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Host selection of the hemiparasitic plant, Rhinanthus minor

by

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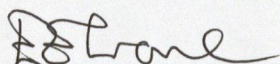
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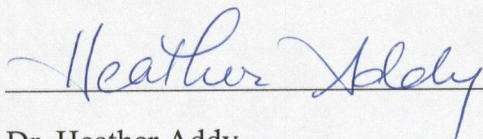
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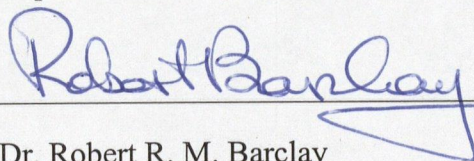
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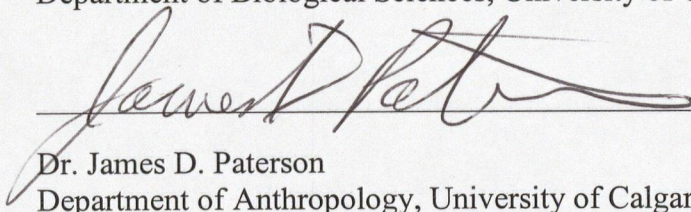
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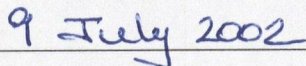
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ABSTRACT

Although ecologists have recognized the importance of active foraging for plant population dynamics, few researchers have studied foraging of parasitic plants. I investigated the relationship between host quality and host selection in the facultative hemiparasite, *Rhinanthus minor* L. (Scrophulariaceae). Seed set by *R. minor* varied according to host species, indicating that hosts differed in quality. In pair-wise combinations with four hosts, *R. minor* exhibited host selectivity and a weak overall preference for the highest quality host, *Bromus inermis*, but did not make more haustoria to better quality hosts. *Rhinanthus minor* did not achieve greater seed set when growing with two host species together than it did when growing with one. In field populations, host species differed in quality, and *R. minor* exhibited selectivity in the number of haustoria it made to different host types. However, as with the experiment, *R. minor* did not invest more haustoria in better quality. Thus, *R. minor* does not exhibit a straightforward preference for better hosts, or appear to benefit from complementary resources gained from different hosts. Possible mechanisms for this mismatch include evolutionary disequilibrium between *R. minor* and nonnative host species, and costs of exploring all possible hosts, rather than using hosts opportunistically as they are encountered.

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1 INTRODUCTION: FORAGING ECOLOGY OF PARASITIC PLANTS

1.1 Foraging by plants

Foraging can be defined as the process in which an organism searches within its habitat for essential resources (Slade and Hutchings 1987a, Hutchings and de Kroon 1994). Foraging involves the placement of “resource-acquiring structures” in favourable areas due to habitat selection (Cain 1994, Hutchings and de Kroon 1994). In contrast, growth is the increase in number or size of resource-acquiring structures in favourable environments and is the consequence of intaking resources. Although foraging is most commonly investigated in animals, the view that plants also forage has recently gained popularity (Table 1.1). Because of spatial and temporal heterogeneity in the distribution of resources, such as nutrients and light, plants that forage may have an advantage over plants that do not.

Numerous plant species express foraging behaviour when living in a patchy environment (Table 1.1). For example, pea plants (*Pisum sativum*) exhibit density-dependent habitat selection in placement of their roots in response to differences in density of competitor plant roots (Gersani *et al.* 1998). This enables plants to avoid competitor roots and allows them to take in more nutrients from the soil. Also, *Portulaca oleracea* seedlings avoid growing towards neighboring plants, even though the neighboring plants are distant and small (Novoplansky *et al.* 1990). In this study, far-red

Table 1.1 Foraging by plants of different growth habits.

Species	Patchy resource	Behaviour	Foraging	Reference
Unitary Plants				
<i>Artemesia tridentata</i> <i>Agropyron desertorum</i> <i>Agropyron spicatum</i>	soil nutrients	root extension into areas of high soil nutrients	yes	Eissenstat and Caldwell 1988
<i>Portulaca oleracea</i>	light	shoot growth away from neighboring plants	yes	Novoplansky <i>et al.</i> 1990
<i>Sorghum vulgare</i>	soil nitrogen	increase fine root biomass in high nutrient areas	yes	Gleeson and Fry 1997
<i>Pisum sativum</i>	soil space	density-dependent placement of roots	yes	Gersani <i>et al.</i> 1998
<i>Pinus sylvestris</i>	light	length of growth increments shortest on shaded branches	no	Stoll and Schmid 1998
		increase production of growth increments and buds in higher light	yes	
<i>Uvularia puberula</i>	soil nutrients	placement of roots	yes	Wijesinghe and Whigham 2001

...continued

Species	Patchy resource	Behaviour	Foraging	Reference
Clonal Plants				
<i>Ranunculus repens</i>	nutrients	no change in internode length with soil nutrient concentration	no	Lovett Doust 1987
<i>Glechoma hederacea</i>	soil nutrients	shorter stolon internodes and more branching in high nutrient soils than in low	yes	Slade and Hutchings 1987a
<i>Glechoma hederacea</i>	light	longer stolon internodes in shaded areas than unshaded	yes	Slade and Hutchings 1987b
<i>Glechoma hederacea</i>	soil nutrients	placement of roots in patches of high nutrient soils	yes	Birch and Hutchings 1994
<i>Hydrocotyle bonariensis</i>	soil resources	increased internode distance in unfavorable patches, rhizome growth is away from colonized patches of soil	yes	Evans and Cain 1995
<i>Elymus lanceolatus</i>	soil nutrients, soil space	more branching in higher nutrient patches	yes	Huber-Sannwald <i>et al.</i> 1998
<i>Uvularia perfoliata</i> <i>Uvularia sessilifolia</i>	soil nutrients	placement of roots in patches of high soil nutrients	no	Wijesinghe and Whingham 2001
...continued				

Species	Patchy resource	Behaviour	Foraging	Reference
Parasitic plants				
<i>Cuscuta costaricensis</i>	hosts	parasitizes high quality hosts over other hosts	yes	Kelly <i>et al.</i> 1988
<i>Cuscuta subinclusa</i>	hosts	mean coiling on a host is proportional to host quality	yes	Kelly 1990
<i>Cuscuta europaea</i>	hosts high in nitrogen content	coiling around ('accepting') higher quality hosts over lower quality hosts	yes	Kelly 1992
<i>Cuscuta europaea</i>	hosts	thin stolons more likely to 'accept' a host than thick stolons	yes	Kelly 1994

light was higher in the direction of the neighboring plants. Therefore, this result was interpreted as *P. oleracea* using the direction of light intensity as a cue for the probability of being shaded in the future (Novoplansky *et al.* 1990).

Clonal plants have been the focus of much work on plant foraging (e.g. Slade and Hutchings 1987a, b, Birch and Hutchings 1994, Cain 1994, Evans and Cain 1995, Huber-Sannwald *et al.* 1998, Wijesinghe and Whingham 2001; Table 1.1). Growth patterns of clonal plants in patchy environments have been considered analogous to the search path of a foraging animal (Sutherland and Stillman 1988). Clonal plants respond to heterogeneities in light and soil environments. For example, in a spatially heterogeneous soil environment, *Hydrocotyle bonariensis* selectively placed ramets in areas of greater soil resources ('good' patches) and avoided areas already inhabited by grass ('poor' patches) (Evans and Cain 1995). Similarly, *Glechoma hederacea* altered stolon length and branching such that it may result in establishment of ramets in more favourable areas (Slade and Hutchings 1987a).

1.2 Parasitic plants

Less attention has been paid to the foraging behaviour of parasitic plants (but see Kelly *et al.* 1988, Kelly 1990, 1992, Kelly and Horning 1999). Worldwide, approximately 3000 angiosperm species are at least partly parasitic on other plants (Kuijt 1969). Parasitic plants are classified based on the degree to which they depend on their

hosts for survival. Holoparasites are non-photosynthetic, acquire water, nutrients and carbon compounds exclusively from their hosts, and are unable to survive without a host (Kuijt 1969). In contrast, hemiparasites are photosynthetic, obtain some of their water, nutrients and carbon from host plants, and are able to survive without a host (Kuijt 1969). However, reproductive output of hemiparasites is greatly improved when attacking a host (Seel and Press 1993).

Because parasitic plants rely on host plants to provide them with water, nutrients, and carbon, success of a parasite depends, in part, on characteristics of the hosts it is attacking. Parasite performance is significantly influenced by host species (Atsatt and Strong 1970, Gibson and Watkinson 1991, Seel *et al.* 1993a, Calladine *et al.* 2000). Typically, parasitic plants have greater growth and reproductive success when parasitizing nitrogen-fixing hosts (Gibson and Watkinson 1991, Matthies 1996, 1997), but this is not always the case (Marvier 1996).

1.2.1 Foraging by parasitic plants

In general, hemiparasites have broad host ranges (Gibson and Watkinson 1989, Calladine *et al.* 2000). Field studies of host selection by parasitic plants show that they do not parasitize all available hosts, but are selective in host parasitism (Gibson and Watkinson 1989, Callaway and Pennings 1998). Parasitic plants may be selective because they obtain different compounds from different host species (Govier *et al.* 1967,

Radomiljac *et al.* 1998, Seel and Jeschke 1999). For example, parasites growing on nitrogen-fixing hosts generally have greater quantities of nitrogen in their xylem sap than when parasitizing non-nitrogen-fixing hosts (Schulze and Ehleringer 1984, Radomiljac *et al.* 1998, but see Seel and Jeschke 1999). Also, parasitic plants may be selective in the compounds that they extract from their hosts (Tennakoon *et al.* 1997).

A recent review compared parasitic plant-host plant interactions to herbivores and their prey plants (Pennings and Callaway 2002). However, in comparison with herbivores, relatively little is known about foraging strategies of parasitic plants and their interactions with hosts.

1.2.2 Host recognition

Parasitic plants explore the environment and invest in resource-acquiring structures before parasitizing hosts, suggesting that parasitic plants are not passively responding to hosts (Kelly 1990). Because of differences in nutrient availability in host tissues, parasitic plants might benefit from identifying their hosts before parasitizing them. Host recognition allows parasitic plants to increase their probability of encountering a suitable host among many potential unsuitable ones. To germinate, many parasites require chemical cues from specific hosts (Kuijt 1969, Cook *et al.* 1972, Atsatt *et al.* 1978). In addition, many parasites show positive chemotropic response to host chemicals. For example, broomrape (*Orobanche* spp.) radicles grow toward host root

exudates (Whitney and Carsten 1981). Also, flavonoids in host bark induce the stem parasite, *Cuscuta subinclusa*, to coil around its host's stem (Kelly 1990). This is the step prior to initiation of haustoria, or foraging organs that enter hosts. Haustorial initiation may also be controlled by host exudates. Haustoria of the hemiparasite *Triphysaria versicolor* are induced by flavonoids, quinones and phenolic acids released by their hosts (Albrecht *et al.* 1999). In contrast, the stem holoparasite, *Cuscuta japonica*, does not rely on chemicals to locate its host, but requires stimulation by far-red light and tactile pressure to initiate haustoria (Tada *et al.* 1996). This is considered to be a unique situation (Tada *et al.* 1996). Although some parasitic plants use chemical cues to detect their hosts (Kuijt 1969, Riopel and Musselman 1979, Whitney and Carsten 1981, Steffens *et al.* 1983, Yoder 1997), it is not known whether they all do.

1.2.3 The haustorium

Once they have located their hosts, parasitic plants exploit host resources by forming foraging organs called haustoria which they attach to their hosts. Haustoria of root hemiparasites penetrate the host root cortex and form a bridge between the host's and parasite's vascular systems, joining the two plants by their xylem (Kuijt 1969). Because transpiration rates of parasitic plants are greater than autotrophic plants (Press *et al.* 1988), parasitic plants are able to rob hosts of resources in the xylem sap through their haustoria (Tennakoon *et al.* 1997, Radomiljac *et al.* 1998).

General haustorial development occurs in four stages. First, the host epidermis is penetrated by elongating distal cells of the parasite. Then, the parasite advances through the host epidermis by division of the distal cells. Next, the distal-most cells divide, creating a palisade arrangement of cells. Last, the parasite penetrates the host endodermis establishing vascular continuity (Heide-Jorgensen and Kuijt 1993, Hood *et al.* 1998). Two additional features function to secure the parasite to the host. Haustorial hairs secure the haustorium to the host root (Heide-Jorgensen and Kuijt 1995). Also, haustorial hairs secrete a carbohydrate substance, which apparently has an adhesive function, and reinforces the link between parasite and host by forming a continuous sheet covering the parasite and the host at the haustorium (Baird and Riopel 1985).

