckera eurekensis*: Is There a Genetic Component of Extinction?

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Abstract

Seed set in *Dedeckera eurekensis*, a recently discovered monotypic genus with a highly restricted geographical distribution, averaged only 3.1 percent for five samples obtained from four populations in different years, spanning an eleven-year period. The largest proportion of fruits (44.5 percent) was fully developed, but contained only aborted ovules; another large group of fruits was partially developed (33.5 percent) and also contained only aborted ovules. A final group of apparently nondeveloped flowers (18.9 percent) was either not pollinated, or abortion occurred prior to any significant ovary development. Normally outcrossing plants such as *Dedeckera* generally abort approximately 50 percent of their ovules. The degree to which this loss is ascribable to relative or absolute manifestations of genetic load as it influences embryo development is a question of considerable interest. Environmental factors are not considered to play a major role in the level of abortion.

But why should virtually the entire seed crop abort as a result of genetic load-developmental selection, especially when there is no compensating vegetative reproduction? An explanation is required that would maintain individual plant vigor, yet permit the reproductive capacity to approach zero. A very tentative evolutionary scenario is postulated whereby greater genetic heterozygosity improves both vigor and longevity. Thus, the surviving members of the population might be heterotically fit for long-term survival, but not necessarily for reproduction. Where environmental conditions are especially unfavorable for seedling establishment (seedlings are unknown in populations of *Dedeckera* examined to date), one might expect to find vegetatively vigorous individuals, comprising largely sterile relictual populations. This argument assumes that individual vigor and longevity are selected for in each generation at the cost of sexual reproductive success. This could occur if increased genetic heterozygosity began to affect reproduction adversely by increasing the probability of exposing deleterious homozygous alleles, as occurs in cases of balanced polymorphisms. If, however, vigor and longevity

continued to be important for survival, selection for increased genetic heterozygosity should nonetheless continue even though it might lead to greatly reduced reproductive success. The accumulation of somatic mutations in long-lived meristems could further exacerbate the problem. Ultimately, the exposure of deleterious homozygous recessive alleles, the accumulation of somatic mutations in long-lived meristems, as well as the occurrence of chromosomal mutations, might eventually lead to extinction through low reproductive rates. Selection is not prescient.

Introduction

The object of this preliminary study was to determine the seed/ovule (S/O) ratio (*i.e.*, the percentage of ovules that develop into seeds) in *Dedeckera eurekaensis* Reveal and Howell (Polygonaceae). The S/O ratio [Wiens, 1984] is a partial measure of reproductive success. Recently, we [Wiens *et al.*, 1987] divided reproductive success into two phases: (1) Pre-emergent (the percentage of eggs developing into seeds that enter the ambient environment) and (2) postemergent (the percentage of progeny surviving to reproduce). Since Polygonaceae produce only a single ovule/flower, the S/O ratio is a direct measure of pre-emergent reproductive success (PERS). In plants with multiple ovuled fruits, PERS must be estimated by analyzing both percentage of surviving fruits (fruit/flower ratio) and the S/O ratio.

Dedeckera eurekaensis is a recently discovered monotypic genus with a highly restricted geographical distribution [Reveal and Howell, 1976]. Presently it is known from about a dozen, mostly small, localized populations in the Last Chance, Panamint, Inyo, and White Mountains bordering the fringes of the northwestern Mojave Desert, where it is common on calcareous soils [Reveal and Howell, 1976; Morefield, 1985; Novak and Strohm, 1981; M. De-Decker, pers. comm.].

The reproductive biology of *Dedeckera* was first examined with respect to its pollination system [Wiens *et al.*, 1986]. The species is protandrous and adapted for outcrossing in spite of its small (1-2 mm) flowers. Preliminary observations of flower visitors at the Coldwater Canyon population, White Mountains, suggested that the species was pollinated by generalist insects, particularly sarcophagid and syrphid flies, and several wasps.

