

Using parasite databases to identify potential nontarget hosts of biological control organisms

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Abstract Biological control organisms undergo host range studies to identify potential nontarget hosts. The selection criterion for host range studies is primarily based on the target host's taxonomy. Thus, inaccuracies in host taxonomy may compromise the validity of host range studies. We propose that biocontrol researchers use internet-available databases to identify potential nontarget organisms that share parasites (biotrophic pathogens and pests) with target hosts, and add these organisms to host range tests. Marijuana (*Cannabis sativa*) has been targeted for biocontrol, and host range studies have focused upon the Moraceae. A list of *Cannabis* parasites was compared with database lists of pests and pathogens for hosts in the order Urticales. The databases revealed seven *Cannabis* biotrophic parasites that were shared by hosts in the family Urticaceae, one biotroph shared by a host in the Celtidaceae, and no biotrophs shared by hosts in the Moraceae, Cercropiaceae, or Ulmaceae. These results suggest that biocontrol host range studies of *Cannabis* parasites should focus on the Urticaceae and Celtidaceae as well as the Moraceae. These results also suggest that taxonomic relationships within the Urticales be reassessed.

Keywords biological control; weeds; *Cannabis sativa*; Urticaceae; Celtidaceae; Moraceae; Fahrenheit's Rule; coevolution

INTRODUCTION

In 1874, agriculturists imported the 11-spotted ladybird (*Coccinella undecimpunctata* L.) from England to Otago, South Island, New Zealand, which was one of the first purposeful introductions of an organism for biological control (Thomas 1989). Since then, New Zealand has become a world leader in the regulation, research, and implementation of biological control technologies for agricultural and natural habitats (Waage 1997). Biological control (biocontrol) generally enjoys strong public approval, engendering a "green" social message, with its emphasis on environmental sustainability, the deployment of natural processes, and non-use of agrichemicals.

The New Zealand biota has a high degree of endemism (typical of an isolated island ecology), which is particularly susceptible to alien weeds. The country has assimilated nearly 20 000 non-indigenous plant species, and about 250 are considered serious weed pests (Fowler et al. 2000). Weeds invade agricultural systems and natural ecosystems and can cause major modifications to indigenous biodiversity and ecosystem function (Williams & West 2000). To combat invasive weeds, New Zealand biocontrol researchers have imported at least 35 alien organisms to serve as natural enemies (Fowler et al. 2000). "Success stories" include the importation of the leaf beetle *Chrysolina hyperici* (Forster) to control St John's wort (*Hypericum perforatum* L.), and the flea beetle *Longitarsus jacobaeae* Waterhouse to control ragwort (*Senecio jacobaea* L.). Ongoing work centres on gorse (*Ulex europaeus* L.), Scotch broom (*Cytisus scoparius* (L.) Link), and Californian thistle (*Cirsium arvense* (L.) Scopoli). Recent research has focused on fungi pathogenic to weeds (Fröhlich et al. 1999, 2000). The investigation of fungi to control New Zealand weeds began in 1910, for control of *C. arvense* (Popay 1997). Fungal biocontrol organisms may occupy intricate niches, acting as tertiary consumers in New Zealand ecosystems (Nicholson 1972). Notwithstanding popular support, the strategy of importing alien biocontrol agents to control alien pests has come

under increased scrutiny (Howarth 1991). Once a self-perpetuating biocontrol agent has been released, it may be impossible to recall or control. Despite host-range testing to identify potential nontarget hosts, biocontrol organisms may spread, switch, or expand their range ("drift") from their intended targets to other organisms (Follett et al. 2000). In New Zealand, no introduced fungal biocontrol organisms are known to have drifted from target hosts, but insects have made unpredicted attacks upon nontarget hosts. The cinnabar moth, *Tyria jacobaeae* (L.), was released for biocontrol of ragwort in 1929, but spread to native species of *Senecio* and *Cineraria*, and *Sonchus oleraceus* L. (Helson 1974). *Chrysolina hyperici* introduced for control of St John's wort drifted to an ornamental, *Hypericum androsaemum* Tutsan (Fowler et al. 2000). The seed beetle *Bruchidius villosus* (F.), a biocontrol agent of *Cytisus scoparius*, spread to tree lucerne, *Chamaecytisus palmensis* (Christ) Hutch. (Fowler et al. 2000). The fungus *Puccinia xanthii* Schweinitz, a biocontrol agent for *Xanthium* weeds in Australia, subsequently attacked sunflower (*Helianthus annuus* L.) and *Calendula officinalis* L. in the field (Auld 1991).

