CHAPTER 6

Aquatic Plants: Patterns and Modes of Invasion, Attributes of Invading Species and Assessment of Control Programmes

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6.1 INTRODUCTION

The natural human inclination to concentrate attention on the strange and the unusual is reflected vividly in the voluminous literature devoted to those aquatic plants that possess anomalously disjunct or cosmopolitan geographical distributions (Sculthorpe, 1967). Since rivers, lakes and other water bodies are separated by tracts of land, it could be expected that aquatic plants would tend to be locally distributed within a particular land mass and that the seas and oceans would provide insurmountable barriers to dispersion between continents. Indeed, approximately 25 to 30% of the known aquatic plants are considered to be true endemics with distributions limited to a single river or portion of a river system (Sculthorpe, 1967; Cook, 1974). In contrast, however, several families and species of aquatic plants are so widely distributed over several continents, some even reaching remote oceanic islands, that they can be described justifiably as cosmopolitan. In addition, some temperate and tropical aquatic plants exhibit curious discontinuities in their ranges, over and above that due to the configuration of seas and land masses (Sculthorpe, 1967). While these continue to attract speculation and discussion, in most cases it is difficult, if not impossible, to show that the discontinuity is genuine and that the plant has not in fact been introduced in historical times to certain parts of its present-day range (Sculthorpe, 1967; Mitchell, 1974).

As a result of the mechanisms of dispersal, invasion, colonization and competition on the one hand, and changing climatic, physical and edaphic factors of the environment on the other, migrations of species continue to occur now as they occurred during geological and historical time. Aquatic floras everywhere are thus in a continual state of flux. The situation has been confounded further by man's relentless expansion of his agriculture, communications, industry and domestic life wherein he has modified existing habitats and created new, artificial habitats. Additional complications have been introduced by man's propensity for

employing aquatic systems for the disposal of his waste products. Human activities that have led to the alteration, disturbance and degradation of aquatic systems have thus served to extend the range of habitats available for colonization by aquatic plants and to accelerate the natural flux of species between habitats.

In this review, we examine the processes of invasion, establishment and dispersal in aquatic plants and address three main questions:

1. What are the properties of an aquatic plant species that enable its individuals to disperse and invade new environments and what features determine their successful establishment?
2. What environmental features render a habitat vulnerable to invasion?
3. What are the most appropriate management strategies for the control of invasive aquatic plants?

In our discussion we have confined our analysis to freshwater species, omitting mention of the large and diverse brackish water and marine flora. Similarly, only vascular plants that habitually grow in flowing or standing water have been included in this review. Phreatophytes (plants which grow in high water tables, such as along streams and river banks) will be referred to where appropriate but will not be considered in detail.

6.2 THE INVASION PROCESS

The processes of plant invasion have attracted considerable attention worldwide (e.g. Elton, 1958; Connel and Slatyer, 1977; Grime, 1979, 1985; Grubb, 1985; Groves and Burdon, 1986; Macdonald *et al.*, 1986; Mooney and Drake, 1986) and are often used to explain features of the diversity and succession of plant assemblages. However, remarkably few theoretical considerations of the invasion process seem to be generally applicable (Harper, 1977; Johnstone, 1986). Part of this problem stems from imprecise definitions of the relationship between invasion and succession. Here, we follow the views expressed by Johnstone (1986) and Breen *et al.* (1987) that the prime cause of invasion can be seen as the removal or overcoming of a barrier that has previously excluded a plant species from an area. Whilst these features can be classified on the basis of time, time is not the *cause* of biological change (Huxley, 1932); rather biological phenomena are described by their dispersion in time and space (Johnstone, 1986). In this context, therefore, plant succession is seen to be caused by sequential, but interlinked, episodes of invasion, establishment, maintenance and decline. Progressive, retrogressive and cyclical successional patterns thus reflect different modes of system instability (Johnstone, 1986).

6.2.1 Natural invasions

Natural invasions are invasions that have taken place in the absence of anthropogenic influences. They occur when an intervening barrier is removed or

through the development of biotic or abiotic transporting mechanisms able to overcome the barrier in question. This leads to the suggestion that barriers and 'transporting mechanisms' oppose one another and provide powerful forces in the direction and timing of successional episodes (Breen *et al.*, 1987).

Examination of the rather scanty fossil record indicates that aquatic plant invasions have occurred naturally for several millennia (Sculthorpe, 1967). Indeed, the Pleistocene fossil record of the heterosporous aquatic fern *Azolla filiculoides* in western Europe suggests that successive waves of invasion occurred during each inter-glacial period, each new invasion restoring communities that had been eliminated during the intervening glacial periods (Moore, 1969).

The process of invasion can be seen as a series of discrete steps; these are summarized in Figure 6.1 and will be discussed in detail later. For an invasion to succeed, each step in the progression from first arrival of the invader to successful colonization of new habitats requires that a series of biotic and abiotic barriers be overcome by the invader. At each stage of the process, both chance and timing play a vital and interactive role in determining, the degree of success attained by the invader (Crawley, 1986; Gray *et al.*, 1987).

The geographical distance between the source of the invading plant and the eventual site of invasion represents perhaps the greatest barrier to natural invasions of aquatic plants. By virtue of their requirement for perennial supplies of freshwater (Sculthorpe, 1967), the adult stages of most freshwater aquatic plants cannot survive periods of transport in the absence of water or even prolonged immersion in seawater (Haller *et al.*, 1974). Thus, the production of
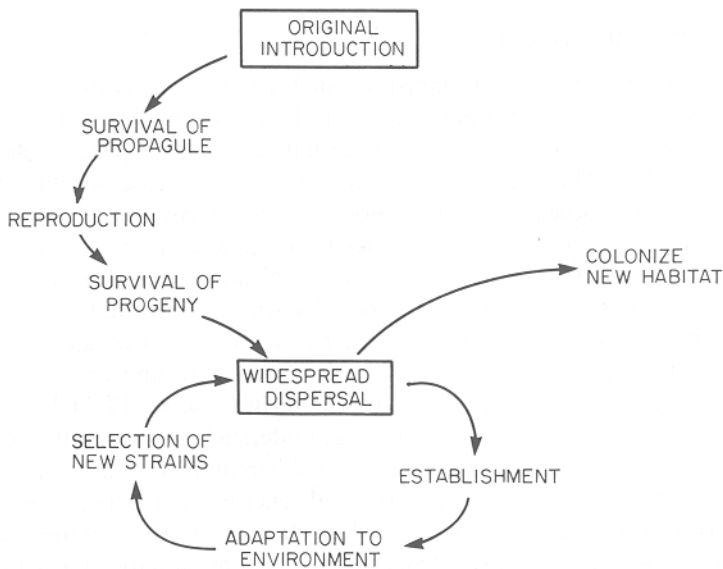

Figure 6.1.   Stages in the invasion and establishment of aquatic plants

resistant seeds and propagules by many aquatic plants provides the only viable means whereby they may survive transport by biotic or abiotic mechanisms. In this regard, the presence of a small population of *Azolla filiculoides* on Inaccessible Island (37° 19′ S; 12° 44′ W) in the Tristan da Cunha group, located on the Mid-Atlantic Ridge, is of great interest (Ashton and Walmsley, 1984; Figure 6.2). As its name implies, the island's isolation makes it highly unlikely that this American fern was deliberately introduced by man and it has been suggested that the fern is a native species (Christensen, 1940; Wace and Dickson, 1965). However, a more likely explanation is that the fern's presence on the island might be due to the transport of spores by winds or waterfowl (Ashton and Walmsley, 1984). This possibility is supported by the several recorded instances where storm-blown American species of waterfowl have arrived at these islands and the east coast of southern Africa (Holdgate, 1965).

Natural invasions can be considered as sporadic events where the likelihood of a successful invasion is determined by interactions between chance and timing (Crawley, 1986). Against this background, man's propensity for modifying his environment and introducing plants into areas where they are not native has largely overcome the barriers to invasion that were previously imposed by geographical isolation. In turn, this has markedly increased the probability that the invasion will be successful. This is clearly evident in the dramatic increase in both the numbers and extent of aquatic plant invasions that have taken place during the 19th, and especially the 20th centuries as a direct consequence of man's activities (Sculthorpe, 1967; Mitchell, 1974; Holm *et al.*, 1977).

6.2.2 Transport mechanisms

Clearly, disruptive forces or mechanisms, which serve to inactivate, overcome or remove barriers, function in a manner that is diametrically opposed to isolating mechanisms and can therefore be conceptualized as 'transport mechanisms' (Breen *et al.*, 1987). These features determine the degree of ease or difficulty with which invasions proceed. Since hydrological characteristics are the principal determinants of all aquatic communities (Gosselink and Turner, 1978), it is logical to expect that they would also be implicated as major transporting mechanisms; this is indeed the case, especially within individual river systems. However, it is important to note that the efficacy of a hydrological transport mechanism depends on both the magnitude of the event and on the temporal scale over which the event occurs or is repeated (Breen *et al.*, 1987). Irregular or episodic high energy events (i.e. of large magnitude, such as extreme floods) bring about catastrophic changes that are quite different from those induced by seasonal or regular low energy events. High energy events therefore remove barriers while low energy events merely breach these barriers temporarily.

Wind may also act as a transport mechanism for some aquatic plants although the distance covered is likely to be short because of the relatively high seed mass
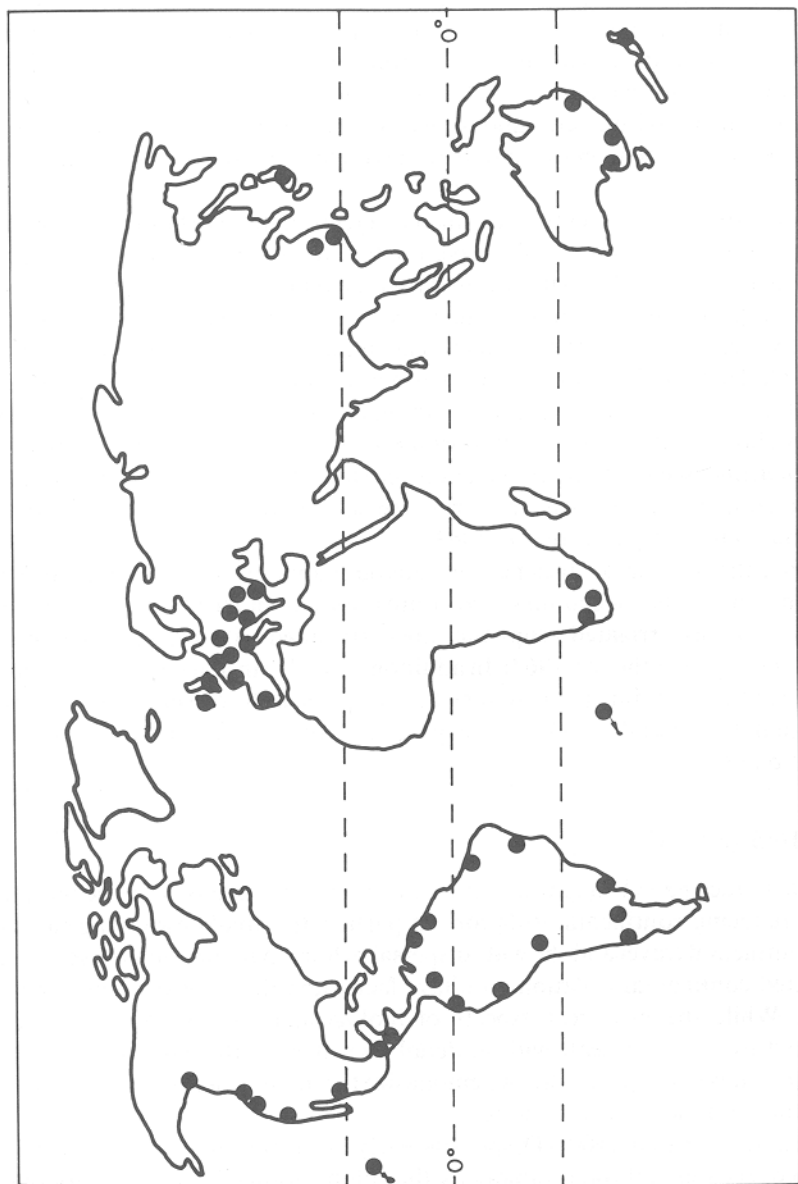
Figure 6.2. World distribution of *Azolla filiculoides*. (Adapted from data in Moore, 1969; Lumpkin and Plucknett, 1980; Ashton and Walmsley, 1984.)

and absence of structures aiding aerial transport (Sculthorpe, 1967). In addition, the likelihood that seeds will be blown onto dry terrestrial soils to desiccate and die, further limits this mode of transport. In contrast, many phreatophytes colonizing the banks of streams and rivers (e.g. *Phragmites, Typha*) produce numerous light seeds which rely on wind transport for dispersal. In these species wind transport is the major mechanism ensuring medium- and long-range dispersal to new environments and probably accounts for their wide distribution over most of the temperate and tropical regions of the world (Sculthorpe, 1967).

