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## **Host Plant Resource Quality, Insect Herbivores and Biocontrol**

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### **Abstract**

Based on research on woody plants, seven fundamentals are advocated on plant and insect herbivore interactions relevant to the biological control of weeds. 1. Plant food is necessary for every individual in an insect herbivore population and is therefore basic to an understanding of herbivore demography. 2. Food of high quality is generally utilized by insect herbivores, usually in the form of vigorously developing plant modules, or highly nutritious seeds, buds, corms, etc. 3. Vigorous, high quality modules are likely to be limiting, providing a low carrying capacity for insect herbivores. 4. Specialized herbivores likely to be used in weed biocontrol generally are adapted to select high quality food, with ovipositing females showing a strong preference for high quality plant modules. 5. This ovipositional preference is linked in many species to larval survival. 6. The results of these evolved plant-herbivore interactions are latent population dynamics defined by bottom-up regulation from plant resources, species that are uncommon or rare in natural landscapes, which rarely if ever become eruptive. 7. Another consequence of the evolved plant-herbivore interaction is that top-down effects in the food web, from carnivores, are frequently weak or inconsequential.

These fundamentals reveal the paradox in weed biocontrol. We wish for outbreaks of insect herbivores but employ insects that virtually never outbreak in natural landscapes. Truly eruptive insect species are very unusual and commonly feed on several or many host plant species making them unsuitable agents for biological control.

Four considerations for the pragmatic biocontrol researcher are proposed, based on the fundamentals and the paradox, to convert insect herbivores with latent population dynamics into outbreak species. 1. During surveys for biocontrol agents the exact details of life history in relation to the host plant should be noted including oviposition site, site of larval establishment and module quality utilized. 2. Determination of optimal host plant quality is basic for successful introductions. 3. At release sites optimal conditions should prevail or be created locally by manipulation. 4. Reservoirs of optimal habitat should be maintained to provide a persistent source of colonists into more marginal zones.

These generalizations were developed based on studies of gall-inducing sawflies and comparative work on many other species that reveal the general scenarios discussed as fundamentals. Not only is plant module quality central to population dynamics but plant architecture also, with completely different dynamics observed on shrubs compared to trees. Examples from biological control are consistent with the suggested scenarios. I conclude that the paradox can be solved after careful study of the insect-plant relationship and adequate local husbandry of the host plant at least at the release site.

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## Fundamentals

Generalizations discussed here were based on research on woody plants, but the fundamentals are likely to be relevant to insect herbivores on herbaceous plants also.

1. Food is necessary for every individual in every population and species, be it humans, insects or in particular biocontrol agents. Food has an overwhelming impact on the distribution, abundance and demography of populations and species. Generally it is the key resource that influences and modifies all other ecological relationships through the trophic system. It is the key to success or failure in biological control of weeds.

2. Food of high quality thus is of central concern for the demographer wishing to regulate plant populations. Again, humans and insects alike find quality to come in the form of young and vigorous plants or plant parts: young plants, young shoots, buds, fruits and seeds. For insect herbivores, early seasonal growth, be it stems, buds or leaves are frequently attacked and gall formers, borers, leaf tiers and rollers and free-feeders largely concentrate on young growth. Many insect herbivore guilds rely on rich resources provided by vigorous plants.

3. Food of high quality is likely to be limiting as a resource for herbivores because rapid growth is usually seasonally brief, optimal sites for plant growth are scattered over a landscape and physiological aging in plants inexorably lowers plant vigor and quality through time. Thus resources over a landscape are patchy and of rapidly changing quality within growing seasons and across seasons.

4. Specialized herbivores utilizing one or a narrow spectrum of plant species, those generally used in weed biocontrol, have evolved with a high preference for certain plant species, and a strong preference for the highest quality plant modules in that species: thick, rapidly-growing shoots for borers, young rapidly developing modules for gall inducers, large young leaves for free-feeders and leaf rollers. The life cycle of these insects is tightly synchronized with host plant phenology such that female herbivores oviposit onto or into very young plant parts or eggs hatch when succulent, new plant growth becomes available.

5. Specialized insect herbivores have evolved a high preference for vigorous plant parts because, generally, larval survival is highest on these parts. *An ovipositional preference is linked to larval performance.* In particular, establishment of first instar larvae in a feeding site is critical, for they are the most vulnerable stage in the life cycle. They need succulent, nutritious food in plants that are generally very low in protein relative to animal needs and very tough for the tiny mouthparts of the neonate insect.

