Biological Control of Indigenous Weeds with Indigenous Insects: *Cirsium arvense* as a Model

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Using indigenous agents as biocontrol agents requires augmentation of their population densities, which are currently insufficient to suppress the weed. It can be assumed that most, if not all, herbivorous insects possess the ability to control their host plant, if they occur in sufficiently high densities. Two keystone questions for the use of native agents need to be addressed: (1) How many agents are needed to sufficiently damage the weed? and (2) What are the factors limiting agent densities? We investigated the effect of density of the shield beetle *Cassida rubiginosa* Muell. (Coleoptera, Chrysomelidae) and two different plant communities on the performance of creeping thistle, *Cirsium arvense* (L.) Scop., plants in an open field experiment. Beetle density had a negative effect on above-ground plant performance while plant community mainly affected below-ground performance. At high densities of *C. rubiginosa* ($greq 20 larvae/plant) we observed 50% weed mortality in the competitively superior plant community. However, such beetle densities rarely occur in the field. Predation was found as a major factor lowering *C. rubiginosa* populations in the field. The probability of a larva being eaten by a predator lies in the order of magnitude of 10% per day. We recently developed a monoclonal antibody to identify the predator complex of *C. rubiginosa* by serological gut contents analysis of field collected predators. These studies will be complemented by continuous long-term video surveillance of *C. rubiginosa* individuals in the field to analyze predation events. Knowledge of the most important predator species of *C. rubiginosa* may provide us with clues on strategies to lower their impact on agent populations and thus achieve a better weed control status.

Prospects of *Septoria cirsii* as a Biocontrol Agent Against *Cirsium arvense*

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Potential of a mycoherbicide candidate is the sum of such biological properties as good inoculum production on cheap media, narrow host range, aggressiveness, and ability to attack a target weed in early stages of its onthogenesis under different natural conditions. A number of experiments were carried out in order to assess the mycoherbicde potential of the fungus, *Septoria cirsii*, against the weed, *Cirsium arvense*. Seedlings of

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the weed were inoculated with conidial suspension ($5x10^5$ conidia ml^{-1}) of the fungus in controlled conditions: at 22°C with varied dew period (0, 12, 24, 36, 48 h), at 24 h dew period with varied temperatures (16, 20, 24, 28°C), and at 36 h dew period, 22°C on different growth stages of *C. arvense* (3-4, 5-6, 7-8 true leaves). The host range of *S. cirsii* was studied on 37 plant species belonging to 13 families. Seedlings of the plants were inoculated with the pathogen at 24°C, 48 h dew period. Disease rating (0-4) was estimated every seventh day after inoculation. The highest levels of the disease were obtained at 36-48 h dew period, 24-28°C during dew period, on plants in the stage of five to six true leaves. During all experiments low older leaves were more susceptible than young leaves. Using staining techniques, it was detected that the pathogen penetrates leaves through stomata of low surface of leaves only. The optimal conditions for natural infection are possible in June when the weed is in the rosette stage. The host range of *S. cirsii* is restricted within the genus *Cirsium*. Requirements of prolonged dew period and specialization on older leaves decrease chances of *S. cirsii* to become a mycoherbicide. However, *S.cirsii* has narrow host range and high reproductive ability on different media. Hence, future investigations should be directed on developing suitable formulation for the fungus to shorten its dew period requirement.

Evaluating the Efficiency of Agent Prioritisation Tools

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In order to optimise research efforts and increase success rates of agent introductions for biological control of weeds, several protocols suggest ways of prioritising promising candidates (Harris 1973; Goeden 1983; Wapshere 1985). Based on data available prior to release, these screening protocols aim to pinpoint future unsuccessful agents at an early stage of exploration to allow for their exclusion from further ecological investigations. At this time, such screening devices have found little application, which may be partly due to the fact that their efficiency is largely unknown, as it has never been addressed for a statistically relevant number of cases. Using data from literature, this contribution assesses the predictive potential of three agent prioritisation tools in a retrospective way. It draws attention to general statistical particularities of screening devices and discusses shortcomings of current agent prioritisation in relation to the conception of future agent selection tools.