Interest in the seed set of *Dedeckera* was stimulated by the discovery in the Cape region of South Africa of two woody, outcrossing shrubs, *Audouinia capitata* (Bruniaceae) and *Retzia capensis* (Retziaceae), with exceptionally low S/O ratios. Both are monotypic genera. *Audouinia* is not known to produce viable seeds, and seeds of *Retzia* are rare (John Rourke, pers. comm.). In *Audouinia*, open pollinated flowers about two months post anthesis showed that only 2.6 percent of the ovules (N = 1153) initiated development. Furthermore, the growth of the few developing ovules appeared to be arrested, and they were apparently inviable. Parisi [1985] also investigated seed set in *Audouinia* and obtained relatively higher values of "seed set" from hand cross pollinations, but she mentions that the "seeds" were in the proembryo stage of development. This supported our supposition that the "seeds" of this

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species aborted at an early stage of development. *Retzia* had an S/O ratio of 6.5 percent (N = 201). At the time of observation, however, the population was not in a major "flush" period of anthesis, and only occasional open flowers with developing fruits were available.

In an extensive study of the S/O ratios in 187 species of plants with different breeding systems, Wiens [1984] showed that the S/O ratios of inbreeding plants (\bar{X} 82 percent) and outcrossing plants (\bar{X} 50 percent) were very significantly different ($P \ll 0.003$). The S/O ratios of *Audouinia*, *Dedeckera*, and *Retzia* are markedly lower than the mean for outcrossing species.

In addition to the apparent absence of seed production (*Audouinia*) or exceptionally low S/O ratios (*Retzia*, < 0.07 percent), both of these genera also exhibited the following characteristics: They are (1) phylogenetically isolated (monotypic genera without close relatives) and apparently the last extant members of their respective clades, (2) known only from a number of relatively small, geographically isolated populations, (3) apparently long-lived shrubs, and most importantly, (4) without known means of vegetative reproduction.

The exceptionally low S/O ratios in both of these genera (coupled with the apparent lack of vegetative reproduction) suggested to us that the factors limiting reproduction in these genera had a genetic basis. Pollination did not appear to be a major factor in the loss of sexual reproductive capability, inasmuch as the S/O ratios were obtained from developing fruits, which is taken as *prima facie* evidence of pollination. Perhaps polli-

nation was inadequate (*i.e.*, too few pollen grains deposited on the stigma), but this seemed unlikely in view of the small number of ovules in the flowers of *Audouinia* (6) and *Retzia* (4). There was no obvious evidence to suggest that resource limitations were responsible for the low S/O ratios, a problem which will be discussed later. Preliminary information suggests that *Dedeckera* duplicates all the basic features of *Audouinia* and *Retzia* mentioned previously, *i.e.*, (1) it has an exceptionally low S/O ratio (3.1 percent), (2) is phylogenetically isolated (a monotypic genus) without obvious close relatives, (3) is known from only a few relatively small populations, and (4) is a long-lived shrub without vegetative means of reproduction.

Methods

The S/O ratios in *Dedeckera* were determined from preserved (pressed) material representing four geographically separated populations in the White, Panamint, and Last Chance mountains (Table 1) and were all made in different years. Flowers and fruits from these collections were scored as follows: those with (1) non-developed ovaries, (2) partially developed fruits with an aborted ovule, (3) fully developed fruits containing an aborted ovule, and (4) fully developed fruits containing a mature seed. Fruits in classes 3 and 4 were approximately similar in length, but the pericarp was conspicuously depressed between the veins in Class-3 flowers (Fig. 1), and the partially developed ovule was aborted. Ovules from Class-2 flowers showed varying degrees of development, but were all smaller than those from Class-3 and 4 fruits. The non-developed ovaries, however, could have resulted from the lack of pollination, or embryo

Table 1
Seed ovule ratios and developmental characteristics of *Dedeckera eurekensis*

