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REVIEW

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Parasitic plants: parallels and contrasts with herbivores

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Abstract Parasitic plants are common in natural communities, but are largely ignored in plant community theory. Interactions between parasitic plants and hosts often parallel those between herbivores and plants: both types of consumers display host preferences, reduce host biomass and alter host allocation patterns, modify plant community structure and dynamics, and mediate interactions between host plants and other organisms. In other cases, basic differences in mobility, hormonal and elemental composition and resource capture between plants and animals lead to different effects: parasitic plants have broad host ranges, affect and are affected by host plant physiology because of similar hormonal pathways between parasite and host, do not alter nutrient cycling as extensively as do herbivores, and may simultaneously parasitize and compete with hosts. Many fundamental aspects of the ecology of parasitic plants remain poorly studied, and research to date has been dominated by laboratory studies and studies of crop pests, rather than by studies of natural communities.

Keywords Parasite · Parasite-host interactions · Parasitic plant · Plant community · Plant-herbivore interactions

Introduction

The typical plant is an autotrophic organism that obtains its necessary resources – sunlight, water and minerals – from the abiotic environment. This perspective, however, overlooks the large number of plants that consume other plants, obtaining much or all of their nutrition from their prey (Govier and Harper 1965; Press and Graves 1995; Press 1998). Parasitic plants number some 3,000 species, about 1% of all angiosperms (Kuijt 1969; Atsatt 1983). They occur within 16 plant families, represent a wide variety of life forms from trees and shrubs to vines and herbs, and are present in most plant communities throughout the world (Musselman and Press 1995). There are also more than 400 species of heterotrophic vascular plants in 87 different genera that lack chlorophyll and parasitize other plants through specialized mycorrhizal connections (Leake 1994). Moreover, even fully autotrophic plants may often participate in mycorrhizally mediated parasitism (Chiarello et al. 1982; Francis and Read 1984; Grime et al. 1987; Moora and Zobel 1996; Walter et al. 1996; Watkins et al. 1996; Simard et al. 1997; Marler et al. 1999; but see Robinson and Fitter 1999). Despite the widespread prevalence of parasitic plants, and extensive research into their role as agricultural pests (Knutson 1979; Parker et al. 1984; Parker and Riches 1993; Riches and Parker 1995), their role in the structure and function of communities has rarely been considered from a theoretical perspective (but see Price et al. 1986; Smith 2000).

Interactions between parasitic plants and their hosts parallel herbivore-host interactions in many ways. Although the obvious analogy between parasitic plants and herbivores was drawn several decades ago (Govier and Harper 1965), we are still a long way from rigorously evaluating Atsatt's (1977) hypothesis that the relationship between plants and herbivorous insects could serve as a model for studying the community ecology of host-parasite relations in plants. Here, we synthesize and analyze the literature in order to compare and contrast herbivores and parasitic plants with respect to host choice, impacts on hosts, and impacts on communities. Although many potential parallels can be developed between herbivores and parasitic plants on the simple basis of mode of nutrition, their fundamental membership in different

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kingdoms of life results in some important differences in their ecological effects.

Host choice

Like herbivores, parasitic plants display strong host preferences, may benefit from dietary mixing and likely benefit from hosts with high nitrogen contents. In contrast to most herbivores, parasitic plants have broad host ranges, and allocation patterns that can be strongly affected by host identity. Many of the possible parallels between diet choice in herbivores and parasitic plants have yet to be investigated. In particular, little is known about the chemical ecology of interactions between parasitic plants and their hosts.

Like herbivores, parasitic plants are able to “choose” among potential hosts (Kelly 1992). In the field, parasitic plants typically attack a subset of the hosts available to them (Gibson and Watkinson 1989; Pennings and Callaway 1996). Parasitic plants are capable of a variety of different foraging patterns. Parasites can forage in time by producing seeds that only break dormancy following cues released by potential hosts (Kuijt 1969; Atsatt 1977, 1983; Press et al. 1990; Press and Graves 1995). Following germination, parasitic plants can forage in space by selectively growing toward or away from hosts, or by selectively penetrating host tissues following contact (Kelly 1990, 1992; Callaway and Pennings 1998; L.S. Adler, personal communication). In both cases, we have an emerging understanding of the proximate chemical cues that are involved (Worsham et al. 1964; Cook et al. 1972; Edwards 1972; Lynn et al. 1981; Steffens et al. 1982, 1983; Atsatt 1983; Press et al. 1990; Appel 1993). Finally, some parasitic plants may rely on animal vectors to move seeds to appropriate hosts (Kuijt 1969; Knutson 1979; Calder 1983).

Despite these foraging patterns, the sedentary nature of parasitic plants constrains their ability to locate hosts, which is likely to result in selection favoring broad host ranges. Host range varies widely among species of parasitic plants (e.g., Atsatt and Strong 1970; Norton and De Lange 1999). Single species of *Cuscuta* and *Castilleja* can parasitize hundreds of host species in many different families, whereas some species of mistletoe parasitize only one host species (Musselman and Press 1995). Although parasitic plants with narrow host ranges exist (Barlow and Wiens 1977), they are the exception rather than the rule (Chuang and Heckard 1971; Watkinson and Gibson 1988; Gibson and Watkinson 1989; Musselman and Press 1995). In this regard, parasitic plants are similar to marine herbivores and mammalian herbivores, which tend to be generalists (Crawley 1983; Hay and Steinberg 1992), but differ from terrestrial herbivorous insects, which tend to be specialists (Price 1983; Strong et al. 1984; Bernays 1989).

Despite the generalist nature of most parasitic plants, the performance of the parasite may vary by an order of magnitude among hosts, with some hosts barely sufficient to support the parasite’s life and others supporting vigorous growth and reproduction (Atsatt and Strong 1970; Chuang and Heckard 1971; Snogerup 1982; Kelly 1990; Gibson and Watkinson 1991; Seel et al. 1993; Matthies 1996, 1997, 1998). Typically, growth of the parasite correlates positively with severity of damage to the host (Atsatt and Strong 1970; Gibson and Watkinson 1991; Matthies 1996; Marvier 1996, 1998a, b; but see Matthies 1998). Different populations of a host may also differ in vulnerability and value to parasites, suggesting the possibility for induction or evolution of resistance; however, the typical pattern of hosts being more resistant to sympatric parasites does not necessarily occur, perhaps because, unlike microbial parasites, parasitic plants do not have a markedly shorter generation time (and thus greater evolutionary potential) than their hosts (Riches and Parker 1995; Koskela et al. 2000; Mutikainen et al. 2000).

Unlike herbivores, allocation patterns in parasitic plants may vary depending on host species (Chuang and Heckard 1971; Snogerup 1982; Seel and Press 1993; Marvier 1996; Matthies 1998). The causes and significance of this variation remain obscure, but could result from host hormones interfering with physiological control of the parasite (Seel and Press 1993). Although herbivores are not likely to be affected by plant hormones, they may be affected by animal hormones (or mimics) produced by plants as anti-herbivore defenses (Harborne 1993); the typical result, however, is reproductive failure (in mammals) or death due to developmental abnormalities (in insects) rather than non-lethal changes in morphology.

Many parasitic plants can simultaneously parasitize multiple host individuals (Gibson and Watkinson 1989; Kelly and Horning 1999). Since different host species may supply a parasite with different resources, including both nutrients and chemical defenses, a mixture of host species may be superior to a single host alone (Govier et al. 1967), much like the fact that “mixed diets” provide better nutrition to animals than “single-item” diets (Pennings et al. 1993; Bernays et al. 1994). Experimental analyses of mixed diets show that they benefit some parasitic plant species, but not all (Matthies 1996; Marvier 1998a, b; Kelly and Horning 1999; Matthies and Egli 1999; Joshi et al. 2000). Future studies of mixed diets may be helpful in understanding the broad host ranges of parasitic plants versus insects. These studies will be most useful if conducted in the field, because the advantages of obtaining nutrients and/or chemical defenses from multiple hosts may only be apparent under conditions of natural resource availability and herbivore load.