A New Microbiological Concept for Weed Control

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Because many weeds are known to take up nutrients earlier and more rapidly than crops, delay of nutrient release would deprive weeds of nutrients early in the growing season. The concept for utilizing soil aggregation and stabilization to prevent rapid leaching and biodegradation of nutrients is proposed. A saprophytic lignin decomposing basidiomycete is being investigated for its ability to produce water stable soil aggregates. This fungus produces a large quantity of extracellular polysaccharides that bind soil particles into aggregates. These binding agents are insoluble and heat resistant. Water stability of artificial fungal amended aggregates and the degree of biodegradation of the binding agents by native soil microorganisms were determined by wet sieving method. [Data demonstrated that soil aggregates supplemented with a source of carbon (millet or lentil straw) were much more water stable and resisted microbial decomposition longer than when they were prepared with or without fungal homogenates.] These results suggest that organic matter inside aggregates is protected from rapid microbial attack and thus their decomposition is slower. If delay of nutrients can favor crop growth over that of weeds in competitive situations, the ability of saprophytic lignin decomposing fungi to aggregate and stabilize soil particles and therefore incorporate organic matter inside aggregates for slow release might have important implications for weed management.

Weed Phenology: Models and Applications

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Management of weeds is facilitated by information on weed growth and development. However, weed phenology has not been an actively researched topic until recently. Several research groups worldwide now are characterizing weed growth, and some are developing microclimate-based predictive weed models. Although the current modeling emphasis is on seedling and shoot emergence, because of the overwhelming importance of this trait for weed management in crops, there also is keen interest in modeling postemergence growth, including reproductive development. All of these traits may have direct bearing on biological control efforts, in that the development of control agents and the weedy plant must be coordinated in time, at least to some degree. Phenological models based on thermal time and hydro-thermal time provide the requisite information for matching prospective control agents, and releasing known control agents, with the overall development of the targeted weed.

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Broomrapes (*Orobanche* spp.) are Excellent Candidates for Imposing Biological Weed Control Methods

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Attempts to impose biological control on weeds were successful when current control measures were inadequate, when the weed had a native habitat, and when no closely related crops or plants of economic/ecological importance are present within the region of weed infestation. Around the Mediterranean region, at least seven broomrape species attack economically important crops. Estimated crop yield losses due to such infestations range between 10 to 100%. Beneficial utilization of broomrapes or any closely related species were not reported. Broomrape control options continue to be scarce, although reports of successful control by Imidazolinone herbicides are accumulating. Accordingly, we believe that broomrapes should receive greater research efforts to explore possible biological control alternatives. The aggressiveness of these parasites and their parasitic nature allocate broomrape species as ideal targets for biological control approaches. Previously, research efforts focused on utilizing some fungi of the genus *Fusarium* as a potential mycoherbicide. In this review, we will provide a thorough and updated revision for the attempts and constraints that face biological control of broomrapes.

The Response of Purple Loosestrife (*Lythrum salicaria*) to Herbivory by Leaf-Feeding Beetles: Can Gas Exchange Measurements Be Used to Predict Herbivore Impact?

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Negative impacts of herbivores on plant biomass allocation and resource acquisition are well documented and a pre-requisite for successful biological weed control. In contrast, the influence of herbivory on plant physiology (such as net photosynthesis and stomatal conductance) has not been well investigated. Knowledge of how leaf carbon fixation rates are altered in response to herbivory may offer important information regarding the impact of different herbivore species on overall plant performance. This study investigated the influence of the leaf feeding biological control agent *Galerucella calmariensis* (Coleoptera: Chrysomelidae) on gas-exchange in purple loosestrife (*Lythrum salicaria*). Net photosynthetic rate (A), stomatal conductance (g), and internal CO_2 concentration

