

AN ABSTRACT OF THE THESIS OF

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Title: Effects of the Biological Control Agent, *Tetranychus lintearius*, on its Host, *Ulex europaeus*.

Abstract approved:

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Invasive plants threaten ecosystems and economies worldwide. Classical biological control, introduction of specialist herbivores on invasive plants, is one of the tools employed to reduce the impact of invasive plants. Gorse, *Ulex europaeus* L. (Fabaceae), an invasive leguminous shrub, is the target of a biological control program in Oregon. The biological control agent, *Tetranychus lintearius* Dufour (Acari: Tetranychidae), the gorse spider mite, was introduced in 1994. Three studies were conducted to quantify the effects of the gorse spider mite on the growth of gorse: a potted plant study, an experimental field study and an observational field study.

The potted plant study quantified the effects of gorse spider mite herbivory at different densities and times of the year under relatively homogenous conditions. Shoot, canopy volume and stem diameter relative growth rates (RGR) and plant dry weights were examined. Average relative mite damage ranged from 1.5 to 4.4% with no significant differences among the inoculation treatments. Shoot RGR was the only plant growth measure affected by mite damage. The late summer high density mite inoculation

resulted in slightly higher shoot RGR compared to the control. The amount of mite damage affected shoot RGR but not stem diameter RGR, canopy volume RGR, aboveground dry weight, belowground dry weight or total dry weight. Unexpectedly, increasing mite damage was associated with slightly increased shoot RGR.

The experimental field study was conducted to assess the effects of gorse spider mite herbivory on individual gorse plant growth rates under field conditions at two inoculation levels. Stem diameter, canopy volume and shoot RGR were examined. Average relative mite damage was 6.5% at the low inoculation level and 7.3% at the high inoculation level and the difference between inoculation levels was not significant. Increased mite damage was associated with decreased shoot RGR. Neither canopy volume RGR nor stem diameter RGR were affected by spider mite damage.

The observational study quantified naturally occurring mite damage and gorse shoot length. Gorse shoot length and the amount of mite damage were measured at several sites throughout the summer. At two of the five sites with mites, mite damage was correlated with shoot length. At one site late in the season, higher mite damage was correlated with greater shoot length. At another site increasing mite damage was associated with shorter shoot length. These contradictory results suggest there may be a damage threshold below which the gorse spider mite either does not affect growth or has a mild stimulatory effect on growth.

The results of this thesis provide evidence that under certain conditions the gorse spider mite affects the growth of gorse over one season. Further research is needed to determine: under what conditions the gorse spider mite reduces shoot growth, what impact reduced shoot growth has over the lifetime of gorse plants and what implications this may have for gorse dominated plant communities.

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Effects of the Biological Control Agent, *Tetranychus lintearius*, on its Host, *Ulex europaeus*.

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Ben Rice, Author

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Effects of the Biological Control Agent, *Tetranychus lintearius*, on its Host, *Ulex europaeus*.

Chapter 1- Introduction

Gorse, *Ulex europaeus* L. (Fabaceae), is an evergreen shrub, native to western Europe. Outside of its native range, gorse has been selected as one of the world's 100 worst invasive species (Lowe et al. 2000). It is invasive in New Zealand, Chile, Australia, Hawaii, and western North America (Hill and O'Donnell 1991b). In western North America, gorse is found primarily in coastal areas from British Columbia to California. Gorse was first reported in Oregon in 1894 and now covers an estimated 20,000 ha in the state (Isaacson and Miller 1992). Gorse forms monocultures which increase fire risk, interfere with recreational activities, interfere with forest regeneration and negatively impact several sensitive species such as the Oregon silver-spot butterfly, *Speyeria zerene* var. *hippolyta* Edwards (Lepidoptera: Nymphalidae).

The gorse spider mite, *Tetranychus lintearius* Dufour (Acari: Tetranychidae), was released as a biological control agent in Oregon in 1994 by the Oregon Department of Agriculture (Coombs et al. 2004). This mite causes chlorosis of gorse shoots by extracting mesophyll cell contents but little is known about the impact at the individual plant level. More information is needed regarding the effects of the gorse spider mite on the growth of individual gorse plants in order to begin assessing its effectiveness as a biological control agent in Oregon. These studies were conducted to quantify the effects of gorse spider mite herbivory on the growth of gorse.

Literature Review

Gorse

Gorse, a spiny, leguminous, evergreen shrub native to western Europe, is just one of a growing number of invasive plants in North America. It is one of 20 species of the genus *Ulex*, native to Europe and North Africa. The rigid spines of this plant are 1-3 cm in length with larger spines developing secondary and tertiary spines. The leaves of mature plants are reduced to scales or spine-like phyllodes (Clements et al. 2001). In its native range vegetative buds burst in late May and elongation continues throughout the summer (Hill 1982).

Flowers are solitary to racemose. The yellow, pea-like flowers are similar in appearance to *Cytisus scoparius* (L.) Link, Scotch broom. Seeds develop within a pod and each pod contains one to seven seeds. Seeds have elaiosomes. Ant mediated seed dispersal has been reported in Europe but has not been reported in western North America (Chater 1931). Dehiscing pods eject seeds up to 5 m from the parent plant (Clements et al. 2001) and seeds remain viable for at least 30 years (Hill and Gourlay 1989). Germination rates for seeds up to 26 years old are as high as 85% (Richardson and Hill 1987). Gorse reproduces vegetatively to a limited extent. Cut gorse readily resprouts from stumps and shoots occasionally root where they contact the ground (Clements et al. 2001).

Gorse is a relatively fast growing plant. Height growth rates in New Zealand average 0.20 m yr^{-1} with 6-10 year old plants growing the fastest (Lee et al. 1986). Gorse height growth averages about 0.30 m yr^{-1} in coastal Oregon (Hermann and Newton 1968). Stem diameter growth rates in New Zealand average 5 mm yr^{-1} , ranging from 0.4 to 14 mm (Lee et al. 1986). During the first 15 years of growth, gorse stands undergo high rates of self-thinning. Recently burnt areas may contain up to $8600 \text{ seedlings m}^{-2}$. Stem density declines markedly with stand age from an average of 32 m^{-2} in intermediate aged stands to 2 m^{-2} in stands older than 20 years (Lee et al. 1986). Gorse stands accumulate biomass up to $40\text{-}60 \text{ t ha}^{-1} \text{ yr}^{-1}$ and about half the annual production is shed as litter (Egunjobi 1971). In the absence of disturbance, single gorse plants may become large. Lee et al. (1986) reported a maximum height of 7 m for gorse and a maximum stem diameter of 217 mm.

The potential geographic distribution of gorse is similar to that of a closely related shrub, Scotch broom. Distribution is limited by the combined effects of temperature and available moisture. The average temperature for the coldest month must be above 2°C . (Richardson and Hill 1987). The southern extent of gorse's range in central coastal California is thought to be moisture limited (Fox and Steinmaus 2001).

Gorse typically occurs in recently disturbed areas and early successional communities (Coombs et al. 1993), often growing in monocultures outside of its native range. These monocultures suppress the growth of trees and other plants (Clements et al. 2001) and

alter local biogeochemistry in several ways. The success of gorse is in part due to its association with nitrogen fixing bacteria, capable of fixing up to $200 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (Clements et al. 2001). Soil becomes acidified under the canopy due to retention of bases, especially calcium, in the litter (Richardson and Hill 1987). Gorse litter also causes the substrate to be drier, which inhibits the establishment of other plants (Clements et al. 2001). The interactions of these factors displace native plants and alter wildlife habitat. For example, in western Oregon gorse negatively affects sensitive species [e.g. *Lycopodium inundatum* L. (Lycopodiaceae), *Phacelia argentea* A. Nelson and J.F. Macbr. (Hydrophyllaceae) and the threatened (federal ESA listed) Oregon silver-spot butterfly, *Speyeria zerene* var. *hippolyta* Edwards (Lepidoptera: Nymphalidae)] (Coombs et al. 1993).

Gorse also poses problems for human communities. In Oregon gorse interferes with land uses such as recreation, reforestation and grazing (Coombs et al. 1993). The high oil content of gorse contributes to its extreme flammability. The town of Bandon, Oregon was destroyed on September 26, 1936 during a fire which was largely attributed to dense gorse stands in the area (Beckham 1985). That fire caused \$1.6 million in damage, 13 deaths and left 1800 area residents homeless.

Gorse often enters plant communities at an early successional stage and continues to dominate sites for extended periods of time. Maximum age of an individual plant is 29-46 years (Clement et al. 2001). The presence of a large long-lived seed bank contributes

to the dominance of gorse stands and its return after disturbance. Gorse seed bank estimates reach 100 million seeds ha⁻¹ (Richardson and Hill 1987). Lee et al. (1986) estimate that a 50-60 year period of relatively low disturbance is required for native plants to replace gorse.

Extent of the gorse problem

Gorse is considered a serious pest plant in New Zealand, Chile, Australia, Hawaii and western North America (Hill and O'Donnell 1991b). Introduction and spread of gorse is associated with human activities (i.e., planting as live fencing and unintentional spread on machinery). Gorse was introduced to New Zealand and Australia for the purpose of live fencing, beginning in the early to mid 19th century (Richardson and Hill 1987). Currently in New Zealand gorse occurs on about 900,000 ha (Hill et al. 1989).

Gorse is found in North America on both the east and west coasts. On North America's eastern coast gorse has been reported from Virginia to Massachusetts. In western North America gorse ranges from central coastal California north to the Queen Charlotte Islands in British Columbia (Coombs et al. 1993). In British Columbia gorse was planted as hedgerows (Clements et al. 2001). Gorse was introduced into California from Ireland by the immigrant tradition of planting gorse on graves and has subsequently spread to all coastal California counties from Monterey north to the Oregon border (Fox and Steinmaus 2001). Gorse was first reported in Oregon in 1894 in the coastal town of Bandon (Isaacson and Miller 1992), introduced by Irishman and town founder, Lord

George Bennett (Beckham 1985). Gorse has spread to cover an estimated 20,000 ha in the state (Isaacson and Miller 1992), occurring primarily in coastal areas with limited but increasing occurrences inland (Coombs et al. 1993). No estimates of the current rate of gorse spread are available. Given the success of gorse in climatically similar areas though, it is reasonable to assume that gorse will continue to spread in Oregon (Isaacson and Miller 1992) with logging roads and equipment providing the primary means of long distance dispersal (Clements et al. 2001).

Gorse Management

Gorse occurs over a large area, much of which is not easily accessible. Chemical and mechanical control methods, while in some cases locally appropriate, are not suited to widespread control. Mechanical control methods, such as mowing, which remove only the canopy are largely unsuccessful, because gorse resprouts. Uprooting gorse with brush rakes kills plants but the soil disturbance may result in high levels of gorse seed germination (Prasad 2003; Anon. 2002). Mechanical control is best used in conjunction with other control methods such as burning or grazing (Richardson and Hill 1987).

Chemical control in the past was locally successful using 2,4,5-T (no longer registered for use in the United States) or combinations of 2,4-D with picloram (Hermann and Newton 1968). Chemical control on a large scale is cost prohibitive and physically difficult (Hill and O'Donnell 1991b). Gorse often requires repeated applications of herbicides to kill individual plants. Herbicides may be effective in temporarily reducing the biomass of

gorse at a particular site, but may not impact gorse populations. Killing individual plants increases the availability of light at ground level. This increase in light can break seed dormancy and promote the growth and development of seedlings. The space previously occupied by a single plant may then be occupied by a number of seedlings. Hence, only a temporary benefit is gained unless herbicide treatment is used in combination with other treatments, such as planting competitive species, burning or grazing. In using herbicides nontarget effects, environmental impacts, human health considerations and public sentiment must also be taken into account.

Control of gorse with domestic grazing animals has been attempted. Clements et al. (2001) cite studies in which grazing with goats in New Zealand was found to be more economical than herbicide applications. Gorse is preferred forage for goats where it occurs as more than 10% of the pasture (Richardson and Hill 1987). Stocking rates of 25-30 goats ha⁻¹ have been found to reduce gorse to negligible levels (Clements et al. 2001). Sheep are moderately successful in preventing establishment of gorse seedlings and may browse gorse when other food is in short supply (Anon. 2002). Grazing has the greatest impact on seedlings and resprouting plants and therefore, effective grazing in established stands of large plants requires some other type of preliminary treatment (Richardson and Hill 1987). Small areas may be effectively controlled with grazing but this method is more problematic over larger areas. Introducing domestic grazing animals in natural areas for gorse control is impractical. In established stands with large plants, much of the gorse foliage is inaccessible to animals. Use of domestic animals may also

have unintended consequences. Feral animals have the potential to be invasive, causing great ecological destruction (van Driesche and van Driesche 2000).

Competitive exclusion of gorse appears to be one of the most effective approaches. This often involves combining some method of gorse biomass reduction, such as herbicide treatment or burning, followed by planting of more desirable species. Agricultural lands can be sown in competitive pasture species. Richardson and Hill (1987) note that gorse competes poorly with aggressive pasture species such as *Trifolium repens* L. and *Lolium perenne* L. In the case of forested land, competitive fast growing tree species may be planted (Hermann and Newton 1968).

In developing and conducting pest control it is essential to consider and exploit the “life-cycle transitions that are both amenable to manipulation and influential on population growth” (McEvoy and Coombs 1999). This approach has led to successful control of tansy ragwort, *Senecio jacobea* L., in northern California and western Oregon (McEvoy and Coombs 1999; McEvoy et al. 1991). In modeling gorse populations Rees and Hill (2001) hypothesize that where gorse produces abundant seed, the key parameters for reducing gorse populations are: decrease the frequency of disturbance, decrease the maximum longevity of individual plants and decrease the probability that the site will be suitable for germination after gorse senescence. Thus, gorse regeneration (seed to juvenile transition) and survival of adult plants (adult to adult transitions) are the life-cycle transitions critical to gorse control. All of the aforementioned treatment options fail

to adequately address these life-cycle transitions. Thus, these management options do not constitute solutions to the gorse problem but offer only short-term relief. For example, foliar herbicide applications, if properly conducted, may provide a one time reduction in the probability of adult to adult transition (i.e. adult plant survival) but do nothing to address the seed to juvenile transition (i.e. germination) that follows.

Biological control of gorse

Biological control is another potential tool for gorse management. Classical biological control involves the release of an approved natural enemy or enemies into an invasive plant's introduced range with the expectation that the agent will control the target species without further human intervention or inputs (Wapshere et al. 1989). Biological control is based on the assumption that plant populations are regulated by natural enemies and that some of these enemies are limited in their host range (Harley and Forno 1992; Wapshere et al. 1989). Biological control is different from other control options. It is fairly permanent, self-perpetuating and has no or only limited recurring costs (Wapshere et al. 1989). In contrast to chemical control, biological control reduces human health risks, reduces resource inputs and avoids the issue of resistance to pesticides (McEvoy and Coombs 2000).

The primary aim of biological control is to reduce populations of the target plant species without damaging other plant species. Thus, classical biological control tends to use specialist herbivores rather than generalists. Use of monophagous and oligiophagous

organisms in biological control carries lower risk to non-target organisms. Specialists may also have a competitive advantage over other herbivores when food resources (i.e., the target plant) are unavailable to generalists, not co-evolved to overcome plant defensive mechanisms (Keane and Crawley 2002). When the host plants occur in monocultures, the advantage to specialists is increased because searching costs are low (Crawley 1983). Alternately, monophagy is a potential barrier to the success of a biological control agent. Depending on resource requirements, biological control agents may become locally extinct before the target plant is reduced to the desired level.