Animals are unquestionably the principal agents in the short range dispersal of all forms of aquatic plants (Sculthorpe, 1967). Over a century ago, in his treatise *The Origin of Species*, Darwin surmised that the remarkably wide distribution of certain freshwater plants had been achieved mainly by the carriage of seeds and vegetative fragments on the plumage and muddy feet of waterfowl (Darwin, 1872). Understandably, direct observations of such dispersal are extremely difficult to obtain (Sculthorpe, 1967) though Agami and Waisel (1986) have recently shown waterfowl to be important for the dispersal and germination of *Najas maritima* seeds. While considerable circumstantial evidence for both exo- and endozoic transport exists, these mechanisms are likely to be less effective in inter-continental dispersal (Löve, 1963).

Finally, the accidental dispersal of aquatic plants by humans must also be borne in mind. Of particular importance are the seeds and fruits of aquatic plants growing amongst irrigated crops that are distributed with the products of the harvested crop (Sculthorpe, 1967). In addition, casual transport by boats, vehicles and agricultural machinery, as well as the escape of seeds or vegetative material from ornamental ponds and botanical gardens, have also increased the spread of aquatic plants.

6.2.3 Human travel

Man's activities have brought about immense changes in global biogeography, greatly reducing continental isolation. In particular, rapidly escalating rates of inter-continental travel and the wide dispersal of human populations have largely eliminated continental isolation and have facilitated the translocation of many species. While the historical aspects of biological invasions that have been facilitated by man are dealt with in detail elsewhere in this volume (di Castri, Chapter 1), it is appropriate that we emphasize the importance of human travel in promoting aquatic plant invasions.

Since approximately 1500 AD, sporadic early European voyages of exploration and discovery were followed rapidly by the colonization of other territories and subsequent trade exchanges around the globe as road, rail and shipping transportation systems improved. Twentieth century developments in air transportation have also boosted considerably the ease, speed and scope of

international travel. Coupled to this trend, man's fascination with strange and exotic organisms and the desire to develop new markets whilst surrounding himself with familiar objects in a new environment have motivated most of the deliberate introductions of aquatic plants to new territories. Typically, ports formed the major foci of human activities and associated plant introductions in these countries (Macdonald *et al.*, 1986). The process of deliberate introduction, followed by escape and subsequent spread, has been repeated in many parts of the world and species such as *Eichhornia crassipes* (Figure 6.3) and *Salvinia molesta* (Figure 6.4) are now widely distributed through the tropical and sub-tropical regions of the globe.

6.2.4 Invasion stages

Extensions to the geographic range of a plant species can only be brought about by the dispersal of breeding populations. When introduced to an area previously unoccupied by its own kind, individuals of a particular species have no chance of becoming established unless the initial immigrants form part of a 'propagule' (Figure 6.1), i.e. the minimum number of individuals able to found a reproducing population under favourable conditions (MacArthur and Wilson, 1967). Despite the fact that several aquatic plants possess some form of dormant stage in their life cycles, adapting them for dispersal, we have seen that few aquatic plants are dispersed between distant unconnected water bodies by natural mechanisms. Indeed, most initial introductions of aquatic plants to new continents have been deliberate in that the introduced species was perceived to have some special attraction and/or intended use for humans (Cook, 1985). A list of the best known invasive aquatic plants and their distribution is given in Table 6.1. In every case, man has been implicated in their deliberate or accidental introduction to continents outside their native range.

As is the case with terrestrial plants, we can recognize three main stages in a successful aquatic plant invasion, namely: the arrival of an individual or propagule, establishment of the population through reproduction, and dispersal to new localities (Figure 6.1). Subsequent adaptation of the invader to the new environment may also favour the selection of new genetic strains.

Each stage involves a series of interactions between the physical, chemical and biological features of the environment and the biological characteristics of the invader. These interactions can either promote, delay or prevent successful completion of the stage (Arthington and Mitchell, 1986). The whole invasion process is then repeated when a propagule is successfully dispersed to a new locality. Clearly, the rate at which the invasion occurs will depend on the number of individuals or propagules present in the initial inoculum and in the dispersal stage. An exponential increase in these will ensure an exponential acceleration in the apparent rate at which the invasion takes place until environmental factors become limiting (Arthington and Mitchell, 1986).
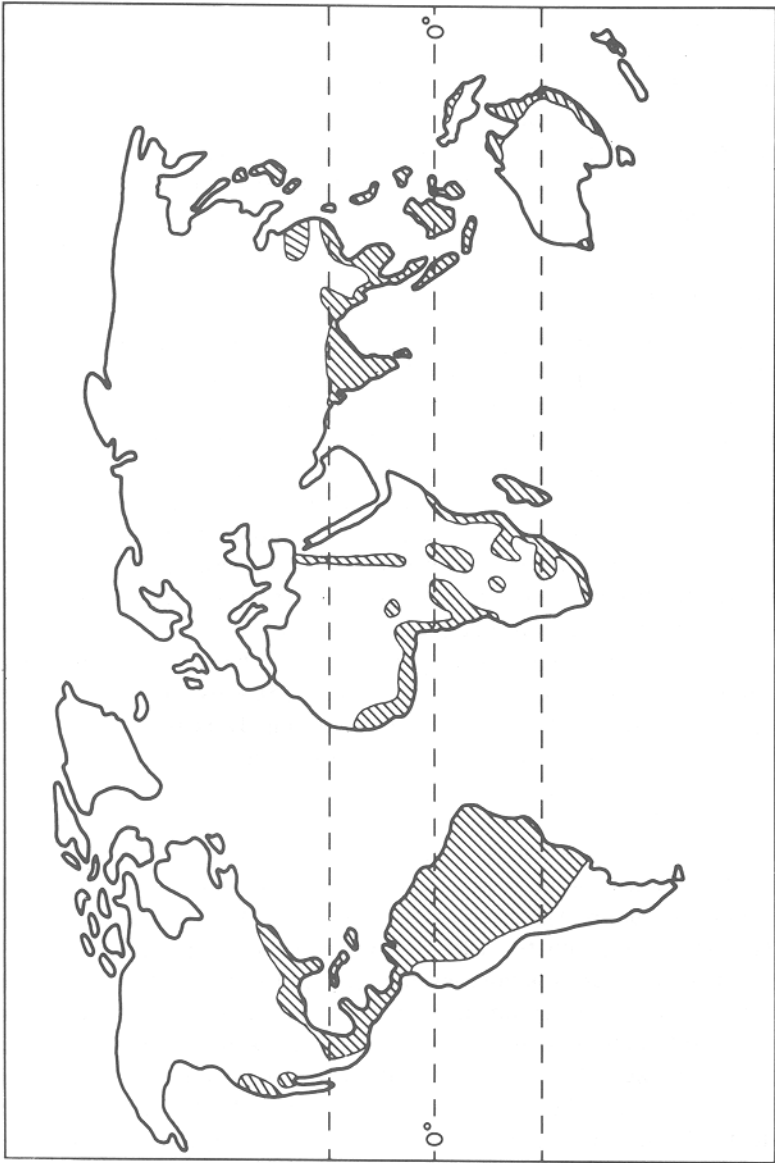
Figure 6.3. World distribution of *Eichhornia crassipes*. (Adapted from data in Sculthorpe, 1967; Robson, 1976; Holm *et al.*, 1977; Jacot Guillarmod, 1979; Gopal and Sharma, 1981; Ashton *et al.*, 1986; Gopal, 1987.)
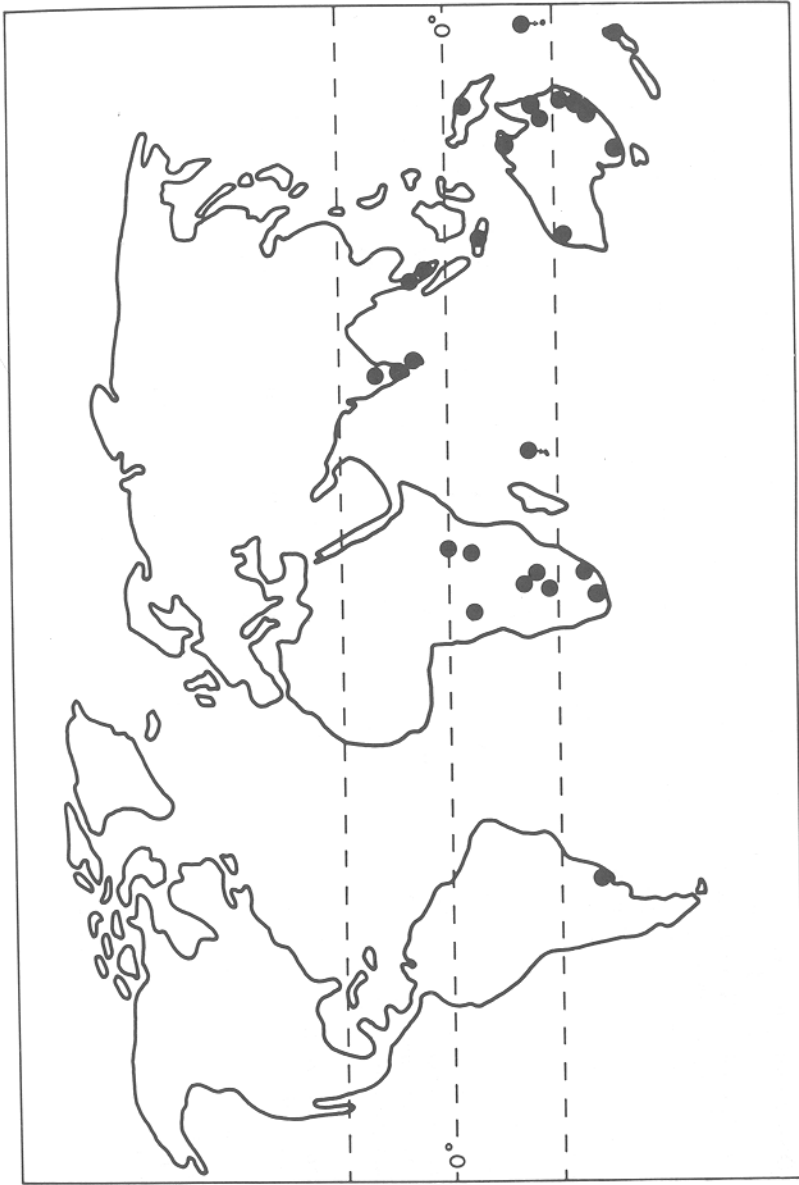
Figure 6.4. World distribution of *Salvinia molesta*. (Adapted from data in Mitchell, 1978, 1979a; Robson, 1976; Harley and Mitchell, 1981; Forno, 1983; Thomas and Room, 1986.)

