PROMYLEA LUNIGERELLA GLENDELLA DYAR (PYRALIDAE) FEEDS ON BOTH CONIFERS AND PARASITIC DWARF MISTLETOE (*ARCEUTHOBIUM* SPP.): ONE EXAMPLE OF FOOD PLANT SHIFTING BETWEEN PARASITIC PLANTS AND THEIR HOSTS

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ABSTRACT. Larvae of *Promylea lunigerella glendella* Dyar (Pyralidae, Phycitinae) feed on *Arceuthobium vaginatum* susp. *cryptopodum* (Hawks.) (Viscaceae), the Southwestern dwarf mistletoe, a parasite of *Pinus ponderosa* (Laws.) *scopulorum* (Pinaceae) at the Manitou Experimental Forest, U.S.D.A. Rocky Mountain Research Station, Woodland Park, Colorado. A previous food plant record for *P. lunigerella* describes the larvae as feeding on a variety of conifers. A careful evaluation of this record suggests it is reliable, and I conclude that *P. lunigerella* is actively shifting between dwarf mistletoe and conifer feeding, or has done so recently. My review of the literature on food plant use by lepidopteran herbivores of dwarf mistletoe and their relatives suggests that food plant shifts between parasitic plants and their hosts, and vice versa, have occurred multiple times and may be common among taxa that feed on parasitic and parasitized plants. These findings support a model of food plant shifting in which the close proximity necessarily maintained by parasitic plants and their hosts provides an ecological opportunity that facilitates food plant shifts between these taxonomically and chemically very dissimilar plants. Finally, I describe the life history of *P. lunigerella* larvae and compare them to those of *Dasypyga alternosquamella* Ragonot (Pyralidae), a closely related phycitine that also feeds on dwarf mistletoe at this same location.

Additional key words: *Mitoura* (Lycaenidae), *Filatima natalis* (Gelechiidae), *Chionodes* (Gelechiidae), *Euthalia* (Nymphalidae).

Insect herbivores, including lepidopterans, often specialize on individual species or groups of closely-related food plants (Ehrlich & Raven 1964, Holloway & Hebert 1979, Vane-Wright & Ackery 1988). The evolutionary and ecological mechanisms by which such specialist herbivores might switch to novel food plants have received considerable attention (Holloway & Hebert 1979, Denno & McClure 1983, Futuyma & Slatkin 1983, Strong et al. 1984, Vane-Wright & Ackery 1988). From these studies comes the prediction that food plant switches are most likely to occur between pants that are similar in phenotypic characters of importance to herbivores such as tissue chemistry. Closely related plants are likely to share such characters due to common ancestry, but taxonomically distant plants may share such characters due to convergence (Judd 1999). There has been relatively little said about how specialist herbivores might shift between taxonomically and phenotypically distinct plants, except to predict that such events are not likely to be common.

Promylea lunigerella glendella Dyar (Pyralidae, Phycitinae) was first described by Ragonot (1887) and the subspecies by Dyar (1906). The species range stretches from coastal British Columbia to California and east to Colorado. Larvae in British Columbia have been reported to feed as solitary defoliators on conifers including grand fir (*Abies grandis* (Doug. ex. D. Don) Lindl. (Pinaceae)), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco (Pinaceae)) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg. (Pinaceae)) (Prentice 1965). I report here on a population of *P. lunigerella* in Colorado that feeds on *Arceuthobium vaginatum* (Willd) Presl susp. *cryptopodum* (Engelm.) Hawksw. & Wiens (Viscaceae), the Southwestern dwarf mistletoe parasitizing ponderosa pine (*Pinus ponderosa* Laws. *scopulorum* (Pinaceae)). This novel food plant record suggests a recent or ongoing food plant shift in this species, despite the fact that dwarf mistletoes (*Arceuthobium* spp.) and conifers differ substantially in chemistry (Buckingham 1994) and are taxonomically unrelated.

