

Fungi Associated with *Eichhornia crassipes* (Water Hyacinth) in the Upper Amazon Basin and Prospects for Their Use in Biological Control

H.C. Evans and R.H. Reeder*

Abstract

Surveys were undertaken in 1998 and 1999 in the upper Amazon basin of Ecuador and Peru to collect and catalogue the mycobiota associated with water hyacinth in the river and lake systems. The results indicate that three groups of fungi, which occupy distinct niches on the plant, can be delimited: biotrophic fungi, colonising green leaf tissue, often without significant visible symptoms (e.g. *Didymella* and *Mycosphaerella*); necrotrophic fungi, causing prominent leaf lesions (e.g. *Leptosphaeria*, *Colletotrichum*, *Myrothecium*, *Phaeoseptoria* and *Stagonospora*); and fungi associated with and isolated from petioles previously invaded by coevolved insect natural enemies, such as *Taosa* and *Thrypticus* spp. (e.g. *Acremonium*, *Cephalosporiospsis*, *Cylindrocarpon*, *Cylindrocladium* and *Stauronema*). Some of these represent new host records, as well as undescribed taxa. A re-analysis of the mycobiota associated with water hyacinth worldwide reveals that most of the records originate from the USA and the Palaeotropics, where the plant is a major invasive species, and where, as a consequence, most research on its control has been concentrated. Fungal genera such as *Alternaria* and *Cercospora*, which traditionally have been favoured as biocontrol agents, seem to be absent or rare on *E. crassipes* in the Upper Amazon.

Introduction

EICHHORNIA crassipes (Mart.) Solms is native to the Neotropics but its precise centre of origin remains speculative. Based on style morphology, it has been suggested that the area of greatest genetic diversity lies in Amazonia (Barrett and Forno 1982); with natural spread from these to other regions of the South American continent, and human-vectored introductions into the Caribbean and Central and North America. Paradoxically, a search of the literature and unpublished herbarium records reveals that few fungi have been reported on water hyacinth in South America. For example, a detailed survey of the fungal pathogens

associated with this host in the Brazilian State of Rio de Janeiro yielded only *Cercospora piaropi*, compared with four species recorded on the closely related *Eichhornia azurea* (Swartz) Kunth. (Barreto and Evans 1996). The same authors also compiled the worldwide records of the mycobiota collected on, or isolated from, *E. crassipes*. A reanalysis of this amended list (Table 1) shows that of the 60 potential pathogens reported, 54 are from countries or regions where water hyacinth is an undisputed alien invasive species, 36 of which are exclusively Old World. Of the New World records, 18 are from the USA, 3 are from the Caribbean or Central America, while only 2 have a South American (ex Brazil) origin.

* CABI Bioscience, Silwood Park, Ascot, Berks. SL5 7TA, UK. Email: h.evans@cabi.org

Table 1. Mycobiota recorded on *Eichhornia crassipes*, worldwide (amended from Barreto and Evans 1996)

