Predicting Effectiveness: Fact and Fantasy

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Man's desire to create order out of the complexities of agent:weed interactions in biological control has led to generalisations, point scoring systems for agents and extensive computer analyses. A brief review suggests that none has been satisfactory and generalisations in particular can be dangerous in neglecting the importance of exceptions. Is there really a case for the pursuit of order or will it only ever be possible to consider each situation case-by-case? Justifications for seeking a pattern have often been weak or loosely defined, yet ad hoc case-by-case consideration can be unguided and of little value to the analysis of new situations in the future. There is a need to carefully examine what is really required. Rather than looking for rules we need to define some questions. Development and application of the full potential of biological control will be dependent on a better understanding and management of herbivory. This needs to include better powers of prediction and the ability to improve and integrate biological control with other systems. The past history of biological control and in particular, analysis of a number of case histories where results have varied with location and agent, shows some of the factors that need consideration. An attempt is made to define the important elements of the weed:herbivore system about which information is required.

Introduction

One of the topics most likely to provoke discussion among workers in biological control is the feasibility of predicting successful control given certain basic information. This often commences as a search for pattern and meaning in what has gone before, which then tends to lead to correlations and generalisations. The translation of these into hypotheses to guide research is basic to scientific methodology, but it is a long way from a correlation to a prediction. This account looks briefly at some of the generalisations that have been debated over recent years or have become standards, and then at a rather different approach using much of the same basic information. A possible series of questions is discussed that may eventually come closer to refining the information required and thence our predictive ability.

The Predictive Value of Generalisations

Burdon and Marshall (1981), in looking at the correlation between the level of success and the reproductive mode of the target weeds, concluded that inbreeding species were more likely to be controlled. The validity of this conclusion has been challenged elsewhere (Chaboudez and Sheppard 1995), but regardless of the rules used for compiling the database and the validity of its subsequent interpretation, it is only a correlation. The data demonstrate that there are a large number of cases of outbreeding species showing successful control and there will no doubt be many more in the future.

Hokkanen and Pimentel (1984) suggested that new agent:host associations were more effective than older, coevolved relationships and should be used as the preferred method in selecting biological control agents. Again, the validity of this conclusion has been challenged (Goeden and Kok 1986) and in a similar manner to the preceding example, there are so many examples of successful control produced by "old associations," that the only value of the proposal is to remind the researcher that new associations should not be neglected when examining all possible agents.
In an analysis of data from biological control programs, Crawley (1986) demonstrated that the majority of successful agents had a high rate of increase and went on to say that agents with a high rate of increase are more likely to succeed. What is implicit in this sort of analysis is the caveat, “all things being equal,” which they seldom are. Some slower-increasing species are effective and it may well be one such species that is under consideration. Other, more relevant questions are required rather than to suggest that a species may be less successful simply because it does not conform to the general description of a species with a high rate of increase.

Even established faiths, for example that annual weeds are more difficult to control than perennials, really need presenting in a different manner. There is perhaps reason to suggest that plant species that are less apparent give less opportunity for the evolution of specialists, but while some annuals may indeed be more or less ephemeral, others may be present for the majority of the year, often in stable habitats and sometimes in the presence of closely related biennial and perennial species that might serve as reservoirs. There is no a priori reason to assume that there may not be suitably specialised and effective natural enemies for an annual species.

The derivation of simplified check lists based on agent characteristics (Harris 1973, Goeden 1983) might be considered a step in the right direction, but there are many factors not considered in such schemes, in particular concerned with the biology and ecology of the weed, while other factors that contribute to the total score may not be relevant to a particular agent or weed. For any given situation, there are often more appropriate and valuable questions than those posed in a formal list of this sort.

If we rely on any or all of these to guide our predictions, we run an enormous risk of excluding potentially effective species and of simply getting it wrong.

So where should the scientist look? If there are so many variables to consider and every situation is different, there is a good argument for saying that each situation can only be considered on a case-by-case basis with a detailed knowledge of the biology and ecology of the plant and of the agent. Unfortunately, this is often impractical. Even it not, it is possible to spend a lot of time gathering data that might turn out to be useless, and given that much of the data can only be collected in the country of origin of the weed, will it really be applicable to a different environment in a different country? There is certainly a school of thought that would maintain that it is not worth the trouble.

An Initial Approach

I believe that if the expenditure of public funds is to be justified and/or if calculated risks have to be taken in introductions, and if we are going to be able to manage the science properly to obtain the maximum benefit, we have to make the effort to predict whether an agent will be effective.