(Ci) of purple loosestrife were measured at two herbivory levels. Stomatal conductance was reduced when herbivory was low but increased at high herbivory levels. When percentage leaf area removed in damaged leaves was used as continuous variable in regression analysis, we found significant positive increases of A, g and Ci with increasing loss of leaf area. This suggests that purple loosestrife attempts to compensate for increased loss of leaf area by increasing rates of carbon fixation. Compensation was not sufficient to completely tolerate damage, however, since total carbon fixation per leaf was much less in damaged leaves. These results indicate that *G. calmariensis* as a biocontrol agent is likely to have a significant impact on purple loosestrife performance. Thus, measurements of gas exchange provide a more complete picture of plant response to herbivory and may enhance our ability to better predict success or failure of weed control programs.

Epidemic Spread of a Rust Fungus in a Weed Population

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The system management approach was proposed as an alternative for the classical and inundative approach. The approach is based on the reduction of competitiveness of a target weed by stimulating epidemics of a pathogen. Mass release of inoculum (inundative approach) or introduction of exotic organisms (classical approach) are excluded. A small amount of inoculum is artificially introduced at one or more points in the field. The epidemic expands from these points with a predictable constant velocity. The velocity of epidemic spread can be calculated using an analytical model which is based on a gross reproduction factor, a latent period, and a contact distribution. The aim of the research presented was to calculate the velocity of epidemic spread of the rust fungus *Puccinia lagenophorae* on the annual weed *Senecio vulgaris* at various temperatures. To calculate the velocity of epidemic spread at various temperatures, the effect of temperature on latent period and aeciospore production was determined in a laboratory experiment. Latent period decreased and aeciospore production increased by increasing temperature in a range from 10 to 22°C. Equations describing the effect of temperature on both parameters were incorporated in an analytical model to estimate the influence of temperature on velocity of epidemic spread. Velocity of epidemic spread increased by increasing temperature. Temperatures tested in the experiment were realistic for conditions during spring in Switzerland, when populations of *S. vulgaris* start to develop. Natural epidemics of *P. lagenophorae* are seldom observed in populations of *S. vulgaris* before the end of summer, probably caused by a lack of inoculum in spring. The results of the research presented indicate that an artificially induced epidemic could develop under spring conditions. The velocity of epidemic spread could then be predicted using the model presented.

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Weed Biocontrol as an Invasion Process

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Biological control programs develop by stages that correspond roughly to those in an invasion process. To investigate three stages (establishment, growth, and spread of control organisms), we combined field observations, experiments, and mathematical models in a case study of two leaf beetle species that were introduced to control purple loosestrife.

Establishment is hampered by factors that put small populations at risk of extinction, including demographic stochasticity, environmental variability, and Allee effects. Simulation models indicated how we might maximize the probability of successful initial establishment given the inherent tradeoff between the size of each release and the number of releases. In most cases, we are unlikely to have estimates of the required parameters for determining the optimum release size (fecundity, survivorship, variance in year to year survivorship, and Allee effect intensity). We develop simple rules of thumb that can tell us whether releases should be “on the large side” or “on the small side” — a significant improvement over the current use of arbitrary release sizes.

Spread of an established organism into a new area is hindered by factors that affect population growth and movement. A scattered colony model incorporating population growth, random diffusion, and long-distance dispersal facilitated our investigation of the interplay between these factors. From knowledge of the mechanism and rate of spread, we refine the optimization of the number, size, and spatial location of secondary releases made to redistribute control organisms.

These approaches illustrate changes in the use of mathematical theory to guide biological control decisions. To take full advantage of these developments, practitioners should replace subjective assessments of the outcomes of releases with quantitative estimates of model parameters. This will create a more reliable basis for comparison, interpolation, and extrapolation.