Table 6.1. Distribution and degree of problem caused by the major submerged, emergent and free-floating invasive plants; x = indigenous, o = has caused minor problems, * = has caused major problems. (Data extracted from Mason, 1960; Sculthorpe, 1967; Moore, 1969; Mitchell, 1974, 1978; Robson, 1976; Holm et al., 1977; Gopal and Sharma, 1981; Cook, 1985; Mitchell and Orr, 1985; Arthington and Mitchell, 1986)

Species	North America	South America	Europe	Africa	India	Southeast Asia	Australia	New Zealand
SUBMERGED								
Egeria densa	*	x	o	o			o	*
Elodea canadensis	x		*	o			*	*
Hydrilla verticillata	*	ox	ox	x	*x	ox	ox	o
Lagarosiphon major			o	x				*
Ceratophyllum demersum	*x	ox	ox	ox	ox	ox	ox	*x
Myriophyllum aquaticum	*	x	*	*		o	o	*
Myriophyllum spicatum	*		x	x	x	ox		
EMERGENT								
Alternanthera philoxeroides	*	x				*	*	*
Phragmites australis	*x	*x	*x	ox	ox	ox	ox	ox
Typha spp.	*x	ox	ox	ox	*x	ox	*x	ox
FREE FLOATING								
Azolla filiculoides	x	x	*	*			ox	x
Eichhornia crassipes	*	*x	*	*	*	*	*	o
Pistia stratiotes	ox	ox		*x	*x	*x	ox	o
Salvinia molesta		x		*	*	*	*	*

6.2.5   Why are some invasions successful while others are not?

Several aquatic plant species have provided spectacular examples of successful invasions when introduced into habitats with which they are not in ecological equilibrium (Sculthorpe, 1967; Mitchell, 1974). In many cases these population growths have been so rapid that the phenomena have been described as biological explosions, with the invading species completely dominating the available habitat at the expence of indigenous species (Arthington and Mitchell, 1986; Ashton *et al.*, 1986). Those aquatic plants that have spread adventively following their introduction to different parts of the world have almost invariably caused problems as weeds (Table 6.1). As a result, these species have attracted considerable attention and therefore provide the best documented cases of aquatic plant invasions. However, while the literature contains several descriptive accounts of the invasive spread of aquatic plants and short-term investigations of suitable control methods, there are few data quantifying the factors responsible for successful invasions (Mitchell, 1974). Still fewer data are available on the causes of unsuccessful invasions.

Several common features can be identified amongst those invasive aquatic plants which have demonstrated a marked capacity for adventive spread when introduced into new environments. Significantly, all of these factors relate to dispersal and reproductive mechanisms:

1. Vegetative reproduction is usually the commonest, and often the only method of reproduction.
2. Human activities are the main mechanism whereby the plants are spread both between and within continents.
3. Plants capable of very rapid rates of reproduction often become serious weeds.
4. Sexually sterile plants become locally naturalized unless they are purposely spread by humans or possess small vegetative propagules that can be widely spread by other means.

Success in the initial stages of aquatic plant invasions is dependent on reproductive capacity (Figure 6.1), provided that there is a fundamental bioclimatic match between the non-native and native environments. Opportunist R- or r- strategists (MacArthur and Wilson, 1967; Grime, 1977, 1979, 1985) with high reproductive rates are well represented among both free-floating (e.g. *Eichhornia crassipes* and *Salvinia molesta*) and submerged (e.g. *Elodea canadensis* and *Hydrilla verticillata*) invasive aquatic plants. Those plants that are capable of prolific vegetative reproduction possess a special advantage since one viable propagule (a single plant) is sufficient to start a new colony. Other attributes of the invading plant, such as the potential to reach a large population size, flexible habitat requirements and the ability to tolerate the stresses of environmental fluctuations and extremes, become more important during subsequent stages in the invasion (Arthington and Mitchell, 1986; Ashton *et al.*, 1986). Clearly, these attributes, in combination, constitute a biological strategy which predisposes a

species for success as an invader However, similar combinations of attributes are not likely to be equally important in all circumstances.

Pre-adaptation to the new environment, perhaps through similarity with its native habitat, is clearly an advantage to an invader. However, such pre-adaptation only *increases* the likelihood of successful invasion; it does not *guarantee* success or decrease the possibility that the invading plant population may subsequently decline. Indeed, the *Elodea canadensis* invasions of Britain, western Europe and Australia, and the *Myriophyllum spicatum* invasions in the eastern United States, have all followed a wave pattern, with a period of rapid increase and stabilization followed by a catastrophic decline (Carpenter, 1980). In each of these cases, the mechanisms causing the population decline would seem to be a complex of interacting factors.

Aquatic ecosystems that have been disturbed by human activities appear to be particularly vulnerable to plant invasions (Cook, 1985). Nevertheless, introduced aquatic plants have also displayed considerable success in invading new ecosystems where there was no apparent disturbance but where suitable habitats and other necessary resources already existed. The *Salvinia molesta* invasion of the flood plain lakes along the Sepik River in Papua New Guinea provides an excellent example of this phenomenon (Mitchell, 1979a; Mitchell *et al.*, 1980; Thomas and Room, 1986; Arthington and Mitchell, 1986). Under these circumstances, successful invasive plants are usually R- or C-strategists (Grime, 1977, 1979) with the additional competitive advantage of freedom from the pests and diseases characteristic of their native range. They are therefore likely to experience considerably lower grazing and predator pressure and thus possess a significant competitive advantage over native species. The possibility that successful invaders may also produce allelopathic substances (Ostrofsky and Zettler, 1986), is an intriguing possibility that is, as yet, untested.

The third essential stage of every successful aquatic plant invasion is the dispersal of the organisms into suitable habitats (Figure 6.1). In the absence of this stage, the introduced organism is properly considered an 'escape' since it has not become truly naturalized (Arthington and Mitchell, 1986). This is clearly illustrated in the case of *Cyperus papyrus*, an emergent species native to Africa and western Asia, that has become established in a number of countries, including Australia. Despite its capacity for vigorous growth and relatively wide latitudinal spread in its native environment, it has shown no evidence of invasive behaviour where it has been introduced. Superficial examination indicates that the naturalized populations do not set seeds; thus the absence of effective dispersal of viable propagules is the most likely explanation for its failure to spread widely and rapidly (Arthington and Mitchell, 1986). Similarly, two other genera of widespread emergent aquatic plants, *Phragmites* and *Typha*, cause serious problems in their native distribution range as a result of rapid spread due to seed dispersal. When established in entirely new areas, however, these plants produce

little seed and seldom pose serious problems unless the habitat becomes eutrophied (Aston 1973).

6.2.6 Why are some environments vulnerable while others are not?

The concept that certain environments are more vulnerable to invasion than others is a recurring theme throughout much of the ecological literature. Though not always stated explicitly, the vulnerability of a particular habitat to invasion does not imply that *any* invasive plant reaching that habitat will succeed automatically. Indeed, it is well known that while many species reach potential new habitats, few are able to invade successfully.

The ease and speed with which certain types of aquatic habitats have been invaded has provided strong support for a variety of hypotheses relating habitat susceptibility to invasion. These hypotheses have variously described the *causes* of successful invasions in terms of: simplified, or species-poor communities (Elton, 1958), poorly adapted native species (Sculthorpe, 1967), absence of predators (Mitchell, 1974; Harper, 1977), gaps generated by disturbance (Mitchell, 1974; Sousa, 1984), chemical changes (Hutchinson, 1975), competitive superiority due to tolerance of lower resource levels (Mitchell, 1974; Connell and Slatyer, 1977; Noble and Slatyer, 1980) and empty niches (Elton, 1958; Harper, 1977; Cook, 1985; Johnstone, 1986). As Johnstone (1986) notes, these concepts represent mechanisms that have facilitated invasions in certain specific circumstances and none of them appear to be applicable to *all* examples of plant invasions. Moreover, as mechanisms, they cannot be considered to be the *causes* of invasion.

Harper (1977) has suggested that all invasions occur as a function of the availability of 'safe sites' that are free of environmental hazards. These may be loosely equated with the 'empty niche' concept proposed by Elton (1958). Johnstone (1986) subsequently expanded this view, stating that 'a plant can successfully invade a site (to grow and reproduce) *only in the absence* of environmental resistance, where environmental resistance is any factor operating to decrease the intrinsic growth rate ... of the invader' (our emphasis). This categorical statement suggests that habitats are either vulnerable or resistant to invasion and takes no account of any special features possessed by the invading plant. In light of our earlier discussions (Sections 6.2.1 and 6.2.2), we can consider an 'environmental resistance' to be synonymous with a 'barrier to invasion'. Further, since we have already noted that barriers may be inactivated, overcome or removed by both biotic and abiotic transporting mechanisms, Johnstone's statement requires modification. In our view, therefore, the vulnerability of a habitat to invasion depends not only on the presence or absence of a barrier or barriers, but also on the *efficacy* of those barriers in resisting any disruptive mechanisms possessed by, or exploited by, the invader in question. Thus, a

hypothetical barrier might easily prevent the ingress of species A into a specific habitat but be inadequate against species B.

Three mechanisms in particular, namely disturbance or alteration of the habitat, the absence of predators and the absence of effective competing species, have been implicated in facilitating the invasions of aquatic habitats (Sculthorpe, 1967; Mitchell, 1973, 1974; Ashton *et al.*, 1986). It is significant that habitat disturbance, for example through the impoundment of a river to form an artificial lake (Mitchell 1973) or the creation of irrigation and transport canals, has been implicated in almost all of the most spectacular examples of aquatic plant invasions. While chance and timing determine whether these mechanisms act simultaneously, sequentially, or not at all, each mechanism increases the vulnerability of a habitat to invasion, particularly by an alien species. Post-invasion successional (autogenic) changes will also modify a habitat's vulnerability to subsequent invasions.

6.3 ATTRIBUTES OF INVADING SPECIES

The r/K concept of plant life-history styles proposed by MacArthur and Wilson (1967) is somewhat over-simplified (Whittaker and Goodman, 1979) and incapable of providing a complete explanation of plant life-history phenomena. Calow and Townsend (1981) proposed that this deficiency could be resolved by the *a priori* testing of life-history strategies on the basis of optimal use of limited resources. However, as Solbrig (1981) points out, our understanding of how a plant functions in a multi-factorial environment is so limited that the optimal adaptations of a plant in any one habitat cannot easily be predicted. Thus, the classification of plant life-history phenomena by Grime (1977, 1979, 1985) into three basic categories, namely: C or competitive plants, S or stress-tolerant plants and R or ruderal plants, appears to be more practical.

6.3.1 Life forms and growth characteristics

In contrast to the terrestrial environment, aquatic environments are often held to be relatively constant thus encouraging species with perennial life cycles and a predominance of asexual reproduction (Sculthorpe, 1967; Hutchinson, 1975). While this assertion may hold true for the wet temperate and tropical latitudes, many aquatic habitats in semi-arid sub-tropical and temperate latitudes experience alternate periods of wetting and drying over both short-term (seasonal) and long-term (aseasonal) cycles (Howard-Williams and Gaudet, 1985; Mitchell and Rogers, 1985). In addition, seasonal cycles of temperature and day length, which are accentuated with increasing distance from the equator, confer further environmental variability. In these more variable habitats, therefore, annual growth patterns, desiccation resistant propagules and multiple regeneration adaptations (Grime, 1979, 1985) are likely to be the rule rather than the

exception, even in those plants whose life cycles extend beyond a single annual cycle. The variability of the environment plays a major role in regulating the growth of aquatic plants and is thus critical to the success or failure of an invasion.