However, it is clear that we need considerably better guidance as to how to do it, what information we need, and how it can be applied. The accumulating history of biological control programs (Julien 1987) is one possible source of guidance. To examine the complete range of case histories listed is a formidable task and is yet to be attempted in detail. The most serious attempt made has been the “Silwood project” whereby, using an earlier edition of Julien (1987) as a base, further information was acquired by questionnaire regarding the agents used. This yielded some interesting correlations regarding agents (Crawley 1986), but attempts to proceed further foundered on disagreements over the type and relevance of the information required concerning the weed. Until there is a clearer idea of what should be looked for, there will remain significant gaps in the information available.

The present attempt has tried to take a more manageable subsample by only looking at programs and agents that have recorded significant control in at least one country or habitat at some time and then look at the reasons given why the system has not been successful elsewhere. The result is a list of 25 different weed/agent associations which yield a total of 30 possible reasons for variation in effect. To help assimilate these cases, they have been arranged in Table 1 in categories.
Most variations in success are explained on the basis of variation in adaptation of the agent to the weed, the effects of temperature and moisture either on the agent or the weed, plus variation in predation on the agent and competition on the weed. Categories were therefore erected on this basis. No attempt is made to suggest that any category is more important than another. If it exists it is important. The aim is guidance and any example is useful in that it is evidence that such an effect is possible.

Implications For Predications From One Situation To Another

Table 1 shows examples of differing levels of damage inflicted by the agent because of genetic variation in the host and the agent, of direct effects of various factors on the survival and reproduction of agents, and of variation in the ability of plants to respond in the face of significant attack. This confirms with the simple model that the ultimate success of an agent is a result of the combination of 3 major factors:
- the damage an individual or population unit of an agent can produce on a plant;
- the ecology of the agent in determining its density and therefore the total damage produced; and
- the ecology of the weed in determining whether that damage is significant in reducing its population (Fig. 1).

The damage produced by the individual agent on its weed host is not only a characteristic of the agent’s biology, but also of the coevolved relation between them. Successful agents include a variety of types, but variation in success is clearly often the result of differences in the agent:weed interaction. If the plant is different, the damage produced may well be different. In trying to predict success in one environment in relation to success in another, there would normally be sufficient known regarding the type of damage, but it is obviously important to know whether there is any variation in the weed.

The effect of climatic factors or other novel aspects of the environment and of predation and parasitism are all examples of variation in the ecology of the agent that affect its population density, and therefore the overall effect it can have.

Under this heading, in comparing different environments, it would be important to know whether:
(a) temperature and moisture are comparable
(b) there are any novel aspects of the new environment that may affect the agent’s ability to persist (e.g., cultivation, loss of refuges, food supply at critical times); and
(c) predation/parasitism are likely to be similar.

The answer to the first two should not be too difficult, but to determine predation levels might require less readily available information. With increasing knowledge of the parasites present that attack similar species in similar situations, the easier it becomes, but there will probably always be some difficulties in predicting a new predator or parasite.

Variation in climatic effects on the weed, often manifested in terms of variation in its ability to recover from damage, and in the level of competition experienced by the weed, are clear examples of variation in the weed’s ecology producing variation in overall success. In comparing different environments, it would be important to establish:
(a) the extent to which the plant is capable of compensating for damage (i.e., whether there are properties of the new environment which will affect this capacity); and
(b) the level of competition (if the weed is of agricultural significance, this may be fairly well known).

The implication from this brief analysis is that if success is achieved in one situation and the above aspects are paid attention to, it should not be too difficult to predict the likelihood elsewhere. The extent to which the information is pursued may well be determined by the accuracy of prediction required, but at least prediction seems possible.

New Situations

In terms of methodology, perhaps all that has been achieved is to gain a better idea of the questions that need to be asked if trying to
### Table 1. Weed: agent associations showing different reasons for variation in success of control.