Understanding why parasitic plants choose the hosts that they do, why the performance of parasitic plants varies between hosts, and why combinations of hosts sometimes are superior to a single host and not at other times, requires a better understanding of the host traits that matter most to parasitic plants. Extensive research on this issue within the context of herbivore-host relations has identified a wide variety of traits, including plant secondary chemistry, toughness, and content of nitrogen and sterols, that mediate host choice in particular cases; however, the importance of these factors often varies between different species of herbivores (Pennings and Paul 1992; Behmer and Grebenok 1998; Joern and Behmer 1998; Pennings et al. 1998; Behmer and Elias 2000). A similar rigorous analysis has not been conducted for parasitic plants; nonetheless, some patterns are evident. Performance of parasitic plants is often better on legumes, suggesting that N content is important to performance (Watkinson and Gibson 1988; Gibson and Watkinson 1991; Seel and Press 1993, 1994; Seel et al. 1993; Matthies 1996, 1998; Tennakoon and Pate 1996; but see Atsatt and Strong 1970; Kelly 1990; Marvier 1996, 1998b). Limited evidence suggests that plants low in minerals or high in secondary metabolites may be poor hosts (Kelly and Horning 1999), and that stressed hosts may be less able to resist infection by parasites (Gehring and Whitham 1992). Most of these studies are correlative, and in only a few cases have plant traits been manipulated to demonstrate that they directly affect parasite preferences or performance (Kelly 1992; Salonen and Puustinen 1996; Puustinen and Salonen 1999a). Open questions that have long been ripe for experimental studies are (1) whether parasitic plants use host secondary metabolites as “feeding” cues, and (2) whether parasites are negatively affected by host secondary metabolites (Atsatt 1977). Two lines of argument support the hypothesis that parasitic plants are less affected, either positively or negatively, by plant secondary metabolites, compared to herbivorous insects. First, the relatively broad host range of most parasitic plants suggests that they are not responding strongly to traits of particular hosts. Second, because the host and parasite share the same primary physiology, it may be difficult for host plants to deploy chemical defenses against parasitic plants without simultaneously poisoning themselves.

Many other aspects of host choice remain relatively unstudied in parasitic plant systems. For example, despite the enormous literature on induced defenses in plant-herbivore systems, it is largely unknown if hosts can induce defenses against parasitic plants (but see Khana et al. 1968; Sahm et al. 1995; Bringmann et al. 1999). The hypothesis that herbivores may choose hosts in order to avoid predators (Bernays and Graham 1988) is analogous to the hypothesis that some parasitic plants gain protection from herbivores by mimicking host foliage (Atsatt 1977; Barlow and Wiens 1977; Ehleringer et al. 1986a); however, experimental tests of this hypothesis are lacking. Finally, although many studies have examined positive and negative induction of feeding preferences of herbivores, only one study has examined whether prior host experience by parasitic plants affects future host preferences of the parasite or its offspring (L.S. Adler, personal communication).

Impacts on hosts

The direct effects of parasitic plants on hosts have been extensively reviewed (Calder 1983; Parker and Riches 1993; Graves 1995). In comparison to herbivores, parasitic plants may have greater effects on their hosts in proportion to the mass of the consumer and the amount of resources removed. For example, several millimeters of shoot of the root hemiparasite *Striga hermonthica* can reduce the biomass of its *Sorghum* host by more than 30 times (Parker et al. 1984). This disproportionate impact of parasitic plants on their hosts is mostly caused by parasite-induced changes in host allocation and/or physiology. *Cuscuta* (dodder) species alter host physiology by acting as a stronger sink for photosynthate than any host organ (Ihl et al. 1984; De Bock and Fer 1992; Parker and Riches 1993). Similarly, although mistletoe leaf area is generally several orders of magnitude lower than that of their hosts, they reduce host growth, partly by diversion of resources (Hull and Leonard 1964; Miller and Tocher 1975; Schulze and Ehleringer 1984; Ehleringer et al. 1985, 1986b; Marshall and Ehleringer 1990; Rey et al. 1991; Marshall et al. 1994), but also by parasite-induced physiological responses that result in abnormal growth patterns and altered resource allocation of the host (Brochot and Tinnin 1986; Wanner and Tinnin 1986; Ihl et al. 1987). Parasitic plants alter the morphology and physiology of their hosts by stimulating production of host growth hormones or by infusing hormones directly into hosts (Drennan and El-Hiweris 1979; Knutson 1979; Livingston et al. 1984).

Perhaps the best-studied example of these parasite-nduced physiological effects on hosts comes from tudies of dwarf mistletoe (*Arceuthobium* spp.). Dwarf mistletoe may constitute less than a tenth of a percent of the living mass of a mature conifer tree, yet it significantly increases whole-tree water use and decreases leaf water potentials (Ehleringer et al. 1986b; Goldstein et al. 1989; Sala et al. 2001). Both infected and uninfected branches on infected trees have lower water use efficiencies than uninfected trees (Fig. 1A). This suggests that mistletoe forces stomata throughout the entire tree to transpire at times that are not favorable, probably explaining why pre-dawn leaf water potentials are lower in infected than control trees (Fig. 1B). Perhaps because of the resource sinks established by dwarf mistletoe infection, uninfected branches above infected branches on the same tree have lower leaf mass per branch diameter (R.M. Callaway, unpublished data). In addition to changes in host physiology, dwarf mistletoe alters host allocation patterns by inducing massive “brooms” on conifers. Brooms impair plant nutrient balance and water relations, and alter photosynthetic and respiration rates (Tinnin and Knutson 1980; Wanner and Tinnin 1986; Parker and Riches 1993; Sala et al. 2001). The net effect of these changes in physiology and morphology is that growth rates of trees infected by mistletoe may be reduced by up to 80% (Fig. 1C).

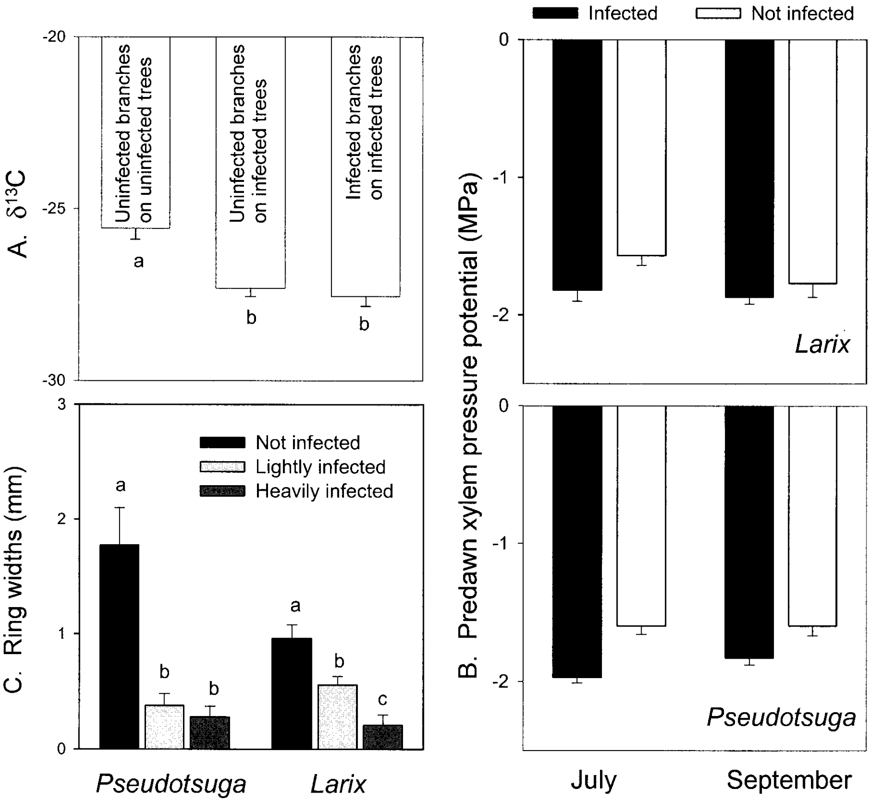

Fig. 1A–C Impact of dwarf mistletoe (*Arcethobium*) on physiology of host trees (*Pseudotsuga menzeisii* and *Larix occidentalis*) in western Montana. Data are means ± 1 SE. **A** Carbon isotope ratios of *Pseudotsuga* leaves (1994 cohort collected in September 1994). Lower values indicate lower water-use efficiencies. Trees were either infected (*Arcethobium* present in >40% of canopy) or uninfected (no *Arcethobium*). All leaves were collected from lower north-facing branches. *Shared letters* indicate no significant difference. **B** Predawn xylem pressure potential for *Pseudotsuga* and *Larix* in 1993. *F*(species)=5.52, *P*=0.34; *F*(infection)=24.59, *P*<0.001. **C** Mean width of the 1993 and 1994 growth rings combined for *Pseudotsuga* and *Larix*. Trees were classified as uninfected (no *Arcethobium*), lightly infected (*Arcethobium* present in 10–30% of canopy) or heavily infected (*Arcethobium* present in 40–80% of canopy). All trees were between 25 and 45 cm DBH. *Shared letters* within a species indicate no significant difference

