gadro's number. Hence D_{Hb}, and the augmentation of O_2 transport, decreases with increasing solvent viscosity.

An interesting possibility arising from the theory described here is in the determination of the oxygen-hemoglobin dissociation curve from diffusion experiments. Thus, from Eq. 1

$$S'(p_{O_2}) = \frac{(\dot{N}_{O_2})\ \max - \dot{N}_{O_2}(p_{O_2})}{(\dot{N}_{O_2})\ \max - (\dot{N}_{O_2})\ \min}$$

where the difference in p_{O_2} is always constant, but p_{O_2} on the high-pressure side is always great enough for $S' = 1$ to be assumed, and p_{O_2} in the equation is on the low-pressure side. Such experiments could be performed with a fixed CO_2 partial pressure on both sides of the membrane. This shows that measurements of $\dot{N}_{O_2}$, and p_{O_2} on the low-pressure side, can be used to determine the dissociation curve.

While the theory described has accounted for all features of enhanced transport of gases O_2, CO_2, or CO which associate with hemoglobin, it in itself does not indicate the role of this mechanism within living organisms. Since the dissociation curves for O_2 and CO_2 are similar in form, it is evident that the mechanism is the same for both of these gases within the living organism. In particular transport of gases within the red blood cell should be described by this theory.

A result of the theory described here is that the effective diffusion coefficient for O_2 in a hemoglobin solution is:

$$D_{O_2} = D_{O_2} + nXD_{Hb}\frac{dS'}{dC_{O_2}}$$

where C_{O_2} is O_2 concentration in the solvent. It is evident that in regions of low concentration of the gas in question the transport of the gas is much greater for a given gradient of concentration than in a region of high concentration. This follows since dS'/dC_{O_2} decreases rapidly with increasing C_{O_2} Thus an important role of this mechanism in living organisms could be to maintain O_2 and CO_2 transport even with lowered gradients of gas concentration. Thus oxygenation of hemoglobin in red blood cells should be more rapid at low oxygen partial pressures in blood plasma. It could also mediate an equitable distribution of gases to tissues, that is, as the concentration of O_2 falls in a given region of tissue the transport of O_2 to that region is spontaneously increased by this mechanism.

In conclusion it should be noted that the theory described here must be modified to include the reaction rate of gas with hemoglobin if the gas concentration in the solution changes rapidly with time.

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References

1. P. F. Scholander, *Science* **131**, 585 (1960).
2. E. Hemmingsen and P. F. Scholander, *Science* **132**, 1379 (1960).
3. R. E. Collins, "Transport of gases through hemoglobin solutions," *Bull. Math. Biophys.*, in press.

27 February 1961

Pollination of Saguaro Cactus by Doves, Nectar-Feeding Bats, and Honey Bees

Abstract. In a large cage, free-flying western white-winged doves, nectar-feeding *Leptonycteris* bats, and honey bees were each effective as cross-pollinators of self-sterile saguaro flowers. Seed production and seed viability were not significantly different in fruit from flowers pollinated by these agents. Pollination is not a limiting factor in saguaro repopulation.

Since the turn of the century the saguaro, or giant cactus [*Carnegiea gigantea* (Engelm.) Britt. & Rose], has failed to repopulate itself in certain areas within the range of its habitat in Arizona (*1*). This report concerns the effect of pollination and of certain pollinating agents on the production of viable seed needed for plant establishment.

The saguaro flower begins to open shortly after nightfall and is usually in full bloom by midnight, when both pollen and nectar are available. The flower usually closes by late afternoon of the same day. Previous work (*2*) showed that the flower may be pollinated both at night and in the daytime and that it is self-sterile and is not wind-pollinated. These findings led to the question: What agents are responsible for pollen transfer?

Preliminary observations indicated that severed saguaro branches (arms), 2 to 5 feet long, would bud, flower, and set fruit satisfactorily. In our experiment 45 arms, removed mainly from windfall plants just before flowering, were placed upright in a 12-mesh plastic-screen cage, 12 by 24 by 9 feet high, located in a cactus forest (*3*).

The prevalence of the day-flying western white-winged doves [*Zenaida asiatica mearnsi* (Ridgway)] during the period of saguaro flowering, and the presence of pollen on their heads, led us to include them as test agents. Six birds of unknown sex were released into the cage (*3*). They soon accepted confinement and were not injured the few times they collided with the plastic screen. These doves fed at will on the nectar in the flowers and on available rolled oats and water.