Free-floating invasive aquatic plants have been responsible for some of the most widespread and serious problems and are considered to be noxious weeds in most countries of the world (Table 6.1). The best-known examples, *Eichhornia crassipes, Salvinia molesta* and *Azolla filiculoides*, all have a free-floating life form, while *Ceratophyllum demersum* is usually unattached and forms large masses that drift about just below the surface of the water (Sculthorpe, 1967; Mitchell, 1974). This group of plants possesses a number of attributes which undoubtedly contribute to their success as invaders. The most important are: a capacity for extremely rapid vegetative multiplication; the ability to regenerate from relatively small portions of vegetative thallus; the complete or partial independence of sexual reproduction, which if possessed, is seldom important in the development of large populations; a growth morphology that results in the development of the largest possible area of photosynthetic tissue in relation to the whole plant, and which rapidly occupies the entire water surface or photic zone; and finally, an independence of substrate conditions and water levels (Mitchell, 1974). Where space is restricted, these plants can also initiate the accumulation of organic matter and promote the development of secondary swamp (emergent) vegetation. Thus they can be regarded as primary colonizers in aquatic ecosystems (Mitchell, 1974; Ashton *et al.*, 1986).

In contrast, submerged and emergent aquatic plants that are rooted in the sediments are dependent on a more stable hydrological regime for survival (Sculthrope, 1967). These plants can tolerate short-term changes in water level though they are unlikely to present problems in situations where rapid or extensive fluctuations occur. Indeed, water level manipulation is often used to control populations of these plants. In this group, *Phragmites, Typha, Myriophyllum aquaticum* and *Alternanthera* possess an emergent growth form while *Myriophyllum spicatum* and the hydrocharitacean genera *Egeria, Elodea, Hydrilla* and *Lagarosiphon* are all submerged plants (Sculthorpe, 1967).

Submerged species can only grow where a suitable substratum exists and where sufficient light penetrates the water column. They are therefore adversely affected by increased turbidity levels due to suspended silt and populations of planktonic algae. Clearly, these species are restricted to certain environmental conditions but, because of their close adaptation to these conditions, they can occupy all the available habitat and rapidly colonize suitable new habitats. Particular attributes possessed by submerged species include: intercellular lacunal systems to provide buoyancy to the photosynthetic organs; reduced structural rigidity; the ability to remain dormant or over-winter in unfavourable environmental conditions (Sastroutomo, 1981); the ability to regenerate from small stem fragments; the virtually complete independence of sexual reproduction; and the production of

large numbers of vegetative propagules (such as tubers, turions and dormant apices) which are important in recolonization of cleared areas and invasions of new areas (Sculthorpe, 1967, Nichols and Shaw, 1986).

Emergent species possess several important attributes which include: long-lived, resistant rhizomes that can act as nutrient stores during unfavourable periods; production of tall, structurally rigid stems and leaves that shade out competing species; variable vegetative growth patterns that can prevent the ingress of competing species or rapidly exploit new colonization sites (Lovett-Doust, 1981; Hutchings and Bradbury, 1986); the production of very large numbers of minute seeds, suitable for long-range dispersal; and remarkable powers of regeneration after cutting (Westlake, 1963).

An additional feature of many invasive aquatic plants is that they are taxonomically close to species which are not invasive or resemble other plants that occupy the same habitat but are not always invasive. The reasons for this are not always clear. For example, *Salvinia molesta* belongs to a complex of four closely related South American species (Table 6.2). Two of these species, *S. molesta* and *S. herzogii*, are capable of very high growth rates but are sexually sterile and depend entirely on vegetative reproduction, thus differing from other species in the complex (Arthington and Mitchell, 1986). Indeed, laboratory studies (Mitchell and Tur, 1975; Cary and Weerts, 1983) suggest that *S. herzogii* would be as invasive as *S. molesta* if it were introduced to a new environment. Thus it would appear that the restricted distribution of *S. herzogii* and *S. molesta* in their native environment (South America) might be caused by the lack of sexual reproduction and by the complex of phytophagous insects that feed on the plants (Arthington and Mitchell, 1986).

Eichhornia crassipes and *E. azurea* provide a second example of two closely related species with similar native distribution patterns that differ in their invasiveness. The attractive flowers of both species have a similar appeal to plant

Table 6.2.   Distribution and reproductive strategies of the four *Salvinia* species in the *Salvinia auriculata* complex (V = vegetative reproduction, S = sexual reproduction; adapted from Forno, 1983)

Species	Chromosome no.	Reproductive strategy	Native distribution	Alien distribution
S. auriculata	54	V and S	South and Central America	United States
S. herzogii	63	V	Southern Brazil and Northern Argentina	
S. biloba	36	V and S	Vicinity of Rio de Janeiro	—
S. molesta	45	V	Southern Brazil	Pantropical

collectors that has promoted their introduction into a number of countries as ornamentals; however, only *E. crassipes* has caused serious problems. Both species are capable of sexual and vegetative reproduction though in *E. azurea*, vegetative reproduction occurs slowly by fragmentation rather than by the rapid production of offsets as in *E. crassipes* (Barrett, 1978). Furthermore, in contrast to the free-floating habit of *E. crassipes, E. azurea* and the other six species in the genus are attached to the substrate. Clearly, the ability to undergo rapid vegetative reproduction, together with a greater degree of mobility, has favoured the spread of *E. crassipes* over that of *E. azurea* (Arthington and Mitchell, 1986; Gopal, 1987).

The members of the family Hydrocharitaceae with a similar morphology of whorls of short sessile leaves and stems with short internodes are another group of plants which may be compared. *Egeria densa, Elodea canadensis, Hydrilla verticillata* and *Lagarosiphon major* are representative of a number of species superficially so similar in morphology that they have often been confused. All are submerged species and occupy similar habitats, but have markedly different native distributions (Sculthorpe, 1967). Each of these four species has been responsible for major troublesome invasions when introduced to habitats outside of their native distribution, though other morphologically similar members of the family have not shown invasive features. Apart from the fact that each invasion has been due to vegetative growth and reproduction alone, no clear explanation exists for the mechanisms of these invasions or the lack of invasions by other members of the family (Arthington and Mitchell, 1986).

6.3.2 Morphological plasticity and the importance of rapid vegetative growth

Morphological plasticity describes the ability of a species to modify the shape and size of its vegetative structures when grown under different environmental conditions. This attribute must be distinguished from heterophylly, the presence on a single individual of two or more distinct types of leaf (Sculthorpe, (1967). Morphological plasticity is well known in aquatic and terrestrial plants, for example the morphological differences between sun-grown and shade-grown individuals of a particular species. Indeed, this feature is so well developed in some free-floating invasive aquatic plants that the different 'growth forms' of a particular species are often scarcely recognizable as belonging to the same species (Sculthorpe 1967; Hutchinson, 1975). Two examples, *Eichhornia crassipes* and *Salvinia molesta*, will suffice to illustrate this point.

Eichhornia crassipes produces two distinctive phenotypes or 'growth forms' which are characteristic of the different habitats occupied (Ashton *et al.*, 1979). The first is a small (5–8 cm high) so-called 'colonizing form', which possesses spherical float-like petioles and flattened, circular laminae. This form is found in open water situations where space is not limiting and multiplies rapidly by the production of stolons. The second is a much larger (up to 1.5 m high), so-called

'mat-form', possessing long elongated petioles and vertically arranged, orbicular laminae. This form is characteristic of dense, well-established mats and, once developed, appears to produce relatively fewer lateral stolons though the mat itself is held together by closely interlinked stolons. When either of these forms is moved from its original site in a dense mat to an open water situation, or vice versa, the plant's morphology changes within 10–20 days to suit its new habitat (Gopal, 1987).

The second example, *Salvinia molesta*, is somewhat more complicated in that three distinct phenotypes are recognizable. These are: the 'survival form', some 1–2 cm is length and bearing four to five pairs of flattened leaves that are each 5–8 mm in length, spaced a few millimeters apart on a very short rhizome; the colonizing form', which resembles the 'survival form' in that it consists of flattened pairs of leaves that are widely spaced on a short rhizome, differs in that the leaves and plants are approximately four to five times larger, the plants reaching a length of 5–10 cm; the 'mat form', with pairs of much larger (up to 5–6 cm wide) leaves that are erect, closely adpressed to each other and closely spaced on a rhizome that can reach 15–20 cm in length. Typically, the 'survival form', is found in adverse conditions, for example where nutrient supplies are low, and has very low growth rates under these conditions. The 'colonizing form' is characteristic of open water situations, where space is not limiting, and is capable of remarkably high growth rates.

The 'mat form', as its name implies, is found in established mats where all the plants are in very close contact with one another and their *in situ* growth rates are relatively low. As is the case with *Eichhornia*, when individual *Salvinia* plants are transferred from one situation to another they adapt their growth form to suit the environmental conditions.

The ability to adapt its phenotype to suit the habitat allows an invasive species to compete for a wide range of habitats and promotes dominance of the invader once a habitat has been occupied. Thus, invasive species such as *Eichhornia* or *Salvinia* possess a distinct competitive advantage over other species that lack this attribute.

In virtually every case of a biological invasion by plants, success in the initial stages depends largely on the invader's reproductive capacity. This is borne out by the spectacular rates of vegetative growth reported for a variety of invasive aquatic plants, particularly free-floating forms that are primary colonizers (Blackman, 1960; Westlake, 1963; Mitchell, 1974; Mitchell and Tur, 1975; Ashton and Walmsley, 1976; Cary and Weerts, 1983; Gopal, 1987). However, reproductive effort per unit time clearly cannot explain the *cause* of all invasions, since many non-invasive plants are equally prolific (Harper, 1977; Johnstone, 1986). Nevertheless, since the success of an invasion depends largely on the invader's ability to compete for available resources, rapid vegetative growth must be advantageous to an invader.

6.3.3 Responses to environmental cues

External environmental factors also act in a third capacity, omitted by Grime (1979), namely as 'cues' or 'signals'. This is clearly seen in cases where changes in the external environment elicit responses in plants which cannot be explained simply in terms of biomass limitation by stress or disturbance; for example, the alternate cycles of drying and wetting that the seeds of several plant species require before germination can occur (Mitchell and Rogers, 1985). Whilst other types of signals result when a stress or disturbance is removed, or is applied, the significance of adaptations to signals lies in the fact that the regulation of growth and dormancy is restricted to favourable and unfavourable periods, respectively (Mitchell and Rogers, 1985). Such adaptations are thus extremely important to invasive plants, promoting their ability to exploit favourable habitats.

The translocation of nutrients to or from underground storage organs and the reproductive events of flowering, setting seeds and the formation of dormant propagules seem to occur largely in response to environmental signals, particularly seasonal changes in photoperiod, light intensity and temperature (Mitchell and Rogers, 1985). In contrast to rooted plants, free-floating aquatic plants respond to both seasonal changes in the environment and to changes in population density (Ashton, 1977; Mitchell and Rogers, 1985). For example, increasing mat density stimulates morphological changes in *Eichhornia crassipes* and *Salvinia molesta* (Section 6.3.2) and the initiation of sporocarp production in *Azolla filiculoides* (Ashton, 1977). Similarly, the initiation of propagule germination is also regulated by environmental signals such as daylength, light intensity, temperature and oxygen saturation (Hutchinson, 1975; Haller *et al.*, 1976; Sastroutomo, 1981; Bowmer *et al.*, 1984; Nichols and Shaw, 1986). While the physiological basis of such regulation is not well understood, hormonal reactions similar to those of terrestrial seeds would appear to be operative (Weber and Nooden, 1976).

6.3.4 Competitive ability in the 'struggle for dominance'

The success of an invasive aquatic plant in a habitat reflects, initially, its genotypic capacity to adapt its morphological, physiological and reproductive strategies to avoid or overcome competition for the acquisition of resources (Breen *et al.*, 1987).

Vegetative and sexual reproductive processes are largely responsible for the success or failure of an invasive plant to survive in a particular habitat. Indeed, the true adaptation of a plant to a particular environment is defined as the capability to undergo successful sexual reproduction in that environment (Solbrig, 1981); in these terms, growth and multiplication by purely vegetative means therefore indicate tolerance of the environmental constraints, rather than

adaptation. A given reproductive strategy reflects the responses elicited by several different cues, stresses and disturbances (Grime, 1979; Menges and Waller, 1983); a single species can thus display contrasting reproductive strategies when grown in different environments. Indeed, the extreme variability of most aquatic environments selects for plants that possess a high degree of reproductive plasticity, favouring species with multiple regenerative adaptations (Grime, 1979).

