The management ecology of aquatic weeds which cause problems in Iranian freshwater systems

by

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Abstract

A wide range of methods are available for managing submerged, floating and aquatic weeds (Pieterse & Murphy, 1990). The efficacy of these methods is well documented for major weed species. However, relatively few investigations have attempted to assess the impacts of aquatic weed control, on specific weed populations, in the context of the different ecological pressures which influence their survival.

This study aimed to assess the response of *Typha latifolia*, *Potamogeton pectinatus* and *Salvinia rotundifolia*, three weed species which cause problems in Iranian fresh waters, to different weed control methods, in relation to naturally occurring and augmented stress and disturbance factors (e.g. shade, nutrient status, sediment type, competition, chemical and physical damage).

The results of germination studies suggested that *Typha latifolia*, grown from seed, was severely inhibited by burial in the soil. After 42 days maximum rates of germination were recorded from seeds buried in sandy sediments to a depth of between 0 and 0.5 cm. In shallow water, newly-germinated *Typha* will die due to lack of light if the time taken to reach the surface is too long (possibly because of the lack of resources available to support initial growth in the tiny *Typha* seed). A statistically significant difference in seed germination was obtained in 0, 0.5 and 1 cm, compared with other depths.

The results of a single cut (carried out at shoot elongation stage) plus shade treatment suggested that *T. latifolia* was very susceptible to physical damage in its early growth stage. Two cuts plus shade had a very severe effect on the plant's ability to regrow. Maximum shoot length for control treatments was 111 cm, one cut with and without shading were 23 and 63 cm, respectively, and two cuts with and without shading were 30, and 27 cm. Some plants were killed by the two cuts plus shade treatment, indicating that the combination of disturbance and stress which this represented is beyond the plant survival capability.

Stress due to shading, when coupled with physical disturbance, had a marked effect on growth of young *T. latifolia* plants. Again the lack of reserves probably plays a

role here: the plants cannot recover from initial loss of their photosynthetic tissue, and the effect is exacerbated if the plants are under stress.

The initial results showed a 15% mortality of *Typha latifolia* after transplanting. Although growth was initially inhibited in a further 35% of transplanted plants, after three months all survivors were growing well, although not as well as non-transplanted plants. Growth after transplanting was slower than that exhibited for the control species. Plants moved to deeper water showed higher mortality (agreeing with results found by Grace & Wetzel, 1982). Flowering was severely inhibited in transplanted *T. latifolia* with no more than 10% of transplants successfully flowering.

Diquat at 1.5 mg l^{-1} gave 100% mortality of *Salvinia rotundifolia* after two weeks. At 1.25 and 1.0 mg l^{-1} the plants did not produce daughter plants and about 50% mortality was observed. The lower rates of diquat (0.25 and 0.5 mg l^{-1}) had no significant effect on any growth or survival parameter measured. Repeating applications, two months after the first treatment, produced some effect within four weeks, at 0.5 and 0.75, but not at 0.25 mg l^{-1} diquat, in terms of root length, leaf area and mortality. Regrowth from injured *Salvinia* tissue began three weeks after second application. One month after the second application, even at the highest dose rate used (1.5 mg l^{-1}), there was 35% regrowth of injured *S. rotundifolia*

Root length, leaf area, production of daughter colonies and dry weight biomass of *Salvinia* all significantly increased, compared with untreated controls, when a single crush (disturbance0 treatment was applied, without shade. Shade stress however significantly decreased growth, as measured by these parameters. In light treatments, the frond form exhibited complicated folding and individuals were large, while a flatter, smaller form was found in shaded treatments.

S. rotundifolia plants proved highly susceptible to stress caused by herbicide treatment, with the lethal concentration of 1.5 mg l^{-1} diquat. At sub-lethal doses of diquat, *S. rotundifolia* showed symptoms of damage (e.g. colour loss) induced by the herbicide stress, which may make the plant more vulnerable to disturbance or competition. However, disturbance alone did not effect *S. rotundifolia* populations, which suggests that the plant is disturbance-tolerant.

S. rotundifolia showed dominance over *Pistia stratiotes* when the species were grown together. Interaction between the two species for space became apparent within the four weeks. The luxuriant growth and high plasticity of *S. rotundifolia* plants enabled them to grow above the *P. stratiotes* plants, thus shading and stressing them.

Responses of *P. pectinatus* to different levels of disturbance (cutting) and stresses (herbicide & shading) were examined. Results from concentration/exposure time showed that diquat provided excellent control of *P. pectinatus* under greenhouse conditions, when that plant was exposed to concentrations ranging from 0.2 to 0.5 mg l^{-1} for 12 to 168 hr. However, there was no significant reduction in treated *P. pectinatus* with these doses under field conditions in a river system.

Results of the studies suggest that varying combinations of treatments causing stress and disturbance produce effects on aquatic weeds which are probably a function of the individual survival strategy of the species concerned.

Physical disturbance, produced by cutting or crushing plants, had very different effects on *Salvinia* and *Typha*. The data suggest that disturbance-tolerance traits are more important in the survival strategy of *S. rotundifolia* than in *T. latifolia*.

Stress caused by herbicide treatment or by shade will obviously produce different physiological effects on a plant, but the net effect is the same: an impairment of photosynthetic production.

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1. Introduction

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Weeds are plants growing where they are not wanted. Other definitions exist, such as "a plant interfering with man's activities" and "a plant growing out of place" for weeds in both the aquatic and terrestrial habitats, but the problems caused by weeds in aquatic and terrestrial habitats are different. They are unwanted in terrestrial habitats because they compete with agricultural plants and cause negative effects on the growth of plants which are wanted by people. Weeds in agricultural lands reduce crop yields by allelopathy, and by competing for moisture, nutrients, light, and space. Control of weeds releases these constraints, to increase crop growth and yield.

An aquatic plant only becomes undesirable when it seriously interferes with the interests of mankind. In aquatic habitats plant density is an important factor which can make plants wanted or unwanted. Calling one plant a weed and not another depends on both these factors. A plant may be tolerable for one recreational use but undesirable for another (Aldrich, 1984). Aquatic plants are usually useful plants which become weeds when their growth becomes excessive, and some type of control or management becomes necessary to ensure continued use of the water body (Barrett, 1978; Pieterse & Murphy, 1990; Nichols, 1991). Pieterse (1990) defined aquatic plants as plants which are able to change their generative with changing habitats from submerged to emergent. He went on to give perhaps the most appropriate definition of an aquatic weed: "an aquatic plant, which when growing in abundance, is not desired by the manager of its place of occurrence" (Pieterse, 1990).

A diversity of aquatic plants occurring in low densities can have a beneficial effect upon waterway ecology (Barko, 1990). They are a natural part which serve many important functions such as preventing excessive erosion, producing oxygen for aquatic ecosystems, preventing turbidity, trapping silt particles, providing habitat and feeding places for fish, and providing food and shelter for waterfowl (Pieterse, 1990; Nelson, 1990).

Weed problems in aquatic habitats are generally caused by the growth of dense vegetation which hampers the use of water bodies. They interfere with irrigation and hydroelectric schemes, fisheries, and navigation. When massive growths occur, they can have an influence on water quality because oxygen is depleted by plant respiration

over-night, often causing fish kills (Mitchell, 1974; Riemer, 1984; Murphy & Pieterse, 1990).

Aquatic plants communities are grouped into five categories by life and growth form (Sculthorpe, 1967; Pieterse, 1990):

(1) Free-floating: includes those species that normally are unattached but float on the surface or just below it. Plants in this category may become attached and firmly rooted in drying mud when water levels drop but the normal growth form is usually readily discernible. Free-floating plants move about with winds and currents. Production of new ramets or daughter plants from meristematic areas on the of parent plant is the main source of reproduction by free-floating plants. *Eichhornia crassipes*, *Salvinia* spp. *Pistia stratiotes*, *Lemna trisulca* and *Azolla* spp. are well-known examples.

(2) Floating attached: includes those species that are rooted in substrate but normally have at least the mature leaves floating on the water surface. Examples are *Nymphaea* spp. and *Nuphar* spp.

(3) Emergent: includes those species that are rooted in the substrate and whose stem, flowers, and most of the mature leaves project above the water surface. These plants are usually rigid and do not depend on the water for support. Emergent plants provide extremely valuable fish and wild life habitats. Also many different fish, frog, bird, and mammal species find food and shelter among emergent plants. The rhizome is a main source of regrowth for most emergent plants. Examples are *Typha* spp. *Phragmites* spp. *Glyceria* spp. and *Carex* spp.

(4) Submerged: submerged plants that are rooted in the substrate, with most of their tissues beneath the water surface (except for flowers, fruits and floating leaves which may either float on the water or are held above it). These plants grow throughout the littoral zone and can grow deeper than most other types of aquatic plants. Submerged plants have leaves that vary significantly in size and shape among the different species. Some leaves may be large and ribbon-like, while others may be feathery in appearance. The flowers are normally pollinated above the surface, but the seeds germinate and the young plants develop only under water. For most submerged species vegetative means such as tubers and turions are likely to be the main source of regrowth. Examples of submerged plants are *Hydrilla verticillata*, *Potamogeton* spp. *Elodea* spp. and *Myriophyllum* spp.

(5) Algae: algae have no true roots, stems, or leaves and range in size from tiny, one-celled organisms to large, multi-celled forms such as *Chara*. Only the macroalgae are usually considered as causing aquatic weed problem. Examples are *Microcystis* spp. *Spirogyra* spp. and *Hydrodictyon* spp.

1.1. Aims

The aim of this study was to develop a better understanding of different methods of control for management of *Typha latifolia, Potamogeton pectinatus*, and *Salvinia rotundifolia* under greenhouse and field conditions, by assessing control impacts on target species in relation to varying intensities of ambient stress and disturbance.

1.1.1. The main objectives were:

. To compare the effectiveness of different approaches to aquatic weed control against selected temperate and sub-tropical macrophyte species, typical of those occurring in Iran.

. To assess the response of the target species to weed control measures, in relation to naturally occurring and augmented stress and disturbance factors (e.g. shade, nutrient status, sediment type, competition, chemical and physical damage), under field and greenhouse conditions.

1.2. Aquatic weed control: background

To meet the aims of this project it was necessary to study a wide range of methods used for management of emergent, submerged, and floating aquatic weeds.

Management refers to controlling nuisance aquatic species and to restoring or reconstructing beneficial aquatic plant communities (Smart & Decell, 1994). Management includes the concepts of prevention, control, and eradication. Weed prevention is concerned with efforts to prevent the introduction and establishment of weed species into an area where they had not previously existed. The control strategy aims to reduce excessive aquatic vegetation in areas where the greatest problems exist. The object of any form of weed control should be to reduce the quantity of weeds to acceptable limits without loss of species diversity and with minimum damage to the environment (Bond, 1990; Henderson, 1990). Riemer (1984) defined aquatic weed control as the reduction of plant population density to an acceptable level, not to eradicate the plants. This is not only impractical, but also the eradication of aquatic plants is likely to cause an undesirable environmental impact on fish, invertebrates and other animals (Smart, 1990). Also eradication is rarely economically viable when large areas are infested.

Removing one plant may result in another filling its niche. Controlling one weed problem may create a worse one. Therefore, in any case of management, it is desirable to have knowledge of the biology, distribution, aggressiveness and tolerance of individual species both to treatment and of ambient conditions, individually and synergistically. An ideal strategy for aquatic weed management should attempt to integrate all possible forms of control (Netherland & Shearer, 1995). For example, the most cost effective method for achieving acceptable reduction in weed levels is often by integration of biological control and the appropriate use of herbicides, or mechanical methods. This is the "maintenance control" concept, used in managing aquatic weeds such as *Eichhornia crassipes* in Florida.

Many techniques including harvesting (mechanical), herbicide, water-level fluctuation, sediment alteration, nutrient limitation, light alteration, and biological controls can be used for managing macrophytes (Pieterse & Murphy, 1990). Methods of control examined here include both physical and chemical approaches, which are

expected to be most easily implemented for control of aquatic weed problems in Iranian fresh waters. Biological techniques were not used in this study.

1.2.1. Physical control

The oldest method of combating aquatic weeds is that of manual and mechanical control. Physical control has always been the most widely used method. It may be defined as the physical destruction or removal of the plants causing trouble. Physical removal of plant material from the water can be done both manually, as is common in many small waterways, and/or by machinery. Physical control has advantages in the treatment of patches of weed. Specific areas can be dealt with; it does not involve the treatment of the whole water body.

For physical methods a knowledge of the biology of the species, equipment, and application time is important. Following removal by cutting in spring and summer, the remaining rooted parts do not die back but often continue to grow during autumn; this increases the probability of high over-wintering biomass and thus higher biomass earlier in the subsequent year. Together this information led to trials of a weed-cut late in the year to reduce over-wintering biomass and thus significantly reduced the growth of many perennial species such as *Ranunculus* species in the subsequent year. A decrease in spring flooding, reduction in the need for a spring cut and a balance between species diversity due to less cutting are some immediate benefits of the late growing season cutting. Also, in order for cutting to be effective, weeds should be removed below the water surface and at frequent enough intervals to deplete the food reserves stored in underground rhizomes, roots, and tubers. The process, even if properly performed, will takes one to three years for control of some aquatic weed likes *Typha latifolia* (Riemer, 1984).

The major problem for mechanical cutting is that weeds recover rapidly from cutting and several cuts may be necessary each year. Eradication of most noxious aquatic weeds by cutting is virtually impossible. On other hand, the weeds must be removed from the water after cutting and this operation is often more difficult and expensive than the initial cut.

Not all aquatic weeds can be cut successfully. For example, *Salvinia* spp. and *Eichhornia crassipes* which are amongst the most problematic aquatic weeds in the world (Mitchell, 1976), can only be removed mechanically by harvesting. Following a herbicide control, raking will be useful for removal of survivors.

1.2.1.1. Hand methods

Hand cutting, hand pulling, and hand raking are probably the oldest, the simplest, and still among the most widely used methods of aquatic weed control in the world. This is still practiced, especially where small bodies of water and streams are involved. Hand cutting followed by removal of the cut weed using forks or rakes is used for control of emergent, floating, and submerged weeds in shoreline, littoral zones, narrow watercourse and/or very small lakes (Mitchell, 1974; Wade, 1990).

Hand methods are slow, laborious, and expensive. Manual techniques are economical only when sufficient, inexpensive labour is available. In countries where labour is not cheap such as UK hand cutting can still be an important weed control method where other methods are impractical (Wade, 1990).

The equipment for hand application includes scythes, sickles, grass hooks, rakes, forks, hoes, chain scythes, and chain knives. After cutting the weeds must be removed from the water, because leaving plants to decompose in situ can cause deoxygenation. The breakdown of the organic material in the water also released inorganic nutrients which can promote the development of algal blooms.

Although hand cutting has been used for hundreds of years and is still used in some areas, it has declined markedly in the last thirty years in the UK, because of the high comparative cost coupled with the lack of suitably skilled labour. The decline of hand cutting has coincided with an increase in the use of weed cutting machines.

Colonisation and recovery of aquatic weeds after hand cutting may occur rapidly, via regeneration from vegetative propagules such as rhizomes and tubers. In rhizomatous species such as *Typha* and *Nuphar* manual clearance is followed by rapid regrowth from the rhizome. The growth of most aquatic species cannot be limited by cutting off the foliage, unless this is done over a long period (Riemer, 1984; Wade, 1990; Nichols, 1991).

The possibility of selective cutting of weeds, to improve species diversity, wildlife conservation management and fisheries, is an advantage of manual methods (Barrett, 1978; Wade, 1990).

1.2.1.2. Mechanical methods

The rapid regrowth and reinfestation of areas after manual control shows that manual methods are inefficient. Also, weed cutting by hand is sometimes impractical, especially in large water bodies. Mechanical methods such as weed-cutting boats and tractor-mounted machines provide rapid and more efficient weed control.

Mechanical equipment for weed control is varied, and machines can be divided into: cutters, shredders, crushers, rakers, and suckers. Some of these machines are fastened on boats and barges, others operate from the shore, mounted on tractors or hydraulic excavators (Riemer, 1984; Wade, 1990).

Among the earliest devices for aquatic weed control were boat-mounted V-shaped cutter bars. A major disadvantage of cutters was that they required relatively flat or gently undulating bottoms and blades dulled easily in contact with solid obstacles such as tree branches and rocks (Riemer, 1984; Wade, 1990).

The next development of weed cutters were U-, L-, and inverted T-shaped cutter bars mounted on an ordinary boat. With hydraulic systems they were able to control the depth and angle of the cutter bars in the water. The rapid regrowth after cutting and the risk of infestation of new sites by downstream movement of cut plant fragments is a major problem with cutting devices. Also the mass of cut plant material, if left in the water, may cause decomposition and consequent deoxygenation problems (Wade, 1990).

Chaining is also among the earliest mechanical methods used to control submerged weeds. With this method the chain is fastened between two tractors, on either side of the canal. The tractors drag the chain along the canal bottom and cut submerged aquatic plants (Riemer, 1984; Fernandez *et al.*, 1990). Such methods remain in regular use in Argentine irrigation systems (Fernandez *et al.*, 1990).

After cutting the removal of cut vegetation is essential to avoid blockage and decomposition problems (Riemer, 1984; Wade, 1990). Harvesting and removing the

weeds from the water body by a mower-harvester was the next step in development of mechanical control. In these harvesters the cut weed removed from the water by a conveyor belt and lifted up onto the boat (Riemer, 1984).

As an alternative to the use of boat-mounted equipment a variety of machines attached to tractors and excavators such as dredging buckets and weed cutting buckets, has been developed, for control of many submerged and rooted floating plants (Riemer, 1984; Wade, 1990).

The most widely used method for control of weeds from the banks is the weed cutting bucket (Wade, 1990). Depending on the skill of the operator, the bucket can cut above or slightly below the sediment. The main problems with this technique are trees and other obstructions which reduce the operation of the bucket from the bank (Riemer, 1984; Wade, 1990).

In the case of the dredger bucket, the whole plant plus sediment is removed. In addition, by deepening the water the amount of light penetrating to the bottom is reduced. Although excavation or deep dredging can keep channels, rivers, and canals clear much longer than other physical control methods, it is far from desirable ecologically. Dredging is slow and costly, and used only when other mechanical methods are ineffective.

1.2.2. Reduction of light

Light is essential for plant growth and photosynthesis. The reduction of light has been considered as a technique for the limitation of excess growth of aquatic macrophytes (Dawson & Kern-Hansen, 1978; Dawson, 1978; Engel, 1982; Wright, 1983; Dawson & Haslam, 1983; Dawson, 1981, 1989; Wade, 1990). The growth of most aquatic weeds is significantly affected by the degree of shading.

An alternative method of control to cutting, herbicide application or grass carp, is light reduction by bankside vegetation (e.g. trees and riparian vegetation), floating plant species, fish, dyes, and plastic sheets (Dawson, 1989).

In flowing waters (> 0.5 m/s), keeping the herbicide close to the target weeds is difficult, and reduction of light by shading seems an ideal alternative method. In some countries, like UK, the use of natural vegetation to create shade condition has

recently been introduced as an effective environmental technique to control aquatic weeds (Dawson & Hallows, 1983; Dawson, 1989).

Brabben and Dawson (1991) reported that the time for optimum control of aquatic weeds by shading varied from six weeks for submerged plants without large rhizomes to 12 weeks for areas of emergent plants with rhizomes. He also mentioned that screens can kill 'green algae' in 8 days.

Dyes like 'Nigrosine' and 'Aquashade' are another method in reducing light in the water which can be successful for control of rooted submerged weeds (Dawson, 1981; Spencer, 1984; Wade, 1990).

1.2.3. Alteration of water level

The growth and reproduction of aquatic weeds is affected by changes in water level (Cooke, 1980; Cooke & Gorman, 1980; Wade, 1990). Aquatic weeds will be effectively controlled by water-level fluctuation in lakes, shallow fish ponds, waterfowl habitats, irrigation systems and reservoirs, at least for the short term control (1-2 years). It will be used for managing macrophytes during the summer/autumn through winter, causing freezing and/or drying of the sediments in order to retard subsequent rooted aquatic plant growth (Wade, 1990).

An increase in water level can be used to control emergent and submerged plants by drowning and limitation of light in the deeper water column above the plants, particularly if submergence continues for long periods (van der Valk, 1981). Also 'washout' and flooding of free-floating species occurs by increasing water level (Wade, 1990).

To provide partial control of most submerged species and possible long-term control of annuals by disrupting seed production, short-term summer drawdown is an effective method. A quick lowering of the water level will cause death or at least reduce growth of submerged weeds. It will be effective on reduction of flowering and formation of vegetative propagules. Drawdown during the late autumn and winter months provides effective control of perennial species such as *Myriophyllum spicatum*. However, this affords a selective advantage to annual species such as *Najas* spp. and

some *Potamogeton* spp. which complete their life cycle during the summer months and survive the drawdowns as seed or functionally similar propagules (Webb, 1990).

The biology of the target vegetation in control by drawdown must be well known for the best results. The rapid establishment of resistant forms and emergent weeds which are, of course, favoured by shallower water may occur. Submerged weed control by drawdown is similar to chemical control because only the above-ground portions of plants are killed by these methods, thus leaving the viable tubers in the hydrosoil to cause reinfestation. Germination of seeds, and seedling establishment of emergent plants such as *T. latifolia* will occur in shallow water.

The degree of control of aquatic weeds by water-level fluctuation is different. At least one month exposure to air under cold (freezing) or hot dry conditions is necessary for the control of most rooted species. Some species such as *P. pectinatus*, which start to form vegetative propagules (tubers) early in the season, are strongly resistant to drawdown in the late summer. Van der Valk and Davis (1978a) reported that seeds and propagules of species such as *P. pectinatus*, *Scirpus validus*, and *Najas flexilis* remained viable one year after drawdown. Drawdown should start before October (before new tubers are formed) and should be continued until water temperatures drop to around 12°C. This inhibits tuber germination and the establishment of new plants, thus preventing new tuber formation.

Although it is not clear that drawdown and exposure of lakes to dry, hot conditions is more effective than exposure to dry, freezing conditions, there is evidence that a winter drawdown is more effective than summer (Cooke, 1980). He suggested that no invasion by terrestrial plants nor emergent plants which become established from seed during drawdown will be observed during winter drawdown. Consecutive drawdowns are usually more effective for controlling aquatic plants and usually two to three consecutive years are required for control (Leslie, 1988).

The drawdown technique is more effective on target species if used in combination with other water management procedures such as dredging, sediment covering, and herbicides.

1.2.4. Chemical control

Herbicides are chemicals which kill plants. Compared with other methods of control, herbicides are economic, effective and fast acting (Murphy & Barrett, 1990). However, they may have side effects which are harmful to aquatic organisms, wildlife in general and, ultimately to man.

Chemical treatment is the most frequently used control method in some parts of the world, like the United States. In many regions of the world, such as Denmark and the Benelux countries, the use of herbicides in aquatic situations is banned or severely restricted (Murphy & Barrett, 1990; Nichols, 1991).

Almost all species of aquatic weeds can be controlled by one or more of chemical which have been approved for use in or near water.

Herbicides may be classified as selective or non- selective. Selective herbicides are those which kill certain plants without significant injury to others. Selectivity based on the nature of the herbicide is determined by whether it is active when applied to the foliage, to the root, or to both foliage and roots. Foliage-active herbicides are generally sprayed on the leaves and foliage of growing plants and can be divided into two basic types: contact and translocated (Murphy & Barrett, 1990).

Contact herbicides (e.g. diquat) kill the plants and/or cause injury to the tissues that are contacted by the chemical. Symptoms appear soon after treatment, and the onset of plant death can be rapid (Sprecher & Netherland, 1995).

Translocated herbicides (e.g. glyphosate) are absorbed by one part of the plant but move within the plant and act on other tissues or growing points. Some herbicides move readily in the phloem and become distributed throughout the plant, while others are limited to the xylem and moved upward in the plant (Murphy & Barrett, 1990; Sprecher & Netherland, 1995).

In aquatic habitats, herbicides are normally used in one of two ways. They are either sprayed directly onto the exposed foliage at or above the water surface or they are added to the water and absorbed by submerged foliage or through the roots (Robson & Barrett, 1977; Barrett, 1978; Barrett & Logan, 1982).

Most aquatic weeds are perennial and spread by vegetative reproduction. They are more susceptible to translocated than contact herbicides because most of them

have well developed rhizome systems. In this case the diluted herbicide is normally sprayed directly on the foliage.

For control of submerged weeds the diluted or undiluted herbicide is normally injected beneath the surface of the water. The successful control of submerged aquatic plants using chemical depends upon the concentration and exposure time of a herbicide with respect to the target plant. Controlled-release (CR) herbicide technology provides several advantages over conventional types of application, especially in flowing water on submerged weeds. CR systems can increase the longevity of herbicide exposure, promote economic saving, reduce the number of herbicide treatments, and target specific areas or be manipulated to obtain the most effective coverage (Murphy & Barrett, 1990).

Herbicide application to small static systems is generally quite successful since the target plants are exposed to a lethal concentration of herbicide for a sufficient period of time (Netherland 1990, 1992). In high water exchange systems, the movement of water can influence herbicide concentration and contact time, resulting in reduced chemical contact time and efficacy.

Regardless of the control methods used, proper timing of applications is often a key for success or failure in aquatic plant management (Luu & Gestinger, 1990). Weeds should be sprayed during their most susceptible growth stages. The best time for control of weeds is in the spring, before the excessive growth can interfere with functionally of the system.

1.2.4.1. Aquatic herbicides: background

Below is a brief discussion of the two herbicides used in this project:

1.2.4.1.1. Diquat

Diquat (6,7-dihydrodipyrido[1,2-a:2′,1′-*c*] pyrazinediium ion) affects within photosystem I the photosynthetic pathway, producing active free radicals. These disrupt cell membranes by lipid peroxidation causing very rapid damage to plant tissues. (Sprecher & Netherland, 1995).

Diquat is a contact herbicide and there must be enough photosynthetic plant material for the herbicide to act upon of it is to be effective. It controls certain free-floating and many submerged plant species, and filamentous algae (Murphy & Barrett, 1990).

Diquat can be either sprayed onto the exposed foliage or added to the water. Diquat is effective against floating weeds when sprayed onto the fronds at 1 kg active ingredient (a.i.) ha^{-1}, but it can also be used against submerged weeds when added to the water at 1 mg a.i. l^{-1} (Murphy & Barrett, 1990).

Viscous gel formulations of diquat, which are applied to the water surface and sink rapidly as strings and droplets which stick to the weed, have been developed. The plants absorb the active ingredient as it is released from the gel (Murphy & Barrett, 1990). Because the gel sinks onto the weed, the recommended dose is not significantly affected by water depth or velocity. Despite this a flow velocity of 100m h^{-1} (2.7 cm sec^{-1}) will carry the formulation downstream.

The activity of diquat is significantly reduced by clay particles, organic matter, and hardness of the water (calcium concentration). It cannot be taken up by plants when it is adsorbed, so it should not be used in turbid waters, very hard waters or when plant surfaces are covered with silt (Murphy & Barrett, 1990).

As diquat works by contact activity the best results are obtained in the early part of the growing season when the plants are actively photosynthesising and the tissues are soft and young (Murphy & Barrett, 1990).

1.2.4.1.2. Glyphosate

Glyphosate [*N*-(phosphonomethyl) glycine] in the form of its isopropylamine salt, is an extremely useful herbicide for the management of many weeds. It is a broad-spectrum, non-selective, post-emergence herbicide with high unit activity on essentially all annual and perennial plants (Bowmer, 1982a; Murphy & Barrett, 1990).

Glyphosate is a translocated, foliar-applied herbicide that can be applied at any stage of plant growth. The rapid translocation of glyphosate from the foliage of treated plants to the roots, rhizomes and apical meristems is one of the most important characteristics. Glyphosate normally enters plants through the leaves and will

translocate to both above and below ground meristems. It kills plants and/or inhibits the germination of buds on rhizome by inhibition of the biosynthesis of aromatic compounds in the shikimate pathway (Murphy & Barrett, 1990).

Glyphosate has been used world-wide for aquatic weed control and has been accepted as safe for use in most countries (Robson & Barrett, 1977).

The translocated mode of action of glyphosate makes it ideally suited against many emergent and floating weeds which have rhizome systems (Grossbard & Atkinson, 1985).

The timing of treatment is important: plants should be sprayed during their most susceptible growth stages. A poor control might be expected during the early stage of growth, due to inadequate leaf area and rhizome systems for herbicide absorption and translocation. Late applications can also provide poor results, and this may be due to the onset of senescence before the glyphosate has been fully translocated into the rhizome system (Murphy & Barrett, 1990).

Adequate control can be achieved by application of the herbicide at mid growing season, when there are sufficient leaves to absorb the herbicide.

Glyphosate is sprayed directly onto exposed foliage. Excellent control of most species has been obtained at rates of 0.34-1.12 kg a.i. ha^{-1} with annual species, and 1.68-2.24 kg a.i. ha^{-1} for some perennial species. Generally, the symptoms start to appear within a few days, resulting in plant death (after 14 days or longer) as a loss of ability to assimilate carbohydrate depletes the plant's reserves.

1.3. Target species

Typha latifolia L., *Potamogeton pectinatus* L., and *Salvinia rotundifolia* were used as the experimental plants, not only because of the need to better understand the mechanisms for controlling the growth of these weeds by different methods but, more importantly, because they are widespread in distribution and they cause serious problems in water bodies over a wide range of conditions.

Below are presented pertinent biological and ecological features relating to the three plant species examined in this study.

1.3.1. Emergent

Typha latifolia

The genus *Typha* has 20 species (Sharma & Gopal, 1980). Four species of *Typha* cause serious aquatic weed problems, of which *T. latifolia*, and *T. angustata* are widespread and possibly amongst the worst.

T. latifolia is a cosmopolitan emergent aquatic weed; its range is from the Arctic Circle to about 30° S. *Typha* is among the most common of emergent weeds and is found in a wide variety of aquatic habitats including canals, drainage channels, shallow standing waters, as well as brackish and fresh water marshes (Krattinger, 1975; Cary & Weerts, 1984; Dickerman & Wetzel, 1985; Grace & Harrison, 1986). It is serious pest in irrigation systems and can block the navigable water. It is considered as undesirable because it often displaces more desirable species and, when uncontrolled, can rapidly cover and desiccate an aquatic area, especially if the area is small and shallow.

Typha is a rhizomatous perennial that usually grows in dense monospecific stands. The juvenile plants can tolerate submerged conditions, while adults prefer emergent or sometimes terrestrial conditions (Sculthrope, 1967; Cook, 1990).

Although very large numbers of seeds are produced by *Typha*, germination from seeds is observed only rarely in natural habitats, and seedlings do not contribute much to population maintenance (Grace & Wetzel, 1981b, c; Dickerman & Wetzel, 1985; Spencer & Bowes, 1990).

In *Typha* the unit of vegetative growth is the ramet. The ramet is a rhizome and its associated leaves, roots, and flowering structures.

Vegetative growth is largely by rhizomes, which is often more than 50% of the total biomass (Fig. 1.1), and the most important component in the colonisation of marshlands, banks, etc. (Djebrouni & Huon, 1988). Rhizomes are perennial, tough, and woody, and can spread over 58 m^2 after 2 years. Rapid growth of the rhizomes leads to a complex underground network and creates serious problems for the recognition of shoots belonging to the same clone (Djebrouni & Huon, 1988). In regions with warm summers and cold winters the dormant rhizome can over-winter, beneath an ice cover, with rapid regrowth occurring in the spring.

The shoots grow up to about 3 m in height, and may or may not develop an apical flowering spike. The leaves of *Typha* are broad and vertical, minimizing self-shading. Leaves develop rapidly in early spring utilising rhizome carbohydrate reserves stored overwinter, and senesce in late summer (Aston, 1973).

Typha flowers develop between the middle of summer and early autumn. The flowers of *Typha* are very small and concentrated in two compound cylindrical, spike-like inflorescences, with the female occurring below the male. *Typha* fruits are equipped with perianth hairs that permit effective wind dispersal.

The airborne seeds of *Typha* germinate well and can establish stands in new water bodies or disturbed areas. *Typha* seeds are small (≈1 mm long) and buried easily during sedimentation. They are capable of germination when shed, but for seed to germinate, there must be sufficient light intensity, light quality, temperature, and moisture, but no standing water. Correll and Correll (1975) reported that through the small easily wind-blown seeds make it easy for *Typha* to invade newly-created water bodies.

Typha possesses the C_3 pathway of photosynthesis, but its above-ground productivity up to 45 tonnes ha^{-1} yr^{-1} is as high as rates reported for many C_4 plants. The absence of water stress in *Typha* habitats contributes to this high productivity.

1.3.2. Submerged

Potamogeton pectinatus

Among submerged weeds *P. pectinatus* is a particular problem. The genus *Potamogeton* is a cosmopolitan group which comprises 100 species, most of which are found in the northern hemisphere (Kadono, 1982; Kantrud, 1990). *P. pectinatus* is widely distributed world-wide, and consequently shows wide ecological tolerances and morphological plasticity (van Wijk, 1988). Typically *P. pectinatus* problems occur in irrigation and drainage channels, where excess submerged weed growth interferes with water flow, with hydroelectric schemes, with navigation, fishing and recreational use (Spencer, 1986; van Wijk, 1988; Kantrud, 1990).

P. pectinatus can start to grow from seeds, subterranean tubers, axillary tubers and sprouting rhizomes. Although *P. pectinatus* can reproduce sexually by means of

seeds, tubers are probably the most important organs of reproduction (van Wijk, 1989; van Vierssen, 1990; Kantrud, 1990).

A main shoot will grow from a sprouted tuber or a germinated seed. After the main shoot has reached a certain biomass, horizontal shoots (rhizomes) will start to grow. From these (branched) rhizomes a constant production of secondary shoots can be observed. Both horizontal (rhizomes) and vertical (main shoot, secondary shoots) growth results in expansion of the shoot complex (van Wijk, 1988) (Fig. 1.1).

Shoot length and branching of the shoot largely determine the architecture of the plant. It can reach 3 m long (Preston, 1996). In some populations a pronounced elongation of the shoot is observed, combined with a strong branching in the upper part of shoots. This results in densely-leaved "brushes" at the water surface.

The narrow-linear leaves which can reach to 15 cm long and 2 mm wide, have conspicuous leaf sheaths and ligules which partly enclose the stem and are variable in length.

Vegetative reproduction starts with the formation of tubers or sprouting rhizomes. Large tuber banks can be found at the end of growing season (Kantrud, 1990; van Wijk, 1988; Yeo, 1965). For that reason vegetative reproduction by means of tubers plays an important role in the survival strategy of *P. pectinatus* (van Vierssen & Hootsmans, 1990; Spencer, 1990; Spencer & Ksander, 1990, 1992; van Dijk *et al.*, 1992).

In many large and running waters *P. pectinatus* has a pseudo-annual life-cycle. The above- and below ground parts die off in autumn (except tubers) while in the next growing season the vegetation starts to grow again from tubers (van Wijk, 1988). In one growing season *P. pectinatus* growing in an area of 24 m^2 was observed to produce 36,000 tubers (Sainty & Jacobs, 1988).

P. pectinatus has a branched rhizome system concentrated in the upper layer of the sediment. The rhizomes produce bare nodes, alternating with nodes from which a shoot as well as a bunch of roots develop. At the end of the growing season, over-wintering tubers will develop at the tip of branched rhizomes. Also aboveground tubers can be formed (axillary tubers) (van Wijk, 1988).

At the end of the growing season *P. pectinatus* can flower abundantly. Initially a compact inflorescence is produced in the axil of a branch. After the penduncle

separates the flowers by stretching, pairs of flowers can be observed. After pollination, four relatively big brown seeds can be formed in each flower (van Wijk, 1988) (Fig. 1.1).

1.3.3. Free-floating

Salvinia rotundifolia

S. rotundifolia is a free-floating weed that is native to South America, but is now widely distributed throughout most tropical and sub-tropical freshwater systems (Mitchell, 1970; Toerien *et al.*, 1983; Forno, 1983). Eight species of the floating fern are capable of causing serious aquatic weed problems (Thomas & Room, 1986; Pieterse & Murphy, 1990), of which *S. molesta*, *S. rotundifolia* and *S. natans* are possibly amongst the worst (Forno & Harley, 1979).

Excessive growth of *S. rotundifolia* can cause serious water quality problems, covering large areas of water, blocking waterways, and hindering fishing and recreation (Usha Rani & Bhambie, 1983; Cary & Weerts, 1983; Room, 1986). Weed mats alter the ecology of the system by preventing the penetration of light into the water, removing nutrients and altering the oxygen content (Thomas & Room, 1986).

The rate of growth of *S. rotundifolia* is determined mainly by temperature and the availability of nutrients (especially nitrogen) in water. Under favourable conditions the species exhibits extremely rapid vegetative growth and spread. It can double the area it covers in as little as 2.5 days (Room & Gill, 1985).

S. rotundifolia is a sterile hybrid. Any spores produced are unable to germinate. It reproduces vegetatively by fragmentation of the main rhizome at the node. The rhizomes of *Salvinia* lie just below the water surface. At each node there is a pair of floating leaves and a stalked, submerged, root-like organ (Room & Kerr, 1983). Most of the leaf and stem tissue is at or above the water surface. The leaves are undivided and in pairs, varying in shape from oval and flat in small isolated plants, to heart-shaped when crowded in dense mats. Leaves of small isolated plants can be as small as 1 cm by 0.5 cm. Leaves on crowded plants can be 3 cm by 6 cm when opened out. The upper surface of the leaves is covered with rows of microscopic columns each ending in four fine hairs joined at the top and resembling an inverted eggbeater. This surface

of the leaf repels water, helping the plant to float. The lower surfaces of the leaves and the roots are covered with pointed, dark, fine hairs (Fig. 1.1).

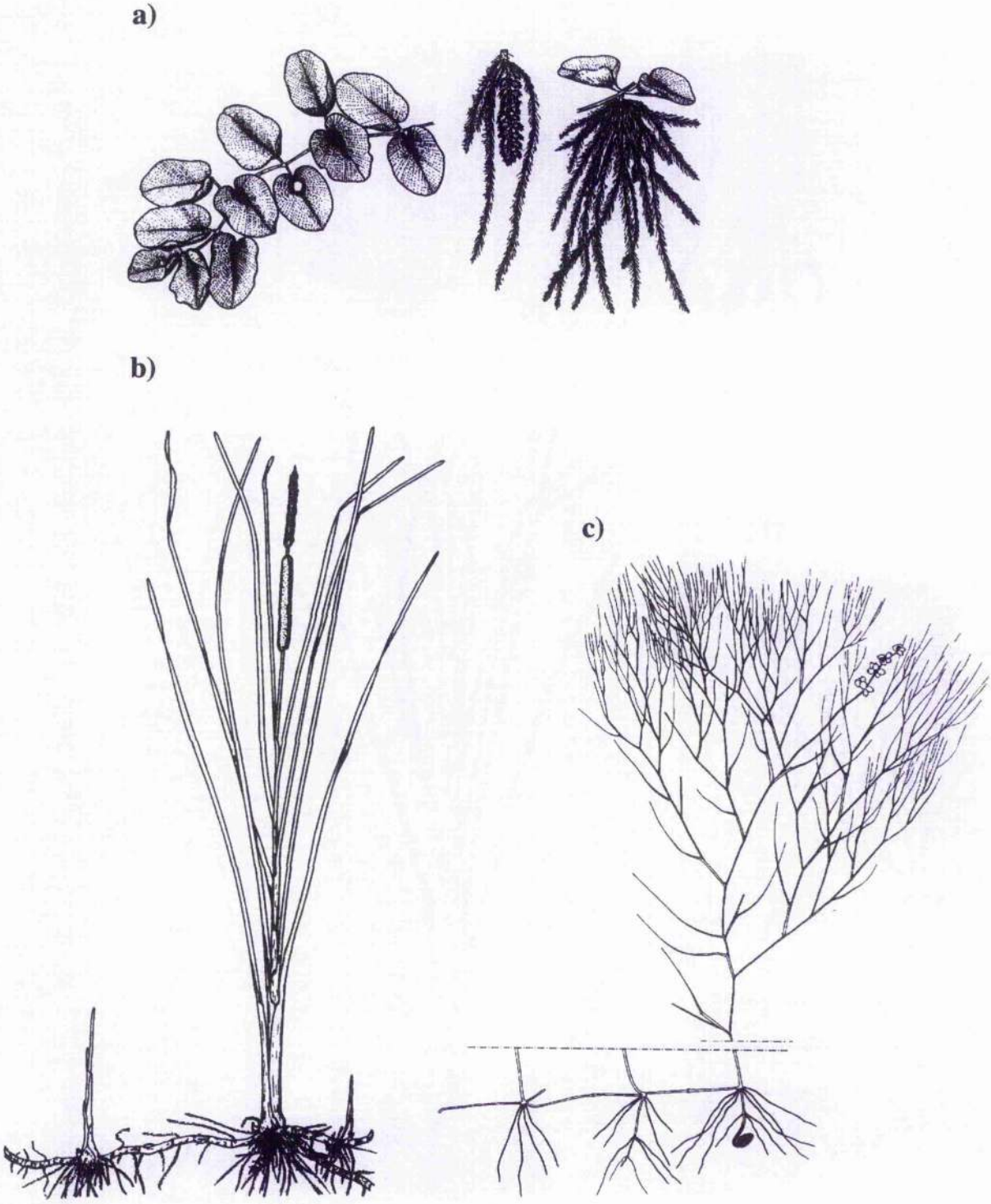


Figure 1.1
a) ***Salvinia rotundifolia;*** **b)** ***Typha latifolia;*** **c)** ***Potamogeton pectinatus***

1.4. Research approach and structure of the thesis

This project combined several greenhouse experiments in the Brian Laboratory of the Division of Environmental and Evolutionary Biology at Glasgow University, and the Netherlands Institute of Ecology (Holland), with field experiments at Possil Marsh, River Kelvin, Lochwinnoch and Lochan Dubh (all Scotland) from 1993 to 1996.

Chapter 2 deals with methodology. All general methods and materials used in this project during three growing seasons (1993-1996) are discussed in this chapter. Chapter 2 also describes experimental locations, methods and materials and all treatments used. Treatments were designed to manipulate stress and disturbance conditions affecting target plants, using (alone or in combination) cutting, crushing, shading, transplanting, competition, water level manipulation, and herbicides. Experimental designs used in this project are also described in this chapter.

Chapter 3 gives results and discussion relating to the 13 experiments undertaken. Experiment 1 determined the effects of sediment depth, sediment type, ethanol, light, temperature and stratification on germination of *Typha* grown from seeds in the greenhouse. In experiment 2, the effects of cutting, shading, competition and water level were tested on *Typha* grown from seeds and rhizomes. Experiment 3 determined the response of *Typha*, grown from seeds and rhizome to transplanting, cutting and water level under field conditions. Experiment 4 was similar except that I sought to determine the effects of water level and cutting on *Typha* grown from seed after transplanting to the field. The effects of glyphosate on *Typha* after transplanting to different water level conditions was examined in experiment 5. Experiment 6 was focused on the effects of glyphosate on *Typha* in late season application. Experiments 7, 8 and 9 were focused on *Salvinia* under greenhouse conditions. Some concentrations of diquat in experiment 7, and different levels of shading with crushing in experiment 8 were chosen as treatments in these experiments. Competition between *S. rotundifolia* and *Pistia stratiotes* in relation to plant density and light was examined in experiment 9.

Experiments 10, 11, 12 and 13 were focused on *P. pectinatus* under greenhouse and field conditions. In experiment 10, the response of *P. pectinatus* to different levels of diquat and exposure times was investigated under greenhouse conditions. The

effects of shading, cutting, and different concentrations of diquat on *P. pectinatus* were determined in experiment 11 and 12. In experiment 13 competition between *P. pectinatus* and *P. perfoliatus* in relation to plant density, sediment types, light, and temperature was examined.

The final chapter (Chapter 4) gives a general discussion of the results in the context of optimal methods for management and control of these three target species.

2. Materials and Methods

2. Materials and Methods

This chapter describes the study sites, including greenhouse and field experiments, undertaken at Possil Marsh, Lochwinnoch, Lochan Dubh and the River Kelvin. The general methodology used for all experiments is presented.

2.1. Experimental sites

2.1.1. Greenhouse

The greenhouse experiments were carried out in the Brian Laboratory facilities of the Division of Environmental and Evolutionary Biology at Glasgow University, Scotland. Typical characteristics for water used in greenhouse experiments are as follows: conductivity: 549 μS cm^{-1}; pH 8.26; nitrate 0.63 mg l^{-1}; calcium 4.6 mg l^{-1}; reactive phosphate 0.53 mg l^{-1}; chlorine 0.31 mg l^{-1}). Each bay in the greenhouse contained 3 fixed benches, each 4 m long and 1 m wide. Twenty-four black and 75 white tanks were used on each bench. Black and white tanks provided a volume of 30 and 3 litres, and a water depth of 30 and 15 cm, respectively. The water in each tank was aerated to encourage macrophyte growth and reduce epiphytic algae.

The greenhouse was maintained at temperature between 18-25°C, with a 16h photoperiod. Midday irradiance (measured as photosynthetically active radiation, PAR), as supplemented by Navilux 400W light at a midpoint in the tanks on a cloudless day, was about 155 μE m^{-2} s^{-1}. Mean and standard error of incident PAR 1 cm above and below water level varied seasonally, but during February-July were in the range 132.8 ± 1.11 and 87 ± 3.08 μE m^{-2} s^{-1}, respectively. A more detailed description of the greenhouse facilities is presented in section 2.4.1 and Fig. 2.1.

2.1.2. Field

2.1.2.1. Possil Marsh

Possil Marsh lies in the catchment of the River Kelvin, a tributary of the Clyde, at approximately 50 m above sea level on the north side of Glasgow (Fig. 2.4). Possil Marsh was part of a much larger wetland prior to the construction of the Forth &

Clyde Canal in 1775. During the late 19th and early 20th centuries most of these wetlands were drained and reclaimed for housing and industrial developments. Possil Marsh probably survived because it lay outside the City of Glasgow limits and because the water from the loch was required to control the level of the adjacent canal (Fig. 2.2).

Possil Loch covers approximately 20% of the total area of the reserve. This is a uniformly shallow loch with a maximum depth of 1.4 m, overlying up to 1m of mud and silt.

The reserve has a wide range of wetland habitats including shallow freshwater, fen, swamp, willow/birch woodland, damp meadows and ditches. There are also drier habitats, dry meadow and a small amount of *Calluna* heath and bryophyte carpets. This range of habitats in turn provides for a wide range of associated flora and fauna.

Typha latifolia is the dominant plant in the marsh but *Glyceria maxima* and *Carex* spp. are also common. Where these stands are not so dense the vegetation is more diverse with *Potentilla palustris*, *Stellaria palustris*, *Ranunculus lingua*, *Lysimachia thyrsiflora*, and a few patches of *Scirpus lacustris*.

The marsh is an important staging post during the spring and autumn migration, especially for waterfowl and warblers. The Swan Mussel (*Anodonta cygnea*) reaches its most north-westerly station in the British Isles here and this century has been recorded from only 5 sites in Scotland.

Heavy metal pollution in the marsh is a major problem which could ultimately effect the entire ecosystem of the reserve. The source of the iron is old ironstone mining veins nearby. Run-off from these flows into the reserve from the Lambhill Cemetery outflow pipes.

2.1.2.2. Lochwinnoch

The R.S.P.B. reserve at Airds Meadow, Lochwinnoch is one of the most extensive areas of wetland in the south west of Scotland (Fig. 2.4). The Lochwinnoch Reserve forms part of Castle Semple and Barr Lochs; together with Kilbirnie Loch (south of Barr Loch) they form one hydrological unit. There is a free exchange of birds

between the three lochs, hence all three lochs are regarded as one 'priority count site' by the Wildfowl and Wetlands Trust (Fig. 2.2).

Lochwinnoch Reserve was established in 1974 and covers 253 hectares of open water and marshlands. Open water forms the major part of the reserve, but there are areas of wet meadow and some woodland.

Diversity of both animal and plant life is Lochwinnoch's most important attribute. Habitats range from open water through marsh/fen, wet and dry grassland to mature semi-natural deciduous woodland, each supporting significant wildlife interest. This diversity of interest, including 173 bird species and 238 vascular plants, is especially important bearing in mind Lochwinnoch's major educational role and large number of general visitors.

Lochwinnich is a large and fine example of the few remaining lowland wetland sites in western Scotland. The shallow eutrophic lochs, together with their associated fringe of botanically rich marsh/fen vegetation, are typical of such sites. The site also holds a typical range of wetland birds, though summer bird populations tend to be low due to flooding.

