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J. Aquat. Plant Manage. 27: 10-15

Isoenzymic Variability in Monoecious Hydrilla in the United States

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ABSTRACT

Monoecious hydrilla, from sites in North Carolina and Washington, D.C., was monitored for heterogeneity by polyacrylamide gel electrophoresis under non-denaturing conditions, followed by staining for isoenzymes. Extracts of subterranean turions from four sites in North Carolina showed a variable distribution of two biotypes. One biotype had patterns of activity for alcohol dehydrogenase, NADP-malic enzyme, aspartate aminotransferase and phosphoglucomutase identical to those for the turions from Washington. The second was different in the first three enzymes. Protein profiles of the two types were slightly different, although the major proteins were identical. Distribution ranged from nearly 100% of one biotype in Lake Anne to nearly 100% of the other in Lake Wheeler, and suggests two separate introductions of the plant in North Carolina. Isoenzymic profiles of turions from three sites near Washington were identical and are in accord with a single introduction.

Key words: electrophoresis isoenzymes, subterranean turions.

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INTRODUCTION

The aquatic plant hydrilla (*Hydrilla verticillata* (L.f.) Royle) may have its center of origin in southeast Asia (Swarbrick et al. 1981), although it is now distributed worldwide. Both monoecious and dioecious strains exist. Additionally, there are a number of biotypes which can be distinguished on the basis of isoenzymic banding patterns after electrophoresis. The electrophoretic and morphological characterization of biotypes has been described in a number of papers (Verkleij et al. 1983; Pieterse et al. 1984, 1985; Verkleij and Pieterse 1986). Two populations have been characterized at present in the United States. The original introduction into Florida (Haller 1978) was dioecious female, and this has now spread throughout the southeast and as far west as California, where it has become established in the Imperial Valley. More recently, a monoecious plant has been noted in the Potomac River and in other bodies of water in the vicinity of Washington, D.C. (Steward et al. 1984). Both of these strains have been characterized by enzymic analysis of the vegetative tissue (Verkleij et al. 1983) or the subterranean turions (Ryan 1988a) and are readily distinguishable by comparison of phosphoglucomutase (PGM) or aspartate aminotransferase (AAT).

The monoecious and dioecious strains of hydrilla have different morphologies and responses to photoperiod. The monoecious plant more rapidly produces subterranean turions in response to short photoperiod than does the dioecious (Spencer and Anderson 1986; Steward and Van 1986). The mean weights of the subterranean turions are different between the two biotypes, as well, with that of the monoecious being considerably smaller under similar conditions of growth and nutrition (Spencer et al. 1987).

Previous reports on the isoenzymic complement of the strains of hydrilla imply that there is little heterogeneity in the isoenzymic complements of the plants from any geographic region (Verkleij et al. 1983; Pieterse et al. 1984, 1985; Verkleij and Pieterse 1986). Isoenzymes of the dioecious strain found in the Unite States were reported to be identical for nine different collections of this plant from California, Texas, Alabama, and Florida (Verkleij and Pieterse 1986). Likewise, four different collections of the monoecious plant from the vicinity of Washington, D.C. were reported to have identical isoenzymic complements. It is not clear how many individuals were tested in each group. Although the hydrilla populations appear homogeneous, it is possible that there could be heterogeneity within the populations. The amount of heterogeneity, among other things, would depend on the size of the founding population for each introduction, the actual number of introductions, and the length of time that genetic drift had been occurring in subpopulations (Loveless and Hamrick 1984).

Recently, it has been reported that monoecious hydrilla from Lake Wheeler, North Carolina, was triploid with a chromosome number of 2n = 24 (Harlan et al. 1984), as opposed to a chromosome number of 2n = 16 for the diploid monoecious plant from Washington, D.C. (Verkleij et al. 1983). Monoecious hydrilla in North Carolina has been reported to produce viable seed (Langeland and Smith 1984) while seed has not been reported in the Washington, D.C. area. This may be due to environmental conditions, however, as plants from both locations have produced seed in Florida (Conant et al. 1984). Earlier reports indicated that the production of viable seed occurred only rarely, if at all, among biotypes of this plant (Ernst-Schwarzenbach 1945). It is doubtful that a triploid plant would produce seed, other than that resulting from apomixis. It is not possible to determine from these papers the distribution of the triploid character, or of the ability to set seed, among this population of plants. These observations raise the question of whether the strains in North Carolina and in the Washington, D.C. area are the same. The increased adaptability of a strain of hydrilla with a sexual reproductive phase, or the increased mobility of even apomictic seeds, are concerns, as well.