Each reproductive stratagem involves a trade-off between the investment of energy and materials in vegetative growth and sexual reproduction (Solbrig, 1981; Menges and Waller, 1983); seed production is thus favoured at the expense of vegetative growth, and vice versa. Whenever resources are in limited supply, sexual reproduction will tend to reduce the competitiveness and survival ability of the adult plant (Solbrig, 1981). On the other hand, the production of resistant seeds by sexual reproduction enables an invading plant such as *Eichhornia crassipes* (Matthews, 1967) to recover and recolonize the habitat after adult plants have been eliminated by catastrophic disturbance (Breen *et al.*, 1987).

In many emergent species such as *Phragmites* and *Typha*, intensive inter- and intra-specific competition for space and light promotes maximum occupancy of above- and below-ground space. The possession of a clonal or phalanx growth form (Lovett-Doust, 1981) provides a powerful barrier against encroachment by competing species, or neighbouring clones of the same species. Survival during unfavourable periods is accomplished in well-developed rhizome systems (Howard-Williams and Gaudet, 1985) which retain control of the substratum. Rapid response to environmental cues triggers mobilization of stored reserves at the onset of favourable conditions, allowing reoccupation of aerial space and expansion of the phalanx, and thus promotes local site domination, often for many years (Hutchings and Bradbury, 1986). The stoloniferous or 'guerrilla' growth form (Lovett-Doust, 1981) possessed by many invasive aquatic plants provides a high degree of parental care for the offshoot while still allowing the stolon to be lost with little or no damage to the adult plant if environmental stresses are too severe (Breen *et al.*, 1987).

Morphological plasticity and the ability to undergo rapid vegetative growth are the key attributes for success in interspecific competition between invasive aquatic plants that have the same growth form. This was shown very clearly by Bond and Roberts (1978) in the Cahora Bassa reservoir, Mozambique, where *Eichhornia crassipes, Salvinia molesta, Pistia stratiotes* and *Azolla nilotica* were in competition soon after the reservoir commenced filling. The smaller species *A. nilotica* and *S. molesta* were eliminated first and the largest and most vigorous species, *E. crassipes*, eventually dominated the flora (Figure 6.5).

6.3.5 Survival during unfavourable periods

Aquatic plant genotypes are exposed to, and thus moulded by, a variety of selective pressures with a seasonal periodicity. These pressures increase in
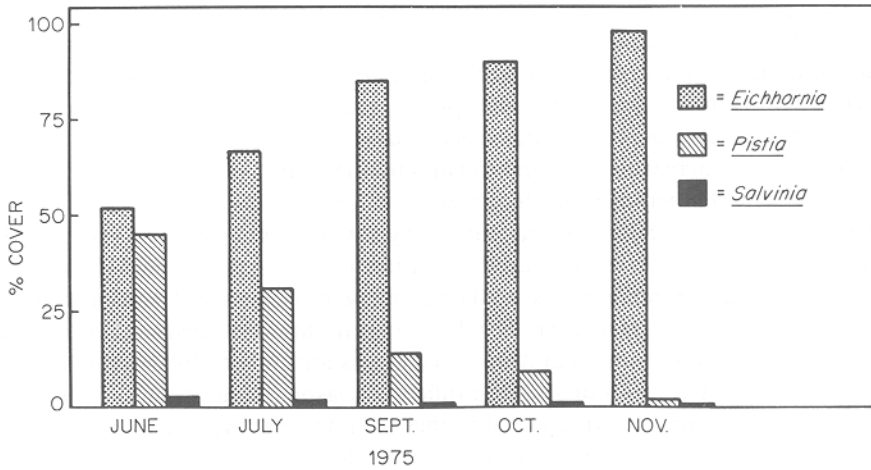
Figure 6.5. Changes in the percentage cover of *Eichhornia crassipes*, *Salvinia molesta* and *Pistia stratiotes* in macrophyte communities of the Carinde and Mucangadze Basins of Lake Cahora Bassa, Mozambique. (Redrawn from Bond and Roberts, 1978.)

magnitude with increasing distance from the equator whilst their predictability varies from a high (e.g. day length) to a low (e.g. atmospheric temperature) probability of occurrence (Mitchell and Rogers, 1985). Different species of aquatic plants can therefore be expected to respond differently to each factor or combination of factors. In addition, several other environmental phenomena, such as droughts, floods and hot or cold periods, also affect aquatic plant growth but do not have a seasonal periodicity. These events are often severe and may eliminate entire populations except for a few sheltered or well-adapted individuals (Mitchell and Rogers, 1985). This periodic screening of genotypes is the basis of 'catastrophic' selection which is an important mechanism leading to adaptive traits and speciation in aquatic plants (Lewis, 1962; Stebbins, 1974).

Several invasive aquatic plants have developed clonal populations or ecotypes as a result of their marked tendency for asexual reproduction (McNaughton, 1986; Hutchinson, 1975). Other invasive species are incapable of setting seed and depend entirely on vegetative reproduction for their survival and spread. These clonal forms allow individual species to occupy widely differing habitats and to take advantage of locally favourable growing seasons. Gopal (1987) has suggested that this may be an important feature of the success achieved by *Eichhornia crassipes*. However, it is important to note that the lack of sexual reproduction in several invasive aquatic plants indicates that these species may have spread from a single introduced clone. Their reduced gene flow and the resultant lack of genetic variability suggest that they might be particularly susceptible to an introduced biocontrol agent (Mitchell, 1974; Arthington and Mitchell, 1986; Ashton *et al.*, 1986).

The submerged species *Potamogeton crispus* provides an excellent example of the ecotypic differentiation of multiple regenerative strategies in plants with this life form. In north temperate ponds, this species over-winters beneath an ice cover either as turions or dormant young plants and seldom flowers or sets seed in summer (stuckey *et al.*, 1978). Turion germination occurs in spring or late summer in response to increasing photoperiod and temperatures in spring or in response to decreasing temperatures at the onset of autumn. In the sub-tropical Pongola River floodplain of South Africa, summer growth is inhibited by unfavourable underwater light conditions due to flood-borne silt loads. Instead, decreasing water temperatures in autumn stimulate turion germination and maximum plant biomass is recorded during winter when large numbers of seeds are produced, enabling survival of aseasonal droughts (Rogers and Breen, 1980; Mitchell and Rogers, 1985). Thus, although quite different seasonal and aseasonal environmental phenomena are experienced in these habitats, ecotypic differentiation of the different regenerative adaptations permits the species to survive over a very wide latitudinal range (Mitchell and Rogers, 1985).

The perennial rhizomes and stolons of many submerged and emergent invasive plants also provide an important survival mechanism during unfavourable conditions when much of the above-ground plant biomass may be lost or senesce (Howard-Williams and Gaudet, 1985). In addition, the possession of underground storage organs permits retention of nutrients within the plant and facilitates rapid growth at the onset of favourable environmental conditions (Sculthorpe, 1967).

6.3.6 Mechanisms facilitating intra- and inter-system transfer

Earlier in our discussion (Section 6.2.2) we emphasized that a variety of transporting mechanisms are important in the arrival and dispersal stages of aquatic plant invasions. Clearly, the efficacy of biotic and abiotic transporting mechanisms will be increased greatly, if the plant in question possesses one or more specialized adaptations that facilitate its dispersal. Indeed, most successful invasive plants possess very efficient dispersal mechanisms, such as sexual or asexual propagules, or are able to disperse widely on flood waters and regrow rapidly following fragmentation.

It is axiomatic that those aquatic plants that are capable of long-distance dispersal will already have done so: they are therefore unlikely to be recognized as invasive alien species in a particular environment. For example, the immense geographical distributions of the anemophilous genera *Phragmites* and *Typha* (Sculthorpe, 1967; Cook, 1974, 1985) suggest that these plants may have spread naturally through wind transportation of their numerous minute seeds (Cook, 1974, 1985; Breen *et al.*, 1987). While anemochory may be a characteristic of most graminaceous phreatophytes, very few truly aquatic plants possess this attribute (Sculthorpe, 1967). Nevertheless, aquatic plants that are capable of a high

reproductive output, in terms of numbers of propagules, increase their chances of dispersal.

In general, therefore, plant attributes that facilitate short-range dispersal increase both the rate and chance of successful invasion. Since large seeds or propagules have a greater germination success but are less easily dispersed, trade-offs between propagule numbers, sizes and ease of dispersal are very important (Sculthorpe, 1967; Hutchinson, 1975). Additional features, such as temporary buoyancy in newly dehisced propagules or the production of fleshy fruits to attract waterfowl (Rogers and Breen, 1980), add to the efficiency of dispersal. Obviously, when dispersal in an invasive plant's native habitat is closely geared to the activities of a specific vector, then dispersal in the new habitat is likely to be very limited. Where dispersal is passive, for example by water currents, flowering and propagule production times can be extended considerably to reduce the chances of mortality. Thus, the development of hardened seed or spore coats protects these propagules from physical damage during transport by water currents and increases their chances of successful intra-system transfer (Ashton, 1977).

6.3.7 The 'perfect invader'—does it exist?

Several authors (e.g. Baker, 1965; King, 1966; Holm *et al.*, 1977; Elmore and Paul, 1983) have described and listed the attributes and characteristics of a hypothetical ideal invader. However, most of these descriptions refer to terrestrial situations and reflect particular concern with the invasion of agricultural crops by weeds. We should, therefore, be cautious when extrapolating them directly to invasions of natural or man-modified aquatic systems. Nonetheless, agricultural weeds and invasive aquatic plants do share several attributes that contribute to their success.

A logical starting point in the search for the 'perfect invader' would be to examine those aquatic species that have provided such dramatic examples of successful invasions that they are now classified as noxious aquatic weeds (Sculthorpe, 1967; Mitchell, 1974; Holm *et al.*, 1977). The most important species that warrant such consideration have been listed in Table 6.1.

Close examination of these invasive aquatic plants and the variety of habitats that each species has invaded successfully, allows assessment of each species against the criteria of the hypothetical 'perfect invader'. On balance, *Eichhornia crassipes* appears to be the closest contender for the title, further substantiating its status as the world's most troublesome water weed (Sculthorpe, 1967; Mitchell, 1974; Holm *et al.*, 1977; Gopal, 1987).

6.4 THE MANAGEMENT OF INVASIVE AQUATIC PLANTS

Excessive populations of invasive aquatic plants not only cause marked changes in the natural vegetation of aquatic ecosystems, they also inhibit or prevent the

management and utilization of water resources (Mitchell, 1974; Ashton *et al.*, 1986). Despite the fact that the biological and economic consequences of these impacts are often difficult to evaluate objectively they are invariably regarded as being undesirable and therefore requiring some form of remedial action (Ashton *et al.*, 1979; Arthington and Mitchell, 1986).

Manipulation of the environment to achieve certain objectives is a well-known characteristic of modern man and forms, for example, the basis of his (largely successful) agricultural practice. However, agricultural systems are highly simplified with a greatly reduced diversity of species. The management of natural or semi-natural aquatic ecosystems that contain large numbers of species is considerably more difficult because of the complex interrelationships that exist between the various components. It is essential that these relationships be understood before management options are formulated and implemented. This situation therefore requires that research aimed at understanding the complexities and interrelationships of the aquatic environment should enjoy a high priority (Arthington and Mitchell, 1986). However, progress and the betterment of the human race cannot always wait for the result of these investigations. Management procedures therefore often have to be designed and instituted on the basis of available knowledge, however inadequate it might be. Thus, it is essential that continual environmental monitoring form part of a management programme which, in turn, must be sufficiently flexible to enable incorporation of viable alternatives if unforeseen developments occur (Mitchell, 1974). However, it must be emphasized from the outset that it is absolutely necessary to clearly define the aims and objectives of any management policy before procedures for its implementation are designed or carried out.