Extensive pure stands of water sedge (*Carex aquatilis*) occur: rare in Scotland. The reeds, cattail's, and sedges along the waters edge provide ideal nesting sites for resident reed buntings, migrant sedge warblers and grasshopper warblers.

The reserve supports wintering populations of seven rare bird species, plus wintering goosander in nationally important numbers. The reserve also supports breeding otters, which are important locally.

2.1.2.3. River Kelvin

The River Kelvin rises in an area of marshy ground 55 metres above sea level near the village of Kelvinhead. It then flows sluggishly (>30 cm sec^{-1}) to join the Clyde Estuary in the west end of Glasgow (Fig. 2.3). In its lower reaches it is the central feature of the Kelvin walkway, an important area of recreation for city dwellers. Figure 2.3 shows a map of the river.

The River Kelvin catchment has eight flow gauging stations sited on it and from this network the flow rates of the main river and the major tributaries are continuously monitored (Fig. 2.3).

The River Kelvin is polluted close to its point of origin by discharges of iron bearing groundwater draining from abandoned coal mines. The situation deteriorates below the confluence of the Dock water, a polluted tributary which joins the Kelvin below the town of Kilsyth.

Aquatic vegetation has become a serious problem in the river. Many areas of the river have limited access due to dense aquatic vegetation. Several species of submerged aquatic macrophytes, including *P. pectinatus*, *P. natans* and *P. crispus*, are present in the River Kelvin. Additionally, numerous emergent macrophytes such as *Phragmites australis* and *Glyceria maxima* are indigenous to the river. Herbicides have been used extensively to control the vegetation, but a more feasible and long-term solution is needed.

Finally, the River Kelvin passes through the west end of Glasgow down a series of short falls. This improves the oxygen concentration in the river before it flows into the Clyde estuary.

2.1.2.4. Lochan Dubh

Lochan Dubh is situated at Rowardennan on the east shore of Loch Lomond, about, 42 km north-west of the centre of Glasgow (Fig. 2.4). It is managed by the Universities of Glasgow and Stirling for field studies in both terrestrial and freshwater ecology (Fig. 2.3).

The area has interesting geological, geomorphological and glaciation features. The flora of the area is quite rich, inhabiting a wide range of habitat types, and there is a similarly diverse fauna.

The climate is typical of Western Scotland. Tittensor and Steele (1971) and Klarer (1978) noted that weekly mean air temperatures illustrated the mildness of the climate, infrequently falling below 0°C or rising above 20°C.

The spread of common reed (*Phragmites australis*), white water lily (*Nymphaea alba*), and yellow water lily (*Nuphar* spp) throughout Lochan Dubh has become particularly marked over the past few years.

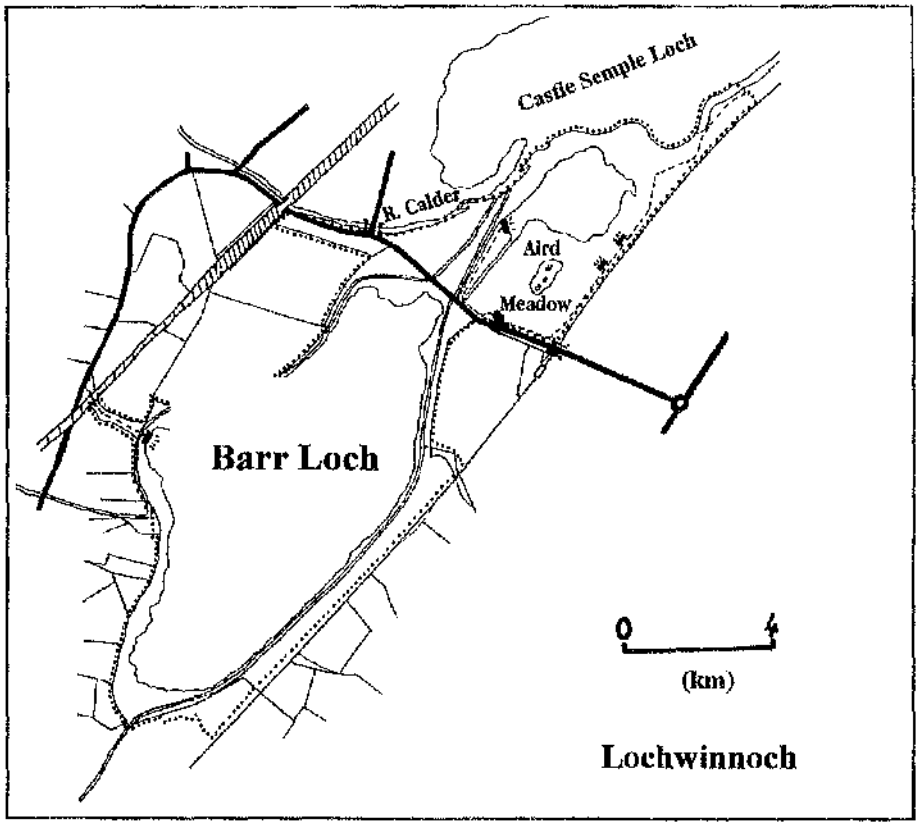
Lochan Dubh is surrounded by a semi-natural woodland with *Quercus petraea*, *Betula pubescens*, *Sorbus aucuparia*, *Larix decidua*, *Fagus sylvatica*, *Hedera helix*, and *Rhododendron ponticum*. The most conspicuous herbaceous plants are *Potentilla erecta*, *Melampyrum pratense*, and *Oxalis acetosella*.

Above Lochan Dubh there are several conifer plantations, the area being husbanded by the Forestry Authority. These are composed mainly of *Picea abies*, *P. sitchensis*, and *Pinus contorta*. At the north end of the loch lies a fen area, through which the loch's outlet drains. Here can be found *Salix cinerea*, *S. aurita* and *Molinia caerulea*.

Table 1. Mean physico-chemical characteristics of Lochwinnoch (LW), Possil Marsh (PM), River Kelvin (RK), and Loch Dubh (LD)

Site	Latitude	Longitude	Average depth (m)	pH	No_3^-	P (mg/l)
LW	55° 47′ N	04° 36′ W	0.38	6.89	0.18	0.01
PM	55° 54′ N	04° 16′ W	1.4	7.2	0.21	0.0096
RK	55° 57′ N	04° 08′ W	0.649	7.73	0.32	0.55
LD	56° 07′ N	04°35′ W	11.1	7.43	0.33	0.0017

Fig. 2.1. Study site, Greenhouse



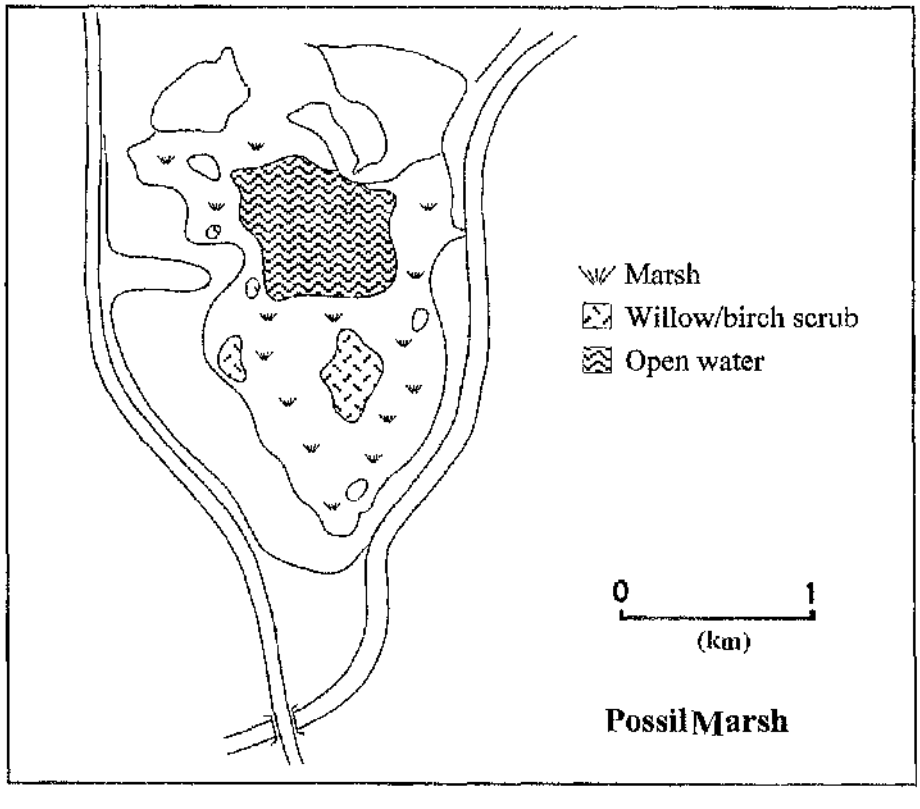
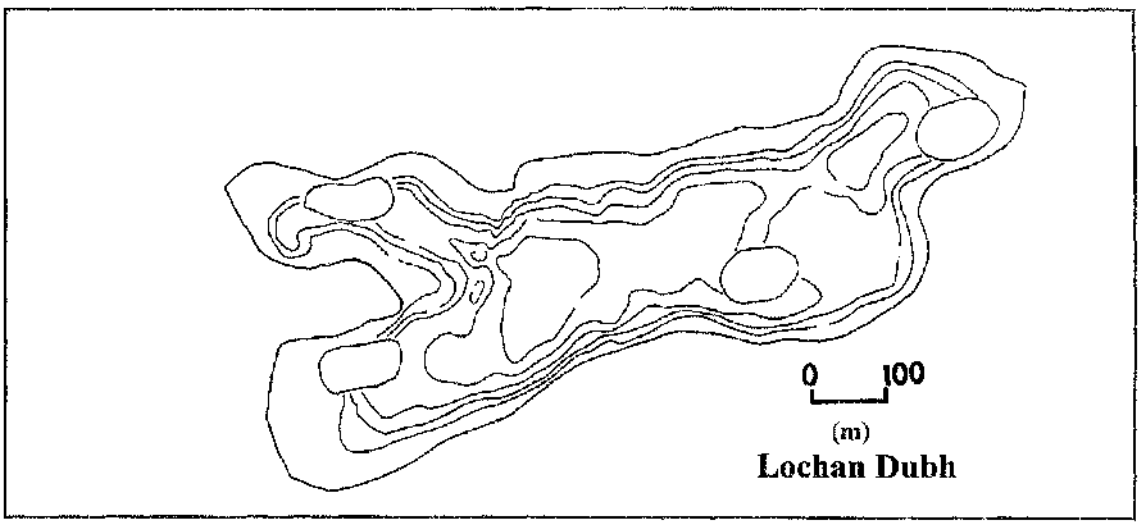


Fig. 2.2 Study sites, Lochwinnoch and Possil Marsh



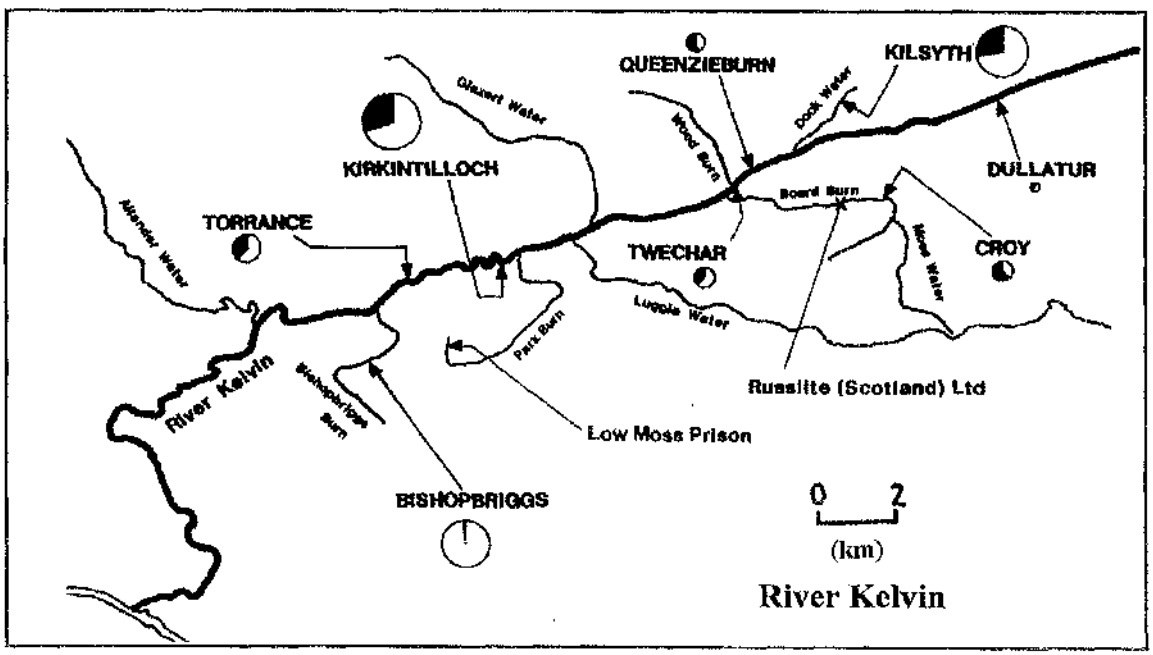


Fig. 2.3 Study sites, Lochan Dubh and River Kelvin

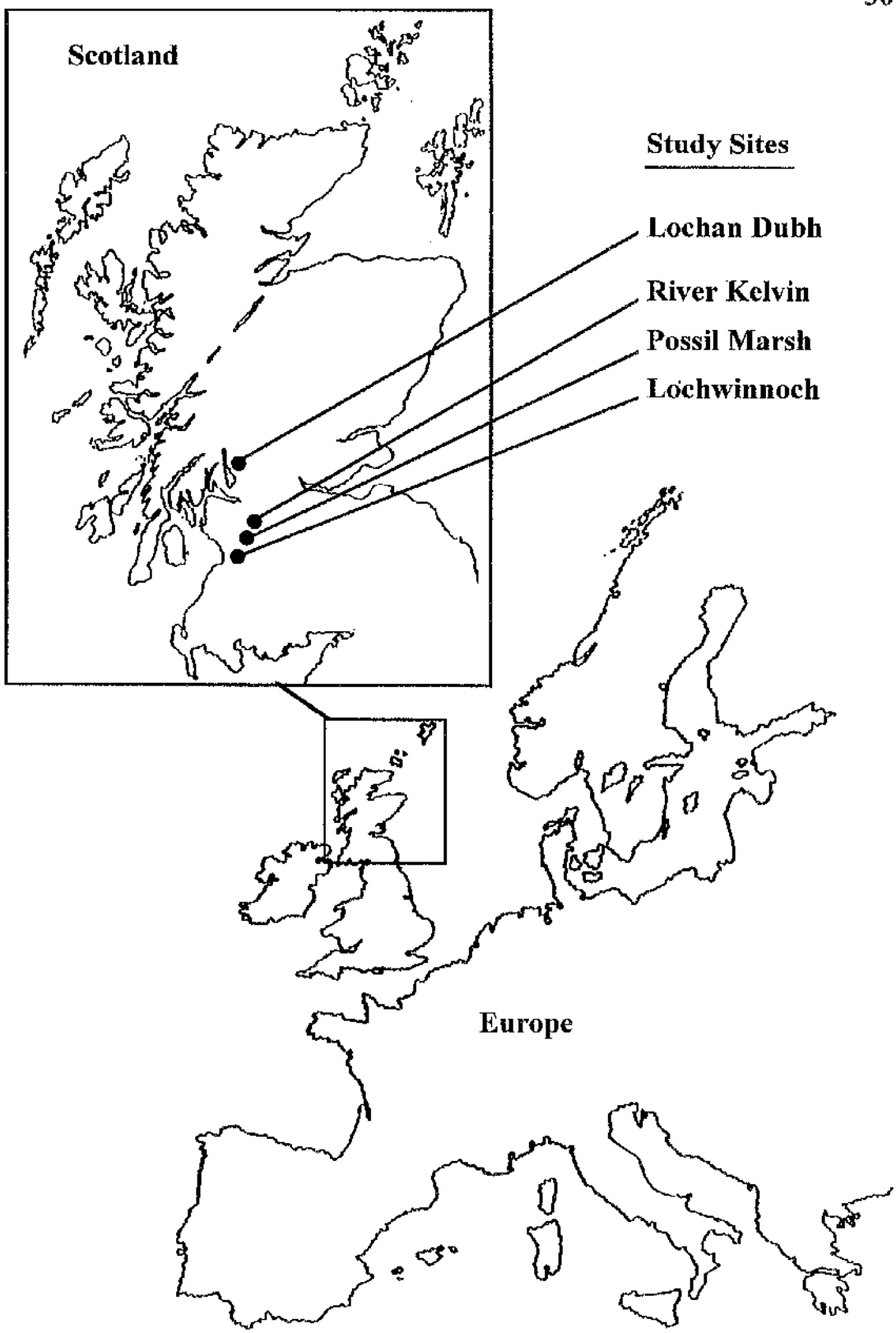


Fig. 2.4 Location of the study sites

2.2. Plant material

2.2.1. Sources of *Typha latifolia* seeds and rhizomes

Seeds of *T. latifolia* for all experiments were obtained from a commercial source (Herbiseed Nurseries, Billingbar Park, Wokingham, England).

Rhizomes of *T. latifolia* were collected at different water levels from 10 cm to 50-60 cm below the water surface at Possil Marsh and Lochwinnoch in two subsequent years (1994-95). Prior to experiments, rhizomes were selected for uniformity of size and stage of development. All rhizomes had attached leaves, which were trimmed to a height of 40 ± 5 cm.

2.2.2. Sources of *Potamogeton pectinatus* tubers and *P. perfoliatus* rhizomes

P. pectinatus winter buds (tubers) were collected from the River Kelvin during July and August, 1993 and again during September and November 1994. Some tubers used in this study were collected by Dr. K. Murphy from a drainage channel (VIRC, Pedro Luro, Buenos Aires Province) in southern Argentina. *P. pectinatus* tubers and *P. perfoliatus* rhizomes for the competition experiment were obtained from Lawesmeer, Lemmer, Holland. There were some small morphological differences, particularly in leaf shape between plants grown from the River Kelvin and Argentine tubers. The plants were excavated from 12 cm at the bottom at the River Kelvin, and Lawesmeer to a depth of 0.25 cm to include all rhizomes, roots and tubers.

2.2.3. Sources of *Salvinia rotundifolia* and *Pistia stratiotes*

For the experiments carried out here *S. rotundifolia* and *P. stratiotes* that had been pre-grown in the greenhouse for some time were used. They originated from Glasgow Botanic Garden and were originally collected in summer 1993. Plants were kept in a greenhouse at the Glasgow University in black tanks filled with River Kelvin sediments. Stock plants remained healthy and reproduced vigorously throughout the project. Temperatures ranged from 18 to 25°C, and light intensity was as previously described for greenhouse conditions.

2.3. Growth of plants

2.3.1. *Typha latifolia*

Seeds of *T. latifolia* were germinated under greenhouse conditions. Prior to sowing, seeds were separated from the mature inflorescence, and repeatedly washed in tap water, then distilled water. Seeds that settled to the bottom of the washing vessel were used, as these were expected to be the most viable. Except for experiment 1, seeds of *T. latifolia* for all experiments were placed on fine sediment (0.25 cm depth) in small white boxes under a 5 cm water layer. Care was taken to prevent seeds sown into the sediment from floating by covering them with a thin layer of pure sand.

2.3.2. *Potamogeton pectinatus*

Tubers were washed thoroughly with tap water to rid them of surface debris. They were transferred to a 2.5 percent hypochlorite solution for 3 min to ensure surface sterilisation and subsequently rinsed in sterile water. They were placed in a refrigeration unit at 4° C for temporary storage until they could be used. Each tuber originating from the same populations as 2.2.2 was planted in a small tanks, filled with 10 cm of the River Kelvin sediment covered with 1-2 cm of washed sand under greenhouse conditions. This sediment supports excellent macrophyte growth in the laboratory and has been used in several previous investigations (K. Murphy, personal communication, 1993). The remaining volume was filled with tap water, and water was renewed twice a week. Tubers were weighed and only those between 250 to 400 mg fresh weight were used to minimize propagule size effects. The tubers were checked for germination at 1-2 day intervals for 15 days.

2.3.3. *Salvinia rotundifolia*

Black tanks, with a thin layer of the River Kelvin sediment on the bottom and filled with fresh water, were used for culturing the plants. As it was not possible to prevent algal growth in the tanks, the plants were transferred every 2 weeks. They were gently washed to remove algae and placed in clean tanks filled with fresh water. *Salvinia* of uniform vigour, selected from clonal material, was used for each

experiment. Each had 10 leaves, with a terminal and 3 axillary buds. The average fresh weight for each plant was 2.5 g.

2.4. Experiment 1: Germination experiments

The germination trials were divided into two experiments. In the first experiment, begun in September 1993, the effects of different levels of light, sediment depth, and sediment types on germination were investigated. In the second, begun in February 1996, the effects of ethanol solution (100, 200, and 350 mM) on germination was studied.

2.4.1. Effect of environmental factors on the seed germination of *Typha latifolia*

The germination experiments were performed by spreading 100 seeds of *T. latifolia* in tanks. Seeds of *T. latifolia* were placed at six different depths in two types of sediment in small tanks. Tanks were positioned into three groups of twelve on three benches. Within all groups a single light level (high, middle, or low) was randomly assigned to each of the three rows tanks. Light intensity was regulated by shading with neutral density screens. A wooden frame with a white and green cover was applied for shading. The sediment used in this study was obtained from the River Kelvin and, in addition a pure horticultural sand was used. The sediment was fine-textured, containing ≈20% sand, 75% silt, and 5% clay by dry mass. Three light levels were provided through the use of neutrally-absorptive polypropylene shade fabrics of variable mesh density manufactured to fit over the aerial dimension of tanks. Mid-day irradiance, photosynthetically active irradience (PAR) measured at a midpoint in the tanks was 200, 100, and 50 $\mu E\ m^{-2}\ s^{-1}$ at high, middle, and high light levels, respectively.

Three replicate containers of each treatment were introduced into each of 36 tanks. Hundred seeds of *T. latifolia* were placed in each type of sediment at depth of 0, 0.5, 1, 1.5, 2, and 2.5 cm. The tanks were filled with 10 cm of each sediment. The water level was maintained 5 to 10 cm above the sediment surface by daily adding tap water and was renewed at 3 to 4 day intervals to prevent the water temperature

increasing above 25°C. Seedling emergence and total percentage germination was recorded every seven days for six weeks. After this period very little additional germination occurred.

2.4.2. Ethanol and germination

Extensive tissue breakdown of *T. latifolia* after cutting the shoots below the water level is associated with the production of ethanol. It has been suggested that ethanol is a major factor preventing seed germination in this species, so this was investigated here.

After 4 weeks of cold stratification, 30 seeds of *T. latifolia* were placed in a petri dish filled with 100, 200, and 350 mM ethanol solution. Also 30 seeds were placed in distilled water as controls. The seeds were allowed to germinate under conditions similar to those described above. The ethanol solution and the distilled water were renewed weekly. Germination was recorded every 4 days for 6 weeks.

2.5. Experiment 2: Responses of *T. latifolia* to cutting, shading, competition, and water levels when grown from seeds and rhizomes

2.5.1. Effect of cutting on *Typha latifolia* in relation to water depth and competition

The experiment was carried out in Possil Marsh, between May to October 1994. Four plots of approximately equal area (400 m^2) were randomly selected. In order to control *T. latifolia* in different levels of water, 24 plants were selected at locations from 20 cm above water level to 60 cm water depth.

On 22 May, when shoots were about 80 cm tall, 6 plants had their shoots cut 20 cm above water level, 6 plants were cut 20 cm below water level, and 6 plants were cut 60 cm below water level. Six plants were left uncut to provide controls.

After 45 days (on 7 July) any regrowth was removed at the same point as the first cut. The third cut was carried out 45 days (on 15 August) after the second cut as above. Five months after the first cutting all plants were harvested. A randomized

block design was used with 4 replicates. Parameters measured were shoot length, leaf length, and plant dry weight.

2.5.2. Cutting and shading effects on *T. latifolia* grown from seed

Seeds were germinated in tanks and seedlings raised at full light for 8 weeks. Seedlings were then transplanted individually to 3 l pots filled with sediment. Sediment was as in Experiment 1.

A factorial, split-plot, experimental design was used, with the main plot being shade, split among cutting treatments. Within a tank, there were three pots of *T. latifolia*, each randomly assigned to one cutting treatment: uncut, 1 cut, and 2 cuts. Shade treatments were as in experiment 1. *T. latifolia* transplants were planted into the same sediment used for experiment 1.

After 2 months, when the *T. latifolia* plants were about 35 cm tall, half of the tanks (selected randomly) had shade barriers placed over them. One week later, two-thirds of the *T. latifolia* were cut close to the first meristems. One third of the *T. latifolia* plants were left intact for the duration of the experiment.

On January 20, 1994, eight weeks after the first cut a second cut, similar to that performed previously was applied. Water in the tanks was replaced every 4-5 days. Daytime water temperature in the tanks , measured weekly, averaged 25°C ± 3°C. Plants were allowed to grow for 45 days after the second cut. The dry weight for one and two cut with shoot length were calculated after first, second, and final stage of experiment.

2.6. Transplantation experiments

Reciprocal transplant experiments were used to study phenotype differentiation and adaptation to local conditions in populations of *T. latifolia* at three different sites. In the first 2 years of study, three reciprocal transplant experiments, two using transplanted rhizomes and one seedlings, were carried out on *T. latifolia*. The modified reciprocal transplant experiment was concerned with how plant survival is influenced by the following factors: (1) site of transplant; (2) disturbance caused by cutting; (3)

pressure of neighbours (competition); (4) water level; and (5) herbicide. The aim of this series of experiments was to answer questions concerning the importance of physical and environmental factors in explaining patch differences.

2.6.1. Experiment 3: Transplant experiment with rhizomes

The first transplant experiment was conducted in Lochwinnoch. Lochwinnoch was chosen for this experiment because of a concurrent gradient of *T. latifolia* patches, from abundant in the north to poor in the south part of the site.

Four areas were selected in Lochwinnoch with standing water depth ranging from 5 cm in plot 4 to 60 cm deep in plot 1. The surface area of each plot measured 10 by 20 m. Distances between plots was approximately 200 m. In each plot, 16 points were randomly chosen along a linear transect. At each point, the nearest two plants were selected. One plant was randomly chosen to be transplanted and the other left as untransplanted. In each area, eight *T. latifolia* ramets with rhizome segments attached were carefully excavated with a spade from a rooting depth of 0.2-0.60 m. Ramets were placed in large (40 x 40 x 20 cm) plastic pond-planting baskets. The ramets were excavated after bud emergence but before major leaf production to minimize transplant shock. Soil for use in these experiments was collected from the same site at the same time, from an area free of *T. latifolia*. The harvested ramets were transplanted into different sites, were chosen to give a wide range of environmental conditions. Another eight ramets were left *in situ* as controls (Fig. 2.5).

In addition, 16 *T. latifolia* ramets collected from Possil Marsh were transplanted to Loch Dubh. The ramets were selected to achieve as similar a size distribution as possible. They were randomly distributed to different levels of water depth (Fig. 2.6).

For one half of the *T. latifolia* plants (whether transplanted or left *in situ*), competing plants were cleared from the circle (radius 0.5 m) around the *T. latifolia*. The plots were naturally dominated by *Glyceria maxima*, *Carex* spp. and *T. latifolia*. The other half had competitors left untouched.

Physical disturbance was applied by cutting *T. latifolia* plants at ground level: one quarter of plants were left as a control (uncut), one quarter were cut once, one quarter twice, and one quarter three times, at 45 day intervals.

2.6.2. Experiment 4: Transplant experiment with seedlings

Survival, growth, and response of *T. latifolia*, grown from seeds, to cutting and transplanting along depth gradients were examined in Possil Marsh and Lochan Dubh. The gradient of water depth for both sites was chosen from 20 to 60 cm. In early May, 1995, 24 uniform-size healthy *T. latifolia* seedlings were transferred into Possil Marsh and Lochan Dubh. Twelve plants were transplanted to Possil Marsh. Six plants were installed in 20 and another 6 in 40 cm water depth. One week later another 12 plants were transferred to Lochan Dubh at similar water depth to those used at Possil Marsh. Sediments were collected at the location involved. Each plant was marked with a cane to distinguish it from natural recruits.

Two levels of cutting, as experiment 3, were applied to *T. latifolia* grown from seeds at different water depth. At monthly intervals the rate of survival, shoot length, leaf length and the number of leaf per plant were determined. Leaves with 50 percent or less green material were considered dead.

2.6.3. Experiment 5: Response of *Typha latifolia* to altered water depth plus different doses of glyphosate

T. latifolia ramets, 40-60 cm tall, were collected at different water depths on 15 April 1994 from Possil Marsh. *T. latifolia* transplants were harvested from a population growing in each plot, during spring, to minimize the impact to the rhizomes. They were transplanted between plots to alter the balance of natural stress affecting the plants. They were randomly assigned to pots and placed in the experimental plots.

On 20 June 1994, 12 *T. latifolia* plants were moved from 60 to 20 cm water depth as well as 12 plants from 20 to 60 cm depth. Also 24 plants were randomly selected in deep and shallow water without transplanting.

On 30 June 1994, glyphosate was applied to transplants and control plants at dose rates of 0, 1, 2, and 4 kg a.i. ha^{-1}.

The experiment was designed as a split-plot with 4 replicates. Parameters measured were plant dry weight, shoot and leaves length, and the number of leaves per plant. Also, regrowth after herbicide application by measuring the shoot and leaf length were recorded.

2.6.4. Problems relating to data analysis in transplant experiments

Although transplant experiments are commonly used to study local adaptation to the native habitat, some difficulties arise in analysis and interpretation, due to the death of plants during the experimental series. This is even more so for traits that are related to reproduction, as only a few ramets produced seeds. A second problem was that unmoved plants have a higher chance for survival under frequent levels of cutting.

The Lochwinnoch site was analysed separately, which permitted a more straightforward test of differences between plants from different water gradient at same site.

The survival of the plants in each plot and the height of each plant were recorded monthly. Leaf length, and whole above-ground dry weight biomass (harvesting) were also measured at 45 days intervals.

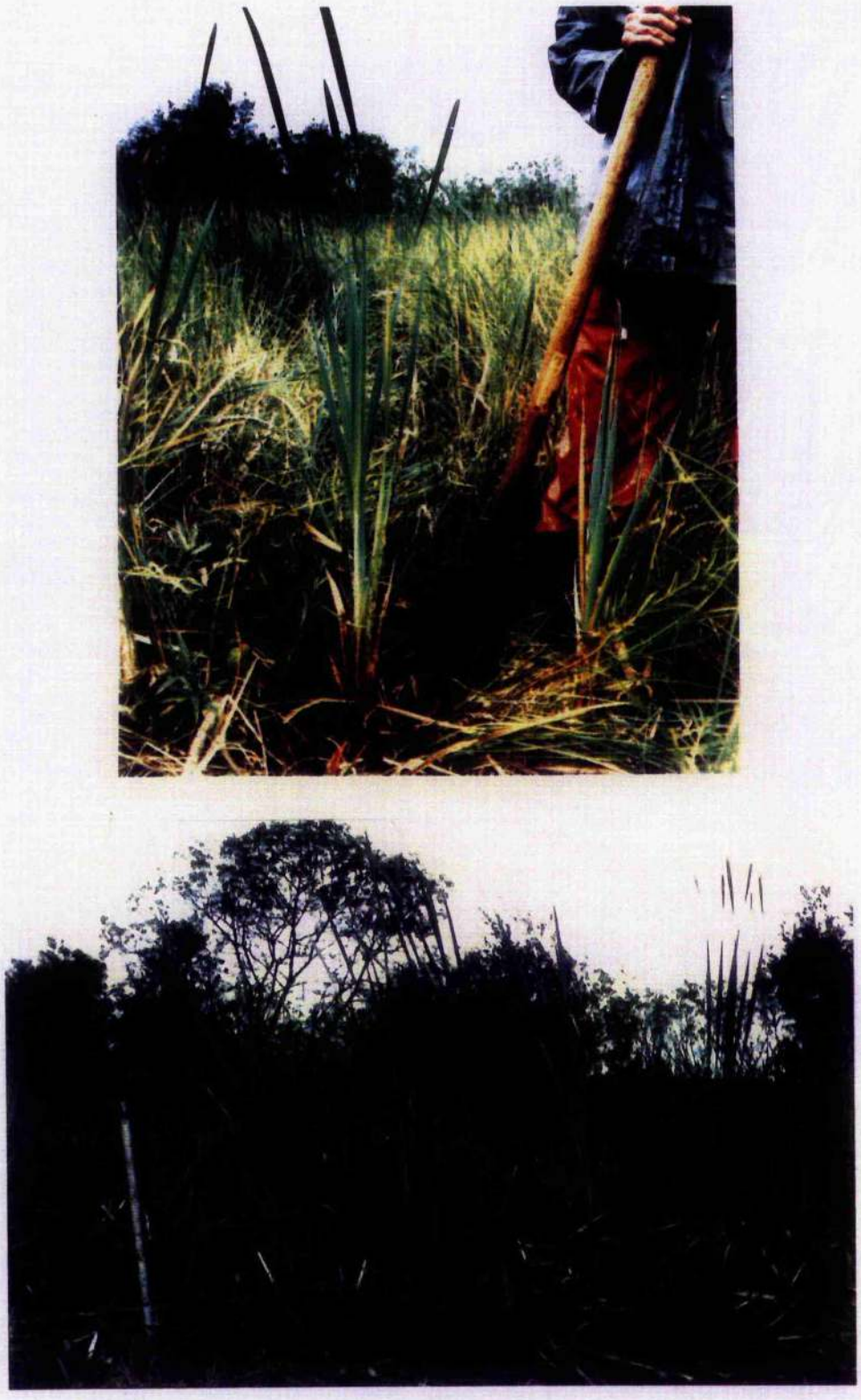


Fig. 2.5. Transplants of *Typha latifolia* ready for planting out in experimental areas of Aird Meadow, Lochwinnoch (Vertical rule = 1m)

Fig. 2.6. Installing transplants of *Typha latifolia* from lower marsh to upper marsh

2.7. Experiment 6: Control of *Typha latifolia* with glyphosate: late season application

On 5 October 1994, 4 equal plots (1 x 6 m^2) were randomly selected in Possil Marsh. As far as possible uniform stands of *T. latifolia* were selected. Each plot was divided into 6 sub-plots.

On 6 October 1994 a range of glyphosate rates (0, 0.5, 1, 1.5, 2, 3, and 4 kg a.i. ha^{-1}) was applied each plot. The depth of water in the plots was about 20 to 40 cm. Experimental design was a randomized complete block with four replications.

The effects of the treatments were assessed by counting the numbers of shoots in each plot, shoot and leaves length, and plant dry weight one year after treatment.

2.8. Experiment 7: Effects of diquat on *Salvinia rotundifolia*

The investigation was conducted during the months of January to June in the greenhouse. *S. rotundifolia* used in the study was obtained from a 5-month-old greenhouse stock. Twenty-eight black tanks were used in the study. Tanks were filled with a 15 cm layer of sediment (sand:clay, 3:1 weight ratio) covered with 1-2 cm washed sand. The tap water used in this experiment had a pH of 6.8.

Before the herbicide application plants were approximately 9 months old and had completely covered the water surface in the tanks.

On 5 January 1994 the plants were treated with diquat at 0, 0.25, 0.75, 1, 1.25, and 1.5 mg l^{-1}. The diluted diquat was injected to 5 cm water depth by syringe.

On 5 April 1994, twelve weeks after the first diquat application, plants were treated a second time with the same herbicide concentrations. Seven days after each herbicide application the tanks were emptied and refilled with fresh water to remove diquat residue. All treatments were replicated four times in a randomized complete block design.

On June 1994 samples were taken by using 10 cm^2 quadrat frame with all plants within the quadrat removed to evaluate a percentage of visual damage, root length, leaf area, and dry weight.

2.9. Experiment 8: Shading and physical disturbance (crush) effects on *Salvinia rotundifolia*

Eighteen tanks (30 l volume), each with a layer of sediment (sand:clay, 3:1 weight ratio) in the bottom, were filled with tap water. When the *S. rotundifolia* had completely covered the water surface, 9 tanks were randomly selected for shading treatments. Tanks were shaded with a layer of white or black material, or left unshaded, to make three levels of shading. White and black layers reduced 50 and 75% of PAR, respectively, at water level in the tanks.

Two weeks after shading, on 18 September 1993, the plants were moved out from the tanks and flattened on the ground. A 75 cm long metal pipe was rolled over the plants 8 times. Then, crushed plants were replaced in the tanks.

On November 18, 1993 plants were crushed for second times according to experimental procedures. The shading application continued by the end of experiment on January 18, 1994.

The number of leaves on each plant, number of daughter plants, root length, leaf area (cm^2), plant dry weight, and clone dry weight was recorded at the end of the experiment.

2.10. Experiment 9: Competition for light between *Salvinia rotundifolia* and *Pistia stratiotes*

To determine the effects of interspecific competition, *S. rotundifolia* and *P. stratiotes* were grown either in monoculture or mixed cultures at a constant total density of 6 plants per tank, using varied proportions of the two species in a replacement series (de Wit, 1960). The densities of plants used were:

S. rotundifolia	0	2	3	4	6
P. stratiotes	6	4	3	2	0

The experiment was conducted in the greenhouse, from 15 February 1996 until 15 May 1996, in 45 black tanks, with a thin layer of River Kelvin sediment on the

bottom and filled with tap water. Healthy green plants, (mean fresh weight 10 ± 2.5 g) were transferred to each tank from the stock culture. Five days after the plants settled in the tanks the shading treatments were applied by reducing the greenhouse light from 150 to 100 and 75 $\mu E\ m^{-2}\ s^{-1}$. The three light levels were achieved by placing green and white nets over two-thirds of the experimental tanks. One-third of tanks were left unshaded. The experiments were replicated three times. To make up the evapotranspiration losses of water, fresh water was added to the tanks at weekly intervals.

Fresh weights were determined at the beginning of the experiment. During the first 10 weeks of the experiment, the plants of each species were removed from the tank biweekly, allowed to drain for 5 min and weighed (fresh weight). They were then returned to their respective tanks. The relative growth rate (RGR) was calculated following Evans (1972):

$$\ln W2 - W1^{(t2\_(t1)-1}$$

where W_1 and W_2 are the fresh weights (g) at times t_1 and t_2, respectively.

At the end of the experiment, the number of plants in each tank was counted and the dry weight of both species was recorded.

2.11. Experiment 10: Response of *Potamogeton pectinatus* to various concentrations and exposure periods of diquat

P. pectinatus tuber were collected from the River Kelvin. Tubers were planted 3 cm deep in 30 l tanks containing well-mixed sediment obtained from the River Kelvin and filled with tap water. Plants were allowed to grow for approximately 6 weeks prior to herbicide treatments. This pre-treatment growth period was for canopy formation and root development. The investigation consisted of 32 treatment combinations of diquat concentration and exposure time: concentrations were 0, 0.1, 0.2 and 0.5 mg l^{-1} diquat, and exposure times were 0, 1, 2, 12, 24, 48, 96 and 168 hr.

On January 21, 1995, a stock solution of diquat was made up from a commercial formulation of diquat ('Midstream') and the calculated concentration was poured into each tank. At the end of the assigned exposure time, each tank was emptied and refilled with tap water at least 3 times to remove diquat residues. Plants

were allowed to grow for 8 weeks after treatment. Weekly visual evaluations were used to characterize the initial response of the treated and untreated plants to diquat. The water was replaced with tap water every 72 hr and air was continuously bubbled through each tank to provide a source of carbon dioxide.

All treatment concentrations were replicated three times in a complete randomized block design. Response variables measured were plant dry weight, shoot length, leaf length, number of leaves per plant, and number of secondary branches per plant.

2.12. Experiment 11: Response of *Potamogeton pectinatus* to diquat, cutting, and shade

Tubers and sediment used in this study were collected as described in section 2.11. Tubers were allowed to germinate in 2.8 l boxes containing tap water for 1 week under greenhouse conditions. After germination, tubers were planted in 30 l black tanks, as for previous experiment. Plants were allowed to grow for 8 weeks prior to treatments application. A split-plot design was used with 3 blocks.

The effects of 4 doses of diquat (0, 0.1, 0.2 and 0.5 mg l^{-1}) in static conditions with three levels of cutting (uncut, one cut, two cut), and 3 levels of shading (unshaded, low, and high shade) on *P. pectinatus* were examined. Shading was as in experiment 8.

In October 1994 when plant height reached about 40 cm, three different light conditions were applied above the tanks. Two thirds of the tanks were shaded by one layer of white or black material. The remainder were left unshaded. One week after shading, herbicide applications were made. Herbicide concentrations were 0, 0.1, 0.2 and 0.5 mg l^{-1}.

Two weeks after implementation of the shade treatments, cutting treatments were applied. Two frequencies of cutting were used, to give a design with 3 levels of the treatment factor: uncut, low (cut 60 days after start of experiment) and high cutting frequency (cut both 60 and 90 days after start). Cutting treatments uniformly reduced plant length to 2 cm after each treatment. Plants were allowed to grow for 8 weeks after the second cut.

Response variables measured were shoot length, leaves length, secondary branches length, number of branches, number of leaves and secondary branch in branches, and biomass dry weight .

2.13. Experiment 12: Response of *Potamogeton pectinatus* to diquat and cutting treatments under field conditions

The study was conducted in 12 plots (120 m^2) located in the River Kelvin. Each plot was divided to one dose of diquat and a level of cutting. The investigations consisted of 12 treatment combinations of diquat concentration and different levels of cutting. The mean water depth was 55 cm. Flow velocities at 10 cm from the substrate was 44 cm s^{-1}. Diquat concentrations were 0, 0.1, 0.2, 0.5, 1 and 1.5 mg l^{-1}. Cutting treatments were uncut, once and twice. Each treatment was replicated 3 times in a complete randomized block design.

On 17 and 18 July 1995, when the plants were at the maximum of vegetative growth, herbicide and cutting application were applied. Treatments were made by injecting the herbicide solution into the water with hypodermic syringes. Replicated cut and untreated sections were located upstream. Immediately after spraying, water samples were collected over 30 minutes, from the downstream end of the treated sections (Table 2). They were analysed for diquat residues with a U.V. spectrophotometer to measure absorbance at 309 nm against a series of standard diquat solutions, with a blank of untreated river water. Also, to determine the effects of diquat on photosynthesis, chlorophyll fluorescence was measured (Appendix. 1) using a Branker portable fluorometer. At the time of application the water flow, pH, and water temperature were determined. Treatments were replicated three times.

The second cut was carried out 45 days after the first cut (on 28 August) as above. The plants were allowed to grow until 15 October, 1995. Parameters measured were plant dry weight, shoot length, and plant width (maximum width of individual ramet in the river)

Table 2. Concentrations of diquat in water at different periods

Concentration (mg l^{-1})	0 min	10 min	20 min	30 min
1.5	1.5	0.038	0.011	0
1	1	0.018	0	0
0.5	0.5	0.016	0	0
0.2	0.2	0	0	0
0.1	0.1	0	0	0

2.14. Experiment 13: Competition Experiment

2.14.1. Introduction

The competition experiments were designed to mimic natural conditions as closely as possible by planting replicated de Wit replacement series in aquaria and tanks (de Wit *et al.*, 1960). Competition between individuals and species is well-documented for terrestrial plants. For aquatic plants, Moen and Cohen (1989), Kautsky (1988, 1991), Agami and Waisel (1985), and Agami and Reddy (1990) have attempted to characterise intra- and interspecific interactions, at the level of individual plants.

2.14.2. Competition between *P. pectinatus* and *P. perfoliatus* under different environmental conditions

The competitive ability of *P. pectinatus* and *P. perfoliatus* was investigated against each other in a de Wit replacement series (de Wit, 1960) between November-February 1995-96, in the ecological laboratory facility, located at the Netherlands Institute of Ecology, Nieuwersluis, Holland. Eighteen aquaria were used in the study. Each aquarium had a volume of 84 l and a water depth of 38 cm. Aquaria were positioned in four phytotron rooms. Aquaria were wrapped in aluminium foil to prevent differential lighting of internal and external compartments within an aquarium, and to maintain the photoperiod regardless of overhead lighting.

To examine possible interactions among the three potential limiting resources, the experiment was conducted in a factorial arrangement with three light levels, two

sediment fertility levels, and two temperature levels, for a total of twelve environmental treatment combinations. Relative competitive abilities of the two species were evaluated by comparing the responses on plants either in monoculture or mixed cultures (i.e. 6:0, 4:2, 3:3, 2:4, 0:6) in each tray. These plant densities was chosen (342 plants m^{-2} sediment surface area) that approximated optimal values observed in natural populations (Kautsky, 1991).

The experiment employed three light levels that were achieved by placing neutral density shade fabric over the two-third of the experimental aquaria. Shading reduced the light to 150 and 75 $\mu E\ m^{-2}\ s^{-1}$, or approximately 50 and 25 percent, respectively, of full light. PAR was measured with a LiCor irradiance meter equipped with an underwater quantum sensor at the mid-point in the aquaria.

Two sediment types were 3:1 and 6:1 sand-clay. Prior to use, the sediments were thoroughly mixed in an electrically driven mortar mixer. After mixing, sediments were placed in 1 l plastic trays, and these were randomly assigned to different experimental treatments. Mean concentrations of available phosphorus in the soil at the beginning of the experiment was 75 $\mu g\ g^{-1}$.

The two rates of temperature (10 and 20°C) were achieved by central heating regulator.

P. pectinatus tubers were obtained from the Institute's stock culture which were collected from Lemmer. *P. perfoliatus* over-wintering rhizomes were collected from Lemmer on 10 November 1995. Uniformly small pieces of *P. perfoliatus* rhizome were chosen to minimize any effects of propagule starting size. Only tubers and rhizomes between 250 - 450 mg fresh weight were used.

Tubers and rhizomes were allowed to germinate at 20°C and at light levels similar to the higher level used in the study, to ensure that they were able to germination, 1 week before planting in the trays. Six propagules (tubers or rhizomes) were planted at the above mentioned densities in each tray and each aquarium received 10 trays (60 plants). Each of the 12 competition-environmental treatment combinations was randomly allocated to a single aquarium. Each combination was replicated three times. Overall, the experiment employed 18 aquaria and 180 trays. The sprouted tubers and rhizomes were planted in trays at 2 cm depth. Sediment surfaces in both 3:1 and

6:1 sediment containers were overlaid with a thin layer of washed silica sand to reduce physical mixing with the overlying solution.

At the end of the 12-week growth period, aquaria were harvested for each treatment combination. In the final stage of the experiment fresh and dry weight biomass yield per species, weight and number of tubers per plant, and percent of allocation dry weight into the different plant parts within each of the trays was determined. pH in the waters was measured several times throughout the experiment.

2.15. Statistical treatment of data

Data were analysed by analysis of variance followed by separation of means only least significant difference tests, at the $P= 0.05$ level, using the programmes GENSTAT and MINITAB.

For each parameter measured, the data were analysed separately, for each time of recording, and together for all data from a given experiment. In analyses carried out with several sampling times, time was not treated as a simple factor. Ten complete randomized block designs and three split-plot designs were used in this work. In the second design, treatments are assigned to main-plots and sampling times are analysed as sub-plots, following standard statistical practice (J. Currall, personal communication).

To determine the significance of comparisons between means, tests of Least Significant Difference (LSD) were applied. Comparisons of results within treatments and between sampling times, or between treatments within a sampling time, were made. All comparisons of means were tested at the 5% level using the number of degrees of freedom associated with the mean square, from the ANOVA.

In all the following presentations and discussions of results the word 'significant' will be used to denote $P< 0.05$.

3. Results and Discussion

3. Experiment 1: Effect of environmental factors on seed germination of *Typha latifolia*

3.1. Introduction

Vegetative propagation is very important to *T. latifolia* (Grace & Wetzel, 1981a, 1982; Krattinger 1983; Dickerman & Wetzel, 1985; Sale & Orr, 1987). Because of this, sexual reproduction in the species has been considered of limited importance. As a result, little is known about the sexual reproduction of this species and of the potential that seed germination represents as a colonization factor. Seed is not only important as a means of maintaining genetic diversity and contributing to plant production, but also as an important dispersal mechanism (Krattinger, 1983; Wade, 1990). Indeed, dispersal of seeds to an unvegetated site may be the only significant mechanism by which clonal perennials are able to colonise new sites. From a practical perspective, if *T. latifolia* is able to create a large seed bank that survives long periods of dormancy and disturbance, then viable germinating seeds would reduce the effectiveness of weed management activities such as herbicide treatments, cutting, and lake drawdown.