Dwarf mistletoes (*Arceuthobium* spp.) are common parasites of conifers in North America, and they are fed upon by a number of specialist herbivores, including several species of Lepidoptera. Dwarf mistletoes are obligate parasites, and for this reason these plants occur in closer physical association than plants without host-parasite relationships. Consistent and close physical association of taxonomically and chemically distinct plants may lead to rates of herbivore food plant shifting higher than that found between plant taxa lacking this physical proximity (Holloway & Hebert 1979, Chew & Robbins 1988) due to what Strong et al. (1984) call increased "ecological opportunity." An opportunity-based model of food plant shifting predicts that herbivores shifting between parasitic plants and the hosts of those plants should be common.

To test this hypothesis I reviewed the food plant literature for dwarf mistletoe herbivores and their close relatives to identify what evidence there is to support the hypothesis that food plant shifts between parasitic plants and their hosts, and vice versa, are common. As part of this review, I also carefully inspected the previous report of *P. lunigerella* feeding on conifers (Prentice 1965) to assess its reliability. Finally, I provide natural and life history data on the larval stages of *P. lunigerella* and compare these larvae to *Dasypyga alternosquamella* Ragonot (Pyralidae), another phycitine herbivore of Southwestern dwarf mistletoe that occurs sympatrically with *P. lunigerella*.

MATERIALS AND METHODS

Life history of *P. lunigerella*. I conducted the field and laboratory work for this project at the Manitou Experimental Forest, an administrative unit of the U.S. Department of Agriculture Forest Service Rocky Mountain Experiment Station located in Woodland Park, Colorado (39°06′00″N, 105°05′00″W). Manitou includes several stands of ponderosa pines (*Pinus ponderosa* var. *scopulorum* Laws.(Pinaceae)) parasitized by Southwestern dwarf mistletoe (*A. vaginatum* subsp. *cryptopodum* Hawks. (Viscaceae)). This field site and the natural history of dwarf mistletoe are described more fully in Mooney (2001).

In a previous report (Mooney 2001), I described the natural- and life-history of *D. alternosquamella* Ragonot (Pyralidae, Phycitinae), a common herbivore of dwarf mistletoes throughout western North America (Heinrich 1920, Reich 1992). It was while conducting this work that I became aware that *P. lunigerella* was also feeding on dwarf mistletoe. Because *D. alternosquamella* and *P. lunigerella* are both phycitine pyralids, it was only after rearing larvae through pupation that I became aware that some of the animals with which I was working were not, in fact, *D. alternosquamella*. Consequently, the life history data reported here are not as complete as they would be had I expressly set out to study *P. lunigerella*.

I collected Southwestern Dwarf Mistletoe from the field between 30 June and 1 August 1999 in individual plastic bags and brought them into the lab on eight separate occasions. Individual plants ranged from 3–10 cm in height and in most cases only one or two plants were taken from any single host-pine. I observed larval feeding in the field, and in most cases the presence of larvae within these plants was indicated by their frass within and surrounding dwarf mistletoe shoots. Larvae were isolated from these plants using a dissecting microscope. In no instance was pine foliage or branch tissue collected, and all larvae were on dwarf mistletoe plants at the time of collection.

I reared *P. lunigerella* individually in clear plastic petri dishes lined with filter paper in a laboratory facility. The larvae were fed small (2–5 cm) shoots of dwarf mistletoe collected from the same general location as the larvae themselves, and they were replenished with fresh plant material approximately every third day. In all cases the larvae readily fed upon the dwarf mistletoe.

I wetted the filter paper linings of each petri dish on a daily basis. The lab building was neither heated nor cooled, and I stored the petri dishes in the open and near a window where they received indirect sunlight. I measured larval head capsule widths daily, and resting body lengths at the time of molting using a stereomicroscope with an ocular micrometer.

Comparison between species. Because these two pyralids are relatively close taxonomically, the larvae can be difficult to distinguish in the field. Anticipating that characters allowing such discrimination may be useful, I formally tested for differences in head capsule width and resting body lengths between the two species using the data presented in this paper on *P. lunigerella* and data on *D. alternosquamella* from Mooney (2001).

