SUBMERGED PLANT SURVIVAL STRATEGIES IN RELATION TO DISTURBANCE AND STRESS IN ARTIFICIAL CHANNELS OF BRITAIN AND ARGENTINA.

A thesis submitted to the University of Glasgow for the degree
of Doctor of Philosophy

by

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DECLARATION

I hereby declare that this thesis is composed of work carried out by myself unless otherwise acknowledged and cited and the thesis is of my own composition. The research was carried out in the period from December 1991 to November 1994. This dissertation has not in whole or in part been previously presented for any other degree.

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ABSTRACT

The aim of this thesis was to make a functional analysis of submerged aquatic plants in relation to management and environmental factors in artificial systems of Britain and Argentina.

In Britain, low-lying plains must have artificial drainage systems to avoid flooding and maintain optimum soil conditions. In Argentina, there are several irrigation districts for agricultural use and two of the most important are the Valle Inferior del Rio Colorado (VIRC) and the Valle inferior del Rio Negro (IDEVI). One of the main problems in these channel networks are the growth of submerged weeds which cause a great deal of damage by blocking the flow of water.

The abundance of submerged weeds were surveyed during 1992 and 1993 in drainage channels located in geographically-distinct areas of Britain and in 1993/1994 in drainage and irrigation channels of VIRC and IDEVI. Environmental and management data were recorded and indices of disturbance and stress constructed from combined data for each site surveyed.

In Britain, a species ordination using Canonical Correspondence Analysis (CCA) showed that the combined disturbance variable explained more of the variability that did stress. Two main groups of species could be distinguished using cluster analysis (TWINSPAN: Two way indicator species analysis). The larger group appear to be those better-adapted to habitats with low disturbance constraints (e.g.. *Myriophyllum spicatum* and *Potamogeton pectinatus*). The smaller group comprised species which tended to occur in sites with higher disturbance (e.g., regular cutting) such *Callitriche stagnalis*.

In Argentina, the same analysis that above showed that each variable (disturbance and stress) explained about half of the constrained variation. Four TWINSPAN species groups were separate in VIRC and IDEVI showing different tolerance to disturbance and stress.

Since the species groups were indicative of different combination of stress and disturbance, each plant community may be defined as different functional groups. When data from Britain and Argentina were analysed together, stress appears as an important factor in determining species variation in Argentina, *Ruppia maritima* being the species most tolerant, especially to water conductivity. Disturbance explained variation in both countries, *Chara contraria*, *Potamogeton crispus, P. pusillus* and the moss *Rynchostegium riparioides* being the most tolerant, especially to management, water velocity and water fluctuation.

Plants were also classified in functional terms on the basis of plant morphological traits, and this study found a relationship between these attributes and the stress and disturbance variables. This suggests the possibility of determined functional groups in submerged vegetation from classic-standardised ecological measures as for example plant length or plant weight.

The inverse relationship between shoot length and total PAR was found in plants of *Potamogeton pectinatus* growing in drainage and irrigation channels of VIRC and IDEVI, showing that the condition of light-limitation for plant growth is frequent in these channels.

Specimens of *P. pectinatus* from the area of VIRC, were grown under laboratory conditions in order to determine its tolerance to disturbance (cutting) and stress (shade). Results suggest that the species has the stress element in its established-phase strategy, and an intermediate tolerance to disturbance.

A field experiment was performed in the Solway drainage area, NW England, to examine the response of populations of *Callitriche stagnalis* and *Potamogeton crispus* to disturbance treatments (manual cutting and dredging) and stress treatments (shade). Results showed that, although the survival strategy of both plants is essentially similar (competitive-disturbance tolerators: CD) *C. stagnalis* was the more competitive of the two species, while *P. crispus* tolerated disturbance and stress better.

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CHAPTER I

AIMS OF STUDY AND GENERAL INTRODUCTION

1. 1 Aims

1.1.1 To ascertain the degree to which submerged species survival strategy could be related to the disturbance and stress pressures present in artificial channels of Britain and Argentina.

1.1.2 To examine the evidence for or against the existence in such habitats of functional groups, in which submerged plant species are associated with different degrees of stress and disturbance or are defined by morphological characters of the plants.

1.1.3 To determine the relative importance of anthropogenic and natural stress and disturbance environmental factors in influencing the distribution of species and hypothesised functional groups in such habitats.

1.1.4 To assess experimentally in the laboratory and in the field, the response of individual plant species representatives of selected functional groups, to imposed stress and disturbance pressures.

1.2 General Introduction

1.2.1. Artificial channel systems in Britain and Argentina

Artificial open channels are important in low-lying agricultural land in both Britain and Argentina.

In Britain, as in most of Europe, the use of land for arable farming or pasture, does not need channel-irrigation networks. However, low-lying plains must have artificial drainage systems to avoid flooding and maintain optimum soil conditions for crop growth. The distribution of drainage channel areas throughout Britain is shown in Fig. 1.1. The problems of drainage are greatest in regions below sea level, where embankment protection is required to prevent tidal inundation. In the Fens (eastern England), the level of the water in the drains is often about 1.3 m below the lowest land level used for agricultural (Miles, 1976). A good functioning of the drainage channel network is vital in winter, when the water table increases, but summer floods are also a potential problem. Such a flood occurred in the Welland and Nene area in 1968 when considerable damage to crops resulted (Miles, 1976).

Price (1981) indicated that the area of agricultural land in England and Wales is approximately 11 million ha, of which some 5.5 million ha are dependent on under drainage and ditch networks. Within this area there are about 27,000 km of main drainage channels, intermediate watercourses discharging generally to main rivers, plus about 100,000 km of subsidiary drainage channels, a vast network of small watercourses and farm ditches (Robinson, 1986). The total area of land drained directly by drainage channels is approximately 800,000 ha (Marshall *et al.*, 1978).

Land drainage systems in Scotland are much less extensive than in England and Wales, and comprise both artificially and canalised or altered natural streams and rivers (Murphy, 1988, 1990). They are concentrated in the low-lying areas of the south-west and north-east (e.g. Moray).

In Argentina, about 70 % of the country is arid or semi-arid, there exist several irrigation districts for agricultural use: mainly cultivation of vegetables, cereals and fruits. Two of the most important are the Valle

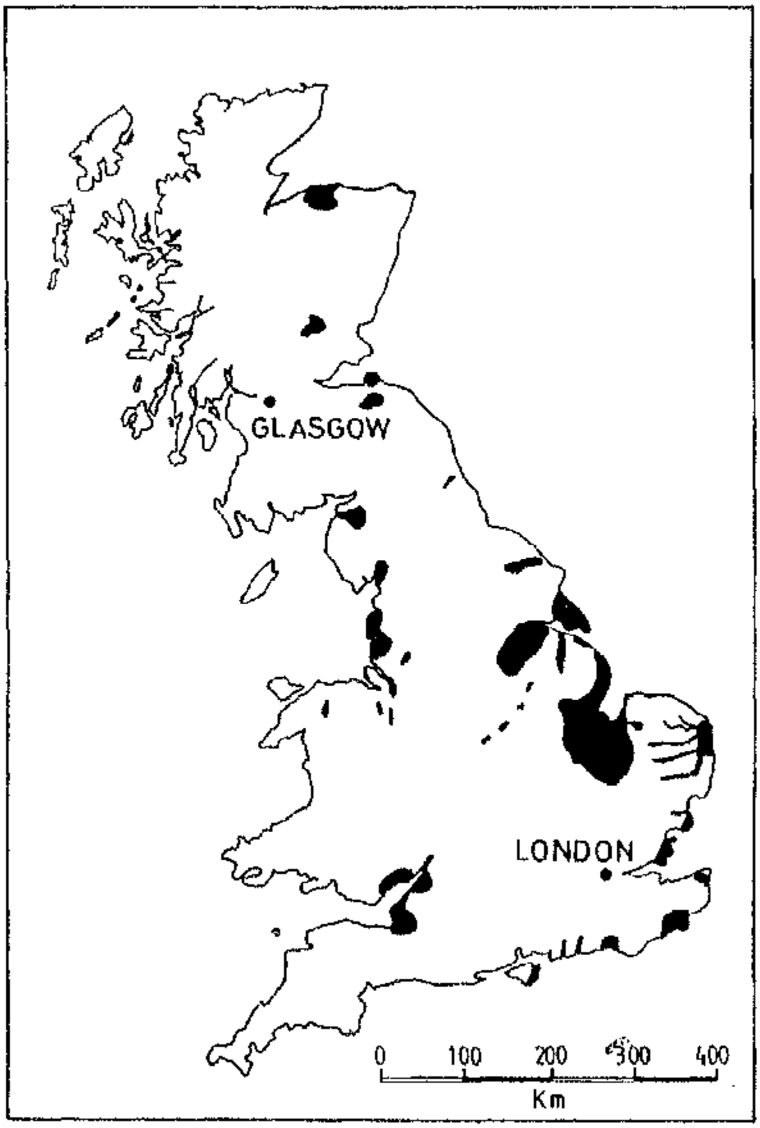


Figure 1.1. Areas of England, Wales and Scotland drained by land drainage channels.

Inferior del Rio Colorado (VIRC) and the Valle inferior del Rio Negro (IDEVI). The location of both districts in Argentina is shown in Fig. 1.2.

In VIRC, 1350 farmers with water rights are responsible for the regional agricultural production represented by horticultural (mainly onion and garlic), cereals, pastures, livestock and forestry. In IDEVI 516 farmers are supplied by irrigation water, the principal production of the area is fruits (apple, pear), horticultural (tomatoes, onion), meat production and non-traditional crops (walnuts, almonds).

VIRC has a jurisdiction over 530,000 ha of land, from which approximately 92,000 ha are currently under various intensities of irrigation and drainage (CORFO, 1992). The climate of the area is temperate semiarid, with an annual rainfall of 350 mm (south) to 450 (north). There is a negative annual water deficit from 300 to 500 mm, hence requiring the irrigation of the crops during all the growing period. Water for irrigation is obtained from the Rio Colorado and distributed by a net of 331 km of primary channels and 5,110 km of secondary and tertiary channels. Water used after irrigation is collected by a network of 397 km of main drainage channels and 3,341 km of secondary and tertiary channels (CORFO, 1992). The drainage network is important in the area specially because its malfunctioning can cause impaired land drainage, which results in salinity problems in the soils of cultivated land (Svachka, 1981).

The IDEVI complex was initiated en 1959, when the government developed a programme with the main objective of transform the surrounding patagonian desert in a productive area. The sector under the administration of IDEVI is 65,000 Ha, but at present 17,500 have irrigation rights. Water comes from the Rio Negro, and the overall irrigation network is composed by

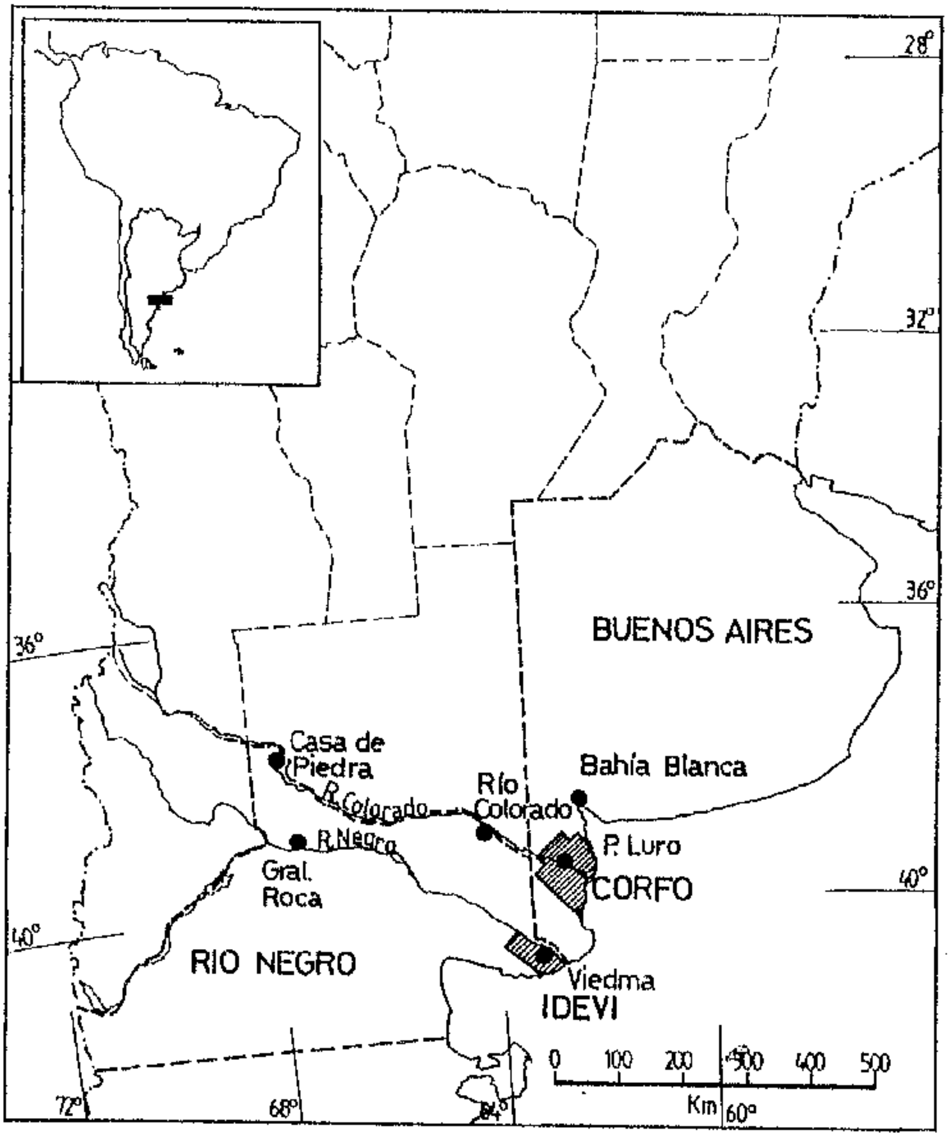


Figure 1.2. Irrigation districts of CORFO (= VIRC) and IDEVI in Argentina.

214.2 km of concrete lined irrigation channels, 70 km of unlined irrigation channels and 1,975 km of farm channels. The drainage channel network comprises 550 km, water is pumped back into the river by means of three pumping stations.

1.2.2 Aquatic weed problems in man-made channel systems

Usually, artificial channels provide a suitable habitat for aquatic vegetation. In general, a moderate growth of aquatic plants is desirable, but when such growth becomes a nuisance there are problems in the functioning of the system. The plants increase channel frictional roughness by increasing "n" in the Manning equation used for the design of open channels, and this leads to impedance of flow (Manning, 1891; Pitlo and Dawson, 1990).

$$v = \frac{1000}{n} R^{2/3} S^{1/2}$$

Where v= mean velocity of flow, n= resistance coefficient, R= hydraulic "radius" or hydraulic mean depth and S= hydraulic gradient or hydraulic energy gradient.

It is difficult to define the taxa which can be described as aquatic weeds in a large area, such as a country, because factors related to climate, biological interactions, the environmental conditions and the management of each water body all contribute to the definition of which species produce nuisance vegetation. Despite this, from a general point of view, there exists a group of submerged aquatic plants that cause most of the problems in channel networks.

In Britain, the typical taxa causing problems in drainage channels are similar to those found elsewhere in Europe, and are filamentous algae (notably *Cladophora, Enteromorpha* and *Vaucheria)* and submerged macrophytes characteristic of slow-flowing eutrophic waters: *Ceratophyllum demersum, Elodea canadensis, Elodea nuttallii, Potamogeton pectinatus and Zannichellia palustris* (Murphy *et al.*, 1990a). Land drainage systems in Scotland are less extensive than in England and Wales, but submerged weeds (*Potamogeton spp., Callitriche spp.*) and filamentous algae seem to cause particular problems (Murphy, 1988; 1990).

The typical submerged weed taxa of drainage and irrigation channels in Argentina are *Potamogeton (P. pectinatus, P. illinoensis*) and *Chara (C. contraria, C. vulgaris*) (Fernández *et al.*, 1990). *Potamogeton* constitutes the principal problem, and is considered the main weed problem requiring control especially in drainage and irrigation channels of VIRC and IDEVI (Fernández *et al.*, 1990; Dall'Armellina *et al.* 1996a).

1.2.3 Biotic and abiotic factors that affect aquatic plant communities

Terrestrial and aquatic plants live under quite different environmental conditions. Water limitation, grazing and temperature stress seem to be important strategy factors in terrestrial environment. Very different factors, such as water velocity, sediment characteristics and hydrostatic pressure, together with light and nutrients, seem to be more important in the aquatic environment (Kautsky, 1988). Several studies have reviewed the influence of the natural environmental on the distribution and abundance of macrophytes species. Fox (1992) stated the importance on river aquatic vegetation of water movement, substratum, light, temperature, water chemistry and water level fluctuations. Barko *et al.* (1986) considered the effect of light, temperature, nutrition, sediment composition and inorganic carbon on submerged aquatic vegetation. A variety of natural abiotic factors controlling submerged aquatic macrophytes declines have been identified including insufficient light caused by biogenic turbidity or suspended sediments, water movement by flow and wave action, temperature, substrate composition, and nutrient availability (Chambers *et al.*, 1993).

The incidence of the external biotic factors able to affect macrophyte vegetation through arthropods (Harley and Forno, 1990), plant pathogens (Charudattan, 1990) or phytophagous fish (Van der Zweerde, 1990) has been specially studied through the possibilities of biological control of aquatic weeds (Pieterse, 1990). One example of the influence of biotic factors in the macrophyte vegetation is the effect of the fish *Cyprinus carpio* on submerged vegetation, that affect plants through uprooting, decreasing turbidity and herbivory (Crivelli, 1983; Fletcher *et al.*, 1985). The effect of this fish and another environmental factors on the macrophyte vegetation was studied recently in the area of VIRC (Fernández *et al.*, 1996subm.).

Anthropogenic factors affecting macrophyte growth and development include weed management, pollution and water bodies engineering (Fox, 1992). About weed management (see 1.2.5) there are a variety of techniques including harvesting, herbicides, water-level fluctuation, light alteration, biological control, etc. (Wade, 1990; Murphy *et al.* 1990; Pieterse, 1990; Nichols, 1991)

All the factors reviewed above are external to the plant community, but also it is important to categorise the interactions that may occur among plant species growing together (Odum, 1971). These general interactions among species or populations within species are termed interference, that is, the effect that the presence of a plant has upon the environment of its neighbours (Radosevich and Holt, 1984). The most important interference effect between plants is competition. Competition is defined by Barbour *et al.* (1980) as the mutually adverse effects of organisms which utilise a resource in short supply. The relationship between interspecific competition and submerged macrophyte community has been little studied, in spite of being an area of great interest to community ecologists (McCreary, 1991).

The influence of both external factors and interference on plant community (e.g. structure and composition) is complex, especially because macrophytes do not respond to each variable independently.

1.2.4 The open channel habitat

Plant population distribution within the submerged aquatic vegetation of a stream or a man-made channel is related to chemical and physical factors of the habitat. According to Haslam (1978), the principal factors in drainage channels are water flow, substrate, width, depth, slope and drainage order of the channels, light regime reaching the water, and the availability of plant nutrients in the sediment and water (Haslam, 1978). The composition of the plant species in channels with little flow, no scour and a fine substrate, is closely related to depth, width, turbidity, substrate type and trophic status (Haslam, 1978).

The water in drainage channels always tends to be eutrophic, receiving agricultural waste, especially from fertiliser runoff. The increase of inorganic nutrient and organic pollutants, producing cultural eutrophication, results in modification of plant community (Scotter *et al.* 1977; Haslam, 1978; Wheeler and Giller, 1982). In lowland waters, the predominantly eutrophic conditions favour species requiring high concentrations of ions, or species indifferent to ionic concentrations, and virtually exclude the 20 - 30 species in the British flora which are closely adapted to low-ionic, nutrient-poor water (Eaton, 1986).

In some drainage channels of Britain, the influence of salinity on the growth of the aquatic macrophytes has been documented. The fluctuation of salinity in the drains of the Monmouthshire Levels, South Wales, was shown to be a factor at least as important as channel management, and the existence of some species is dependent upon the influx of the salt water to the channels (Scotter *et al.*, 1977; Wade and Edwards, 1980). In the Norfolk Broads, the high water salinity of some channels permits only the growth of tolerant species (Driscoll, 1986) and sites deficient in macrophytes had higher levels of sodium in the water and sediment (Wheeler and Giller, 1982).

In the drainage network of VIRC, Argentina, water salinity and turbidity limited the presence of submerged weeds, and long stretches without submerged vegetation exist in channels with high levels of turbidity or salinity (Sabbatini, 1989). The salinity of the water in such drainage channels was shown to be between 3 and 20 g. l^{-1} and the pH a constant level of 7.2 (Peinemann *et al.*, 1979). However, drainage channels of VIRC have a longer history of aquatic weed problems.

In drainage channels of VIRC, water which used to be completely transparent in the overall drainage network became very turbid in many places, expanding in some channels over the whole extension of the channels. The first report of the presence of a permanent increased turbidity for the drainage channels was that of Sabbatini (1989). This phenomena was associated with the appearance of a new fish, *Cyprinus carpio*, in the system. Recently, a clear relationship was found between fish and channel environmental with aquatic macrophytes, and the data is strong to support that *C. carpio* have a substantial, and predictable, impact on channel turbidity, which in turn is associated with the reduction of submerged plant growth (Fernández *et al.*, 1996).

In the irrigation channels of VIRC, substantial changes in water clarity and macrophyte abundance have occurred during the past recent years in both the irrigation and drainage channels. At the irrigation channels prior to the construction of a the dam Casa de Piedra on the Rio Colorado (Fig. 1.2), the suspended sediment content of the river water was very high. Since closure of the dam in July 1989, river turbidity has declined, owing to the settlement of the sediment load in the Casa de Piedra reservoir, leading to the increase of transparency in irrigation channels of the VIRC system, fed by the water of the Rio Colorado. This in turn was followed by increased growth of submerged weeds in the irrigation system.

The channel network of IDEVI appears as a very suitable habitat for submerged plant growth, being *P. illinoensis* dominant in irrigation and *P. pectinatus* in drainage channels (Dall' Armellina *et al.* 1996a; 1996b).

1.2.5 Management of aquatic weeds

In England and Wales approximately 30,000 km of main channel receive manual, mechanical and chemical maintenance each year (Marshall *et al.*, 1978). Robson (1975) showed that hand weeding was the most widely used technique, following by mechanical removal and chemical control in that order.

On the main drains the principal weed control operations are mechanical, such as cutting, harvesting and dredging. Other physical methods of control, less widely used, are burning, shading, alterations of water level (Wade, 1990b), and recently algal control with straw (Newman and Barrett, 1993).

Manual clearance of submerged weeds (hand pulling, raking, cutting) may be inefficient: regrowth to nuisance density tends to be rapid, and more than one cut per season is usually required (Wade, 1990b). Price (1981) reported that three manual cuts per year are the norm for drainage channels in the UK. However, apart from certain rivers in which there is an important game fishing interest, these methods have been largely surpassed by mechanical techniques (George, 1976).

Cutting and/or harvesting, including operating from floating and bank machines, is now the commonest method of control. Where flow has to be maintained in a channel throughout the summer, weed control will usually repeated two or three times a year (Robson, 1973). After weed cutting certain species will escape control. For example, a close autumn cut of *Ranunculus calcareous* in the lower reaches of a large chalk-stream reduced the biomass present at the time of the following spring cut by 20 - 40 % (Westlake and Dawson, 1986).

Dredging includes the use of machines which have other functions apart from weed cutting and/or removal. Excavator or dragline is used, and the weed is removed with the accumulated silt from the bottom and sides of the channel (Robson, 1973). The dredging had results in the creation of a deep channel in the centre with steep sides, and a new substrate for vegetation to recolonise.

While re-vegetation is often rapid following clearance, the recovery of the plant community after dredging is usually a slow process, taking a long time (Wade, 1990b). The re-establishment of the vegetation after dredging in drainage channel habitats might take a cyclical nature, and has been described by Scotter *et al.* (1977) and Wade (1978).

Chemical control of aquatic weeds in Britain (Robson, 1973, 1975; Holland, 1977) is widespread compared with some other countries of Europe, although their use is strictly regulated. In Britain, there is a considerable reliance on herbicides for ditch maintenance (Robinson, 1986; Murphy, 1988). There are nine herbicides legally permitted in Britain to be used in or near water, of which three may be used against submerged vegetation: dichlobenil, diquat and terbutryne (Barrett *et al.*, 1990; Murphy *et al.*, 1990a; Holloway and Greenfield, 1992).

There is some evidence that the vegetation of ditches subject to a long-term treatment with herbicides may be maintained by the management regime at an early-successional stage, dominated by opportunist plant species, of which filamentous algae are a good example (Murphy and Barrett 1990). In the short-term, herbicide treatments causes a hydroseral regression to an earlier stage of the freshwater plant succession including the immigration of opportunist (disturbance tolerance) species followed by slower growing, but more competitive species (Newbold, 1976). In the long term, development of a plant community very similar to the pre-spraying community both in terms of species composition and abundance, was shown to occur by Wade (1981).

Biological control by means of grass carp (*Ctenopharyngodon idella*) has severe limitations on its use in British waters, including strict licensing by requirements (van der Zweerde, 1990; Murphy *et al.*, 1990a).

Management may refer either to controlling nuisance species, or to restoring or restructuring plant communities. Producing stable, diverse aquatic plant communities containing high percentages of desirable species is a primary goal (Nichols, 1991). However, in many cases the need is simply to minimise Manning's "n" (see 1.2.2) in the channel, for as great a proportion of the year as possible.

The relationships between drainage channel management and the aquatic plant community have been documented in Britain (Haslam, 1978; Wade and Edwards 1980; Driscoll, 1986; Robinson, 1986; Wolseley, 1986). Despite being artificial, the drainage systems have acquired a conservation value, specially where traditional cyclical vegetation clearance is a practicality, tending to maintain plant diversity against the tendency to succession to reedswamp (Eaton, 1989). However, a more rigorous management made changes in several channels that leads to a impoverishment of the vegetation. The loss of plant diversity after changes in land use from management for livestock to arable production have been described by Scotter *et al.* (1977), Wade and Edwards (1980) and Driscoll (1986).

In the drainage and irrigation channels of VIRC and IDEVI, the principal method used for aquatic weed control is mechanical (cutting, dredging, chaining), that is too costly and slow to clean the large area involved. Since 1994, chemical control has been extensively used in VIRC with the herbicide acrolein ("Magnacide H 92%"; BPCI, 1989). Acrolein, banned in many countries, is expensive, dangerous and harmful for the environmental (Hansen *et al.*., 1983; Murphy and Barrett, 1990).

Since 1980, a multi-disciplinary approach has been considered in VIRC the most appropriate way of approaching channel management minimise the harmful affects of weeds, including studies on the biology and ecology of the aquatic weeds (Irigoyen, 1981a, Sabbatini *et al.* 1986a, 1987), chemical control (Irigoyen, 1981b, Sabbatini *et al.*, 1986b), timing of control methods and prevention (Fernández *et al.*, 1987a, b). From 1992 the Commission of the European Communities funded the project "Biological management of irrigation channel weed problems in irrigated semi-arid agriculture", that included research in VIRC and IDEVI on the biology and ecology of submerged weeds and on biological control with phytophagous fishes (Hootsmans *et al.*, 1994).

1.2.6 Survival strategies of plants

The "primary ecological strategies" are recurrent types of specialisation of animals and the plants associated with particular habitat conditions or niches. The recognition of these primary strategies provides a key to understand the structure and dynamics of communities and ecosystems, and therefore is the baseline for the development of a universal functional classification of organisms (Grime *et al.*, 1988). Strategy is defined by Grime (1979) as "a grouping of similar or analogous genetic characteristics which recurs widely among species or populations and causes then to exhibit similarities in ecology". A primary strategy involves therefore the more fundamental activities of the organism: resource capture, growth and reproduction. Each primary strategy may exhibit sets of traits which are predictably related to the ecology of species showing that strategy.

A detailed description of the growing literature dealing with the strategy approach is out of place here, but it is worth noting that historically there have been two different approaches: The two- and three- primary strategy models (Pianka, 1970; Grime, 1979).

The r - K selection theory of Mac Arthur & Wilson (1967) and Pianka (1970) is based on the logistic equation of population growth, "K" refers to carrying capacity and "r" is the maximal intrinsic rate of natural increase. On this approach, K-selection leads to increasing efficiency of utilisation of environmental resources and r-selection leads to high productivity.

Grime (1979) placed the external factors which affect vegetation into two broad categories: stress and disturbance. Stress consists of those phenomena which restrict photosynthetic production, and occurs in resource-limited habitats or those with suboptimal conditions. Disturbance is associated with the partial or total destruction of plant biomass and arises from activities or phenomena such as herbivores, anthropogenic impacts, frost and fire.

According to Grime, there are three primary dimensions of environmental constraints limiting plant growth: competition, disturbance and stress, and therefore three types of primary strategies can be distinguished in plants: competitors (C), stress-tolerators (S) and disturbance-tolerators (D: also called ruderals by Grime). The three are extremes of evolutionary specialisation. Obviously, there are others which exploit the various intermediate conditions which correspond to particular equilibria between the three strategies. In the real world the C-D-S equilibrium varies from place to place, even within a plant community, and on diurnal, seasonal and successional times scales (Grime *et al.*, 1988).

For the location of the populations or species in the C-D-S equilibrium it is necessary to identify the most consistent traits characterising each survival strategy. For example, Grime *et al.* (1988) determined attributes of morphology, life-history and physiology and used these to classify plant species of the Sheffield region, England, into the C-D-S model.

A distinctive feature of the three-strategy model of Grime (1979) is the separation of the strategy exhibited in the established (adult) phase from that of the regenerative (juvenile) stages. In plants, this has led to the suggestion that there are distinct regenerative strategies which differ in such respects as grade of resource investment, mobility and dormancy, and which confer different but predictable sets of ecological capacities and limitations upon the organisms.

This study will be based on an application of the C-D-S model of Grime (1979). An advantage of this approach is that the strategy concept has proved useful in analysing the major effects of management within large areas of vegetation. Recognition of the major types of strategies provides an insight into the processes controlling the structure, species composition and dynamics of vegetation. This, in turn, can suggest a number of guidelines for management (Grime, 1980).

1.2.7 Functional vegetation groups

A functional vegetation group may be defined as a plant community which performs a given ecological function, expressed as a similar set of strategy traits, for survival of a given combination of stress and disturbance pressures. A functional group may be considered as a set of similarly-adapted species occurring together at one or more locations experiencing similar suites and intensities of stress and disturbance pressures. The advantage of using this unit of vegetation is that it identifies sets of plants in functional terms. Any set of plant populations adapted to the same set of environmental conditions (i.e. exhibiting similar sets of survival traits for survival of a given combination of C, S and D pressures) may be viewed as belonging to a definable functional group, regardless of precise taxonomic composition.

The concept of functional group (or "guild") is frequently discussed in the literature but with a wide array of definitions (Reader, 1988; Simberloff and Dayan, 1991; De Kroon and Olff, 1995). Belsky (1992) defined functional groups as communities in which all species respond in a similar manner to all major environmental factors. This concept differ from those based exclusively on anatomical and morphological characteristics (Steneck and Watling, 1982), and from the concept of "guild" (sensu Root 1973) which is based strictly on similarities in resource utilisation. Recently, Kindscher and Wells (1995) defines plant guilds as being groups of species with similar morphological, physiological and ecological traits. They stated that taxonomically, a single guild may include widely unrelated species, genera, families or higher taxa that have evolved similar ecological attributes as a result of convergent evolution.

Most of the determinations of the survival strategies were made in this study by assessing the direct relationship between species composition and abundance, and the external factors that affect submerged plant growth. Thus, groups associated with precise intensities of stress and disturbance determined its survival strategy. Recently Grime (1995), supported attempts to recognise functional types by relating the spatial distribution of organisms to independent measurements of potential productivity and disturbance. This approach is an advanced on methods which rely upon subjective assessments and complements the experimental approach in which communities and ecosystems are allowed to assemble under strictly controlled conditions of productivity and disturbance (for example Heal and Grime, 1991; Campbell and Grime, 1992).

An alternative way to classify vegetation in functional terms is on the basis of plant attributes (Keddy, 1992). For example, Grime *et al.* (1988) used a devised dichotomous key of plant traits to determine the strategies of herbaceous plant species of the Sheffield area of Britain. This approach was also explored in this study (see 4.3.2).

In geographically widely separated areas (such Argentina and Britain) the species and populations within the plant community of defined habitat types may be quite distinct, but similar functional groups probably exist as a consequence of the same environmental and management regime pressure.

CHAPTER II

SUBMERGED PLANT SURVIVAL STRATEGIES IN RELATION TO MANAGEMENT AND ENVIRONMENTAL PRESSURES IN DRAINAGE CHANNELS OF BRITAIN

Part of this Chapter is in press in *Hydrobiologia*, 1996 (see Appendix 1)

2.1 Introduction

In recent years, several studies have been published using the strategy approach (see 1.2.6 and 1.2.7) to assess relationships between the aquatic vegetation and environmental conditions. Grime *et al.* (1988) included some submerged plants in their established-phase strategy descriptions of plant species from northern England. Kautsky (1988) constructed a square model with four basic life strategies, which was proposed as a replacement for the triangular model, for aquatic soft-bottom macrophytes in the Baltic sea. Farmer and Spence (1986) classified the isoetids in Scottish freshwater lochs into the extremes of evolutionary specialisation. Shipley *et al.* (1989) established the relationship between juvenile and adult traits of emergent macrophytes occurring along the Ottawa River, Canada. Rørslett (1989) suggested that submerged macrophytes frequently exhibit combined trait strategies and used 16 major features to classify the vegetation of Norwegian lakes. A further development of this approach was the strategy analysis technique, for use at population and community level by Murphy *et al.* (1990b). This paper assessed the relationship between submerged macrophyte vegetation and environmental (natural and anthropogenic) pressures acting in lakes. Steneck and Dethier (1994) derived a general model that provides a simple way to predict marine algae community composition based on two environmental axes: disturbance and stress (presented here as it inverse, "productivity potential").

The management of aquatic weeds, especially when herbicides or mechanical methods are used, is probably a major disturbance pressure regulating the vegetation in drainage channels. Wade (1990a) assessed aquatic weed communities according to their ecophysiological and morphological adaptations, using the triangular strategy model. Kvet & Hejny

(1986) described some aquatic weeds in relation to control methods, including examples of each extreme of evolutionary specialisation.

Murphy (1989) indicated that a limited range of established-phase survival strategies appears to characterise the plant populations which make up the aquatic weed communities to the drainage channels. The application of strategy analysis to the submerged vegetation of drainage channels, which may experience widely differing aquatic weed control regimes, might lead to an improvement in the state of existing knowledge about the relationship between functionally-defined groups of plants and the environment in which they occurs.

The aims of this chapter are to ascertain, using a multivariate approach:

(a) the degree to which species survival strategy could be related to the environmental and management factors that affect plant growth in man-made drainage channel of Britain and

(b) the existence in those habitats of functional aquatic plant groups in which species are associated with different degrees of disturbance and stress pressures.

2.2 Materials and Methods

2.2.1 Site location.

For the study, it was selected a set of drainage channels showing a broad range of environmental conditions and management regimes typifying this habitat in Britain. In total 24 sites were located in the following drainage areas: The Fens (10 sites, E England: 0°15'E, 52°40'N); Crossens (5 sites, W England: 3°00'W, 53°35'N); Solway (6 sites, NW England: 3°15'W, 54° 50'N) and the Spynie Canal (3 sites, NE Scotland: 3°20'W, 57°40'N). Fig. 2.1 shows the map of Britain with the target drainage areas. Sites were located in the following places:

SITES	UK NATIONAL GRID REFERENCE
THE FENS	
1. Whittlesey Dike. Burnt House Farm	TL 334 942
2. King's Dike (Field's End bridge).	TL 235 965
3. 4th. District Main Drain (Pode Hole) by Bailey Bridge.	TF 210 220
4. Counter Drain (by Bailey bridge)	TF 210 220
5. Well Creek (Upwell) Mullicant Aqueduct	TF 531 029
6. Well Creek Marmory Priory Lock	TF 488 013
7. Old Bedford River (Welney)	TL 523 392
8. Old Bedford River (Welches Dam)	TL 472 860
9. Counter Drain (Rickwood Hide)	TL 465 853
10. Forty Foot Drain (Welches Dam)	TL 468 859
CROSSENS	
1. Three Pools Waterway	SD 373 178
2. Back Drain	SD 394 178
3. Low Wood Watercourse	SD 397 175
4. Tarleton Runner	SD 406 175
5. Drain 42A. Mere Hall	SD 402 162
SOLWAY	
1. Cormire Twins	NY 209 511
2. Colmire Sough High Level	NY 225 505
3. Roods Sough	NY 223 506
4. Cuddy Arch	NY 234 508
5. Cuddy Arch (at Lawrenceholme Drain)	NY 239 524
6. Tarn Sough (South of Martin Tarn)	NY 258 515

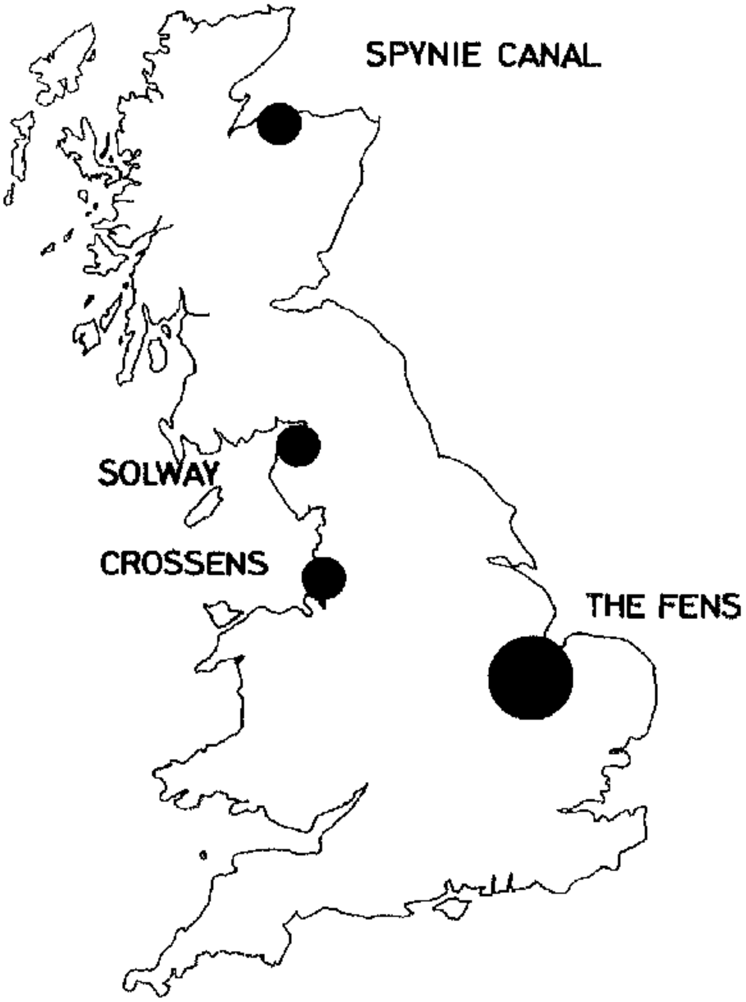
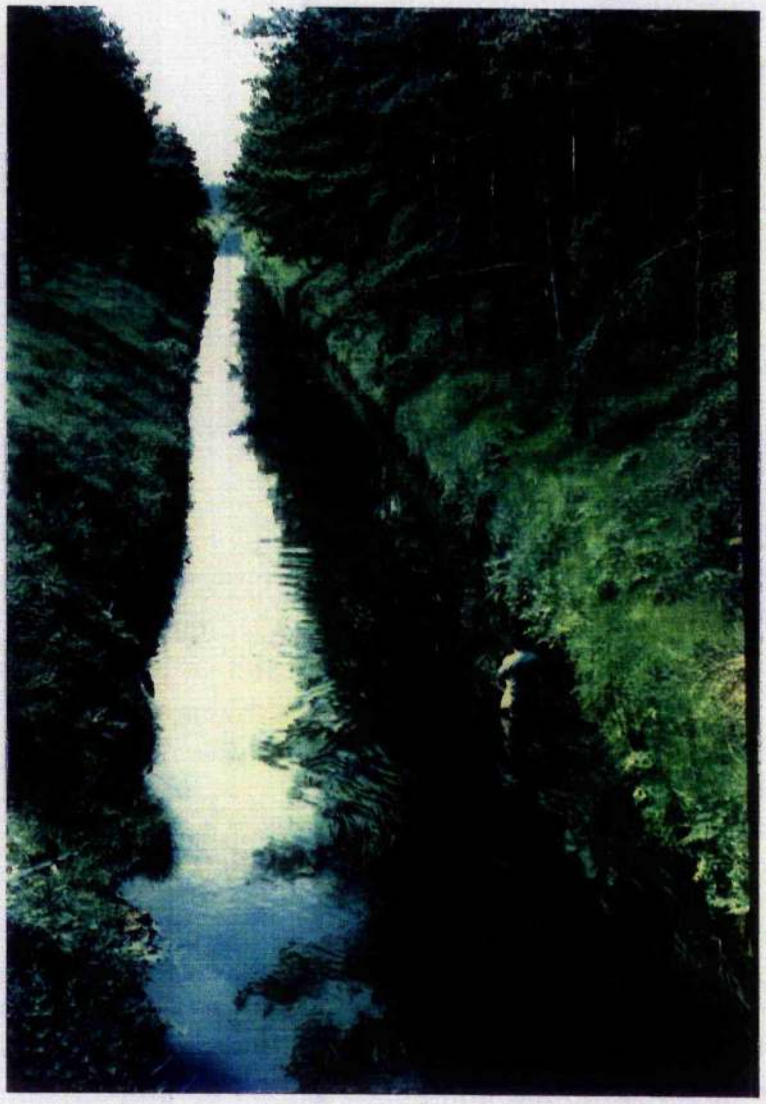


Fig. 2.1 Location of the drainage areas of England and Scotland under study.



Photograph 1: A site in the Spynie Canal, a drainage channel in NE Scotland, covered by *Sparganium emersum*.

SITES	UK NATIONAL GRID REFERENCE
SPYNIE CANAL	
1. Waterton	NJ 178 659
2. Salterhill	NJ 204 661
3. Oakenhead	NJ 246 687

2.2.2 Sampling

Following a preliminary site examination early in the 1992 season, a 50 m stretch was sampled during 1992 in early, middle and late season and in 1993 in early and late season. Two sites were not sampled again in 1993 because on them the routine management regime changed that year. They were site 5 of the Fens, and site 1 of the Spynie Canal (see 2.2.1). Sites were always sampled at least one month after the most recent weed control treatment. 10 random grapnel hauls were taken to sample submerged macrophyte species, following the grapnel-sampling technique of Murphy *et al.* (1981). The procedure was to divide the 50 m stretch in approximately 5 m channel length, and at each point collected one sub-sample. For the collection was used a eight-pronged plant grapnel on a cord 5 m in length, which was thrown into the water channel at right angles to the bank, and dragged back along the bottom. Each species present in each sub-sample was registered and the abundance rated as 0, none; 1, scarce; 2, common and 3, abundant. The frequency of each species in every site was calculated as the presence or absence of the species in the ten sub-samples. For example, if the species was present in 7 of the 10 sub-samples taken in a site, the frequency was 0.7. The abundance of each species was calculated as the average of the 10 values taken at each site.

2.2.3 Physico-chemical characteristics of the habitat.

Following are indicated the different on-site electrometric measurement carried out at each site in each visit:

2.2.3.1 Light attenuation

The extinction coefficient *k* describes the fraction of light energy that is converted to other forms per unit depth and its value depends on the nature of the water. There is a significant regression between light availability and maximum depth of plant growth (Hutchinson, 1975; Chambers and Kalff, 1985; Canfield *et al.* 1985; Dennison, 1987). The depth in the water column at which light intensity falls below the value in which net photosynthesis is theoretically possible is called the euphotic depth (z_{eu}). Moss (1988) states that as a rule of thumb, the z_{eu} for phytoplankton corresponds to that at which about 1 % of the surface light still remains, and that it lies higher in the water column for bulkier aquatic plants. Also, Moss (1988) define that z_{eu} for a number of experiments corresponds to a depth in which 2.47 % of the surface light remains. In this study a value of 3 % of surface light as limit of the euphotic depth was assumed. Other studies show different values of minimal light requirements for aquatic vegetation. For example, the average minimal value for freshwater angiosperm in lakes in Canada was determined to be 21.4 % of surface light levels (Chamber and Kalff, 1985) and for marine submerged plants, 10.8 % (Duarte, 1991).

Photosynthetically-active radiation (PAR) was measured in each visit using a twin-sensor SKYE SKP210 linked to a SKYE Datahog SDL 2540 logger. From the PAR- light data (photo flux density) the extinction coefficient k (also called net downward attenuation coefficient), was calculated:

$$k = 1/d \ . \ ln \ I°/I$$

where d is the distance between the light intensity at water surface ($I°$) and a determinate depth (I). From this, the euphotic depth z_{eu}, in which about 3 % of the surface light still remains was calculated as

$$z_{eu} = 3.51/k$$

and then the relationship z_{eu}/d evaluated, where d is the average depth measures in each site. A value = 1 means that on average the bottom of the channel was receiving only 3 % of surface PAR. Low values imply that the channel bed is below the euphotic zone.

2.2.3.2 Management regime

The management regime applied during the three years prior to sampling was rated as the likely degree and timing of destruction of plant biomass produced by the different management operations (Fig. 2.2).

Information on management regime at each site was provided by the National Rivers Authority (NRA: Ely, Crossens, Carlisle), Middle Level Commissioners (March) and Maintenance Committee of the Spynie Canal.

2.2.3.3 Other measures and site data information

On-site electrometric measurement of dissolved oxygen (mg. l^{-1}), conductivity (μS. cm^{-1}), water depth (cm), channel wide (cm), pH and temperature (C) were recorded in each visit. All the measures were taken in daytime and no corrections were made for likely diurnal variations in these variables during daylight hours: it is accepted such variation inevitably increases the noise associated with these data (Moss, 1988). Nitrate-N was measured in the lab using ion-specific electrodes from water samples taken at each site during summer 1993.

Fig. 2.2 Management procedures in relation to the likely degree and timing of destruction of the plant biomass in the target sites. (D: disturbance).

LOW D - Weed boat: every 1 - 2
- Manual weed rake (from banks in deep channels): every year
- Shallow dredge (Bradshaw bucket): every year
- Shallow dredge and manual control: every year

↓ - Manual control (scythes, forks): 2 or more for year (shallow channels)
- Herder bucket + manual control; dredged every 3 - 4 years + annual manual clearance

LOW D - Deeper dredging: every year

Data for additional water chemistry determinands were provided by the National River Authority (NRA) Anglian Region, NRA North West Region and North East River Purification Board (Scotland). The data included last 3 years monthly values of TON as N, ammonia as N, P- ortho, conductivity, temperature, oxygen, pH. Samples for this data were taken on a routine-basis sampling in or close to the following sites (see 2.2.1): Fens: 1, 2, 7, 8, 9, and 10; Crossens: 1, 2 and 4; Spynie canal: 1,2 and 3.

2.2.4 Disturbance and stress indices.

Parameters likely to constrain the growth of submerged plant species were measured and transformed into a numerical index which increased with increasing pressure on plant survival.

(i) Water fluctuation: The coefficient of variation *cv* of the different measures of water depth recorded during each visit, in both years, were transformed onto a 0-5 index range, of equal-interval classes covering the full range of *cv* obtained. Water depth was correlated with water fluctuation and showed that shallow waters had maximum values (see Fig. 2.10). Water level fluctuation can affect both disturbance and stress (Kautsky, 1988), however it was observed that high water fluctuation values occurred at sites that had very low water level during some weeks and a substantial loss of above-ground biomass. On these grounds, it was considered that water level fluctuation was primary acting as a disturbance in the channels studied.

(ii) Management: the indices were calculated from 2.2.3.2 on a scale 0 to 5 as the likely degree and timing of destruction of plant biomass (Fig. 2.2).

(iii) Light attenuation: Indices were calculated from the ratio z_{eu}/d (2.2.3.1). The range of values calculated for the ratio was divided in a series of equal-interval classes to give an index on a scale of 0 - 5 for each site.

(iv) Other stress factors: These included saline intrusions, low oxygen, eutrophication and shade (from emergent plants or trees). Their likely effect on macrophyte was rated as low (1) , medium (2) or high (3) , and were summed for each site to give a 0 - 5 index range.

The disturbance index (I_D) was constructed as the sum of (i) plus (ii) and the stress index (I_S) as the sum of (iii) plus (iv).

Filamentous algae were included together, and treated as one taxon in the analysis: these included *Cladophora glomerata, Vaucheria dichotoma* and *Enteromorpha intestinalis*. Certain taxonomically-close vascular species, with marked similarities of morphological and reproductive survival traits were also included together in the analysis. They were *Elodea canadensis - E. nuttallii, Callitriche stagnalis -C. platycarpa* and *Potamogeton berchtoldii - P. pusillus*.

2.2.5 Multivariate analysis of the vegetation

Field data on frequency and abundance were analysed using cluster and ordination analysis, as follows:

2.2.5.1 Cluster analysis:

Cluster analysis is an explicit way of identifying groups in row data and helps to find structure in the data. However even if there is a continuous structure in the data, the analysis may impose a group structure. Van Tongeren (1987) indicates the aim of cluster analysis:

-to give information of the concurrence of species

-to establish community types for descriptive studies.

-to detect relations between communities and the environment by analysis of the groups formed by the cluster analysis with respect to the environmental parameters.

There are several types of cluster analysis. TWINSPAN (Two Way INdicator SPecies Analysis: Hill 1979a, 1979b) was used in this study. It was undertaken using the PC version 1.2 (1989), option in the VESPAN II statistical package. TWINSPAN provides a hierarchical divisive classification of the data matrix. It is one of the most widely used programs in community ecology, especially because it classifies the sites- by- species matrix. "Indicator species", differentiating sample- groups, identified at each level of abundance ("cut levels"), are considered as separate entities ("pseudospecies") by the program. A limited set of levels of abundance is needed if an unduly large number of pseudospecies is not to be generated (Hill, 1979b).

2.2.5.2 Ordination

Ordination is the collective term for multivariate techniques that arrange sites along axes on the basis of data on species composition. The aim of ordination is to arrange the points in a diagram such that points that are close together in the ordination space correspond to sites that are similar in species composition, and sites that are far apart correspond to sites that are dissimilar in species composition. The way in which abiotic environmental variables influence biotic composition could be explored using ordination in two ways: indirect and direct analysis.

In indirect gradient analysis the data is summarised and arranged in a ordination diagram (e.g. samples in terms of species), which is then interpreted in the light of whatever is known about the environmental characteristics of the samples. One of the advantages over direct gradient analysis is that species composition may be a more informative indicator of environment than any given set of measured environmental variables (ter Braak, 1987).

CA (Correspondence analysis) is an indirect analysis which is based on a unimodal response model. In this model any species occurs in a limited range of values of each of the latent variables, which is determined by the observation that species commonly show bell- shaped response curves with respect to environmental gradients. CA constructs from the data matrix the theoretical variable that best explains the species data, which is termed the first ordination axis. Further axes are constructed in CA, which maximise the dispersion of the species scores but may be subject to the constraint of being only poorly correlated with previous CA axes. This constraint is intended to ensure that new information is expressed on the later axes. Thus the axes may then be correlated with the associated environmental variables, and the variables which are significantly correlated with the axes can be postulated to control the variation in species composition (Gauch, 1982). This analysis was made in this study with DCA (Detrended Correspondence Analysis), which is similar to CA but with a modification designed to correct two "faults" of CA, both related to linear dependence between axes (Hill and Gauch, 1980).

By contrast with the above, direct analysis is impossible without explicit environmental data. Canonical ordination techniques, one type of direct analysis, are designated to detect the patterns of variation in the species that are best explained by the observed environmental variables. The resulting ordination diagram expresses not only a pattern of variation in species composition but also the main relations between the species and each of the environmental variables included. Canonical ordination thus combines aspects of regular ordination with aspects of regression (ter Braak, 1987).

CCA (Canonical Correspondence Analysis) is a technique that selects the linear combination of environmental variables that maximises the dispersion of the species scores, and gives the first axis. The second and further axes also select linear combinations of environmental variables that maximise the dispersion of the species scores, but subject to the constraint of being uncorrelated with previous CCA axes. CA also maximises the dispersion of the species scores, though irrespective of any environmental variable. CCA is therefore "restricted correspondence analysis" in the sense that the site scores are restricted to be linear combination of measured environmental variables (ter Braak, 1986, 1987, 1988).

The ordination diagram in DCA displays sites and species. In CCA displays sites, species and environmental variables; the variables are represented by arrows if they are continuous or by points (centroids) if they are nominal variables. Generally speaking, the arrow for an environmental variable points in the direction of maximum change of that variable across the diagram, and its length is proportional to the rate of change in this direction. The order of the projection point of a species corresponds approximately to the position of a species distribution along an environmental variable (ter Braak 1989).

DCA and CCA were undertaking using CANOCO version 3.1 (ter Braak, 1988, 1989). ANOVA analysis were made using MINITAB realise 8.

2.3 Results

2.3.1 Macrophyte community and weed status.

In total 62 macrophyte species taxa were recorded from the targets area of the UK during the survey both years (Table 2.1). This included 5 filamentous algae, 35 submerged and floating taxa (also bryophyte and charophyte) and 22 emergent species. Except one, all the species recorded were included by Holmes and Newbold (1984) in the community group described as being "either base-rich or nutrient rich, and usually both". The exception was *Equisetum palustre* (mesotrophic) found in some sites in the Solway Drainage Area. Other features confirm the generally eutrophic nature of the drained system examined: (a) none of the 26 aquatic plant species recorded exclusively in the groups dystrophic, oligotrophic or mesotrophic by Palmer *et al.* (1992) were found in the area, and (b) Nitrate-N water concentration during summer 1993 measured in all sites under study was high, between 1.4 and 13.5 mg. l^{-1} (Table 2.4). However, few sites seem to have a mesotrophic nature (see below).

In a study of river plant communities, Newbold and Palmer (1979) and Holmes and Newbold (1984) proposed a ranking system to assess the trophic status of most freshwater habitats. They assigned "trophic rank" to 150 aquatic plant species, starting with those confined to oligotrophic water and working up to those tolerant of hypertrophic conditions. Recently, a similar botanical classification of standing waters was made by Palmer *et al.* (1992). From these studies and by using the "species trophic scores", the trophic mean score of each site was calculated (Table 2.2). This shows that 6 of the 24 sites under study are mesotrophic, rather than eutrophic. A low species diversity and the presence of *Glyceria fluitans, Agrostis stolonifera,* *Juncus effusus* and *Potamogeton natans*, all with low trophic scores, differentiated these sites.

Table 2.1. Aquatic plant species recorded in the examined sites of Britain

Submerged and floating vegetation

Callitriche hamulata Kuetz. ex Kotch
Callitriche stagnalis Scop.
Callitriche obtusangula Le Gall
Callitriche platycarpa Kuetz
Ceratophyllum demersum L.
Charophyta
Cladophora glomerata (L.) Kutz.
Elodea canadensis Michaux
Elodea nuttallii (Planchon) H.St. John
Enteromorpha intestinalis (L) Grev
Fontinalis antipyretica Hedw.
Glyceria fluitans (L.)R.Br.
Hippuris vulgaris L.
Hottonia palustris L.
Lemna gibba L
Lemna minor L
Lemna trisulca L
Myriophyllum spicatum L.
Nuphar lutea(L.) Smith
Nymphaea alba L.
Nymphoides peltata Kuntze
Persicaria amphibia (L.) Gray
Potamogeton berchtoldii Fieber
Potamogeton crispus L.
Potamogeton lucens L.
Potamogeton natans L.
Potamogeton pectinatus L.
Potamogeton perfoliatus L.
Potamogeton pusillus L.
Ranunculus aquatilis L.
Ranunculus circinatus Sibth.
Rhizoclonium Kützing
Riccia fluitans L.
Rorippa nasturtium-aquaticum (L.) Hayek
Rynchostegium riparioides (Hedw.) C. Jens
Sagittaria sagittifolia L.
Sparganium emersum Rehmann
Spirogyra Link
Vaucheria dichotoma (L.) C.A. Agardh
Zannichellia palustris L.

Table 2.1 (cont.).Aquatic plant species recorded in 24 studied sites of Britain.

Emergent species

Agrostis stolonifera L.
Alisma plantago-aquatica L
Alisma lanceolatum With
Apium nodiflorum (L.)Lag.
Caltha palustris L.
Carex spp.
Carex riparia Curtis
Epilobium hirsutum L.
Equisetum palustre L.
Galium palustre L.
Glyceria maxima (Hartman) O. Holmb.
Iris pseudacorus L.
Juncus articulatus L.
Juncus effusus L.
Mentha aquatica L.
Myosotis scorpioides L.
Phalaris arundinacea L.
Phragmites australis (Cav) Trin.ex Steudel
Persicaria hydropiper (L.) Spach
Sparganium erectum L.
Typha latifolia L.
Veronica beccabunga L.