How to Favour a Rust Fungus to Reduce a Weed Population

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The system management approach of biological weed control was proposed as an alternative to the well established classical and microbial herbicide approaches. Its aim is to shift the competitive weed-crop relationship in favour of the latter, mainly by stimulating the build-up of a disease epidemic or insect outbreak on the target weed population. Main emphasis is given to native or naturalized antagonists. Plant disease epidemics relate both to the spatial and temporal spread of the disease, and to the increase in disease severity on a given host plant. Constraints on disease development involve: (i) lack of adequate inoculum at the right time, (ii) host resistance, and (iii) environmental deficiencies. We study these factors using the weed-pathogen system *Senecio vulgaris-Puccinia lagenophorae* as a research model. The plant is considered a weed in most parts of the world, and the rust fungus is the potential control organism, originating most probably from Australia and now naturalized in most parts of Europe. Relating disease epidemics to crop-weed interactions at the population level became the major issue of this research project. The weed-pathogen system is first described. Studies on the population biology of both the plant and the antagonist, on the impact of the rust fungus on plant individuals and populations, and on resistance mechanisms will then be presented. Emphasis will be given to experiments to determine the genetic differentiation and plasticity of *S. vulgaris* populations, and their relevance for biological control.

Supercooling Capacity of *Urophora affinis* and *U. quadrifasciata* (Diptera: Tephritidae): Effect of Site, Time of Season, Differences among Plants, and Gall Density

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The supercooling capacities of *Urophora affinis* and *U. quadrifasciata* larvae were evaluated during the 1991-1992 fall/winter time period with respect to differences among sites, fall/winter time periods, differences among plants, and gall densities. Significant differences in supercooling points for *U. affinis* were found among sites in three out of four fall/winter time periods examined and two of four time periods examined for *U. quadrifasciata*. Significant differences in supercooling points for *U. affinis* were found among the four fall/winter time periods in all six sites examined and two of four sites examined for *U. quadrifasciata*. Only two of six sites and three out of 24 cases examined showed significant differences in supercooling points for *U. affinis* among plants. Significant differences in supercooling points for *U. quadrifasciata* among plants were found at two of four sites and four of nine cases examined. No relationship was found between larval supercooling points and gall densities of the respective fly species. Significantly lower supercooling points were found for *U. affinis* compared to *U. quadrifasciata* in three out of four fall\winter time periods examined.

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INVADERS Weed Tracking and Alert System

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The INVADERS Database <http://invader.dbs.umt.edu> is an interactive web site that tracks the historic spread of approximately 900 exotic plants that have invaded the five Pacific northwest states of United States since 1875. Core data include 80,000 distribution records from herbaria, weed identification laboratories, agency surveys, and other various sources. All distribution records have at least county level spatial resolution. Data can be verified as to source, and most have voucher specimens or originate from experienced weed taxonomists. Online outputs include county level distribution maps, time lapse spread maps, spread rate curve graphics, lists of exotics by user specified state or county groupings, and a database engine with live links to other URL's with species specific descriptions. Point location records can be extracted and imported to GIS for climate matching, determination of habitats at risk to invasion, and other forms of spatial analyses. The site also includes examples of how regulatory agencies, weed program, and land managers have been using INVADERS data for risk assessment, environmental impact statements, selection of target weeds, legal noxious designations, and various on-the-ground projects. Taxonomically qualified users can submit new weed findings directly to the INVADERS web site. The new distribution records are immediately available for inclusion in output graphics and lists. Users can request automatic next morning e-mail notification of new reports of specific weeds. http://invader.dbs.umt.edu is a Java driven web site. It was designed to work best with the Microsoft Internet Explorer 4.01 browser, which allows full delivery of INVADERS web site graphics. The INVADERS team hopes to expand geographic coverage from the current five northwestern US states to at least the 50 US states or continental North America, if not the entire western hemisphere.