6. Resulting from these factors, the population dynamics of specialized insect herbivores used in biocontrol of weeds, in their native habitat, are likely to be heavily constrained by shortage of high quality food. Bottom-up regulation in the food chain, from plant food to insect herbivores will be the norm. Over a landscape there will be small patches of vigorous plants that sustain insect herbivore populations with many areas of host plant largely unavailable and irrelevant to the insects needs. Populations are likely to be latent, meaning that abundance is generally low, distribution is sparse, and outbreak or eruptive dynamics are seldom if ever observed. These conditions prevail for the majority of insect herbivore species, which are uncommon or rare over a landscape.

7. Another consequence of these evolved and ecological relationships is that natural enemies of insect herbivores, the carnivores in the food web, are largely inconsequential in herbivore population dynamics. Larvae establish feeding sites readily in protected places and grow rapidly, reducing availability to carnivores. Populations are sparse and

individuals hard to find in a landscape, and the changing mosaic of suitable habitat results in an ever-changing availability of herbivores for carnivores. Top-down regulation of insect herbivore populations is unlikely and rare, and very local if it occurs at all.

### **The Paradox**

These scenarios reveal the almighty paradox for the weed biocontrol practitioner. We wish to create eruptive populations of insects that decimate plant populations using insect species with preponderantly latent, non-eruptive population dynamics. A sea of alien weeds is not necessarily food for specialized insects, for adequate, high quality resources may be rare.

Adding to the dilemma in weed biocontrol is that eruptive insect herbivores, which we would like to use, have unsuitable traits. First, they are very uncommon, unusual insects, constituting a very small percentage of insect herbivores in any one fauna. Therefore, there are few opportunities to use them. Second, life cycles which predispose species to eruptive dynamics also result in a catholic diet including several to many host plant species. Females of many eruptive species do not show a preference for any food-plant-quality trait valuable for larval performance. In fact, oviposition time and place is usually separated significantly from the time and place when larvae will commence feeding. Oviposition may be on tree bark in the late summer while larvae will feed on buds or leaves in the following early spring. In extreme cases eggs are dropped from the tree canopy and lie on the ground for 6-18 months before eclosion. A consequence of this female behavior is larvae evolved to be general in their capacity to utilize most of what is available to feed upon because very small young larvae must find food quickly and establish a feeding site. Ultimately, such species are able to defoliate a population of host plants, often causing economic damage and being categorized as pests, even in more or less natural vegetation.

The most usual place to observe specialized insect herbivores with latent population dynamics in natural habitats, becoming pest species is in unnatural habitats. That is in agriculture, horticulture, nurseries, and plantations. Humans optimize plant growth converting species into optimal food and habitat for insect herbivores. Young, vigorous and nutritious plants are desired by humans and insect herbivores alike, as stated early in this essay.

### **Applications to Biocontrol**

The lessons for the pragmatic biocontrol researcher are clear.

1. During surveys for insect biocontrol agents attention should be given, for each insect species, to:
  - a) the exact location of oviposition on the plant host, especially in relation to plant age and module vigor relative to the distribution of module sizes in a plant population;
  - b) the exact location of larval feeding in relation to plant age and module vigor; and
  - c) the plant age and module vigor in which occurs the highest survival at the end of feeding.

Such observations are critical to the eventual success of a biocontrol research program in my opinion. They may be expanded using experimental gardens that maximize differences in plant quality using water and fertilizer treatments and perhaps plant age treatments.

2. Optimal host plant quality for the insect herbivore should be determined in relation to ovipositional preference and larval performance using quantitative data collected in natural populations and, if possible, in experimental plots.
3. At a release site these optimal conditions should be recreated locally as well as possible, especially concerning host plant age and vigor. Either (a) optimal sites may be found which occur without manipulation, or (b) populations should be established in optimal sites, or (c) plant populations should be modified locally by watering, fertilizing, pruning, mowing, thinning, fencing or other such husbandry. Manipulation is expensive, but in its absence biocontrol agents may be released into a sea of what is largely nonfood.
4. Reservoirs of optimal habitat for herbivores should be maintained throughout a biocontrol program to ensure persistent sources of colonists. Such reservoirs should be distributed throughout the range of the weed species if biocontrol proves to be difficult. Also, reservoirs should act as refuges for insect populations during adverse conditions for plant hosts involving drought, fire, flooding, successional vegetation changes and other natural variation.

### Justification

The forgoing generalizations and conclusions are based on research principally involving insect herbivores on woody plants, but I contend that they apply to many herbaceous plants and their herbivores as well, even if in a weaker manner in some cases. The most general introductory literature includes *Insect Ecology* (Price 1997) and several overviews with specific insect examples, some covering both latent and eruptive species (Price *et al.* 1990, Price 1991, 1994, Price *et al.* 1995, 1998).