Most of these errant biocontrol organisms were released before the advent of rigorous host range testing, or they were tested by criteria hopelessly inadequate by current standards. In the case of *P. xanthii*, it should be noted that this fungus arrived in Australia without official help or sanction, and had not been subjected to host range testing prior to its unexpected arrival (Auld 1991).

Today, all potential biological control agents are subjected to host range testing to identify potential nontarget hosts. The plants chosen for host range testing are selected by internationally recognised criteria, known as the centrifugal method of Wapshere (1974): the first plants to be tested are taxonomically related species in the same genus as the target plant. Next tested are plants in the same family, with an emphasis on economically and environmentally important plants, especially threatened and endangered species. Next tested are species in the same taxonomic order if they share morphological or phytochemical similarities with the target host, or if they share the same habitat. Lastly, any host on which the biological control agent (or its close relatives) has been previously reported should also be tested.

These criteria caused Syrett et al. (1995) to reject a Scotch broom control agent, the weevil *Pirapion immune* Kirby, because of its risk to kowhai, *Sophora microphylla* Ait. Similarly, Barratt et al.

(1997) identified nearly a dozen nontarget hosts of the biocontrol parasitoids *Microctonus aethiopoidea* Loan and *Microctonus hyperodae* Loan, ironically including another biocontrol agent, *Rhinocyllus conicus* Fröhlich. *Dictyonota strichnocera* Fieber, a promising control of *Ulex europaeus*, was rejected because it attacked *Lupinus arboreus* Sims and *Chamaecytisus palmensis* (Christ) Hutch. (Fowler et al. 2000). The fungus *Sclerotinia sclerotiorum* effectively controlled *Cirsium arvense* and other pasture weeds, but its wide host range has hampered its development (Bourdôt et al. 1995).

Despite these successes in identifying potential problems, the Wapshere protocol has its shortcomings. Funasaki et al. (1988) estimated that 27% of biocontrol organisms introduced into Hawai'i have spread to nontarget species. Indeed, Howarth (1991) described nearly 100 cases where errant biocontrol organisms have driven nontarget hosts to extinction, mostly in island ecosystems. The Wapshere protocol, with its emphasis on traditional taxonomy of host plants, may break down if the taxonomy of the host plant is not well characterised (Evans et al. 2001). Traditional plant taxonomy relies primarily on morphological characters to estimate phylogenetic relationships. New molecular methods have improved the accuracy of plant systematics and demonstrated errors in morphology-based taxonomy (Ueda et al. 1997). The use of molecular methods would help prevent "embarrassing and costly mistakes" made in the past (Evans et al. 2001). Unfortunately, molecular methods are costly and such taxonomic advances are slow in forthcoming.

A novel and less costly approach to taxonomy involves the study of host plant-parasite relationships. Many obligate parasites evolve with their plant hosts, eventually becoming dependent on single species. Thus, parasite phylogeny mirrors host phylogeny; this has become known as Fahrenholtz's Rule (Hoberg et al. 1997). Some fungi show high degrees of host specificity; they have been considered highly specialised "plant taxonomists" (Hijwegen 1979). Fungal specificity may be restricted to one host species, to several host species in one family, or to several families in one order (Parlevliet 1986). Klebahn (1904) may have been the first to use a fungus for angiosperm taxonomy, when he established the identity of a willow by its susceptibility to *Melampsora ribesii-purpurea* Klebahn. This approach to angiosperm systematics has long been championed by Savile (1954, 1979). Savile, however, asserted that the various fungi are not equally discriminate taxonomists. He considered

obligate pests and pathogens (biotrophic parasites) to be highly host-specific, whereas facultative pests and pathogens (necrotrophic organisms) were considered nonspecific.

We propose adding Fahrenheit's Rule to the centrifugal method of Wapshere, to assay plant genera that share biotrophic pests or pathogens with the target host. The advent of computerised host-pathogen and host-pest databases makes this relatively easy to implement.

