Reprinted from Nature, Vol. 338, No. 6210, pp. 65-67, 2nd March, 1989

Developmental failure and loss of reproductive capacity in the rare palaeoendemic shrub *Dedeckera eurekensis*

Delbert Wiens*, Daniel L. Nickrent†, Cedric I. Davern*‡, Clyde L. Calvin§ & Nancy J. Vivrette‖

* Department of Biology, University of Utah, Salt Lake City, Utah 84112, USA
† Department of Plant Biology, University of Illinois, Urbana, Illinois 61801, USA
§ Department of Biology, Portland State University, Portland, Oregon 97207, USA
‖Ransom Seed Laboratory, PO Box 300, Carpinteria, California 93013, USA

EVOLUTIONARILY successful outcrossing plants have spontaneous seed sets that are, on average, around 50% (±20%), but those of woody species are lower (33%) and herbaceous perennials higher (57%); self-pollinating (autogamous) species average about 85%[1–3]. *Dedeckera*, an outcrossing (protandrous) evolutionary relict from the Mojave desert of California has a seed set of only 2.5% and no means of vegetative reproduction. We show here that the most probable explanation for this exceptional result is that there are genetically mediated embryonic abnormalities. The percentage of fully viable seeds is further reduced by low viability, germinability, and post-germination developmental failure. Genetic studies involving extinction have emphasized inbreeding depression and homozygosity[4–8], but *Dedeckera* is highly heterozygous (27%). Outcrossing does not significantly increase seed set over selfing, suggesting that a high segregational genetic load is primarily responsible for the low seed set in *Dedeckera*. Such loss of reproductive capacity could explain the relictual nature of *Dedeckera* and might ultimately result in its extinction.

A histological analysis of post-fertilization development of 27 ovules of *Dedeckera* showed a pattern of genetically controlled embryo abortion similar to that reported in *Epilobium*[3] (Onagraceae), and *Arabidopsis*[9,10] (Brassicaceae), and in species hybrids[11]. Three ovules showed no evidence of fertilization.

Spontaneous seed germination in seven trials was only 3.5% ($N = 460$ filled seeds). Sixty days of stratification had no effect, but scarification and gibberellic acid treatment increased germination to 33%. Only 11.1% of spontaneously germinating seeds developed normally, but the sample size was small ($N = 9$). Thus the percentage of fully viable seeds in *Dedeckera* is probably less than 0.5%. *Dedeckera* may produce about 64,500 flowers and ovules (ovaries are uniovulate). Given seedling survivorship values for desert perennials[12,13] of 10^{-4} to 10^{-5}, the loss of reproductive capacity in *Dedeckera* may be critical for its continued survival.

Neither prezygotic genetic self-incompatibility nor inadequate pollination explain the exceptionally low fecundity of *Dedeckera* because about 90% of the ovaries initiate growth, which is taken as *prima facie* evidence for fertilization (Table 1). The consistency of the data, both between populations and in different years, indicates that resources do not limit seed set (Table 1), and also argues against gametic imbalance and hybrid dysgenesis as explanations for low seed set. *Dedeckera* is not a chromosome translocation heterozygote (n is about 12 bivalents). Herbivory was uncommon and there was no overt evidence of pathogen activity.

Intraplant self-pollination (geitonogamy) may be common in *Dedeckera*[14], but inbreeding depression resulting from selfing in a normally outcrossed population (segregational genetic load) is not a major factor contributing to the low seed set (Table 2). The seed set for controlled self-pollinations (6.3%) and cross-pollinations (11.4%) do not differ significantly (d.f. = 1, $\chi^2 = 2.95$, $P > 0.05$) and all population sizes exceed 150 (Table 2).

Allozyme analyses were completed from each of the six populations studied (Table 1) to determine the amount of genetic polymorphism and heterozygosity. F-statistics[15] were used to examine apportionment of variation within and between populations. Mean values, summed for all populations, are $F_{IS} = 0.192$, $F_{IT} = 0.299$ and $F_{ST} = 0.133$, which indicate that there is a limited degree of interpopulational differentiation with most variance

‡ Deceased.