6.4.1 Available options

Management strategies employed against invasive aquatic plants can conveniently be divided into two basic groups, namely: protectionist and interventionist. The former group attempts to retain particular ecosystems in a hypothetical 'natural' or pristine state by preventing invasions and usually contains a strong legislative element (discussed in Section 6.4.6). Typically, these strategies involve some form of environmental or ecological management that is designed to reduce habitat disturbance. The most important invasive aquatic plants, the primary colonizers of disturbed systems, are thereby excluded.

In contrast, interventionist strategies seek to suppress or remove existing invaders from a particular habitat, thereby reducing their population size to a more 'acceptable' level and minimizing their impact on ecosystem functioning. Typical strategies include various forms and combinations of manual, mechanical, chemical and biological control techniques that confine the invader to a low level. These actions almost invariably return the habitat to an earlier successional stage, and increase the probability that the first invader may be replaced by a

second, more problematic, invasive species (Cook, 1985). Because of financial considerations, complete eradication of the invader is seldom attempted.

At present, six groups of control techniques can be used to manage invasive aquatic plants:

1. Manual removal, as its name suggests, is a labour intensive and low efficiency technique that is hampered by water depth and the physical quantities of material that can be handled in a given time interval.
2. Mechanical control usually involves the use of mechanized or power-driven equipment to harvest plant material a remove it from a water body. High rates of removal are possible but the process is often inefficient in dealing with very extensive invasions where the rates of regrowth often exceed the removal capacity of the machines.
3. Chemical control involves the use of inorganic or organic herbicides, usually as a last resort, to treat extensive infestations. The herbicide is either applied directly into the plants in the case of free-floating and emergent species or into the water in the case of submerged species. A serious disadvantage is the prohibitively high cost of most chemical control programmes. Modern developments in herbicide formulation have considerably improved the performance of appropriate herbicides and at the same time have reduced many of the deleterious side effects on other aquatic organisms. Safety to other water users is of paramount importance when using herbicides to control aquatic plants.
4. Biological control techniques use one or more host-specific natural enemies from a target plant's native range to attack the plant and maintain its population at a low level. Unfortunately, the initial stages of identification, collection and screening of the organism for host specificity, followed by its breeding and dissemination on the target plant can be expensive and take several years. However, when successful, these control measures are self-sustaining. Ultimately, this technique probably holds the greatest promise in terms of minimizing the ecological impacts of control programmes.
5. Environmental manipulation involves modification of the aquatic environment, for example by lowering water levels, to disadvantage the invasive plant of interest. Significant successes have been achieved in this manner though the techniques are not entirely suitable in areas where water supplies are scarce. A further disadvantage is that unless the dead plant material is removed, a subsequent rise in water level causes rapid nutrient release and enrichment of the water.
6. Direct use of the invasive plant for economic benefit, for example as a stock feed, requires that the maintenance of a particular plant population is compatible with other uses to which the water may be put. A serious disadvantage is that the plant population serves as a source for further invasions.

So wide is the range of aquatic plant life forms and growth characteristics that a method of control appropriate to one species is often unsuitable for another species in the same habitat (Sculthorpe, 1967). In addition, the control of invasive aquatic plants often presents many specialized problems. For example, if all the aerial, rooted and submerged growing regions of a plant are not destroyed, new growth is soon produced and the problem recurs. Additional problems can arise due to the inefficient disposal of plants killed *in situ*, which can cause oxygen depletion and elevated levels of dissolved nutrients that, in turn, can promote the regrowth of surviving plant fragments.

Ideally, each problem should be treated as unique and all the local factors investigated thoroughly before a particular technique or combination of techniques is chosen. In almost every case, it is clearly advantageous to commence operations as soon as possible before the problem becomes critical and necessitates the use of drastic measures (Sculthorpe, 1967; Mitchell, 1974; Ashton *et al.*, 1979).

6.4.2 Eradication versus control and the costs of inaction

Once the successful invasion and establishment of an aquatic plant has been found to have adverse ecological and economic effects, every attempt must be made to reduce its population size and prevent further spread. The severity of the actual and potential problems posed by the invading plant influence the choice of whether to opt for total eradication of the invader or undertake a control programme to maintain the invader's population at a lower, more acceptable level. Both options employ the same techniques but differ in the degree of vigour and persistence with which they are carried out. In the short term, control is cheaper than eradication. However, maintenance of control programmes over long periods of time invariably raises their long-term cost above that of eradication.

Vigorously growing plants such as *Eichhornia* and *Salvinia* can be eradicated if the infestation is identified and dealt with at an early stage or is confined to a small body of water. However, once an infestation is well established in a large water body with inaccessible areas, eradication attempts are less likely to succeed. In either case, it is critically important that control or eradication programmes are well planned and thorough and that they are persistently carried out. Regular surveys and follow-up control of outbreaks from surviving plants or newly germinated seedlings are required for a number of years (Mitchell, 1974; Ashton *et al.*, 1979). In particular, this follow-up procedure is crucial to the success of programmes aimed at eradicating *Eichhornia crassipes* (Ashton *et al.*, 1979), whose seeds can remain viable for 10–15 years (Matthews, 1967; Gopal, 1987). The necessity to sustain expensive follow-up programmes to ensure successful control or eradication, emphasizes further the benefits of self-sustaining biological control measures (Arthington and Mitchell, 1986).

Delays in the identification of an invasive aquatic plant problem and failure to limit the plant's initial spread will allow rapid expansion of the population. This will increase the size of the problem and expand the scope, impact and costs of the remedial action required (Ashton *et al.*, 1986). Inaction, or action that is too little too late, is thus both ecologically and economically expensive.

6.4.3 Successful control programmes—why did they succeed?

Numerous control and eradication programmes directed against submerged, emergent and free-floating invasive aquatic plants in many parts of the world have been reported in the literature. Whilst considerable attention has been paid to submerged and emergent plants (e.g. Jacot Guillarmod, 1979; Bowmer *et al.*, 1984), the majority of these programmes have been aimed at the free-floating species *Salvinia molesta* and, more especially, *Eichhornia crassipes* (e.g. Sculthorpe, 1967; Gopal, 1987), a direct reflection of the latter's world-wide weed status (Gopal and Sharma, 1981). A wide variety of local ecological and economic constraints has dictated the use of an enormous array of control techniques and strategies in these programmes. As could be expected, different degrees of success have been achieved (e.g. Blackburn, 1974; Mitchell, 1974; Crafts, 1975; Soerjani, 1977; Ashton *et al.*, 1979, 1986; Mayer, 1981; Julien, 1982; Forno and Bourne, 1985; Thomas and Room, 1986; Gopal, 1987). Given the extreme variability of the data set and the fact that the 'success' of a particular programme will depend largely on its original objectives, can we identify any common features that distinguish *effective* control and eradication programmes?

Two important features have virtually guaranteed the success of programmes directed at small infestations of invasive aquatic plants, i.e. those measuring less than 20–30 hectares in extent. These were a high degree of isolation or confinement of the infestation to a single, accessible water body and the early identification of the aquatic plant problem followed by prompt and sustained remedial action (Mitchell, 1974; Mayer, 1981). The reduced cost involved in treating small infestations has favoured the choice of eradication rather than control and has promoted the widespread use of a range of herbicides in those situations involving free-floating plants (Blackburn, 1974; Newbold, 1975). Where the infestations involve submerged plants, fish such as grass carp (*Ctenopharyngodon idella*) are often used as biocontrol agents with great success (Van Zon, 1981; Julien, 1982; Wiley and Gorden, 1984). An invasive aquatic plant infestation in a river is far more difficult to control and requires extensive checks of the river catchment to reduce the frequency of reinfestation.

In contrast, the scale of operations required to deal with most of the more extensive invasions of aquatic plants (> 1000 hectares) has greatly limited the variety of control procedures that could be implemented. Typically, high rates of plant growth render the use of manual or mechanical techniques alone inappropriate; usually only chemical techniques, specific biocontrol agents or

integrated programmes that con ' 'ne several techniques stand any chance of success. Where an ecologically undesirable technique is used, for example the large-scale application of herbicides, special precautions are needed to minimize the risks of adverse ecological impacts and any deterioration in water quality (Blackburn, 1974; Mitchell, 1974).

The *Eichhornia crassipes* eradication programme at Lake Hartbeespoort, a heavily enriched, multi-purpose reservoir in South Africa, provides one of the best example of successful large-scale use of herbicides (Figure 6.6; Ashton *et al.*, 1979, 1980). Extended planning, herbicide tests and inclement weather delayed initiation of the spraying programme such that the rapidly growing *E. crassipes* infestation covered 1200 hectares (60% of the lake's surface area) by the time herbicide application started. The spraying programme consisted of four separate aerial applications of herbicide supplemented with intermittent spot-treatments of marginal plants using hand-held and boat-mounted sprayers. Impacts on the environment and other water users were minimal and all adult *E. crassipes* plants in the reservoir were successfully eliminated (Ashton *et al.*, 1979, 1980). A follow-up surveillance programme initiated in 1978 has monitored the lake shores for *E. crassipes* seedlings and is scheduled to continue until 1995 to
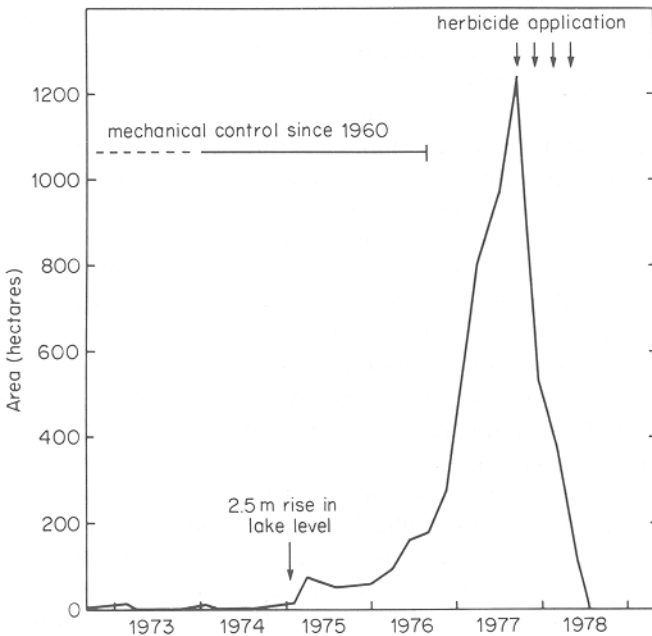

Figure 6.6. Changes in the area covered by *Eichhornia crassipes* on Lake Hartbeespoort, South Africa, before and after herbicide application. (Adapted from data in Ashton *et al.*, 1979.)

minimize the risk of reinfection. Concomitant checks are made of streams and rivers in the catchment above the lake to avoid the development of new *E. crassipes* infestations (Ashton *et al.*, 1979, 1980). In the case of Lake Hartbeespoort, success was entirely dependent on careful planning, diligent and sustained implementation of the chosen techniques and the maintenance of an efficient, vigilant follow-up operation over many years (Ashton *et al.*, 1986).

The two biological control programmes directed against *Salvinia molesta* in Australia (Room *et al.*, 1981, 1984) and Papua New Guinea (Mitchell, 1981; Thomas and Room 1985, 1986) are outstanding examples of the success that can be achieved against both small and large infestations with a host-specific control agent.