| Fungi | Distribution |
|---|--|
| Ascomycotina and Deuteromycotina | |
| <i>Acronium crotocigenum</i> (Schol-Schwarz) W. Gams | Australia (IMI 288071 ^a) |
| <i>Acronium implicatum</i> (Gilman & Abbott) W. Gams | Australia (IMI 271067) |
| <i>Acronium sclerotigenum</i> (F. & R. Moreau ex Valenta) W. Gams | Sudan (IMI 284343) |
| <i>Acronium strictum</i> W. Gams | Australia (IMI 288318, 288319) |
| <i>Acronium zonatum</i> (Sawada) W. Gams | Australia, India, Pakistan, Panama, USA, Sudan |
| <i>Alternaria alternata</i> (Fr.) Keissler | Egypt |
| <i>Alternaria eichhorniae</i> Nag Raj & Ponnappa | Egypt, India, Thailand, USA, Kenya, Ghana, South Africa, Zimbabwe |
| <i>Alternaria tenuissima</i> (Nees ex Fr.) Wiltshire | Hong Kong |
| <i>Bipolaris urochloae</i> (Putterill) Shoemaker | Egypt (IMI 324728) |
| <i>Bipolaris</i> sp. | USA, Brazil |
| <i>Blakeslea trispora</i> Thaxter | Thailand |
| <i>Cephalotrichum</i> sp. | USA |
| <i>Cercospora piaropi</i> Tharp | India, Sri Lanka, USA |
| <i>Cercospora rodmanii</i> Conway | USA–India (IMI 329783), Nigeria (IMI 329211) |
| <i>Chaetomella</i> sp. | Malaysia |
| <i>Cladosporium oxysporum</i> Berk. & Curt. | Hong Kong–Nigeria (IMI 333543) |
| <i>Cochliobolus bicolor</i> Paul & Parbery | India (IMI 138935) |
| <i>Cochliobolus lunatus</i> (= <i>Curvularia lunata</i>) Nelson & Haasis | Egypt (IMI 318639), India (IMI 162522, 242961), Sri Lanka (IMI 264391), Sudan (IMI 263783) |
| <i>Coleophoma</i> sp. | Sudan (IMI 284336) |
| <i>Curvularia affinis</i> Boedijn | USA |
| <i>Curvularia clavata</i> B.L. Jain | India (IMI 148984) |
| <i>Curvularia penniseti</i> (M. Mitra) Boedijn | USA |
| <i>Cylindrocladium scoparium</i> var. <i>brasiliense</i> Batista | India |
| <i>Didymella exigua</i> (Niessl) Saccardo | Trinidad, USA |
| <i>Drechslera spicifera</i> (Bainier) V. Arx | Sudan |
| <i>Exserohilum prolatum</i> K.J. Leonard & E.G. Suggs | USA |
| <i>Fusarium acuminatus</i> Ellis & Everhart | Australia (IMI 266133) |
| <i>Fusarium equiseti</i> (Corda) Saccardo | India–Sudan (IMI 284344) |
| <i>Fusarium graminearum</i> Schwabe | Australia (IMI 266133) |
| <i>Fusarium moniliforme</i> Sheldon | Sudan (IMI 284342) |
| <i>Fusarium oxysporum</i> Schlechtendal | Australia (IMI 288317) |
| <i>Fusarium solani</i> (Martin) Saccardo | Australia (IMI 270062) |
| <i>Fusarium sulphureum</i> Schlechtendal | India (IMI 297053) |

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Table 1. (Cont'd) Mycobiota recorded on *Eichhornia crassipes*, worldwide (amended from Barreto and Evans 1996)