We tested this approach on marijuana (*Cannabis sativa* L.), a plant targeted for biological control since the 1970s (McPartland & West 1999). Currently, fungal pathogens are the focus of biological control evaluations. Host range tests of *Cannabis* fungal pathogens have centred on the family Moraceae (Taber & Taber 1983; McCain & Noviello 1985; Tiourebaev 1999), because nearly half of modern taxonomists follow Engler & Prantl (1889) and place *Cannabis* in the Moraceae (e.g., Greuter et al. 1993). Other taxonomists classify *Cannabis* in the Cannabaceae (e.g., Cronquist 1981; Thorne 1992). The Cannabaceae is a small family consisting of *Cannabis* and its sister genus *Humulus*.

In a previous study we identified four invertebrate specialist pests of *Cannabis* that also infested other hosts in Urticales (McPartland et al. 2000). In this study we sought to identify, from on-line databases, fungal pathogens of *Cannabis* that also attack other plants in Urticales.

METHODS

A catalogue of all known *Cannabis* fungal pathogens was compiled, subtracting misidentifications and synonyms (McPartland et al. 2000). Next we compiled lists of fungal pathogens for every genus in the Urticales (*sensu* Cronquist 1981), including members of the families Moraceae, Urticaceae, Ulmaceae, Celtidaceae, Cecropiaceae, and Cannabaceae. The lists of fungal pathogens were collated from two databases: the specimen records of the US National Fungus Collections (herbarium BPI), and the Host-Pathogen database derived from the John Stevenson Mycological Library at the Systemic Botany and Mycology Laboratory of the United States Department of Agriculture (USDA). Combining these databases provided a representative sample. BPI is the largest fungal herbarium the world, holding over 1.1 million specimens (Palm 1999). The Host-Pathogen database includes over 340 000 reports of over 62 000 fungal species on

14 500 plant hosts throughout the world (Farr & Rossman 1999). Both databases are accessible on line (<http://nt.ars-grin.gov>), and can be searched by host name or fungus name.

The list of *Cannabis* pathogens and lists of Urticales pathogens were then compared. *Cannabis* fungi shared by other plants in the Urticales were categorised as either biotrophic (obligate parasites) or necrotrophic (facultative pathogens). Holomorphic fungi (species that produce teleomorphic and anamorphic stages in their life cycles) were cited by the stage in which they were listed in the databases; if both teleomorphs and anamorphs were listed in the databases, only the teleomorph was cited. Herbarium specimens of shared biotrophs were personally examined to ascertain the identity of both fungi and hosts. This was not done with the necrotrophs, because they would have required loans from dozens of herbaria. SYSTAT 5.2 (Evanston, Illinois) was used to compute Pearson correlations and Bartlett Chi-square analyses.

RESULTS

Both databases proved to be rich sources of fungal names (Table 1). The BPI specimen database contained 7631 records associated with hosts in the Urticales (mean 54.9 specimens per host genus). The Host-Pathogen database contained 7393 citations (mean 53.2 citations per host genus). The number of specimens and citations per host genus correlated with the economic value of the host genus; valuable genera included *Ulmus* (2872 specimens and 1639 citations), *Ficus* (1183 specimens and 2306 citations), *Morus* (870 specimens and 945 citations), and *Urtica* (792 specimens and 347 citations). Genera with little economic value often did not have any records in either database.

Biotrophic fungi

Cannabis shared two biotrophic fungi (obligate pathogens) with its sister genus *Humulus*: *Pseudoperonospora humuli* (Miyabe & Takahashi) G.W. Wilson and *Sphaerotheca macularis* (Wallroth:Fries) Lind (see Table 1). *Cannabis* shared three biotrophic fungi with other hosts in the Urticaceae: *P. humuli* and *Leveillula taurica* (Léveillé) with *Urtica* species, and *S. macularis* and *L. taurica* with *Parietaria* species. *Cannabis* shared one biotrophic fungus with a member of the Celtidaceae: *P. humuli* with a *Celtis* species.

Cannabis shared no biotrophic fungi with plants in the Moraceae, Cecropiaceae, or Ulmaceae.

Necrotrophic fungi

Cannabis shared 12 necrotrophic fungi with *Humulus*: *Botrytis cinerea* Persoon: Fries, *Fusarium oxysporum* Schlechtendahl: Fries, *Fusarium roseum* Link emended Snyder et al., *Gibberella cyanogena* (Desmazières) Saccardo (= *Fusarium sulphureum* Schlechtendahl), *Gibberella pulicaris* (Fries: Fries) Saccardo (= *Fusarium sambucinum* Fuckel), *Leptosphaeria acuta* (Hoffman: Fries) P. Karsten, *Phoma exigua* Desmazieres, *Phoma herbarum* Westendorp, *Pythium ultimum* Trow, *Sclerotinia sclerotiorum* (Libert) deBary, *Verticillium albo-atrum* Reinke & Berthier, and *Verticillium dahliae* Klebahn. Indeed, 52% of *Humulus* pathogens also infested *Cannabis*.