Fig. 2.3 includes the number of submerged plant vegetation species recorded in the study. Under the title "submerged plants" are included here not only true-submerged (as for example the rooted *Potamogeton pusillus* or the non-rooted *Ceratophyllum demersum)*, but also floating-rooted species such as *Persicaria amphibia* or *Potamogeton natans*. Both the different drainage areas and sites in the same area, show important differences in the number of species present. The Fens and Crossens drainage areas support more than the double the Solway and Spynie canal species diversity. As will be seen later, in some cases this is clearly explained by the management of the site, but in others, environmental variables rather than the management (like the light regime or the water column), appear to especially affect species diversity.

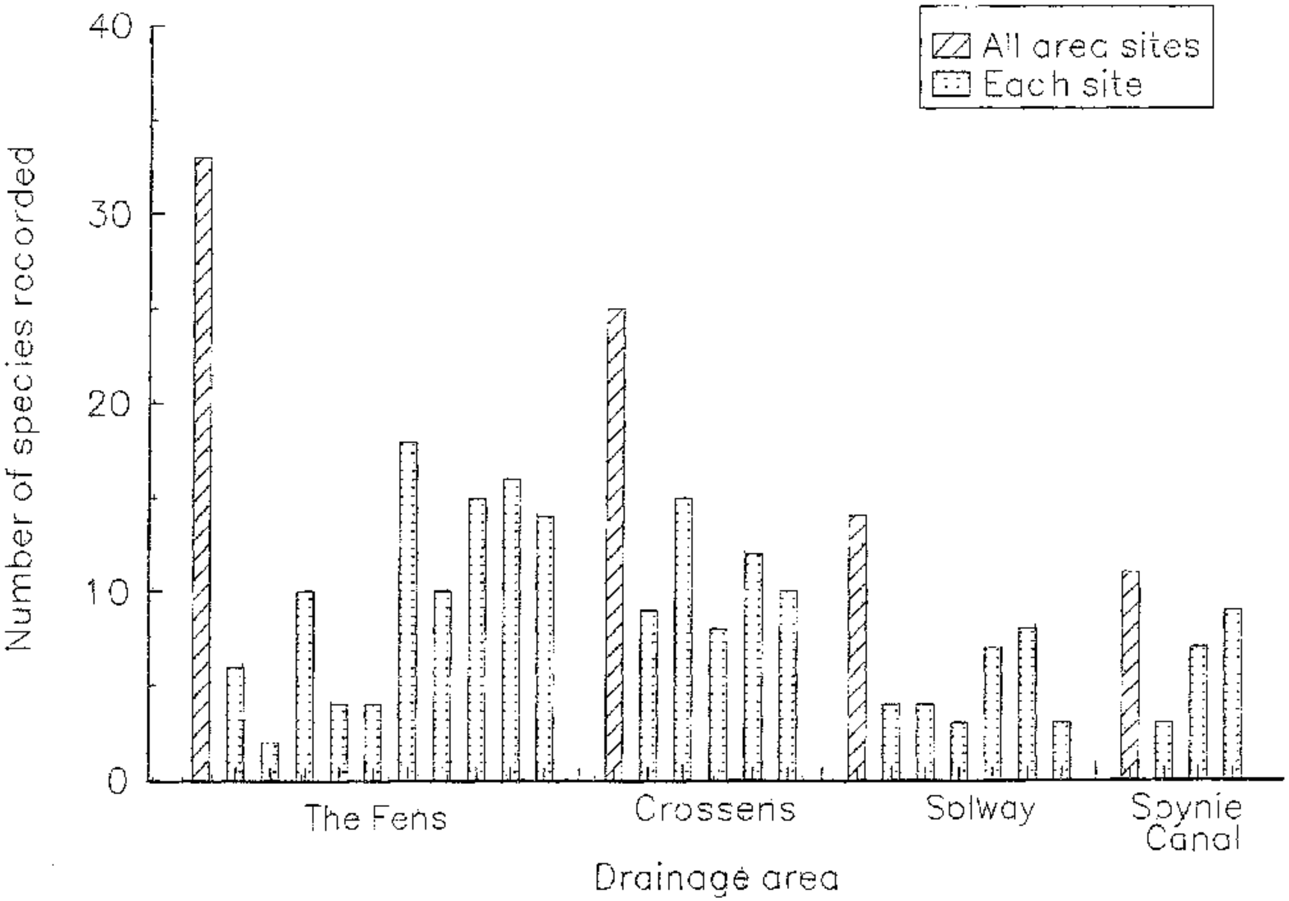


Fig. 2.3 Number of species recorded in 24 drainage channels sites surveyed in 1992 and 1993. "All sites" bars show the diversity in each drainage area.

Table 2.2. Trophic status of each site calculated from the Trophic Ranking Scores (TRS) schemes given by Palmer *et al.* 1992 (*) and by Holmes and Newbold , 1979 (**).

Drainage Area	Site	TRS (*)	TRS (**)	Trophic status of the site
FENS	1	9.3	113	Eutrophic
	2	9.1	131	"
	3	9.4	124	"
	4	9.8	119	"
	5	9.8	120	"
	6	8.7	111	"
	7	9.2	112	"
	8	8.8	110	"
	9	8.5	116	"
	10	9.2	105	"
CROSSENS	1	8.7	110	"
	2	9.1	105	"
	3	8.8	104	"
	4	9.0	108	"
	5	8.6	108	"
SOLWAY	1	7.9	87	Mesotrophic
	2	8.5	98	Eutrophic
	3	7.2	85	Mesotrophic
	4	7.8	85	Mesotrophic
	5	8.3	97	Meso-eutrophic
	6	8.4	87	Mesotrophic
SPYNIE CANAL	1	8.1	81	Mesotrophic
	2	8.3	109	Eutrophic
	3	8.6	104	Eutrophic

Fig. 2.4 shows mean species frequency (*f*) and abundance (*a*) for all sites studied. The figures only included angiosperm species found at least in 2 different drainage areas and with a value of $f > 0.10$. This information, specially abundance, is a good measure of the extent of the vegetation nuisance in the drainage network.

Only *Callitriche stagnalis* and *C. platycarpa* were present in every site surveyed in the Solway drainage area ($f = 1$). Other frequent species were

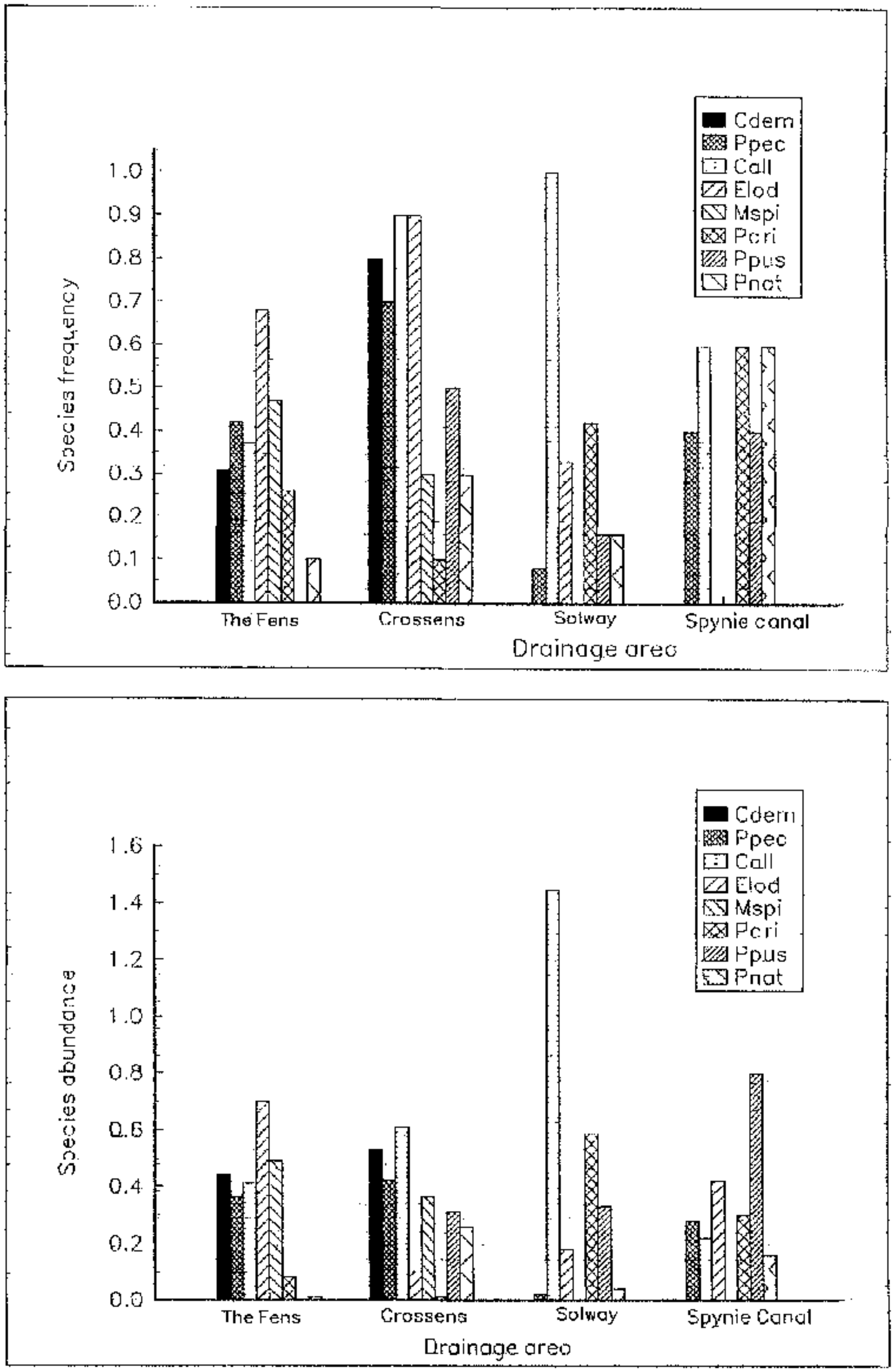


Fig. 2.4. Average frequency (above) and abundance (below) of submerged and floating-rooted plant species. Abundance was rated as 1, scarce; 2, common and 3, abundant. Only included species found at least in 2 drainage areas and with a frequency > 0.10. For species codes see Fig. 2.8.

Ceratophyllum demersum, Potamogeton pectinatus, Elodea canadensis, E. nuttallii and *P. crispus* (*f* = 0.6 - 0.8).

Fig. 2.4 shows that in terms of abundance *Callitriche* species were the most abundant (*a* = 1.45, in a range from 0 to 3) in the Solway drainage area. The next most abundant species were *P. pusillus* and *P. berchtoldii* in the Spynie Canal (*a* = 0.80), that is a relatively small value in the measured range. Thus, it can be state that there is a group of at least 10 vascular plants that cause most of the problems in the studied drainage channels, but the abundance of each one varies in a great measure between different drainage areas and also between different sites within the same area.

Table 2.3 shows the mean annual values of TON as N , ammonia as N and orthophosphate as P in some of the surveyed sites. Phosphate and ammonia concentration are both key determinants of water quality which may influence macrophyte communities. In natural waters that support aquatic vegetation, the values of these nutrients usually show a seasonal pattern of summer minimum and winter peaks, corresponding to aquatic plant uptake from the water. This can be see in a report to NRA Anglian Region (see Appendix 2: Aquatic vegetation, management and physico-chemical status of the Old Bedford/ Counter Drain and Forty Foot Drain), that involve 4 sites of this study located in the Fens Drainage Area. From monthly data it is clear from this report that the values of T.O.N. were very high during the wintertime and low during the growing season.

Table 2.4 shows the ranges of 8 environmental variables measured in each site, expressed as averages for each drainage area. The studied sites showed a wide spectrum of physico-chemical characteristics, not only between different drainage areas, but also between sites in the same area.

Table 2.3. Annual 1992/ 1993 water quality averages taken from database. In brackets are maximum and minimum values measured. Samples were taken in or close to 6 sites in the Fens, 3 sites in the Crossens and 3 sites in the Spynie canal.

Measured parameter	**FENS**	**CROSSENS**	**SPYNIE CANAL**
Ammonia-N (mg .l^{-1})	0.62 (0.01 - 5.20)	1.06 (0.06 - 8.70)	0.13 (<0.02 - 0.43)
T.O. N. - N (mg .l^{-1})	7.74 (0.10 - 23.35)	11.02 (2.7 - 27.0)	4.13 (0.05 - 2.39)
Ortho- P (mg .l^{-1})	0.35 (0.01 - 1.46)	1.27 (0.08 - 6.20)	0.05 (<0.02 - 0.16)

Table 2.4. Maximum and minimum environmental parameters values measured during the 92/93 survey in Britain in all the examined sites.

Measured parameter	**FENS**	**CROSSENS**	**SOLWAY**	**SPYNIE CANAL**
pH	7.3 - 8.7	6.5 - 8.7	5.1 - 7.8	7.1 - 7.8
Dissolved oxyg. (mg .l^{-1})	1.7 - 12.5	4.1 - 16.6	1.6 - 9.6	8.4 - 12.7
Conductivity (µS. cm^{-1})	845 - 3800	758 - 1235	252 - 685	489 - 1070
Channel wide (m)	2.50 -14.80	1.90 - 17.70	0.70 - 2.10	1.80 - 7.70
Channel depth (m)	0.60 - 1.50	0.40 - 1.18	0.13 - 0.50	0.21 - 0.60
Light attenuation (z_{eu}/ d)	0.87 - 3.90	0.84 - 8.70	0.95 - 6.28	5.56 - 7.51
Water fluct.(c.v., %)	5 - 23	20 - 58	22 - 86	15 - 37
Nitrate (mg .l^{-1} as N)	1.8 - 7.2	1.45 - 13.50	1.45 - 2.40.	1.80 - 2.70.

It is of interest to determine the phytosociologically-defined aquatic plant communities present in the target drainage channels of Britain, in terms of the 24 communities of aquatic vegetation recognised by the National Vegetation Classification (NVC; Rodwell, 1995). In Appendix IV are included the NVC plant community types present at survey sites within the four drainage areas surveyed in Britain during this study. This shows that seven plant communities and several sub-communities were recognised (with different degree of goodness of fit) as the aquatic vegetation of the drainage channels.

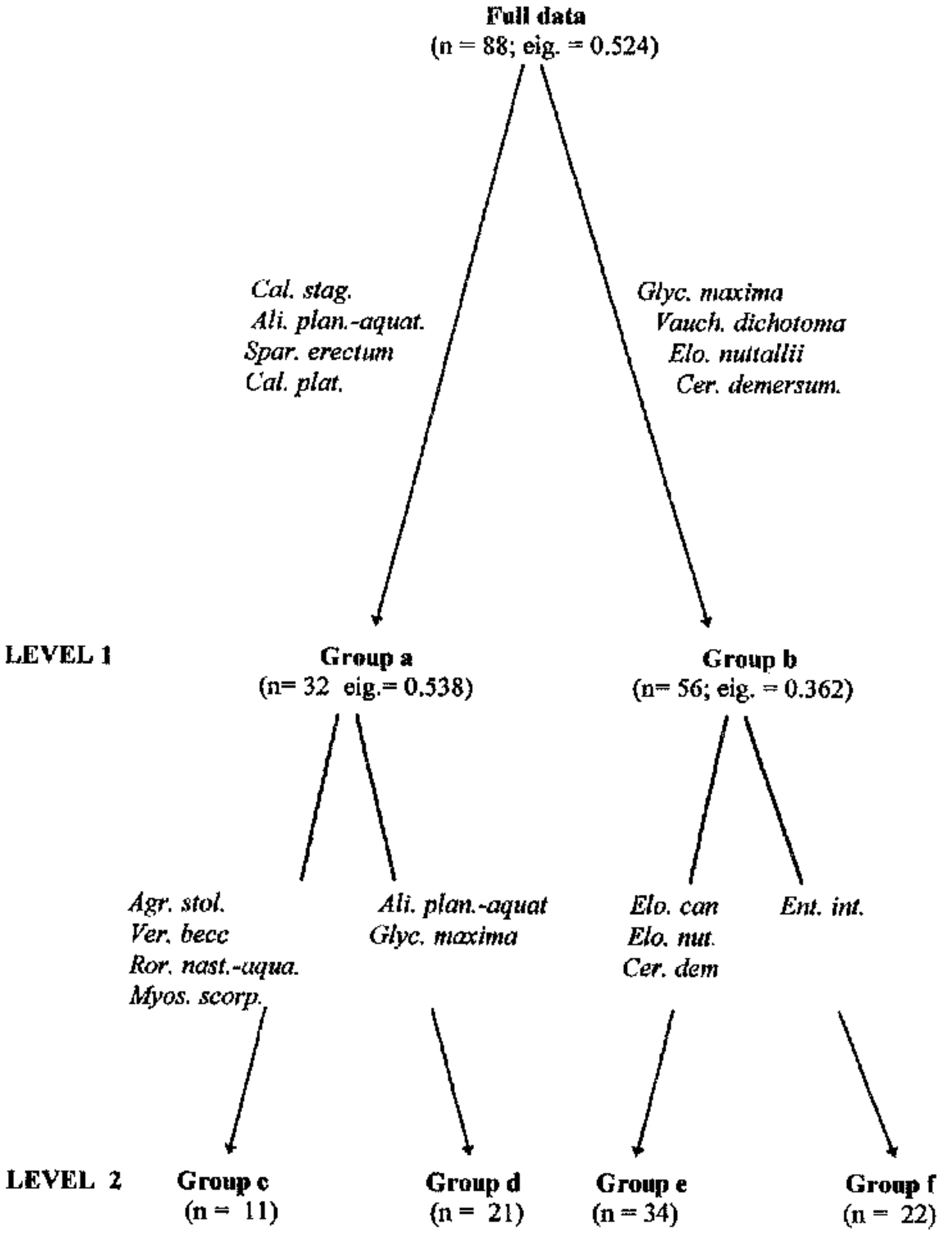


Fig. 2.5. Results of the TWINSPAN analysis expressed as a dendogram showing hierarchical subdivisions of the samples x submerged, floating and emergent frequency to level 2. Only the indicator species are in the diagram. For references and further details see text.

2.3.2 Multivariate analysis of the vegetation

The first species x sites matrix used covered each time of sampling as a separate sample-group, and including submerged, free-floating and emergent vegetation. From this matrix it is possible not only to find distinction between sites, but also vegetation type differences within the growing season. Fig. 2.5 shows the result of TWINSPAN analysis of the matrix sites x emergent, floating and submerged species frequency, expressed as a dendogram showing hierarchical subdivisions of the data set to give 4 end-groups at level 2 of the division process. At level 1 the analysis divided the samples largely according to a geographical pattern, with a large right-side group (n = 56) covering most of the Fens and Crossens drainage area sites and other with sites from Solway, Spynie Canal and a small group from Crossens drainage area. Filamentous algae *(Vaucheria dichotoma, Enteromorpha intestinalis*) tended to come out as major indicators of samples falling into the right- side (groups b, e, f), with the emergent *Glyceria maxima* and the submerged plants *Elodea spp.* and *Ceratophyllum demersum.* The left-side groups (a, c, d) contain 7 emergent indicator species plus one submerged indicator: *Callitriche* species. The data showed no separation between early, mid and late season, and also that in general the same sites, sampled in different seasons, fell in the same group.

Fig. 2.6 shows DCA sites scores (eigenvalue = 0.67) using a data matrix containing only submerged vegetation. The displaying plot shows in axis 1 a length of more than 4.0 (Fig. 2.6). In DCA, the axis units are standard deviations of species turnover, and an axis length of 4.0 or more, would indicate that sites at either end of the axis have not species in common (ter Braak, 1987). Overlaying the time of sampling (Fig. 2.6) in the sample scores, again showed no evidence of separation of early, mid and

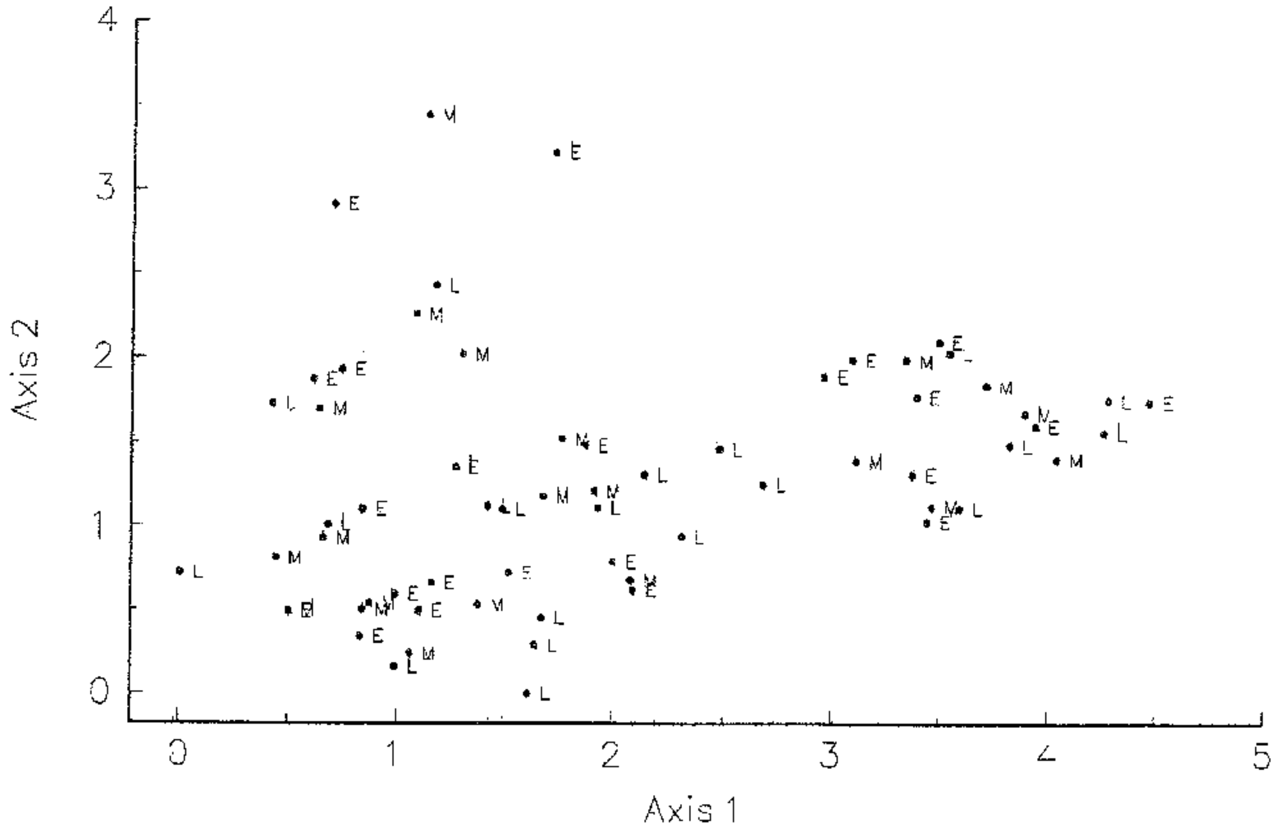


Fig. 2.6. DCA ordination of submerged vegetation plotting site scores during the season. E: early season, M: middle season, L: late season.

late-season. Habitats usually under disturbance or with the influence of environmental parameters that strongly affect plant growth, are expected to show a pattern of plant growth or species composition more adapted to these alterations than a seasonal growth pattern. Fox and Murphy (1990) found some evidence of different macrophyte communities in early and late season in British rivers. However, they include in the survey emergent species, that tend to increase their percentage of frequency in late season.

For further analysis, seasonal average abundance of the species were used for multivariate analysis. Species were excluded *a priori* if they were not likely to be directly affected by the stress and disturbance parameters evaluated in this study. Example include *Lemna,* unlikely to be affected by underwater shade stress owing to its surface- floating life- form; and for the same reason *Hippuris vulgaris,* which showed an emergent growth form in the target sites. Also excluded were species found in only one site and species with few occurrences located in sites with extreme conditions. Such species have little influence on the analysis and tend to be ordinated the edges of the plot. To enlarge the remainder of the diagram it may be convenient to omit them (ter Braak, 1988; 1989).

Fig. 2.7 shows the result of TWINSPAN analysis of the matrix sites x submerged species, expressed as a dendogram showing hierarchical subdivisions of the data set to give 4 end groups at level 2. Analysis was stopped at this point because eigenvalues were too low or subgroups contained too few sites, to justify further subdivision. 3 abundance cut levels were used and the data from 1992 and 1993 were considered as different (site-year) cases in the analysis. The figure contain also eigenvalues of each division, number of sites and indicator species with their abundance value ("pseudospecies" Hill, 1979b) . At level 1 TWINSPAN separates two plant

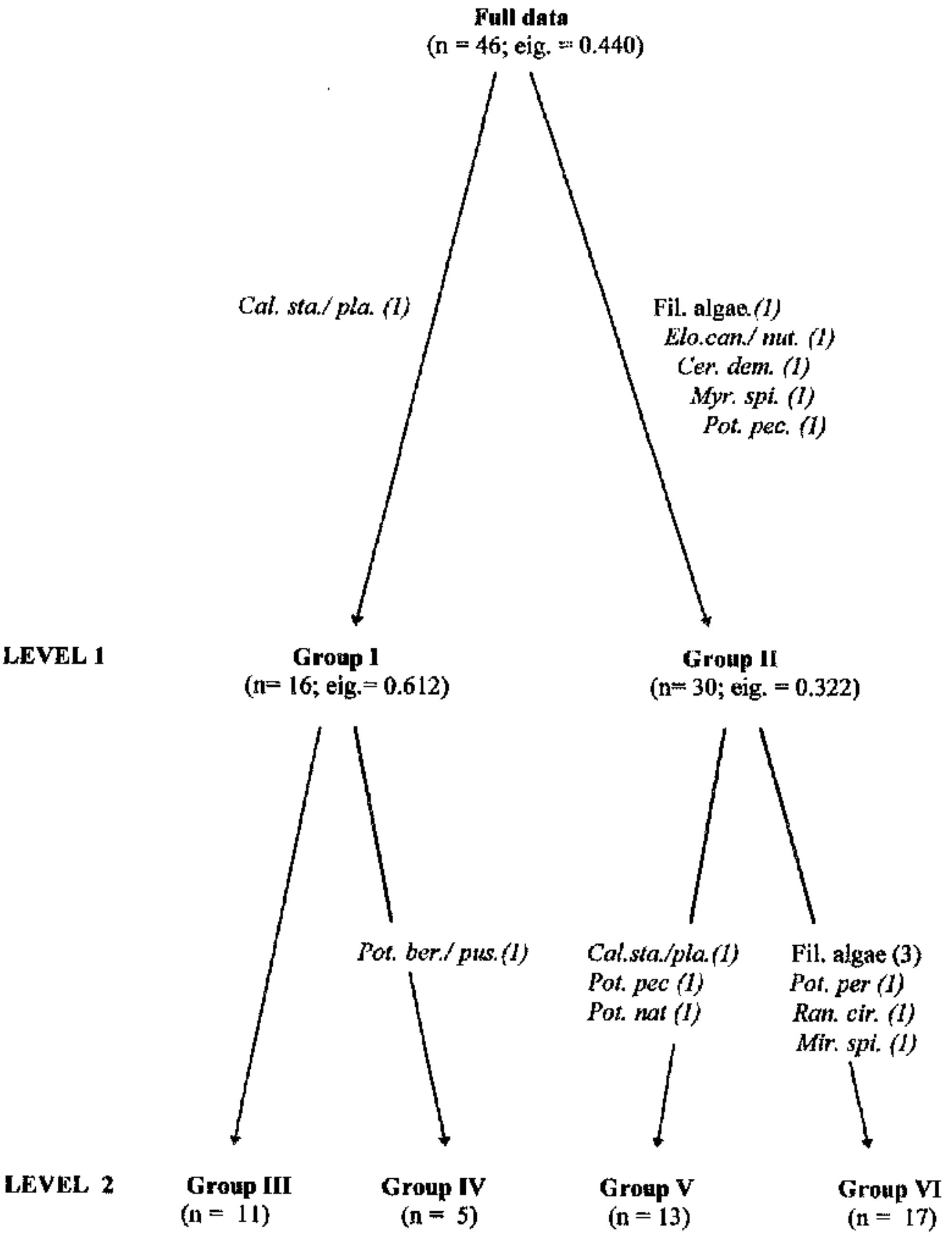


Fig. 2.7. Results of the TWINSPAN analysis expressed as a dendogram showing hierarchical subdivisions of the samples x species abundance to level 2. Only the indicator pseudospecies are in the diagram. n = number of sites for group. For further details see text.

groups according to a geographical pattern, group I included especially sites of the Solway Area and Group II sites of the Fens and Crossens Area (Table 2.5). Three sites of the Spynie canal were included in group I and two in group II. From this, comes up that the vegetation data did not change enough between the two years to cause much a shift in group content. In fact, this happened only in two sites: site 1 of the Fens and site 5 of the Spynie canal (see 2.2.1). This suggest that the vegetation in drainage channels is fairly stable and adapted to site conditions, so long as management regime remains stable.

C. stagnalis and *C. platycarpa* appears as indicator species of group I, but also in group V that is a division of group II (Fig. 2.7). The presence of filamentous algae characterised group II, especially because they are indicator species in it subdivition group VI with their maximum abundance (Fig. 2.7). Groups I and II were compared statistically to each other on terms of the environmental parameters measured for each site, using t- test (Table 2.5). From the 7 parameters evaluated, there were significant differences in all of them, except dissolved oxygen and light attenuation.

The 4 TWINSPAN end groups at level 2, identified as III, IV, V and VI in Fig. 2.7 were compared to each other using one-way analysis of variance and multiple comparisons by Tuckey' s test, with a family error rate of 0.05 (Table 2.6). As in level 1, in level 2 there were not significant differences in light attenuation and dissolved oxygen between groups but the other parameters show different patterns of significance.

Table 2.5. TWINSPAN end group at level 1 and means of different environmental parameters in British sites. Means labelled in each column with different letters (a - b) are significantly different (t-test, $p < 0.05$). In column 1 are indicated in each group the number of sites and the drainage area where they were located.

Site Group (Fig. 2.7)	**Light Atten. (Z_{eu}/D)**	**Water Fluct. (C.V. %)**	**Water Depth (Cm)**	**Conduc. (μS. Cm^{-1})**	**pH**	**Diss. Oxyg. (Mg .L^{-1})**	**Manag. (0 - 5)**
I (16 sites: 12 Solway 3 Spynie C. 1 Crossens)	4.10 a	45.8 a	26.87 a	510.2 a	6.70 a	5.57 a	3.56 a
II (30 sites: 19 Fens, 2 Spynie C. 9 Crossens)	3.38 a	18.70 b	99.60 b	1265.5 b	7.64 b	7.09 a	1.76 b

Table 2.6. TWINSPAN end-groups at level 2 (Fig. 2.7) means and different environmental parameters in British sites. Means labelled in each column with different letters (a - c) are significantly different (Tukey's test, $p<0.05$). In column 1 are indicated in each group the number of sites and the drainage area where they were located.

SITE TWINSPAN GROUP	**LIGHT ATTEN. (z_{eu}/d)**	**WATER FLUCT. (c.v. %)**	**WATER DEPTH (cm)**	**CONDUC. (μS. cm^{-1})**	**pH**	**DISS. OXYG. (mg .l^{-1})**	**MANAG. (0 - 5)**
III (11 sites: 10 Solway, 1 Spynie C.)	3.93 a	54.09 a	23.55 a	489.8 a	6.52 a	5.08 a	3.81 a
IV (5 sites: 2 Solway, 1Crossens 2 Spynie C.)	4.30 a	27.60 bc	34.20 a	555.2 ab	7.09 ab	6.66 a	3.00 ab
V (13 sites: 3 Fens, 8Crossens, 2 Spynie C.)	3.64 a	28.23 b	92.92 b	948.2 b	7.32 b	7.32 a	1.92 bc
VI (17 sites: 16 Fens, 1 Crossens)	3.10 a	11.41 c	104.71 b	1508.2 c	7.89 b	6.92 a	1.65 c

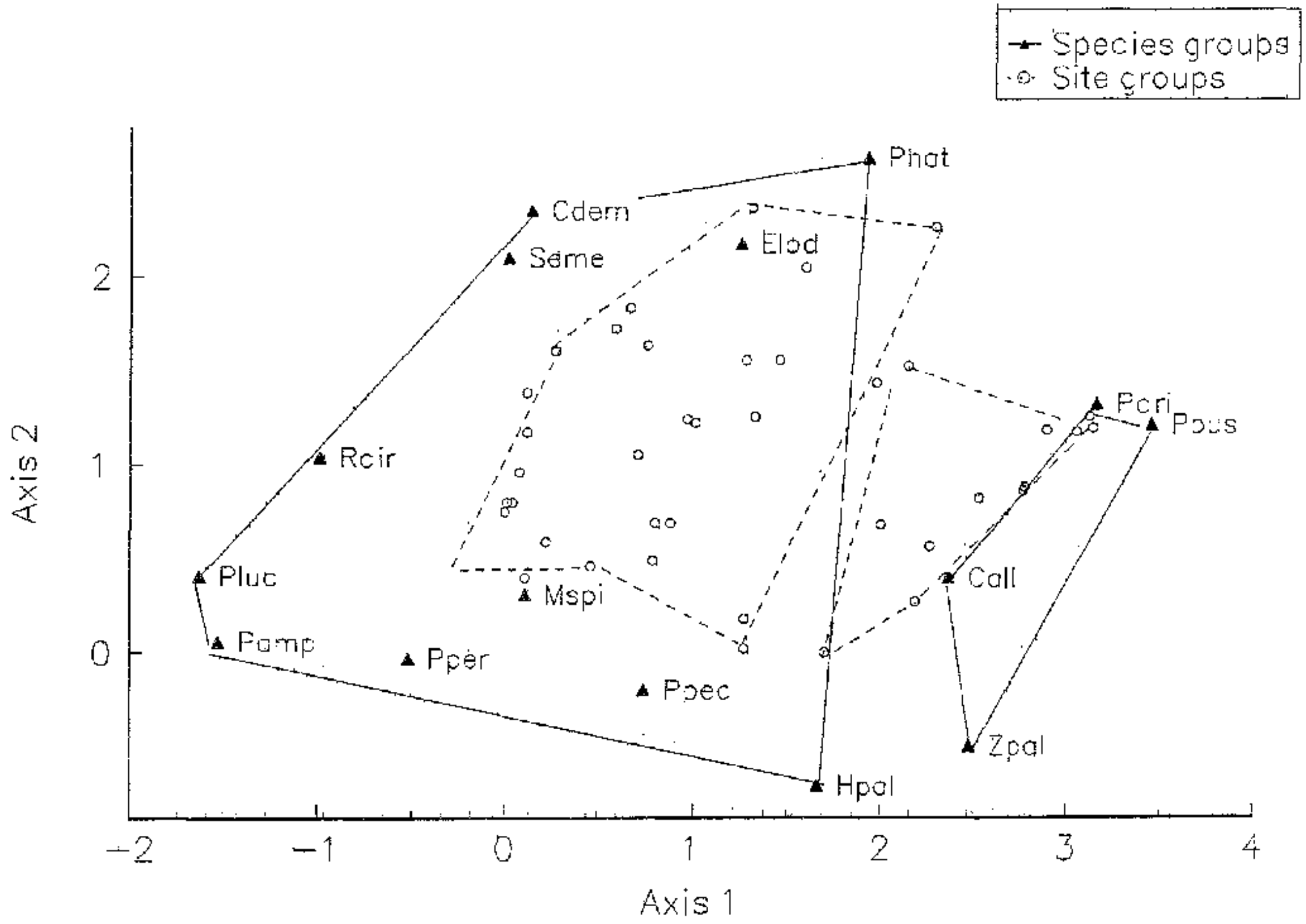


Fig. 2.8. DCA ordination of vegetation samples plotting the sites (✲) and species (♦) scores. The boundaries are shown two site groups (I and II) and two species groups (A and B) identified at level 1 of TWINSPAN classification. Species codes: Call, *Callitriche stagnalis* and *C. platycarpa;* Cdem, *Ceratophyllum demersum*; Elod, *Elodea canadensis* and *E. nuttallii*; Falg, filamentous algae; Hpal, *Hottonia palustris*; Mspi, *Myriophyllum spicatum*; Pamp, *Persicaria amphibia*; Pcri, *Potamogeton crispus;* Pluc, *P. lucens;* Pnat, *P. natans;* Ppec, *P. pectinatus*; Pper, *P. perfoliatus;* Ppus, *P. pusillus* and *P. berchtoldii*; Rcir, *Ranunculus circinatus*; Rrip, *Rynchostegium riparioides* (moss); Seme, *Sparganiun emersum*; Zpal, *Zannichellia palustris.*

Fig. 2.8 shows DCA ordination plot of the abundance of submerged vegetation displaying species and site scores. In this analysis the eigenvalues were 0.61 and 0.36 for the first and second axis, respectively. The length of the first axis gradient was 3.15, and the second axis 2.36. In addition, Fig. 2.8 indicates the sites included in both groups (I and II) in the TWINSPAN sample classification at level 1 (Fig. 2.7). TWINSPAN besides a site ordination made a species classification. Fig. 2.8 also shows the two species groups (A and B) at level 1 (eigenvalue = 0.83). The figure shows that there is a clear correspondence between both analysis, DCA and TWINSPAN.

Fig. 2.9 shows the CCA ordination plot displaying species scores and arrows of environmental variables. This was plotted from the same species x sites matrix as the last DCA analysis, plus an environmental data x sites matrix. The environmental variables used were the same as those used for compared the different TWINSPAN site groups (see Tables 2.5 and 2.6). Water temperature was not included because this variable was not significant in previous analyses. The influence of boat traffic in the species data was also included in previous analysis as a nominal variable, but it was not significant. About boat traffic, there were boat movements by powered pleasure craft through 5 sites of the Fens area. In 1992, in the sites from the Old Bedford/ Counter drain there was an annual top estimate of only 24 passages at all. However, at sites located in Well Creek (Upwell) traffic was estimated as up to 1000 movements per year. The main mechanism of boat damage is the disturbance of the water by propeller action and by boat wash, that damages plant tissues and stirs up sediments which reduce the available light for submerged plant photosynthesis (Murphy and Eaton 1981, 1983).

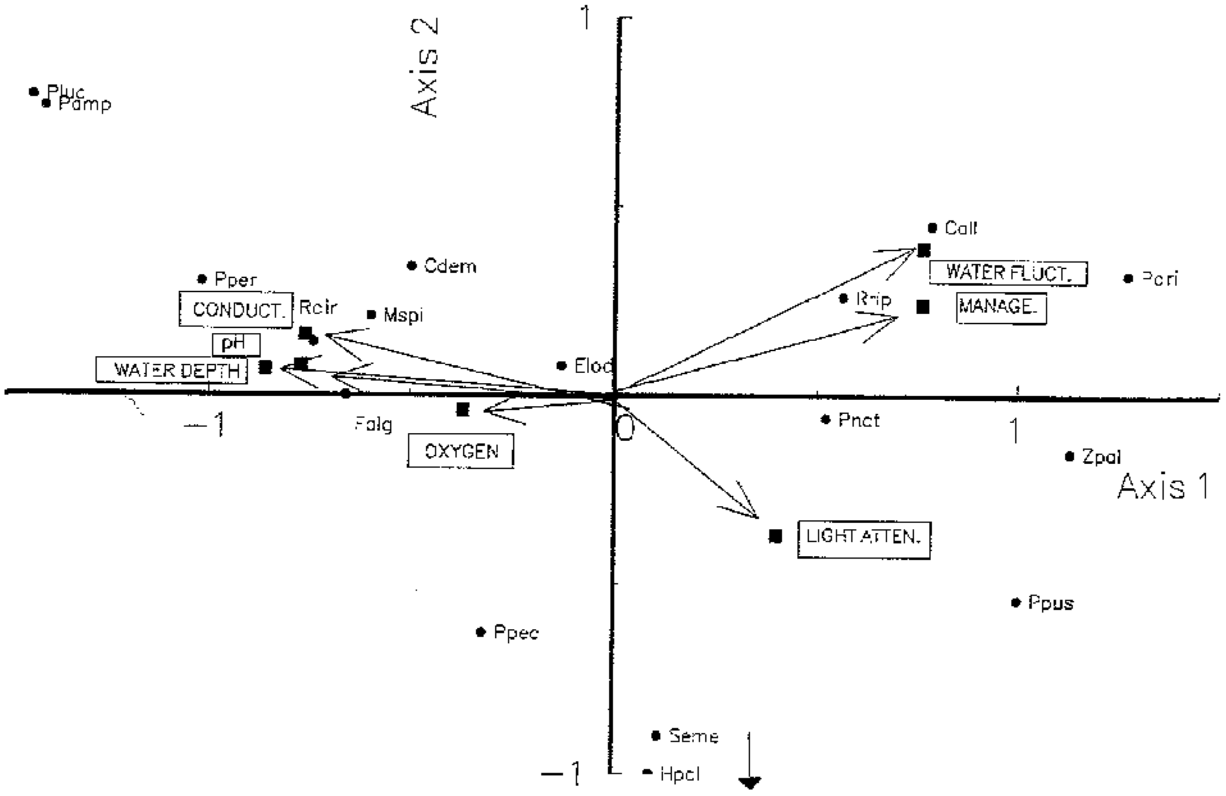


Fig. 2.9 CCA ordination of species scores (•) and arrowed biplot scores of environmental variables (■). For species codes see Fig. 2.8. Values on axis 2 for *S. emersum* and *H. palustris* were -1.43 and -1.51, respectively.

A summary of CCA analysis is given in Table 2.7. The eigenvalues, an indication of the amount of inherent variability within the data set accounted for along a given principal axis, were 0.46 and 0.27 for the first and second axis, respectively. These values are quite normal for this kind of study, ter Braak (1988) stated that eigenvalues of ca. 0.3 and higher are quite common in ecological applications. The ratio of the unconstrained eigenvalues to the canonical eigenvalues indicates that 35 % of the variation expressed in DCA is explained in the CCA using the environmental variables. To investigate whether the observed differences could be accounted for by pure chance the Monte Carlo permutation test with the first eigenvalue was used. The 99 random data set generated by random permutation all yielded a lower eigenvalue. It is therefore concluded that there are significant differences in vegetation among environmental variables ($p \leq 0.01$).

Table 2.7. Summary on CCA of submerged vegetation in relation to seven environmental variables (see text).

Axis	1	2	3	4	Total inertia
Eigenvalues:	0.460	0.275	0.215	0.157	3.574
Species-environ. correlations:	0.895	0.810	0.811	0.738	
Cumulative % variance					
of species data:	12.1	20.6	26.6	31.0	
of species-environ. relation:	36.4	58.1	75.1	87.5	
Sum of all unconstrained eigenv.					3.574
Sum of all canonical eigenvalues:					1.265

Table 2.8 shows the canonical coefficients and the interset correlations of the CCA analysis. The canonical coefficients define the ordination axes as linear combinations of the environmental variables, and the interset correlations are the correlations between the environmental variables and the site scores that are derived from the species data (ter Braak, 1986). The inter-set correlation is *R* times the intra-set correlations,

where *R* is the species-environmental correlation of the axis, and the intra-set correlation are the correlation coefficient between the environmental variables and the ordination axis. When the environmental variables are strongly correlated with each other the effects of different environmental variables on community composition cannot be separated out and, consequently, the canonical coefficients are unstable. This is the multicollinearity problem and, when this problem arises one should abstain from attempts to interpret the canonical coefficient (ter Braak, 1986). The intra and inter set correlations do not suffer from this problem and can still be used for interpretation purposes.

Table 2.8. CCA . Inter- set correlations of environmental variables with axes and canonical coefficient for standardised variables, in the analysis of the relation between submerged plant species and six environmental variables.

	Canonical coefficient		**Correlation coefficient**	
Axis variable	**Axis 1**	**Axis 2**	**Axis 1**	**Axis 2**
Depth	-0.482	-0.350	-0.771	0.064
Light attenuat.	-0.006	-0.712	0.358	-0.303
Water fluct.	0.158	0.936	0.687	0.323
Management	0.214	0.800	0.688	-0.201
pH	-0.013	0.609	-0.694	0.065
Dissol. oxygen	0.123	-0.201	-0.333	-0.037
Conductivity	-0.437	0.452	-0.688	0.136

Comparison of the different interset correlations on axis 1 (Table 2.8), show that several environmental variables explain the same variation in axis 1. This is clear from Fig. 2.9. Thus, the inter-set correlations of environmental variables with axis 1 were -0.77 for water depth and ± 0.69 for pH, conductivity, water fluctuation and management (Table 2.8). The environmental variables most strongly correlated with axis 2 were water fluctuation, light attenuation and management regime, with values of interset correlations of -0.32, -0.30 and 0.20, respectively.

An interested option in CANOCO 3.1 is the "forward selection of environmental variables" (ter Braak, 1990). The purpose of this selection is to find a minimal set of variables that explain the species data about as well as the full set. At each step, the variable is selected that adds most of the explained variance of the species data. When this option was added to the CCA analysis, it was found that water depth explained 28.6 % of all the variables selected (sum of all constrained eigenvalues = 1.26, see Table 2.7). With the addition of light attenuation the value rose to 44.0 %, with water fluctuation to 59.5 % and with conductivity to 74.0 %. It is interested to point out that light attenuation, which showed an interset correlation of 0.36 and - 0.30 with axis 1 and 2 respectively, come out as the second most important environmental variable explaining plant species variation in the analysis. It is clear that the five environmental variables that show high interset correlations with axis 1, are highly correlated to each other, and light- limitation is the second variable that best describes plant variation.

2.3.3 Functional grouping in terms of disturbance and stress pressures

Up to this point the vegetation data has been related to a set of selected environmental variables. In the analysis that follows only 4 environmental variables will be considered, which represent the condensed variation of different environmental parameters expressed on a 1 to 5 index (see 2.2.4). Each variable increases in proportion to increasing pressure on plant survival. Other environmental parameters that might also contribute to the explain plant variation, such as water salinity and pH, were not included because neither pH or salinity was considered likely have contributed significant stress or disturbance on plant growth, at least within the range of observed values found in this data set. Water depth was the variable that best explained plant variation (Table 2.8), but it was not included in the indices because it was assumed that its effect on vegetation are better represented by water fluctuation and light attenuation, two variables

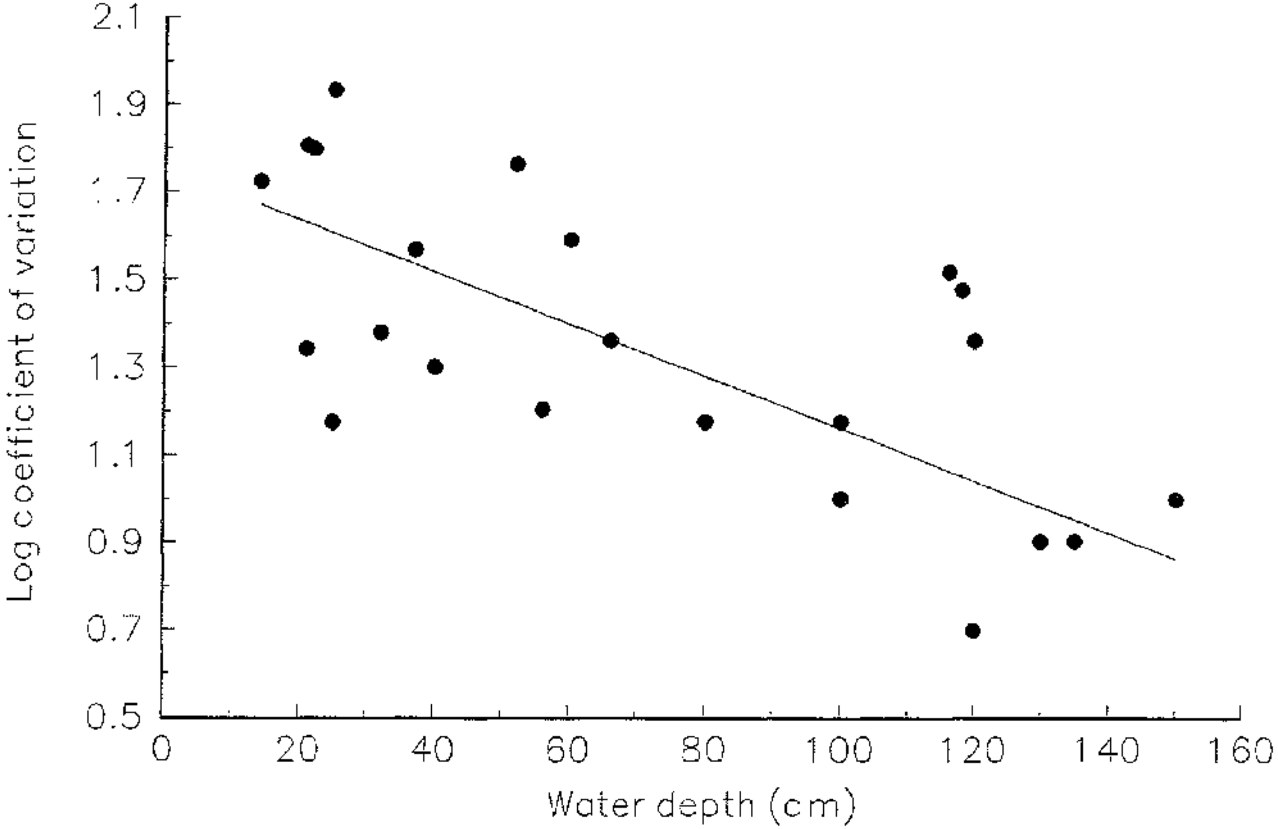


Fig. 2.10. Relationship between means of water depth and water fluctuation in the 24 examined sites of Britain, describing by a single regression line model (r = 0.71; P < 0.001).

measured separately in this study. Fig. 2.10 shows a simple regression ($r = 0.71$; $P < 0.001$) that confirms the correlation between water depth and water fluctuation: shallow waters had maximum fluctuation values. About light attenuation, several published paper relate water depth with light limitation to plant growth (e.g. Blindow, 1992; Kautsky, 1988), but the direct measure of light availability in relation to water depth (z_{eu}/d) is a better measure of this parameter.

Fig. 2.11 shows the CCA ordination plot displaying species scores and arrows for environmental variables. A summary of the CCA analysis is given in Table 2.9. It is worth to point out that the first axis of CCA practically explained the same variation when four (Table 2.9) or seven (Table 2.7) variables were included in the analysis. Parameters not included in the analysis with four variables were water conductivity, pH and water depth. The 99- point random Monte Carlo permutation test was used in this CCA and all the data set generated yielded a lower eigenvalue for the first axis and the overall analysis ($p \leq 0.01$).

Table 2.10 shows the canonical coefficients and the interset correlations of the CCA analysis shown in Fig. 2.11. The inter-set correlations of environmental variables with axis 1 were 0.76 for both management regime and water fluctuation. Light attenuation and management were best correlated with axis 2. In the study it was expected that there would be a correlation between water depth and management regime, because some kinds of weed control procedures are related to water depth. For example, manual control is only possible in shallow waters, and the use of weed-cutting boats is possible only in relatively deep waters. The total or partial loss of plant biomass was in this study rated according with the observed effect that these control measures made on the target vegetation. For this reason, and because all the study sites were

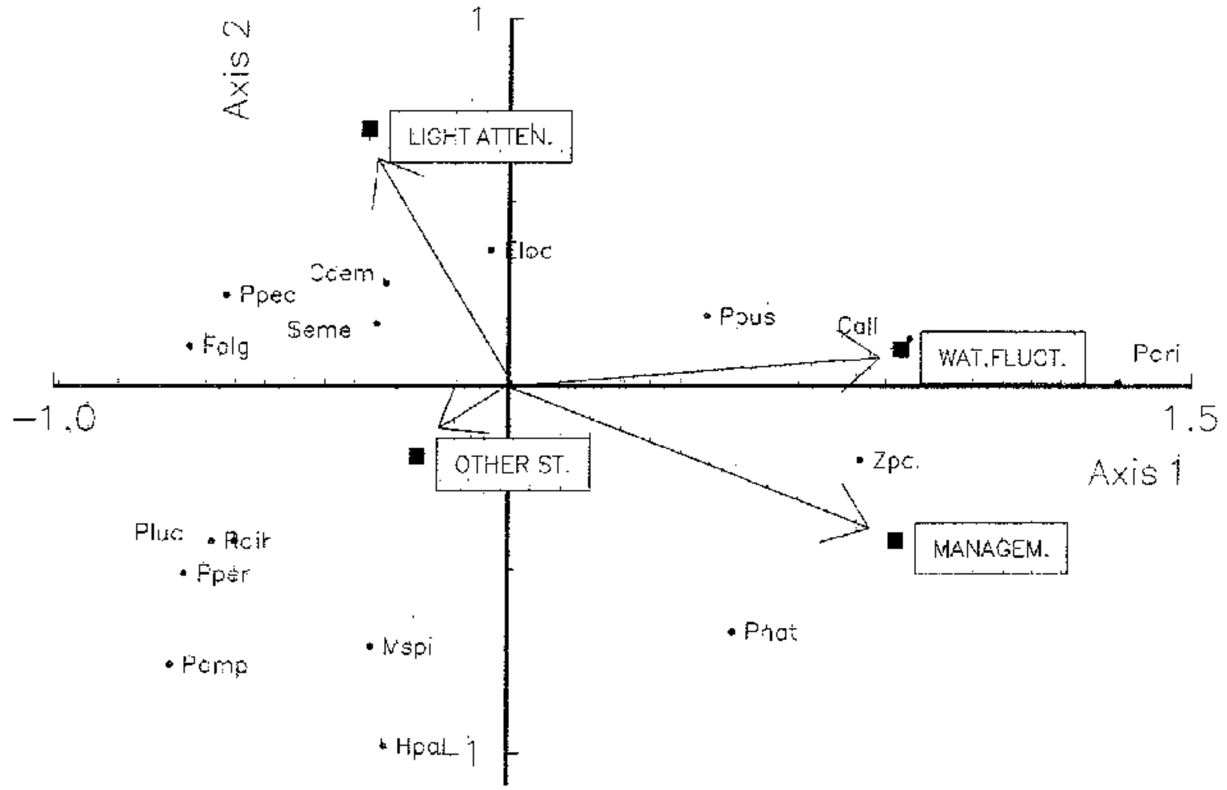


Fig. 2.11 CCA ordination of species scores (•) and arrowed biplot scores of environmental variables (■) showing species and environmental parameters names. For species codes see Fig. 2.8.

experiencing disturbance of one sort or another, these two apparently uncorrelated variables were in fact related in this study.

Table 2.9. Summary on CCA of submerged vegetation in relation to four environmental variables (see text).

Axis	1	2	3	4	Total inertia
Eigenvalues:	0.425	0.155	0.108	0.079	3.574
Species-environ. correlations:	0.884	0.703	0.565	0.526	
Cumulative % variance					
of species data:	11.9	16.2	19.3	21.5	
of species-environ. relation:	55.3	75.6	89.7	100.0	
Sum of all unconstrained eigenvalues					3.574
Sum of all canonical eigenvalues:					1.265

The "forward selection of environmental variables" showed that the management regime explained 45.5 % of the variation (sum of all constrained eigenvalues = 0.77, see Table 2.9). With the addition of water fluctuation the value rose to 66.2 % and with "other stress" to 83.1 %. Management appears as the variable that best explains plant community alteration.

Table 2.10. CCA . Inter- set correlations of environmental variables with axes and canonical coefficient for standardised variables, in the analysis of the relation between submerged and floating plant species and four environmental variables.

	Canonical coefficient		**Correlation coefficient**	
Axis variable	**Axis 1**	**Axis 2**	**Axis 1**	**Axis 2**
Water fluct.	0.53	0.41	0.76	0.68
Light attenuat.	0.23	1.03	-0.28	0.50
Other stress	-0.32	-0.72	-0.18	-0.14
Management	0.64	-0.21	0.76	-0.30

The next step in this analysis was to condense the environmental variables in terms of disturbance or stress to plant survival, by calculate a disturbance (I_D) and stress (I_S) index in each site (see 2.2.4).

Fig. 2.12 shows the CCA ordination plot displaying site scores and arrows for environmental variables (ter Braak, 1988). The eigenvalues were 0.40 and 0.11 for the first and second axes, respectively. In addition, Fig. 2.12 indicates the sites included in both groups (I and II) in the TWINSPAN sample classification at level 1 (eigenvalue 0.44). In CCA, the first axis explained 79 % of the variance in the weighted average of the species scores, and the inter-set correlation of environmental variables with axis 1 was 0.87. To investigate whether the observed differences could be accounted for by pure chance the Monte Carlo permutation test was used in CCA. The 99-point random data set generated by random permutation all yielded a lower eigenvalue for the first axis and the overall analysis ($p \leq 0.01$).

Fig. 2.13 shows the diagram of the same CCA analysis of Fig. 2.12 but displaying the species scores. Overlaid on Fig. 2.13 are the strategy type for species given by Grime *et al.* (1988) and Murphy *et al.* (1990), together with the boundaries of TWINSPAN species groups (A and B) at level 1 (eigenvalue: 0.83).

