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Evolutionary processes in aquatic plant populations

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ABSTRACT

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Aquatic plants exhibit striking taxonomic, morphological and ecological diversity. This variation limits the ability to pose general hypotheses with regards to evolutionary processes in aquatic plants. Here we ask whether the population structure, reproductive systems, gene flow and patterns of genetic differentiation in aquatic plants are likely to differ in any significant way from terrestrial plants. Defining the limits of aquatic plant populations is best attempted using demographic and genetic techniques for estimating effective population size (N_e). Data available for terrestrial species suggest that N_e in many annual aquatics is likely to be small, a fraction of the census number. In highly clonal species, especially those with water-dispersed vegetative fragments, effective population sizes may differ widely from those of related terrestrial taxa. However, measuring N_e in such species will probably require approaches more similar to those used to study vagile parthenogenetic animals than those used in plant populations.

Reproductive systems in aquatic plants, though well described, have only begun to receive quantitative study. Levels of inbreeding and other mating-system parameters have been measured in several emergent species but are lacking for floating-leaved, submerged or free-floating taxa. Extensive clonal propagation presents analytical difficulties but also provides experimental opportunities for studying mating-system variation, particularly the relationship between large clone size and self-fertilization. Limited sexual reproduction has been observed in many highly clonal, aquatic species; there has been little attempt, however, to investigate the extent to which sterility can be attributed to genetic and environmental factors, or to explore whether sterility accumulates in clonal lineages.

Gene flow in aquatic plants may be greatly affected by the discrete and patchy nature of many aquatic habitats and the directional transport of propagules in running waters. While the extent of gene movement may be influenced by habitat structure, genetic consequences of local and long-distance dispersal are likely to depend on the type of propagule involved. Transport of vegetative fragments may lead more frequently to successful gene establishment than dispersal of seed, and may, in part, explain the extensive geographical ranges of many clonal aquatic species.

A survey of electrophoretic variation in 81 aquatic taxa revealed that the distribution of genetic diversity within and among populations of emergent species, as in their terrestrial counterparts, ap-

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pears to be determined primarily by their breeding systems and life histories. In contrast, data for several submerged groups suggest widespread genetic monomorphism. The data, however, are limited, making interpretation of this pattern difficult, especially in cases where uniformity at isozyme loci appears to be associated with morphological and physiological differentiation. Further microevolutionary studies of aquatic plant populations may help to clarify the apparent conservative macroevolutionary pattern exhibited by certain aquatic plant families.

INTRODUCTION

Aquatic vascular plants hold a special fascination for naturalists and plant biologists because of their distinctive growth forms and ubiquitous presence wherever wetland habitats occur. Along with trees, grasses and cultivated plants, aquatic plants are usually among the first groups to be singled out for special attention. Manuals of aquatic plants have been completed for many geographical areas; magazines and scholarly journals are devoted solely to their study; a thriving horticultural and aquarium trade is based on their culture and sale. In addition, because of their economic importance as weeds, work on the control of aquatic vegetation is an active area of research in many countries.

Aside from weed control, most research on aquatic plants has been concerned with their systematics and ecology. Many taxa of aquatics are notoriously difficult to classify, because of extensive phenotypic plasticity, reduced growth forms and convergent morphology associated with the invasion of water. The specialized morphological and physiological attributes of aquatic plants have also raised many ecological questions concerned with the relationships between structure and function (Crawford, 1987). This somewhat classical, botanical tradition is evident from a perusal of recent articles in this journal as well as earlier works by Arber (1920) and Sculthorpe (1967) which are largely devoted to empirical studies of the taxonomy, morphology and ecology of particular groups.

Despite the attention aquatic plants have received from systematists and ecologists, relatively little is known of their population genetics and evolution, especially in comparison with the growing body of data on terrestrial plants (reviewed in Gottlieb and Jain, 1988; Brown et al., 1990a). Moreover, our limited understanding of the population genetics of aquatic plants is in striking contrast to the rapidly accumulating body of information on other groups of aquatic organisms including fish (Turner, 1984), invertebrates (Hebert, 1978; Ryland and Tyler, 1989; Browne and Bowen, 1990), and algae (Innes, 1984). This gap in our knowledge of aquatic plants has led to inferences about the nature of evolutionary processes being made in the absence of a sound body of quantitative data. This is unfortunate because aquatic plants provide several interesting macroevolutionary problems which would probably be clarified by input from microevolutionary studies at the population level.

The purpose of this essay is to assess why so little population genetic data are available for aquatic plants, whether the conventional methods used to study terrestrial plant populations are likely to provide such data and, if not, how alternative approaches can be devised to investigate the mechanisms of evolutionary change. Our approach is to focus on four issues which we think are critical to understanding the mode and tempo of evolution in plant populations: (1) What constitutes a population? (2) What kinds of reproductive systems operate in aquatic plants and how can they be quantified? (3) How important is gene flow in aquatic plants and what are the evolutionary consequences of long-distance dispersal? (4) What levels of genetic diversity are likely to be found in aquatic species and how is this diversity structured? Throughout we attempt to raise unanswered questions, highlight deficiencies in our existing knowledge and discuss whether measures of key population genetic parameters can be obtained with methods currently used in terrestrial populations. Before we address these issues, however, we briefly discuss the diversity of life forms found in aquatic plants and the difficulties this creates when attempting to define an aquatic plant.

WHAT IS AN AQUATIC PLANT?

While constituting a relatively small proportion of the vascular plants (less than 1–2%) (Cook, 1990), aquatic plants exhibit considerable morphological, taxonomic and ecological heterogeneity. This diversity is represented by a continuum from species capable of tolerating flooded soils, through amphibious groups that are equally at home on land or in water, to submerged aquatic plants adapted to growing in deeper lake and marine environments. The various life forms of aquatic plants not only present difficulties in defining what an aquatic plant is, but are also likely to prevent any broad generalizations from being made on the nature of evolutionary processes in aquatic plant populations. Despite attempts to define and classify aquatic plants (see Sculthorpe 1967, pp. 3–10; Hutchinson, 1975, pp. 118–132), the growth form, life history and reproductive system possessed by an individual species will be the prime determinants of its population genetic structure, not the fact that the species lives in an aquatic environment. Nevertheless, aquatic plants possess some characteristics that set them apart from terrestrial groups. Although most traits found in aquatic plants are also represented in related terrestrial taxa, certain attributes are either unique or reach a high degree of specialization (Table 1). It is, therefore, instructive to explore whether the distinctive features of aquatic plants are likely to have significant genetic and evolutionary consequences.

In this essay, we use the term 'aquatic plant' in its broadest sense to include

TABLE 1

Distinctive ecological features of aquatic plants and their potential evolutionary consequences

Feature	Occurrence	Evolutionary consequences
High phenotypic plasticity	Most groups	Buffers genotypes against environmental heterogeneity and reduces selection intensities
Prolific clonal propagation	Perennial species, especially submerged and free-floating	Can lead to genetically uniform populations and reduces the risk of genotype mortality
Limited sexual reproduction	Clonal species and those of hybrid origin	Limits recombination and reduces genetic diversity
Precocious reproduction	Annual species of ephemeral habitats	Enables radiation into unpredictable environments
Hydrophilous pollination	Many submerged species	Limits gene flow via pollen to the confines of the water body
Water-dispersed diaspores	Many groups	Provides opportunities for both local and long-distance dispersal

all plants that occur in permanently or seasonally wet environments. For convenience we include under this general term species that have been described elsewhere as hydrophytes, limnophytes, macrophytes, amphiphytes, helophytes, as well as amphibious, wetland, or simply water plants. Our rationale for such a broad usage of the term, in contrast to Raunkiaer (1934), Iversen (1936) and Den Hartog and Segal (1964) who exclude amphibious and emergent species, is two-fold. First, including all growth forms along the ecological continuum from plants in saturated soil to deep water facilitates comparisons among species at various locations on the terrestrial–aquatic gradient. Second, since these life forms represent an evolutionary continuum, we believe it would be quite arbitrary to exclude species commonly found in aquatic habitats but that do not complete their entire life cycle in water. We follow Sculthorpe (1967) in classifying aquatic plants as either emergent, floating-leaved, submergent or free-floating. In using this broad definition, it becomes particularly important that our discussion of evolutionary processes is made within the context of particular life forms. We therefore make a special attempt to distinguish life forms that are likely to differ in this regard.

WHAT IS AN AQUATIC PLANT POPULATION?

One of the major difficulties in applying population genetic approaches to aquatic plants is the problem of determining what constitutes a population, the fundamental unit of population genetics. Theoretical models used to provide a conceptual framework for population biology generally assume that populations are discrete, diploid, infinite in size and composed of randomly mating individuals with a Poisson distribution of progeny per parent. Natural populations of any species seldom satisfy all of these criteria. Populations of many aquatic plants are likely to violate all of the above conditions. The diversity among aquatic plants in ecology and growth form, however, prevents any broad generalization as to what constitutes a population and hence how they should be sampled for genetic studies.

At one end of the spectrum, annual species occurring in discrete habitats such as seasonal ponds, salt marshes, ditches or rice fields may be relatively straightforward to sample and, not surprisingly, considerable progress has been made in characterizing their population genetic structure (species of *Echinochloa, Eichhornia, Mimulus, Limnanthes, Salicornia* — Table 2). The difficulties in sampling these populations are the same as those encountered in studies of their terrestrial counterparts — what are the physical limits to a single population, and how should one deal with the subterranean population of dormant seeds?

Increasing difficulty is encountered in deciding what constitutes a population in perennial species of aquatic habitats. The problem ranges from minor in those species which grow in discrete clumps where the limits to genetically distinct individuals (genets) are easily identified (*Lythrum salicaria* L. — Haldane, 1936; *Crinum erubescens* Ait. — Manasse and Pinney, 1991) to difficult where clumps intermingle and clonal propagation obscures boundaries between genets (*Pontederia cordata* L. — Barrett et al., 1983; *Spartina patens* (Ait.) Muhl. — Silander, 1984), to near impossible in highly clonal species which regularly fragment during growth, resulting in the wide dispersal of individual genets throughout continuous water systems (*Azolla, Elodea, Lemna, Myriophyllum* — Sculthorpe, 1967). This latter group presents the most serious challenge to population geneticists and requires approaches more similar to those used in vagile parthenogenetic animals than plants. At the very least, investigators should explicitly report the sampling strategies used in terms of scale and sampling units.