1.2.4 Consequences of foraging of parasitic plants

Parasitic plants are important components of plant communities because they can alter individual host performance (Matthies 1995, Seel and Press 1996), species composition (Pennings and Callaway 1996, Davies *et al.* 1997), total plant community biomass (Davies *et al.* 1997, Joshi *et al.* 2000), and rates of nutrient flux (Quested *et al.* 2002). Parasitic plants have strong negative effects on their hosts and have the ability to greatly decrease their hosts' growth and fecundity (Gibson and Watkinson 1991, Matthies 1996, 1997, Puustinen and Salonen 1999ab, Davies and Graves 2000). For example, when hemiparasitic plants *Castilleja miniata* and *Orthocarpus purpurascens* were grown

with *Lolium perenne* (Poaceae) and *Medicago sativa* (Fabaceae), the host's aboveground biomass decreased by 24 to 71% (Matthies 1997). Also, parasitism in consecutive years significantly reduced reproductive success of hosts in comparison with unparasitized hosts and hosts parasitized in only one year (Puustinen and Salonen 1999a).

Species composition of plant communities tends to differ depending on the presence or absence of parasitic plants (Pennings and Callaway 1996, Joshi *et al.* 2000). Through non-random parasitism of hosts, parasitic plants can strongly influence and alter plant community structure by mediating competition between host species (Gibson and Watkinson 1991, Pennings and Callaway 1996). For example, parasitic plants can selectively parasitize and suppress the dominant plant in the community, allowing less competitive plants to flourish (Pennings and Callaway 1996, Callaway and Pennings 1998, Marvier 1998b). Consequently, parasitic plants have been considered as a management tool for grasslands to increase biodiversity (Davies *et al.* 1997). In contrast, parasitic plants may decrease species diversity if the preferred host is rare or a competitively non-dominant species in the community (Watkinson and Gibson 1988, Gibson and Watkinson 1992, Pennings and Callaway 1996, Davies *et al.* 1997).

Parasitic plants may alter species diversity through increasing nutrient cycling in soils (Quested *et al.* 2002). Leaf litter from parasitic plants is high in nitrogen compared with that of autotrophic plants, and leaf nitrogen concentration is positively correlated with decomposition rates (Taylor *et al.* 1989). Leaf litter from parasitic plants has the potential to increase decomposition rates and nutrient cycling in nutrient-poor

environments (such as sub-arctic systems) by mixing with leaf litter from autotrophic plants (Quested *et al.* 2002). This may enable more nutrient-demanding plant species to invade and coexist with the present species (Quested *et al.* 2002).

1.2.5 Host defense mechanisms

Host species differ in their susceptibility to attack by parasitic plants (Musselman and Mann 1979, Hariri *et al.* 1991, Olivier *et al.* 1990, Visser *et al.* 1990, Yan 1993, Singh and Singh 1997). Plants that are exposed to parasitism develop defense mechanisms, such as production of polyphenolic substances at the haustoria-root interface (Hariri *et al.* 1991, Neumann *et al.* 1999), increased bark thickness, production of wound periderm (Yan 1993), and inhibitors of cell-wall degrading enzymes (Singh and Singh 1997), to counter the attack. For example, transgenic tobacco plants can detect parasitism and attachment of haustoria stimulates expression of pathogenesis-related genes in response to parasitism by *Orobancha aegyptiaca* (Joel and Portnoy 1998). Despite these defense mechanisms against parasitism, host plants may still be susceptible to attack by parasitic plants (Neumann *et al.* 1999).

Time spent coexisting with a parasitic plant affects host resistance (Koskela *et al.* 2001). For example, the host species *Urtica dioica* growing with the stem holoparasite *Cuscuta europaea* is more resistant to parasitism than plants of the same species but not coexisting with the holoparasite (Koskela *et al.* 2001).

1.3 Conclusions

Foraging behaviour appears to be common in plants across a range of growth habits (Table 1.1). In particular, parasitic plants can be said to forage in that they have specialized mechanisms for detecting hosts before haustorial attachment, and specialized foraging organs to exploit hosts. However, to my knowledge, there have been only four studies that examine active foraging behaviour of parasitic plants (Kelly *et al.* 1988, Kelly 1990, Kelly 1992, Kelly 1994), two of which explicitly use models traditionally applied to explain animal behaviour, to parasitic plants (Kelly 1990, Kelly 1994). In this thesis, I will characterize foraging by *Rhinanthus minor* by examining the quality of its hosts and the relationship between host selection and host quality.

2 HOST SELECTION BY *RHINANTHUS MINOR*

2.1 Introduction

Among recent studies in plant foraging, most have focused on clonal plants, while studies on foraging by parasitic plants have been under-represented (Table 1.1). Parasitic plants are model systems for plant foraging studies because they forage with distinctly visible haustoria which they form to their hosts. Parasitic plants use haustoria to extract water, nutrients and carbon from their hosts (Kuijt 1969). It is generally accepted that non-parasitic plants forage for spatially heterogeneous resources such as soil nutrients and light (e.g. Slade and Hutchings 1987a, b, Birch and Hutchings 1994, Evans and Cain 1995, Gleeson and Fry 1997, Gersani *et al.* 1998, but see Wijesinghe and Whigham 2001). Because parasitic plants receive much of their water and nutrients from hosts, the resources that they are foraging for are host plants. Root parasites have not received as much attention as non-parasitic plants and conclusions as to their foraging proficiency (host selection) are still in debate. My research will test the extent to which *Rhinanthus minor*, a hemiparasitic annual plant, follows general foraging theories that were developed primarily for animal populations. Currently, there is little evidence testing the applicability of foraging theory to plants (but see Kelly 1990).

Parasitic plants are exposed to many potential host individuals and host species. However, they do not parasitize all available hosts in proportion to their availability

(Kelly *et al.* 1988, Gibson and Watkinson 1989, Helton *et al.* 2000). One reason why parasites do not use hosts equally may be because hosts differ in their quality to parasitic plants. I define host quality in terms of relative parasite reproductive output when parasitizing that host in comparison with other hosts, when investment into parasitizing the hosts is equal. Hosts may differ in quality because of differences in characteristics such as tissue nutrient composition and concentration (Seel and Press 1993, Seel and Jeschke 1999), secondary chemistry (Marvier 1998a, Adler 2000), physical root characteristics (Riopel and Timko 1995, Davies and Graves 2000), and amount of leaf area lost due to herbivory (Puustinen and Salonen 1999b).

There is strong evidence supporting the idea that hosts differ in quality to parasitic plants (Atsatt and Strong 1970, Chuang and Heckard 1971, Snogerup 1982, Schulze and Ehleringer 1984, Calladine *et al.* 2000). Because hemiparasitic plants tap into their hosts' xylem to extract nutrients and water, nitrogen concentration of the host's xylem is likely to be an important factor influencing host quality. Past research points to nitrogen-fixing legumes as better quality hosts than other plants. Generally, parasitic plants achieve greater growth and reproductive success when parasitizing leguminous hosts than non-nitrogen fixing hosts (Schulze and Ehleringer 1984, Gibson and Watkinson 1991, Seel and Press 1993, Seel *et al.* 1993a, Matthies 1996, 1997, Radomiljac *et al.* 1998, Seel and Jeschke 1999, but see Marvier 1996). This increase in performance is attributed to the greater availability of nitrogen in host plant tissues that can be extracted by the parasite (Seel *et al.* 1993a, Radomiljac *et al.* 1998).

Host nitrogen content may be linked to host selection by parasitic plants. For example, in a host-choice experiment, the stem parasite, *Cuscuta europaea*, was more likely to parasitize hosts supplemented with a fertilizer containing higher concentration of nitrogen than other hosts (Kelly 1992). In a greenhouse study, host selection of the generalist parasite, *Schwalbea americana*, was related to the hosts' ability to use ammonium (Helton *et al.* 2000). Also, in a field study, *Rhinanthus minor* parasitized legumes over other species (except grasses) (Gibson and Watkinson 1989). Although there is a link between nitrogen content of hosts and host selection, there is conflicting evidence as to whether nitrogen-fixing plants make better hosts for parasitic plants than others and what characteristics of the host cause them to be selected (e.g. Matthies 1996, Seel and Jeschke 1999).

Classical foraging theory predicts that animals spend more time and energy exploiting more profitable prey than less profitable prey (MacArthur and Pianka 1966, Charnov 1976). The extension of this to foraging by parasitic plants predicts that there will be more haustorial connections with better quality hosts than with poorer quality hosts (Kelly 1990). Therefore, if hosts differ in quality, and parasitic plants are foraging, I expect a non-random distribution of haustoria to host plants. If host plants are analogous to foraging 'patches' and parasitic plants are following ideal free distribution (Fretwell and Lucas 1969), then I expect there will be more haustoria to better quality hosts than to other hosts, and the number of haustoria to each acceptable host will be related to the relative quality of that host compared to other hosts.

Generalist herbivores experience improved growth and reproduction by including mixed resources into their diet (Belovsky 1978, Rapport 1980, Dearing and Schall 1992, Pennings *et al.* 1993, Bernays *et al.* 1994). Including many prey species into their diet may be beneficial to consumers because it improves the nutrient balance of the diet as well as dilutes any toxic secondary compounds of prey plants (Bernays *et al.* 1994). For example, the generalist grasshopper, *Schistocera americana*, grew faster when fed a mixture of three plant species than when fed any one alone (Bernays *et al.* 1994). Analogously, some parasitic plants experience increased reproductive success when parasitizing more than one host species at a time (Marvier 1998a, Kelly and Horning 1999). Host species differ in the amount and type of nutrients they can supply to parasitic plants (Tennakoon *et al.* 1997, Radomiljac *et al.* 1998) and parasitic plants extract different nutrients (Govier *et al.* 1967, Seel and Jeschke 1999) as well as toxic secondary compounds (Adler 2000) from different host species.

While it is well documented that animals forage for complementary resources (e.g. Belovsky 1978, references in Rapport 1980), less is known about plants foraging for complementary resources. By parasitizing multiple host species simultaneously, parasitic plants might gain synergistic benefits from the resources they extract from their hosts (Marvier 1998a). To date, some studies have concluded that parasitic plants do not express reproductive benefits from parasitizing more than one species (Matthies 1996, Marvier 1998b, Matthies and Egli 1999), while others concluded the opposite (Marvier 1998a, Kelly and Horning 1999).

2.1.1 Objectives

Few published studies focus on plant foraging and even fewer attempt to link resource choice with resource quality and plant fitness. In this study I address three aspects of the foraging behaviour of *R. minor*: 1) the effect of host availability and quality on host selection, 2) whether *R. minor* forages for complementary resources, and 3) host range and selection in Kananaskis Country, AB. I address the first objective with an experiment in which I grew *R. minor* with four host species and examined the effect of host root length and host species on host selection. Next, I examine whether host selection and investment in exploiting a host is related to host quality. I address the second objective by comparing performance of *R. minor* when grown in pot cultures with either one or two host species. Finally, to address the third objective, I compare my experimental results to an observational study of *R. minor* foraging and performance in two natural populations in Kananaskis Country, AB.

2.2 Methods

2.2.1 Study system

2.2.1.1 *Rhinanthus minor*

Rhinanthus minor L., commonly known as Yellow Rattle, is an annual root hemiparasite that commonly occurs in semi-disturbed areas such roadsides, ditches, and

human-altered grasslands (Kuijt 1969, Gibson and Watkinson 1989, Watkinson and Gibson 1988). It is a generalist hemiparasite because it has a broad host range which exceeds 50 species, spanning 18 families (Gibson and Watkinson 1989). Despite being a generalist, *R. minor* exhibits selectivity in the hosts that it parasitizes (Gibson and Watkinson 1989, 1991) showing selection for hosts in the Fabaceae (legumes) and Poaceae (grasses) over others (Gibson and Watkinson 1991).

2.2.1.2 Hosts

As hosts, I used four perennial plants that commonly co-occur with *R. minor* in montane regions, and that potentially differ greatly in root morphology, foliar and root nitrogen concentration and secondary chemistry. I chose Common Yarrow, *Achillea millefolium* L. (Asteraceae, hereafter *Achillea*), Smooth Brome, *Bromus inermis* Leyss. (Poaceae, hereafter *Bromus*), Silky Lupine, *Lupinus sericeus* Pursh (Fabaceae, hereafter *Lupinus*), and Red Clover, *Trifolium pratense* L. (Fabaceae, hereafter *Trifolium*).

Trifolium and *Lupinus* are nitrogen-fixing legumes. *Trifolium* is not known to produce harmful compounds that can be passed on to parasitic plants and has an extensive root system. In contrast, *Lupinus* produces quinolizidine alkaloid compounds (Hartman 1991) which are harmful to parasitic plants (Marvier 1996). *Lupinus* has the thickest roots and the least branched root system of the four hosts. In contrast with *Trifolium* and *Lupinus*, *Bromus* and *Achillea* do not fix atmospheric nitrogen. *Bromus* is not known to produce harmful compounds that can be passed on to parasitic plants and

has the finest and most extensively branched root system of the four host species. *Achillea* roots are characterized by a branching pattern intermediate between that of *Lupinus* and *Trifolium*. *Achillea* roots may contain sesquiterpene lactones, which are produced by the majority of tribes in the Asteraceae family (Seaman 1982). These compounds are toxins and deter herbivory by insects.

Bromus seeds were collected from field populations along roadsides in Bragg Creek, AB in August 1999 and stored at room temperature. I obtained *Trifolium* seeds from Evergro Canada Inc., and local *Achillea* and *Lupinus* seeds from ALCLA Native Plant Restoration Inc. Based on differences in host root morphology and chemistry, I predict that *Trifolium* will be the most frequently parasitized host followed by *Bromus*, *Lupinus* and *Achillea*.