Observation on the biology of *T. latifolia* in many different areas of the world indicates that, although *T. latifolia* seeds are viable for long periods and each individual ramet produces enormous numbers of seeds, only a few survive into the seedling phase (Rivard & Woodard, 1989; Grace & Wetzel, 1981a). *T. latifolia* can establish from seed only during periods when there is no standing water and in the spring or summer (van der Valk *et al.*, 1983; van der Valk & Davis, 1978a, b; Baskin *et al.*, 1993). The small size of seeds, remaining in the soil, impact of the established living plant canopy on seed, and the competition among seedlings all contribute to high seedling mortality. McNaughton (1968) and Szczepanska (1971) demonstrated that seedling mortality is also partly produced by an allelopathic effect of decaying aerial parts of *T. latifolia* on the germination of its own seeds.

Improved knowledge of seed germination in *T. latifolia* would be helpful to understand species distribution, vegetation patterns and successional processes in wetlands as well as giving greater insight into reproductive strategies in this species.

In an aquatic system the germination of seeds can be related to many environmental factors such as depth, sediment texture, irradiance, temperature, and disturbance. Percentage seed germination for *T. latifolia* was highest in the surface soil layer and declined sharply when seeds were covered by as little as 1 cm of sand (Galinato & van der Valk, 1986).

This study was designed to examine the impact of the following environmental factors on the germination of *T. latifolia*:

(1) depth of burial;

(2) stratification, sediment texture, light, and temperature regime;

(3) different concentrations of ethanol.

3.1.1. Effects of burial on germination

Under greenhouse conditions germination normally began within 2-5 days; after 35 days maximum germination had been achieved with no further germination taking place during the following 47 days. Percent seed germination at all depths in the greenhouse (20°C) was significantly greater than seed germination *in situ* ($P<0.01$). Irrespective of substrate or light conditions, *T. latifolia* seeds showed significant reductions in germination percentages when depth of burial was increased over the range 0 to 2.5 cm ($P<0.01$) (Fig. 3.1). Unburied seeds of *T. latifolia* had the highest mean germination percentage (95%) with a sharp decline when the seeds were buried even only to 1 cm (Fig. 3.1). In both greenhouse and *in situ* treatments, there was no further significant difference in germination between 1 and 2.5 cm depth (Fig. 3.1). Germination was reduced to less than 10%, once the depth of seed burial exceeded 2 cm. The maximum depth from which any *T. latifolia* seedling could still reach the surface of the sediment was 2 cm (raw data in Appendix 2).

3.1.2. Effects of light and temperature on germination

Seed germination in the presence of light was greater for all depths than germination in the shade. Light also enhanced the germination of seeds in both sand and River Kelvin sediment. Experimental results showed that different levels of light

did not significantly stimulate the germination of *T. latifolia* seeds in the sand and the River Kelvin sediment (P=0.552). Maximum germination of *T. latifolia* seeds when grown in the surface under full light conditions varied from 95% on the sand to 45% for River Kelvin sediment. The mean percentage seed germination in the full light was 2 and 4 times higher than in the half and one third of full light reductions respectively.

T. latifolia proved to be quite sensitive to low temperatures. Analysis of variance for seed germination indicated that there was a highly significant difference in germination at all temperatures in greenhouse and outside. Within the range used here, germination at ~22°C was the greatest, with a significant decline observed at 5-10°C. Maximum seed germination was observed on the substrate surface at a temperature of 20°C, and in full light. Practically zero germination was observed at the temperature regimes of 5 and 10°C at all of burial depths.

3.1.3. Effect of sediment type on germination

Percent seed germination in sand was greater than seed germination in River Kelvin sediment (P=0.001). Nearly all seeds in sand and 40% in the River Kelvin sediment had germinated when they were sown at the surface in full light (Fig. 3.1).

Seedlings of *T. latifolia* grown in the sand were significantly smaller than those in River Kelvin sediment. The average shoot length for *T. latifolia* grown in the River Kelvin sediment was 10-20 cm, but for *T. latifolia* grown in sand were only 4.5-8 cm in length, 6 weeks after planting. Differences in shoot length between treatments increased through time and by 8 weeks, in the River Kelvin sediment, shoot height was nearly 12 times as great as on sand sediment.

Mortality and establishment percentage of seedlings (by 6 weeks after germination) were recorded. A large number of young seedlings, mostly grown on the sand, started to die 1 week after germination. This loss of seedlings may reflect a lack of nutrient in the sand. After 4 weeks, most surviving seedlings grown in the River Kelvin sediment had started to develop leaves. However, all surviving *T. latifolia* in the sand were still in seedling phase.

3.1.4. Effect of stratification on germination

Cold stratification did not significantly increase the germination of *T. latifolia* seeds (Fig. 3.2a). Experimental results showed that at 10°C and above the mature seeds of *T. latifolia* were able to germinate. Unlike seeds of *T. glauca*, which had higher germination after stratification (Galinato & van der Valk, 1986), unstratified seeds of *T. latifolia* germinated better than stratified seeds.

3.1.5. Ethanol and germination

Experimental results showed no significant differences (P=0.19) between seed germination in ethanol or in distilled water over a period of 6 weeks. However, the total number of germinated seeds of *T. latifolia* in distilled water was low compared to those in ethanol (Fig. 3.2b).

3.1.6. Discussion

Seeds must be able to sense their environment and to recognise suitable site conditions for germination and seedling establishment. In this process physical conditions and/or the presence of compounds that are characteristic of a certain niche, and that influence the germination of seeds, may play an important role.

The germination of *T. latifolia* seeds was strongly inhibited when covered with 2.5 cm of sediment. It is thus likely that buried seeds remain ungerminated. Although *T. latifolia* seeds are able to germinate under a wide range of environmental conditions, but the seeds will not germinate in the first place if they are buried.

In situations where the seeds are buried, seedling emergence depends on the depth of burial; those buried deep in the soil will not emerge. Results of this study showed that when the depth of burial was lower (< 0.5 cm), germination of *T. latifolia* seeds was higher. Once the seeds were placed below 1.5 cm sediment, germination rates dropped below 10%. Therefore, sedimentation is a key factor limiting the germination of *T. latifolia* seeds. Agreeing with my results Galinato and van der Valk, (1986), van der Valk (1986), Baskin *et al.* (1993), and Smits (1994), found that a layer

of sediment ≥ 1 cm will significantly reduce seed germination of *T. latifolia*. In a similar experiment Galinato and van der Valk, (1986) found that small seeded species like *Typha* failed to germinate at sediment depth below 1.5 cm.

Seed size, which is directly related to the quantity of food reserve stored, is likely to be an important influence on seedling establishment and rate of germination in *Typha*. Several studies have shown a negative association between seed size and relative growth rate (Fenner, 1983; Shipley & Keddy, 1988; Leishman & Westoby, 1994). My studies revealed that when *T. latifolia* seeds germinated in deep water, the seedlings might not be able to grow to the surface and thus would die. This is probably because seed of *T. latifolia* has a small store of starch in the endosperm.

T. latifolia seeds have a strong innate dormancy and may remain dormant for several years until suitable conditions arise to break the dormancy (Gopal & Sharma, 1983). The period after seed fall is usually an unfavourable period for seedling establishment. Dormancy of the seeds then serves to postpone germination. The innate dormancy of the seeds prevents germination in autumn (Smits, 1994). *T. latifolia* requires high temperature and light for germination to take place.

As the temperature increases all *T. latifolia* seeds situated on the sediment surface start to germinate. Seeds exposed to higher temperature (18-24°C) in greenhouse at the sediment surface and exposed to different levels of light showed an average of 90% germination. As in this study, Moore *et al.* (1993) for *Zostera marina*, and Hartleb *et al.* (1993) for *Myriophyllum spicatum*, found that temperature is a key environmental factor regulating germination.

Low temperatures (5-10°C) prevent germination of *T. latifolia* seeds. Seeds which were exposed to lower temperature (5-10°C) *in situ*, exhibited lowest rates (5%) of germination. *T. latifolia* seeds require a temperature higher than 10°C before they begin to show significant germination rates. The requirement for water temperature higher than 10°C may have adaptive significance.

I suggest that the period between seed release and the onset of germination in the field is a dormancy induced partly by low water temperature. I found virtually no germination when temperatures were between 5-10°C. Germination will start when temperature increases above this level, and end when temperature drops to this point again.

The germination results under different levels of light in both greenhouse and outdoor were not consistent with the findings of Sifton (1959), Sharma and Gopal (1978) and Rivard and Woodard (1989) who determined that light significantly affected germination success. There is some evidence that factors associated with the burial environment other than absence of light may prevent seed germination of *T. latifolia*. My results, as well as those of Holm (1972); Baskin and Baskin (1985); Hartleb *et al.* (1993), showed that the absence of light alone does not prevent seed germination, and a combination of other factors such as temperature and depth of burial, plus light, must be responsible for the lack of seed germination.

Although the percent of seed germination in sand was more than in the River Kelvin sediment, few seedlings survived. The high mortalities of seedlings were presumably due to nutrient limitation in the sand.

This study supports the view of van der Valk (1986) that the impact of competition among seedlings can influence seedling mortalities. The River Kelvin sediment clearly served as a rich source of nitrogen (N) and phosphorus (P) for *T. latifolia* seedlings. *T. latifolia* seedlings appear to be highly sensitive to N and P deficiency.

Seeds which were located at more than 1.5 cm depth do not germinate, but stay viable and contribute to the production of a persistent seed bank. Smits (1994) suggests that dormancy in most aquatic plants seeds is enforced by burial. The buried seeds germinate as soon as they experience germination-favourable conditions, i.e. when the available oxygen concentration, light and temperature are sufficient.

Under anaerobic conditions in *Typha* plants which are cut below water, a substantial amount of ethanol and methane is produced and released into the surrounding water (Sale and Wetzel, 1983). Under these conditions McNaughton (1968) reported these plant products inhibited germination. Although *T. latifolia* was not tested, Smits (1994) reported that ethanol addition to seeds in the light under aerobic conditions had in fact stimulated the germination of *Nymphaea* and *Nuphar* seeds.

The observations made in this study indicated that ethanol did not inhibit germination and seedlings mortalities of *T. latifolia*. Other limiting factors such as

depth, temperature, light and sediment types that are described above were more likely to be responsible for inhibition of seed germination.

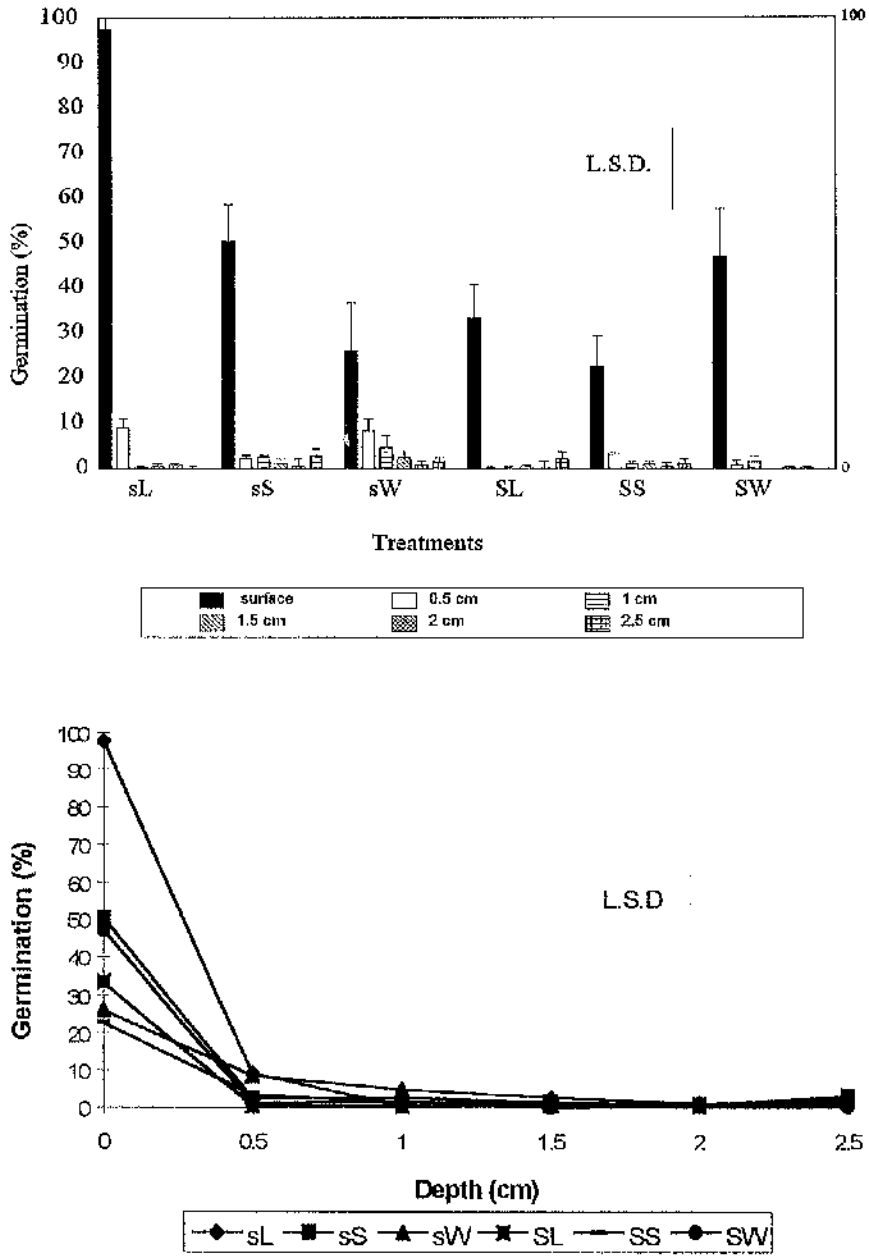


Fig. 3.1. Mean number of seedlings (± 1 S.E.) of *Typha latifolia* grown from seed at seven different soil depths, 3 levels of light and 2 sediment types. Bars on histograms represent ± 1 s.e., separate bars represent least significant difference (P<0.05). Key to treatments: sL = sand & full light; sS = sand & 40% light reduction; sW = sand & 60% light reduction; SL = River Kelvin sediment & full light; SS = River Kelvin sediment & 40% light reduction; SW = River Kelvin sediment & 60% light reduction.

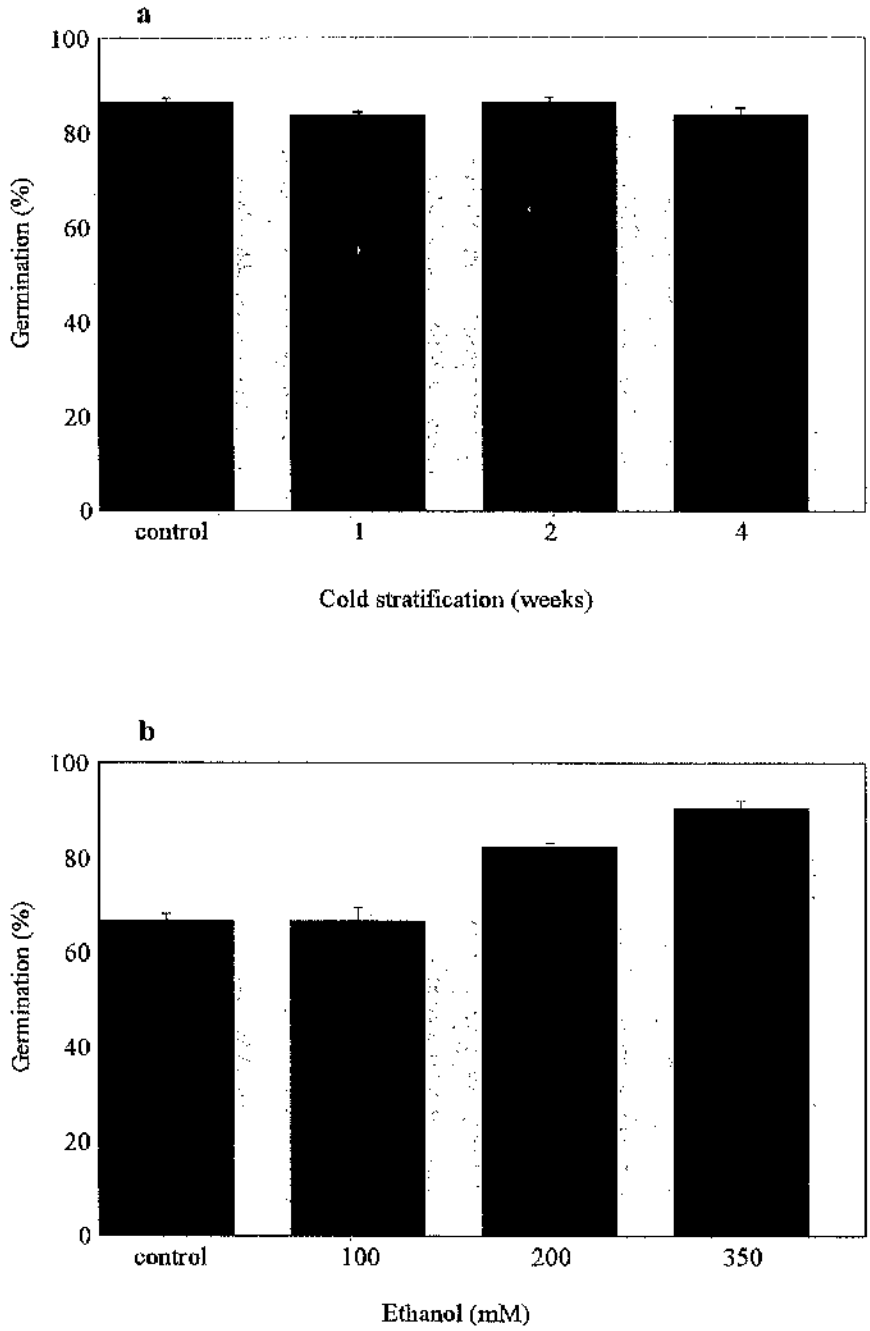


Fig. 3.2. Percentage germination of *Typha latifolia* seeds after various periods of cold stratification (a), and in different ethanol concentrations (b). Bars on histograms represent ± 1 s.e.

3.2. Experiment 2: Responses of *Typha latifolia* grown from seed to cutting and shading, and to water depth and competition when grown from rhizome

3.2.1. Introduction

In many parts of the world *T. latifolia* is a major component of wetland ecosystems. *T. latifolia* grows most vigorously in shallow waters and competes very successfully with other emergent macrophytes (Grace & Wetzel, 1982). Rapid and excessive growth of *T. latifolia* may cause problems such as impeding drainage and creating problems in rice paddies, and in natural and artificial lakes.

Sexual reproduction of *T. latifolia* has received little research attention; however, previous studies indicate that regrowth from seeds may explain why the plant returns after apparently successful control programmes (van der Valk, 1983; Baskin *et al.*, 1993). An understanding of the complete life cycle of this plant is needed if we are to more successfully control its growth.

After a habitat is fully colonized by *Typha*, seed germination may occur (McNaughton, 1968; Grace & Wetzel, 1981a, b; 1982). Populations of *T. latifolia* are largely maintained by vegetative reproduction and seed serves mainly for long range dispersal (Krattinger, 1983; Grace & Harrison, 1986). Several works have shown that seedlings of perennial emergents such as *T. latifolia* become established during water drawdown (Grace, 1983; van der Valk, 1981; Rivard & Woodard, 1989). It is clear that *Typha* plants growing directly from seed are less vigorous than vegetative plants of a similar age, but many questions are unanswered about the response of *Typha* to stress and disturbance when grown from seeds. *T. latifolia* grown from seed has thinner, softer leaves and fewer, larger rhizomes than plants grown vegetatively.

The commonest method for control of *T. latifolia* is cutting, which is no more than a short term solution. *T. latifolia* is particularly difficult to control just by cutting because networks of underground rhizomes rapidly give rise to new shoots. Several reports by Singh and Moolani (1973); Singh *et al.* (1976); Husak (1978); Wright (1983); Ricmer (1984); Husak and Kvet (1986), Jordan and Whigham (1988)and Wade (1990) suggested that cutting the shoots below the water and keeping the

stubble submerged under water for a long time is effective for control of *T. latifolia*. Past experiences (Wright, 1983) suggest that growth of *Ranunculus* spp. did not become limited by cutting off the foliage, unless this is done over a long period.

The use of shade for reduction of macrophyte biomass could be a useful alternative to weed cutting. Dawson (1989) reported that direct removal of plants is only a short term control and is currently becoming more expensive. He proposed that the reduction of light by shading is an alternative technique for the limitation or reduction of excessive growth of aquatic macrophyte.

The objective of these experiments was to investigate (i) the possibility of controlling *T. latifolia* grown from rhizomes by frequently cutting the shoots close to the substrate at the different levels of water and (ii) to determine the effects of cutting and shading on *T. latifolia* when grown from seeds under greenhouse conditions.

3.2.2. Effects of cutting, water levels, and competition on *T. latifolia* grown from rhizomes

The analysis of variance showed that *T. latifolia* dry weight decreased significantly ($P<0.001$) after cutting, compared to the control plants. Dry weights were uniformly reduced at all treatments after 1 and 2 cuttings (Fig. 3.3). The highest plant dry weight obtained for control, compared to 53, 84 and 100% reduction after 1, 2 and 3 cuttings (Fig. 3.3). The experiment showed that a single cut in the early or middle stage of the growth season did not produce satisfactory control. Except for a few plant's survival, there was no regrowth after second cut. In both cases where plants were cut twice and three times, regrowth of *T. latifolia* was not significant at the time of final cut in early-autumn.

A significant decrease ($P<0.01$) in shoot length was observed after 1 and 2 cuts. The reductions were 22, 58 and 100% respectively. The highest shoot length (202 cm) was recorded for the treatment combination of uncut *T. latifolia* at 60 cm depth, without competitors (Fig. 3.3) (raw data in Appendix 3).

Experimental results showed that water depth did not have a significant influence on dry weight and shoot length, although *T. latifolia* dry weight in 60 cm depth was 12 and 30% more than 5 and 20 cm depth, respectively. There were also 8

and 44% increases in shoot length at 60 cm water depth, compared to 5 and 20 cm depth respectively. However, variability in shoot length led to a lack of statistical significance between treatments (Fig. 3.3).

The analysis of variance showed that intraspecific competition had little influence on shoot length and plant dry weight in all water depths. However, there was approximately 3 and 10% reduction in dry weight and shoot length, respectively, in the presence of competitors. The highest dry weight for *T. latifolia* (27.71 g) was observed in 60 cm depth, without competitors (raw data in Appendix 3).

After three cuts, at 50 cm below water 90% of *T. latifolia* had died. Regular observation showed a discolouring of leaves for more than 70% of uncut plants in different water depths, but new shoots were beginning to emerge from sediment at the last stage of the experiment. Extensive tissue breakdown was observed in the stubble of *T. latifolia* which was cut and submerged for more than 3 weeks.

The results suggest that length of time of submergence had a significant effect on the control of *T. latifolia*.

3.2.3. Effects of cutting and shading on *T. latifolia* grown from seeds

Shading significantly (P=0.05) affected plant dry weight and shoot length after 1 and 2 cuttings. Figure 3.4 shows that shading significantly reduced the dry weight and shoot length of uncut plants but did not significantly affect the performance of plants subject to 1 and 2 cuts. The greatest control was achieved in twice cut, shaded plants. Cutting plants showed a similar pattern of higher plant dry weight and shoot length in light than shade. The control effect of all frequencies of cutting were more pronounced when the cut was with shading.

A significant decrease was observed in plant dry weight and shoot length after one and two cuts (Fig. 3.4). One cut without shading decreased the plant dry weight and shoot length by 93 and 55%, respectively, compared with control plants (Fig. 3.4). However, a second cut did not significantly further the reduction in plant dry weight and shoot length. Significant differences in shoot length relative to the control were found after 1 and 2 cuttings under light and shade conditions (Fig. 3.4). Under light, the reduction of shoot length were 52 and 73% after 1 and 2 cuttings respectively,

compared to control plants. Shoot length were also 73 and 80% less under shade than light compared with control plants after 1 and 2 cuttings (Fig. 3.4).

The percentage re-emergence after the second cut with and without shading was less than 10 and 20%, respectively. The highest shoot dry weights for uncut, one cut, and two-cut were 2.80, 0.276 and 0.202g, respectively (raw data in Appendix 4).

3.2.4. Discussion

This experiment illustrates the importance of understanding the interactive effects of cutting and shading in plant communities if we wish to predict the outcome of plant management operations with reasonable confidence. Light intensity appears to be the major controlling factor not only in seed germination, but in plant survival under the disturbance caused by cutting, and the stress caused by shading, for *Typha* when grown from seeds and rhizomes.

Very little work has been done on the responses of *T. latifolia* to cutting and shading when grown from seeds. Similarly, the cause of dry weight and shoot length decline of *T. latifolia* under light limitation has been investigated by Grace and Wetzel (1981a). They found that the reduction was partly because of light limitation over a long period. It was found that during cutting, a great quantity of shade was produced through on accumulation of cut foliage, resulting in the suppression of *T. latifolia* growth and subsequent shoot length. Sale and Wetzel (1983) found that the *T. latifolia* after cutting below the water, produced toxic substances that suppressed its own growth. However, Sculthorpe (1967) reported that *T. latifolia* plants, when grown from seeds, are more tolerant of an anaerobic environment than when grown from rhizomes.

The results for shoot length indicated that two cuts plus shade most efficiently reduced the length of regenerated shoots. Two cuts caused the regenerating of new shoots to be greatly retarded. There was almost no regeneration after two cuts with or without shade treatments. The experiment found that after the second cut some shaded plants died, hence *Typha* when grown from seed should be virtually eradicated after two cuts with shading.

An increase in shoot and leaf length was observed with increasing water depth, agreeing with the results of Grace and Wetzel (1982). However, there was no significant difference between plants at different water depths. *T. latifolia*, by increasing allocation to leaves and shoots, could enhance growth and subsequently survival. Grace and Wetzel (1982) also found that, with increasing water depth, *T. latifolia* diverted resources away from flowering to leaf production. However, none of my experimental plants grown from seeds and rhizomes, either in their natural habitats and/or greenhouse sites had initiated flowering by the time they were harvested. Sale and Orr (1987) reported that lack of flowering by plants grown from seeds after 6 months is not uncommon. My field observations and the results of Sale and Orr (1987) indicated that the leaves on non-flowering shoots remained green and photosynthetically active for longer than in flowering *T. latifolia*, as a results of a lack of carbohydrate transfer to the reproductive organs. This result supports the findings of Grace and Wetzel (1982) with regard to resource allocation.

Experimental results showed that three cuts during the growth season resulted in almost complete death of the plants. These results were in agreement with those proposed by Shekhov (1974), Sale and Wetzel (1983), Riemer (1984), Husak (1986), and Wade (1990) who found that cutting off shoots below the water surface two or three times during the one growing season has a strong controlling effect on *Typha* stands. Leaves of *Typha*, by absorbing oxygen and passing it to below ground parts, are able to sustain aerobic respiration in an anaerobic environment. Reduced regeneration and height of shoots brought about by the increase in the period of submergence thus inhibits respiratory activity of the stubble and underground rhizomes.

Unlike submerged plants, the submerged parts of emergent plants like *Typha* are not adapted to low light conditions, and are unable to photosynthesise beneath the water surface (Spencer & Bowes, 1990). Thus, it would seem that the limited penetration of light into the water was also important in retarding regrowth of cut stems.

Visual observation showed that decomposition of the below-ground parts started after 4 weeks submergence. Unlike seedling *T. latifolia*, which is able to cope with anaerobic conditions (Sculthorpe, 1967), adult *Typha* starts to breakdown after 4

weeks submergence when all shoots are cut below the water level. The rate of shoot regeneration depended on the duration of submergence. It appears that water entered slowly into the stubble shoots filling the aerenchyma, thus preventing gaseous exchange. This result supports the findings of Sale and Wetzel (1983) who found large amounts of methane production around the plants cut below water, presumably resulting from an increase in anaerobic bacteria. These bacteria are able to break down the cell walls of the *Typha* root and rhizomes.

Another factor which has a significant effect on inhibition of the regeneration of *Typha* after cutting is the reduction of food reserves in submerged stubble due to decay of the stubble (Singh & Moolani, 1973; Husak & Kvet, 1986). Poor regrowth after two cuts may also be due to exhaustion of carbohydrate reserves which are largely consumed in the flowering process. Therefore, control will be most effective if plants are cut once they have started to flower. Sale and Wetzel (1983), and Singh *et al.* (1976) reported that one cut of aerial shoots at the time of flowering and keeping the stubble submerged were effective in controlling *T. latifolia* (Fig. 3.5). This is probably because, at the time of flowering the rhizome's carbohydrate reserves are at their lowest following much translocation to the aerial plant parts. These data show that the growth rate of new shoots was more affected by submergence than by frequent cutting

One cut at or above the water surface had no effect on growth of *Typha* in the next year. Despite a significant reduction of plant dry weight, substantial regrowth in the same year was observed after a single cut above water level. These results agree with those of Singh and Moolani (1973), Shekhov (1974), Singh *et al.* (1976), Husak (1978), Riemer (1984), Husak and Kvet (1986) and Wade (1990), who all found poor control after a single cut during the early and/or middle of growing season. The ability of *T. latifolia* to recover declined after even one cut at 60 cm below the water depth. It is suggested that control of *T. latifolia* with one cut strongly depends on water depth. It is clear that fast regrowth after one cut is due to a lack of significant depletion of carbohydrate reserves in the rhizomes. Like Sale and Wetzel (1983), my conclusions are that, for long term control of *Typha*, two below-water cuts may be necessary in one season.

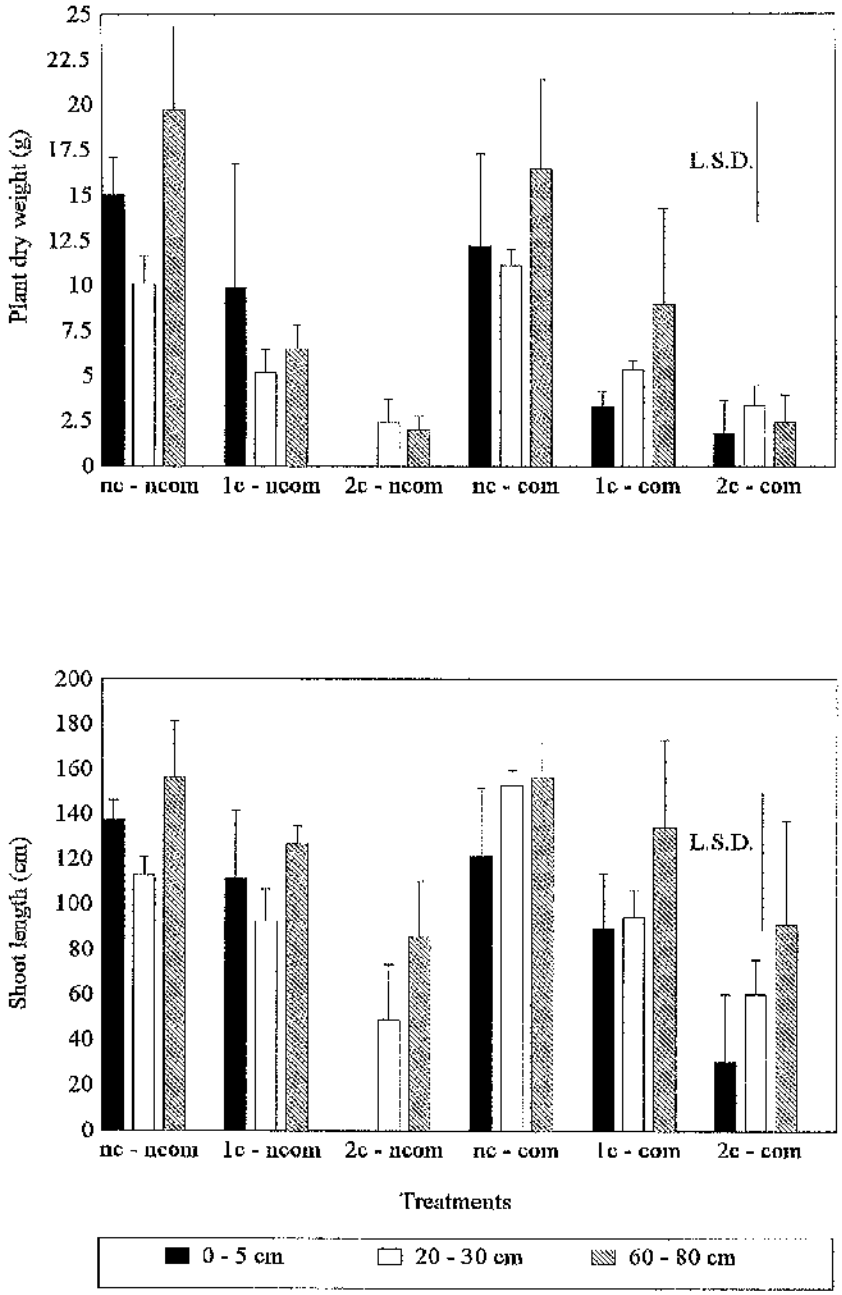


Fig. 3.3. Plant dry weight (g) and shoot length (cm) of *Typha latifolia* along a gradient of water depth with and without competitors, and different levels of cutting. Bars on histograms represent ± 1 s.e.; separate bars represent least significant difference (P<0.05). Key to treatments: c = cutting; nc = no cutting; 1c = one cut; 2c = two cuts com = competition; ncom = no competition

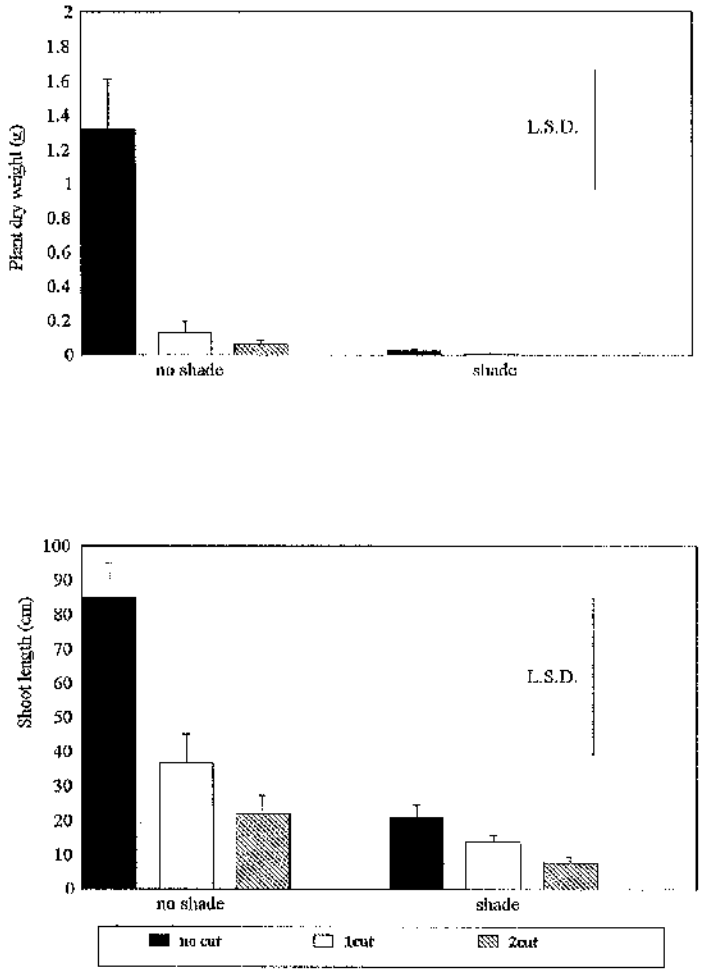


Fig. 3.4. Effects of various levels of cutting and shading on dry weight (g) and shoot length (cm) in *Typha latifolia* when grown from seeds. Bars on histograms represent ± 1 s.e.; separate bars represent least significant difference (P<0.05).

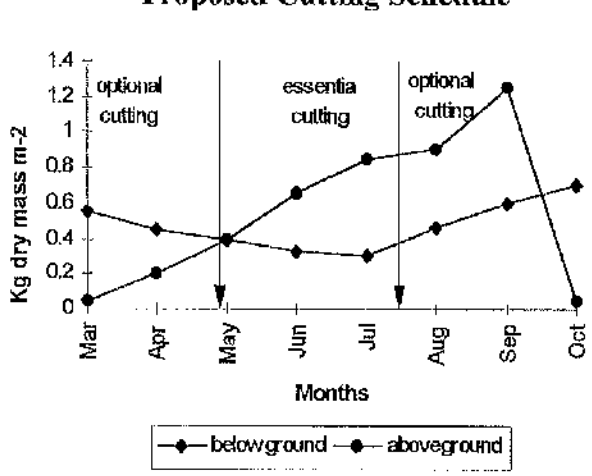


Fig. 3.5. A cutting scheme which will provide effective *Typha* control (Djebrouni & Huou, 1988)

3.3. Experiments 3-5: Transplantation experiments

3.3.1. Introduction

T. latifolia is a variable species, both in morphology and life history, that occurs in a variety of habitats (Grace & Wetzel, 1981a, b). For example, phenological differences in growth response of field populations, discovered by Grace and Wetzel (1981a, 1982), showed that *T. latifolia*, in competition for light, was better able to grow and survive in shallow than deep water.

Grace and Wetzel (1981a, b) found that *Typha* populations in deep marshes (50-100 cm), as compared to damp (0-20 cm) roadside populations, were characterized by a higher density of adult plants, by increasing leaf length and leaf surface area, decrease in sexual structures, and higher mortality during a severe winter and lower mortality during the growing season. Plants in deep marshes (with increased leaf weight per unit height) produced smaller rhizomes, although these were capable of producing emergent leaves in 80 cm of water (Grace, 1981; Grace & Wetzel, 1981a, 1982). In contrast, plants in damp roadsides were characterized by a much greater leaf surface area, earlier in the growing season. They were also more tolerant of shading (Grace & Wetzel, 1981b). These two morphological types can be considered as the extremes of a range of phenotypes that occur when different populations are grown under uniform conditions.

The establishment of environmental criteria for the control, protection, and restoration of aquatic vegetation, especially of perennial species, requires an understanding of the temporal variation in environmental quality of the habitat as well as ecological performance of the species in question. One way to determine the source of limitation is through a transplant experiment. Transplant experiments are thus among the principal tools of the ecologist interested in species distributions.

In order to gain an ecologically-based understanding of this system, three reciprocal transplant experiments were carried out in three contrasting habitats. These differed in depth, nutrient status and competitors. The use of a water-depth gradient was chosen to facilitate a comparison of niche characteristics and because soil moisture and water depth both strongly influence *Typha*'s establishment and growth (Grace, 1983; Rivard & Woodard, 1989).

In all three experiments, potential distribution, natural biomass allocation, and management of *T. latifolia* were determined by observing the growth of moved and unmoved ramets in the presence and absence of competitors, at different water depths, and with different levels of control by cutting and glyphosate application.

The aims of these investigations, i.e. the reciprocal transplant trials conducted on the *Typha* populations grown from seeds and rhizomes under different levels of disturbance (cutting) and stress (competition) were: (1) to confirm the observed variation patterns in response to environmental differences; (2) to assess the importance of one of the prime environmental characters associated with littoral zone differences, i.e. depth; (3) to assess the plasticity of population response to growth in different plots and in the presence of different competitors; (4) to assess the response of ramets from different plots to different levels of cutting; and (5) to evaluate the effectiveness of glyphosate in controlling transplanted *T. latifolia* in different water depth.

3.3.2. Experiment 3: Effects of cutting, competition, and water levels on transplanted and untransplanted *Typha latifolia*

Performance of transplanted and untransplanted *Typha* under new environmental conditions and different levels of cutting and competition was evaluated by measuring mean biomass (dry weight) and plant length. The average mortality rate was lowest at plots 2 and 4 in Lochwinnoch and plot 1 in the Lochan Dubh (~25 cm depth). Transplant success was excellent in plots 2 and 4 (60-85% of plants survived), good in plot 1 (60% of plants survived), and poor in plot 3 (50% of plants survived). The higher mortality recorded in plots 1 and 3 may have been due to the higher water level, in which the numbers of native plants was also reduced. On the other hand, the transplanted *Typha* may have been installed in a poor condition, or may have died when competition with other vegetation was high. In plots 2 and 4, where water depth was less than 20 cm, *Typha* exhibited a considerable increase in length and dry weight throughout the growing season.

The statistical analysis indicated that transplanted *Typha* in Lochan Dubh had a significantly lower mortality rate than transplanted Lochwinnoch plants but,

unexpectedly, no difference was found between the plots in Lochwinnoch. It is also possible that low mortality and the high biomass of *Typha* at the Lochan Dubh was due to the excellent growing conditions in 1995 compared with weather conditions at Lochwinnoch in 1994. In general the rates of mortality was higher in moved plants compared with unmoved *Typha*. Mortality was concentrated in the winter following the first season of transplanting.

Depth had a major effect on transplant survival. Loss rate was highest in deep water (over 50 cm deep) at plot 3 in Lochwinnoch, while vegetative propagation in shallow water (less than 50 cm) resulted in an increase of the population biomass. Growth was highly correlated ($P<0.01$) with depth at plots 1 and 3 in Lochwinnoch. The subsequent rate of mortality was also lower in shallow water than in deep water. Almost 75% of the *Typha* transplanted to shallow water survived the first year. *Typha* transplanted to deep water at plots 1 and 3 suffered dramatic losses after two and three cuts. Less than 30% of the *Typha* transplants survived after 3 cuts. There were no plants below 80 cm depth in plot 3 after 3 times cuts.

During the growing season the development of plants was recorded at about monthly intervals. Plant growth at the three sites (Possil Marsh, Lochwinnoch, and Lochan Dubh) differed considerably. At Lochan Dubh *Typha* showed a rapid increase in shoot and leaf length during the summer. At Lochwinnoch the growth of leaves and shoots was relatively constant by two months after transplanting.

Environmental features of the transplant site, and cutting, influenced survival of *Typha* plants more than competition from neighbouring plants. Previous ecological studies conducted by Grace and Wetzel (1981a, b, c, & 1982) have provided evidence for differences in growth characteristics and flowering time between populations of *Typha* in the absence and presence of competitors across a water depth gradient. They also reported that *T. angustifolia* and *T. domingensis* were poorer competitors than to *T. latifolia*. Although, competition was assume to be the cause of mortality of *T. latifolia* after transplanting, there was no significant ($P=0.806$) increase in plant dry weight in the absence of competitors at the end of experiment (Fig. 3.6). *T. latifolia* had a 6.3% decrease in height in moved and 10.8% increase in unmoved plants in the absence of competitors compared with control plants in the end of experiment.

T. latifolia had also 3.6 and 9.8% greater biomass in moved and unmoved plants in the absence of competitors.

A significant decrease in height and biomass was observed after two and three cuts compared with uncut treatments (Fig. 3.6). Because of the high mortality rates, data from three cuts are not presented. At plots 1 and 3 a few plants survived after two cuts, but no plants survived after three cuts. At plot 2 most transplants of *Typha* did well until they were clipped 3 times. Only two plants survived after three cutting. A reduction in plant biomass of between 53 and 61% for two cuts, and 97 and 99% for three cuts, respectively (Fig. 3.6). Compared with control plants, dry weight decreased 13 and 26% after one cutting in moved and unmoved *Typha*, respectively (Fig. 3.6).

A significant reduction (86.5 and 94%) in plant height was observed after three cuts in moved and unmoved plants, respectively (Fig. 3.6). A 21 and 41% reduction in plant height were observed after two cuts in transplanted and untransplanted *Typha*, respectively (Fig. 3.6). Despite a high mortality of *Typha* in plots 1 and 3, transplanting did not significantly (P=0.583) influence plant height. Also, the presence and/or absence of competitors had no significant effect (P=0.734) on height of transplanted or untrasplanted *Typha* (Fig. 3.6).

Plants in cut plots and/or transplants of *Typha* often produced no inflorescence and were therefore omitted from the ANOVA since the data would not be normally distributed. In the second year, inflorescence production in all plots was too low to test for treatment effects. Variability in time of flowering in transplanted and untransplanted *Typha* following the clipping was considerable during the experiment. In the first year, cutting or transplanting reduced flowering, with cutting having the greatest effect. Flowering in the transplant *Typha* was significantly dependent on the cutting times. Transplanted *Typha* did not flower after they were clipped. Although no statistically significant between-plot differences (P=0.665) were observed, there was some evidence for differential population response. Eighty percent of the *Typha* plants surviving at the end of growing season failed to flower and only two of the transplants in plot 2 were vigorous enough to flower. Flowering of untransplanted *Typha* occurred approximately 2 months earlier than that of transplanted *Typha*. However, the short growing season may be the main control on flowering in *Typha* populations in Scotland.

Although initial losses were high in plots 1 and 3 these transplants that survived were able to persist over the subsequent year. Three weeks delay in the regrowth of plants was observed after transplanting at plot 3. However, despite varied and often unsuitable growth conditions at plots 1 and 3, most of the transplanted *Typha* continued to grow (raw data in Appendix 5).

3.3.3. Experiment 4: Responses of *T. latifolia* to cutting and water depth when grown from seed

Analysis of variance of the results showed no significant differences in plant mortality, plant dry weight, shoot length, leaf length, and the number of leaves per plant due to water level because of the great variability between plots, but the effect of cutting did prove to be highly significant. However, there were no significant differences in growth responses between the two sites, although high mortality of transplanted seedlings was observed in the Lochan Dubh.

A significant reduction in dry weight, shoot and leaf length was observed after the first and second cut in both Possil Marsh and Lochan Dubh (Figs. 3.7 & 3.8). The highest above ground biomass was observed at the controls and the lowest where two cuts were applied. Except for a few plants, most had died after a second cut, especially in the Lochan Dubh (Fig. 3.7) (raw data in Appendix 6).

In both sites, plant dry weight, leaf and shoot length generally increased with the decrease of water level. In support of this, *Typha* dry weight, shoot and leaf lengths were generally much higher at all levels of cutting treatments in the shallower Possil Marsh than Lochan Dubh (Figs. 3.7 & 3.8).

3.3.4. Experiment 5: Response of *Typha latifolia* to altered water depth plus different doses of glyphosate

The results of this experiment showed that *T. latifolia* is susceptible to glyphosate at doses of 2 kg a.i. ha^{-1} and above (Fig. 3.9). In this experiment glyphosate at doses of 2 and 4 kg a.i. ha^{-1} caused a significant reduction in plant dry weight, shoot

length, leaf length, and number of shoots per plant. In all treatments mortality was compared with controls (Figs. 3.9 & 3.10).

A very rapid and complete die-off occurred at 4 kg a.i. ha^{-1} glyphosate in both moved and unmoved plants at both water depths. At 2 kg a.i. ha^{-1} glyphosate the die-off was a little slower, but 54 and 81% mortality in both moved and unmoved respectively, was observed 60 days after glyphosate application. At 1 kg a.i. ha^{-1} glyphosate mortality was 34 and 41% in both moved and unmoved *Typha*, respectively.

Despite a reduction of 5 and 50% in the number of shoots treated with 1 kg a.i. ha^{-1} glyphosate in moved and unmoved plants, respectively, there were no significant differences compared with controls. Glyphosate at 2 kg a.i. ha^{-1} significantly reduced (46 and 73%) the number of shoots in moved and unmoved plants, respectively (Fig. 3.10).

The results indicated that in moved and unmoved *Typha* shoot length was significantly reduced (46 and 73%) at 2 kg a.i. ha^{-1} glyphosate. Despite 22 and 35% reductions in 1 kg a.i. ha^{-1} glyphosate, no significant differences in shoot length were observed compared to untreated plants (Fig. 3.10).

Glyphosate at 2 kg a.i. ha^{-1} significantly reduced leaf length (34 and 84%) and number of leaves per shoot (42 and 83%) in both moved and unmoved *Typha* (Figs. 3.9 & 3.10). No significant differences were observed in leaf length and number of leaves per plant, despite a 14 and 38% reduction in moved and 38 and 33% reduction in unmoved plants, respectively (Fig. 3.9).

There were no obvious differences in mortality between transplanted and untransplanted plants after glyphosate application. Experimental results showed that transplanting from shallow to deep and deep to shallow water did not significantly influence plant dry weight, shoot length, leaf length and number of shoots (raw data in Appendix 7).

A small amount of regrowth in both moved and unmoved *Typha* had been observed at 1 kg a.i. ha^{-1} some 3 months after application. The majority of this regrowth occurred in shallow water.

3.3.5. Discussion

There were some problems in the transplant experiments. Despite starting with a large number of plants there was such high mortality and low incidence of flowering among the survivors that little data could be collected. Moreover, only differences in survival plant length, plant dry weight, and competition among successful transplants were evaluated. The reciprocal transplant experiments revealed the complexity of the environmental influence, cutting, and competition on the growth response *T. latifolia* when grown from seeds and rhizomes.