| Fungi | Distribution |
|--|--|
| <i>Fusidium</i> sp. | South Africa (IMI 318345) |
| <i>Gliocladium roseum</i> Bainier | Australia (IMI 278745) |
| <i>Glomerella cingulata</i> (Stonem) Spauld & Schrenk | Sri Lanka (IMI 264392) |
| <i>Helminthosporium</i> sp. | Malaysia |
| <i>Leptosphaeria eichhorniae</i> Gonzales Fragoso & Ciferri | Dominican Rep., Panama |
| <i>Leptosphaerulina</i> sp. | USA |
| <i>Memmoniella subsimplex</i> (Cooke) Deighton | USA |
| <i>Monosporium eichhorniae</i> Sawada | Taiwan |
| <i>Mycosphaerella tassiana</i> (De Notaris) Johanson | USA |
| <i>Myrothecium roridum</i> Tode ex Fr. | India, Philippines Thailand–Burma (IMI 79771), Malaysia (IMI 277583) |
| <i>Pestalotiopsis adusta</i> (Ellis & Everhard) Steyaert | Taiwan–Hong Kong (IMI 119544) |
| <i>Pestalotiopsis palmarum</i> (Cooke) Steyaert | India (IMI 148983) |
| <i>Phoma sorghina</i> (Saccardo) Boerema, <i>et al.</i> | Sudan–Australia (IMI 288313, 288311, 288312, 288315, 333325) |
| <i>Phoma</i> sp. | USA |
| <i>Phyllosticta</i> sp. | Nigeria (IMI 327627, 327628) |
| <i>Spegazzinia tessarthra</i> (Berk. & Curt.) Saccardo | Sudan 284335 |
| <i>Stemphylium vesicarium</i> (Wallroth) E. Simmons | USA |
| Basidiomycotina | |
| <i>Doassansia eichhorniae</i> Ciferri | Dominican Rep. |
| <i>Marasmiellus inoderma</i> (Berk.) Singer | India |
| <i>Mycoleptodiscus terrestris</i> (J.W. Gerdermann) Ostazeki | USA |
| <i>Rhizoctonia oryzae-sativae</i> (Sawada) Mordue | Australia (IMI 289087) |
| <i>Rhizoctonia solani</i> Kuhn | India, Panama, Thailand and USA |
| <i>Rhizoctonia</i> sp. | India, USA |
| <i>Thanatephorus cucumeris</i> (Frank) Donk | China, Taiwan–India (IMI 3075) |
| <i>Tulasnella grisea</i> (Raciborski) Saccardo & Sydow | Indonesia (Java) |
| <i>Uredo eichhorniae</i> Gonzales Fragoso & Ciferri | Argentina, Brazil, Dominican Rep. |
| Chromista | |
| <i>Pythium</i> sp. | USA |

^aInternational Mycological Institute isolate reference number

Most of the records in the exotic range, and especially in the Palaeotropics, comprise a heterogeneous assemblage of generalist, opportunistic pathogens, with a minority group of apparently more specialised species not yet recorded from the native range. For example, *Cercospora piaropi* was reported from Asia, Africa and North America only, before the aforementioned survey in southern Brazil (Barreto and Evans

1996). Thus, Table 1 reflects the distribution of water hyacinth research workers rather than the true co-evolved mycobiota. As Barreto and Evans (1996) concluded, the doubts and speculation surrounding the area of origin or diversity of *E. crassipes* need to be resolved and addressed in order to open the way for more targeted and, potentially, more meaningful surveys for exploitable natural enemies.

The Surveys

Strategy employed

The Amazon basin, and specifically Amazonian Brazil, is most frequently cited as the probable centre of origin of *E. crassipes* (Harley 1990; Holm et al. 1991). However, ad hoc pathology surveys along the lower Amazon and its tributaries in the early 1990s, in the vicinities of Belém (Pará State) and Manaus (Amazonas State) yielded few fungi of interest (H.C. Evans and R.W. Barreto, pers. obs.). This led to speculation that perhaps the true origin lay further south in the great basins of the Paraná or São Francisco rivers (Barreto and Evans 1996), particularly since the earliest record of the plant was from the Rio São Francisco (Seubert 1847). Nevertheless, an exploratory survey along this river in 1996 failed to find any new or exploitable pathogens (R.W. Barreto and H.C. Evans, unpublished data). The only major area in South America for which there were no natural enemy records, and hence in which no surveys appeared to have been conducted, is the northwestern region; specifically, the upper Amazon basin, which comprises a confluence of many river systems and interlinked or isolated lakes or 'cochas'. It was hypothesised that in such ecosystems, natural enemies of water hyacinth may have coevolved in isolation and, as the plant spread naturally down the Amazon to reach the Atlantic and the other river systems of South America, these natural enemies were filtered out, especially those with poor survival or dispersal strategies. Thus, the biota associated with *E. crassipes* in the lower Amazon basin and elsewhere may be depauperate compared with that in the Upper Amazon, some 5500–7000 km upriver. The theory was put to the test, initially by opportunistic surveys, followed-up later by a more organised collecting trip, in the upper Amazon basin of both Peru (in Oct. 1988 and May 1999) and Ecuador (in May and Sept. 1999, and May 2000).

