Angiosperm Parasite and Host: Coordinated Dispersal

Abstract. *Seeds of the root parasite* Orthocarpus densiflorus *may be dispersed by the propagules of its host,* Hypochoeris glabra. *Such coordinated transport, which includes seed clustering, reinforces the integration and stability of populations of this host and parasite.*

The self-incompatible annual herb *Orthocarpus densiflorus* (Scrophulariaceae) is an obligate parasite of other flowering plants. Self-incompatibility, especially in annual plants, imposes the strict necessity for clustering of individuals, since annuals must produce seed each year in order to persist. Obligate parasitism necessitates coordination between the dispersal of the seeds of the parasite and its host. This report describes a system of coordinated seed dispersal involving self-incompatibility, parasitism, and a unique seed morphology in *Orthocarpus densiflorus* (owl's clover) and *Hypochoeris glabra* (cat's-ear).

The natural population studied is located in Isla Vista, near Santa Barbara, California. The species grows there in abandoned pasture land, composed of numerous grasses, composites, legumes, and other annuals. At early stages of its growth it becomes apparent that the *Orthocarpus* individuals are not randomly distributed, but they are highly clustered and associated spatially with the common annual *H. glabra.* Although the *Orthocarpus* is a normal-appearing, green, flowering plant, in the Isla Vista population these two annual plants have entered into a close parasitic relationship, as demonstrated by the following facts. Unattached individuals of the *Orthocarpus* grow weakly in our greenhouse (being unbranched and, at most, up to 15 cm tall) and almost never survive under the more rigorous field conditions. When grown with *H. glabra,* individuals of *O. densiflorus* are vigorous and often attain a height of 40 cm, producing as many as 15 to 20 robust flowering branches. In order to grow *O. densiflorus* in the greenhouse its seed is placed in a suitable soil adjacent to an achene of *Hypochoeris*. This achene germinates within 6 days, and 4 or 5 days later the *Orthocarpus* seed germinates. Root grafts (*1*) are formed as soon as contact is made between seedling roots, usually within 4 or 5 weeks. Numerous root grafts have been observed between these plants in the Isla Vista population. An *Orthocarpus* individual may become attached to the roots of one or several *Hypochoeris* individuals.

While it has been demonstrated clearly that *O. densiflorus* is an obligate parasite (*2*) for which *Hypochoeris* serves as a host, it is also true that individuals of this species parasitize other plants, both in the Isla Vista population and in other areas. However, a clear distinction must be made between the physiological act of parasitism and the ecological success of such a relationship. The successful integration of the *Orthocarpus* population with its host population depends on many factors. *Hypochoeris glabra* has proved to be the primary host of *O. densiflorus* in this locality. This species alone meets such requirements as: a life cycle synchronized with that of *O. densiflorus*; sufficient densities to support the tens of thousands of individuals which may make up the *Orthocarpus* population; adequate germination, growth, and reproduction under severe drought conditions; intrapopulation competition among hosts favoring establishment of parasite seedlings; and interpopulation competition (exclusion of vegetation with rank foliage).

The seeds of both *Orthocarpus* and *Hypochoeris* are quite unusual. Those of *O. densiflorus* are surrounded by a rigid net, about 1 mm in diameter, that is formed from the outer integument. The portion of the seed that contains the embryo is only about 0.5 mm in length, and it is completely free within the loose fitting net. Seeds of *Hypochoeris,* actually achenes, are of two kinds. The outer whorl of florets produces achenes with a pappus of barbed bristles and a central mass of hairs. The pappus of the inner