Most targets for biological control are invasive species (Crawley 1989). Biological control of plants introduces herbivores with the expectation that the herbivore will reduce the invasiveness of the target plant (Bellows and Headrick 1999). Approximately 259 species of arthropods have been used in the biological control of plants worldwide. This number includes 254 insect species and 5 mite species (Bellows and Headrick 1999). Targets of biological control programs include 101 species of “weeds” in 33 families (Goeden and Andres 1999). Approximately 25% of these biological control programs have been successful (van Driesche and Bellows 1996). Success is a subjective term often based on qualitative measures rather than quantitative ones. Even when quantitative measures are available they tend to be of low quality (Keane and Crawley 2002). Schooler (1998) divided quantitative biological control agent evaluation into six measures: 1) establishment, 2) increase in the population, 3) geographic spread, 4) effects

on individual target plants, 5) effects on target plant populations and 6) indirect effects on the plant community.

Several surveys have been conducted of the phytophagous invertebrates attacking gorse in its native range, including those by Hill, O'Donnell and Zwoelfer (Hill and Gourlay 1989). Sixteen invertebrate species were found to be host specific enough to warrant further study as potential gorse biological control agents (Hill and Gourlay 1989). A number of these species have been introduced as gorse biological control agents throughout the world. Some of the first gorse biological control programs involved the use of *Exapion ulicis* (= *Apion ulicis*) Forster (Coleoptera: Brentidae (=Apionidae)). The larvae of this univoltine weevil destroy gorse seeds in the spring. In New Zealand 85-95% of the spring pods are attacked by *E. ulicis* (Hill et al. 1989). The weevil was released in California in 1953 and Oregon in 1956 (Coombs et al. 1993). It attacks 40-90% of seed pods in Oregon, but has not influenced gorse populations (Coombs et al. 1993). Failure of this agent to affect target plant populations is in part due to the fact that *E. ulicis* is univoltine. Therefore, all seed and flower production outside the active period are not subject to attack, including fall flowering which can be substantial in some areas. *Cydia succedana* Denis and Schiffermüller (Lepidoptera: Tortricidae), a bivoltine moth species was released in New Zealand to attack both spring and fall seed pods (Hill and Gourlay 2002). However, the effect of these two seed feeding insects is expected to be negligible in most areas because gorse is usually not seed limited. A very small number of viable seeds are required for gorse to become established and dominate a site. Other

gorse biological control agents that attack vegetative plant parts have been introduced around the world. Many of these have been relatively recent and the effectiveness of these species has not yet been thoroughly assessed. Two shoot feeders, *Agonopterix ulicitella* Stainton (Lepidoptera: Oecophoridae), the gorse shoot-tip moth, and *Pempelia genistella* Duponchel (Lepidoptera: Pyralidae), have been released in Hawaii and New Zealand (Julien and Griffiths 1998). The gorse thrips, *Sericothrips staphylinus* Haliday (Thysanoptera: Thripidae), has been released in New Zealand, Hawaii and Australia (Julien and Griffiths 1998; Anon. 2002).

Several accidentally introduced herbivores in the western United States have been discovered attacking gorse outside of intentional biological control introductions.

Agonopterix nervosa Haworth (Lepidoptera: Oecophoridae), a moth of European origin and typically associated with Scotch broom, was found to attack gorse in 1966 (Coombs et al. 1993). In California an exotic gall mite, *Aceria genistae* Nalepa (Acari: Eriophyoidea), was discovered feeding on gorse (Clements et al. 2001).

Gorse spider mite

Tetranychus lintearius Dufour, the gorse spider mite, is a stenophagous mite that feeds on gorse. It belongs to the same genus as agricultural pest mites such as *Tetranychus urticae* Koch and *Tetranychus cinnabarinus* Boisduval. The gorse spider mite occurs at higher densities than these spider mite species. The gorse spider mite is arrhenotokous; haploid males develop from unfertilized eggs (Hill and O'Donnell 1991a). Eggs are 128 μm in

diameter and are initially a translucent white color becoming an opaque brown as they mature. Males average 360 μm in length and 161 μm in width. Females are substantially larger averaging 561 μm by 288 μm . Both sexes are green in immature stages and red in the adult phase. Mature males do not move with feeding colonies but remain behind to mate with females directly after ecdysis. Inactive chrysalids and eggs are also left behind. Upon emerging or hatching, mites move along webbing or disperse to other areas to seek food (Stone 1986). Average generation times (egg to egg) for this species range from 17.7 days at 25°C to 45.8 days at 15°C (Stone 1986). Average temperatures greater than 13° C are required to complete development (Hayes et al. 1994). There is no evidence of diapause in the gorse spider mite.

The gorse spider mite disperses to new food patches both passively and actively.

Dispersal behavior in other *Tetranychus* species is triggered by low relative humidity (Kennedy and Smitley 1985; Rodriguez and Rodriguez 1987). The gorse spider mite moves actively along webbing into adjacent shoots and plants and may also drop to the ground to crawl to other bushes. Spider mites move passively by positioning themselves to increase the probability of being carried away by wind. As a gorse spider mite colony reaches the tip of a gorse shoot some individuals move to the edges of the colony, increasing the chance of being carried by wind to new sites.

A great deal of research was conducted prior to the use of the gorse spider mite as a biological control agent. It was found to be reproductively isolated from other

tetranychid species (Hill and O'Donnell 1991a). Host specificity testing was conducted for each country before the mite was released. Initially, a wide range of plants was tested. Hill and O'Donnell (1991b) found that only legumes were suitable for survival of this species. Subsequent host specificity testing was then restricted to legumes. The mite successfully completed its life cycle on *Phaseolus vulgaris* L., bean, and *Glycine max* L., soybean, but these plants did not support a second generation. Furthermore, gorse spider mites have never been recorded on either species throughout its native geographical range. It was concluded that the gorse spider mite posed no threat to these agriculturally important species. Later testing found little threat to native and economically important legumes in North America (Hill and Gourlay 1991).

Spider mite feeding removes cell contents, which directly and indirectly disrupts the physiological functions of plants. Feeding can cause a variety of plant responses including changes in growth, flowering and seed output (Tomczyk and Kropczynska 1985). The most common consequence of spider mite feeding is reduction of growth in all plant parts (Tomczyk and Kropczynska 1985). Gorse spider mite feeding causes foliage to become mottled white or green. Individual shoots may die and flowers may be spontaneously aborted (Hill et al. 1991). Observations suggest that mite feeding reduces the growth of individual shoots and early season feeding reduces flowering (E.M. Coombs personal communication).

The gorse spider mite was introduced in New Zealand in 1989 from Cornwall, England. Establishment, overall, was successful but with some localized failures associated with heavy rainfall during warm temperatures. These conditions cause mites to become entangled within the webbing, leading to high levels of mortality (Hayes et al. 1996). Due to these failures to establish, five additional “strains” of the mite from other areas of Europe were subsequently imported into New Zealand (Hayes et al. 1996).

English and Spanish/Portuguese gorse spider mite strains from New Zealand were released in Oregon in 1994 by the Oregon Department of Agriculture (Coombs et al. 2004). The mite is now considered established in Oregon but its effectiveness as a biological control agent is largely unknown. However, to date the mite has had no observable effects on the target plant populations or plant communities. The apparent lack of success is in part attributed to predator associations formed in the introduced range. A native coccinellid beetle, *Stethorus bifidus* Kapur (Coleoptera: Coccinellidae), and a predatory mite, *Phytoseiulus persimilis* Athias-Henroit (Acari: Phytoseiidae), were reported to feed on the gorse spider mite in New Zealand (Hill et al. 1991). Pratt et al. (2003) identified several predatory species associated with the gorse spider mite in Oregon. Of particular concern was the presence of *Phytoseiulus persimilis* in the Bandon, Oregon area and *Stethorus* species in the Florence, Oregon area. These species appear able to substantially reduce the number and size of gorse spider mite colonies and any effects of the gorse spider mite may be minimized by high levels of predation.

Damage to gorse may also be limited by the quality of food resources, specifically by the available nitrogen content of gorse foliage. Gorse total soluble nitrogen content peaks immediately after initiation of new growth then decreases. Nitrogen content reaches a low point after six weeks and remains at this level for the duration of the growing season (Hill 1982). In coastal Oregon the gorse spider mite does not become abundant until well after foliar nitrogen content decreases and this may limit the seasonal increase of mite populations.

Objectives

Very little is currently known about the impact of the biological control agent, the gorse spider mite, on its target plant, gorse. Pratt et al. (2003) noted that “it remains unclear what level of spider mite density is needed to reduce the competitive superiority of *U. europaeus*.” There have been several attempts to quantify the effects of gorse spider mite herbivory but these have not provided conclusive results (G.P. Markin unpublished data; T.R. Partridge personal communication). Anecdotally, there is a general opinion that the gorse spider mite has been a failure as a biological control agent, but empirical support for this hypothesis is lacking.

This thesis addresses one aspect of biological control agent evaluation in Schooler's (1998) evaluation assessment scheme, effects on individual target plants. This project examined the effects of mite herbivory on gorse over one growing season in three parts: a potted plant study, an experimental field study and an observational field study. The

potted gorse study quantified the effects of gorse spider mite herbivory following inoculations with different densities of mites at different times of the year under relatively homogenous conditions. The experimental field study was conducted to examine the effects of gorse spider mite herbivory on individual gorse plants under field conditions. The observational study quantified naturally occurring mite densities and damage. The results of these studies will be useful in understanding the effects of the mite over one growing season and as a step towards evaluating the gorse spider mite as a biological control agent in Oregon.

Literature cited

- Anonymous. 2002. Service sheet: Gorse *Ulex europaeus* (L.). Department Of Primary Industries, Water and Environment. Tasmania, Australia.
- Beckham, C. 1985. The Night Bandon Burned. Myrtle Point Printing, Myrtle Point, Oregon.
- Bellows, T.S. and Headrick, D.H. 1999. Arthropods and vertebrates in biological control of plants. In T.S. Bellows and T.W. Fisher [eds.], Handbook of Biological Control: Principles and Applications of Biological Control. Academic Press, San Diego, CA.
- Chater, E.H. 1931. A contribution to the study of the natural control of gorse. Bulletin of Entomological Research 22: 225-235.
- Clements, D.R., Peterson, D.J. and Prasad, R. 2001. The biology of Canadian weeds 112 *Ulex europaeus*. Canadian Journal of Plant Science 81: 325-337.
- Coombs, E., Isaacson, D., Miller, G. and Turner, C. 1993. Petition for the introduction and field release of the gorse spider mite, *Tetranychus linteraius* Dufour (Tetranychidae: Acari), for the biological control of gorse, *Ulex europaeus* L. (Leguminosae), in North America. TAG Report 93-04.

- Coombs, E.M., Markin, G.P., Pratt, P.P. and Rice, B. 2004. Gorse. *In* E.M. Coombs, J.K. Clark, G.L. Piper, and A.F. Cofrancesco Jr. [eds.], *Biological Control of Invasive Plants in the United States*. Oregon State University Press, Corvallis, OR.
- Crawley, M.J. 1989. Insect herbivores and plant population dynamics. *Annual Review of Entomology* 34: 531-564.
- Crawley, M.J. 1983. *Herbivory: The Dynamics of Animal-Plant Interactions*. University of California Press, Berkeley, CA.
- Egunjobi, J.K. 1971. Ecosystem processes in a stand of *Ulex europaeus* L.: I. Dry matter production, litter fall and efficiency of solar energy utilization. *Journal of Ecology* 59: 31-38.
- Fox, J.C. and Steinmaus, S. 2001. Climatic prediction of an invasive plant in California: *Ulex europaeus* (Gorse). *Proceedings of the California Weed Science Society* 53: 34-37.
- Goeden, R.D. and Andres, L.A. 1999. Biological control of weeds in terrestrial and aquatic environments. *In* T.S. Bellows and T.W. Fisher [eds.], *Handbook of Biological Control: Principles and Applications of Biological Control*. Academic Press, San Diego, CA.
- Harley, K.L.S. and Forno, I.W. 1992. *Biological Control of Weeds: A Handbook for Practitioners and Students*. Inkata Press, Melbourne, Australia.
- Hayes, A.J., Gourlay, A.H. and Hill, R.L. 1996. Population dynamics of an introduced biological control agent for gorse in New Zealand: a simulation study. *In* V.C. Moran and J.H. Hoffman [eds.], *Proceedings, IXth International Symposium on Biological Control of Weeds*, 19-26 January, 1996, Stellenbosch, South Africa, University of Cape Town.
- Hayes, A.J., Gourlay, A.H. and Hill, R.L. 1994. Temperature-dependent phenology of gorse spider mite. *Proceedings of the New Zealand Plant Protection Conference* 47: 98-102.
- Hermann, R.K. and Newton, M. 1968. Tree Planting for the Control of Gorse on the Oregon Coast. Research Paper 9. Forest Research Laboratory, School of Forestry, Oregon State University, Corvallis, Oregon.
- Hill, R.L. 1982. Seasonal patterns of phytophage activity on gorse (*Ulex europaeus*) and host plant quality. *In* J.H. Visser and A.K. Minks [eds.], *Proceedings of the 5th International Symposium on Insect/ Plant Relationships*, Wageningen, the Netherlands.

- Hill, R.L. and Gourlay, A.H. 2002. Host-range testing, introduction and establishment of *Cydia succedana* (Lepidoptera: Tortricidae) for biological control of gorse, *Ulex europaeus* L., in New Zealand. *Biological Control* 25: 173-186.
- Hill, R.L. and Gourlay, A.H. 1991. Safety testing of *Tetranychus lintearius* (Dufour), a potential control agent for gorse in Oregon. Unpublished report to the Oregon Department of Agriculture.
- Hill, R.L. and Gourlay, A.H. 1989. *Ulex europaeus* L., gorse (Fabaceae). In P.J. Cameron, R.L. Hill, J. Bain, W.P. Thomas [eds.], Technical Communication No. 10, A Review of Biological Control of Invertebrate Pests and Weeds in New Zealand 1874-1987. CAB International, Walingford, UK.
- Hill, R.L. and O'Donnell, D.J. 1991a. Reproductive isolation between *Tetranychus lintearius* and two related mites *T. urticae* and *T. turkestanii* (Acarina: Tetranychidae). *Experimental and Applied Acarology* 11: 241-251.
- Hill, R.L. and O'Donnell, D.J. 1991b. The host range of *Tetranychus lintearius* (Acarina: Tetranychidae). *Experimental and Applied Acarology* 11: 253-269.
- Hill, R.L., Gourlay, A.H. and Wigley, P.J. 1989. The introduction of gorse spider mite, *Tetranychus lintearius*, for biological control of gorse. *Proceedings of New Zealand Weed and Pest Control Conference* 42: 137-139.
- Hill, R.L., Grindell, J.M., Winks, C.J., Sheat, J.J. and Hayes, L.M. 1991. Establishment of gorse spider mite as a control agent for gorse. *Proceedings of the New Zealand Plant Protection Conference* 44: 31-34.
- Isaacson, D.L. and Miller, G. 1992. A comparison of gorse (*Ulex europaeus* L.) in New Zealand and the United States. In *Proceedings of the Washington State Weed Conference*, Nov 4-6, Yakima, WA.
- Julien, M.H. and Griffiths, M.W. 1998. *Biological control of weeds: A World Catalogue of Agents and their Targets*, 4th Edition. CABI, New York.
- Keane, R.M. and Crawley, M.J. 2002. Exotic Plant Invasions and the enemy release hypothesis. *Trends in Ecology and Evolution* 17: 164-170.
- Kennedy, G.G. and Smitley, D.R. 1985. Dispersal. In W. Helle and M.W. Sabelis [eds.], *Spider Mites: Their Biology Natural Enemies and Control*. Elsevier, New York.