At all sites plant size was the most important trait determining survival. At each site, transplanted *Typha* was relatively smaller than the native populations. As yet it is not clear which conditions of the native habitats led to these differences, either biotic factors (such as competition) or abiotic factors (such as water depth and water nutrients). Grace (1985) found no genetic differences in ramet survival in a transplant experiment with both seedlings and rhizomes, but sample sizes were small due to a heavy mortality.

Typha height was shown to be an important ecological factor determining survival of plants at all sites. The rate of increase in plant height and biomass was low during the first two months of the experiment, due to the transplant shock and water depth. After two months, plants had recovered from transplant shock and increased in size at a similar rate to that observed for natural patches.

Although determination of the precise reasons for the transplant failure were not easy, water depth may have been partially responsible. The difference in regrowth after transplanting was probably not the results of genetic differences among the *Typha* population. It may be due to installing plants into deep water. This agrees with the results of Grace and Wetzel (1982) who suggested that with increasing water depth, light is the main limiting resource for *T. latifolia*. A decrease in light penetration, due to increased water depth, is therefore suggested as the cause of the *Typha* decline in plots 1 and 3. Light limitation at higher depth may produce a negative carbon balance, leading to cessation of growth and even death. An increase in transplant mortality was observed in plot 3 due to increase of water depth (agreeing with the results found by Grace & Wetzel, 1982). These results indicated that stress caused by water depth

contributed to production of biomass in the natural population. This agrees with results for populations of *T. latifolia*, in which the deep water plants showed a high increase in shoot-to-root ratio at low light intensities relative to a shallow water population (Grace & Wetzel, 1982). Therefore, a small average rhizome size of *T. latifolia* compared with *Typha angustifolia* in depth of water (>50 cm) reduced the ability of the plant to produce enough emergent leaves.

Despite the insignificant effects of competition on survival, transplanted *Typha* plants showed considerably greater growth in plots 2 and 4. This is because they were mostly free from competition for light with other competitors like *Glyceria maxima* and *Carex* species. Especially in plot 2 many plants were still alive at the end of summer. Growth of *Typha* which originated from seeds and rhizomes was inhibited at 60 cm water depth. An increase in plant mortality after transplanting in the presence of competitors, was presumably at least partly due to competition for light with other plants. Although the high leaf surface area produced by *T. latifolia* is an additional advantage in competing for available light, the greater mortality and reduction of *Typha* growth in plot 1 was probably due to interspecific competition for light with *Glyceria maxima*. These results did not support the results of similar experiments undertaken by Grace and Wetzel (1982), who found that, under extremely low light intensities, *T. latifolia* is a better competitor.

Light penetration and cutting may have a synergistic effect on *Typha* survival. When environmental conditions are marginal suitable for the establishment of *Typha*, because of poor light penetration a minimum disturbance caused by cutting may be required for successful plant control. The long-term survival of the moved and unmoved *Typha* increased after cutting in shallow water depth. These results showed that transplanted *Typha*, after cutting, were sensitive to low light levels.

It is possible that the major damage to the transplanted *Typha* was due to early cutting after transplanting. My initial hypothesis, that emergent plants would eventually die when clipped frequently underwater, was based on field clipping studies by Middleton (1990) on *Paspalum distichum* and *Ipomoea aquatica*. My study demonstrates that *T. latifolia* has different abilities to survive and grow after clipping; its tolerance depends both on the water depth and the frequency with which the plants are clipped. The results of these experiments suggest that, not only did *T. latifolia*

survive a single underwater cut, but, clipped plants produced the same or even amount biomass than unclipped plants.

In these experiments only two years of the life cycle of *Typha* grown from both seeds and rhizomes was covered and not all plants were followed until their death. Results revealed that *T. latifolia* plants had a very low flowering frequency when transplanted to an alien site. Apparently, local adaptation between *T. latifolia* populations is very important. Populations in these experiments may be separated into three groups on the basis of their habitats, treatments, and associated flowering responses: water depth, weather conditions, and disturbance caused by cutting. Data from plots 1 and 3 indicated that flowering was completely controlled by clipping. Earlier flowering in the uncut and one clipped *Typha* probably was due to greater above and below ground biomass. The size of a plant has been found to be positively related to flowering (Grace & Wetzel, 1981a, 1982). At all sites, differences in plant size were found between clones. It is not clear what has caused the rather unexpected result that some clones apparently were larger and thus contributed more to flowering. It might be partly due to differences in initial condition of transplants that have no genetic background. Alternatively, clones might be adapted to certain conditions common to all three sites, such as weather conditions during the experiment. The chemical analysis of the water showed no significant differences in P (phosphorus) and N (nitrogen) concentrations in the three habitats.

A plausible alternative explanation is that plants may differ in allocation of resources to vegetative growth and seed production. Vegetative size positively affects survival at the sites studied, so that increased allocation to growth may result in a higher longevity and a higher reproductive potential. It seems unlikely that climatic differences were more important than other factors.

Flower development may be retarded as a result of photosynthetic area. Because most material for the flowering process comes from rhizome storage (Grace & Wetzel, 1982), insufficient biomass in the rhizomes may result in non-flowering. A seasonal abundance of C reserves and their rates of mobilisation play an important role in *Typha* flowering. In this respect, C reserves in the rhizomes may be particularly critical to transplant success and flowering. Past studies by Grace and Wetzel (1981a, b, c; 1982) generally indicated that rhizome size is related to flowering since an

average of almost 30 g dry mass must be stored in the rhizome in order to produce an inflorescence. The significant decrease in plant dry weight after frequent cuttings and transplanting compared with uncut and unmoved plants can be dependent on rhizome size.

The low frequency of flowering in transplants compared with unmoved plants would be influenced by stress due to transplanting and decreased sexual allocation with increasing water depth. Grace and Wetzel (1982) have also shown that flowering in *T. latifolia* occurred only when extra resources were available. Also the suppression of flowering after transplantation could be related to variation in root biomass which might limit the potential uptake of nutrients.

Other factors affecting flowering were light and temperature. Temperature and light, more than other environmental factors are strongly correlated with time of flowering. *Typha* reacted as a short-day plant, as evidenced by its inability to flower over a 9-hr photoperiod, even though flowering occurred under longer day length treatments.

The average mortality in the seedlings after transplanting was higher than *Typha* grown from rhizomes. Especially in the second plot (~50 cm) at Lochan Dubh many seedlings died early. These results indicated that seedling mortality may be caused by a higher water depth in this plot. Adult plants with established rhizomes and carbohydrate reserves may be better able to tolerate increased inundation.

Although experiment 5 was conducted to determine the effects of glyphosate on *Typha* after transplanting shock, there were no statistical differences in the effects of the different levels of glyphosate on moved and unmoved *Typha*. Transplant *Typha* even had a better growth after low glyphosate dose application. It might be due to transplant stress and/or dormancy of rhizomes after changing the habitat, which accelerates natural die back. Murphy and Barrett (1990) found that the best time for application of glyphosate is before senescing. Seddon (1981) and Barrett (1976) found a similar phenomenon that natural die back of plants may reduce the effectiveness of glyphosate. Seddon (1981) suggested that the effect of glyphosate depends upon its translocation from the leaves to the rhizomes. The best time for control of *Typha* with glyphosate must coincide with active growth of the plants and when the transfer of photosynthetic products from the leaves to the rhizomes occurs. As the translocation

of glyphosate is associated with the movement of food materials from the leaves to rhizomes (Barrett & Robson, 1971) earlier shock due to transplanting may have restricted the transport of herbicide to the rhizomes. Evans (1978) suggested that the optimum time for herbicide treatment of most aquatic species is likely to be around the time of flowering or just after.

Another factor that may be involved in the *Typha* response to glyphosate is the rate of application. Excellent control in both the moved and unmoved *Typha* at a middle-season application was found at 2 kg a.i. ha^{-1} glyphosate. The results of my experiment conform with those of Murphy and Barrett (1990) who found good control of *T. latifolia* by glyphosate at 2 kg a.i. ha^{-1}. These results did not support those of Evans (1978) who indicated that good control of *T. latifolia* was only possible where rates of at least 2.7 kg a.i. ha^{-1} were used. However, he did not mention the time of application.

Like other rhizomatous species, *Typha* is resistant to the activity of glyphosate. It is suppressed in the season of application but regrowth occurs the following spring. In order to obtain long term control (>24 months) of *Typha*, the rhizomes must be controlled (Barrett, 1976; Shilling *et al.*, 1990). *Typha* rhizomes, were not as sensitive as shoots to glyphosate except at the highest concentration. Complete inhibition of rhizomes regrowth therefore requires a higher herbicide rates.

McNaughton (1968) and Szczepanska (1971) reported that an allelopathic effect of decaying aerial parts of *Typha* caused the absence of *Typha* seedlings within a stand of this species. However, McNaughton (1968) found that soil water and the extracts of *T. latifolia* affect seedling growth more than the germination of seeds themselves. Further experimental results by Sharma and Gopal (1978) and Grace (1983) showed that general absence of seedlings in nature was not due to the autotoxic effect of *Typha* itself on the germination of *Typha* seeds. Sharma and Gopal, (1978) indicated that the absence of *Typha* seedlings was because of heavy shading by *Typha* and other water plants. Grace (1983) conducted a series of experiments in the greenhouse and laboratory and reported that leaf and litter extracts did not inhibit the germination of *Typha* seeds.

Only an increase of water depth to more than 40 cm was found to be the responsible for increasing *Typha* seedling mortality in this experiment. This finding is in

agreement with results reported by Sharma and Gopal (1978) and Grace (1983), who found that physical pressure like water depth, light, and competition were more important influences on seedlings than allelopathy. Good growth of *Typha* seedlings after transplanting to both Possil Marsh and the Lochan Dubh at low water levels showed that critical time for survival was germination. These findings clearly indicated that the chance of *Typha* seedling survival was not less than other water plants, and support the findings of Grace (1983) that the absence of *Typha* seedlings in nature could be due to a suppression of seedling growth and survival rather than inhibited germination. Therefore, this experiment did not support the findings of McNaughton (1968), who believed that allelopathy affected seedlings rather than seeds.

The lack of inhibition of seed germination in the presence of established *Typha* plants is in strong contrast with the reported absence of *Typha* seedlings in nature (van der Valk & Davis 1976; Grace 1983). It seems more likely that water depth, wave action and sediment types are more important in regulating the *Typha* populations in nature than autotoxic properties reported by McNaughton (1968) and Szczepanska (1971).

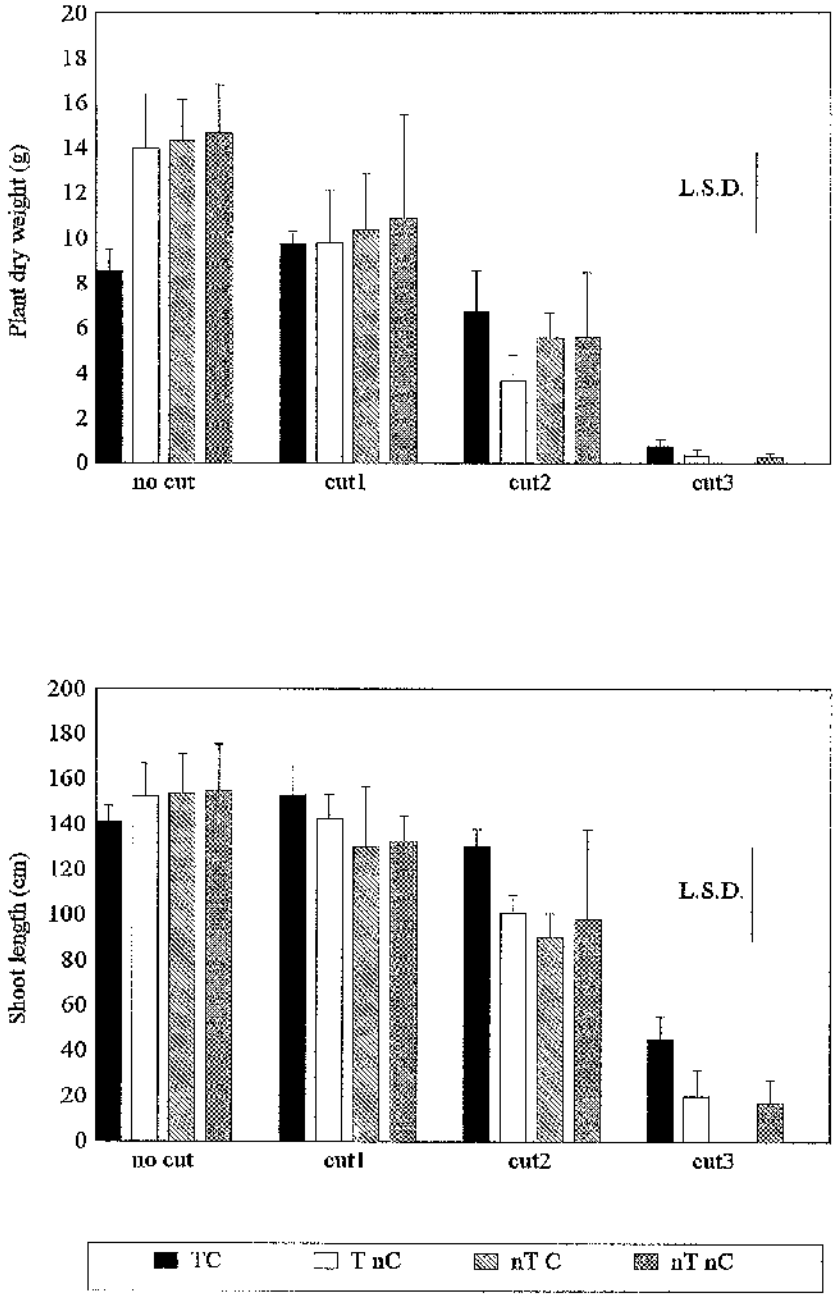


Fig. 3.6. Potential and realized distribution of *Typha latifolia* in relation to competition, transplants and disturbance (cutting) in plant dry weight (g) and plant shoot length (cm). Bars on histograms represent ± 1 s.e.; separate bars represent least significant difference ($P<0.05$). Key to treatments: T = transplant; C = competition; nC = no competition; nT = no transplant

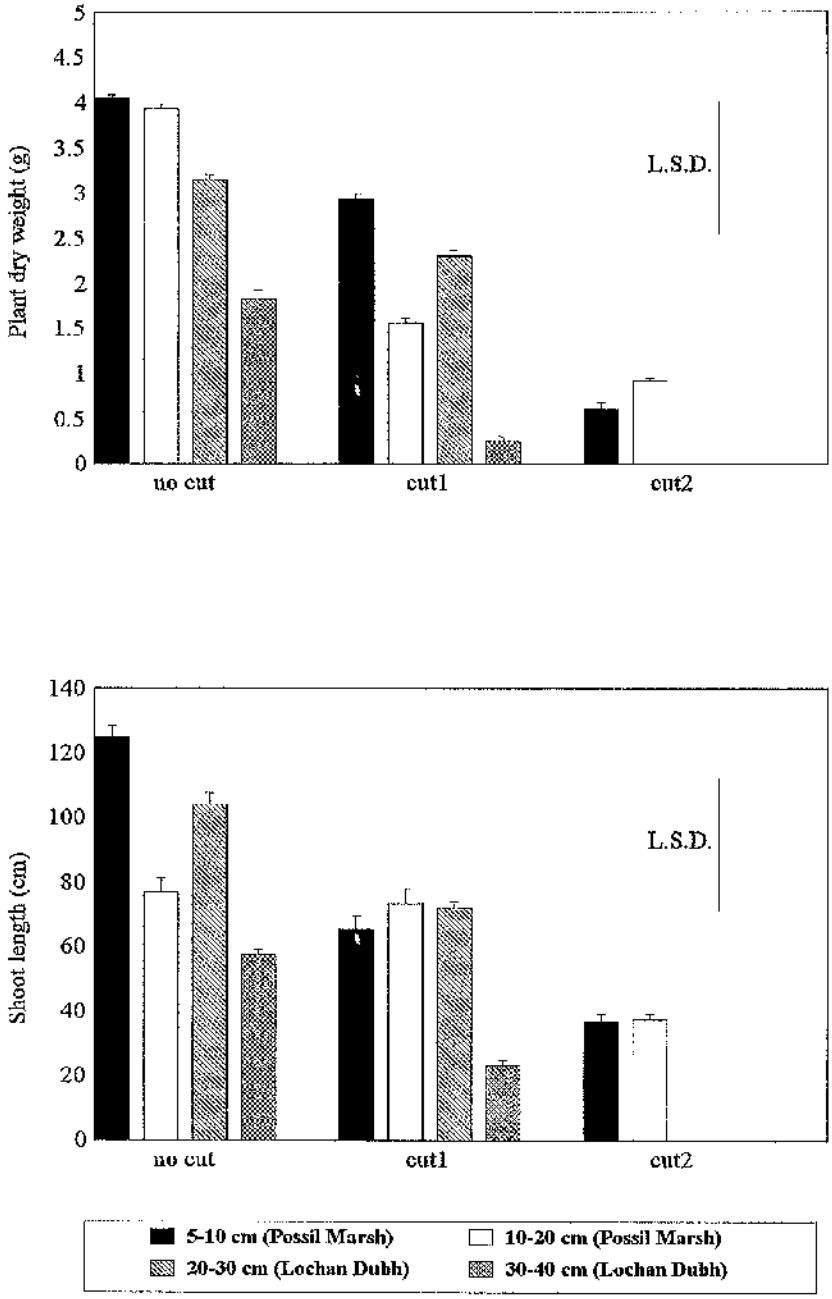


Fig. 3.7. Potential and realized distribution of *Typha latifolia* grown from seeds in relation to transplants and disturbance (cutting) in plant dry weight (g) and plant shoot length (cm). Bars on histograms represent ± 1 s.e.; separate bars represent least significant differences (P<0,05).

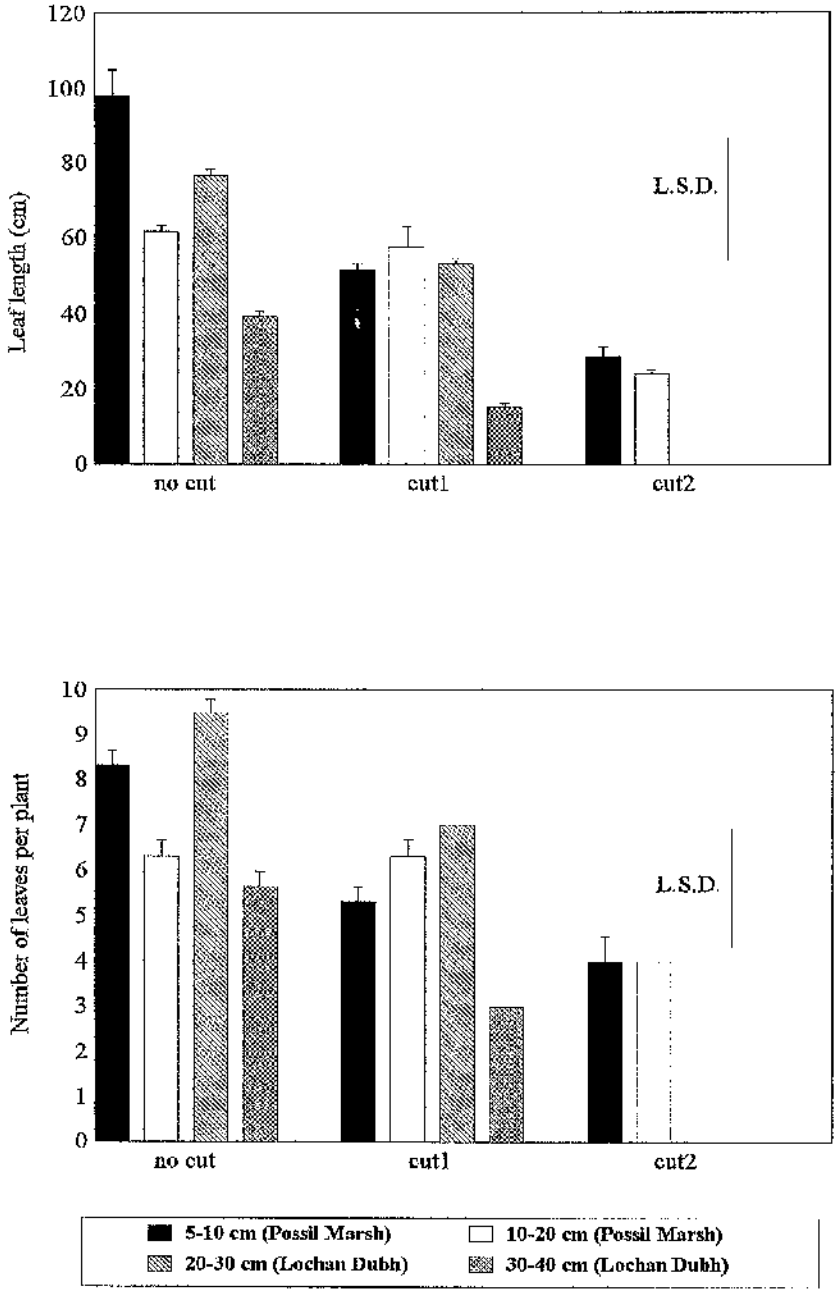


Fig. 3.8. Potential and realized distribution of *Typha latifolia* grown from seeds in relation to transplants and disturbance (cutting) in leaf length (cm) and number of leaves per plant. Bars on histograms represent ± 1 s.e., separate bars represent least significant difference (P<0.05).

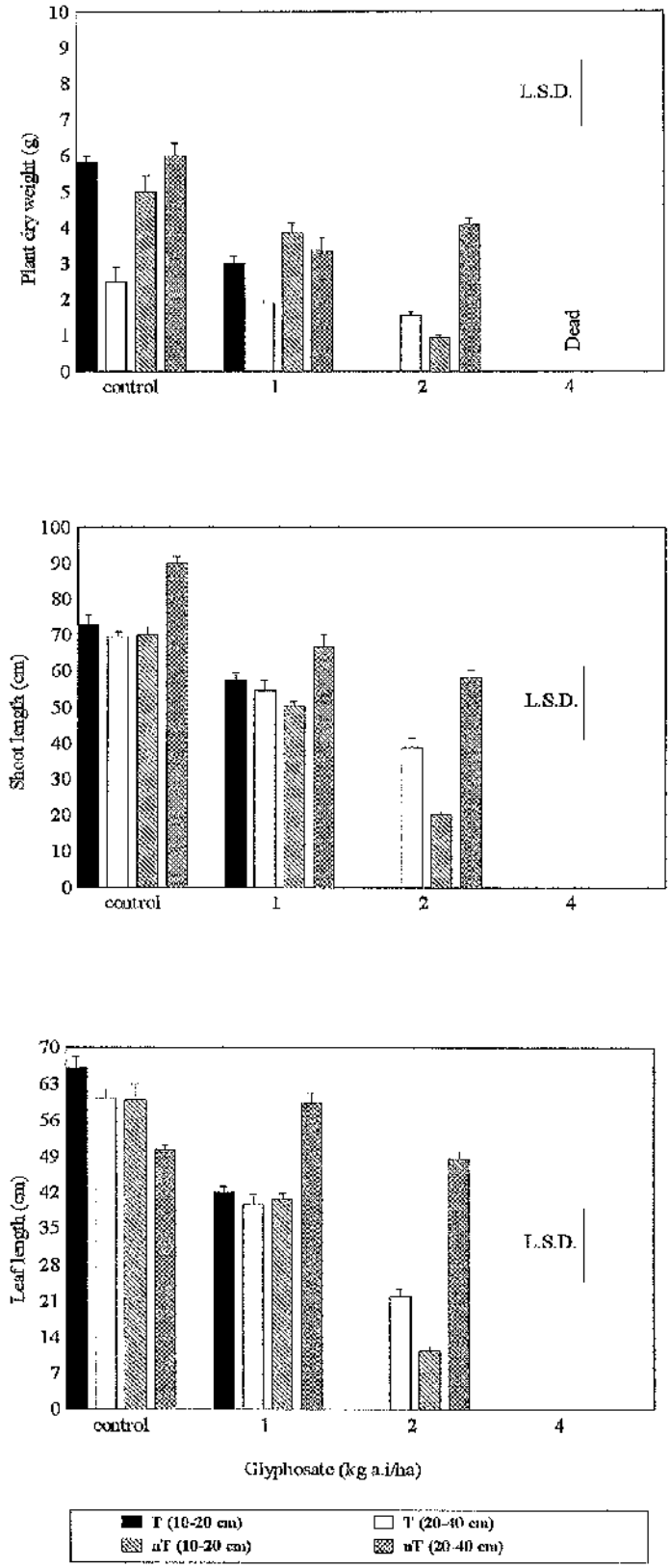


Fig. 3.9. Average plant dry weight, shoot length and leaf length (cm). Bars on histograms represent ±1 s.e.; separate bars represent least significant difference (P<0.05).

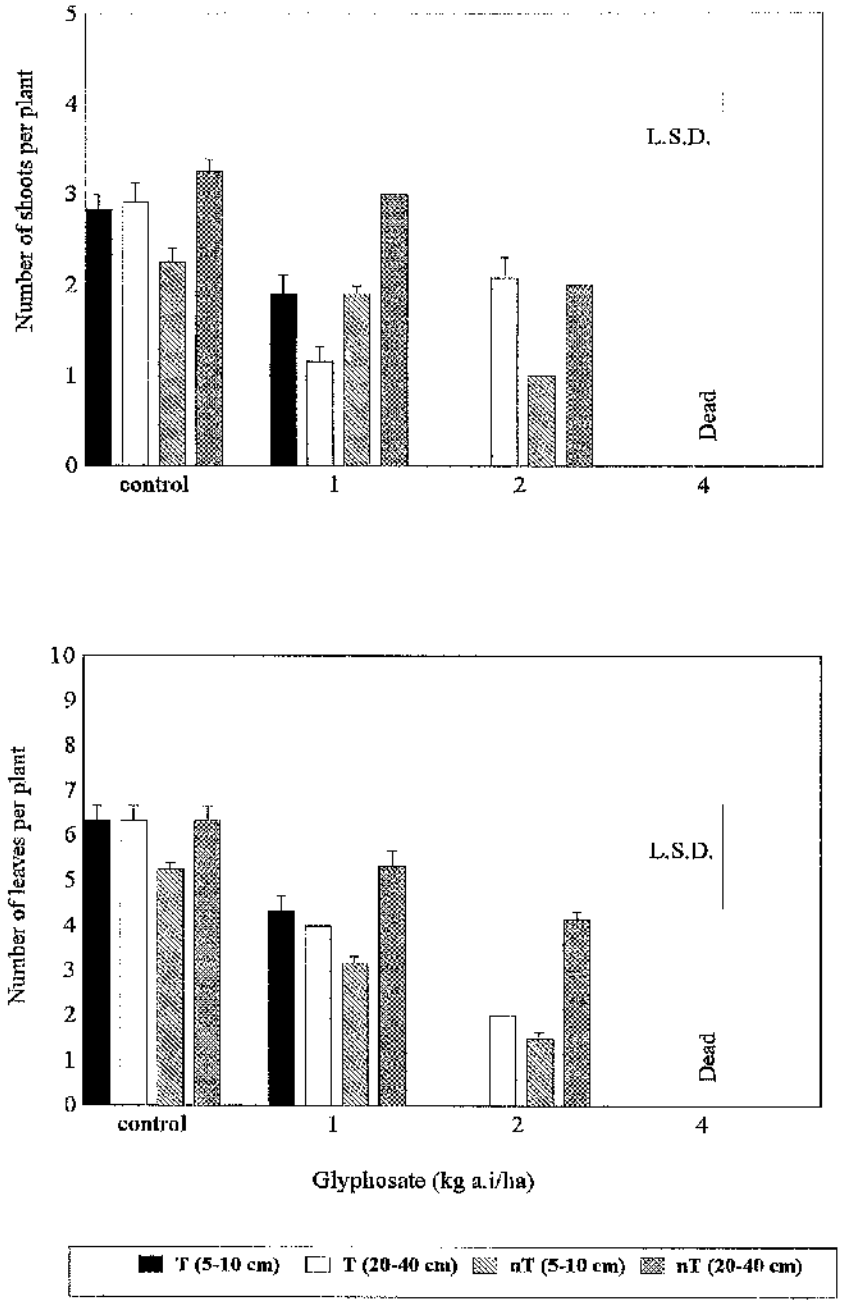


Fig. 3.10. Average number of shoots per plant and average number of leaves per plant. Bars on histograms represent ± 1 s.e.; separate bars represent least significant difference (P<0.05).

3.4. Experiment 6: Control of *Typha latifolia* with glyphosate: late season application

3.4.1. Introduction

A series of tests similar to those undertaken in experiment 5 were conducted to assess the susceptibility of *T. latifolia* to glyphosate during the mid-autumn period. A secondary objective was to evaluate any differences in the susceptibility to glyphosate between moved and unmoved *Typha*.

3.4.2. Results

A significant (P<0.001) increase in *Typha* mortality at 1.5, 2, 3 and 4 kg a.i. ha^{-1} glyphosate was observed some two months after application (Fig. 3.11). Mortality was 100% at 4 kg a.i. ha^{-1} glyphosate. The areas treated with glyphosate at 2, 3, and 4 kg a.i. ha^{-1} glyphosate were completely clear of all *Typha* growth. Glyphosate at 2, 3 and 4 kg a.i. ha^{-1} treatments caused a severe injury and an increased mortality to *T. latifolia* in the year of application. However, there was significant regrowth to the control level in the next year. Different doses of herbicide produced different levels. Visible effects were the gradual wilting and yellowing of the treated plants at lower doses after 1 week to complete browning, deterioration of plant tissue and ultimate decomposition of the underground roots and rhizomes at higher doses 3 weeks after application.

A 43, 59, 68 and 78% reduction in *Typha* dry weight was found at 1.5, 2, 3 and 4 kg a.i. ha^{-1} glyphosate respectively, compared to control, but no significant differences (P=0.05) were observed at lower doses (Fig. 3.11). Plant dry weight in all treated areas never exceeded that observed in the control (Fig. 3.11). Reduction of growth rate was directly proportional to increasing glyphosate concentrations.

Frequent visual observations of the *Typha* treated with 0.5 and 1 kg a.i. ha^{-1} glyphosate and measurement of shoot length failed to reveal any significant herbicidal effect. The number of shoots and leaves were also strongly reduced by increasing glyphosate and the strongest effects were observed at the highest glyphosate

concentration (4 kg a.i. ha^{-1}) (Figs. 3.11 & 3.12). Compared with the untreated control, glyphosate at 1.5, 2, 3 and 4 kg a.i. ha^{-1} significantly ($P<0.01$) (30, 40, 43 and 50% respectively) reduced the shoot length (Fig. 3.11), although the reduction was not significantly greater at 4 kg a.i. ha^{-1} than at 2 kg a.i. ha^{-1}. Significant reductions of number of leaves per plant at 1.5, 2, 3 and 4 kg a.i. ha^{-1} glyphosate were 21, 25, 32 and 43%, respectively (Fig. 3.12).

Glyphosate at 0.5 and 1 kg a.i. ha^{-1} had no effect on the number of shoots in each plot and, though a reduction (10 and 16%) was indicated for number of plants in each plot, these values were not significantly different ($P=0.05$) (Fig. 3.12). Higher concentrations of glyphosate reduced significantly (34, 53, 59 and 70%) the number of plants in each plot. Experimental results showed that none of *Typha* treated with more than 1 kg a.i. ha^{-1} glyphosate went on to flower by the end of experiment (raw data in Appendix 8).

3.4.3. Discussion

In order to control *T. latifolia* with glyphosate the response of rhizomes must be considered. At the time of herbicide application the rhizome carbohydrate reserves must be at the lowest level. Under field conditions the *T. latifolia* rhizomes should absorb sufficient glyphosate from the treated shoots to kill the plants. Small quantities of glyphosate translocated to the rhizome may play a relatively minor role in controlling *T. latifolia*.

Experimental results showed that *T. latifolia* was susceptible to glyphosate at a dose of 1.5 kg a.i. ha^{-1} and above. These findings were similar to those of a study of *Glyceria maxima* by Barrett (1976) who concluded that survival rate for a short time after treatment with 2 kg a.i. ha^{-1} glyphosate was very low. Despite a large decrease in plant dry weight at 2, 3, and 4 kg a.i. ha^{-1} glyphosate compared with untreated plants, there was a substantial recovery of *T. latifolia* one year after treatments. This finding agrees with that of Smith *et al.* (1993) who concluded that for complete control of a rhizomatous species for a relatively long period a single application rarely suffices. Glyphosate must be absorbed and translocated to the rhizomes in quantities that are phytotoxic. Although high rates (1.5, 2, 3 and 4 kg a.i. ha^{-1}) of glyphosate provided

excellent initial control of *T. latifolia*, long-term control was not achieved. Experimental results suggested that a late season application caused poorer control due to a lack of the movement of photosynthate to areas of high metabolic activity. Agreeing with Murphy and Barrett (1990) these results suggest that late-season treatments of glyphosate produce a poor result due to senescence of plants before the glyphosate has been fully translocated into the rhizome system. The main factor that influence the translocation of glyphosate in plants is growth stage (Grossbard & Atkinson, 1985). It must be pointed out that satisfactory control of *Typha* by using low doses of glyphosate could be achieved if applied during intensive growth i.e. before and during flowering (Arsenovic & Konstantinovic, 1990) (Fig. 3.13).

The low degree of control at 1.5, 2 and 2.5 kg a.i. ha^{-1} glyphosate suggests that for obtaining a low regrowth in the following season the rate of herbicide must be increased. At 0.5, 1 and 1.5 kg a.i. ha^{-1} glyphosate no symptoms of having been sprayed were observed, and treated plants were indistinguishable from untreated plants.

It must be emphasized that this experiment did not consider other potentially important ecological effects of herbicide use, such as nutrient release, pH reduction, enhancement of dissolved CO_2 concentrations, destruction of habitat for non-target species, or any additional direct effects of the chemical on non-target species.

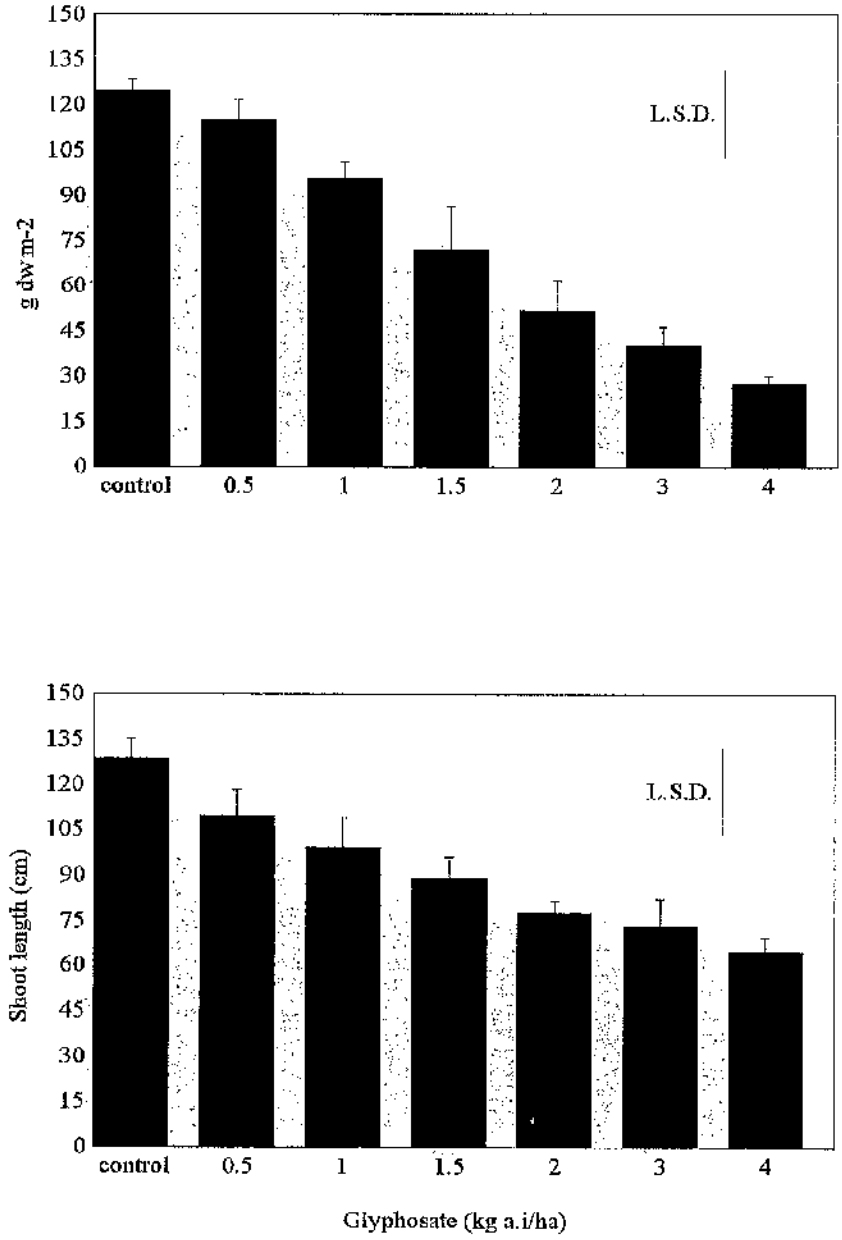


Fig. 3.11. Average biomass dry weight (g) in m^2 and shoot length in the late season application with glyphosate. Bars on histograms represent ± 1 s.e.; separate bars represent least significant difference (P<0.05).

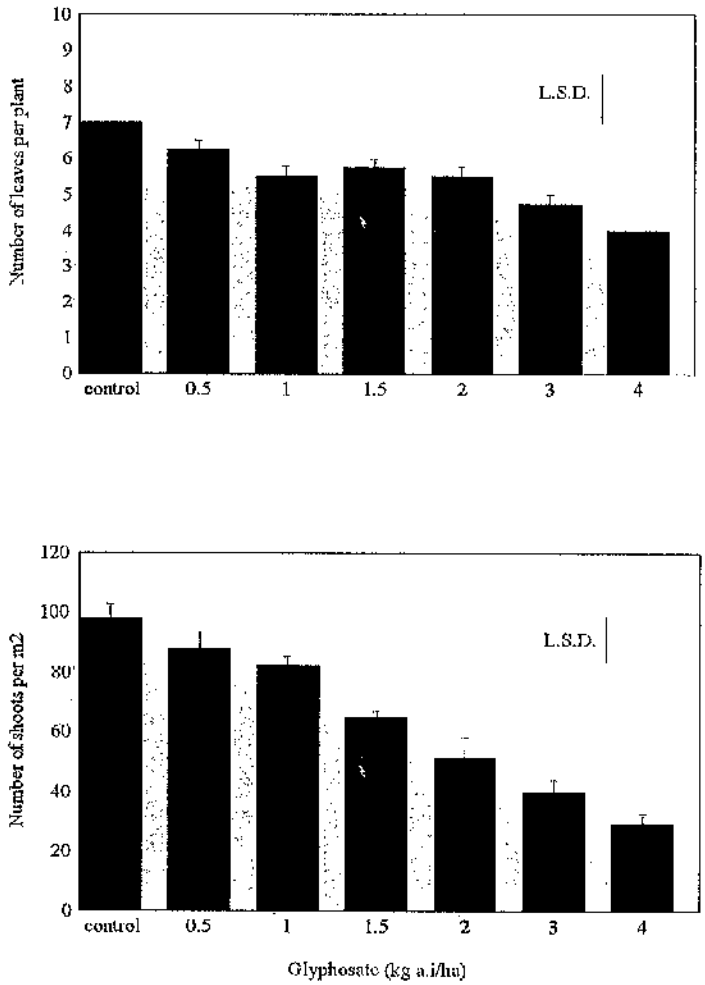


Fig. 3.12. Average number of leaves per plant, and shoots per m^2 in the late season application with glyphosate. Bars on histograms represent ± 1 s.e.; separate bars represent least significant difference (P<0.05).

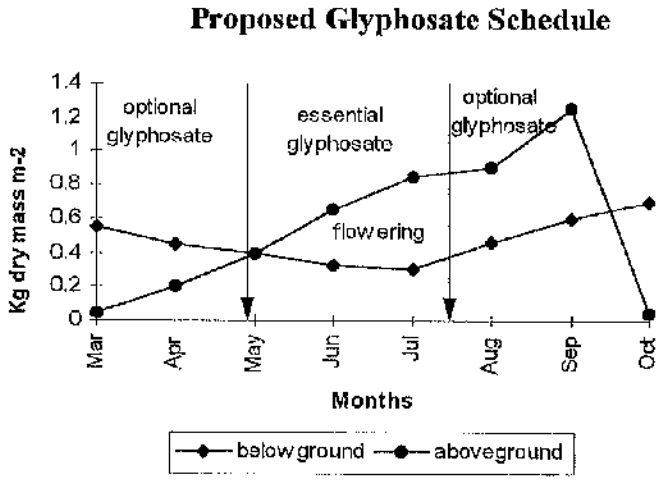


Fig. 3.13. A glyphosate scheme which will provide effective *Typha* control

3.5. Experiments 7-8: The effects of diquat, crushing and shading on *Salvinia rotundifolia*

3.5.1. Introduction

S. rotundifolia has an extremely fast rate of growth (Mitchell, 1976). Since the rapid production of ramets (daughter plants) is the key to the prolific spreading of *S. rotundifolia*, a method that will reduce or suppress ramet production would greatly enhance *S. rotundifolia* control. A variety of control methods is available for *S. rotundifolia* management purposes, including mechanical, biological, and chemical technologies. Chemical control techniques employ herbicides with different modes of action, and are therefore applied with product-specific application rates and environmental usage considerations.

The ability of *S. rotundifolia* to reproduce at a faster rate than mortality produced by control methods is a limiting factor to the success of these methods. Therefore, use of methods which included additional stress, such as reduction of light to slow the growth rate of *S. rotundifolia* are likely to improve the efficacy of control.

To assess methods for controlling the growth and spread of *S. rotundifolia* two experiments evaluated the effectiveness of diquat and crushing plus shading on plant mats.

The objectives of these investigations were to:

(i) determine the susceptibility of *S. rotundifolia* to diquat;

(ii) provide information on the minimum dose which can control *S. rotundifolia*;

(iii) examine the effects of disturbance and stress (physical crushing and shading) on *S. rotundifolia*;

(iv) compare shading and crushing with previous methods (herbicide and raking);

(v) identify potential vulnerable stages in the life cycle of *S. rotundifolia* for improving control.

3.5.2. Experiment 7: Effects of diquat on *Salvinia rotundifolia*

Preliminary results indicate that growth of *S. rotundifolia* can be suppressed with application of diquat. Growth of *S. rotundifolia*, as measured by plant dry weight,

clone dry weight, root length, and leaf area, was clearly inhibited at 1.25 and 1.5 mg l^{-1} diquat over 14 days compared to the untreated plants (Fig. 3.15). At 3 weeks post-treatment, a 95% mortality and reduction in plant number as compared to the untreated controls was observed with application of diquat at 1.5 mg l^{-1}. Significant reduction in fresh weight was also observed with 1.5 mg l^{-1}. Three weeks after the first application, leaf size and root length of treated plants with 1, 1.25 and 1.5 mg l^{-1} diquat were smaller than other doses and control plants (Fig. 3.16).

Three weeks after the first application a 98% reduction in plant dry weight had occurred with 1.5 mg l^{-1} diquat. At 1 and 1.25 mg l^{-1} diquat, 75 and 95% mortality respectively, was recorded, and the remaining plants showed no sign of growth for at least 8 weeks. No significant decrease in plant dry weight, clone dry weight, root length and leaf area was observed at the lower doses of diquat (0.25 and 0.5 mg l^{-1}). At 0.25 and 0.5 mg l^{-1} diquat reductions in plant dry weight, clone dry weight, root length, and leaf area were 11 and 27%, 18 and 32%, 22 and 41%, and 32 and 43%, respectively (Figs. 3.16 & 3.17) (raw data in Appendix 9).

In contrast, the second application did significantly reduce plant dry weight, clone dry weight, root length, and leaf size at lower doses (Figs. 3.16 & 3.17). The mean plant dry weight, clone dry weight, root length, and leaf area reductions after second application were 79, 64, 57 and 31%, respectively, compared with the first application (Figs. 3.16 & 3.17).

Despite a slight reduction in plant dry weight, clone dry weight, root length, and leaf area after the first application with 0.25 and 0.5 mg l^{-1} diquat, there was no significant difference between treated and untreated plants (Figs. 3.16 & 3.17).

Regrowth of injured *S. rotundifolia* tissue began 5 weeks after the second application. The levels of regrowth were varied with dose rate of diquat. Eighty percent of treated plants exhibited some regrowth after the first application. The second application significantly reduced the plant biomass with just 21% regrowth by final harvest. Due to the reduction in size of plants after application with ≥1 mg l^{-1} diquat, there was no marked increase in coverage of the water surface. In addition, all the new leaves were becoming progressively smaller.

3.5.3. Experiment 8: Shading and physical crush effects on *Salvinia rotundifolia*

There was a significant ($P<0.001$) increase in average plant and clone dry weight with one crush compared with two crush and control treatments (Fig. 3.18).

Experimental results showed that crushing increased clone and plant dry weight. (Fig. 3.18). The mean of clone and plant dry weight were 1.329 and 0.1372 g in one crush without shading compared with 0.876 and 0.0882 in two crush and 0.806 and 0.0891 in control (raw data in Appendix 10).

There was significant increase in root length, leaf area, number of daughter plants, and number of plants in each clone compared with control (Figs. 3.18 & 3.19). Mean number of plants in each clone, root length, leaf area, and daughter plants in one crush without shading were 17.443, 70.22, 11.42 and 9.42 compared with 9.22, 45.77, 7.88 and 7.106 in the control respectively. There was also a significant increase (34 and 23%) in root length and leaf area in one crush without shading compared with two crush (raw data in Appendix 10).

Experimental results showed that *S. rotundifolia* had better growth in light than shade (Figs. 3.18 & 3.19). Root length, leaf area, clone and single plant dry weight of shaded plants were significantly smaller than unshaded treatments (Figs. 3.18 & 3.19). Shaded plants had a less dry weight and were 56.4% smaller than unshaded plants. Root length in shaded plants were 72% smaller than unshaded plants. 23% reduction observed of leaf area in shaded plants compared with unshaded plants. Daughter plants also decreased 50% at shaded treatments. No significant difference was observed between control and two crush treatments.

Severe plant damage, including whole plant necrosis and leaf browning was observed after second crush plus shading. Growth of *S. rotundifolia* with two crush and shading was suppressed for approximately 4 weeks after treatments.

3.5.4. Discussion

S. rotundifolia that had been treated with 1, 1.25 and 1.5 mg l^{-1} of diquat generally became bleached white or grey, due to a loss of carotenoids and chlorophyll, and cessation of growth occurred. Regrowth of *S. rotundifolia* suggested that a

contact herbicide like diquat desiccates the surface layer of *S. rotundifolia* leaves. However, in *S. rotundifolia* mats the leaves are compressed and deeply folded, so the inner parts of the plants are protected from herbicide, and small plants can remain hidden. One month after the first spray with diquat, the water surface was covered with a high density of small and healthy shoots. The poor control following the first application at lower doses was probably due to increase density and size of the *S. rotundifolia* mats.

Like other floating plants, the stembase of *S. rotundifolia* performs an important function by providing a chemical energy source for future growth and survival. First application with doses lower than 1 mg l^{-1} did not significantly reduce stembase biomass. Thus the plant could recover from the treatment stress. The decline in plant density after a second application was due to the penetration of diquat to the inner parts of the plants.

Regrowth of the treated plants after the second application was probably due to complete disappearance of diquat in the water column. It seems that fast adsorption of the diquat onto suspended matter and algal around the *S. rotundifolia* was the main factor for a poor control results at lower doses.

S. rotundifolia stored maximum carbohydrates in leaves during the vegetative stage. Ramets (daughter plants) are the over-wintering structures of the plants. These structures play an important role in the seasonal carbohydrate cycle of the plant by providing energy for dormant buds and new growth in the spring. Based on the growth characteristics and carbohydrate allocation, potential control points of *S. rotundifolia* by both physical (crushing) and chemical (diquat) treatments are shown in Figure 3.14. These periods include (a) early spring, when the leaves are small and carbohydrate reserves in the plants are low; (b) shortly before the second peak of ramet production; and (c) shortly before mid-September, when plants are actively translocating carbohydrates to daughter plants.