TABLE 1 Seed sets in *Dedeckera eurekensis*

Population*	Collection year	% Developed (filled)	%Developed (aborted)	% Partially developed	% Non-developed	n (ovaries)	n (plants)
Bishop†	1988	1.6	6.5	39.9	52.0	1,624	10
	1987	0.6	20.2	72.5	5.8	1,046	10
	1984	4.6	50.1	24.5	20.8	351	1
Coldwater Cyn‡	1988	4.7	25.8	67.4	2.0	2,875	10
	1987	4.2	48.7	44.3	2.8	1,112	10
	1985	1.9	33.3	44.8	20.0	105	1
Gunter Cyn§	1988	0.8	41.3	32.9	25.0	1,482	10
	1987	1.9	54.1	36.2	7.8	1,238	10
Dedeckera Cyn	1988 (upper)‖	4.0	29.0	65.1	1.7	1,682	10
	1987	1.7	67.3	28.5	2.4	1,230	10
	1988 (lower)¶	4.3	44.3	49.6	1.8	1,464	10
	1987	2.9	61.3	33.2	2.6	1,265	11
	1978	1.7	46.0	42.5	9.7	113	1
	1975	2.9	29.7	50.5	16.8	101	1
Last Chance Mts#	1987	1.9	70.4	26.7	1.0	1,184	10
Panamint Mts**	1980	0.9	49.5	26.6	22.9	109	1
Means or totals (overall)		2.5	42.3	42.8	12.2	16,981	116
Means or totals	1988	3.1	29.4	51.0	16.5	9,127	50
Means or totals	1987	2.2	54.6	39.5	3.7	7,075	61
Means or totals	1975–85	2.4	44.5	33.5	18.9	779	5

The structures scored are anatomically indehiscent, single-seeded, post-anthesis ovaries or maturing fruits (achenes), although functionally they behave essentially as seeds. Developed (aborted) fruits reach approximately full length, but the ovary wall is partially collapsed between the ribs and the ovule has atrophied. Partially developed fruits did not reach full size, but all initiated ovary expansion before ovule abortion, which is taken as *prima facie* evidence for fertilization. Non-developed ovaries showed no evidence of expansion. They were probably not pollinated, or the ovules were unfertilized, or abortion occurred at the earliest stages of embryogenesis or endosperm development.

* All locations on Universal Transverse Mercator grid ticks, zone 11; Cyn, Canyon; Mts, mountains. † 385500E-4136800N; ‡ 384000E-4149000N; § 388100E-4146200N; ‖443700E-4101900N; ¶ 443600E-4101300N; # 442000E-4094800N; ** 434400E-4083100N.

TABLE 2 Controlled pollinations in *Dedeckera eurekensis*

Pollination treatment	Per cent seed types recovered					
	Developed (filled)	Developed (aborted)	Partially developed	Non-developed	*N* 1-ovuled (ovaries)	*N* (plants)
Intrapopulation crosses	11.4	21.1	66.7	0.88	228	10
Self-pollinations (geitonogamous)	6.3	7.9	85.7	0	63	4
Interpopulation crosses (× Gunter Cyn.)	12.9	37.1	48.4	1.6	62	2
Spontaneous seed set in parental plants	4.7	25.8	67.4	2.0	2,875	10
Flowers isolated in nylon exclosures	3.9	26.0	65.5	4.6	281	3

Coldwater Canyon population, 2–29 July 1988 (see Table 1 legend for locality and explanation of fruit types). Control flowers were taken from unmanipulated portions of experimental plants and left open so that pollination was spontaneous. Isolated flowers were those simply left under nylon exclosures (after removing all open or fruiting flowers), thus excluding all insect pollen vectors. All open or fruiting flowers were removed from the experimental inflorescences after which they were enclosed with removable fine-mesh nylon covers mounted over a wire frame to prevent contact of the nylon with the flowers. Flowers were emasculated daily before anthesis. All three stigmas were pollinated by contacting their sticky surfaces with a dehiscing anther after the styles had diverged and the stigmas became receptive. The small flowers (2–3 mm) required that all floral manipulations be effected under a dissecting microscope mounted on a camera tripod. The nylon covers were removed after the completion of all pollinations.

residing within populations.