**Variation in adaptation/effectiveness of agent on form of weed**

- **Phragmidium violaceum** (Schultz) Winter (Uredinales) on *Rubus fruticosus* L. (Rosaceae)
  - Chile, Australia
- **Puccinia chondrillina** Bubak & Sydenham (Uredinales) on *Chondrilla juncea* L. (Asteraceae)
  - Australia, USA
- Several agents on *Lantana camara* L. (Verbenaceae)
  - Australia, Hawaii

**Direct temperature effects on agent**

- **Agasicles hygrophila** Selman & Vogt (Coleoptera: Chrysomelidae) on *Alternanthera philoxeroides* (Martius) Grisebach (Amaranthaceae)
  - USA
- **Neochetina eichhorniae** Warner (Coleoptera: Curculionidae) on *Eichhornia crassipes* (Martius) Solms-Laubach (Pontederiaceae)
  - Australia, USA?
- **Erytenna conspucta** Pascoe (Coleoptera: Curculionidae) on *Hakea sericea* Schrader (Proteaceae)
  - South Africa
- **Cyllotabago salviniae** Calder & Sands (Coleoptera: Curculionidae) on *Salvinia molesta* D.S. Mitchell (Salviniaeaceae)
  - Australia
- **Uroplata giardi** Pic (Coleoptera: Chrysomelidae) on *L. camara*
  - Australia
- **Micrarinus** spp. (Coleoptera: Curculionidae) on *Tribulus terrestris* L. (Zygophyllaceae)
  - USA

**Variation in temperature; effect on agent and on weed not distinguished**

- **Rhopalomyia californica** Felt (Diptera: Cecidomyiidae) on *Baccharis halimifolia* L. (Asteraceae)
  - Australia
- **Cactoblastis cactorum** (Bergroth) (Lepidoptera: Pyralidae) and *Dactylopius opuntiae* on *Opuntia ficus-indica* (L.) Millr (Cactaceae)
  - Hawaii

**Variation in moisture affecting agent**

- **Aceria chondrillae** (Canestrini) (Acari: Eriophyidae) on *C. juncea*
  - Australia
- **Chrysolinia quadrigemina** (Suffrian) (Coleoptera: Chrysomelidae) on *Hypericum perforatum* L. (Clusiaceae)
  - Australia
- **Teleonema scrupulosa** Stål (Hemiptera: Tingidae) on *L. camara*
  - Fiji

**Variation in moisture; effect on agent and on weed not distinguished**

- **Procecidochares utilis** Stone (Diptera: Tephritidae) on *Ageratina adenophora* (Sprengel) R. King & H. Robinson (Asteraceae)
  - Hawaii
- **Liothrips urichi** Karny (Thysanoptera: Phlaeothripidae) on *Clidemia hirta* (L.) D. Don (Melastomataceae)
  - Fiji, Hawaii?
- Several agents on *L. camara*
  - Hawaii

**Variation in other environmental factors directly affecting agent**

- Culture: *A. chondrillae* on *C. juncea*
- Sun/shade: *C. quadrigemina* on *H. perforatum*
- Summer shelter/resources: *Perapion antiquum* (Gyllenhal) (Coleoptera: Apionidae) on *Emex* spp. (Polygonaceae)

**Effect of predation/parasitism on agent**

- *P. utilis* on *A. adenophora*
  - Australia, India, NZ
Table 1. Continued.

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<thead>
<tr>
<th>Species/Host Table</th>
<th>Country of Origin</th>
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<tbody>
<tr>
<td>C. schmidtii on C. juncea</td>
<td>Australia, USA</td>
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<tr>
<td>Dactylopius australis De Lotto (Hemiptera: Dactylopiidae) on Opuntia aurantiaca Lindley</td>
<td>South Africa</td>
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<tr>
<td>Dactylopius ceylonicus (Green) on Opuntia vulgaris Miller</td>
<td>Mauritius</td>
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<tr>
<td>T. scrupulosa on L. camara</td>
<td>Fiji</td>
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**Variation in ability of weed to recover from damage**

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<tr>
<th>Species/Host Table</th>
<th>Country of Origin</th>
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<tr>
<td>Tyria jacobaeae (L.) (Lepidoptera: Arctiidae) on Senecio jacobaea L. (Asteraceae)</td>
<td>Canada</td>
</tr>
<tr>
<td>C. quadrigemina on H. perforatum</td>
<td>Australia</td>
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**Variation in level of competition experienced by the weed**

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<th>Species/Host Table</th>
<th>Country of Origin</th>
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<tr>
<td>Rhinocyllus conicus (Frölich) (Coleoptera: Curculionidae) on Carduus nutans L. (Asteraceae)</td>
<td>Canada</td>
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**Regional variation; cause unknown**

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<tr>
<th>Species/Host Table</th>
<th>Country of Origin</th>
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<tr>
<td>Longitarsus jacobaeae (Waterhouse) (Coleoptera: Chrysomelidae) on S. jacobaeae</td>
<td>Canada vs. USA</td>
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<tr>
<td>Zeuxidiplosis giardi (Kieffer) on H. perforatum</td>
<td>Australia vs. South Africa</td>
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</tbody>
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**Figure 1. Major factors determining effectiveness of an agent.**

Damage produced by agent

Ecology of agent

Total damage produced

Ecology of the weed

Final effect

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predict from one situation to another. How might this be relevant to new situations?