Diquat provided effective control against young *S. rotundifolia* plants. By using this herbicide on young plants in the early stage of the growing season and/or after a first application when the plants became completely flat, the active ingredient contacted all parts of the small plant, providing good control. Maximum plant biomass occurred in late August to early September. The highest proportion of plant dry weight

was found in mature leaves when plants were in the vegetative stage. When diquat was applied at this stage, the plants life cycle was minimal due to the density and height of the *S. rotundifolia* canopy which prevented the herbicide from contacting all aerial parts of the plant.

These experiments did not support the results of Finlayson and Mitchell (1982) who advocated repeated use of herbicide. The present study showed that days after herbicide application a large number of daughter clone survived the herbicide stress.

The increase in rate of growth after crushing is associated with a strong disturbance-tolerance response to physical damage in *S. rotundifolia*. Damage to plants stimulates growth of dormant buds and/or daughter plants into branches and subsequently an increase in plant numbers following separation into independent plants. Harley and Mitchell (1981) reported that damage to plants which even causes the death of a large amount of plants tissue, frequently stimulates dormant buds into branches and subsequently will increase the plant growth.

Reduced plant growth was observed after the reduction of light by shading, agreeing with results found by Dawson and Hallows (1983) and Gopal (1976). The population of *S. rotundifolia* was severely reduced in numbers and size by shading. The results suggest that the optimum period of cover required for control of at least 50% of plants was 3 months, which was probably related to the age of plants, degree of infestation, and the availability of nutrients in water.

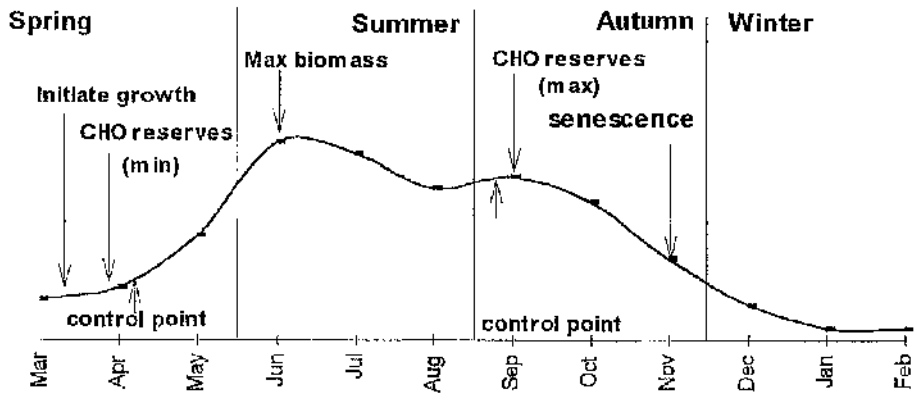


Fig. 3.14. Potential control points in the growth cycle of *S. rotundifolia*

a

b

c

Fig. 3.15. ***Salvinia rotundifolia*****: treated with 0.5 (a) and 1.5 (b) mgl^{-1} diquat, compared with untreated controls (c): 14 days after treatment in greenhouse tanks.**

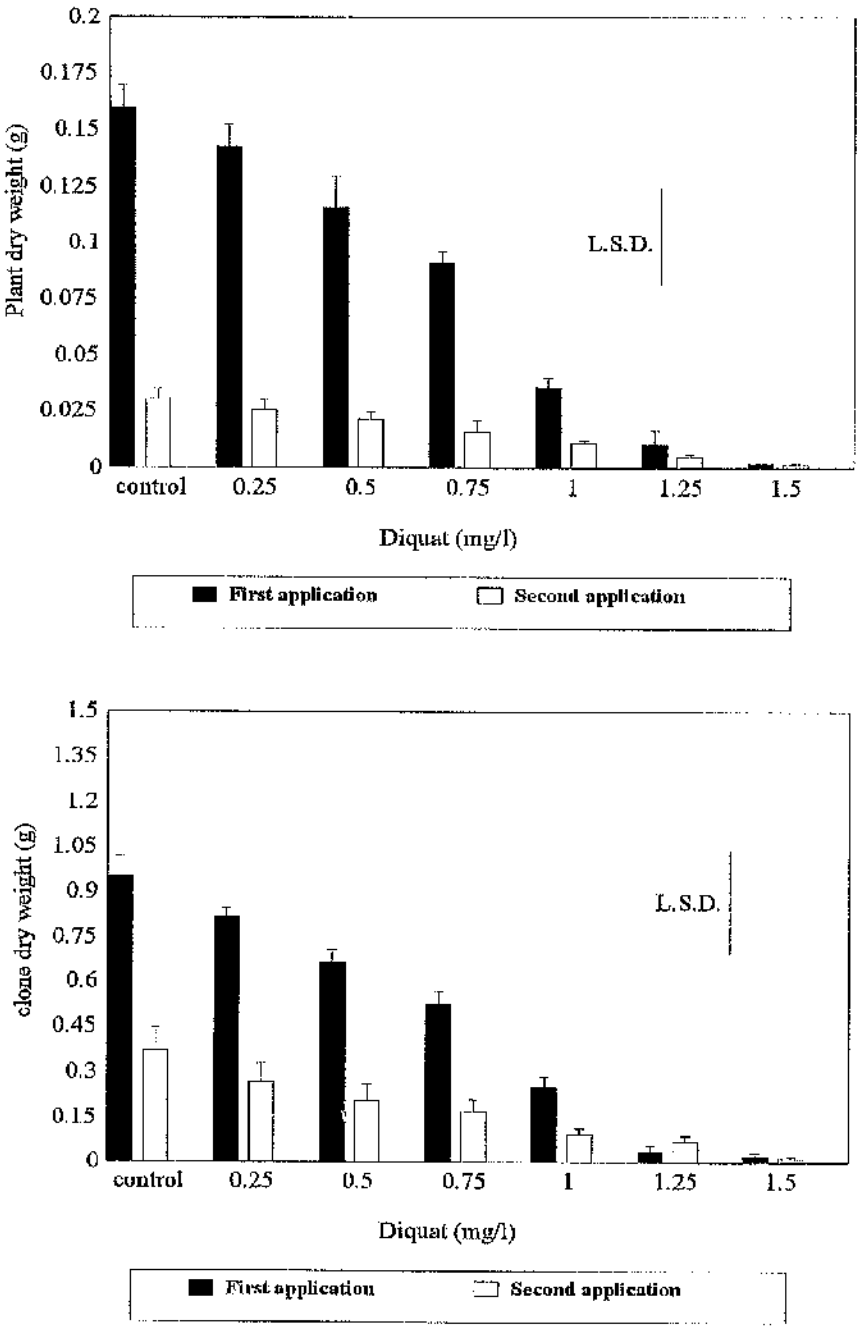


Fig. 3.16. Effects of various concentrations of diquat on plant and clone dry weight (g), in *Salvinia rotundifolia*. Bars on histograms represent ± 1 s.e.; separate bars represent least significant difference (P<0.05).

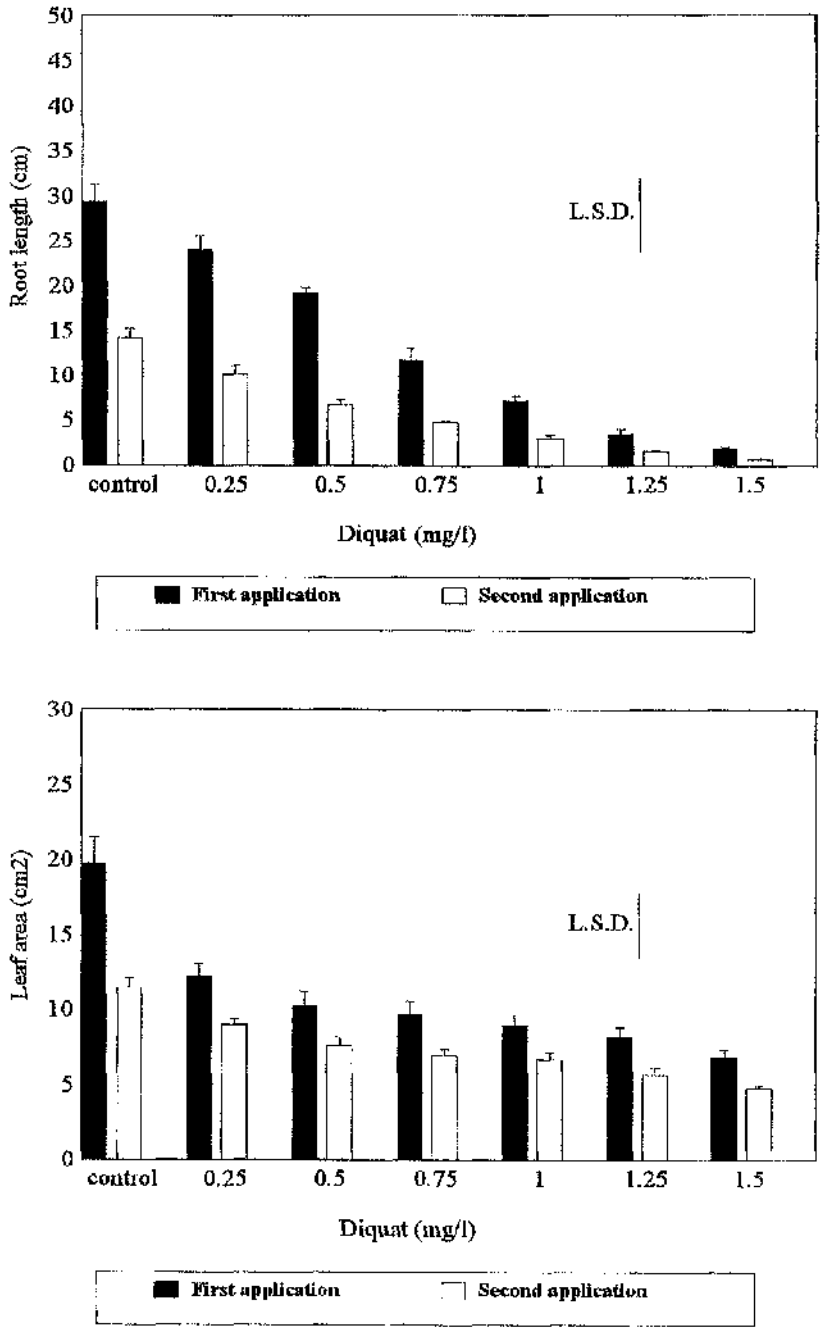


Fig. 3.17. Effects of various concentrations of diquat on root length (cm) and leaf area (cm^2) in *Salvinia rotundifolia*. Bars on histograms represent ± 1 s.e.; separate bars represent least significant difference (P<0.05).

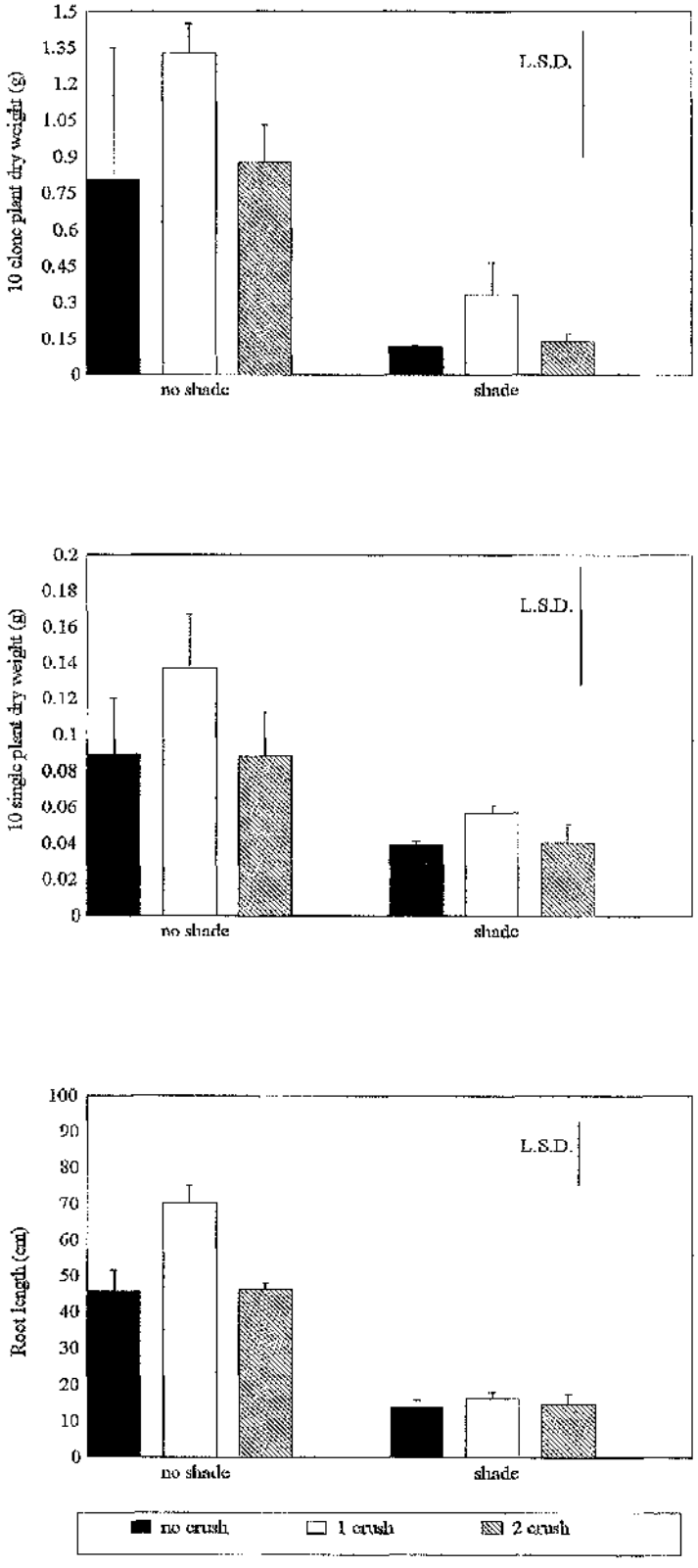


Fig. 3.18. Effects of shading and crushing on *Salvinia rotundifolia*: Effects of treatments on 10 clone plant dry weight (g), 10 single plant dry weight (g) and root length (cm). Bars on histograms represent ± 1 s.e.; separate bars represent least significant difference (P<0.05).

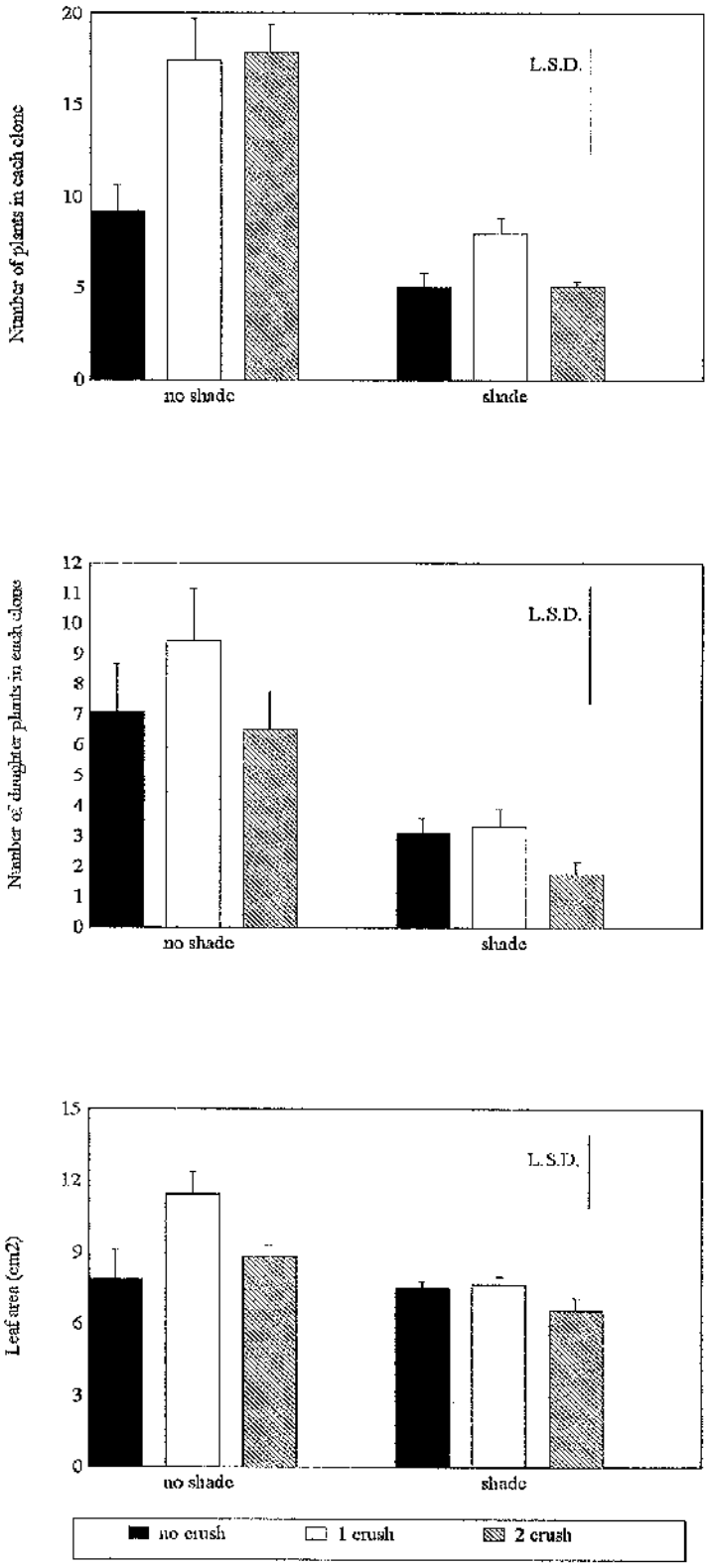


Fig. 3.19. Effects of shading and crushing on *Salvinia rotundifolia*:
Effects of treatments on number of plants in each clone, number of daughter plants in each clone and leaf area (cm^2). Bars on histograms represent ± 1 s.e.; separate bars represent least significant difference ($P<0.05$).

3.6. Experiment 9: Competition for light between *Salvinia rotundifolia* and *Pistia stratiotes*

3.6.1. Results

The research reported here involved an evaluation of the relative competitive abilities of two problem exotic species, *S. rotundifolia* and *P. stratiotes*, under different light and density conditions. The objectives of the research were to identify the factors and mechanisms involved in short-term competition between these two species.

During the first 3 weeks of the experimental period (until 21 February 1996), both species grew freely without any interspecific interference. Their biomass in mixed culture was similar to that in monoculture. After 5 weeks, the biomass of each species and especially *S. rotundifolia* had doubled and gradually covered the water surface (Figs. 3.20, 3.21 & 3.22).

Biomass yields of *S. rotundifolia* and *P. stratiotes* were usually in direct proportion to the number of plants at all densities in both mixed culture and monoculture. Maximum growth of *S. rotundifolia* was obtained at the high levels of light and without competition after 4 weeks (Fig. 3.20). In contrast the maximum growth of *P. stratiotes* was obtained in low light treatments (Fig. 3.22). After six weeks, the biomass of *S. rotundifolia* in 6-0, 4-2, 3-3 and 2-4 density proportions had increased by 2, 1.87, 2 and 2.12 fold, respectively, in high light treatments (Fig. 3.20). In contrast the biomass of *P. stratiotes* in the same light regime and density proportions had increased 1.41, 1.53, 1.62 and 1.55 fold, respectively. However, by the end of the experiments, the highest plant biomass and number of plants was obtained only from those combinations in which *S. rotundifolia* were grown, in mixed culture as well as in monoculture (Figs. 3.20, 3.21 & 3.22). In mixed and monoculture with the same initial density, *S. rotundifolia* produced a 2-fold greater biomass than *P. stratiotes*. In addition, the number *S. rotundifolia* plants was 6 times greater than *P. stratiotes* over with the same initial number after 9 weeks of competition (Figs. 3.20, 3.21 & 3.22).

The cumulative biomass and density of plants, which grew in mixed cultures, by end of the experiment was higher than that of the plants grown in monoculture. The

highest total biomass at harvest, as well as the highest growth rates, were generally found in high light, except for monoculture in *P. stratiotes* which grew better in 75 μE m^{-2} s^{-1}.

Experimental results indicated that light did not significantly influence the total biomass in both species (Figs. 3.20, 3.21, 3.22 & 3.24). While total biomass of *S. rotundifolia* was slightly affected by light, total biomass of *P. stratiotes* was more affected by both light and density. In the absence of competition, *S. rotundifolia* was more responsive to an increase in light availability. In contrast, *P. stratiotes* responded to an increase in light in both absence and presence of competition. Total biomass production of *P. stratiotes* was affected mainly by increases of plant density. In contrast, total biomass production of *S. rotundifolia* was affected by reductions of light. Despite a slight increases in biomass, suppression of *P. stratiotes* by *S. rotundifolia* had increased after 6 weeks. Nine weeks after the start of experiment (on 5 April 1996) the *P. stratiotes* were significantly suppressed by the *S. rotundifolia* (Fig. 3.24).(raw data in Appendix 11)

A significant ($P<0.001$) decrease in *P. stratiotes* reproduction was observed with increases in *S. rotundifolia* density. These results indicate that, under different light conditions, the growth of *S. rotundifolia* was more rapid than that of *P. stratiotes*, and *S. rotundifolia* was the superior competitor (Fig. 3.23)

Under the different light levels and plant density, both species exhibited a morphological plasticity. Root length in *P. stratiotes* increased two-fold to four-fold under conditions of high *S. rotundifolia* density and light reduction. In contrast, under low light conditions, *S. rotundifolia* decreased the rate of leaf mortality by producing smaller leaves. Although leaves produced under low light were smaller than those produced under higher light, the relationship between leaf size and root length was similar for both plants grown under all light levels.

3.6.2. Discussion

In spite of the suppression of *P. stratiotes* by *S. rotundifolia*, these two species grow together in natural ecosystems (Mitchell, 1970). These types of studies (short term studies) especially on floating plants provide only a brief insight into competitive

interactions occurring during particular time periods, usually during the middle stages of growth. Information obtained from these studies is not easily extrapolated to larger spatial and longer time scales (Smart, 1992). Long-term studies, on the other hand, are difficult to conduct and to control, and require a long period of time to produce results.

In these experiments, the levels of light used (75, 100, & 150 $\mu E\ m^{-2}\ s^{-1}$) most likely did not limit the growth of both species. Decreased light slightly increased *P. stratiotes* growth, and marginally decreased *S. rotundifolia* biomass. This was due to slower growth of *S. rotundifolia* under low light conditions.

Results from these experiments indicate that outcome of competition between two species can vary dramatically depend on the environmental conditions and growth rate. By the end of this study, the dominance of *S. rotundifolia* over *P. stratiotes* was not only for mixed cultures in which these two plant species started at the same density, but also for mixed cultures in which *S. rotundifolia* started at a density of 2 plants per tank (25%) and *P. stratiotes* started at a density of 4 (75%) per tank. The plant density and doubling time (which was faster in *S. rotundifolia*) was most likely to affect the outcome of competition between these two species. Since *S. rotundifolia* showed high growth rates in both mixed and monoculture, it is not surprising that the outcome of competition between them depended on plant density.

In both mixed and monocultures, the production of new leaves was much faster in *S. rotundifolia* than *P. stratiotes*. This characteristic provides greater exposed leaf surface area for photon capture and increased photosynthesis efficiency in a competitive situation. Thus, the luxuriant productivity and high plasticity of *S. rotundifolia* plants enable them to flourish by growing above *P. stratiotes* plants, consequently shading and stressing them. In three similar experiments on floating plants, Center and Spencer (1981) and Agami and Reddy (1989, 1990) found the dominating effects of *E. crassipes* and *S. rotundifolia* on *P. stratiotes* and *Spirodela polyrhiza* at various interaction stages.

The two species studied in this experiment clearly differ in terms of their plant growth strategies. *S. rotundifolia* allocates much of its biomass and nutrients to leaves, has a high requirement for light and nutrients, tolerates low light levels, exhibits a high degree of morphological plasticity in response to different environmental conditions,

and loses a significant proportion of its accumulated biomass and nutrients during seasonal senescence. Rapid growth rates, by producing an excessive number of daughter plants under suitable conditions, give this species an ability to exploit habitats left open by indigenous vegetation. By contrast *P. stratiotes* allocates its biomass and nutrients to leaves and roots portions. It can also tolerate lower light and lower nutrient supply.

Results of this study and those of Agami and Reddy (1990) show that *P. stratiotes* has a greater capacity than *S. rotundifolia* for root elongation. With additional consideration for its heterophyllous life form and its capacity to produce high shoot densities, *S. rotundifolia* may be superior to *P. stratiotes* in its canopy-forming capabilities. Perhaps the most important advantage that *S. rotundifolia* has over *P. stratiotes* is its ability to rapidly produce daughter plants. In *P. stratiotes*, the production of new ramets is sustained at the expense of root elongation, suggesting a strategy to grow away from *S. rotundifolia*. This mechanism in *P. stratiotes* is facilitated in part by its efficient use of nutrients. This adjusts the ratio of root-to-shoot biomass and may increase tolerance of spatial and temporal gradients in sediments nutrients availability; thus differences among species in this capacity may effect changes in the composition of aquatic plant communities.

In the presence of *S. rotundifolia*, *P. stratiotes* daughter plants which were attached to parents became detached more slowly than those grown alone. This was confirmed by end of experiment that *S. rotundifolia* produced more ramets than *P. stratiotes*.

Based on my findings, intraspecific competition did not result in significant reductions in the biomass of individual plants. At high density both *S. rotundifolia* and *P. stratiotes* produced more biomass than at low density. The mechanisms of intraspecific competition of this kind are undoubtedly linked with nutrients and space, but as yet are poorly understood.

In conclusion, the results of this study indicate that the biomass yields, rates of growth, and number of *S. rotundifolia* plants were higher at all densities than for *P. stratiotes* when grown in monoculture. In mixed cultures, 6 weeks after the start of experiments, the growth of *P. stratiotes* was suppressed by *S. rotundifolia* shading. This suggests that *S. rotundifolia*, through high productivity and high plasticity, has

the capacity to suppress *P. stratiotes* through shading. In both mixed and monocultures the interspecific effects were stronger than the intraspecific ones. This may be explained by the similar growth forms. Thus two species may not be able to coexist by occupying similar zones in the water.

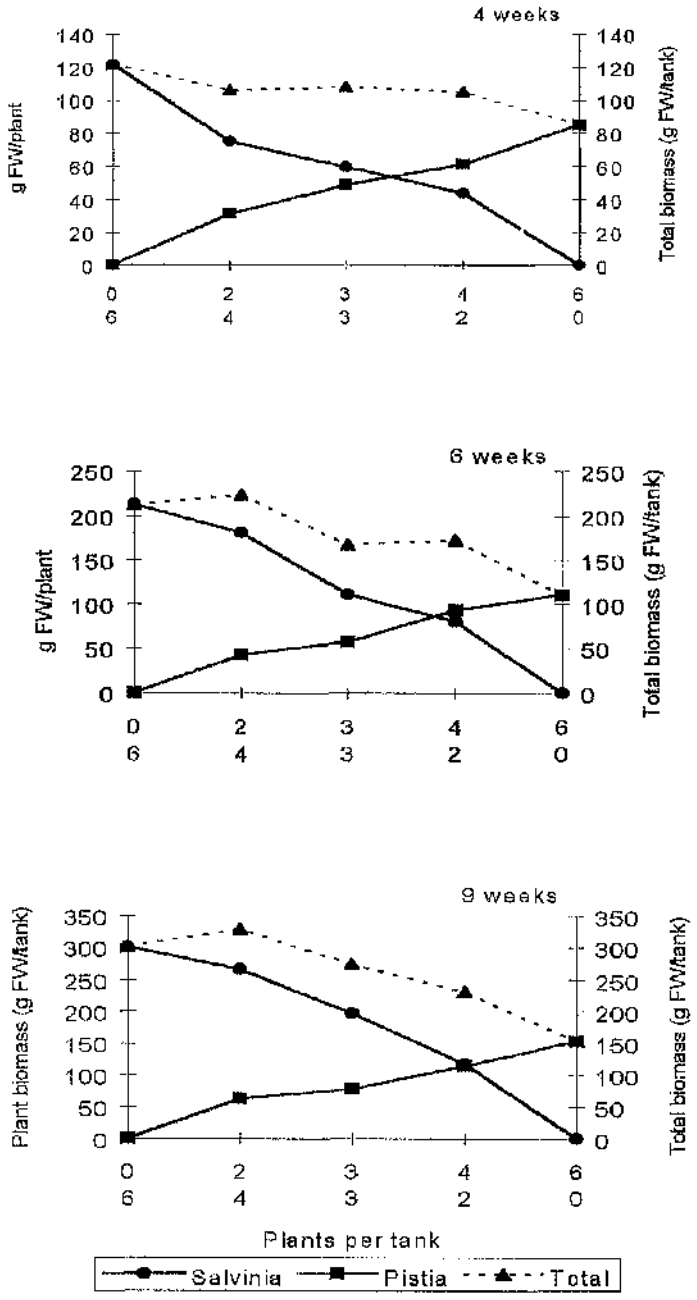


Fig. 3.20. Relative fresh weight diagrams for total biomass production of *S. rotundifolia* and *P. stratiotes* grown in tank mixtures under high light conditions (150 µE m^{-2} s^{-1}) at the indicated densities, throughout the 4, 6 and 9 weeks of the experiment. The broken --♦-- indicates the arithmetic sum of yields of both species. Values are means of three replicates.

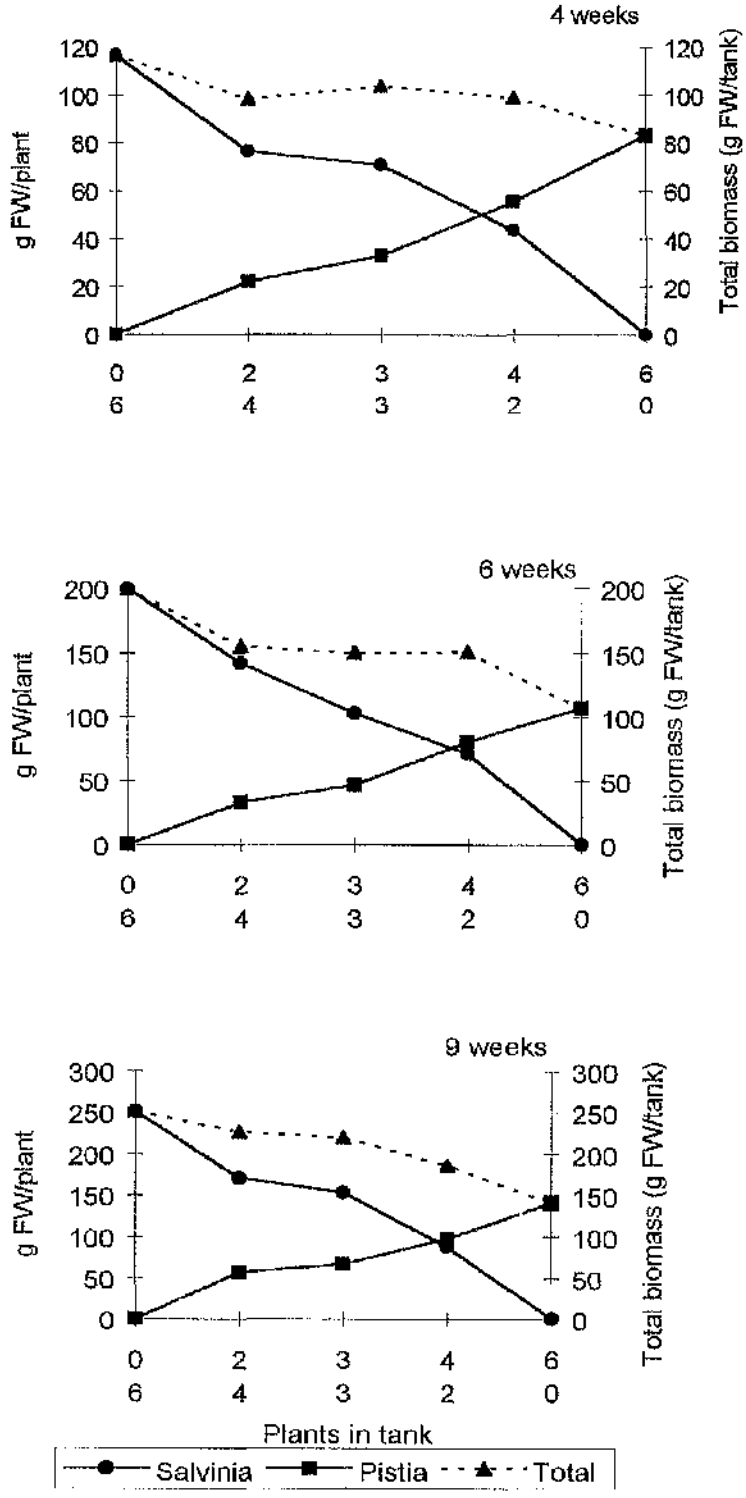


Fig. 3.21. Relative fresh weight diagrams for total biomass production of *S. rotundifolia* and *P. stratiotes* grown in tank mixtures under middle light conditions (100 µE m^{-2} s^{-1}) at the indicated densities, throughout the 4, 6 and 9 weeks of the experiment. The broken --♦-- indicates the arithmetic sum of yields of both species. Values are means of three replicates.

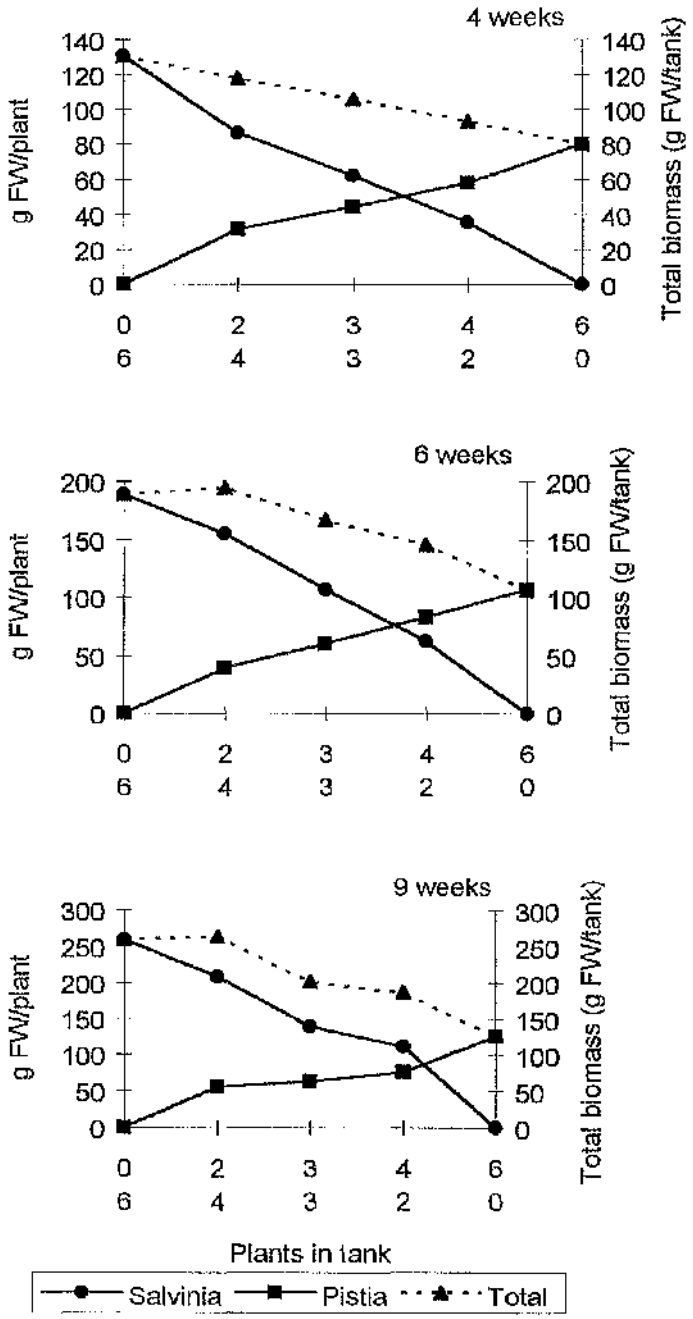


Fig. 3.22. Relative fresh weight diagrams for total biomass production of *S. rotundifolia* and *P. stratiotes* grown in tank mixtures under low light conditions (75 μE m^{-2} s^{-1}) at the indicated densities, throughout the 4, 6 and 9 weeks of the experiment. The broken --♦-- indicates the arithmetic sum of yields of both species. Values are means of three replicates.

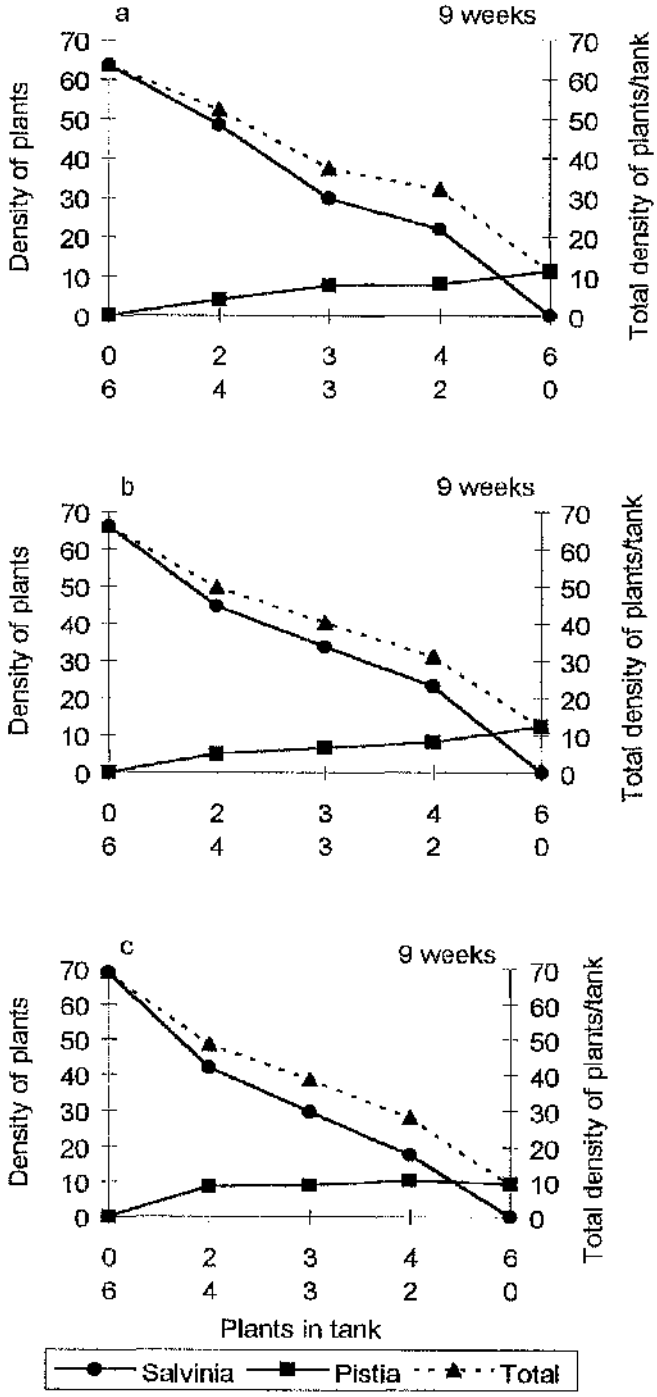


Fig. 3.23. Density responses of *S. rotundifolia* and *P. stratiotes* grown in monoculture and tank mixtures under different light levels. The broken --♦-- indicates the arithmetic sum of plants of both species. Values are means of three replicates.

Key to treatments: a = 150 μE m^{-2} s^{-1}, b = 100 μE m^{-2} s^{-1}, and c = 75 μE m^{-2} s^{-1}

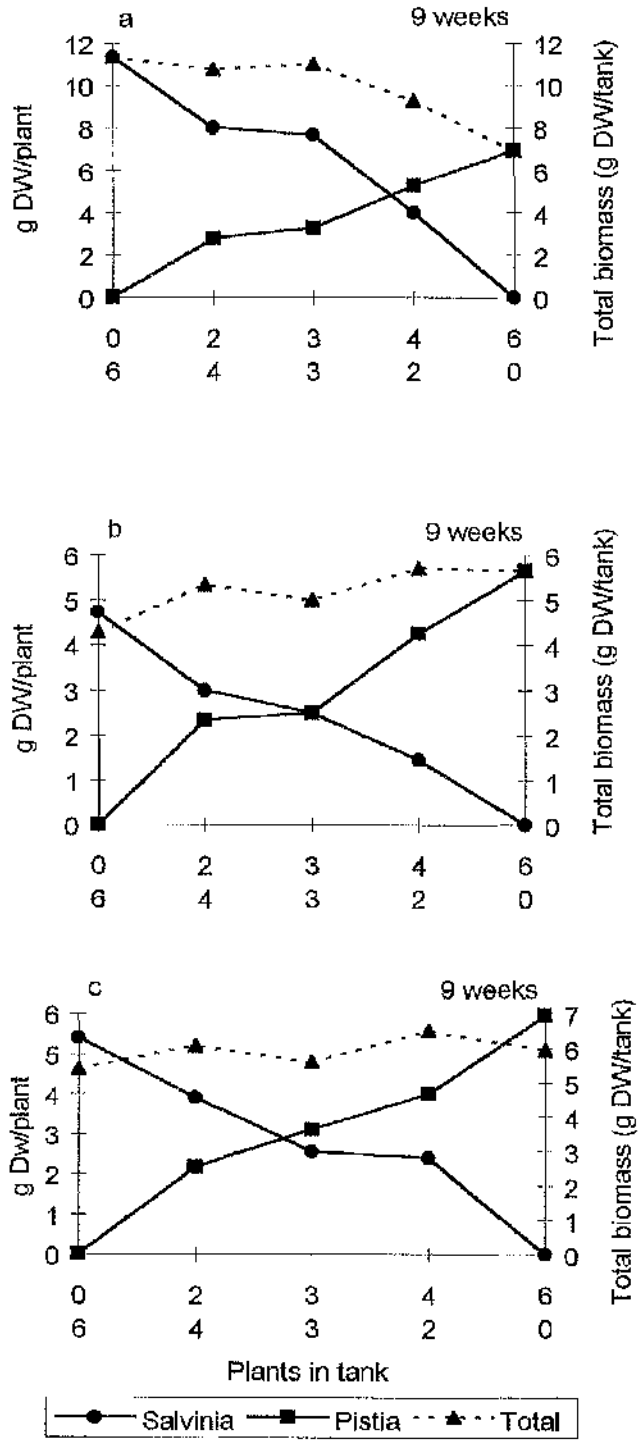


Fig. 3.24. Relative dry weight diagrams for total biomass production of *S. rotundifolia* and *P. stratiotes* grown in tank mixtures under different light conditions. The broken --♦-- indicates the arithmetic sum of yields of both species. Values are means of three replicates.

Key to treatments: a = 150 µE m^{-2} s^{-1}, b = 100 µE m^{-2} s^{-1}, and c = 75 µE m^{-2} s^{-1}

3.7. Experiments 10-12: Response of *Potamogeton pectinatus* to diquat, cutting, and shade under greenhouse and field conditions

3.7.1. Introduction

For many multiple-use water bodies the ideal aquatic plant management strategy is to suppress nuisance vegetation while allowing desirable, non-weedy species to flourish. Various methods have been used in the last 30 years to control unwanted aquatic vegetation. Although herbicides and plant growth regulators can control many weed species there are limitations on using them in water bodies. The success of a chemical treatment against submerged aquatic plants depends on the concentration of the herbicide that comes into contact with the target plant, the length of time a target plant is exposed to the herbicide, and timing of application. The response is also related to the properties of individual herbicides and the sensitivity of the target species to each herbicide (Langeland & Laroche, 1994).

Information on herbicide uptake and lethal concentration in plant tissues is extremely limited for aquatic macrophytes, especially submerged species (Van & Conant, 1988). Rapid dilution and dispersal of herbicide residues from the treatment area following herbicide application (due to diffusion and water movement) can reduce both concentration and exposure time to a level less is required for complete control. Previous studies have focused on the use of a contact herbicide like diquat for control of submerged weeds, to provide a temporary weed-free period in the target area for up to one year (Caffrey, 1990; Van & Conant, 1988; Fox *et al.*, 1986). However, the fact that weed growth resumes in the following year suggests that herbicides alone are not necessarily the best approach for management.

An alternative is to use an integrated approach which might include a low dose of herbicide (which has the added benefit of environment protection) to cause chronic stress to the target weeds, and then top up control using other methods, such as mechanical clearance. Shading and cutting can be an effective alternative to the use of herbicides. Shading was suggested by Dawson and Kern-Hansen (1978, 1979) and Dawson (1978, 1989) as an ecologically-based alternative management technique to mechanical and chemical weed control.

In order to evaluate the potential of different methods for controlling the growth and spread of *P. pectinatus* three experiments were evaluated under greenhouse and field conditions. The first experiment was to determine the effects of diquat on *P. pectinatus* at different concentrations and exposure times. The effects of diquat plus shading and cutting were examined in the second experiment. The third experiment aimed to determine the sub-lethal effects of diquat against *P. pectinatus*, either using the herbicide alone, or in combination with cutting, under field conditions. A chlorophyll fluorescence technique for measuring the herbicide penetration into the plant tissue was used in these 3 experiments.

3.7.2. Experiment 10: Response of *P. pectinatus* to various concentrations and exposure periods of diquat

Rapid and serious injury to *P. pectinatus* shoot biomass occurred at most concentrations and exposure times tested. The significant concentration by exposure interaction indicated differential levels of plant response to increasing concentrations of diquat when exposure to herbicide varied. An exposure to 0.5 mg l^{-1} diquat for all times resulted in circa 100% kill of *P. pectinatus*. Complete inhibition of plant growth and tuber production was observed at 0.5 mg l^{-1} diquat in all exposure times (Fig. 3.27)

P. pectinatus response was variable following herbicide treatments. Several leaves and shoots at 24, 48, 96, and 168 hr exposure times became brown and necrotic, and began to sink to the bottom within 3 days post-treatment. At 9 days post-treatment, all *P. pectinatus* shoots in the treated tanks at 24, 48, 96 and 168 hr exposure times lay prostrate on the sediment, with leaves browning and dropping from the shoots (Fig. 3.27). During this period, *P. pectinatus* in the untreated control tanks remained vigorous and healthy. Diquat symptoms were delayed following treatments at 1 and 2 hr exposure times. Despite a complete knockdown of *P. pectinatus* treated with diquat at longer exposure times, some shoots were still attached to the roots and tubers (Fig. 3.27). However, these shoots were completely brown and were not considered viable.

Analysis of variance and observation indicated that diquat provided good control of *P. pectinatus* in 12, 24, 48, 96 and 168 hr exposure times in both 0.1 and 0.2 mg l^{-1} (Figs. 3.25, 3.26, 3.28, 3.29 & 3.30). Increasing diquat concentrations to 0.2 mg l^{-1} did not increase the level of control at all exposure times. The 0.1 and 0.2 mg l^{-1} treatments diquat in all exposure times significantly ($P<0.001$) reduced *P. pectinatus* biomass dry weight (Fig. 3.28). The reductions ranged from 51% in 1 hr to 95% in 96 hr exposure times when compared to untreated plants. The maximum decrease (95%) was in 0.2 mg l^{-1} at 96 hr exposure period. At the 0.1 and 0.2 mg l^{-1} diquat, little differences were observed between the 12, 24, 48, 96 and 168 hr exposure periods (raw data in Appendix 12).

Treatments with 0.1 and 0.2 mg l^{-1} diquat for 2, 12, 24, 48, 96 and 168 hr exposure times significantly reduced shoot length (Fig. 3.28). Reduction ranged from 44 to 77%. The maximum reduction was observed at 48 hr for 0.1 mg l^{-1} and at 168 hr for 0.2 mg l^{-1} diquat exposure times. Most shoots in 0.1 and 0.2 mg l^{-1} diquat concentrations at 48, 96 and 168 hr exposure times were completely brown and were not considered viable. Rapid regrowth occurred at short exposure times, indicating the ineffectiveness of these treatments.

Treatments with 0.1 and 0.2 mg l^{-1} for 2, 12, 24, 48 and 96 hr exposure times significantly reduced leaf length from 38 to 78%. The maximum reduction (78%) was observed at 0.2 mg l^{-1} for 96 hr exposure times (Fig. 3.28).

The inhibition of tuber production persisted long after the plants had recovered from the initial herbicidal effects. The duration of effect on tuber suppression increased with increasing treatment rates. The 0.1 and 0.2 mg l^{-1} treatments with 12, 24, 48, 96 and 168 hr exposure reduced tuber production from 58 to 100%, respectively. After 2 months, untreated control *P. pectinatus* produced an average of 34.5 tubers per tank, while no tubers were found in plants treated with 0.1 and 0.2 mg l^{-1} at 48 and 96 hr exposure. The tubers produced in the 0.1 and 0.2 mg l^{-1} treatments at all exposure times were much smaller compared to tuber weight in untreated plants (Fig. 3.30).