Reliability of previously published food plant record. It is possible that the previous claim of *P. lunigerella* feeding on conifers (Prentice 1965) is erroneous and that in fact the larvae were feeding on dwarf mistletoe in those trees. To evaluate this possibility, I carefully inspected the methods and dataset presented by Prentice (1965). I then consulted Hawksworth et al. (1996) and summarized the ranges for species of dwarf mistletoe known to parasitize the conifers from which *P. lunigerella* were reportedly collected. Dwarf mistletoes are of great commercial importance as parasites of conifers in North America and have been called "the single most destructive pathogen of commercially valuable coniferous timber trees in . . . western Canada and western United States" (Hawksworth et al. 1996). For these reasons, they have been thoroughly studied, and the compendium by Hawksworth et al. (1996) is widely accepted as the authoritative source of information about the geographic distributions of these parasites and the coniferous hosts they use. By cross referencing data from Hawksworth et al. (1996) and Prentice (1965) I assessed the likelihood that dwarf mistletoes occurred on the conifers from which *P. lunigerella* larvae were collected.

Literature review. Lepidopteran larvae known to specialize on dwarf mistletoe (*Arceuthobium* spp.) are the following: *Mitoura spinetorum* Hewitson (Lycaenidae), *Mitoura johnsoni* Skinner, *Filatima natalis* Heinrich (Gelechiidae), *D. alternosquamella* Ragonot (Pyralidae) (Stevens & Hawksworth 1970, Hawksworth et al. 1996, Mooney 2001), and now *P. lunigerella*. In order to identify possible examples of food plant shifts between dwarf mistletoes and conifers I conducted a literature review to identify whether the relatives of any or all of these taxa include conifer feeders. Although examples of sister taxa feeding on dwarf mistletoe and conifers provides evidence for a recent food plant shift, more data are needed to infer the direction of the food plant shift. Such sister taxa examples by themselves not indicate whether the shift was from conifers to dwarf mistletoe, or vice versa.

TABLE 1.   Mean values for head capsule width, pre- and post-molt body lengths of resting larvae, and instar duration for *Promylea lunigerella*. Sample sizes and standard errors follow each measurement.

Instar	x̄ head capsule width mm (N, SE)	x̄ post-molt body length mm (N, SE)	x̄ pre-molt body length mm (N, SE)	x̄ instar duration days (N, SE)
1	—	—	—	—
2	—	—	2.09 (1, —)	—
3	0.31 (3, 0.0008)	2.1 (1, —)	2.71 (3, 0.14)	9.0 (2, 3.0)
4	0.44 (9, 0.0016)	2.72 (3, 0.14)	3.71 (6, 0.25)	8.0 (4, 1.2)
5	0.58 (11, 0.0020)	3.72 (6, 0.25)	5.84 (8, 0.49)	8.3 (7, 0.68)
6	0.76 (16, 0.00003)	5.85 (8, 0.49)	9.12 (3, 1.16)	12.2 (10, 1.00)

RESULTS

Life history of *P. lunigerella*. I reared 16 *P. lunigerella* larvae through pupation, although none of these were collected as eggs. One larva passed through five instars before pupating, but I believe this species normally has six instars for several reasons. *Dasypyga alternosquamella* has six larval instars (Mooney 2001) and *Dasypyga* and *Promylea* are likely sister genera (Heinrich 1956). The head capsule width and length of this earliest *P. lunigerella* larvae were nearly identical to those of a second instar *D. alternosquamella*. The last three larval instars of *P. lunigerella* are significantly smaller than the last three larval instars of *D. alternosquamella* (see below). For *P. lunigerella* to have only five instars would require that this species hatch at a size 30% larger than the relatively closely related *D. alternosquamella*, but pupate at a size only half that of *D. alternosquamella*.