Parasitic plants other than mistletoes and dodder also intensify their effects on hosts by altering host physiology. For example, Press et al. (1988) found that eight species of root hemiparasites transpired at high rates during the night, with some species transpiring more during the night than the day. All of the hemiparasites studied acquired large amounts of nutrients from their hosts, and nighttime transpiration would allow the parasites to continue to acquire nutrients in the xylem stream. Many parasitic plants have the ability to deregulate host stomatal control (Press et al. 1988, 1990; Graves et al. 1990; Seel and Press 1994). Stomatal deregulation may decrease host water-use-efficiency and whole plant water relations (Goldstein et al. 1989; Sala et al. 2001). Herbivores such as aphids and gall-making insects may also act as resource sinks and manipulate host physiology and/or morphology (Crawley 1983; Louda et al. 1990), and the saliva of chewing herbivores can affect plant growth (Dyer 1980; McNaughton 1985a). Thus, herbivores and parasitic plants may both alter host physiology in various ways; however, the magnitude of the effects supports the hypothesis that the impacts of parasitic plants on host plant physiology exceed those of herbivores.

Consumption of hosts by parasitic plants and herbivores may not only differ in degree, but also in ecosystem impacts. Plant biomass consumed by herbivores may be transported to new locations, and returned to the soil as concentrated, labile waste materials that can have large impacts on plant production and community composition (Crawley 1983; McNaughton 1985b; Ruess et al. 1989; McNaughton et al. 1997; Steinhauer and Collins 2001). In contrast, plant biomass consumed by parasitic plants remains in the same general location without large changes in chemical composition or ecosystem properties (but see Press 1998).

Host-parasite interactions among animals and between animals and plants have provided models for understanding coevolution (Price 1980; Spencer 1988; Toft et al. 1991; Marquis 1992; Thompson 1994; Yan and Stevens 1995); studies of parasitic plants as selective forces, and of the reciprocal response of the parasite, are far fewer (Norton and Carpenter 1998). The lack of narrow host ranges among most parasitic plants suggests that coevolutionary selection is weak (but see above for exceptions such as dwarf mistletoe). Parasitic plants frequently reduce the reproductive output of their hosts (Silva and Martinez del Rio 1996; Puustinen and Salonen 1999b), but there is little evidence for directional selection, perhaps because the traits that mediate host choice are poorly understood. Medel (2000) studied the potential for *Tristerix aphyllus* mistletoes to select for defensive traits in two cactus species in northern Chile. He found that *Tristerix* decreased fruit production, seed number per fruit, and total seed output of one of the species, *Echinopsis chilensis*, and appeared to select for longer spines that deter the birds that disperse *Tristerix* seeds.

The net effect of herbivory on the growth rate, final biomass, or reproduction of a plant can be negative, neutral, or positive, with the latter generally referred to as 'compensatory growth'. The large and controversial body of literature on compensatory responses of plants to herbivory (Owen and Wiegert 1976; Belsky 1986; Crawley 1987; Paige and Whitham 1987; Machinski and Whitham 1989; Belsky et. al. 1993; Trumble et al. 1993; de Mazancourt et al. 2001) is paralleled by only a few studies of plant responses to damage by parasitic plants (Seel and Press 1996; Puustinen and Salonen 1999b). Comparing the responses of hosts to consumption by parasitic plants versus herbivores may provide new insights into the general phenomenon of compensatory growth.

Impacts on communities

Like herbivores, parasitic plants can have strong impacts on the communities in which they occur, altering plant community biomass, species composition, diversity and dynamics. Herbivores and parasitic plants both mediate interactions between host plants and other species such as parasitic nematodes and mycorrhizal fungi, and both may benefit from sequestered secondary metabolites. Interactions between parasitic plants and hosts, however, can differ from plant-herbivore interactions because some parasites simultaneously compete with the host plants that they consume.

Parasitic plants can be divided into holoparasites, which lack chlorophyll and derive all their resources from their host, and hemiparasites, which contain chlorophyll and derive only part of their resources from their host. Like herbivores (McNaughton 1985b; Hay and Fenical 1988), holoparasites commonly reduce the total biomass of the plant community (Pennings and Callaway 1996). Although hemiparasitic plants also reduce the biomass of their host community, this reduction can occasionally be compensated for, or even exceeded by, the production of the parasite (Marvier 1996; Joshi et al. 2000). Thus, the net effect of a hemiparasite on total plant community biomass can be negative, neutral or positive, although negative effects are most typical (Mizianty 1975; Matthies 1995, 1996, 1998; Marvier 1998b; Matthies and Egli 1999; Joshi et al. 2000).

The fact that hemiparasites are partially autotrophic means that they compete (primarily for light) with their hosts. This difference in resource capture between herbivores and hemiparasites causes the latter to be limited in distribution to relatively nutrient-poor, low-biomass habitats (Matthies 1995; Smith 2000). In sites with low productivity, competition for light is minimal, and hemiparasites can be highly successful. In contrast, at sites with high vegetation biomass, the negative effects of competition for light may outweigh the benefits of parasitism such that autotrophic plants outcompete hemiparasites. In comparison, the abundance of herbivores generally increases with plant productivity (Oksanen et al. 1981; Crawley 1983; McCauley et al. 1988).

Herbivores commonly alter the composition of plant communities (Bryant et al. 1991; Louda et al. 1990). In the same way, since parasitic plants selectively depress the biomass of preferred host taxa, plant parasitism can alter the competitive balance between preferred and non-preferred hosts (Gibson and Watkinson 1991; Matthies 1996; Callaway and Pennings 1998; but see Matthies and Egli 1999). As a result of this indirect effect, the species composition of the non-parasitic vegetation may differ between communities with and without parasitic plants (Gibson and Watkinson 1992; Pennings and Callaway 1996; Joshi et al. 2000). The strength of the impact has been suggested to depend on the virulence and degree of host-specificity of the parasite, with the most virulent and specialized parasites having the largest impact on community structure (Gibson and Watkinson 1992).

Virulence may differ not only between species of parasites but also across environmental gradients, as illustrated by our studies of the dodder, *Cuscuta salina*, in a southern California salt marsh (Fig. 2). *Cuscuta* is more virulent at higher elevations in the marsh than at lower elevations (Fig. 2A). The reason for this variation has not been explored, but it is likely due to increased tidal flooding at lower elevations causing stress in *Cuscuta*. In higher marsh zones, *Cuscuta* prefers to infect *Salicornia* and avoids *Arthrocnemum*, *Frankenia* and *Limonium* (Fig. 2B). In lower marsh zones, *Cuscuta* slightly prefers to attack *Jaumea* versus *Salicornia*, but both are readily attacked (Pennings and Callaway 1996). In the absence of the parasite, plants compete to create vegetation pattern across the marsh landscape. *Arthrocnemum* and *Salicornia* strongly compete at their border (Pennings and Callaway 1992), and *Salicornia* appears to be competitively dominant over *Frankenia* and *Limonium* in the high-*Salicornia* zone (Pennings and Callaway 1996). At lower elevations, *Jaumea* is competitively dominant over *Salicornia* (Fig. 2C). These differences in virulence, host-preference, and community interactions combine to produce different types of parasite effects at different elevations. At the *Arthrocnemum*-*Salicornia* border, *Cuscuta* preferentially attacks *Salicornia* and indirectly favors *Arthrocnemum*, releasing it from competition and allowing it to expand to lower elevations (Fig. 2D). In the high-*Salicornia* zone, *Cuscuta* again preferentially attacks S*alicornia*, indirectly favoring *Limonium* and *Frankenia* (Fig. 2E). In the deep-*Salicornia* zone, *Cuscuta* is not very virulent, and it readily attacks both *Salicornia* and *Jaumea*. Because both virulence and preference are weak in this marsh zone, *Cuscuta* has no effect on the competitive interaction between the two potential hosts (Fig. 2F).