- Lee, W.G., Allen, R.B. and Johnson, P.N. 1986. Succession and dynamics of gorse (*Ulex europaeus* L.) communities in the Dunedin Ecological District, South Island, New Zealand. *New Zealand Journal of Botany* 24: 279-292.
- Lowe, S.J., Browne, M. and Boudjelas, S. 2000. 100 of the World's Worst Invasive Alien Species. IUCN/SSC Invasive Species Specialist Group (ISSG), Auckland, New Zealand.
- McEvoy, P.B. and Coombs, E.M. 2000. Why things bite back: unintended consequences of biological weed control. *In* P.A. Follett and J. Duan [eds.], *Nontarget Effects of Biological Control*. Kluwer Academic Publishers, Boston, MA.
- McEvoy, P.B. and Coombs, E.M. 1999. Biological control of plant invaders: regional patterns, field experiments, and structured population models. *Ecological Applications* 9: 387-401.
- McEvoy, P., Cox, C. and Coombs, E. 1991. Successful biological control of ragwort, *Senecio jacobaea*, by introduced insects in Oregon. *Ecological Applications* 1: 430-442.
- Prasad, R. 2003. Management and Control of Gorse and Scotch Broom in British Columbia. Technology Transfer Note Number 30. Canadian Forest Service, Pacific Forestry Centre, Victoria, BC.
- Pratt, P.D., Coombs, E.M. and Croft, B.A. 2003. Predation by phytoseiid mites on *Tetranychus lintearius* (Acari: Tetranychidae), an established weed biological control agent of gorse (*Ulex europaeus*). *Biological Control* 26: 40-47.
- Rees, M. and Hill, R.L. 2001. Large-scale disturbances, biological control and the dynamics of gorse populations. *Journal of Applied Ecology* 38: 364-377.
- Richardson, R.G. and R.L. Hill. 1987. *Ulex europaeus*. *In* F.D. Panetta, R.H. Groves and R.C.H. Shepherd [eds.], *The Biology of Australian Weeds*, Volume 2. R.G. and F.J. Richardson, Melbourne, Australia.
- Rodriguez, J.G. and Rodriguez, L.D. 1987. Nutritional ecology of phytophagous mites. *In* F. Slansky Jr. and J.G. Rodriguez [eds.], *Nutritional Ecology of Insects, Mites, Spider and Related Invertebrates*. John Wiley and Sons, New York.
- Schooler, S.S. 1998. Biological control of purple loosestrife *Lythrum salicaria* by two chrysomelid beetles *Gallerucella pusilla* and *Gallerucella calamaiensis*. M.S. Thesis, Oregon State University.

- Stone, C. 1986. An investigation into the morphology and biology of *Tetranychus lintearius* Dufour (Acari:Tetranychidae). *Experimental and Applied Acarology* 2: 173-186.
- Tomczyk, A. and Kropczynska, D. 1985. Effects on the Host Plant. *In* W. Helle and M.W. Sabelis [eds.], *Spider Mites: Their Biology Natural Enemies and Control*. Elsevier, New York.
- van Driesche, R.G. and Bellows, T.S. 1996. *Biological Control*. Chapman and Hall, New York.
- van Driesche, J. and van Driesche, R. 2000. *Nature out of place: biological invasions in the global age*. Island Press, Washington, D.C.
- Wapshere, A.J., Delfosse, E.S. and Cullen, J.M. 1989. Recent developments in biological control of weeds. *Crop Protection* 8: 227-250.

Chapter 2- Effects of gorse spider mite, *Tetranychus lintearius* Dufour (Tetranychidae: Acari), on growth of potted gorse, *Ulex europaeus* L. (Fabaceae)

Introduction

Gorse, *Ulex europaeus* L. (Fabaceae), is an evergreen shrub, native to western Europe. Outside of its native range, gorse has been selected as one of the world's 100 worst invasive species affecting several regions of the world (Lowe et al. 2000; Richardson and Hill 1987). In western North America, gorse is found primarily in coastal areas from British Columbia to California, including an estimated 20,000 ha in Oregon (Issacson and Miller 1992). Gorse forms monocultures that increase fire risk, interfere with recreational activities, interfere with reforestation and negatively affect sensitive species, such as the endangered Oregon silver-spot butterfly, *Speyeria zerene* var. *hippolyta* Edwards (Lepidoptera: Nymphalidae) (Coombs et al. 1993). In 1994 a gorse biological control agent, the gorse spider mite, *Tetranychus lintearius* Dufour (Tetranychidae: Acari), was released in Oregon by the Oregon Department of Agriculture (Coombs et al. 2004). The gorse spider mite is in the same genus as several agricultural and horticultural pests, such as *Tetranychus urticae* Koch and *Tetranychus cinnabarinus* Boisduval.

Spider mite feeding removes cell contents, which directly and indirectly disrupts plant physiological functions, causing a variety of responses including changes in growth, flowering and seed output. The most common consequence is a reduction in growth of all plant parts (Tomczyk and Kropczynska 1985). Plant responses to herbivory are dependent on both the timing and amount of feeding damage (Bellows and Headrick

1999; Crawley 1989). The gorse spider mite was introduced as a biological control agent with the expectation that it would reduce the growth of gorse and consequently affect gorse populations in Oregon. This study was designed to quantify the effects of gorse spider mite herbivory following inoculations with different numbers of mites at different times of year under relatively homogenous conditions.

Methods

Experimental design

Fifty-six gorse plants less than 1 m tall were collected from field sites on the Oregon Coast 6-10 months prior to the first mite inoculation treatment. During the first year gorse is usually a single-stemmed, unbranched plant. During the second year axillary buds produce branches which elongate until vegetative buds burst the following year. Thus, the age of gorse plants can be determined. Plants with aboveground parts approximately two years old were selected for this study. Root systems may be older than the aboveground parts due to resprouting. Plants with noticeably older root systems were rejected. Gorse proved sensitive to transplanting and therefore, methods were developed to increase transplanting success. Plants were dug from the soil, retaining as much root and surrounding soil as possible, and were immediately placed into a 1:1 mixture of field sand and commercial yard waste compost in a 20 cm diameter by 22 cm tall pot. Plants were immediately watered to completely saturate the soil. Potted plants were transported to a growing area, a covered structure with open sides, on the campus of Oregon State University, Corvallis, OR and fertilized with 6.1 g of a commercial 16-12-12 granular

fertilizer. To avoid repotting plants, the smaller pots were placed in the center of larger pots, 41 cm diameter by 38 cm tall, that were half filled with field collected sand. Then, large pots were filled with sand and watered to saturation. Pots were arranged in rows approximately 40-50 cm apart. The sides of pots were coated with a ring of Teflon paint to prevent mites from crawling between pots. A barrier constructed of window screen and wire fencing was placed around each plant, preventing mites from being passively transported between plants by wind. An automated drip irrigation system was installed to standardize watering and to avoid disturbing mites and their webbing. Plants were watered to keep the soil moist but not saturated. Competing vegetation in gorse pots was manually removed until the first mite inoculation. Eight plants were randomly assigned to each of the experimental treatments which were combinations of mite inoculation time and density. There were three inoculation times: early summer (June 21, 2003), mid summer (August 5, 2003) or late summer (September 19, 2003) and two inoculation densities: low, one inoculation shoot, or high, two inoculation shoots. The remaining eight plants were maintained as a control, receiving no mite inoculations.

Mite colonies were collected from field sites on the Oregon Coast one or two days prior to inoculations. Mite infested gorse shoots 15-20 cm in length, containing an area of 2-3 cm² of dense adult mite colonies, were collected, placed in plastic bags and kept cool until needed. Several arthropod species, primarily *Phytoseiulus persimilis* Athias-Henroit (Acari: Phytoseiidae) and *Stethorus* spp. (Coleoptera: Coccinellidae), have been identified as predators of the gorse spider mite in Oregon (Pratt et al. 2003). All inoculation shoots

appeared to be free of known predators based on examination of webbing under a dissecting microscope. Plants were inoculated by lodging the appropriate number of mite infested shoots in the lower portion of the canopy.

Gorse plants were measured prior to the first inoculation in June and then monthly until December. Height was recorded to the nearest cm from the soil to the tallest point in the plant. Canopy diameter was measured along two axes: one at the widest point, major diameter, and the second at the narrowest point, minor diameter. Current year shoots were selected by randomly choosing a point within the canopy. Random numbers were chosen along the major and minor diameters. The corresponding point was located and the length of the shoot with the shoot tip closest to that point was measured. The length of four current year shoots selected in this manner on each sampling date was measured to the nearest cm and used to calculate an average shoot length. Stem diameters were measured at ground level using a digital caliper. For plants with more than three stems, the three largest diameter stems were marked and measured on each sampling date.

Canopy volume was calculated as a sphere, with the diameter equal to the average of the height, major diameter and minor diameter. Monthly average relative growth rates (RGR) were calculated using the first and last month data for stem diameter, canopy volume and average shoot length. Relative growth rates were calculated as $[\ln(\text{measurement at time}_2) - \ln(\text{measurement at time}_1)] / (\text{time}_2 - \text{time}_1)$. At the end of the study, plants were harvested, cleaned, separated into above- and belowground

components and dried to constant weight. The final weights of above and belowground components were recorded.

Mite damage was assessed on each sampling date. Each patch of webbed and unwebbed mite damage was measured (length, width and height) to the nearest 5 cm. Volume of each mite damaged patch was determined and the volumes were summed to produce total mite damage volume for each plant. Relative mite damage was calculated as total mite damage volume divided by the total plant canopy volume from data collected on the last sampling date.

Statistical analysis

The effect of inoculation treatment on relative mite damage data was tested with an analysis of variance (ANOVA) using PROC MIXED in SAS version 8.2 (SAS 2001). Relative mite damage was logit transformed to better meet assumptions of normality. Back-transformed means are reported. Residual distribution was within the expected range given the small sample sizes for each treatment. Means were compared using a Tukey adjustment for unplanned comparisons.

The effects of mite herbivory were examined in two ways. An analysis of covariance (ANCOVA) was conducted to examine the effects of inoculation time and density on relative growth rates and plant weights, with initial canopy volume as a covariate. An ANCOVA was conducted independently for each growth variable using PROC MIXED

in SAS version 8.2 (SAS 2001). Mean responses of mite inoculated groups were compared to the control using a Dunnett adjustment for multiple comparisons. ANCOVA assumptions were tested for each model. Residuals were graphically examined for normal distribution and constant variance. In the case of the belowground, aboveground and total biomass, plots of predicted vs. residual biomass showed increasing variance with increasing values and thus, biomass values were log transformed to better meet the assumption of constant variance. Assumption of residual normal distribution was within the expected range given the small sample sizes for each treatment. In all cases the relationship between the covariate and the response variables was approximately linear. For each response the assumption of homogeneity of slopes for all treatments was tested (Littell et al. 2002). A significant p -value (<0.05) for the interaction of treatments and the covariate indicates slopes are heterogeneous. Slopes for all treatment groups were homogeneous.

Relative growth rate and biomass data were analyzed individually as a function of initial canopy volume and relative mite damage, using regressions in SAS version 8.2 (SAS 2001). Residuals were graphically examined for constant variance. A plot of predicted vs. residual belowground biomass showed increasing variance with increasing values. Therefore, belowground biomass was log transformed to better meet the assumption of constant variance. Variance of all models was relatively constant after this transformation.

Results

Relative mite damage

The amount of relative mite damage was significantly affected by mite inoculation ($p < 0.001$, $F_{6,49} = 31.16$). The relative mite damage of all inoculation treatments was significantly different from the control but not from each other. Median relative mite damage ranged from 4.42% in the late summer high density inoculation to 1.48% in the mid summer low density inoculation (Table 2.1).

Relative growth rates

Stem RGR was not significantly affected by mite inoculations ($p = 0.4923$, $F_{6,48} = 0.92$) but did vary with initial canopy volume ($p = 0.0265$, $F_{1,48} = 5.24$). Similarly, canopy volume RGR was not significantly affected by mite inoculation ($p = 0.4852$, $F_{6,48} = 0.93$) but did vary with initial canopy volume ($p < 0.0001$, $F_{1,48} = 46.26$) (Figure 2.1). The effect of mite inoculation treatments on shoot growth was marginally significant ($p = 0.0567$, $F_{6,48} = 2.22$) and again the effect of initial canopy volume was also significant ($p = 0.0005$, $F_{1,48} = 13.99$). The late summer high inoculation treatment had greater shoot RGR compared to the control. Shoot growth in this group was $0.07 \text{ cm cm}^{-1} \text{ month}^{-1}$ greater than in the control (95% CI: 0.002 to 0.14).

The regression analyses indicated that relative mite damage did not significantly affect stem RGR ($p = 0.9093$, $t_{53} = -0.11$) or canopy volume RGR ($p = 0.7586$, $t_{53} = 0.31$). Shoot RGR was significantly affected by relative mite damage ($p = 0.0343$, $t_{53} = 2.17$) (Table 2.2).

After accounting for initial canopy volume, a 1% increase in relative damage is estimated to increase average shoot RGR by $0.33 \text{ cm cm}^{-1} \text{ month}^{-1}$ (95% CI: 0.03 to 0.64).

Plant biomass

Total plant biomass was not affected by mite inoculations ($p=0.1818$, $F_{6,48}=1.55$) but did vary with initial canopy volume ($p<0.0001$, $F_{1,48}=62.34$). Aboveground biomass was not significantly affected by mite inoculations ($p=0.3333$, $F_{6,48}=1.18$) but varied with initial canopy volume ($p<0.0001$, $F_{1,48}=44.99$). Similarly, mite inoculations did not affect belowground biomass ($p=0.1711$, $F_{6,48}=1.59$) and belowground biomass varied with initial canopy volume ($p<0.0001$, $F_{1,48}=0.1711$) (Figure 2.2).

The regression analyses indicated that there were no significant relationships among relative mite damage and biomass (Table 2.2). Relative mite damage did not significantly affect log belowground biomass ($p=0.4787$, $t_{53}=0.71$), aboveground biomass ($p=0.9042$, $t_{53}=-0.12$) or total biomass ($p=0.7169$, $t_{53}=0.3646$).

Discussion

Overall the results of this study do not provide strong evidence that gorse spider mite damage, within the range observed, affects the growth of young gorse plants. Of the growth responses measured in this study, only average shoot RGR was marginally affected by spider mite herbivory. Contrary to expectations, mite herbivory was associated with higher shoot growth rates. The late summer high density mite inoculation

had a greater shoot RGR, $0.07 \text{ cm cm}^{-1} \text{ month}^{-1}$, compared to the control. However, the late summer low density inoculation did not yield higher shoot growth even though relative mite damage did not differ between the late summer low and high density inoculations. It is noteworthy that while not statistically significant, the overall trend was towards slightly increased growth responses in inoculated vs. control plants. Results from the regression analysis indicated shoot growth increased with increasing mite damage; each 1% increase in relative mite damage is estimated to increase average shoot RGR by $0.33 \text{ cm cm}^{-1} \text{ month}^{-1}$. It is likely that the lack of a clear effect of the gorse spider mite is related to the low mite damage observed during this study. Mites were quick to disperse after inoculations which may have been caused by ambient conditions or plant quality.