Following this assumption of six larval instars, the 16 larvae I reared through pupation were collected from the field in the following life-stage distribution: One second instar, three third instar, five fourth instar, three fifth instar, and four sixth instar. Head capsule widths and larval resting lengths for *P. lunigerella* are presented in Table 1 according to this assumption, and the same data for *D. alternosquamella* from Mooney 2001 are presented in Table 2.

Promylea lunigerella and *D. alternosquamella* were collected at the same time and from the same dwarf mistletoe plants. A comparison of the instar distributions from these collections (Fig. 1) suggests that the time of emergence and oviposition of *P. lunigerella* is substantially earlier than that of *D. alternosquamella*, which occurs in mid-June (Mooney 2001). The median and modal life-stage for *P. lunigerella* was fourth instar larvae and for *D. alternosquamella* was egg-first instar larvae, i.e., the former precedes the later by three to four instars. Based on instar duration data I estimate *P. lunigerella* emergence precedes *D. alternosquamella* by approximately three weeks, i.e., *P. lunigerella* emerges in late May.

Comparison between species. There were sufficient sample sizes to compare larval lengths, head capsule widths, and instar duration between fourth, fifth, and sixth instar *P. lunigerella* and *D. alternosquamella*. I tested for differences between species in these three characters using separate one-way ANOVAs for each instar. I accounted for the increased likelihood of type I error with multiple tests using a Bonferroni adjustment (Zar 1999).

Promylea lunigerella was significantly smaller in length than *D. alternosquamella* in fourth ($F_{1,11}$ = 32.98, p < 0.0001), fifth ($F_{1,16}$ = 18.60, p = 0.0005) and sixth ($F_{1,6}$ = 13.13, p = 0.011) instars and had significantly smaller head capsule widths in fifth ($F_{1,18}$ = 11.13, p = 0.0037) and sixth ($F_{1,23}$ = 389.36, p < 0.0001) instars at the Bonferroni adjusted alpha of 0.016. There were not significant differences in fourth instar head capsule widths ($F_{1,16}$ = 0.69, p = .487), nor in duration of fourth ($F_{1,11}$ = 2.42, p = 0.1483), fifth ($F_{1,15}$ = 1.77, p = 0.2035), and sixth ($F_{1,17}$ = 0.71, p = 0.4104) instar larvae.

I reared 25 larvae through pupation for the life history work described here and in Mooney 2001. Of

TABLE 2.   Mean values for head capsule width, pre- and post-molt body lengths of resting larvae, and instar duration for *Dasypyga alternosquamella*. Sample sizes (N) are given in column two. Standard errors follow each measurement. Post-molt body length for instar one is size at time of hatching. Reproduced from Mooney (2001).

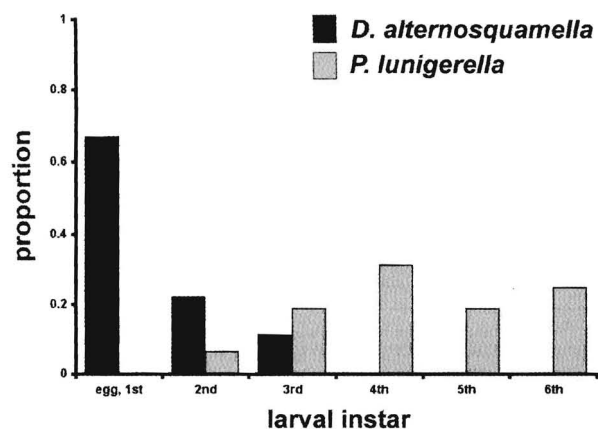| Instar	N	x̄ head capsule width mm (SE)	x̄ post-molt body length mm (SE)	x̄ pre-molt body length mm (SE)	x̄ instar duration days (SE)
1	5	0.15 (0.005)	1.19 (0.048)	1.61 (0.093)	7.33 (0.558)
2	8	0.20 (0.004)	1.62 (0.093)	2.30 (0.088)	6.5 (0.563)
3	9	0.29 (0.010)	2.31 (0.088)	3.25 (0.124)	6.38 (0.263)
4	9	0.43 (0.012)	3.26 (0.124)	5.36 (0.288)	6.33 (0.471)
5	9	0.64 (0.011)	5.37 (0.288)	8.25 (0.310)	7.11 (0.351)
6	9	0.96 (0.111)	8.26 (0.310)	16.56 (1.034)	14.78 (0.760)