2.2.2 Experiment

2.2.2.1 Design

I germinated host seeds in Peat Pellets (Jiffy-7, Shippagan Canada) and, as seedlings, transferred them to cylindrical pots (4 cm in diameter, 21 cm deep) in which they grew in the University of Calgary greenhouse for 1 month. I then transplanted the seedlings into pots 20 cm in diameter and 15 cm in depth with a 5:2 soil:sand mixture. Four host individuals were transplanted in each pot such that their stems formed the corners of a square 10-cm on a side. Host plants were set up into ten treatment

conditions: monocultures, hereafter referred to as the No Choice Test (4 treatments, initial $n = 24$), and in pair-wise combinations, hereafter referred to as the Choice Test (6 treatments, initial $n = 24$). Hosts of the same species were transplanted diagonally from each other (Fig. 2.1).

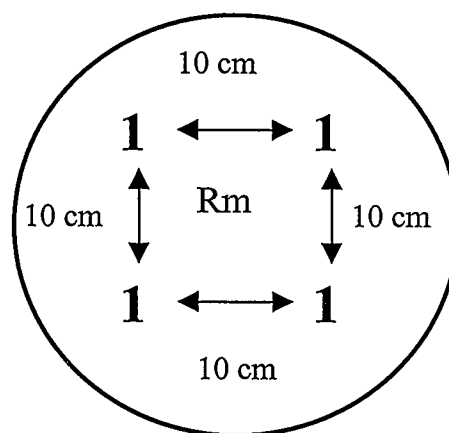
On 10 June 2000, pots were placed into the ground at the University of Calgary Kananaskis Field Station, AB (50° 00' North, 115° 05' West, elevation 1390 m) such that the top of the pots were level with the ground. Pots were placed in this way to best resemble natural light and temperature conditions. Pots were randomly positioned in a 30 x 8 grid formation, 30 cm apart. To increase the opportunity for natural water flow, I cut out the bottoms of the pots and replaced them with nylon cloth. The nylon also served to contain host roots in the pots as well as exclude foreign roots from the experiment. Observation of the nylon after pots were removed from the plot confirmed that roots were contained within the pots and other roots excluded.

I collected *R. minor* seedlings from Fortress Mountain, AB, Canada (50° 48' North, 115° 12' West, elevation 2025 m) at the four-leaf stage of development and transplanted them into the middle of the experimental pots, approximately 5 cm from all hosts, in mid-June 2000. The experiment was contained within a metal mesh cage to exclude herbivory by deer (*Odocoileus virginianus*) and ground squirrels (*Spermophilus* spp.).

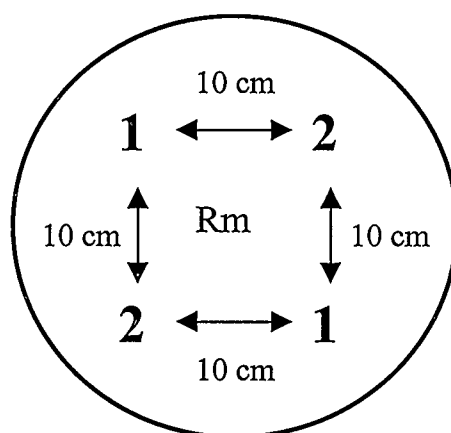
I fertilized plants with 100 mL of 10-52-10 Nitrogen-Phosphorus-Potassium and micronutrients (PLANT-PROD® Plant Products Co. Ltd., Brampton, Ontario, Canada)

Figure 2.1. Schematic representation of the top view of the Choice and No Choice Tests. Hosts were planted in square formation, 10 cm apart. The circle represents the pot rim, numbers represent host species, and 'Rm' indicates placement of *R. minor*.

No Choice Test



Choice Test



twice during the experiment, on 30 June and 30 July. I left all plants to be naturally pollinated. I watered plants when needed.

I recorded the number of flowers and seeds for each *R. minor*. *Rhinanthus minor* plants were allowed to grow until they set seed, after which the pots were immediately removed from the field plot. Time of seed set spanned from 15 August to 4 September 2000. After *R. minor* set seed, I measured each plant's final height.

2.2.2.2 Host selection

To prepare roots for observation, I washed roots thoroughly in water and separated them into species groups. Haustoria to each host species in each pot were identified using a dissecting microscope and the number of haustoria to each species was recorded. I assumed that all haustoria were functional and that all were equal in their ability to intake water and nutrients from the host. Haustoria broken off during the washing process leave a scar on the host root enabling me to identify past points of attachment.

2.2.2.3 Host availability

I used host root length as an indicator of host availability to a foraging *R. minor*. Previous work on host selectivity of parasitic plants used dry root biomass as the estimate of host availability (Gibson and Watkinson 1989). However, the four species in my experiment differ in the relationship between mass and length of roots (ANOVA,

$F_{3,100} = 12.62, P < 0.001$), such that by using root biomass as the estimate of host availability, I overestimate the availability of hosts with thick, short roots, and underestimate the availability of hosts with long, fine roots.

I measured root length, following the methods of Tennant (1975), on 27 plants per host species. I cut roots into 1 cm long pieces and took subsamples of varying wet mass. I dispersed the subsample of roots in a 22 cm x 22 cm glass pan filled with water approximately 1 cm in depth. A 2 cm x 2 cm grid was placed underneath the pan such that the grid lines were visible through the glass and water. I then recorded the number of intersections between the dispersed roots and gridlines. If a root section crossed a gridline, ended touching a gridline or a curved portion of root touched a gridline, it received a count of one. If a root section lay on top of a gridline, it received a count of two (Tennant 1975). I then estimated root length in the sample using the equation

$$\text{Root length (cm)} = \# \text{ intersections} \times 11/14 \times \text{grid size (cm)}$$

Roots were dried at 70° C for 5 days and dry mass was recorded. Regression equations of root length and dry mass for the four hosts were then used to estimate the length of roots in the experimental pots from dry mass (*Achillea*: length = 81.104 x mass + 0.34, $R^2 = 0.88$; *Bromus*: length = 42.123 x mass + 3.14, $R^2 = 0.71$; *Lupinus*: length = 13.64 x mass + 0.16, $R^2 = 0.58$; *Trifolium*: length = 59.26 x mass + 1.43, $R^2 = 0.90$).

2.2.2.4 Nutrient analysis

To prepare roots and shoots for analysis, I dried the tissue at 70° C for 5 days and ground the dry material in a Wiley Mill with size 40 mesh (Arthur H. Thomas Co., Philadelphia, PA, USA). I then dried the material for an additional 24 hours at 70° C. I analysed ammonium and phosphate concentration with a Technicon Autoanalyser II (Technicon Industrial Systems, Tarrytown, NY 10591) for nine randomly chosen individuals of each host species from the No Choice Test after using the micro-Kjeldahl digestion procedure (no pre-treatment and no catalysts) (Bremner and Mulvaney 1982).

2.2.2.5 Statistical analyses

I used generalized linear models (Nelder and Wedderburn 1972) to determine differences in host quality among hosts in the No Choice test, and host selection in Choice and No Choice Tests. I used Poisson-distributed error and the log link function for these analyses. Poisson regression is appropriate for my data because the dependent variable is a count with few large values (Neter *et al.* 1996). To determine the probability of parasitism and differences in proportion of *R. minor* that produced seeds, I used logistic regression with binomially-distributed residuals and the logit link function. For all analyses, I began with a saturated model and removed non-significant interactions to arrive at the simplest model to fit the data.

I estimated host quality from differences in *R. minor* reproductive output in the

No Choice Tests and differences in nitrogen and phosphorous concentration in host tissues. I separated reproduction into two parts: 1) whether *R. minor* set seed, and 2) the number of seeds produced. To determine differences in the proportion of *R. minor* that set seed, I used logistic regression with host species as the independent variable and *R. minor* seed production (yes or no) as the dependent variable. I used linear regression with Poisson-distributed error to assess differences in *R. minor* reproductive output when grown with different host species. I treated host species and number of haustoria to hosts as independent variables and *R. minor* seed set as the dependent variable. I tested differences in root and shoot nitrogen and phosphorus concentrations among host species using ANOVA and parametric contrasts.

To determine factors influencing the probability of parasitism in No Choice Tests, I used logistic regression with host species and root length as independent variables and state of the host (parasitized or not) as the dependent variable. To determine differences in the number of haustoria to hosts among treatments, I used the same independent variables, and analyzed differences with Poisson regression.

I assessed factors influencing host selection in samples from the Choice Test. Before analysing host selection, I assigned host species in each pot as Host 1 (the focal host species) and Host 2 (the partner species). Each pot was therefore analyzed twice, once with the two host species arbitrarily assigned Host 1 and Host 2 and again with the host assignments reversed. Across all treatments, the number of haustoria made to Host 1 and Host 2 were not correlated (Spearman's rank correlation, $n = 90$, $r = 0.18$, $P > 0.05$).

I summed the root lengths of the two individuals of each host species in each pot. I analyzed host selection in two steps. First, I looked at the probability of parasitism (i.e. presence or absence of haustoria), and second, the number of haustoria to hosts. I used logistic regression to determine the effects of host species and host availability on the probability of parasitism. The dependent variable was whether Host 1 was parasitized or not, and the independent variables were the species of Host 1 and 2, and root length of Host 1 and 2. Using the same independent variables, I determined differences in the number of haustoria to hosts using Poisson regression.

To assess host selection when *R. minor* was grown with each pair-wise combination of host species, I compared the least squares mean number of haustoria to hosts while controlling for differences in host root length. Because of small sample sizes for this analysis, I pooled data for each host species across the various host combinations and compared least squares mean number of haustoria to each host species while controlling for differences in root length.

To determine if parasitizing two host species produced synergistic effects on *R. minor* seed set relative to parasitizing only one host species, I compared average seed production of *R. minor* between the No Choice Test and the Choice Test.

I determined whether host selection by *R. minor* was related to host quality by comparing relative quality of pairs of hosts with host selection of *R. minor* when grown with each pair of hosts. I used Spearman's rank correlation with relative quality of combinations of two hosts as the independent variable and host selection index as the

explanatory variable. To calculate relative quality of two host species, I used results from the No Choice Test and the symmetrical index

$$\text{Quality}_{\text{host 1: host 2}} = (\text{Host 1}_{\text{seed}} - \text{Host 2}_{\text{seed}}) / (\text{Host 1}_{\text{seed}} + \text{Host 2}_{\text{seed}})$$

where $\text{Host 1}_{\text{seed}}$ and $\text{Host 2}_{\text{seed}}$ are the least squares mean number of seeds produced by *R. minor* when growing with Host 1 and Host 2, respectively.

To calculate selection between two hosts I used results from the Choice Test and the selection index,

$$\text{Selection}_{\text{host 1: host 2}} = (\text{Host 1}_{\text{haust}} - \text{Host 2}_{\text{haust}}) / (\text{Host 1}_{\text{haust}} + \text{Host 2}_{\text{haust}})$$

where $\text{Host 1}_{\text{haust}}$ and $\text{Host 2}_{\text{haust}}$ are the number of haustoria to Host 1 and Host 2 in each pot, respectively.

2.2.3 Field Survey

2.2.3.1 Study site and sample collection

I collected *R. minor* from a roadside population near Fortress Mountain, Kananaskis Country, AB (50° 48' North, 115° 12' West, elevation 2025 m) and near

King Creek, in Peter Lougheed Provincial Park, AB (50° 43' North, 115° 07' West, elevation 1700 m). On 21 August and 27 August 2001, I removed from each site 15 soil blocks, 20 cm long x 20 cm wide x approximately 10 cm deep, each containing one *R. minor* and the surrounding plants. Care was taken so that no other parasitic plants (such as *Castilleja miniata*, another root hemiparasite present at the sites) were present in the samples. I chose samples arbitrarily within a 20-m² area at each site, but attempted to include a range of sizes of *R. minor*. Samples were placed in 8-inch pots and transported to the University of Calgary where they were kept in refrigeration chambers at 4° to 8° C until they were processed.

2.2.3.2 *Rhinanthus minor* growth and reproduction

I measured *R. minor* height, basal stem diameter, number of branches, and fruit set. Since I needed to identify hosts by their shoots for host selection identification and most host shoots senesce towards the end of summer, I collected *R. minor* plants before they set seed. Also, *R. minor* fruit production is highly correlated with seed set (Pearson correlation, $n = 27$, $r = 0.93$, $P < 0.001$), and therefore I believe fruit production to be a suitable substitute for seed set.

2.2.3.3 Host selection

I identified hosts in each sample by their above-ground features. Initial

observations revealed that *R. minor* roots at King Creek and Fortress Mountain did not extend beyond approximately 5 cm from the stem. To ensure that I examined the entire root system of each *R. minor*, I cut out a cylinder of soil and roots 14 cm in diameter from the original sample with *R. minor* in the centre. I washed soil from the roots in water and separated host roots from each sample while keeping roots connected to their shoots as much as possible. I separated unattached roots into groups based on morphology and colour and identified them by comparing them to known roots. Because of difficulties identifying grasses to species by root morphology and colour, all grass species were grouped together. Using a dissecting microscope, I observed and recorded the number of haustoria to each host species present in each sample.

