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Factors affecting the extinction or survival of parasitic higher plants

Abstract

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Holoparasites in primary habitats mostly have a limited distribution. They grow in some sort of equilibrium with the flora of their natural ecosystem, due to particular adaptive habits like limited dispersal and restrained infestability. Their survival depends on a combination of biological and demographic characters of their hosts, their own ecological demands, and environmental conditions that affect their development. Significant change of any of these factors may result in severe reduction of the parasite's population and eventually in its elimination. Such changes can be caused by human interferences, by catastrophes, or by natural succession; they may affect the parasite directly, or its host's population, or the whole vegetation. The higher the specificity of the parasite, the higher are the chances of its going extinct. Parasites in secondary habitats, many of which have become cosmopolitan in distribution, are less prone to extinction than those in primary habitats, owing to their weed-like adaptations; only if host-specific they may become rare or extinct when culture of their particular host crop is abandoned. Parasitic higher plants in both habitat types do not endanger the existence of their host species. Examples from the *Cuscutaceae* are briefly discussed.

Introduction

Two major questions arise when one deals with the diversity of parasitic higher plants within the general context of endangered species: (1) Are there threatened species among these plants? (2) Do they pose a threat upon the existence of their host species?

There are about 3300 species of parasitic higher plants (i.e. 1.1-1.3 % of the seed plants), more than four fifths of which are semiparasites (mainly stem-parasitic *Loranthaceae* and root-parasitic *Santalaceae* and *Scrophulariaceae*) and less than one fifth are holoparasites (mainly root-parasitic *Rafflesiaceae* and stem-parasitic *Cuscutaceae*). Most of the species, over twenty two hundred, are found in the tropical and subtropical regions of the world (Table 1, based on Engler 1964, Kuijt 1969, Willis 1973,

Heywood 1978, Mabberley 1987). However, half of the families (*Orobanchaceae*, *Santalaceae* and *Scrophulariaceae* in particular) contain many representative species growing in the Mediterranean region.

Table 1. Families of plant parasites and their distribution. – hp = holoparasite, sp = semiparasite, r = root parasite, s = stem (and leaf) parasite.

	species N°	parasitism		main distribution
<i>Balanophoraceae</i>	< 120	hp	r	tropical
<i>Cuscutaceae</i>	160	hp	s	tropical to temperate
<i>Cynomoriaceae</i>	1	hp	r	mediterranean, temp. Eurasia
<i>Hydnoraceae</i>	18	hp	r	tropical
<i>Krameriaceae</i>	> 15	sp	r	tropical
<i>Lauraceae</i> (<i>Cassytha</i>)	20	hp	s	tropical
<i>Lennoaceae</i>	6	hp	r	subtropical (USA, Mexico)
<i>Loranthaceae</i>	< 1300	sp	s	tropical to temperate
<i>Misodendraceae</i>	11	sp	s	southern S America
<i>Olacaceae</i> (incl. <i>Opiliaceae</i>)	240	sp	r	palaeotropical
<i>Orobanchaceae</i>	230	hp	r	temperate Eurasia
<i>Rafflesiaceae</i>	50	hp	r	tropical & subtropical
<i>Santalaceae</i>	> 400	sp	r	tropical to temperate
<i>Scrophulariaceae</i> p.p.	760	sp	r	temperate to tropical

Several parasitic species have a wide, multiregional or even cosmopolitan distribution, whereas many others are confined to certain areas or habitats, or plant formations. In general, distribution patterns are related to the ecological demands and adaptations, and to the reproductive and demographical characters of the plants. In plant parasites, the host-parasite-habitat association is a more complex type of relationship. According to habitat and host preference of the parasite, three general categories can be discerned: (1) species that grow in primary (natural) habitats, probably as an integral part of the flora; (2) species that occupy secondary habitats and are usually hosted by cultivated plants; and (3) species that occur in both habitat types.

Also, as some host species (principal hosts) are preferred and more frequently infested than other species (casual or temporary hosts), there are different levels of parasite-host specificity: specificity to a particular species or group of species (e.g. *Cuscuta epithymum* Murray on *Coridothymus*, *Cytinus hypocistis* (L.) L. on *Cistus*); specificity to a higher systematic entity (e.g. species of *Centranthera* on monocots, *Arceuthobium* on conifers); specificity to certain life-forms (e.g. *Cuscuta monogyna* Vahl on phanerophytes, species of *Viscum* on trees, *Thesium humile* Vahl on annual herbs); and generalized parasitism on annuals and perennials of various families (e.g. *Cuscuta palaestina* Boiss., *Orobanche cernua* Loebl.).