The problem in defining the population unit for many aquatic species stems primarily from the occurrence of prolific clonal growth and the resulting difficulty in distinguishing between ramets and genets. While clonal propagation may be particularly well developed in many aquatic plants, the problem of separating the genetic individual (genet) from its constituent fragments (ramets) has long been a thorn in the side of workers studying terrestrial plants (Harper, 1977; Abrahamson, 1980). The use of genetic markers to distinguish genets can alleviate some of the problems, and a growing literature on the clonal demography of terrestrial plant populations has accumulated in recent years (Ellstrand and Roose, 1987). For some questions in population

TABLE 2

Electrophoretically detectable variation at isozyme loci in aquatic plants

Species[1]	Enzymes or loci[2]	*N*(*n*)[3]	Variation			Source
			A[4]	W[4]	H[5]	
(A) Emergent						
Aeschynomene indica L.	20	11 (19–46)	+	+	+	Carulli and Fairbrothers, 1988
Aeschynomene rudis Benth.	20	1 (25)	na	0	0	Carulli and Fairbrothers, 1988
Aeschynomene virginica (L.) B.S.P.	20	8(5–30)	+	+	+	Carulli and Fairbrothers, 1988
Aeschynomene sensitiva Sw. var. *amazonica* Rudd	5	11 (nr)	+	+	+	Hill et al., 1978
Aeschynomene sensitiva Sw. var *sensitiva* Rudd	5	10 (nr)	+	+	+	Hill et al., 1978
Alisma lanceolatum With.	16	2 (ML)	+	nr	+	Triest et al., 1988
Ambrosia maritima L.	13	5 (M)	+	+	+	Triest et al., 1989
Carex crinita Lam. var. *brevicrinis* Fern.	18	7 (15–20)	+	+	+	Bruederle and Fairbrothers, 1986
Carex crinita Lam. var. *crinita*	18	12 (15–20)	+	+	+	Bruederle and Fairbrothers, 1986
Carex gynandra Schwein	18	12 (15–20)	+	+	+	Bruederle and Fairbrothers, 1986
Carex mitchelliana M. Curtis	18	5 (15–20)	+	+	+	Bruederle and Fairbrothers, 1986
Decodon verticillatus (L.) Ell.	4	12 (30–90)	+ +	+ +	+	C.G. Eckert and S.C.H. Barrett, unpublished data, 1992
Echinochloa crus-galli (L.) Beauv.	31	11 (nr)	+	+ +	+	Barrett, 1988
Echinochloa microstachya (Wieg.) Rydb.	25	40 (15)	+	0	0	Barrett, 1992
Echinochloa oryzoides (Lam.) Hitchc. ex Chase	32	12 (15)	+	0*	0*	Barrett, 1988
Echinochloa phyllopogon (Lam.) Hitchc. ex Chase	25	12 (15)	+	+	0*	Barrett, 1988
Eichhornia paniculata (Spreng.) Solms.	21–27	23 (40–200)	+ +	+ +	+	Glover and Barrett, 1987; Husband and Barrett, 1991
Howellia aquatilis Gray	18	4 (30–60)	0	0	0	Lesica et al., 1988
Limnanthes alba Hartw. in Benth.	15	7 (160–300)	+ +	+	+	Jain, 1978
Limnanthes douglasii R.Br.	9	2 (10–40)	+	+ +	+	Kesseli and Jain, 1985
Lythrum tribracteatum Salzm. ex Ten.	18	6 (M)	+ +	+ +	+	Baker and Baker, 1976
Mimosa pigra L.	5*	5 (nr)	+	+	+	Hill et al., 1978
Mimulus caespitosus Greene	15	22 (36)	+ +	+ +	+	Ritland, 1989
Mimulus guttatus Fisch. ex DC.	6	5 (426–648)	+	+ +	+	Ritland and Ganders, 1987
Puccinellia × *phryganodes* (Trin.) Scriber and Merr.	7–12*	3 (5–15)	+ +	+ +	?	Jefferies and Gottlieb, 1983

Salicornia europaea L. (sensu stricto)	21–30	52 (20–30)	0*	0*	0*	Jefferies and Gottlieb, 1982; Wolff and Jefferies, 1987a,b
Salicornia ramosissima J. Woods	21–30	23 (20–30)	0*	0*	0*	Jefferies and Gottlieb, 1982; Wolff and Jefferies, 1987b
Salicornia rubra A. Nels.	21	12 (30)	0*	0	0	Wolff and Jefferies, 1987a
Spartina alterniflora Loisel.	S*	1 (M)	na	+ +	?	McMillan, 1980
Spartina patens (Ait.) Muhl.	31	3 (75–90)	+ +	+	+	Silander, 1984
Typha angustifolia L.	16*	23 (3–40)	0*	0	0	Lee and Fairbrothers, 1973; Lee, 1975; Sharitz et al., 1980
Typha domingensis Pers.	10*	83 (3–244)	0	0	0	Liu et al., 1978; Mashburn et al., 1978; Sharitz et al., 1980
Typha latifolia L.	2–10*	143 (3–277)	0*	0*	0*	Lee and Fairbrothers, 1973; Lee, 1975; Suda, 1976; Liu et al., 1978; Mashburn et al., 1978; Sharitz et al., 1980; Krattinger, 1983
Typha × *glauca* Godr.	2–10*	9 (3–40)	0*	0*	0*	Lee and Fairbrothers, 1973; Lee, 1975; Sharitz et al., 1980
Veronica peregrina L.	5*	3 (40)	+	+	+	Keeler, 1978
Zizania aquatica L.	17	24 (12–24)	+	+	+	Warwick and Aiken, 1986
Zizania palustris L.	17	9 (12–24)	+	+ +	+	Warwick and Aiken, 1986
(B) Floating-leaved						
Hydrocharis morsus-ranae L.	29	2 (20–76)	0	0	+	Scribailo et al., 1984
(C) Submergent						
Amphibolis antarctica (Labill.) Sonder and Aschers.	7*	1 (S)	na	0	?	McMillan et al., 1981
Amphibolis griffithii (J.M. Black) Den Hartog	7*	1 (S)	na	0	?	McMillan et al., 1981
Ceratophyllum demersum L.	14–16	S (20–25)	+ +	+	+	Les, 1986, 1989, 1991
Ceratophyllum echinatum Gray	16	S (25)	+ +	+	0*	Les, 1989, 1991
Cymodocea rotundata Ehrenb. and Hempr.	8*	3 (nr)	0	0	?	McMillan, 1981
Cymodocea serrulata (R.Br.) Aschers. and Magnus	8*	3 (nr)	0	0	?	McMillan, 1981

TABLE 2 (*continued*)

Species[1]	Enzymes or loci[2]	$N(n)$[3]	Variation			Source
			A[4]	W[4]	H[5]	
Enhalus acoroides (L.f.) Royle	S*	1 (S)	na	0	?	McMillan, 1982
Halodule pinifolia (Miki) Den Hartog	5*	S (nr)	0	0	?	McMillan, 1982
Halodule uninervis (Forsk.) Aschers.	5*	3 (nr)	0	0	?	McMillan, 1980
Halodule wrightii Aschers.	5*	6 (nr)	0	0	?	McMillan, 1980
Halophila decipiens Ostenfeld	7*	1 (nr)	na	0	?	McMillan and Williams, 1980
Halophila engelmannii Aschers.	S*	1 (nr)	na	0	?	McMillan, 1982
Halophila hawaiiana Doty and Stone	7*	1 (nr)	na	0	?	McMillan and Williams, 1980
Halophila johnsonii Eiseman	7*	1 (nr)	na	0	?	McMillan and Williams, 1980
Halophila minor (Zoll.) Den Hartog	7–8*	1 (S)	na	0	?	McMillan and Williams, 1980; McMillan and Bridges, 1982
Halophila ovalis (R.Br.) Hook. f.	7–8*	17 (S)	+	0	?	McMillan and Williams, 1980; McMillan and Bridges, 1982
Halophila stipulacea (Forsk.) Aschers.	7*	1 (nr)	na	0	?	McMillan and Williams, 1980
Heterozostera tasmanica (Mart. ex Aschers.) Den Hartog	S*	S (nr)	0	0	?	McMillan, 1982
Hydrilla verticillata (L.f.) Royle	8*	36 (1–S)	+	0*	?	Verkleij et al., 1983; Pieterse et al., 1985
Najas marina L. spp. *armata* (Lindb. f.) Horn and Rantzien	4*–24	5 (20–90)	+	+	+	Triest and Symoens, 1985; Triest, 1989
Najas marina L. spp. *intermedia* (Gorski) Casper	1*–24	31 (2–90)	++	++	+	Triest and Symoens, 1985; Triest et al., 1986; Van Geyt et al., 1987; Triest, 1989
Najas marina L. ssp. *marina*	1*–24	44 (7–90)	+	+	+	Triest and Symoens, 1985; Triest et al., 1986; Van Geyt et al., 1987; Triest, 1989
Phyllospadix scouleri S. Wats.	10*	S (5–15)	+	0	?	McMillan and Phillips, 1981
Phyllospadix serrulatus Rupr. ex Aschers.	10*	2 (5–15)	0	0	?	McMillan and Phillips, 1981
Phyllospadix torreyi Hook.	10*	S (5–15)	0	0	?	McMillan and Phillips, 1981
Podostemon ceratophyllum Michx.	19	11 (21)	+	0*	0*	Philbrick and Crow, 1992
Posidonia australis Hook.	8*	1 (S)	na	0	?	McMillan et al., 1981
Posidonia sinuosa Cambridge and Kuo	8*	1 (S)	na	0	?	McMillan et al., 1981

Potamogeton pectinatus L.	5*	7 (S)	+	0	?	Van Wijk et al., 1988
Syringodium filiforme Kütz.	5*	8 (nr)	0	0	?	McMillan, 1980
Syringodium isoetifolium (Aschers.) Dandy	5*	2 (nr)	0	0	?	McMillan, 1980
Thalassia hemprichii (Ehrenb.) Aschers.	5*	3 (M)	0	0	?	McMillan, 1980
Thalassia testudinum Banks ex König	5*–29	20 (M)	+	+	+	McMillan, 1980; D. Porter and J. L. Hamrick, unpublished data, 1992
Thalassodendron ciliatum (Forsk.) den Hartog	5*	S (nr)	0	0	?	McMillan, 1980
Vallisneria americana Michx.	16	nr(nr)	+	+	+	Laushman, 1993
Zostera capensis Setchell	7*	1 (F)	na	0	?	McMillan et al., 1981
Zostera capricorni Aschers.	7*	1 (F)	na	0	?	McMillan et al., 1981
Zostera marina L.	7–17*	M (3–40)	+	+	+	Gagnon et al., 1980; McMillan, 1982; Laushman, 1993
Zostera muelleri Irmisch ex Aschers.	7*	1 (F)	na	0	?	McMillan et al., 1981
Zostera novazelandica Setchell	7*	1 (F)	na	0	?	McMillan et al., 1981
(D) Free-floating						
Lemna gibba L.	17	28 (1)	++	na	?	Vasseur et al., 1991
Lemna minor L.	17	4(1)	++	na	?	Vasseur et al., 1991
Spirodela polyrhiza (L.) Schleid.	17	4 (1)	++	na	?	Vasseur et al., 1991

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[1] Species have been classified by life form following Sculthorpe (1967).