Polymorphism over 17 loci and six populations is 56.8%. Heterozygosity averaged over the subset of the 12 polymorphic loci is 26.9% (Table 3). Heterozygotes range from 11.9% for MDR-1 to 58.3% for GPI-2. These heterozygosity averages are underestimated because they include the zero values for those markers that are not polymorphic in the particular population sampled. This amount of variation is much higher than that reported for other species of desert shrubs[16], but is similar to other woody, outcrossing perennials[17–18].

Dedeckera is vegetatively vigorous and flowers profusely. Its longevity (at least 140 years and probably much more) may be correlated with heterozygosity as reported in *Liatris*[19] (Asteraceae). In *Dedeckera*, vegetative fitness may be largely dependent upon rare, highly heterotic (or possibly epistatic) genotypes. The uniquely heterozygous genotypes that do survive may, however, have low reproductive potential because of the excessively high segregational genetic load. Reproduction could be further compromised by the accumulation of recessive lethals in long-lived meristems[20] and chromosomal mutations[21].

The persistence of palaeoendemics may depend on rare multiple-locus heterotic genotypes that could arise as a result of tracking some protracted secular environmental change, for example, increasing aridity. The pace and extent of such change could easily exhaust the species' additive genetic variance relevant to adapting to that change. Heterosis may be the only survival strategy available to such species, in spite of the negative reproductive consequences. Thus the 13% increase in mean heterozygosity for the populations of *Dedeckera* in the Last Chance Mountains, as opposed to those in the White Mountains (Table 3), may be important because the former localities are both hotter and drier. In fact, many palaeoendemics may be ecologically 'out of place', in that they may not possess many of the adaptations typical of plants occupying that habitat—thus *Dedeckera* flowers in mid-summer when desert perennials are typically dormant.

Rabbits[22] and humans[23] have genetically mediated spontaneous embryo abortion rates of about 50% and 70%, respectively. The loss of reproductive capacity stemming from early embryonic genetic load should not be overlooked as a possible element in the decline of higher animal palaeoendemics. Such cases may be observed rarely because higher animals generally have much shorter life-spans, relatively limited reproductive potentials, and because early abortion is more difficult to detect than in plants.

Other palaeoendemic plants in North America, Africa and Australia also seem to have exceedingly low seed sets. Reproductive capacity should be given careful consideration in management decisions regarding rare and/or endangered species. □

Received 8 November 1988; accepted 16 January 1989.

1. Wiens, D. *Oecologia* **64**, 47–53 (1984).
2. Harper, J. L. & Wallace, H. L. *Oecologia* **74**, 31–38 (1987).
3. Wiens, D., Calvin, C., Wilson, C. A., Frank, D. & Seavey, S. *Oecologia* **71**, 501–509 (1987).

TABLE 3 Genetic variability at 12 loci

	Mean sample size per locus	Mean no. of alleles per locus	% Loci polymorphic	Mean heterozygosity
White Mountains populations				
Bishop	15.8	1.9	66.7	0.211
Coldwater Cyn	18.8	2.6	75.0	0.218
Gunter Cyn	16.3	2.3	75.0	0.194
Means	17.0	2.3	72.2	0.207
Last Chance Mountains populations				
Dedeckera Cyn (upper)	14.8	2.7	91.7	0.384
Dedeckera Cyn (lower)	16.7	3.3	91.7	0.293
Last Chance Mts	13.3	2.7	83.3	0.318
Means	14.9	2.9	88.9	0.332

Values in this table are derived from analysis of 12 loci—EST-2 (esterase), GSR-2 (glutathione reductase), IDH-2 (isocitrate dehydrogenase), MDH-1, MDH-2, MDH-4 (malate dehydrogenase), MDR-1 (menadione reductase), GPI-2 (glucose phosphate isomerase), PGM-1, PGM-2, PGM-3 (phosphoglucomutase) and SKDH (shikimate dehydrogenase)—that were polymorphic in at least one of the six populations. When five additional loci ADK-1 (adenylate kinase), GPI-1, GSR-1, LAP (leucine amino peptidase), and MDH-3], monomorphic for all populations, are included, the mean polymorphism is 56.8%. A locus was considered polymorphic if any allelic variant was detected. Mean proportion of heterozygotes (direct count) is less than the expected Hardy–Weinberg (unbiased estimate)[24]. The fixation index F[25] showed that only two loci (PGM-1 in the Gunter Cyn population and SKDH in the population of the Last Chance Mountains) had significant ($P < 0.001$) deviations in genotype proportions.