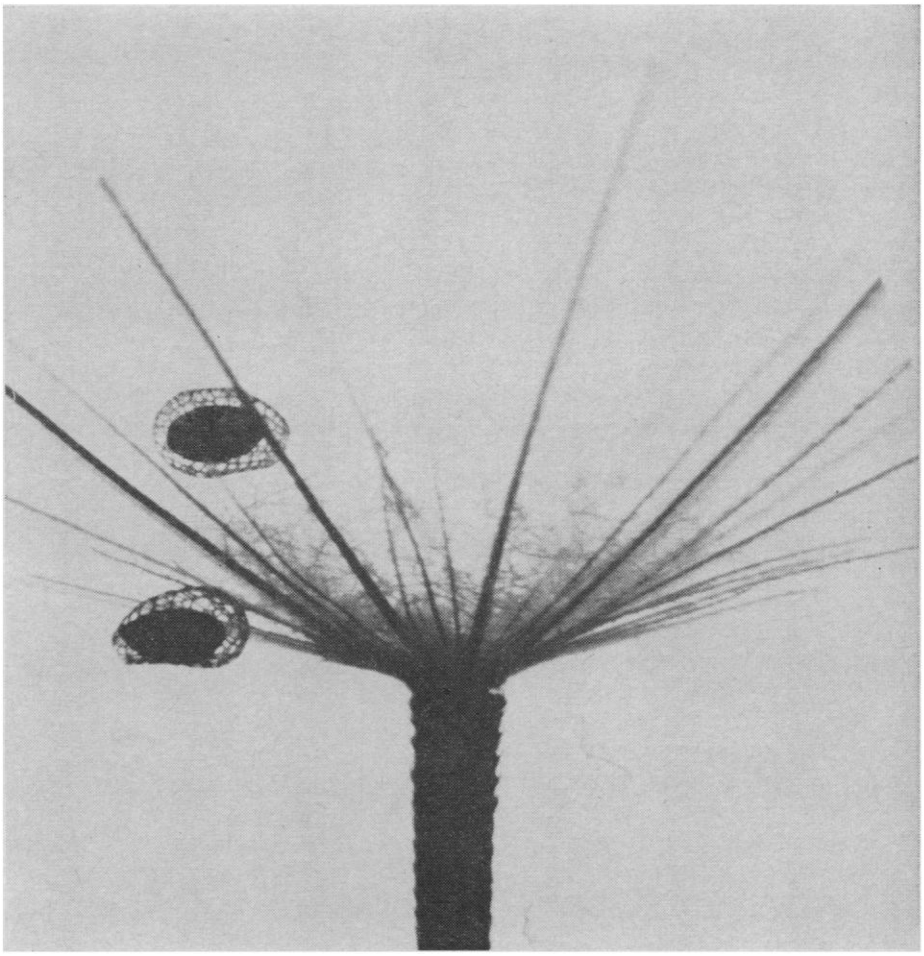

Fig. 1. Two seeds of the root parasite *Orthocarpus densiflorus* attached to an achene of its host, *Hypochoeris glabra.* The net of the lower seed is lanced by one of the lateral bristles. The upper seed was rolled slightly from its central position to bring it into focus. Actual length of seed cage is 1 mm (× approximately 17).

achenes is less open and lacks the fine central hairs.

In natural populations the seeds of both *Orthocarpus* and *Hypochoeris* mature at approximately the same time. The *Hypochoeris* achenes fall to the ground with the upwardly directed pappus forming a sea of bristles. The entanglement of these achenes is so dense at times that falling *Orthocarpus* seeds often become attached to the pappus—either the net of the *Orthocarpus* seed is pierced by a pappus bristle or the seed becomes entangled by the fine hairs of the outer achene (Fig. 1). The percentage of *Orthocarpus* seeds which become attached to achenes is, of course, highly variable; and I have no good data for the general frequency of this event except that examination of the *Hypochoeris* achenes surrounding *Orthocarpus* individuals usually reveals several achenes with one or more attached seeds.

Several handfuls of *Hypochoeris* achenes were scraped from around mature *Orthocarpus* plants, placed in a large paper bag, and taken to the laboratory. The total numbers of both types of achenes were estimated to be about 5000, and the sample was carefully examined for attached *Orthocarpus* seeds. Only 11 (0.3 percent) of the 4000 inner achenes retained single seeds. However, 7 percent of the 1000 outer achenes carried one or more firmly attached seeds; 57 achenes each retained a single seed, 10 achenes carried 2 seeds, and one achene held 3 seeds. The outer achenes with the central mass of fine hairs are far more efficient than the inner achenes in retaining *Orthocarpus* seeds. It is important that several of the outer achenes carried two or more such seeds.