The first species we studied that provided insights into the existence of tight preference-performance linkage and consequent population dynamics was a gall-inducing sawfly, *Euura lasiolepis* Smith (Hymenoptera: Tenthredinidae). A brief synopsis is provided here with key supporting papers by Craig *et al.* (1986, 1989), Price and Clancy (1986), Preszler and Price (1988), and Price *et al.* (1995, 1998). We revealed the critical importance of plant module vigor and the evolved behavior of females in response to rapidly growing modules. In fact the plant-herbivore interaction is the key to the whole population dynamics of the sawfly, modified by water supply affecting plant growth. Dynamics are driven by bottom-up forces with top-down effects of minimal consequence.

Female sawflies emerge in synchrony with rapidly growing shoots of the only host plant, arroyo willow, *Salix lasiolepis* Bentham (Salicaceae). The sawfly is a specialist. Females show a strong preference for the most rapidly growing shoots that eventually become the longest shoots in a population of shoot modules. Larvae establish feeding sites and survive best in galls on long shoots. On vigorous shoots, galls grow large providing effective refuge from some parasitic wasps. The general trend in population dynamics is for increases in density after heavy winter precipitation which promote plant growth and decreases in drier conditions. Disturbance results in young plants or young ramets favorable to sawflies, while its lack results in plant senescence and steep declines in population density.

In a comparative manner we have extended studies to many other gall-inducing sawflies (e.g. Price *et al.* 1998, Price *et al.* 1999), other gall-inducers (e.g. Price *et al.* 1990), free-feeding sawflies (Carr 1995, Carr *et al.* 1998) and shoot borers (Price *et al.* 1990, Spiegel and Price 1996). There is a very general case to be made for a coupling of

female preference and larval performance related to high plant module vigor. However, in some species larval performance is not correlated with shoot length, perhaps when females become so selective that virtually all modules attacked are suitable for larval survival.

### Plant Architecture

One important consideration in terms of general understanding of insect herbivore population dynamics and biocontrol of woody plants is the different responses of herbivores to shrubs and trees. This concerns herbivores with high preference-performance linkage. Shrubs lack apical dominance, producing new young ramets from the base, creating vigorous modules for herbivores over the long term. Herbivore populations may remain relatively stable over decades on such resources, as is the case for *Euura lasiolepis* (Price *et al.* 1990, 1995, 1997, 1998). However, in the same genus, *Euura*, those on trees colonize very young trees, or rapid growth on damaged trees and go locally extinct rapidly. Trees have apical dominance such that ontogenetic and physiological aging are inevitable, with both probably playing a role in the precipitous decline of populations with host or ramet age (e.g. Roininen *et al.* 1993, 1996, Price *et al.* 1997). Consequently host plant architecture impacts strongly the population dynamics of populations, a factor noted also by Kearsley and Whitham (1989).

### Biocontrol-Related Examples

Biocontrol of saltcedar (*Tamarix* spp.) has been a longstanding target in the southwestern United States (e.g. DeLoach *et al.* 1996). The spindle-gall moth, *Amblypalpis olivierella* Rag. (Lepidoptera: Gelechiidae) is a biocontrol candidate for *T. ramosissima* Ledebour in the U.S. (Jack DeLoach, personal communication). This plant-insect interaction illustrates the kinds of concerns relevant to weed biocontrol.

Larvae of the spindle-gall moth on *T. nilotica* (Ehrenb.) Bge. in Israel emerge during the wet season and bore into young, rapidly growing shoots of *Tamarix* and each forms a gall (Lupo and Gerling 1984, Price and Gerling 2000). There is a strong positive relationship between number of larvae establishing in galls per shoot and shoot length, provided that shoots are vigorous. On young trees with many vigorous ascendant shoots populations of gall-inducers are high and cause severe dieback. *Amblypalpis* could be a significant contributor to biocontrol if it were necessary on *T. nilotica*, but only in young, vigorous populations of the host. Perhaps it could be equally effective on *T. ramosissima* in the U.S.A.

My brief exposure to the biocontrol of weedy legumes in South Africa, thanks to Cliff Moran and Johnny Hoffmann, reinforced the view that vigorous plants are susceptible to herbivore attack. Evidently legumes grow very well in South African coastal conditions fostering success in biocontrol. The three weevils on *Sesbania punicea* (Cav.) Benth. have been extraordinarily successful (e.g. Hoffmann 1990, Moran and Hoffmann 1989, Hoffmann and Moran 1991). At the time of my visit I was especially impressed by the large-scale death of shoot tips on very vigorous young plants caused by the shoot-boring weevil, *Neodiplogrammus quadrivittatus* (Olivier) (cf. Hoffmann and Moran 1991).