Locality ^a	Date of Voucher ^b	Dev. Fruit (Full) ^c		Dev. Fruit (Aborted ovule)		X̄ Ovule Length (Aborted ovule mm)		Part Dev. Fruit		X̄ Ovule Length (Part. dev. fruit, mm)		Non. Dev. Flowers		Total Ovules
		Number	Number	Number	Number	Range	N	Range	N	Number	N	Number	N	
White Mts. Coldwater Cyn.	7/5/85 MD5821	2	35					47				21	105	
White Mts. S. Bishop	8/24/84 MD5700	16	176					86				73	351	
Panamint Mts.	8/10/80 MD5144	1	54			0.97 (0.33)	13	0.63-1.68	29		0.57 (0.08)	6	109	
Last Chance Mts. Dedeckera Cyn.	7/22/75 MD3909	3	30			1.08 (0.32)	9	0.81-1.65	51		0.56 (0.06)	10	101	
Last Chance Mts. Dedeckera Cyn.	9/13/78 MD4794	2	52			0.91 (0.15)	7	0.72-1.05	48		0.54 (0.11)	9	113	
Totals and S/O ratios		24 (3.1%)	347 (44.5%)	0.99	29	0.53-1.68	29	0.42-0.72	261 (33.5%)	0.55	25	147 (18.9%)	779	

^a All localities from Inyo and Mono Counties, California

^b All data from herbarium collections by Mary Dedecker

^c Pooled data for X fruit length (1.85 mm), S.D. (0.19 mm), and range (1.62-1.19) (N=12)

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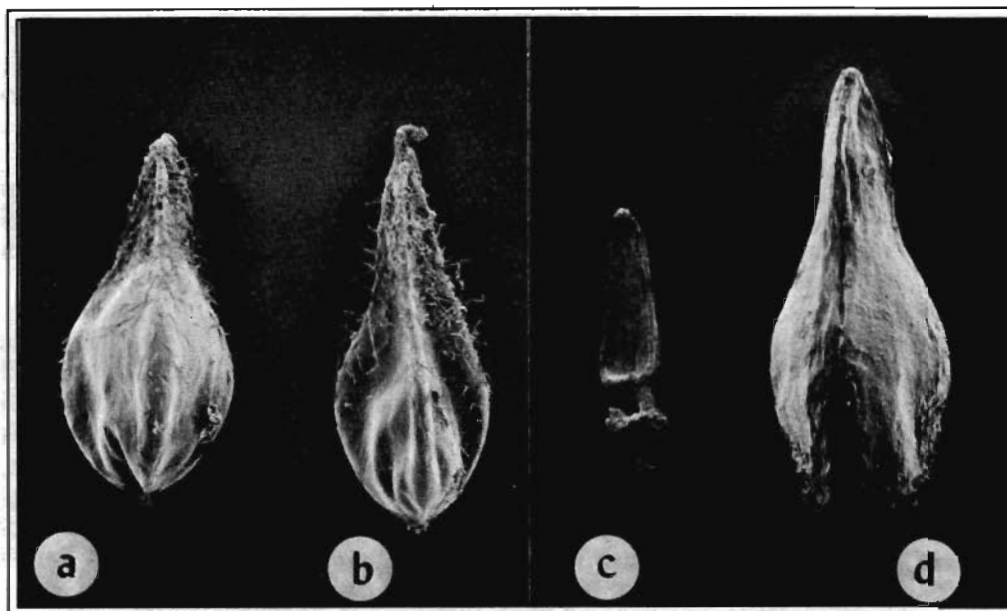


Figure 1. Fruits, seeds and aborted ovules in *Dedeckera eurekensis*. (a) Fruit with fully developed seed. (b) Fruit with aborted ovule. (c) Aborted ovule from (b). (d) Fully developed seed from (a). (a) and (b) ca. 40X; (c) and (d) ca. 60X.

and/or endosperm abortion at very early developmental stages prior to significant enlargement of the ovary. Since the anthers had apparently dehisced, they could not represent young unpollinated flowers (flowers typically close following anthesis). Seed and ovule lengths were measured under a dissecting microscope utilizing an eyepiece micrometer.