Fig. 2.12 shows that I_D clearly varies along axis 1. Sites supporting macrophyte communities more resistant to the disturbance produced by water fluctuations and management regime were located to the right of the diagram. The gradient also follows a geographical pattern, indicated by the drainage area location of each site. This may be explained by the fact that within an individual drainage area a relatively uniform set of weed control

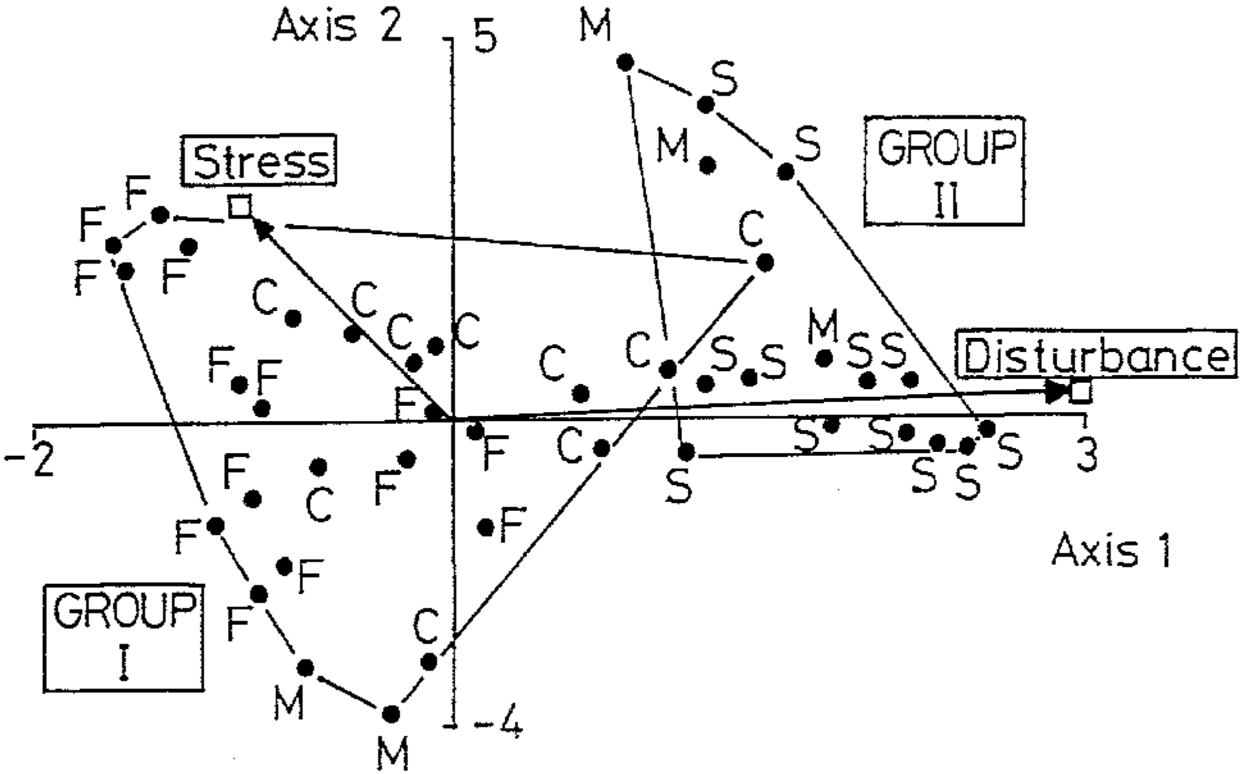


Fig. 2.12. CCA ordination of sample scores (•) identified by region (F, Fens; C, Crossens; S, Solway and M, Spynie Canal) and arrowed biplot scores of environmental variables (□). The boundaries of two site groups (I and II) identified at level 1 of TWINSPAN classification are overlaid on the ordination plot.

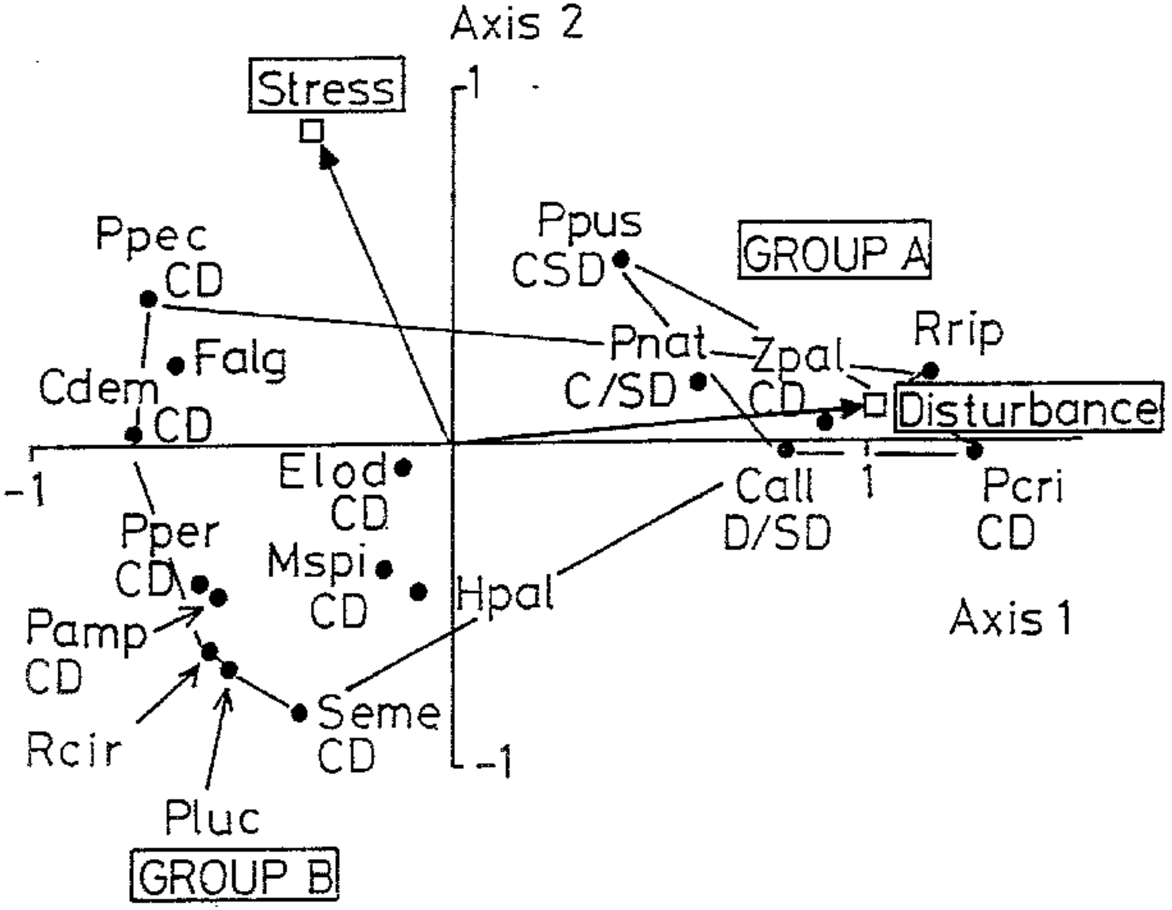


Fig. 2.13 CCA ordination of species scores (•) and arrowed biplot scores of environmental variables (□) showing species name plus strategy type codes (where available). C, D and S indicate competition, disturbance and stress elements, respectively. For species codes see Fig. 2.8.

procedures is used, and that environmental characteristics are likely more similar within than between geographically separated areas.

TWINSPAN analysis can classify both samples and species into groups based on species assemblage data only and is not, as in canonical techniques, constrained by the environmental data. I_D was found to explain most of the variation shown by TWINSPAN at level 1 (Fig. 2.7). The indicator species for the large group (I) are *Elodea canadensis, E. nuttallii, Ceratophyllum demersum, Myriophyllum spicatum*, and *Potamogeton pectinatus.* All these species are considered to be high-nuisance submerged weeds (Pieterse & Murphy, 1990). The indicator species for the smaller group (II) are *Callitriche* species. These species are noted for their survival in channels occasionally dry for short periods or in temporary pools and they also have a strong tolerance of management based on disturbance, such as cutting (Haslam, 1978; Grillas & Duncan, 1986). Grime *et al.* (1988) allocated a strategy type with a strong element of disturbance-tolerance to *C. stagnalis*. In Chapter VI, the survival strategy of *C. stagnalis* and *P. crispus* is studied in order to improve understanding of the vulnerability of these plants to different forms of weed control.

In Fig. 2.13, the small group A comprised *P. crispus, P. pusillus, P. berchtoldii, Zannichellia palustris,* and *Callitriche* species. All these species scored high on the disturbance gradient, and are frequently mentioned in the literature as being disturbance-tolerant (e.g. Newbold *et al.*, 1983). The larger species group B showed more varied tolerance of disturbance, although most species scored much lower on the disturbance gradient than group A species (Fig. 2.13).

In Fig. 2.12, the stress variable may permit differentiation of plant communities growing in sites with low disturbance, but affected by different intensities of stress, especially light availability. *P. pectinatus* scored highest on the stress-tolerant gradient (Fig. 2.13); tolerance to shade and to high salinity is a well-known feature of this plant (e.g. van Wijk, 1988). In Chapter V the response of *P. pectinatus* to disturbance and stress is examined in artificial channels and experimental cultures.

A number of species appeared most characteristic of intermediate conditions of disturbance and stress: examples here included *P. berchtoldii, P. pusillus* and *P. natans.*

2.4 Discussion

The most frequent and abundant species recorded in this study (Fig. 2.4) are widely distributed around the world (Sculthorpe, 1967; Cook 1985). For example *P. pectinatus* occurs circumboreally to about 70°N (Hulten, 1968) and can also be found in South America, South Eurasia, South Africa and New Zealand (Kantrud, 1990). *P. pectinatus* and *C. demersum* are unlikely to be native throughout their wide range, but it is not possible today to determine where they are native and where they are introduced (Cook, 1985). *E. canadensis and E. nuttallii* are native to North America, but have been spread to Europe, South Africa and New Zealand (Cook, 1985; Cook and Urmi- Konig, 1985). *M. spicatum, C. stagnalis* and *P. crispus,* natives from Eurasia, also spread in a wide range from North America to Australia (Sculthorpe, 1967; Aiken *et al.*, 1979; Cook; 1985; Cook 1990).

With the exception of the *Callitriche* species, all the more abundant species in this study (Fig. 2.4) are also important aquatic weed species around the world. *C. demersum* is for instance named as weed in Europe (Murphy *et al.* 1990a), Asia (Gopal, 1990), Africa (Mitchell *et al.* 1990), Australasia (Mitchell and Bowmer, 1990) and North America (Anderson, 1990; Steward, 1990). The introduced *M. spicatum* has an estimated extent of infestation in US waters of about 202,000 ha (Murphy, 1988). The introduced *E. canadensis* continues to cause major problems in Europe (Simpson, 1984; Pokorny *et al.*, 1984; Murphy *et al.*, 1990), but it seems that it is being replaced by *E. nuttallii*, especially in eutrophic waterways of northern Europe (Chandler 1975; Weber-Oldecop, 1977). *C. stagnalis* and *C. platycarpa* are not quoted in general as important weeds, but they are normally included as weeds in lowland rivers and canals of Europe and seem to produce problems especially in Britain (Murphy *et al.*, 1990; Haslam and Wolseley, 1981, 1987).

The objective of this study was to determine the relationships between the submerged vegetation, management, and selected environmental variables in drainage channels. Environmental variables not included in the data analysis that affect submerged and floating plant distribution in slow waters, are sediment particle size (Haslam 1978; Holmes 1983) and nutrient availability from substratum (Barko and Smart, 1981b). Also the effect of eutrophication can affect vegetation by enhancing the growth of phytoplankton and epiphytes, especially in slow- moving waters (Phillips *et al.*, 1978; Sand- Jensen and Borum, 1984; Brierley *et al.*, 1989).

Several authors have found a relationship between the structure and composition of the aquatic vegetation and chemical composition of water (Hutchinson, 1975; Raven, 1988; Gacia *et al.*, 1994). Palmer *et al.* (1992)

classified 10 site-groups, based on an indicator species analysis of the vegetation of 1124 fresh and brackish standing water sites in Great Britain. They found these groups related to the alkalinity, pH and conductivity of the water. By comparing data on pH and conductivity from this study (Table 2.4) with the published data, it is possible to characterised mostly of the sites as eutrophic-base rich, and a few in the mesotrophic group.

Jeffries (1989) presented general tables indicating ranges for various water quality determinants associated with natural, degraded and severe loss conditions. When that ranges are compared with Table 2.3, the Fens and (especially) the Crossens drainage area both have severe loss status. The Spynie Canal data are more suggestive of "natural condition" status. From the nitrate -N data took in every site (Table 2.4), and from the trophic rank calculated using the aquatic plant community (Table 2.2) it is possible to state that also the Solway Drainage area is a "natural condition" for the macrophyte community.

The correlation of macrophytes with nutrient (particularly phosphorus and nitrogen) concentrations is complicated by the ability of many species to obtain minerals either by foliar uptake from the water or from the substratum via their roots (Fox, 1992). In terms of species tolerance, the concentration of phosphorus and nitrogen with which species are best correlated varies between them, and for example is < 0.3 mg l^{-1} P for *E. canadensis* and *P. natans*, but between 1.2 - 3.0 mg l^{-1} P for *Sparganium emersum* (Haslam 1978). Anyway, the nutrient range presented in Table 2.3 are within the suitable range for the growth of most of the submerged plants present in the examined sites (Haslam, 1978; Newbold and Palmer, 1979; Jeffries, 1989; Caffrey, 1987; Palmer *et al.,* 1992).

The effect of water depth on aquatic vegetation is well known (Schieder and Prosser, 1976; Kiørboe, 1980; Dale, 1981; Barrett *et al.*, 1989, Nichols, 1992; Nichols, 1994). Water plants may be limited by mechanical damage (disturbance) from ice, waves, or changes in water level, or by restricted light penetration. In the drainage channels under study, water fluctuation and light penetration were probably the variables of major importance in explaining the effect of water depth on submerged vegetation.

The influence of water level fluctuations on submerged vegetation is well known (Erixon, 1979; Kautsky, 1988, Rørslett, 1989, Wilcox and Meeker, 1991). In shallow waters, water level fluctuations affect macrophyte development particularly through desiccation (Haslam, 1978). As was stated before, the occurrence of very low water level during part of the growing season is probably a major factor influencing vegetation in relation to water level changes in this study.

Extended ranges of lake level alterations impoverish the macrophytic vegetation in Scottish lochs (Smith *et al.*, 1987) and in Norwegian hydro-electric lakes (Rørslett, 1984). The impact of water level alterations introduces a shift in the probability distribution of the underwater light regime, the result of which could be a significant reduction in the niche size attainable for a given macrophyte species (Rørslett, 1984; 1987b). Water level fluctuation is widely used for aquatic weed management, especially by the air exposure of part or all of the bed of a water body (Cooke, 1980; Nichols, 1991, Wade, 1990). Researchers generally conclude that the results of the use of this drawdown technique, are species selective: some are destroyed, some enhanced, and some are unaffected when exposed to drawdown (Nichols, 1991).

Weed control procedures in shallow drainage channels are usually based on manual clearance using scythes, rakes, forks, etc. Sometimes some mechanical control as the Herder- bucket is used also. The effect on vegetation of this kind of management regime is similar to the desiccation effect, affecting the above-ground biomass, but normally leaving part of the plant biomass in the sediment. From these remaining stems or underground reproductive propagules, a rapid regrowth occurred. Manual control may be inefficient as it can leave 10 % or more of the weed untouched (Soulsby 1974; Wade 1990b).

From the above, it is clear that the importance of water alterations and the management regime on species diversity is critical in drainage channels. In this study, both variables were not complete independent: weed control procedures were applied less frequently in the target sites when the effect of desiccation clearly provokes a weed biomass reduction. Increasing values of water level fluctuation (related to more effect from desiccation) or management clearly impoverished species composition in this study: the species group exhibiting maximal values of disturbance had six species, whereas the other large group, with lower disturbance, supported twelve different species (Fig. 2.8; Fig. 2.13).

Light availability is one of the major factor that affects community composition and abundance of submerged plants (Barko *et al.*, 1986; Spencer and Bowes, 1990). The maximum depth at which submerged plants can survive increases with increasing light penetration. In general, there is a signification regression between light availability and maximum depth of plant growth (Dennison, 1987; Chambers and Kalf, 1985; Canfield *et al.*, 1985; Dennison *et al.*, 1993). Light attenuation was a factor not related to the 4 geographical-distanced areas: there were no significant differences between the 4 TWINSPAN groups (Tables 2.5 and 2.6), that showed a clear geographical pattern. However, differences were important between sites in the same area (Table 2.4). In fact, 5 of the examined sites received, on average at the bottom of the channel, less than 3 % of surface PAR ($z_{eu} / d < 1$; see 2.2.1.3); two of them were located in the Fens, two in the Crossens area and one in the Solway drainage area.

Most of the species included in this study probably have a rather similar established-phase survival strategy, particularly in relation to competitiveness and disturbance-tolerance (CD). Disturbance- tolerance is likely to be a vital survival feature for channel plants in Britain, at least in part because of the widespread use of management based on disturbance-causing methods. All sites in this study experienced at least some disturbance from aquatic plant management (the lowest management index values were associated with a single annual weed-cut by boat; the highest with dredging - see Fig. 2.2).

In spite of the fact that the based categorization of strategies of these vegetation is CD, this study demostrate significant differences between species in terms of response to the disturbance and stress pressures. This also have been shown in experimental cultures with *Elodea canadensis* and *Myriophyllum spicatum*, two CD species that showed however different responses to disturbance, stress and competition (see Additional Paper: Response of *Elodea canadensis* Michx. and *Myriophyllum spicatum* L. to shade, cutting and competition in experimental culture). This paper shown that *E. canadensis* is more tolerant to shade and cutting than *M. spicatum*., and agreed with results of this study where also *E. canadensis* showed more tolerance to light attenuation and management regime than *M. spicatum* (Fig. 2.9 and Fig. 2.11).

The area of the ordination plot with low scores for disturbance and stress, on the I_D and I_S gradients (i.e. the lower left corner of Fig. 2.13) is were plants whose strategy incorporates a stronger C-element would be expected to occur. In fact species with competitive strategies were located throughout the ordination diagram. This suggests that drainage channels habitats provided a rather productive environmental for macrophyte growth. The observed variation in I_S probably represents a range of habitats in which stress is very low in absolute terms.

The use of only two indices to summarise the complex influences of the environment on the growth of submerged plants is of value only up to point. Take, for example, water depth. This effects light availability for euhydrophytes (Kautsky, 1988; Blindow, 1992) and is therefore a stress factor, but changes in water level may provoke physical damage to plant tissues by partial or total desiccation, which is clearly a disturbance. However, the use of integrated indices of stress and disturbance affecting channel sites proved successful in allowing us to distinguish two groups of plants showing differential disturbance tolerance. These may be considered as two separate functional groups, under the definition given in Chapter I (1.2.7), and their importance in this study will be discussed below (see 4.4 and 7.1).

CHAPTER III

SUBMERGED PLANT SURVIVAL STRATEGIES IN RELATION TO MANAGEMENT AND ENVIRONMENTAL PRESSURES IN DRAINAGE AND IRRIGATION CHANNELS OF SOUTHERN ARGENTINA

3.1 Introduction

There are no aquatic plant keys or previous survey data on freshwater vascular plants growing in the irrigation zones of VIRC and IDEVI. However, several studies of the life- history and physiology of selected aquatic plants species have been made during the past 13 years. *Potamogeton pectinatus* (previously identified as *P. striatus*: see Table 3.1) and *Chara contraria* are the most troublesome species in VIRC. The first studies of the life-history of these plants in VIRC were published by Irigoyen (1981) on *P. pectinatus (=P. striatus),* and by Sabbatini *et al.* (1986b) on *C. contraria*. Other studies include work on the biology and ecology of *C. contraria* (Sabbatini *et al.*, 1986a, 1987) and on timing of control methods, prevention and integrated weed management (Fernández *et al.*, 1987a, b; 1990). There are no previous publications on the aquatic plants in the area of IDEVI, prior to those noted below.

From October 1992 The Commission of the European Communities funded a project named "Biological management of irrigation channel weed problems in irrigated semi-arid agriculture" that involved studies in both target irrigation districts. From this project, new information is available on submerged plant species in southern Argentina. Initial results from the project were communicated in September 1994 at the 9th International Symposium on Aquatic Weeds, Dublin, Ireland (Bezic and Dall' Armellina, 1994; Dall' Armellina and Bezic, 1994; Hootsmans *et al.* a, b, 1994; Sidorkewicj *et al.*, 1994). At present, several papers involve this project are in press or were submitted for publication, for example Dall'Armellina *et al.*, 1996a (in press), 1996b (in press), Fernández *et al.* 1996 subm., Sidorkewicj *et al.*, 1996a (in press), 1996b (subm.).

The aim of this study was the same as in Chapter II for drainage channels of Britain. As in that study the objectives are to ascertain, using a multivariate approach:

(a) the degree to which species survival strategy could be related to the environmental and management factors that affect plant growth in man-made drainage and irrigation channels of southern Argentina.

(b) the existence in those habitats of functional aquatic plant groups in which species are associated with different degrees of disturbance and stress pressures.

3.2 Materials and Methods

3.2.1 Site location.

For the study, 114 sites were selected to cover a wide spectrum of geo-climatic and management regime in Argentine irrigation systems. The number of sites selected in each area was related to the relative size of the areas: in VIRC the total area with irrigation rights is eight times larger than in IDEVI. Three irrigation channels selected in IDEVI were in a concrete-lined channel, but with sediment accumulated on the lining in which aquatic plants were growing. All the other sites studied were located in earth-bottom channels. Maps of the target systems are shown in Fig. 3.1 and 3.2, with the location of individual sites as below:

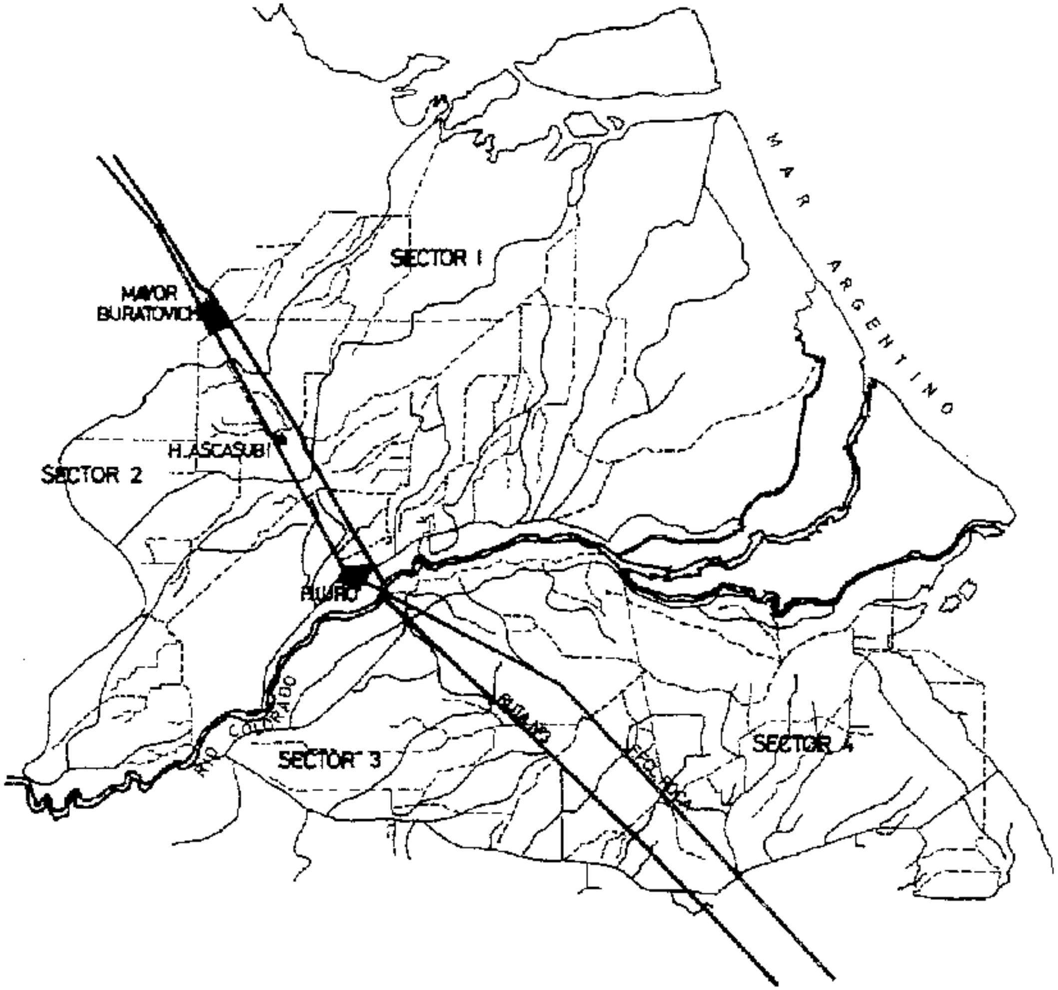


Fig. 3.1 Main Irrigation (——) and drainage (- - -) network of VIRC.
For number of sites sampled in each sector see text.

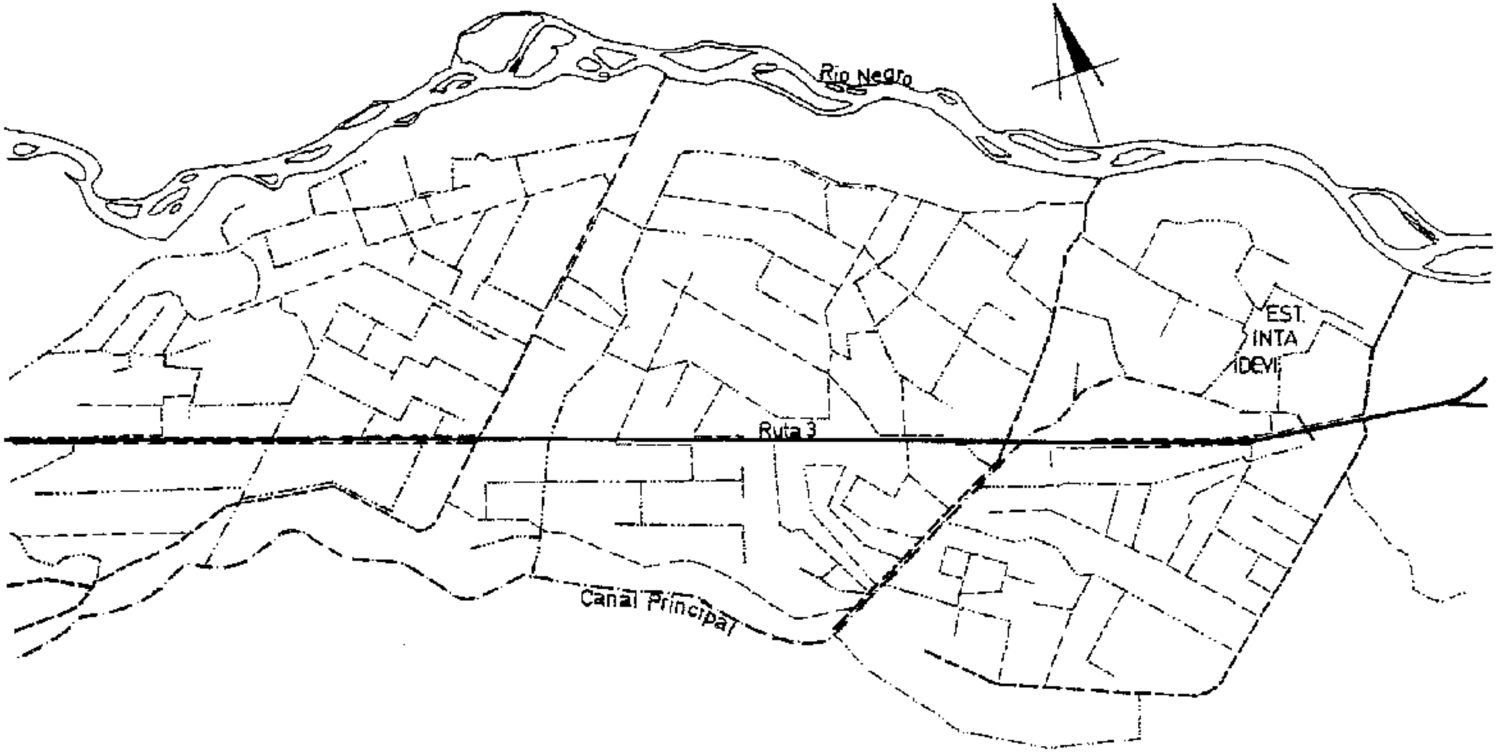


Fig. 3.2 Main irrigation and drainage network of IDEVI

(–·–·) , (—·—·—) and (–·–·–) showed the principal , secondary and tertiary irrigation channels , respectively.

(–––) and (– - –) showed the principal and secondary drainage network

Photograph 2: A dense cover of *Potamogeton pectinatus* (above) and *Chara contraria* (below) in two drainage channels of the Valle Inferior del Río Colorado, Argentina.

SITE LOCATION	Number of sites	
	IRRIGATION	DRAINAGE
VIRC-Sector 1 (North of Río Colorado, East of Ruta 3)	17	18
VIRC-Sector 2 (" , West ")	18	10
VIRC-Sector 3 (South " , East ")	13	9
VIRC-Sector 4 (" " , West ")	12	5
IDEVI	6	6
TOTAL	66	48

3.2.2. Plant sampling.

Following a preliminary site examination, a 50 m stretch was selected at each survey location. The target stretches were sampled twice, in middle (December 1993- January 1994) and late season (March- April 1994). Sites were always sampled at least one month after the most recent weed control treatment. 10 random grapnel hauls were taken to sample submerged and floating macrophyte species. The abundance of each species was rated on a scale of 1 = scarce; 2 = common and 3 = abundant.

3.2.3. Physico-chemical characteristics of the habitat.

3.2.3.1. Light attenuation and turbidity

Photosynthetically-active radiation (PAR) was measured, as possible, in each visit, using a Licor-192 5B underwater quantum sensor, or a SKYE SKP210 sensor linked to a SKYE - SDL 2540 logger. From the PAR-light data the extinction coefficient *k*, the euphotic depth z_{eu}, and the relationship $z_{eu} .d^{-1}$ were calculated. (see 2.2.3.1).

When it was not possible to take PAR data during the site visit, it was estimated retrospectively from turbidity data measured as NTU (NephelometricTurbidity Units; APHA, 1985; Clesceu *et al.*, 1989). Turbidity decreases light penetration and acts selectively, favouring species more adapted to turbid conditions (Nichols, 1992; Engel and Nichols, 1994). Fig. 3.3 shows that a simple linear regression model gave a good fit ($r = 0.98$; $p < 0.001$) for the relationship between NTU and PAR for the water of these channels. Water turbidity was measured using a portable turbidimeter (Hach, model 2100P), which measures turbidity from 0.01 to 1000 NTU. From the regression equation the extinction coefficient *k* was estimated as:

$$k \ (1.\ m^{-1}) = \mathbf{NTU}\ .10.97^{\ -1}$$

3.2.3.2 Management regime

The management regime applied at each site during the three years prior to sampling was rated in relation to the likely degree and timing of destruction of plant biomass produced by the different management operations (Fig. 3.4). Traditional methods for submerged weed control in the target areas are mechanical. Hydraulic grab-buckets, which extract vegetation together with some of the sediment, work at a rate of 40 m of canal length per hour. The buckets are frequently replaced by rakes, which eliminate 60 or 70 per cent of the vegetation, and are capable of covering around 100 m of channel lenght per hour (Fernández *et al.*, 1990). Also, in both areas "chaining" is a common technique. This method uses a heavy chain of sharp blades slung between two tractors, one on each bank. The chain is then dragged upstream ripping out weed growth as it goes.

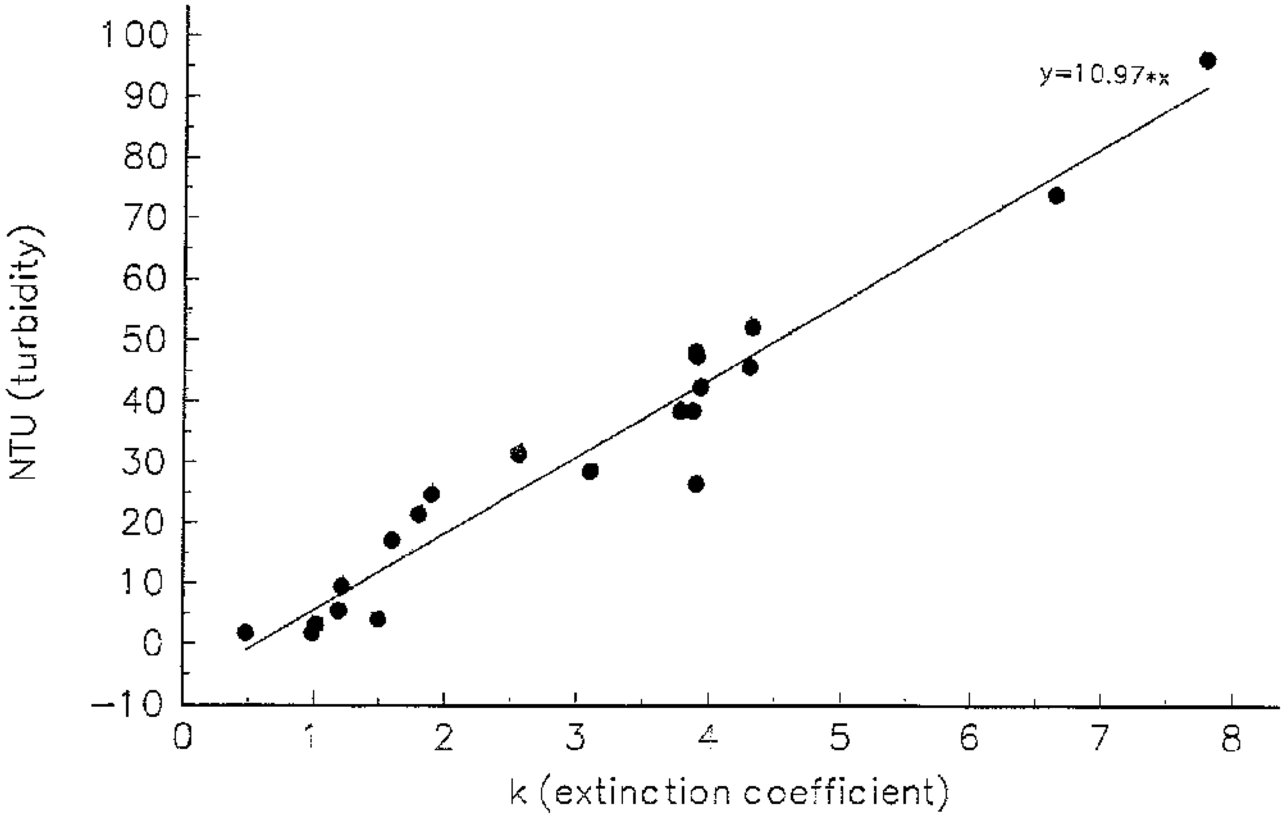


Fig. 3.3. Relationship between means of water turbidity (NTU) and extinction coefficient *k* in measures taken simultaneity in different channels of VIRC, describing by as single regression model ($r = 0.985$; $p < 0.001$).

Information on management regime at each site was provided by CORFO (Corporacion del Fomento del Valle Inferior del Rio Colorado), CURZA (Centro Regional Zona Atlantica) and by IDEVI (Instituto de Desarrollo del Valle Inferior del Rio Negro).

3.2.3.3 Water movement

Water velocities ranged approximately between 0.01 and 0.21 m. sec^{-1} in drainage channels and between 0.20 and 0.40 m. sec^{-1} in secondary irrigation channels. Water velocity in primary channels ranged from 0.30 to 0.62 m. sec^{-1}.

LOW D
- Shallow dredge (Hydraulic with mechanical rakes) every 3- 4 years
- Deep dredge (Hydraulic with grab-buckets) every 3- 4 years
- Dredging every 1- 2 year.
- Bank-mounted hydraulic excavators in irrigation channels during water recess

↓
- Deep dredge every year with excavators during irrigation recess (May-September)
- Dredging every year during irrigation recess plus summer weed control with heavy chains pulled by tractors, or bank- mounted hydraulic machines.
- Deep dredge every 1 - 2 years during irrigation recess plus summer weed control (chains, hydraulic excavators) up to 8 times a year.

HIGH D

Fig. 3.4. Management procedures in relation to the likely degree and timing of destruction of the plant biomass in the target sites (D: disturbance)

It was not possible to measure the velocity directly at every site, but discharge data are collected regularly by CORFO and IDEVI at sample points on channels in both areas. It was expected that changes in water velocity in each site were related to abundance of aquatic vegetation: vegetation affects the resistance coefficient ("n") in Manning 's equation (Manning 1891; Pitlo & Dawson 1990) used for the calculation of flow resistence (see 1.2.2). Actual velocity values depend on slope and wetted perimeter of every stretch. Water velocity was rated in each site on a scale of 1-10 (1: pond, 2: slack, 3-5: slow, 6-8: fast, 9-10: riffle) and subsequently adjusted to incorporate additional information from CORFO and IDEVI.

3.2.3.4 Winter drought:

Due to crop water requirements, the irrigation channels are dry in both systems every year during winter time, typically from May to August. This is an important plant growth difference from drainage networks which contain water all the year round. This variable was incorporated as nominal (present/ absent) in the analysis.

3.2.3.5 Other measures.

The following on-site measurements were taken at each site in each visit: dissolved oxygen (measured with a microprocessor OXI 96, WTW), pH (pH tester 2 with ATC, Cole-Palmer), conductivity and temperature (with a conductimeter LF 96-A/ WTW), water depth, and channel wide. All the measures were taken in daytime and no corrections were made for likely diurnal variations in these variables during daylight hours: it is accepted such variation inevitably increases the noise associated with these data (Moss, 1988).

3.2.4 Disturbance and stress indices

Each of several parameters likely to constrain the growth of submerged plant species was summarised and transformed into a numerical index (1- 5) which increases with increasing pressure on plant survival. Appendix 4 records the indices for the 114 sites, calculated as follows:

(i) Conductivity and water depth: from the values measured at each site (see 3.2.3.5).

(ii) Water velocity and management: from the rated scales calculated at each site (see 3.2.3.2 and 3.2.3.3)

(iii) light attenuation: from the relationship z_{eu}/d (see 3.2.3.1).

(iv) winter drought: was included as a nominal variable (absent/ present).

The disturbance (I_D) and stress (I_S) indices were constructed for each site in three steps:

(1) Each numerical index was multiplied by the CCA inter set correlation of environmental variables with axis 1. This made it possible take in to account the weight of each variable in the vegetation under study and not under- or over- estimate the influence of one variable in relation to another.

(2) The I_D value for each site was then calculated as the sum of the values calculated in step (1) for the variables water velocity, winter drought, management and water depth.

(3) The I_S value for each site was constructed as the sum the variables water conductivity and z_{eu}/d.

2.5 Multivariate analysis

Field data on plant abundance were analysed using TWINSPAN (Two Way Indicator Species Analysis, Hill 1979) PC version 1.2, 1989, option in the VESPAN statistical package. DCA (Detrended Correspondence Analysis) and CCA (Canonical Correspondence Analysis) were undertaking using CANOCO version 3.1 (ter Braak, 1988, 1989). See 2.2.5 for general features of these multivariate analyses. Statistic analysis were made using MINITAB release 8.

3.3 Results

3.3.1 Macrophyte community and weed status.

In total 12 macrophyte taxa were recorded from the two irrigation areas, since December 1993 to March 1994 (Table 3.1). This included two filamentous algae, one macroalga and one fern; the remainder being angiosperms. In VIRC, of the 102 sites studied, 21 irrigation and 4 drainage channels sites had no floating or submerged vegetation. All the IDEVI sites had aquatic vegetation.

Fig. 3.5 shows plant species frequency in irrigation and drainage channels of VIRC and IDEVI. Both species richness and frequency are higher in IDEVI than in VIRC. In the irrigation network eight different species were found in IDEVI and five in VIRC, whereas in the drainage network the numbers were ten and eight taxa, respectively.

Table 3.1. Code and name of macrophyte species collected in both irrigation districts and considered in the analysis.

CODE	SPECIES	CLASSIFICATION
PPEC	*Potamogeton pectinatus* L.	Angiosperm
ZPAL	*Zannichellia palustris* L.	"
ECAL	*Elodea callitrichoides* (Rich.) Casp.	"
CDEM	*Ceratophyllum demersum* L.	"
PPUS	*Potamogeton pusillus* L. (**)	"
PILL	*Potamogeton illinoensis* Morong	"
RMAR	*Ruppia maritima* L.	"
MAQU	*Myriophyllum aquaticum* (Vell) Verd.	"
AZOL	*Azolla filiculoides*	Fern
CHAR	*Chara contraria* A. Braun ex Kütz (***)	Macrophytic alga
EFLE	*Enteromorpha flexuosa* (Kutzing) Blibing	"
CSUR	*Cladophora surera* Parodi et Caceres and *Rhizoclonium hieroghyphicum* (Ag.) Kütz.	"

(*) Tur (1982) identified specimens from Argentina as *Potamogeton striatus* Ruiz et Pavon, and this was the authority used for specimens of this plant from VIRC (e.g. see Fernández *et al.* 1990). In 1992, and after the study made by different researchers involved in the CEC project, it was decided to name *P. pectinatus* the species present in VIRC. In 1993, using isozyme techniques, was found substantial differences between the VIRC specimens and the Northern European populations of *P. pectinatus* (see Appendix 3: Hollingsworth and Gornall, 1993).

(**) (= *Potamogeton berteroanus* R.A. Phil; Tur, 1982).

(***) In the VIRC area the only species present during the survey was *C. contraria.*, but in IDEVI confirmation of charophyte species present has not yet been made.

Species present in more than 80 % of the evaluated drainage sites from IDEVI were *P. pectinatus, C. demersum* and the alga *C. surera,* whereas in the irrigation network were *P. pectinatus, M. aquaticum* and *E. callitrichoides* (Fig. 3.5).

In the irrigation network of VIRC *P. pectinatus* and *C. contraria* were the most frequent species present in 47 % and 53 % of the studied sites, respectively (Fig. 3.5). *C. contraria* was the only charophyte species found in VIRC. The remaining species were all present in less than 12 % of sites. In VIRC, the drainage channels showed more variability than the irrigation channels, *P. pectinatus, Z. palustris* plus the filamentous algae *C. surera* and *E. flexuosa* were present in more than 30 % of the sites. The macroalga *C. contraria*, the most frequent species in the irrigation network of VIRC, was present in only 15.5 % of the drainage sites.

Fig. 3.6 shows mean species abundance in both areas for all the sites. Abundance is better than frequency as a measure of the blockage of water flow in the channels caused by aquatic plant growth, because abundance is a rough measure of population density and can be more precise in the estimation of channel frictional roughness (see 3.2.3.3). Species with high mean abundance scores of more than 1.5 (scarce to common) were present in IDEVI: *P. pectinatus, C. demersum, E. callitrichoides* and *M. aquaticum*. In VIRC, scores tended to be lower and only *P. pectinatus* and *C. contraria* had mean abundance values of 0.6 or lightly higher. In the drainage channels of VIRC several species are present with similar abundance values, all minor to 0.72 in average (Fig. 3.6).

In VIRC, 41.6 % of the irrigation and 45 % of the drainage sites showed at least one species with an abundance value of 1.5 or higher,

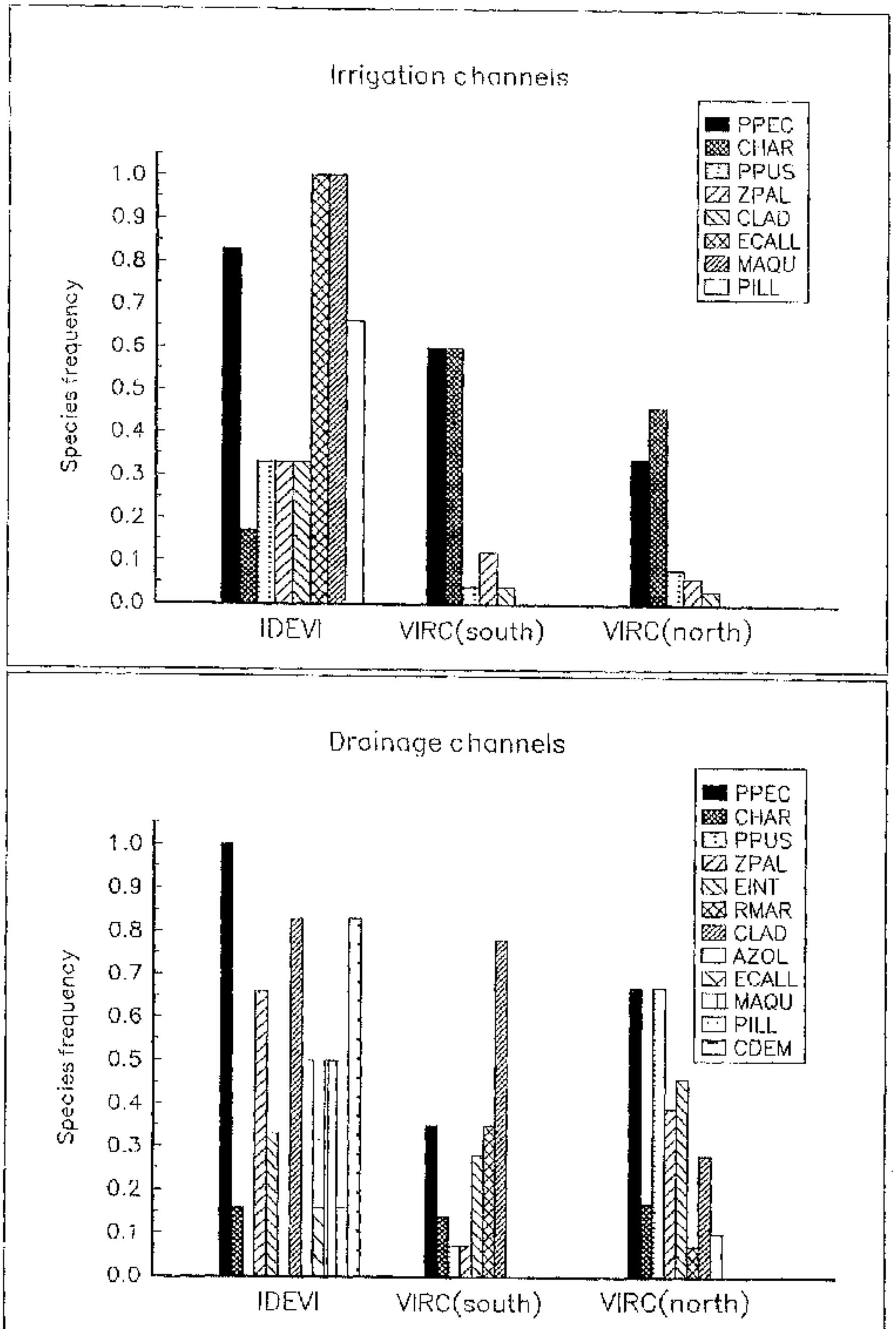


Fig. 3.5. Submerged and floating species richness in irrigation (above) and drainage (below) channels of VIRC and IDEVI. For species codes see Table 3.1.

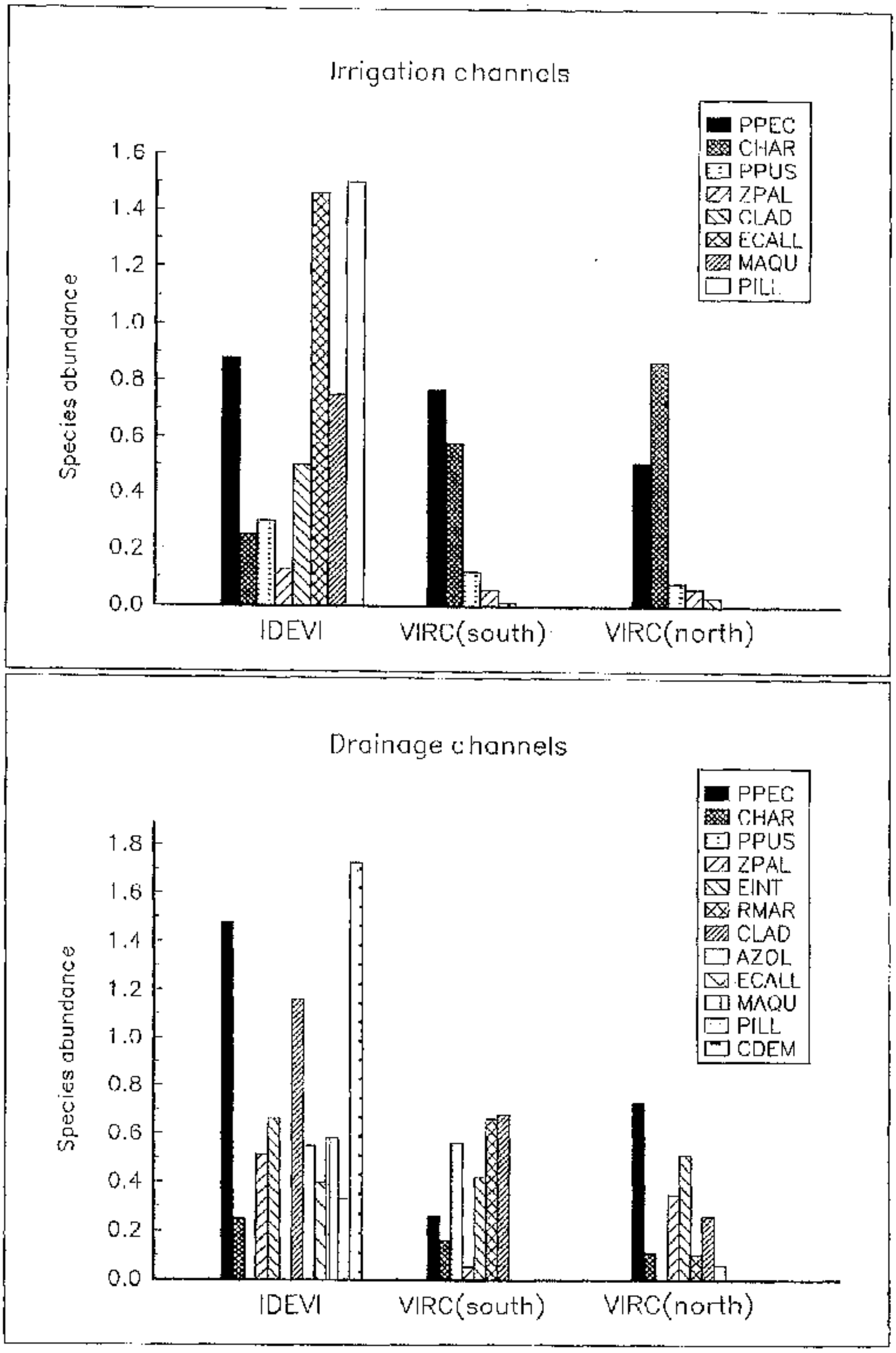


Fig. 3.6. Average abundance of submerged and floating plant species in irrigation (above) and drainage (below) channels of VIRC and IDEVI. For species codes see Table 3.1.

whereas in IDEVI the values were respectively 83 % and 100 %. This is a clear difference between the two areas, with IDEVI being an area with a heavy infestation of weeds, and VIRC an area with aquatic weed problems limited to only that part of the channel network, where the environmental conditions and management regime are adequate to support aquatic plant growth.

Table 3.2. Maximum and minimum values of environmental parameters values measured in 1993/94 for VIRC and IDEVI

Measured parameter	VIRC	IDEVI
pH	7.5 - 8.5	8.5 - 10.3
Oxygen concentration (mg .l^{-1})	6 - 18	8.0 - 19
Water temperature (C)	20 - 30 C	20 - 30
Conductivity (μS. cm^{-1})	1010 - 14300	160 - 6450
Channel width (m)	1.8 - 20.00	1.00 - 20.00
Channel depth (m)	0.10 - 2.00	0.15 - 3.00
Water velocity (cm. sec^{-1})	1 - 65	1 - 62
Water turbidity (NTU)	1.20 - 177.00	1.09 - 15.1
Light attenuation ($z_{eu} . d^{1}$)	0.41 - 58.88	0.85 - 32.36

3.3.2. Species grouping and relation to management and environmental pressures

Fig. 3.7 shows the results of TWINSPAN analysis of the matrix sites x submerged and floating species, expressed as a dendogram of hierarchical subdivisions of the data set to level 3. Analysis was stopped at this point because eigenvalues were too low, or subgroups contained too few sites, to

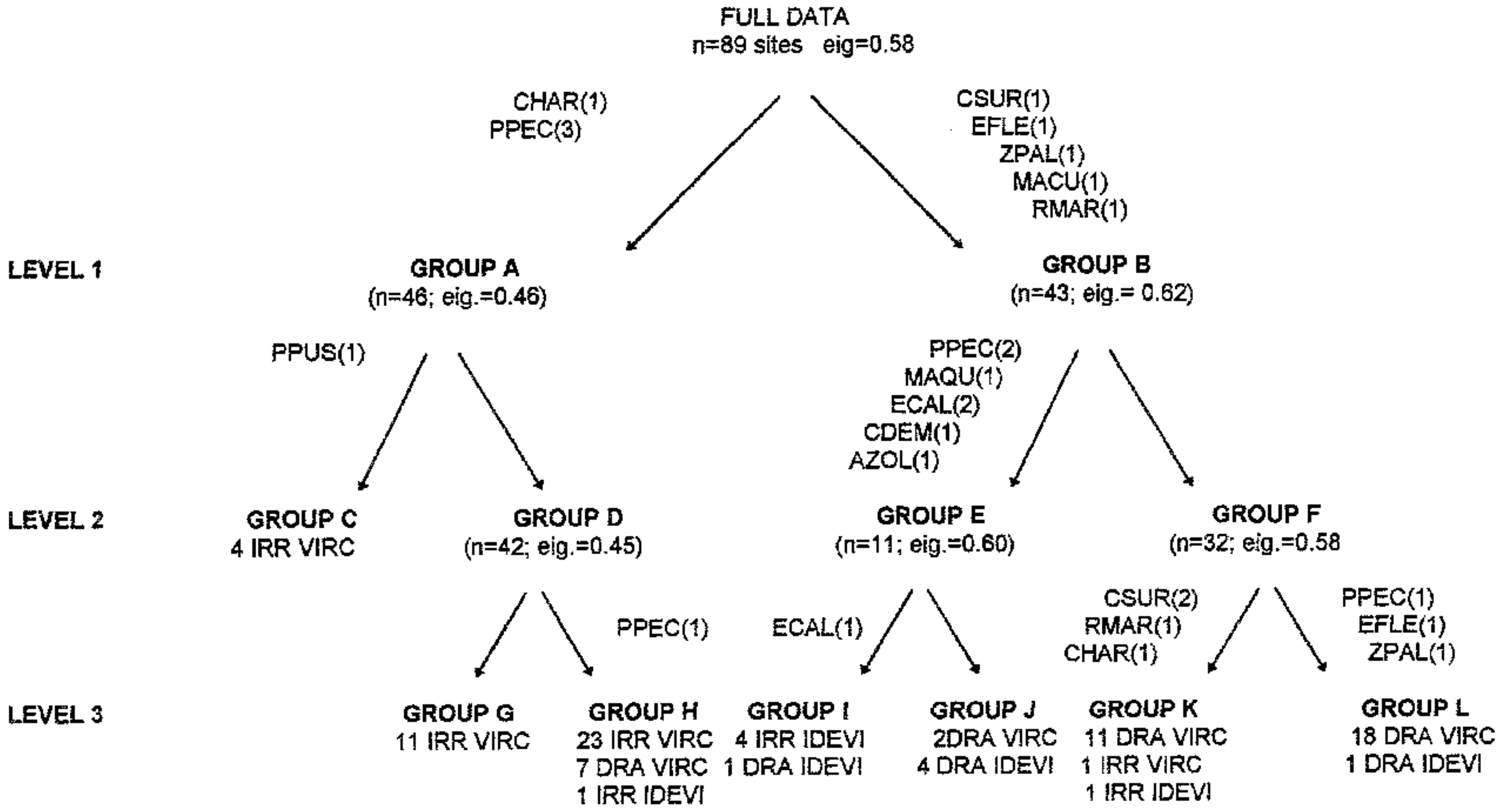


Fig. 3.7. Results of the TWINSPAN analysis expressed as a dendogram showing hierarchical subdivisions of samples abundance to level 3. Only the indicator species are labelled in the diagram. n: number of sites for groups. For species codes see Table 3.1.

justify further subdivision. Fig. 3.7 shows eigenvalues of each division, number of sites and indicator species with their abundance value (pseudospecies). At level 1, the TWINSPAN analysis separates to the left a site group which included 45 channel sites of VIRC and only one of IDEVI, from a second group (to the right) comprising 32 sites of VIRC and 11 of IDEVI.