Collecting and isolation

Collecting was done using motorised canoes, travelling down the Napo River in Ecuador from the port of Coca, and up the Amazon River from Iquitos in Peru and along the major feeder rivers of the Nanay and Marañón. In addition, a short survey was undertaken along the Ucayali River around the port of Pucallpa. Diseased leaves were collected and dried in a plant press for processing in the UK. In addition, plants were lifted and petioles, stems and roots exam-

ined for disease symptoms. Such fleshy material was stored in waxed packets for later isolation in the UK.

Isolations were made either: directly from spores present on the diseased tissues, using a stereomicroscope; or tissues were aseptically-dissected, surface sterilised (30% hydrogen peroxide for 5 minutes) and rinsed several times in sterile distilled water. All samples were plated directly onto tap-water agar (TWA) or potato-carrot agar (PCA) containing antibiotics (penicillin, streptomycin sulfate), and incubated at 25°C, with a 12-hour black light regime to stimulate sporulation.

Results

Field assessment

The striking, and initially depressing, observation of water hyacinth populations in the rivers and lakes of the upper Amazon basin is that there is little visible evidence to signify the presence of fungal pathogens, especially compared to *E. crassipes* in its exotic range where patches of senescing or dying plants are not uncommon (caused by both abiotic and biotic factors). However, closer examination reveals that there is a range of fungal pathogens occurring on water hyacinth (see Table 2), and that these fungi fall into three groups. Genera, such as *Didymella* and *Mycosphaerella*, produce their discrete, black ascostromata singly but abundantly in the still green leaf tissues and, thus, apart from some yellowing (chlorosis), symptoms are cryptic. These species represent highly coevolved or biotrophic fungi, living within the host without seriously disrupting its physiology. The second group includes fungi which belong to the genera *Colletotrichum*, *Leptosphaeria*, *Myrothecium*, *Phaeoseptoria* and *Stagonospora*, and which cause necrotic leaf spots: some restricted and discrete (e.g. *Colletotrichum*); others spectacular, such as a prominent target spot (*Leptosphaeria*). However, it is only when the plants are lifted, and the petioles examined, that the high incidence of disease becomes evident. Many petioles were attacked by species of *Taosa* (Dictyopharidae; Homoptera) and *Thrypticus* (Dolichopodidae; Diptera), with their characteristic feeding and egg-laying patterns, and a significant proportion of these showed a positive association with fungal necrosis, as evidenced by lesion development around and subsequent spread from the insect punctures. It is considered that these wounds permit the ingress of both specialist and opportunistic fungal pathogens into the petiole, resulting in colonisation and invasion of

the stele, with decline or eventual death of the plant caused, in part, by the actions of this third group of fungi. There is a less clear association with the tunnels of *Neochetina* larvae, although microorganisms readily invade such damaged tissues. Interestingly,

there was no association of fungi with the feeding scars of *Neochetina* adults on the leaves. The fungi isolated from these tissues, excluding well-documented and ubiquitous saprophytic species, are listed in Table 2.

Table 2. Mycobiota associated with *Eichhornia crassipes* in the Upper Amazon basin