The control agent in question, a Brazilian curculionid beetle found feeding only on *Salvinia molesta*, was initially identified as *Cyrtobagous singularis* and introduced to Australia as a potential biocontrol agent against *S. molesta* (Forno and Bourne, 1985). When released on Lake Moondarra in Australia, the beetle destroyed a 200 hectare *S. molesta* infestation in 14 months (Figure 6.7; Room *et al.*, 1981). Subsequent studies have shown the beetle to be a separate species, *Cyrtobagous salviniae* Calder and Sands, and it is being used with great success to control *S. molesta* elsewhere in Australia (Room *et al.*, 1984) as well as in Namibia
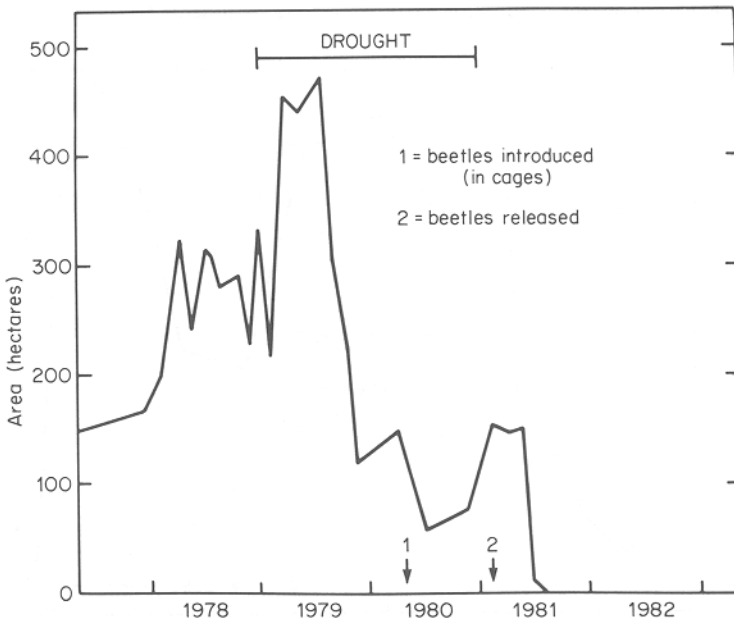

Figure 6.7. Changes in the area covered by *Salvinia molesta* on Lake Moondarra, Australia, before and after introduction of *Cyrtobagous salviniae*. (Redrawn from Thomas and Room, 1986.)

(Schlettwein, 1985), India (Room and Thomas, 1986) and Papua New Guinea (Thomas and Room, 1986).

The rapid control exerted by *C. salviniae* on the *S. molesta* infestation in the Sepik River floodplain lakes in Papua New Guinea has provided the most spectacular example so far of successful biological control of an aquatic weed (Figure 6.8; Thomas and Room, 1985, 1986). Within a two year period, *C. salviniae* destroyed an estimated two million tonnes of *S. molesta*, reducing the plant's cover from approximately 200 km² to 2 km² (Thomas and Room, 1986).

The success of *C. salviniae* in controlling *S. molesta* contrasts markedly with the failures of other insects, particularly the related *C. singularis*, the pyralid moth *Samea multiplicalis* and the lesser success of the aquatic acridid grasshopper *Paulinia acuminata*. Intensive investigations have shown that the success of *C. salviniae* can be attributed to the deliberate dispersal of the beetles over the whole *S. molesta* infestation, the lack of predators, parasites and diseases in its new environment, and the selective feeding behaviour of both the larvae within the rhizome and the adults that destroy *Salvinia* growing points (Thomas and Room, 1986). This feeding pattern has considerable significance for *S. molesta* which relies entirely on vegetative propagation (Mitchell, 1974). High nitrogen levels within *S. molesta* plants increase their 'palatability' to *C. salviniae* and, together with elevated water temperatures, amplify the beetle's feeding rate and promote rapid development of *C. salviniae* populations (Forno and Bourne, 1985; Room
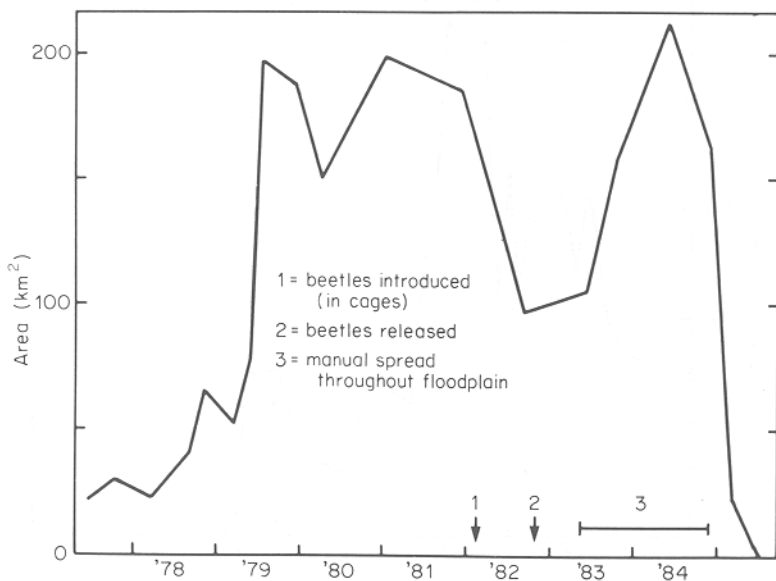

Figure 6.8.   Changes in the area covered by *Salvinia molesta* on 100 lakes in the Sepik River floodplain, Papua New Guinea, before and after introduction of *Cyrtobagous salviniae*. (Redrawn from Thomas and Room, 1986.)

and Thomas, 1985; Thomas and Room, 1986). *C. salviniae* is thus a highly cost-effective and environmentally sound means of biological control against *S. molesta* invasions in the tropics. However, the insect's sensitivity to lower temperatures precludes its use in cool temperate areas where *S. molesta* can still grow (Cary and Weerts, 1983; Room and Thomas, 1986).

Another example of successful biological control of an invasive aquatic plant has been the use of the flea beetle (*Agasicles hygrophila*) against alligator weed (*Alternanthera philoxeroides*) in Australia and several of the southeastern states of the United States. As in the case of *Cyrtobagous* and *Salvinia*, the *Agasicles* success can be largely attributed to its host-specific selective feeding behaviour and possession of similar environmental tolerances to those of *Alternanthera* (Andres, 1977; Julien, 1982).

6.4.4 Unsuccessful control programmes—why did they fail?

In our preceding discussion we emphasized the importance of careful planning, use of appropriate techniques and the need to maintain a vigilant follow-up operation. Indeed, failure to comply with one or more of these three requirements has led to the failure of several attempts to chemically control or eradicate infestations of invasive plants.

For example, at Lake Bon Accord, South Africa, two aerial herbicide applications reduced an *Eichhornia crassipes* infestation that covered the entire surface of the lake (200 hectares) to less than one hectare. However, failure to maintain a follow-up programme resulted in complete reinfestation of the impoundment within a period of 8 months (Ashton *et al.*, 1980). A second series of herbicide applications, this time combined with an efficient follow-up operation, has since eradicated *E. crassipes* from this lake (Ashton *et al.*, 1986). In another, more tragic example, a 30-year period (1952–1982) of successful *E. crassipes* control with the herbicide 2, 4-D on Lake McIlwaine, Zimbabwe (Jarvis *et al.*, 1982), has since been negated by a failure to maintain the required follow-up programme (P. J. Ashton, personal observation). In those situations where funds are limited, the increasing costs of both herbicides and the equipment for their application can lead to a loss of continuity in a chemical control programme and thus allow the invasion to return.

Another very important feature that can thwart attempts to chemically control invasive aquatic plants, is the problem of inaccessible terrain. For example, early attempts at aerial applications of herbicide to control the *Eichhornia crassipes* infestation in the newly flooded Lake Brokopondo, Surinam, were frustrated by the highly indented shoreline, dense riparian forests and the shelter afforded to *E. crassipes* by partly inundated trees (Van Donselaar, 1968; Leentvaar, 1973). Similarly, attempts to chemically control the *Salvinia molesta* infestation in the rivers, lakes and swamps of northern Botswana and the eastern Caprivi area of Namibia were also largely unsuccessful. Here, control of *S. molesta* plants

growing in the open water areas was effective, while plants sheltered by the dense *Phragmites* reedswamps were unaffected by the herbicide and rapidly reinvaded the cleared areas (Edwards and Thomas, 1977).

An important point to remember is that the large-scale use of herbicides to control extensive aquatic plant infestations is ecologically undesirable; such a course of action should be reserved for crisis conditions only (Ashton *et al.*, 1979, 1980). Furthermore, an inadequate knowledge of the invasive plant's ecology can lead to the choice of an inappropriate herbicide, for example one which cannot control all of the invader's life stages. Chemical control techniques are thus seldom effective in the long term unless they are integrated with other control techniques (e.g. manual or mechanical removal, ecosystem manipulation, biological control; Soerjani, 1977).

Biological control is widely considered to be the ideal solution to all invasive aquatic plant problems. Indeed, this view is strongly reinforced by the spectacular successes achieved, for example, against *Salvinia molesta*. However, a recent survey (Julien, 1982) has shown that less than half of the programmes undertaken have been effective and the likelihood of success in a particular programme can rarely be predicted. The use of an inappropriate organism or deployment of the organism in an unfavourable environment appear to be the most frequent reasons for the failure of biological control programmes (Julien, 1982; Gopal, 1987).

Biological control programmes directed against *Eichhornia crassipes* in India and North America using the Chinese grass carp (*Ctenopharyngodon idella*) provide good examples of the use of an inappropriate organism. These (and other) herbivorous fish fed preferentially on submerged aquatic plants (Van Zon, 1981; Wiley and Gorden, 1984), and consumed *E. crassipes* only as a last resort (Mehta and Sharma, 1972). Thus, their preferential feeding pattern, combined with a poor reproductive performance outside of their native range, necessitated very high stocking rates (Baker *et al.*, 1974), which rendered this species totally unsuited for *E. crassipes* control in most instances.

In contrast, an organism that is a successful biocontrol agent in one environment may prove to be far from effective when it is introduced elsewhere. A case in point is provided by the curculionid beetle *Neochetina eichhorniae* which has achieved a reasonable degree of success as a biological control agent against *E. crassipes* in Australia (Harley and Wright, 1984; Wright, 1984) and the United States (Manning, 1979). However, this organism appears to have had little impact on *E. crassipes* in South Africa despite the fact that it has maintained large populations at several sites for many years (P. J. Ashton, personal observation). In this case, it is possible that climatic and local environmental differences may have altered the host plant's chemistry and cuticle structure, thereby reducing its palatability and decreasing its susceptibility to the introduced beetles (Wright, 1984). However, the effects of *N. eichhorniae* on *E. crassipes* can be augmented when a plant pathogen such as the fungus *Cercospora rodmanii* is inoculated

onto the insect-damaged plants. Trials in the southeastern United States have shown that this and other combinations of insects and plant pathogens have considerable potential for the biological control of *E. crassipes* and deserve far greater attention in future (Freeman, 1977).

