During such bloom periods, the seawater-to-atmosphere flux we quantify in this model will enhance the already large pCO_2 gradients that exist. Furthermore, because the O_2 used in bird and mammal respiration is derived from the atmosphere rather than from the ocean, the anticipated Redfield O_2:CO_2 relations (*28*) will also be affected. This phenomenon may be a characteristic feature of especially productive Antarctic marine ecosystems caused by seasonally intensive feeding and respiration of highly concentrated birds and mammals. We conclude that the CO_2 respired by birds and mammals may represent a significant inefficiency in the ability of the Southern Ocean to act as a carbon sink. We suggest that similar determinations be made for birds and mammals in other oceans to assess their global role in the biological carbon pump.

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Evolution of Pollen Morphology

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Over evolutionary time, the morphology of angiosperm pollen has evolved toward an increasing number of apertures, among other things. From a neo-Darwinian point of view, this means that (i) some polymorphism for aperture number must exist and (ii) there must be some fitness increase associated with increasing the aperture number. Pollen types with different aperture numbers often occur in the same species. Such is the case in *Viola diversifolia*. Comparison of pollen with three and four apertures in this species showed that four-apertured grains germinated faster than three-apertured ones but that the four-apertured ones experienced other disadvantages. These results obtained on the gametophyte can be interpreted in terms of strategies of the sporophyte.

THE REDUCTION OF THE HAPLOID phase is one of the most striking characteristics of the evolution of animals and plants. Unlike animals, plants still produce multicellular haploid life stages, the gametophytes. In higher plants, the male gametophyte is the pollen grain. The evolution of pollen has been studied both from a morphological and a physiological point of view. The morphological analyses have been mainly (if not exclusively) devoted to systematics and used in stratigraphic applications. (The exine of pollen is extraordinarily resistant and can easily be extracted from sediments.) This approach relied on the implicit assumption that pollen morphology is constant within a species or a group of species. The view of pollen morphology has thus been very typological. More consideration must be given to the importance of pollen variation within species. Three main features of pollen evolution have been described; only the first two have been studied.

First, there has been an increase through evolutionary time in the speed of pollen tube growth (*1, 2*). For example, from gymnosperms to angiosperms the rate of pollen tube growth has increased by a factor of 2000 (from 10 to 20,000 μm/hour) (*3*). These increases in germination and growth rates of pollen tubes have been interpreted as adaptative responses to enhance pollen competitive ability in the style (*4*). Such competition can play a very important role in the structure and quality of the next sporophytic generation (*5–7*): pollen grains that have fast growing pollen tubes will be the first to fertilize and thus will transmit more of their genes to the next generation than will slower growing types.

Second, there has been a decrease through evolutionary time in the life expectancy of pollen grains: generally, "primitive" pollen grains are long-lived, whereas "highly

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Table 1. Number of three- and four-apertured pollen grains in white (A_1), intermediate (A_2), and violet (A_3) flowers from population A, and populations B, C, and D. From two to six flowers were sampled per plant, all five anthers were sampled per flower. The proportions of three- and four-apertured grains are different among the three colors of population A ($\chi^2 = 26.37$; $P < 0.001$; df = 2).

Population	Plants (n)	Pollen grains/aperture (n)		Three-apertured grains (%)	χ^2	P
		3	4			
A_1	8	3094	6582	32.0	6.37	>0.50
A_2	6	2197	5514	28.5	1.84	>0.75
A_3	4	562	1554	26.6	5.44	>0.10
B	6	1145	2317	33.0	3.22	>0.50
C	6	1348	2415	35.8	9.43	>0.05
D	3	1460	2476	37.1	2.39	>0.25

evolved" grains die within a few hours of release into the atmosphere (*1, 3, 8–10*). So-called advanced species release pollen grains that are able to germinate immediately when put on a style; unlike those of "primitive" species, they show no dormancy. Furthermore, the increasing efficiency of pollination in animal-pollinated species has made the selection of short-lived but quickly germinating pollen grains possible (*11*).

Finally, the fossil record strongly suggests that evolution has resulted in an increase in aperture number (*12, 13*). Because the aperture is the place where pollen tubes are initiated as well as the place where pollen and stigma interact, it seems logical to hypothesize that this increase in aperture number has led to a higher probability of germinating quickly. Until now, this hypothesis has been unexplored.

We tested the relation between pollen aperture and components of fitness such as germination and survival. To our knowledge, the fitness of pollen grains with different aperture numbers but with identical or at least similar genetic background have not been described.