| Identification | Country | Associated tissue | Isolate reference no. ^c |
|--|---------------------|-------------------|------------------------------------|
| Ascomycotina and Deuteromycotina | | | |
| <i>Acroniella</i> sp. | Peru | Petiole | _d |
| <i>Acronium</i> sp. (New species) | Peru | Petiole | 384422 |
| <i>Acronium</i> sp. (New species) | Peru | Petiole | 384429 |
| <i>Acronium</i> sp. ^a | Peru | Petiole | 384427 |
| <i>Asteroma</i> sp. | Peru | Petiole | 379974 |
| <i>Cephalosporiopsis</i> sp. | Peru | Petiole | – |
| <i>Cephalosporium</i> sp. | Ecuador | Leaf | – |
| <i>Chaetophoma</i> sp. | Ecuador | Leaf | – |
| <i>Cochliobolus lunatus</i> R.R. Nelson & F.A. Haasis | Peru | Petiole | 379965 |
| <i>Cochliobolus pallescens</i> (Tsuda & Ueyama) Sivan | Peru | Petiole | 379971 |
| <i>Coniothyrium</i> sp. | Ecuador | Petiole | – |
| <i>Curvularia</i> sp. | Ecuador | Petiole | – |
| <i>Fusarium</i> sp. (New species) | Peru | Petiole | 384418 |
| <i>Cylindrocladium</i> sp. ^a | Peru | Petiole | 384414 |
| <i>Fusarium poae</i> (Peck) Wollenw. | Peru | Petiole | 384424 |
| <i>Fusarium sacchari</i> (E.J. Butler & Hafiz Kahn) W. Gams. | Peru | Petiole | 384423 |
| <i>Fusarium</i> sp. (New species) | Ecuador | Petiole | 384434 |
| <i>Fusarium</i> sp. | Peru | Petiole | – |
| <i>Fusarium</i> sp. | Peru | Petiole | – |
| <i>Fusarium</i> sp. ^a | Ecuador | Petiole | 384433 |
| <i>Gliocladium roseum</i> Bainier | Ecuador | Petiole | 384435 |
| <i>Gliocladium</i> sp. | Peru | Petiole | – |
| <i>Glomerella cingulata</i> (Stoneman) Spauld. & H. Schrenk. | Brazil ^b | Leaf | 384437 |
| <i>Glomerella cingulata</i> (Stoneman) | Ecuador | Leaf | 384432 |
| <i>Glomerella cingulata</i> (Stoneman) | Peru | Leaf | 384416 |
| <i>Glomerella</i> sp. | Peru | Leaf | – |
| Hyphomycete sp. 1 ^a | Ecuador | Petiole | 384431 |
| Hyphomycete sp. 2 ^a | Ecuador | Petiole | 384430 |
| Hyphomycete sp. 3 | Ecuador | Petiole | – |
| Hyphomycete sp. 4 | Ecuador | Petiole | – |
| Hyphomycete sp. 5 with dictyochlamydo spores (New species). | Peru | Petiole | 379967 |

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Table 2. (Cont'd) Mycobiota associated with *Eichhornia crassipes* in the Upper Amazon basin

| Identification | Country | Associated tissue | Isolate reference no. ^c |
|---|---------------------|-------------------|------------------------------------|
| <i>Idriella</i> sp. ^a | Peru | Petiole | 384417 |
| <i>Leptosphaeria</i> sp. | Brazil ^b | Leaf | – |
| <i>Leptosphaeria</i> sp. ^a | Peru | Leaf | 384425 |
| <i>Leptosphaerulina</i> sp. | Peru | Leaf | 379972 |
| <i>Mycosphaerella</i> sp. (New species) | Peru | Leaf | 384426 |
| <i>Myrothecium verrucaria</i> (Alb. & Schwein.) Ditmar | Peru | Leaf | 379973 |
| <i>Myrothecium</i> sp. | Brazil ^b | Leaf | – |
| <i>Phaeoseptoria</i> sp. | Peru | Leaf | 379966 |
| <i>Phoma chrysanthemicola</i> Hollós | Peru | Petiole | 384421 |
| <i>Phoma leveillei</i> Boerema & Bollen | Ecuador | Petiole | – |
| <i>Phoma</i> section <i>Peyronellaea</i> (Goid. ex Togliani) Boerema | Peru | Petiole | 384420 |
| <i>Phoma</i> sp. ^a | Brazil ^b | Petiole | 384436 |
| <i>Phoma</i> sp. ^a | Peru | Petiole | 384428 |
| <i>Phoma</i> spp. | Ecuador | Petiole | – |
| <i>Phoma</i> spp. | Peru | Petiole | – |
| <i>Pseudocercospora</i> sp. | Peru | Leaf | 384415 |
| <i>Sarocladium</i> sp. | Peru | Petiole | – |
| <i>Stagonospora</i> sp. | Peru | Leaf | – |
| <i>Stauronema</i> sp. ^a | Peru | Petiole | 384419 |
| Basidiomycotina | | | |
| Basidiomycete sp. 1 | Peru | Petiole | – |
| Basidiomycete sp. 2 | Peru | Petiole | – |
| Basidiomycete sp. 3 | Peru | Petiole | – |
| <i>Rhizoctonia</i> sp. | Ecuador | Petiole | – |
| <i>Rhizoctonia</i> sp. | Peru | Petiole | – |
| <i>Thanetophorus</i> sp. | Peru | Petiole | – |