It is possible that ambient conditions in the growing facility caused an unintended behavioral response in the mites. Within several days of inoculations the majority of mites moved to the top of the plants and barriers. *T. urticae* dispersal behavior is known to be triggered by low relative humidity (Kennedy and Smitley 1985; Rodriguez and Rodriguez 1987). Low relative humidity, common in Corvallis during summer months, may have caused the gorse spider mites to disperse rather than settle and feed on gorse plants.

Favorable growing conditions in this study may have also decreased the quality of gorse as a food resource for the mites. Quality of plants as a food resource is a combination of

positive, accessible energy and nutrients, and negative factors, toxins, indigestible materials and deterrents (Crawley 1983). Mites may have dispersed or died due to the low quality of food resources.

Within the limited range of mite damage observed in this study, the positive relationship between mite damage and shoot growth and the lack of relationships between mite damage and other growth parameters suggest plant tolerance to gorse spider mite herbivory under certain conditions. Tolerance of plants to herbivory is a possible defensive mechanism (Strauss and Agrawal 1999) and the strength of this defense is limited by other demands placed upon the plant, such as damage by multiple herbivores, abiotic stresses (e.g. drought and extreme temperatures), disease and intra- and interspecific competition (Bellows and Headrick 1999; Maschinski and Whitman 1989; Strauss and Agrawal 1999). In this experiment biotic and abiotic stress was limited by the experimental design. Plants were likely neither resource limited nor subject to intra- or interspecific competition and it is under such "highly favorable but improbable environmental conditions" that tolerance to herbivore damage is expected (Belsky et al. 1993).

Anecdotal evidence suggests there is a threshold of damage below which gorse spider mite herbivory does not affect gorse. This experiment provides support for this assertion and furthermore, under favorable growing conditions mite damage within a certain range may have a mild stimulatory effect on shoot growth over one growing season. Future

research should determine under what conditions increased shoot growth occurs and assess what the implications of increased shoot growth are for gorse fitness over time.

No firm conclusions can be drawn from this study about the efficacy of the gorse spider mite as a biological control agent in part due to the restricted nature of this study. This research was severely constrained by its short duration; in some cases the effects of spider mite feeding are not manifested until the following growing season (Rodriguez and Rodriguez 1987). This study was also constrained by the narrow range of mite damage observed. To better understand the effects of the gorse spider mite, future research should quantify the effects of mite feeding in consecutive seasons and over a wider range of mite damage.

Literature Cited

- Bellows, T.S. and Headrick, D.H. 1999. Arthropods and vertebrates in biological control of plants. *In* T.S. Bellows and T.W. Fisher [eds.], *Handbook of Biological Control: Principles and Applications of Biological Control*. Academic Press, San Diego, CA.
- Belsky, A.I., Carson, W.P., Jensen, C.L. and Fox, G.A. 1993. Over-compensation by plants: herbivore optimization or red herring? *Evolutionary Ecology* 7: 109-121.
- Coombs, E.M., Markin, G.P., Pratt, P.P. and Rice, B. 2004. Gorse. *In* E.M. Coombs, J.K. Clark, G.L. Piper and A.F. Cofrancesco Jr. [eds.], *Biological Control of Invasive Plants in the United States*. Oregon State University Press, Corvallis, OR.
- Coombs, E., Isaacson, D., Miller, G. and Turner, C. 1993. Petition for the introduction and field release of the gorse spider mite, *Tetranychus linteraius* Dufour (Tetranychidae: Acari), for the biological control of gorse, *Ulex europaeus* L. (Leguminosae), in North America. TAG Report 93-04.

- Crawley, M.J. 1989. Insect herbivores and plant population dynamics. *Annual Review of Entomology* 34: 531-564.
- Crawley, M.J. 1983. *Herbivory: The Dynamics of Animal-Plant Interactions*. University of California Press. Berkeley, CA.
- Kennedy, G.G. and Smitley, D.R. 1985. Dispersal. *In* W. Helle and M.W. Sabelis [eds.], *Spider Mites: Their Biology, Natural Enemies and Control*. Elsevier, New York.
- Isaacson, D.L. and Miller, G. 1992. A comparison of gorse (*Ulex europaeus* L.) in New Zealand and the United States. *In* Proceedings Washington State Weed Conference, Nov 4-6, Yakima, WA.
- Littell, R.C., Stroup, W.W. and Freund, R.J. 2002. *SAS for Linear Models*, 4th edition. SAS Institute, Cary, NC.
- Lowe, S.J., Browne, M. and Boudjelas, S. 2000. 100 of the World's Worst Invasive Alien Species. IUCN/SSC Invasive Species Specialist Group (ISSG), Auckland, New Zealand.
- Maschinski, J. and Whitman, T.G. 1989. The continuum of plant responses to herbivory: the influence of plant association, nutrient availability and timing. *The American Naturalist* 134: 1-19.
- Pratt, P.D., Coombs, E.M. and Croft, B.A. 2003. Predation by phytoseiid mites on *Tetranychus lintearius* (Acari: Tetranychidae), an established weed biological control agent of gorse (*Ulex europaeus*). *Biological Control* 26: 40-47.
- Richardson, R.G. and Hill, R.L. 1987. *Ulex europaeus*. *In* F.D. Panetta, R.H. Groves and R.C.H. Shepherd [eds.], *The Biology of Australian Weeds*, Volume 2. R.G. and F.J. Richardson, Melbourne, Australia.
- Rodriguez, J.G. and Rodriguez, L.D. 1987. Nutritional ecology of phytophagous mites. *In* F. Slansky Jr. and J.G. Rodriguez [eds.], *Nutritional Ecology of Insects, Mites, Spider and Related Invertebrates*. John Wiley and Sons, New York.
- SAS. 2001. *SAS Version 8.2 for Windows*. SAS Institute, Cary, NC.
- Strauss, S.Y. and Agrawal, A.A. 1999. The ecology and evolution of plant tolerance to herbivory. *Trends in Ecology and Evolution* 14: 179-18.

Tomczyk, A. and Kropczynska, D. 1985. Effects on the Host Plant. *In* W. Helle and M.W. Sabelis [eds.], Spider Mites: Their Biology, Natural Enemies and Control. Elsevier, New York.

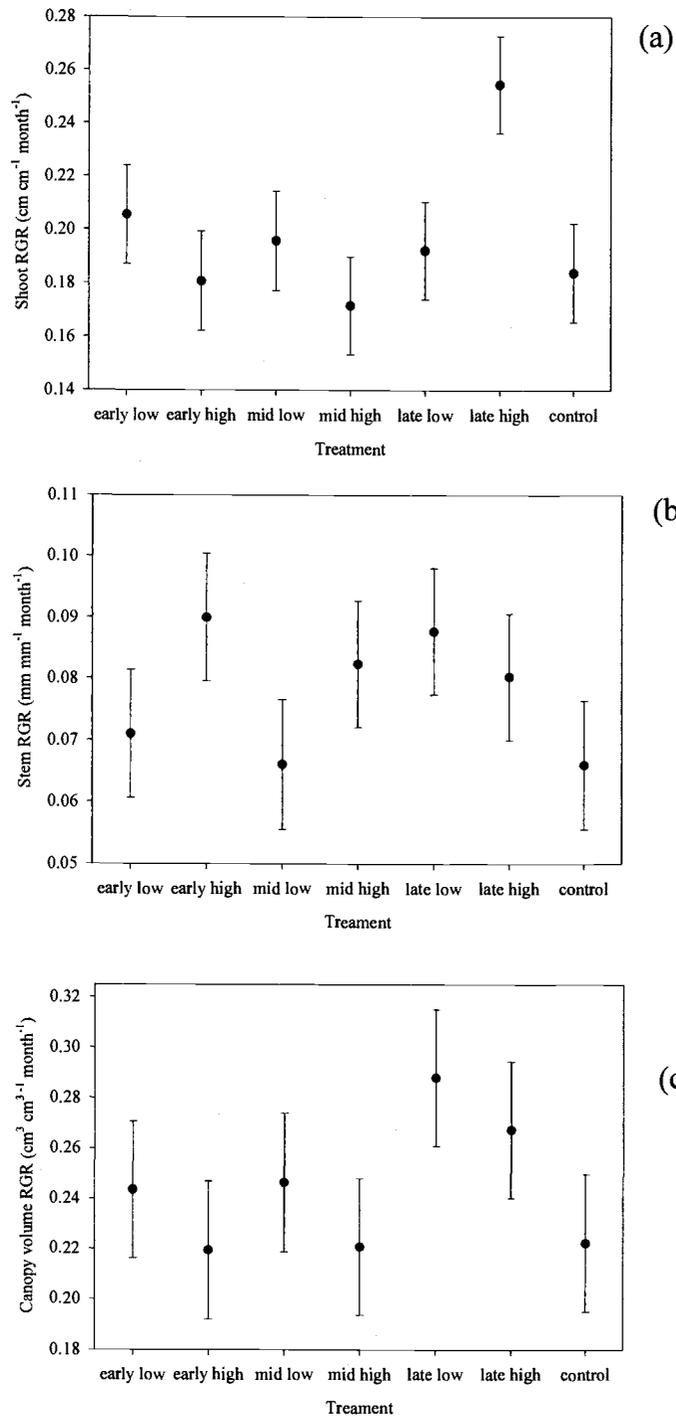


Figure 2.1. Adjusted mean relative growth rates for shoot (a), stem (b) and canopy volume (c). Treatments were high and low mite inoculation densities applied early, mid and late summer. Bars indicate standard errors.

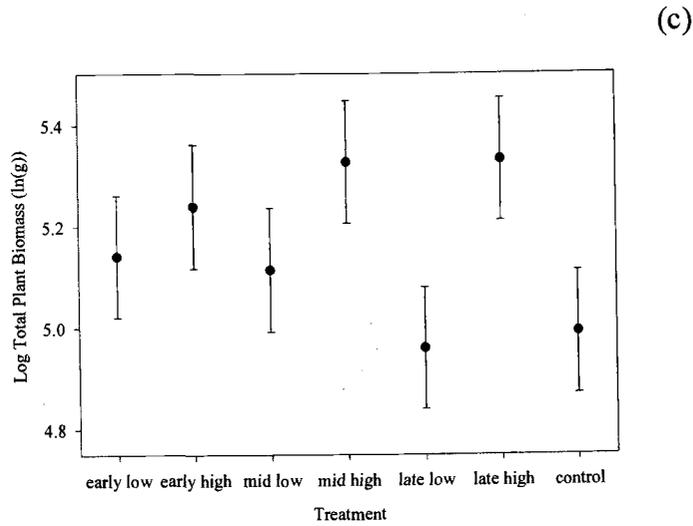
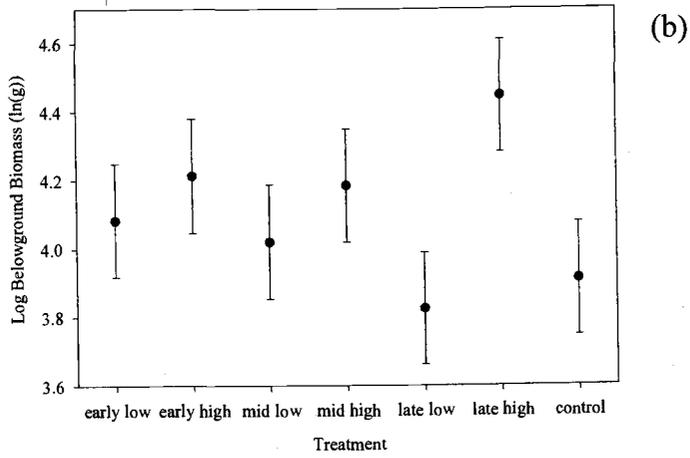
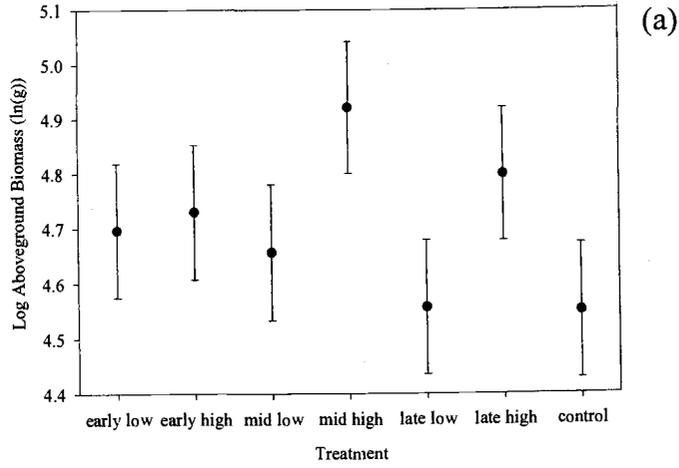


Figure 2.2. Adjusted mean relative growth rates for log aboveground biomass (a), log belowground biomass (b) and log total biomass (c). Treatments were high and low mite inoculation densities applied early, mid and late summer. Bars indicate standard errors.

Table 2.1. Median relative mite damage and 95% confidence intervals for each mite inoculation treatment.

Inoculation time	Inoculation density	Relative mite damage (%)	Tukey adjusted 95% confidence interval	
Early summer	Low	2.03 a	0.69	5.79
	High	2.30 a	0.79	6.53
Mid summer	Low	1.48 a	0.50	4.28
	High	3.11 a	1.07	8.70
Late summer	Low	4.06 a	1.40	11.15
	High	4.42 a	1.53	12.07
Control		0.00 b	0.00	0.00

Note: Values in a column followed by the same letter are not significantly different ($p > 0.05$).

Table 2.2. Regression equations relating shoot, stem and canopy relative growth rates and aboveground, belowground and total biomass to relative mite damage and initial canopy volume. Standard errors are in parentheses.

Response	Regression equation	R ²
Shoot RGR (cm cm ⁻¹ month ⁻¹)	Y=0.2241 + 0.3342 * relative mite damage – 0.7997 * initial canopy volume (m ³) (0.0149) (0.1539) (0.2267)	0.2426
Stem RGR (mm mm ⁻¹ month ⁻¹)	Y=0.0951 - 0.0097 * relative mite damage – 0.3392 * initial canopy volume (m ³) (0.0082) (0.0844) (0.1244)	0.1233
Canopy RGR (cm ³ cm ³ ⁻¹ month ⁻¹)	Y=0.3546 + 0.0686 * relative mite damage – 2.2533 * initial canopy volume (m ³) (0.0215) (0.2221) (0.3274)	0.4723
Belowground biomass ln(g)	Y=3.3128 + 0.9901 * relative mite damage + 14.7564 * initial canopy volume (m ³) (0.1341) (1.3879) (2.0454)	0.4985
Aboveground biomass (g)	Y=68.7366 - 12.2776 * relative mite damage + 1051.87 * initial canopy volume (m ³) (9.8194) (101.5512) (149.65)	0.4824
Total biomass (g)	Y=89.5906 + 57.1328 * relative mite damage + 2036.00 * initial canopy volume (m ³) (15.1462) (156.7126) (230.95)	0.5952

Chapter 3- Impact of gorse spider mite on growth of gorse in coastal Oregon

Introduction

Invasive species threaten ecological and economic systems throughout the world, costing at least \$137 billion annually in the United States (Pimentel et al. 2000) and posing one of the greatest threats to global biodiversity (Reichard and White 2001). The ecological effects of invasive plants include disturbance regime alteration, changes in resource cycling and changes in trophic structures (Vitousek 1990). It has been suggested that plants become invasive when freed from the constraints of their co-evolved native herbivores (Morin 2001; Keane and Crawley 2002; Harris 1986). Classical biological control involves reassociating invasive plants with native specialist herbivores with the expectation they will control targeted plant species without further human intervention or inputs (Wapshere et al. 1989). At least 259 species of invertebrates, 254 insect and 5 mite species, have been used in the biological control of plants (Bellows and Headrick 1999). Targets of biological control programs include at least 101 species of “weeds” in 33 families (Goeden and Andres 1999). Approximately 25% of these programs have been deemed successful (van Driesche and Bellows 1996).