Initial work in this laboratory with subterranean turions from North Carolina indicated that there was heterogeneity among isoenzymes for alcohol dehydrogenase (ADH), NADP-malic enzyme (NADP-ME), and aspartate aminotransferase (AAT). The work reported here was undertaken to determine the extent of heterogeneity in the North Carolina and the Washington, D.C. populations of hydrilla.

MATERIALS AND METHODS

Subterranean turions were collected from sieved samples of hydrosoil in November and December, 1987. Plants from North Carolina were collected by Dr. David DeMont and colleagues, Aquatic Weed Control Program, Department of Natural Resources and Community Development, State of North Carolina, Raleigh, N.C. Collections from the Washington, D.C. area were conducted by Dr. Richard Hammerschlag and Dianne Ingrahm, National Park Service, U.S. Department of the Interior, Washington, D.C. Collections were generally from a single site within each body of water. Turions were immediately sent to Davis, California, where they were kept at 10 C until analysis. Analyses were carried out within three weeks of receipt of the plant material.

For electrophoresis, turions were ground in a chilled mortar and pestle with one ml buffer per 100 mg fresh weight of turion. The buffer was 50 mM Na-HEPES, 1 mM phenylmethylsulfonylfluoride, pH 8.0, 10% (v/v) glycerol, with 20 ml 2-mercaptoethanol added per ml of grinding buffer. Tissue was homogenized at 4 C, then centrifuged at 7700 x g for 30 min. The supernatant was loaded on polyacrylamide gels without further treatment. The non-denaturing buffers of Davis (1964) were used for electrophoresis. Slab gels were 0.75 mm thick, 14 cm wide and 16 cm long and were 7.5% in total acrylamide. The gels had 20 wells and 40 µl of extract was loaded per well. The tracking dye was bromphenol blue; 30 µl of 0.02% (w/v) solution were added to 750 ml of the upper buffer. Electrophoreses were run at a constant current of 15 mA per gel, for approximately 2.5 h, until the dye front approached the end of the slab. Four gels with the same samples were run at the same time. Gels were stained for ADH, AAT, NADP-ME and PGM by the methods of Siciliano and Shaw (1976). Some gels were stained for protein. When the electrophoresis was completed, the gel was placed in a fixative of 5% (v/v) methanol and 7.5% (v/v) acetic acid in water. The ratio of fixative to gel volume was ca. 5 to 1. After one hour, the gel was stained for 20 min. with a solution of 0.25% (w/v) Coomassie Brilliant Blue R-250 in 45% (v/v) H_2O, 45% (v/v) methanol, 10% (v/v) acetic acid. Destaining was carried out overnight in the fixative.

Protein transfers to nitrocellulose were conducted in a semi-dry electroblotting apparatus (Sartorius GmbH, Göttingen, FRG)[2] using a buffer of 48 mM Tris, 39 mM glycine, 1.3 mM sodium dodecyl sulfate, made 20% (v/v) in methanol (Bjerrum and Schäfer 1986). Primary antiserum was prepared in rabbits against one of the major groups of proteins of subterranean turions of the dioecious biotype of hydrilla. The proteins were purified by electrophoresis under non-denaturing conditions. The characteristics of this protein and the antiserum raised against it are described elsewhere (Ryan 1988b). The binding of primary antiserum to protein was visualized by use of a secondary goat anti-rabbit lgG covalently labelled with alkaline phosphatase (BioRad, Richmond, CA)[2]. Alkaline

[2]Mention of a manufacturer does not constitute a warranty or guarantee of the product by the U.S. Department of Agriculture nor an endorsement by the Department over other products not mentioned.