2.2.3.4 Host availability

I used root length as the measure of host availability and estimated it for all host species with the line-intersect method of Tennant (1975). This method is described in section 2.2.2.3. Because of the large amount of grass roots in the samples, I used subsamples of varying mass from the grasses to estimate regression lines predicting root length from dry mass. I dried the remaining grass roots at 70° C for 5 days and estimated root length using the regression equations (Fortress Mountain: $\text{Length (m)} = 106.50 \times \text{mass (g)} - 0.86$, $R^2 = 0.96$; King Creek: $\text{Length (m)} = 63.01 \times \text{mass (g)} - 1.03$, $R^2 = 0.90$).

2.2.3.5 Statistical analyses

I used multiple regression and ANCOVA to determine if *R. minor* exhibited selectivity in host parasitism. To meet the assumption of normality, I square-root transformed the number of haustoria made to hosts, which is the typical transformation made for count data (Sokal and Rohlf 1995). To determine if there were differences in host selection between sites, I used the number of haustoria to each host type as the dependent variable and site, host root length and host identity (grass, legume, other) as explanatory variables. Beginning with the saturated model, I removed non-significant interactions to arrive at the simplest model to fit the data. Because there was a significant site effect, I separated the data by site with the same explanatory variables, excluding site, to analyze the relation between host type and root length on number of haustoria.

When analyzing host selection at Fortress Mountain, I only used samples containing root lengths less than 140m for each host type. This was done to ensure that I was considering host selection over a range of root length where all hosts had representation. I regressed number of haustoria against root length and compared slopes between host species with paired t-tests. To determine ranks of host preferences at King Creek, I adjusted the number of haustoria to each host type to account for significant differences in root length among hosts and compared least squares mean number of haustoria made to each host type.

I used multiple regression with backward step-wise elimination to analyze the dependence of fruit production by *R. minor* on number of haustoria formed to grasses,

legumes, and other hosts. Variance inflation factors were all less than 1.2, indicating that the independent variables were not correlated substantially (variance inflation factors greater than 10 indicate multicollinearity, Neter *et al.* 1996). Because there was a significant site effect, I separated the data by site with the same explanatory variables, excluding site, to analyze the relation between forming haustoria to different hosts and *R. minor* fruit production.

To estimate host quality, I used the ‘net’ regression coefficients for each main effect. I took the partial derivative of *R. minor* fruit production with respect to each host type (grass, legume, other) in the final model separately to arrive at equations for the relationships between haustoria to the other host types and *R. minor* fruit production. I evaluated the effect of haustoria to a focal host type at the average number of haustoria made to the other host types and summed the terms in the equation to arrive at the ‘net’ regression coefficient for the focal host type. I used the average number of haustoria to the other hosts to consider the average situation that *R. minor* experienced in my samples. These regression coefficients represent the effect of one explanatory variable when the other explanatory variables are in the model and held constant (Neter *et al.* 1996). In my models, the regression coefficients are the effect of forming haustoria to each host type on fruit production. These summarize the reproductive value to *R. minor* of making haustoria to each host type.

I used ANCOVA to determine differences in *R. minor*’s growth and reproduction between sites. I used fruit set of *R. minor*, its height, and number of branches separately

as dependent variables and number of haustoria to grasses, legumes, and other hosts, and site as independent variables. I used SAS (SAS Institute 1990) with a Type I error level of 0.05 to determine significance for these analyses. For *post hoc* comparisons, I adjusted the Type I error level using the Dunn-Šidák method (Sokal and Rohlf 1995).

2.3 Results

2.3.1 Experiment

Due to *R. minor* mortality during the experiment, replication of each treatment was reduced (No Choice Tests: *Achillea* = 19, *Bromus* = 18, *Lupinus* = 16, and *Trifolium* = 16; Choice Tests: *Achillea-Bromus* = 13, *Achillea-Lupinus* = 12, *Achillea-Trifolium* = 18, *Bromus-Lupinus* = 18, *Bromus-Trifolium* = 13, and *Lupinus-Trifolium* = 16). I observed *R. minor* parasitizing all host species and producing flowers and seeds when growing with all hosts in the No Choice test. However, not all host individuals in the experiment were parasitized. Visual inspection of *Trifolium* and *Lupinus* roots confirmed that they were nodulated indicating that they were capable of fixing atmospheric nitrogen (Allen and Allen 1933, Harris *et al.* 1949). Haustoria made to *Lupinus* were approximately twice the size of those made to the other hosts.

2.3.1.1 Host quality

Hosts differed significantly in foliar and root nitrogen concentrations (ANOVA, foliar: $F_{3,30} = 110.75$, $P < 0.001$; root: $F_{3,32} = 71.09$, $P < 0.001$). In particular, the legumes, *Trifolium* and *Lupinus* had higher root nitrogen concentrations than *Achillea* or *Bromus* (Fig. 2.2b). Also, foliar nitrogen concentration in *Trifolium* was almost twice as high and significantly greater than other hosts (Fig. 2.2a). Hosts also differed in foliar and root phosphorous concentrations (ANOVA, foliar: $F_{3,32} = 31.26$, $P < 0.001$; root: $F_{3,30} = 8.50$, $P < 0.001$). *Lupinus* had significantly lower foliar phosphate than the other hosts (Fig. 2.2c). *Bromus* had significantly lower root phosphorous than other hosts (Fig. 2.2d).

The proportion of *R. minor* that produced seeds did not differ among hosts in the No Choice Tests ($G_{3,65} = 4.37$, $P > 0.05$). However, number of seeds that *R. minor* produced differed significantly when grown with the four hosts in the No Choice Test. *Rhinanthus minor* made significantly fewer seeds when parasitizing *Trifolium* than when parasitizing any other host ($G_{3,65} = 21.04$, $P < 0.001$). When I controlled for differences in number of haustoria to the hosts, the trends in differences in *R. minor* seed production remained. *Rhinanthus minor* produced the fewest seeds when parasitizing *Trifolium* (Table 2.1, Host effect; Fig. 2.3). Host quality ranking from greatest to least was *Bromus* $\geq$ *Achillea* $\geq$ *Lupinus* $>$ *Trifolium* (Fig. 2.3).

Figure 2.2. Concentrations (mean $\pm$ SE) of a) foliar and b) root nitrogen and c) foliar and d) root phosphorous in host tissue from the No Choice Test. Means labelled with different letters were significantly different. Note the different y-axis scales among panels.

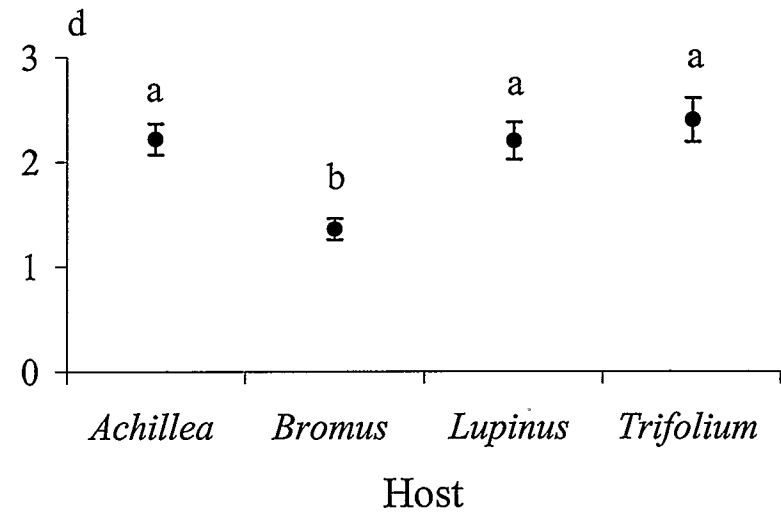
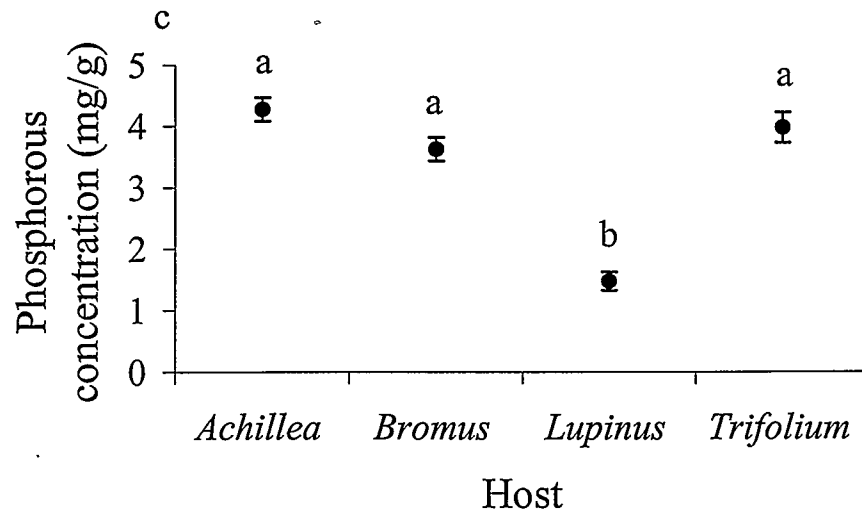
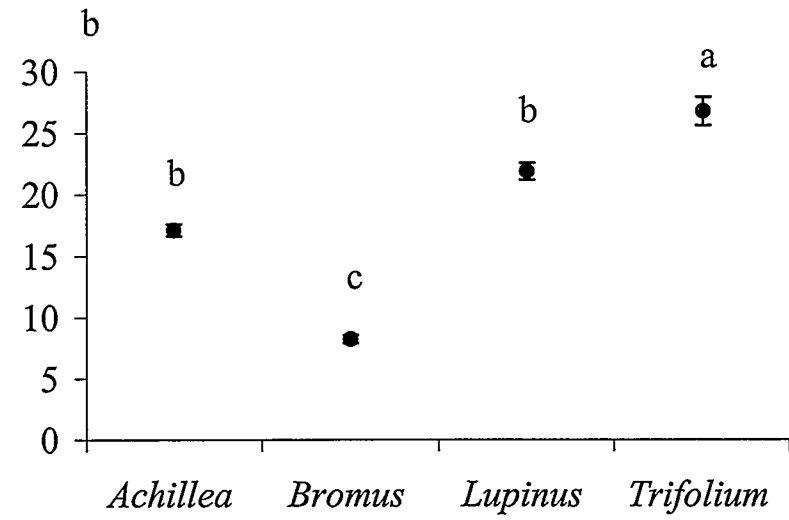
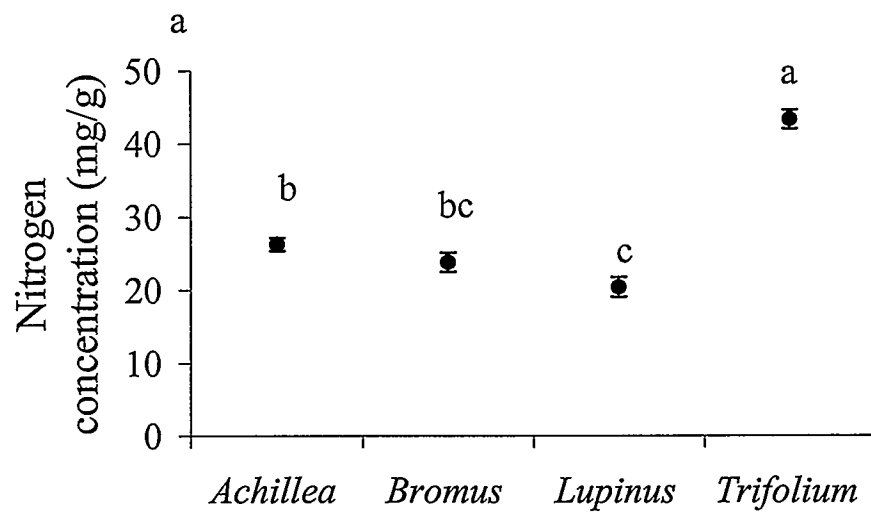
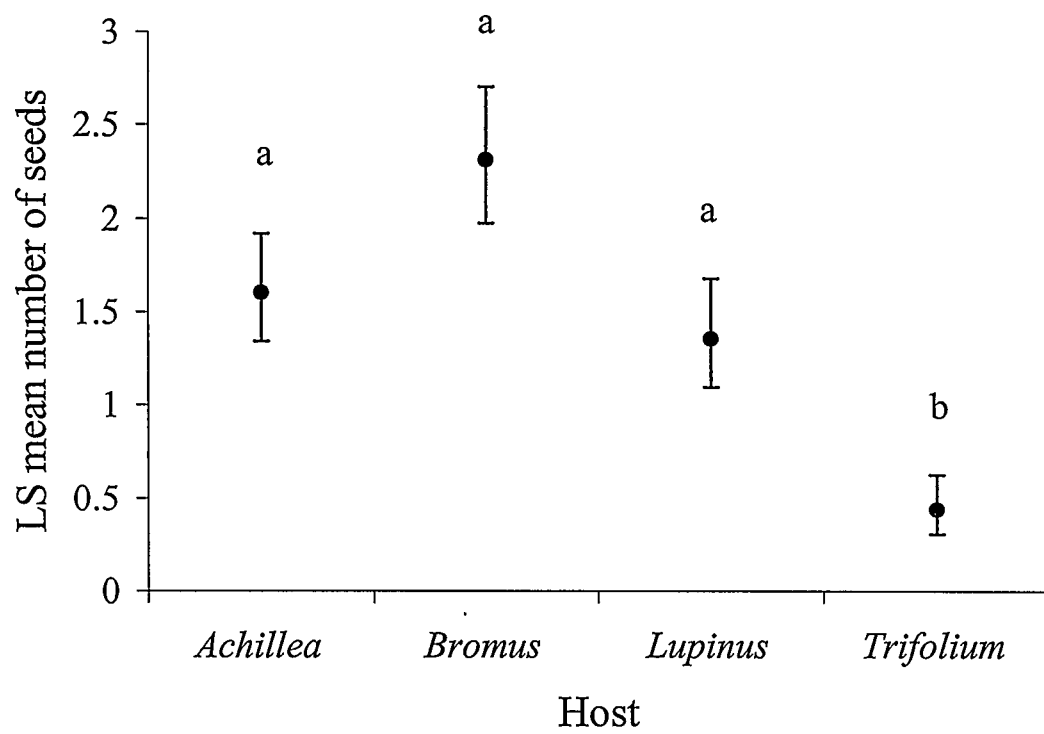


Table 2.1. Logistic and Poisson regression results of factors influencing host parasitism, number of haustoria formed, and seed production by *R. minor* in No Choice Tests.