Gorse, *Ulex europaeus* L. (Fabaceae), a spiny, leguminous, evergreen shrub native to western Europe has become invasive in New Zealand, Chile, Australia, Hawaii and western North America (Hill and O’Donnell 1991). Introduction and spread of this plant is associated with human activities. In Oregon gorse was first reported in 1894 in the

coastal town of Bandon (Isaacson and Miller 1992), introduced by Irishman and town founder, Lord George Bennett (Beckham 1985). Gorse now covers an estimated 20,000 ha in Oregon (Isaacson and Miller 1992), primarily in coastal areas with limited but increasing occurrences inland (Coombs et al. 1993).

The gorse spider mite, *Tetranychus lintearius* Dufour (Acari: Tetranychidae), is one of several biological control agents introduced around the world for gorse control within the past 20 years. It was first brought to New Zealand in 1989 from Cornwall, England. Since then five strains of the mite have been imported from elsewhere in Europe (Hayes et al. 1996). In 1994 the gorse spider mite was imported from New Zealand and released in Oregon by the Oregon Department of Agriculture (Coombs et al. 2004). The mite is now considered established in Oregon but it remains unclear what effects gorse spider mites have on gorse (Pratt et al. 2003).

Spider mite feeding removes cell contents, which directly and indirectly disrupts the physiological functions of plants, leading to a variety of plant responses. The most common consequence of spider mite feeding is reduction in growth of all plant parts (Tomczyk and Kropczynska 1985). Observations suggest gorse spider mite feeding reduces the growth of individual gorse shoots and early season feeding reduces flowering (E.M. Coombs personal communication). This study was conducted to quantify the effects of gorse spider mite herbivory on the growth of individual gorse plants within established gorse infestations.

Methods

Study sites

Four study sites were located on the Oregon Coast from near Florence in the north to Port Orford in the south (Figure 3.1). Those sites were: Baker Beach on the Mapleton Ranger District of the Siuslaw National Forest (44° 05' North 124° 07' West); Umpqua Eden on the Coos Bay District of the USDI Bureau of Land Management (43° 41' North 124° 08' West); Knapp Ranch, a privately owned ranch in Curry County (42° 46' North 124° 28' West) and Elk River, a private campground on the Elk River (42° 46' North 124° 28' West).

Experimental design

At each site mature gorse plants with no conspicuous mite or herbicide damage were selected. Where plants occurred as continuous gorse thickets, surrounding plants were trimmed to expose and isolate study plants. Individual study plants were located approximately 1 to 15 m from each other. Plants were selected far enough away from each other to decrease the likelihood of mites moving between them. At the Umpqua Eden, Knapp Ranch and Elk River sites 18 plants were selected and at the Baker Beach site 24 plants were selected. Additional plants were selected at the Baker Beach site to buffer against the potential loss of study plants to herbicide application. Ultimately, data were collected for 20 plants at Baker Beach.

At each site one-third of the plants were randomly assigned to each of three treatments: control, low mite inoculation level and high mite inoculation level. Control plants

received no mites and were periodically inspected to ensure they did not become infested. The low inoculation treatment received 1 mite colony per 4 m² of canopy surface area with a minimum of one colony and the high inoculation treatment received 1 mite colony per 2 m² canopy surface area with a minimum of 2 colonies. Canopy surface area was calculated as a sphere as described below. Mite inoculation treatments were conducted in early summer as mites became available. Mite infested gorse shoots 15-20 cm in length, containing an area of approximately 2 to 3 cm² of dense adult mite colonies, were clipped, placed in plastic bags and sealed. Several predatory arthropod species, such as *Phytoseiulus persimilis* Athias-Henroit (Acari: Phytoseiidae) and *Stethorus* spp., have been identified as predators of the gorse spider mite in Oregon (Pratt et al. 2003). All inoculation shoots were determined to be free of predators. Plants were inoculated by tying the appropriate number of mite infested shoots with cotton twine to live shoots throughout the canopy.

Plants were measured prior to inoculations. Canopy diameter was measured along two axes one at the widest point, major diameter, and the second at the narrowest point, minor diameter. Height from the soil to the tallest point in the plant canopy was recorded. Canopy volume was calculated as a sphere, with a diameter equal to the average of the height, major diameter and minor diameter measurements. Current year shoots were selected by randomly choosing a point within the canopy and measuring the length of the shoot closest to that point. The length of two current year shoots selected in this manner was measured and an average shoot length was calculated. Stem diameters were measured at ground level using a digital caliper. Individual gorse plants may be single or

multi-stemmed. On plants with more than four stems, four stems were randomly selected from all stems. The selected stems were tagged and measured. At the end of the season, plants were measured as described above, with the exception that four randomly selected current year shoots were measured rather than two. Monthly average relative growth rates (RGR) were calculated for stem diameter, canopy volume and average shoot length. Relative growth rates were calculated as $[\ln(\text{size at time2}) - \ln(\text{size at time1})] / (\text{time2} - \text{time1})$.

During the end of season sampling, mite damage was measured. Each patch of webbed and unwebbed mite damage was measured (length, width and height) to the nearest 5 cm. Volume of each patch was calculated and the volumes were summed to produce a total mite damage volume per plant. Relative mite damage was calculated as the total mite damage volume divided by the total plant canopy volume.

Statistical analysis

Regression analyses were performed independently for each of the three relative growth rates using a linear mixed effects regression model in S-PLUS version 6.1 (Insightful 2002). Site, initial plant height and relative mite damage were used as explanatory variables. Site was included as a random effect and both initial plant height and relative mite damage were included as continuous independent variables. In the analysis of stem diameter RGR, stems which died between measurements, due to either wind damage or animal browsing, were removed from the analysis.

Relative mite damage for the low and high inoculation treatments was analyzed using an analysis of variance (ANOVA) to test the effect of inoculation treatment. Relative damage rates were logit transformed to better meet assumptions of normality. The transformed relative damage rates were analyzed as a function of treatment and site with a linear mixed effect ANOVA model in S-PLUS version 6.1 (Insightful 2002). Site was treated as a random effect in this analysis.

Results

Plant growth

Relative mite damage was found to significantly affect average shoot RGR ($p=0.0106$, $t_{71}=-2.61$) but initial height was not related to average shoot RGR ($p=0.6062$, $t_{71}=-0.5178$). After accounting for initial height and the random effect of site, each 1% increase in relative damage decreased average shoot RGR $0.28 \text{ cm cm}^{-1} \text{ month}^{-1}$ (95% CI: -0.48 to -0.07) (Table 3.1).

Other growth parameters were not affected by mite damage (Table 3.1). After accounting for the random effect of site, stem diameter RGR was related to initial plant height ($p<0.0001$, $t_{71}=-5.3983$) but was not affected by spider mite damage ($p=0.7766$, $t_{71}=-0.2848$). Similarly, canopy volume RGR also varied with initial plant height ($p=0.0016$, $t_{71}=-3.2854$) but was not affected by spider mite damage ($p=-0.5717$, $t_{71}=0.5693$).

Mite damage

Some inoculations failed in both high and low mite inoculation treatments but generally webbing appeared relatively dense, indicating few, if any, predators within the colonies. After accounting for site, the amount of relative mite damage did not differ between inoculation levels ($p=0.6967$, $F_{1,47}=0.1538$). Relative damage rates were generally below 25% and only 4 plants had relative damage rates over 50% in both the low and high inoculation treatments (Figure 3.2). After accounting for the effect of site, the back-transformed mean relative mite damage was 6.5% (95% CI: 0.7 to 40.6%) at the low mite inoculation level and 7.3% at the high inoculation level (95% CI: 0.4 to 60.3%).

Discussion

The invasiveness of related shrubs, such as Scotch broom, *Cytisus scoparius* (L.) Link, has been attributed to high relative growth rates (Prevosto et al. 2004). Higher growth rates outside of a plant's native range compared to growth rates within the native range are likely due to decreased herbivore pressure (Keane and Crawley 2002; Mack et al. 2000). Indeed, the high growth rate of gorse poses problems for forest regeneration in Oregon (Hermann and Newton 1968). As expected, shoots attacked by the gorse spider mite appeared stunted and over one growing season increasing gorse spider mite damage significantly decreased average shoot RGR. This finding agrees with the results of Partridge (unpublished data) which associated higher rates of gorse spider mite damage with reductions in shoot growth.

The effects of spider mite herbivory on shoot growth observed in this study are contrary to the results of a potted plant study in which mite damage was associated with a small but significant increase in average shoot RGR month⁻¹. These contradictory results likely reflect differences in growing conditions. Herbivores tend to have their greatest impact when combined with other forms of plant stress. In the potted plant study plants were watered regularly and intraspecific competition was low. Under field conditions plants are subject to a wide array of biotic and abiotic stressors. Mite damage coincides with the dry season in western Oregon when plant growth may be moisture limited.

During the course of this study, reductions in stem diameter or canopy volume growth due to gorse spider mite herbivory were not detected. Though, the scope of this study may have been too limited to detect changes in these parameters. Only four plants had more than 50% relative mite damage. Perhaps at higher levels of damage stem diameter and/or canopy volume growth rates are affected by mite damage. Furthermore, the duration of this study may have been too short to detect changes in these growth parameters. Plant growth is in part a function of available photosynthetic area. Thus, it is likely that over several seasons repeated mite attacks and consequent chronic reductions in total photosynthetic area may affect other growth parameters.

This study is the first step in quantifying the impacts of gorse spider mites in Oregon. Successful gorse control and desired plant community changes will likely depend on the interaction of multiple stressors (Bacher and Schwab 2000). It is possible that the gorse

spider mite could be used effectively in conjunction with other stressors to alter gorse population structures. The long-term performance of the gorse spider mite is questionable, as it has not yet produced noticeable changes in plant community composition. The effects of the gorse spider mite may be limited by predation (Pratt et al. 2003), quality of food resources (Hill 1982) and/or failure to infest plants in consecutive years (T.R. Partridge unpublished data). Given these limitations, it may be that the mite is not well suited as a classical biological control agent. Although, in light of the effect of gorse spider mite feeding on shoot growth found in this study, further research is warranted. The gorse spider mite could be an effective inundative biocontrol agent. For example, the mite could be used in situations where short-term reductions in shoot growth allow competing vegetation to become established. Future research should investigate what effect higher levels of inoculation have on growth rates and whether reduced shoot RGR over several seasons affects plant fitness.

Literature cited

- Bacher, S. and Schwab, F. 2000. Effect of herbivore density, timing of attack and plant community on performance of creeping thistle *Cirsium arvense* (L.) Scop. (Asteraceae). *Biocontrol Science and Technology* 10: 343-352.
- Beckham, C. 1985. *The Night Bandon Burned*. Myrtle Point Printing, Myrtle Point, Oregon.
- Bellows, T.S. and Headrick, D.H. 1999. Arthropods and vertebrates in biological control of plants. *In* T.S. Bellows and T.W. Fisher [eds.], *Handbook of Biological Control: Principles and Applications of Biological Control*. Academic Press, San Diego, CA.
- Coombs, E., Isaacson, D., Miller, G. and Turner, C. 1993. Petition for the introduction and field release of the gorse spider mite, *Tetranychus linteraius* Dufour (Tetranychidae:

- Acari), for the biological control of gorse, *Ulex europaeus* L. (Leguminosae), in North America. TAG Report 93-04.
- Coombs, E.M., Markin, G.P., Pratt, P.P. and Rice, B. 2004. Gorse. *In* E.M. Coombs, J.K. Clark, G.L. Piper and A.F. Cofrancesco Jr. [eds.], *Biological Control of Invasive Plants in the United States*. Oregon State University Press, Corvallis, OR.
- Goeden, R.D. and Andres, L.A. 1999. Biological control of weeds in terrestrial and aquatic environments. *In* T.S. Bellows and T.W. Fisher [eds.], *Handbook of Biological Control: Principles and Applications of Biological Control*. Academic Press, San Diego, CA.
- Harris, P. 1986. Biological control of weeds. *In* J.M. Franz [ed.], *Biological Control of Plant Pests and of Vectors of Human and Animal Diseases: International Symposium of the Akademie der Wissenschaften und der Literatur, Mainz, November 15th-17th, 1984 at Mainz and Darmstadt*. *Fortschritte der Zoologie* 32: 124-138. G. Fischer Verlag, New York.
- Hayes, A.J., Gourlay, A.H. and Hill, R.L. 1996. Population dynamics of an introduced biological control agent for gorse in New Zealand: a simulation study. *In* V.C. Moran and J.H. Hoffman [eds.], *Proceedings IXth International Symposium on Biological Control of Weeds, 19-26 January, 1996, Stellenbosch, South Africa*, University of Cape Town.
- Hermann, R.K. and Newton, M. 1968. Tree Planting for the Control of Gorse on the Oregon Coast. Research Paper 9. Forest Research Laboratory, School of Forestry, Oregon State University, Corvallis, Oregon.
- Hill, R.L. 1982. Seasonal patterns of phytophage activity on gorse (*Ulex europaeus*) and host plant quality. *In* J.H. Visser and A.K. Minks [eds.], *Proceedings of the 5th International Symposium on Insect/ Plant Relationships, Wageningen, the Netherlands*.
- Hill, R.L. and O'Donnell, D.J. 1991. The host range of *Tetranychus lintearius* (Acarina: Tetranychidae). *Experimental and Applied Acarology* 11: 253-269.
- Insightful. 2002. S-PLUS 6.1 for Windows. Insightful Corporation, Seattle, WA.
- Isaacson, D.L. and Miller, G. 1992. A comparison of gorse (*Ulex europaeus* L.) in New Zealand and the United States. *In* *Proceedings Washington State Weed Conference, Nov 4-6, Yakima, WA*.
- Keane, R.M. and Crawley, M.J. 2002. Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology and Evolution* 17: 164-170.

Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M. and Bazzaz, F.A. 2000. Biotic invasions: causes, epidemiology, global consequences and control. *Ecological Applications* 10: 689-710.

Morin, L. 2001. Classical biological control of weeds- update and global issues. *In* Proceedings of the Third International Weed Science Congress; 2000 June 6-11; Foz do Iguassu, Brazil, Manuscript number 353. CD ROM available from: International Weed Science Society, Oxford, MS, USA.

Pimentel, D., Lach, L., Zuniga, R. and Morrison, D. 2000. Environmental and economic costs of nonindigenous species in the United States. *BioScience* 50: 53-65.

Pratt, P.D., Coombs, E.M. and Croft, B.A. 2003. Predation by phytoseiid mites on *Tetranychus lintearius* (Acari: Tetranychidae), an established weed biological control agent of gorse (*Ulex europaeus*). *Biological Control* 26: 40-47.

Prevosto, B., Robert, A. and Coquillard, P. 2004. Development of *Cytisus scoparius* L. at stand and individual level in a mid-elevation mountain of the French Massif Central. *Acta Oecologica* 25: 73-81.

Reichard, S.H. and White, P. 2001. Horticulture as a pathway of invasive plant introductions in the United States. *BioScience* 51: 103-113.