^a Preliminary identification awaiting confirmation from CABI Bioscience, International Mycological Institute (Egham) or Centraalbureau voor Schimmelcultures (Baarn, Netherlands).

^b Recent survey along the Xingu River (Pará).

^c International Mycological Institute Herbarium

^d – = not yet accessed in collections.

Laboratory assessment

An analysis of the fungi collected on, and isolated from, diseased water hyacinth samples in the upper Amazon basin shows some notable differences from those fungi reported from other countries or regions (see Discussion). Notable among the Amazonian records are undescribed species of *Acremonium* (2 spp.), *Fusarium* (2 spp.), *Mycosphaerella* (1 sp.) and probably undescribed taxa, belonging to the genera

Phaeoseptoria, *Stagonospora* and *Pseudocercospora*, since there are no previous records of these genera from *E. crassipes*. In addition, there are still some tentative identifications which may represent novel species and/or genera, and for which more taxonomic inputs are awaited. In this context, of particular interest is Hyphomycete sp. 5, which cannot be assigned to any known genus or indeed a taxonomic group. In culture, this fungus produces masses of

hydrophobic, greenish-grey resting bodies ('sclerotia') within which are produced more thick-walled resting structures or dictyochlamydospores. It can be hypothesised that the 'sclerotia' are adapted for floating and for dispersal of the resting spores, perhaps attaching to the leaves and petioles of water hyacinth plants, but the rest of the fungal life-cycle, and specifically its invasion of the host, remains highly speculative.

Greenhouse assessment

Several of the *Acremonium* species and other verticillid Hyphomycetes have been screened on water hyacinth plants (ex Africa) in a quarantine greenhouse facility in the UK. Only one species (*Cephalosporiopsis*) has demonstrated high pathogenicity; causing a spreading necrosis and death of inoculated, unwounded petioles. Clearly, more in-depth screening, particularly with and without wounding (to simulate insect attack), is necessary before the potential of these Amazonian fungi as biocontrol agents of *E. crassipes* can be properly evaluated.

Discussion

These essentially preliminary surveys demonstrate that there is a rich mycobiota associated with *E. crassipes* in the upper Amazon basin. Moreover, few of these species share a common link with the mycobiota recorded in other regions or countries where the plant is an alien invasive species. For example, of the ubiquitous pathogens which have been targeted and assessed as biocontrol agents of water hyacinth, only *Myrothecium roridum* has been found in both situations. This suggests that other common taxa and potential biocontrol agents such as *Alternaria eichhorniae*, *Acremonium zonatum* and *Cercospora rodmanii* (= *C. piaropi*), which have been recorded during routine surveys in the USA (Freeman et al. 1974), South Africa (Morris et al. 1999) and India (Evans 1987), are altogether absent or rare on *E. crassipes* in the upper Amazon.