Effect	Probability of parasitism	Number of haustoria	Number of seeds
Host	$G_{3,64} = 2.28$	$G_{3,61} = 21.77^{***}$	$G_{3,64} = 24.46^{***}$
Haustoria	-	-	$G_{1,64} = 6.05^*$
Root length	$G_{1,64} = 5.41^*$	$G_{3,61} = 34.46^{***}$	-
Host x Root length	-	$G_{3,61} = 30.62^{***}$	-

* $P < 0.05$, *** $P < 0.001$

Figure 2.3. Least squares mean number of seeds ($\pm$ SE) produced by *R. minor* in the No Choice Tests. Different letters indicate significant differences in number of seeds.



2.3.1.2 Host selection

In total, number of haustoria to host species did not differ among No Choice Tests (Kruskal-Wallis $\chi^2 = 3.84$, $df = 3$, $P > 0.05$). In No Choice Tests, host root length significantly affected probability of parasitism, with hosts with longer total root length in the pots having a higher probability of parasitism than hosts with shorter roots (Table 2.1, Length effect). Host species did not affect probability of parasitism (Table 2.1, Host effect). Host root length significantly affected number of haustoria made to hosts (Table 2.1, Length effect). However, the relationship between number of haustoria and root length differed among host species (Table 2.1, Length x Host effect). Considering only *R. minor* that made haustoria to hosts, the number of haustoria per root length was significantly larger for *Lupinus* than for other host species ($G_{3,19} = 43.45$, $P < 0.001$).

In Choice Tests, the species of Host 1 (the focal host) and 2 (partner host) and root length of Host 1 significantly affected the number of *R. minor* forming haustoria to Host 1 (Table 2.2, Model 1). Number of haustoria to the focal host varied positively with the root length of that host (slope: 0.008, $P = 0.04$). When Host 2 was included in the model, significance of Host 1 decreased (Table 2.2, Model 2). Although not statistically significant, the trend of number of haustoria to Host 1 varied positively with Length 1 remained (slope: 0.007, $P = 0.06$). In addition, number of haustoria to Host 1 varied negatively with root length of Host 2 (slope: -0.007, $P = 0.18$).

Accounting for differences in root length between the two host species in each Choice Test, least squares mean number of haustoria to host species did not differ

Table 2.2. Generalized linear regression statistics for the effect of host species and root length on number of haustoria made by *R. minor* in Choice Tests.

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Effect	Number of haustoria	
	Model 1	Model 2
Host 1	$G_{3,172} = 61.15^{***}$	$G_{3,171} = 62.53^{***}$
Host 2	$G_{3,172} = 52.11^{***}$	$G_{3,171} = 43.53^{***}$
Length 1	$G_{1,172} = 4.35^*$	$G_{1,171} = 1.85 (P = 0.17)$
Length 2	-	$G_{1,171} = 3.47 (P = 0.06)$
* $P < 0.05$, *** $P < 0.001$		

significantly between hosts in any host combination (Fig. 2.4). Considering trends in host selection in the six Choice Tests, only *Lupinus* was consistently under-used. Of the other three host species, *R. minor* did not select any one species consistently over the other hosts. For example, in the *Achillea-Bromus* treatment, *R. minor* formed more haustoria to *Achillea* than to *Bromus* (Fig. 2.4a). However, in the *Achillea-Trifolium* treatment, *R. minor* formed more haustoria to *Trifolium* than to *Achillea* (Fig. 2.4b). When grouped together, number of haustoria to hosts differed significantly among host species in Choice Tests ($G_{3,176} = 110.52, P < 0.001$). *Bromus* and *Trifolium* had significantly more haustoria than *Achillea* and *Lupinus*. This difference was maintained even when accounting for differences in host root length (Figure 2.5, $G_{3,175} = 34.29, P < 0.001$).

2.3.1.3 Host selection vs. Host quality

Host selection in Choice Tests was not related to host quality from No Choice Tests, either when I consider all *R. minor* (Spearman's rank correlation, $n = 90, r = -0.17, P > 0.05$, Fig. 2.6a), or only those *R. minor* that made detectable haustoria to hosts (Spearman's rank correlation, $n = 24, r = -0.37, P > 0.05$, Fig. 2.6b). The non-significant trend was for *R. minor* to select the poorer quality host over the better quality one in Choice Tests.

Figure 2.4. Least squares mean number of haustoria ($\pm$ SE; a-d) and number of haustoria (e, f) *R. minor* made to hosts in the Choice Tests. Panels e and f illustrate host selection of one *R. minor* each. Note the different scales in the y-axis between panels.

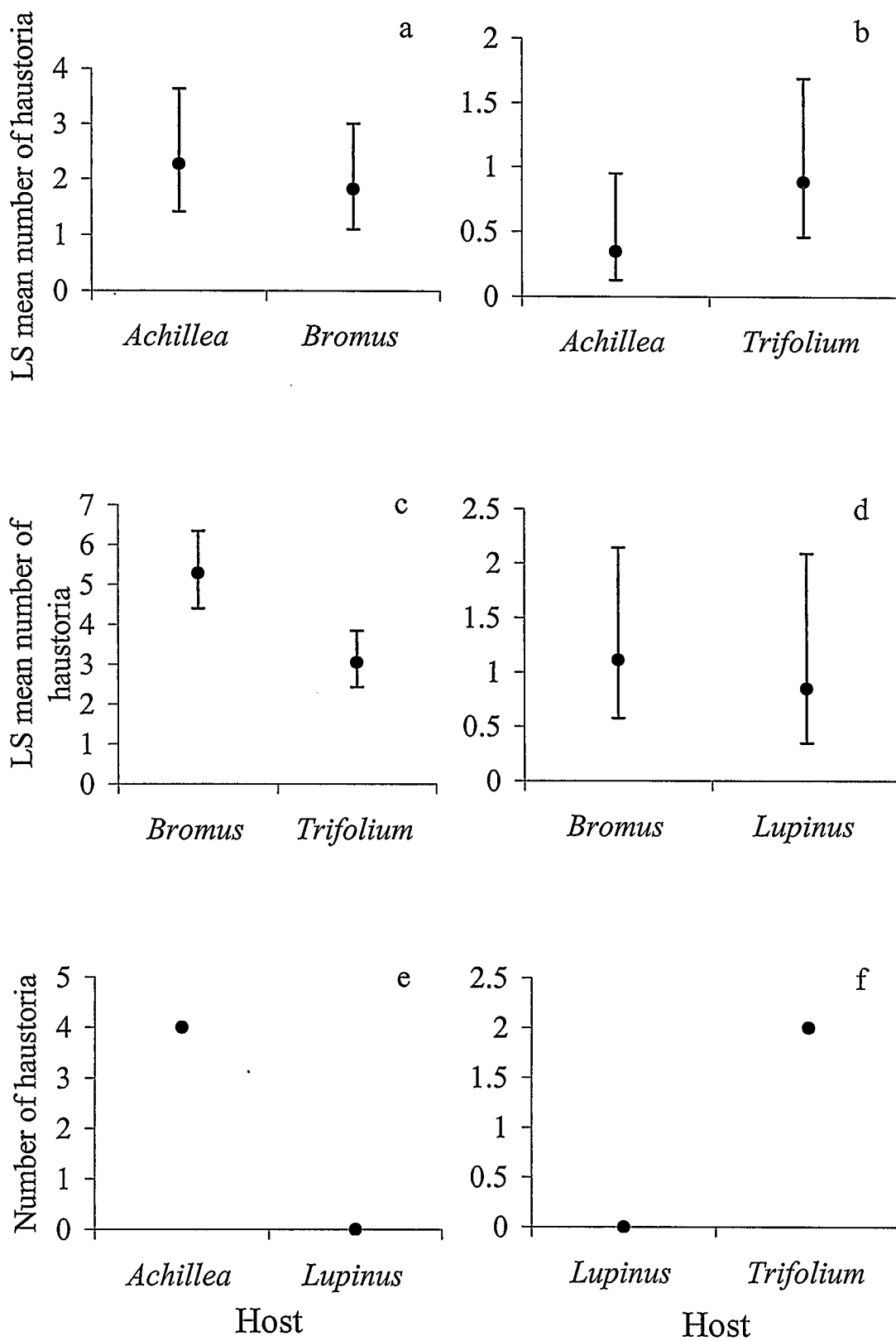


Figure 2.5. Least squares mean number of haustoria ($\pm$ SE) made by *R. minor* to hosts in the Choice Tests. Hosts from all treatments are grouped together by species. Different letters indicate significant differences in number of haustoria.

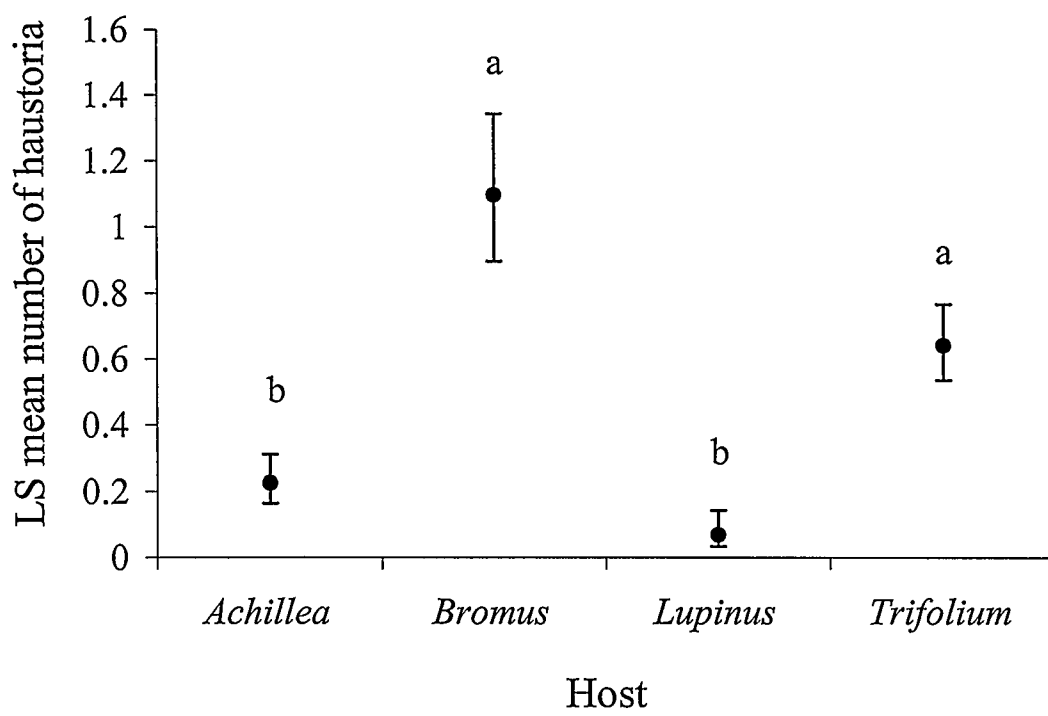
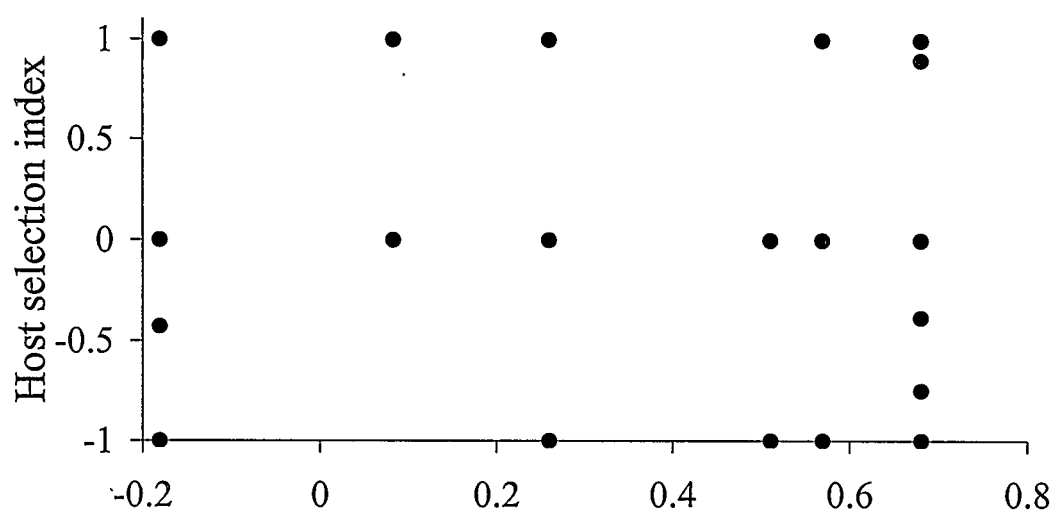
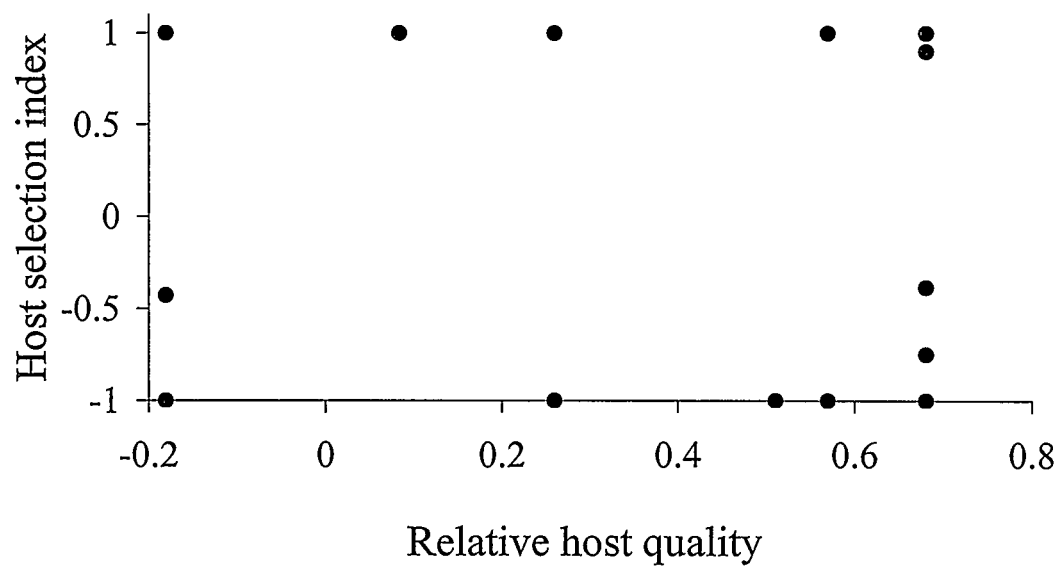