Seven TWINSPAN end- groups, identified as C, G, H, I, J, K and L in Fig. 3.7, and an eighth group (W: sites without vegetation) were selected for statistic analysis. These groups were compared to each other in terms of the environmental parameters measured for each site, using one-way analysis of variance and Tukey's test of multiple comparisons, with a family error rate of 0.05 (Table 3.3). Analysis of variance was carried out for five environmental variables, and significant differences (<0.05) between the groups were detected in each case (Table 3.3). Comparing the 8 groups in terms of location of their sites, it is clear that both geographical factors (irrigation district) and winter drought (= channel type: irrigation or drainage) are very important sources of variation in the data set (Table 3.3 and Fig. 3.7).

Fig. 3.8 shows the DCA ordination plot displaying site scores. In this analysis, the eigenvalues were 0.58 and 0.42 for the first and second axis, respectively. Overlaid on this diagram are the boundaries of the approximate location of the 7 TWINSPAN site groups analysed in Table 3.3.

TWINSPAN classifies species as well as sites, and Fig. 3.9 is an overlay plot of the DCA ordination diagram showing species scores and the TWINSPAN species groups boundaries at level 2. The eigenvalue was 0.94 at iteration 1 (first division), 0.30 at iteration 2 (groups I and II) and 0.34 at iteration 3 (groups III and IV).

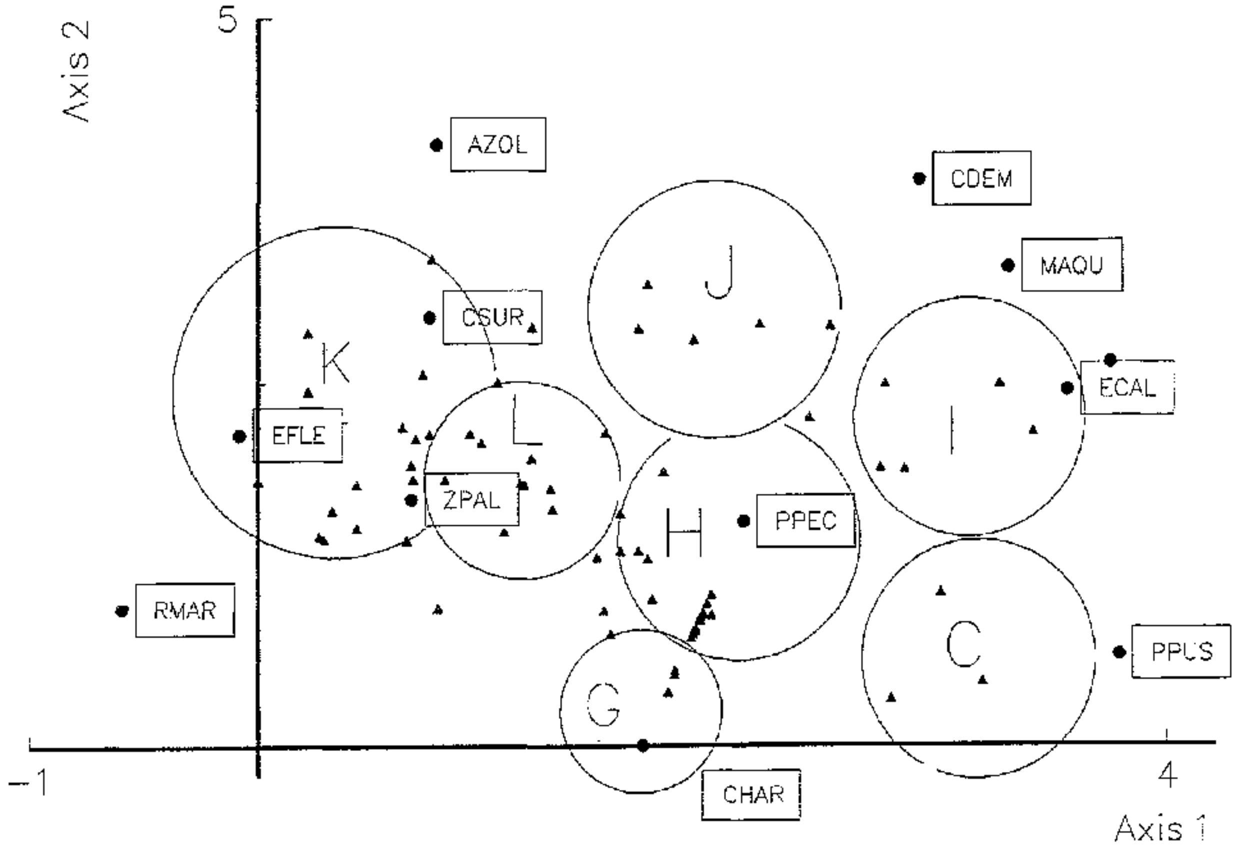


Figure 3.8 DCA ordination of submerged and floating species displaying sites (▲) and species (•) scores, showing the approximate boundaries of the seven TWINSPAN groups recognised in Fig. 3.7. For species codes see Table 3.1.

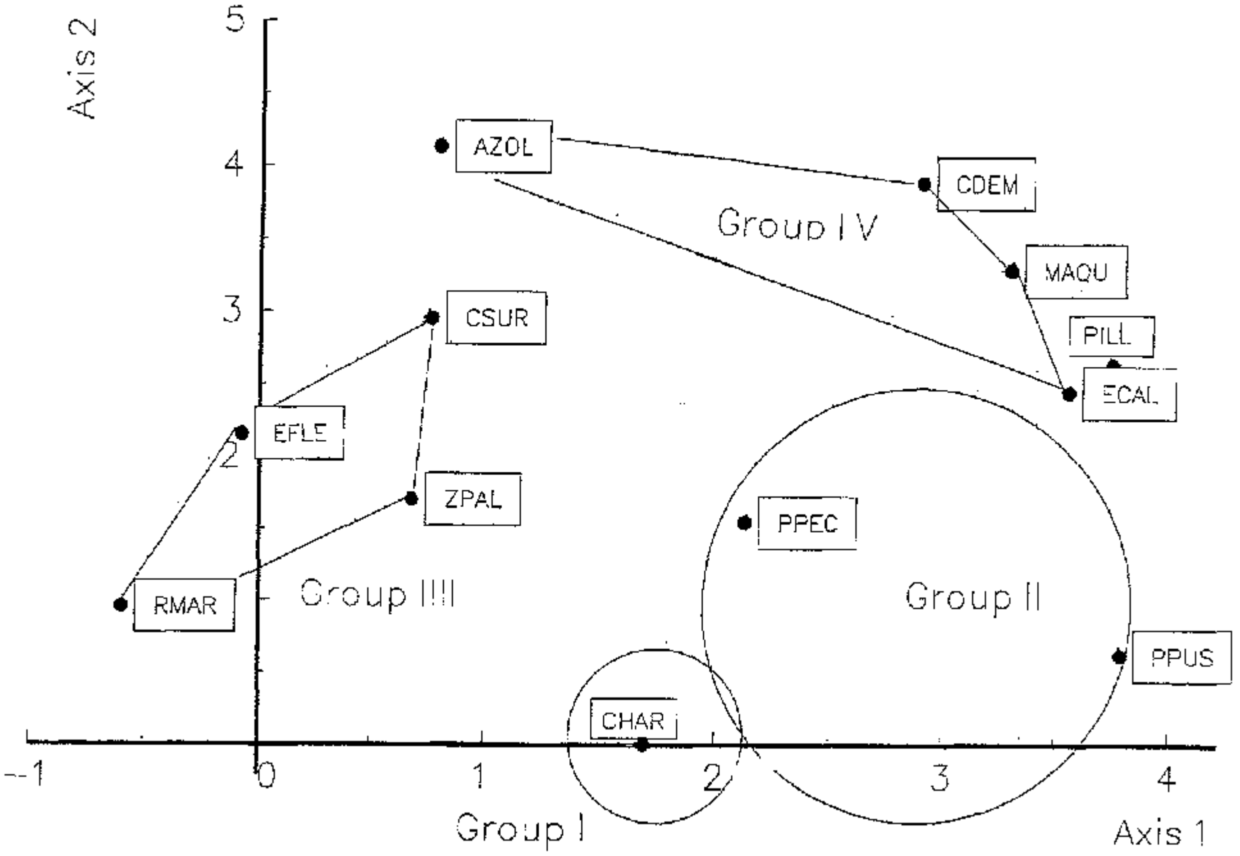


Fig. 3.9. DCA ordination of submerged and floating species displaying species scores (•) and the boundaries of the four TWINSPAN species groups at level 2. For species codes see Table 3.1.

Table 3.3. TWINSPAN group means for different environmental parameters. Gro W is a site without vegetation. Means labelled in each column with different letter (a -d) are significantly different (Tukey's test, $p<0.05$). Information on site location in Fig. 3.7.

TWINSPAN Site Group	Winter drought % (*)	Water depth (m)	Water conductivity (μS. cm^{-1})	Water movement (1 - 10; 1:pond, 10: riffle)	Light attenuation (z_{eu}/ d) (m. m^{-1})	Management regime (0 - 4; 0: low intensity 4: high intensity)
K	16	0.36 a	7030 a	2.23 a	16.49 a	1.23 a
L	100	0.59 ab	6260 a	2.16 a	3.88 b	1.05 a
I	20	1.72 d	160 b	2.60 ab	5.14 ab	1.80 ab
J	100	1.02 bcd	2370 b	1.50 a	9.94 ab	1.33 ac
G	0	0.65 ab	1050 b	3.81 ab	11.59 ab	3.18 b
H	22	0.79 bc	1940 b	4.45 b	6.68 ab	2.96 b
C	100	0.72 abc	1040 b	3.50 ab	11.72 ab	3.00 b
W	16	1.12 cd	1030 b	7.32 c	2.58 b	2.80 b

(*) percentage of drainage channel sites present in the group.

Fig. 3.10 shows the CCA ordination plot displaying species scores and arrows of environmental variables. The same site x plant data set as in the DCA analysis was used in CCA but sites without vegetation were now included in the species scores as "no submerged", to permit examination of

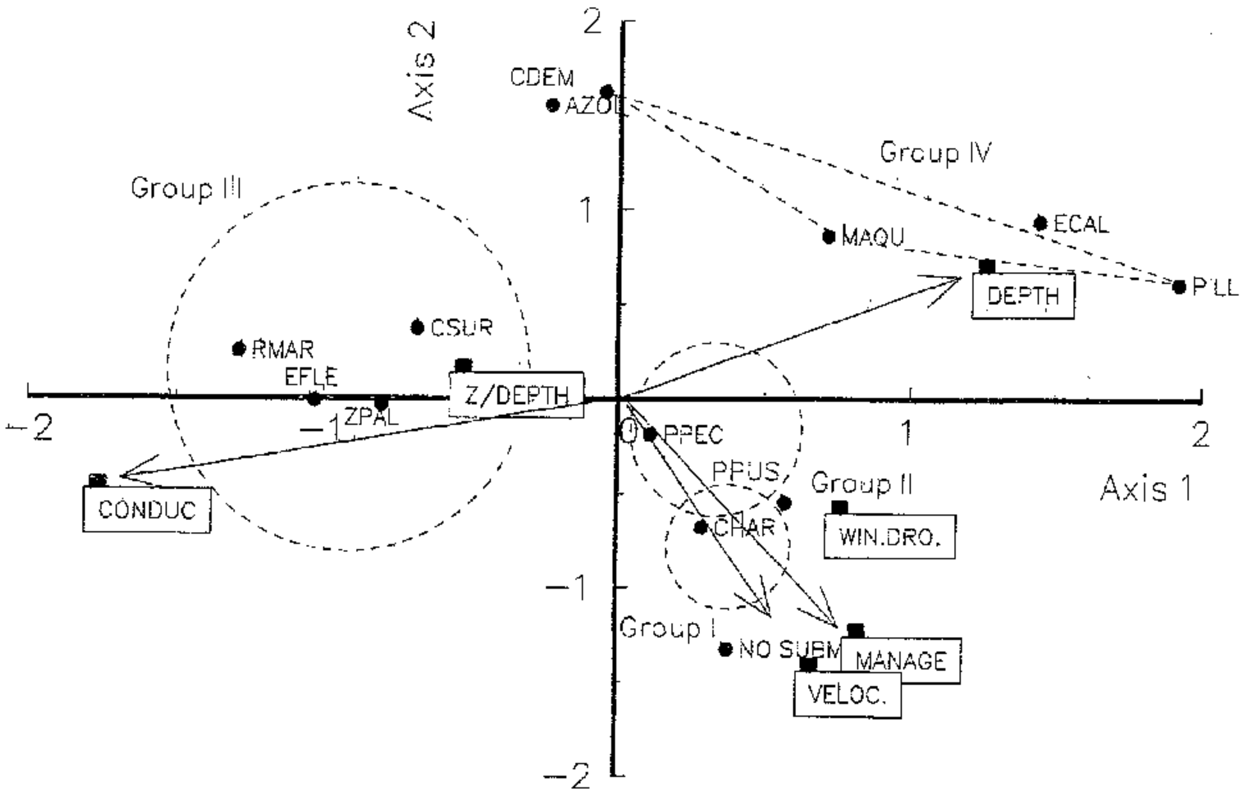


Fig. 3.10. CCA ordination of species scores (•), arrowed biplot scores of environmental variables (■) and the centroid of the nominal environmental variable "winter drought". The approximate boundaries of the TWINSPAN species groups to level 2 are overlaid on the ordination plot. For species codes see Table 3.1.

potential influence of environmental factors on these sites. In the CCA analysis, the eigenvalues were 0.52 and 0.38 for the first and second axis, respectively, and these axes explained 65.1 % of the variance in the weighted average of the species scores (Table 3.4).

Table 3.4. Summary information for CCA of submerged and floating vegetation in relation to six environmental variables (see text).

Axis	1	2	3	4	Total inertia
Eigenvalues:	0.525	0.380	0.232	0.163	4.989
Species-environ. correlations:	0.901	0.805	0.598	0.608	
Cumulative % variance					
of species data:	10.5	18.1	22.8	26.1	
of species-environ. relation:	37.8	65.1	81.8	93.5	
Sum of all unconstrained eigenvalues					4.989
Sum of all canonical eigenvalues:					1.391

Table 3.5 shows for each environmental variable in CCA the canonical coefficient for standardised variables and the inter-set correlation of environmental variables with axes. The inter-set correlation is *R* times the intra-set correlation; *R* is the species-environmental correlation of the axis. The ratio of unconstrained eigenvalues to the canonical eigenvalues indicates that 28 % of the variation expressed in DCA is explained in CCA using the environmental variables included in the analysis. To investigate whether the observed differences could be accounted for by chance a Monte Carlo permutation test was applied to the dataset (ter Braak, 1988). The 99-point random data set generated by random permutation yielded a

significant lower eigenvalue for the first axis and the overall analysis ($p < 0.01$).

Table 3.5. CCA . Inter-set correlations of environmental variables with axes and canonical coefficient for standarized variables, in the analysis of the relation between floating and submerged plant species and six environmental variables.

	Canonical coefficient			**Correlation coefficient**		
Axis variable	**Axis 1**	**Axis 2**	**Axis 3**	**Axis 1**	**Axis 2**	**Axis 3**
Conductivity	-0.34	-0.68	-0.25	-0.80	-0.19	0.04
Water depth	0.39	0.28	0.36	0.57	0.29	0.27
Water velocity	-0.15	-0.24	1.22	0.30	-0.58	0.23
Winter drought	0.72	-0.72	-1.25	0.68	-0.47	-0.11
Management	-0.15	-0.15	0.02	0.37	-0.50	-0.04
log. $z_{eu} \cdot d^{-1}$	-0.05	0.28	- 0.33	-0.24	0.06	-0.29

The inter-set correlations show that conductivity (r= -0.80), winter drought (r= 0.68) and depth (r= 0.57) are most strongly correlated with axis 1 (Table 3.5). Values of conductivity are very different in drainage and irrigation channels. Thus, in the studied sites of VIRC conductivity ranged from 1020 to 1170 μS. cm^{-1} in irrigation channels and from 2070 to 14110 μ S. cm^{-1} in drainage channels. In IDEVI, these values fluctuated between 156 - 160 and 166 - 6450 μS. cm^{-1} in irrigation and drainage channels, respectively. The nominal variable "winter drought" also separates both channel types, because only the irrigation channels are dry during the winter, in both systems. The strongest correlations on axis 2 were with water velocity (r= -0.58), management (r = -0.50) and winter drought (r= 0.47). Water movement and management regime are also factors that show different ranges in drainage and irrigation channels (see 3.2.3.1 and 3.2.3.2).

Fig. 3.11 shows the CCA site ordination plot. From this it is clear that submerged plant distribution in terms of abundance is strongly affected by several parameters that show different range in drainage and irrigation channels, and this explain, at least in part, the correlation found between channel type, irrigation district and site groups.

High conductivity showed a strong affinity with the TWINSPAN species group III and with the sample groups K and L (Fig. 3.10 and Table 3.3). Group III is associated with high conductivity, shallow waters, low water flow and low-intensity management in the CCA analysis (Fig. 3.10). Species group IV was closely associated with low conductivity and high water depth, and species groups I and II with high water flow, high intensity of management and winter drought (Fig. 3.10).

Environmental variation between the eight TWINSPAN site groups, analysed using ANOVA and Tukey's test, permits further examination of plant species-environmental relationships (Table 3.3). Groups K and L (mostly VIRC drainage channels) are differentiated by light attenuation: the ratio $z_{eu} . d^{-1}$ is on average 16.49 in group K and 3.88 in group L. Thus, the group with *P. pectinatus, Z. palustris* and *E. flexuosa* as indicator species occurs in more turbid waters than the group indicated by *C. surera, R. maritima* and *Charophyta.* Between groups I and J, including most of the sites in IDEVI, the only difference is the winter drought that occurs in irrigation channels (Table 3.3). There were not significant differences in environmental characteristics between groups C, G and H, that include especially sites located in the irrigation channels of VIRC, between them

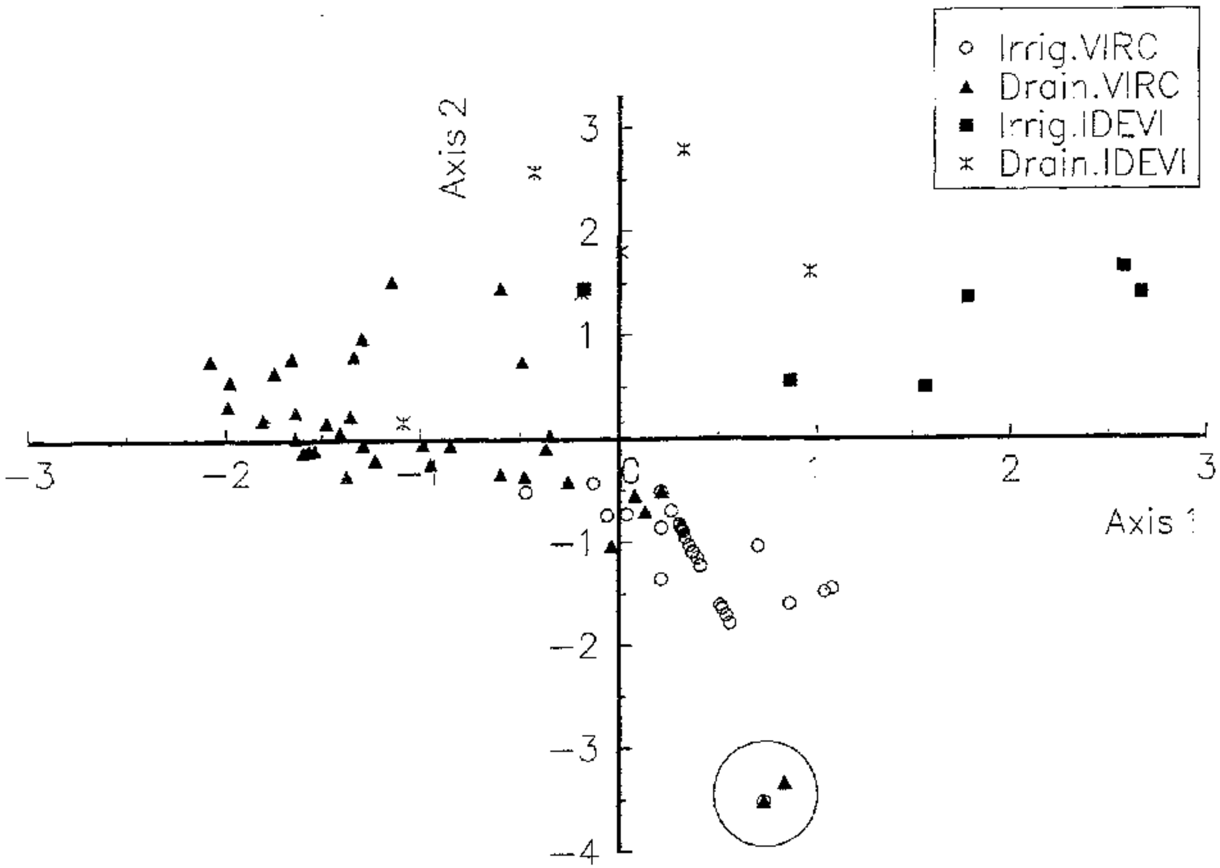


Figure 3.11. CCA ordination plot of site scores identified by channel type ande district area. The circled area contains sites without vegetation. Species scores and environmental variables of the same analysis are displaying in Fig. 3.10.

(Table 3.3), and then other factors seems to affect plant variation. Only the variable water flow separates very clearly Group W (sites without vegetation) from the others. The velocity of the water, very high in primary channels, appears to be an important variable that prevents plant growth in such channels.

3.3.3 Functional grouping in terms of disturbance and stress pressures

Fig. 3.12 shows the CCA ordination plot displaying the species scores and arrows of environmental variables when I_D and I_S were used in the analysis. The eigenvalues were 0.40 and 0.38 for the first and second axis, respectively. The first axis explained 51.6 % of the variance of the species-environmental relation, so each variable explained about half of the constrained variation. The inter-set correlations of environmental variables with axes were 0.80 for I_S and -0.37 for I_D in axis 1 and 0.01 for I_S and -0.71 for I_D in axis 2. The Monte Carlo permutation test was used in CCA and the 99- point random data set generated by random permutation all yielded a lower eigenvalue for the first and both axis ($p < 0.01$).

The TWINSPAN species groups I, II, III and IV are differentiated in the CCA analysis when I_D and I_S were included as environmental variables (Fig. 3.12). These groups may be considered as different functional groups, under the definition given in Chapter 1 (see 1.2.7). Groups I and II appear as disturbance-tolerance with intermediate tolerance to stress, (strategy type *D(S)*, following Murphy *et al.*, 1990), while Group III was more stress tolerant (strategy type *S*). Group IV showed *E. callitrichoides, P. illinoensis* and *M. aquaticum* as tolerant to disturbance under low stress (strategy type *D (C))* and *C. demersum* and *Azolla* sp. located far from both environmental constraints that affect vegetation: named competitors by Grime (strategy

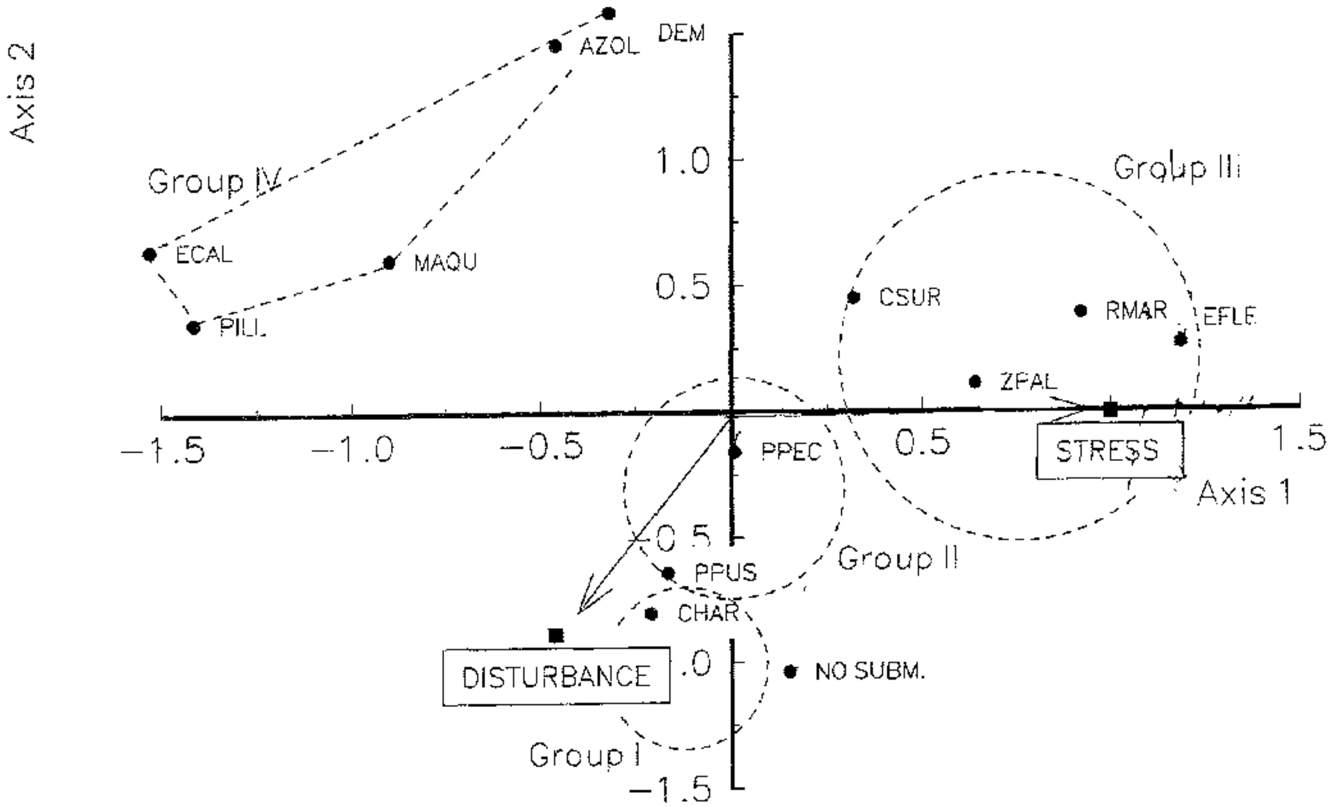


Figure 3.12. CCA ordination of species scores (•) and arrowed biplot scores of disturbance and stress variables (■). The approximate boundaries of the TWINSPAN species groups are overlaid on the ordination plot. For species codes see Table 3.1.

type *C*). Sites without plants appears in the area with maximum stress and disturbance, in agreement with the general theory of Grime (1979) for terrestrial plants.

3.4 Discussion

Of the eight submerged angiosperm plants species recorded in both irrigation districts, four were not found in VIRC and one was not in IDEVI (Fig. 3.5). As is explained below, low species richness in VIRC may be associated, at least in part, with the relatively short time available for colonisation since the irrigation channels developed suitable plant growing conditions and by the continued absence of suitable environmental conditions to support submerged macrophytes in some sites.

In the irrigation network of VIRC, very important changes occurred only few years ago. Irrigation activities in VIRC started on the end of last century, and the management organisation of the irrigation scheme (CORFO) started officially by 1960. It is interested to point out that until few years ago (by 1990) the water of the irrigation network was completely unsuitable for the growth of submerged plants, and no vegetation at all was recorded in primary and secondary irrigation channels at least until 1990 (Sabbatini *et al.*, 1986b; Fernández *et al.*, 1987a,b; 1990). This was because the water of the irrigation channels, taken from the Rio Colorado, used to contain a high load of suspended silt. This resulted in very turbid water, which impeded submerged plant growth owing to the extreme high light attenuation. The construction of a new dam at Casa de Piedra, approximately 500 km upstream (Fig. 1.2), caused an important reduction in sediment loading of the river water downstream. This significantly reduced water turbidity and caused a substantial transparency in the water of the irrigation channels. As a result, weed problems in irrigation channels started only few years ago, becoming a real management problem by 1992.

Weed problems in the irrigation network of VIRC are caused especially by *P. pectinatus* and *C. contraria* (Fig. 3.6). These species grew profusely in the drainage network when the water turbidity changed in the irrigation scheme (Fernández *et al.,* 1987a, b; Fernández *et al,* 1990). The dispersal mechanisms of these two species (by seeds, tubers, oospores or fragments) from drainage to irrigation channels favoured the spread of plants between the closely-adyacent irrigation and draiange channel systems. Propagules could be carried from one to another by flooding, birds, but probably especially by human activities related to channel maintenance. Other submerged macrophytes could not have reached the sites because the short time that passed since the water became clear. Invasion of additional submerged species can be expected into the irrigation scheme of VIRC in the next few years.

Examples may include *P. illinoensis, E. callitrichoides* and *M. aquaticum,* species abundant in the irrigation channels of IDEVI but absent in VIRC (Fig. 3.6). In fact, *M. aquaticum* was found in 1995 in one channel of VIRC, not included in the survey. Are these species absent because the conditions in the irrigation network of VIRC are not suitable for their growth or just because the species simply have not reached the channels yet? CCA analysis (Fig. 3.10, 3.14) can help predict the answer, at least in relation to the studied environmental and management factors. In the CCA diagram, it is possible to inferring a ranking of the species along each environmental variable using the biplot. This could be made by the projection of the species points on each arrow (axis), and the order of the projection points correspond approximately to the ranking of the species with respect to the environmental variable (ter Braak, 1986, 1987). If is compared the projection of the three species recorded exclusively in IDEVI with the projection for *C. contraria* and *P. pectinatus,* they are differentiated especially by water depth and water conductivity (Fig. 3.10). Water conductivity in both irrigation channels were very different being on average 1080 (±47) µS. cm^{-1} in VIRC and 178 (±12) µS. cm^{-1} in IDEVI. However, from the literature, water conductivity values of the irrigation channels of VIRC are within the range suitable for the growth of *P. illinoensis* (Westerdahl and Getsinger, 1988), *M. aquaticum* (Sutton, 1985) and *E. callitrichoides* (Haslam *et al.*, 1975). In fact, *M. aquaticum* was found to be one of the most tolerant of ten plants exposed to various concentrations of seawater (Haller *et al.*, 1974), and *P. illinoensis* occurs in hardwater lakes such as those of Florida, USA (K. Murphy, pers. comm., 1995). The other feature that is inferred from Fig. 3.10 is that the three species found only in IDEVI occurred at higher water depth than *C. contraria* and *P. pectinatus.* From this, *E. callitrichoides, M. aquaticum* and. especially *P. illinoensis* could find more suitable conditions for growth in deep irrigation channels in VIRC.

Differences in species composition were found also in the drainage networks. *P. pusillus* and *R. maritima* were recorded in VIRC but not in the IDEVI drainage channels. On the other hand, *E. callitrichoides, M. aquaticum, P. illinoensis* and *C. demersum* were present in drainage channels of IDEVI but not in VIRC (Fig. 3.5). By making the projections of the species scores on each arrow representing the conductivity and water depth variables, CCA analysis separates *R. maritima* from *E. callitrichoides, M. aquaticum* and *P. illinoensis* (Fig. 3.10). *Ruppia maritima* is a species that occurs mainly in saline or brackish waters and in shallow waters (Kiørboe, 1980; Kautsky, 1988; Costa and Seeliger, 1989; Vaquer and Heurteaux, 1989; Lazar and Dawes, 1991; Martinez-Taberner and Moya, 1993). The location of the *R. maritima* species score was in the region of highest conductivity and low water depths (Fig. 3.10). where most of the drainage channel sites scores of VIRC are located (Fig. 3.11).

The absence from drainage channels of VIRC of *C. demersum* and from drainage channels of IDEVI of *P. pusillus*, is more difficult to explain in this study. *C. demersum*, one of the most widespread submerged freshwater plant species in the world, was recorded in sites with very low intensity of management and water movement (Fig. 3.10). Also in drainage channels of Britain, *C. demersum* was found in the most undisturbed sites (Fig. 2.13), and in sites with low water movement. The literature indicates that this species is usually found growing in ponds or slow-moving streams, in fertile and hardwaters, adapting to different water levels and turbidity (Haslam *et al.*, 1975; Westerdahl and Getsinger, 1988). According to this, drainage channels of VIRC, mostly with slow water movements and low intensity of management, could be open to invasion by *C. demersum*, at least for those with relatively low water conductivity.

From the above, it is clear that the submerged vascular plants are not randomly distributed in both irrigation districts, and their dispersion is clearly related to selected environmental variables, especially water conductivity, winter drought, water depth, water movement and management regime. However, it seems that the ecological amplitude of some species, unless in terms of the more important abiotic factors that affect plant distribution, is broader than the actual species occurrence in the area. Difficulties in the dispersion of some species owing to the relatively short existence of these man-made water systems, is probably one cause that explains the rather low species richness of the area. A second cause is the isolation of both catchment areas: both districts are separated from other river catchment areas for more than 100 km.

The objective of this part of the study was to ascertain the relationship between the aquatic vegetation and channel management plus some selected environmental parameters. One of the environmental variables not included in the data set is the effect on the vegetation of the fish *Cyprinus carpio* (common carp). In Argentina common carp, were introduced many years ago (Ringuelet *et al.* , 1967; Mac Donagh, 1948) and are now naturalised in the channels of VIRC. They are predominantly benthic feeders, which stir up the sediments in their foraging activities, thereby disturbing and uprooting plants, and increasing the suspended sediment load in the water. This increases turbidity, thereby reducing the underwater light availability for photosynthesis, and reducing submerged plant production (Bregazzi *et al.*, 1984; Crivelli, 1983; Fletcher *et al.*, 1985). Since 1983, observations made in parts of the drainage channel system of VIRC have suggested that the presence of common carp has been the indirect cause of a marked reduction in submerged weed growth in the channels (Sabbatini, 1989). The current levels of turbidity present in the channels are probably at least in part a consequence of the presence of carps, with greater effects occurring where there is a combination of fine sediment and high fish density (Fernández *et al.*, 1996subm.).

CCA analysis suggested that water movement and management regime are both important factors which limited the growth of submerged plants in some sites (Fig. 3.10). In Table 3.3 water velocity appears as the only environmental factor that differentiate significantly the group of sites without vegetation (Group W) from the others. However, as was stated above, similar velocity and management did prevent the growth of such species as *P. illinoensis* in IDEVI. Maximum values of water velocity found in both drainage areas are around 60 cm. sec^{-1}; higher velocities could start an erosive process in the channels, and for this are avoided by CORFO and IDEVI. Water velocity has different effects on plant growth, and can influence photosynthetic rates and exposure to nutrients (Westlake, 1967; Westlake, 1975; Madsen and Sondergaard, 1983), produce mechanical damage (Haslam, 1978) or affect propagule establishment. Chambers *et al.* (1991) studied the effect of water velocity on a plant community dominated by *Potamogeton* species and *Z. palustris* on the Bow River, Canada, and showed that plant biomass decreased with increasing current velocity over the range 0.01 to 1 m. sec^{-1}, and at current speeds higher than 1 m. sec^{-1}, aquatic macrophytes were rare.

According to Fig. 3.10, light attenuation is not important in influencing species distribution. However, the figure shows the first two axes of the ordination and hides the minor, but significant, importance of other axes in the analysis. The inter-set correlation coefficients shows that the variable best correlated with axis 3 was light attenuation (Table 3.5). The possible influence of light regime on submerged vegetation is also showed up in this study in the environmental comparisons of the TWINSPAN site groups. Group W (sites without vegetation), comprising most of the primary irrigation channels of VIRC, had the highest light attenuation and highest water velocity (Table 3.3). This suggest that both are important factors reducing plant growth at these sites to low quantities or zero. However, it is relevant to point out that differences were statistically significant for water movement but not for light attenuation (Table 3.3).

It is interested to examine the statiscally significant differences found in light availability between groups K and L, that comprise mostly of the drainage channels sites of VIRC (see Table 3.3 and Fig. 3.8), being *C. contraria* and *R. maritima* species less tolerant to shade than *P. pectinatus* and *Z. palustris.* In part, this agrees with the literature: charophytes are algae usually found in clear waters (Forsberg, 1965; Boyd, 1971), and significant reductions in underwater light may be most important for the growth of *R. maritima* (Dunton, 1990). On the other hand, *P. pectinatus* is a species that has important adaptations that allow it to succeed in highly turbid waters unfavourable to several common potential competitors (Kantrud, 1990).

Of the eight vascular submerged plants found in the target areas, four have been previously classified into the Grime strategy type, by Murphy *et al.* (1990) and Grime *et al.* (1988). The classified species, *Z. palustris, P. pectinatus, P. pusillus* and *C. demersum*, have the same established-phase survival strategy: CD, related to competitiveness and disturbance-tolerance. As in drainage channels of Britain, disturbance-tolerance is a vital survival feature in VIRC and IDEVI, especially because weed control procedures, that with different extent are widespread in both areas. In some channels, water fluctuation (estimated in this study from water depth), winter drought, and water movement are also relevant as disturbance-caused variables (Fig. 3.11). A widespread competitive element is also expected in channels that provided a rather productive environmental for submerged plant growth. On this sense, we can add to the information provided before about the studied environmental parameters, that nutrient water concentration (particularly phosphorus and nitrogen) in the channel network of VIRC and IDEVI, are into the suitable range published for the growth of mostly of the submerged plants (A. Lazzari, personal communication).

I discussed in point 2.4 the problems of using only two indices to summarise the complex influences of the environmental on the growth of submerged plants. However, the use of the integrated indices of stress and disturbance proved successful in allowing me to distinguish four groups of plants showing differential stress and disturbance tolerance. These may be considered as different functional vegetation groups (FVTs).

Important differences were found between the TWINSPAN species group in relation to the stress and disturbance variables (Fig. 3.12), and then may be considered as different functional groups. Group I and II, comprising Charophyte, *P. pusillus* and *P. pectinatus*, are especially related to disturbance-tolerance but with an intermediate tolerance to stress. The ecological amplitude of each species according to the literature agree with the strategy-type of the group. Species of *Chara* have a propensity for colonising water bodies disturbed by weed control, especially dredging (Nichols, 1984b; Wade 1990), and *C. contraria* is a species frequent in waters with mid-salinity content (Pereyra-ramos, 1981; Guerlesquin and Podlejski, 1980; Grillas and Duncan, 1986). *P. pectinatus* and *P. pusillus* are species tolerant to disturbance and shade (Newbold *et al.*, 1983).

Group I includes species of charophytes, mainly *C. contraria*. In irrigation and drainage channels of VIRC, *C. contraria* frequently is present in extensive monospecific meadows anchored to the bottom of the channels, and extending vertically up towards the water surface (Sabbatini, 1989; Fernández *et al.*, 1990). Similar types of charophyte stands are usually found in a wide range of water bodies as for example brackish lakes of the north of Poland (Pereyra-Ramos, 1981) or farm ponds of the rural portion of Madison County, New York (Crawford, 1977; 1979).

Group III, comprising *R. maritima, Z palustris* and two filamentous algae were, according to CCA, stress-tolerant species (Fig. 3.12). Both species, but especially *R. maritima*, can tolerate high water salinity (Verhoeven *et al.*, 1982; Haslam *et al.*, 1975). A difference with the literature is that *Z. palustris* is considered a disturbance-tolerance species (e.g. Newbold *et al.* 1983) and also fell into this category in drainage channels of Britain (see Fig. 2.13). *Z. palustris* and *R. maritima* are both annual species that base their regenerative strategies on possession of a large seed bank (Verhoeven *et al.*, 1982; Kautsky, 1989). These regenerative characteristics differentiate these species from all the others found in VIRC and IDEVI, which mainly reproduce vegetatively. It is possible to infer that this feature facilitates the survival of these two species on environmental with high stress and low disturbance. However, according to the general theory of Grime for terrestrial plants, annual species with persistent seed banks are characteristics of disturbance-tolerant species, a no stress- tolerators. More studies, related for example with the life-history, seed bank, salinity or disturbance-tolerance of these two species are needed for improve the interpretation of the data.

Group IV was clearly related to non stress conditions (low water conductivity and high light availability). but is not homogeneous in its tolerance to disturbance (Fig. 3.12). As was state above, the literature review of each species present in the group agree in general with the location of each species in the diagram. For example, *M. aquaticum* is a species that show traits clearly correlated to competitiveness: it growth is luxuriant under favourable conditions, and high concentrations of nutrients are required for good growth under field conditions (Sutton, 1985; Fernández *et al.*, 1990). On the other hand, this species growth in disturbed areas as for example the irrigation and drainage channels of California

(Bernhardt and Duniway, 1984), and in IDEVI, *M. aquaticum* growth in main irrigation channels that are "chained" up to eight times a year (Murphy, 1995).

CHAPTER IV

FUNCTIONAL ANALYSIS OF SPECIES AND PLANT TRAITS IN RELATION TO MANAGEMENT AND ENVIRONMENTAL PRESSURES IN ARTIFICIAL CHANNELS OF BRITAIN AND ARGENTINA

4.1 Introduction

In chapters II and III species groups associated to external factors were defined in artificial channels in two geographically widely separated areas, Britain and Argentina. Both target areas are located in temperate zones with comparable environmental and management conditions, and so were expected to support similar functional groups regardless of precise taxonomic composition. Few attempts have been made to use multivariate analysis techniques on aquatic plant data taken from different countries, and very few using data from different continents. One such was a strategy analysis of submerged lake macrophyte communities, using data from Norway, Egypt and Scotland (Murphy *et al.*, 1990b).

Species traits of macrophytes have been little studied, partly because these plants rarely flower, and because it is difficult to study aquatic plants *in situ* (Bornette *et al.*, 1994). Despite this difficulty, several studies on the relationship between aquatic plant traits and the environmental have been undertaken (Van der Valk, 1981; Shipley *et al.*, 1989; Mitchell and Rogers, 1985; Boutin and Keddy, 1993; Bornette *et al.*, 1994; Abernethy, 1995). Strategy analyses using submerged plant species trait data were published by Kautsky (1988) and by Murphy *et al.* (1990b). Recently, as part of a large-scale multidisciplinary program on European Wetland Ecosystems, analysis of biological trait data was linked to analysis of distribution data, to define functional groupings of organisms in relation to the environmental characteristics of the wetland habitat (Hills *et al*, 1994; Wu *et al.*, 1992; Obrdlik *et al.*, 1992; Murphy *et al.*, 1994). No such studies have been made in artificial channels, where the management regime produces clear differences from others water bodies such as lakes or rivers.

The aims of this chapter are:

1) By using multivariate approach with mixed vegetation data taken in both countries, to determine (a) the existence of functional groups in which submerged plants are associated to environmental and management factors; and (b) the degree to which species survival strategy could be related to the disturbance and stress pressures present in those habitats.

2) By using species morphological traits measured in submerged angiosperm species, (a) to identify functional groups of species present in both countries differentiated by selected morphological traits; (b) to determine the association between the measured traits and the disturbance and stress pressures that affect the studied channels.

4.2 Materials and Methods

For the multivariate analysis, data recorded during 1992 and 1993 in Britain were combined with data collected in Argentina in 1994/95: the species-site matrix thus comprised data on submerged plant composition and abundance at 160 sites (see 2.2 and 3.2).

A second set of data included those environmental physico-chemical variables that were measured in both surveys and were significant in determine species variation in Britain (see Fig. 2.9) and Argentina (see 3.10). They were management, light attenuation, water conductivity, water depth, water movement and light attenuation, expressed as:

(i) log of water conductivity (μS. cm^{-1});

(ii) log of water depth (cm);

(iii) water movement on a 1-10 scale (see 3.2.3.3.);

(iv) management regime, rated on a scale of 0 to 5 (see 2.2.3.2 and 3.2.3.2)

(v) log light attenuation (see 2.3.2.1 and 3.2.3.1)

Log transformation of some variables was necessary for normalise the data. Water fluctuation was a parameter that explains variation in Britain, but was not included here because was not measured in Argentina. Channels with "winter drought" (winter water recess) were only present in Argentina, and then it inclusion would not contribute to explain species variation in the mixed data.

The stress and disturbance indices were constructed from the numerical indices calculated in Chapter II for vegetation in Britain and in Chapter III for vegetation in Argentina. To standardise the indices from both countries, each index was transformed into a numerical 0-9 index which increased with increasing pressure on plant survival. As a consequence of this transformation, it was assumed in the study that minimum and maximum pressures were the same in both systems.

Between 3 and 6 ramets (plants) of each species were collected from different sites for laboratory measurement of the following morphological traits: LEN: above-sediment length of plants; WST: weight of stems per plant; and WLE: weight of leaves per plant. Only angiosperm plants were included, leaving out Charophyte, filamentous algae and the moss *Rynchostegium riparoides*. *Sparganium emersum* was excluded because is a species without above-ground stem.

Data were analysed using TWINSPAN (Two Way Indicator Species Analysis), DCA (Detrended Correspondence Analysis) and CCA (Canonical Correspondence Analysis). For methodology and general features of these multivariate analysis see 2.2.5.

4.3 Results

4.3.1 Analysis using species frequency and abundance

Twenty two taxonomic groups were included as items for the analysis. These comprised either single species or sets of species as is shown in Table 4.1. Filamentous algae were included together, and treated as one taxon in the analysis.

Fig. 4.1 shows the result of TWINSPAN analysis of the submerged species x site matrix covering 160 sites in Britain and Argentina, expressed as a dendogram showing hierarchical subdivisions of the data set to give 4 end groups at level 2. From the 160 sites, 25 were not analysed because they had no submerged plants when they were surveyed. Three abundance cut levels were used in the analysis, and the diagram also shows eigenvalues of each division, number of sites identified according to the country and indicator species with their abundance value.

At both levels TWINSPAN analysis divided the samples largely but not entirely according to a geographical pattern, with a left-side group A with 80 sites of VIRC and IDEVI, two sites from the Fens and one from the Crossens area. The presence of *P. pectinatus* in abundance in these three British sites made them more similar in terms of species composition and

Table 4.1. Submerged weed taxa from Britain and Argentina using in the multivariate analysis.

TAXON (Code)	*SPECIES*	CLASS	COUNTRY
RCIR	*Ranunculus circinatus*	Angiosperm	Britain
CALL	*Callitriche stagnalis*	"	"
	C. platycarpa	"	"
HPAL	*Hottonia palustris*	"	"
ELOD	*Elodea canadensis*	"	"
	E. nuttallii	"	"
MSPI	*Myriophyllum spicatum*	"	"
PPER	*Potamogeton perfoliatus*	"	"
PCRI	*Potamogeton crispus*	"	"
PNAT	*Potamogeton natans*	"	"
SEME	*Sparganiun emersum*	"	"
PLUC	*Potamogeton lucens*	"	"
PAMP	*Persicaria amphibia*	"	"
RRIP	*Rynchostegium riparoides*	Moss	"
CHAR	*Chara contraria*	Macroalga	Argentina
RMAR	*Ruppia maritima*	Angiosperm	"
ECAL	*Elodea callitrichoides*	"	"
MAQU	*Myriophyllum aquaticum*	"	"
PILL	*Potamogeton illinoensis*	"	"
PPEC	*Potamogeton pectinatus*	"	Britain and Argentina
CDEM	*Ceratophyllum demersum*	"	"
ZPAL	*Zannichiellia palustris*	"	"
PPUS	*Potamogeton pusillus*	"	"
	Potamogeton berchtoldii	"	Britain
FALG	*Cladophora glomerata*	Alga	"
	Enteromorpha intestinalis	"	"
	Vaucheria dichotoma	"	"
	Enteromorpha flexuosa	"	Argentina
	Cladophora surera	"	"
	Rhizoclonium hieroglyphicum	"	"

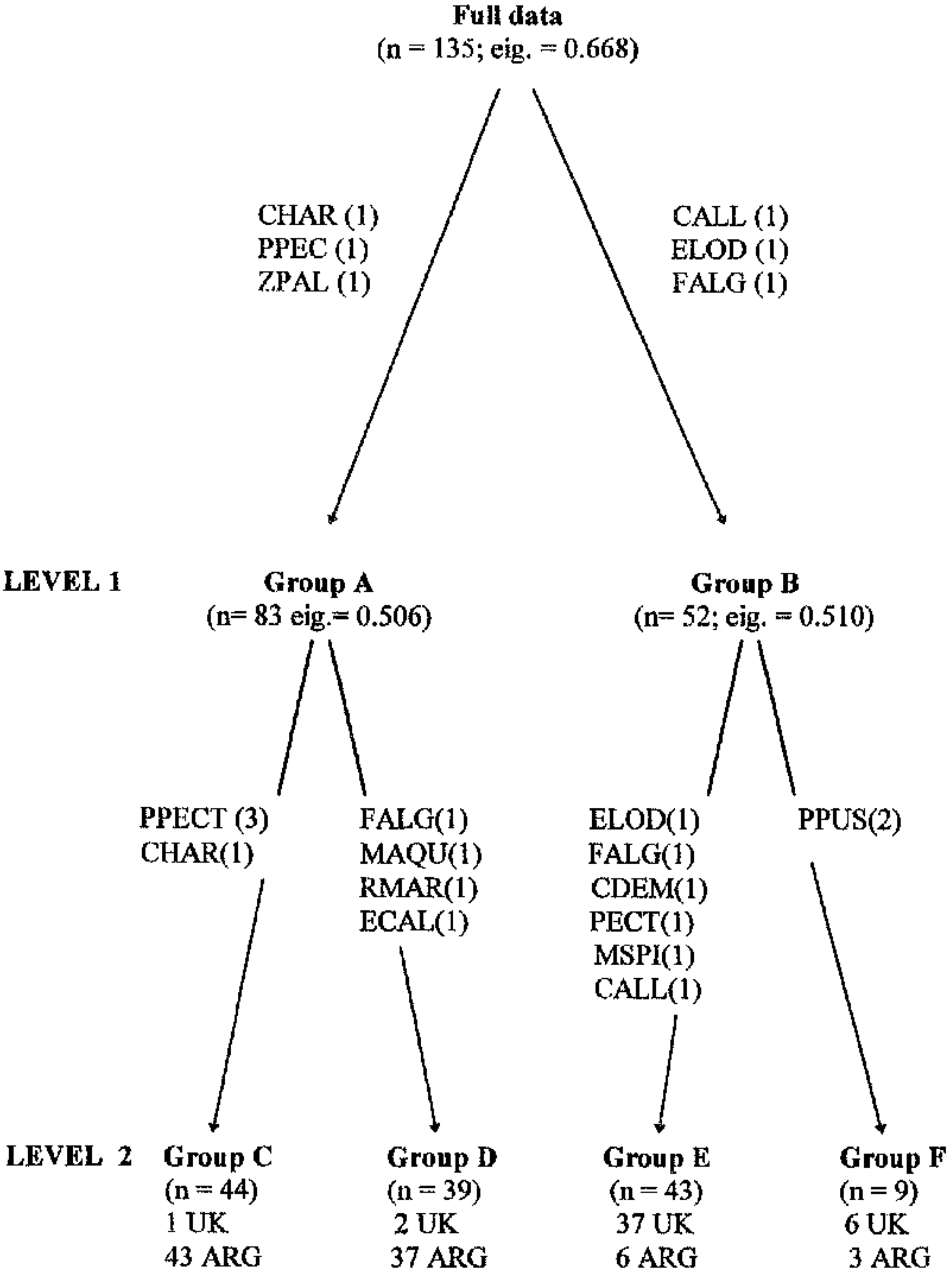


Fig. 4.1 Results of the TWINSPAN analysis expressed as a dendogram showing hierarchical subdivisions of the samples x species abundance to level 2. Only the indicator pseudospecies are labelled in the diagram. n: number of sites for group. ARG: Argentina. For species codes see Table 4.1.

abundance to channels of Argentina than other channels of UK. In group B are most of the British sites, with the addition of 9 sites of VIRC. Sites of VIRC with only filamentous algae and others with *P. pusillus* made them similar to British sites. At level 2 of the analysis, group A is divided following a geographical pattern but also channel type. Thus, all the irrigation channel sites of VIRC are in group C, and the indicator species are *C. contraria* and *P. pectinatus*, species abundant in that channels. Group D comprises drainage channel sites of VIRC, where *R. maritima* grew exclusively, and channel sites of IDEVI, where *M. aquaticum* and *E. callitrichoides* grew exclusively. Group E comprised mostly British sites, and group F included 6 of Britain and 3 of VIRC, that had in common the growth in abundance of *P. pusillus* or *P. berchtoldii*, analysed together as one taxon.

TWINSPAN classifies species as well as sites, and Fig. 4.2 is an overlay plot of the DCA ordination diagram showing species scores and the TWINSPAN species group (I and II) boundaries at level 1. The eigenvalues of the DCA analysis were 0.761 and 0.575 for the first and second axis, respectively. The eigenvalue of the species classification in the TWINSPAN analyses was 0.89 at iteration 1.

Fig. 4.3 shows the CCA ordination plot displaying species scores and arrows of five environmental continuous variables: water velocity, water depth, light attenuation, water conductivity and management regime. A summary of CCA analysis is given in Table 4.2, the eigenvalues were 0.439 and 0.405 for the first and second axis, respectively. The 99- point random Monte Carlo permutation test was used in this analysis and all the data set generated yielded a lower eigenvalue for the first axis and the overall analysis ($p \leq 1$).

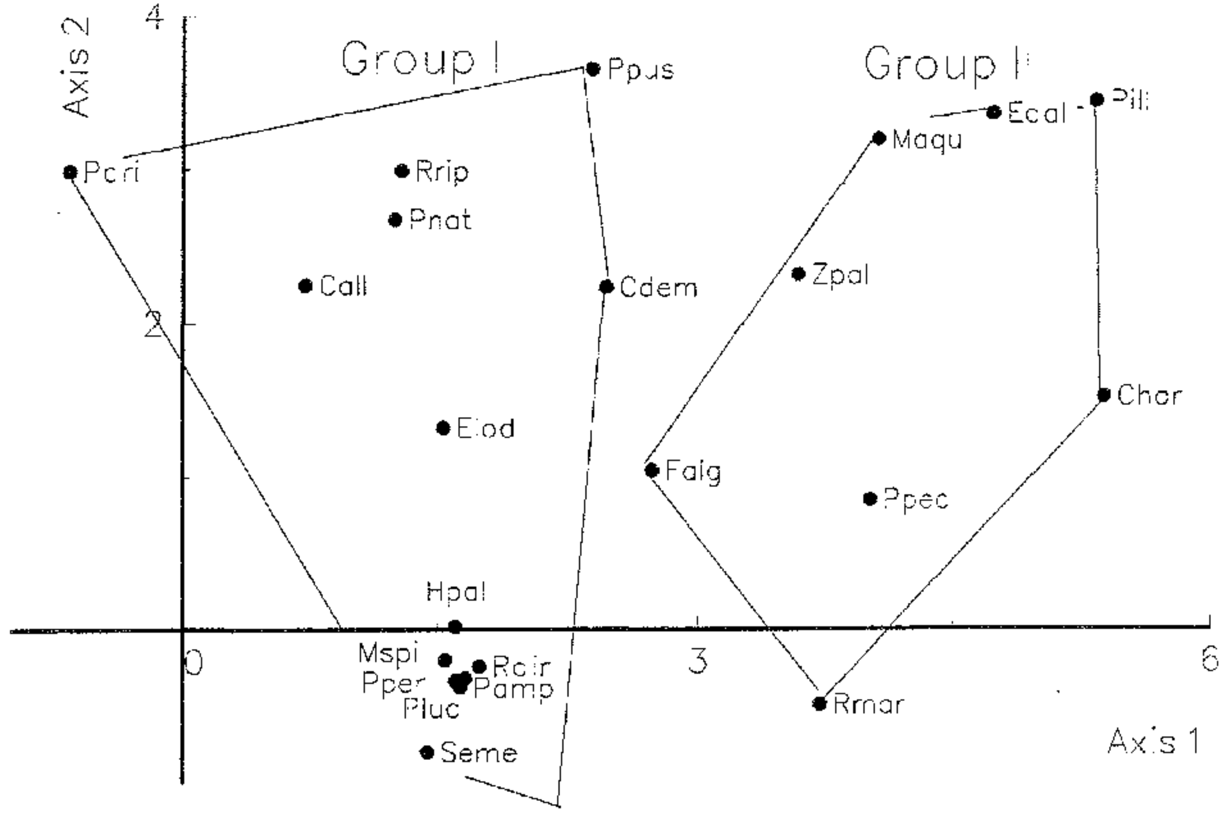
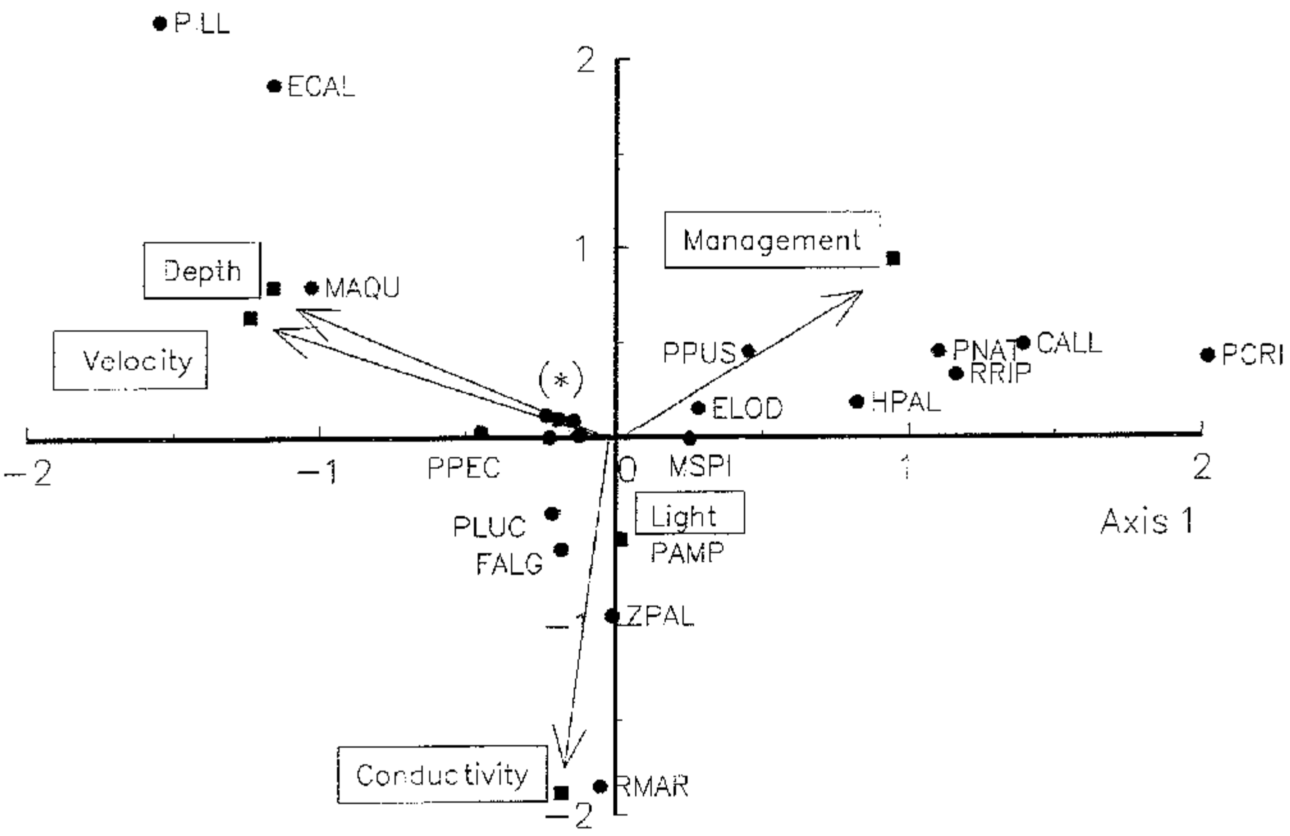


Fig. 4.2 DCA ordination diagram of species scores (•). The boundaries shown the two species groups (I and II) identified at level 1 of TWINSPAN classification. For species codes see Table 4.1.