Saguaro pollen has been found in the stomach and fecal material of nectar-feeding bats (*Leptonycteris nivalis* Saussure) (*4*). This finding, and our observations that pollination may occur at night, suggested that we try these bats. Nine females, three of which were gravid and four with living young, were collected in nearby Colossal Cave (*3*). They were kept in a 12 by 24 by 24 in. screen-bottomed box. Screen was also provided in the ceiling of the container for them to cling to. Because of their sensitivity to excessive temperatures, the bats were kept in an air-conditioned building during the daytime. At nightfall the box with bats was suspended in the cage and gently opened. However, the bats did not break their cluster for an hour or more; they always returned to the box voluntarily before dawn.

Flowering stalks of the century plant (*Agave schottii* Engelm.) were placed in the cage as an attractant for the bats in the early evening before the saguaro

Table 1. Saguaro fruit set, seed production, and seed viability as related to mode of pollination, Tucson, Arizona, 1960.

Mode of pollination	Flowers exposed			Seeds*	
	Dates (inclusive)	No.	Set (%)	Per fruit† (No.)	Germination‡ (%)
Doves	9–18 May	338	44.7§	2634	83.5
Bats	24–26 May	86	61.6§	1887	80.2
Honey bees	27 Apr.- 8 May	193	51.8§	1751	90.4
Natural, field-pollinated	8–16 May	132	53.8	2721	83.4
Hand cross-pollinated	26 Apr.– 23 May	79	70.9§	2439	91.9
Self-pollinated	26 Apr.– 20 June	124	0	—	—

* Data not significantly different at 5-percent level. † Based on counts of seed in ten fruits. ‡ Based on three 100-seed replicates from each of ten fruits. § Includes all fruits harvested plus injured buds that dropped after 7 days.

flowers opened. The yellow pollen from *A. schottii* was found on the stigmas of the saguaro flowers, among the cream-colored pollen from the saguaro, indicating that flowers of both species were visited. There were no claw marks or other signs of damage to the saguaro flowers by the bats. Details of their activity in the cage are described elsewhere (*5*).

Honey bees (*Apis mellifera* L.) have been in the Southwest only since 1872 (*6*), which is not long enough to account for many of the more mature saguaros. However, the bees are attracted to saguaro flowers (*7*) and were included in this test because of their versatility as pollinators.

The bees were housed in a single-body Langstroth hive, well stocked with bees of all stages, honey, and pollen. Water was constantly available. Bee activity in the cage was similar to that in the open (*7*).

Appropriate checks of hand cross-pollinated and of naturally self-pollinated flowers were made intermittently. Such flowers were covered with cheesecloth if pollinating agents were in the cage; otherwise the flowers were left open. For comparison, records were also kept on some naturally pollinated "field" blossoms.

Each day throughout the flowering period all caged flowers were tagged and the fruits that were shed were recorded. As fruits matured they were harvested and the seeds were removed and counted. Germination percentages were determined under conditions of natural light and temperature in the laboratory (*8*).

The results (Table 1) show that viable seeds were produced in considerable quantity by both night- and day-pollinating agents. The effectiveness of the agents tested and the probable effectiveness of similar pollinators in the area (*7*) would indicate that failure of the saguaro to repopulate is not due to lack of cross-pollination.

To our knowledge this is the first experimental proof (*9*) that honey bees can pollinate the saguaro or that white-winged doves and *Leptonycteris* bats can pollinate any plant (*10*).

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References and Notes

1. F. Shreve, *Plant World* **13**, 235 (1910); R. M. Turner and J. R. Hastings, unpublished data.
2. S. M. Alcorn, S. E. McGregor, G. D. Butler, Jr., E. B. Kurtz, Jr., *Cactus and Succulent J.* **31**, 39 (1959).
3. Appreciation is expressed to John C. Cook, superintendent, Saguaro National Monument, for permission to collect saguaro arms and conduct this experiment on the Monument grounds; to Gilbert Ray, executive director, Pima County Parks and Recreation Department, for permission to collect saguaro arms in Tucson Mountain Park; to the University of Arizona Arid Lands Program for incidental funds; to Lyle K. Sowls and E. Lendell Cockrum for cooperation in collecting the white-winged doves and bats, respectively.
4. L. D. Beatty, thesis, University of Arizona (1955), 51 pp.
5. E. L. Cockrum and B. Hayward, *Natural History of the Long-Nosed Bat* (Leptonycteris nivalis *Saussure*), Univ. of Arizona Press, in press.
6. F. E. Todd, *Ariz. Highways* **26**, 4 (1950).
7. S. E. McGregor, S. M. Alcorn, E. B. Kurtz, Jr., G. D. Butler, Jr., *J. Econ. Entomol.* **52**, 1002 (1959).