Cannabis shared 19 necrotrophic fungi with urticaceous genera: *B. cinerea*, *F. oxysporum*, *L. acuta*, *P. exigua*, and *S. sclerotiorum*, plus *Alternaria alternata* (Fries: Fries) Keissler, *Athelia epiphylla* Persoon, *Curvularia lunata* (Wakker) Boedijn, *Diaporthe artii* (Lasch) Nitschke, *Hymenoscyphus herbarum* (Persoon: Fries) Dennis, *Myrothecium roridum* Tode: Fries, *Periconia byssoides* Persoon, *Phoma herbarum* (Persoon: Fries) Rabenhorst, *Phymatotrichopsis omnivora* (Duggar) Hennebert, *Pythium aphanidermatum* (Edson) Fitzpatrick, *Sclerotium rolfsii* Saccardo, *Thanatephorus cucumeris* (Frank) Donk (= *Rhizoctonia solani* Kühn), *Torula herbarium* (Persoon: Fries) Link, and *Trichoderma viride* Persoon. *Cannabis* shared 23 necrotrophic fungi with genera in the Moraceae: *A. alternata*, *A. epiphylla*, *B. cinerea*, *F. oxysporum*, *F. roseum*, *G.*

cyanogena, *G. pulicaris*, *M. roridum*, *P. byssoides*, *P. omnivora*, *P. ultimum*, *S. sclerotiorum*, *S. rolfsii*, *T. cucumeris*, plus *Botryosphaeria obtusa* (Schwein.) Shoemaker, *Botryosphaeria rhodina* (Berk. & Curtis in Curtis apud Cooke) (= *Lasiodiplodia theobromae* (Pat.) Grif. & Maub.), *Cladosporium herbarum* (Persoon) Link, *Epicoccum pururascens* Ehrenberg: Schlecht., *Gibberella baccata* (Wallroth) Saccardo (= *Fusarium lateritium* Nees: Fries), *Nectria haematococca* Berk. & Broome (= *Fusarium solani* (Martius) Saccardo), *Pithomyces chartarum* (Berk. & Curtis apud Berk.) M.B. Ellis, *Rosellinia necatrix* Prillieux, and *Trichothecium roseum* (Persoon: Fries) Link. *Cannabis* shared four necrotrophic fungi with plants in the Cecropiaceae: *B. rhodina*, *G. baccata*, *G. cyanogena*, and *N. haematococca*. *Cannabis* shared six necrotrophic fungi with plants in the Celtidaceae: *B. obtusa*, *G. baccata*, *P. omnivora*, *R. solani*, *S. sclerotiorum*, and *T. roseum*. *Cannabis* shared nine necrotrophic fungi with plants in the Ulmaceae: *B. cinerea*, *B. obtusa*, *C. herbarum*, *F. oxysporum*, *P. omnivora*, *R. solani*, *T. roseum*, *V. albo-atrum*, and *V. dahliae*.

The largest family, the Moraceae (67 genera), shared more necrotrophic fungi with *Cannabis* than did the other plant families (Table 1). The number of shared necrotrophs correlated with the size of the plant family (number of genera, $r = 0.93$, $P < 0.007$). Thus, the number of shared necrotrophic fungi appeared to be a function of family size rather than host relatedness. This differed from the data for the biotrophic fungi, where the size of the plant family was not a predictor of the number of biotrophs shared

Table 1 Characteristics of six families examined in this study.

Character set	Cannabaceae	Moraceae	Urticaceae	Cecropiaceae	Celtidaceae	Ulmaceae
Number of biotrophic fungi in common with <i>Cannabis</i>	2*	0	3	0	1	0
Number of necrotrophic fungi in common with <i>Cannabis</i>	12*	23	19	4	7	9
Number of genera in each family	2	67	48	6	12	4
Number of species in each family	5	1607	983	244	281	51
Number of records per family in BPI specimen database	369	2465	980	143	796	2878
Number of records per family in Fungus-Host database	367	3808	710	75	784	1652

*Biotrophic and necrotrophic fungal pathogens of *Humulus* species in common with *Cannabis*.

with *Cannabis* ($r = 0.12$, $P > 0.8$). There were no significant correlations between the number of shared pathogens and the number of BPI specimens, or the number of Host-Pathogen citations.