Results

The overall S/O ratio of 3.1 percent of *Dedeckera* (Table 1) is one of the lowest ever obtained in over 200 species so analyzed [Wiens, 1984; Wiens *et al.*, 1987; Wiens, unpubl. data]. The four populations surveyed showed relatively little variation in S/O ratios (0.9-4.5 percent), and the five collections (the Last Chance Mountains population was sampled twice in different years) were obtained over a period spanning 11

years. Such preliminary results indicate relatively consistent S/O ratios through both space and time and suggest a genetic explanation for the unusually low S/O ratios in *Dedeckera*; such consistency is also in accordance with previous studies of S/O ratios covering a wide range of species over a period of six years [Wiens, 1984, Wiens *et al.*, 1987]. Herbarium specimens should also represent random samples or bias in favor of higher S/O ratios, since most collectors consciously select "good" specimens.

The wide range of ovule sizes at the time of abortion (Table 1) is somewhat unusual, since most abortion generally tends to occur early in embryogenesis [Casper and Wiens, 1981; Casper, 1983; Wiens, 1984; Nakamura, 1986; Wiens *et al.*, 1987]. In this regard the high proportion of fully and partially developed

fruits with aborted ovules is especially noteworthy (Fig. 1). The relatively wide range of lengths among fully developed seeds suggests the sample might also contain a significant proportion of inviable seeds, but initial attempts to test for viability among two-year-old seeds using a 0.1 percent aqueous solution of 2,3,5 triphenol tetrazolium chloride were not successful and require further experimentation.

Discussion

The exceptionally low S/O ratios in *Dedeckera* and the South African Cape genera *Audouinia* and *Retzia* are difficult to explain. Outcrossing plants generally have S/O ratios averaging around 50 percent [Wiens, 1984]. Woody outcrossers have lower S/O ratios (38 percent) than herbaceous outcrossers (57 percent), but this figure is likely skewed low in woody plants because many species produce dry, indehiscent fruits that are generally single-seeded by fixed patterns of abortion, e.g., *Acer*, *Dalea*, *Fraxinus*, *Quercus*, etc. [Casper and Wiens, 1981, Wiens *et al.*, 1987]. Thus, S/O ratios in such woody plants mostly begin at 50 percent and proceed lower, depending on the number of ovules. Genera with such fixed rates of abortion have S/O ratios ranging from 50 to 15 percent. Some fleshy fruited groups also have fixed or consistently low S/O ratios [Wiens, 1984], e.g., all Prunoideae (50 percent) and especially *Ribes* (15-6 percent). We suspect, however, that this abortion pattern is also related to the dispersal system, which in this case involves birds. We propose that there is selection against sib competition which would result if a number of seeds were dispersed together in closed fruits.

There is no indication, however, that the high abortion rates in *Dedeckera* are in any way related to dispersal. The flower is single ovuled, a feature typical of the Polygonaceae as a whole; however, in *Dedeckera* the fruit is also invested by the pubescent perianth which possibly assists in dispersal or provides protection against desiccation, or both. The fruit of *Audouinia* is apparently indehiscent, but this would hardly explain the apparent abortion of all the ovules. Fixed abortion rates related to dispersal might, however, well play a role in the ultimate explanation of the extraordinary reproductive situation in *Audouinia*. *Retzia* has a typical capsular fruit.

We have not at this time determined the S/O ratios of other shrubby or woody species with characteristics similar to *Dedeckera* or the South African genera, nor have we systematically searched the literature for additional cases. Some examples, however, have come to light. We determined the S/O ratios of several species of rare *Astragali* from herbarium material; they are phylogenetically isolated and have restricted geographic distributions. It is not known if they reproduce vegetatively. These include: *A. cronquistii* (21.4 percent), *A. duchesnensis* (61.6 percent), *A. johannis-howellii* (28.1 percent) and *A. monoensis* (26.1 percent). These species show relatively low S/O ratios, except for *A. duchesnensis*. This species is more typical of the S/O ratios of outcrossing species of perennial herbs in general. One example from the literature indicates that *Pleuropogon oregonus*, a rare grass from Oregon (But *et al.*, 1985) has an S/O ratio of only 10.6 percent. A number of *Protea* species from the Cape region of South Africa also show unusually