FIG. 1.   Distributions of life-stages of *P. lunigerella* (N = 16 larvae) and *D. alternosquamella* (N = 9) collected between 30 June and 1 August 1999.

these, 16 were *P. lunigerella* and nine were *D. alternosquamella*. These data suggest a relative abundance of approximately 2:1. The precision of this estimate is reduced by the following facts: (1) the two species were at different stages in their phenology and likely had experienced different rates of mortality prior to my collections, (2) differences in larval sizes due to phenological differences likely resulted in unequal rates of detection during larval collection, and finally, (3) not all larvae collected survived through pupation and the two species may have suffered different rates of mortality in the laboratory.

Reliability of previously published food plant record. The *P. lunigerella* host plant data from Prentice (1965) are summarized in Table 3. A total of 347 larvae were found feeding on *Abies amabilis* (Dougl.) Forbes (Pinaceae), *A. grandis* (Pinaceae), *Picea sitchensis* (Bong.) Carr. (Pinaceae), *Pseudotsuga menziesii* and *Tsuga heterophylla* in the southern coastal area of British Columbia near Vancouver ("coastal B.C.") and in interior B.C. near Lillooet ("interior B.C."). These larvae were from 118 separate collections, where each collection is from a separate locality, but distance between localities is unclear. The number of collections and the number of larvae from the coastal and interior regions were not specified.

Using dwarf mistletoe species range data from Hawksworth et al. (1996) I determined which species of dwarf mistletoes parasitize the conifers listed by Prentice (1965), and whether the parasite range extends to either coastal or interior B.C. Of the six dwarf mistletoe species parasitizing these five conifers, only *A. tsugense* (Rosendahl) G. N. Jones occurs in British Columbia, and its range is limited to the coastal region. Furthermore, while *A. tsugense* commonly parasitizes

Abies amabalis, it very rarely parasitizes *A. gandis* and *T. heterophylla* (Hawksworth et al. 1996). Cross referencing these data on dwarf mistletoe ranges and larval host plant records (Table 3) demonstrates that a minimum of 46 larval collections (number of larvae is not determinable) were from trees on which there could not have been dwarf mistletoe. If I discount the possibility that larvae were collected from *A. tsugense* on its rare hosts then 110 of the 118 collections were made from trees without dwarf mistletoe. I therefore conclude that most, and probably all, of Prentice's records of *P. lunigerella* feeding on conifers are reliable food plant records.

Literature review. *Mitoura johnsoni* Skinner (Lycaenidae) and *M. spinetorum* Hewitison both feed on dwarf mistletoes while *M. gryneus* Hübner and several species in the sister genus *Callophrys* (*C. eryphon* Boisduval, *C. niphon* Hübner, *C. lanoraieensis* Sheppard, *C. hesseli* Rawson & Ziegler) are conifer feeders (Scott 1986). Given that there are no dwarf mistletoe feeders reported in *Callophrys*, it would be reasonable to assume that the ancestral character for *Mitoura* is conifer feeding and that either one or two shifts from conifers to dwarf mistletoe have occurred.

Filatima natalis Heinrich (Gelechiidae) is a dwarf mistletoe feeder (Heinrich 1920, Stevens & Hawksworth 1970, Hawksworth et al. 1996) while several species of *Chionodes* Hübner (Gelechiidae) feed on conifers (Heinrich 1920, Hedlin et al. 1981). While these species are not congeners, there is evidence to suggest that *Filatima* and *Chionodes* are sister taxa (R. Hodges pers. com.). There is not a great deal of information on food plants for other species of *Filatima*, but at least some feed on *Salix* (Karshold & Razowsky 1996). Feeding within *Chionodes* is diverse (Hodges 1999). Without an accurate phylogeny of this clade, and more complete food plant records, it is difficult to ascertain whether the taxonomic proximity of conifer and dwarf mistletoe feeding is the result of a past food plant shift or simply a coincidence.