Tomczyk, A. and Kropczynska, D. 1985. Effects on the Host Plant. *In* W. Helle and M.W. Sabelis [eds.], *Spider Mites: Their Biology, Natural Enemies and Control*. Elsevier, New York.

van Driesche, R.G. and Bellows, T.S. 1996. *Biological Control*. Chapman and Hall, New York.

Vitousek, P.M. 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. *Oikos* 57: 7-13.

Wapshere, A.J., Delfosse, E.S. and Cullen, J.M. 1989. Recent developments in biological control of weeds. *Crop Protection* 8: 227-250.

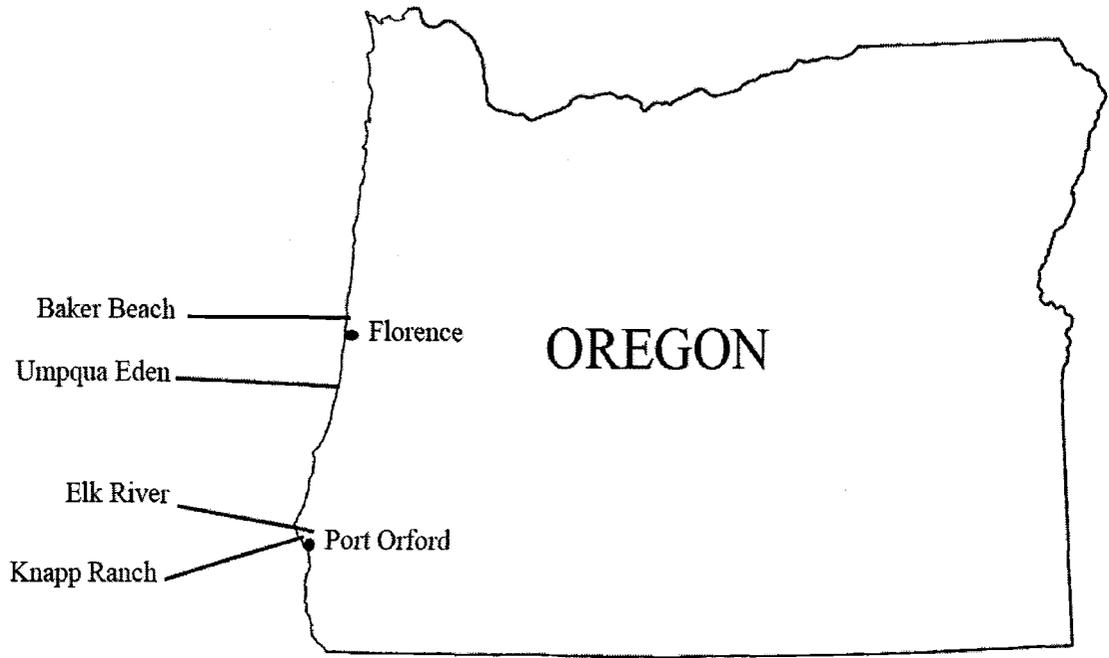


Figure 3.1 Experimental field sites on the Oregon Coast.

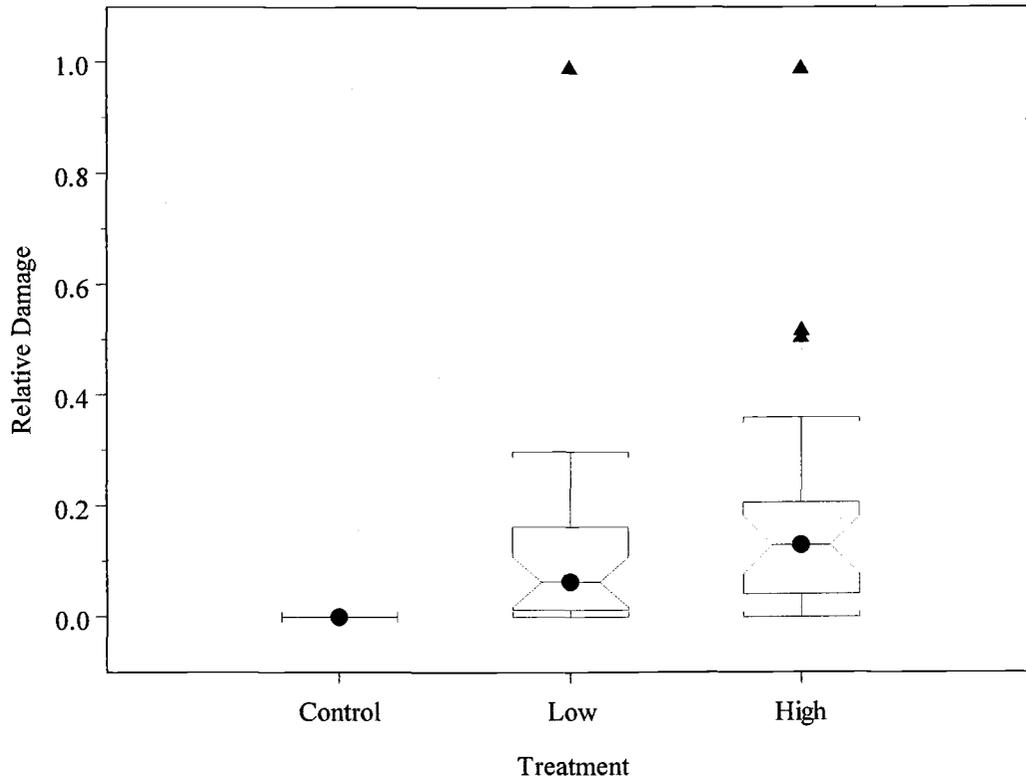


Figure 3.2 Box plots of relative mite damage (webbed and unwebbed) distribution by treatment level. Boxes encompass 1st to 3rd quartile. Circles represent median values. Whiskers span 1.5 * inter-quartile range and values beyond that are shown by triangles.

Table 3.1. Regression equations relating relative growth rate (RGR) of gorse to relative mite damage (RMD) and initial plant height (IPH). Standard errors are in parentheses.

Response	Regression equation
canopy RGR $\text{m}^3 \text{m}^{-3} \text{month}^{-1}$	$Y = 0.2078 - 0.0366 * \text{RMD} - 0.0579 \text{IPH (m)}$ (0.0307) (0.0588) (0.0176)
stem diameter RGR $\text{mm mm}^{-1} \text{month}^{-1}$	$Y = 0.1017 - 0.0048 * \text{RMD} - 0.0265 * \text{IPH (m)}$ (0.0089) (0.0167) (0.0049)
average shoot RGR $\text{cm cm}^{-1} \text{month}^{-1}$	$Y = 0.1949 - 0.2752 * \text{RMD} - 0.0156 * \text{IPH (m)}$ (0.0618) (0.1048) (0.0301)

Chapter 4- Impact of gorse spider mite on gorse shoot length: an observational study along the Oregon Coast

Introduction

Gorse, *Ulex europaeus* L. (Fabaceae), a leguminous shrub native to western Europe, has been classified as one of the world's 100 worst invasive species (Lowe et al. 2000). The invasive nature of gorse was recognized by the beginning of the twentieth century and more than one-hundred years later this plant continues to be a wide-spread problem (Richardson and Hill 1987). Due to large persistent seed banks and the ability to resprout following disturbance, management of gorse has proven extremely difficult.

Biological control has been employed as one of the tools to control gorse. In 1989 the gorse spider mite, *Tetranychus lintearius* Dufour (Acari: Tetranychidae), was first introduced as a biological control agent in New Zealand (Hayes et al. 1994). The gorse spider mite lives in densely webbed colonies feeding on mesophyll cell contents. It has multiple generations per year and all life stages feed exclusively on gorse (Coombs et al. 1993). The mite preferentially feeds on older hardened foliage, usually avoiding newer soft foliage. During the winter months mites retreat to the interior of plants where they aggregate in small clusters. When weather allows, mites move out to the foliage, feeding and building webs. Mite populations increase exponentially during favorable weather reaching peak population levels in late summer.

In 1994 the Oregon Department of Agriculture introduced the gorse spider mite in Oregon (Coombs et al. 2004). It is now considered established, though subject to high levels of predation by ladybird beetles, *Stethorus* spp. (Coleoptera: Coccinellidae), and a predatory mite, *Phytoseiulus persimilis* Athias-Henroit (Acari: Phytoseiidae), which is used in the biological control of agricultural and horticultural pest spider mites (Pratt et al. 2003). Quantitative information on gorse spider mite populations and their effects on host plants is lacking. This observational study was conducted as part of an effort to quantify the effects of the gorse spider mite in Oregon.

Methods

Study design

At many sites on the Oregon Coast, the buildup of mite populations begins in May or June and peaks in late August and early September. Gorse infested sites were visited throughout this time period in coastal Lane, Douglas, Coos and Curry Counties. Sites included two in the Port Orford area, Elk River and Knapp Ranch; two in the Bandon area, Faber and Whiskey Run State Park; one in Coos Bay; one in the Reedsport area, Umpqua Eden and one in the Florence area, Baker Beach (Figure 4.1). Sampling was conducted between June 26 and October 18, 2003 and each site was sampled between 2 and 4 times (Table 4.1).

On each sampling date transects of accessible plants were haphazardly chosen along the edges of gorse infestations. Sampling points were randomly selected along each transect.

The number of randomly selected points was equal to the total transect length divided by three. For example, a 24 meter transect would have eight sampling points. The number of points sampled on each date varied from twelve to forty-eight (Table 4.1). A 1 by 1 m frame constructed of plastic tubing was placed at each sampling point. If frames overlapped by less than 25 cm, one of the frames was moved until they no longer overlapped. When frames overlapped by more than 25 cm another random point was selected. Within the frame, several plant and mite damage parameters were recorded. Plant height was measured from the soil surface to the tallest point within the frame. Vegetative bud burst occurs in spring and apical elongation of these current year shoots continues throughout the year. Current year shoots were selected by randomly choosing a point within the frame. The length of the shoot closest to that point was measured. Initially, two shoots were measured per frame but four shoots per frame were measured after July 11, 2003. The length, width and height of each webbed and unwebbed mite damaged area within the frame was measured to the nearest 5 cm. Volume of each area was calculated and the volumes were summed to produce a total mite damage volume per frame. Relative mite damage was calculated as the total mite damage volume divided by the total frame volume (plant height x 1m x 1m).

Statistical analysis

Mean shoot lengths and mite damage volume were calculated for each site and sampling date using PROC MEANS in SAS version 8.2 (SAS 2001). Due to the unbalanced nature of the data, comparison of means on particular dates among sites was not possible.

The association of gorse spider mite damage and average shoot length was examined independently for each site. The Umpqua Eden and Whiskey Run sites were not analyzed because they had no mites. Umpqua Eden, an isolated gorse infestation, had never been inoculated with mite infestations. At Whiskey Run the mite population has been extirpated by the predatory mite, *Phytoseiulus persimilis* (E.M. Coombs personal communication). Because sampling dates within a month tended to be only several days apart at the different sites, dates are reported as months. Sampling conducted during the last week of June was included in July.

Regression analyses were performed to examine the correlation of shoot length and relative mite damage after accounting for month and transect using a mixed effect regression model in SAS version 8.2 (SAS 2001). Relative mite damage was $\log(\text{relative damage} + 0.00001)$ transformed and treated as a continuous fixed effect. Month was treated as a categorical fixed effect. Transects were nested within months and included as random effects. The initial regression model for each analysis included a relative mite damage by month interaction, indicating heterogeneous regression slopes. Slope homogeneity was tested with a Type III F -test. If the F -test indicated homogeneous slopes ($p > 0.05$) or the interaction term was not appropriate (i.e. mite damage was only measured on one sampling date), the interaction was removed from the final regression model.

Results

Description of mite damage and shoot length

Based on the data from sites that were sampled three or four times, shoot elongation appeared to decrease from August to September (Figure 4.2). At two sites shoot length remained largely unchanged after this period and at two other sites there appeared to be an increase in shoot growth from September to October. The amount of shoot growth varied considerably among sites. Shoot lengths in October ranged from 18 cm at Knapp Ranch to 40 cm at Umpqua Eden.

Based on the data from sites that were sampled three or four times, gorse spider mite damage increased from August to October (Figure 4.3). At the end of the season, the highest average mite damage volume per frame was found at the Faber site in Bandon, the site furthest inland. Of the sites with mites, Knapp Ranch had the lowest average spider mite damage per plot.

Average shoot length

The association of log relative mite damage and average shoot length at the Faber site was significant ($t_{27}=-3.28, p=0.0028$). It is estimated that average shoot length decreased 0.79 cm (95% CI: -1.28 to -0.30) for each doubling of relative mite damage at the Faber site. At the Baker Beach site the interaction of month and log relative damage was significant ($F_{3,82}=3.12, p=0.0305$). Thus, at this site the correlation of the log relative gorse spider mite damage and average shoot length varied by month (Table 4.2). Mite

damage was significantly associated with changes in shoot length only in October at Baker Beach, when it is estimated that shoot length increased 0.48 cm (95% CI: 0.09 to 0.88) for each doubling of relative mite damage. Log relative mite damage was not significantly associated with average shoot length at the Elk River site ($t_{55}=1.29$, $p=0.2033$), the Knapp Ranch site ($t_{70}=-1.13$, $p=0.2644$) or the Coos Bay site ($t_{34}=-0.62$, $p=0.5411$).

Discussion

Average shoot length varied greatly from site to site, likely due to differences in unmeasured site conditions, such as soil attributes, competition and precipitation.

Hermann and Newton (1968) reported average height growth of approximately 0.30 m yr⁻¹ for gorse in coastal Oregon, which is towards the upper range of shoot lengths observed in this study. Thus, there may be substantial year to year variation in shoot growth which was not captured by this study.

It appears that there is a mid-summer decrease in gorse shoot growth. A similar shoot growth pattern is seen in the closely related invasive shrub, *Cytisus scoparius* (L.) Link (e.g. Fogarty and Facelli 1999). This decrease in growth may be important in evaluating future biological control agents. The effects of herbivory depend not only on the magnitude but also on the timing of damage to a plant (Bellows and Headrick 1999; Crawley 1989). More research is needed to determine if there is a critical point or points

during seasonal gorse growth, which could be targeted by biological control programs using herbivores.

Results suggest that in some cases gorse spider mite damage is correlated with gorse shoot growth. Average shoot length was associated with relative mite damage at two of the five sites which had mites. At the Baker Beach site there was a positive relationship between log relative mite damage and shoot lengths on the October sampling date. In contrast mite damage and shoot lengths were inversely related at the Faber site in Bandon. It is likely that these inconsistent results are related to different levels of spider mite damage. It has been suggested that gorse spider mites only affect gorse growth above some damage threshold (T.R. Partridge unpublished data). Perhaps mite populations only reached damaging levels at the Faber site.

Lack of consistent evidence for a relationship between gorse spider mite damage and shoot length may be related to the low frequency of mite damage sampled. Of the 385 frames sampled, only 79 contained mite damage. The cause of infrequent mite damage is unknown. Unfavorable weather or high levels of predation may have negatively impacted mite populations. However, *P. persimilis* was only observed within gorse spider mite webbing at the Knapp Ranch site. Further research is needed to investigate which factors regulate gorse spider mite populations in Oregon and what effect changes in those regulating factors have on gorse growth.