→ S. M. Alcorn and E. B. Kurtz, Jr., *Am. J. Botany* **46**, 526 (1959).

9. This report is Arizona Agricultural Experiment Station technical paper No. 616.
10. A report giving greater details of these tests is in preparation.

3 January 1961

Chemotaxis of Zoospores for Root Exudates

Abstract. A chemotactic response of the zoospores of a soil-inhabiting plant pathogenic fungus, *Phytophthora cinnamomi*, for roots of avocado seedlings was observed. The chemotaxis of the zoospores and chemotropy of their germ tubes were directly related to infection and disease production. Indications were obtained of specificity of the pathogen-attracting root exudate, and interesting implications are evident with regard to mechanisms of invasion and pathogenicity, and to disease resistance.

Plant pathogenic fungi invade their hosts by means of several different avenues including natural openings in host tissue, wounds, and direct penetration of living tissue (*1*). Invasion through such avenues has been attributed to (i) attraction of the fungus mycelium or the germinating spore to stimulatory chemicals exuding from roots or leaves, (ii) attraction of the fungus to a nutrient gradient, or (iii) mere chance.

The complex medium of soil provides a difficult but highly interesting area in which to study attraction of plant roots for plant pathogenic microorganisms. The motile infective zoospores of pathogenic species of the fungus genus *Phytophthora* serve as an excellent tool for investigating such phenomena. Other investigators have demonstrated chemotaxy of motile plant units such as bracken spermatozoids and gametes of *Allomyces* (*2*) to specific chemicals, electric fields, or hormones. Goode (*3*) reported a nonspecific attraction of zoospores of *Phytophthora fragariae* to the root tips and the root-hair zones of strawberry roots. Flentje (*4*) has recently summarized information on means by which plant pathogenic fungi reach their host, and on subsequent invasion of the host.

In the present investigation young, vigorously growing roots of avocado (*Persea americana* Mill.) seedlings were found to have strong attraction for the zoospores of the avocado root pathogen, *Phytophthora cinnamomi* Rands. A preliminary report has been published (*5*). Young excised root tips (1 to 2 cm long, 1 to 2 mm in diameter) from avocado varieties highly susceptible to the pathogen were placed in petri dishes containing actively swimming zoospores of *P. cinnamomi*. Zoospores were liberated from sporangia produced at 24°C for these tests by a method previously described (*6*), involving use of a nonsterile soil extract.

Chemotaxy of the zoospores for the roots occurred within a few minutes and was demonstrated by an obvious accumulation of the motile spores in the immediate vicinity of the root pieces. The concentration of spores was notably greater in the region of elongation on the root, just above the root tip, than it was at the root tip or in the region of differentiation. The avocado root does not produce root hairs.

In 30 to 60 minutes, as a rule, spores settling on and in the vicinity of the roots began to encyst and to germinate. Quantitative evidence of the attraction was then obtained by examining the root pieces under a dissecting microscope and counting numbers of spores settling on different areas of the root and adjacent to the root. These observations showed:

1) That the zoospores were particularly attracted to the region of elongation above the root tip, and that spores also encysted at different distances from the root as if in response to a concentration gradient of some stimulatory chemical exuding from the root (Table 1).

2) Positive chemotropism of germ

Table 1. Attraction of zoospores of *Phytophthora cinnamomi* to roots of a host plant (avocado) and a nonhost plant (citrus).

Distance from root (mm)	Av. No.* of zoospores settling in areas 0.5-mm square
	Avocado
0–0.5	34.0
0.5–1.0	14.7
1.0–1.5	11.1
1.5–2.0	8.7
2.0–2.5	5.0
2.5–3.0	4.2
	Citrus (*mandarin orange*)
0–0.5	0.6
0.5–1.0	1.4
1.0–1.5	0.9
1.5–2.0	1.3
2.0–2.5	0.9
2.5–3.0	1.3

* Figures represent mean of ten fields counted.