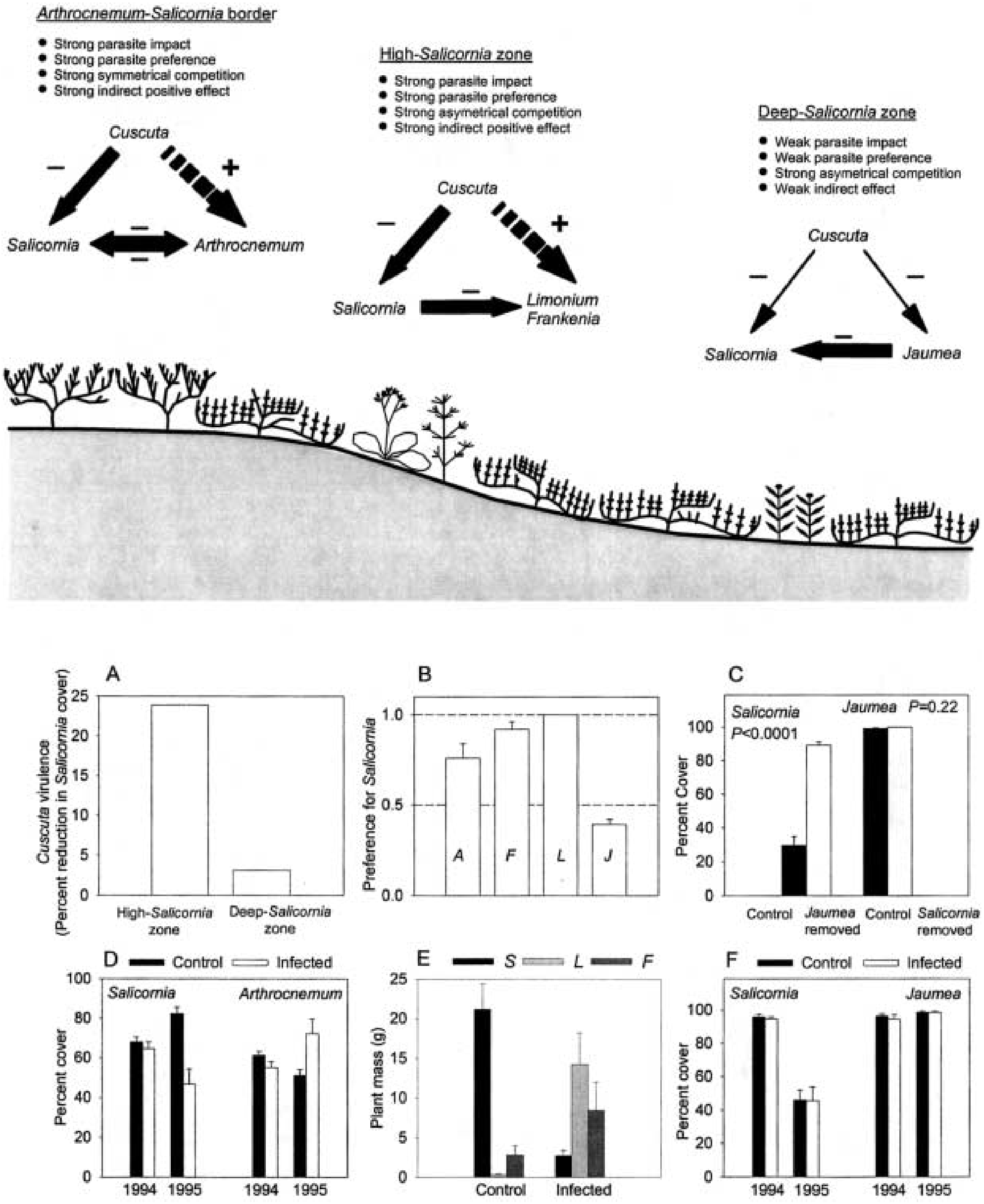

Fig. 2A–F Community impacts of dodder, *Cuscuta salina*, at three elevational zones in a southern California salt marsh. Zones differ in elevation and plant composition (Pennings and Callaway 1992, 1996; Callaway and Pennings 1998). *Top*: schematic of marsh zones and biological interactions. *Solid arrows* indicate direct effects, *dashed arrows* indicate indirect effects, effect strength is indicated by width of arrow. *Bottom*: **A** Virulence of *Cuscuta* (also see Pennings and Callaway 1996). Forty 0.5×0.5 m plots were marked in the high-*Salicornia* and deep-*Salicornia* zones in May 1994. All plots initially had 100% cover of *Salicornia*. In each zone, 10 "infected" plots had 98–100% cover of *Cuscuta* and 10 control plots had no *Cuscuta*. Cover of *Salicornia* was measured again the following May, and virulence calculated by subtracting the mean values for infected plots (High-*Salicornia* zone: 76±7 (SE); deep-*Salicornia* zone: 97±1) from mean values for control plots (High-*Salicornia* zone: 100±0; deep-*Salicornia* zone: 100±0). (B) Preference for *Salicornia* versus "A", *Arthrocnemum*; "F", *Frankenia*; "L", *Limonium*; "J", *Jaumea*. Preference index (±SE) varies from 0 (strongly avoided) to 1 (strongly preferred); 0.5 indicates no preference. All bars are significantly different from 0.5 (data from Pennings and Callaway 1996; also see Callaway and Pennings 1998). **C** Competitive interactions between *Salicornia* and *Jaumea*. *Jaumea* occurs as discrete patches in the low marsh. Twenty 0.5×0.5 m plots were established on each side of the border between *Salicornia* and *Jaumea* in June 1997. S*alicornia* was removed from half of the patches that it dominated, and *Jaumea* from half of the patches that it dominated. Weeding was repeated in 1998. In April 1999, plant cover was recorded in each patch. Data are means±SE. Removing *Jaumea* strongly increased *Salicornia* cover, but removing *Salicornia* had no effect on *Jaumea* cover, indicating that *Jaumea* was competitively dominant over *Salicornia*. These experiments were conducted during a period when *Jaumea* was expanding in cover, and may not reflect the long-term competitive balance between these two species. **D** Impact of *Cuscuta* at the *Arthrocnemum*-*Salicornia* border. Over time, *Salicornia* decreased and *Arthrocnemum* increased in plots infected with *Cuscuta* (data from Callaway and Pennings 1998). **E** Impact of *Cuscuta* in the high-S*alicornia* zone. Large patches of *Cuscuta* suppress *Salicornia* and favor *Limonium* and *Frankenia* (data from Pennings and Callaway 1996). **F** Impact of *Cuscuta* in the deep-*Salicornia* zone. Twenty-two plots were located on the edges of *Jaumea* patches in the deep-*Salicornia* zone in May 1994; plots initially had >90% cover of both *Jaumea* and *Salicornia*; 11 "infected" plots also had 98–100% cover of *Cuscuta* whereas 11 control plots had no *Cuscuta*. Plant cover was measured again in May 1995. *Cuscuta* infection did not affect cover of *Salicornia* or *Jaumea*, but cover of *Salicornia* decreased over time as *Jaumea* patches expanded (these long-term changes in *Jaumea* patch size were probably driven by long-term variation in climate)

In cases where parasites mediate changes in species composition, these changes may increase or decrease plant diversity, depending on whether the preferred hosts are common or rare in the absence of the parasite (Gibson and Watkinson 1992; Joshi et al. 2000). Parasitic plants might also mediate community diversity in nutrient-poor systems by altering the distribution and recalcitrance to decomposition of plant litter (Press 1998); however, this hypothesis remains to be tested.

If parasites have strong effects on host survival, they may drive preferred hosts locally extinct, and then go locally extinct themselves. Once the parasite disappears, conditions should then favor the re-establishment of the original vegetation. The dodder *Cuscuta salina* may drive this kind of vegetation cycle in coastal salt marshes (Pennings and Callaway 1996). Similarly, in a tidal freshwater marsh, abundances of *C. gronovii* and its preferred host, *Impatiens capensis* (both annuals), appear to cycle over time, suggesting that *Cuscuta* limits seed production of *Impatiens*, and *Impatiens* abundance in turn limits *Cuscuta* success (Leck and Simpson 1995). In the same way, interactions between herbivores and plants may also lead to various types of cyclical behavior (Yeaton 1978; Bryant 1981; Oksanen et al. 1981; Bryant et al. 1983, 1985; McNaughton 1985b; Louda et al. 1990).