(*) CDEM, RCIR, PPER, SEME & CHAR

Fig. 4.3 CCA ordination of species scores (•) and arrowed biplots scores of environmental variables (■) showing species codes (Table 4.1) and environmental variables names.

Table 4.3 shows the canonical coefficient and the inter-set correlations of the CCA analysis indicated above. The inter-set correlations of environmental variables with axis 1 were -0.506 for water velocity, -0.470 for water depth and 0.383 for management regime. Water conductivity was best correlated with axis 2, with a inter-set correlation of -0.773.

In the CCA biplots, the species points can be projected on to each arrow representing an environmental variable. The order of the projection points corresponds approximately to the ranking of the weighted averages of the species with respect to that variable, and then the position of a species along an environmental variable (Ter Braak, 1987). In Fig. 4.4 the diagram shows the projections for each variable of the species scores, in the CCA analysis of Fig. 4.3. Taxa are differentiated according to the country where they were recorded. The arrows of the variables water depth and water velocity were very close each other (Fig. 4.3), and so were included together in Fig. 4.4b. The range that covers the species recorded in one country shows the gradient of environmental or management where they survive, and then if the variables have influenced the distribution of the vegetation.

Fig. 4.5 shows the CCA ordination plot displaying species scores and arrows of both external survival factors that affect plant growth: disturbance and stress. As was stated before, the indices used here were calculated from those calculated in Chapter II and III, and using the same weightings of pressure (in absolute terms) for the data collected in Britain and Argentina. For example, sites under maximum disturbance pressure in Britain and Argentina had both the same index value (I_D = 9) while undisturbed sites had an I_D of 0 in both data. The eigenvalues of the CCA analysis were 0.34 and 0.30 for the first and second axis, respectively. The first axis explained 52.8 % of the variance of the species-environmental relation, so each

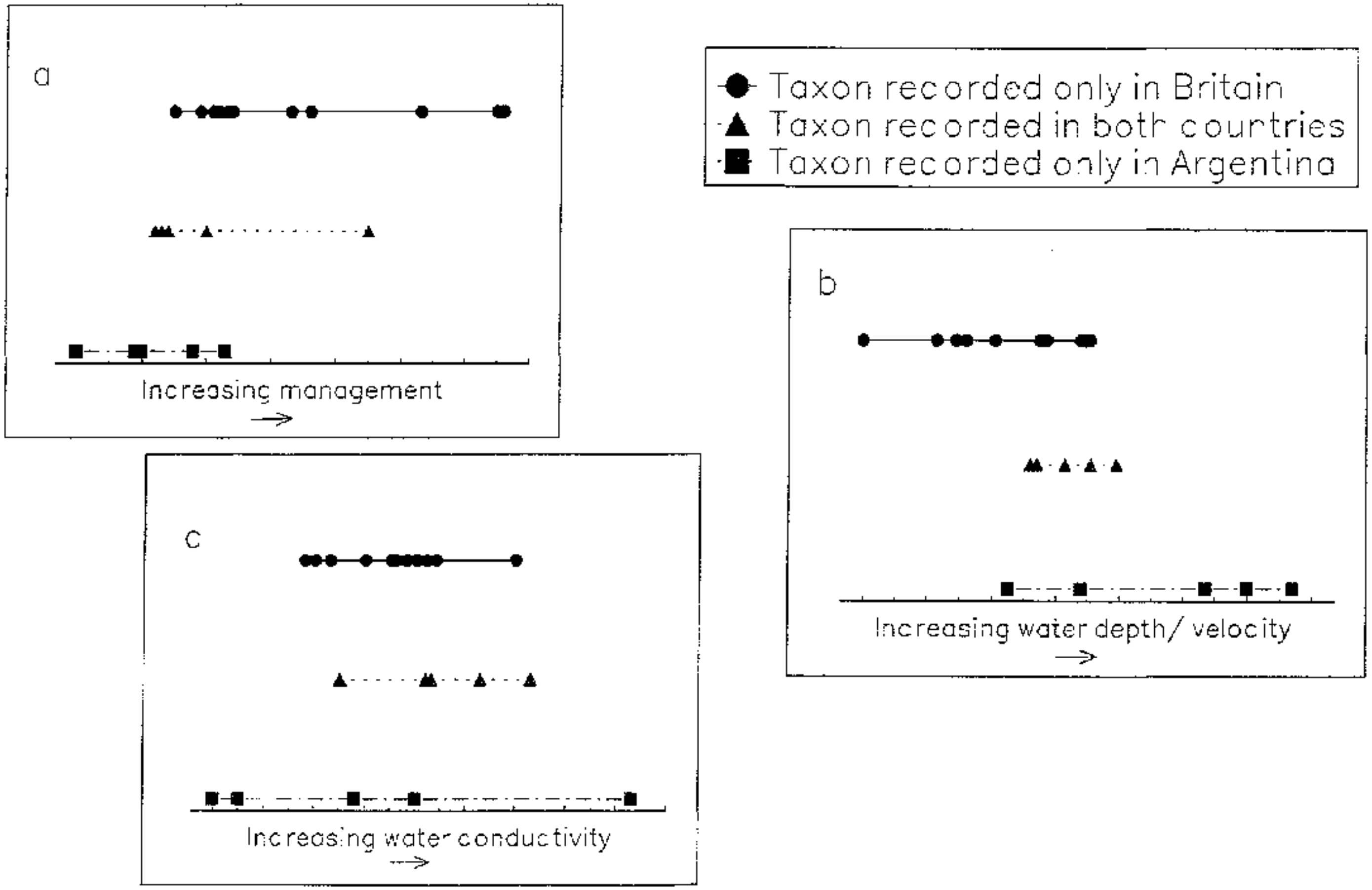


Fig. 4.4 Relative projections of the species scores on to each arrow representing an environmental variable (a, b, c), in the CCA analysis of Fig. 4.3. Taxa are differentiated according to the country where they were recorded.

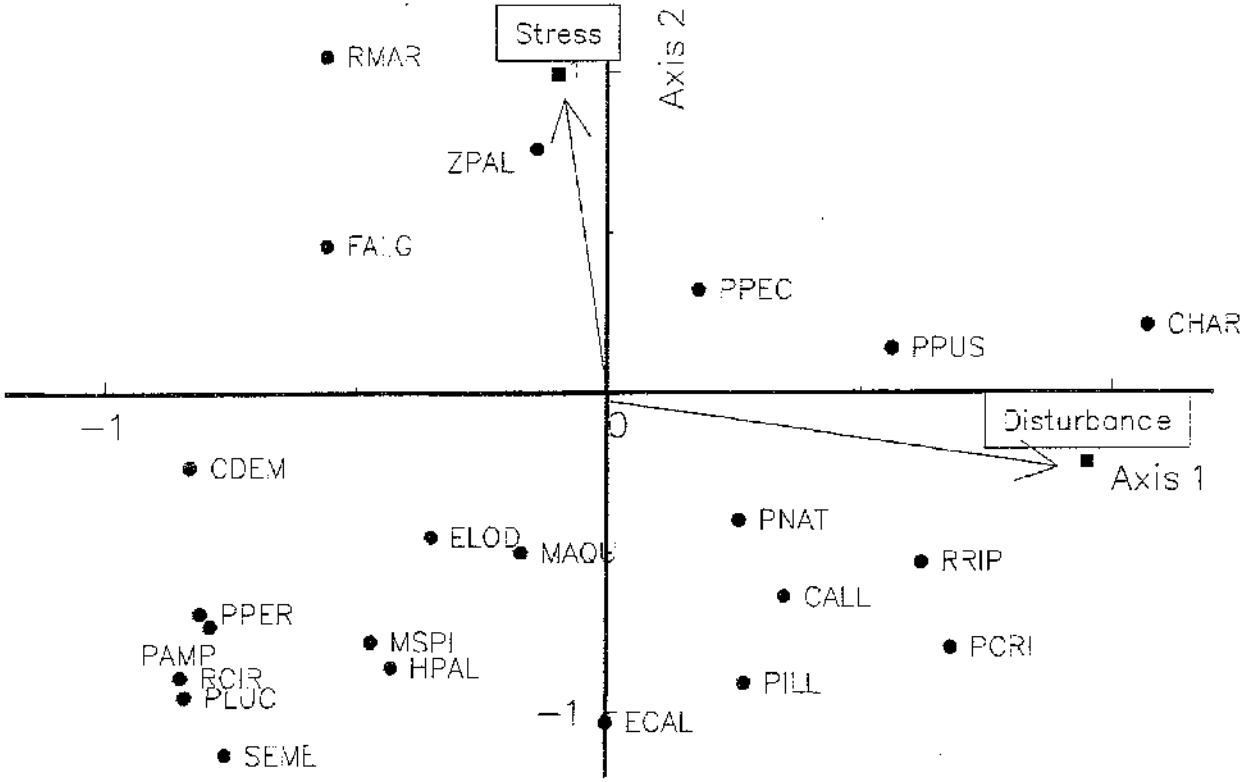


Fig. 4.5 CCA ordination of species scores (•) and arrowed biplots scores of the disturbance and stress variables (■) showing species codes (Table 4.1) and environmental variables names.

variable explained about half of the constrained variation. Fig. 4.6 shows the projections of the species scores for each variable with the taxa differentiated according to the country where they were recorded.

Table 4.2. Summary on CCA of submerged vegetation of Britain and Argentina in relation to five environmental variables (see text).

Axis	1	2	3	4	Total inertia
Eigenvalues:	0.439	0.405	0.250	0.129	6.179
Species-environ.correlations:	0.808	0.815	0.646	0.602	
Cumulative % variance					
of species data:	7.1	13.7	17.7	19.8	
of species-environ. relation:	33.6	64.6	83.8	93.7	
Sum of all unconstrained eigenvalues					6.179
Sum of all canonical eigenvalues:					1.306

Table 4.3. CCA. Inter-set correlations of environmental variables with axes and canonical coefficient for standarized variables, in the analysis of the relation between submerged plant species of Britain and Argentina to five environmental variables

	Canonical coefficient			**Correlation coefficient**		
Axis variable	**Axis 1**	**Axis 2**	**Axis 3**	**Axis 1**	**Axis 2**	**Axis 3**
Log water cond.	-0.16	-0.77	0.23	-0.079	-0.773	0.001
Log water depth	-0.49	0.25	-0.52	-0.470	0.325	0.368
Water velocity	-0.73	-0.06	0.72	-0.506	0.262	0.458
Management	-0.51	0.24	0.36	0.383	0.386	0.370
Log. z_{eu}/ *depth*	-0.15	-0.11	-0.07	0.015	-0.222	-0.214

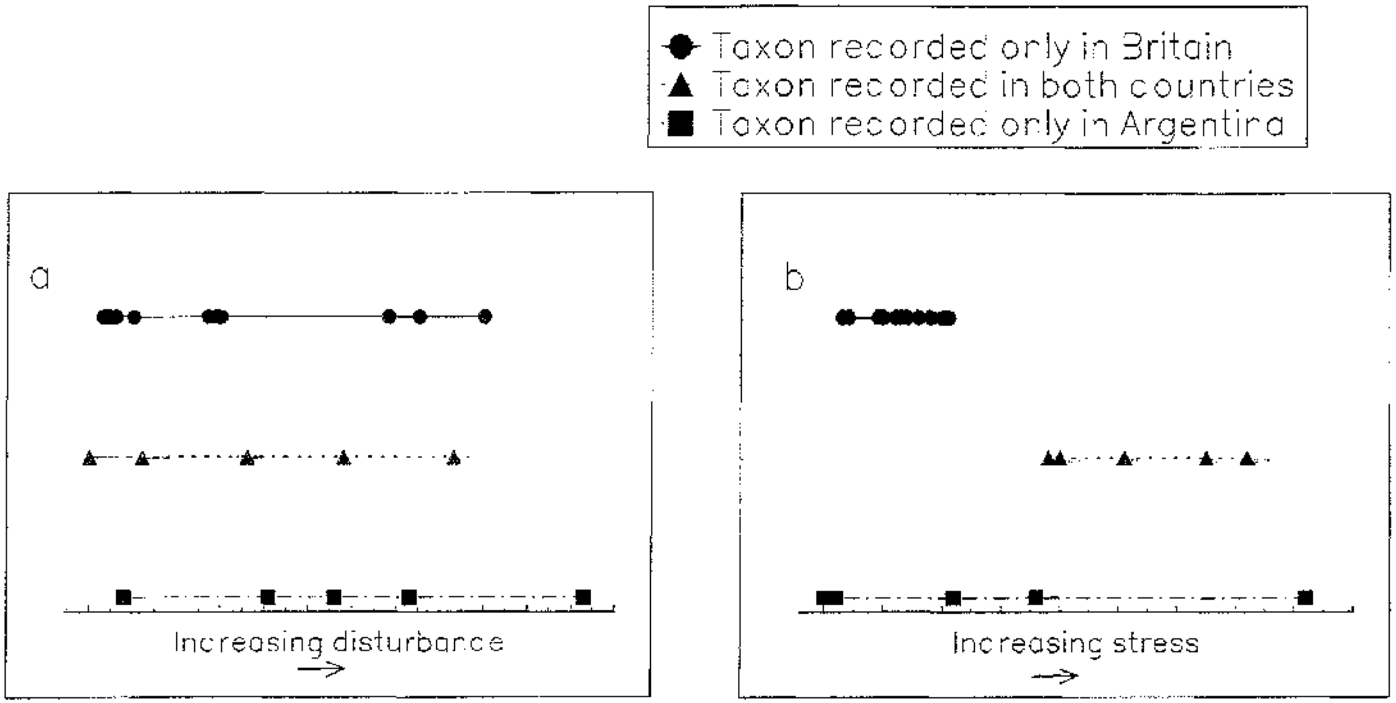


Fig. 4.6 Relative projections of the species scores on to each arrow representing an environmental variable (a, b), in the CCA analysis of Fig. 4.5. Taxa are differentiated according to the country where they were recorded.

4.3.2. Analysis using species morphological plant traits

Table 4.4 shows the average of the three morphological plant traits measured in different sites of Britain and Argentina. Means of the measured trait data taken in each country were considered for the four taxa that were common to both areas: *P. pectinatus, C. demersum, P. pusillus* and *Z. palustris*.

Table 4.4 shows that besides the important differences between populations, there are also significant differences between some groups of species. Fig. 4.7 displays the average by species of the 3 measured traits in a 3 dimensional graph, showing that some species, for example *Callitriche* or *R. maritima*, are in average much smaller plants, compared with big species such as *P. lucens* or *P. illinoensis*. Fig. 4.7 shows also that the different sets of traits are mutually related. The correlation coefficient of the average by species of the 3 measured traits were calculated and lead to the following values: 0.89 (LEN x WST), 0.86 (LEN x WLE) and 0.95 (WST x WLE). All the coefficient are high, and reveal that longer plants lead in general with heavy stems and leaves and short plants with light stems and leaves.

Is it possible to construct groups of species differentiated by traits, in spite of the evident gradient present in the data? For answering this question data was cluster using TWINSPAN, to produce a hierarchical divisive classification. At level 1 (eigenvalue = 0.30), TWINSPAN divided the species into two groups, that differentiated "small" (group 1) from "big" (group 2) plants. At level 2, the eigenvalues decreased to low values (0.01 and 0.18): so further clustering was inappropriate. Groups comprised the following species:

GROUP 1

Callitriche stagnalis and *C. platycarpa*
Hottonia palustris
Elodea canadensis and *E. nuttallii*
Ranunculus circinatus
Ruppia maritima
Potamogeton crispus
Elodea callitrichoides
Myriophyllum aquaticum
Potamogeton pectinatus
Zannichiellia palustris
Potamogeton pusillus and P. berchtoldii

GROUP 2

Myriophyllum spicatum
Potamogeton perfoliatus
Potamogeton natans
Potamogeton lucens
Persicaria amphibia
Potamogeton illinoensis
Ceratophyllum demersum

In addition, in Fig. 4.7 is overlaying the TWINSPAN species groups boundaries at level 1, showing that the two groups are clearly separated in the sequence of the species in the three dimensional graph.

Fig. 4.8 is the same diagram of the CCA analysis displayed in Fig. 4.5, but the labels on the species scores have been changed to show their membership of TWINSPAN groups 1 and 2. In Fig. 4.9a, b the diagrams display the projections of the species scores in the CCA analysis of Fig. 4.5, showing the relationship between the stress and disturbance indices and the above-ground plant weight (WLE+WST). As was stated above, the projections show the position of the species scores in the environmental gradient in terms of its frequency and abundance along the range. Linear or curvilinear regression analysis showed that neither stress nor disturbance indices were significantly correlated with WLE, WST or WLE+WST.

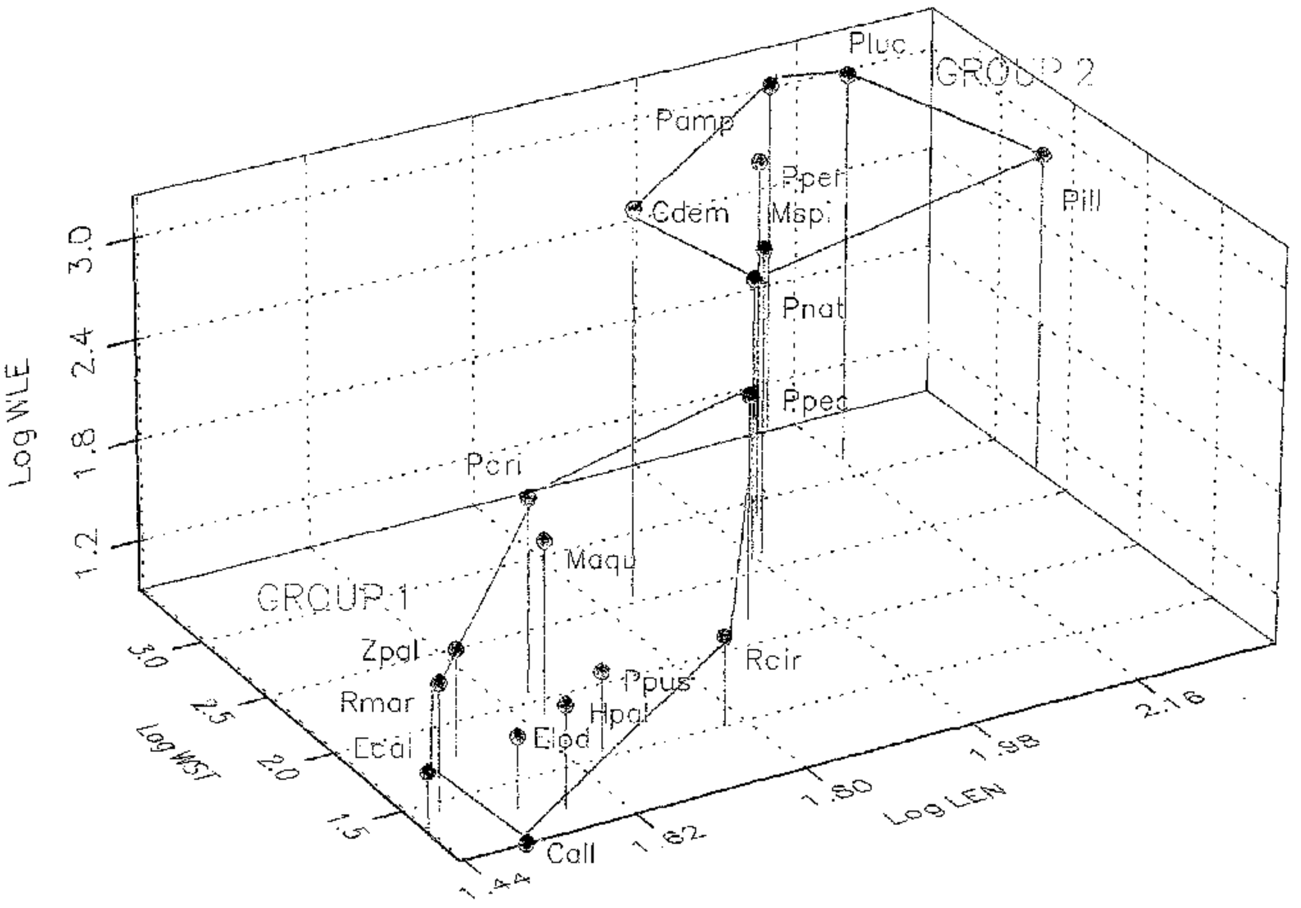


Fig. 4.7 Three dimensional graph showing the relationship between species average values for three measured morphological plant traits. WSE: weight of stems; WLE: weight of leaves; LEN: plant length. The boundaries shown the TWINSPAN groups at level 1. For species codes see Table 4.1.

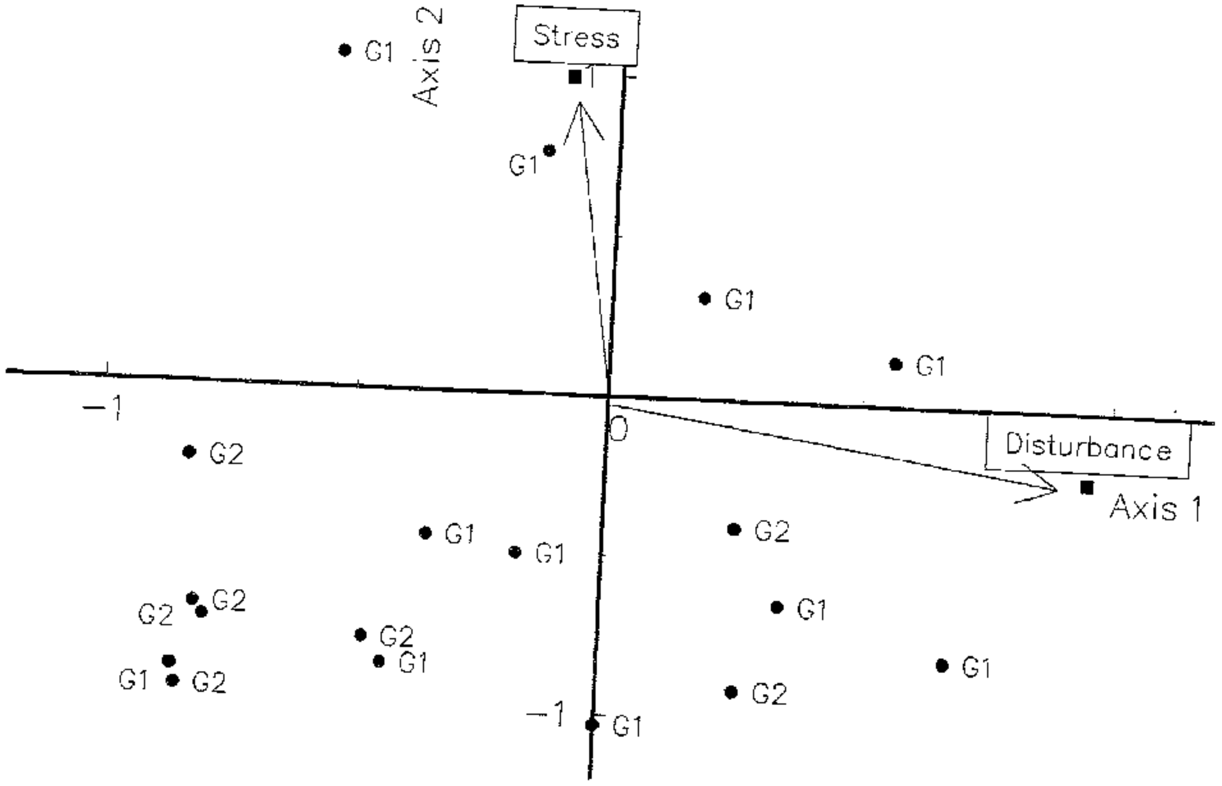


Fig. 4.8 CCA ordination of species scores (•) and arrowed biplots scores of the disturbance and stress variables (■) in the analysis displayed in Fig. 4.5. The label of the species codes were replaced by the TWINSPAN species groups were they belonged. G1: small plants; G2: big plants.

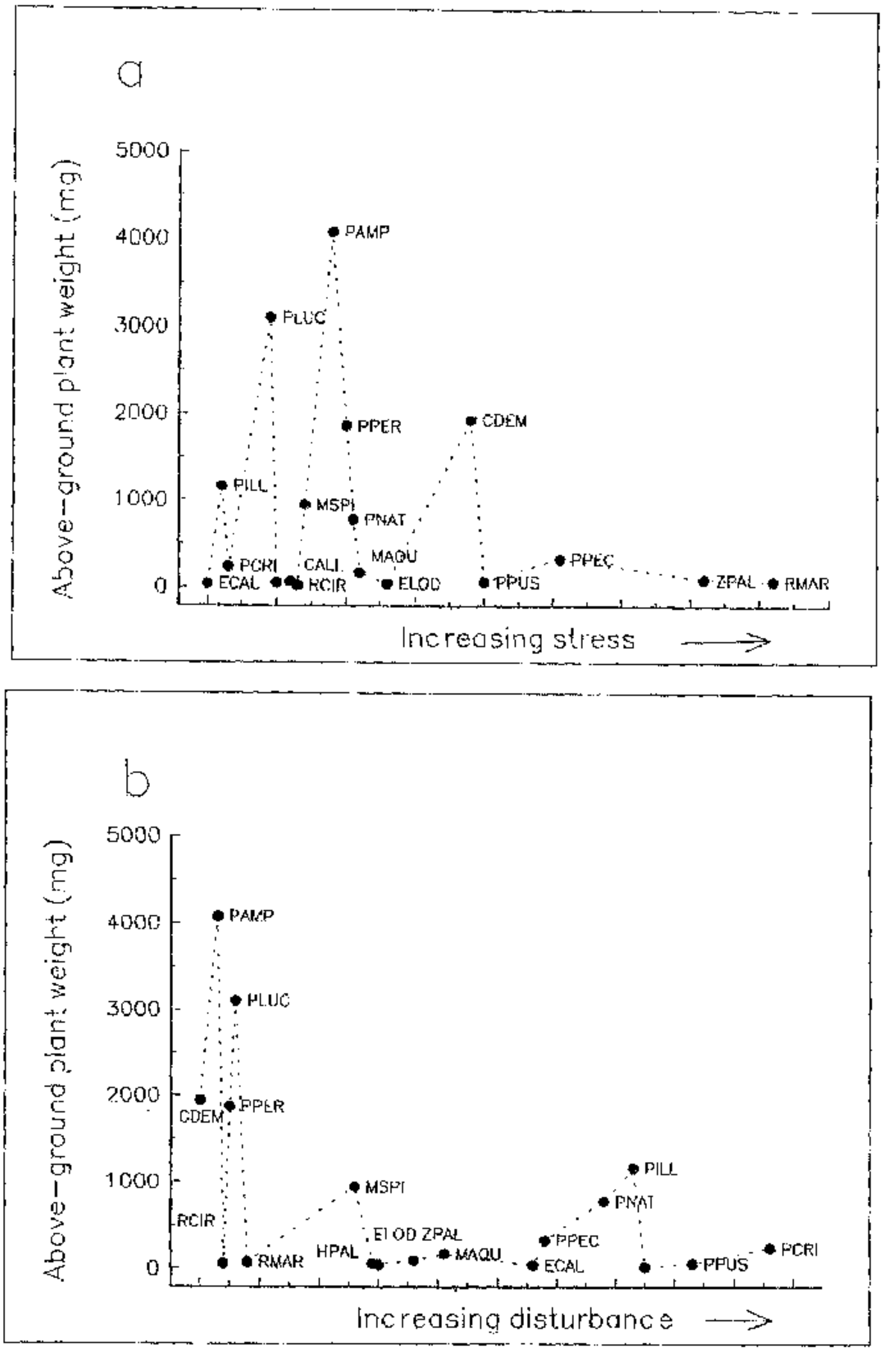


Fig. 4.9 Relationship between the above-ground plant weight and the relative projections of the species scores on to each arrow representing stress (a) or disturbance (b), in the CCA analysis of Fig. 4.5. For species codes see Table 4.1.

Table 4.4 Morphological trait data for 18 submerged species harvested in Britain and Argentina. Data are means ± standard deviation of the average of 3 to 6 plants taken at each site. LEN: above-sediment length of plants; WST: weight of stems per plant; WLE: weight of leaves per plant. For species codes see Table 4.1.

Species code	Number of sites	LEN	WST	WLE
PPEC	24 (Arg.)	84.1 (± 40.0)	149.3 (±149.2)	179.3 (±119.8)
PPEC	7 (UK)	77.8 (± 22.4)	143.7 (±113.7)	170.1 (±183.3)
PPEC	Arg. + UK	80.9	146.5	174.7
PPUS	5 (Arg.)	52.3 (± 27.7)	42.8 (±49.6)	33.5 (±32.2)
PPUS	4 (UK)	38.0 (± 24.1)	28.0 (±31.4)	14.7 (±13.1)
PPUS	Arg. + UK	45.1	35.4	24.1
ZPAL	3 (Arg.)	24.1 (± 11.7)	34.2 (±7.2)	27.3 (±11.4)
ZPAL	3 (UK)	43.5 (± 13.5)	81.1 (±20.2)	43.3 (±11.6)
ZPAL	Arg. + UK	33.8	57.7	35.3
CDEM	2 (Arg.)	85.5 (± 24.7)	564.5 (±396.6)	2356.6 (±1607.2)
CDEM	2 (UK)	53.1 (± 2.9)	164.0 (±33.9)	803.0 (±226.3)
CDEM	Arg. + UK	69.3	364.2	1577.7
RMAR	4 (Arg.)	30.0 (± 8.4)	27.3 (±11.7)	45.2 (±47.9)
PILL	2 (Arg.)	206.4 (± 173.8)	503.2 (±363.1)	660.7 (±217.3)
MAQU	2 (Arg.)	44.4 (± 11.7)	78.3 (±24.3)	87.3 (±17.4)
ECAL	2 (Arg.)	27.3 (± 3.5)	20.3 (±6.9)	18.3 (±11.7)
PCRI	3 (UK)	45.4 (± 13.5)	119.3 (±122.4)	114.7 (±71.7)
MSPI	4 (UK)	98.7 (±20.0)	421.7 (±219.5)	528.0 (±367.1)
ELOD	5 (UK)	34.6 (± 10.7)	21.2 (±10.6)	21.2 (±7.63)
CALL	5 (UK)	32.0 (± 11.8)	12.4 (±5.03)	7.6 (±5.2)
HPAL	2 (UK)	36.9 (±14.3)	17.0 (±1.4)	33.0 (±4.2)
RCIR	4 (UK)	60.6 (± 7.9)	32.5 (±10.0)	27.5 (±12.2)
PNAT	3 (UK)	95.5 (± 29.7)	402.0 (± 127.0)	379.0 (±176.9)
PAMP	2 (UK)	135.0 (±49.5)	3050.0 (±762.3)	1030.0 (±274.4)
PPER	2(UK)	105.8 (± 1.2)	760.0 (±212.1)	1107.0 (±109.6)
PLUC	2 (UK)	145.0 (± 35.3)	1345.0 (±247.5)	1760.0 (±1216.2)

4.4 Discussion

During the survey, 41 submerged and floating taxa were identified in drainage channels of UK (Table 2.1) and 12 in irrigation and drainage channels of Argentina (Table 3.1). In the species matrix used in this Chapter for multivariate analysis, 10 taxa included species from Argentina and 18 species from the UK (Table 4.1). Differences in plant species diversity between both channel systems could be explained in part by differences in their age. In the UK, several drainage channels were made centuries ago. For example, the fens, rivers, defensive banks and washes in the Fens drainage area, are almost entirely man-made, and the area as adjudged to be "drained" by the 17th century (NRA, 1992). The "King's Dike", where site 2 was located (see 2.2.1), was built by King Canute in 1030 (G. Cave, personal communication). On the other hand, artificial channel network in VIRC and IDEVI started officially by 1960 (see 1.2.1 and 3.4). The important difference in age between both systems, suggest that channels of UK have had more opportunities for plant colonisation from other water bodies than channels of Argentina.

DCA analysis diagram shows the distribution of the species according to a geographical pattern, being species recorded only in Britain to the left and only in Argentina to the right (Fig. 4.2). Taxa that were common to both countries fall in the centre of the diagram. In DCA, the distribution of the species scores in the diagram are related to the abundance and species composition of every site analysed, 135 in this study. Fig. 4.2 shows that some species from different countries are closer than species from the same country, and this shows that the five taxa that have in common both countries, define some species arrangements not connected by a geographical pattern. For example, Fig. 4.2 shows that *R. maritima* (present only in Argentina during the survey) and *R. circinatus* (present only in UK) are closer each other than the first from *P. illinoensis* (only in Argentina) and the second from *P. crispus* (only in UK).

Fig. 4.3 and Fig. 4.4a show that management determines differences especially between species in Britain, with strong CD species as *P. crispus* or *Callitriche* spp.. Populations of *Z. palustris* showed in Britain high tolerance to disturbance (Fig. 2.9), but joined with the data of populations of Argentina the species appears now to be a species with medium to low tolerance to management (Fig. 4.3). In IDEVI, *P. illinoensis* and *E. callitrichoides* were found in sites of high water depth and flow (Fig. 4.3). In Britain, a range of species as *P. crispus, C. stagnalis* or *C. platycarpa*, were found in abundance in sites with shallow and very slow water movements (Fig. 4.3, 4.4b). Fig. 4.4c shows that in channels of Argentina a wide range of species are adapted to different water conductivity, from *P. illinoensis* and *E. callitrichoides* (found in sites of IDEVI with values as low as 160 μS. cm^{-1}) to *R. maritima* (found in sites of VIRC with more than 14,000 μS. cm^{-1}).

Fig. 4.5 displays a clear picture on the distribution of submerged species in artificial channels of Britain and Argentina, showing that the simplification of the external constraints that affect plant growth in disturbance and stress was useful to improve the understanding of these plant communities. Charophyta, *P. crispus, P. pusillus,* between others, appear as disturbance-tolerant plant species with intermediate to low tolerance to stress. *R. maritima, Z. palustris* and filamentous algae as stress-tolerants with intermediate to low tolerance to disturbance. A group of species, recorded exclusively in Britain (*P. amphibia, R. circinatus, P. lucens, P. perfoliatus*, between others), that grew far from the environmental constraints that affect plant growth, could be named "competitive plants" (strategy type C, sensu Grime, 1979). The area where both variables were high is empty of species, in agreement with the general theory of Grime (1979) for terrestrial plants.

Fig. 4.6a shows that disturbance is an important factor in determining the distribution of the aquatic submerged taxa in artificial channels of both countries. On the other hand, stress is important in channels of Argentina (by far for the influence of water conductivity), but has less influence on the species present exclusively in Britain, unless in relation to the variables measured in this study (Fig. 4.6b).

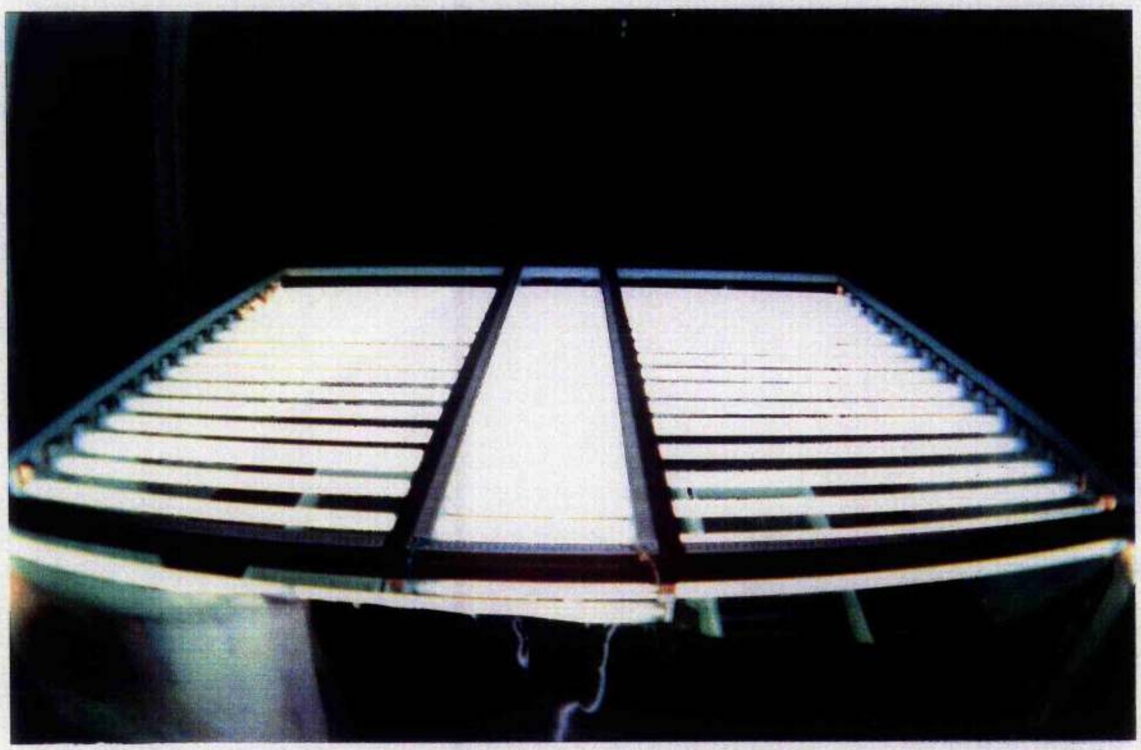
One characteristic survival trait of competitive plant species is to form large peaks of biomass, in both terrestrial (Grime, 1979) and freshwater habitats (Murphy *et al.*, 1990). This was corroborated in part in this study, since species included in Group 2 (big plants) were not present in the stress or disturbance extremes (Fig. 4.8). However, species from Group 1 (small plants) were present everywhere along the stress and disturbance range (Fig. 4.8).

Fig. 4.9a shows that the seven "big plant" species, with more than 700 gDW of total weight, all fell in the unstressed half of the range. Fig. 4.9b shows that species from group 2 cover approximately 80 % of the disturbance range, but the four species with more than 1500 g.DW of total above-ground weight fell in a narrow range, located in the undisturbed extreme. As above, Fig. 4.9a, b shows that "small plant" species are located along all the range of disturbance and stress evaluated.

Hills *et al.* (1994) reported that wetland plant populations that were tall and had a large dry weight of leaves tended to have a high competitive ability. Similar conclusion is possible to assert for submerged vegetation in this study at species level (Fig. 4.8 and Fig. 4.9). Plant height is frequently quoted as a trait positively related to competitive ability of the plants. For example, Grime *et al.* (1988) use the possession of tall shoots as an attribute of "competitive plants". Gaudet and Keddy (1988) found that taller plants suppressed more the growth of a species phytometer than lower-growing plants. Keddy and Shipley (1989) and Menges and Waller (1983) found similar results in lake-shores and in flood plain forest herbs.

Stress tolerant submerged plants were morphologically constrained to a low total above-ground plant weight (Fig. 4.9a). Since the highly correlation between morphological traits showed in Fig. 4.7, it can be suggested that short species (low LEN) are also characteristic of habitats under high stress. This agrees with results found for terrestrial (Grime, 1974; Grime *et al.*, 1988) and aquatic (Hills *et al.*, 1994) vegetation. Results in relation to disturbance are not so clear, but show the same tendency.

These results show that some morphological features that permit classified terrestrial plants in terms of their survival strategy, are useful also for classified submerged vegetation. This is specially interested because in submerged plants the application of the general strategy concepts have been frequently under controversy, specially because is often not clear what factors exactly limit growth of aquatic macrophytes (Verhoeven *et al.*, 1982; Brux *et al.*, 1987; Wiegleb and Brux, 1991; van Wijk, 1988).



Photograph 3. Above: growth chamber where *Potamogeton pectinatus* was studied under laboratory controlled conditions. Below: Site 2 (Low Level) located in the Solway drainage area in NW England. Light attenuation made by geotextile material is measured using a light-sensor linked to a datalogger.

CHAPTER V

RESPONSE OF *POTAMOGETON PECTINATUS* L. TO DISTURBANCE AND STRESS PRESSURES IN ARTIFICIAL CHANNELS AND IN EXPERIMENTAL CULTURE

5.1 Introduction

Potamogeton pectinatus, present in 39 % of the sites of Britain and in 55 % of the sites of Argentina, was one of the most widespread species in this study. *P. pectinatus* is a submerged macrophyte of near cosmopolitan distribution. The plant is of world-wide importance as a waterfowl food but is also often a nuisance in irrigation districts and recreational waters. Yeo (1965) outlined the life history of *P. pectinatus;* many other papers have reported on the effects of environmental factors influencing the distribution and abundance of this species through the world (e.g. Kollman and Wali, 1976; Anderson, 1978; Howard-Williams and Liptrot, 1980; Verhoeven 1980a, 1980b; Van Vierssen and Verhoeven, 1983).

Potamogeton species have a wide ecological flexibility (Heathcote *et al.*, 1987; Pip, 1987). The broad ecological amplitude of *P. pectinatus* has been demonstrate by Kautsky (1987), van Wijk (1988) and Kantrud (1990), although certain biological constraints still operate (Wiegler and Brux, 1991).

The general established-phase survival strategy of *P. pectinatus* has been related to competitiveness and disturbance-tolerance (Murphy *et al.*, 1990). However, several attributes of *P. pectinatus* appear to be related also with stress-tolerance, as for example it wide tolerance to turbidity compared with other submerged species (Stukey, 1971; Davis and Carey, 1981; Reese and Lubinski, 1983), its high tolerance to shade (Wilson 1958; Hynes 1970; Vermaat and Hootsmans, 1991) and its wide tolerance to water salinity (e.g. Kantrud, 1990). Van Wijk (1989) also suggested that *P. pectinatus* has several characteristics of a "stress-tolerator".

In Chapters II, III and IV, CCA analysis contributed to determine the survival strategy of several submerged plant species (Fig. 2.13, Fig. 3.14, Fig. 4..5). For example, *R. maritima* as a stress-tolerant plant, Charophyta or *P. crispus* as disturbance-tolerants and *P. lucens* or *P. amphibia* as competitors (Fig. 4.5). The interpretation of the CCA diagrams is more difficult when the species scores fall at intermediate positions, because not always mean intermediate tolerance to the variables involved (ter Braak, 1987). In Fig. 4.3 and 4.5, *P. pectinatus* lie close to the centre of the CCA diagrams, and then more analysis is necessary for determine if it is an intermediate tolerant species or a species with a wide tolerance to the stress and disturbance pressures.

Another way to study the effect of environmental and management pressures on *P. pectinatus* is through their effects on selected species plant traits. The effect of environmental on some morphological traits of *P. pectinatus* have been reported (Spence, 1976; Spence and Dale, 1978; Vermaat & Hootsmans, 1991; Hootsmans and Vermaat, 1991; Madsen, 1991; Sher-Kaul *et al.*, 1995). It is important to study the response of the species to cutting disturbance and to shade stress, especially because plants are heavily disturbed in artificial channels with different mechanical weed control procedures, and the effect of water turbidity on the growth of the plants seems to be an important environmental constraint that affects the growth of *P. pectinatus* in channels of VIRC.

The aims of this chapter were:

1) To determine if differences between populations of *Potamogeton pectinatus* (in terms of frequency, abundance and morphological traits) could be related to the stress and disturbance pressures that these populations encounter in the field.

2) To ascertain, under standardised experimental laboratory conditions, the response of juvenile and adult plants of *P. pectinatus* to artificially imposed stress (shade) and disturbance (cutting).

5.2 Materials and Methods

5.2.1 Field data

Survey data from Chapters II and III were utilised in this chapter to study the relationship between the frequency and abundance of *P. pectinatus* across a range of environmental and management variables.

Morphological trait data on *P. pectinatus* used at species level in Chapter IV, were utilised here, differentiated at population level. The measured traits were:

LEN: above-sediment length of plants
WST: dry weight of stems per plant
WLE: dry weight of leaves per plant
WRE: dry weight of spikes per plant (not included in Chapter IV)

From these data other indices were calculated: the total above-ground plant weight (WAG) was calculated as the addition of WST, WLE and WRE. The stem above-ground weight ratio (STWAG), leaves above-ground weight ratio (LEWAG) and spikes above-ground weight ratio (REWAG) were calculated as the ratio between WST, WLE and WRE to WAG, respectively. Dry weight was determined for oven-dried (48 hr, 80°C) material.

5.2.2 Laboratory data

Two experiments were carried out in the laboratory under a temperature regime of 21 (± 3) °C. In both experiments, plants were grown from tubers collected from the sediment of a drainage channel of VIRC. Tubers were placed in individual pots of 60 cm^2 x 9 cm height (1 plant/ pot), filled with terrestrial sandy loam soil. 15 pots were placed into each polypropylene tank (0.24 m^2 x 0.7 m height) filled with tap water. Nine and twelve tanks were utilised in experiment 1 (EXP.1) and experiment 2 (EXP. 2), respectively. Periodically, a variable number of pots were removed from the tanks for measured morphological plant traits. Dry weight was determined on oven-dried (48 hs, 80°C) material.

Full light was provided by a panel of 32 fluorescent tubes (120 cm length; 36 W) supplemented with 60-W incandescent bulbs. The intensity of light expressed as photosynthetically-active radiation PAR, was 48.99 (± 6.82) $\mu E.m^{-2}. s^{-1}$, just above water level (air) and 31.7 (± 3.11) $\mu E.m^{-2}. s^{-1}$ just below water level (sub-surface). Light was measured using a SKYE SKP210 PAR sensor linked to a SKYE Datalog SDL 2540 logger. Different thickness of geotextile material produced the light attenuation of the treatments.

A complete-random design was used as standard with three replicates (tanks). Prior to the statistical analysis, normality and homoscedasticity were checked in the data. Normality was examined using a MINITAB 8 powerful test which is essentially equivalent to the Shapiro-Wilk test, and homogeneity of variances was checked using Bartlett's test (Sokal and Rohlf, 1981). Analysis was performed using one- way ANOVA followed by mean comparations using Tukey's test. When data was not normal or had not homogeneity of variances, means comparations were performed using Student t-test. The number of individual pots (within-treatment replicates) collected at each sampling date was two in EXP. 1 and three in EXP. 2, except for WTOT that was six for EXP. 1 after 122 days of planting, and ten for EXP. 2 after 76 days of experiment set up.

In EXP.1, the experimental set up was made 12 days after tuber planting, and then treatments were made to juvenile plants. Treatments included 3 light levels: (1) full light (2) 60 % full light and (3) 30 % full light. The measured traits in this experiment were:

LEN: total-above plant length
WTOT: total plant dry weight
WST: dry weight of stems per plant
WLE: dry weight of leaves per plant
WRO: dry weight of below-ground part of the plant
WRE: dry weight of spikes

In EXP. 2, treatments were made to adult plants, three months old and with 20 % of flowering. The experiment included four treatments: (1) full light, (2) full light, cutting, (3) 30 % full light, (4) 30 % full light, cutting. Cuts were made at ground level, and all the above-ground plant was removed. The measured traits were the same than in EXP. 1 plus:

NSSH: number of secondary shoots
NLEA: number of leaves per plant
TLEN: total principal plus secondary shoots length
LA: Leaf area per plant

For the measurement of the leaf area (LA), 50 leaves were random-selected per plant and spread evenly between two plastic sheets. The area occupied by the leaves was drown onto the top transparent sheets, and measured using a portable area meter Li-COR model LI-3000A.

From trait data the following indices were calculated: leaf weight ratio (LWR: WLE/ WTOT); stem weight ratio (SWR: WST/ WTOT); root weight ratio (RWR: WRO/ WTOT); specific leaf area (SLA: LA/ WLE) and leaf area ratio (LAR: LA/ WTOT).

5.3 Results

5.3.1 *P. pectinatus* abundance in relation to disturbance and stress pressures.

Fig. 5.1 shows the abundance of *P. pectinatus* in the 114 sampled sites of Argentina in relation to the disturbance and stress indices calculated at each site. Fig. 5.2 show the same relationships than Fig. 5.1 but in the 46 sampled sites of Britain.

No relationship was found between the disturbance indices and the abundance of the species in Argentina (Fig. 5.1a). Note that few sites were surveyed in Argentina with intermediate values of disturbance (i.e. between 3 and 5 in the scale), and then is not possible to state if the species was present in abundance only in both disturbance extremes. Data from Britain show that an increasing disturbance reduced the presence and abundance of *P. pectinatus* (Fig. 5.2a). The species was found in a wide range of stress in both countries and no relationship determined (Fig. 5.1b and Fig. 5.2b),

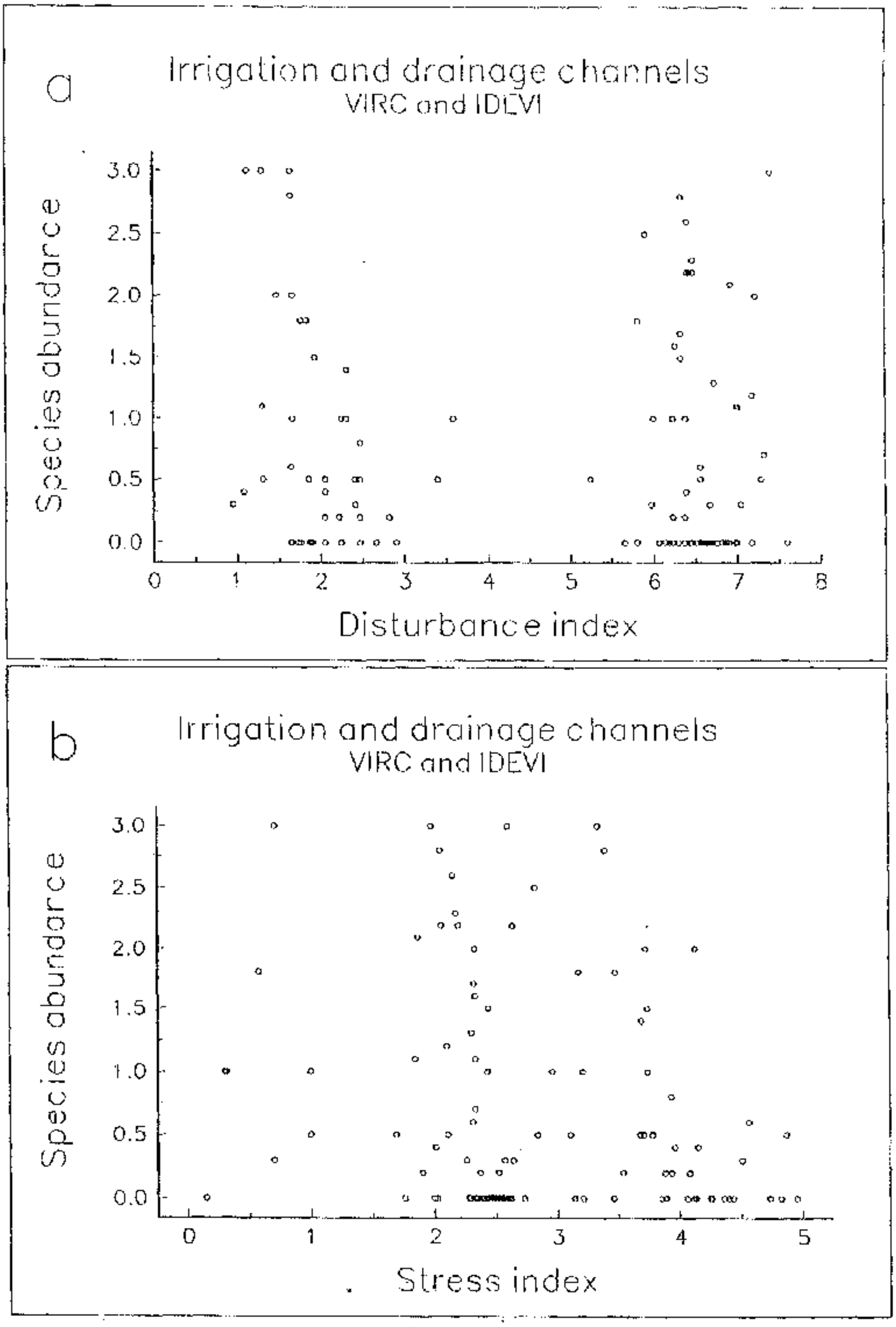


Fig. 5.1 Relationship between the disturbance (a) and stress (b) indices and the abundance of *P.pectinatus* in sites located in artificial channels of VIRC and IDEVI.

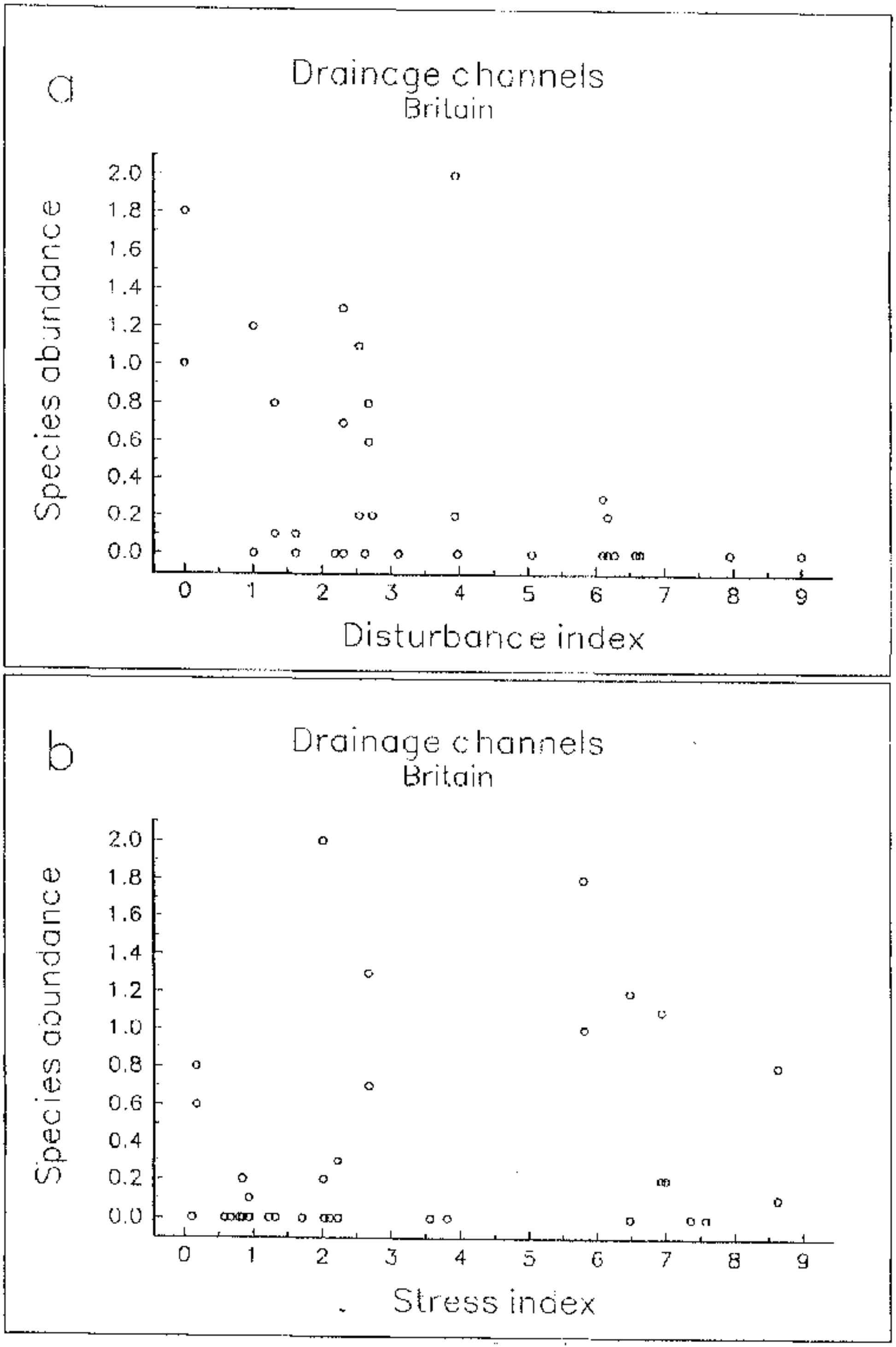


Fig. 5.2 Relationship between the disturbance (a) and stress (b) indices and the abundance of *P.pectinatus* in sites located in drainage channels of Britain.

even if it was absent or at low abundance at the highest values recorded in Argentina (Fig. 5.1b).