[2] Figures marked with asterisks are number of enzyme systems resolved, when no interpretation of the number of loci involved was attempted.

[3] Number of populations examined (*N*) is given with number of individuals sampled per population (*n*). *In some cases, sample sizes were not reported* (*nr*) *or reported only qualitatively* (*M, many; S, several; F, few*).

[4] The amount of variation within (W) and among (A) populations is presented qualitatively as none (0), negligible (0*), some (+) or considerable (++). In cases where only one population or only one individual per population was sampled, information on among population differentiation or variation within populations, respectively, was not available (na).

[5] Heterozygosity (H) is presented as either present (+), negligible (0*) or absent (0). In cases where no genetic interpretation of isozyme bands was attempted, the level of heterozygosity is unknown (?).

biology, however, the distinction between ramets and genets is not critical, and considerable progress has been made in demographic studies of plant parts using modular approaches (Caswell, 1985; Sackville Hamilton et al., 1987). Nevertheless, in evolutionary studies where measurement of parameters such as effective population size, outcrossing rates and variance in survival and reproductive success of individual genotypes are central to the issues under investigation, rampant clonal propagation presents a major challenge.

EFFECTIVE POPULATION SIZE

Even if the number of genetic individuals can be determined in populations of aquatic plants using genetic markers, this measure of population size is unlikely to be directly relevant for evaluating the mechanisms of evolutionary change. How a population responds genetically to selective pressures is better predicted using estimates of the effective population size (N_e) which represents the number of individuals in an 'ideal' population with the same variance in allele frequencies or level of inbreeding as observed in the actual population (Wright, 1931; Kimura and Crow, 1963). Disparities between measures of N and N_e stem from temporal variation in population size, gene flow, unequal sex ratios, non-random mating, variation in fecundity among individuals, overlapping generations, and skewed size and age structures (Crow, 1954). Measures of N_e can be derived using ecological approaches based on estimates of the number of breeding individuals in a population and incorporating quantitative estimates of the sex ratio, mating system and variation in reproductive output among individuals (Begon et al., 1980). Alternatively, a variety of genetic approaches have been used (Dobzhansky and Wright, 1941; Hill, 1981; Chakraborty and Neel, 1989). These methods arise from the direct relationship between N_e and genetic variability, and are particularly appealing since estimates are inferred directly from the genes themselves in a retrospective manner.

Unfortunately, estimates of N_e in the plant literature are particularly sparse (Jain and Rai, 1974; Heywood, 1986; Fenster, 1991a,b), although what data are available suggest that N_e is usually much smaller than N. This is supported by a recent attempt to estimate N_e using both ecological and genetic approaches in ten populations of the tristylous, annual, emergent aquatic *Eichhornia paniculata* (Spreng.) Solms (Pontederiaceae) from Brazil (Husband and Barrett, 1992). N_e was inferred from temporal changes in allele frequency at isozyme loci using the method of Waples (1989) and from five demographic variables including the number of individuals in populations (N), year to year fluctuations in N, variance in flower number per individual, style morph frequencies and the selfing rate. The average N_e based on isozyme data was 15.8 (range 3.4–70.6), a fraction (mean $N_e/N=0.106$) of the census population size (mean $N=762.8$, range 30.5–5040). Temporal variation in

N and variance in flower number among individuals each reduced N_e to about half of N, whereas variation in morph frequencies and self-fertilization had relatively minor effects. All estimates of N_e based on demographic variables were consistently larger than those obtained from genetic data; the two kinds of estimates were, however, in general agreement when all demographic variables were combined into a single measure.

The low values of N_e estimated for *E. paniculata* indicate that genetic drift is likely to play a dominant role in natural populations of this species. This raises the question of whether low values of N_e and hence opportunities for genetic drift are likely to occur in other aquatic plants. *Eichhornia paniculata* occurs in seasonal ponds and ditches and relies exclusively on seed for population persistence and dispersal. This life history is common in many annual taxa of seasonally inundated environments such as *Ammania, Dopatrium, Echinochloa, Heteranthera*, and *Rotala*. Population sizes in annual species vary greatly depending on available moisture and the coexistence of perennial competitors. Moreover, two other features of annuals are likely to reduce N_e from N: first, they are highly plastic in their reproductive output creating the potential for much variation in reproductive success among individuals (Heywood, 1986); second, their life history is commonly associated with high rates of self-fertilization. Since many annual aquatic plants are adapted to ephemeral environments, regular population bottlenecks and cycles of colonization and extinction are likely to be a feature of their life histories. This makes it particularly likely that effective population size will often be small and hence genetic drift will play an important role in influencing population genetic structure.

Genetic drift associated with small population size is not only a feature of annual populations of selfers living in ephemeral habitats. Reductions in population size are likely to occur in most species during episodes of colonization, habitat degradation or simply from restrictions on the size of suitable habitat patches. Loss of genetic variation from small populations of a long-lived, outcrossing, emergent aquatic is exemplified by data from North American populations of tristylous *Lythrum salicaria* (Lythraceae). A native of Eurasia, *L. salicaria* has proved to be an aggressive colonizer of disturbed wetland habitats in eastern central North America over the last century (Thompson et al., 1987). A survey of 102 populations in eastern and central Ontario, Canada, indicates a significant negative correlation between population size and the loss of style morphs (Eckert and Barrett, 1992) (Fig. 1). Small populations were more likely to lack one of the style morphs than larger populations. In addition, more than 30% of the populations surveyed consisted of less than 50 plants indicating that small population size is an important feature of this species, at least in its adventive range.

Estimating effective population size in clonal aquatic plants, particularly those with fragmentary growth patterns, will be particularly difficult since

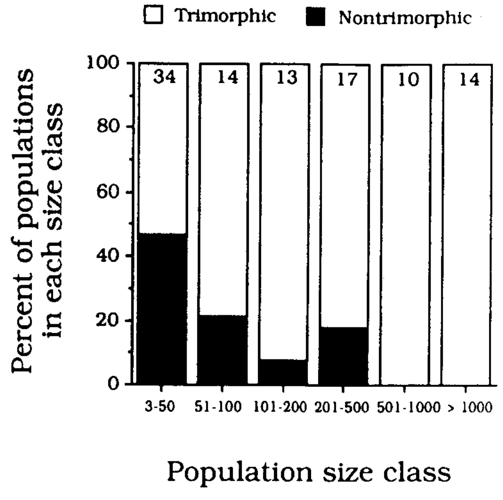

Fig. 1. Population size and style morph number in populations of tristylous *Lythrum salicaria* from Ontario, Canada. Data are based on a survey of 102 populations conducted during 1988 and 1989. In each population, the presence of the three style morphs, long-, mid- and short-styled, was determined from a sample of flowering individuals. Non-trimorphic populations lacked one or two style morphs. The proportion of populations lacking a morph was significantly higher in the smaller size classes. Sample sizes for each class are indicated (after Eckert and Barrett, 1992).

population limits are hard to define. Water-dispersed vegetative fragments may effectively unite spatially isolated colonies within a water system so that large areas may be considered a single breeding unit. However, since sexual reproduction is often infrequent in clonal species (Table 1 and below), opportunities for gene exchange may be quite limited. The influence of clonal propagation on effective population size is a largely unexplored area (but see Gliddon et al., 1987) and theoretical work is needed to determine how different types of clonal growth (e.g. guerilla versus phalanx, fragmentary and non-fragmentary — see Harper, 1985) influence N_e.

REPRODUCTIVE SYSTEMS

No other group of vascular plants displays such a wide diversity of reproductive systems as are found in aquatic plants. Virtually all the major flowering plant breeding systems are represented among aquatic plants, including the various forms of dicliny (e.g. dioecy, monoecy), self-incompatibility (e.g. multiallelic systems, distyly, tristyly), autogamy and agamospermy, and these are often combined with a wide range of methods for clonal propagation including rhizomes, runners, stolons, tubers and turions. While the developmental basis and general morphology of organs used for clonal propagation are similar to those in terrestrial plants, it has been suggested that the frequency of clonal reproduction in aquatic plants may be higher (Sculthorpe, 1967; Hutchinson, 1975). This has led to the suggestion that "the excessive vegetativity of water plants acts, in all probability, as a deterrent to sexual reproduction" (Arber, 1920). Comparative data on the reproductive systems of related aquatic and terrestrial taxa would be most useful in examining this idea.

Most of the pollination systems observed in terrestrial plants involving both wind (Cook, 1988) and insect vectors (C.T. Philbrick, unpublished data, 1992) are found in aquatic plants. In addition, many submerged aquatic plants exhibit hydrophily, a pollination system unique to aquatic plants (Cox, 1988; Philbrick, 1991). A recent symposium on the reproductive biology of aquatic plants reviewed many aspects of the pollination biology and breeding systems of particular aquatic groups (see Philbrick, 1988). However, many of the interesting features of both aerial and hydrophilous pollination in aquatic plants remain uninvestigated, or have only begun to receive much quantitative study. For instance, Hutchinson (1975) points out an observation made by Nehemia Grew more than three centuries ago that many aquatic plants with aerial, insect pollination tend to possess white flowers in contrast to the colored flowers of related terrestrial groups (e.g. *Ranunculus*). Unfortunately, little is known of the comparative pollination biology of groups including both terrestrial and aquatic taxa.