Homogeneity of the genetic background is important in such studies as it has been shown (*5*) that the genotype of the pollen grain can influence its ability to fertilize. Therefore, the best way to compare the fitness of pollen grains with different aperture numbers is to use pollen grains obtained from the same or closely related individuals. Variability of pollen morphs within one species is a fairly common phenomenon in angiosperms. About one out of three families has genera or species that exhibit variation in aperture number (*14*). It is known that pollen morphology is determined by the sporophyte and not by the gametophyte (*15*). Therefore, the term "pollen polymorphism" is misleading for the geneticist because differences in pollen morphology are not caused by differences in pollen genotype. Of course, there must be genetic variation underlying a sporophyte's different proportions of pollen morphs (*16*). So-called pollen polymorphism thus raises specific questions: why should a plant produce different kinds of pollen, and why should pollen grains be different?

In *Viola diversifolia* (Violaceae), an en-

Table 2. Total numbers of three- and four-apertured germinated pollen grains (G), three- and four-apertured nongerminated pollen grains (NG), and the percentages of three- and four-apertured germinated pollen grains. Each sample subject to germination tests was also sampled for the frequency of three- and four-apertured grains. The "3(%)" is the global percentage of three-apertured pollen grains in each one of the 22 independent experiments; 325 germinated grains were counted after 1 hour on the germinating medium, 757 after 2 hours, 717 after 3 hours, and 692 after 4 hours. Overall χ^2 after 1 hour of germination: 45.63; 3 df; $P < 0.001$; after 2 hours: 14.57; 6 df; $P < 0.25$; after 3 hours: 11.64; 5 df; $P < 0.05$; and after 4 hours: 4.45; 4 df; $P > 0.25$.

Population	Plants (n)	Apertures	Germination at 1 hour			2 hours			3 hours			4 hours		
			G	NG	G (%)	G	NG	G (%)	G	NG	G (%)	G	NG	G (%)
A_1	9	3	27	625	4	103	500	17	81	321	20	84	385	18
		4	146	1047	12	284	1103	21	207	753	21	163	782	18
		3(%)			35.3			30.3			29.5			33.2
					(32.3†)			(2.4)			(0.3)			(0.1)
A_2	7	3	19	405	4	45	356	11	55	351	14	65	410	14
		4	110	1103	9	114	924	11	178	976	15	164	803	17
		3(%)			25.9			27.9			26.0			32.9
					(7.9‡)			(0.03)			(0.8)			(1.9)
A_3	2	3		61		9	44	17	3	39	8	3	24	13
		4	4	113	4	23	99	39	7	101	7	9	81	11
		3(%)			35.1			47.7			27.9			22.9
								(0.1)						
B	2	3				20	53	27	12	79	13		28	
		4				29	58	33	26	73	26	3	50	6
		3(%)					45.6				47.9		35.9	
							(0.3)				(3.8)			
C	4	3				12	118	9	10	103	9	23	82	22
		4				41	195	17	33	166	17	54	153	26
		3(%)						35.5			36.2			33.7
								(4.1‡)			(3.6)			(0.5)
D	5	3	7	226	3	18	198	8	39	214	15	49	277	15
		4	12	407	3	59	368	14	66	388	15	78	504	13
		3(%)			35.7			33.6			35.8			35.9
					(0)			(3.7)			(0.04)			(0.3)

*Numbers in parentheses represent χ^2 values. †$P < 0.001$. ‡$P < 0.05$.

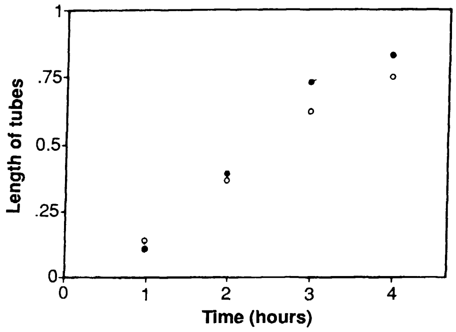

Fig. 1. Mean pollen tube length (in millimeters) of three- (●) and four- (○) apertured grains (average overall populations) after different germination times. The number of plants and germinated pollen grains studied are the same as in Table 2. The standard errors of the means for each of the points are too small to be drawn (values between 1.58×10^{-3} mm and 0.18×10^{-3} mm). The slope (growth rate) is significantly greater in three-apertured pollen grains than in four-apertured ones ($F = 6.76$; $P < 0.001$; df = 1).

demic of schisteous screes of the Alpine vegetation zone of the Pyrenees (Europe), all individuals produce pollen with three to six apertures (*17*). Four populations (A, B, C, and D) (*18*) were sampled. All flowers from given individuals and all individuals within populations B, C, and D produced similar proportions of three- and four-apertured pollen (about one-third three-apertured to two-thirds four-apertured grains, with five- and six-apertured grains being relatively rare). In population A, however, there is a flower color polymorphism and the proportions of three- and four-apertured pollen differ significantly between the different flower colors (Table 1). There is statistically significant variation in pollen aperture number among populations (*19*). This species therefore provides a system for comparing the fitness of pollen with different aperture numbers.