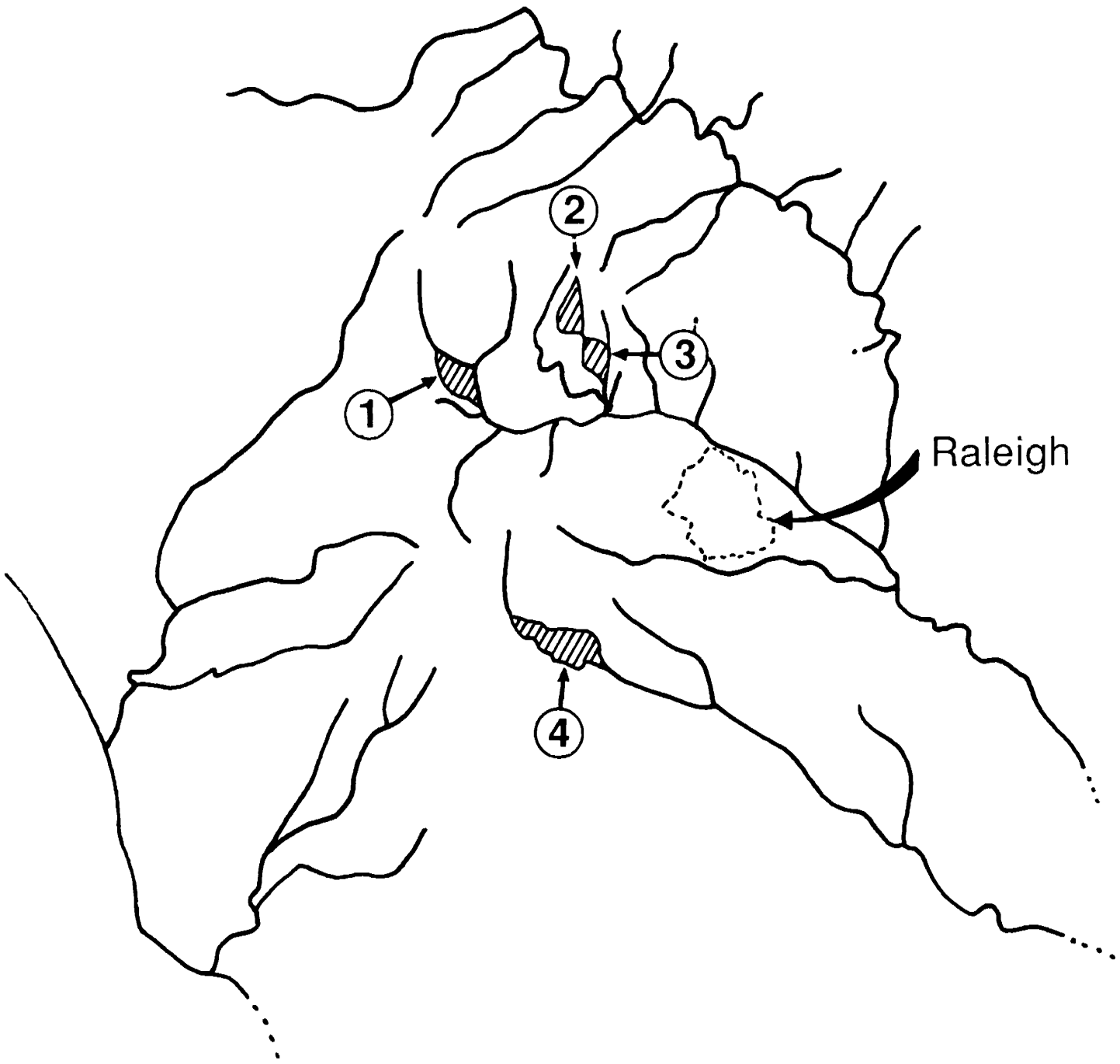

Figure 1. Map of sites of collection of subterranean turions in Wake County, North Carolina. 1) Page Lake, 2) Dunnaway's Pond, 3) Lake Anne, 4) Lake Wheeler. The principal regional streams are shown as well.

phosphatase was detected using 5-bromo-4-chloro-3-indolyl phosphate toluidine salt and nitroblue tetrazolium in 100 mM sodium carbonate, 1 mM $MgCl_2$, pH 8.9 (Blake et al. 1984).