Another case in coastal South Africa, in which very vigorous plants are susceptible, involves *Acacia longifolia* (Andr.) Willd. and the gall-inducing pteromalid wasp, *Trichilogaster acaciaelongifoliae* Froggatt. The remarkably high densities of large galls, even on old trees, has not been observed in natural conditions in my experience, and I sus-

pect bottom-up effects are involved. *Trichilogaster* is not so effective in drier inland sites according to Dennill and Donnelly (1991) and Dennill *et al.* (1999), although the situation needs reevaluation apparently.

## Conclusions

Bottom-up regulation of insect herbivore populations through plant quality is more prevalent than top-down regulation from carnivores. Host plants have dramatic impact on herbivore populations with plant architecture, age and module vigor as critical factors. Thus management of plant quality in biocontrol of weeds can be a basic necessity for success.

The most favorable plant hosts in relation to species and quality within species reduce the impact of carnivores on herbivores either because of rapid development or by providing vigorous modules in which herbivores are well concealed.

The paradox in weed biocontrol is that herbivores likely to be used are also likely to be uncommon with latent population dynamics and yet we wish them to be outbreak species. Herbivore species that are specific in their host preference are likely to be specific to module quality with a consequent ovipositional preference and larval performance linkage. Such species are likely to be regulated by a very limited supply of high quality modules, occur as uncommon or rare species under natural conditions, with latent population dynamics. True outbreak species in nature are usually generalists attacking several to many host plant species and are unsuitable as agents of biocontrol. The solution apparently is to raise host plant quality, at least in patches that simulate agricultural crops in which specialized insects can utilize an abundance of high quality modules and populations can become eruptive.

Herbivore species with a strong preference for high quality modules can become abundant locally when the carrying capacity is high, often after disturbance when young plants establish or when rootstocks resprout. Relatively high fecundity coupled with abundant oviposition sites, and rapid larval development in safe feeding sites results in weak top-down effects from carnivores. Many specific insects are endophagous, such as gallers, seed feeders, shoot, stem and root borers, limiting access to natural enemies.

During the exploration, testing and release phases in biocontrol research, the details of the plant and herbivore interaction should become understood. Optimal conditions at release sites should be simulated to maximize establishment, and perhaps refugia of high quality habitat should be maintained to provide a supply of new colonizing herbivores after generally adverse conditions.

## Acknowledgments

I am grateful to the organizers for their invitation to contribute to this symposium. Financial support for research was provided by the U.S. National Science Foundation for 20 years, with the last grant being DEB-9318188.

## References

- Carr, T.G. 1995. Oviposition preference – larval performance relationships in three free-feeding sawflies. M. S. Thesis, Northern Arizona University, Flagstaff.
- Carr, T. G., H. Roininen, and P. W. Price. 1998. Oviposition preference and larval performance of *Nematus oligospilus* (Hymenoptera: Tenthredinidae) in relation to host plant vigor. *Environ. Entomol.* 27: 615-625.