Other parameters of growth such as number of leaves per plant, number of secondary branches per plant, number of leaves per secondary branch, and secondary branch length, were also significantly affected by both diquat concentrations (0.1 and 0.2 mg l^{-1}) at different exposure times (Figs. 3.29 & 3.30). The reductions were 40 to

93% in the number of leaves per plant, 34 to 87% in the number of secondary branch per plant, 25 to 67% in the number of leaves per secondary branch, and 12 to 74% in the secondary branch length respectively at both 0.1 and 0.2 mg l^{-1} diquat concentrations.

The degree of initial injury of 1, 2 and 12 hr exposure in both 0.1 and 0.2 mg l^{-1} was less than other treatments and recovery occurred quickly. The ability of plants to recover from diquat and produce a new healthy shoots decreased as exposure times increased. Most plants at 1, 2 and 12 hr exposure times at the end of experiment were healthy and green. An interesting result was the better regrowth of treated plants in 168 hr exposure time.

3.7.3. Experiment 11: Response of *Potamogeton pectinatus* to shading, cutting, and diquat

The effects of the presence and absence of shading, herbicide and cutting were analysed 120 days from the start of the experiment. The analysis of variance showed significant effects of diquat and shading on *P. pectinatus*. Diquat was taken up rapidly by plant tissue within 4 days of application. The plants treated with 0.5 mg l^{-1} began to decompose after 5 days.

Chlorophyll fluorescence was examined at different times after application. Significant differences ($P<0.001$) were found between untreated plants and the treated with different concentration of diquat. The rate of fluorescence [=(P-I) / I] in plants treated with 0.5 mg l^{-1} was significantly higher ($P<0.05$) than that in the control plants two days after application. Five days after application, the fluorescence ratio in plants which were treated with lower doses (0.1 and 0.2 mg l^{-1}) also showed a more significant increase than control plants. At 2 days after application, there were no significant differences between the values of fluorescence at 5, 10, 50 and 100 second in the treated and untreated leaf tissue, but by 7 days after application, the values of fluorescence in the treated plants was significantly higher ($P<0.05$) than in the untreated plants. The differences in values of fluorescence between treated and untreated plants became more significant until 10 days after application. By 2 weeks after application the fluorescence ratio in treated leaves decreased slowly.

Statistical tests revealed a significant difference among the three levels of light. The above-ground biomass at the highest level of shading started to decay 4 weeks after application. Experimental results showed a significant (51 and 81%) reduction in plant dry weight at low and high shade respectively compared with unshaded plants (Fig. 3.32).

The results showed that the plant dry weight was not significantly affected by the cutting treatments. Compared with uncut plants, 23% of dry weight increased after one cut (Fig. 3.32). A 53% reduction of biomass was observed after 2 cuts compared with control plants (Fig. 3.32).

Compared with control plants there was a significant reduction in plant dry weight after herbicide application. Reductions were 78, 83 and 90% in 0.1, 0.2 and 0.5 mg l^{-1} diquat, respectively (Fig. 3.32).

The combination of cutting, shading and diquat, resulted in a higher control of *P. pectinatus* than a single method. A significant decrease of plant dry weight was observed by one cut in present of low and high shading. Two cuts had a greater effect in reducing plant dry weight under shade. The reductions were 67 and 96% for 2 cuttings with low and high shade, respectively (Fig. 3.32).

Analysis of variance and observations indicated that high shade significantly reduced plant length. The plant length reductions were 15 and 51% in low and high shade, respectively. Three levels of diquat (0.1, 0.2 and 0.5 mg l^{-1}) significantly reduced the plant length. The reduction were 36, 42, and 65%, respectively. Despite a 22% reduction in plant length, there were no significant differences between treatments after cutting. However, a slight increase (1%) was observed in plant length after 1 cut. Experimental results showed that the reductions of plant length at low dose diquat (0.1 and 0.2 mg l^{-1}) in presence of shade were greater (Fig. 3.33). Reductions were 62 and 41% higher than when diquat was used without shade treatments (Fig. 3.33).

The results indicated that shading, diquat, and two cuts significantly reduced the number of leaves per plant. Compared with unshaded controls, 48 and 68% reductions in number of leaves per plant were observed at low and high shade. Compared with control plants, there were 13 and 50% reductions in number of leaves per plant after 1 and 2 cuts, respectively. The reductions of number of leaves per plant at 0.1, 0.2 and 0.5 mg l^{-1} were 69, 78.5 and 78%, respectively (Fig. 3.36).

There was also a significant decrease in other growth parameters such as leaf length, number of secondary branches per plant, number of leaves per secondary branch, and secondary branch length after treatment with diquat, shading, and cutting (Figs. 3.34, 3.35, 3.37 & 3.38).

Leaf length increased 2% in low shade, but a significant (30%) reduction was observed in high shade compared with unshaded controls. Despite 7.5 and 12% reductions, there were no significant effects of cutting on leaf length compared with control plants. There was no significant effect of diquat at 0.1 and 0.2 mg l^{-1} on leaf length with only 1 and 16%, reduction respectively. A significant (37%) reduction in leaf length was observed in plants treated with 0.5 mg l^{-1} (Fig. 3.37).

Significant reductions in the number of secondary branches per plant at low and high shade were 44 and 65%, respectively. Compared with control plants, significant (67, 75 and 76%) reductions in the number of secondary branches per plant were observed at 0.1, 0.2 and 0.5 mg l^{-1} diquat. There was no significant change after 1 cut in the number of secondary branches per plant (20% reduction). Two cuts decreased the number of secondary branches per plant significantly (50%) compared with uncut plants (Fig. 3.34).

Analysis of variance showed significant reductions in the number of leaves per secondary branch at low (3%) and high (14%) shade, compared with controls. There were significant (10%) increases in the number of leaves per secondary branch after one cut. Despite a slight increase (1%) in the number of leaves per secondary branch, there was no significant change between two cuts and controls. Diquat at 0.1, 0.2, and 0.5 mg l^{-1} significantly (8.5, 14 and 18% respectively) reduced the number of leaves per secondary branch (Fig. 3.35).

Immediately following the 7-days treatment period, *P. pectinatus* no longer exposed to diquat began to recover. Regrowth from 1, 2 and 12 hr exposure times was rapid and plants reformed a canopy within 3 weeks. No residual response to diquat was noted during the recovery period. *P. pectinatus* regrowth from the 24, 48, 96 and 168 hr exposure times was delayed, and some of the early regrowth showed symptoms of residual diquat. After 6 weeks it was difficult to distinguished diquat-treated plants from untreated plants.

3.7.4. Experiment 12: Response of *Potamogeton pectinatus* to diquat and cutting treatments under field condition

Although some slight symptoms of diquat could be seen with 1 and 1.5 mg l^{-1} diquat, there was no significant control. The growing tips in high levels of diquat (1 and 1.5 mg l^{-1}) after a second application were slightly chlorotic. However, this effect did not significantly reduce the plant growth. Although the higher doses showed slightly higher activity and produced better long-term control, there were no significant differences in weed control between the high and low doses. The weed at all doses was unchanged even after the second application. It was not possible to show any differences between treated and control. Because the current had washed the diquat from plant mats. However, it was difficult to quantify the degree of weed control by observation, loss of chlorophyll has been used as an early indication of diquat injury (Fig. 3.39).

By the end of experiment, the cutting treatments had a significant effect on biomass dry weight, plant length, and plant width. Compared with the control, biomass dry weight significantly increased (77%) after one cut. Biomass dry weight significantly decreased after second cut compared with control and one cut. The reductions were 48 and 70%, respectively (Fig. 3.40).

Significant decreases (50 and 55%) in plant length were observed after a second cut, compared with control and the single cut. Despite a 13% increase in plant length after one cut, there were no significant differences between this and control plants (Fig. 3.40)

Plant width significantly decreased after two cuts, compared with control and one cut. The reductions were 43 and 50% respectively. There were no significant differences between control and one cut (Fig. 3.40).

3.7.5. Discussion

The key to a successful diquat treatment is maintaining herbicidally-active concentrations for periods exceeding 24 hr. The results from greenhouse and field studies suggest that providing an adequate herbicide contact time would be crucial for

the success of a chemical treatment. A minimum concentration of the herbicide must be maintained near the target plant in the water column for a minimum contact time. Barrett (1980) stated that the recommended treatment rate of diquat for control of submerged vegetation is 1 mg l^{-1} with a minimum contact time of 24 hr.

A fast flow velocity was probably the main factor producing poor results after diquat application (Fig. 3.31). Water analysis showed that more than 90% of diquat concentrations was washed out of the treatment area in less than 10 minutes (Table 2). Previous studies suggest that for control of submerged plants a minimum of 6 and 24 hr contact to 2 and 1 mg l^{-1}, respectively, is required (Barrett, 1980; Van & Conant, 1988). This experiment showed that diquat, even in its alginate formulation, is not a good choice for control of submerged plants in a fast flowing river (>50 cm s^{-1}).

High and turbid water conditions during the spring made it impossible to apply treatments before July. The early stage of growth in submerged plants is more susceptible to the contact herbicide because soft and young tissues take up the chemical readily. Chemical applications to submerged species are more successful before peak biomass conditions, and prior to the plant reaching the water surface. Therefore, a further reason for the poor level of control may have been the late season application (Barrett, 1980; Van & Conant, 1988). In addition, in *P. pectinatus* developed from tubers, early growth depends largely on stored food reserves. Therefore, the recovery of submerged weeds after applying herbicide in early stage of season will take a long time.

Previous aquatic testing (Barrett & Murphy, 1982; Bowmer, 1982; Bowmer & Smith, 1984; Fox *et al.*, 1986) has shown that diquat can become inactivated by adsorption on to clay minerals and organic matter attached to the plants. Heavily coated *P. pectinatus* plants in the River Kelvin with aufwuchs of inorganic detritus, and bacterial and algal epiphytes may act as a barrier to diquat reaching the plant surface. This is in agreement with the findings of Barrett (1980), Fox *et al.*, 1986 and Caffrey (1990).

High calcium concentrations also antagonise diquat activity (Fox *et al.*, 1986), but can be ruled out here because the Kelvin is not a hard-water river (Clyde RPB unpublished data).

It is clear from this experiment that as concentration and exposure time are increased, plant control is increased. Previous studies using endothall and 2,4-D on *Myriophyllum spicatum* (Green, 1988, 1989), triclopyr and 2,4-D on *Hydrilla* and *Myriophyllum spicatum* (Netherland, 1992; Turner *et al.*, 1992), and bensulfuron on *Hydrilla* (Van & Vandiver, 1994) showed that higher concentrations and/or exposure times resulted in increased plant injury. Although the data indicated significant reductions in biomass dry weight, shoot length, leaf length, and other growth parameters, visual observation showed rapid regrowth at 1 and 2 hr exposure times. Results of short-term static exposures of diquat on *P. pectinatus* indicate that diquat at 0.1 and 0.2 mg l^{-1} for 1, 2 and 12 hr exposure was inefficient in significantly reducing *P. pectinatus* biomass. New growth of treated plants remained bleached and necrotic while in contact with diquat; however, when the diquat was removed, plants began to regrow from tubers.

Results indicate that increased exposure time is the key to improving *P. pectinatus* control with diquat. Regrowth from tubers suggests a lack of transport of diquat to *P. pectinatus* tubers which agrees with the results of Van and Stewart (1985). Also Van and Stewart (1985) reported that tubers may become physiologically independent from the plant as a result of forming during pre-treatment growth. Therefore to inhibit the *P. pectinatus* growth the tubers must absorb sufficient diquat at the surface of the soil. The level of regrowth depended on the exposure times.

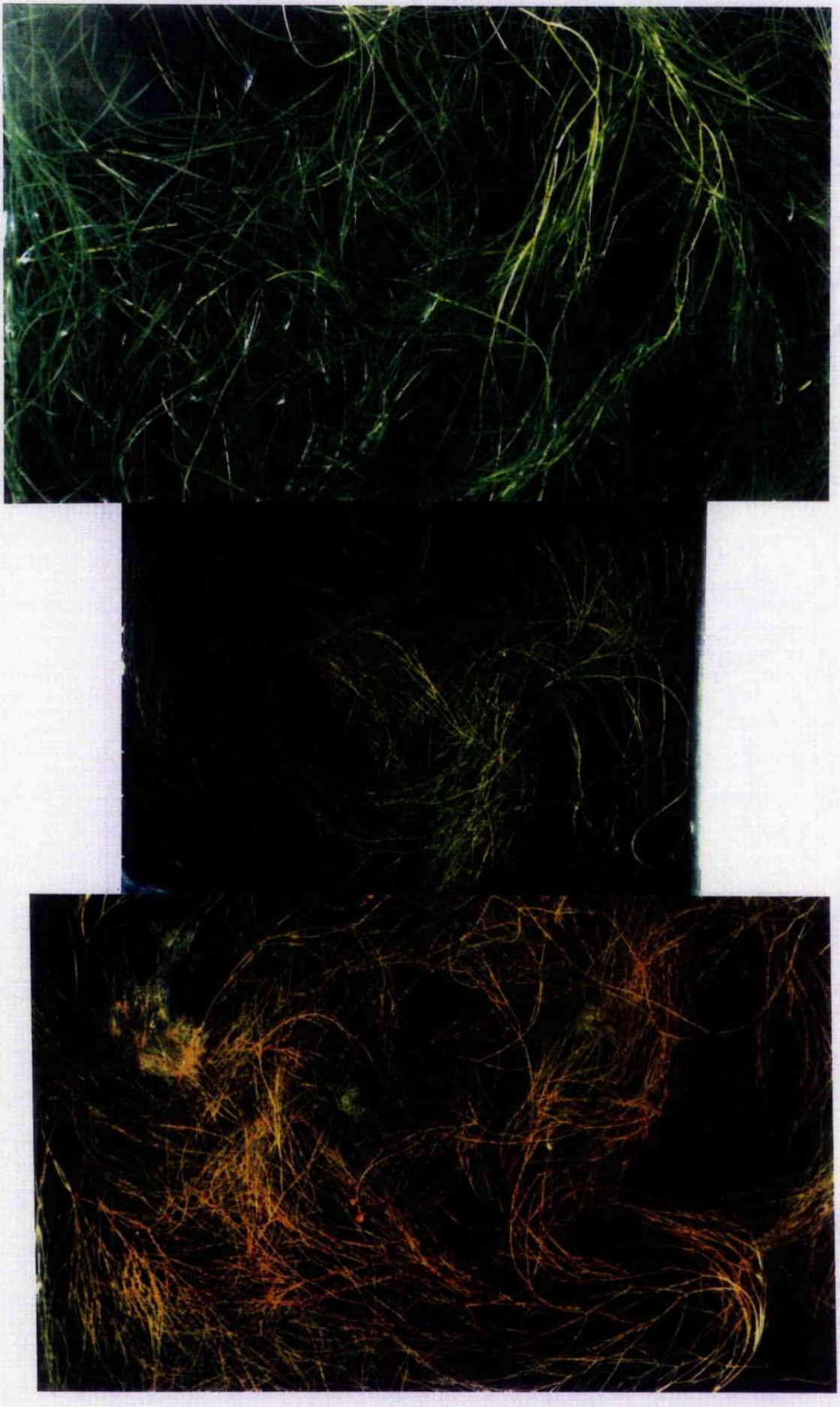
No viable shoots were observed at 0.2 mg l^{-1} for 48, 96 and 168 hr and 0.1 mg l^{-1} for 96 and 168 hr exposures in one replicate at the end of the experiment. The experimental results showed that increasing diquat concentration up to 0.2 mg l^{-1} did not increase the levels of control when exposure time was ranging from 1 24 hr. A minimum 24 hr contact time with 0.2 mg l^{-1} diquat is required to control *P. pectinatus*.

The results of this study suggest that following initial injury from 0.1 and 0.2 mg l^{-1} at 24, 48, 96 and 168 hr exposure times diquat can control *P. pectinatus* at low concentrations combined with long exposure times. Although some unexpected growth was observed at 168 hr exposure time in one replicate, evidence from this study suggests that diquat can control *P. pectinatus* at 168 hr exposure times even at lower concentrations.

Experimental results showed that *P. pectinatus* responds to cutting with increased growth. These results are in agreement with Caffrey (1990) and Dawson (1978) who found that the maximum biomass in *P. pectinatus* was observed after cutting. The increase in plant biomass will probably be due to a decrease in self-shading. There was a significant reduction in biomass after two cuts. These also suggest that by an exhaustion of stored carbohydrate after intensity of cutting, plant is not able to respond with increased growth, but instead shows decreased growth.

The experimental results led to the development of a proposal for management by shading. These experiments showed significant difference between the *P. pectinatus* in shaded and unshaded tanks after treatment with diquat and cutting. *P. pectinatus* was unable to survive a combination of different stress and disturbance-based control methods (herbicide, cutting and shading). Diquat at low doses (0.1 and 0.2 mg l^{-1}) and cutting alone, were not enough to provide long-term control. A rapid regrowth in *P. pectinatus* after cutting and herbicide application showed that the reduction in light at treated sites was a key factor for a control success. However, when these two factors (herbicide and cutting) were applied with shading, the *P. pectinatus* showed a significant decrease in growth. These data support the results of Dawson (1989) and Dawson and Kern-Hansen (1979) who reported 50% decrease in plant growth by 50% reduction in light. They also proposed that further reduction in light to below half will lead to disappearance of the aquatic plants from a water body.

The experimental results suggest that the direct application of greenhouse results to the field should be viewed with some caution. Exposure times in the field are dynamic in that the plant is exposed to a dissipating concentration of herbicide over time. In addition, differences in sensitivity between mature field plants and plants grown from small tubers in greenhouse require caution.



a

b

c

Fig. 3.25. *Potamogeton pectinatus*: treated with 0.1 mg l^{-1} diquat at 2 (a), 12 (b), and 168 (c) hr exposure times: 7 days after treatment in greenhouse tanks.

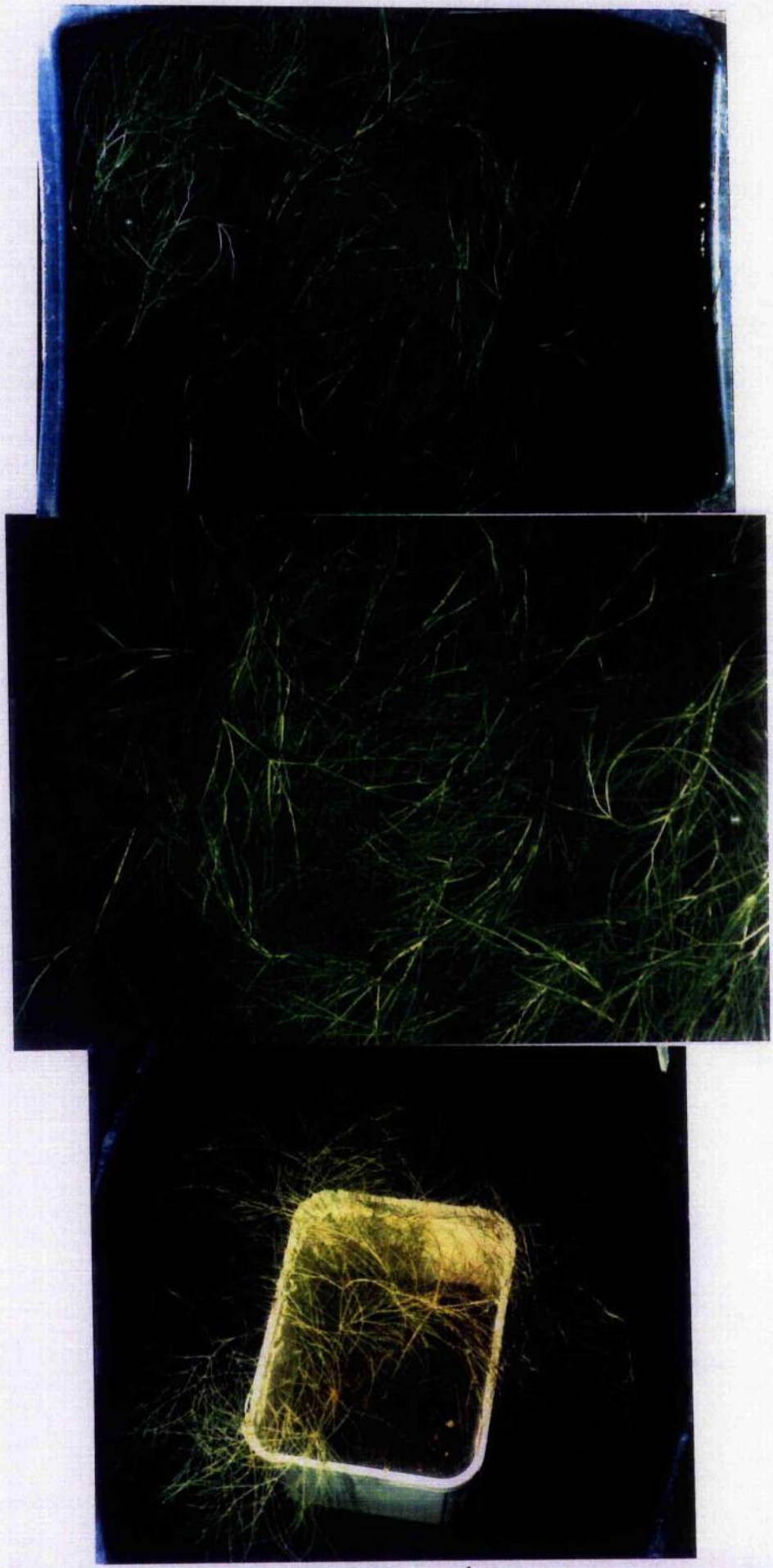
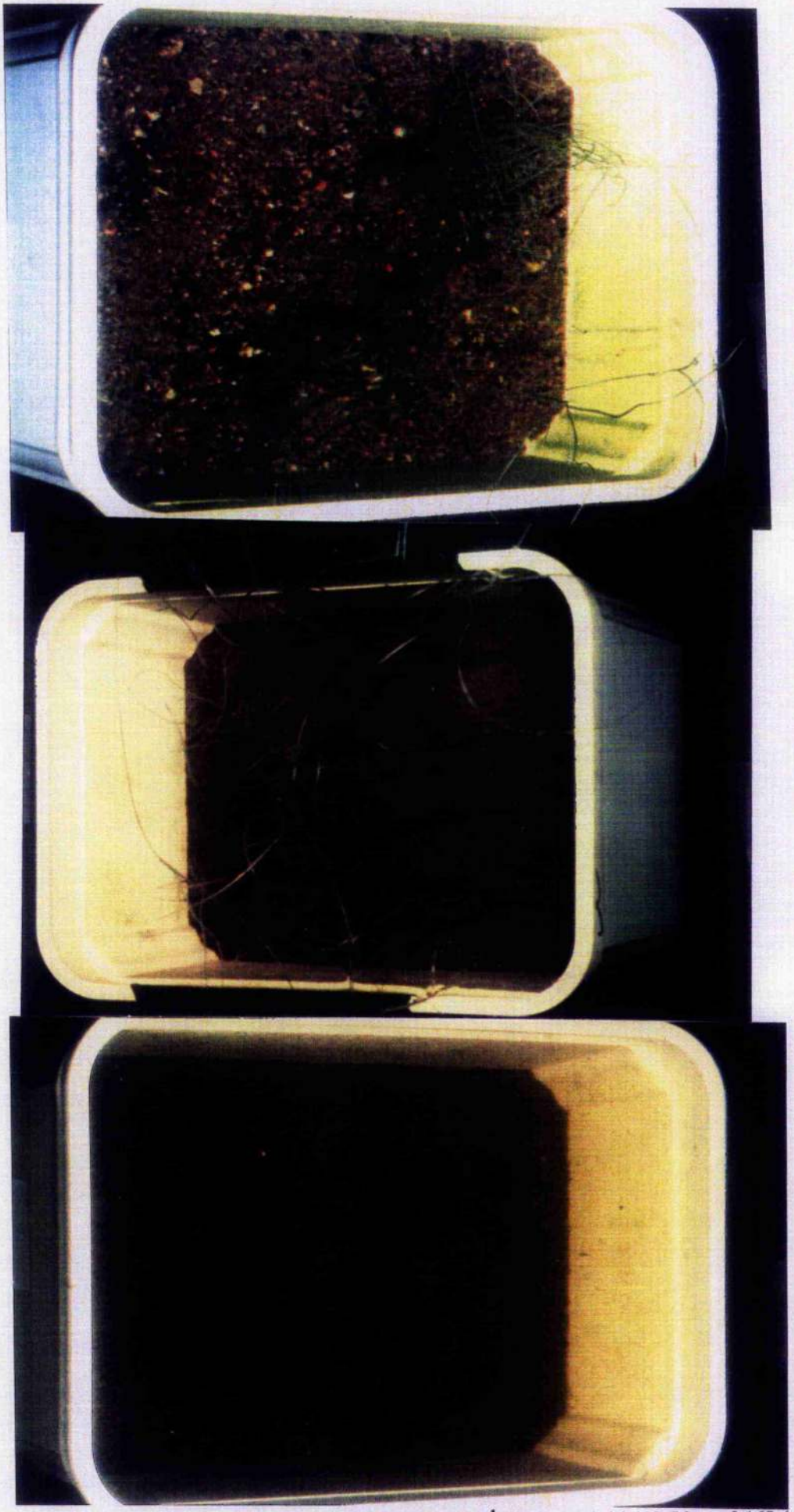


Fig. 3.26. ***Potamogeton pectinatus*****: treated with 0.2 mg l^{-1} diquat at 2 (a), 12 (b), and 168 (c) hr exposure times: 7 days after treatment in greenhouse tanks.**



a

b

c

Fig. 3.27. ***Potamogeton pectinatus*****: treated with 0.5 mg l^{-1} diquat at 2 (a), 12 (b), and 168 (c) hr exposure times: 7 days after treatment in greenhouse tanks.**

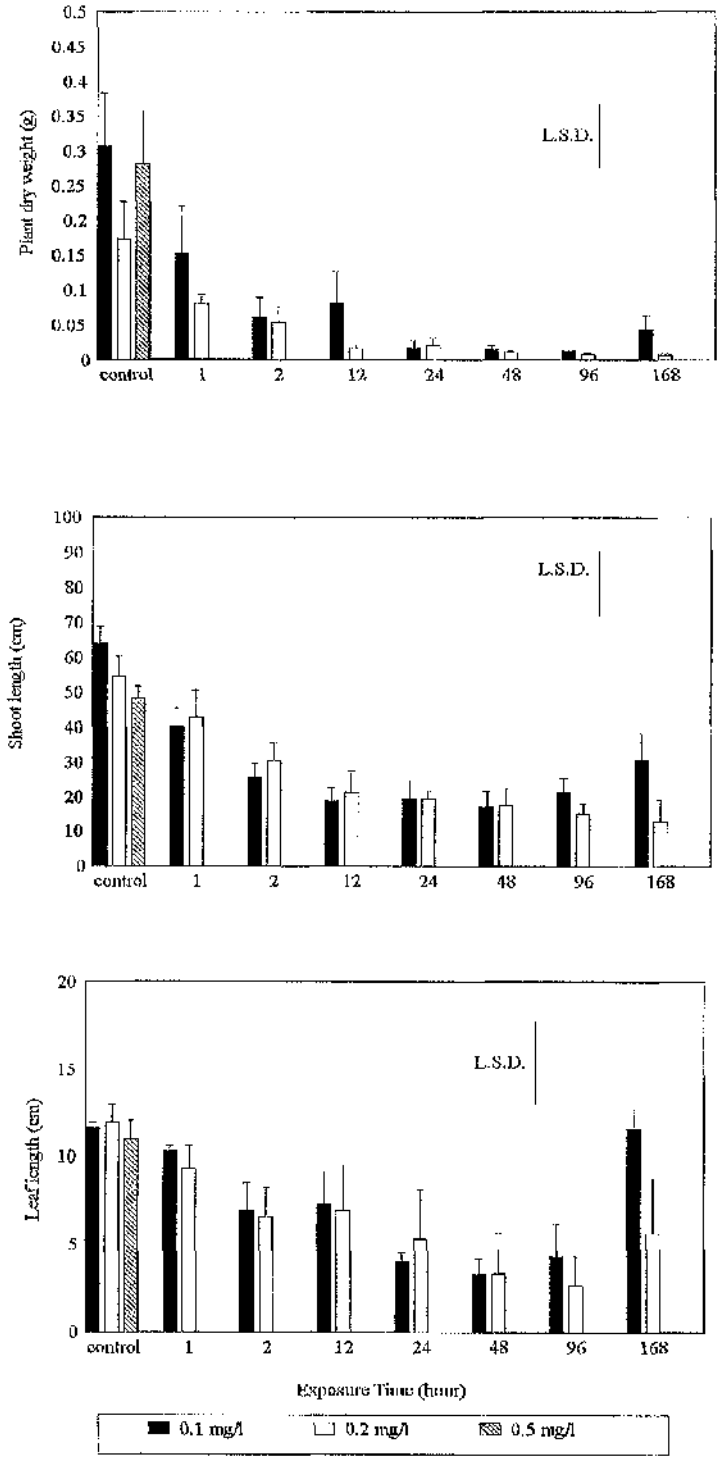


Fig. 3.28. Effects of various concentrations and exposure times of diquat on plant dry weight (g), shoot length (cm) and leaf length (cm) in *Potamogeton pectinatus* at 8 weeks post-treatment. Bars on histograms represent ± 1 s.e.; Separate bars represent least significant difference (P<0.05).

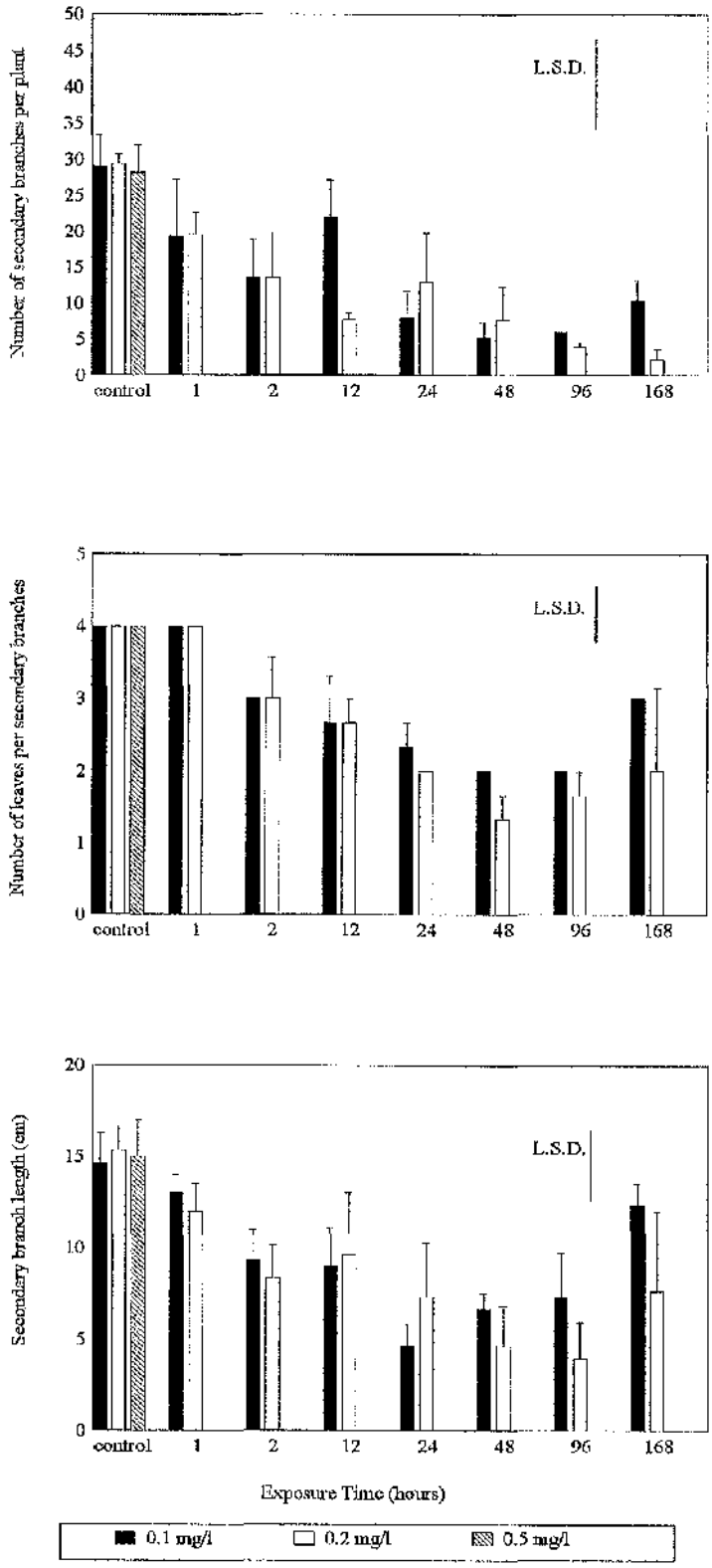


Fig. 3.29. Effects of various concentrations and exposure times of diquat on number of secondary branches, number of leaves per secondary branches and secondary ranch length (cm) in *Potamogeton pectinatus* at 8 weeks post-treatment. Bars on histograms represent ± 1s.e.; separate bars represent least significant difference (P<0.05).

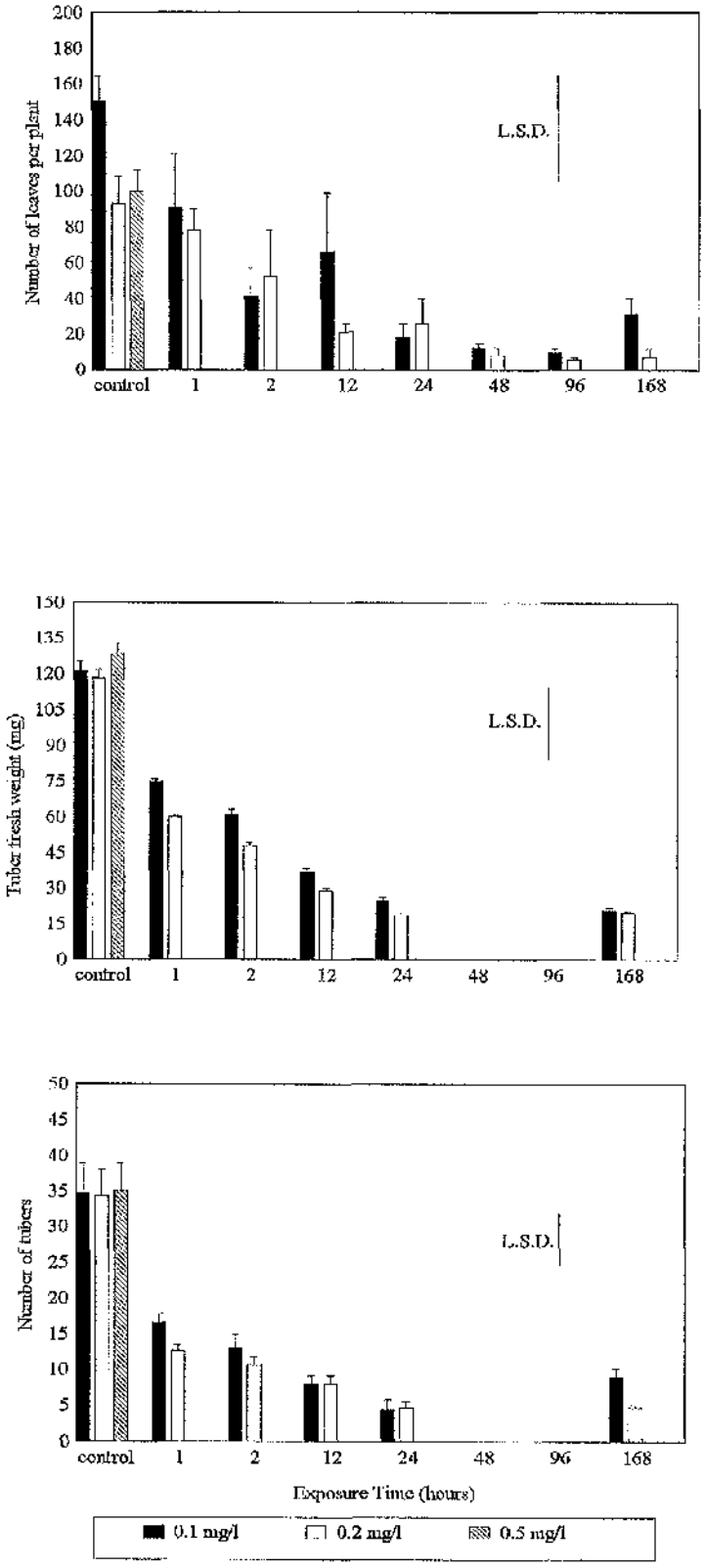


Fig. 3.30. Effects of various concentrations and exposure times of diquat on number of leaves per plant, tubers per plant and tubers weight in *Potamogeton pectinatus* at 8 weeks post- treatment. Bars on histograms represent ± 1 s.e.; separate bars represent least significant difference (P<0.05).

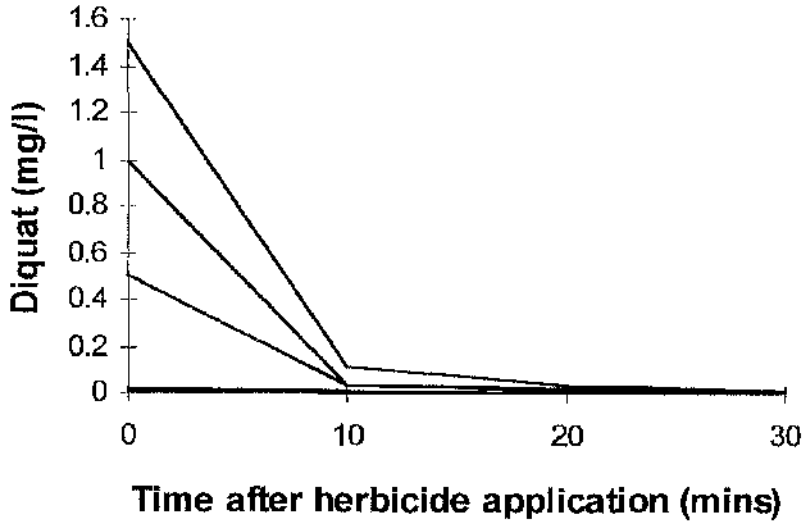


Fig. 3.31. Diquat disappearance from the treated plots in the River Kelvin

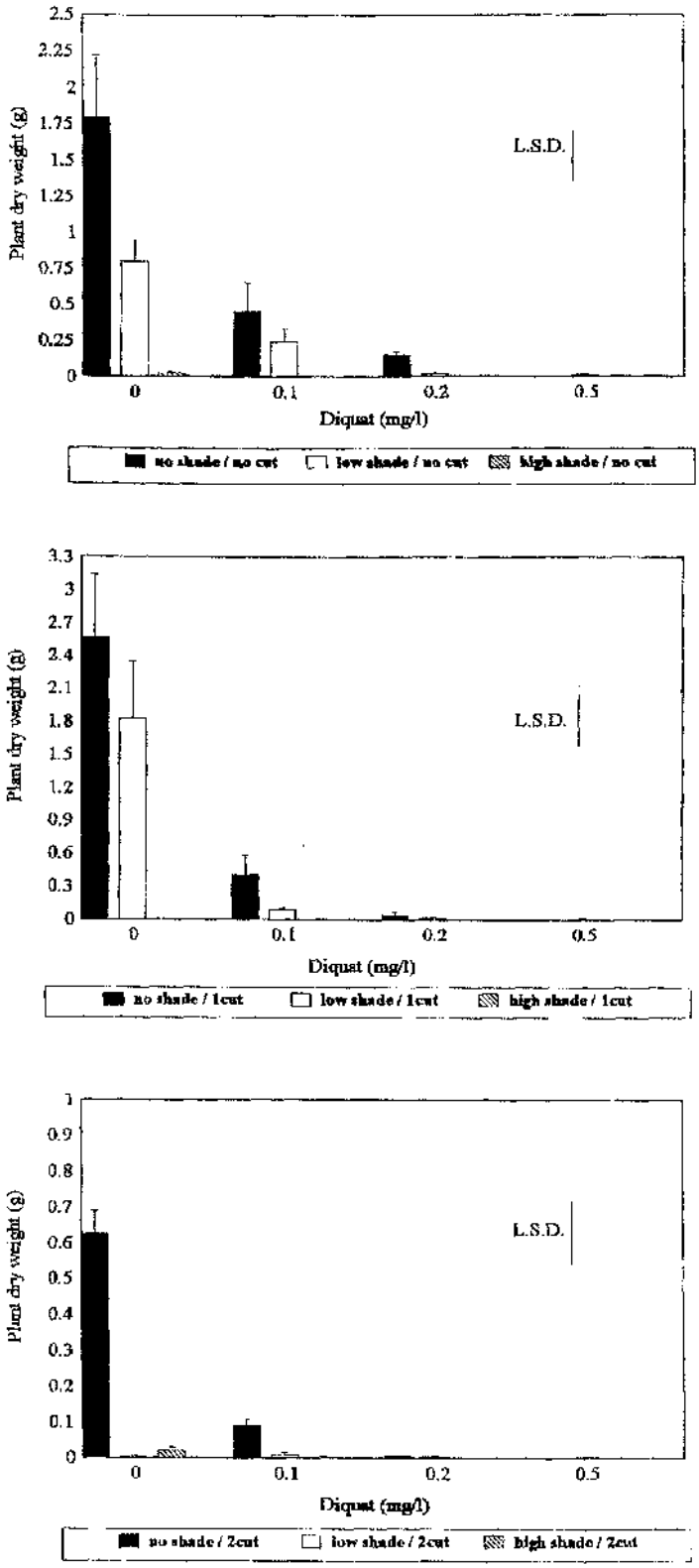


Fig. 3.32. Effects of different levels of diquat, cutting and shading on plant dry weight (g) in *Potamogeton pectinatus*. Bars on histograms represent ± 1 s.e.; separate bars represent least significant difference (P<0.05).

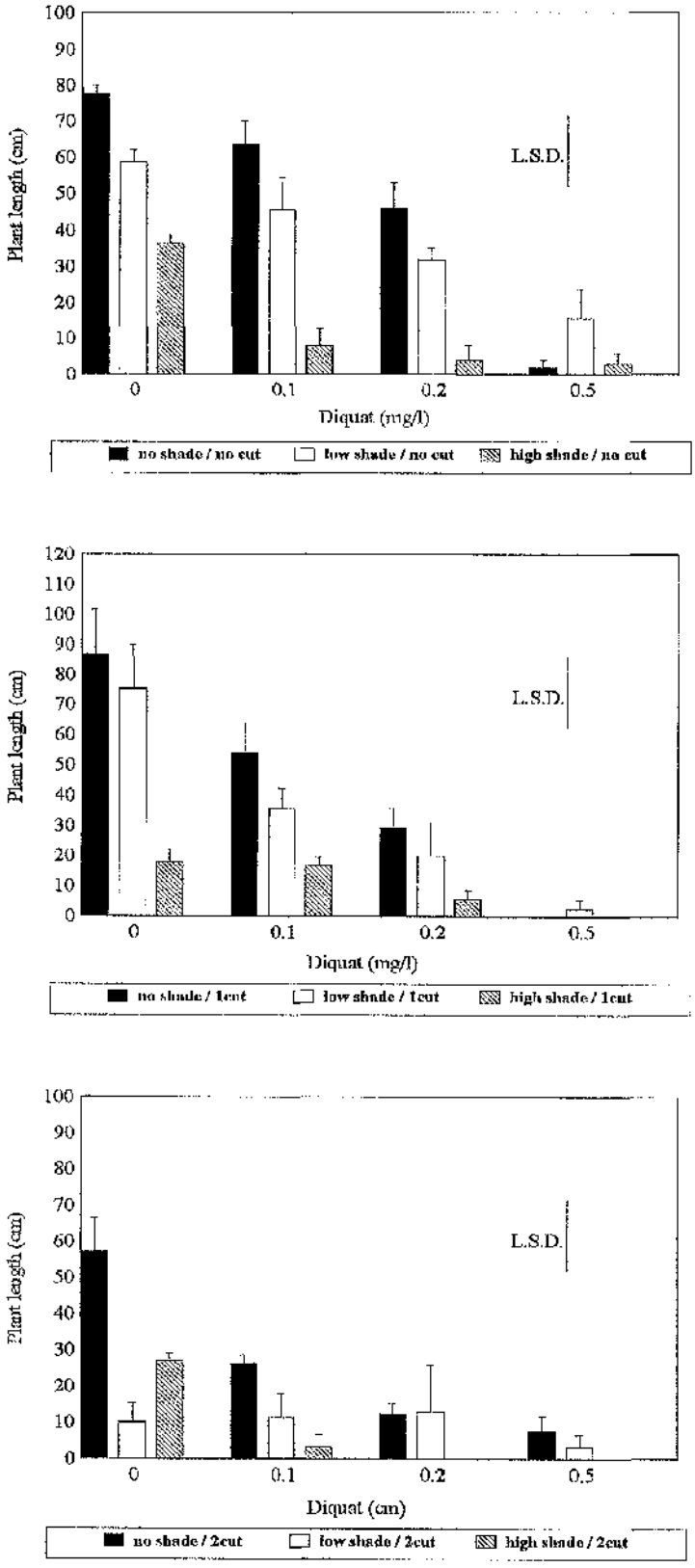
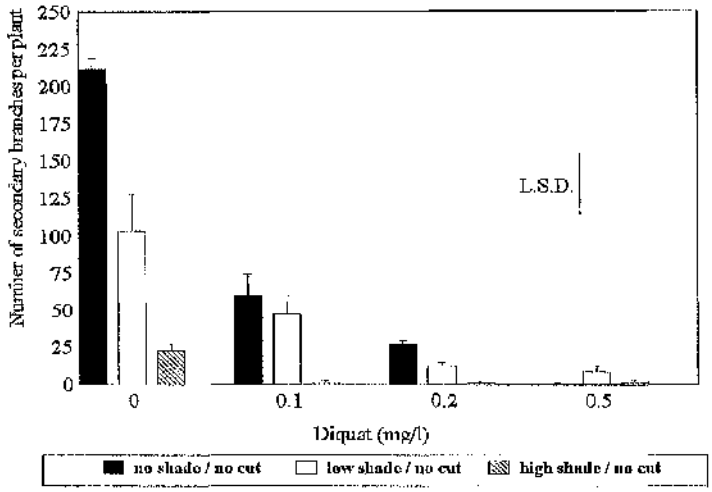
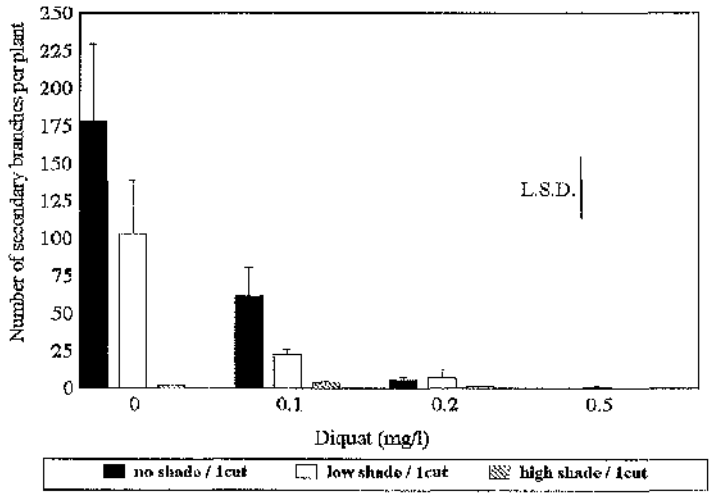


Fig. 3.33. Effects of different levels of diquat, cutting and shading on plant length (cm) in *Potamogeton pectinatus*. Bars on histograms represent ± 1 s.e.; separate bars represent least significant difference (P<0.05).