We shall demonstrate that among parasitic higher plants in natural habitats there are several species which are prone to potential extinction, and the higher their specificity, the higher their vulnerability.

Parasites in natural habitats

We regard higher plant parasites in primary habitats as “prudent parasites” which are an integral component of the natural ecosystem (Plitmann 1991). By analogy to predators, such parasites should be less frequent or have a lower biomass than their hosts. *Cuscuta palaestina*, for example, infests about 20 % of the shrublets in a *Sarcopoterium* community, covers 2-55 % of each and 10-16 % of the whole vegetation (Table 2). Likewise, *Cuscuta costaricensis* Yuncker was found to occupy 50 % of the total available cover, and the two most frequently affected hosts had 31-57 % of infested cover (Kelly & al. 1988).

The level of specificity, combined with the distribution pattern of the host, may in part account for the total amount of infestation and for the rarity of the parasite, as exemplified by *Cuscuta monogyna* and *C. babylonica* Choisy in Israel (Table 2).

Table 2. Rates of infestation by some *Cuscuta* species.

Species	N° of sites	principal hosts	% cover on each infested plant	% cover of parasite in vegetation
<i>Cuscuta babylonica</i>	4	<i>Prosopis</i> , <i>Atriplex</i>	7-60	2-9
<i>C. campestris</i>	4	roadside herbs & grasses	15-90	30-70
<i>C. monogyna</i>	2	<i>Ziziphus</i>	30-50	1-2
<i>C. palaestina</i>	4	<i>Sarcopoterium</i>	4-55	10-16
<i>C. planiflora</i>	2	desert annuals	40-70	1-2

We assume that selection acting on parasitic plants in natural habitats favours genotypes of mild or restricted infestation (“harmlessness” sensu May 1985, “nice” parasites sensu Michalakakis & al. 1992). Aggressive mutants might be suicidal. Thus, in *Cuscuta*, there are certain adaptations that limit the distribution of and/or the damage caused by the parasite: delayed flowering and fruiting, in-situ dispersal, very low germination rates (Plitmann 1991).

In addition, parasitic plants in natural habitats should be adapted, as are their hosts, to the environmental conditions.

Since many species are tropical/subtropical by origin, they are susceptible to cold and prefer warm places with plenty of water available. Examples are *Cuscuta babylonica* and *Loranthus acaciae* Zucc. in Israel, or species of the *Balanophoraceae* which grow in moist forests. Some species, like *Cuscuta planiflora* Ten., *Cistanche tubulosa* (Schenk) Hook., *Cynomorium coccineum* L., and species of *Krameria*, succeed to survive in arid zones where their life span is relatively short. Others are found in special habitats (coastal sands, saline marshes, water courses).

Parasites in secondary habitats

This category includes species that grow either in cultivation or as ruderals. They behave like weeds (Musselman 1982), adapted to human agricultural activities, and, by analogy to bacterial pests, they may be epidemic. In most cases their host specificity is

low (e.g., *Cuscuta campestris* Yuncker and *Orobancha crenata* Forssk. grow on various crop plants), fecundity is high (e.g. in *Orobancha aegyptiaca* Pers. each capsule contains thousands of tiny seeds), and they show wide phenotypic plasticity and phenological variability. *Cuscuta campestris* may serve as an example: it has spread from N. America into most regions of the Old World, including the Mediterranean; it can be disseminated with the crops or inadvertently transported by humans; it is able to propagate vegetatively and features fast growth and branching; its fecundity (in number of fruits and seed per plant) is high, and the germination rate higher than in dodder species of natural habitats (over 23 % vs. less than 10 %, respectively); it has a long flowering season – throughout the summer and autumn – and is fruiting simultaneously with the crop; it occupies roadsides and fields, heavily infesting annual and perennial herbs (even grasses) as well as shrublets; it is resistant to pest-control substances (Danin, pers. comm.); it may infest over 60 % of the available area and cover up to 90 % of the host (Table 2).

Endangered species or populations in *Cuscuta*

The monogeneric family *Cuscutaceae* comprises 160 species, 84 of which have a very limited distribution. Moreover, most grow in primary habitats and belong to the natural ecosystem in their respective areas (Table 3, based on Yuncker 1932, Hunziker 1949-1950, and personal information). Within this family, we have data on three cases in our region in which species or populations have become extinct or very rare.