The dwarf mistletoe herbivores discussed here, *P. lunigerella* and *D. alternosquamella*, are both phycitine pyralids. There were a sufficient number of shared characters for Heinrich (1956) to at least preliminarily group these genera together: Heinrich's key separates the genera within a single couplet and they are treated on adjacent pages in his text (Heinrich 1956). While no phylogenetic work has been done on these groups, more recent inspection of genital characters support Heinrich's groupings (H. Neunzig pers. com.). The only food plant records within these two genera are those already discussed, i.e., *P. lunigerella*, which feeds on both conifers and dwarf mistletoe, and *D. alter-*

TABLE 3. Conifer species from which Prentice (1965) reports *P. lunigerella* were isolated in coastal and interior British Columbia, the dwarf mistletoes (*Arceuthobium* spp.) known to parasitize those conifers (Hawksworth 1996), and whether the dwarf mistletoes ranges include the regions where larvae were found (Hawksworth 1996). "Coastal" refers to southern coastal BC including Vancouver, "interior" refers to the Lillooet area. The 118 larval collections (Σ = 347 larvae) were made from separate localities from 1950–1957. Neither the number of collections from coastal vs. interior B.C., nor the larvae per collection were determinable.

| Dwarf mistletoe | Conifer species of larval collections | | | | | Dwarf mistletoe range | |
	Abies amabilis	*Abies grandis*	*Picea sitchensis*	*Pseudotsuga menziesii*	*Tsuga heterophylla*	coastal BC?	interior BC?
A. abietinum	x	x				no	no
A. abietis-religiosae	x	x				no	no
A. douglasii				x		no	no
A. microcarpum			x			no	no
A. pusilum			x			no	no
A. tsugense	x	x			x	yes	no
P. lunigerella							
Collections	8	53	1*	45*	11	Σ = 118	

* These collections were made from trees outside of the range of any possible dwarf mistletoe parasitism.

nosquamella, a dwarf mistletoe feeder (Heinrich 1956). These records suggest that the congeners of these species may also be conifer and/or dwarf mistletoe feeders. Based on the fact that *D. alternosquamella* is a dwarf mistletoe feeder, it appears the ongoing shift observed in *P. lunigerella* is from an ancestral condition of dwarf mistletoe feeding to a derived condition of conifer feeding.

DISCUSSION

Both *P. lunigerella* and *D. alternosquamella* were abundant and occurred sympatrically at the Manitou Experimental Forest. This is somewhat surprising as it would seem that competitive exclusion should prevent two species of such close taxonomic relation and ecology from occurring sympatrically in the same habitat (Hardin 1960). The two species do differ significantly in size, and possibly this difference facilitates their coexistence.

The previous record of *P. lunigerella* feeding on conifers is reliable, as are my observations of the species feeding on dwarf mistletoe. It is notable that these two accounts are separated by several thousand kilometers and multiple decades. These data suggest that either a food plant shift is actively occurring within this species, or perhaps that *P. lunigerella* is actually two geographically separated, cryptic species that are more easily diagnosed by dietary preference than morphology.

My review of the dietary literature suggests that shifts in feeding between parasitic plants and the hosts of those plants, and vice versa, have occurred multiple times and may be common among lepidopteran taxa that feed on parasitic and parasitized plants. Every one of the five species of Lepidoptera known to feed on dwarf mistletoe has a relative in the same or sister genus that feeds on conifers. In three of those cases

(the two *Mitoura* and *P. lunigerella*) a food plant shift almost certainly occurred. The evidence for a shift in the gelechiids is suggestive but far from clear.

The evidence to-date suggests that the shift in *Mitoura* was from conifer to dwarf mistletoe, while the shift in the phycitine pyralids was from dwarf mistletoe to conifer. Holloway and Hebert's (1979) review of the Canadian Forest Insect Survey Data (e.g., Prentice 1965) suggested that forest lepidopterans feeding on conifers are less specific in their food plant choice than angiosperm-feeding species. This suggests that switches from conifers to dwarf mistletoes may be more common.