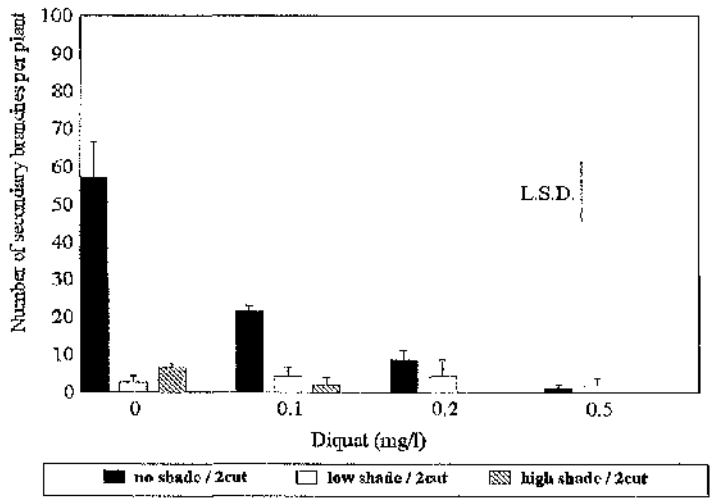


Fig. 3.34. Effects of different levels of diquat, cutting and shading on number of secondary branches per plant in *Potamogeton pectinatus*. Bars on histograms represent ± 1 s.e.; separate bars represent least significant difference (P<0.05).

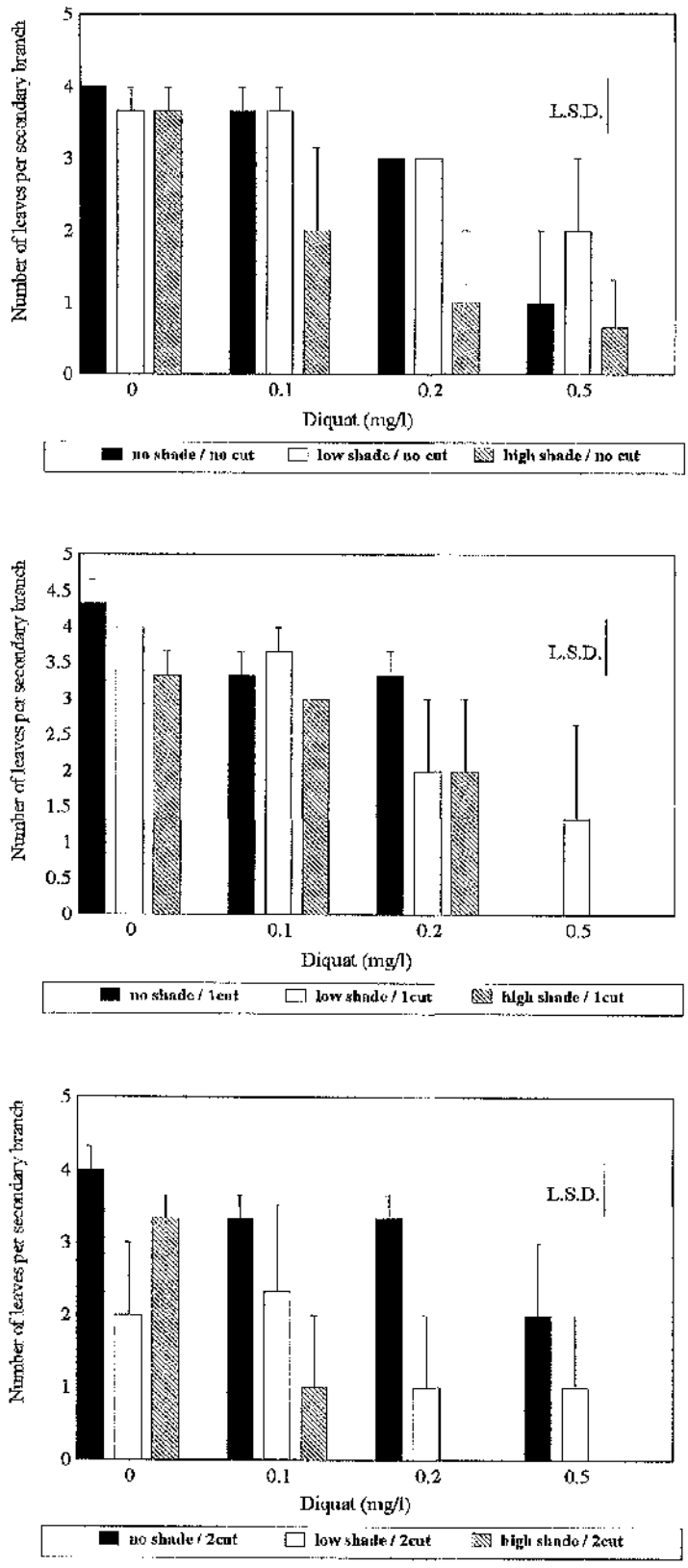
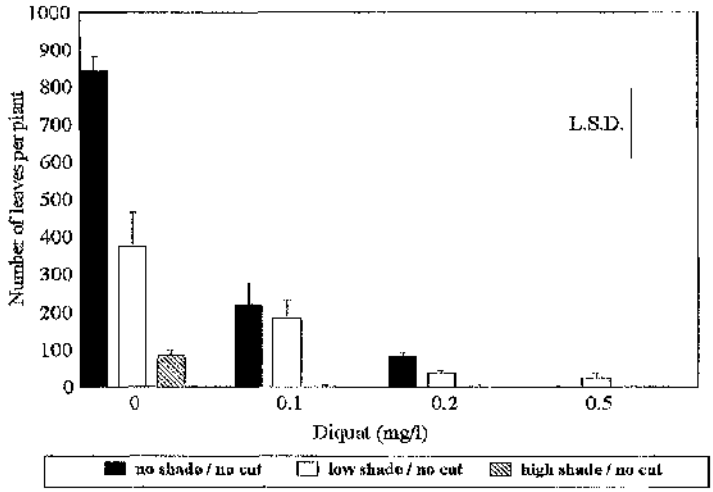
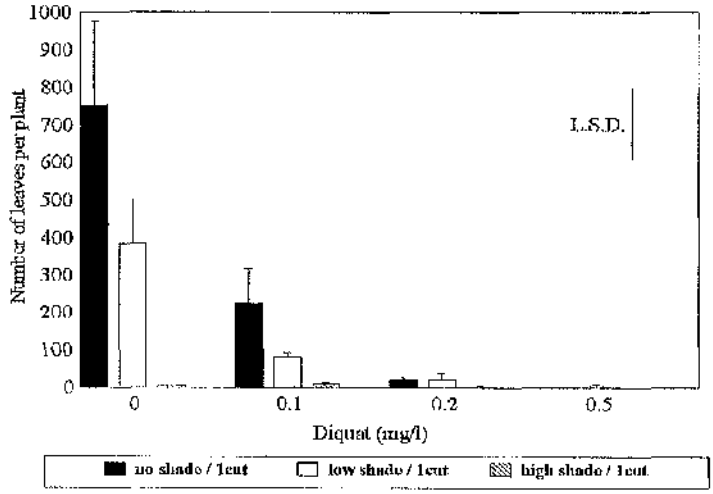


Fig. 3.35. Effects of different levels of diquat, cutting and shading on number of leaves per secondary branch plant in *Potamogeton pectinatus*. Bars on histograms represent ± 1 s.e.; separate bars represent least significant difference (P<0.05).





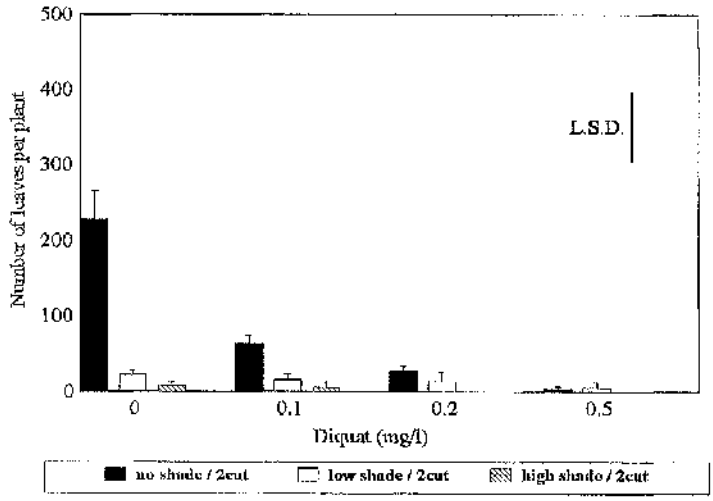


Fig. 3.36. Effects of different levels of diquat, cutting and shading on number of leaves per plant in *Potamogeton pectinatus*. Bars on histograms represent ± 1 s.e.; separate bars represent least significant difference (P<0,05).

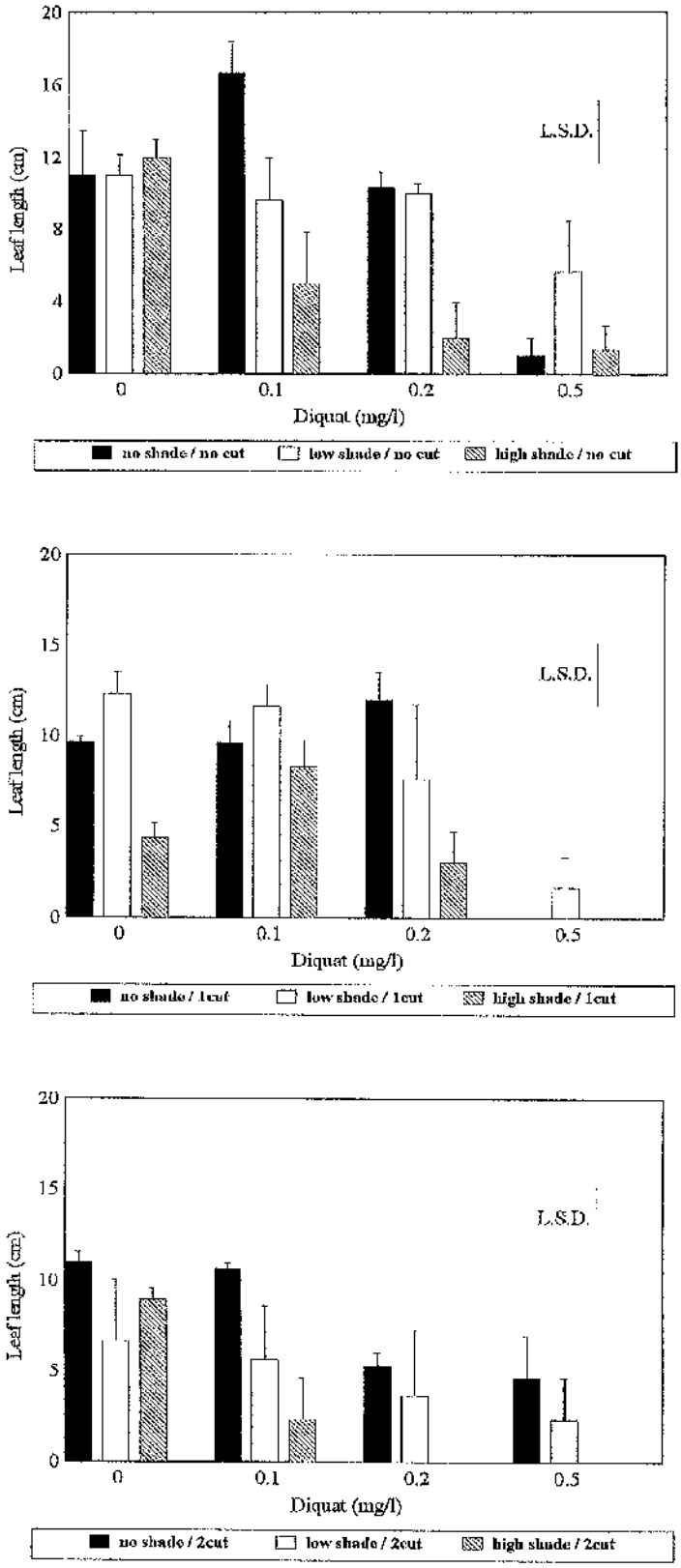


Fig. 3.37. Effects of different levels of diquat, cutting and shading on leaf length (cm) in *Potamogeton pectinatus*. Bars on histograms represent ± 1 s.e.; separate bars represent least significant difference (P<0.05).

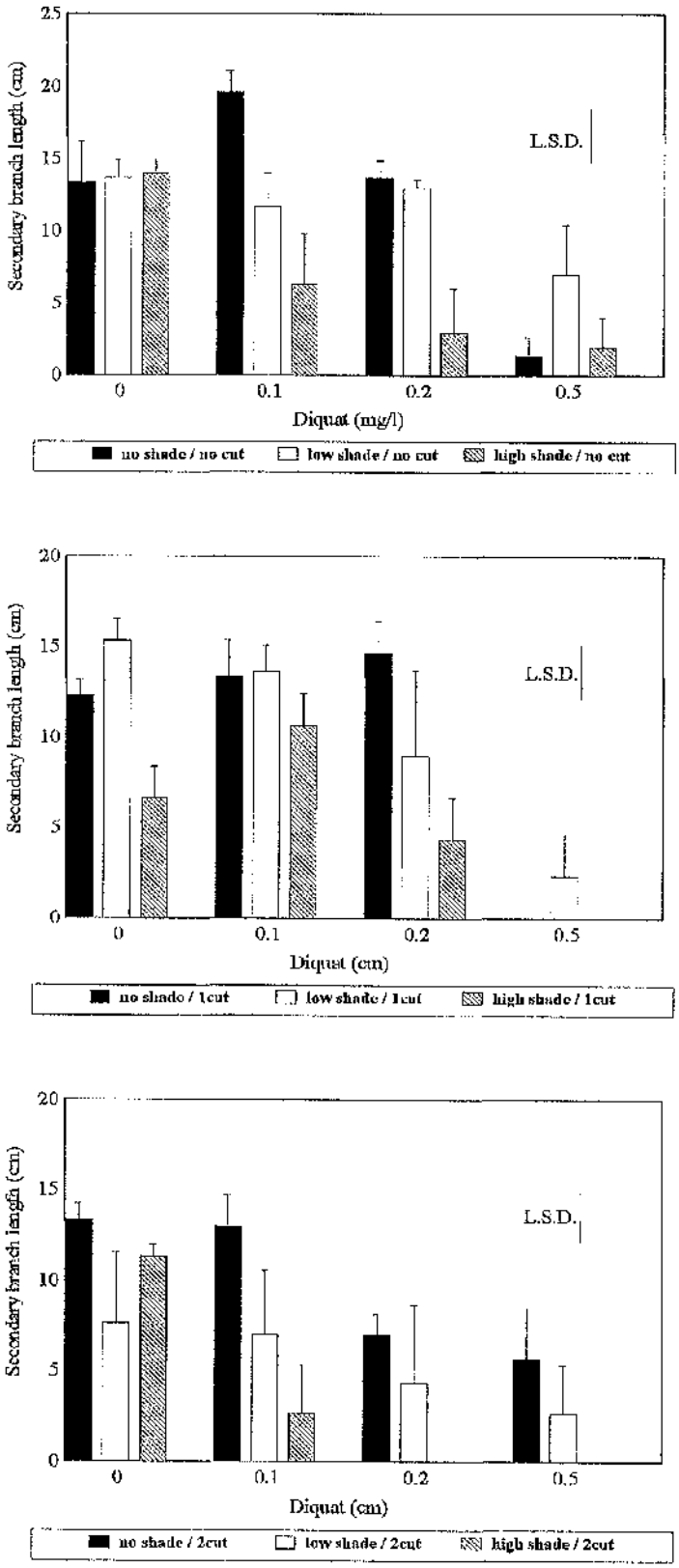
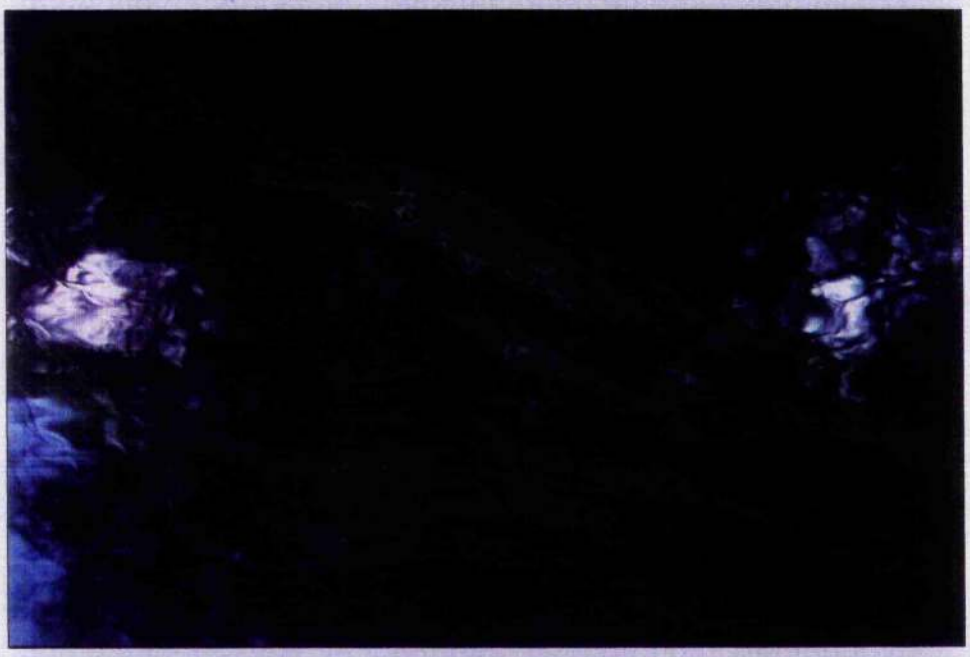
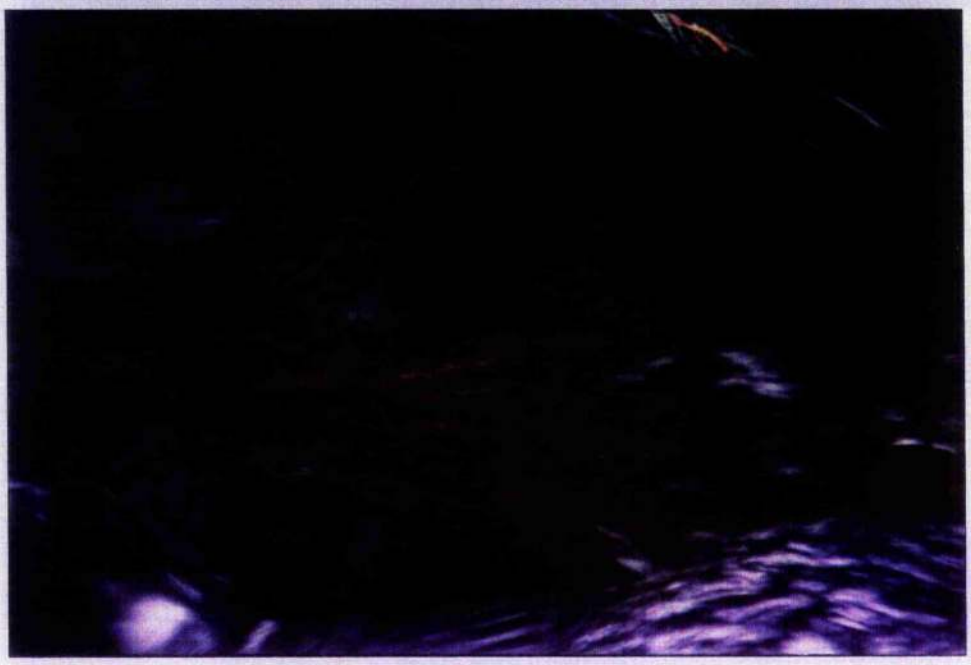


Fig. 3.38. Effects of different levels of diquat, cutting and shading on secondary branch length (cm) in *Potamogeton pectinatus*. Bars on histograms represent ± 1 s.e.; separate bars represent least significant difference (P<0,05).

a



b



c

Fig. 3.39. ***Potamogeton pectinatus*****: treated with 0.1(a), 0.5 (b), and 1 (c) mg l^{-1} diquat: 3 days after treatment in field condition.**

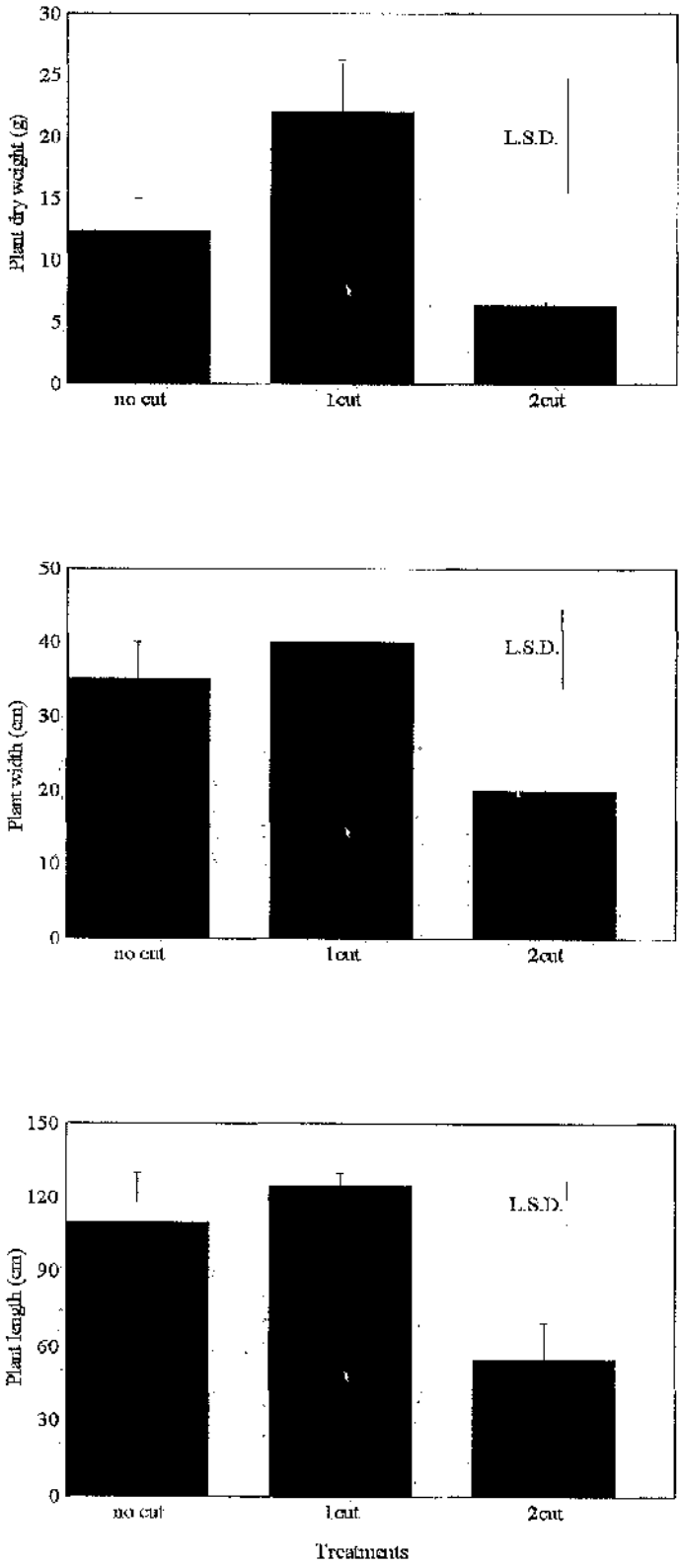


Fig. 3.40. Effects of different levels of cutting on plant dry weight (g), plant width (cm) and plant length (cm) in *Potamogeton pectinatus*. Bars on histograms represent ± 1 s.e.; separate bars represent least significant difference (P<0.05).

3.8. Competition between *P. pectinatus* and *P. perfoliatus* under different environmental conditions

3.8.1. Results

The results from this experiment were unexpectedly influenced by an unknown toxic material flushing from the material used to constract the new phytotron which killed all plants in 14 aquaria (W. van Vierssen, personal communication). Only 4 aquaria at 100 $\mu E\ m^{-2}\ s^{-1}$ and 20°C survived. Despite this setback, which was outwith my control, it was felt worthwhile to present the remaining results. However the conclusives to be down are clearly of only limited value under these circumstances.

P. pectinatus tubers began to grow soon after planting. Growth was initially from the main shoot; later, new shoots from underground runners emerged. *P. pectinatus* grew to the water surface, producing a canopy with the most leaves floating on the water surface.

P. perfoliatus began growing about one week later than *P. pectinatus*. Initial growth was from the original rhizome cuttings with one leaf in the main stem. In contrast with *P. pectinatus*, there was no significant differences in canopy formation of *P. perfoliatus* at above and below the water levels. Within 5 weeks of planting, both species had reached the surface of the water and was beginning to produce new shoots.

The results from the de Wit replacement series are summarized in Figs. 3.41, 3.42, 3.43 and 3.44. The highest amount of shoots, roots with rhizomes, number of tubers, and tubers fresh weight in *P. pectinatus* and shoots and roots with rhizomes dry and fresh weight in *P. perfoliatus* were generally produced in 1:3 clay:sand sediment compared to 1:6 clay:sand sediment (Figs. 3.41, 3.42 & 3.43). The reductions were 32, 20 and 30% in shoots, roots with rhizomes, and tubers in *P. pectinatus* and 17 and 6% in *P. perfoliatus*, respectively. However, there was an increase in weight and number of tubers at 2-4 density in 1:6 clay:sand than 1:3 clay:sand. A slight increase in below-ground biomass of both species was observed in the 3-3 and 2-4 mixtures in the 1:6 (clay:sand) sediment. However, *P. perfoliatus* accumulated substantially more

below-ground biomass (~2.5 times) than *P. pectinatus* on both sediment (Figs. 3.41 & 3.42).

P. pectinatus showed considerable suppression of growth under both sediment fertility regimes (Figs. 3.41 & 3.42). The experimental results for both species indicated that interspecific effects were more than intraspecific, thus resulting in a higher yield per plant in monoculture than in the presence of the other species (Figs. 3.41 & 3.42). The opposite was found for tubers, where the maximum weight was observed in the 3-3 density. Here the two species in each combination are assumed to compete for the same environmental resources, while at the same time one of the species suffers more from within-species competition (Harper, 1977). However, despite a 23% increases in tuber weight in the 3-3 density, there was no significant differences between treatments (Fig. 3.44).

Since both above and below-ground parts of *P. pectinatus* were significantly lighter than *P. perfoliatus*, it will be concluded that *P. perfoliatus* exerted an interspecific competitive effects on both shoots and roots of *P. pectinatus*.

A significant decreases in tuber production in the 4-2, 3-3 and 2-4 densities observed compared with 6-0 density. The reductions were 50, 70 and 76%, respectively (Fig. 3.44).

Differences in accumulation of nitrogen in above and below-ground biomass did not demonstrate such a striking response to sediment fertilization. Despite a more nitrogen incorporated in below and above parts of *P. perfoliatus*, there was not a significant differences between species (Fig. 3.43).

3.8.2. Discussion

This study and others (Kautsky, 1991) showed that *P. pectinatus* was significantly suppressed when combined with *P. perfoliatus*. This may be explained by *P. pectinatus* and *P. perfoliatus* similar growth forms and occupying the same sediment layer. *P. perfoliatus* with having the higher growth rate at the mid-stage of growth slowed the fast initial growth of *P. pectinatus*. These results suggests that the two species have the same environmental demands and compete for the same resources (e.g. nutrients).

Biomass production on *P. perfoliatus* was only slightly suppresses at 2-4 and 3-3 densities due to the presence of *P. pectinatus*. Given the no significant reduction of *P. perfoliatus* above and below-ground biomass in mixture relative to monocultures, *P. perfoliatus* appeared to be unaffected by the presence of *P. pectinatus*.

Both species did demonstrate a variety of morphological responses to the competitive situation. Among these, the growth of neighbouring species may become limited through reduction in available light (McCreary *et al.*, 1990). Although *P. pectinatus* is known to be capable of forming extensive canopies (van Wijk 1988; Moen & Cohen, 1989), canopy formation was one reason why *P. perfoliatus* was competitively superior to *P. pectinatus*. This suggests that *P. perfoliatus*, by produced similar leaves at different levels of water, was able to suppress *P. pectinatus* through shading. Therefore, the *P. perfoliatus* by forming a floating-leaf canopy had limiting light availability to *P. pectinatus*. Moen and Cohen (1989) planted *P. pectinatus* and *Myriophyllum exalbescens* together in aquaria in a replacement series experiment. Results of this experiment suggested that *P. pectinatus* with higher initial growth and growth form held a competitive ability over *M. exalbescens* at all plant densities.

In combinations of *P. pectinatus* and *P. perfoliatus* at the tested densities, the interspecific effects on tuber weight were less strong than the interaspecific ones. This may be explained by the different growth forms and rooting depth of *P. pectinatus* and *P. perfoliatus*. Thus two species may be able to coexist by occupying different zones in the sediment and in the water. Similar results have been shown by McCreary and Carpenter (1983) for two submerged species, *Eleocharis acicularis* and *Juncus pelocarpus*.

In conclusion, this experiment demonstrated the ability of a rhizome growth species, *P. perfoliatus*, to strongly outcompete a tuber growth species, *P. pectinatus*. Under different experimental conditions (e.g. light levels, alkalinity, nutrient availability etc.), the competitive ability of both species might be different. Further work is however needed to confirm these observations in view of the incomplete nature of my experimental results.

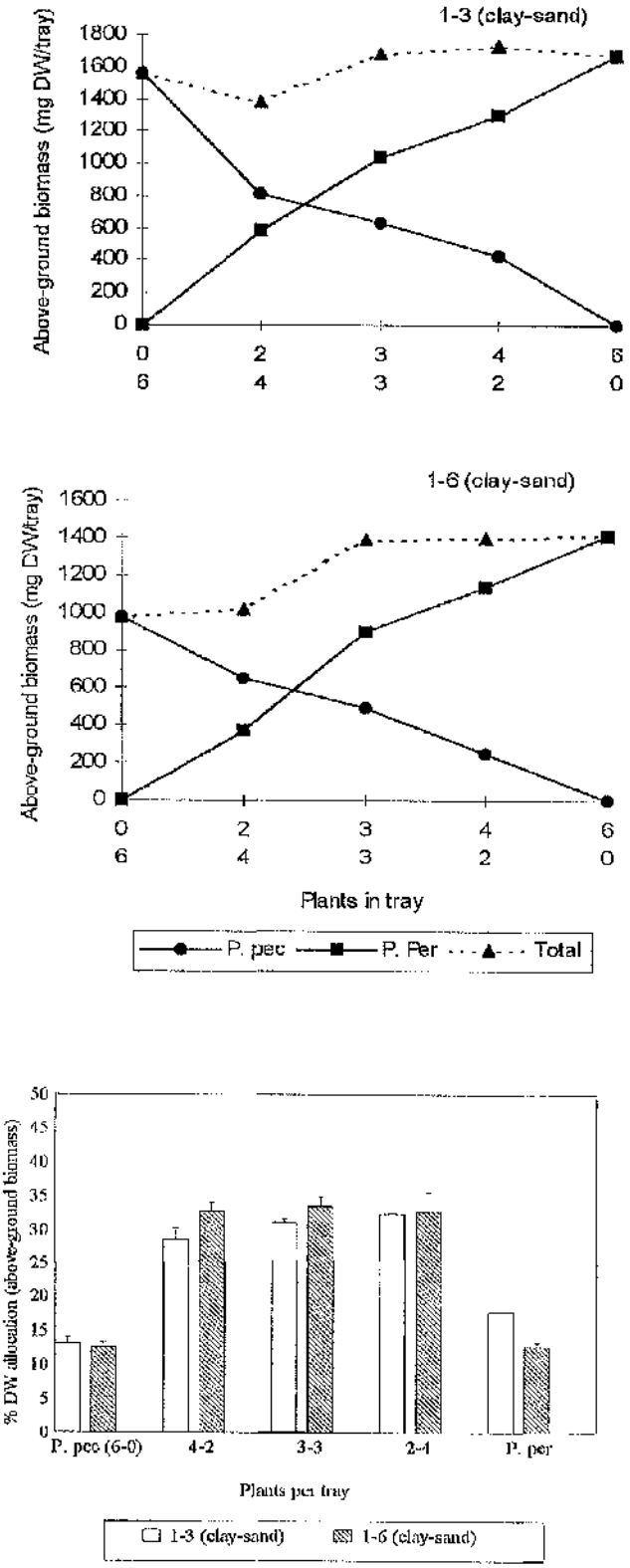
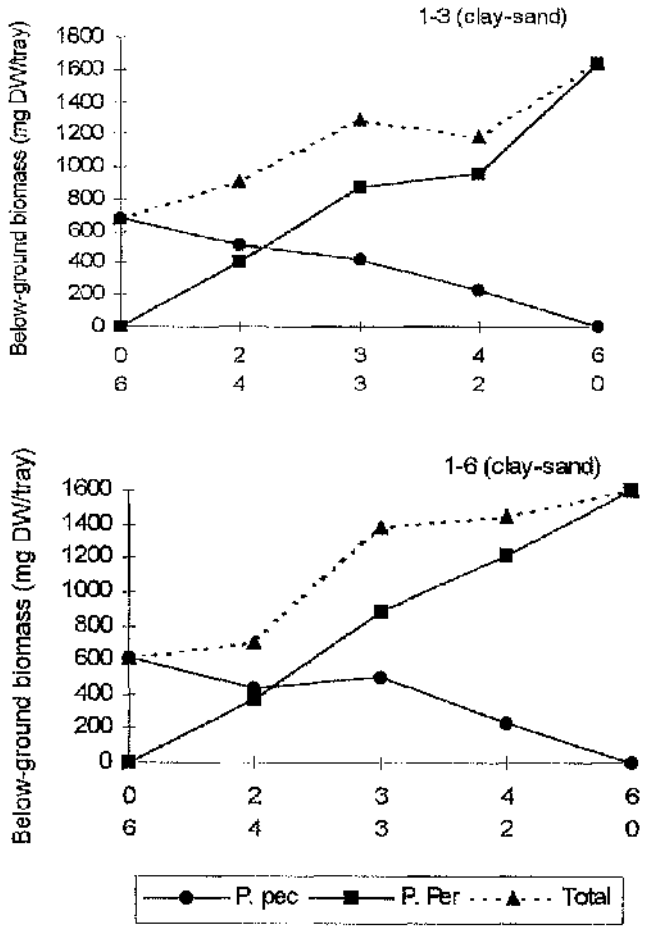


Fig. 3.41. Replacement series of *P. pectinatus* (–●–) vs. *P. perfoliatus* (–■–) under 1:3 (clay: sand) and 1:6 (clay:sand) sediments. The broken ----- indicate the arithmetic sum of the yields of both species. Values represent means of two replicates.



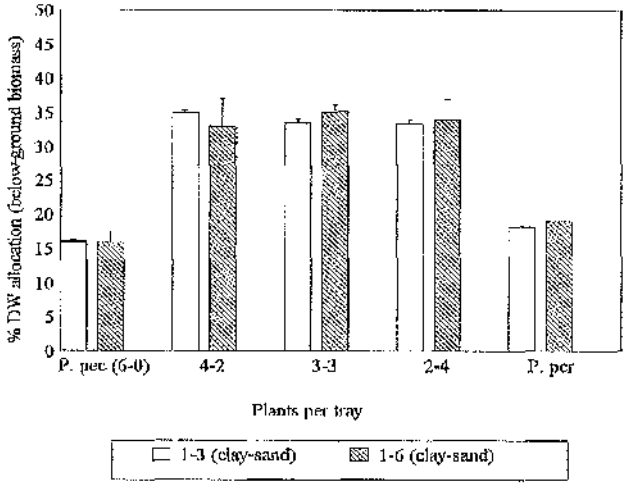


Fig. 3.42. Replacement series of *P. pectinatus* (–•–) vs. *P. perfoliatus* (–■–) under 1:3 (clay: sand) and 1:6 (clay:sand) sediments. The broken ------ indicate the arithmetic sum of the yields of both species. Values represent means of two replicates.

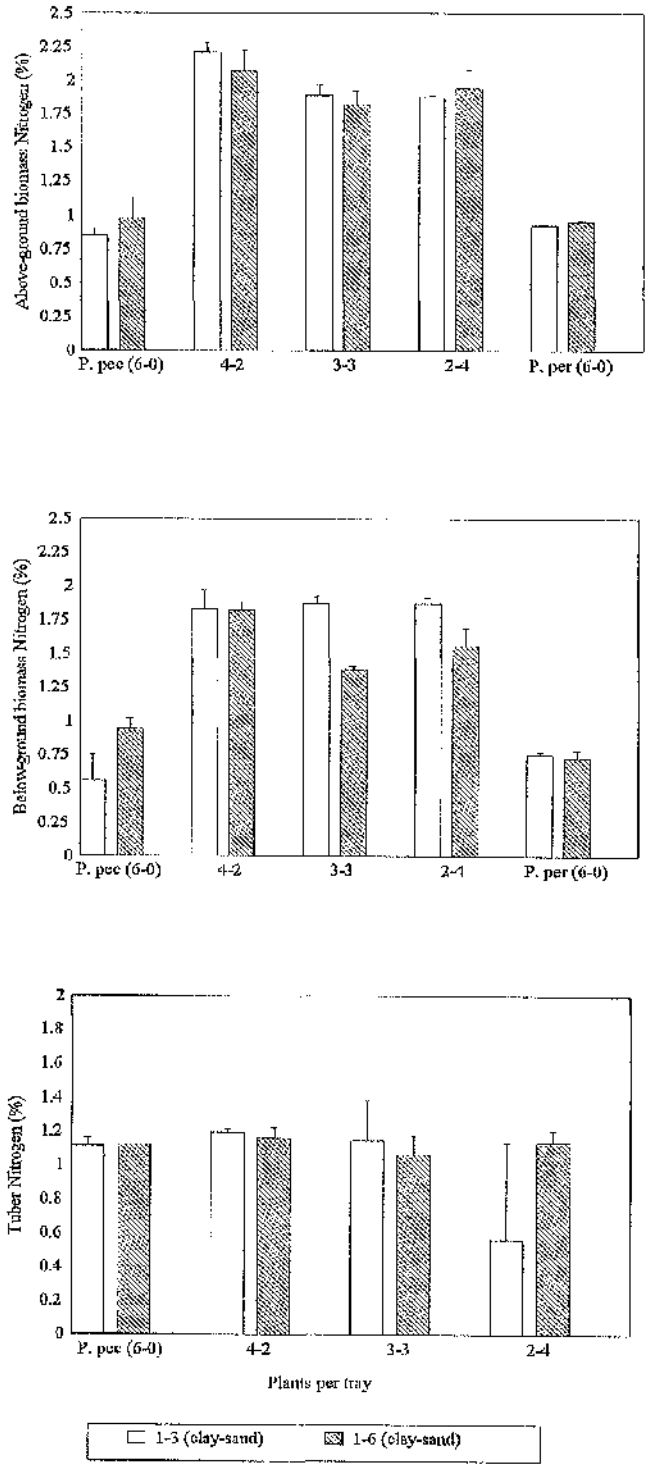


Fig. 3.43. Mean (n=2) nitrogen percentages in above-ground, below-ground and tuber in *P. pectinatus*, *P. perfoliatus*, and 4-2, 3-3, and 2-4 mixtures under 1:3 (clay:sand) and 1:6 (clay:sand) sediments.

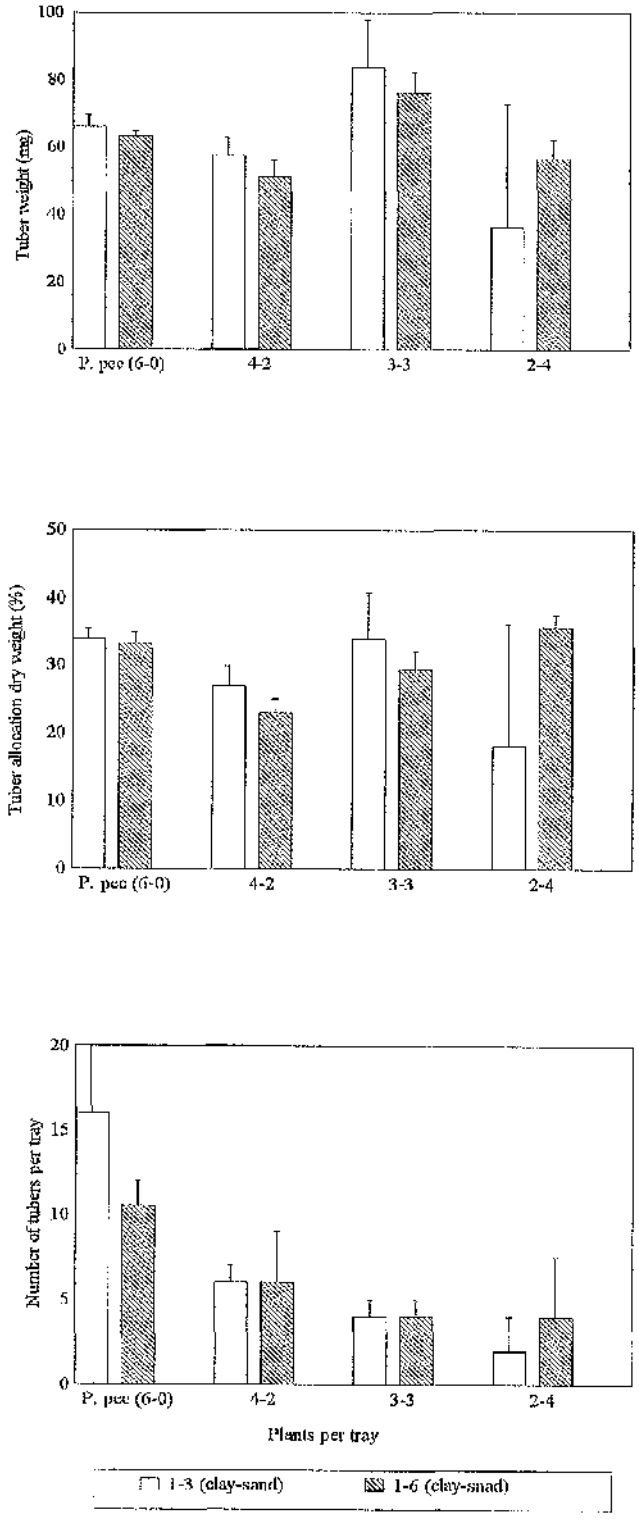


Fig. 3.44. Mean (n=2) tuber weight (mg), tuber allocation dry weight (%), and number of tubers per tray in full density (6-0) of *P. pectinatus*, 4-2, 3-3 and 2-4 mixtures under 1:3 (clay: sand) and 1:6 (clay:sand) sediments.

4. General Discussion and Conclusions

4. General Discussion and Conclusions

Determination of the optimal control methods, at both species and community levels, is clearly desirable for any aquatic weed problem. Unfortunately, in most studies the physiological consequences of various control techniques are unknown, or incompletely understood, which raises the question of what are the intensities of cutting and/or herbicide required to get a significant reduction in aquatic weed biomass.

Timing is important in aquatic plant management techniques if optimum results are to be required. The amount of rhizomes storage carbohydrate is an excellent time indicator for control application. A plant phenological study indicates the weakest life cycle stages, during which optimum control effect can be gained. The greatest biomass reduction in the year following treatment was obtained when cutting and/or herbicide was applied at the lowest carbohydrate reserved, generally during the flowering stage. It is recommended that shoots should be removed when their carbohydrate content is higher than that of the underground parts. However, a single cut and/or herbicide application during any stage (including the above) of the growing season is inadequate to obtain an effective aquatic weed control. Therefore, frequency and intervals of control application must be considered.

4.1. *Typha latifolia*

The present study suggests that the success of control measures is affected by several factors. Frequent cutting of *T. latifolia* in one growing season caused a high biomass reduction, and the rhizomes became weaker. After one cut, *T. latifolia* produces longer and thinner shoots which compensate the carbohydrate storage in the rhizomes. Sundblad (1990) reported that shoot density of *Glyceria maxima* increased after a single cut and reached its maximal competitive ability. In contrast, competitive ability of *T. latifolia* decreased after cutting. Tall foliage leaves of *T. latifolia* gave it a greater potential competitive interaction than other neighbour plants. *T. latifolia*'s high competitive ability could be due to its fast regenerative growth rate and its growth form. Shade produced by the uncut control plant canopies suppresses the

growth of the associated plant species. After cutting above the water level, reserves of carbohydrates were assigned to growth and elongation of rhizomes rather than developing new leaves. However, no differences in shoot biomass were observed between control and one cut treated sites.

Aquatic plant management by cutting mainly depends on water depth, frequency of cutting, and time of cutting. Ideally, *T. latifolia* shoots should be cut below the water surface and just before flowering when most of the plant reserves nutrients are located in the foliage. Shoot growing points were deeper than the cutting level and some were embedded in soil, at mid-May before flowering. Therefore, cutting was not effective at this time. After early cutting, new thinner shoots grew from nodes on the underground rhizomes resulting in high shoot density later in the season. Thus, there was no difference between earlier cut and uncut shoots. Similar results were obtained by van der Toorn and Mook (1982) on *Phragmites australis* and Ham *et al.* (1982) on *Ranunculus penicillatus*. They concluded that cutting during early growth stages leads to a new crop of similar density as the previous crop, with biomass only been reduced after a late second cut.

At most of the experimental sites uncut *T. latifolia* flowered from mid-July to early September. Plants cut in mid-May regrew but did not flower. Many studies agreed with these research findings (e.g. Sale & Wetzel, 1983; Husak, 1986). The present study shows that late-June to early-August is the best time for cutting (in Northern Hemisphere conditions), when carbohydrate reserves in the rhizomes are low, and just before the inflorescence appears. Westlake (1968), Dawson (1976) and Singh and Moolani (1976) suggested that cutting *T. latifolia* before flowering in spring may stimulate further growth. In Possil Marsh the cutting results confirmed this and indicated that when *T. latifolia* was cut before flowering, extensive regrowth at the beginning of August resulted. Similar rapid regrowth of *T. latifolia* after cutting was observed at Lochwinnoch and Lochan Dubh sites. Despite a change in canopy formation, there were no significant differences in biomass between the control and cut, in the early growing season, in all experimental sites.

The findings of the present study suggest that regrowth of *T. latifolia* was not severely inhibited after cutting. Studies on *T. latifolia* regrowth following various

cuttings regimes confirmed the above results. It is convenient to segregate short-term (the year of the cutting) and long-term (one or more years after cutting) effects.

4.1.1. Short-term effects

The present study indicates that substantial regrowth occurred following an early single cut in the same year, but two and three cuts were more effective in reducing the plant regrowth.

4.1.2. Long-term effects

The present study indicates that cutting, even once per growing season, can reduce *T. latifolia* growth, but greater reduction occurred after two or three cuts. A single cut at flowering time decreased carbohydrate reserves for the following year, which in turn reduced plant biomass and carbohydrate stored in the next year. Consequently, changes in carbohydrate allocation patterns were responsible for changes in biomass dynamics. Soulsby (1974) suggested that there is an optimum time for removal of each species. This study showed that cutting at flowering time (late-June to late-August) had great influence on the growth pattern of *T. latifolia*.

Results from experiments 5 and 6 indicated that stress caused by glyphosate had reduced the growth rate of *T. latifolia*. Slower growth rate was observed when stress combined by disturbance (e.g. cutting and water level fluctuation). Despite a better growth in absence of competitors, there was no effect of neighbour species on *T. latifolia*. *T. latifolia*, is a competitive species and with some stress-tolerance potential. Grime *et al.* (1988) allocate a 'competitive' (C) strategy to *T. latifolia*. My findings suggest at least some element of stress-tolerance, but little ability to tolerate disturbance in the population of this plant studied here. Using the terminology of Murphy *et al.* (1990) might perhaps be the best strategy of *T. latifolia* designated as C to C (S).

Grace and Wetzel (1981a, b; 1982) indicated that *T. latifolia* has a high population variability in vegetative growth, flowering, and survival under different environmental conditions. Transplanting *T. latifolia* from deep to shallower water enhanced its vegetative growth and flowering compared with *T. latifolia* transplanted from shallow to deeper water. *T. latifolia* transplanted from shallow to deeper water

at Lochwinnoch were more susceptible to water depth and disturbance (cutting) than Possil Marsh and Lochan Dubh plants. The reserved plant carbohydrate and light were the most important factors affecting transplanting (as described in section 3.3.5). Successful transplants may require more incident light than the is required to maintain established populations, particularly during the early stage after transplanting. Poor growth of *T. latifolia* after transplanting may be due to the dark water colour which in turn caused low light intensity.

4.2. *Salvinia rotundifolia*

Salvinia has lower carbohydrate content at its early growth stage, which is divided between the root and shoot systems.

During the middle phase of growth, density increased. However, there is a slow increase in average plant size as a result of intraspecific competition. Root carbohydrate allocation stabilises, then begins to decline. Leaves change to the folded form, and the mass of the mat provides the buoyancy needed to remain at the surface. The production and separation of daughter plants in this stage were high.

In the mature stage, density starts to decrease as a result of competition and self-thinning. Intense competition resulted with a rapid increase of average plant size. Root allocation continues to decline in mature stands.