The abundance of *P. pectinatus* was related to the environmental variables measured during the surveys made in Argentina and Britain. Fig. 5.3a shows that water conductivity appears as the variable that explain best the distribution of *P. pectinatus* in VIRC and IDEVI: the plant was found in abundance in sites where water conductivity was lower than approximately 7000 $\mu S.\ cm^{-1}$.

Water depth limited the abundance of *P. pectinatus* in Argentina and Britain (Fig. 5.3b, Fig. 5.4a). At water depths lower than approximately 30 cm, the species was found at low abundance in VIRC and IDEVI (Fig. 5.3b) and was not found in drainage channels of Britain (Fig. 5.4a). Water fluctuation explains as water depth the distribution of *P. pectinatus* in Britain, being the species absent in sites with high water fluctuations through the season (Fig. 5.4b).

5.3.2 *P. pectinatus* morphological traits in relation to the disturbance and stress pressures.

Table 5.1 indicated the means of the four morphological traits recorded in Britain and Argentina at each site. Table 5.2 shows the total above-ground plant weight (WAG) of the species in each system, and also the fraction of the WAG allocated to stems (STWAG), leaves (LEWAG) and spikes (REWAG).

No differences (t-test; $p \leq 0.05$) were found between plant traits measured in irrigation channels, drainage channels of Argentina and in

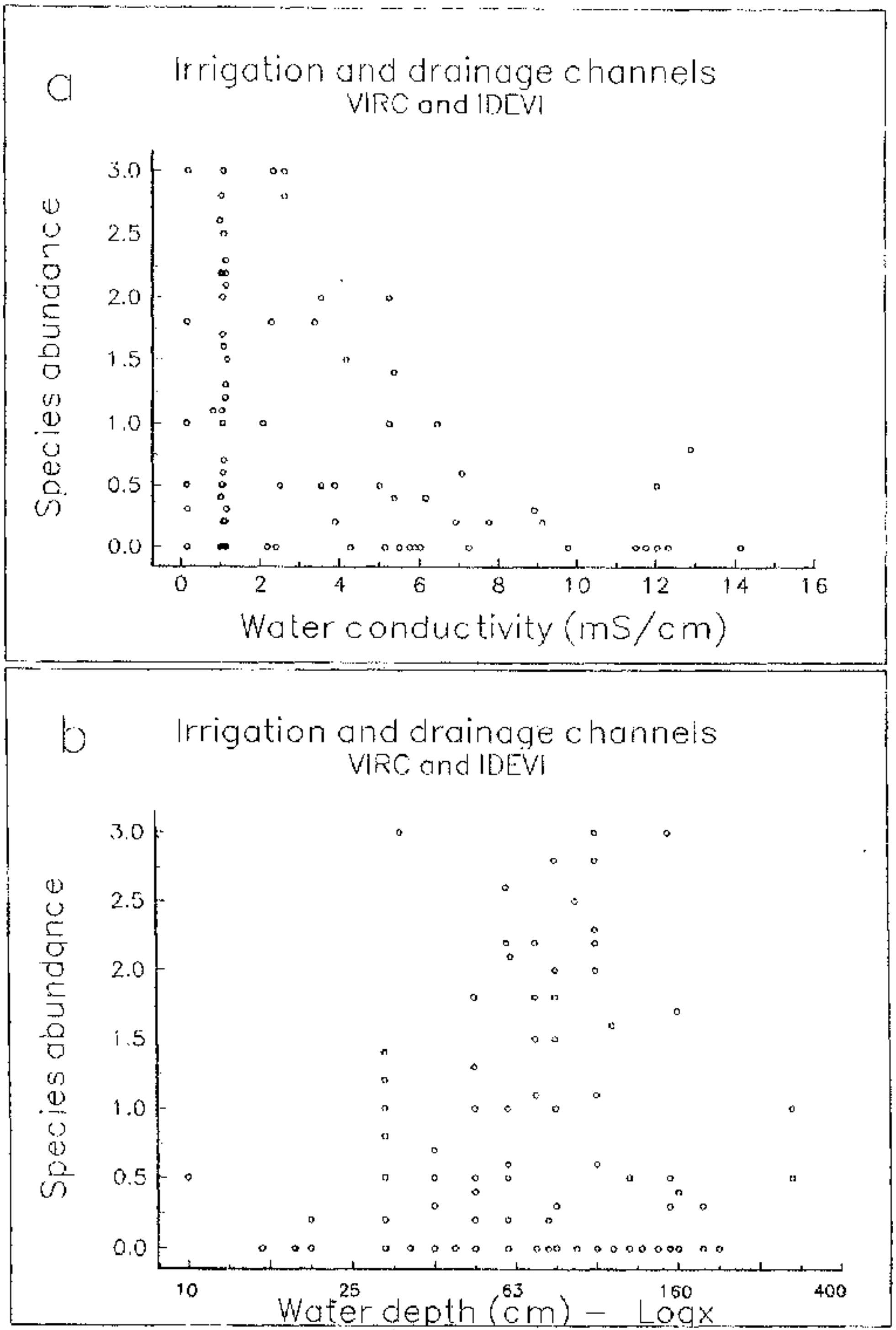


Fig. 5.3 Relationship between water conductivity (a) and water depth (b) and the abundance of *P. pectinatus* in sites located in VIRC and IDEVI.

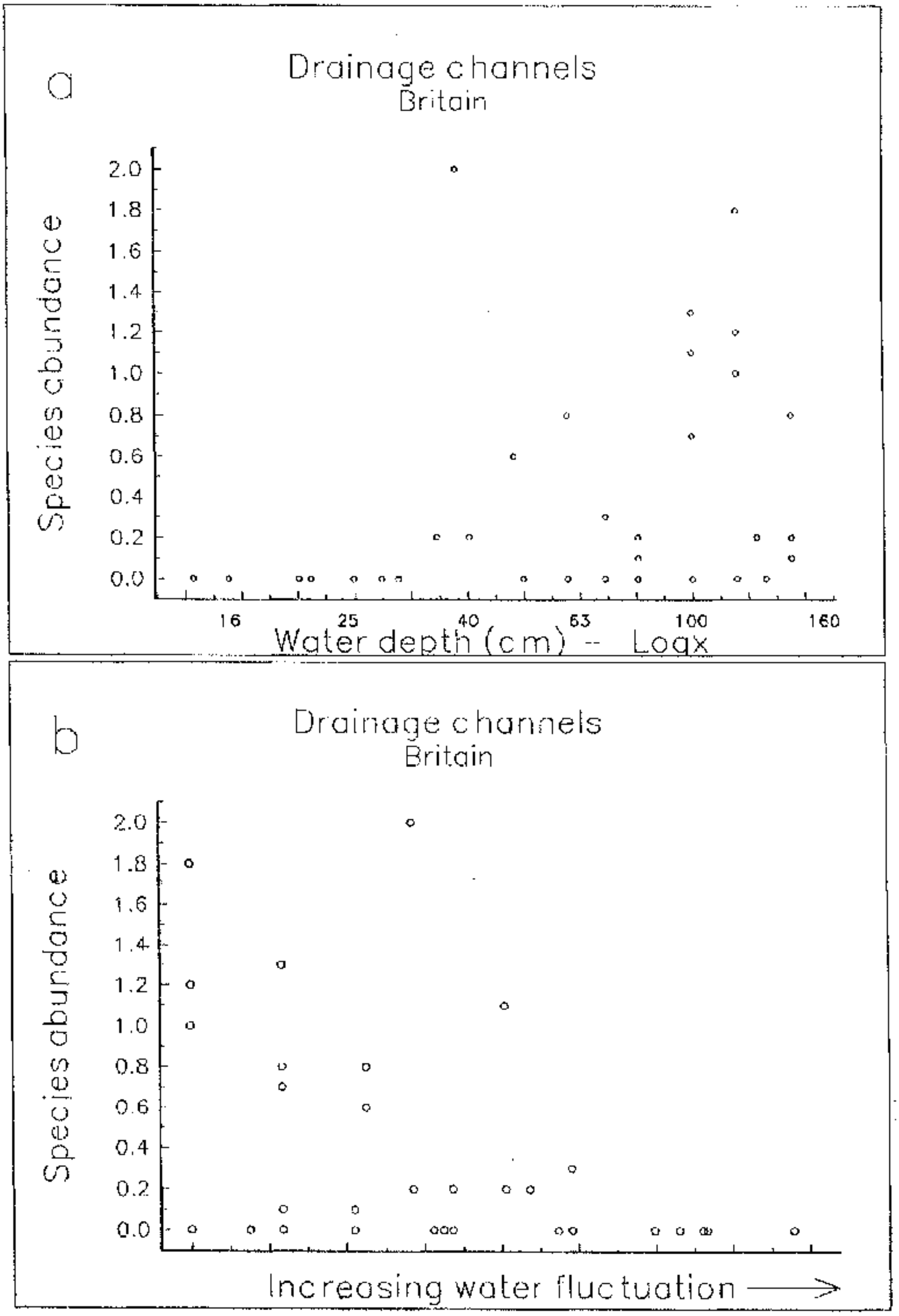


Fig. 5.4 Relationship between water depth (a) and water fluctuation (b) and the abundance of *P. pectinatus* in sites located in drainage channels of Britain.

Table 5.1. Morphological trait data for *P. pectinatus* in Britain and Argentina. Data are means ± standard deviation of three plants taken at each site. For trait codes see text.

Site code and Country	LEN	WST	WLE	WRE
I- 4 - Arg.	70.3 (± 3.8)	66.6 (± 17.6)	72.6 (± 24.4)	0
I- 6 - Arg.	113.0 (± 21.5)	119.6 (± 18.9)	205.0 (± 97.1)	3.0 (±4.0)
I- 13 - Arg.	106.6 (± 35.8)	182.3 (± 80.1)	162.3 (± 71.0)	12.7 (± 2.1)
I- 15a - Arg.	69.5 (± 22.3)	146.6 (± 85.6)	364.0 (± 230.5)	30.6 (± 26.3)
I- 15b - Arg.	71.6 (± 9.1)	80.6 (± 4.5)	174.6 (± 17.6)	52.7 (±24.2)
I- 29 - Arg.	44.6 (± 16.8)	80.0 (± 36.5)	191.3 (± 136.1)	23.6 (± 6.6)
I- 38 - Arg.	72.3 (± 18.2)	72.6 (± 28.4)	113.3 (± 75.8)	11.0 (± 17.3)
I- 49 - Arg.	92.5 (± 4.8)	116.0 (± 22.1)	82.0 (± 6.2)	25.7 (± 2.5)
I- 54 - Arg.	52.6 (± 13.5)	54.0 (± 24)	37.3 (± 28.4)	15.3 (± 9.9)
I- 56 - Arg.	105.0 (± 17.3)	255.0 (± 115.7)	322.2 (± 124.6)	46.0 (± 52.0)
I- 60 - Arg.	113.2 (± 3.5)	295.0 (± 58.7)	209.2 (± 74.6)	13.7 (± 16.5)
I- 103 - Arg.	68.3 (± 30.9)	66.0 (± 15.1)	166.7 (± 48.6)	6.3 (± 7.1)
IRRIGATION VIRC -IDEVI	81.6 (± 23.6)	127.8 (±78.8)	175.0 (± 96.2)	20.0 (± 16.4)
D 110	88 (± 25.9)	88 (± 21.6)	245 (± 42)	30.6 (± 35.1)
D 113	49 (±12.7)	32.6 (± 22.7)	52.6 (± 15.0)	0
D 114	90.0 (± 15.9)	103.5 (± 41.20)	103.5 (± 46.7)	0
D 112	128 (± 28.8)	766.5 (± 563.8)	569.0 (± 309.5)	49.0 (± 42.9)
D 61	99.0 (± 13.0)	86.6 (± 12.9)	95.3 (± 21.0)	19.7 (± 10.6)
D 68	130.3 (± 62.5)	155.7 (± 120.7)	179.0 (± 70.8)	1.7 (± 1.5)
D 73	134.3 (± 9.6)	159.0 (± 123.4)	182.6 (± 120.8)	0
D 77	27.0 (± 3.6)	33.3 (± 16.1)	61.3 (± 24.5)	0
D 76	42.0 (± 8.9)	161.3 (± 42.2)	167.6 (± 64.5)	0
D 78	47.3 (± 11.1)	77.3 (± 36.5)	142.3 (± 32.6)	11.7 (± 16.9)
D 81	14.3 (± 2.1)	116.6 (± 129.6)	86.6 (± 35.9)	0.7 (± 1.1)
D 85	190.3 (± 49.8)	269.3 (± 112.4)	317.6 (± 183.6)	0

Table 5.1. Cont. Morphological trait data for *P. pectinatus* in Britain and Argentina. Data are means ± standard deviation of three plants taken at each site. For trait codes see text.

DRAINAGE Argentina	86.6 (± 52.7)	170.8 (± 198.4)	183.5 (± 144.0)	9.45 (± 15.9)
F 1 - UK	38.0 (± 5.0)	25.3 (± 10.6)	28.0 (± 10.4)	0
F 3 - UK	97.5 (± 35.8)	93.6 (± 23.1)	73.5 (± 17.5)	0
F 4 - UK	62.8 (± 12.0)	52.5 (± 11.9)	30.0 (± 23.1)	1 (± 1.7)
F 10 - UK	91.6 (± 17.6)	87.5 (± 19.7)	126.5 (± 33.1)	37.6 (± 32.8)
C 6 - UK	88.5 (± 14.9)	146.0 (± 72.5)	127.0 (± 26.9)	0
C 9 - UK	70.5 (± 19.0)	286.0 (± 119.1)	261.0 (± 133.2)	2.0 (± 2.0)
SP 3 - UK	97.0 (± 38.8)	315.2 (± 175.9)	545.0 (± 167.5)	0
DRAINAGE Britain	77.8 (± 22.4)	143.7 (± 146.5)	170.1 (± 183.3)	5.8 (± 14.0)

Table 5.2. Growth parameter data for *P.pectinatus* in Britain and Argentina. Data are means ± standard deviation of site averages. For codes see text.

	WAG	STWAG	LEWAG	REWAG
IRRIGATION ARGENTINA	322.8 (± 162.7)	0.40 (± 0.11)	0.53 (± 0.12)	0.07 (± 0.05)
DRAINAGE ARGENTINA	363.7 (± 348.6)	0.43 (± 0.09)	0.54 (± 0.08)	0.02 (± 0.03)
DRAINAGE BRITAIN	319.7 (± 289.1)	0.48 (± 0.10)	0.49 (± 0.08)	0.02 (± 0.05)

drainage channels of Britain. When WRE was compared between systems, was considering only sites were spikes of *P. pectinatus* were present in the plants. Spikes were present in 91.7%, 50.0% and 42.8% of the plants sampled in irrigation channels of Argentina, drainage channels of Argentina and drainage channels of Britain, respectively.

No correlation was found between the disturbance or the stress indices and the four morphological traits. However, when the trait data of VIRC and IDEVI were correlated with each individual environmental variable, LEN was significantly correlated ($r = 0.707$; $p < 0.001$) with water depth in the linear simple regression model (Fig. 5.5a). Also, LEN was significantly correlated to the ratio $z_{eu}\ d^{-1}$ ($r = 0.608$; $p < 0.01$) in the same regression model. Both environmental measures, specially $z_{eu}\ d^{-1}$, are related to light availability (2.2.3.1).

5.3.3 Response of juvenile plants of *P. pectinatus* to shade (EXP. 1).

Fig. 5.6a and Fig. 5.6b show the dry weight of below-ground, leaves and stems in juvenile plants under different light-regimes, after 34 and 97 days of planting, respectively. After 34 days maximum light attenuation affected the formation of leaves (Fig. 5.6a), with a significant reduction of 64.3 % in WLE. After 97 days, at 30 % full-light all the measured traits (WRO, WLE and WST) were significantly reduced in 91.6%, 63.8% and 86.5%, respectively (Fig. 5.6b). At 60 % full light, there were no significant differences in the measured traits after 34 days, but after 97 days light attenuation significantly reduced WRO by 53.2 %.

At every date, no significant differences (Tukey test, $p \leq 0.05$) were found in plant length (LEN) between treatments (Fig. 5.7a). However, and using the same statistic test, differences were significant between treatments in total plant weight (WTOT) after 97 and 122 days (Fig. 5.7b). The evidence suggests that the plants showed significantly reduced growth under the shade treatments when WRO, WLE, WST and WTOT were considered, but plants did not show changes in LEN at every light exposures.

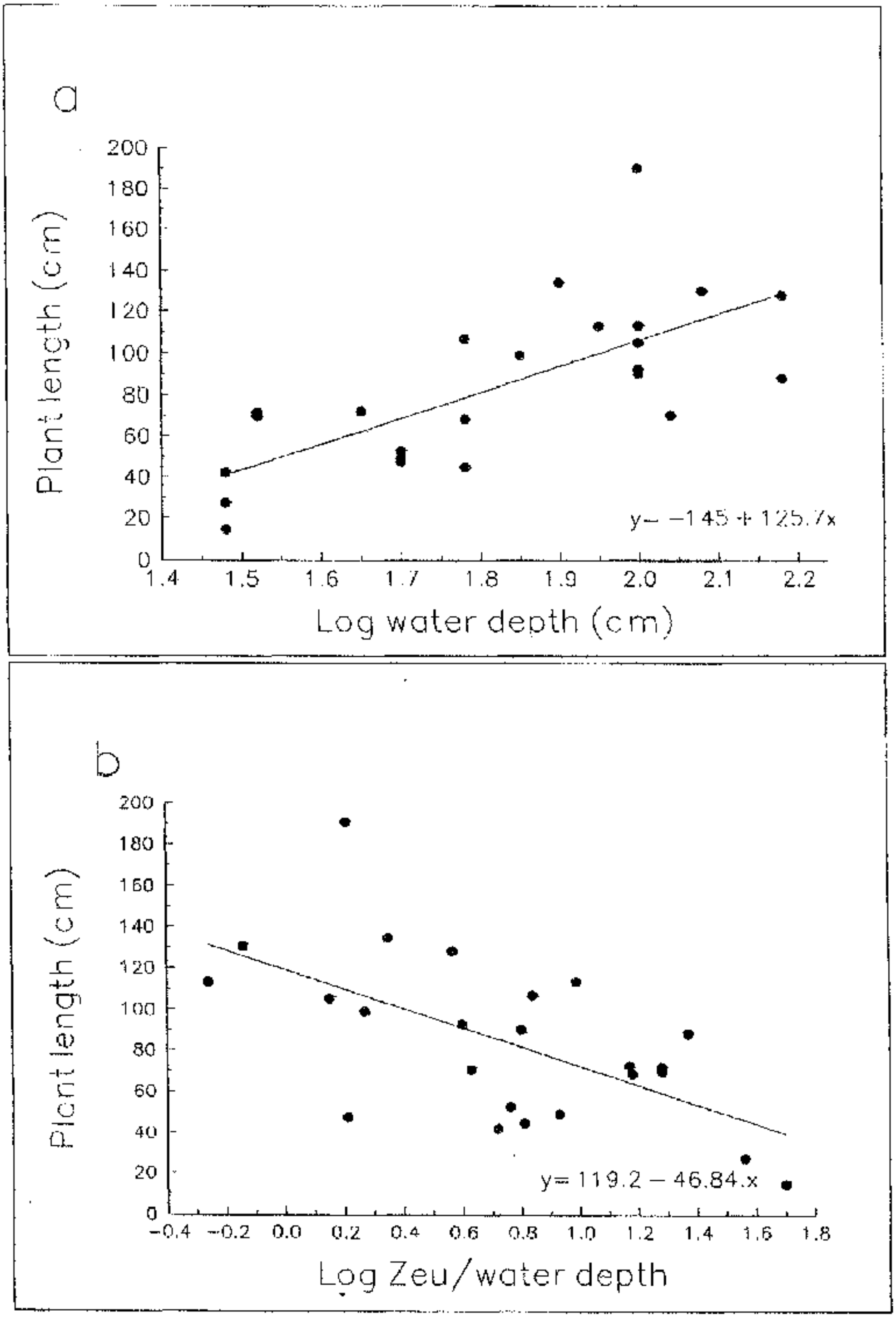


Fig. 5.5 Simple linear regression between water depth (a) and the ratio euphotic depth to water depth (b) and the plant length of *Potamogeton pectinatus* in artificial channels of VIRC and IDEVI. For more information see text.

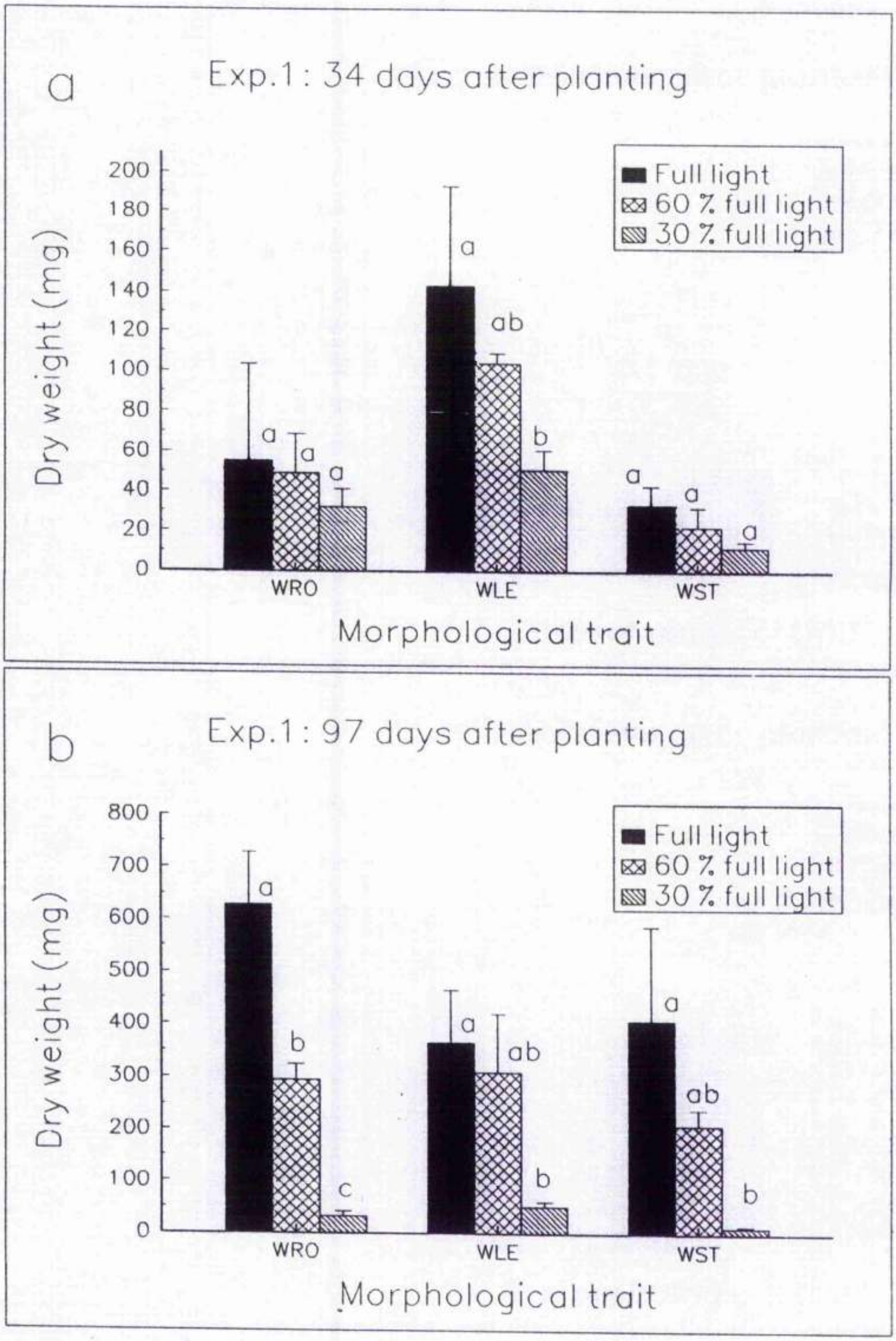


Fig. 5.6 Changes in the weight of below-ground (WRO), weight of leaves (WLE) and weight of stems (WST) under 3 light regimes in EXP. 1, after 34 (a) and 97 (b) days after planting.

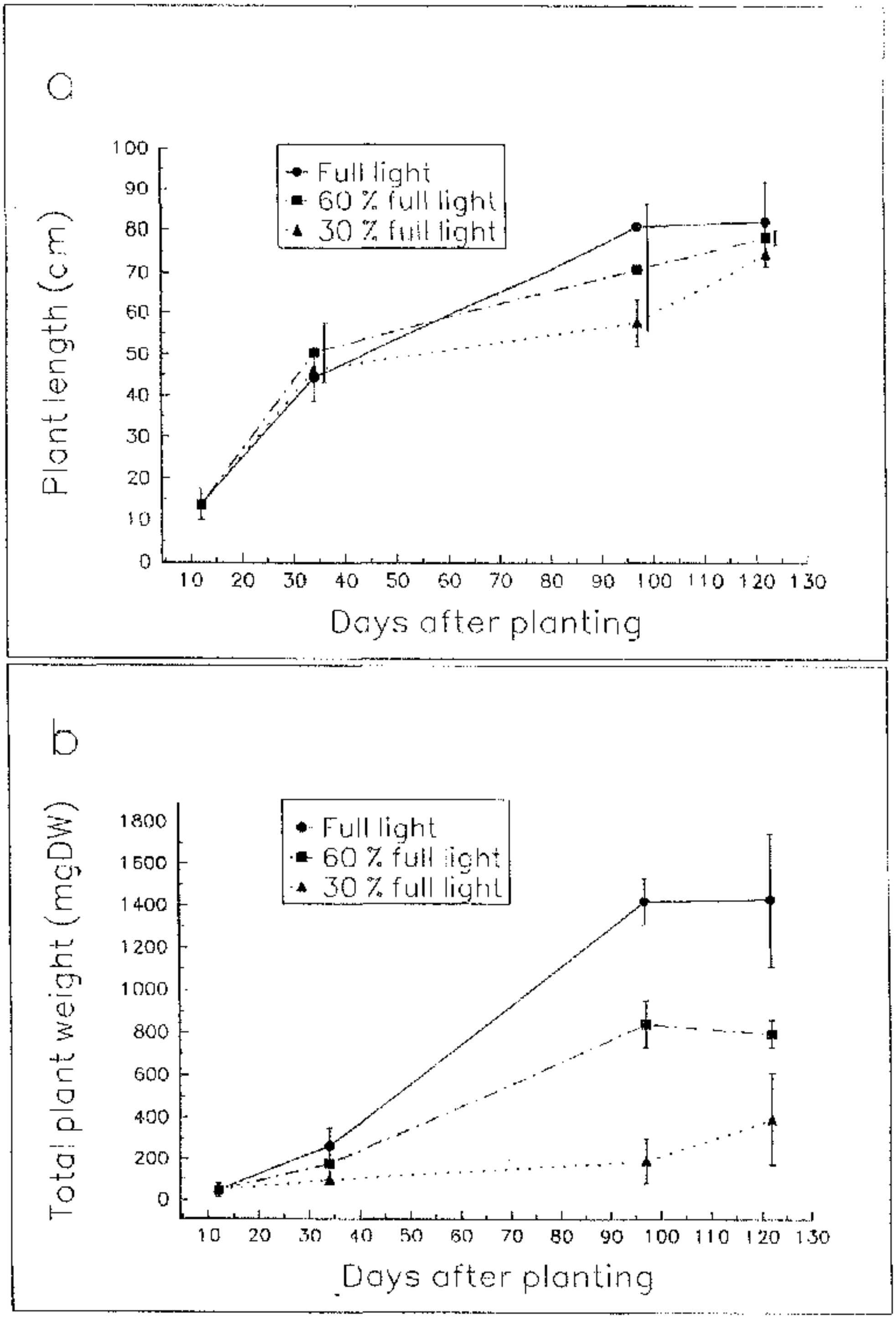


Fig. 5.7 Changes in the length of plants (a) and total plant weight (b) under 3 light regimes during EXP. 1.

Plants were able to flower under every treatment. After 97 days flowered 33 %, 19% and 9% of the plants that grew under full-light, 60 % full-light and 30 % full-light, respectively.

5.3.4 Response of adult plants of *P. pectinatus* to cutting and shade (EXP. 2)

There were no differences between morphological plant traits under full- light and 30 % full-light (Table 5.3). However, as a consequence of the reduction in total PAR, significant changes were found for specific leaf area (SLA) and for leaf area ratio (LAR), two important parameters of plant growth analysis (Evans, 1972; Table 5.4). SLA, the ratio of leaf area and leaf weight, was 46.8 % higher in plants under 30 % full-light. LAR, the ratio of leaf area and total plant weight, was 127 % higher in the light-reduced treatment. LAR is the product of a morphological component (SLA) and the leaf weight ratio (LWR), indicating the fraction of total plant weight allocated to the leaves.

Plants that were cut showed after 76 days significant reductions in number of secondary shoots (NSSH), weight of leaves (WLE) and stems (WST), total length of stems (TLEN) and total plant weight (WTOT). Differences were no significant in weight of below-ground biomass (WRO), plant length (LEN), leaf area (LA), percent of flowering (%FLO) and in all the plant growth parameters calculated (Table 5.3). Results suggested that after the disturbance made on the plants the main shoot recuperated after approximately two months, but there was a significantly reduction in the formation of secondary shoots. The presence of more secondary shoots in the undisturbed plants, resulted in higher values of biomass and total length.

There were no significant differences between the cutting treatments under full and reduced light, and then the recovery of *P. pectinatus* emerge not related to the total PAR available.

Fig. 5.8a and Fig. 5.8b show differences in plant length and in total plant weight during EXP. 2, respectively. Certainly, the recovery of the plants after cutting were very affected in terms of plant biomass, but not in the growth of the principal shoot (LEN). Plants that were disturbed reached the same length of plants that were not cutting.

If it is compare the absolute growth rate (in dry weight terms) of the plants of EXP. 1 and EXP. 2, it is clear that the recuperation of the plants that were cut was slower that the growth of juvenile plants. Thus, if it is added WSH plus WLE (weight of the above-ground part) in EXP. 1, juvenile plants grew under full light in a rate of 7.95 mg. day^{-1} during the first 97 days. On the other hand, in EXP. 2 and under the same light regime, plants that were disturbed grew during the first 76 days on a rate of 2.69 mg. day^{-1}. Thus, the rate of the regrowth represented 33.8 % of the growth of juvenile plants.

Table 5.3. Morphological trait data for *P. pectinatus* after 76 days of experiment set up in EXP. 2. Data are averages of three replicates. Each replicate result from the mean of three plants, except WTOT that result of the mean of 10 plants. Means labelled in columns with different letters (a,b) are significantly different (tukey test, t-test; $p \leq 0.05$). For trait codes see text.

	LEN (cm)	NSSH	WLE (g)	WST (g)	WRO (g)	NLEA	TLEN (cm)	WTOT (g)	LA (cm^2)	LWR	SWR	RWR	SLA $m^2.kg^{-1}$	LAR $m^2.kg^{-1}$	FLO %
Full light	89.66 (± 16.75) a	21.33 (± 5.24) a	0.264 (± 0.04) a	0.336 (± 0.08) a	0.542 (± 0.09) a	316.33 (± 55.29) a	820.10 (± 183.64) a	1.200 (± 0.17) a	94.88 (± 40.00) ab	0.236 (± 0.02) a	0.297 (± 0.03) a	0.461 (± 0.02) a	34.646 (± 92.28) a	7.982 (± 17.80) a	22.66 (± 15.53) a
Full light, cutting	82.21 (± 34.18) a	6.22 (± 2.71) b	0.115 (± 0.05) b	0.090 (± 0.06) b	0.241 (± 0.17) a	129.66 (± 54.23) b	250.44 (± 64.35) b	0.522 (± 0.28) b	51.20 (± 2.23) a	0.310 (± 0.16) a	0.199 (± 0.02) a	0.490 (± 0.17) a	48.249 (± 153.80) ab	15.557 (± 112.62) ab	22.85 (±35.71) a
30% Full light	85.10 (± 0.38) a	15.0 (± 0.33) ab	0.277 (± 0.02) a	0.212 (± 0.01) ab	0.292 (± 0.12) a	321.44 (± 23.62) a	764.10 (± 49.57) a	0.954 (± 0.22) ab	140.1 (± 21.17) b	0.357 (± 0.05) a	0.275 (± 0.05) a	0.355 (± 0.09) a	50.862 (±132.65) b	18.188 (± 46.26) b	9.33 (± 9.02) a
30% Full light, cutting	74.76 (± 17.92) a	8.45 (± 4.02) b	0.156 (± 0.08) ab	0.096 (± 0.04) b	0.229 (± 0.16) a	181.22 (± 96.54) ab	454.44 (± 232.27) ab	0.529 (± 0.248) b	81.14 (± 42.64) ab	0.344 (± 0.09) a	0.224 (± 0.05) a	0.438 (± 0.11) a	52.071 (± 80.50) b	18.36 (± 69.07) ab	12.66 (± 13.57) a

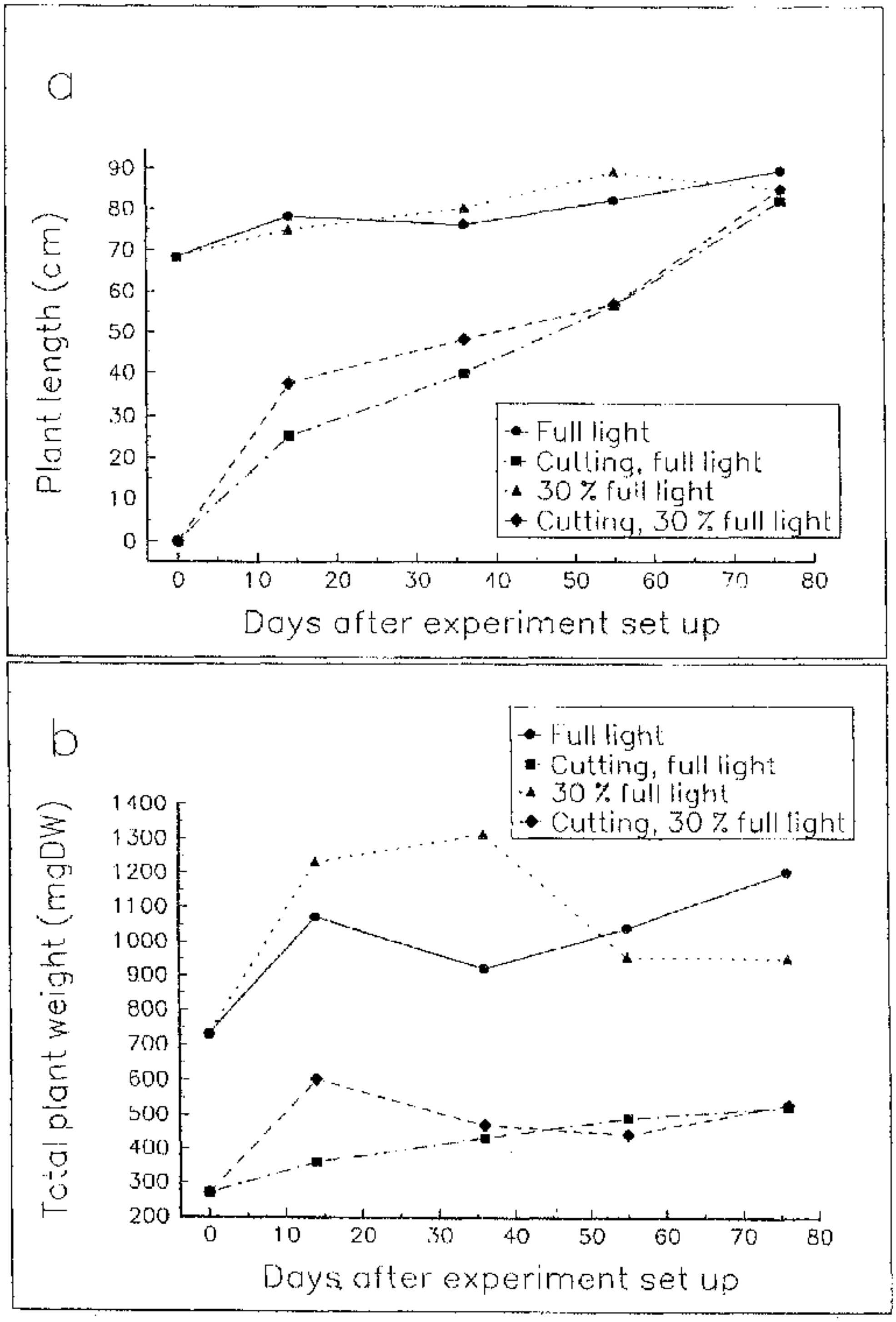


Fig. 5.8 Changes in the length of plants (a) and total plant weight (b) under four treatments that combined shade and plant cutting in EXP. 2.

5.4 Discussion

From Fig. 5.1 it is clear that *P. pectinatus* occurs in the drainage and irrigation channels of VIRC and IDEVI across a wide range of stress and disturbance. This indicates that the "intermediate" position of the species in the CCA diagrams of VIRC and IDEVI (Fig. 3.10 and Fig. 3.14) is a consequence of the broad ecological amplitude of the species. However, the distribution of the species in both areas of Argentina appears to be limited by water depth and water conductivity (Fig. 5.3). In British drainage channels, disturbance limited the growth of *P. pectinatus* (Fig. 5.2a), especially through water depth and water fluctuation (Fig. 5.4).

From the data of both countries, it seems that the species survives at water depth higher than 25-40 cm in the studied channels (Fig. 5.3b; Fig. 5.4a), which is within the previously reported depth limit range for *P. pectinatus* of 0.07 - 0.40 m. (Robel, 1962; Andersen, 1976; Kiørboe, 1980; Verhoeven 1980a, 1980b). In British drainage channels, a clear correlation was found between water depth and water fluctuation (Fig. 2.10). In Chapter II the disturbance effect of water fluctuation on submerged vegetation was ascribed to the physical damage to plant tissues produced by partial or total desiccation. A question arises on this point: is the limited distribution of *P. pectinatus* in relation to water depth, a consequence of the actual depth, or of changes in water level? Water fluctuation was not measured in VIRC and IDEVI, but levels fluctuate largely with rainfall and abstraction of water by farmers for crop irrigation. It may be that the effect of water fluctuation is similar to the disturbance effect provoke by wave action on the species in such other water bodies as lakes. Boltt *et al.* (1969) reported that *P. pectinatus* occurrence at selected water depths was influenced by wave disturbance.

Water conductivity higher than 7000 μS. cm^{-1} limited the distribution of the species in artificial channels of VIRC and IDEVI (Fig. 5.3a). This is equivalent to approximately 5.6 g. l^{-1} of total dissolved solids, according to studies made in waters of the channels of VIRC (Peinemann *et al.*, 1979). Several studies indicated the presence of *P. pectinatus* in a similar range of salinity (Haslam *et al.*, 1975; Getsinger *et al.*, 1982; Kautsky, 1987; Brock and Lane, 1983; Pip, 1987). However, other authors found the species also in more saline water, for example Sloan (1970): optimum between 1 and 15 g. l^{-1}, or Thorne-Miller *et al.* (1983): 4 and 15 g. l^{-1}. Kantrud (1990) found from an extensive review that world-wide *P. pectinatus* grows in natural waters with salinity up to 104 g. l^{-1}. In the waters of VIRC and IDEVI, the growth of the species is limited to relative low conductivity, probably being excluded from more saline waters by competition from other species better adapted to saline conditions (e.g. *Ruppia maritima)*. The replacement of *P. pectinatus*-dominated communities by *Ruppia*-dominated communities at increased salinity is well documented elsewhere (Verhoeven and Van Vierssen 1978a, 1978b; Spence *et al.*, 1979).

One difficulty when light attenuation is compared between artificial channels of Britain and Argentina is that the global insolation, and as a consequence the light PAR quantity, is quite different between the two countries. Using long-yearly average measured provided by the Royal Dutch Meteorological Institute, daily global insolation for the Netherlands was of 382 cal cm^{2} day^{-1} during summer time, (M. Hootsmans, personal communication). Roughly, Britain is in the same latitude and experiences the same average weather, and then it is possible to estimate a similar value. In Bahia Blanca, located approximately 110 km from the centre of the irrigation area of VIRC, daily global isolation during the summer time is 682 cal cm^{2} day^{-1} (P. Varela, personal communication). These data implicate that the total light energy received in the target area of Argentina is approximately double that in Britain. Comparisons of the average measures of sub-surface PAR taken during this study in drainage channels of Britain average 345 (± 297) μE. m^{-2} s^{-1}, and in the irrigation district of VIRC and IDEVI, 993 (± 394) μE. m^{-2} s^{-1}, also suggest a substantial difference between the two target locations. Simple comparison for water in % PAR attenuation values for water in British and Argentine channels would therefore be misleading because the absolute light energy involved is substantially different. More light energy is available to support plants at the same water depth and turbidity in an Argentina channel than in a British channel.

P. pectinatus growth can be greatly reduced by light attenuation caused by both organic and largely inorganic materials suspended in the water (Kantrud, 1990). However, it was found to have an intermediate to high tolerance to turbidity if it is compared to other submerged species (Reese and Lubinsky, 1983; Haslam, 1978). In a study of three submerged species, Barko and Smart (1981) found that all responded similarly to decreasing light through an increase in shoot length, a reduction in the numerical density of shoots, and the associated development of a canopy. These changes represent morphological adaptations to low light. The inverse relationship between shoot length and total PAR was also found in algae (Stross, 1979) and in several *Potamogeton* species (Spence, 1976; Spence and Dale, 1978). Fig. 5.5 shows that the same relationship was possible found in drainage and irrigation channels of VIRC, showing that the condition of light-limitation for plant growth is frequent in artificial channels of VIRC and IDEVI. Using the regression models of Fig. 5.5 is possible to estimate the length of the plants from field data on water depth (Fig. 5.5a) and water turbidity plus water depth (Fig. 5.5b).

In order to know if a plant could be consider a shade-tolerant species, it should have a higher capacity to maintain its relative growth with decreasing irradiance (Bjorkman, 1981). Vermaat and Hootsmans (1991) stated that in terms of maintenance of relative growth rates under low irradiance, *P. pectinatus* can be seen as a comparatively shade-tolerant. They postulated that most aquatic macrophytes are comparatively shade-tolerant, with some exceptions as *Potamogeton polygonifolius*, generally being restricted to open, shallow water habitats.

The experiments in the laboratory (Exp. 1 and Exp. 2) were made under very low light regime. Light quantity (PAR) under full-light just above the water surface was around 50 μE. m^{-2} s^{-1}, that is lower than the suitable level (between 300 and 1000 μE. m^{-2} s^{-1}) for the culture of most submerged species (Bowes *et al.*, 1977; Titus and Adams, 1979; Smart and Barko, 1984). Total PAR level used in experiments of light levels irradiance were for example between 100 and 1500 μE. m^{-2} s^{-1} (Barko and Smart, 1981; Barko *et al.*, 1984) and between 50 and 200 μE. m^{-2} s^{-1} (Hootsmans and Vermaat, 1991). The values registered at sub-surface level in the experiments represented between 2 to 13 % of the average light quantity received by the plants during the summer time in the channels of VIRC. The fact that juvenile plants were able to growth (and flowering) under those light conditions, and adult plants survive without significant changes in plant weight, are indicative of the strong tolerance to low light conditions of these specimens of *P. pectinatus*.

The response of juvenile plants to shade shows a strong reduction in biomass production (Fig. 5.7b) but not in plant length (Fig. 5.7a). In these plants, the significant reduction in the weight of leaves after 34 days (Fig. 5.6a), affected the biomass allocation afterward (Fig. 5.6b). However, the length of the plant did not varies between treatments, showing as above the typical adaptation to low light: the relative length promotion of the principal shoot.

In EXP. 2, the recovery of the species after cutting disturbance was poor taking into account the higher growth rates measured in juvenile plants. There were no differences between both light levels in the treatments where the plants were cut , showing that the PAR level influence was not important unless at these very low levels. Preliminary results measured in one irrigation channel of VIRC ("Puma") showed that after the application of the contact herbicide acrolein, the above-ground part of individual plants of *P. pectinatus* recovered with an average absolute growth rate of 7.8 mg. d^{-1} (D. Bentivegna, personal communication). This value is three times higher than the rate calculated in this laboratory culture in the cutting treatments (see 5.3.4). Field observations indicated that the species has a strong ability to recover quickly after cutting, but it is important to state the high difference in total PAR between the target channels and the experimental cultures.

The specific leaf area (SLA) calculated in this study for undisturbed plants growing under full-light was 34.64 m^{-2}. kg (Table 5.3), similar to 37.6 m^{-2}. kg reported by Sher-Kaul *et al.* (1995) for plants of *P. pectinatus* collected in Lake Geneva, Switzerland. The significant increases in SLA found in EXP. 2 in plants under 30% full-light, was also reported in several macrophytes in response to shade (Spence and Christal, 1970; Spence *et al.*, 1973; Stross. 1979). Apparently plants under light stress produce leaves with low investments in biomass. Differences in SLA can be ascribed either to morphological factors (thickness of the leaves, vein structure) or to the chemical composition of leaf biomass (Poorter and Remkes, 1990). Under the light-stress condition, *P. pectinatus* produced leaves with a high light-intercepting area per unit carbon invested.

Van Wijk *et al.* (1988) found marked intraspecific variation between populations of *P. pectinatus* with respect to several plant traits, as for example biomass production or shoot-length distribution. As is shown in Appendix III, consistent isoenzyme differences were found between the Argentine and the European populations of *P. pectinatus*. The plastic adaptation of this species to a range different habitat conditions, is indicative that the results found in this study for populations from Argentina, could hardly be generalised for other biotypes, such as European specimens, without comparative experiments.

It is important to remark that this chapter examined the regrowth of adult plants of the species after cutting (e.g. the established phase), and the strategy classification of Grime was made only for this phase. In irrigation and drainage channels there is important re-growth of the species after mechanical procedures from the tubers present in the sediment. This is probably the most important characteristic of the species that made it one of the more widespread weeds in disturbed areas as, for example, irrigation districts.

The wide range in which *P. pectinatus* occurs in relation to the stress pressures in the studied channels and the tolerance of the species to shade in the experimental cultures, suggests that the populations of *P. pectinatus* present in the target area have the S-element in its established-phase strategy. On the other hand, the apparent poor tolerance of *P. pectinatus* to water fluctuation and low water levels in target channels and the low tolerance to the disturbance cutting treatments imposed in the laboratory cultures, suggests an intermediate tolerance to disturbance of the established-phase of this species.

CHAPTER VI

RESPONSE OF *CALLITRICHE* AND *POTAMOGETON* TO CUTTING, DREDGING AND SHADE IN ENGLISH DRAINAGE CHANNELS.

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6.1. Introduction

Changes in standing crop and morphology provide useful measures of how submerged plants respond to pressures on survival. These pressures may be produced by the natural environment, or by human activities such as aquatic plant management operations. In this study was measured the response, in terms of standing crop and plasticity of selected morphological traits, of established populations of two submerged weeds, common water-starwort (*Callitriche stagnalis* Scop.) and curled pondweed (*Potamogeton crispus* L.), to disturbance treatments (manual cutting and dredging) and stress treatments (shade) in English drainage channels under field experimental conditions. The aim was to assess the survival strategy of the two species, in order to improve understanding of the vulnerability of these plants to different forms of weed control.

Starwort is widespread in shallow, disturbed freshwater systems, including small rivers, streams and man-made channels, in northern Europe (Soulsby 1974, Eaton *et al.* 1981, Newbold *et al.,* 1983, Haslam 1987, Murphy *et al.* 1990a). The established-phase strategy of starwort was given by Grime *et al.* (1988) as intermediate between ruderal (= disturbance-tolerant: D) and competitive ruderal (CD). Starwort is a plant which produces a rosette of floating leaves, with the rest of its photosynthetic canopy at or just below the surface (Sculthorpe 1967), a competitive trait in submersed macrophytes (Murphy *et al.*, 1990b). In drainage channels in Great Britain, *C. stagnalis*, together with the closely-related long-styled water starwort *Callitriche platycarpa* Kütz., were the indicators for a functional vegetation type characterised by high tolerance of disturbance (see Fig. 2.13). Similarly, in Dutch drainage channel systems, Pot (1993) observed that *C. platycarpa* was a dominant in submerged vegetation types that experienced regular disturbance from weed control by mowing bucket or cutting boat, repeated up to five times per year.

The established-phase strategy of curled pondweed was designated (using traits characteristic of lake populations of the species) as competitive disturbance-tolerant (CD) by Murphy *et al.* (1990b). The shade adaptation of curled pondweed is well documented (Nichols and Shaw 1986). This species causes weed problems both in its native European range (Murphy *et al.* 1990a) and as an introduced species in temperate regions of North America (Nichols and Shaw 1986, Anderson 1990, Steward 1990).

In British drainage channel systems, both starwort and curled pondweed are widely distributed, often abundant weeds, that persist as stable components of the submersed community. For example, Wade and Edwards (1980) found that both species had a consistently wide distribution in drainage channels in South Wales throughout the period 1840-1976, despite fairly substantial changes in weed control practice during that period. Both are dominant weed species, which cause substantial blockage of water flow, in the drainage channels of the Solway Drainage Area (DA) of north-western England, where was carried out the experiments reported here during 1993. Standard submersed weed control regimes used during the 1980-90s in the Solway DA used manual and mechanical procedures, on an annual basis.

6.2. Materials and Methods

6.2.1. Site descriptions

Two adjoining drainage channels, were selected in spring 1993 within the Solway DA in north-western England (3°15' W, 57°40' N). The experimental channels were typical for the area, being narrow, shallow and with reasonably clear water.

Site 1 (High Level) was located in a channel stretch (2 m wide; averaging 0.35 m deep during summer) with a mobile, soft sediment, mechanically-dredged annually in winter. Average water conductivity was 0.550 mS cm^{-1}, mean pH 7.6, and mean underwater light (as PAR) extinction coefficient, *k*, 3.20 m^{-1} (Moss 1988). A patchy, low-density submersed plant community was present, with well-separated stands likely to be experiencing little or no direct interspecific competition. Starwort was dominant at the outset, with occasional patches of small pondweed (*Potamogeton berchtoldii* Fieb.) and Canadian waterweed (*Elodea canadensis* Michx.). Emergent plants were sparse.

Site 2 (Low Level) had a width of 0.8 m and average depth of 0.2 m during summer 1993, with a thick , ochreous sediment, less mobile than that of Site 1. Average conductivity was 0.553 mS cm^{-1}, mean pH 6.4, and mean *k* 3.97 m^{-1}. The standard weed control regime was one-two manual clearances per summer. At the outset high-density beds of starwort, closely intermixed with beds of curled pondweed, were present throughout, with a much higher probability of interspecific competition effects than in Site 1. Emergent vegetation was absent.

6.2.2. Methods

An identical complete random design with three treatment replicates was used in both sites. The treatments were:

T1: Low shade stress (LSH): white geotextile material, producing on average 38.6 ± 2.4% attenuation of photosynthetically-active radiation (PAR) at water surface: measured in the centre of the treatment plot, using a twin-sensor SKYE SKP210 PAR linked to a SKYE Datahog SDL 2540 logger. Taking into account the value of *k*, and depth of water, light attenuation at the channel bed in Site 1 was calculated as 80.5% of above-barrier incident PAR, and in Site 2, 72.6%.

T2: High shade stress (HSH): black geotextile material, producing on average 91.6 ± 1.5% PAR attenuation, measured as above. Light attenuation at the channel bed was between 96 and 98% of above-barrier incident PAR in both sites.

T3: Cutting disturbance (CUT): manual control by scythe.

T4: Dredging disturbance (DRE): manual removal of plants plus sediment by shovel.

T5: Untreated (UNT).

Treatment plots comprised a 5 m stretch of channel, with intervening 5 m stretches left untreated as separators. Shade barriers used material stretched over a wooden frame 5 m long and the width of the channel, supported on wooden corner posts driven into the bank so that the material was positioned approximately 1 m above water surface.

Above-sediment weed standing crop samples were collected using a Lambourn sampler (Hiley *et al.* 1981) to remove all vegetation from 25 x 20 cm sample subplots, located in randomly-chosen beds of the target species within each treatment plot. In the laboratory samples were oven-dried at 90C prior to weighing. Sampling was undertaken on two occasions, 2 and 3 months after the experiment was set up, respectively in August and September 1993. Physico-chemical, management history and species differences ruled out direct statistical comparisons between channels of the effects of treatment on starwort (Hurlbert 1984). Standing crop data were initially analysed separately for each site, using ANOVA with mean separation by Tukey's test. There were no significant differences between sampling dates, so samples from the two visits were pooled for final analysis, to result in within-treatment replication of n = 6 for each site. Use of the term "significant" in the results and discussion below implies means different at $P \leq 0.05$ from Tukey's test.

Ramets of each species were collected for laboratory measurement of four morphological traits: above-sediment length of plant (LEN); individual stem dry weight (WST); dry weight of leaves per ramet (WLE) and leaf area per leaf (LA: measured with a Delta-T video leaf area meter). The data from the two sampling occasions were pooled and t-tests used to examine within- and between-site differences. Because the effects on standing crop of high shade were so intense, no trait data were collected for high shade treatments.

6.3. Results and Discussion

Standing crop response of plants to treatments is shown in Figures 6.1 and 6.2. Site 1 supported only about half (57%) as much submersed standing crop as Site 2 (comparing untreated control plots: t=2.52, p = 0.04), with a substantially lower probability of interspecific competition than in Site 2. Such differences between adjacent channels are common in the Solway DA: suggesting a substantial degree of habitat patchiness, a feature which is reflected also in the observed patchiness of plant distribution in the target channels.

When competitor plants were absent, in Site 1, low shade stress (LSH) significantly reduced starwort standing crop, by 53% compared to untreated control (Figure 6.1). Disturbance treatments (CUT, DRE) had a similar effect to LSH: reducing standing crop values by 55 - 65% below UNT control values. High shade stress (HSH) eliminated starwort within 2 months.

When competitors (curled pondweed) were present, in Site 2, the standing crop responses of starwort to CUT and DRE disturbance treatments were magnified, giving reductions of 90 - 95% below UNT control values (Figure 6.2). Again high shade stress had a very severe effect on starwort standing crop compared with untreated plots, but in this case low shade stress had no significant effect.

Curled pondweed, in the presence of competitor starwort plants, showed a standing crop response to stress and disturbance quite different from that of starwort. Shade (LSH or HSH) had no significant effect. Disturbance increased the standing crop of curled pondweed compared to untreated control, significantly so for CUT plots, which experienced a three-fold increase (Figure 6.2).