The impacts of parasitic plants on their hosts create the potential for a diverse suite of indirect interactions between parasitic plants and other species in the community. Parasitic plants may compete with other species that consume plants, such as herbivores and parasitic nematodes, because all consumers are likely to have negative effects on the host, which represents a shared and potentially limiting resource (Gomez 1994; Salonen and Puustinen 1996; Puustinen and Salonen 1999a; Puustinen et al. 2001; Puustinen and Mutikainen 2001). Alternatively, by weakening hosts, parasitic plants might make them more vulnerable to attack by other consumers (Stevens and Hawksworth 1970; Scharpf 1975). Parasitic plants may also interact with the mycorrhizae of their hosts. Infection by parasitic plants, like damage caused by herbivores (Gehring and Whitham 1991, 1994, 1995), can reduce levels of mycorrhizal colonization on host plants (Gehring and Whitham 1992; Davies and Graves 1998). Whether herbivores and parasitic plants suffer or benefit from mycorrhizal colonization of the host depends on whether mycorrhizae most affect host defenses or host biomass and nutritional quality (Sanders et al. 1993; Gehring and Whitham 1994; Davies and Graves 1998; Salonen et al. 2000). Finally, because parasitic plants can change the morphology of their hosts, they are likely to affect species that use plants as a habitat. For example, mistletoe infection increases the density and diversity of forest insects and birds (Stevens and Hawksworth 1970; Scharpf 1975; Bennetts et al. 1996). We are just beginning to scratch the surface of all these types of indirect effects involving parasitic plants, and more studies of these interactions are needed. In particular, since interactions among parasitic plants and other organisms may be mediated by a wide variety of biotic and abiotic factors, results of pot and mesocosm studies need to be corroborated by studies conducted in the field.

Finally, the composition of the plant community may in turn affect interactions between parasitic plants and their herbivores. Like herbivores (Rowell-Rahier and Pasteels 1992; Harborne 1993), parasitic plants obtain a wide variety of compounds from their host plants (Govier et al. 1967; Wallace et al. 1978; Rozema et al. 1986; Seel and Press 1993; Graves 1995; Marvier 1996; Kelly and Horning 1999), including both compounds of nutritional value (Govier et al. 1967; Klaren and Janssen 1978; Page 1995; Tennakoon and Pate 1996; Marvier 1998a) and others such as secondary metabolites that may function as defenses (Boonsong and Wright 1961; Stermitz et al. 1989, 1993; Boros et al. 1991; Mead et al. 1992; Adler and Wink 2001; L.S. Adler, unpublished data). As a result, which host species a parasitic plant is attached to can affect its vulnerability to herbivores (Harvey 1966; Marvier 1996, 1998a; Adler 2000; L.S. Adler, in preparation; Adler et al. 2001; but see Stermitz et al. 1989).

Future directions

Parasitic plants provide a novel opportunity to explore the kingdom-level generality of plant-herbivore and parasite-host theories. Moreover, the ability of parasitic plants to sequester a variety of compounds from their hosts provides an under-utilized approach to studying effects of plant secondary metabolites and hormones (e.g., Adler 2000). There appear to be broad similarities between parasitic plants and herbivores. Where exceptions occur, these are linked to fundamental differences between plants and animals in mobility, hormonal and elemental composition, and resource capture. Some of the comparisons drawn in this paper are based on very few studies and are quite speculative, and there are many areas that are ripe for further research. In particular, we know relatively little about the basis for host preferences of parasitic plants, about defenses of host plants and traits of hosts that affect parasite vigor, about the selective pressures that parasitic plants impose on hosts, and about multi-species interactions mediated by parasitic plants. Finally, our current knowledge of the biology of parasitic plants is dominated by laboratory studies, and by studies of crop pests. In order to place the knowledge gained from these studies into context, there is a need for more field studies of parasitic plants in the communities in which they naturally occur.

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References

Adler LS (2000) Alkaloid uptake increases fitness in a hemiparasitic plant via reduced herbivory and increased pollination. Am Nat 156:92–99

Adler LS, Wink M (2001) Transfer of alkaloids from hosts to hemiparasites in two *Castilleja-Lupinus* associations: analysis of floral and vegetative tissues. Biochem Syst Ecol 29:551–561

Adler LS, Karban R, Strass SY (2001) Direct and indirect effects of alkaloids on plant fitness via herbivory and pollination. Ecology 82:2032–2044

Appel HM (1993) Phenolics in ecological interactions: the importance of oxidation. J Chem Ecol 19:1521–1552

Atsatt PR (1977) The insect herbivore as a predictive model in parasitic seed plant biology. Am Nat 111:579–612

Atsatt PR (1983) Host-parasite interactions in higher plants. In: Lange OL, Nobel PS, Osmond CB, Ziegler H (eds) Encyclopedia of plant physiology, vol 12C. Springer, Berlin Heidelberg New York, pp 519–535

Atsatt PR, Strong DR (1970) The population biology of annual grassland hemiparasites. I. The host environment. Evolution 24:278–291

Barlow BA, Wiens D (1977) Host-parasite resemblance in Australian mistletoes: the case for cryptic mimicry. Evolution 31:69–84

Behmer ST, Elias DO (2000) Sterol metabolic constraints as a factor contributing to the maintenance of diet mixing in grasshoppers (Orthoptera: Acrididae). Physiol Biochem Zool 73:219–230

Behmer ST, Grebenok RJ (1998) Impact of dietary sterols on life-history traits of a caterpillar. Physiol Entomol 23:165–175

Belsky AJ (1986) Does herbivory benefit plants? A review of the evidence. Am Nat 127:870–892

Belsky AJ, Carlson WP, Jensen CL, Fox GA (1993) Over-compensation by plants – herbivore optimization or red herring? Evol Ecol 7:109–121

Bennetts RE, White GC, Hawksworth FG, Severs SE (1996) The influence of dwarf mistletoe on bird communities in Colorado ponderosa pine forests. Ecol Appl 6:899–909

Bernays EA (1989) Host range in phytophagous insects: the potential role of generalist predators. Evol Ecol 3:299–311

Bernays E, Graham M (1988) On the evolution of host specificity in phytophagous arthropods. Ecology 69:886–892

Bernays, EA, Bright KL, Gonzalez N, Angel J (1994) Dietary mixing in a generalist herbivore: tests of two hypotheses. Ecology 75:1997–2006

Boonsong C, Wright SE (1961) The cardiac glycosides present in mistletoes growing on *Nerium oleander*. Aust J Chem 14:449–457

Boros CA, Marshall DR, Caterino CR, Stermitz FR (1991) Iridoid and phenylpropanoid glycosides from *Orthocarpus* spp. Alkaloid content as a consequence of parasitism on *Lupinus*. J Nat Prod 54:506–513

Bringmann G, Schlauer J, Rückert M, Wiesen B, Ehrenfeld K, Proksch P, Czygan F-C (1999) Host-derived acetogenins involved in the incompatible parasitic relationship between *Cuscuta reflexa* (Convolvulaceae) and *Ancistrocladus heyneanus* (Ancistrocladaceae). Plant Biol 1:581–584

Brochot NE, Tinnin RO (1986) The effect of dwarf mistletoe on starch concentration in the twigs and needles of lodgepole pine. Can J For Res 16:658–660

Bryant JP (1981) Phytochemical deterrence of snowshoe hare browsing by adventitious shoots of four Alaskan trees. Science 213:889–890

Bryant JP, Chapin FS III, Klein DR (1983) Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. Oikos 40:357–368

Bryant JP, Wieland GD, Clausen T, Kuropat P (1985) Interactions of snowshoe hare and feltleaf willow in Alaska. Ecology 66:1564–1573

Bryant JP, Provenza FD, Pastor J, Reichardt PB, Clausen TP, du Toit JT (1991) Interactions between woody plants and browsing mammals mediated by secondary metabolites. Annu Rev Ecol Syst 22:431–446

Calder DM (1983) Mistletoes in focus: an introduction. In: Calder D, Bernhardt P (eds). The biology of mistletoes. Academic Press, Sydney, pp 1–18

Callaway RM, Pennings SC (1998) Impact of a parasitic plant on the zonation of two salt marsh perennials. Oecologia 114:100–105

Chiarello N, Hickman JC, Mooney HA (1982) Endomycorrhizal role in interspecific transfer of phosphorus in a community of annual plants. Science 217:941–943