Another topic of particular interest is the occurrence in many aquatic species of pseudocleistogamy (e.g. *Hydrothrix gardneri* J. Hook. — Goebel, 1913; *Ottelia alismoides* (L.) Pers. — Ernst-Schwarzenbach, 1956), where some normally aerial flowers develop underwater and because they never fully open are self-fertilized. The evolution of mixed-mating systems in plants has been at the center of considerable debate among theoreticians throughout the last decade (reviewed in Barrett and Eckert, 1990) hence terrestrial species producing both self-pollinating cleistogamous and outcrossing chasmogamous flowers have received much attention (Schoen and Lloyd, 1984; Waller, 1986). Mixed floral strategies have also provided experimental tools for developmental biologists (Lord, 1981) and it would seem likely that any of the scattered reports of cleistogamy and pseudocleistogamy in aquatic plants (see Sculthorpe, 1967, pp. 290–291) would repay more detailed investigation.

Mating-system measurement

During the past two decades much progress has been made in obtaining quantitative estimates of various mating parameters from natural plant populations using electrophoretic techniques (reviewed in Brown et al., 1990b). These measurements have enabled a more accurate assessment of the mating systems of populations, and have shown that earlier inferences based on observations of floral biology and pollinator behavior may be misleading. Along with the use of electrophoretic techniques has been the development of statistical models for the estimation of specific mating parameters such as the rates of self-fertilization, biparental inbreeding, correlated mating and multiple paternity (reviewed in Brown, 1990). The study of plant mating systems has also involved much theoretical work investigating the conditions under which various systems of mating are likely to evolve (reviewed in Uyenoyama and Antonovics, 1987; Hedrick, 1990; Holsinger, 1992). Today, a sizeable body of data on outcrossing rates in natural populations is available for many species of terrestrial plants. This has enabled some generalizations to be made on the associations between mating system, life form and pollination system (Barrett and Eckert, 1990).

Although quantitative estimates of mating system are available for some aquatic plants, these almost exclusively involve annual emergent species (*Eichhornia paniculata* — Barrett and Husband, 1990a) or plants of wet environments (*Limnanthes alba* Hartw. in Benth. — Jain, 1978; *Mimulus guttatus* Fisch. ex DC. — Ritland and Ganders, 1987). At present we know of no mating system estimates for any species in the remaining aquatic groups. This is unfortunate since the lack of data hampers interpretation of other genetic information on population structure and our ability to assess the potential for gene flow and population differentiation.

Comparison of mating-system estimates between species with hydrophilous pollination and those with wind pollination would allow comparative assessment of patterns of mating-system evolution associated with abiotic pollen transport. Among terrestrial species, there appears to be a difference in the patterns of mating-system variation between insect and wind-pollinated groups. The distribution of outcrossing rates among species is more strongly bimodal in the latter than in the former (Aide, 1986; Barrett and Eckert, 1990). Aide (1986) suggested that since wind is a fairly reliable pollen vector, anemophilous species could achieve either predominant selfing or outcrossing, the two theoretically stable end-points of mating-system evolution (Lande and Schemske, 1985). Insect-pollinated species, on the other hand, would show much more variation in outcrossing rates within and among species due to spatial and temporal vagaries of pollinator service. Clearly, comparison of the distribution of outcrossing rates between entomophilous and hydrophilous aquatic plants would provide an independent test of Aide's hypothesis.

A major technical difficulty associated with estimating mating-system parameters in clonal aquatic plants involves the highly structured nature of their populations. Like other population genetic models, the mixed-mating model, upon which statistical techniques for estimating mating parameters are based, assumes an ideal population structure (Clegg, 1980). First, all parents should practice the same combination of self-fertilization and random mating. Second, the population should not be spatially or temporally substructured with respect to the marker loci used, and outcrossed matings should be random such that all maternal parents experience the same pollen pool. Finally, there should be no association (i.e. disequilibrium) among alleles at different marker loci.

Obviously extensive clonal reproduction in aquatic plant populations could result in violation of these assumptions. Populations consisting of a few genetically distinct clones may be substructured spatially (*Spartina patens* (Ait.) Muhl. — Silander, 1984) or temporally (*Phragmites australis* (Cav.) Trin. ex Steudel — Björk, 1967) such that mating will not be random and pollen allele frequencies may vary widely among parents. Limited clonal diversity within populations may also result in significant disequilibrium among marker alleles. Another problem is that highly clonal populations may lack sufficient variation at isozyme loci with which to study the mating system (Table 2). Despite these problems, electrophoretic data from clonal terrestrial species (reviewed in Ellstrand and Roose, 1987) suggest that genetic uniformity and/or extreme substructuring may not characterize all clonal aquatic plants. Violation of the idealized mixed-mating model may be remedied by the use of more flexible estimation procedures incorporating some of the troublesome features of clonal populations. Lack of variation at isozyme loci, however, presents a more serious problem and may require the use of more variable molecular markers at the DNA level (Clegg, 1990).

Mating patterns in clonal species

If mating systems can be successfully measured, what levels of outcrossing are likely to characterize populations of clonal aquatic plants? Outcrossing mechanisms may be compromised by extensive clonal spread, particularly in species which are hermaphroditic and self-compatible. Large clone size increases the likelihood of geitonogamous pollen transfer leading to self-fertilization and the potentially harmful effects of inbreeding (Silander, 1985). Despite observations of pollinator behavior that support this notion (Handel, 1985), the relationship between clone size and selfing has, to our knowledge, never been tested explicitly using experimental approaches. Moreover, there are few mating-system estimates from highly clonal species.

Extensive clonal spread may not always be associated with high levels of self-fertilization. Populations of the self-compatible, emergent aquatic *Decodon verticillatus* (L.) Ell. (Lythraceae) are often highly clonal; mating-system estimates for three populations from Ontario, however, indicate relatively low selfing rates (mean, 0.20; range, 0.14–0.28 — C.G. Eckert and S.C.H. Barrett, unpublished data, 1992). One explanation for this result involves the potential occurrence of physiological mechanisms resulting in facultative or 'cryptic' self-incompatibility in *D. verticillatus*. Although this species is highly self-compatible in that self-pollinations yield almost as many seeds as cross-pollination (Fig. 2), studies in several apparently self-compatible species using

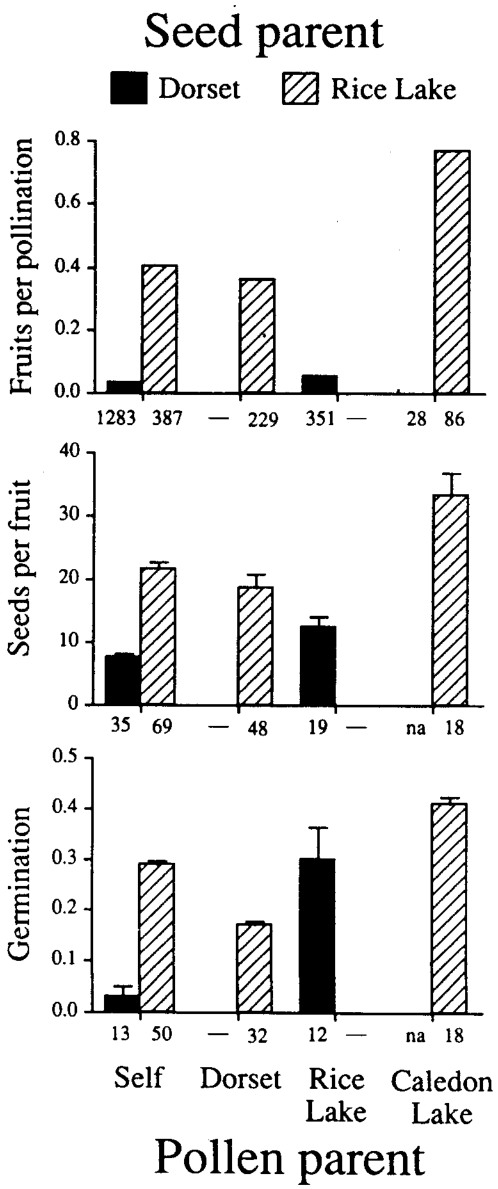

Fig. 2. Sterility in a northern population of *Decodon verticillatus* from Dorset, Canada. Data are from controlled crosses and a germination experiment conducted on five plants from each of three Ontario populations: Dorset, Rice Lake and Caledon Lake. Plants from Dorset and Rice Lake were used as both seed and pollen parents, plants from Caledon Lake were used as pollen parents only. Only self-pollinations and between-population crosses were conducted. Sample sizes are indicated below each bar. Sample sizes for the proportion of seeds germinated are the number of replicate pots containing 20 seeds each. Bars are one standard error (C.G. Eckert and S.C.H. Barrett, unpublished data, 1992).

mixtures of genetically marked self and cross pollen, have revealed a competitive disadvantage to self pollen (e.g. *Eichhornia paniculata* — Glover and Barrett, 1986). Thus, even if the availability of outcross pollen in the middle of large clonal patches is low compared with self pollen, outcrossing rates may be disproportionately high. Alternatively, mating patterns of flowers in different parts of extensive clones may be strikingly different. Such heterogeneity may require modifications to existing estimation methods which assume that outcrossing rates are uniform throughout a population. Finally, in geographically marginal populations of clonal species such as *Eichhornia crassipes* (Mart.) Solm. (Barrett, 1980b) or *Decodon verticillatus* (Eckert and Barrett, 1992) every seed is likely to be the product of self-fertilization despite insect-mediated cross-pollination because populations are frequently composed of single clones.