Figure 2.6. Relationship between host selection of *R. minor* in Choice Tests and relative host quality considering a) all samples and b) only samples in which *R. minor* made at least one haustorium.

a



b



2.3.1.4 Complementary resources

Although both selection and performance depend on the combination of hosts, in general, *R. minor* did not show a reproductive gain from growing with two host species over one (Fig. 2.7). *Rhinanthus minor* produced significantly more seeds when growing with one host species than when growing with two (mean $\pm$ SE: No Choice, 2.09 ± 1.15 ; Choice, 0.88 ± 1.24 , $G_{1,158} = 5.00$, $P < 0.05$). *Trifolium* appeared to decrease seed production. *Rhinanthus minor* growing with *Trifolium*, either alone or in combination with any other host, produced significantly fewer seeds than *R. minor* not growing with *Trifolium* (alone: $G_{1,65} = 21.04$, $P < 0.001$; combination: $G_{1,89} = 25.60$, $P < 0.001$).

On a species pair basis, *R. minor* made significantly more seeds when growing with *Bromus* in monoculture than with *Bromus* and *Achillea* together ($G_{1,150} = 6.90$, $P < 0.01$) and *Bromus* and *Trifolium* together ($G_{1,150} = 19.11$, $P < 0.001$). *Rhinanthus minor* also made more seeds when growing with *Achillea* in monoculture than with *Achillea* and *Trifolium* together ($G_{1,150} = 11.64$, $P < 0.001$). *Rhinanthus minor* flower production and height did not differ significantly when growing with two host species and one (flower: $G_{1,158} = 0.33$, $P > 0.05$; height: ANOVA, $F_{1,159} = 0.55$, $P > 0.05$).

2.3.2 Field Survey

At the two study sites, I observed *R. minor* parasitizing all available host species, including itself, except black spruce (*Picea mariana*) (Table 2.3). Single *R. minor* plants

Figure 2.7. Mean number of seeds ($\pm$ SE) produced by *R. minor* in Choice and No Choice Tests. Abbreviations: No Choice Test; AA = *Achillea*, BB = *Bromus*, LL = *Lupinus*, TT = *Trifolium*: Choice Test; AB = *Achillea-Bromus*, AL = *Achillea-Lupinus*, AT = *Achillea-Trifolium*, BL = *Bromus-Lupinus*, BT = *Bromus-Trifolium*, LT = *Lupinus-Trifolium*.

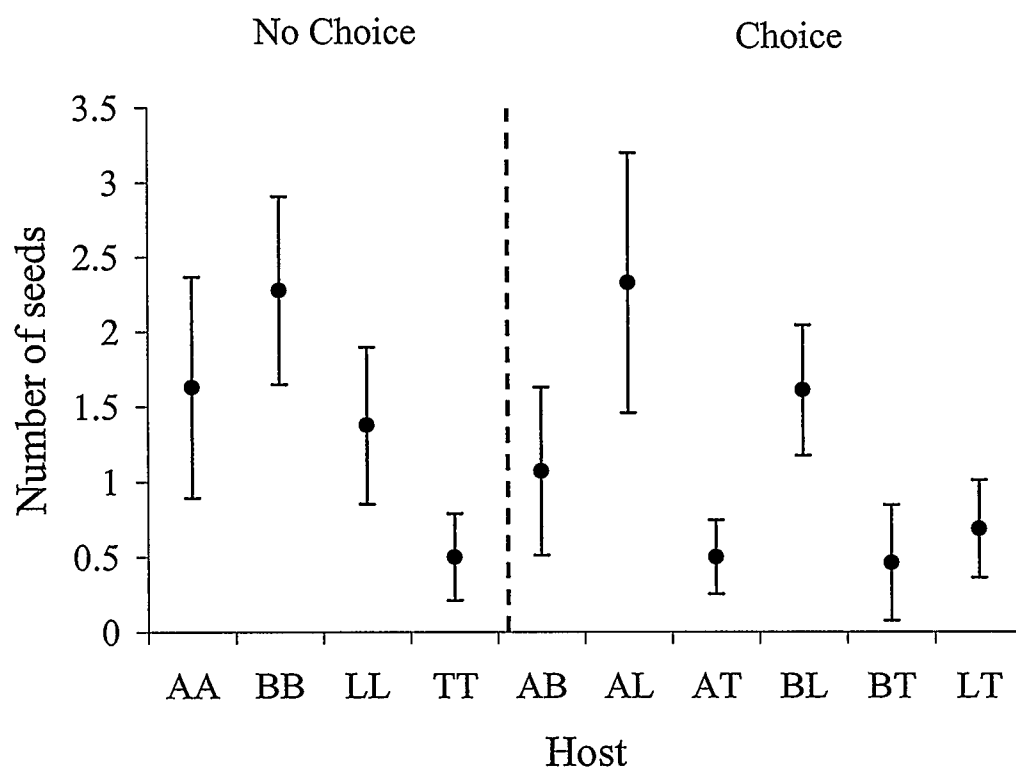


Table 2.3. Host type classification and plants parasitized by *R. minor* at Fortress Mountain and King Creek.

Host Type	Species
Grass	<i>Bromus inermis</i>
	<i>Festuca rubra</i>
	<i>Phleum commutatum</i>
	<i>Poa alpina</i>
	<i>Poa pratensis</i>
Legume	<i>Hedysarum alpina</i>
	<i>Oxytropis splendens</i>
	<i>Trifolium hybridum</i>
	<i>Trifolium pratense</i>
Other	<i>Achillea millefolium</i>
	<i>Equisetum arvense</i>
	<i>Fragaria virginiana</i>
	<i>Parnassia</i> sp.
	<i>Salix</i> sp.
	<i>Solidago multiradiata</i>
	<i>Taraxacum officinale</i>

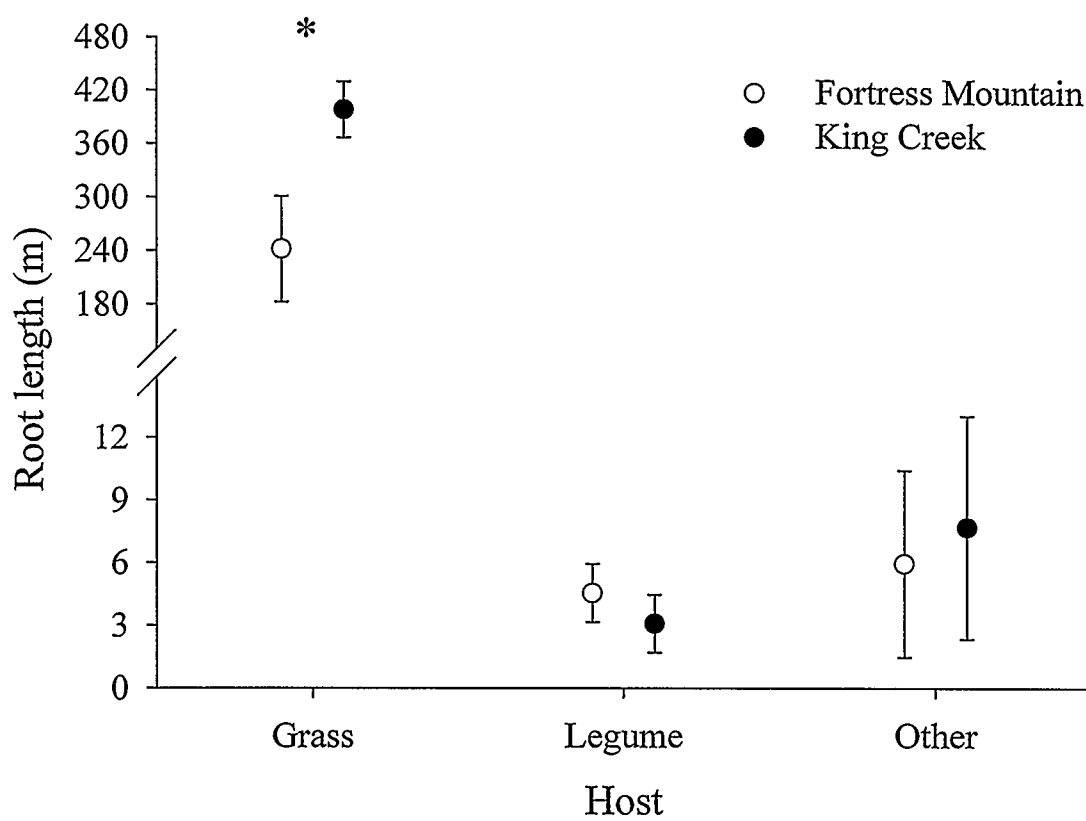
parasitized two to six host species simultaneously from at least two host types (i.e., grass, legume, and other). I also observed *R. minor* with haustoria attached to small stones, although these instances were rare. *Rhinanthus minor* made more haustoria to hosts at King Creek (mean $\pm$ SE: 245.9 ± 37.6) than at Fortress Mountain (185.3 ± 32.7), although, this difference was not significant ($F_{1,25} = 1.49$, $P > 0.05$). *Rhinanthus minor* invested the greatest proportion of haustoria to parasitizing grasses. At King Creek I observed 91.3% of haustoria attached to grasses, 4.3% to legumes and 4.4% to other hosts. At Fortress Mountain, 83.6% of haustoria were attached to grasses, 10.2% to legumes and 6.2% to other hosts.

Hosts differed in root abundance within and between sites (Fig. 2.8). Within each site, there were significantly greater total root length for grass than legume or other host roots (Fortress Mountain: Kruskal-Wallis $\chi^2 = 29.05$, $P < 0.001$; King Creek: Kruskal-Wallis $\chi^2 = 27.36$, $P < 0.001$). There were significantly greater total grass root length in samples from King Creek (mean $\pm$ SE: $398.48 \text{ m} \pm 31.49$) than from Fortress Mountain ($241.71 \text{ m} \pm 59$) ($F_{1,26} = 11.49$, $P < 0.01$).

2.3.2.1 *Rhinanthus minor* growth and reproduction

Controlling for differences in number of haustoria to the three host types, *R. minor* produced significantly more fruit at Fortress Mountain (least squares mean $\pm$ SE: 22.0 ± 2.6) than at King Creek (6.9 ± 2.8 ; $F_{1,23} = 13.95$, $P < 0.05$). Also, at Fortress

Figure 2.8. Mean ($\pm$ SE) root length of hosts in samples from Fortress Mountain and King Creek. The asterisk indicates a significant difference in root length between sites. At both sites, grass roots were significantly longer than legumes and other hosts. Note the change in scale of the y-axis at the axis break.