Indeed, the origins and, in particular, the original host(s) of *A. eichhorniae* can only be speculated upon. Since its description on *E. crassipes* in India (Nag Raj and Ponappa 1970), it has been recorded from various countries in Africa, as well as from Egypt and the USA (Table 1). However, pathogenicity tests in the latter two countries showed contrasting results, with virulent strains being reported in Egypt (Shabana et al. 1997) but only weakly pathogenic isolates in the

USA (Freeman et al. 1974). This fungus is also regarded as a weak pathogen in South Africa (Morris et al. 1999), although virulent strains have recently been found in both East and West Africa (Bateman 2001). Nag Raj and Ponappa (1970) reported that *A. eichhorniae* has a narrow host range, at least in the tests that were conducted, and attacked only a related member of the Pontederiaceae (*Monochoria vaginalis* Pers.). If *E. crassipes* is South American in origin, and if, as the present survey suggests, *A. eichhorniae* is not present in South America (or at least the upper Amazon), then what is its natural host range? A confirmed record of this species on *Bupleurum falcatum* L. (Umbelliferae) from Germany (Evans 1987) only fuels the speculation.

Despite the spectacular success of *Neochetina* weevils as classical biocontrol agents in a number of countries or regions, such control has not always proven to be sustainable or universal, and hence the search for, and assessment of, other arthropod natural enemies still continues apace (Cordo 1999; Hill and Cilliers 1999). The essentially provisional results reported here indicate that new and potentially exploitable fungal pathogens can be found in the upper Amazon basin. The case for this being the centre of origin or diversity of *E. crassipes*, therefore, has been strengthened but there are still some anomalies. For instance, two biotrophic fungi, the rust *Uredo eichhorniae* and the smut *Doassansia eichhorniae*, which were described by the great Italian mycologist R. Ciferri on water hyacinth in the Dominican Republic in the 1920s (Evans 1987), were not found during the Amazonian surveys. A rust, however, was common on *E. azurea* in the same habitats. If these represent coevolved taxa, then this would suggest that the Caribbean is the true centre of origin. Nevertheless, to support this conclusion, the host range of the rust requires clarification, and the identification of the smut needs to be verified. Unfortunately, a recent survey in the Dominican Republic failed to locate either of these natural enemies (R.W. Barreto, pers. comm.).

It is relevant here to ask whether or not classical fungal biocontrol agents could make a useful addition to the armoury to be deployed against *E. crassipes* in its exotic range, and, if so, is it an acceptable strategy? A judgment cannot yet be made on this question since classically introduced fungi have never been used for management of water hyacinth in most of the countries affected by the weed, where the introduction of exotic pathogens as biocontrol agents is still viewed with considerable scepticism (Evans 2000). However,

based on recent results in South Africa and Australia (Evans 2000), this can be a potentially highly successful strategy and one which can be approached from three possible directions.

Firstly, the traditional classical approach can be adopted, involving the release of a virulent, coevolved fungal agent producing abundant inoculum with highly efficient dispersal and survival mechanisms, such as a rust or smut. However, from the mycobiota documented so far (Tables 1 and 2), there is no indication that a suitable candidate has been found. In fact, the majority of fungi recorded in the upper Amazon are either poor sporulators (e.g. *Didymella* and *Mycosphaerella*), producing relatively few, delicate ascospores; or possess slime-spores (conidia) which are adapted for short-distance, rain-splash dispersal only (e.g. *Colletotrichum*, *Acremonium*, *Fusarium*, *Phaeoseptoria* and *Stagonospora*). This restricted dispersal ability may account for the fact that they appear not to have spread with the plant during its migration from the headwaters of the Amazon. The exploitation of such fungi as 'classical' mycoherbicides could be considered, in which the strategy would be to spot-spray rather than blanket-spray, allowing for natural spread (rain or water-splash) within contiguous populations, and perhaps a single application, rather than repeated doses, relying on the specialised survival propagules to ensure carryover and thus provide long-term or sustainable control.

However, perhaps the most potent use of these fungi would be in conjunction with insects, as recommended by Charudattan et al. (1978), and there is evidence from the current surveys that there is a close association between certain fungal species listed in Table 2 and insect natural enemies such as *Taosa* and *Thrypticus* species. Indeed, an analysis of the early data relating to prickly pear control in Australia, reveals that success was achieved through a combination of *Cactoblastis cactorum* and the introduction of exotic microorganisms (Mann 1970).

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