Clonal propagation and sterility

Extensive clonal reproduction may also influence a species' reproductive strategy by affecting its ability to reproduce sexually. Several authors have suggested that the sexual capacity of a population may decline as somatic mutations affecting sexual function and/or early life-history stages accumulate in clonal lineages (Buss, 1983; Gill and Halverson, 1984; Silander, 1985; Klekowski, 1988a). The rate at which somatic variants are fixed in clonal populations depends on the frequency of sexual reproduction, the strength of selection against the somatic variants, and a variety of morphological and ontogenetic factors (Klekowski, 1988b). While somatic variation has been examined and used by plant breeders for some time (Hartmann and Kerster, 1975), studies investigating the importance of somatic mutation in natural populations are few (Breese et al., 1965; Whitham and Slobodchikoff, 1981; Klekowski, 1988a). The diverse array of mechanisms for clonal propagation in aquatic plants provides excellent opportunities for empirical investigation, especially considering the numerous reported instances of infrequent flowering and low seed set in aquatic species (Arber, 1920; Sculthorpe, 1967; Hutchinson, 1975; Les, 1988).

The causes of limited sexual reproduction in clonal aquatic plants need more thorough investigation. In particular, it is crucial in our view to distinguish whether the lack of sexual reproduction results from ecological or genetic factors or an interaction of both. The term sterility is frequently used in a general way to describe the absence of sexual reproduction in a particular species often in reference to a particular population, regardless of its underlying basis. We think, however, that this term should be restricted to refer to cases where sexual reproduction is prevented because of either the build-up of mutations impairing reproductive function or meiotic irregularities associated with polyploidy. Absence of sexual reproduction in clonal aquatic plants can also occur because of: (1) unsuitable ecological conditions for seed maturation or germination (*Acorus calamus* L. in the northeastern USA — Jervis and Buell, 1964), or seedling establishment (*Eichhornia crassipes* in California — Barrett, 1980a,b); (2) the presence of a single mating type in a population or region in self-incompatible (*Butomus umbellatus* L. in Sweden and northern USA — Hutchinson, 1975 and Cook, 1988, respectively), heterostylous

(*Lythrum flagellare* Shuttl. ex Chapm. in Florida, USA — C.G. Eckert, personal observation, 1988; *Nymphoides indica* (L.) Griseb. in the Lower Amazon — Barrett, 1980c; *Pontederia rotundifolia* L. in Costa Rica — Barrett, 1977) or dioecious species (*Egeria densa* Planchon and *Elodea canadensis* Michx. in Europe — Sculthorpe, 1967; *Hydrilla verticillata* (L.f.) Royle in North America — Verkleij et al., 1983; *Myriophyllum brasiliense* Camb. in California — Baker, 1972; *Stratiotes aloides* L. in Europe — Hutchinson, 1975); (3) sterility arising from hybridization (*Potamogeton* spp. — Hutchinson, 1975; *Acorus calamus* in Europe — Wulff, 1954). Few studies, however, have attempted to determine the relative importance of genetic and ecological factors in impairing sexual function in natural populations of clonal aquatic plants.

We have recently investigated this phenomenon in *Decodon verticillatus*. Field observations indicated that in many populations at the northern periphery of the range seed production is low or non-existent. One northern population at Dorset, Ontario, Canada has shown virtually no seed set over the past 3 years, despite high levels of flower production. This could be due to environmental effects such as lack of pollinators and/or low temperatures for fertilization and seed maturation; however, data from controlled crosses using plants from this and other populations conducted in a glasshouse environment provided evidence of sterility (Fig. 2). Self-pollinations conducted on ramets collected from Dorset resulted in extremely low fruit and seed set as well as poor seed germination compared with self-pollinations conducted on material from another population located further south at Rice Lake, Ontario. Further, comparisons of the performance of plants from these two populations as both seed and pollen parents indicated that the genetic factors involved, negatively affected both male and female reproductive function in plants from Dorset. The absence of sexual reproduction in northern populations of *D. verticillatus* is associated with extensive genetic uniformity at isozyme loci (C.G. Eckert and S.C.H. Barrett, unpublished data, 1992) suggesting that many populations may consist of single clones maintained by vegetative propagation. Indeed, a study of the patterns of style morph variation occurring at the northern limits of the range of this tristylous species in Michigan, Ontario and New England revealed that more than 40% of populations surveyed were composed of a single style morph and thus potentially, single clones (Eckert and Barrett, 1992).

Mating-systems and life history

Surveys of outcrossing rates and information on the distribution of breeding systems among different taxonomic and ecological groups in terrestrial plants generally indicate a relationship between plant longevity, size and mating patterns (Barrett and Eckert, 1990). As originally pointed out by Darwin (1859), large organisms such as trees are mostly outcrossing whereas short-lived species, particularly annuals, frequently display moderate to high levels of self-fertilization. Similar patterns occur in aquatic plants. Most annual species are self-compatible and many are highly autogamous. In contrast, large clonal perennials frequently possess breeding systems that are believed to promote outcrossing (e.g. heterostyly, dioecy). Les (1988) has suggested that these associations are particularly evident in hydrophilous taxa (see also Cox, 1988). Dioecy tends to be characteristic of perennial species, especially those in which most reproduction is through clonal propagation. Annual species, on the other hand, show a higher frequency of sexual reproduction and tend to possess monoecious or hermaphrodite breeding systems. Les goes on to pose the hypothesis that dioecy in clonal perennial hydrophiles is simply a relictual trait persisting from terrestrial ancestors and is of little adaptive significance in contemporary populations.

There are two aspects of Les' hypothesis that require closer examination. The first concerns the apparent association between dioecy, clonal reproduction and hydrophilous pollination. There have been repeated attempts in terrestrial plants to show that dioecy is associated with particular features such as fleshy fruits, woody growth form, inconspicuous flowers and island habitats (reviewed in Thomson and Brunet, 1990). While there is some support for all these correlations, few have stood up to more rigorous applications of the comparative method (Charlesworth, 1985; Thomson and Brunet, 1990). Establishing an association between dioecy and life history in hydrophilous aquatic plants will require comparative analysis (Pagel and Harvey, 1988). The second issue involves the sequence of evolutionary events responsible for the association between particular traits. Is it dioecy followed by hydrophily, or the reverse sequence?

Distinguishing between alternative sequences is best attempted using phylogenetic analysis as illustrated by Donoghue (1989). This approach requires phylogenies including hydrophilous taxa along with their terrestrial relatives. Because of extensive convergent evolution in morphology among hydrophilous taxa, phylogenies based on molecular characters such as restriction fragment length polymorphisms (RFLPs) or DNA sequence data are required to avoid some of the homoplasy associated with convergent evolution of vegetative and reproductive characters in aquatic groups (Eckenwalder and Barrett, 1986). Once phylogenies have been constructed, the traits of interest are mapped onto the tree using parsimony (Soltis et al., 1992). Les' hypothesis would be supported if hydrophily generally appeared as a derived condition with respect to dioecy.

GENE FLOW AND MIGRATION

Gene flow is the movement of alleles from one population to another and occurs through several different mechanisms, including migration of individuals, dispersal of gametes or recolonization of entire populations after extinction (reviewed by Slatkin, 1985a). The term migration is often used synonymously with gene flow in the population genetic literature whereas aquatic botanists usually use it with reference to the movement of species rather than genes. Gene flow is an important evolutionary process since it determines the degree to which local populations behave as independent evolutionary units. Local differentiation caused by genetic drift or selection is diminished by recurrent gene flow from other populations. Alternatively, if gene flow occurs episodically and involves few individuals, founder effects may enhance differentiation. Ultimately, the consequences of gene flow will depend on the geographic structure of populations, and the extent and scale of gene movement among them. Here, we discuss ways of measuring gene flow and consider the important features of aquatic plants that influence its evolutionary significance.

Measurement of gene flow

Gene flow is defined in population genetic theory by the parameter m, which is the proportion of individuals in a population that are immigrants each year (Wright, 1931). It can be measured by observing migration directly or by inferring past levels of gene flow from spatial patterns of genetic variation (Slatkin, 1985a). Gene flow can be inferred directly from the activity of pollinators (Levin and Kerster, 1974) or from the dispersal of marked propagules or genes (Ellstrand et al., 1989). These measures are useful only to the extent that they are measures of gene dispersal, not gene establishment (Fenster, 1991a,b). Alternatively, gene flow can be inferred from the observed geographic distribution of alleles. Several different methods are available; however, we will only discuss the most widely used ones.

Wright (1951) showed that for an infinite number of local populations the degree of genetic differentiation among populations, measured as F_{ST} (standardized variance in allele frequencies), is related to m by the formula:

$$F_{ST}=\frac{1}{(1+4Nm)}$$

where N is the effective population size. Under the assumption that alleles are selectively neutral, this method is reasonable when several gene loci are screened, and is robust to variation in mutation rates and whether gene flow is random (island model) or among neighboring populations (stepping stone model, Slatkin and Barton, 1989). Nei (1972) suggested that estimates of m could also be inferred from other measures of differentiation, such as genetic distance. Slatkin (1985b) later developed a method based on the frequency of rare alleles in populations. He found that the frequency of alleles found in only a single population was dependent on the average level of gene flow, regardless of selection or mutation rates among loci. Slatkin's method has since been used by several workers to estimate values of m for terrestrial plant populations (Soltis and Bloom, 1986; Golenberg, 1987; Soltis and Soltis, 1987).

Gene flow in aquatic plants

Whether aquatic plants establish after dispersal may depend on the propagules involved. To the extent that dispersal involves vegetative fragments, a relatively high proportion of dispersal events may lead to successful colonizations since such propagules can often root in the water column before actually reaching a site suitable for establishment. In addition, subsequent population growth does not depend on the presence of compatible mates for sexual reproduction. Clonal growth can have important consequences for gene flow. By increasing the likelihood of establishment, dispersal by clonal propagules should enhance the rates of gene flow among aquatic plant populations. At the same time, however, if the source of dispersing propagules is comprised a limited number of clonal genotypes and if sexual reproduction is limited, then genetic diversity in the migrant pool will be much lower than in sexually reproducing species. This effectively leads to a reduction in gene flow among populations.