Climate Matching between the Western United States and Eurasia to Target Foreign Exploration for Natural Enemies of Spotted Knapweed

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Twelve species of insect natural enemies have been introduced to North America for biological control of spotted knapweed (*Centaurea biebersteinii* DC. = *C. maculosa* auct. non Lam). However, only a few of these species have established well in the interior of the continent, suggesting that many of the introduced populations are not well adapted to

the climate. Three climate matching techniques were used to compare areas where spotted knapweed occurs in the western United States with its native range in Eurasia. One approach used 1,292 point location records for spotted knapweed in the western U.S., compiled from several sources, in conjunction with a global 0.5 climate grid. The other two approaches used climate matching functions provided in the CLIMEX system, based on meteorological data for the specific set of locations included with CLIMEX. Analyses focused on the western United States region as a whole, and separately on the core range of spotted knapweed in Montana. There was good agreement among the three approaches used. Areas in the eastern and northern portions of the palearctic range of spotted knapweed appear to be similar in climate to much of the area of spotted knapweed infestation in the western U.S., but particularly to the core range of spotted knapweed in Montana.

Patch Size, Herbivore Dispersal, and Spatial Scale: Landscape Effects Promoting Herbivore Outbreaks

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We examine the effect of patch size on the ability of herbivore populations to reach an outbreak density that results in host-plant defoliation. The intent of this study was to identify whether there were threshold amounts of habitat above which herbivores could outbreak and below which they would not. Theory suggests that when patches are the same size or larger than the typical dispersal distance of the herbivore, populations can build up more readily within those patches. In effect, herbivores would be dispersing within patches. Data were collected from 130 populations of forest tent caterpillar from 1993 through 1999 and the peak density reached at each of those sites was estimated. Around each sample point, the proportion forested vs unforested land was estimated from a classified photo-mosaic; no forest was recorded as zero, and complete forest cover as one. Forest cover estimates were taken from the mosaic at six spatial scales (53m, 106m, 212m, 425m, 850m and 1700m). The relationships between point estimates of tent caterpillar density and forest structure at each of the six spatial scales were examined to identify the [respective] patterns.

At all spatial scales, there were higher densities of tent caterpillar in areas where there was more forest. Among these six spatial scales however, only at the 850 m^2 scale was there evidence of a threshold amount of forest cover above which outbreaks occurred and below which they never occurred, thus producing a distinct 'step' in the relationship between cover and population size. With only one exception, all outbreak populations

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were in areas with more than 72% forest cover (measured at 850m by 850m), whereas no sites with less than 72% forest cover ever reached outbreak density.

The presence of a distinct threshold of forest cover for outbreaks, at the 850 m^2 scale, suggests that habitat patches of this size or greater equal or exceed the distance over which moths typically disperse and result in population build-up. This threshold is obscured at spatial scales of less than 850 m^2 because moths typically disperse beyond the scale at which structure is estimated; they are able to leave this area and still be within the larger single patches. At 1700 m^2 scale, the relationship also disappears because multiple patches are incorporated, increasing the variation of percentage forest cover relative to the occurrence of insect outbreaks. Although the 'typical' dispersal distance of forest tent caterpillar is not known, the scale of about 800 - 1000m seems reasonable.

Although this study was done on a non-weed feeding insect, the observed pattern suggests that there will be a specific threshold patch size of a weed that will facilitate the establishment and outbreak of each biocontrol agent. A similar approach could be used to indirectly estimate dispersal distances of established biocontrol control agents, such as *Aphthona* beetles on leafy spurge. Spread of the root beetles can be estimated by examining the relationship between spurge patch size and beetle population densities at multiple spatial scales. The spatial scale where a threshold response for an outbreak population occurs may provide an indirect estimate of beetle dispersal distances. Taking these patterns one step further, dispersal distance could dictate the optimal patch size into which releases are done in order to create an herbivore outbreak. As a rule of thumb, the pattern observed with forest tent caterpillar suggests that releases of biocontrol agents should be done in large patches of weeds where possible. Small patches, although not supporting outbreak populations, may still, however, serve as stepping stones for dispersal of the biocontrol agent once the insect has established and reached outbreak status.

Seedling Establishment of Invasive and Non-Invasive Populations of Sulphur Cinquefoil, *Potentilla recta* L.