Chuang T-I, Heckard LR (1971) Observations on root-parasitism in *Cordylanthus* (Scrophulariaceae). Am J Bot 58:218–228

Cook CE, Whichard LP, Wall ME, Egley GH, Coggon P, Luhan PA, McPhail AT (1972) Germination stimulants. II. The structure of strigol–a potent seed germination stimulant for witchweed (*Striga lutea* Lour.). J Am Chem Soc 94:6198–6199

Crawley MJ (1983) Herbivory: the dynamics of animal-plant interactions. University of California Press, Berkeley

Crawley MJ (1987) Benevolent herbivores? Trends Ecol Evol 2:167–168

Davies DM, Graves JD (1998) Interactions between arbuscular mycorrhizal fungi and the hemiparasitic angiosperm *Rhinanthus minor* during co-infection of a host. New Phytol 139:555–563

De Bock F, Fer A (1992) Effects of abscisic acid on the transfer of sucrose from host, *Pelargonium zonale* (L.) Aiton, to a phanerogamic parasite *Cuscuta reflexa* Roxb. Aust J Plant Physiol 19:679–691

De Mazancourt C, Loreau M, Dieckmann U (2001) Can the evolution of plant defense lead to plant-herbivore mutualism? Am Nat 158:109–123

Drennan DSH, El-Hiweris SO (1979) Changes in growth substances in *Sorghum vulgare* infected by *Striga hermonthica*. In: Musselman LJ, Worsham AD, Eplee RE (eds) Proceedings, 2nd International Symposium on Parasitic Weeds, Raleigh. North Carolina State University, Raleigh, pp 144–145

Dyer MI (1980) Mammalian epidermal growth factor promotes plant growth. Proc Natl Acad Sci USA 77:4836–4837

Edwards WGH (1972) *Orobanche* and other plant parasite factors. In: Harborne JB (ed) Phytochemical ecology. Academic Press, New York, pp 235–248

Ehleringer JR, Schultze E-D, Ziegler H, Lange OL, Farquhar GD, Cowan IR (1985) Xylem mistletoes: water or nutrient parasites? Science 227:1479–1481

Ehleringer JR, Ullmann I, Lange OL, Farquhar GD, Cowan IR, Schulze E-D, Ziegler H (1986a) Mistletoes: a hypothesis concerning morphological and chemical avoidance of herbivory. Oecologia 70:234–237

Ehleringer JR, Cook CS, Tiezen LL (1986b) Comparative water use and nitrogen relationships in a mistletoe and its host. Oecologia 68:279–284

Francis R, Read DJ (1984) Direct transfer of carbon between plants connected by vesicular-arbuscular mycorrhizal mycelium. Nature 307:53–56

Gehring CA, Whitham TG (1991) Herbivore-driven mycorrhizal mutualism in insect–susceptible pinyon pine. Nature 353:556–557

Gehring CA, Whitham TG (1992) Reduced mycorrhizae on *Juniperus monosperma* with mistletoe: the influence of environmental stress and tree gender on a plant parasite and a plant-fungal mutualism. Oecologia 89:298–303

Gehring CA, Whitham TG (1994) Interactions between aboveground herbivores and the mycorrhizal mutualists of plants. Trends Ecol Evol 9:251–255

Gehring CA, Whitham TG (1995) Duration of herbivore removal and environmental stress affect the ectomycorrhizae of pinyon pines. Ecology 76:2118–2123

Gibson CC, Watkinson AR (1989) The host range and selectivity of a parasitic plant: *Rhinanthus minor* L. Oecologia 78:401–406

Gibson CC, Watkinson AR (1991) Host selectivity and the mediation of competition by the root hemiparasite *Rhinanthus minor*. Oecologia 86:81–87

Gibson CC, Watkinson AR (1992) The role of the hemiparasitic annual *Rhinanthus minor* in determining grassland community structure. Oecologia 89:62–68

Goldstein G, Rada F, Sternberg L, Burguera M, Orozco A, Montilla M, Zabala O, Azocar A, Canales MJ, Celis A (1989) Gas exchange and water balance of a mistletoe species and its mangrove hosts. Oecologia 78:176–183

Gómez JM (1994) Importance of direct and indirect effects in the interaction between a parasitic angiosperm (*Cuscuta epithymum*) and its host plant (*Hormathophylla spinosa*). Oikos 71:97–106

Govier RN, Harper JL (1965) Angiospermous hemiparasites. Nature 205:722–723

Govier RN, Nelson MD, Pate JS (1967) Hemiparasitic nutrition in angiosperms. I. The transfer of organic compounds from host to *Odontites verna* (Bell.) Dum. (Scrophulariaceae). New Phytol 66:285–297

Graves JD (1995) Host-plant responses to parasitism. In: Press MC, Graves JD (eds) Parasitic plants. Chapman & Hall, London, pp 206–225

Graves JD, Wylde A, Press MC, Stewart GR (1990) Growth and carbon allocation in *Pennisetum typoides* infected with the parasitic angiosperm *Striga hermonthica*. Plant Cell Environ 13:367–373

Grime JP, Mackey JML, Hillier SH, Read DG (1987) Floristic diversity in a model system using experimental microcosms. Nature 328:420–422

Harborne JB (1993) Introduction to ecological biochemistry, 4th edn. Academic Press, London

Harvey TL (1966) Aphids, dodder (*Cuscuta campestris*), and dodder-host plant interrelations. Ann Entomol Soc Am 59:1276–1282

Hay ME, Fenical W (1988) Marine plant-herbivore interactions: the ecology of chemical defense. Annu Rev Ecol Syst 19:111–145

Hay ME, Steinberg PD (1992) The chemical ecology of plant-herbivore interactions in marine versus terrestrial communities. In: Rosenthal GA, Berenbaum MR (eds) Herbivores: their interactions with secondary plant metabolites, 2E, vol II. Evolutionary and ecological processes. Academic Press, New York, pp 371–413

Hull RJ, Leonard OA 1964 Physiological aspects of parasitism in mistletoes (*Arceuthobium* and *Phoradendron*). I. The carbohydrate nutrition of mistletoes. Plant Physiol 39:996-1007

Ihl B, Jabob F, Sembdner G (1984) Studies on *Cuscuta reflexa* Roxb. V. The level of endogenous hormones in the parasite, *Cuscuta reflexa* and its host, *Vicia faba* L. and a suggested role of in the transfer of nutrients from host to parasite. J Plant Growth Regul 2:77–90

Ihl B, Jabob F, Sembdner G (1987) Investigation on the endogenous levels of abscisic acid in a range of parasitic phanerogams. J Plant Growth Regul 5:191–205

Joern A, Behmer ST (1998) Impact of diet quality on demographic attributes in adult grasshoppers and the nitrogen limitation hypothesis. Ecol Entomol 23:174–184

Joshi J, Matthies D, Schmid B (2000) Root hemiparasites and plant diversity in experimental grassland communities. J Ecol 88:634–644

Kelly CK (1990) Plant foraging: a marginal value model and coiling response in *Cuscuta subinclusa*. Ecology 71:1916–1925

Kelly CK (1992) Resource choice in *Cuscuta europaea*. Proc Natl Acad Sci USA 89:12194–12197

Kelly CK, Horning K (1999) Acquisition order and resource value in *Cuscuta attenuata*. Proc Natl Acad Sci USA 96:13219–13222

Khana SK, Viswanathan PN, Tewari CP, Krishnan PS Sanwal GG (1968) Biochemical aspects of parasitism by the angiosperm parasites: phenolics in parasites and hosts. Physiol Plant 21:949–959

Klaren CH, Janssen G (1978) Physiological changes in the hemiparasite *Rhinanthus serotinus* before and after attachment. Physiol Plant 42:151–155

Knutson DM (1979) How parasitic seed plants induce disease in other plants. In: Horsfall JG, Cowling EB (eds) Plant disease, an advanced treatise. Academic Press, San Diego, pp 293–312

Koskela T, Salonen V, Mutikainen P (2000) Local adaptation of a holoparasitic plant, *Cuscuta europaea*: variation among populations. J Evol Biol 13:749–755

Kuijt J (1969) The biology of parasitic plants. University of California Press, Berkeley

Leake JR (1994) The biology of myco-heterotrophic (‘saprophytic’) plants. New Phytol 127:171–216

Leck MA, Simpson RL (1995) Ten-year seed bank and vegetation dynamics of a tidal freshwater marsh. Am J Bot 82:1547–1557