DISCUSSION

Taken together with previous data concerning invertebrate pests (McPartland et al. 2000), these results suggest that *Cannabis* shares no biotrophic pests and pathogens with moraceaceous hosts, but shares the biotrophic pathogen *P. humuli* with a host in the Celtidaceae, and shares seven biotrophic organisms with urticaceous hosts: the fungi *P. humuli*, *S. macularis*, and *L. taurica*, and the narrowly oligophagous hops cyst nematode (*Heterodera humuli* Felipjev), hops aphid (*Phorodon humuli* Pass.), and leafminer flies *Agromyza reptans* Fallén and *Melanogromyza urticivora* Spencer.

Previous host range studies of *Cannabis* fungal pathogens, based on traditional plant taxonomy-based selection criteria, focused on plants in the Moraceae (Taber & Taber 1983; McCain & Noviello 1985; Tiourebaev 1999). Our results suggest that these researchers should have been testing hosts in the Urticaceae and the Celtidaceae, because these hosts share fungal pathogens with *Cannabis*. These findings support our proposal to add Fahrenholtz's Rule to the centrifugal method of Wapshere.

We implemented Fahrenholtz's Rule by using databases to identify potential nontarget organisms that share parasites with target hosts. This procedure has one major shortcoming: the accuracy of information within the databases. Some researchers (including one anonymous reviewer of this paper) have reported mistakes to be endemic in most databases, a direct result of having nonspecialist people entering specialist information. These mistakes often become perpetrated because of inadequate quality controls. In the current study, however, database information was confirmed by personal examination of herbarium voucher specimens, asserting the identity of both fungi and hosts. The databases concerning biotrophic fungi proved to be 100% accurate. That is not to say mistakes do not appear in the literature; a previous study of herbarium specimens (McPartland 1994) demonstrated misidentifications of several necrotrophic fungi reported on *Cannabis*, or the correct fungi were cited on the wrong host plant. Results obtained from computerised databases should be confirmed by inspection of voucher specimens.

The assertion by Savile (1979) that necrotrophic fungi make poor "taxonomists" was corroborated by our results. The number of necrotrophic fungi that *Cannabis* shared with hosts in other families was simply a factor of host family size. This is a corollary of Eichler's Rule: host groups that are large and diverse will harbour a greater number of parasites than smaller, less diverse host groups (Hoberg et al. 1997). Biotrophic fungi, in contrast, showed no such correlation with family size.

Interpreting our results with Fahrenholtz's Rule suggests that researchers need to re-evaluate taxonomic relationships within the Urticales. Shared biotrophic fungi indicate that *Cannabis* and *Humulus* are phylogenetically related, with closer affinities to the Urticaceae and the Celtidaceae than to the Moraceae, Cecropiaceae, or Ulmaceae. These results agree, in part, with a phylogenetic analysis of the Urticales based on morphological characters in which Judd et al. (1994) concluded that the Cannabaceae shares as much in common with the Urticaceae as with the Moraceae (a departure from contemporary taxonomic opinion), and that the Celtidaceae is closer to the Cannabaceae-Urticaceae-Moraceae complex than to the Ulmaceae (sens. str.). Similarly, in a molecular phylogeny based on *rbcL* nucleotide sequences, Ueda et al. (1997) linked *Celtis* with the Urticaceae. Sytsma et al. (2002) allied the Celtidaceae and the Cannabaceae, based on three molecular character sets, *rbcL*, *trnL-F*, and *ndhF* sequences.