Table 3. Ecogeographical distribution of species of the *Cuscutaceae*.

	single locality	uni-regional	multiregional	others	total
primary habitats	43 (27 %)	41 (25.5 %)	52 (32.5 %)	10 (6.25 %)	146 (91.2 %)
secondary habitats	–	–	12 (7.5 %)	2 (1.25 %)	14 (8.8 %)
totals	84 (52.5 %)		64 (40 %)	12 (7.5 %)	160 (100 %)

Cuscuta gennesaretana Sroëlov was first described by Feinbrun & Taub (1964) as a dodder that grows sporadically from Lebanon to the Lower Galilee in Israel and along the Jordan Rift. Its recorded distribution area and original description were based on herbarium specimens collected between 1922 and 1952. Since, vast areas in these districts were turned into cultivated land, and spring waters were channelled in pipes. All our efforts to find this species again have been futile, and we regard it as extinct.

In the same districts of Israel, we located two populations of *Cuscuta monogyna*, each consisting of a few plants growing on *Ziziphus* trees and shrubs. Due to road construction near one of the populations (foothill of Mt. Tabor), the host trees were cut down and the parasite population disappeared completely.

Cuscuta epilinum Weihe is a parasite specific to the cultivated flax, *Linum usitatissimum* L. A substantial reduction of the areas of flax cultivation during the last decades, together with effective weed control measures, contributed to the rarity of this parasitic species. To our knowledge, however, this is the only case in which a weedy parasite's survival has been endangered, probably due to its high specificity.

Discussion and conclusions

Comparing the adaptive characters of parasites in regard to their environment and hosts, it is obvious that those species growing in primary habitats are more prone to extinction. Several of them are rare to begin with. They are all “host-dependent”, and their existence is conditioned by several factors affecting either host or parasite. The change of any single such factor may have an impact on the parasitic population, either directly or indirectly (through the host), and eventually lead to its disappearance. Such a process is probably enhanced by a low variability of the parasite population, as in clones of *Cuscuta*. Adverse changes may be caused by natural succession resulting in a gradual decrease in the host population, or by catastrophes like consecutive years of extreme drought, or – most effectively – by human disturbance affecting the habitat and its flora. We therefore believe that many parasitic higher plants, especially those that are already limited in distribution or are rather rare, face a real danger of extinction.

Recent studies on parasitic animals and micro-organisms, and models of host-parasitoid associations (Anderson 1978, 1980, Price 1980, May 1985, Rollinson & Anderson 1985, Cohen & Newman 1989, Seger & Hamilton 1988, Hamilton & al. 1990, Toft & al. 1991, Godfray & Pacala 1992, Hochberg & al. 1992, Rennie 1992), support the assumption that there are co-evolutionary relationships between hosts and parasites, such that correlated diversities and life-spans may have evolved in both, leading to some stability of their interactions. In this kind of coexistence the parasites are the agents of selection and regulate the host populations. More, “under certain conditions a parasitized host may be better off than an uninfected one” (Michalakis & al. 1992). We assume that similar evolutionary or ecological relationships exist between parasitic higher plants and their hosts. In primary habitats, or in natural ecosystems, elimination of the parasitic component, whether intentional or not, may impinge upon the demographic equilibrium in the community.

There is another implication of the loss of a parasitic higher plant, which concerns the scientific value of parasitism per se. Parasitic higher plants provide excellent material for studies of interactions between living organisms at various levels – chemical, physiological, anatomical, demographic, and evolutionary (e.g. Kuijt 1969, Tsivion 1978, Hedberg 1979, Atsatt 1983, Stewart & Press 1990, Linhart 1991). In addition, certain species feature biologically unique phenomena, either reproductive (like the huge flowers of *Rafflesia*, the “naked” embryos in *Balanophoraceae*, *Loranthaceae* and *Santalaceae*) or cytological (like the chromosome systems in species of *Cuscuta*, or of *Loranthaceae*).

In view of their distribution patterns and adaptations, parasitic plants in primary habitats do not pose an immediate threat to the existence of their host species. In secondary habitats, particularly on arable land, the impact of an aggressive parasite is mainly economic: the parasite does not endanger the survival of the crop species but decreases its productivity. The various pest control measures (see, for example, Visser & Musselman 1986, Weber & Forstreuter 1987) may reduce weed parasite populations, though they seemingly would not bring about their total extinction, due to the parasite’s abundance and adaptability.

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