While I made no attempt to review the literature beyond those species feeding on dwarf mistletoes, in doing this work I became aware of another example in a different parasitic plant-host system: The nymphalid *Euthalia lubentina* Cramer feeds on several species of the mistletoe *Loranthus* (Loranthaceae) (Wynter-Blyth 1957) parasitizing Anacardiaceae, including mango *Mangifera indica* L. and *Anacardium occidentale*. These two Anacardiaceae species are fed upon by *Euthalia aconthea garuda* Moore (Corbet et al. 1978). A more exhaustive literature search would likely reveal more such examples.

Despite the high degree of chemical dissimilarity and taxonomic distance between conifers and dwarf mistletoe, food plant shifting appears to have happened repeatedly. These data provide support for a model of opportunity-based food plant shifting in which consistent physical association between plants may facilitate such shifts (Fig. 2). While the parasite-host relationship between dwarf mistletoes and conifers guarantees an unusual degree of close and consistent physical association, other associations might be predicted to produce the same phylogenetic patterns of food plant use. In their discussion of ecological opportunity and host shifting, Strong et al. (1984)
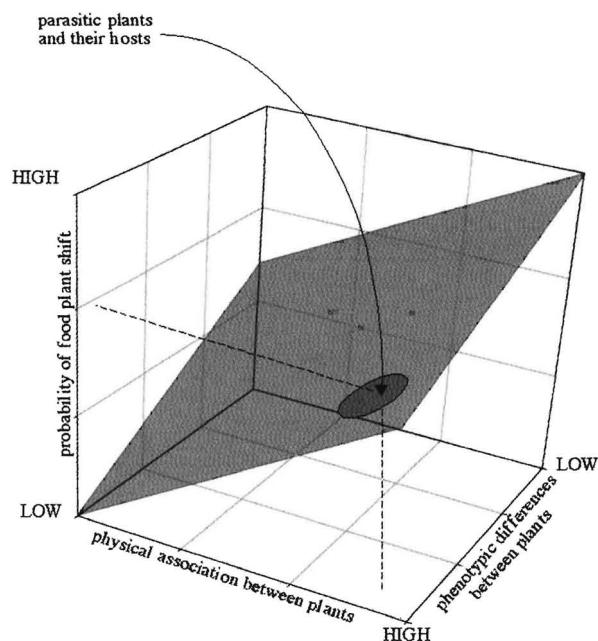
FIG. 2.   Schematic model demonstrating how (1) phenotypic differences between food plants and (2) physical association between food plants affect the (3) likelihood of specialist herbivores shifting between those food plants. Food plant shifts are most likely between plants that are phenotypically similar and between plants that are consistently in close physical association. Dwarf mistletoes and conifers are phenotypically very distinct, but are in close physical association.

cite Winter's (1974) findings of food plant shifts by insects from Myricaceae and Ericaceae moorland plants to the conifers with which they are frequently associated. Strong et al. (1984) also cite multiple examples of laboratory studies in which, following initially high rates of mortality, insects shifted and adapted to novel and often dissimilar food plants. For example, Gould (1979) was able to induce phytophagous mites to shift from Curcurbitaceae to Fagaceae. Chew and Robbins (1988) review literature suggesting that lycaenid and riodinid mutualisms with ants have resulted in shifts to feeding on the lichens frequently associated with these ants, and to carnivorous feeding on the ants themselves and on ant-tended homopterans.

Shifting among food plants has been an active topic of evolutionary and ecological research, but to-date there has been little work suggesting the mechanisms by which food plant shifts occur among dissimilar plants. While parasitic plants are but a small proportion of the flora available to lepidopteran larvae, the unusually consistent physical association these plants must maintain with their hosts make these systems ideal for investigating the role of physical proximity among plants in food plant shifts by specialist herbivores.

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