Another feature of many aquatic plants that may influence the magnitude and patterns of gene flow is habitat distribution. Most aquatic habitats within continental land masses are not continuously distributed, but occur as discrete islands in a terrestrial landscape. As a result, populations are frequently isolated from one another and may be restricted in size. These physical limits will decrease the probability of gene flow among populations and thus enhance differentiation through genetic drift. Populations of *Eichhornia paniculata* occur in temporary pools and ditches in the otherwise arid region of northeastern Brazil. Our surveys of genetic variation in this species have suggested that gene flow among these discrete populations is indeed restricted. Based on surveys of isozyme variation at 25 loci in 44 populations, the average genetic distance between pairs of populations was 0.10, a value significantly higher than the mean value of 0.05 reported for other conspecific populations (Gottlieb, 1977; Crawford, 1990). Assuming that populations are at drift-migration equilibrium, this amount of differentiation would result from levels of gene flow of $Nm = 0.30$. Wright (1931) showed that if Nm is less than 1, that is each population receives less than one migrant per generation, there will be significant differentiation among populations.

Since the average effective population size (N_e) in this species has been estimated as 15.8 (see above), we can infer that $m = 0.02$, that is at any given time only 2% of the population are immigrants. These average levels of gene flow assume that migrants are chosen at random from all populations examined. However, an examination of average genetic distance for population pairs at six geographic distance classes indicates that after about 100 km the average genetic distance between populations increases as the geographic distance separating them increases (Fig. 3). This suggests that most gene flow occurs between neighboring populations and that long-distance gene flow, while of biogeographic importance (see below), is of less significance to local population genetic structure.

The distribution of aquatic habitats has also influenced the patterns of genetic differentiation among populations of *Mimulus caespitosus* Greene, a clonal perennial of mountain streams (Ritland, 1989). While *M. caespitosus* readily produces seed, observations indicate the species can also disperse by vegetative fragments. An electrophoretic analysis revealed strong differentiation (Nei's $D=0.07$) among 22 populations sampled in the Cascade mountains of Washington, USA. Moreover, populations from the same stream system showed lower differentiation compared with populations from the same mountainside, mountain or region. This suggests that gene flow occurs predominantly within streams, as might be expected when dispersal is water mediated. We might further anticipate unidirectional gene flow in populations associated with running waters, however, the exact pattern of within-stream differentiation one would predict is not obvious. Would populations located further downstream be more or less variable than populations upstream? Would genetic distance increase along the course of a stream, or is dispersal

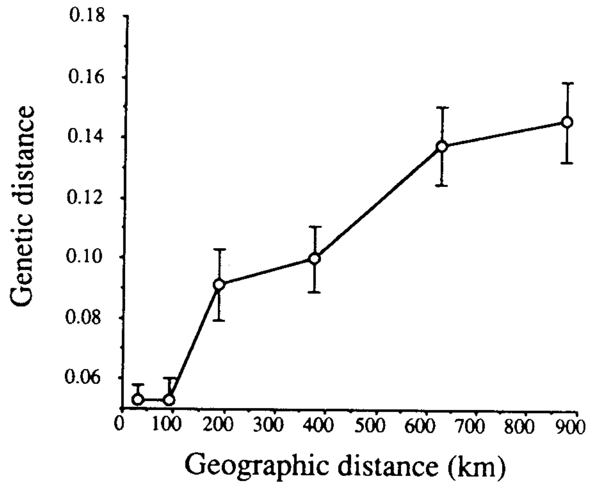

Fig. 3. Relationship between genetic distance and geographic distance in a sample of 44 Brazilian populations of *Eichhornia paniculata*. Genetic distance was measured following Nei (1972) using data from 25 allozyme loci. All pairwise genetic distance measures were classified into six geographic distance categories. To avoid the non-independence involved in using all pairwise comparisons, each population was used once in the calculation of mean distance for a given class. Each mean is based on between 15 and 20 distance values. Bars are one standard error. The overall correlation between genetic and geographic distance was significant using a permutation test ($K_c=16792$; $P<0.0001$; B.C. Husband and S.C.H. Barrett, unpublished data, 1992).

random with respect to distance in running water? Unfortunately, little theoretical work is available to guide predictions with respect to these issues. Furthermore, the limited empirical data are equivocal. A statistical analysis used by Ritland (1989) failed to reveal any effect of unidirectional gene flow on the pattern of genetic variation in *M. caespitosus.* Qualitative interpretation of genetic data in three amphibious species of leguminaceous shrubs inhabiting river edges in Brazil, on the other hand, gave some indication of genetic structuring with respect to water flow (Hill et al., 1978). In any case, the potential peculiarities of gene flow in running waters clearly warrant further attention.

Genetic consequences of long-distance dispersal

The extensive geographical ranges of many aquatic plants have been widely recognized since Darwin's time (Darwin, 1859; Ridley, 1930; Good, 1964; Cook, 1987; Sauer, 1988). Sculthorpe (1967) estimated that 60% of aquatic species have ranges spanning more than one continent. The widespread distribution of aquatic plants indicates a well-developed facility for long-distance dispersal of seed and vegetative parts over inhospitable territory such as land and sea. Unfortunately, few data are available on the mechanisms of long-distance dispersal in aquatic plants, although it is generally assumed that migratory birds and, more recently, humans are the major agents responsible for most intercontinental transport. Since long-distance dispersal events, especially via biotic agents such as birds, are likely to be infrequent their study defies quantitative analysis. However, in cases where human introduction has occurred in recent times, opportunities are provided to study genetic and evolutionary changes that occur following introduction. Cook (1985) has recently reviewed range extensions in 172 aquatic vascular plants, many of which are likely to provide fertile ground for microevolutionary investigations. Of particular interest are dispersal events associated with the migration of rice weed floras since in some cases historical information on the source of rice stocks containing weed seed contaminants is available (Barrett and Seaman, 1980; McIntyre and Barrett, 1985). Such information has been used to interpret the genetic consequences of colonization in annual species of *Echinochloa* introduced to Australian rice fields from California (Barrett, 1988,1992).

Some long-distance dispersal events in aquatic plants can have profound ecological consequences, as exemplified by the rapid invasion of many free-floating aquatic weeds into suitable habitats following their accidental introduction (e.g. *Eichhornia crassipes, Pistia stratiotes* L., *Salvinia molesta* Mitchell — Sculthorpe, 1967; Barrett, 1989; Ashton and Mitchell, 1989). However, whether dispersal events in aquatic plants have any evolutionary consequences depends on whether local adaptation following introduction occurs. Three factors need to be taken into account in assessing this possibility: (1) the amount and kinds of genetic variation in the founding genotype(s); (2) the opportunities for sexual reproduction in the introduced region; (3) the ecological characteristics of their adopted homes with regards to the types of selection pressures to which they are exposed. In many cases of the adventive spread of clonal aquatic weeds, the limited occurrence of sexual reproduction effectively precludes any opportunities for adaptive responses in the alien range.

Several studies of genetic variation in adventive populations of aquatic weeds indicate that they are genetically depauperate at isozyme loci (e.g. *Hydrilla verticillata* — Verkleij et al., 1983; *Hydrocharis morsus-ranae* L. — Scribailo et al., 1984; *Echinochloa microstachya* (Wieg.) Rydb., *Echinochloa oryzoides* (Lam.) Hitchc. and Chase — Barrett, 1988, 1992). Care is required in interpreting such patterns, however, particularly if one is attempting to make evolutionary deductions. Several examples serve to illustrate this point. *Monochoria vaginalis* (Burm. f.) Presl. and *Heteranthera limosa* (Sw.) Willd. (Pontederiaceae) are both annual weeds of rice that have been introduced to rice fields in California (Barrett and Seaman, 1980). The former is a common Asian rice weed restricted in North America to the vicinity of Biggs Rice Research Station, Butte County, California, where it has flourished but not spread for more than 35 years. One hypothesis to account for its inability to invade other rice-growing areas within the state is a possible lack of genetic variability. *Heteranthera limosa* is also a common weed of rice occurring in the southern USA and other rice-growing areas of Central and South America. Since its initial discovery in California in 1948, the species has spread throughout much of the rice-growing region. If the amount of genetic variation in founding populations has influenced the subsequent spread of these rice weeds, one would predict higher levels of diversity in populations of *Heteranthera limosa* compared with *Monochoria vaginalis*. However, our electrophoretic studies have revealed no variation at 25 (*Monochoria vaginalis*) and 26 loci (*Heteranthera limosa*) surveyed in 75 plants sampled from two populations of each species. Clearly, the isozyme data do not support the genetic hypothesis to explain differences in the spread of these species following their introduction to California. Isozymes are, however, only one assay of genetic variation, and it is possible that differences in the amount of quantitative genetic variation between the two species may contribute to their contrasting migration patterns following introduction to California. Many cases exist where colonizing species depauperate in isozyme variation have on further study been shown to contain considerable quantitative genetic variation (reviewed in Barrett and Shore, 1990). In fact, a study of variation in open-pollinated progeny arrays of *Monochoria vaginalis* and *Heteranthera limosa* grown under uniform glasshouse conditions revealed significant differences for a range of life-history traits in both these weed species, indicating the presence of quantitative genetic variation in spite of monomorphism at isozyme loci.

Generalizations as to the likely evolutionary responses following long-distance dispersal in aquatic plants can be aided if genetic information is available for both the source and the migrant populations (Barrett and Husband, 1990b). Unfortunately, for most aquatic introductions the source regions are not known with any certainty, making comparisons between introduced populations and those from the native region difficult. This problem has occurred in our comparison of population genetic structure in continental and island populations of *Eichhornia paniculata* (Glover and Barrett, 1987). Several lines of evidence suggest that Caribbean island populations represent a secondary center derived from long-distance dispersal from South America. However, it is not known whether populations on Jamaica were derived directly from the mainland or were secondarily colonized from Cuba, the other Caribbean island where the species occurs. Since analysis of isozyme patterns in Jamaican populations indicate two separate dispersal events are involved (Husband and Barrett, 1991) it is possible that introductions from both potential source areas have occurred.

Dispersal events in aquatic plants that possess distinct mating types (e.g. separate sexes in dioecy or two or three style morphs in heterostyly) can effectively preclude opportunities for evolutionary responses to novel environments if only one mating type is introduced to parts of the adventive range (see above). Leaky dioecy or self-compatibility systems may enable some seed to be produced in such situations but such seed rarely appears to establish, perhaps because of inbreeding depression. In the case of *Eichhornia crassipes*, the occurrence of a single style morph in many parts of the adventive range was earlier thought to account for the apparent absence of sexual reproduction (Baker, 1965; Sculthorpe, 1967; Richards, 1986). However, this is not the case since the species is thoroughly self-compatible and seed is produced in most populations monomorphic for style length (Barrett, 1980a,b).