Literature cited

- Bellows, T.S. and Headrick, D.H. 1999. Arthropods and vertebrates in biological control of plants. *In* T.S. Bellows and T.W. Fisher [eds.], *Handbook of Biological Control: Principles and Applications of Biological Control*. Academic Press, San Diego, CA.
- Coombs, E.M., Markin, G.P., Pratt, P.P. and Rice, B. 2004. Gorse. *In* E.M. Coombs, J.K. Clark, G.L. Piper and A.F. Cofrancesco Jr. [eds.], *Biological Control of Invasive Plants in the United States*. Oregon State University Press, Corvallis, OR.
- Coombs, E., Isaacson, D., Miller, G. and Turner, C. 1993. Petition for the introduction and field release of the gorse spider mite, *Tetranychus linteraius* Dufour (Tetranychidae: Acari), for the biological control of gorse, *Ulex europaeus* L. (Leguminosae), in North America. TAG Report 93-04.
- Crawley, M.J. 1989. Insect herbivores and plant population dynamics. *Annual Review of Entomology* 34: 531-564.
- Fogarty, G. and Facelli, J.M. 1999. Growth and competition of *Cytisus scoparius*, an invasive shrub, and Australian native shrubs. *Plant Ecology* 144: 27-35.
- Hayes, A. J., Gourlay, A.H. and Hill, R.L. 1994. Temperature-dependent phenology of gorse spider mite. *Proceedings of the New Zealand Plant Protection Conference* 47: 98-102.
- Hermann, R.K. and Newton, M. 1968. Tree Planting for the Control of Gorse on the Oregon Coast. Research Paper 9. Forest Research Laboratory, School of Forestry, Oregon State University, Corvallis, Oregon.
- Lowe, S.J., Browne, M. and Boudjelas, S. 2000. 100 of the World's Worst Invasive Alien Species. IUCN/SSC Invasive Species Specialist Group (ISSG), Auckland, New Zealand.
- Pratt, P.D., Coombs, E.M. and Croft, B.A. 2003. Predation by phytoseiid mites on *Tetranychus linteraius* (Acari: Tetranychidae), an established weed biological control agent of gorse (*Ulex europaeus*). *Biological Control* 26: 40-47.
- Richardson, R.G. and R.L. Hill. 1987. *Ulex europaeus*. *In* F.D. Panetta, R.H. Groves and R.C.H. Shepherd [eds.], *The Biology of Australian Weeds*, Volume 2. R.G. and F.J. Richardson, Melbourne, Australia.
- SAS. 2001. SAS Version 8.2 for Windows. SAS Institute, Cary, NC.

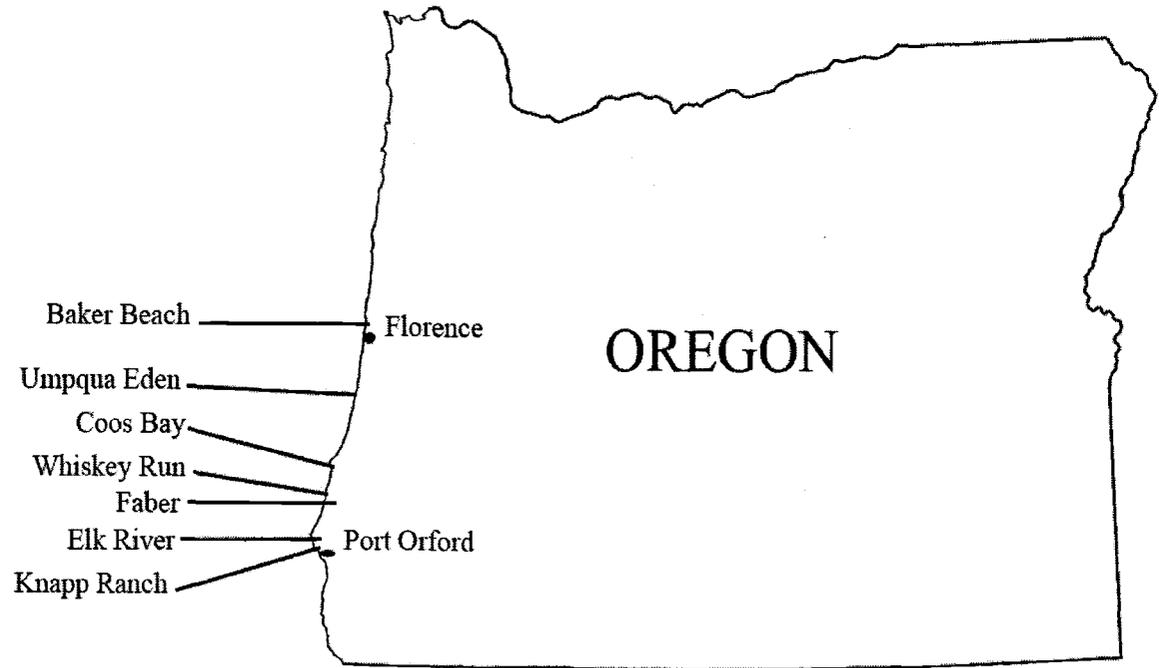


Figure 4.1. Seven sites along the Oregon Coast where gorse spider mite damage and gorse shoot length were surveyed.

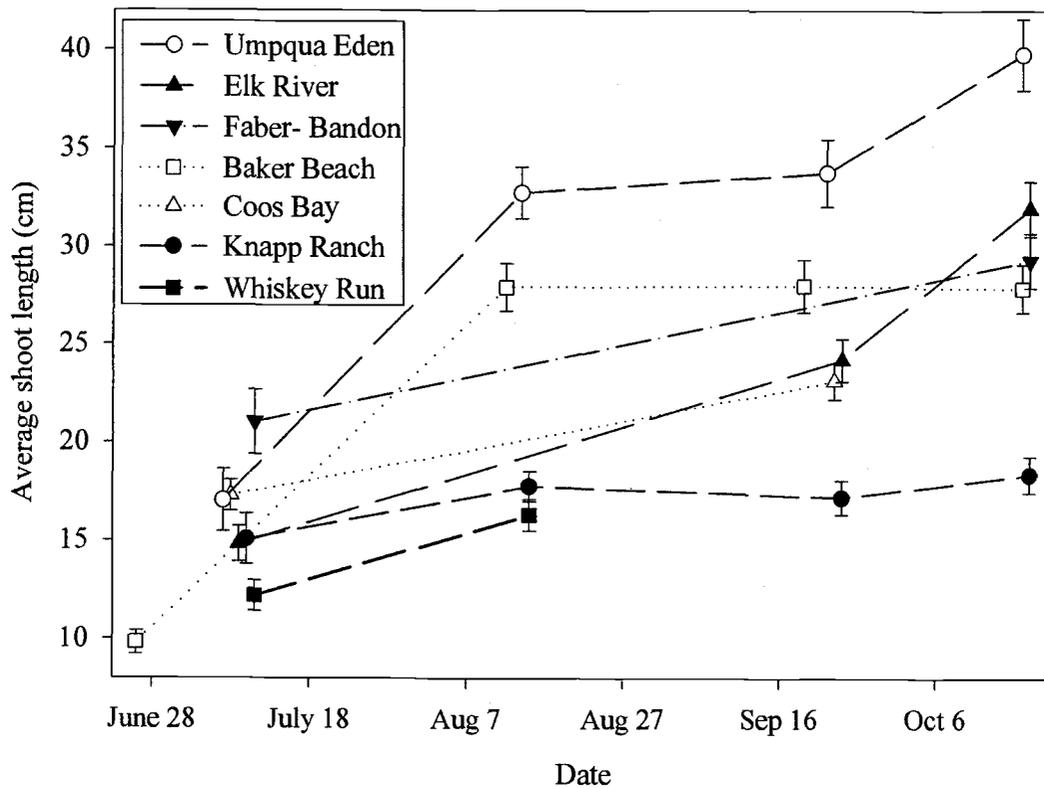


Figure 4.2. Average gorse shoot length at seven sites along the Oregon Coast, 2003. Bars represent 1 standard error.

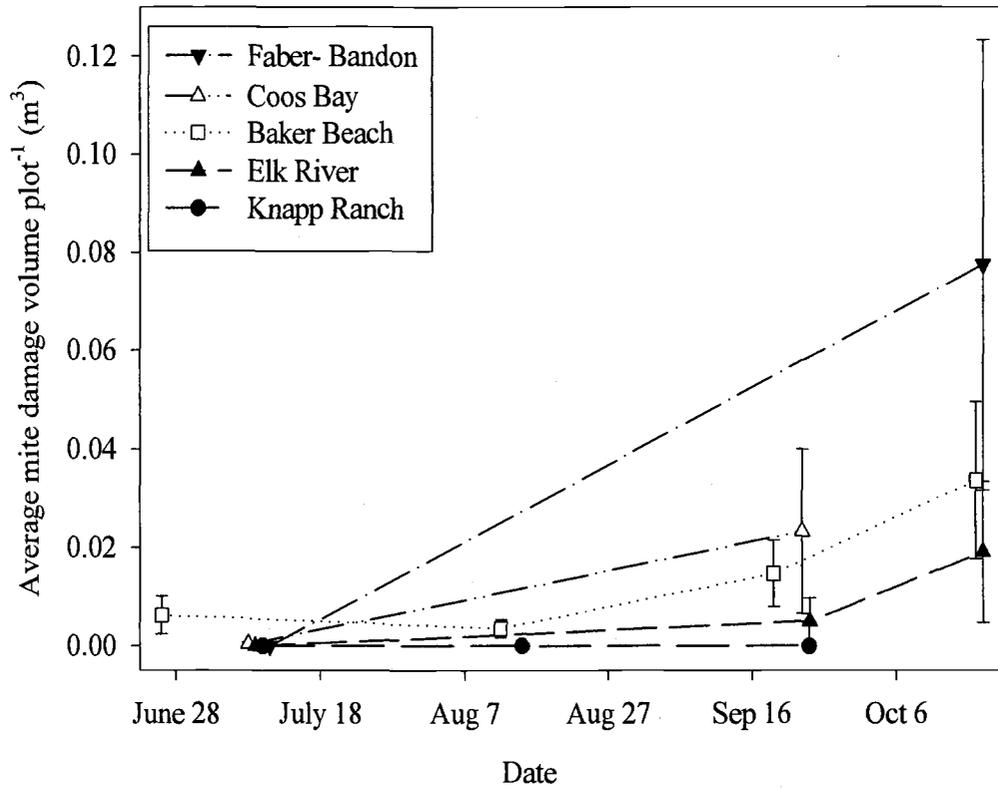


Figure 4.3. Average mite damage volume at five sites along the Oregon Coast, 2003. Bars represent 1 standard error.

Table 4.1. Number of points sampled over four months at seven sites along the Oregon Coast, 2003.

Sample dates	Baker Beach	Faber- Bandon	Knapp Ranch	Coos Bay	Umpqua Eden	Elk River	Whiskey Run
July (6/26 - 7/11)	48	12	12	22	12	24	24
August (8/12 - 8/15)	24		24		24		24
September (9/19 - 9/24)	24		24	24	24	24	
October (10/17 - 10/18)	24	24	24		24	24	

Table 4.2. Regression equations for the relationship of shoot length to month and log relative mite damage. Standard errors are in parentheses. “*” indicates a significant slope ($p < 0.05$).

Site	Month	Regression equation
Baker Beach	July	$8.85 - 0.04 \times \log \text{ relative mite damage}$ (5.74) (0.44)
	August	$34.09 + 0.55 \times \log \text{ relative mite damage}$ (5.11) (0.37)
	September	$23.81 - 0.45 \times \log \text{ relative mite damage}$ (4.14) (0.29)
	October	$35.21 + 0.70 \times \log \text{ relative mite damage}^*$ (3.77) (0.29)
Bandon- Faber	July	$5.34 - 1.14 \times \log \text{ relative mite damage}^*$ (5.37) (0.35)
	October	$16.67 - 1.14 \times \log \text{ relative mite damage}^*$ (4.21) (0.35)
Elk River	July	$21.87 + 0.51 \times \log \text{ relative mite damage}$ (5.89) (0.39)
	September	$30.39 + 0.51 \times \log \text{ relative mite damage}$ (5.38) (0.39)
	October	$37.56 + 0.51 \times \log \text{ relative mite damage}$ (5.47) (0.39)
Knapp Ranch	July	$9.84 - 0.40 \times \log \text{ relative mite damage}$ (5.20) (0.35)
	August	$12.27 - 0.40 \times \log \text{ relative mite damage}$ (5.07) (0.35)
	September	$11.79 - 0.40 \times \log \text{ relative mite damage}$ (5.03) (0.35)
	October	$13.32 - 0.40 \times \log \text{ relative mite damage}$ (4.72) (0.35)
Coos Bay	July	$19.12 + 0.14 \times \log \text{ relative mite damage}$ (3.25) (0.22)
	September	$24.48 + 0.14 \times \log \text{ relative mite damage}$ (2.96) (0.22)

Chapter 5- Conclusions

Biological control can be a powerful tool in the control of invasive plants (Andres 1971; Bellows and Headrick 1999). Yet, classical biological control has been referred to as a series of "uncontrolled and unmonitored experiments on a grand scale" (Shea et al. 2002). Much of the literature on biological control agent impacts is not quantitative (Keane and Crawley 2002) and measurements of biological control agent success tend to be "subjective and impressionistic" (McEvoy and Coombs 2000). Evaluation of biological control agent effects is an important, yet largely neglected, element of biological control programs (Keane and Crawley 2002; McEvoy and Coombs 2000). Understanding biological control efforts, successes and failures, is essential not only to improving the understanding of ecology, herbivory and invasions but also to improving biological control. Quantitative evaluation of the ecological effects of biological control agents can be divided into six measures: 1) establishment, 2) increase in the population, 3) geographic spread, 4) effects on individual target plants, 5) effects on target plant populations and 6) indirect effects on the plant community (Schooler 1998). This thesis begins the formal evaluation process of the gorse spider mite, *Tetranychus lintearius* Dufour (Acari: Tetranychidae), by quantifying the effects on individual gorse, *Ulex europaeus* L. (Fabaceae), growth.

Experimental inoculation of potted gorse plants with mites found that slightly increased shoot growth was associated with increased mite damage. Tolerance to mite damage was

likely due to mite dispersal and/or the highly favorable growing conditions maintained during this experiment. Late season high density inoculations led to higher shoot growth rates. However, the late summer low density inoculation did not yield higher shoot growth and relative mite damage was not statistically different between the late summer low and high density inoculations. Canopy RGR and stem diameter RGR were unaffected by mite inoculations and damage.

Gorse spider mite damage was associated with reduced shoot growth of plants in the field over the course of a single growing season. Canopy and stem diameter RGR were unaffected. Mite damage did not significantly vary between the two densities tested. Higher density inoculations may be needed to severely retard gorse growth.

In the observational study increasing mite damage was not consistently associated with decreasing average shoot lengths. Higher mite damage was associated with decreased shoot length at one site and increased shoot length at one site on one sampling date. These inconsistent results are likely due to differences in the level of mite damage between these sites, but further research is needed.