Using Fahrenholtz's Rule to make taxonomic judgements regarding host taxa is controversial (Parlevliet 1986). The use of parasites in taxonomy fell into disfavour after Hennig (1966) challenged the validity of Fahrenholtz's Rule. Hennig suggested that host-parasite specificity reflected *ecological, geographical, or phytochemical* associations, independent of *phylogenetic* relationships. Recently, however, Fahrenholtz's Rule has been re-accepted, thanks to new methodologies such as parsimony analysis and component or reconciliation methods (Hoberg et al. 1997). Notably, New Zealand research led this renewed interest in host-parasite relationships. Humphries et al. (1986) studied *Nothofagus* plant hosts and their *Cyttaria* fungal pathogens. They compared cladograms based on Fahrenholtz's Rule with cladograms based on morphological characters and they found significant matches between the cladograms. Farrell & Mitter (1990) used morphological criteria to suggest cospeciation between *Phyllobrotica* leaf beetles and their *Scutellaria* host plants; subsequently these researchers combined

morphological data with allozyme data to show cladogram correspondence between *Tetraopes* beetles and *Asclepias* milkweed species (Farrell & Mitter 1998). Six & Paine (1999) used a panel of allozymes to detect parallel cladogenesis between *Dendroctonus* bark beetles and their common symbiotic fungi (*Ceratocystiopsis*, *Leptographium*, and *Ophiostoma* species). Hinkle et al. (1994) used morphological and gene sequence data to show congruent cladogenesis between leaf-cutting ants and antine fungi. DNA sequencing studies have convincingly documented coevolution between gophers (e.g., *Geomys* and *Orthogeomys*) and their parasitic lice (Page 1996), and between *Nesoydne* planthoppers and their plant hosts (Roderick 1997).

It is worth discussing that Fahrenholz's Rule is not necessarily synonymous with "coevolution". Fahrenholz's Rule describes a parasite phylogenetically tracking its evolving host. The process involves biological specialisation, and is one source of parallel cladogenesis, a form of cospeciation. Coevolution in the sense of Ehrlich & Raven (1964) necessitates *reciprocal* evolutionary change in interacting organisms *in response to each other*, or a progressive, mutual evolution of non-mixing gene pools, leading to interdependence (Pirozynski & Hawksworth 1988; McPartland & Guy 2003). Coevolution implies host specialisation, but the reverse may not be true (Parlevliet 1986). For example, in toxin-producing fungi such as *Fusarium oxysporum* Schlechtendahl: Fries, host specialisation depends on the expression of specific toxins. A toxin point mutation may cause *F. oxysporum* to "jump" to distantly related hosts, hypothetically from *Cannabis* to cotton (McPartland & West 1999). Thus, toxin specialisation has little to do with coevolution. Similarly, host specialisation may imply mutualism, but the reverse is not always true. The best known *Cannabis* mutualist is *Pyrrhocoris apterus* L., a seed-dispersing beetle (Vavilov 1926), but *P. apterus* is quite polyphagous (McPartland et al. 2000). Similarly, the mutualistic mycorrhizal fungus *Glomus mosseae* (Nic. & Gerd.) Gerd. & Trappe associates with *Cannabis*, but the fungus exhibits a broad host range (McPartland & Cubeta 1997).

Plant pathologists and mycologists recognised the concept of coevolution long before the term was coined by Ehrlich & Raven (1964). Coevolutionary concepts are implicit in the work by Klebahn (1904). Savile's "coevolutionary" publications began in 1954, although he studied cospeciation and not coevolution sens. str. Flor's coevolutionary "gene-for-gene" hypothesis was formulated in 1956; it has

been experimentally demonstrated in over 40 fungi and their plant hosts (reviewed by Thompson & Burdon 1992). Knowledge of fungus-host relationships has periodically propelled plant pathologists and mycologists into the field of angiosperm systematics. Persoon (1807) was the first to synonymise *Cannabis indica* under *Cannabis sativa*, a taxonomic debate that continues today (McPartland 1992). Vavilov earned his PhD in plant pathology, used fungi as tools in angiosperm taxonomy (Vavilov 1915), and made numerous contributions to *Cannabis* systematics (e.g., Vavilov 1926).

The ultimate challenge of *Cannabis* biocontrol researchers is to identify organisms that selectively infest drug biotypes and not fibre biotypes. New Zealand is one of approximately 20 countries that permits the cultivation of high-fibre, low-drug biotypes of *Cannabis*. Hemp is resistant to many New Zealand pests of potatoes, maize, peas, and grains, so it could serve as a rotation crop with these pest-susceptible plants (McPartland & Glass 2001). Hemp is susceptible, however, to all the biocontrol organisms currently recommended for deployment against marijuana (McPartland & West 1999). The release of these biocontrols would endanger hemp cultivation. We recommend that further searches be done for more specific agents, and that new host range studies include plants from the Urticaceae and the Celtidaceae as well as the Moraceae.

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