4. Bonnell, M. L. & Selander, R. K. *Science* **184**, 908–909 (1974).
5. O'Brien, S. J. *et al. Science* **227**, 1428–1434 (1985).
6. Wildt, D. E. *et al. Nature* **329**, 328–331 (1987).
7. Ledig, F. T. & Conkle, M. T. *Evolution* **37**, 79–85 (1983).
8. Waller, D., O'Malley, D., & Gawler, S. *Cons. Biol.* **1**, 335–340 (1987).
9. Meinke, D. W. & Sussex, I. M. *Devl Biol.* **72**, 50–61 (1979).
10. Marsden, M. P. F. & Meinke, D. W. *Am. J. Bot.* **72**, 1801–1812 (1985).
11. Raghaven, V. *Embryogenesis in Angiosperms* (Cambridge University Press, New York, 1986).
12. Steenbergh, W. F. & Lowe, C. H. *Ecology* **50**, 825–834 (1969).
13. Turner, R. M., Alcorn, S. M. & Olin, G. *Ecology* **50**, 835–844 (1969).
14. Wiens, D., DeDecker, M. & Wiens, C. D. *Madroño* **33**, 302–305 (1986).
15. Nei, M. *Ann. hum. Genet.* **41**, 225–233 (1977).
16. Hamrick, J. L., Mitton, J. B. & Linhart, Y. B. *Proc. Symp. Isozymes of North American Forest Tress and Forest Insects* (ed. Conkle, M. T.) 35–41 (USDA, Forest Service Gen. Tech. Rep. PSW-48, 1981).
17. Ledig, F. T. *Cons. Biol.* (ed. Soulé, M. E.) 77–104 (Sinauer, Sunderland, Massachusetts, 1986).
18. Gottlieb, L. D. *Progress in Phytochemistry* (eds Rheinhold, L., Harborne, J. B. & Swain, T.) 1–40 (Pergamon, New York, 1981).
19. Schaal, B. & Levin, D. A. *Am. Nat.* **110**, 191–206 (1977).
20. Klekowski, E. Jr, Mohr, H. & Kazarinova-Fukshansky, N. *Genetics, Development, and Evolution* (eds Gustafson, J. P., Stebbins, G. L. & Ayala, F. J.) 79–113 (Plenum, New York, 1986).
21. Sankaranarayanan, K. *Mutat. Res.* **61**, 1–26 (1979).
22. Brambell, F. W. R. *Biol. Rev.* **23**, 370–407 (1948).
23. Biggers, J. D. *New Engl. J. Med.* **304**, 336–342 (1981).
24. Nei, M. *Genetics* **89**, 583–590 (1978).
25. Wright, S. *Evolution and Genetics of Populations* (University of Chicago Press, 1978).

ACKNOWLEDGEMENTS. We thank J. Chesnut, J. Neuhauser, M. Kobler, S. Wroe, W. Owen, O. Pollak, C. Scheidlinger, S. Hodges and M. Weiss for field and laboratory assistance, and the staff of the White Mountain Research Station, Bishop, California, for laboratory facilities. J. Ehleringer, T. Hazelrigg, D. Mansfield, K. Paige, P. Raven, R. K. Vickery Jr, E. O. Wilson, and especially J. Endler, have read and commented on the manuscript. M. DeDecker, J. Dickinson and W. Wiens offered various suggestions. J. Rourke first mentioned the existence of plants with exceptionally low sexual reproductive capacity in Africa. The study was supported by grants from the NSF, the USDA (Forest Service, Rocky Mountain Forest and Range Experiment Station) and the University of Utah, College of Science.

Printed in Great Britain by Turnergraphic Limited, Basingstoke, Hampshire