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One of the basic ecological questions in the field of biological invasion is why a species becomes invasive outside its natural distribution area, while it does not show invasive characters in its native range. It has been hypothesized that invasive populations of plant species are better competitors than non-invasive populations, and that this difference may be due to a) the lack of natural enemies in the new range, and/or to b) changes in life-history traits of the plant species which may reflect bottleneck effects during establishment or altered selection pressure compared to the native area. Sulphur cinquefoil is a Eurasian plant species which has invaded North America some 100 years ago. Field studies in the native area have shown that seedling establishment is a critical factor in population dynamics which is very variable between the years. On the other hand, mortality rates of plants older than six months were always very low. Hence, if the increased invasiveness in North America is based on changes in the life history of *P. recta*, these changes may be expected to be most prominent during the early life stages. In order to address this question, 17 populations from southeastern Asia, Europe, and North America were compared for early seedling growth.

Modelling the Population Interactions Between *Echium plantagineum* and the Crown Weevil *Mogulones larvatus*

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Population models have been used to understand the ecological mechanisms involved in a variety of biological control systems. Host-parasitoid models are commonly used in insect biological control systems and have achieved levels of complexity, which have provided detailed evidence of some subtle stabilising mechanisms in the interactions between populations of predator and prey. Such models in weed biological control systems have, in general, been quite simple by comparison. In most cases the models used have been based on the dynamics of the target weeds incorporating the impact of the biological control agent as a constant or stochastic variable within a range defined from field observation. Such modelled systems are either unregulated (matrix models) or regulated by density dependence only in the target. We have been constructing and exploring a suite of models for the interactions between a root-crown boring weevil (*Mogulones larvatus*) introduced into Australia and locally wiping out populations of the annual pasture weed (*Echium plantagineum*). A simple cohort-based model, like others in the past, incorporates weevils simply as a constant impact change in survival and/or fecundity of the weed. The results are over-optimistic about the impact of the weevil on the populations of its host. A more complex individual-based model incorporates: a) a seedbank, b) variation in weevil impact, and c) integrates the dynamics associated with how the agent population responds to changing densities of its host. Density dependence is present therefore in both agent and weed components of this model. Outputs from this model highlight the following conclusions. Firstly, including a seedbank in the model increased weed population stability in the face of impact from the weevil. Secondly, including variation in weevil impact amongst plant individuals greatly decreased the effects of the weevils at the population level and this critically depended on the form that this variation took (i.e poisson or negative binomial). Finally, including density dependence in both the weed and the weevil populations in the model increased the stability of the interactions between them. This study shows that it is valuable to move beyond simple population models for understanding the interactions between weeds and their biological control agents, but it is vital in this process that field data on agent impact assesses variation as well as the mean of the impact and attack levels they cause. (Paper submitted to Journal of Applied Ecology).

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Comparing Weed Vigour in Indigenous and Non-Indigenous Environments

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An often observed phenomenon is that invasive plants appear to grow more vigorously in their introduced range compared to conspecifics growing in their native range. Indeed, such increases in the vigour of weedy species are a central premise of biological weed control: freedom from natural enemies facilitates the 'uncontrolled' growth and population expansion of introduced species. Implicit in this scenario is the assumption that plastic phenotypic responses to changes in key environmental variables are responsible for the increased vigour, although this has been investigated experimentally only rarely. We present data from an experiment aimed at testing the hypothesis that the increased vigour of invasive plants results from a plastic response to a relatively benign environment, free of co-evolved natural enemies. Four species native to Britain and continental Europe but non-indigenous invaders of Australia and New Zealand were grown in a common experimental garden from seeds sampled in both the indigenous and non-indigenous distributions of the species. If the apparent vigour of non-indigenous samples was a plastic response to a novel environment, we expected that the growth of these samples would not differ from their indigenous conspecifics when grown in the same environment. Preliminary analyses suggest that the growth of indigenous and non-indigenous samples does not, in general, differ significantly, thereby supporting the 'benign environment' hypothesis. We discuss the results of this experiment and its implications for biological weed control.