It would seem legitimate to regard control of a weed in its country of origin as an example of success that can be compared elsewhere (i.e., a country of introduction) in the same way. If the natural enemy(ies) exerting control in the original environment is(are) known, it should be possible to get close to predicting the possibility of success by the natural enemy, now a biological control agent, elsewhere. The new environment need not be the same, but to the extent that it is similar, prediction will be easier and more accurate. Where it is known to be different, it is a matter of whether the differences am important.

The situation is obviously a little more complex, especially perhaps where several natural enemies interact, but with a combination of information from the country of origin and from the country of introduction (plant growth, competition, ability to compensate, etc.) considerable prediction should be possible.

**Situations With No Prior Information**

At this point it might be thought that the argument has come full circle; i.e., we are back to requiring some good ecological information from the country of origin. However, it is now possible to better define the information required and to see the way it can be profitably applied. Nevertheless, this leaves a myriad of situations where this simply is not possible. Situations where perhaps it is not known whether there is successful control, or if so, why. There is
therefore no information to suggest that the agent is successful anywhere. Are there agents that are never going to be successful? In neglecting consideration of those that have never been successful, has this abbreviated analysis missed other factors that are important? It is likely that the majority of cases of no success could be explained by one or more of the factors considered, but perhaps not all. It might require some generalising of the questions that might be asked or perhaps breaking some of the questions into smaller component parts to yield answers that might not only suggest variations in success but the likelihood of success in the first place.

A Questioning Approach

The best hope for a reasonable approach is going to be to arrive at a set of questions that might be posed. It might be a large set, but it might act rather like a computerised taxonomic key and function as a form of expert system. For any one situation only a selection would be relevant. An initial separation could be envisaged on the basis of the principal ways in which a weed population persists from season-to-season. This would tend to sort between the different major groups; e.g., annuals, herbaceous perennials, woody perennials, etc. These would affect subsequent questions with regard to the significance of the different types of damage.

The type of damage would in fact be another major separator, with subsequent questioning according to the type of agent. As examples (Table 2), one might consider 2 subsets, 1 for a flower- or seed-feeder, and 1 for a defoliator.

| Table 2. Damage produced on a target weed by a flower- or seed-feeder and a defoliator. |
| Flower- or seed-feeder |
| Does the agent's period of activity coincide with the phenology of the susceptible stage of the weed? |
| Is this likely to vary from season-to-season or site-to-site? |
| What percentage seed production is likely to be destroyed? |
| Is this going to be significant in the dynamics of the weed? | See “seed dynamics” under “weed dynamics” |
| Can the weed compensate for the loss of heads/buds/seed? | See “compensation” |
| Is the effect limited to seed loss or are there other physiological effects; e.g., energy loss by gall formation? | See “storage reserves” under “weed dynamics” |

| Defoliator |
| Is there a significant effect of defoliation on: |
| - root reserves? | See “storage reserves” under “weed dynamics” |
| - flower and seed production? | See “seed dynamics” under “weed dynamics” |
| - competition? | See “competition” |
| - growth rate? | See “competition” or “seed dynamics” |
| Will this have an effect on: |
| - competition or seed production by the end of the season? |
| - susceptibility to frost and thence survival and reproduction of critical parts? | See “frost susceptibility” |
The eventual aim would be to obtain an estimate of the probability that a given agent would reduce a weed's density by a required percentage. This would obviously be based primarily on effects on the dynamics of the weed. Initially however, the main advantage might be to serve as a guide to the knowledge that might be important and that might therefore be gathered during the course of working on an agent. At the beginning of a program there would be enormous gaps, but it would at least point to those that would be important to fill in.

Conclusion

Any form of accurate prediction will clearly take some time, and while there remains just a chance that we might be wrong, there will always be the possibility of considering those agents that seem to logically offer little hope. However, at least it will allow a more objective assessment relative to the costs and possible risks of a particular introduction.

References