Pollen was germinated on an artificial medium (*9*) with a series of four preparations made for each experiment. Germination was stopped and pollen tubes were stained [with Alexander's stain (*20*)] after 1 hour for the first preparation, 2 for the second, 3 for the third, and 4 for the fourth. Tube length and aperture number were then measured.

Our results (Fig. 1 and Table 2) showed that four-apertured pollen grains germinated faster than three-apertured ones, and in vivo experiments of pollen germination on stigmas gave similar results (*21*). These data were collected on pooled pollen within the different populations but the same results were obtained for individual plants. This would indicate a selective advantage for four-apertured grains if the pollen grains that are the first to germinate were more likely to fertilize, as would be the case if all other things were equal. Two-way analyses of variance were performed to compare the length of tubes from three- and four-apertured pollen and from the different populations for each hour class. These results show that the tubes of four-apertured pollen grow significantly slower than those of three-apertured pollen (Fig. 2). Thus, even if four-apertured pollen grains germinate earlier, they may very well "lose the race." Furthermore, an important side effect of germinating quickly is that the longevity of many-apertured pollen grains is less than in grains with few apertures. When pollen grains were separated for increasing amounts of time from the mother plant, the proportion of three-apertured germinated pollen increased steadily, indicating that three-apertured grains have a greater longevity than four-apertured ones.

We have demonstrated three factors as relevant to pollen fitness: speed of germination, tube growth rate, and survival. The last two may be the consequences of a common cause, as shown below, pollen deteriorates faster when it has more apertures, and this is likely to result in reduced tube growth. Four-apertured pollen grains are better at germination and three-apertured pollen have better tube growth and better survival. A problem of evolutionary interest is to know whether these factors can lead to a "polymorphism" in pollen grain morphology. A preliminary game theory model has been developed and shows that when germination is traded off with tube growth, no mixed strategy is maintained, whereas when germination is traded off with survival, mixed strategies are often stable (*22*).

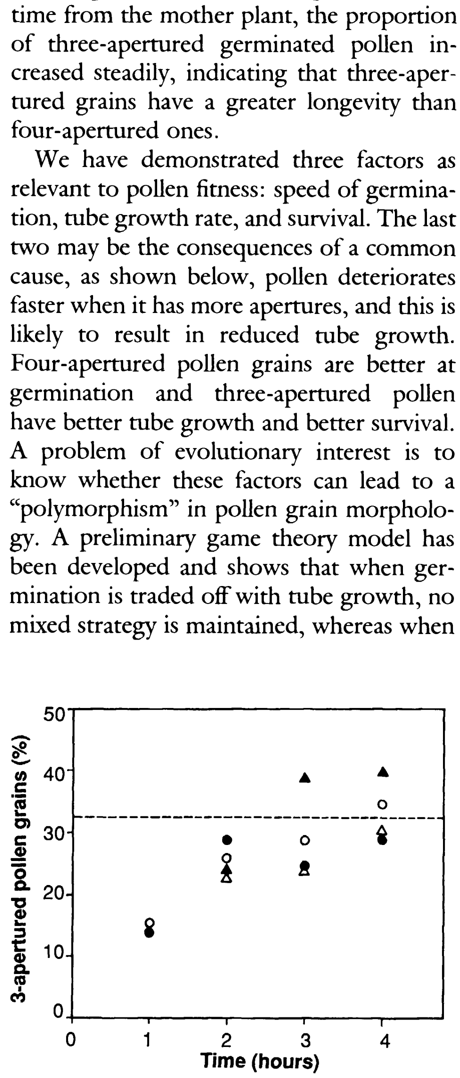

Fig. 2. Observed frequencies of three-apertured germinated pollen grains at each sampling time, for flower colors A_1 (○) (white flowers) and A_2 (●) (intermediate), and populations C (△) and D (▲). The other populations (A_3 and B) are not represented because of their small sample size. The dotted line represents the mean percentage of three-apertured pollen grains in the anthers. After 1 hour on the germination medium, the percentage of three-apertured germinated grains for population D was not taken into account because only 19 grains germinated. No pollen grains germinated after 1 hour on the medium in population C.

As in the hare and tortoise, running fast (that is, germinating quickly) can be less reliable than walking (that is, germinating slowly). In this regard, four-apertured grains play "hare." If they are in good condition (removed rapidly from the anthers), they win. But if pollinators take some time to collect them, they become less reliable than three-apertured "tortoise" strategists.

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