RESULTS

The sites of collection in North Carolina are shown in Figure 1, along with the principal streams of the watershed. The type of isoenzymic heterogeneity observed in the material from North Carolina is shown in Figure 2. In lanes 2, 3, and 4, the more common variants for ADH, NADP-ME, and AAT are shown in the left lane, while the less common forms are shown in the right lanes. For NADP-ME (lane 3) a single, more rapidly moving variant of the enzyme is present, while for AAT (lane 4), a pair of more rapidly moving enzyme forms are present. For ADH (lane 2), at least one more rapidly moving form is associated with each of the three major allozymic forms of the activity. In no case was variation found in one enzymic activity without variation in the other two. Thus, it was possible to classify the plants as Type A, the most common

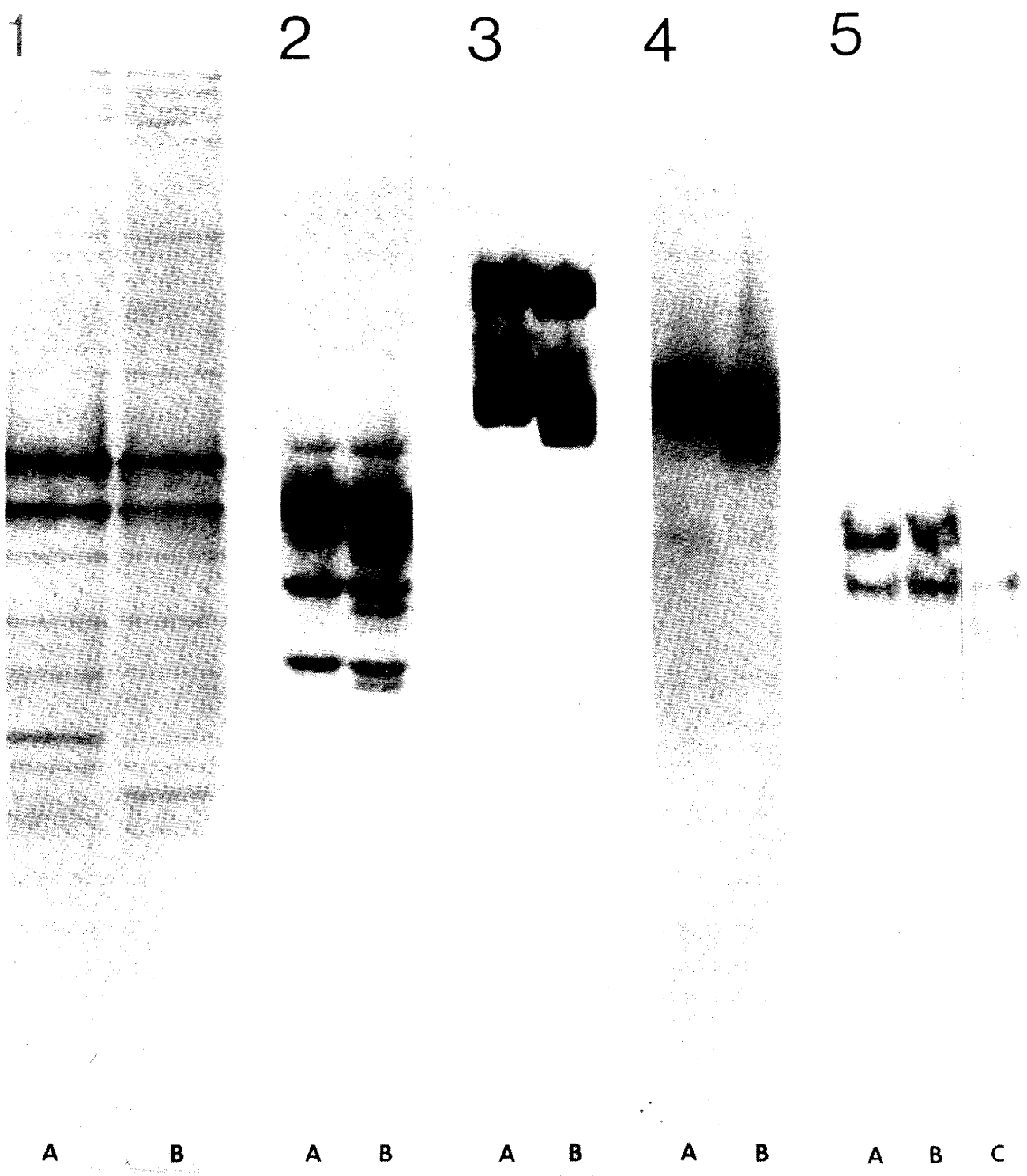

Figure 2. Protein and isoenzymic profiles of extracts of turions from North Carolina after electrophoresis under non-denaturing conditions. Lane 1: Protein after staining with Coomassie Brilliant Blue R-250. Lane 2: ADH. Lane 3: NADP-ME. Lane 4: AAt. Lane 5: Immunblot of turion extracts after electrophoresis under non-denaturing conditions. In all cases. A and B denote the extracts from turions of Type A and Type B, respectively. In lane 5, C denotes the extract from a dioecious turion.

form, or Type B, the less common. The enzyme PGM, monitored in all cases, displayed no heterogeneity in the samples from North Carolina or Washington, D.C. Three principal bands were seen in all cases, as reported previously for monoecious hydrilla (Ryan 1988a).

In Figure 2, lane 1, are shown the protein profiles of

extracts from turions of Type A (left lane) and Type B. The differences are changes in the relative intensities of some of the more rapidly moving protein bands. There is no evidence of extensive proteolytic degradation associated with either Type A or B. When gels run under non-denaturing conditions were transferred to nitrocellulose and probed with anitbody against the major proteins of the turions of dioecious hydrilla, no differences were noted among the cross-reactive proteins from turions of Type A or B (Figure 2, lane 5). The pattern was typical of that observed previously for extracts of monoecious turions from the Washington, D.C. area (Ryan 1988b). The extract from dioecious turions gave a pattern which was distinct (Figure 2, lane 5, c).