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low S/O ratios, a number of which are less than 10 percent [Wiens *et al.*, 1983]. Many of these proteas are likewise narrowly restricted in distribution, are without close interspecific relatives, and do not reproduce vegetatively. These few data indicate that rare species without close relatives may generally have lower S/O ratios than more common species with closely related, extant relatives. More experimental and field data are needed, however, before firm conclusions can be drawn.

There is a consensus among most students of plant reproduction that S/O ratios are controlled by resource limitations [Lloyd, 1978] and sociobiological factors [Stephenson and Winsor, 1986]. These hypotheses were discussed in detail and rejected by Wiens *et al.* [1987] in favor of a simpler genetic load-developmental selection explanation. This conclusion was based on the fact that autogamous and outcrossing species in general exhibit S/O ratios of ca. 85 percent and ca. 50 percent, respectively. In *Epilobium* (Onagraceae) these S/O ratios were maintained among autogamous and outcrossing species throughout their geographical distributions, in different years, as well as when growing sympatrically in the same habitat with their roots intertwined. Furthermore, *Epilobium angustifolium*, a strongly outcrossing species, exhibited a consistent and successful pattern of embryo development to the late globular phase, at which time greater than 95 percent of the ovules contained developing embryos. When the major differentiation events are initiated, however, many embryos began to abort and showed numerous indications of physiological and structural abnormalities indicative of genetic vulnerability of these differentiation

events. These stages include (1) the blocking out of tissue systems, (2) the formation of lateral appendages (cotyledons and foliage leaves), (3) a change from axial to bilateral symmetry, (4) the establishment of organized shoot and root meristems, and (5) the synthesis of seed storage proteins. We also suggested that developmental selection might explain some of the embryonic deaths, which appeared to be much higher (up to 70 percent) than should be expected theoretically on the basis of the frequency of homozygous lethal allelic combinations in outcross progeny. Because embryos of outcrossing species are likely to differ genetically, inter-embryo competition might occur locally along the placenta of the developing fruits or among closely neighboring single-ovuled fruits. In effect, these two types of proposed abortion mechanisms can be referred to as relativistic (competitive) and absolutistic (genic lethals).

The role of chromosome mutations, so common in human abortions [Sankaranarayanan, 1979], and the possible accumulation of deleterious somatic mutations to a level countered by their elimination through somatic crossing over, somatic segregation and self-pruning in long-lived meristems that give rise to inflorescences [Klekowski *et al.*, 1985, 1986] need to be explored as possible causes of additional genetic deaths. Another type of genetically based reduction in PERS might occur as the result of nonfertilization of ovules even in the presence of available pollen tubes. This situation was reported in alfalfa by Cooper *et al.* [1937], where approximately half of the ovules were not fertilized although pollen tubes were in close proximity to them. Very preliminary data suggest that this might be the case in *Lupinus*

argenteus, where a large proportion of ovules fail to develop [Wiens, 1984]. We propose that resources are generally instrumental in determining plant size and total module numbers produced (including flowers), whereas the above-mentioned genetic and developmental factors are more important in determining the number of surviving fruits and embryos.

The low S/O ratio in *Dedeckera* (3.1 percent) and other species remains to be confirmed by outcrossing the flowers through hand-pollination and increasing the number of populations sampled. If these procedures do not significantly alter the S/O ratio of 3.1 percent, an explanation based on genetic considerations must be accepted as the reason for these low S/O ratios, assuming that water and mineral resources do not limit reproduction in this C_3 plants (the C_3 status of *Dedeckera* was recently determined by J. Ehleringer, pers. comm.). Our experience suggests that the preliminary data on S/O ratios reported here for *Dedeckera* are indicative of the situation in nature.