- Craig, T.P., P.W. Price, and J.K. Itami. 1986. Resource regulation by a stem-galling sawfly on the arroyo willow. *Ecology* 67: 419-425.
- Craig, T.P., J.K. Itami, and P.W. Price. 1989. A strong relationship between oviposition preference and larval performance in a shoot-galling sawfly. *Ecology* 70: 1691-1699.
- DeLoach, C.J., D. Gerling, L. Fornasari, R. Sobhian, S. Myartseva, I.D. Mityaev, Q.G. Lu, J.L. Tracy, R. Wang, J.F. Wang, A. Kirk, R.W. Pemberton, V. Chikatunov, R.V. Jashenko, J.E. Johnson, H. Zheng, S.L. Jiang, M.T. Liu, A.P. Liu, and J. Cisneroz. 1996. Biological control programme against saltcedar (*Tamarix* spp.) in the United States of America: progress and problems. pp. 253-260. In V. C. Moran and J. H. Hoffmann [eds.] Proc. IX Int. Symp. Bio. Control Weeds, University of Capetown, South Africa.
- Dennill, G.B., and D. Donnelly. 1991. Biological control of *Acacia longifolia* and related weed species (Fabaceae) in South Africa. *Agric. Ecosystems Environ.* 37: 115-135.
- Dennill, G.B., D. Donnelly, K. Stewart, and F.A.C. Impson. 1999. Insect agents used for the biological control of Australian *Acacia* species and *Paraserianthes lophantha* (Willd.) Nielsen (Fabaceae) in South Africa. *African Entomol. Mem.* 1: 45-54.
- Hoffmann, J.H. 1990. Interactions between three weevil species in the biocontrol of *Sesbania punicea* (Fabaceae): the role of simulation models in evaluation. *Agric. Ecosystems Environ.* 32: 77-87.
- Hoffmann, J.H., and V.C. Moran. 1991. Biological control of *Sesbania punicea* (Fabaceae) in South Africa. *Agric. Ecosystems Environ.* 37: 157-173.
- Kearsley, M.J.C., and T.G. Whitham. 1989. Developmental changes in resistance to herbivory: implications for individuals and populations. *Ecology* 70: 422-434.
- Lupo, A., and D. Gerling. 1984. Bionomics of the *Tamarix* spindle-gall moth *Amblypalpis olivierella* Rag. (Lepidoptera: Gelechiidae) and its natural enemies. *Bolletino Lab. Ent. Agr. Filippo Silvestri* 41: 71-90.
- Moran, V.C., and J.H. Hoffmann. 1989. The effects of herbivory by a weevil species, acting alone and unrestrained by natural enemies, on growth and phenology of the weed *Sesbania punicea*. *J. Appl. Ecol.* 26: 967-977.
- Preszler, R.W., and P.W. Price. 1988. Host quality and sawfly populations: A new approach to life table analysis. *Ecology* 69: 2012-2020.
- Price, P.W. 1991. The plant vigor hypothesis and herbivore attack. *Oikos* 62: 244-251.
- Price, P.W. 1994. Phylogenetic constraints, adaptive syndromes, and emergent properties: from individuals to population dynamics. *Res. Pop. Ecol.* 36: 3-14.
- Price, P.W., and K.M. Clancy. 1986. Interactions among three trophic levels: gall size and parasitoid attack. *Ecology* 67: 1593-1600.
- Price, P.W., and D. Gerling. 2000. Complex architecture of *Tamarix nilotica* and resource utilization by the spindle-gall moth *Amblypalpis olivierella* (Lepidoptera: Gelechiidae). *Israel J. Entomol.* In press.
- Price, P.W., N. Cobb, T.P. Craig, G.W. Fernandes, J.K. Itami, S. Mopper, and R.W. Preszler. 1990. Insect herbivore population dynamics on trees and shrubs: new approaches relevant to latent and eruptive species and life table development. pp. 1-38. In E. A. Bernays [ed.]. *Insect-plant interactions*. Vol. 2. CRC Press, Boca Raton, Florida.
- Price, P.W., T.P. Craig, and H. Roininen. 1995. Working toward theory on galling sawfly population dynamics. pp. 321-338. In N. Cappuccino and P. W. Price [eds.]. *Population dynamics: new approaches and synthesis*. Academic Press, San Diego.
- Price, P.W., H. Roininen, and T. Carr. 1997. Landscape dynamics, plant architecture and demography, and the response of herbivores. pp. 319-333. In K. Dettner, G. Bauer and W. Völkl [eds.]. *Vertical food web interactions: evolutionary patterns and driving forces*. Springer Verlag, Berlin.
- Price, P.W., T.P. Craig, and M.D. Hunter. 1998. Population ecology of a gall-inducing sawfly, *Euura lasiolepis*, and relatives. pp. 323-340. In J. P. Dempster and I. F. G. McLean

[eds.]. Insect populations: in theory and in practice. Kluwer, Dordrecht.

- Price, P., H. Roininen, and T. Ohgushi. 1999.** Comparative plant-herbivore interactions involving willows and three gall-inducing sawfly species in the genus *Pontania* (Hymenoptera: Tenthredinidae). *Ecoscience* 6: 41-50.
- Roininen, H., P.W. Price, and J. Tahvanainen. 1993.** Colonization and extinction in a population of the shoot-galling sawfly, *Euura amerinae*. *Oikos* 68: 448-454.
- Roininen, H., P.W. Price, and J. Tahvanainen. 1996.** Bottom-up and top-down influences in the trophic system of a willow, a galling sawfly, parasitoids and inquilines. *Oikos* 77: 44-50.
- Spiegel, L.H., and P.W. Price. 1996.** Plant aging and the distribution of *Rhyacionia neomexicana* (Lepidoptera: Tortricidae). *Environ. Entomol.* 25: 359-365.