An interesting aspect of this interaction is the accuracy with which its origin can be dated. While *O. densiflorus* is restricted to western regions of California, *H. glabra* is a native of western Eurasia and North Africa and has only recently been introduced into the range of *Orthocarpus. Hypochoeris glabra* was common in the San Francisco area by 1870 but apparently did not reach Southern California until 1900 (*3*). While other species native to the California area have and still do serve as hosts for *Orthocarpus*, the *Orthocarpus–Hypochoeris* system is less than 100 years old. Intricate and complex interactions do not necessarily indicate a long evolutionary development but can be a fortuitous combination of features evolved independently.

Hypochoeris glabra is not only ecologically and physiologically a suitable host for *O. densiflorus* but also the seeds of host and parasite fit together so that the seeds may be clustered and the dispersal coordinated. Clustering is an important factor in all outbreeding populations, though it has primarily been discussed in specialized cases of founder populations. Baker (*4*) has pointed out the difficulty of long-range dispersal in self-incompatible plants, and Raven (*5*) has suggested a selective advantage in a self-incompatible plant of a multiseeded unit but he noted that known examples are relatively heavy and unlikely to be dispersed. The attachment of more than one *Orthocarpus* seed to a single *Hypochoeris* achene not only provides the potential for long-range migration and establishment, but at the same time produces a degree of clustering within populations of these self-incompatible annuals.

The advantage of a coordinated dispersal of host and parasite is readily visualized, but perhaps the less obvious phenomenon of seed clustering in self-incompatible plants is of greater general significance, and may be an important aspect of plant-population interactions where parasitism is not a factor.

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References and Notes

1. Details of root grafting in *Orthocarpus* are similar to those for *Castilleja* reported by L. R. Heckard in *Bot. Gaz.* **124**, 21 (1962).
2. The term "obligate" is used because it describes the dependency of the natural population on the presence of a host. The fact that *individuals* of some species will complete their life cycle without a host should not be confused with the fact that natural populations growing without a host do not exist and, therefore, presumably cannot exist.
3. S. B. Parish, *Bull. Southern Calif. Acad. Sci.* **19** (No. 4), (1920); W. W. Robbins, *Univ. Calif. Agr. Exper. Station Bull. 637* (1940), p. 1.
4. H. G. Baker, *Evolution* **9**, 347 (1955).
5. P. H. Raven, *Quart. Rev. Biol.* **38**, 151 (1963).

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Prostaglandin: Release from the Rat Phrenic Nerve–Diaphragm Preparation

Abstract. *Release of a substance that stimulates smooth muscle was detected from a phrenic nerve–diaphragm preparation from the rat upon direct and indirect stimulation. On thin-layer chromatography most of the active material behaved as a mixture of prostaglandins. The effect of electrical stimulation was mimicked by catecholamines but not by acetylcholine or eserine. The effect of nerve stimulation was not antagonized by* d-*tubocurarine.*

There is a spontaneous and evoked release not only of acetylcholine (*1*) but also of unsaturated hydroxycarboxylic acids from the somatosensory cortex of the anesthetized cat (*2*). These acidic substances, which are also released from the perfused spinal cord of the frog on stimulation (*3*), produced a slow contraction of the isolated uterus of the rat and have now been identified with a mixture of prostaglandins (*4*), a class of substances whose chemical structure and pharmacological properties have now been elucidated (*5*). In order to study the mechanism of release and the possible function of these lipid acids, we attempted to detect their release from a simple nerve structure, namely the phrenic nerve–diaphragm of the rat. This isolated preparation was first introduced by Bulbring (*6*) and is very useful for studying the effects of drugs on cholinergic synapses. Despite the comment that the "behaviour of this preparation is sufficiently predictable to allow observations to be repeated and therefore confirmed" (*7*), there is no agreement concerning the release of acetylcholine from the nerve terminals (*8*).

Hemidiaphragms were dissected from female Wistar rats (150 g), suspended in a 2-ml bath of Tyrode solution at 37°C, and aerated with O_2 containing 5 percent CO_2. The costal margin of the diaphragm was attached to one side of the bath, and contractions of the muscle were recorded on a polygraph by connecting the central tendinous part of the diaphragm to a strain gauge. A pair of flexible platinum electrodes mounted on the lucite frame of the tissue bath served to stimulate the nerve or muscle directly. The bath fluid was changed every 15 minutes, and at least two resting samples were collected before maximum stimulation of either the nerve or the muscle at 25 stimuli per