It is understandable that plants that reproduce primarily vegetatively should lose sexual reproductive efficiency. Many such instances are known among cultivated plants selected for their vegetative structures [Zohary, 1984] and various grasses that reproduce extensively by rhizomes, e.g., various Eragrostideae [Bhanwra, 1986] and *Phragmites* [Tsvelev, 1984]. Sexual reproduction is a complex function; and, if selection does not continuously maintain the process, it could easily degenerate by virtue of the accumulation of deleterious genetic combinations and mutations. However, why should sexual capability be virtually lost in the absence of vegetative

reproduction? This is the fundamental problem posed by the data. Such a situation is "evolutionary suicide," and genera such as *Dedeckera* are in effect "living dead." Most studies of reproductive loss have centered around the idea of inbreeding depression resulting from the loss of genetic variability in small populations. This is clearly a problem, particularly in captive animal populations (see Schoenwald-Cox *et al.* [1983] for examples and references). Two species of pine are known to be largely homozygous genetically [Ledig and Conkle, 1983; Fowler and Morris, 1977], but reproductive data are not available. We suspect, however, that this is not necessarily the case in genera such as *Dedeckera* and tentatively suggest another possible explanation.

One evolutionary scenario that might explain such a situation is based on a study of *Liatris* (Asteraceae) by Schaal and Levins [1976]. They demonstrated the presence of age classes in this genus and reported that the oldest class was also the most heterozygous, as determined by electrophoretic analysis. Heterozygosity should therefore increase vegetative fitness; since older individuals are larger, they should also leave more progeny, and selection should continue to favor both increased vigor and longevity. Schaal and Levins [1976] also cite a number of studies indicating selection for heterozygosity, particularly in extreme habitats. Others have also suggested that longevity and various other life-history parameters are associated with increased genetic heterozygosity [Guries and Ledig, 1977; Mitton *et al.*, 1981; Epperson and Allard, 1984].

In relictual populations occurring in extreme habitats, the vigor

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associated with heterozygosity could be expected to enhance the survival of increasingly heterozygous individuals as the population declines. The increase in average vegetative vigor of the survivors should also correlate with longevity and flowering propensity, even though the latter might result in only febrile reproductive success. Indeed, a considerable sample bias should exist in the observability of the various modes of extinction displayed by plant species that favors the discovery of long-lived, vegetatively vigorous relicts with severely compromised sexual reproductive capacity.

If subvital alleles contribute significantly to heterotic vigor, then one would expect a very large proportion of genetically defective zygotes, since chance homozygosis for subvital alleles should arise in crossings among the hyper-heterozygous individuals comprising these relictual populations. In addition to the segregational burden, there could be the added problem of recessive lethal alleles, as well as balanced structural chromosomal rearrangements accumulated during the lifetime of an individual.

If the accumulation of recessive deleterious somatic mutations [Klekowski *et al.*, 1985, 1986] are of significance, they might be correlatable with isozyme divergence between branch systems that have been isolated for very long periods of time. The accumulation of recessive lethals in such long-lived meristems could further compromise sexual reproductive success.

In addition to these purely genetic considerations, it is possible that in the context of infrequent sexual reproduction, natural selection might

favor increasing vegetative vigor and longevity at the expense of post zygotic embryonic development--or at least in benign neglect of it! In fact, the long-term persistence of these reproductively compromised genera might be favored by very infrequent capacity for seedling establishment. The prolific flowering of *Dedeckera* (also *Audouinia*), however, would appear to negate the possibility of a trade-off between increased vegetative growth at the expense of reduced sexual reproductive capacity, as occurs in the grasses previously mentioned as well as some other groups. Flowering is likely coupled to vegetative vigor in *Dedeckera* and might compensate to some extent for the exceptionally low S/O ratio. In absolute terms, therefore, sufficient seeds might be produced that would permit the establishment of a rare seedling under favorable circumstances.

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