Mountain, *R. minor* had significantly more primary branches (2.39 ± 1.65) than at King Creek (0.03 ± 1.65 ; $F_{1,25} = 33.82$, $P < 0.001$), as well as greater basal stem diameter (Fortress Mountain: $2.22\text{mm} \pm 1.06$; King Creek $1.52\text{mm} \pm 1.06$; $F_{1,25} = 15.59$, $P < 0.001$). Height of *R. minor* did not differ between the populations.

2.3.2.2 Host selection

Number of haustoria to host types differed between and within sites. There was inconsistency in *R. minor*'s host selection among individuals from the same site. In general, *R. minor* exhibited selectivity at both sites (Table 2.4, Host effects, Fig. 2.9, 2.10); however, host selection was not in the same order at the two sites. At Fortress Mountain, the number of haustoria per root length differed among host types (Table 2.4, Length x Host effect, Fig. 2.10). *Rhinanthus minor* made significantly more haustoria per length to legumes than to grasses (Paired sample t-test, $t = -9.83$, $df = 19$, $P < 0.001$) and other hosts (Paired sample t-test, $t = -14.67$, $df = 26$, $P < 0.001$). Number of haustoria per root length of grasses and other hosts did not significantly differ after adjusting the Type I error rate for three contrasts. At King Creek, *R. minor* made significantly more haustoria to grasses than to legumes ($F_{1,37} = 157.72$, $P < 0.001$) and to others ($F_{1,37} = 156.44$, $P < 0.001$), after controlling for differences in root length among hosts (Fig. 2.9).

Table 2.4. ANCOVA statistics describing the effects of host root length, host type and collection site on the number of haustoria *R. minor* made to hosts.

Effect	All data	Fortress Mt.	King Creek
Length	$F_{1,72} = 28.99^{***}$	$F_{1,36} = 20.62^{***}$	$F_{1,38} = 4.09^{\circ}$
Host	$F_{2,72} = 32.6^{***}$	$F_{2,36} = 32.43^{***}$	$F_{2,38} = 17.35^{***}$
Site	$F_{1,72} = 8.07^{**}$	-	-
Length x Host	$F_{2,72} = 15.67^{***}$	$F_{2,36} = 9.84^{***}$	-
Length x Site	$F_{1,72} = 7.24^{**}$	-	-
Host x Site	$F_{2,72} = 1.25$	-	-
Length x Host x Site	$F_{2,72} = 3.18^{*}$	-	-
$^{\circ}P = 0.05, *P < 0.05, **P < 0.01, ***P < 0.001$			

Figure 2.9. Least squares mean number of haustoria ($\pm$ SE) to hosts at Fortress Mountain and King Creek. Different letters indicate significant differences among number of haustoria to hosts. Capital letters refer to King Creek, lower case letters refer to Fortress Mountain. Grasses and legumes differed significantly in number of haustoria between sites.

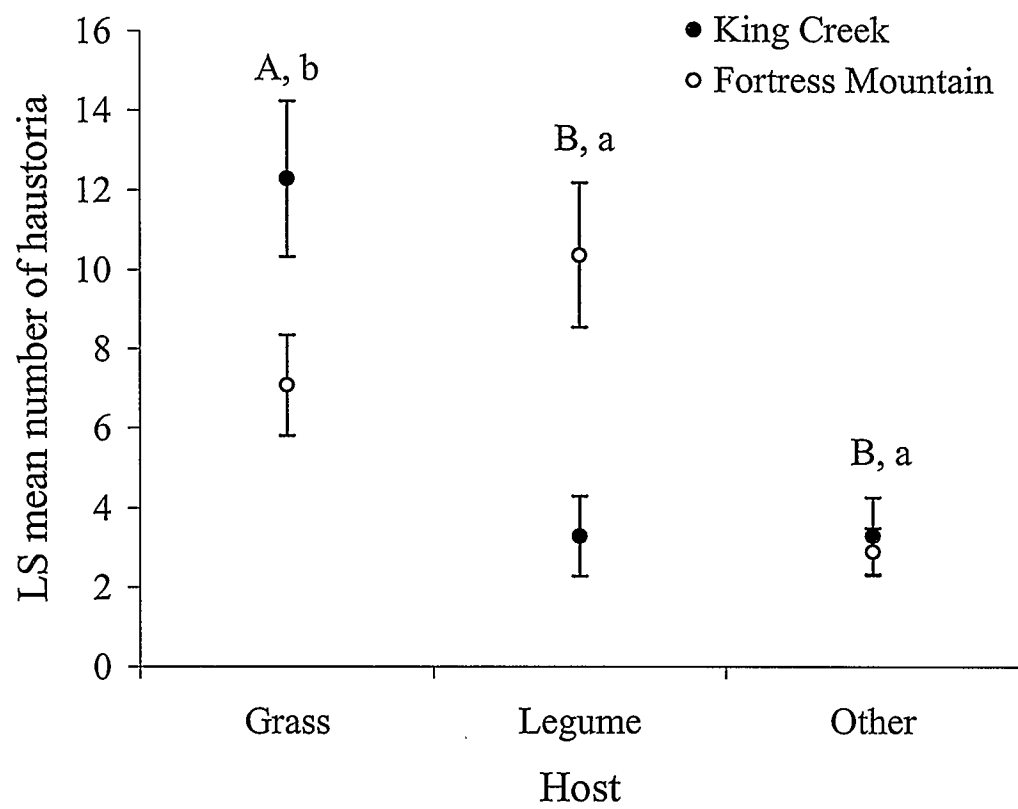
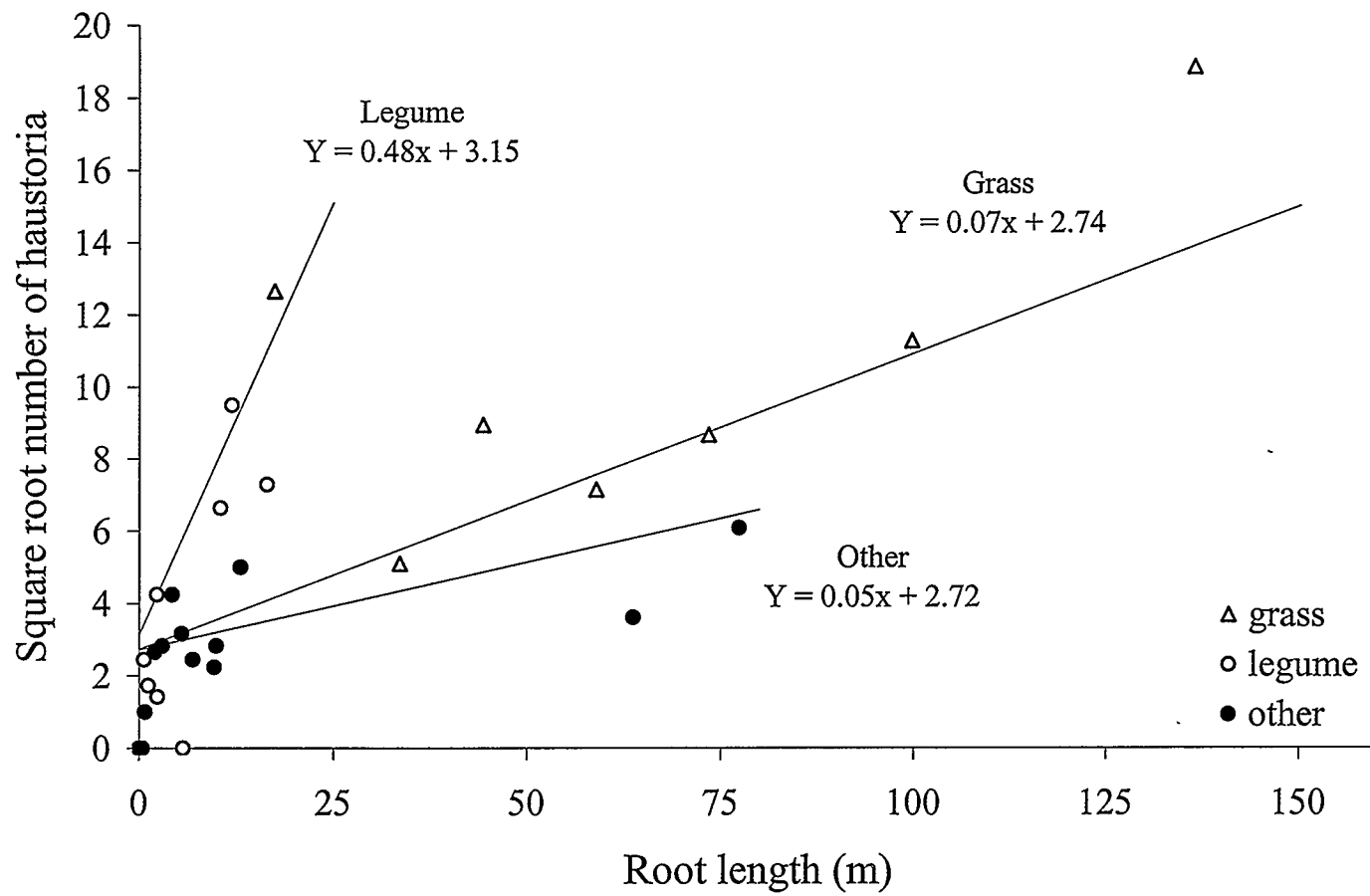


Figure 2.10. Relationship between host root length and square root number of haustoria at Fortress Mountain.



2.3.2.3 Host quality

Host types differed in quality between sites (Table 2.5). At Fortress Mountain, hosts did not differ significantly in quality (Table 2.5). Number of haustoria to each host type or total haustoria did not significantly affect *R. minor* flower production (Table 2.5). However, the highest quality host was grass followed by other and legumes. At King Creek, legumes were the highest quality host to *R. minor* followed by grasses and other (Table 2.5).

To explore the significant Grass x Legume and Other x Legume interactions on *R. minor* fruit production at King Creek, I divided the King Creek data into two groups based on the numbers of haustoria to legumes. Samples containing greater than five haustoria to legumes were grouped into the 'high legume' category and samples containing five or fewer haustoria to legumes were grouped into the 'low legume' category. I then substituted this new categorical variable into the final model of host selection at King Creek, in place of the continuous variable of number of haustoria to legumes. When there were many haustoria to legumes, there was a significantly positive effect of having haustoria also to grasses (estimate: 0.054, $P < 0.01$). When there were few haustoria to legumes, there was a non-significant negative effect of having haustoria also to grasses (estimate: -0.005, $P > 0.05$). In contrast, there was a significantly negative effect of having haustoria to other hosts when there were many haustoria to legumes (estimate: -0.801, $P < 0.05$) and a non-significant positive effect of having haustoria to other hosts when there were few haustoria to legumes (estimate: 0.158, $P > 0.05$).

Table 2.5 ANCOVA statistics describing the effect of haustoria to grasses, legumes and other hosts, and site, on fruit production by *R. minor*, and regression statistics and coefficients describing the effect of haustoria to grasses, legume and other hosts on fruit production by *R. minor* at Fortress Mountain and King Creek. Net regression coefficients are in bold type.

Effect	Together	Fortress Mt.			King Creek		
			Coefficient	Std. Err.		Coefficient	Std. Err.
Grass	$F_{1,23} = 5.20$	$F_{1,10} = 2.05$	0.0832	0.0581	$F_{1,8} = 0.06$	-0.0051 0.0477	0.0199
Legume	$F_{1,23} = 0.21$	$F_{1,10} = 0.10$	-0.0544	0.1754	$F_{1,8} = 0.89$	0.3399 0.5813	0.3595
Other	$F_{1,23} = 0.13$	$F_{1,10} < 0.01$	0.0079	0.3666	$F_{1,8} = 3.36$	0.3054 -0.3425	0.1665
Site	$F_{1,23} = 14.32^{**}$	-	-	-	-	-	-
Grass x Legume	-	-	-	-	$F_{1,8} = 6.42^*$	0.0042	0.0016
Legume x Other	-	-	-	-	$F_{1,8} = 18.03^{**}$	-0.0639	0.0150
Total haustoria	-	$F_{1,13} = 2.88$	0.0455	0.0269	-	-	-

* $P < 0.05$, ** $P < 0.01$

2.4 Discussion

Rhinanthus minor made haustoria to all host species in my experiment, indicating that all were suitable hosts. My experimental results show poor reproduction by *R. minor*, which is comparable to some field populations in Kananaskis Country and the greenhouse study of Salonen *et al.* (2001). At my field sites, *R. minor* parasitized all available host species, except black spruce, which was present in only one sample at very low abundance. These findings are in agreement with previous studies that concluded that *R. minor* is a generalist hemiparasite with a broad host range (Kuijt 1969, Gibson and Watkinson 1989, Seel *et al.* 1993a). Also in agreement with my results, previous studies found that host selection was inconsistent between and within populations and that *R. minor* parasitized many host species simultaneously (Gibson and Watkinson 1989). In the field, I observed *R. minor* parasitizing two to six host species simultaneously; Gibson and Watkinson (1989) observed *R. minor* parasitizing two to seven hosts simultaneously.