Livingston WH, Brenner ML, Blanchette RA (1984) Altered concentrations of abscisic acid, indole-3-acetic acid and zeatin riboside associated with eastern dwarf mistletoe infections on black spruce. In: Hawksworth FG, Scharpf RF (eds) Biology of dwarf mistletoes. Proceedings of the Symposium. Fort Collins, Colorado. Gen Tech Rep RM-111. USDA Forest Service, Fort Collins, Colorado, pp 53–61

Louda SM, Keeler KH, Holt RD (1990) Herbivore influences on plant performance and competitive interactions. In: Grace JB, Tilman D (eds) Perspectives on plant competition. Academic Press, San Diego, pp 413–444

Lynn DG, Steffens JC, Kamat VS, Graden DW, Shabanowitz J, Riopel JL (1981) Isolation and characterization of the first host recognition substance for parasitic angiosperms. J Am Chem Soc 103:1868–1870

Machinski J, TG Whitham (1989) The continuum of plant responses to herbivory: the influence of plant association, nutrient availability, and timing. Am Nat 134:1–19

Marler MJ, Zabinski CA, Callaway RM (1999) Mycorrhizae indirectly enhance competitive effects of an invasive forb on a native bunchgrass. Ecology 80:1180–1186

Marquis RJ (1992) Selective impact of herbivores. In: Fritz RS, Simms EL (eds) Plant resistance to herbivores and pathogens. Ecology, evolution, and genetics. University of Chicago Press, Chicago, pp 301–325

Marshall JD, Ehleringer JR (1990) Are xylem-tapping mistletoes partially heterotrophic? Oecologia 84:244–248

Marshall JD, Dawson TE, Ehleringer JR (1994) Integrated nitrogen, carbon, and water relations of a xylem-tapping mistletoe following nitrogen fertilization of the host. Oecologia 100:430–438

Marvier MA (1996) Parasitic plant-host interactions: plant performance and indirect effects on parasite-feeding herbivores. Ecology 77:1398–1409

Marvier MA (1998a) A mixed diet improves performance and herbivore resistance of a parasitic plant. Ecology 79:1272–1280

Marvier MA (1998b) Parasite impacts on host communities: plant parasitism in a California coastal prairie. Ecology 79:2616–2623

Matthies D (1995) Parasitic and competitive interactions between the hemiparasites *Rhinanthus serotinus* and *Odontites rubra* and their host *Medicago sativa*. J Ecol 83:245–251

Matthies D (1996) Interactions between the root hemiparasite *Melampyrum arvense* and mixtures of host plants: heterotrophic benefit and parasite-mediated competition. Oikos 75:118–124

Matthies D (1998) Influence of the host on growth and biomass allocation in the two facultative root hemiparasites *Odontites vulgaris* and *Euphrasia minima*. Flora 193:187–193

Matthies D, Egli P (1999) Response of a root hemiparasite to elevated CO2 depends on host type and soil nutrients. Oecologia 120:156–161

McCauley E, Murdoch WM, Watson S (1988) Simple models and variation in plankton densities among lakes. Am Nat 132:383–403

McNaughton SJ (1985a) Interactive regulation of grass yield and chemical properties by defoliation, a salivary chemical and inorganic nutrition. Oecologia 65:478–486

McNaughton SJ (1985b) Ecology of a grazing ecosystem: the Serengeti. Ecol Monogr 55:259–294

McNaughton SJ, Banyikwa FF, McNaughton MM (1997) Promotion of the cycling of diet-enhancing nutrients by African grazers. Science 278:1798–1800

Mead EW, Looker M, Gardner DR, Stermitz FR (1992) Pyrrolizidine alkaloids of *Liatris punctata* and its root parasite, *Castilleja integra*. Phytochemistry 31:3255–3257

Medel R (2000) Assessment of parasite-mediated selection in a host-parasite system in plants. Ecology 81:1554–1564

Miller JR, Tocher RD (1975) Photosynthesis and respiration of *Arceuthobium tsugense* (Loranthaceae). Am J Bot 62:765–769

Mizianty M (1975) Influence of *Rhinanthus serotinus* (Schönheit) Obomy on the productivity and floristic composition of the meadow plant association. Fragm Florist Geobot (Krakow) 21:491–505

Moora M, Zobel M (1996) Effect of arbuscular mycorrhiza on inter- and intraspecific competition of two grassland species. Oecologia 108:79–84

Musselman LJ, Press MC (1995) Introduction to parasitic plants. In: Press MC, Graves JD (eds) Parasitic plants. Chapman and Hall, London, pp 1–13

Mutikainen P, Salonen V, Puustinen S, Koskela T (2000) Local adaptation, resistance, and virulence in a hemiparasitic plant-host plant relationship. Evolution 54:433–440

Norton DA, Carpenter MA (1998) Mistletoes as parasites: host specificity and speciation. Trends Ecol Evol 13:101–119

Norton DA, De Lange PJ (1999) Host specificity in parasitic mistletoes (Loranthaceae) in New Zealand. Funct Ecol 13:552–559

Oksanen L, Fretwell SD, Arruda J, Niemelä P (1981) Exploitation ecosystems in gradients of primary productivity. Am Nat 118:240–261

Owen DF, Wiegert RG (1976) Do consumers maximize plant fitness? Oikos 27:488–492

Page HM (1995) Variation in the natural abundance of ^{15}N in the halophyte, *Salicornia virginica*, associated with groundwater subsidies of nitrogen in a southern California salt-marsh. Oecologia 104:181–188

Paige KN, Whitham TG (1987) Overcompensation in response to mammalian herbivory: the advantage of being eaten. Am Nat 129:407–416

Parker C, Riches CR (1993) Parasitic weeds of the world: biology and control. CAB International, Wallingford, UK

Parker C, Musselman LJ, Polhill RM, Wilson AK (eds) (1984) Proceedings of the third international symposium on parasitic weeds, ICARDA/International Parasitic Seed Plant Research Group, 7–9 May 1984, Aleppo, Syria. ICARDA, Aleppo, Syria

Pennings SC, Callaway RM (1992) Salt marsh plant zonation: the relative importance of competition and physical factors. Ecology 73:681–690

Pennings SC, Callaway RM (1996) Impact of a parasitic plant on the structure and dynamics of salt marsh vegetation. Ecology 77:1410–1419

Pennings SC, Paul VJ (1992) Effect of plant toughness, calcification, and chemistry on herbivory by *Dolabella auricularia*. Ecology 73:1606–1619

Pennings SC, Nadeau MT, Paul VJ (1993) Selectivity and growth of the generalist herbivore *Dolabella auricularia* feeding upon complementary resources. Ecology 74:879–890

Pennings SC, Carefoot TH, Siska EL, Chase ME, Page TA (1998) Feeding preferences of a generalist salt-marsh crab: relative importance of multiple plant traits. Ecology 79:1968–1979

Press MC (1989) Autotrophy and heterotrophy in root hemiparasites. Trends Ecol Evol 4:258-263

Press MC (1998) Dracula or robin hood? A functional role for root hemiparasites in nutrient poor ecosystems. Oikos 82:609–611

Press MC, Graves JD (1995) Parasitic plants. Chapman and Hall, London

Press MC, Graves JD, Stewart GR (1988) Transpiration and carbon acquisition in root hemiparasitic angiosperms. J Exp Bot 39:1009–1014

Press MC, Graves JD, Stewart GR (1990) Physiology of the interaction of angiosperm parasites and their higher plant hosts. Plant Cell Environ 13:91–104

Price PW (1980) Evolutionary biology of parasites. Princeton University Press, Princeton, N.J. USA

Price PW (1983) Hypotheses on organization and evolution in herbivorous insect communities. In: Denno RF, McClure MS (eds) Variable plants and herbivores in natural and managed systems. Academic Press, New York, pp 559–598

Price PW, Westoby M, Rice B, Atsatt PR, Fritz RS, Thompson JN, Mobley K (1986) Parasite mediation in ecological interactions. Annu Rev Ecol Syst 17:487–505

Puustinen S, Mutikainen P (2001) Host-parasite-herbivore interactions: implications of host cyanogenesis. Ecology 82:2059–2071

Puustinen S, Salonen V (1999a) The effect of host defoliation on hemiparasitic-host interactions between *Rhinanthus serotinus* and two *Poa* species. Can J Bot 77:523–530

Puustinen S, Salonen V (1999b) Effects of intensity and duration of infection by a hemiparasitic plant, *Rhinathus serotinus*, on growth and reproduction of a perennial grass, *Agrostis capillaris*. Ecography 22:160–168

Puustinen S, Järvinen O, Tiilikkala K (2001) Asymmetric competition between a hemiparasitic plant and a cyst nematode on a shared host plant. Ecoscience 8:51–57

Rey L, Sadik A, Ferf A, Renaudin S (1991) Trophic relations of the dwarf mistletoe *Arceuthobium oxycedri* with its host *Juniperus oxycedrus*. J Plant Physiol 138:411–416

Riches CR, Parker C (1995) Parasitic plants as weeds. In: Press MC, Graves JD (eds) Parasitic plants. Chapman & Hall, London, pp 226–255

Robinson D, Fitter A (1999) The magnitude and control of carbon transfer between plants linked by a common mycorrhizal network. J Exp Bot 50:9–13

Rowell-Rahier M, Pasteels JM (1992) Third trophic level influences of plant allelochemicals. In: Rosenthal GA, Berenbaum MR, Herbivores:their interactions with secondary plant metabolites, 2E, vol II. Ecological and evolutionary processes. Academic Press, San Diego.