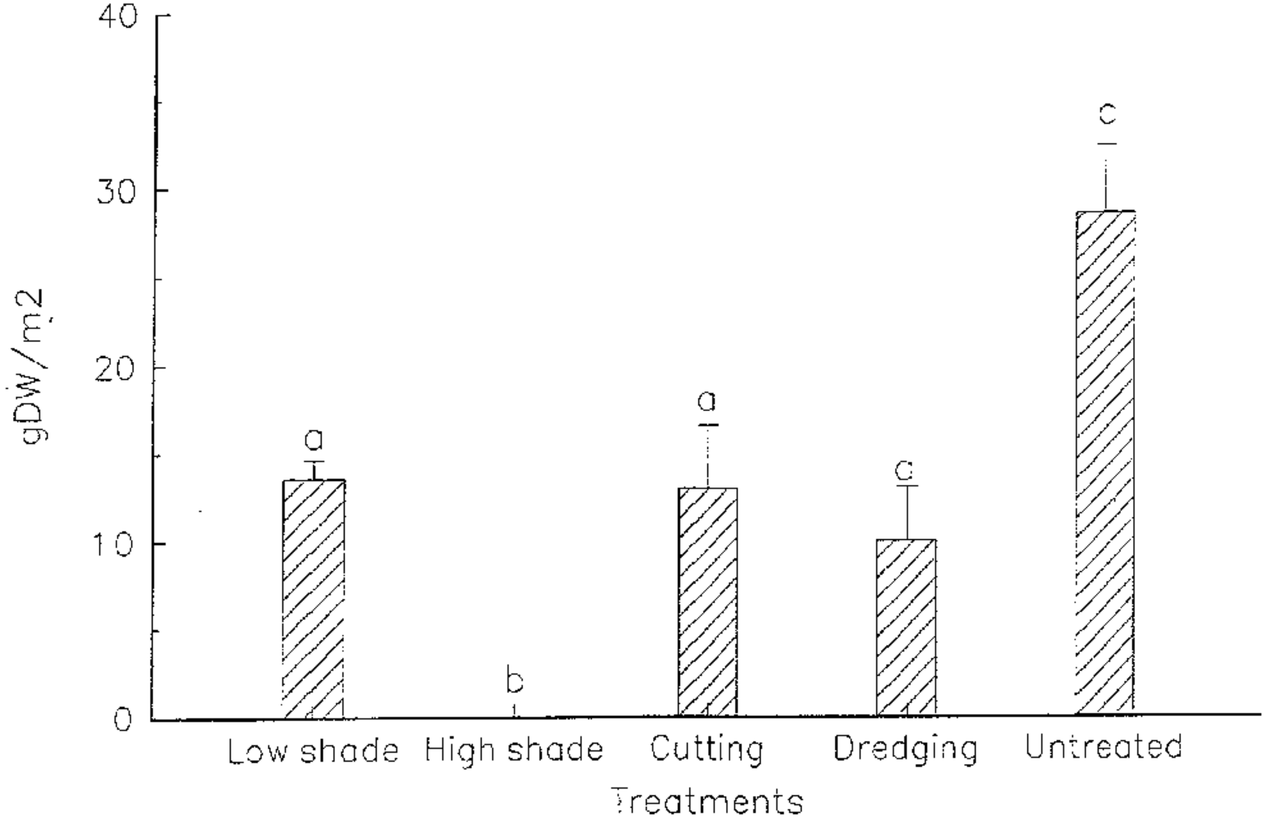

Fig. 6.1. Standing crop of *Callitriche stagnalis* in August - September 1993 in Site 1 (mean ± SE; n = 6 samples). Treatments labeled with different letters (a - c) are significantly different (Tukey's test; $P < 0.05$).

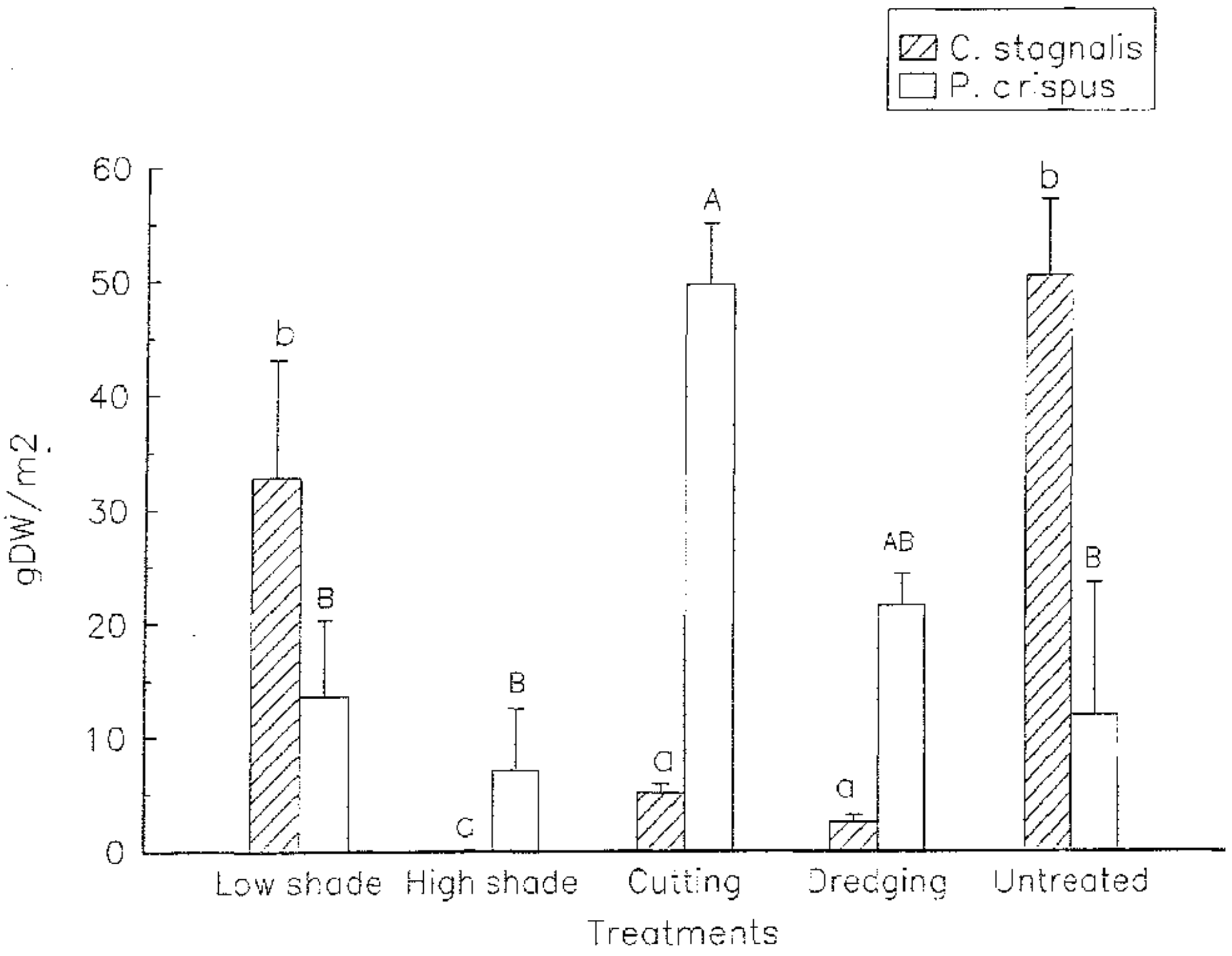

Fig. 6.2. Standing crop of *Callitriche stagnalis* and *Potamogeton crispus* in August - September 1993 in Site 2 (mean ± SE; n = 6 samples). Treatments labeled with different letters for each individual species (a - b; A - B) are significantly different (Tukey's test; $P < 0.05$).

Table 1. Morphological trait data[1] for starwort and curled pondweed populations in two drainage channels of the Solway Drainage Area, England.

Population	LEN	WST	WLE	LA
C. stagnalis Site 1	12.3 ± 1.01 (24)	4.2 ± 0.64 (24)	4.4 ± 0.48 (24)	0.30 ± 0.008 (80)
C. stagnalis Site 2	19.5 ± 0.92 (24)	7.62 ± 0.57 (24)	5.7 ± 0.33 (24)	0.34 ± 0.010 (80)
P. crispus Site 2	29.0 ± 1.62 (32)	42.9 ± 4.23 (32)	46.2 ± 5.2 (32)	1.56 ± 0.029 (110)

[1] LEN = above-sediment length of plant (cm); WST = individual stem weight (g); WLE = weight of leaves per stem; LA = leaf area per leaf (cm^2). Data are means ± standard error, with value of n given in brackets.

For both species, treatments had no significant effects on any of the traits measured in either Site 1 or Site 2. However, individual starwort plants from Site 2 (Table 6.1) were overall significantly longer (LEN), and significantly heavier (WST, WLE) than plants from Site 1, perhaps reflecting the more intense disturbance-history of Site 1. The trait data also show that curled pondweed plants were significantly longer, heavier, and had a higher LA than starwort plants (Table 6.1). Since weed control treatments caused no morphological trait changes for individual plants, the standing crop were probably produced by changes in ramet density.

In this study, low shade stress (LSH treatments) produced none of the typically-observed morphological responses of young submersed plants to shade (e.g. Vermaat and Hootsmans 1991; Tobbiesen and Snow 1984). The likely explanation is that shade stress produced by LSH treatments was not strong enough to produce such responses. The average sub-surface (0 m) PAR recorded in unshaded channels in north-west England during the course of this study, was 345 μE m^{-2} s^{-1} (range 48-960 μE m^{-2} s^{-1}). Even though the low shade treatments reduced these incident light values by a further 39%, it is probable that plants, with foliage at or close to the surface, rarely experienced shade stress from light levels as low as the 20 - 200 μE m^{-2} s^{-1} normally reported as necessary to produce morphological trait changes.

In North European populations of curled pondweed and starwort, the established-phase of the life cycle is in early to mid summer (Scotter *et al.* 1977; van Vierssen 1990). Results showing here demonstrated how phenology may be affected by management disturbance: removal of standing crop produced a strong regrowth response in curled pondweed in mid to late summer, but in starwort the standing crop showed no such recovery (Figure 6.1 and 6.2).

The results suggest that curled pondweed was outcompeted by starwort in non-stressed, undisturbed (UNT) conditions, but was much more tolerant of disturbance when competition from starwort was reduced by management treatments. It is possible that in the crowded conditions and shallow waters of the Site 2, populations of starwort may outcompete curled pondweed by overgrowing the deeper-water foliage of the latter. While the shade adaptation of curled pondweed may permit it to survive such conditions at reduced standing crop, it is only when the abundance of its competitor is reduced that curled pondweed can develop a large standing crop.

For submersed vascular plants minimum light requirement is often in the range 4 and 29% of incident light measured just below water surface (e.g. Dennison *et al.* 1993). In this study, when underwater light was reduced by 90%, starwort populations could not survive, but curled pondweed tolerated this stress better.

There were measurable differences in disturbance-tolerance between the two species: curled pondweed being the better disturbance-tolerator under the field conditions of the experiment. The starwort populations present in the experimental channels were better competitors than curled pondweed. The tolerance shown by both species to low shade in site 2 was not expected, but it may be that the treatments simply did not reach the intensity of shade needed to put the plants under significant stress. The results, suggesting that curled pondweed was slightly the more stress-tolerant, are in line with what was expected from the literature (Haslam and Wolseley 1981; Nichols and Shaw 1986)

The results of the experiment support the designation of established-phase strategy for both species as essentially between disturbance-tolerants and competitors, but with a minor stress element, stronger in the strategy of curled pondweed than in that of starwort. In starwort the competitive element emerged as stronger than in curled pondweed. Further work is needed to confirm the findings, but at least in relation to anthropogenic pressures on plant survival, this experiment suggests (using the terminology of Murphy *et al.* 1990b) the strategy of starwort as competitive disturbance tolerator, with a small element of stress tolerance: CD(S); and that of curled pondweed as a disturbance tolerator with smaller strategy elements of competitiveness and of stress-tolerance: (C)D(S).

From the practical management point of view, the results of this study imply that the disturbance-causing weed control measures used in the Solway DA at present will tend to favour species with stronger disturbance-tolerant strategies, such as curled pondweed. It is quite likely that the less-competitive curled pondweed is maintained and encouraged in the Solway DA system by the effects of the present weed control regime in reducing competition from starwort.

CHAPTER VII

OVERVIEW AND CONCLUSIONS

7.1 Survival strategies and functional grouping

When the data from Britain were analysed (Chapter II), the disturbance gradient separates two main TWINSPAN submerged species groups (Fig. 2.13). One was a large group that included 12 species and the other a smaller group with 6 species. The smaller group scored high in the disturbance gradient (see 2.3.3). Even though some species showed more tolerance to light limitation or saline intrusions, differences in the tolerance to stress were not a significant feature of the vegetation, and no groups were separate by this variable. The observed variation in the stress variable probably represents a range of habitats in which stress is low in absolute terms.

Since the two species groups were indicative of different combinations of disturbance pressures, each plant community may be defined as different functional groups present in drainage channels of Britain. As functional groups, differences between them should be expressed as differences in the strategy traits of the species that belong to each group (see 1.2.6). On Fig. 2.13 is overlaying the strategy type given by Grime *et al.* (1988) and by Murphy *et al.* (1990) for most of the recorded species, showing that they have a similar established-phase survival strategy, particularly in relation to competitiveness and disturbance-tolerance (CD). Thus, the six species that cover the most disturbance-tolerance group A (Fig. 2.13) were CD or variant of this, but also the 12 species that belong to the other group (less disturbance-tolerance).

Therefore, this thesis has identified a problem in the use of the strategy terminology put forward by Grime (1979) to classify and distinguish functionally defined groups of species of closely-similar established-phase strategy (here, mainly variants of CD). The two functional groups determined in drainage channels of Britain show clear differences in their tolerance to disturbance (especially management regime and water fluctuation), and then is possible to suggest a number of guidelines for management. However, a more precise and detailed description of sub-categories of plant strategies appears to be necessary for identified these groups in functional terms. Probably, the best way for determine that sub-categories is the experimentation, and was explored in Chapters V and VI.

Standardised-field experiments have the advantage over multivariate analysis that all the environmental variables correlated to the variable of interest could be standardise and then have not influence in the analysis. In Chapter V, a field experiment was performed to examine the response of populations of the submerged species *Callitriche stagnalis* and *Potamogeton crispus,* to disturbance (manual cutting and dredging) and stress treatments (shade) in drainage channels in the Solway Drainage Area. These two species scored high in the disturbance variable in the CCA analysis performed with data from Britain, and both were included in the same functional group (see Fig. 2.13).

Results of the experiment showed that, although the survival strategy of both plants is essentially similar (competitive-disturbance tolerators: CD) *C. stagnalis* was the more competitive of the two species, while *P. crispus* tolerated disturbance and stress better. Also in the CCA analysis, *P. crispus* appears as more disturbance-tolerance than *Callitriche* (see Fig. 2.9, Fig. 2.11 and Fig. 2.13). it is interested to point out that, two very close species in terms of survival strategies were clearly separated in the experiment, and sub-categories defined: *P. crispus* as (C)D(S) and *C. stagnalis* as CD(S), (See 6.3). Also in experiments carried out in the laboratory with *Elodea* *canadensis* and *Myriophyllum spicatum,* was found that, although the broad categorisation of "competitive-disturbance tolerators" is probably correct for the two species, it is possible to demonstrate significant differences in terms of response to disturbance and competition (see Additional paper: Response *of Elodea canadensis* Michx. *and Myriophyllum spicatum* L. to shade, cutting and competition in experimental culture).

In the literature, the general established-phase of *Potamogeton pectinatus* is related to competitiveness and disturbance-tolerance, even though appears to be associated also to stress-tolerance (see 5.1). In the multivariate analysis made with data from Britain and Argentina, the species appeared with intermediate tolerance to stress and disturbance, and belonging to the less disturbance-tolerance group (Fig. 2.13, Fig. 3.12 and Fig. 4.5). In Chapter V, specimens of the species from the area of VIRC, were grown under controlled laboratory conditions in order to determine its tolerance to disturbance (cutting) and stress (shade). Results suggest that *P. pectinatus* has the S element in its established-phase strategy, and an intermediate tolerance to disturbance.

In drainage and irrigation channels of VIRC and IDEVI, the system is characterised by a low submerged plant diversity, with eight angiosperm species recorded during the survey. From these species, *Potamogeton pectinatus, P. pusillus, Ceratophyllum demersum* and *Zannichellia palustris* have been identified in the literature as CD (Murphy *et al.*, 1990), *Chara* sp. as CSD (Murphy *et al.*, 1990) and *Ruppia maritima* as CS (Kautsky, 1988), being the other species unclassified in the current bibliography. Thus, as in drainage channels of Britain, species have close-similar established-phase strategy (mainly variants of CD). The exception is *Ruppia maritima* that, in agreement with Kautsky (1988), appears related in this study with low disturbance and high stress (see Fig. 3.12).

The low species diversity, the lack of enough information on the strategy type of some species (for example *Potamogeton illinoensis*), and the similar strategy type showed for most of the species, turn difficult to characterise functional groups from the established-phase strategy of the species included in them.

Four species groups were separate in VIRC and IDEVI by the disturbance and stress variables (Fig. 3.12). Group I (that comprises charophyta) and Group II (*Potamogeton pectinatus* and *P. pusillus*) showed a disturbance-tolerance strategy, with intermediate tolerance to stress. Group III (*Ruppia maritima* and *Zannichellia palustris*) appears as stress-tolerants, and Group IV *(Elodea callitrichoides, Ceratophyllum demersum, Potamogeton illinoensis* and *Myriophyllum aquaticum*) is clearly related to non stress conditions, but it is not homogeneous in its tolerance to disturbance.

As in drainage channels of Britain, the analysed data shows that the submerged vegetation present in artificial channels of VIRC and IDEVI have specific adaptations to the environmental that permit to separate functional groups. Results suggest that, even though the characteristics of these open channels are similar, differences in stress and disturbance (conductivity, winter drought, management, water depth), affect the composition and abundance of the channel plant community. However, the ecological amplitude of some species is broader than the actual species occurrence in the area. Difficulties in the dispersion of some species owing to the relative short existence of these man-made water bodies, and the isolation of the system from other river catchment areas, are probably other causes that affect plant distribution.

In Chapter IV, mixed data on plant composition and abundance from Britain and Argentina was analysed together. Only four submerged angiosperm species were common to both countries, and thus the species **TWINSPAN** groups were divided largely (but not entirely) by a geographical pattern (Fig. 4.2).

Fig. 4.5 is a clear picture on the relationship between all the surveyed submerged species and the two broad external factors that affect plant growth. If the **TWINSPAN** groups of above are overlapping in Fig. 4.5, it is possible to see that, regardless of the different species taxonomy, functional groups that belong to different countries are similar in terms of their tolerance to stress and disturbance. About stress tolerance, Fig. 4.5 displays 15 taxa showing low tolerance, 3 high tolerance and 4 intermediate tolerance to that variable. Stress appears as an important factor in determining species distribution only in Argentina, feature clearly showed in Fig. 4.6b. On the other hand, the disturbance variable explains species variation in both countries (Fig. 4.6a), Charophyta, *Potamogeton crispus, P. pusillus* and the moss *Rynchostegium riparoides* being the most tolerant, especially to management, water velocity and water fluctuation.

As was stated before (see 1.2.6), an alternative way to classify vegetation in functional terms is on the basis of plant attributes. Several studies on the relationship between aquatic plant traits and the environmental have been undertaken, as for example Hills *et al.* (1994) and Abernethy (1995). In this study, three morphological plant traits were measured in every submerged plants: length of plants, weight of stems and weight of leaves. It was difficult to construct groups from the data, because there were an evident gradient in the measures (see Fig. 4.7). However, clustering using TWINSPAN analysis at level 1 (eigenvalue = 0.30) differentiated "small" from "big" plants. These morphological plant groups were only partially related to the functional groups showed above: if it is overlay these groups on the CCA diagrams made with data of Britain (Fig. 2.13), data of Argentina (Fig. 3.12) or mixed data from both countries (Fig. 4.8) is possible to see that "big plants" are not located in the stress or disturbance extremes, but also that "small plants" are located everywhere along the stress and disturbance variables. This is clearly shown in Fig. 4.9, where the above-plant weight was related to the disturbance and stress projections of the species scores on the stress and disturbance axes: no big plants are present on its extremes.

Van Wijk (1989) stated that because of several complicating factors, the classification of water plants into general strategy concepts is still largely speculative. The presence in abundance of "big plants" in sites where the environmental was more suitable for plant competition (sensu Grime), agrees with current literature on terrestrial and aquatic plants (e.g. Grime *et al.*, 1988; Gaudet and Keddy, 1988; Hills *et al.* 1994). Results suggest the possibility of found functional groups in submerged vegetation from classic-standardised ecological measures (e.g. plant length or plant weight), showing that some traits that permit classified terrestrial plants in terms of their survival strategy, are useful also for classified submerged plants.

7.2 Influence of anthropogenic and natural environmental factors on species community

The four drainage areas surveyed in Britain showed differences in their phisico-chemical environmental. For example, the trophic status of the Solway drainage area showed a mesotrophic feature, rather than eutrophic as the others (see Table 2.2). The measured parameters during this study also shown important differences between drainage areas. When the data recorded in the Fens and the Crossens was contrasted with the data taken in the Solway area, former areas showed more water conductivity, more pH and less water fluctuation (Table 2.4).

These differences on environmental between drainage areas of Britain were important in the separation of the site groups in the TWINSPAN analysis, because it follows until level 2 a clear geographical pattern (Table 2.5 and Table 2.6). At level 1 the separation of the site groups was explained by several parameters (management, water fluctuation, water depth, conductivity and pH) but at level 2 the sub-groups of each group at level 1, appear especially separated by water fluctuation (Table 2.6).

Table 2.8 shows that when CCA analysis was performed using data from drainage channels of Britain, the first axis of variation was explained by several variables (water depth, water fluctuation, management, pH and conductivity) and the second axis by water fluctuation, light attenuation and management regime. When were selected the four variables considered likely contributed significant stress or disturbance on plant growth, practically the same species variation was explained (Table 2.9). Fig. 2.11 shows the importance of the management regime and water fluctuation on species distribution: both parameters explain similar species variation, showing some species high tolerance (*P. crispus*) whereas other low tolerance to these variables (e.g. *P. lucens*).

In the field-based experiment of Chapter VI, *P. crispus* was more tolerant to shade than *C. stagnalis*, and this agrees with the position of both species in the CCA analysis, when are contrasted the projections of the species scores on the "light attenuation" variable (Fig. 2.9). Light availability is one of the major factor that affects community composition and abundance of submerged plants, and come up as one of the environmental variables explaining species variation in drainage channels of Britain

The two irrigation districts surveyed in Argentina showed differences in environmental especially in water conductivity and water turbidity. Water of VIRC showed during the survey a variation of conductivity that ranged from 1000 μS. cm^{-1} (irrigation channels) to between 3000 and 14300 μS. cm^{-1} (drainage channels), whereas in IDEVI that values ranged between 160 and 6500 μS. cm^{-1} (Table 3.2). Water turbidity also showed higher variation in VIRC, being some channels with very high values, and as a consequence the calculated values of light attenuation (Table 3.3).

It is important to point out that both irrigation districts (VIRC and IDEVI) started officially approximately 35 years ago, and then the opportunities for plant colonisation and dispersion in the artificial channels have been minor than in drainage channels of Britain, that were most made centuries ago (see 4.4). Also, the short time that passed since the irrigation channels of VIRC have suitable conditions for submerged plant growth (since 1989, see 1.2.4), could cause that some species, from these channels or from other water bodies, have not reached the sites yet (see 3.4).

The seven TWINSPAN site groups selected for analysis, were clearly correlated to the measured environmental variables (Fig. 3.3). District areas (VIRC or IDEVI) and winter drought (= channel type: drainage or irrigation) were important sources of variation of the data set (Fig. 3.7). Channel type was a variable correlated with water conductivity (higher in drainage channels), water movement (higher in irrigation channels) and management regime (usually applied more frequently in irrigation channels). Besides these variables, water depth appears as the parameter that differentiated more the groups (Table 3.3). Between the site groups K and L, that comprised most of the drainage channels of VIRC, the only parameter that was statistically different was light attenuation, and this implicate that *Z. palustris* and *P. pectinatus* are species more tolerant to light attenuation than *R. maritima* and *C. contraria*, result that agrees with the literature. The group that included sites without vegetation, was statistically different to the others in water velocity (Table 3.3).

When CCA analysis was applied to the data from VIRC and IDEVI, water conductivity was the variable that best explained species variation on the first axis, followed by winter drought and water depth. In axis 2, variation was explained by water velocity, management and winter drought (Table 3.5). Some species appear clearly related to some environmental variables, and this is discussed in Chapter III (see 3.4). Examples are *C. demersum* and *Azolla sp.* with low tolerance to management and low tolerance to water movement, and *R. maritima, Enteromorpha flexuosa* and *Z. palustris* with high tolerance to high water conductivity.

Light attenuation explained few species variation in this analysis on axes 1 and 2, but was the variable best correlated to axis 3 (Table 3.5). As an adaptation to low light availability, submerged plants respond similarly through an increase in shoot length (see 5.4). The inverse relationship between shoot length and total PAR was found in plants of *P. pectinatus* growing in drainage and irrigation channels of VIRC and IDEVI (Fig. 5.5), showing that the condition of light-limitation for plant growth is frequent in these channels.

When mixed data of both countries were analysed together (Chapter IV), CCA analysis emphasises the importance of the management in determine species variation in Britain, and water conductivity in Argentina (Fig. 4.3). The Figure also shows that water depth explained an important part of plant variation in both countries, but few light attenuation. It is worth to point out that the comparison between light attenuation in both countries would be misleading because the absolute light received in the target area of Argentina is approximately double than in Britain (see 5.4).

7.3 Effect of management regime on submerged vegetation

The factor of major interest affecting submerged vegetation in this study was the management regime: if determined functional groups or submerged species would be correlated to determined weed control procedures, the information could be useful for the suggestion of a number of guideless for management. It was difficult in this study found a relationship between the different procedures with the existing vegetation at each site, especially because in several sites more than one management operation had been carried out during the three years before the survey. For this, the construction of indices that synthesise the intensity and frequency of the destruction of the plant biomass during that period was used for analysis.

As was stated above, in drainage channels of Britain the disturbance variable was strongly correlated to species composition and abundance. Even though a similar species variation was explained by other environmental factors (especially water fluctuation), it was clear that higher intensities and frequencies of weed control procedures have as a consequence two principal features: (a) an impoverish in the species diversity of the plant community and (b) the presence in abundance of a group of species adapted to severe conditions of disturbance. It is clear from Fig. 2.2 and 2.9 that species as *Potamogeton lucens* or *P. perfoliatus* are best adapted to drainage channels where the management regime is not heavy and not frequent, as for example based on the use of weed boats or manual weed rakes once during the season. On the other hand, the presence in abundance of species as *P. crispus* or *C. stagnalis* is indicative of a more frequent and intense weed control regime, as for example the application, three or more times during the season, of the combination of manual and mechanical weed control operations.

These last two species showed different tolerance to manual cutting and dredging in the field experiment showed in Chapter VI: both treatments significantly reduced the standing crop of *C. stagnalis*, but increased the standing crop of *P. crispus* compared to untreated control, significantly so for the cutting treatments.

P. pectinatus comes up as a species with low tolerance to management in Britain (Fig. 2.9 and Fig. 2.11) and with intermediate tolerance in VIRC and IDEVI (Fig. 3.10). The recovery of *P. pectinatus* after cutting in the experimental cultures was poor (Fig. 5.8), compared to field observations. However, total PAR light were very low in the experimental cultures, and plants growing under conditions of severe stress are likely to exhibit slow rates of recovery from defoliation (Grime, 1979).

In VIRC and IDEVI, the management regime was highly correlated to channel type. For example, in VIRC most of the irrigation channels received during the winter (water recess) a deep dredge with excavators, whereas most of the drainage channels were dredged every 3 - 4 years. Likewise, irrigation channels have faster water movement, lower water conductivity and they only have winter droughts. For this, it was difficult to separate the effect of the different environmental parameters and stated clearly the influence of management on species distribution. Furthermore, when mixed data from Britain and Argentina was analysed together, the management regime explained less species variation in Argentina than in Britain (Fig. 4.4a).

In this thesis, into the variable "management regime" was included only operations related directly to weed control procedures (see Fig. 2.2 and Fig. 3.4). In drainage channels of both Britain and Argentina, these procedures are the most important anthropogenic influence on plant growth. However, in irrigation channels of VIRC and IDEVI, water velocity and the winter water recess are factors that clearly affected vegetation and are under the control of the water management organisations. For this, channel management in its broad sense, that comprise all the human activities involved in the channel network organisation, explains an important part of the species variation (Fig. 4.5).

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APPENDICES

APPENDIX I

SUBMERGED PLANT SURVIVAL STRATEGIES IN RELATION TO MANAGEMENT AND ENVIRONMENTAL PRESSURES IN DRAINAGE CHANNEL HABITATS

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ABSTRACT

The abundance of submerged weeds, in relation to management regime and environmental factors, was surveyed during 1992 and 1993 in drainage channels located in four geographically-distinct areas of Britain. The aim of the study was to ascertain, using a multivariate approach, the degree to which species survival strategy and vegetation could be related to disturbance and stress pressures on plant survival.

Indices of disturbance and stress were constructed from combined environmental data for each site. A species ordination using Canonical Correspondence Analysis showed that the combined disturbance variable explained more of the variability that did stress. Two main groups of species could be distinguished. The larger group scored low on the disturbance gradient and these species, with different tolerances to stress (especially light-limitation), appeared to be those better-adapted to habitats with low disturbance (e.g. *Potamogeton pectinatus* and *Potamogeton lucens*). The smaller group comprised species which tended to occur in sites with higher disturbance (e.g. regular cutting) such as *Callitriche stagnalis*.

Using the terminology of strategy theory, most of the dominant species could be classed as "competitive/ disturbance tolerators (CD)" or variants of this established-phase strategy. The limitations are discussed of applying the strategy approach at species level in a defined habitat-type which shows a high degree of uniformity between sites, such as artificial drainage channels.

Grime (1979) classified the external factors which affect vegetation into two broad categories: stress (phenomena which restrict photosynthetic production), and disturbance (pressures causing partial or total destruction of plant biomass). In the aquatic environment, factors such as light availability, water level fluctuation, desiccation and management regime are examples of such pressures acting to restrict the survival of submerged plants (Kautsky, 1988; Murphy *et al.*, 1990; Nichols, 1991). Grime *et al.* (1988) included some submerged plants in describing the strategies of English plant species. For lake macrophytes, Murphy *et al.* (1990) attempted to produce a species-strategy classification using survival traits relevant to life cycle, morphology, regeneration and plant physiology.

A functional group of plant populations may be considered as a set of similarly-adapted species occurring together at one or more locations experiencing similar suites and intensities of stress and disturbance pressures. The application of strategy analysis to the submerged vegetation of drainage channels (which commonly experience widely differing aquatic weed control regimes) should lead to an improvement in knowledge of the relationship between functionally-defined groups of plants and the channel environment in which they occur.

The aim of this study was to ascertain the degree to which species survival strategy could be related to the disturbance and stress pressures present in British drainage channels, and to investigate the evidence for the existence of functional groups of channel plants which might be related to such pressures.

MATERIALS AND METHODS

Twenty four drainage channel stretches showing a broad range of environmental conditions and management regimes typical of this habitat in Britain were selected from four drainage areas: The Fens (10 sites, E England: 0°15' E, 52°40' N); Crossens (5 sites, W England: 3°00' W, 53°35' N); Solway (6 sites, NW England: 3°15' W, 54°50' N) and the Spynie Canal (3 sites, NE Scotland: 3°20' W, 57°40' N). In each stretch, a 50 m channel length (site) was sampled during 1992 and 1993 in early, middle and late summer. Sites were always sampled at least one month after the most recent weed control treatment. 10 random grapnel hauls were taken to sample submerged macrophyte species. Abundance of each species present per sample was rated as 1, scarce; 2, common or 3, abundant.

On-site electrometric measurement of underwater light (PAR) penetration was determined for each site on each sampling date using a twin-sensor SKYE SKP210 PAR linked to a SKYE Datahog SDL 2540 logger. Dissolved oxygen, pH, temperature and conductivity were measured using Hanna and WPA instruments. Additional water chemistry data were provided by the National River Authority (NRA Anglian Region, NW Region) and NE River Purification Board (Scotland). Information on management regime was provided by NRA (Ely, Crossens, Carlisle), Middle Level Commissioners (March) and the Maintenance Committee of the Spynie Canal.

Parameters likely to constrain the growth of submerged plant species were measured and transformed into a numerical index which increased with increasing pressure on plant survival, as follows:

(i) Water fluctuation: The coefficients of variation *cv* of the measures of water depth recorded during each visit, in both years, were transformed onto a 0-5 index, of equal-interval classes covering the full range of *cv* obtained. Water depth was correlated with water fluctuation and showed that shallow waters had maximum values. Water level fluctuation can affect both disturbance and stress (Kautsky, 1988), however we observed that high water fluctuation values occurred at sites that had very low water level during some weeks and a substantial loss of above-ground biomass. On these grounds, we considered that water level fluctuation was primarily acting as a disturbance in the channels studied.

(ii) Management: The management regime applied during the three years prior to sampling was subjectively rated on a scale of 0 to 5 as to the likely degree and timing of destruction of plant biomass (see Fig. 1).

(iii) Light attenuation: From the PAR data determined for each site on each sampling date, the average extinction coefficient k was calculated (Moss, 1988). The euphotic depth z_{eu}, at which about 3 % of the surface light still remains was then calculated as $z_{eu} = 3.51/k$, and the ratio of z_{eu} to average depth, d, determined. An increased value of this ratio suggested more light availability at the channel bed. The range of values calculated for the ratio was divided into a series of equal-interval classes to give an index on a scale of 0 - 5 for each site.

(iv) Other stress factors: These included saline intrusions, low oxygen, eutrophication and shade (from emergent plants or trees). Their likely effect on macrophyte survival was rated subjectively as low (1), medium (2) or high (3), and were summed for each site to give a 0 - 5 index range.

The disturbance index (I_D) was constructed as the sum of (i) plus (ii) and the stress index (I_S) as the sum of (iii) plus (iv).

Filamentous algae were included together, and treated as one taxon in the analysis: these included *Cladophora glomerata, Vaucheria dichotoma* and *Enteromorpha intestinalis*. Certain taxonomically-close vascular species, with marked similarities of morphological and reproductive survival traits were also combined as single taxa for the purposes of the analysis (see Fig. 3).

Field data on plant abundance were analyzed using TWINSPAN (Two Way Indicator Species Analysis; Hill, 1979). The vegetation-environment dataset was analysed with CCA (Canonical Correspondence Analysis; ter Braak, 1989) using CANOCO (ter Braak, 1988).

RESULTS

In total 40 euhydrophyte taxa were recorded from the target sites during 1992-93, including five filamentous algae, two bryophytes and one charophyte, the remainder being vascular plants. Of these, the 22 commonest, mainly submerged, taxa were included in the multivariate analysis. Excluded were species found at only one site and species with few occurrences located in sites with extreme conditions. We also excluded euhydrophytes with free-floating habit (e.g. *Lemna* spp.), or with most of their foliage above the water surface (e.g. *Hippuris)* because these were unlikely to be directly affected by the stress and disturbance pressures included in the I_D and I_S indices.

All the species recorded were included by Holmes & Newbold (1984) in the community group described as being typical of habitats which are "either base-rich or nutrient-rich, and usually both". The eutrophic condition of British drainage channels is shown by the nitrate concentrations in channel water recorded during summer 1993 at the study sites, which was in the range 1.4 - 13.5 mg. l^{-1}. The study sites showed a wide range of physico-chemical characteristics: pH (5.6 - 8.6); oxygen concentration (2.3 - 11.0 mg l^{-1}). Conductivity (252 - 2088 μS. cm^{-1}), with salinity intrusions at certain sites raising the maximum value to 3800 μS. cm^{-1}; water depth (0.14 - 1.50 m); z_{eu}/d (0.85 - 8.70) and fluctuation of water depth (*cv:* 5 - 86 %)

Fig. 2 shows the CCA ordination plot displaying site scores and arrows for environmental variables (ter Braak, 1988). The eigenvalues, an indication of the amount of inherent variability within the data set accounted for along a given principal axis, were 0.40 and 0.11 for the first and second axes, respectively. In addition, Fig. 2 indicates the sites included in both groups (I and II) in the TWINSPAN sample classification at level 1 (eigenvalue 0.44). In CCA, the first axis explained 79 % of the variance in the weighted average of the species scores, and the inter- set correlation of environmental variables with axis 1 was 0.87. To investigate whether the observed differences could be accounted for by pure chance the Monte Carlo permutation test was used in CCA (ter Braak, 1988). The 99-point random data set generated by random permutation all yielded a lower eigenvalue for the first axis and the overall analysis ($p \leq 0.01$).

Fig. 3 shows the diagram of the same CCA analysis of above but displaying the species scores. Overlaid on Fig. 3 are the strategy type for species given by Grime *et al.* (1988) and Murphy *et al.* (1990), together with the boundaries of TWINSPAN species groups (A and B) at level 1 (eigenvalue: 0.83).

Fig. 2 shows that I_D clearly varies along axis 1. Sites supporting macrophyte communities more resistant to the disturbance produced by water fluctuations and management regime were located to the right of the diagram. The gradient also follows a geographical pattern, indicated by the drainage area location of each site. This may be explained by the fact that within an individual drainage area a relatively uniform set of weed control procedures is used, and that environmental characteristics are likely more similar within than between geographically separated areas. Other environmental parameters that might also contribute to the observed gradient are average water salinity and pH. These parameters were not included in this study because the values we recorded were unlike to have contributed significant stress or disturbance to plant growth.

TWINSPAN analysis can classify both samples and species into groups based on species assemblage data only and is not, as in canonical techniques, constrained by the environmental data. I_D was found to explain most of the variation shown by TWINSPAN at level 1. The indicator species for the large group (I) are *Elodea canadensis* , *Elodea nuttallii, Ceratophyllum demersum, Myriophyllum spicatum,* and *Potamogeton pectinatus.* All these species are considered to be high-nuisance submerged weeds (Pieterse & Murphy, 1990). The indicator species for the smaller group (II) are *Callitriche* species. These species are noted for their survival in channels occasionally dry for short periods or in temporary pools and they also have a strong tolerance of management based on disturbance, such as cutting (Haslam, 1978; Grillas & Duncan, 1986). Grime *et al.* (1988) allocated a strategy type with a strong element of disturbance-tolerance to *Callitriche stagnalis.*

In Fig. 3, the small group A comprised *Potamogeton crispus, Potamogeton pusillus, Potamogeton berchtoldii, Zannichellia palustris,* and *Callitriche* spp. All these taxa scored high on the disturbance gradient, and are frequently mentioned in the literature as being disturbance-tolerant (e.g. Newbold *et al.*, 1983). The larger species group B showed more varied tolerance of disturbance, although most species scored much lower on the disturbance gradient than group A species (Fig. 3).

In Fig. 2, the stress variable may permit differentiation of plant communities growing in sites with low disturbance, but affected by different intensities of stress, especially light availability. *Potamogeton pectinatus* scored highest on the stress-tolerant gradient (Fig. 3); tolerance to shade and to high salinity is a well-known feature of this plant (e.g. van Wijk, 1988). A number of species appeared most characteristic of intermediate conditions of disturbance and stress: examples included *Potamogeton berchtoldii, Potamogeton pusillus* and *Potamogeton natans.*

DISCUSSION

Most of the species included in this study probably have a rather similar established-phase survival strategy, particularly in relation to competitiveness and disturbance-tolerance.

Disturbance-tolerance is likely to be a vital survival feature for channel plants in Britain, at least in part because of the widespread use of management based on disturbance-causing methods. All sites in this study experienced at least some disturbance from aquatic plant management: the lowest management index values were associated with a single annual weed-cut by boat; the highest with dredging (Fig. 1).

The area of the ordination plot with low scores for disturbance and stress (i.e. the lower left corner) is were plants whose strategy incorporates a stronger competitive element would be expected to occur. In fact species with competitive strategies were located throughout the ordination diagram. This suggests that drainage channels habitats overall provide a rather productive environment for macrophyte growth.

The use of only two indices to summarize the complex influences of the environment on the growth of submerged plants is of value only up to point. Take, for example, water depth. This effects light availability for euhydrophytes (Kautsky, 1988; Blindow, 1992) and is therefore a stress factor, but changes in water level may provoke physical damage to plant tissues by partial or total desiccation, which is clearly a disturbance. Nevertheless, the use of integrated indices of stress and disturbance affecting channel sites proved successful in allowing us to distinguish two groups of plants showing differential disturbance tolerance. These may be considered as two separate functional vegetation groups, under the definition given in the introduction to this paper.

The study has identified a problem in the use of the strategy terminology put forward by Grime (1979) to classify and distinguish functionally defined groups of species of closely-similar established-phase strategy (here, mainly variants on competitors and disturbance-tolerators). If the functional analysis approach is to be successfully applied in these circumstances it would be useful to develop a terminology which would allow for more precise and detailed description of sub-categories of plant strategies. One such approach has recently been described by Hills *et al.* (1994) for wetland vegetation. Further work is needed to develop appropriate methods applicable to submerged plants.

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FIGURE CAPTIONS

Fig. 1. Management procedures in relation to the likely degree and timing of destruction of the plant biomass in the target sites.

Fig. 2. CCA ordination of sample scores (•) identified by region (F, Fens; C, Crossens; S, Solway; M, Spynie Canal) and arrowed biplot scores of environmental variables (☐). The boundaries of two sample groups (I and II) identified at level 1 of TWINSPAN classification are overlaid on the ordination plot.

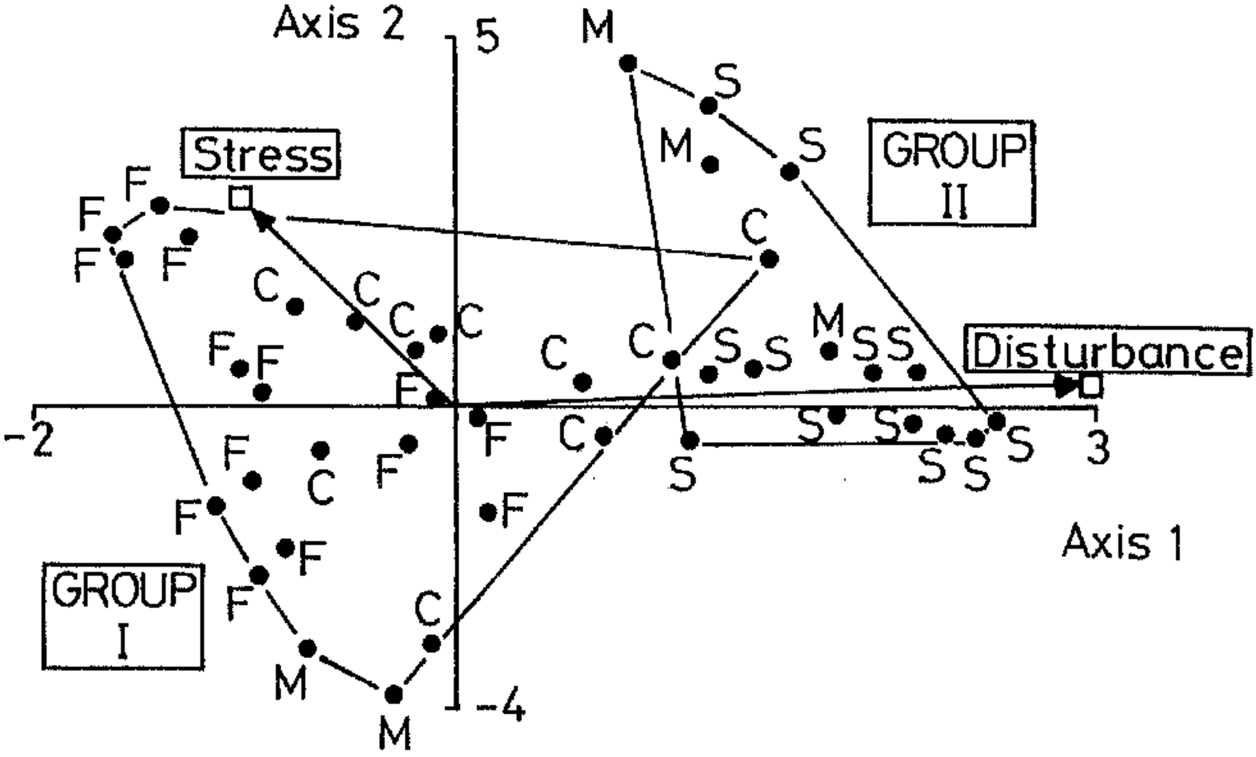
Fig. 3. CCA ordination of species scores (•) and arrowed biplot scores of environmental variables (☐) showing species name plus strategy type codes (where available): Call, *Callitriche stagnalis* and *C. platycarpa;* Cdem, *Ceratophyllum demersum*; Elod, *Elodea canadensis* and *E. nuttallii*; Falg, filamentous algae; Hpal, *Hottonia palustris*; Mspi, *Myriophyllum spicatum*; Pamp, *Persicaria amphibia*; Pcri, *Potamogeton crispus;* Pluc, *P. lucens;* Pnat, *P. natans;* Ppec, *P. pectinatus*; Pper, *P. perfoliatus;* Ppus, *P. pusillus* and *P. berchtoldii*; Rcir, *Ranunculus circinatus*; Rrip, *Rynchostegium riparioides* (moss); Seme, *Sparganium emersum*; Zpal, *Zannichellia palustris.* C, D and S indicate competition, disturbance and stress elements, respectively.

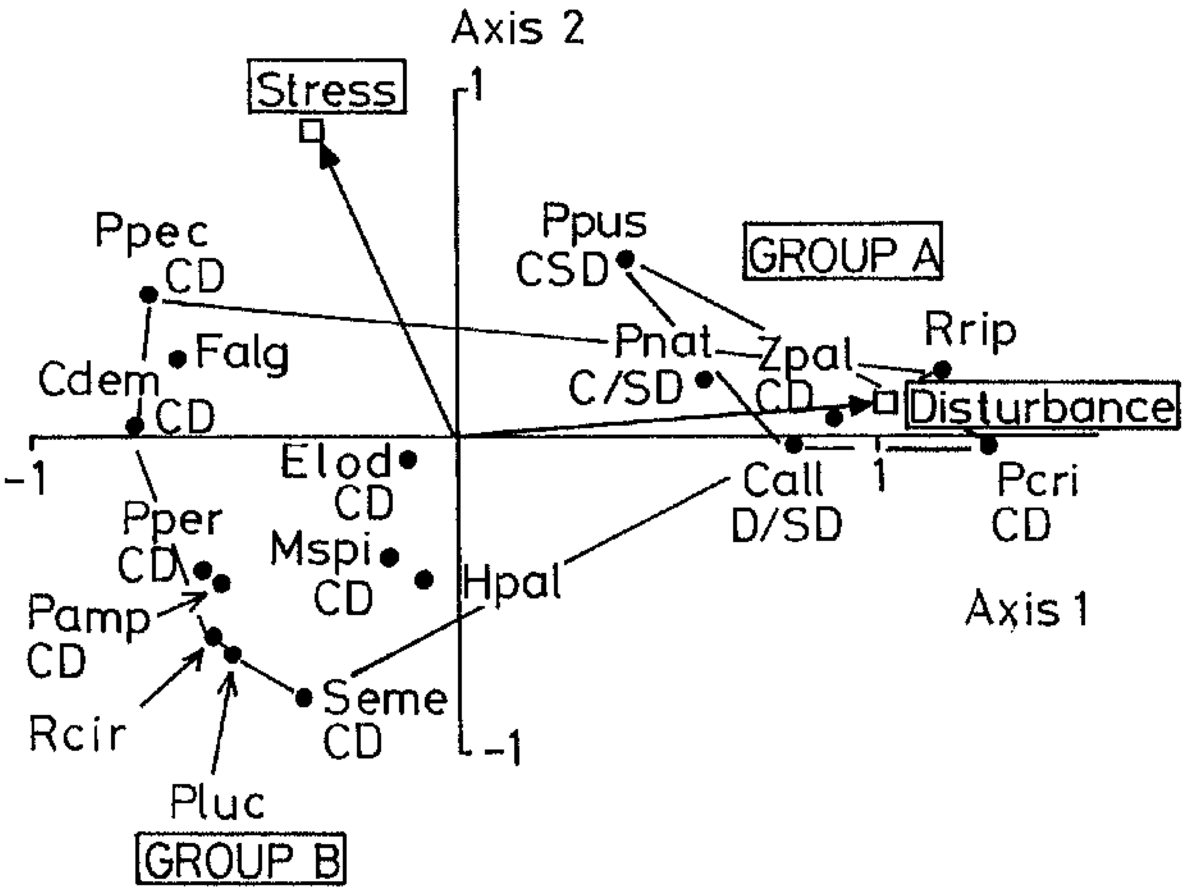
LOW DISTURBANCE

- Weed boat: every 1 - 2 years
- Manual weed rake (from banks in deep channels): every year
- Shallow dredge (Bradshaw bucket): every year
- Shallow dredge and manual control: every year
- Manual control (scythes, forks): 2 or more per year (shallow channels)
- Herder bucket + manual control
- Dredged every 3 - 4 years + annual manual clearance
- Deeper dredging: every year

↓

HIGH DISTURBANCE


Axis 2
5
-4
-2
3
Axis 1
Stress
Disturbance
GROUP I
GROUP II
F
C
M
S


Axis 2
Stress
1
Ppec
CD
Ppus
CSD
GROUP A
Falg
Cdem
CD
Pnat
C/SD
Zpal
CD
Rrip
Disturbance
-1
Elod
CD
Call
D/SD
1
Pcri
CD
Pper
CD
Mspi
CD
Hpal
Axis 1
Pamp
CD
Seme
CD
Rcir
-1
Pluc
GROUP B

APPENDIX II

AQUATIC VEGETATION, MANAGEMENT AND PHYSICO-CHEMICAL STATUS OF THE OLD BEDFORD/COUNTER DRAIN AND FORTY FOOT DRAIN 1992

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Anglian Region

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1. INTRODUCTION

In 1992, 24 sites located in different drainage areas of Great Britain were sampled on three occasions during the plant growth season. The survey is part of the study "Aquatic plant survival strategy in relation to drainage channel management regime", a postgraduate project being undertaken by the University of Glasgow. This report includes information about the four sites located in the Old Bedford/Counter Drain and Forty Foot Drain. The purpose is to follow up reports (Murphy 1991, 1992) about the environmental impact of channel management, water quality and boat traffic on the aquatic plant vegetation.

2. METHODOLOGY

2.1 Following a preliminary site examination in early May 1992, the target stretch were sampled on 3 occasions during 1992 (26 May, 5 August and 7 October). The site located in Welney was not sampled in October because the area was flooded.

A 50 m stretch was selected for survey at the sites:

(i) Forty Foot Drain (Welches Dam Lock): TL 465859
(ii) Counter Drain, upstream of Welches Dam: TL 462849
(iii) Old Bedford River, Welches Dam Pumping Station TL 471860
(iv)Old Bedford River, upstream of Delph Bridge,Welney:TL 522930

2.2 At each site 10 random grapnel hauls were taken to sample submerged macrophyte growth. The frequency of the species in each sample was recorded, and the abundance was rated as 1, present; 2, frequent and 3, abundant. The biomass of the more abundant species was calculated by using a quantitative grapnel standing crop assessment procedure. The presence of emergent aquatic plants was recorded during each visit.

2.3 On-site electrometric measurement of underwater light (as photosynthetically-active radiation, PAR) penetration, dissolved oxygen, pH, temperature and conductivity of the water were carried out.

Data on additional water-chemistry determinands were provided by NRA from 1990 to August 1992, for the Old Bedford River at Welches Dam Pumping Station and at Delph Bridge Welney, for the Counter Drain at Welches Dam and for the Forty Foot at R. Carter Rd. Br. Chatteris. The data for boat traffic was provided by Mrs. Lyn Shotbolt of IWA.

3. MACROPHYTE COMMUNITY

3.1 Diversity

In total 37 macrophyte taxa were recorded from the target site area during May - October 1992 (Table 1). This included 3 filamentous algae taxa, 22 submerged taxa and 12 emergent species. The total is below the totals for channel-growing species of 50 and 52 recorded in 1990 and 1991 by Murphy (1991, 1992) but it is important to point out that the length of channel studied in 1992 is only one third of that surveyed in 1991.

All the species recorded were included by Newbold and Palmer (1984) in the group community described as being "either base-rich or nutrient rich, and usually both". Study river plant communities, Newbold and Palmer (1979) and Holmes and Newbold (1984) proposed a ranking system to assess the trophic status of most freshwater habitats. they assigned "trophic rank" to 150 aquatic plant species, starting with those confined to oligotrophic water and working up to those tolerant of hypertrophic conditions. By using this methodology, the "trophic mean score" of the four sites included in this study are:

-Forty Foot:	105
-Counter Drain:	116

-Old Bedford River:

Welches Dam:	110
Welney:	112

According to Holmes and Newbold (1984) plant communities with these trophic scores are the most eutrophic examples found in British rivers, suggesting that the species which typify it favour enriched water: some are clearly tolerant of pollution. None of the 20 aquatic plant species included exclusively in the groups mesotrophic or oligotrophic were found in the area, again confirming the eutrophic nature of the system.

Even though the area under study was smaller, it worth pointing out that only four species of *Potamogeton* were recorded during 1992, a lot less than the totals of 10, 7 and 8 recorded in 1986, 1990 and 1991 in the same area. This could be further evidence for the apparent trend of reduction in *Potamogeton* diversity in the system during the last few years, noticed by Murphy (1992).

One uncommon species, *Lemna trisulca*, recorded in the Forty Foot Drain in 1990 but not found in 1991, was recorded again in 1992.

3.2 Frequency and abundance

All the species found with a frequency of more than 10 % during the 1991 survey (Murphy 1992), were found again in 1992. Table 2 shows that filamentous algae (specially *Vaucheria dichotoma*), *Ceratophyllum demersum*, *Elodea canadensis*, *E. nuttallii*, *Lemna minor*, *Ranunculus circinatus* and *Myriophyllum spicatum* are the most wide spread submerged and floating weeds in the area.

In the 1991 survey, *P. pectinatus* and *Nuphar lutea* were spread throughout the system but were recorded in only one site in 1992. On the other hand, the values of frequency of *Elodea* on both years seem to show a rise in the spread and abundance of this genus in 1992 compared with early years.

3.3. Biomass

Submerged weeds impede channel flow by increase frictional roughness. The biomass of submerged plants present is a good measure of the extent of the vegetation nuisance in a channel.

The total dry biomass was between 300 and 500 gDW. m^{-2} in the four sites. The values of biomass per species in each site (Fig. 1) show seasonal changes in relative importance of weed species at each site. In the Forty Foot Drain there were in May significant growth of *Elodea, V. dichotoma, C. demersum* and *C. obtusangula,* but in August and October more than 50 % of the total biomass was *Elodea.*

The filamentous algae, specially *V. dichotoma,* had an important biomass during all the growing season, with values between 100 and 200 gDW. m^{-2}. Besides the algae, *R. circinatus* and *C. demersum* dominated the submerged vegetation in the sites located in the Counter Drain and the Old Bedford River, respectively.

4. WATER PHYSICO-CHEMISTRY

4.1. Mean values of T.O.N. as N, Ammonia N, P-Ortho, pH, turbidity and conductivity from July 1991 to September 1992 in the NRA sampled points, are shown in Fig. 2 - 7. The data confirm the eutrophic nature of the system with high to very high values of nutrients and pH.

According to Newbold and Palmer (1979) the nutrient status in the system would be between eutrophic and hypertrophic, changing with the seasonal fluctuations of the nutrient levels. The authors pointed out that these types of water bodies are characterised by a high algae productivity.

The values of P-Ortho were very high throughout all the period, except during the winter time in the Counter Drain (Fig. 4). The values of T.O.N. (Fig. 2) were very high during the winter time and low during the growing season, showing the normal seasonal pattern of summer minimum and winter peaks, corresponding to plant uptake of N from the water. The ammonia levels (Fig. 3) shown some variations, but in general the values are very high all the year.

4.2. pH (Fig. 5) was consistently high throughout the season, showing values consistent with a high submerged plant biomass.

4.3. Turbidity data (Fig. 6) in the Old Bedford/Counter Drain showed that the water in the system is generally clear, but the Forty Foot Drain rose in turbidity during 1992. The average values of the light extinction coefficient (k) were 2.23, 1.64, 1.46 and 2.76 m^{-1} in the sites at Welney, Welches Dam, Counter Drain and Forty Foot Drain, respectively. Thus, the most turbid water was found too in the Forty Foot site.

As in 1991 (Murphy, 1992), the pattern of B.O.D. during 1992 closely followed the pattern shown by the turbidity, which may suggest that some disturbance of the channel sediment detritus was responsible.

4.4. Conductivities were high during 1992, especially in the Counter Drain with values between 1090 and 3000 $\mu S.\ cm^{-1}$ (Fig. 7). The chloride data followed the conductivity pattern with values between 129 and 311 $mg.\ l^{-1}\ Cl^{-}$. The conductivity was between 800 and 1600 $\mu S.\ cm^{-1}$ in the other points, with chloride values between 60 and 150 $mg.\ l^{-1}$. The data confirm that the high chloride values are the likely cause of the high conductivities seen in the system, and suggested that saline intrusions were occurring from time to time, especially in the Counter Drain (Murphy, 1992).