The isoenzymic profiles of collections of turions from four sites in North Carolina were run and individual turions were classified as belonging to Type A or Type B, as described above. Samples from the entire collection were run twice. These data, with the mean weights, are shown in Table 1. The turions from each site had a ratio of the two types that was similar upon repetition. The mean weights of the turions from each site were not statistically different for the two repetitions (ANOVA, followed by Fisher's PLSD test), suggesting that there was little bias in the selection of turions for electrophoretic analysis. The mean weights were similar to those noted previously for monoecious turions grown at this laboratory (Spencer et al. 1987).

Similar measurements of heterogeneity were conducted on turions from the Washington, D.C. area. Subterranean turions were from Belle Haven Marina on the Potomac River, from Kenilworth Gardens, and from Frederick, MD. Two repetitions of 18 samples from each site were run. There were no detectable variations in the patterns for ADH, NADP-ME, AAT or PGM after electrophoresis. The patterns were identical to those of the so-called Type A from North Carolina.

DISCUSSION

The homogeneity of the isoenzymic complement in the Washington, D.C. population of monoecious hydrilla is expected if the introduction had only a small number of similar individuals, and reproduction were exclusively clonal. This tendency toward a genetically uniform population seems to be a characteristic of aquatic and water-associated plants, and may be due to the predominantly clonal reproduction in these plants. For instance, populations of *Phyllospadix scouleri* Hook., *P. torreyi* S. Wats., and *P. serrulatus* Rupr. ex Aschers. were reported to have a high degree of genetic uniformity (McMillan and Phillips, 1981). In a study of *Typha* species in the United States, Sharitz et al. (1980) found little variation in the isoenzymic patterns within each of four species across a wide range of habitats, even when there was evidence of differences in adaptation among different members of the range. Even long-established, cosmopolitan populations of aquatic weeds seem to have relatively small amounts of genetic variability. In a study of isoenzymic variability in *Potamogeton pectinatus* L. from Europe, Hettiarachchia and Triest (1986) found that superoxide dismutase, xanthine dehydrogenase and NADP-ME exhibited no variability among the populations tested, while ADH, AAT, peroxidase, and shikimate dehydrogenase were more heterogeneous. Evidence has been presented that *Najas marina* L. subsp. *marina* from western Europe has no heterogeneity in isoenzymes for malic enzyme and only a very low level in ADH (Triest et al. 1986). *Najas marina* L. subsp. *intermedia* had a higher degree of polymorphism in the four isoenzymes which were monitored.