Throughout the history of biological control, there have been some extremely successful programs, such as the control of *Opuntia* cacti (Cactaceae) in Australia and St John's wort, *Hypericum perforatum* L. (Clusiaceae) and tansy ragwort, *Senecio jacobaea* L. (Asteraceae), in the Pacific Northwest (Andres 1971; McEvoy et al. 1991). Despite these

extraordinary cases, herbivores typically influence plant populations and community dynamics not by eating their host plant to extinction, but by altering the competitive ability of their host (Crawley 1983). The gorse spider mite could be classified as a successful biological control agent in coastal Oregon at this stage of the evaluation process, evaluation of effects on individual host plants. Overall the results of this thesis provide evidence that the gorse spider mite damage is associated with significant shoot growth decreases under certain conditions but it is not known whether these decreases are sufficient to alter the competitive advantage of gorse. Ultimately, biological control is concerned with the effects on target plant populations and on plant communities. Future research should determine what effect the gorse spider mite has on the competitive advantage of individual gorse plants and what consequences reduced competition has on gorse populations. Mites will likely have the greatest effect on small plants and seedlings yet the effects of the mite may be limited by predation (Pratt et al. 2003). In fact, mite damage in the observational study was generally low and infrequent, which may be due in part to the influence of predators. However, even if predators limit the success of the gorse spider mite as a classical biological control agent, the mite may have some value as an inundative biological control agent for use in conjunction with other control methods. Much remains to be learned about the effects of the gorse spider mite as a biological control agent and given the risks involved with gorse range expansion, further research is warranted.

Literature cited

- Andres, L.A. 1971. The suppression of weeds with insects. *In* Proceedings from the 3rd Tall Timbers Conference on Ecological Animal Control by Habitat Management, February 25-27, 1971, Tallahassee, Florida.
- Bellows, T.S. and Headrick, D.H. 1999. Arthropods and vertebrates in biological control of plants. *In* T.S. Bellows and T.W. Fisher [eds.], *Handbook of Biological Control: Principles and Applications of Biological Control*. Academic Press, San Diego, CA.
- Crawley, M.J. 1983. *Herbivory: The Dynamics of Animal-Plant Interactions*. University of California Press, Berkeley, CA.
- Keane, R.M. and Crawley, M.J. 2002. Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology and Evolution* 17: 164-170.
- McEvoy, P.B. and Coombs, E.M. 2000. Why things bite back: unintended consequences of biological weed control. *In* P.A. Follett and J. Duan [eds.], *Nontarget Effects of Biological Control*. Kluwer Academic Publishers, Boston, MA.
- McEvoy, P., Cox, C. and Coombs, E. 1991. Successful biological control of ragwort, *Senecio jacobaea*, by introduced insects in Oregon. *Ecological Applications* 1: 430-442.
- Pratt, P.D., Coombs, E.M. and Croft, B.A. 2003. Predation by phytoseiid mites on *Tetranychus lintearius* (Acari: Tetranychidae), an established weed biological control agent of gorse (*Ulex europaeus*). *Biological Control* 26: 40-47.
- Schooler, S.S. 1998. Biological control of purple loosestrife *Lythrum salicaria* by two chrysomelid beetles *Gallerucella pusilla* and *Gallerucella calamaiensis*. M.S. Thesis, Oregon State University.
- Shea, K., Possingham, H.P., Murdoch, W.M. and Roush, R. 2002. Active adaptive management in insect pest and weed control: intervention with a plan for learning. *Ecological Applications* 12: 927-936.

Bibliography

- Andres, L.A. 1971. The suppression of weeds with insects. *In* Proceedings from the 3rd Tall Timbers Conference on Ecological Animal Control by Habitat Management, February 25-27, 1971, Tallahassee, Florida.
- Anonymous. 2002. Service sheet: Gorse *Ulex europaeus* (L.). Department Of Primary Industries, Water and Environment. Tasmania, Australia.
- Bacher, S. and Schwab, F. 2000. Effect of herbivore density, timing of attack and plant community on performance of creeping thistle *Cirsium arvense* (L.) Scop. (Asteraceae). *Biocontrol Science and Technology* 10: 343-352.
- Beckham, C. 1985. *The Night Bandon Burned*. Myrtle Point Printing, Myrtle Point, Oregon.
- Bellows, T.S. and Headrick, D.H. 1999. Arthropods and vertebrates in biological control of plants. *In* T.S. Bellows and T.W. Fisher [eds.], *Handbook of Biological Control: Principles and Applications of Biological Control*. Academic Press, San Diego, CA.
- Belsky, A.I., Carson, W.P., Jensen, C.L. and Fox, G.A. 1993. Over-compensation by plants: herbivore optimization or red herring? *Evolutionary Ecology* 7: 109-121.
- Chater, E.H. 1931. A contribution to the study of the natural control of gorse. *Bulletin of Entomological Research* 22: 225-235.
- Clements, D.R., Peterson, D.J. and Prasad, R. 2001. The biology of Canadian weeds 112 *Ulex europaeus*. *Canadian Journal of Plant Science* 81: 325-337.
- Coombs, E., Isaacson, D., Miller, G. and Turner, C. 1993. Petition for the introduction and field release of the gorse spider mite, *Tetranychus linteraius* Dufour (Tetranychidae: Acari), for the biological control of gorse, *Ulex europaeus* L. (Leguminosae), in North America. TAG Report 93-04.
- Coombs, E.M., Markin, G.P., Pratt, P.P. and Rice, B. 2004. Gorse. *In* E.M. Coombs, J.K. Clark, G.L. Piper and A.F. Cofrancesco Jr. [eds.], *Biological Control of Invasive Plants in the United States*. Oregon State University Press, Corvallis, OR.
- Crawley, M.J. 1989. Insect herbivores and plant population dynamics. *Annual Review of Entomology* 34: 531-564.
- Crawley, M.J. 1983. *Herbivory: The Dynamics of Animal-Plant Interactions*. University of California Press, Berkeley, CA.

- Egunjobi, J.K. 1971. Ecosystem processes in a stand of *Ulex europaeus* L.: I. Dry matter production, litter fall and efficiency of solar energy utilization. *Journal of Ecology* 59: 31-38.
- Fogarty, G. and Facelli, J.M. 1999. Growth and competition of *Cytisus scoparius*, an invasive shrub, and Australian native shrubs. *Plant Ecology* 144: 27-35.
- Fox, J.C. and Steinmaus, S. 2001. Climatic prediction of an invasive plant in California: *Ulex europaeus* (Gorse). *Proceedings of the California Weed Science Society* 53: 34-37.
- Goeden, R.D. and Andres, L.A. 1999. Biological control of weeds in terrestrial and aquatic environments. *In* T.S. Bellows and T.W. Fisher [eds.], *Handbook of Biological Control: Principles and Applications of Biological Control*. Academic Press, San Diego, CA.
- Harley, K.L.S. and Forno, I.W. 1992. *Biological Control of Weeds: A Handbook for Practitioners and Students*. Inkata Press, Melbourne, Australia.
- Harris, P. 1986. Biological control of weeds. *In* J.M. Franz [ed.], *Biological Control of Plant Pests and of Vectors of Human and Animal Diseases: International Symposium of the Akademie der Wissenschaften und der Literatur, Mainz, November 15th-17th, 1984 at Mainz and Darmstadt*. *Fortschritte der Zoologie* 32: 124-138. G. Fischer Verlag, New York.
- Hayes, A.J., Gourlay, A.H. and Hill, R.L. 1996. Population dynamics of an introduced biological control agent for gorse in New Zealand: a simulation study. *In* V.C. Moran and J.H. Hoffman [eds.], *Proceedings IXth International Symposium on Biological Control of Weeds, 19-26 January, 1996, Stellenbosch, South Africa, University of Cape Town*.
- Hayes, A.J., Gourlay, A.H. and Hill, R.L. 1994. Temperature-dependent phenology of gorse spider mite. *Proceedings of the New Zealand Plant Protection Conference* 47: 98-102.
- Hermann, R.K. and Newton, M. 1968. Tree Planting for the Control of Gorse on the Oregon Coast. Research Paper 9. Forest Research Laboratory, School of Forestry, Oregon State University, Corvallis, Oregon.
- Hill, R.L. 1982. Seasonal patterns of phytophage activity on gorse (*Ulex europaeus*) and host plant quality. *In* J.H. Visser and A.K. Minks [eds.], *Proceedings of the 5th International Symposium on Insect/ Plant Relationships, Wageningen, the Netherlands*.

- Hill, R.L. and Gourlay, A.H. 2002. Host-range testing, introduction and establishment of *Cydia succedana* (Lepidoptera: Tortricidae) for biological control of gorse, *Ulex europaeus* L., in New Zealand. *Biological Control* 25: 173-186.
- Hill, R.L. and Gourlay, A.H. 1991. Safety testing of *Tetranychus lintearius* (Dufour), a potential control agent for gorse in Oregon. Unpublished report to the Oregon Department of Agriculture.
- Hill, R.L. and Gourlay, A.H. 1989. *Ulex europaeus* L., gorse (Fabaceae). In P.J. Cameron, R.L. Hill, J. Bain, W.P. Thomas [eds.], Technical Communication No. 10, A Review of Biological Control of Invertebrate Pests and Weeds in New Zealand 1874-1987. CAB International, Walingford, UK.
- Hill, R.L. and O'Donnell, D.J. 1991a. Reproductive isolation between *Tetranychus lintearius* and two related mites *T. urticae* and *T. turkestanii* (Acarina: Tetranychidae). *Experimental and Applied Acarology* 11: 241-251.
- Hill, R.L. and O'Donnell, D.J. 1991b. The host range of *Tetranychus lintearius* (Acarina: Tetranychidae). *Experimental and Applied Acarology* 11: 253-269.
- Hill, R.L., Gourlay, A.H. and Wigley, P.J. 1989. The introduction of gorse spider mite, *Tetranychus lintearius*, for biological control of gorse. *Proceedings of New Zealand Weed and Pest Control Conference* 42: 137-139.
- Hill, R.L., Grindell, J.M., Winks, C.J., Sheat, J.J. and Hayes, L.M. 1991. Establishment of gorse spider mite as a control agent for gorse. *Proceedings of the New Zealand Plant Protection Conference* 44: 31-34.
- Insightful. 2002. S-PLUS 6.1 for Windows. Insightful Corporation, Seattle, WA.
- Isaacson, D.L. and Miller, G. 1992. A comparison of gorse (*Ulex europaeus* L.) in New Zealand and the United States. In *Proceedings of the Washington State Weed Conference*, Nov 4-6, Yakima, WA.
- Julien, M.H. and Griffiths, M.W. 1998. *Biological Control of weeds: A World Catalogue of Agents and their Targets*, 4th edition. CABI, New York.
- Keane, R.M. and Crawley, M.J. 2002. Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology and Evolution* 17: 164-170.
- Kennedy, G.G. and Smitley, D.R. 1985. Dispersal. In W. Helle and M.W. Sabelis [eds.], *Spider Mites: Their Biology, Natural Enemies and Control*. Elsevier, New York.

- Lee, W.G., Allen, R.B. and Johnson, P.N. 1986. Succession and dynamics of gorse (*Ulex europaeus* L.) communities in the Dunedin Ecological District, South Island, New Zealand. *New Zealand Journal of Botany* 24: 279-292.
- Littell, R.C., Stroup, W.W. and Freund, R.J. 2002. SAS for Linear Models, 4th edition. SAS Institute, Cary, NC.
- Lowe, S.J., Browne, M. and Boudjelas, S. 2000. 100 of the World's Worst Invasive Alien Species. IUCN/SSC Invasive Species Specialist Group (ISSG), Auckland, New Zealand.
- Maschinski, J. and Whitman, T.G. 1989. The continuum of plant responses to herbivory: the influence of plant association, nutrient availability and timing. *The American Naturalist* 134: 1-19.
- Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M. and Bazzaz, F.A. 2000. Biotic invasions: causes, epidemiology, global consequences and control. *Ecological Applications* 10: 689-710.
- McEvoy, P.B. and Coombs, E.M. 2000. Why things bite back: unintended consequences of biological weed control. *In* P.A. Follett and J. Duan [eds.], *Nontarget Effects of Biological Control*. Kluwer Academic Publishers, Boston, MA.
- McEvoy, P.B. and Coombs, E.M. 1999. Biological control of plant invaders: regional patterns, field experiments, and structured population models. *Ecological Applications* 9: 387-401.
- McEvoy, P., Cox, C. and Coombs, E. 1991. Successful biological control of ragwort, *Senecio jacobaea*, by introduced insects in Oregon. *Ecological Applications* 1: 430-442.
- Morin, L. 2001. Classical biological control of weeds- update and global issues. *In* Proceedings of the Third International Weed Science Congress; 2000 June 6-11; Foz do Iguassu, Brazil, Manuscript number 353. CD ROM available from: International Weed Science Society, Oxford, MS, USA.
- Pimentel, D., Lach, L., Zuniga, R. and Morrison, D. 2000. Environmental and economic costs of nonindigenous species in the United States. *BioScience* 50: 53-65.
- Prasad, R. 2003. Management and Control of Gorse and Scotch Broom in British Columbia. Technology Transfer Note Number 30. Canadian Forest Service, Pacific Forestry Centre, Victoria, BC.

Pratt, P.D., Coombs, E.M. and Croft, B.A. 2003. Predation by phytoseiid mites on *Tetranychus lintearius* (Acari: Tetranychidae), an established weed biological control agent of gorse (*Ulex europaeus*). *Biological Control* 26: 40-47.

Rees, M. and Hill, R.L. 2001. Large-scale disturbances, biological control and the dynamics of gorse populations. *Journal of Applied Ecology* 38: 364-377.

Prevosto, B., Robert, A. and Coquillard, P. 2004. Development of *Cytisus scoparius* L. at stand and individual level in a mid-elevation mountain of the French Massif Central. *Acta Oecologica* 25: 73-81.

Reichard, S.H. and White, P. 2001. Horticulture as a pathway of invasive plant introductions in the United States. *BioScience* 51: 103-113.

Richardson, R.G. and R.L. Hill. 1987. *Ulex europaeus*. In F.D. Panetta, R.H. Groves and R.C.H. Shepherd [eds.], *The Biology of Australian Weeds, Volume 2*. R.G. and F.J. Richardson, Melbourne, Australia.

Rodriguez, J.G. and Rodriguez, L.D. 1987. Nutritional ecology of phytophagous mites. In F. Slansky Jr. and J.G. Rodriguez [eds.], *Nutritional Ecology of Insects, Mites, Spider and Related Invertebrates*. John Wiley and Sons, New York.

SAS. 2001. SAS Version 8.2 for Windows. SAS Institute, Cary, NC.

Schooler, S.S. 1998. Biological control of purple loosestrife *Lythrum salicaria* by two chrysomelid beetles *Gallerucella pusilla* and *Gallerucella calamaiensis*. M.S. Thesis, Oregon State University.

Shea, K., Possingham, H.P., Murdoch, W.M. and Roush, R. 2002. Active adaptive management in insect pest and weed control: intervention with a plan for learning. *Ecological Applications* 12: 927-936.

Stone, C. 1986. An investigation into the morphology and biology of *Tetranychus lintearius* Dufour (Acari:Tetranychidae). *Experimental and Applied Acarology* 2: 173-186.

Strauss, S.Y. and Agrawal, A.A. 1999. The ecology and evolution of plant tolerance to herbivory. *Trends in Ecology and Evolution* 14: 179-18.

Tomczyk, A. and Kropczynska, D. 1985. Effects on the Host Plant. In W. Helle and M.W. Sabelis [eds.], *Spider Mites: Their Biology, Natural Enemies and Control*. Elsevier, New York.

van Driesche, R.G. and Bellows, T.S. 1996. *Biological Control*. Chapman and Hall, New York.

van Driesche, J. and van Driesche, R. 2000. *Nature out of place: biological invasions in the global age*. Island Press, Washington, D.C.

Vitousek, P.M. 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. *Oikos* 57: 7-13.

Wapshere, A.J., Delfosse, E.S. and Cullen, J.M. 1989. Recent developments in biological control of weeds. *Crop Protection* 8: 227-250.