2.4.1 Host Quality

Typically, parasitic plants have their highest growth and reproduction when parasitizing hosts high in nitrogen content (Snogerup 1982, Gibson and Watkinson 1991, Seel and Press 1993, Matthies 1996). In particular, parasitic plants growing with legumes have better performance than those growing with other hosts. However, trends in host quality from my experiment and the Fortress Mountain population do not support this

generalization. Host quality in my experiment was not related to host nitrogen concentrations. The host with the highest mean nitrogen concentration, *Trifolium*, was the lowest quality host for *R. minor*, as determined by *R. minor* seed set. This was surprising since *R. minor* growth is positively correlated with nitrogen supply (Seel *et al.* 1993a). Similar results to mine were obtained by Kelly (1990) and Matthies and Egli (1999), who found that host nitrogen content was not correlated with parasite biomass.

In addition to nitrogen, phosphorous is an important nutrient to parasitic plants (Seel *et al.* 1993b). Phosphorous affects successful haustorial attachment (Davies and Graves 2000), and phosphorous fertilization increases *R. minor* growth and photosynthetic rate (Seel *et al.* 1993b). However, in my experiment, host phosphorous concentration was not related to host quality in terms of *R. minor* seed set.

Overall, grasses were the best quality host. *Bromus* was the best host in the experiment, and grasses were the only hosts that had a positive net regression coefficient (host quality) at both field sites. My experimental results support those by Seel and Jeschke (1999) who found that *R. minor* grown with *Hordeum vulgare*, a grass, had greater performance than *R. minor* grown with *Trifolium alpestre*, a legume. In Seel and Jeschke's experiment, *H. vulagare* had higher nitrogen concentration than *T. alpestre*, so *R. minor* growth increased with host nitrogen concentration.

2.4.2 Host Selection

Rhinanthus minor did not parasitize hosts equally, indicating that *R. minor* exhibited selectivity in host parasitism, although in different ways at the two field sites. Host species or type, and availability significantly affected the number of haustoria *R. minor* made to hosts in the experiment and in field populations. At King Creek, *R. minor* parasitized grasses over legumes and other species. In the experiment, *R. minor* parasitized *Bromus* (grass) and *Trifolium* (legume) over the other species. These findings are consistent with those of Gibson and Watkinson (1989) who found that *R. minor* host selection in natural populations was not random and that it selected grasses over legumes and other hosts. At Fortress Mountain, however, *R. minor* selected legumes over grasses and others.

Although grasses were the most selected host species overall, there was no clear correlation between host selection and host quality. A positive relationship in pair-wise differences between relative host quality and host selection would suggest that *R. minor* made more haustoria to the better quality host of the two that it was growing with. Instead, I found a non-significant negative slope to this relation, indicating that *R. minor* made more haustoria to the poorer quality host. When I consider hosts in Choice tests pooled by species, *R. minor* did make the most haustoria to the best quality host, *Bromus*. However, the number of haustoria to *Bromus* was not statistically greater than the number of haustoria to *Trifolium*, the poorest quality host. The same trend of mismatch between host quality and selection occurred at both field sites. At King Creek, where legumes

were the highest quality host, grasses were selected most. At Fortress Mountain, where grasses were the highest quality host, legumes were selected most.

Foraging involves the placement of resource-acquiring structures in favourable areas due to habitat selection (Kelly 1990, Cain 1994, Gersani *et al.* 1998). This action increases the foraging plants' rate of resource acquisition. I assessed foraging in *R. minor* by the relationship between its host selection and expected reproductive gain from parasitizing the selected hosts. If *R. minor* invests more haustoria parasitizing hosts that give it greater reproductive gain than other available hosts, then *R. minor* is expressing foraging behaviour. According to trends in host quality, at Fortress Mountain *R. minor* did not invest more haustoria parasitizing the better quality hosts than the poorer quality ones. My experimental and field results therefore suggest that *R. minor* did not express foraging behaviour.

2.4.3 Complementary resources

One reason why *R. minor* did not appear to forage as I predicted may be because resources are complementary. *Rhinanthus minor* may need different resources from different host species. If *R. minor* needed less nutrients from the hosts that I have defined as better quality, it may, therefore, make fewer haustoria to them. However, my results do not support the hypothesis that *R. minor* is foraging for complementary resources. *Rhinanthus minor* did not achieve greater seed set when parasitizing two host species

simultaneously than when parasitizing one host species in the experiment. In this respect, my experimental results are supported by Matthies (1996) and (Marvier 1998b) who found that parasitic plants did not achieve greater growth and reproduction when simultaneously parasitizing a legume and grass host. My field results provide weak support for the complementary resources hypothesis. The significantly positive regression coefficient of the Grass x Legume interaction at King Creek indicates synergistic effects of forming haustoria to both host types; fruit production increased significantly when *R. minor* made haustoria to grasses, as long as there were many haustoria also made to legumes. However, the significantly negative Legume x Other interaction suggests that there may be a reproductive cost to parasitizing two host types simultaneously, which does not support the complementary resource hypothesis.

2.4.4 Other possible explanations

Several other factors may influence the relationship I observed between host quality and use. Like many other researchers (Musselman and Mann 1979, Gibson and Watkinson 1989, Prati *et al.* 1997, Davies and Graves 2000), in my study, I assumed that I was observing all of the haustoria on a host and that all were functional and made by the *R. minor* in the sample. There are three reasons why this assumption may be incorrect. First, because most hosts that I observed are perennial, some haustoria on hosts in the natural populations may have been made by *R. minor* in previous years and were not

functional. Second, if hosts have defense mechanisms, such as necrosis of host cells near the point of haustorial attachment, I would be unable to detect this unless I examined the histology of all haustoria (Hood *et al.* 1998), which was not logistically feasible. Third, inevitably, some haustorial connections may have broken during the root washing process rendering them undetectable, which could lead to incorrect conclusions as to which hosts were selected versus avoided. For example, if smaller, weaker haustorial connections were broken more frequently than stronger connections, then species with small haustoria attached to them, such as grasses, would appear to be avoided.

Alternatively, *R. minor* foraging may not be at evolutionary equilibrium with host quality. Of the hosts in my experiment, *Achillea* and *Lupinus* are native to Alberta whereas *Bromus* and *Trifolium* were recently introduced. *Bromus inermis* was introduced into western Canada from Eurasia in 1896 (Heinrichs 1969). The more time the native species have had coexisting with *R. minor* may have enabled them to develop defense mechanisms to counter parasitism, whereas the introduced species have not.

Alternatively, more *R. minor* may not respond adaptively to non-native hosts, because local populations have not had time to evolve to match host quality. Either could explain why there were significantly fewer haustoria with the native species than the exotic species and why the exotic species are relatively of better quality.

In addition, environmental conditions and host quality differed between natural populations. *Rhinanthus minor* is a subalpine species with a circumpolar distribution

(Hitchcock and Cronquist 1973, Moss 1983). The collection sites for my study contain *R. minor* at the southern limit of its range. The Fortress Mountain population is higher in elevation than King Creek and thus likely experiences cooler conditions. The difference in temperature may be a reason why Fortress Mountain *R. minor* had greater fruit production than the King Creek individuals. Also, if a site had a low amount of nitrogen available for plants, then nitrogen-fixing hosts may be of relatively high quality in comparison with the others available, because they can provide parasitic plants with more nitrogen than non-nitrogen-fixing hosts can. Dispersal among populations in a heterogeneous environment would slow local adaptation (Ridley 1996), and could cause a mismatch between behaviour of experimental plants collected at Fortress Mountain, and conditions at the Kananaskis Field Station, the lowest, warmest of the three sites, where the experiment was conducted.

Rhinanthus minor may form haustoria non-randomly to host species not because it is selective, but because of a differential ability to form haustoria to hosts. This may be caused by hosts preventing parasitism by defense mechanisms or being cryptic by chemical mimicry. Chemical mimicry is present in a number of plant species. For example, it occurs in *Arum* lily species to lure in pollinators (Dormer 1960, Smith and Meeuse 1966). Chemical mimicry also occurs in host plants of insect herbivores where hosts mimic non-hosts as protection against herbivory (Dethier 1980). Chemical mimicry may also occur in hosts of parasitic plants, although, to my knowledge, it has not been studied. In my experiment, the significantly greater number of haustoria formed to

Bromus and *Trifolium* than to *Achillea* and *Lupinus* in the Choice Tests may be the outcome of *Bromus* and *Trifolium* being easier to parasitize than the other hosts and not selection for them. This may be why there were more haustoria to *Trifolium* (worst quality host) than *Achillea* and *Lupinus* in the Choice Tests.

Finally, although *R. minor* did not express foraging behaviour, it may still be behaving adaptively. *Rhinanthus minor* is a summer annual with only three to four months in which to make haustoria and gather resources for reproduction. It has a reduced root system in comparison to autotrophic plants (Fitter and Hay 1987) and lives in areas where grass roots are abundant and always available (Tansley 1965, van Hulst *et al.* 1987, Gibson and Watkinson 1989). Selective pressure for host preferences may not be great since the difference in host quality among available hosts is not very large. This may be especially true at Fortress Mountain where there were no significant differences in host quality that I could detect. Therefore, the best strategy for *R. minor*, in terms of foraging, may be to parasitize all hosts that it comes in contact with. Classical foraging theories predict that, as costs such as search time and travel among foraging patches increase, foragers should use resources more opportunistically (Stephens and Krebs 1986). Construction of roots to explore possible hosts may be too costly to make up for the subtle differences in host quality.

Discriminating among the above hypotheses would require either extensive additional experimentation or empirically-based models of the individual-level costs and benefits. Future work to investigate costs and benefits of host selectivity of parasitic

plants may be possible using dynamic optimization models (Mangel and Clark 1988, Clark and Mangel 2000). In contrast to static optimization models (Stephens and Krebs 1986), dynamic optimization models do not assume that the organism maximizes long-term energy intake, but incorporate the organism's current state into its future decisions. This technique has already been applied to model oviposition decisions of parasitoids, such as when to accept or reject a host, when to feed on the host, and how many eggs to oviposit at a time (Collier 1995). Analogously, one could model foraging and reproductive decisions of parasitic plants, such as when to invest energy in extending the root system, produce haustoria, leaves, and reproductive structures, and under what host or environmental conditions it is beneficial to be selective in parasitism.

3 CONCLUSIONS

The goal of this project was to quantify host quality and host selection and use predictions of animal foraging theory to explain foraging by *R. minor*. Differences between the modes of foraging between animals and plants limit the usefulness of such models. For example, plants are not mobile and therefore the cost of searching for a new patch in which to forage is more energetically costly than in animals since new plant material (e.g., roots, stolons) must be constructed. Also, the assumption that searching for resources and exploiting them are mutually exclusive activities may not apply to plants since they do not 'leave' patches like animals do, but continue to forage there while exploiting new patches. However, *R. minor* foraging may be analogous to animals that collect food from multiple patches, and store the food for later use; such animals would use resources from multiple patches simultaneously. Although animal foraging theory may not be directly applicable to parasitic plants because of the violations of assumptions of the models, the general theory may still be used to predict *R. minor* foraging behaviour.

Analogies can be made between aspects of animal and parasitic-plant foraging. Handling time in animal foraging models is analogous to the energetic cost of making an haustorium to a host. This may be greatest for *Lupinus* (thick roots, large haustoria) and smallest for *Bromus* (fine roots, small haustoria). Search time is analogous to the energetic cost of extending the root system to encounter new host roots to parasitize. In

my experiment, on average, search costs would be greatest for *Lupinus* and least for *Bromus* because of the difference in root abundance and architecture.

Authors of a recent review of optimal diet theory make the distinction between diet preferences and active predator choice in foraging behaviour (Sih and Christensen 2001). Organisms with diet preferences have non-random diets relative to prey abundance. Organisms with active predatory choice have unequal attack probabilities given encounters with different prey types (Sih and Christensen 2001). By these definitions, *R. minor* has diet preferences since the relationship between number of haustoria and host availability was different among host types in the experiment and in both field populations. Unfortunately, I am not able to assess whether *R. minor* exhibited active prey choice by Sih and Christensen's (2001) definition, since I do not know if it encountered hosts but did not make haustoria to them.

In conclusion, host selection of *R. minor* did not conform well to the predictions of optimal foraging theory (Fretwell and Lucas 1969, Charnov 1976, Pyke *et al.* 1977). *Rhinanthus minor* did not invest more energy (make more haustoria) parasitizing better quality hosts over poorer quality ones. However, the application of optimal foraging theory to *R. minor* requires the consideration of search costs, which may alter the relative quality of hosts. *Rhinanthus minor* also did not appear to switch among hosts to obtain complementary resources. Nonetheless, *R. minor* was selective in host use, suggesting that individuals were not simply responding passively to resource availability.

Thus, parasitic plants appear to fall somewhere between classical foraging theory,

which was developed for animals using nutritionally similar prey, and classical plant ecology, in which individuals respond passively to resource availability. In fact, as suggested by Pennings and Callaway (2002), my observations may be most parallel to plant-herbivore interactions, in which feeding is cued by complex chemical cues and responses, and for which broad general patterns have been more difficult to find.

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