The importance of local environmental conditions and natural successional changes in the aquatic vegetation should not be underestimated. Indeed, successional changes can mask or amplify the impact of an introduced biological control agent and thereby complicate assessments of the control programme's efficacy. The biological control programme directed against the *Salvinia molesta* infestation on Lake Kariba, Zimbabwe, highlighted this dilemma. After closure of the dam wall in December 1958, the rising waters of the new lake inundated huge areas of vegetation. Scattered *S. molesta* colonies began to proliferate rapidly in the calm, nutrient-enriched waters and the mats became securely anchored amongst partly inundated trees. The area covered by the plant rose to a peak in May 1962 when it occupied 1003 km² (21.5%) of the lake's surface (Figure 6.9; Mitchell and Rose, 1979; Marshall and Junor, 1981). Subsequently, the area decreased and then fluctuated between about 400 and 800 km². Approximately 2 years after the introduction of the Trinidad strain of an aquatic acridid grasshopper (*Paulinia acuminata*), there was a dramatic drop in the area covered by *S. molesta*, to approximately 100 km² (Mitchell and Ross, 1979). However,
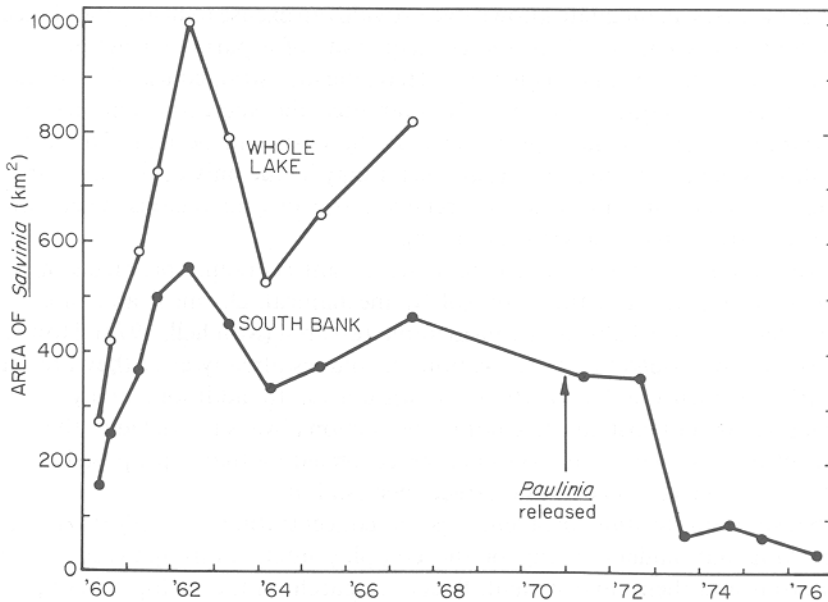

Figure 6.9. Changes in the area covered by *Salvinia molesta* on Lake Kariba, Zambia/Zimbabwe, before and after release of *Paulinia acuminata*. (Redrawn from Mitchell and Rose, 1979.)

while *P. acuminata* did feed actively on the *S. molesta* plants, a combination of environmental factors was also implicated in the plant's decline. As the lake matured, decomposition of the trees that had previously anchored *Salvinia* mats plus increasing competition from native aquatic plants and the declining nutrient content of the lake water were considered to be the main factors responsible (Mitchell and Ross, 1979; Marshall and Junor, 1981). Thus, while the introduction of *P. acuminata* as a biological control agent may have contributed to reducing the *S. molesta* population, biological control alone was not effective.

6.4.5 Can programme success be predicted?

The ability to predict the outcome of particular management strategies is one of the prime objectives of water managers concerned with counteracting the adverse effects of invasive aquatic plants. Ideally, accurate predictions regarding the consequences of a particular action require a sound understanding of the system under consideration and the ecology of the invasive plants as well as the likely impacts on the environment of the proposed course of action. Sadly, however, our present knowledge of aquatic ecosystems is often inadequate to meet these criteria and formulate ecologically sound management programmes (Mitchell, 1979b); many control programmes continue to be implemented on a 'best guess' or trial and error basis (Mitchell, 1974; Ashton *et al.*, 1986).

In some cases, inadequate knowledge provides an excuse to justify the choice of an alternative scenario where the consequences of a particular action on the environment are conveniently ignored. Here, the unrestrained use of chemical or mechancial techniques can virtually guarantee the successful elimination of undesirable aquatic plants, provided that the costs can be met. This type of situation is obviously undesirable and yet it may be the only option available to water management authorities, especially those in arid regions where water resources are scarce (Ashton *et al.*, 1986).

Invasive aquatic plants have caused significant economic problems in most areas of the world and their control by mechanical, chemical and biological means has been the subject of considerable research (Mitchell, 1978). However, whilst effective control and eradication techniques already exist they are often remarkably ineffectual in certain circumstances. In addition, many control techniques are not cost-effective nor is their action always restricted to the target plant of interest. This situation must be corrected so that a proposed control measure can be confined to the target species alone.

The solution to this problem lies in concentrating our efforts towards improving our understanding of the complex interactions between invasive organisms and their environment. Recent research on the biological control of *Salvinia molesta* has emphasized the subtleties of many of these interactions and has highlighted their importance as determinants of successful control (Thomas and Room, 1986).

Therefore, in the case of *Salvinia molesta* invasions, our improved understanding now enables us to make reasonable predictions as to whether or not *Cyrtobagous salviniae* will be an effective biological control agent in a particular environment. While this is a tremendous achievement in itself, further studies are still required to refine this predictive ability for *S. molesta*. A wealth of biological information is available on another notorious invader *Eichhornia crassipes* (Gopal, 1987), a species which has been controlled or eradicated successfully in a number of different countries. However, despite these successes, we still cannot make accurate predictions as to whether a particular management option will succeed or not.

6.4.6 The role of legislation

Legislation plays a vital role in two major arenas of invasive aquatic plant control: namely, avoiding the establishment of invasive plants, and determining the means and manner by which such plants may safely be controlled or eradicated.

Legislation preventing the establishment of invasive plants aims to prevent entry into a country and restrict spread within the country. For both components, specific plants are identified as being undesirable on the basis of their known invasive behaviour. However, legislation seldom prevents the entry of a 'new' species unless it is recognized as a problem in another country. Legislation cannot prevent the unauthorized or accidental introduction of invasive plants.

Where problems have been experienced due to invasive aquatic plants, legislation restricting their spread within the country has received considerable attention. In general terms, such legislation is only feasible when humans are the main, if not the only, dispersal agent (Arthington and Mitchell, 1986). A far more common course of action is to promulgate dangerously invasive plants as 'noxious weeds' and promote public participation in their control. For example, public participation in the dispersal of *Cyrtobagous salviniae* over the Sepik River floodplain was vital to the successful control of *Salvinia molesta* (Thomas and Room, 1986). Noxious weed legislation is important in that it not only empowers water management authorities to control the plant wherever it may be found, it makes such control obligatory (Ashton *et al.*, 1986).

The second important role of invasive aquatic plant legislation lies in its regulation of the control techniques that may be used in particular situations and in the stipulations as to the safety precautions that are required For example, the use of herbicides in or near water supplies used for human or stock consumption is a highly sensitive issue and all possible precautions must be taken to ensure the safety and well-being of every water user (Bates, 1976; Ashton *et al.*, 1980).

Regional and international legislation relating to invasive plants is gradually changing as we improve our knowledge of the invasive characteristics of particular plant groups (Navaratnam and Catley, 1986). The apparent trend

towards a greater stress on preventive measures, away from a more retrospective stance where legislation is only enacted against a particular plant after it has caused a problem, is worthy of special emphasis. At present, the most urgent requirement for improved legislation relates to the nursery, aquarium and aquaculture trades who are responsible for the importation and sale of a considerable number of aquatic plants. Far stricter controls are required to limit their trade in invasive aquatic plants (Ashton *et al.*, 1986).

6.4.7 Integrated control strategies

Our preceding discussions have emphasized the fact that many of the methods currently used to control or eradicate invasive aquatic plants are not always successful when used individually. Furthermore, many of the more effective techniques have undesirable effects on the environment and other aquatic biota and therefore should be used with extreme caution. Ideally, control or eradication strategies must strive to minimize adverse ecological impacts. Such sensitivity to ecological constraints requires the use of an array of techniques, each carefully integrated to coincide with different phases of the target plant's life cycle and, most importantly, geared to the dynamics of the affected ecosystem. This type of approach is increasingly being referred to as 'integrated control'.

Integrated control programmes have a definite advantage over more conventional single-option programmes in that they are highly flexible and are thus better able to deal with unexpected situations. Furthermore, integrated control tends to retain biotic diversity, and thus has the potential to stabilize the system and render it less prone to further invasions. In contrast, the use of a single method, particularly chemical or mechanical techniques, tends to interrupt the existing successional trend by an abrupt simplification of the system. The system reverts to an earlier, less stable successional stage that is once again susceptible to invasion.

Some of the most pressing aquatic plant problems today concern the need to control invasions of nature reserves and natural ecosystems as well as artificial water supply reservoirs where external perturbations must be kept to an absolute minimum. Both types of problems would benefit by the use of integrated control strategies.

To date, several control and eradication programmes directed at specific target plants have employed a range of techniques to accomplish their objectives (Mitchell, 1978; Ashton *et al.*, 1980; Gopal, 1987). However, very few programmes have deliberately integrated a variety of control techniques with the dynamics of the plant and ecosystem. Once again, the greatest barrier to the realization of this ideal is our inadequate knowledge of plant–environment interactions and ecosystem dynamics.

6.5 CONCLUSIONS

It has been stressed that the art and science of controlling water flows is probably the one branch of engineering science that has contributed most to the development of civilization (Baxter and Glaude, 1980). In the process, a wide range of new aquatic ecosystems has been created and numerous existing systems have been modified. Unfortunately, man's skill at, and knowledge of engineering systems have not been matched by his understanding of the intricacies of biological systems and his ability to maintain them in a stable condition (Mitchell, 1974). Coupled to this, the tremendous increase in international travel dramatically increased the ease with which invasive plants are transported around the globe. Consequently, man is not only responsible for the introduction of invasive plants to an area, he also creates conditions which promote their excessive growth. Indeed, most successful aquatic plant invaders are primary colonizers of disturbed habitats (Cook, 1985) and are well represented in the early successional stages of plant communities.

In the light of man's frequent involvement in aquatic plant introductions, it is not surprising that the absence of a long-distance dispersal mechanism does not hinder a plant's invasive potential. Instead, the possession of an efficient short-range dispersal mechanism is sufficient to increase both the likelihood and rate of successful invasion. Another essential attribute of successful invaders is their high reproductive output. Here, the ability to undergo rapid vegetative reproduction is far more important than sexual reproduction. However, the ability to multiply rapidly also places constraints on an invasive plant since the available resources of light, nutrients and space become limited with time unless the plant can regulate its own population size (Gopal, 1987). Invaders such as *Eichhornia crassipes* and *Salvinia molesta* have largely achieved this with their high degree of morphological plasticity, competitive ability and tolerance of a wide range of environmental conditions. Indeed, their success as invaders can be gauged both by their wide distribution and by the attention they have attracted. However, whilst we know most of the attributes that increase the probability of notorious species such as *E. crassipes* and *S. molesta* becoming successfully established in a new environment, we are still unable to make accurate predictions about individual situations.

Sadly, our knowledge of the biology and ecology of other invasive aquatic plants is far less extensive, particularly with regard to their responses to environmental cues and their interactions with the biotic and abiotic features of new environments. This situation is further confounded by the interacting effects of chance and timing (Crawley, 1986) which can either amplify, modify or remove invasion barriers (Breen *et al.*, 1987). Consequently, our predictive ability is limited to the rather banal generalization that the probability of an invasion succeeding will increase as the bioclimatic match between the plant's native and invaded environments improves.

Excessive populations of invasive aquatic plants are a direct consequence of, and an expanding obstruction to, man's increased management and utilization of water resources (Mitchell, 1974). Inevitably, such populations are considered to be undesirable and therefore requiring remedial action. While a wide variety of management options are available, the choice of technique requires a sound understanding of the ecosystem under consideration and the ecology of the invasive plant as well as the likely impacts on the environment of the proposed course of action.

Preference should therefore be given to a stratagem that is both ecologically sound and cost-effective (Mitchell, 1974; Ashton *et al.*, 1986). In this regard, the use of specific biological control agents against target plants is now receiving increased attention as a result of the successes that have been achieved against *Salvinia molesta* (Thomas and Room, 1986). Yet another approach, the use of plant pathogens in combination with phytophagous insects, is also receiving greater attention (Freedom, 1977). Whatever option is chosen, the success or failure of a control programme depends on careful planning, diligent and sustained implementation of the chosen techniques and maintenance of efficient and vigilant follow-up operations. Failure to comply with one more of these requirements will lead to the failure of the programme.

Ultimately, the use of biological control techniques and the development of carefully integrated control programmes hold the greatest promise for the future. Ideally, integrated control programmes against invasive aquatic plants should form part of an overall catchment management programme (Van Schayck, 1986). Unfortunately, our presently inadequate knowledge prevents realization of this ideal. However, since the scale and scope of aquatic plant invasions are increasing world-wide, urgent attention must be given to remedying this deficiency. In addition, it is particularly important that everyone who is involved with the ecology and management of invasive aquatic plants should adopt a far broader outlook and appreciation of the problems involved. We hope that this review will stimulate such an approach.

ACKNOWLEDGEMENTS

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