GENETIC VARIATION AND POPULATION DIFFERENTIATION

The amount of genetic variation within a species and how it is partitioned within and among populations is a major determinant of evolutionary diversification (Wright, 1982). Aquatic plants pose an interesting problem in this regard. It has been repeatedly pointed out that aquatic plants show relatively little taxonomic differentiation compared with terrestrial groups (Sculthorpe, 1967; Hutchinson, 1975; Les, 1988; Cook, 1990). Of the 33 strictly aquatic plant families, 30 include fewer than ten genera, 17 contain only one genus and three consist of a single species (Sculthorpe, 1967). Moreover, the amount of evolutionary diversification dwindles as one moves from amphibious and emergent groups to fully submergent hydrophilous taxa.

Genetic variation in aquatic plants

Les (1988) has suggested that the conservative macroevolutionary pattern in hydrophilous aquatic plants is associated with low genetic variability and weak population differentiation below the species level, as well as the general uniformity of aquatic environments. Testing this hypothesis requires data on the relative amounts and partitioning of genetic variation within and among aquatic plant populations. Electrophoretic variability at isozyme loci provides one class of data with which to index the amount and distribution of genetic variation. Although isozyme data are available for more than 600 species of terrestrial plants (Hamrick and Godt, 1990), electrophoretic investigation of population genetic structure in aquatic plants is in its infancy. In Table 2 we present a survey of isozyme studies in aquatic plants. Although data are available for more than 81 taxa, for 33 of these isozyme phenotypes have been resolved for use as taxonomic characters with no genetic interpretation of the banding patterns (e.g. McMillan and co-workers' studies of sea grasses, McMillan, 1982). Measurement of isozyme variability within and among populations in a population genetic framework has been attempted for 44 taxa; however, 33 of these are primarily short-lived emergent aquatic plants with no clonal reproduction (*Echinochloa* spp., *Eichhornia paniculata, Limnanthes* spp., *Mimulus* spp.). Data from these species mirror some of the patterns and correlations commonly found among terrestrial species (Hamrick and Godt, 1990): breeding system and life history are the major determinants of genetic structure and not the fact that they live in or around water.

For the remaining aquatic groups, data on isozyme variation are available for only a handful of species (*Ceratophyllum* spp., *Hydrocharis morsus-ranae, Lemna* spp., *Najas marina* L., *Podostemum ceratophyllum* Michx., *Spirodela polyrhiza* (L.) Schleid., *Thalassia testudinum* Banks ex König, *Vallisneria americana* Michx., *Zostera marina* L. — Table 2). Obviously, this limited database puts us a long way from making any comparison of patterns of genetic variation in these groups, usually considered to be 'true aquatics'. Nevertheless, the limited data available suggest widespread monomorphism and weak population differentiation in many hydrophilous species, particularly sea grasses such as species of *Halodule, Syringodium* and *Thalassia* in which populations scattered over an entire ocean system express a single multilocus electrophoretic phenotype (McMillan, 1980, 1982). Extensive monomorphism, however, is not restricted to submergent species. Large-scale studies of North American *Typha* spp. have revealed the most severe case of isozyme monomorphism reported for any plant species (Mashburn et al., 1978; Sharitz et al., 1980). Similarly, extensive surveys of three species of annual halophytes *Salicornia* spp. also detected negligible amounts of electrophoretic variation (Jefferies and Gottlieb, 1982,1983; Wolff and Jefferies, 1987a,b).

What mechanisms might be responsible for low allozymic diversity within and among populations of some aquatic plants? Low variability within populations might be expected in highly selfing or clonal species since a single individual may successfully found a population. However, in terrestrial plants the available data suggest that clonal reproduction or selfing, while leading to monomorphism within populations, is not necessarily associated with low levels of variation among geographically disjunct populations or within the species as a whole (Ellstrand and Roose, 1987; Hamrick and Godt, 1990). Though selfing and clonal reproduction are undoubtedly involved, other mechanism(s) must also be at work. These could potentially include: (1) extreme population bottlenecks associated with pleistocene glaciation, colonization or speciation; (2) fixation of a single dominant general-purpose genotype; (3) loss of variation through selection resulting in adaptation to a uniform environment.

Extreme bottlenecks affecting species-wide variation have been invoked to explain low isozyme variability in terrestrial species (reviewed in Barrett and Kohn, 1991). Bottlenecks may be especially important in rare or threatened species such as the endangered annual, emergent aquatic *Howellia aquatilis* Gray in which a sample of four populations completely lacked variation at 18 isozyme loci (Lesica et al., 1988). Similarly, bottlenecks occurring at speciation may restrict the amount of variation with which a species originates (e.g. *Stephanomeria malheurensis* Gottlieb — Gottlieb, 1973). The main problem with accepting bottlenecks as a mechanism producing such extensive monomorphism is that electrophoretic variation should be replenished by mutation over time. Thus bottlenecks are most satisfactory as an explanation for monomorphism in species of recent origin or those which experience recurrent episodes of small population size.

The next two hypotheses both involve the selective fixation of a single coadapted genotype. However, they differ in that the general-purpose genotype is competitively superior across a range of environmental variation while the genotype fixed through selection to a uniform environment does best only in the particular uniform environment to which it is adapted. Thus, it can be considered a 'single-purpose genotype'. Fixation of a general-purpose genotype has been presented as a likely mode of evolution in selfing and clonal species (Baker, 1965). However, recent studies have provided conflicting evidence for the existence of general-purpose genotypes (Lynch, 1984). Moreover, two other considerations do serious damage to both hypotheses. First, since electrophoretic variation at isozyme loci is thought to be selectively neutral, it should eventually accumulate through mutation so that the general- or single-purpose genotype remains monomorphic at loci controlling environmentally relevant traits while expressing variation at neutral loci. Second, some evidence from aquatic plants suggest genetic differences among individuals in the absence of isozyme variation. McMillan (1978, 1979, 1980, 1981) has shown differentiation with respect to morphology and response to chilling in several species of seagrasses which appear to possess no electrophoretic variation. Genetically based variation in the absence of electrophoretic variation has also been reported in *Typha* spp. for a variety of characters including response to temperature and salinity, photosynthetic activity, morphology and phenology (reviewed in Mashburn et al., 1978; Sharitz et al., 1980). Thus, it appears that these aquatic plants display a pattern of genetic variation opposite to that expected under the two hypotheses: variability at selectively important loci and monomorphism at neutral isozyme loci. Population differentiation for traits of adaptive significance also fails to support the idea that aquatic habitats are necessarily uniform. Hence, at the present time no satisfactory explanation fully accounts for the apparent genetic monomorphism of certain aquatic groups.

Ecotypic differentiation

Phenotypic variation in morphology and life-history traits has been observed within and among populations of many aquatic plants. However, this variation might be accounted for by the extensive phenotypic plasticity exhibited by many aquatic species (Table 1). It is, therefore, important to determine how much of this variation has an underlying genetic basis. Studies of genetic differentiation in terrestrial plants have commonly used ‘common garden’ experiments involving the comparison of genotypes under uniform growing conditions and reciprocal transplants under field conditions (Heslop-Harrison, 1964; Briggs and Walters, 1984). With few exceptions, genetically based population differentiation appears to be a universal feature of terrestrial plant populations, although how much of this variation is adaptive remains uncertain (Antonovics, 1976). Studies of population differentiation in emergent aquatic plants have also revealed clear evidence of local race formation (see below). Fewer data are, however, available for submersed and free-floating groups. Because of the potential for extensive gene flow via floating vegetative fragments and infrequent sexual reproduction, it will be of particular importance in species with these life forms to determine whether genetically based variation exists and if so the extent and scale of differentiation.

Experimental estimates of the genetic components of phenotypic variation should ideally involve randomly sampled half-sib families grown in a common environment (Mitchell-Olds and Rutledge, 1986). This may pose difficulties in many clonal aquatic plants which reproduce by seed infrequently. In these cases, clonal replicates and analyses using measures of repeatability will be required to assess the degree of genetic differentiation (Falconer, 1980). Another difficulty for genetic studies of population differentiation, particularly in free-floating species, concerns the problems of sampling associated with arbitrary nature of population limits (discussed above). Obscure population boundaries require that the unitary concept of population be abandoned for more rigorous, hierarchical approaches to sampling (Wright, 1978).

While these features of aquatic plant populations pose some hurdles for conventional genetic analysis, we feel that they should not prevent workers from investigating these issues. As long as the sampling schemes used are carefully reported, valuable data will inevitably be obtained. Moreover, clonal aquatic plants offer many advantages for these kinds of investigations since transplant studies are more powerful for investigating differentiation if they involve clonal replicates since genotype and environmental effects will not be confounded. Because cloning is easily achieved in aquatic plants, and for many species experimental field manipulations are easily undertaken, aquatic plants can offer outstanding experimental systems for the study of local adaptation. Several examples serve to illustrate this point.

Genetic differentiation occurs among lake populations of the submerged perennial *Ruppia maritima* L. (formerly *R. occidentalis* S. Wats., Potamogetonaceae) in Alberta, Canada. The species occurs in coastal waters throughout the world and is the dominant species of many saline lakes in western Canada; occasionally it is found in fresh water. In most lakes, particularly those with fresh water, seed is produced sporadically and at low levels (Husband and Hickman, 1985). Consequently, population growth and colonization is achieved primarily through fragmentation of the rhizome and dispersal of vegetative propagules produced at the end of each growing season. Despite this extensive clonal propagation, colonization of freshwater lakes has been accompanied by marked genetic differentiation. In a growth chamber study, Husband (1985) compared relative growth of ramets from a freshwater (Pigeon Lake) and a saline (Miquelon Lake) population grown in four water salinity treatments and four lake sediments, in all combinations (Fig. 4). He found significant differences in growth rates and biomass among populations. On average, clones grew best in water treatments that were most similar to their native lakes. However, the differences in their water salinity optima depended on the substrate in which the plants were rooted. Results from reciprocal transplants in the field involving the same two populations corroborated findings from the growth chamber studies. Populations grew best in the lake from which they were originally collected, and in this sense, differentiation among these populations of *Ruppia* appears to be adaptive. Further investigations of additional populations would be valuable in establishing whether a freshwater race of *R. maritima* has differentiated from the more commonly occurring saline-adapted forms in other areas of western Canada.