TABLE 1. CLASSIFICATION OF SUBTERRANEAN TURIONS FROM FOUR SITES IN NORTH CAROLINA.

Site		Weight turions (±s.d.)	Percentage Type A	Percentage Type B
Lake Anne	(N = 17)	144 ± 47 mg	0.00	1.00
	(N = 19)	127 ± 36	0.00	1.00
Dunnaway's Pond	(N = 19)	161 ± 34	0.79	0.21
	(N = 19)	170 ± 51	0.74	0.26
Page Lake	(N = 19)	120 ± 20	0.95	0.05
	(N = 19)	116 ± 18	1.00	0.00
Wheeler Lake	(N = 19)	155 ± 34	1.00	0.00
	(N = 19)	147 ± 47	0.90	0.10

The presence of two apparent biotypes in the monoecious population of hydrilla in North Carolina is unexpected. The reports that this population is triploid (Harlan et al. 1984) and that it sets seed (Conant et al. 1984) indicated that it differs from the monoecious population from Washington, D.C. The distribution of the two biotypes, as shown in this report, indicates that this population is not at equilibrium, since the ratio of the two biotypes is not constant. The proportion of Type B ranged from nearly 100% of the population in Lake Anne to close to 0% in Lake Wheeler and Page Lake. According to Harlan et al. (1985), hydrilla was first identified in Wake County, North Carolina, in 1981, and had already been established for a number of years. It is possible that there have been two introductions of monoecious hydrilla into this area of North Carolina and that the more recent introduction is a secondary introduction from the Washington area, thus explaining the distribution of Type A. The older infestation is Type B. If this is the case, then Type A would be diploid and Type B triploid, since the determination of chromosome number (Harlan et al. 1984) may have been conducted before a significant amount of Type A appeared in the population.

Another explanation which must be considered is that differences in isoenzymic patterns are due to environmental factors, such as the age of the tuber. Lakes with a relatively new population of hydrilla have low amounts of Type B. Lake Anne was stocked with triploid grass carp (*Ctenopharyngodon idella* Val.) before 1987, with complete suppression of plant growth during that year (D. deMont, personal communication). This lake has the highest proportion of Type B. Further research needs to be conducted to confirm the variable ratio of the two biotypes in these bodies of water, and to follow changes in the populations by observing the isoenzymic profiles during the course of several years.

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J. Aquat. Plant Manage. 27: 15-20

Integration of *Myrothecium roridum* and 2,4-D in Waterhyacinth Management

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ABSTRACT

Sub-lethal doses of the commonly used herbicide 2,4-D had no adverse effect on *in vitro* mycelial growth and *in planta* damage by *Myrothecium roridum* on waterhyacinth (*Eichhornia crassipes*). Efficacy of *M. roridum* as a biocontrol agent of waterhyacinth was augmented when used sequentially with low rates (5-10% recommended rate) of 2,4-D both under greenhouse and field conditions.

Key words: Sri Lanka, weed control, biocontrol, herbicide, pathogen.

INTRODUCTION

Success of biocontrol in one region of the world stimulates its adoption in other regions. On this basis the choice of a fungal pathogen for biocontrol of waterhyacinth (*Eichhornia crassipes* (Mart.) Solms) in Sri Lanka would have been *Cercospora rodmanii*, the efficacy of which has been well established (1, 2, 3, 4). This fungus has not been encountered as a pathogen of waterhyacinth in Sri Lanka (5, 7). Considering local pathogens of waterhyacinth the choice fell on *Myrothecium roridum* which was found to be highly pathogenic to waterhyacinth and well distributed in Sri Lanka. However, lack of host specificity excluded it from being tried as a biocontrol agent in other countries (9, 10, 11).

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