Rozema J, Broekman R, Arp W, Letschert J, Van Esbroek M, Punte H (1986) A comparison of the mineral relations of a halophytic hemiparasite and holoparasite. Acta Bot Neerl 35:105–109

Ruess RW, Hik DS, Jefferies RL (1989) The role of lesser snow geese as nitrogen processors in a sub-arctic salt marsh. Oecologia 79:23–29

Sahm A, Pfanz H, Grünsfelder M, Czygan F-C, Proksch P (1995) Anatomy and phenylpropanoid metabolism in the incompatible interaction of *Lycopersicon esculentum* and *Cuscuta reflexa*. Bot Acta 108:358–364

Sala A, Carey EV, Callaway RM (2001) Dwarf mistletoe affects whole-tree water relations of Douglas-fir and western larch primarily through changes in leaf to sapwood ratios. Oecologia 126:42–52

Salonen V, Puustinen S (1996) Success of a root hemiparasitic plant is influenced by soil quality and by defoliation of its host. Ecology 77:1290–1293

Salonen V, Setälä H, Puustinen S (2000) The interplay between *Pinus sylvestris*, its root hemiparasite, *Melampyrum pratense*, and ectomycorrhizal fungi: influences on plant growth and reproduction. Ecoscience 7:195–2000

Sanders IR, Koide RT, Shumway DL (1993) Mycorrhizal stimulation of plant parasitism. Can J Bot 71:1143–1146

Scharpf RF (1975) Dwarf mistletoe-insect relationships.In: Proceedings of the joint meeting, 26th annual Western Forest Insect Work Conference and 22nd annual Western International Forest Disease Work Conference (23–28 February, Monterey, California). U.S. Department of Agriculture Forest Service, Intermountain Forest and Range Experimental Station, Ogden, Utah, USA, pp 72–75

Schultze E-D, Ehleringer JR (1984) The effect of nitrogen supply on growth and water-use-efficiency of xylem-tapping mistletoes. Planta 162:268–275

Seel WE, Press MC (1993) Influence of the host on three sub-Arctic annual facultative root hemiparasites. I. Growth, mineral accumulation and above-ground dry-matter partitioning. New Phytol 125:131–138

Seel WE, Press MC (1994) Influence of the host on three sub-Arctic annual facultative root hemiparasites. II. Gas exchange characteristics and resource use-efficiency. New Phytol 127:37–44

Seel WE, Press MC (1996) Effects of repeated parasitism by *Rhinanthus minor* on the growth and photosynthesis of a perennial grass, *Poa alpina*. New Phytol 134:495–502

Seel WE, Cooper RE, Press MC (1993) Growth, gas exchange and water use efficiency of the facultative hemiparasite *Rhinanthus minor* associated with hosts differing in foliar nitrogen concentration. Physiol Plant 89:64–70

Silva A, Martinez del Rio C (1996) Effects of the mistletoe *Tristerix aphyllus* (Loranthaceae) on the reproduction of in cactus host *Echinopsis chilensis*. Oikos 75:437–442

Simard SW, Perry DS, Jones MD, Myrold DD, Durall DM, Molina R (1997) Net transfer of carbon between ectomycorrhizal tree species in the field. Nature 388:579–582

Smith D (2000) The population dynamics and community ecology of root hemiparasitic plants. Am Nat 155: 13–23

Snogerup B (1982) Host influence on northwest European taxa of *Odontites* (Scrophulariaceae). Ann Bot Fenn 19:17–30

Spencer KC (1998) Chemical mediation of coevolution. Academic Press, San Diego

Steffens JC, Lynn DG, Kamat VS, Riopel JL (1982) Molecular specificity of haustorial induction in *Agalinis purpurea* (L.). Ann Bot 50:1–7

Steffens JC, Roark JL, Lynn DG, Riopel JL (1983) Host recognition in parasitic angiosperms: use of correlation spectroscopy to identify long-range coupling in an haustorial inducer. J Am Chem Soc 105:1669–1671

Steinhauer EM, Collins SL (2001) Feedback loops in ecological hierarchies following urine deposition in tallgrass prairie. Ecology 82:1319–1329

Stermitz FR, Belofsky GN, Ng D, Singer MC (1989) Quinolizidine alkaloids obtained by *Pedicularis semibarbata* (Scrophulariaceae) from *Lupinus fulcratus* (Leguminosae) fail to influence the specialist herbivore *Euphydras editha* (Lepidoptera). J Chem Ecol 15:2521–2530

Stermitz FR, Foderaro TA, Li YX (1993) Iridoid glycoside uptake by *Castilleja integra* via root parasitism on *Penstemon teucrioides*. Phytochemistry 32:1151–1153

Stevens RE, Hawksworth FG (1970) Insects and mites associated with dwarf mistletoes. Research Note RM-59. U.S. Department of Agriculture Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo. USA

Strong DR, Lawton JH, Southwood TRE (1984) Insects on plants: community patterns and mechanisms. Blackwell, Oxford

Tennakoon KU, Pate JS (1996) Heterotrophic gain of carbon from hosts by the xylem-tapping root hemiparasite *Olax phyllanthi* (Olacaceae). Oecologia 105:369–376

Thompson JN (1994) The coevolutionary process. University of Chicago Press, Chicago, Ill. USA

Tinnin RO, Knutson DM (1980) Growth characteristics of the brooms on Douglas-fir caused by *Arceuthobium douglasii*. For Sci 26:149–158

Toft CA, Aeschlimann A, Bolis L (1991) Parasite-host associations: coexistence or conflict? Oxford University Press, Oxford

Trumble JT, Kolodny-Hirsch DM, Ting IP (1993) Plant compensation for herbivory. Annu Rev Entomol 38:93–119

Wallace A, Romney EM, Alexander GV (1978) Mineral composition of *Cuscuta nevadensis* Johnston (dodder) in relation to its hosts. Plant Soil 50:227–231

Walter LEF, Hartnett DC, Hetrick BAD, Schwab AP (1996) Interspecific nutrient transfer in a tallgrass prairie plant community. Am J Bot 83:180–184

Wanner J, Tinnin RO (1986) Respiration in lodgepole pine parasitized by American dwarf mistletoe. Can J For Res 16:1375–1378

Watkins NK, Fitter AH, Graves JD, Robinson D (1996) Carbon transfer between C_3 and C_4 plants linked by a common mycorrhizal network. quantified using stable carbon isotopes. Soil Biol Biogeochem 28:471–477

Watkinson AR, Gibson CC (1988) Plant parasitism: the population dynamics of parasitic plants and their effects upon plant community structure. In: Davy AJ, Hutchings MJ, Watkinson AR (eds) Plant population ecology. Blackwell, Oxford, pp 393–411

Worsham AD, Moreland DE, Klingman GC (1964) Characterization of the *Striga asiatica* (Witchweed) germination stimulant from *Zea mays* L. J Exp Bot 15:556–567

Yan G, Stevens L (1995) Selection by parasites on components of fitness in Tribolium beetles: the effects of intraspecific competition. Am Nat 146:795–813

Yeaton, RI (1978) A cyclical relationship between *Larrea tridentata* and *Opuntia leptocaulis* in the northern Chihuahuan desert. J Ecol 66:651–656