Unlike *T. latifolia*, managing *Salvinia* spp. at early growth stages resulted in an higher control efficiency and reduced treatment costs. Early herbicide applications also improved their effectiveness, since growth rates at the early stages are slower, there is less biomass to control, and most of the leaves are unfolded.

As discussed in experiments 7 and 8 *Salvina* plants proved highly susceptible to the stress caused by shading and herbicide treatment, with the lethal concentration at least 1.5 mg l^{-1} diquat. At sub-lethal doses of diquat *Salvinia* showed symptoms of damage (e.g. colour loss) induced by the herbicide stress. They damage may make the plant more vulnerable to disturbance or competition. However disturbance alone was highly ineffective as a means of damaging *Salvinia*. *Salvinia* by producing more daughter plants after crushing is highly disturbance tolerant. This characteristic allows *Salvinia* to exploit and monopolize new sites very quickly and, once established this

At flowering time, most of the tuber nutrients are translocated to the upper shoots. When stored carbohydrate are at their minimum, management techniques will have the maximum effects (Fig. 4.1). In order to prevent excessive summer growth and destroy the aboveground biomass before new tuber production in autumn, management should be applied at late-May to early-June. During this period plants have a low carbohydrate content.

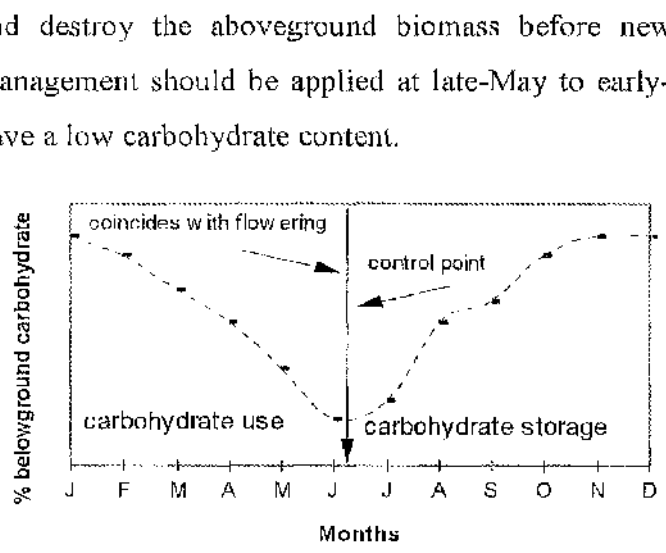


Fig. 4.1. Below-ground carbohydrate concentration and control point identification

light is a major factor for growth and control of the *P. pectinatus* (van Vierssen, 1990; van Dijk & van Vierssen, 1991). In aquatic ecosystems, however, light availability can be strongly reduced by both abiotic and biotic factors. Because of this shading aquatic macrophytes have generally been considered as shade plants (Spencer & Bowes, 1990).

Damage caused by cutting is an important factor in reducing plant growth, but it does not seem likely that *P. pectinatus* growth will be severely effected by cutting. Cutting could be an important factor in succession process in most freshwater systems. *P. pectinatus* is a competitive species (Grillas, 1988). Disturbing the dense canopy of *P. pectinatus* by cutting may give other species to take over (Grillas, 1988).

In experiments 10-12 *P. pectinatus* recovered following cutting, this being strongly dependent on tuber pressure below-ground. In order to obtain a more effective control the cutting regime should be applied to the most vulnerable part of the life cycle. The plants are cut when they are already full grown and have become a nuisance. However, by that time the plants will have developed new tubers which will

enable regrowth. If the plants are cut during the flowering, when maximum carbohydrate reserves are in the shoots, and prior to new tubers formation, the growth of *P. pectinatus* will be reduced. Van Wijk (1988) suggested that the best time for controlling *P. pectinatus* by cutting is at the beginning of the growing season, when tubers have not been formed. However, this study showed that the weakest life cycle stage varies from year to year, for two reasons. In many areas water levels were too high and plants were small at the early stage of the growing season. Second, plants such as *P. pectinatus* stored high carbohydrate contents at the beginning of the growing season at high levels when application of cut at this stage will not retarded the plant regrowth.

Considering the results from this thesis, the control of *P. pectinatus* by cutting the above-ground biomass did not highly affect the plant growth. In addition to the potential increase in sexual reproduction, cutting plants may also lead to an increase in vegetative reproduction (Caffrey, 1990). Removal of the above-ground parts had increased branching and biomass, and number of tubers may increase. Finally, an increase in the biomass of photosynthetically active parts of the plants could lead to an increase in starch production. Starch is usually stored in the tuber and rhizome system. Excess starch could lead to an increase in the rhizomatous shoots, faster growth rates of the existing shoots, and increase in numbers or growth rates of shoots in the next growing seasons. The present research indicated that even two cuts in one growing season had no impact on the next year's population development.

The experimental results showed that the control of *P. pectinatus* largely depends on managing the tuber bank. This finding agrees with the results of van Vierssen and Hootsmans (1990) who reported that for species such as *P. pectinatus*, tubers play an essential role in reproduction. Bottom dredging seems to be a very effective control method since this directly affects the below-ground propagule banks.

Van Wijk (1988, 1989) provided evidence that *P. pectinatus* can survive as a 'competitor' a ' stress-tolerating' or a 'ruderal' species. According to this study and that of by van Wijk (1989), *P. pectinatus* has several characteristics of a 'stress-tolerator', but there are still many unanswered questions into general strategy concepts of water plants. In most aquatic systems it is not clear exactly what factors limit the growth of macrophytes. Therefore, it is sometimes difficult to determine

which factor must be defined as 'stress'. Various light regimes caused high differences in total biomass. Van Dijk van Vierssen and (1991) reported that under low light conditions *P. pectinatus* allocated more carbohydrate to the tubers. In contrast, under stress caused by herbicide (experiments 10-12) there was a significant reduction in number and weight of tubers. On the other hand, different populations of *P. pectinatus* under greenhouse and field conditions sometimes show different responses to stress and disturbance. Although previously allocated a CR stategy category (= CD: Murphy *et al.* 1990), evidence for stress-tolerance suggests that its strategy is probably more intermediate: CSR in Grime's (1979) classification.

An extensive review of life cycles and survival strategies among aquatic plants, combined with data on terrestrial plant ecology and population biology is necessary for further research. A broad range of research focusing on ecology, genetics, population biology and ecophysiology on macrophytes species is necessary to make survival strategies of aquatic macrophytes clearer and more specific.

The present study demonstrates that focusing on the survival strategy is an effective way to understand the ecological functioning of populations. The greenhouse and field studies were useful to understand the important parts of the survival strategy and ecology of target species. Other parts such as factors limiting growth, factors inducing tuber, rhizome and daughter plant formation, and the differentiation of these three species in relation to life cycles still remain unclear and need some further research. The more competitive interaction of target plants and relevant species should also be investigated.

5. References

5. References

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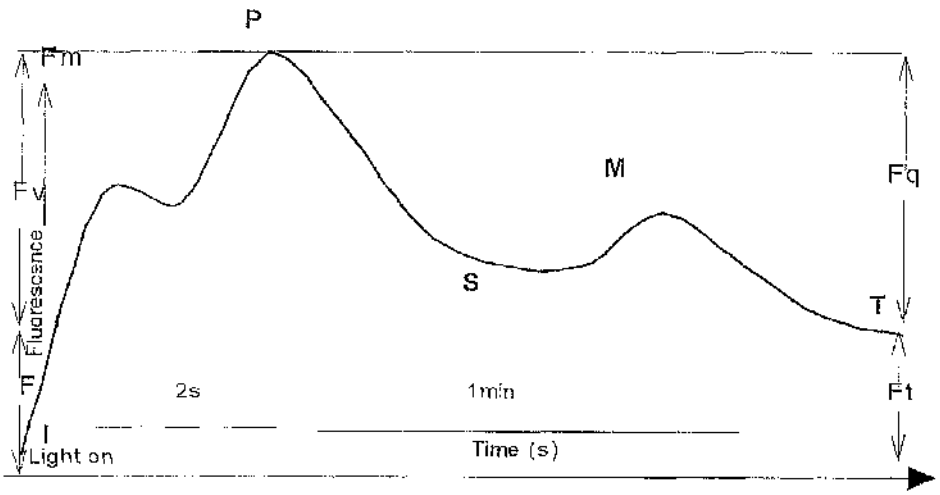
6. Appendices

Appendix 1.



Appendix 1. The kinetics of *in vivo* fluorescence induction. The light is turned on at zero time following pre-darkening of the leaf for 15 minutes. The symbols I-P-S-M-T are listed to describe the various transients of the induction curve. Fo, initial level of fluorescence, attained within a few milliseconds of the onset of illumination. Fm, maximum fluorescence during induction period, attained at P; Fv, variable fluorescence [=(Fm-Fo) / Fo]; Ft, steady state level of fluorescence attained at T; Fq, fluorescence quenching [=(Fm-Ft) / Fo) (Smith, 1981).

Appendix 2. Seed germination of *Typha latifolia* under different environmental conditions

Sand sediment

Depth (cm)	Full light	Low shade	High shade
Rep1			
0	95	53	27
0.5	12	3	3
1	0	3	10
1.5	0	3	6
2	1	1	1
2.5	0	2	2

Clay- Sand sediment

Depth (cm)	Full light	Low shade	High shade
Rep1			
0	20	35	63
0.5	3	3	3
1	0	1	1
1.5	0	1	0
2	1	0	0
2.5	2	3	0

Sand sediment

Depth (cm)	Full light	Low shade	High shade
Rep2			
0	100	63	44
0.5	10	1	10
1	1	3	3
1.5	0	1	1
2	1	1	2
2.5	1	1	3

Clay-Sand sediment

Depth (cm)	Full light	Low shade	High shade
Rep2			
0	34	21	51
0.5	1	4	0
1	0	2	4
1.5	1	2	0
2	0	1	1
2.5	0	0	1

Sand sediment

Depth (cm)	Full light	Low shade	High shade
Rep3			
0	95	35	7
0.5	5	3	12
1	0	2	1
1.5	2	0	0
2	1	0	0
2.5	0	6	0

Clay-Sand sediment

Depth (cm)	Full light	Low shade	High shade
Rep3			
0	46	12	27
0.5	0	3	0
1	1	1	0
1.5	0	1	0
2	0	1	0
2.5	5	1	0

Appendix 3. Effects of cutting, water level and competiton on *Typha latifolia* when grown from rhizomes

Treatments	Depth (5-10 cm)		Depth (20-30 cm)		Depth (60-80 cm)	
Plot 1	Dw (g)	S l* (cm)	Dw (g)	S l (cm)	Dw (g)	S l (cm)
no cut / no com*	20.06	129	13.37	127	30.83	151
1 cut / no com	36.53	158	4.68	74	13.90	142
2 cut / no com	0	0	4.61	69	3.39	48
3 cut / no com	0	0	0	0	0	0
no cut / com	6.73	74	17.3	155	27.23	170
1 cut / com	6.11	59	9.532	116	8.28	146
2 cut / com	8.61	91	7.99	88	8.18	145
3 cut / com	0	0	0	0	0	0
Treatments	Depth (5-10 cm)		Depth (20-30 cm)		Depth (60-80 cm)	
Plot 2	Dw (g)	S l* (cm)	Dw (g)	S l (cm)	Dw (g)	S l (cm)
no cut / no com*	20.21	129	20.52	112	18.08	117
1 cut / no com	2.95	55	11.58	120	9.37	115
2 cut / no com	0	0	6.70	78	5.08	132
3 cut / no com	0	0	0	0	0	0
no cut / com	15.61	110	19.7	141	11.69	126
1 cut / com	2.86	72	8.56	75	3.25	62
2 cut / com	0	0	5.645	58	0	0
3 cut / com	0	0	0	0	0	0
Treatments	Depth (5-10 cm)		Depth (20-30 cm)		Depth (60-80 cm)	
Plot 3	Dw (g)	S l* (cm)	Dw (g)	S l (cm)	Dw (g)	S l (cm)
no cut / no com*	29.82	155	13.31	99	43.09	202
1 cut / no com	6.79	121	7.90	84	7.10	123
2 cut / no com	2.84	96	0	0	0.90	77
3 cut / no com	0	0	0	0	0	0
no cut / com	33.71	179	14.86	163	38.02	174
1 cut / com	7.35	137	7.09	93	30.23	195
2 cut / com	0	0	2.2	36	3.28	129
3 cut / com	0	0	0	0	0	0

Sl = shoot length
com = competition

Appendix 4. Effects of cutting and shading on *Typha latifolia* grown from seeds

Treatments	no shade		shade	
	Shoot length (cm)	Dry weight (g)	Shoot length (cm)	Dry weight (g)
no cut	45	1.325	16	0.010
cut 1	13	0.0185	11	0.0066
cut 2	10	0.0045	7	0.0029
Treatments	no shade		shade	
	Shoot length (cm)	Dry weight (g)	Shoot length (cm)	Dry weight (g)
no cut	46	0.182	18	0.0122
cut 1	16	0.0149	14	0.0088
cut 2	12	0.0063	8	0.0035
Treatments	no shade		shade	
	Shoot length (cm)	Dry weight (g)	Shoot length (cm)	Dry weight (g)
no cut	111	2.2	9	0.010
cut 1	23	0.169	7	0.0096
cut 2	9	0.141	4	0.0049
Treatments	no shade		shade	
	Shoot length (cm)	Dry weight (g)	Shoot length (cm)	Dry weight (g)
no cut	91	0.641	19	0.0536
cut 1	43	0.020	11	0.0152
cut 2	13	0.0034	3	0.00716
Treatments	no shade		shade	
	Shoot length (cm)	Dry weight (g)	Shoot length (cm)	Dry weight (g)
no cut	45	1.325	16	0.010
cut 1	13	0.0185	11	0.0066
cut 2	10	0.0045	7	0.0029
Treatments	no shade		shade	
	Shoot length (cm)	Dry weight (g)	Shoot length (cm)	Dry weight (g)
no cut	101	1.276	16	0.0195
cut 1	49	0.0686	10	0.00295
cut 2	18	0.036	14	0.0024
Treatments	no shade		shade	
	Shoot length (cm)	Dry weight (g)	Shoot length (cm)	Dry weight (g)
no cut	74	0.979	20	0.011
cut 1	42	0.276	17	0.00715
cut 2	38	0.202	4	0.0017
Treatments	no shade		shade	
	Shoot length (cm)	Dry weight (g)	Shoot length (cm)	Dry weight (g)
no cut	90	1.09	32	0.024
cut 1	19	0.0062	26	0.0124
cut 2	27	0.0715	17	0.0059
Treatments	no shade		shade	
	Shoot length (cm)	Dry weight (g)	Shoot length (cm)	Dry weight (g)
no cut	122	2.802	39	0.071
cut 1	87	0.104	16	0.0063
cut 2	49	0.0486	6	0.0037

Appendix 5. Transplant experiment in Lochwinnoch

Treatments	Transplanted		Untransplanted	
Plot 1	Dw (g)	S l* (cm)	Dw (g)	S l (cm)
no cut / no com*	31.22	167	13.45	123
1 cut / no com	10.279	122	38.39	161
2 cut / no com	2.116	84	19.19	168
3 cut / no com	0.248	33	0	0
no cut / com	10.45	143	19.09	110
1 cut / com	15.20	128	8.22	87
2 cut / com	6.314	126	6.78	75
3 cut / com	0.793	58	0	0
Treatments	Transplanted		Untransplanted	
Plot 2	Dw (g)	S l (cm)	Dw (g)	S l (cm)
no cut / no com	23.11	170	26.57	196
1 cut / no com	18.95	158	11.08	139
2 cut / no com	3.54	99	2.519	68
3 cut / no com	2.037	47	0	0
no cut / com	14.41	143	22.34	182
1 cut / com	14.29	165	20.03	183
2 cut / com	6.049	115	13.54	118
3 cut / com	0	0	0	0
Treatments	Transplanted		Untransplanted	
Plot 3	Dw (g)	S l (cm)	Dw (g)	S l (cm)
no cut / no com	19.72	163	22.146	185
1 cut / no com	8.21	126	8.60	120
2 cut / no com	7.60	123	13.2	157
3 cut / no com	0	0	0.715	29
no cut / com	17.07	157	30.31	182
1 cut / com	12.87	136	24.88	168
2 cut / com	18.18	150	5.66	95
3 cut / com	0.824	17	0	0
Treatments	Transplanted		Untransplanted	
Plot 4	Dw (g)	S l (cm)	Dw (g)	S l (cm)
no cut / no com	12.89	109	28.97	166
1 cut / no com	23.65	164	9.64	111
2 cut / no com	9.73	98	0	0
3 cut / no com	0	0	1.04	39
no cut / com	11.35	122	11.84	142
1 cut / com	16.87	1	11.60	84
2 cut / com	11.46	133	8.80	73
3 cut / com	0	0	0	0

Appendix 6. Transplants of *Typha* grown from seeds to Possil Marsh and Lochan Dubh

Possil Marsh

Treatments				
20 cm depth	Dw (g)	sl (cm)	ll (cm)	nl
no cut	6.34	118	85	9
1 cut	4.40	66	51	5
2 cut	1.11	37	28	5
40 cm depth				
no cut	6.06	76	61	6
1 cut	2.30	85	68	6
2 cut	1.53	41	26	4

Lochan Dubh

20 cm depth	Dw (g)	sl (cm)	ll (cm)	nl
no cut	4.93	102	76	10
1 cut	3.51	69	51	7
2 cut	0	0	0	0
40 cm depth				
no cut	2.87	55	39	6
1 cut	0.373	21	15	3
2 cut	0	0	0	0

Appendix 7. Mean results of the effects of herbicide (glyphosate) and transplanting on *Typha* in Possil Marsh

Treatments	Transplanted					Untransplanted				
0-10 cm depth	Dw (g)	sl (cm)*	ll (cm)*	ns*	nl*	Dw (g)	sl (cm)	ll (cm)	ns	nl
control	9.08	73	66	2.83	6.33	7.90	70	60	2.25	5.25
1 kg a.i/ha	4.69	57.6	42	1.90	4.33	6.29	50.33	40.66	1.91	3.16
2 kg a.i/ha	0	0	0	0	0	1.49	20.33	11.33	1	1.5
4 kg a.i/ha	0	0	0	0	0	0	0	0	0	0
20-40 cm depth										
control	3.88	69.5	60.16	2.91	6.33	5.96	90.08	50.33	3.25	6.33
1 kg a.i/ha	3.01	54.66	39.66	1.16	4	3.27	58.33	48.66	3	4.16
2 kg a.i/ha	2.42	39	22	2.08	2	4.06	66.66	59.33	2	5.33
4 kg a.i/ha	0	0	0	0	0	0	0	0	0	0

sl = shoot length
ll = leaf length
ns = number of shoots per plant
nl = number of leaves per plant

Appendix 8. Late season application of glyphosate on *Typha latifolia*

Treatments				
Plot 1	Dw (g)	sl (cm)*	nl*	ns*
control	205.64	134	7	85
0.5 kg a.i/ha	185.06	125	7	73
1 kg a.i/ha	171.53	111	5	80
1.5 kg a.i/ha	176.82	103	6	60
2 kg a.i/ha	123.98	88	5	38
3 kg a.i/ha	82.59	92	5	31
4 kg a.i/ha	51.74	69	4	23
Plot 2				
control	185.5	128	7	99
0.5 kg a.i/ha	156.39	101	6	91
1 kg a.i/ha	136.84	91	5	79
1.5 kg a.i/ha	82.70	89	5	66
2 kg a.i/ha	50.23	69	6	50
3 kg a.i/ha	44.05	50	4	50
4 kg a.i/ha	35.25	50	4	39
Plot 3				
control	182.93	111	7	101
0.5 kg a.i/ha	174.16	89	6	100
1 kg a.i/ha	134.41	76	6	80
1.5 kg a.i/ha	80.17	70	6	65
2 kg a.i/ha	76.32	77	5	49
3 kg a.i/ha	70.01	69	5	42
4 kg a.i/ha	48.81	70	4	26
Plot 4				
control	202	142	7	107
0.5 kg a.i/ha	165.69	123	6	88
1 kg a.i/ha	153.11	119	6	91
1.5 kg a.i/ha	108.86	94	6	69
2 kg a.i/ha	73.26	77	5	48
3 kg a.i/ha	48.04	82	5	37
4 kg a.i/ha	36.03	69	4	30

sl = shoot length (cm)
nl = number of leaves per plant
ns = number of shoots per m^2

Appendix 9. Effects of diquat on *Salvinia rotundifolia*

Treatments	First application				Second application			
Block 1	cdw (g)*	pdw*	rl (cm)*	la (cm2)*	cdw (g)*	pdw*	rl (cm)*	la (cm2)*
control	0.8139	0.1455	27.5	21	0.45	0.0334	14	13
0.25 mg l^{-1}	0.7499	0.1432	22	12	0.3814	0.0309	8.5	8
0.5 mg l^{-1}	0.613	0.1181	19.68	12	0.3573	0.0239	5	6
0.75 mg l^{-1}	0.4832	0.098	9.43	9	0.2905	0.0127	4.33	6
1 mg l^{-1}	0.1706	0.0332	6.66	9	0.1318	0.0087	2	6
1.25 mg l^{-1}	0.0099	0.0043	3.07	8	0.1185	0.0054	1.32	5
1.5 mg l^{-1}	0.0171	0.0021	1.99	7.5	0.0139	0.0007 7	0.75	4.5
Block 2								
control	1.1090	0.191	30.7	24	0.5415	0.0409	15.5	12
0.25 mg l^{-1}	0.8726	0.1693	26.8	14	0.3185	0.0139	11	9
0.5 mg l^{-1}	0.7962	0.1545	20.75	12	0.2071	0.0116	7.8	8
0.75 mg l^{-1}	0.6527	0.1020	14.33	12	0.1088	0.0091	4.5	8
1 mg l^{-1}	0.2914	0.0318	8.75	10	0.0466	0.0144 6	3.33	8
1.25 mg l^{-1}	0.0141	0.0043	4.78	88	0.077	0.0027	1.7	6
1.5 mg l^{-1}	0.0534	0.0013	2.2	8	0.0029	0.0017	0.99	5
Block 3								
control	1.027	0.1524	25.5	16	0.2449	0.0287	16	10
0.25 mg l^{-1}	0.8572	0.1340	21	13	0.077	0.0351	12.5	10
0.5 mg l^{-1}	0.6388	0.095	17.76	8	0.1567	0.023	7.5	8
0.75 mg l^{-1}	0.5194	0.083	13.5	8	0.1496	0.0306	5	7
1 mg l^{-1}	0.3119	0.049	6.7	7	0.1213	0.0118	3.75	6
1.25 mg l^{-1}	0.0891	0.0045	2.5	7	0.0671	0.0077	1.5	5
1.5 mg l^{-1}	0.0079	0.00124	1.35	6	0.0346	0.002	0.75	5
Block 4								
control	0.8508	0.1480	34	18	0.2419	0.0183	11.66	11
0.25 mg l^{-1}	0.7067	0.1233	26.5	10	0.3	0.0222	8.75	9
0.5 mg l^{-1}	0.6087	0.095	18.75	99	0.1118	0.0273	6.5	8.5
0.75 mg l^{-1}	0.4407	0.0813	10	10	0.1362	0.0121	5.23	7
1 mg l^{-1}	0.2377	0.0295	7	10	0.0824	0.0093	3	7
1.25 mg l^{-1}	0.0311	0.0295	4	10	0.0147	0.0051	1.86	7
1.5 mg l^{-1}	0.0051	0.0029	2	6	0.0066	0.0026	0.5	5

cdw = clone dry weight (g)
pdw = plant dry weight
rl = root length (cm)
la = leaf area (cm^2)

Appendix 10. Effects of shading and crushing on *salvinia rotundifolia*

Treatments						
Block 1	pcdw (g)	pdw (g)	la (cm2)	rl (cm)	dpec	npec
control	1.889	0.1508	8.66	56.66	4.66	12
1 crush \ no shade	1.473	0.1928	9.6	75	6.33	15.33
2 crush \ no shade	0.762	0.0651	9.5	43.33	5	20.66
1 crush \ no shade	0.1199	0.0384	8	11.66	4	3.5
1 crush \ shade	0.1794	0.0561	7	13	3.33	7
2 crush \ shade	0.1138	0.0259	6	19.66	2.33	4.66
Block 2						
control	0.2589	0.0505	5.5	37.33	10	7
1 crush \ no shade	1.429	0.1301	12.66	75.33	9.6	15
2 crush \ no shade	0.684	0.1362	8	46.33	9	17.66
1 crush \ no shade	0.1250	0.0365	7.5	17.33	2.33	6
1 crush \ shade	0.2228	0.0499	8	17.5	2.33	7.33
2 crush \ shade	0.0987	0.0345	6	9.66	2	5
Block 3						
control	0.2706	0.0662	9.5	43.33	6.66	8.66
1 crush \ no shade	1.087	0.0889	12	60.33	12.33	22
2 crush \ no shade	1.183	0.0634	9	49	5.5	15.33
1 crush \ no shade	0.1051	0.0438	7	13	3	5.66
1 crush \ shade	0.5937	0.0654	8	18.28	4.33	9.66
2 crush \ shade	0.2037	0.0608	7.66	14.33	1	5.66

pcdw = plant clone dry weight (g)
pdw = plant dry weight (g)
la = leaf area (cm^2)
rl = root length (cm)
dpec = daughter plant in each clone
npec = number of plants in each clone

Appendix 11. Competition between *Salvinia rotundifolia* and *Pistia stratiotes*.

Block 1

Initial plant density	Initial plant FW (g) 3. Feb. 1996		FW (g) 3. Mar. 1996		FW (g) 17. Mar. 1996		FW (g) 3. Apr. 1996	
150 µE. m^{-2} s^{-1}	*Salvinia*	*Pistia*	*Salvinia*	*Pistia*	*Salvinia*	*Pistia*	*Salvinia*	*Pistia*
6-0	60	0	142	0	221	0	300	0
4-2	43	24	87	44	156	29	357	94
3-3	32	35	83	59	149	78	228	100
2-4	20	40	65	60	109	90	173	105
0-6	0	66	0	80	0	104	0	145
Initial plant density	Initial plant FW (g) 3. Feb. 1996		FW (g) 3. Mar. 1996		FW (g) 17. Mar. 1996		FW (g) 3. Apr. 1996	
100 µE. m^{-2} s^{-1}	*Salvinia*	*Pistia*	*Salvinia*	*Pistia*	*Salvinia*	*Pistia*	*Salvinia*	*Pistia*
6-0	60	0	115	0	175	0	252	0
4-2	43	24	110	20	186	32	264	45
3-3	32	35	77	33	122	45	192	67
2-4	20	40	67	55	102	77	144	90
0-6	0	66	0	95	0	86	0	123
75 µE. m^{-2} s^{-1}	*Salvinia*	*Pistia*	*Salvinia*	*Pistia*	*Salvinia*	*Pistia*	*Salvinia*	*Pistia*
6-0	60	0	168	0	220	0	318	0
4-2	43	24	86	26	163	35	212	46
3-3	32	35	59	47	116	59	133	80
2-4	20	40	63	45	102	63	132	76
0-6	0	66	0	77	0	102	0	137

Block 2

150 µE. m^{-2} s^{-1}	*Salvinia*	*Pistia*	*Salvinia*	*Pistia*	*Salvinia*	*Pistia*	*Salvinia*	*Pistia*
6-0	60	0	125	0	230	0	343	0
4-2	43	24	59	25	154	41	258	55
3-3	32	35	53	41	123	49	178	61
2-4	20	40	40	62	75	85	100	115
0-6	0	66	0	100	0	86	0	139
100 µE. m^{-2} s^{-1}	*Salvinia*	*Pistia*	*Salvinia*	*Pistia*	*Salvinia*	*Pistia*	*Salvinia*	*Pistia*
6-0	60	0	126	0	225	0	260	0
4-2	43	24	69	18	140	25	157	54
3-3	32	35	84	31	124	46	178	57
2-4	20	40	42	58	80	84	82	105
0-6	0	66	0	94	0	106	0	152
75 µE. m^{-2} s^{-1}	*Salvinia*	*Pistia*	*Salvinia*	*Pistia*	*Salvinia*	*Pistia*	*Salvinia*	*Pistia*
6-0	60	0	119	0	186	0	249	0
4-2	43	24	93	30	146	39	204	55
3-3	32	35	60	59	90	85	128	52
2-4	20	40	26	67	51	88	73	99
0-6	0	66	0	83	0	127	0	128

Block 3

150 µE. m^{-2} s^{-1}	*Salvinia*	*Pistia*	*Salvinia*	*Pistia*	*Salvinia*	*Pistia*	*Salvinia*	*Pistia*
6-0	60	0	98	0	187	0	260	0
4-2	43	24	79	24	233	60	183	40
3-3	32	35	42	46	60	44	184	70
2-4	20	40	26	62	56	104	79	122
0-6	0	66	0	75	0	141	0	176
100 µE. m^{-2} s^{-1}	*Salvinia*	*Pistia*	*Salvinia*	*Pistia*	*Salvinia*	*Pistia*	*Salvinia*	*Pistia*
6-0	60	0	109	0	198	0	245	0
4-2	43	24	50	28	100	50	89	70
3-3	32	35	51	35	62	51	90	76
2-4	20	40	21	53	31	79	38	98
0-6	0	66	0	60	0	127	0	146
75 µE. m^{-2} s^{-1}	*Salvinia*	*Pistia*	*Salvinia*	*Pistia*	*Salvinia*	*Pistia*	*Salvinia*	*Pistia*
6-0	60	0	106	0	161	0	212	0
4-2	43	24	80	39	157	44	209	65
3-3	32	35	67	26	115	37	156	56
2-4	20	40	17	61	34	99	128	52
0-6	0	66	0	80	0	92	0	112

Number of plants

Initial plant density (3.Feb.96)	Number of plants 3. Apr. 1996 150 µE. m^{-2} s^{-1}		Number of plants 3. Apr. 1996 100 µE. m^{-2} s^{-1}		Number of plants 3. Apr. 1996 75 µE. m^{-2} s^{-1}	
Block 1	*Salvinia*	*Pistia*	*Salvinia*	*Pistia*	*Salvinia*	*Pistia*
6-0	58	0	51	0	80	0
4-2	60	6	72	7	25	8
3-3	38	11	22	8	42	12
2-4	29	8	29	7	25	8
0-6	0	12	0	15	0	8
Block 2	*Salvinia*	*Pistia*	*Salvinia*	*Pistia*	*Salvinia*	*Pistia*
6-0	76	0	80	0	65	0
4-2	48	3	25	3	36	7
3-3	35	5	43	7	18	7
2-4	23	7	26	8	14	9
0-6	0	8	0	12	0	9
Block 3	*Salvinia*	*Pistia*	*Salvinia*	*Pistia*	*Salvinia*	*Pistia*
6-0	57	0	67	0	62	0
4-2	37	3	37	5	65	11
3-3	16	7	36	5	29	8
2-4	14	9	14	9	14	14
0-6	0	14	0	10	0	11

Plant Dry weight

Initial plant density (3.Feb.96)	Plant Dry weight (g) 3. Apr. 1996 150 µE. m^{-2} s^{-1}		Plant Dry weight (g) 3. Apr. 1996 100 µE. m^{-2} s^{-1}		Plant Dry weight (g) 3. Apr. 1996 100 µE. m^{-2} s^{-1}	
Block 1	*Salvinia*	*Pistia*	*Salvinia*	*Pistia*	*Salvinia*	*Pistia*
6-0	7.48	0	4,38	0	6.37	0
4-2	5.96	3.97	4.37	1.6	3.57	1.67
3-3	4.09	4.41	3.12	2.45	2.56	3.15
2-4	2.72	4.7	2,16	3.57	2.36	3.05
0-6	0	8.132	0	6.16	0	5.3
Block 2	*Salvinia*	*Pistia*	*Salvinia*	*Pistia*	*Salvinia*	*Pistia*
6-0	5.7	0	5.132	0	5.64	0
4-2	4.89	2.53	3.03	1.49	4.38	2.31
3-3	4.05	3.23	1.99	2.21	1.8	3.94
2-4	2.6	5.53	1.42	4.78	1.29	4.18
0-6	0	5.84	0	5.83	0	5.8
Block 3	*Salvinia*	*Pistia*	*Salvinia*	*Pistia*	*Salvinia*	*Pistia*
6-0	5.72	0	4.65	0	4.19	0
4-2	4.22	1.724	1.58	3.94	3.79	2.53
3-3	3.14	2.17	2.42	2.83	3.28	2.29
2-4	1.67	5.66	0,771	4.42	3.58	4.97
0-6	0	6.86	0	4.94	0	6.73

Appendix 12. Effects of diquat concentrations and exposure times on *Potamogeton pectinatus*

Block 1

Treatment	Con (mg l^{-1})*	E.T. (hr)*	Dw (g)*	SL (cm)*	LL (cm)*	NSPP*	NLSB*	SBL*	NLP*	NT*
control	0.00	-	0.2710	65	12	22	4	13	168	34.66
1		1	0.1166	48	11	13	4	14	90	16.66
2		2	0.0665	42	8	11	3	11	33	13
3	0.1	12	0.0199	13	6	15	2	6	30	8
4		24	0.0376	28	4	15	2	4	30	4.33
5		48	0.0082	15	2	2	2	8	10	0
6		96	0.0073	14	2	6	2	4	12	0
7		168	0.083	42	12	16	3	14	48	9
control	0.00	-	0.2835	44	11	32	4	14	64	34.33
1		1	0.0539	28	8	14	4	11	55	12.66
2		2	0.02037	22	5	6	2	6	27	10.66
3	0.2	12	0.0101	10	2	6	2	3	12	8
4		24	0.0423	24	3	26	2	6	52	4.66
5		48	0.0073	10	1	4	1	2	4	0
6		96	0.0052	17	1	5	1	2	55	0
7		168	0	0	0	0	0	0	0	4.66

Block 2

Treatment	Con (mg l^{-1})*	E.T. (hr)*	Dw (g)*	SL (cm)*	LL (cm)*	NSPP*	NLSB*	SBL*	NLP	NT
control	0.00	-	0.2018	72	11	28	4	18	124	36
1		1	0.0544	43	10	10	4	14	40	14.33
2		2	0.01228	29	4	6	3	6	18	10
3	0.1	12	0.05723	18	5	19	2	8	38	9.5
4		24	0.01524	21	5	7	3	7	21	5
5		48	0.0079	11	3	5	2	5	10	0
6		96	0.0225	24	3	6	2	6	6	0
7		168	0.0377	34	14	9	3	13	29	7
control	0.00	-	0.2835	57	14	29	4	18	116	32
1		1	0.089	54	12	21	4	15	84	11
2		2	0.093	40	10	26	4	12	104	11.25
3	0.2	12	0.02706	32	9	8	3	12	24	6.5
4		24	0.0094	17	2	3	2	3	6	5.5
5		48	0.0138	27	1	17	1	3	17	0
6		96	0.0085	19	1	3	2	2	5	0
7		168	0.0125	18	11	4	4	15	16	4.5

Block 3

Treatment	Con (mg l^{-1})*	E.T. (hr)*	Dw (g)*	SL (cm)*	LL (cm)*	NSPP*	NLSB*	SBL*	NLP	NT
control	0.00	-	0.4522	55	12	37	4	13	160	33
1		1	0.2855	30	10	35	4	11	143	15
2		2	0.1099	37	9	24	3	11	72	9.5
3	0.1	12	0.1702	26	11	32	4	13	132	4.75
4		24	0.0026	10	2	2	2	3	4	5
5		48	0.0297	26	5	9	2	7	18	0
6		96	0.01166	27	9	6	2	12	12	0
7		168	0.0124	17	8	6	3	10	18	8
control	0.00	-	0.1172	63	11	27	4	13	112	30
1		1	0.0999	47	8	24	4	10	96	12.5
2		2	0.0513	30	5	9	3	7	27	13
3	0.2	12	0.0147	22	10	9	3	14	28	7
4		24	0.0136	18	11	10	2	13	20	4.5
5		48	0.0125	16	8	2	2	9	4	0
6		96	0.01119	10	6	44	2	8	88	0
7		168	0.01059	21	6	3	2	8	6	5.25

* = no plant survived at 0.5 mg l^{-1}

con = concentration, E.T. = exposure time, Dw = dry weight, SL = shoot length, LL = leaf length
NSPP = number of secondary branches per plant, NLSB = number of leaves per secondary branch
SBL = secondary branch length, NLP = number of leaves per plant, NT = number of tubers per plant

Appendix 13. Competition between *Potamogeton pectinatus* and *Potamogeton perfoliatus*.

phy	S	T	P	D	part	cup.w.	cup+fw	cup+dw	fw	dw	%dw	%N	%C	%H	T1	Tuber Fresh Weight (mg)											
						mg	mg	mg	mg	mg						1	2	3	4	5	6	7	8	9	10	11	12
9/1	1-3			4-2	pect.above	4217	10491	4965	6274	748	11.9	1.35	37.56	5.88													
					pect.ro+rh	4217	8434	4845	4217	628	14.9	0.80	34.23	5.15													
					pect.tubers	4212	4648	4342	436	130	29.8	1.17	40.50	6.49	7	114	67	56	61	66	44	29					
					perf.above	4232	7870	4524	3638	692	19.0	0.99	37.03	5.76													
					perf.below	4200	6356	4601	2156	401	18.6	0.66	35.65	5.60													
9/2	1-6			2-4	pect.above	4205	5899	4376	1694	171	10.1	1.21	38.01	5.62													
					pect.ro+rh	4209	5605	4388	1396	179	13.8	0.92	35.52	5.35													
					pect.tubers	4206	4614	4358	408	152	37.3	1.07	40.79	6.74	8	8	34	49	76	66	20	78	79				
					perf.above	4215	9661	5354	5446	1139	20.9	0.95	38.72	6.29													
					perf.below	4230	8778	5109	4548	879	19.3	0.69	38.64	6.15													
9/3	1-6			4-2	pect.above	4219	8395	4725	4176	506	12.1	0.93	37.52	5.63													
					pect.ro+rh	4215	6878	4603	2663	388	14.6	0.84	37.40	5.62													
					pect.tubers	4215	4626	4300	411	85	20.7	1.22	40.25	6.23	9	4	10	46	24	23	54	9	10	14			
					perf.above	4215	6912	4580	2697	465	17.2	1.30	37.34	5.70									5	2			
					perf.below	4216	6653	4685	2437	473	19.4	0.70	39.14	6.18													
9/4	1-6			0-6	pect.above																						
					pect.ro+rh																						
					pect.tubers																						
					perf.above	4220	12224	5680	8004	1460	18.2	0.96	38.24	6.18													
					perf.below	4210	12400	5672	8190	1462	17.9	0.74	38.72	6.16													
9/5	1-3			3-3	pect.above	4229	9949	4550	5720	721	12.6	0.95	38.16	5.83													
					pect.ro+rh	4202	7302	4686	3100	484	15.6	0.90	38.96	5.95													
					pect.tubers	4198	4407	4254	209	56	26.8	1.38	40.37	6.59	3	103	78	27									
					perf.above	4203	10637	5386	6434	1183	18.4	0.86	34.51	5.37													
					perf.below	4222	8760	5109	4538	887	19.5	0.69	39.34	6.00													
9/6	1-3			0-6	perf.above	4223	8869	5033	4646	812	17.5	0.87	38.26	5.89													
		1	2		perf.below	4219	7141	4769	2922	550	18.8	0.76	34.05	5.37													
9/6	1-3			0-6	perf.above	4209	6461	4680	2252	471	20.9	0.86	38.85	6.14													
		2	2		perf.below	4205	7175	4784	2970	579	19.5	0.70	37.08	5.77													
9/6	1-3			0-6	perf.above	4219	7076	4675	2857	456	16.0	1.13	38.41	5.89													
		3	2		perf.below	4210	7119	4754	2909	544	18.7	0.70	37.95	5.91													

phy	S	T	P	D	part	cup.w.	cup+fw	cup+dw	fw	dw	%dw	%N	%C	%E	T1	Tuber Fresh Weight (mg)											
						mg	mg	mg	mg	mg						1	2	3	4	5	6	7	8	9	10	11	12
	1-3			0-6	perf.above				9755	1739	17.8	0.95	38.51	5.97													
		6	6		perf.below				8801	1673	19.0	0.72	36.36	5.68													
9/7	1-6			6-0	pect.above	4203	10660	4987	6457	784	12.1	1.13	37.87	5.55													
					pect.ro+rh	4213	7290	4659	3077	446	14.5	1.02	39.17	5.91													
					pect.tubers	4227	5033	4481	806	254	31.5	1.12	40.38	6.33	12	167	10	94	84	62	54	72	23	43	69	10	24
					perf.above												8										
					perf.below																						
9/8	1-3			2-4	pect.above	4219	7752	4689	3533	470	13.3	0.89	36.19	5.38													
					pect.ro+rh	4220	6309	4501	2089	281	13.5	0.83	36.78	5.22													
					pect.tubers	4226	4515	4330	289	104	36.0	1.13	40.34	6.56	4	102	45	87	56								
					perf.above	4227	11172	5472	6945	1245	17.9	0.98	38.49	6.15													
					perf.below	4206	9410	5241	5202	1033	19.9	0.63	38.12	6.15													
9/9	1-3			6-0	pect.above	4210	8674	4765	4464	555	12.4	0.89	39.15	6.18													
		1	2		pect.ro+rh	4209	6242	4554	2033	345	17.0	0.64	38.47	5.32													
	pla				pect.tubers	4222	4651	4355	429	134	31.2	1.10	41.01	6.74	3	221	16	46									
9/9	1-3			6-0	pect.above	4208	9025	4767	4817	559	11.6	0.90	38.40	5.84			4										
		2	2		pect.ro+rh	4204	6319	4530	2115	326	15.4	0.81	38.03	5.76													
					pect.tubers	4198	4633	4368	435	170	39.1	1.03	41.01	6.73	4	190	10	52	93								
9/9	1-3			6-0	pect.above	4211	7226	4597	3015	386	12.8	0.92	38.56	5.78			5										
		3	2		pect.ro+rh	4218	5703	4465	1485	247	16.6	0.80	36.22	5.50													
					pect.tubers	4231	4399	4274	168	43	25.6	1.37	41.34	6.74	7	39	7	30	12	16	24	44					
9/9	1-3			6-0	tubers(rest	4219	4632	4382	413	163	39.5	1.13	39.99	6.51	7	7	30	28	11	61	94	80					
					tubers (all)	16870	18315	17380	1445	510	35.3	1.16	40.84	6.68	21				2								
	1-3			6-0	pect.above				1229	1500	12.2	0.90	38.70	5.90													
		6	6		pect.ro+rh				5633	918	16.3	0.75	37.57	5.53													
					pect.tubers				1445	510	35.3	1.16	40.84	6.68													
9/10	1-6			3-3	pect.above	4229	7448	4660	3219	431	13.4	0.94	38.38	6.05													
					pect.ro+rh	4204	6469	4565	2265	361	15.9	0.71	32.82	4.98													
					pect.tubers	4217	4564	4328	347	111	32.0	1.17	40.76	6.70	5	120	72	54	62	40							
					perf.above	4203	9581	5267	5328	1064	20.0	0.97	38.33	6.07													
					perf.below	4213	9117	5155	4904	942	19.2	0.78	36.19	5.80													

phy	S	T	P	D	part	cup.w.	cup+fw	cup+dw	fw	dw	%dw	%N	%C	%E	T1	Tuber Fresh Weight (mg)											
						mg	mg	mg	mg	mg						1	2	3	4	5	6	7	8	9	10	11	12
10/1	1-6			6-0	pect.above	4220	13048	5393	8828	1173	13.3	0.82	39.08	6.20													
					pect.ro+rh	4196	8624	4957	4428	771	17.4	0.86	39.29	6.09													
					pect.tubers	4218	4750	4403	532	185	34.8	1.12	38.64	6.13	9	121	61	89	79	48	40	29	37	25			
					perf.above																						
					perf.below																						
10/2	1-3			2-4	pect.above	4206	7281	4658	3075	452	14.7	1.02	38.51	6.05													
					pect.ro+rh	4204	5825	4451	1622	247	15.2	0.81	37.42	5.69													
					pect.tubers	*																					
					perf.above	4220	11533	5570	7313	1350	18.5	0.97	39.64	6.23													
					perf.below	4209	12088	5620	7879	1411	17.9	0.86	38.84	6.10													
10/3	1-6			2-4	pect.above	4205	6470	4540	2265	335	14.8	0.97	38.51	6.15													
					pect.ro+rh	4212	5811	4485	1599	273	17.1	0.76	36.00	5.67													
					pect.tubers	4200	4262	4221	62	21	33.9	1.20	40.45	6.57	1	62											
					perf.above	4215	10017	5362	5802	1147	19.8	0.92	38.84	5.99													
					perf.below	4213	9810	5235	5597	1022	18.3	0.88	38.21	6.11													
10/4	1-3			6-0	pect.above	4206	7312	4659	3106	453	14.6	0.77	38.33	5.86													
		1	1		pect.ro+rh	4201	5877	4449	1676	248	14.8	0.72	35.50	5.64													
					pect.tubers																						
10/4	1-3			6-0	pect.above	4225	7292	4627	3067	402	13.1	0.79	37.86	5.70													
		2	2		pect.ro+rh	4205	5779	4457	1574	252	16.0	0.67	34.87	5.08													
					pect.tubers																						
10/4	1-3			6-0	pect.above	4222	9575	4986	5353	764	14.3	0.85	37.83	5.75													
		3	3		pect.ro+rh	4215	6937	4659	2722	444	16.3	0.85	38.85	5.83													
		6	6		pect.tubers	4217	4782	4400	565	183	32.4	1.06	40.62	6.75	11	63	56	62	56	46	11	11	11	88	16	55	
	1-3			6-0	pect.above				1152	1619	14.0	0.80	38.01	5.77							6	5					
		6	6		pect.ro+rh				5972	944	15.8	0.73	36.41	5.52													
					pect.tubers				565	183	32.4	1.06	40.62	6.75													
10/6	1-3			3-3	pect.above	4206	8688	4757	4482	551	12.3	0.97	38.10	6.08													
					pect.ro+rh	4214	6364	4512	2150	298	13.9	0.80	38.88	6.27													
					pect.tubers	4209	4703	4411	494	202	40.9	0.91	40.48	6.57	5	126	12	93	45	10							
					perf.above	4209	8955	5112	4746	903	19.0	1.00	38.67	6.13			1			4							
					perf.below	4229	9033	5204	4804	875	18.2	0.73	38.79	6.32													

phy	S	T	P	D	part	cup.w.	cup+fw	cup+dw	fw	dw	%dw	%N	%C	%E	T1	Tuber Fresh Weight (mg)											
						mg	mg	mg	mg	mg						1	2	3	4	5	6	7	8	9	10	11	12
10/7	1 6			3-3	pect.above	4212	7930	4765	3708	553	14.9	0.78	39.10	6.36													
					pect.ro+rh	4203	8042	4852	3839	649	16.9	0.65	38.71	6.14													
					pect.tubers	4216	4466	4283	250	67	26.8	0.95	40.39	6.43	3	75	53	11									
					perf.above	4208	8167	4948	3959	740	18.7	0.95	39.17	6.16				9									
					perf.below	4209	8502	5009	4293	802	18.6	0.93	38.58	6.16													
10/8	1-6			0-6	pect.above																						
					pect.ro+rh																						
					pect.tubers																						
					perf.above	4225	12245	5592	8020	1367	17.0	0.95	38.74	6.13													
					perf.below	4220	14035	6031	9815	1811	18.5	0.77	38.49	6.37													
10/9	1-3			4-2	pect.above	4219	10309	5087	6090	868	14.3	0.99	38.68	5.98													
					pect.ro+rh	4218	7834	4610	3616	592	16.4	0.88	39.32	6.28													
					pect.tubers	4205	4464	4267	259	62	22.9	1.21	40.63	6.50	5	133	70	33	14	10							
					perf.above	4221	8126	4687	3905	466	11.9	1.09	39.60	5.84													
					perf.below	4209	6558	4545	2349	336	14.3	1.05	38.39	5.94													
10/10	1-6			4-2	pect.above	4206	9708	5008	5502	802	14.6	0.83	38.44	5.93													
					pect.ro+rh	4207	8810	4691	2603	484	18.6	1.10	39.44	6.06													
					pect.tubers	4217	4289	4260	172	43	25.0	1.10	40.87	6.55	3	87	56	25									
					perf.above	4212	5753	4481	1541	269	17.5	1.08	39.51	6.24													
					perf.below	4224	5922	4552	1698	328	19.3	1.28	39.84	6.16													

Phy – Phytotron
S = sediment
T = Tuber
P = Plant
d = density
dw = dry weight
fw – fresh weight
T1 – number of tubers