Studies of inter- and intra-population differentiation in heterophylly in *Ranunculus flammula* L. conducted by Cook and Johnson (1968) provided evidence that genotypes that were most heterophyllous were associated with unpredictable environments characterized by frequent water-level fluctua-

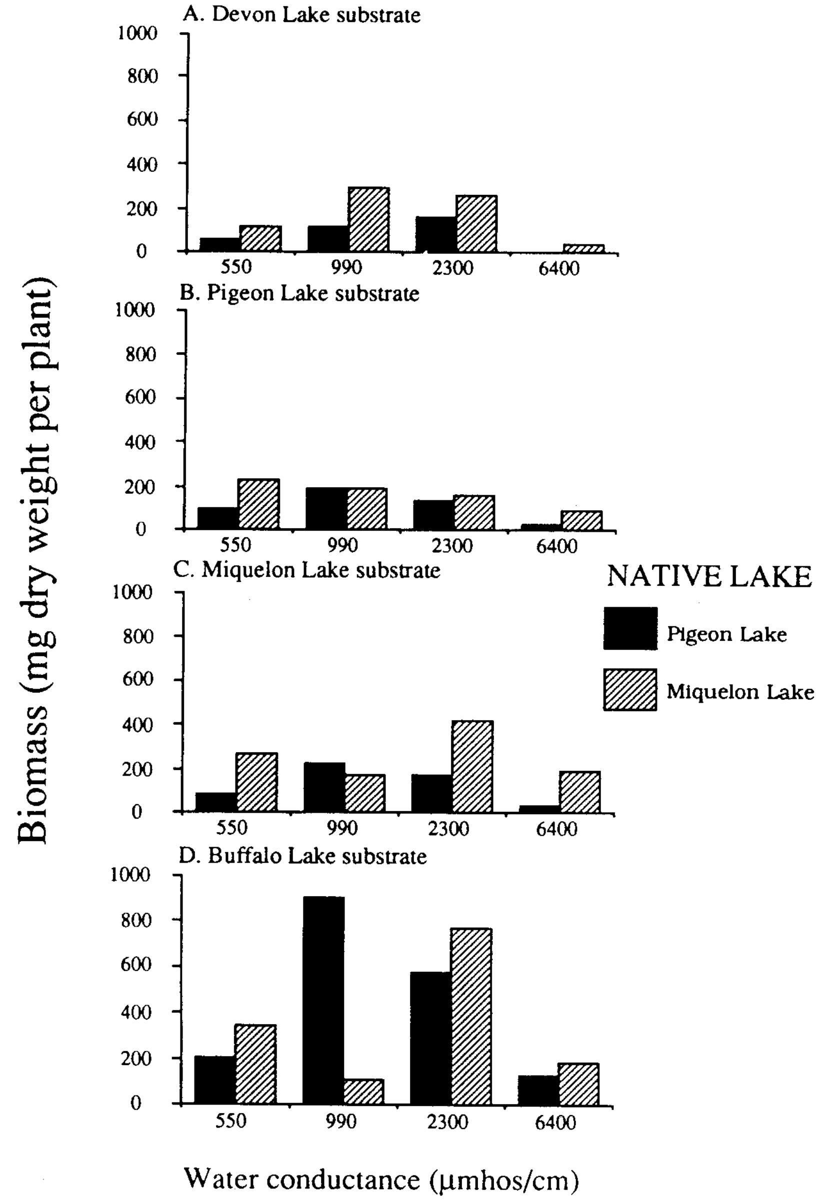

Fig. 4. Genetic differentiation between a fresh water (Pigeon Lake) and a saline lake (Miquelon Lake) population of *Ruppia maritima*. Plants were grown in a growth chamber experiment involving all combinations of four substrate types and four water salinity treatments, ranging from freshwater (550–990 μS cm^{-1}) to saline (2300–6400 μS cm^{-1}). The substrates used represent a gradient from coarse, freshwater lake substrates with low organic content (Devon Lake) to fine, saline lake substrates with high organic content (Buffalo Lake). Four ramets were grown in each combination of water and substrate (B.C. Husband, unpublished data, 1985).

tions. Genotypes with little heterophylly were commonly found in more terrestrial environments. Reciprocal transplant experiments and controlled studies involving long-term submergence and desiccation further supported the conclusion that heterophyllous genotypes were best adapted to changing environments. A particularly interesting finding of Cook and Johnson's work is the scale at which population differentiation occurred. While a mosaic of locally adapted populations were evident within Oregon, similar types of differentiation involving morphology and developmental flexibility were also found within populations over distances ranging from 4 to 75 m. Judging by the wide geographical range of *Ranunculus flammula* it seems unlikely that the water-dispersed seeds of this species would be restricted in their dispersal. It appears, therefore, that selection pressures are sufficiently strong to bring about fine-scale differentiation with respect to heterophylly.

Similar fine-scale patterns of local differentiation have been shown by Linhart (1974, 1988) in the annual *Veronica peregrina* L. occurring in vernal pools in California. Despite extensive gene flow via seeds, genotypes from the center of pools differed from those occurring at the periphery for a range of life-history traits, suggesting that the disruptive effects of selection can overcome the homogenizing effects of gene flow. Electrophoretic studies comparing allozyme variation between central and peripheral plants indicated little differentiation between the two subpopulations (Keeler, 1978), although samples from the periphery were more variable, a pattern also found for morphological traits by Linhart (1974).

These patterns suggest that local differentiation in response to seasonal variation in water availability may be a common feature of short-lived aquatic plants occurring in ephemeral environments. The strong selection pressures that the drying of seasonal ponds, pools and ditches are likely to have on the timing of growth and reproduction appear to be responsible for the occurrence of precocious reproduction in many short-lived taxa. Flowering in juvenile individuals of *Alisma gramineum* Gmel. and *Nuphar luteum* (L.) Sm. has been reported by Arber (1920) and several rice field weeds (e.g. *Monochoria* spp.) flower precociously in the vegetative state presumably to avoid desiccation associated with the harvest of the crop (Van Steenis, 1957). Similar selection pressures on reproductive timing may also be exerted on aquatic weeds by regular herbicide sprays and may account for the rapid flowering of California rice field populations of the annual *Sagittaria montevidensis* Cham. and Schlecht. ssp. *calycina* (Engelm.) Bogin which occurs within a month of flooding. Because of the intense nature of selection associated with such environmental changes it would seem likely that genetic responses would be common. However, as yet there has been little attempt to investigate the evolutionary consequences of seasonality in aquatic plants.

FUTURE PROSPECTS

The considerable heterogeneity in growth form, life history and reproductive systems among plants adapted to life in aquatic environments makes any generalizations concerning their population genetics and evolution difficult. Not unexpectedly, amphibious and emergent taxa are likely to most resemble terrestrial plants in the types of selection pressures they encounter and in their evolutionary responses. From the existing, albeit, limited database for these groups it would appear that they exhibit a range of population genetic structures similar to that found in strictly terrestrial plants. A wealth of different ecological niches is associated with life at the margins of streams, rivers and lakes, in fresh and saltwater marshes, fens, bogs, swamps and seasonally wet habitats such as vernal pools, ditches and rice fields. Moreover, many amphibious and emergent groups exhibit extensive adaptive radiation associated with evolutionary diversification in these habitats. This variation provides plant evolutionary biologists with almost unlimited scope for future comparative and experimental studies of a range of interesting problems. Several issues which the authors believe deserve particular attention in amphibious and emergent aquatic plants are, therefore, briefly listed.

(1) Is self-fertilization a general feature of species inhabiting ephemeral or unpredictable aquatic environments? Is this simply a consequence of neoteny associated with precocious reproduction or has it evolved independently of major changes in life history?

(2) Are there significant differences between pollination systems of emergent aquatic plants and their terrestrial relatives? Are the kinds, amounts and patterns of insect visitation and hence gene flow different between aquatic and terrestrial environments?

(3) Is phenotypic plasticity a general solution to unpredictability in seasonal aquatic environments? How much genetic variation for phenotypic plasticity occurs within natural populations, and does this vary along gradients of environmental uncertainty?

(4) What kinds of population structures are associated with different aquatic habitats? For example, do populations occurring along streams and rivers exhibit linear structure and unidirectional gene flow? Are populations occurring in discrete water bodies more highly differentiated than those in continuous water systems?

Floating-leaved, free-floating and submergent life forms exhibit progressive specialization to life in water and as such are often considered as 'true aquatics'. Because of the exclusively aquatic habitats in which they occur, they are more likely to be subject to distinctive microevolutionary forces. Quantitative studies of evolutionary processes in these groups are in their infancy (e.g. Cox, 1988; Les, 1988; Philbrick, 1988, 1991) but clearly indicate that considerable progress can be made despite some of the practical and conceptual difficulties discussed above. While studies of the population biology of these groups could involve unlimited possibilities, several areas where investigation is likely to yield data of value for evolutionary interpretation are listed below.

(1) How can the concept of effective population size (N_e) be usefully applied to clonal aquatic plants with widespread dispersal of vegetative propagules? What are the theoretical consequences of different modes of clonal propagation on N_e?

(2) What is the distribution of mating systems in taxa exhibiting hydrophilous pollination, and how does the distribution of outcrossing rates compare with that observed in wind-pollinated terrestrial species?

(3) What ecological and genetic mechanisms account for the low capacity for sexual reproduction in clonal populations, and is there differentiation among populations in this regard? How important is somatic mutation in contributing to sexual dysfunction?

(4) What is the evolutionary significance of dicliny in hydrophilous aquatic plants? Is it associated with perenniality and clonal propagation, and if so, what is the functional basis of these associations and the phylogenetic sequence of trait evolution?

(5) What are the amounts and distribution of genetic variation within and among populations of submerged aquatic plants, and how is the pattern of genetic variation related to reproductive and life-history traits (e.g. dicliny, clonal propagation, perenniality)?

(6) What is the relationship between isozyme variation and genetic differentiation for morphological and life-history traits? Is the electrophoretic monomorphism observed within many taxa also associated with limited ecotypic differentiation?

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