5. CHANNEL MANAGEMENT REGIME

Information on weed cutting and dredging in 1992 was provided by NRA (Ely) as follows:

-In the Counter Drain-Old Bedford a weed cutting from a boat and a shallow hydraulic dredging were carried out in the Counter Drain and Welney sites in September. By the first days of October this work had not been undertaken in Welches Dam because the area was flooded.

-In the Forty Foot Drain no work had been made until the first days of October, but a weed cutting with weedrake was expecting to carry out soon.

It is interesting to point out that the weed cutting carried out in the Counter Drain did not in general affect the frequency and abundance of the submerged/floating plants, though the biomass of *Ranunculus circinatus* was significantly reduced (Table 2, Fig. 1).

6. BOAT TRAFFIC

There were 12 boat passages through Welches Dam between Easter and October 1992. As all boats also made the return trip, this gave a top estimate of only 24 passages in all. This value is similar to the data for 1991, with c. 20 boat traffic movements (Murphy, 1992).

The baseline study (Murphy 1991) suggested that low traffic (in the order of 10 movements per "navigation day") would have a measurable effect on the Forty Foot. There is no evidence that the 1991-1992 traffic, which averaged less than one movement per navigation day, produced any measurable environmental effect on the channel.

7. ACKNOWLEDGEMENTS

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Table 1. Aquatic weed species recorded in 4 sites of the Old Bedford River/Counter Drain and Forty Foot Drain 1992.

Submerged and floating species

Callitriche stagnalis Scop.
Callitriche obtusangula Le Gall
Ceratophyllum demersum L.
Cladophora glomerata
Elodea canadensis Michaux
Elodea nuttallii (Planchon) H.St. John
Enteromorpha intestinalis (L) Grev
Glyceria fluitans (L.)R.Br.
Lemna gibba L
Lemna minor L
Lemna trisulca L
Myriophyllum spicatum L.
Nuphar lutea(L.) Smith
Nymphaea alba L.
Nymphoides peltata Kuntze
Persicaria amphibia (L.) Gray
Potamogeton crispus L.
Potamogeton lucens L.
Potamogeton pectinatus L.
Potamogeton perfoliatus L.
Ranunculus aquatilis L.
Ranunculus circinatus Sibth.
Sagittaria sagittifolia L.
Sparganium emersum Rehmann
Vaucheria dichotoma

Emergent species

Agrostis stolonifera L.
Apium nodiflorum (L.)Lag.
Caltha palustris L.
Carex riparia Curtis
Epilobium hirsutum L.
Glyceria maxima (Hartman)O.Holmb.
Juncus articulatus L.
Juncus effusus L.
Mentha aquatica L.
Phalaris arundinacea L.
Phragmites australis (Cav) Trin.ex Steudel
Sparganium erectum L.

Table 2. Ocurrence of species iin four sites of the Old Bedford/Counter Drain and Forty Foot Drain 1992. %F: mean % frequency for submerged/floating plants from ten records. In brackets is the abundance average recording as 1, present; 2, frecuent and 3, abundant.

Site:	OLD B.(WELNEY)		OLD BEDFORD (WELCHES DAM)		
Date:	26/5	5/8	26/5	5/8	7/10
Cal. stagnalis					
Cal. obtusang.					
Cer.demer.	80	100 (3)	80	100 (2.7)	90 (1)
Fil. algae	100	100 (2.6)	100	100 (2.2)	100 (2.5)
Elo. can./nut	100	100 (1.4)	100	80 (1.1)	60 (1.3)
Gly.fluitans	20				
Jun.bulbosus					
Lemna minor	100	100 (2)	100	100 (1)	40 (0.4)
Lemna gibba		100 (2)	40	100 (1)	
Lem. trisulca					
Myr.spicatum		60 (0.6)		80 (1.1)	60 (0.9)
Nup. lutea					
Nym. alba				20 (0.2)	
Nym.peltata				100 (1.9)	50 (0.5)
Per. amphibia					
pot. crispus					
Pot. lucens				10 (0.3)	
Pot. pect.					
Pot. perf.			30		
Ran. aquat.					
Ran. circ.	80		40	90 (1.1)	80 (0.8)
Sag. sagit.					
Spar. emer.					

Table 2 (cont.). Ocurrence of species iin four sites of the Old Bedford/Counter Drain and Forty Foot Drain 1992. %F: mean % frequency for submerged/floating plants from ten records. In brackets is the abundance average recording as 1, present; 2, frecuent and 3, abundant.

Site:	COUNTER DRAIN			FORTY FOOT		
Date:	26/5	5/8	7/10	26/5	5/8	7/10
Cal. stagnalis				70 40		
Cal. obtusang						
Cer.demer.		10 (0.3)		40	100 (1.2)	40 (0.4)
Fil. algae	80	100 (2.5)	100 (1.9)	100	80 (1.4)	100 (1.5)
Elo. can./nut	20	100 (1.2)	100 (1.2)	100	100 (3)	100 (3)
Gly.fluitans						
Jun.bulbosus			50 (0.5)			
Lemna minor					100 (1.5)	100 (2)
Lemna gibba					60 (0.7)	100 (1)
Lem. trisulca						20 (1)
Myr.spicatum	50	30 (0.8)	70 (1.6)		60 (0.6)	
Nup. lutea	20					
Nym. alba						
Nym.peltata	40					
Per. amphibia	20					
pot. crispus	40			30		
Pot. lucens						
Pot. pect.	100	100 (1.3)	20 (2)			
Pot. perf.	50	60 (0.7)	70 (0.7)			
Ran. aquat.				20	30 (0.3)	100 (1.4)
Ran. circ.	100	100 (1.9)	90 (1.2)	30	40 (0.4)	30 (0.3)
Sag. sagit.						20 (0..3)
Spar. emer.	10					

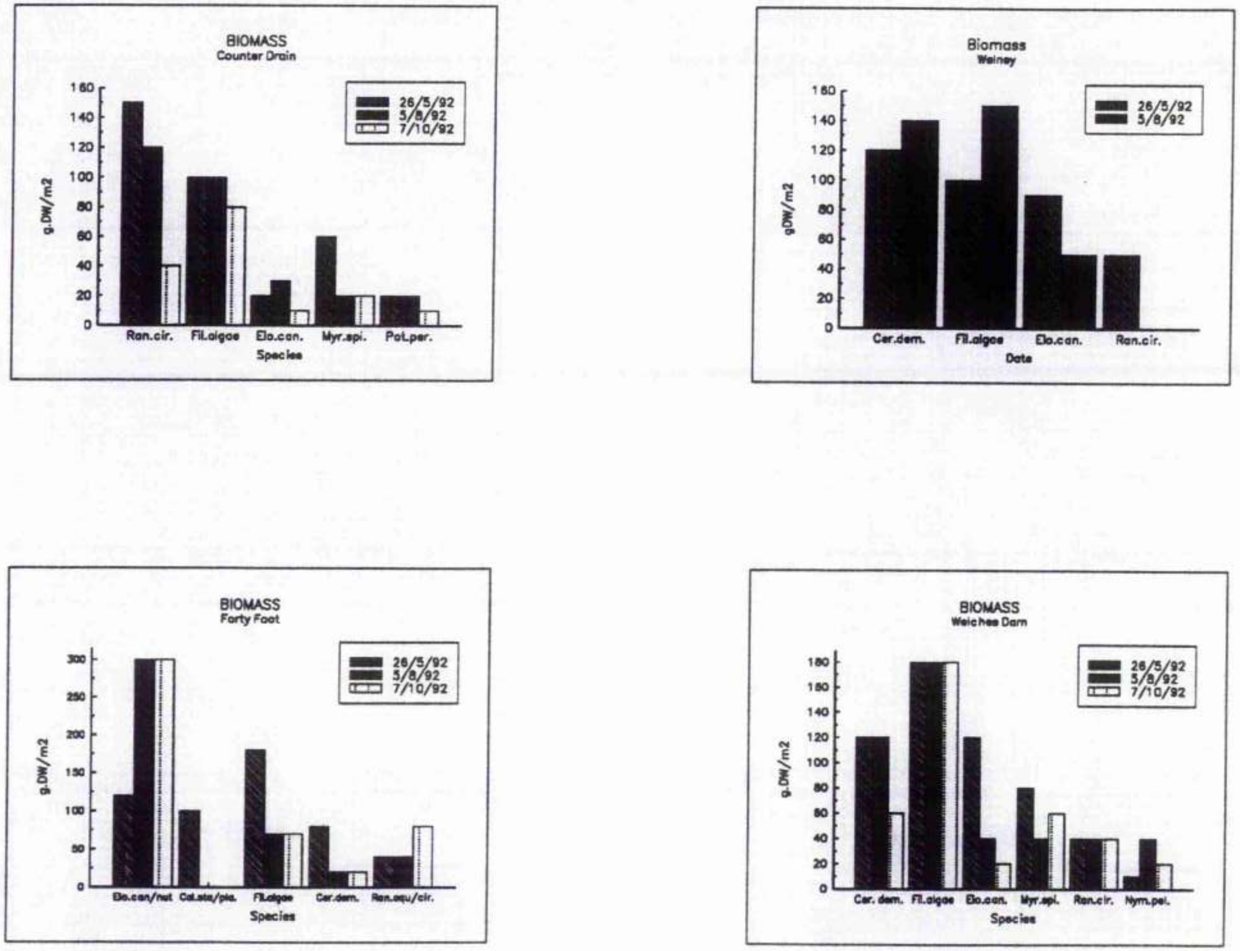


Fig.1 . Biomass data of the Old Bedford/Counter Drain and Forty Foot 1992.

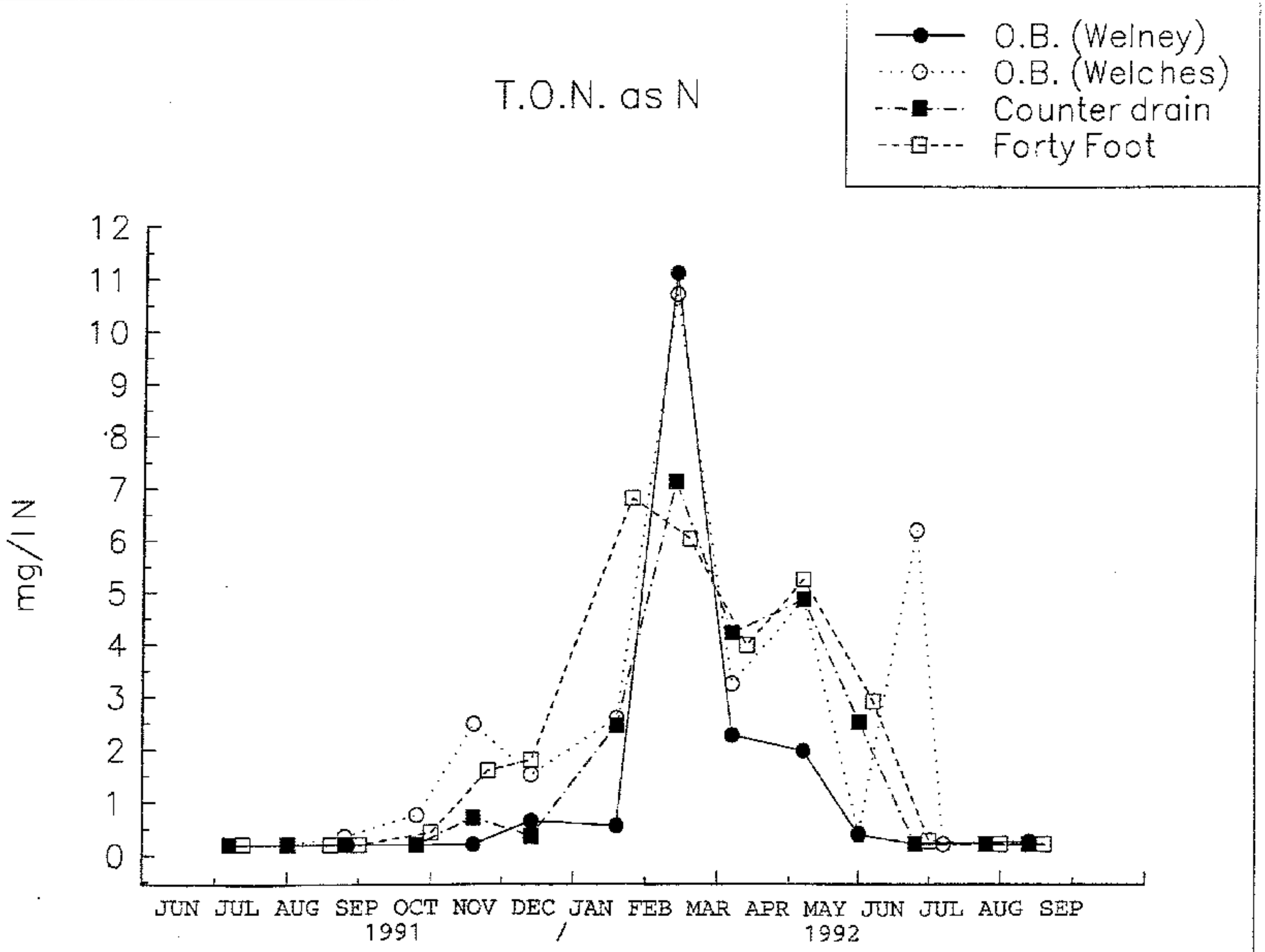


Fig.2. Monthly values of total oxidised nitrogen recorded in the area.

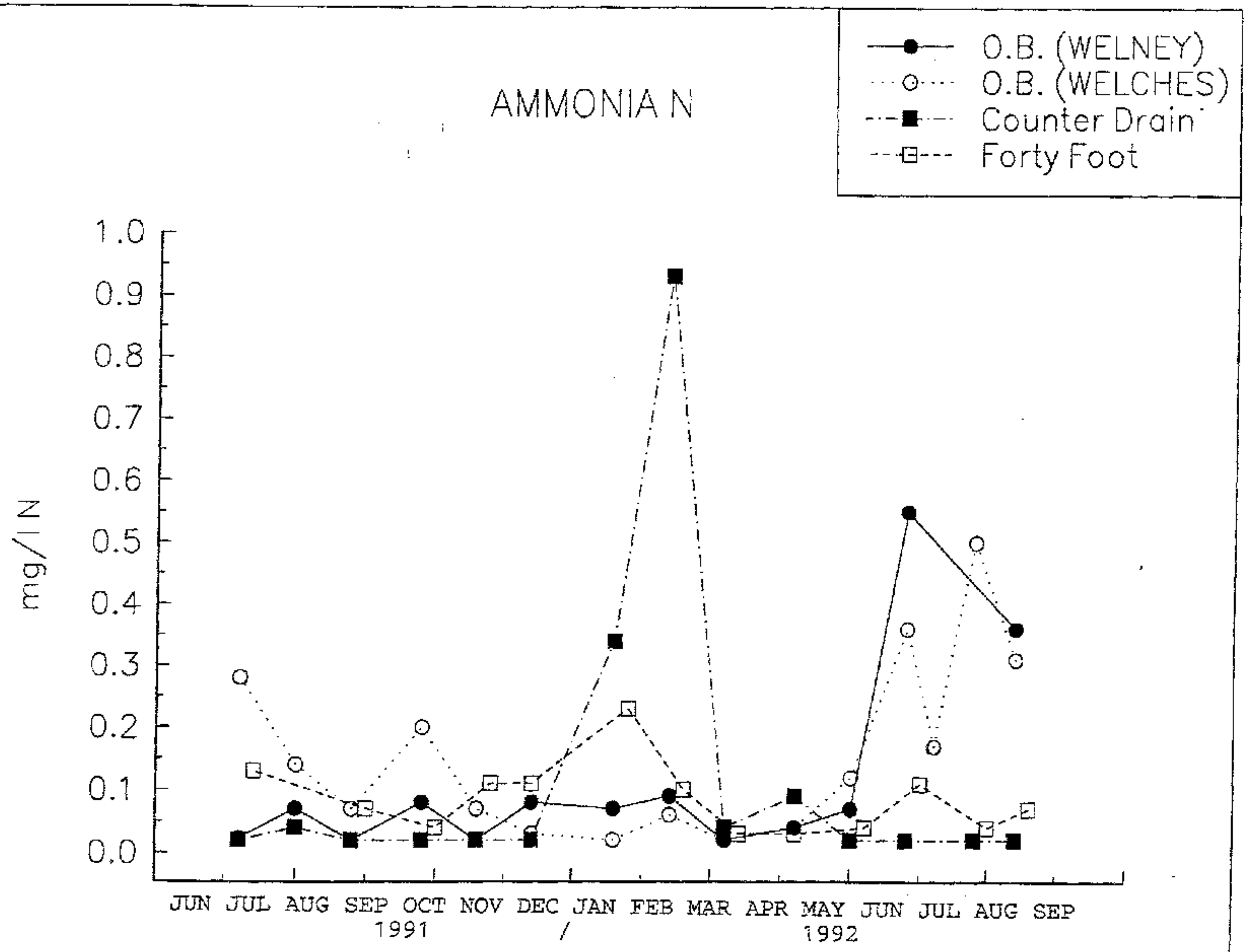


Fig.3. Monthly values of ammonia-nitrogen recorded in the drainage area.

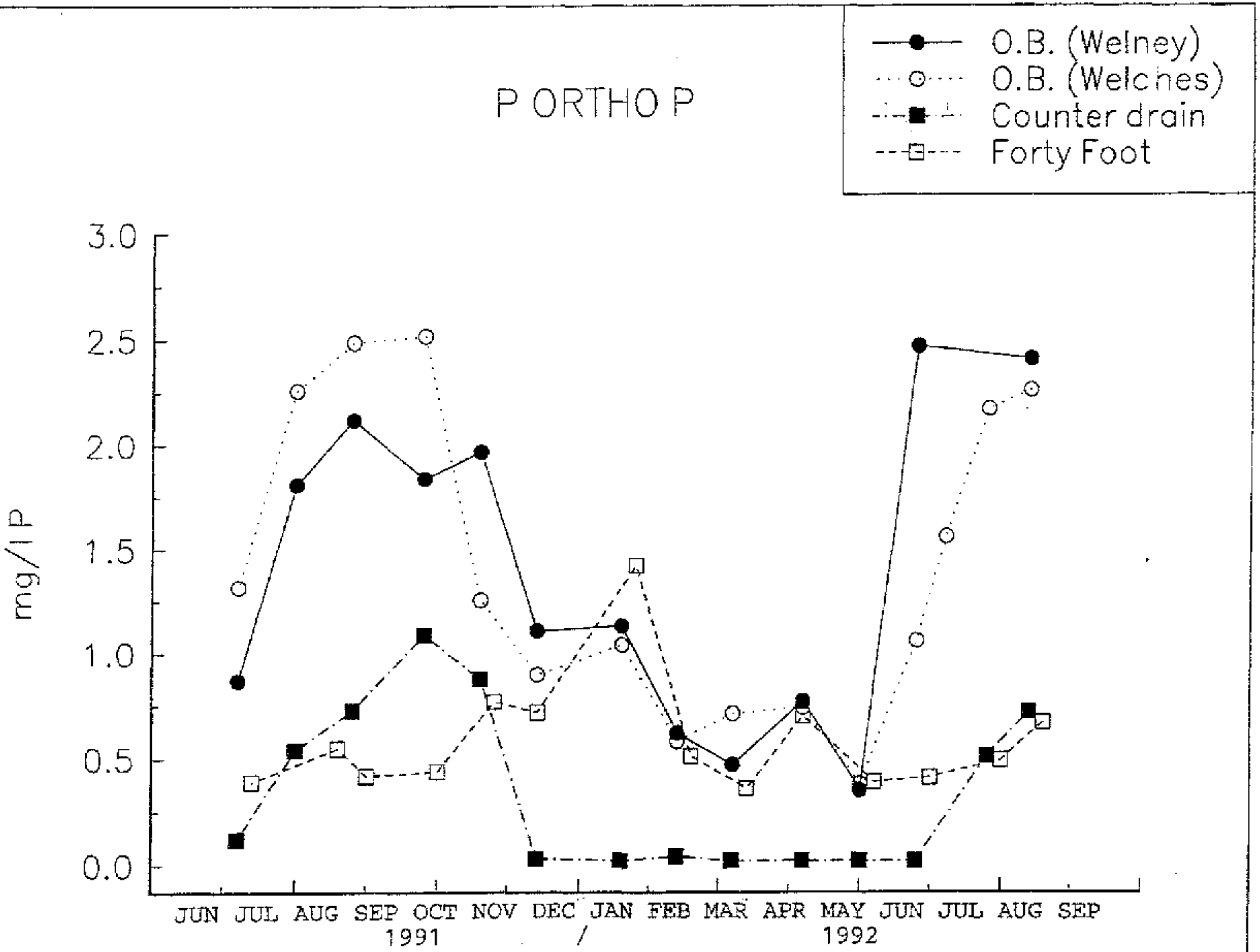


Fig.4. Monthly values of orthoposphate–phosphorus recorded during 1991/92

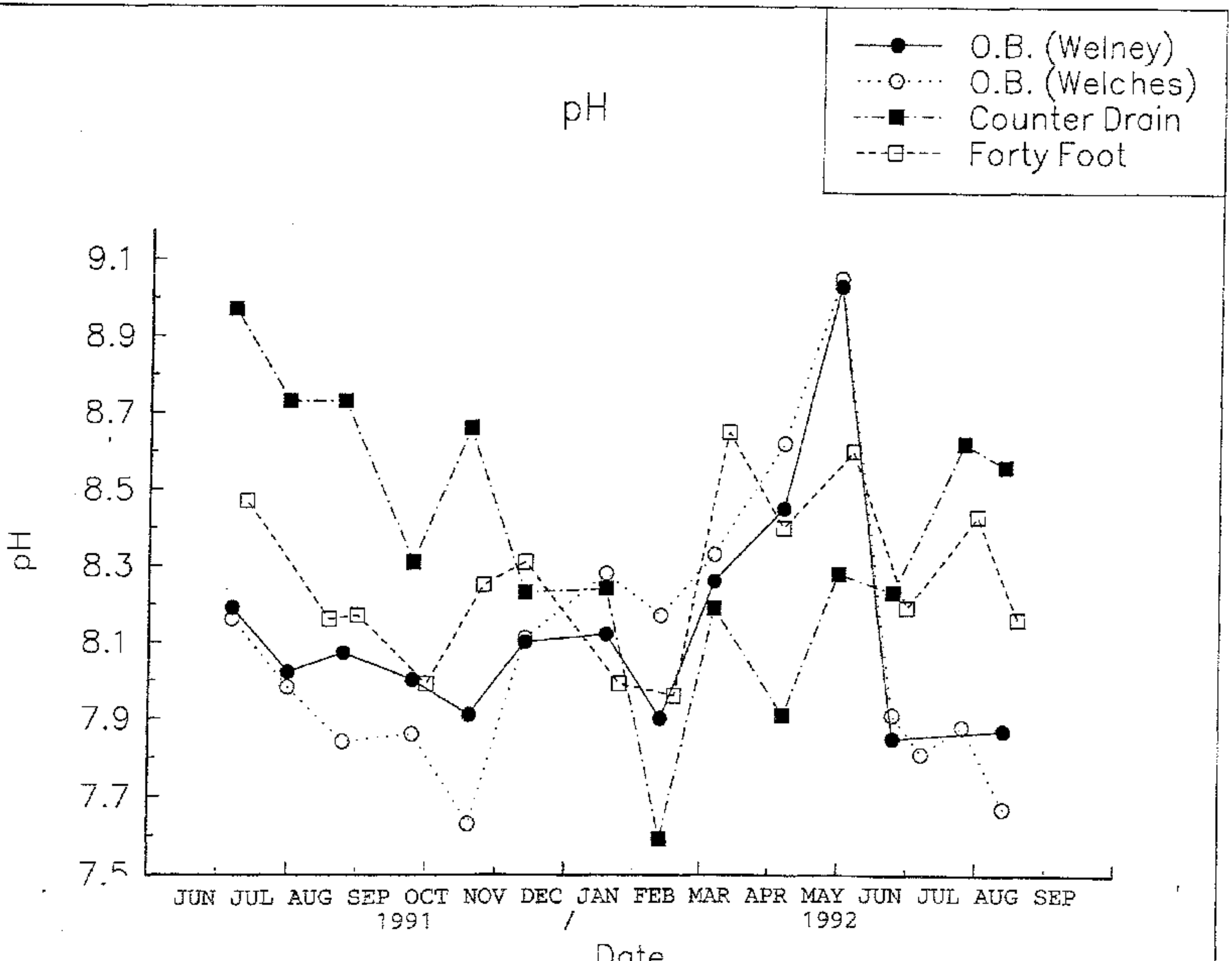


Fig.5. Monthly values of pH recorded in the drainage area.

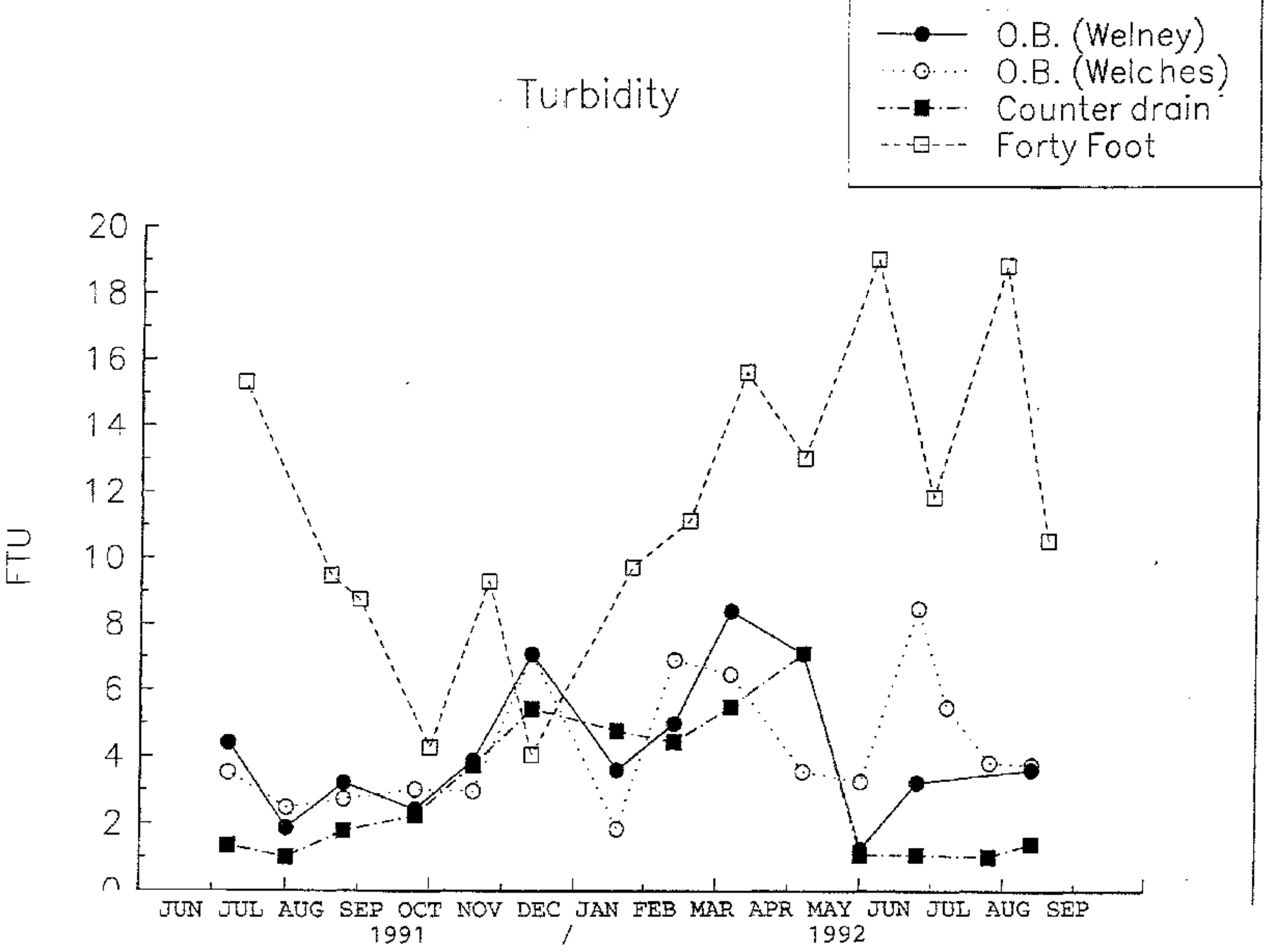


Fig.6. Monthly values of turbidity recorded in the drainage area 1991/1992

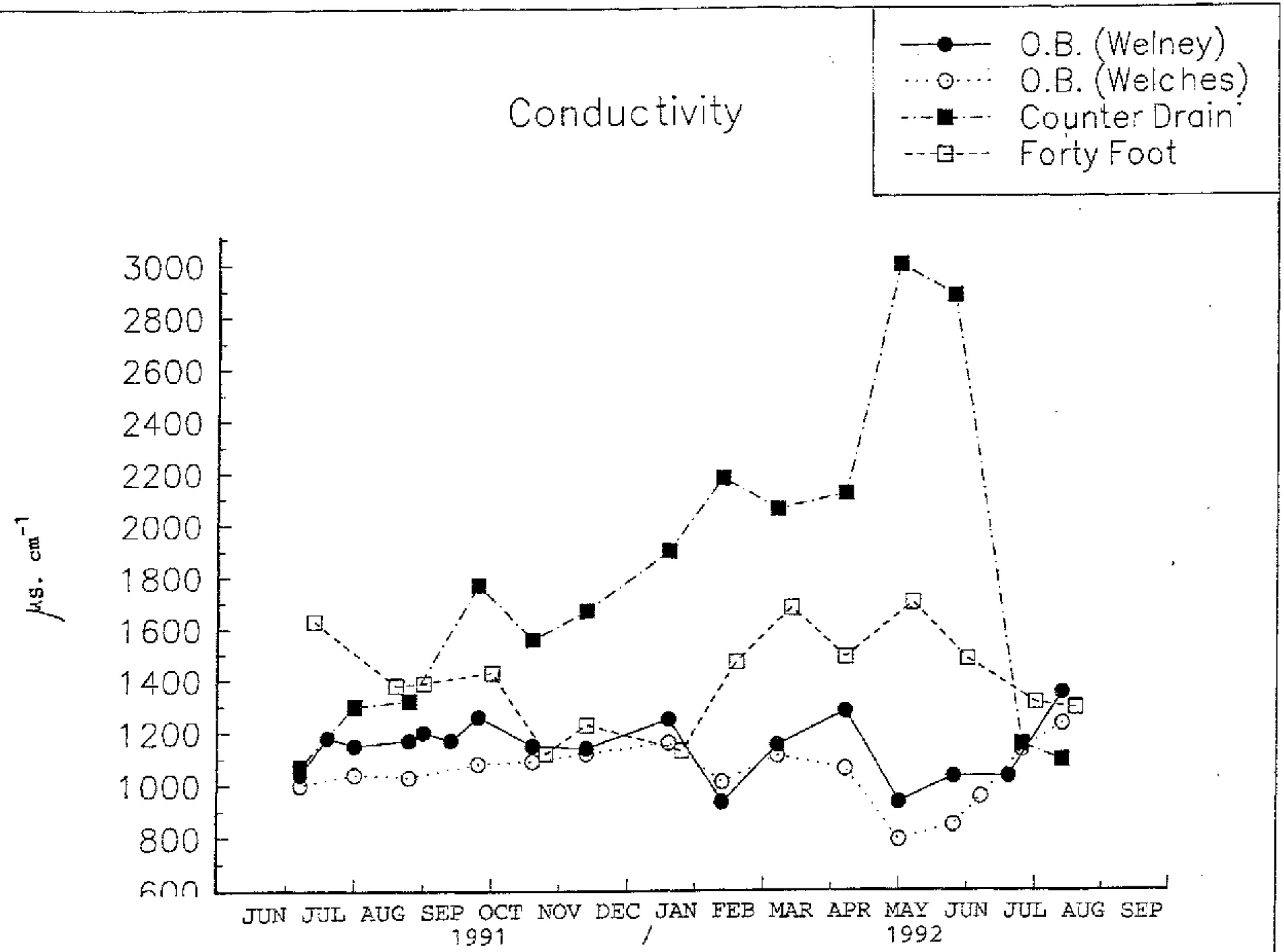


Fig.7.Monthly values of conductivity 25 C recorded in the drainage area.

APPENDIX III

REPORT ON SAMPLES OF *COLEOGETON* FROM ARGENTINA

P.M.HOLLINGSWORTH
R.J.GORNALL

Samples from the following localities were analysed using standard horizontal starch gel electrophoresis of isozymes (Wendal & Weeden 1990).

1. Irrigation channel, Rio Colorado, CORFO system. *P.pectinatus*, var. *striatus*. 20 plants analysed.

2. Drainage channel, Irizo, CORFO system. *P.pectinatus*, var. *pectinatus*. 10 plants analysed.

3. Drainage channel, Pradere, CORFO system. *P.pectinatus*, var. *pectinatus*. 8 plants analysed.

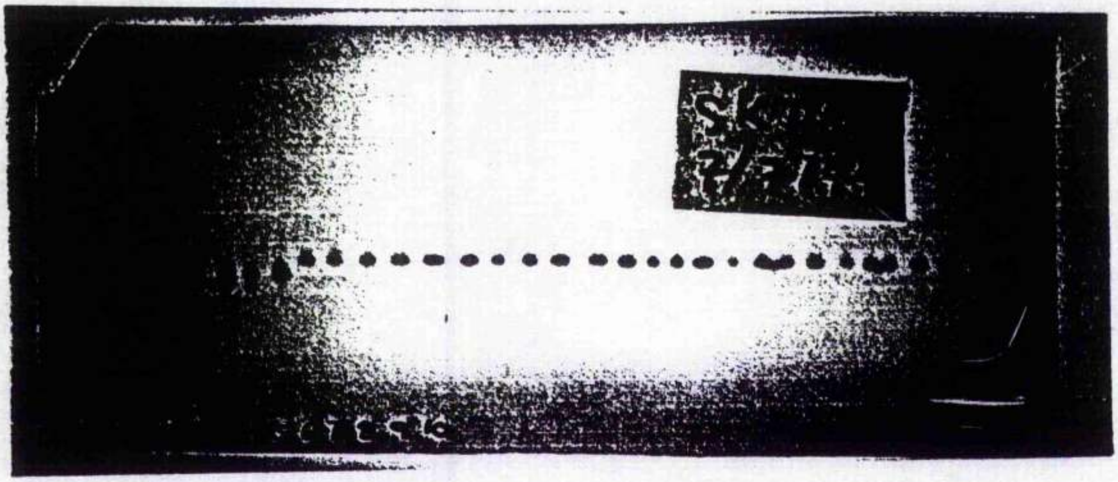
4. Drainage channel, Miscellaneous sites, CORFO system *P.pectinatus*, var. *pectinatus*. 15 plants analysed.

Nine enzyme systems, representing 14 putative loci were visualised for the above samples. No variation was found between any of the samples. Using the same techniques on British and Swedish material of the European members of the sub genus *Coleogeton* namely *P.pectinatus, P.filiformis and P.vaginatus* infraspecific variation has been noted within and between populations. Consistent differences between these species has been observed at 3 of the 9 enzyme systems, with additive inheritance of the parental 'marker bands' noted in a putative hybrid.

The Argentinian material differs greatly from the European *P.pectinatus* with only two out of the nine enzymes showing the same banding patterns.

The combined data show no difference between *P. pectinatus* var. *pectinatus* and var. *striatus* in the Argentinian populations examined. They do however show substantial differences from Northern European populations of *P. pectinatus* (fig. 1)

Fig. 1. SKD 07.07.1993 British and Argentinian *Coleogeton* sp.



Lanes 1-2 *P.filiformis* (UK) , 3 *P.filiformis* x *P.pectinatus* (UK), 4 *P. pectinatus* (aberrant UK form), 5 *P.pectinatus* (standard UK form), 6-7 *P.pectinatus* var. *striatus* (Argentina), 8-9 *P.pectinatus* var. *pectinatus* (Argentina), 10-29 misc. *P.pectinatus* var. *striatus* and var. *pectinatus* (Argentina).

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APPENDIX IV

Aquatic plant communities present in the target drainage channels of Britain, in terms of the vegetation types recognised by the National Vegetation Classification.

The aquatic vegetation types described in British Plant Communities (Rodwell, 1995) were used to classify the 24 sites surveyed in Britain. The identification of the plant communities was made using the computer program TABLEFIT (Hill, 1993). The code identified the community as named by Rodwell (1995), and a brief summary of each community is given below the table. In brackets are the goodness-of-fit values of each community in every site; a value of >50 probably assign a good fit of the vegetation to the recognised community (Hill, 1993). The first three plant communities most closely related to the vegetation are included for each site. For sites location see 2.2.1.

FENS	Aquatic vegetation types
1	A11b (92), A16b (78), A11 (75)
2	Only filamentous algae present
3	A12 (80), A5 (69), A5b (60)
4	A12 (80), A11a (74), A11 (63)
5	Only filamentous algae present
6	A16a (64), A16 (63), A11b (61)
7	A5a (99), A5(91), A5b (72)
8	A5a (86), A5 (71), A11 (62)
9	A11b (98), A11 (93), A11c (67)
10	A5a (91), A5 (82), A15 (67)
CROSSENS	
1	A5 (77), A11b (73), A5a (71)
2	A11b (89) A11(82), A5a (76)
3	A5a (84), A5 (80), A16a (69)
4	A11b (77), A5 (77), A5a (75)
5	A11 (84), A11a (74), A11c (70)
SOLWAY	
1	A16a (82), A16 (80), A16b (67)
2	A16a (82), A16 (80), A16b (67)
3	A16a (71), A16 (69), A16b (88)
4	A9c (65), A16a (69), A16 (64)
5	A16a (71), A16 (100), A16b (88)
6	A16a (100), A16 (100), A16b (100)
SPYNIE C.	
1	A9c (85), A9 (81), A16a (80)
2	A13a (44), A11b (41)
3	A11b (93), A11 (70), A16b(66)

A5 (*Ceratophyllum demersum* community): This community is characterised by often dense free-floating masses of *C. demersum*, usually with at least a little, sometimes much, *Elodea canadensis*. Is typical of still or slow-moving, eutrophic waters, mainly in the warmer, south-eastern lowlands of Britain.
A5a: *Ranunculus circinatus* sub-community.
A5b: *Lemna minor* sub-community.

A9 (*Potamogeton natans* community): This community includes all those stands where *P. natans* is a clear dominant over the water surface, often to the total exclusion of other free floating or floating-leaved species and with just very sparse submerged or emergent associated. This community is typical of mesotrophic to fairly nutrient-poor, standing to moderately fast-flowing waters.
A9c: *Juncus bulbosus-Myriophyllum alterniflorum* sub-community.

A11 (*Potamogeton pectinatus-Myriophyllum spicatum* community): This community includes most of the richer and more diverse pondweed vegetation in which *P. pectinatus* and *M. spicatum* play a prominent role. The community is best developed on finer mineral substrates in clear, standing to moderately fast-moving waters, which are generally mesotrophic to eutrophic and base rich, sometimes marly, occasionally slightly saline.
A11a: *Potamogeton pusillus* sub-community.
A11b: *Elodea canadensis* sub-community:
A11c: *Potamogeton filiformis* sub-community.

A12 *(Potamogeton pectinatus* community): This community comprises species-poor vegetation dominated by this fine-leaved pondweed. It can make rapid growth in early summer to form bushy clumps, often very luxuriant. This vegetation is characteristic of still to quite fast-moving, eutrophic waters, often with some measure of artificial enrichment, and frequently polluted and turbid.

A13 (*Potamogeton perfoliatus-Myriophyllum alterniflorum* community): This community subsumes the bulk of the richer and more varied pondweed assemblages in which the broader-leaved *P. perfoliatus* and *P. gramineus*, together with *M. alterniflorum*, provide the most consistent floristic element. Largely confined to the north and west of Britain, this community is typical of shallow to quite deep, mesotrophic and rather base-poor waters.
A13a: *Potamogeton berchtoldii* sub-community.

A15 (*Elodea canadensis* community): This community comprises species-poor vegetation in which this particular kind of North American pondweed has became dominant. Most characteristic of still to sluggish, nutrient-rich waters, shallow to quite deep, and generally with fine mineral beds.

A16 (Callitriche stagnalis community): Community usually dominated by *C. stagnalis,* occasionally accompanied or locally replaced by *C. platycarpa* or, in southern England by *C. obtusangula*. This community can be found throughout lowland Britain in a variety of more shallow open waters with but sluggish flow or none, as in dikes, canals, ponds, and in such habitats conditions can be eutrophic with the substrates often of silt or clay.
A16a: *Callitriche spp.* sub-community
A16b: *Potamogeton pectinatus* sub-community.

ADDITIONAL PAPER

(Paper relating to the main subject of the thesis, but which do not form part of the thesis itself; included in support of the application)

RESPONSE OF *ELODEA CANADENSIS* MICHX. AND *MYRIOPHYLLUM SPICATUM* L. TO SHADE, CUTTING AND COMPETITION IN EXPERIMENTAL CULTURE

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Abstract

Elodea canadensis Michx. and *Myriophyllum spicatum* L. are widespread nuisance aquatic plant species. Their ecology is regarded as similar. Both species have been previously classified in terms of established-phase survival strategy as "competitive disturbance-tolerant" species. Experimental data are presented to show that although this broad categorisation of strategy is probably correct for the two species, it is possible to demonstrate significant differences in terms of response to disturbance and competition. Less difference was discernible in their comparative response to stress. The drawbacks of applying broad descriptive terminology when dealing with two species of similar strategy are addressed. The results help explain reports of variable success in attempting to manage these two species using disturbance-based weed control measures, and suggest that *Elodea* is even less susceptible to such measures than *Myriophyllum*.

Introduction

Elodea canadensis Michx. and *Myriophyllum spicatum* L. are two submerged macrophyte species, which have successfully crossed the Atlantic during the past century, in the former case from North America to Europe, and in the latter from Europe to North America, to cause weed problems in a range of freshwater systems (Murphy *et al.* 1990a; Anderson 1990; Steward 1990; Simpson 1984). Despite their differing provenances, both species are currently problem aquatic weeds in Europe.

The ecology of the two species is usually considered to be quite similar. Their established phase strategies both show strong elements of competitiveness and disturbance-tolerance (Grime *et al.* 1988; Murphy *et al.* 1990b). The two species tend to occur in similar freshwater habitats, and occur under broadly similar sets of physico-chemical environmental conditions (Simpson 1984; Smith & Barko 1990). The available evidence (as, for example, reviewed by Nichols & Shaw 1986) therefore suggests that populations of the two species exhibit rather similar sets of phenotypically-expressed traits for tolerance of stress, disturbance and competition from other species (*sensu* Grime 1979). When in direct competition there is some evidence that one species may successfully displace the other, but field observations are far from consistent (e.g. Madsen *et al.* 1991).

The question arises whether the application of management measures (which impose artificial stress or disturbance on weed populations) is likely to have similar effects on *E. canadensis* and *M. spicatum*, and whether such effects are modified in the presence of competitor plant populations.

The aims of the study were:

(i) to determine, under standardised experimental glasshouse conditions, the response of *Elodea canadensis* and *Myriophyllum spicatum* to artificially-imposed stress, disturbance, and interspecific competition; and

(ii) to use the information gained to refine knowledge of the established-phase survival strategy of the two species.

Methods

In all experiments plants were grown in tapwater, in aerated 30 l black polypropylene tanks, under 16 hr light regime (Navilux 400W sodium floodlights augmenting natural daylight) in a heated glasshouse (20 C). The rooting medium was well-mixed natural river sediment. Plants were established as 12 cm stem sections, each with a viable bud, and subjected in a series of experiments to varying intensities of stress, competition, and disturbance. A random-block design was used as standard, with 3 blocks; except in Experiment 4 where an incomplete factorial design was used, with 4 blocks. Variables measured were plant length, biomass per plant, and resource allocation, (as biomass per stem, leaves and roots: Experiment 1 only). For each variable, and each species, % changes compared to untreated controls were calculated. Four experiments were conducted:

Experiment 1. Effects of stress caused by shade

Plants were grown in individual pots (1 plant/pot), with 2 plants of each species per tank. Individual tanks were shaded with one or more layers of shade material, or left unshaded (9 tanks used), to give a design with 3 levels of the treatment factor: UNSHADED, LOW (23% reduction in photosynthetically-active radiation, measured using a Skye PAR meter at water level in the tank), and HIGH-shade (40% reduction in PAR).

Experiment 2. Effects of disturbance caused by cutting

Plants were grown in individual pots (1 plant/pot), with 11 pots/tank (18 tanks, each containing a random mix of treatment units). Cutting treatments were standardised to reduce individual plant length to 5 cm after each treatment. Two frequencies of cutting were used, to give a design with 3 levels of the treatment factor: UNCUT, LOW (cut 35 days after start of experiment) and HIGH cutting frequency (cut both 35 and 66 days after start).

Experiment 3. Effects of interspecific competition

An additive approach (Martin & Snaydon 1982) was used to compare MIXED v. PURE stands of *Elodea canadensis* and *Myriophyllum spicatum*. Either 25 plants of each species in monoculture, or 25 + 25 plants of each species in mixed culture, were planted in trays (360 x 220 mm), with 1 tray/tank.

Experiment 4. Combined effects of shade stress and disturbance caused by cutting

The experiment was set up with plants grown in individual pots at a density of 10 plants per tank, of which 2 replicates per tank of each species were harvested. In total there were 6 treatment-combinations: untreated (UNTR), low shade (LS), high shade (HS), single cut (C1), two cuts (C2), and low shade + single cut (LS/C1). Shade treatments were as in Experiment 1.

Statistical treatments

Data were analyzed using GENSTAT, as follows: Experiments 1 - 3: ANOVA followed by orthogonal mean separation using Tukey's LSD test; Experiment 4: two-way ANOVA with orthogonal contrasts (UNTR v. LS; UNTR v. C1; LS v. HS; C1 v. C2; LS/C1 interaction). In the results outcomes are treated as significant at $P<0.05$ throughout.

Results

Experiment 1. Effects of stress caused by shade

Data shown in Fig. 2 are 77 days from start of the experiment. Shade stress produced little significant response by either species. Both showed no significant change in length per plant (except for *Myriophyllum* under high shade: 19% increase) in response to reduced light availability. There were no significant effects on biomass per plant for either species. In terms of resource allocation no significant response was observed by either *Elodea* or *Myriophyllum* in biomass allocation to stem or leaves as a result of shading. For *Elodea* there was no change in root biomass either, but *Myriophyllum* showed a significant (71%) reduction in root biomass at high shade, compared with unshaded controls. The results for *Myriophyllum spicatum* mirror the findings of previous work, for example by Barko & Smart (1981).

Experiment 2. Effects of disturbance caused by cutting

Data shown in Fig. 1 are 123 days from start of the experiment. Compared with untreated controls *Myriophyllum* showed a significant response to both single and double cut treatments: for both biomass (45 and 90% reduction after 1 and 2 cuts respectively), and length per plant: (22 and 70% reduction). For *Elodea* the effect was less, especially for length response, where there was no significant change after 1 cut, and only 44% reduction after two cuts. The biomass response of *Elodea* was more marked, with reductions of 41 and 59% after 1 and 2 cuts respectively.

Experiment 3. Effects of interspecific competition

Data shown in Fig. 3 are 84 days post-treatment. The two species responded differently to interspecific competition. Compared with growth in monoculture, there was a significant reduction (25%) in plant length of *Elodea*, but no significant reduction in plant biomass, when grown with *Myriophyllum*. The converse was seen for the two variables measured in *Myriophyllum*: a significant reduction (33%) in plant biomass, but with no significant reduction in plant length, when grown with *Elodea*.

Experiment 4. Combined effects of shade stress and disturbance caused by cutting

The results shown in Table 1 are % changes, for the orthogonal comparisons shown, two for variables measured 74 days after treatment. A stronger response to shade stress was seen in *Myriophyllum,* with biomass being significantly reduced by LS treatment, whereas no significant response was observed under low shade conditions for *Elodea*. Adding in cutting disturbance to low shade stress produced a greater effect on *Myriophyllum* than on *Elodea*. The effect on *Myriophyllum* was similar to that of high-disturbance treatment; much less for *Elodea*. The effects of cutting disturbance alone were similar for both species.

Discussion and conclusions

Tolerance of stress and disturbance

Myriophyllum showed a more plastic growth response to shade stress: by reducing resource allocation to roots, and increasing its length. These results are suggestive of a rather low tolerance of stress (Grime 1979). The results of Experiment 4 also suggested that *Elodea* was slightly more tolerant of shade stress than *Myriophyllum*.

Elodea was slightly more disturbance-tolerant than *Myriophyllum*. In both **Experiments 1 and 4 the responses** of *Myriophyllum*, in **terms** of biomass-reduction, and reduced plant length, were usually similar to, or greater than for *Elodea*. *Elodea* was more tolerant than *Myriophyllum* of combined stress and disturbance, at moderate intensities of both pressures.

These results are of relevance when considering the response of the two species to weed control measures based on stress and disturbance. *M. spicatum* has frequently been observed to respond positively to disturbance produced by cutting or harvesting (Smith & Barko 1990). The results of our study suggest that applying disturbance-based weed control to *Elodea canadensis* is likely to produce an even worse result in weed control terms.

Competitiveness

From the results of Experiment 3, *Elodea* was the more competitive of the two species when grown in mixed culture with each other under standard glasshouse conditions. Although *Elodea* produced shorter plants in competition with *Myriophyllum*, *Elodea* showed no significant loss of biomass compared with monoculture controls. In contrast, *Myriophyllum* plants competing with *Elodea* showed significant biomass loss.

Separation of strategies of Elodea *and* Myriophyllum

The two freshwater plant species studied here, both of which act as opportunistic weeds, and which tend to occur in similar habitats (Nichols & Shaw 1986), had measurably different responses to stress, disturbance and competition, under standardized experimental conditions.

Field evidence from comparison of drainage channel habitats of the two species in Britain (Sabbatini & Murphy, these Proceedings) has suggested that there is a tendency for *Elodea* to occur in slightly higher-stress conditions than *Myriophyllum*. Sheldon & Boylen (1979) found that *E. canadensis* had the deepest maximum depth (compared with *M. spicatum* and *Potamogeton crispus*) in US lakes. Nichols & Shaw (1986) considered that *E. canadensis* is the "most efficient" of these three submerged macrophyte species in surviving low light conditions. There is further evidence in the literature that *M. spicatum* is only poorly-tolerant of shade stress (e.g. Chambers & Kalff, 1985). In neither species, however, does stress-tolerance seem to play a major role in established-phase strategy. Much more important are traits for disturbance-tolerance and competitiveness.

The established-phase strategies of these two species are certainly close (for most populations of the two species, probably competitive disturbance-tolerant CD), but there are interspecific differences in response to environmental pressures on survival, which indicate that their strategies can be separated. This highlights the problem of relying on a descriptive terminology for plant strategy, such as that put forward by Grime (1979). When two species have closely-similar strategies, as in the case of *Elodea canadensis* and *Myriophyllum spicatum*, classification into broad categories such as "competitive disturbance tolerator" do not adequately reflect the functional differences between the species. What is needed is a numerically-based methodology to describe strategy and functional type of plant species, which would allow better quantification of the differential responses of plants to pressures on their survival and reproduction. An increasing amount of work is currently being devoted to developing functional analysis methods along these lines, for aquatic and wetland vegetation as well as terrestrial plants (e.g. Hills *et al.* 1994; Abernethy 1994 in prep.; Pantou & Arens 1994; Bornette *et al.* 1994; Hendry & Grime 1993). The appropriate application of approaches such as these may lead to an improved understanding of both the ecology, and susceptibility to control measures, of nuisance species such as *Elodea canadensis* and *Myriophyllum spicatum*.

Acknowledgements

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Table 1. Percentage response of *Elodea canadensis* and *Myriophyllum spicatum* length and biomass per plant for 5 orthogonal comparisons. Treatment codes are given in text. NS: not significant (P>0.05); other values are significant at P<0.05 for comparison)

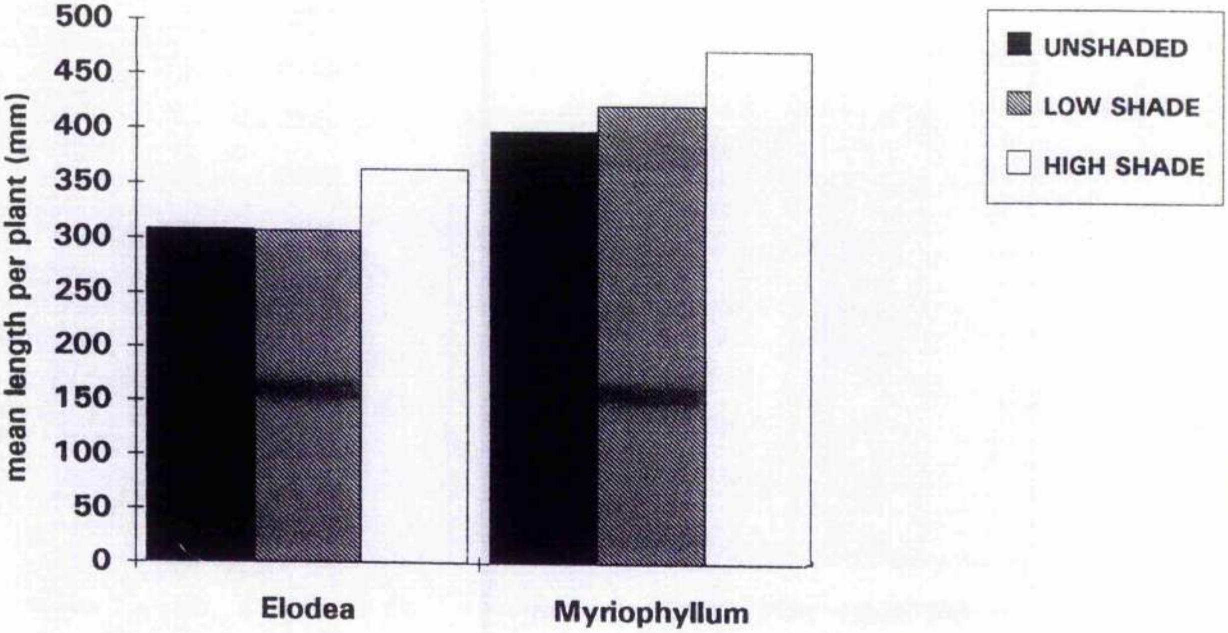
Treatment comparison	Reduction (%)			
	Elodea		*Myriophyllum*	
	Length	Biomass	Length	Biomass
UNTR v. LS	NS	NS	NS	53
LS v. HS	NS	77	NS	NS
UNTR v. LS/C1	NS	49	62	85
UNTR v. C1	37	38	NS	38
C1 v C2	43	88	66	83

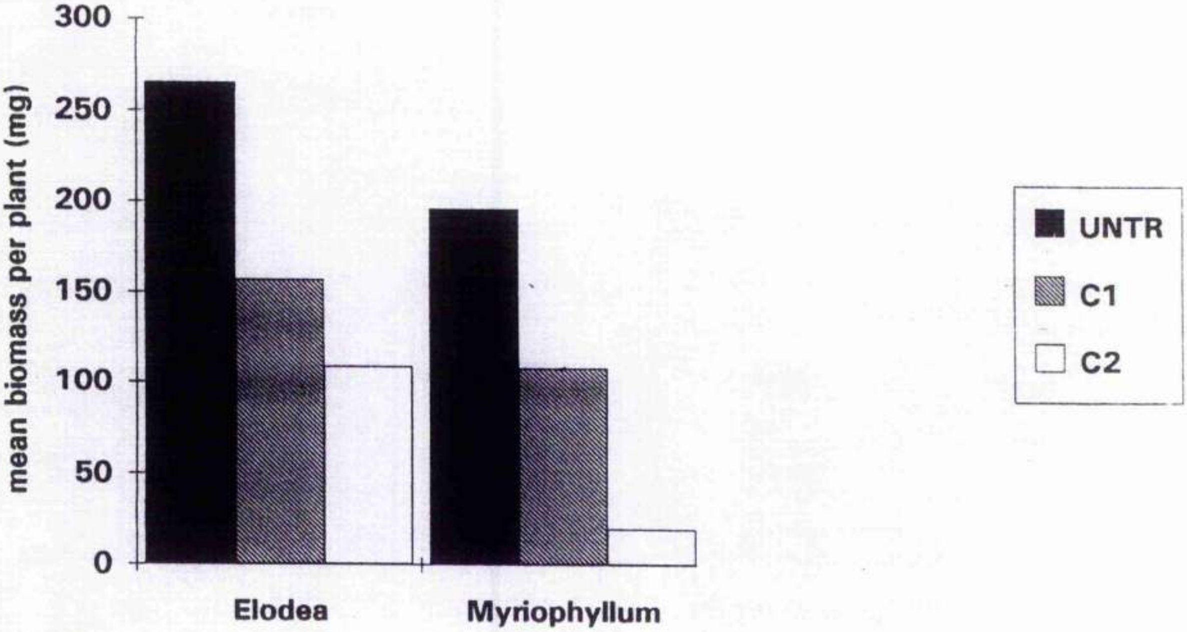
Figure captions

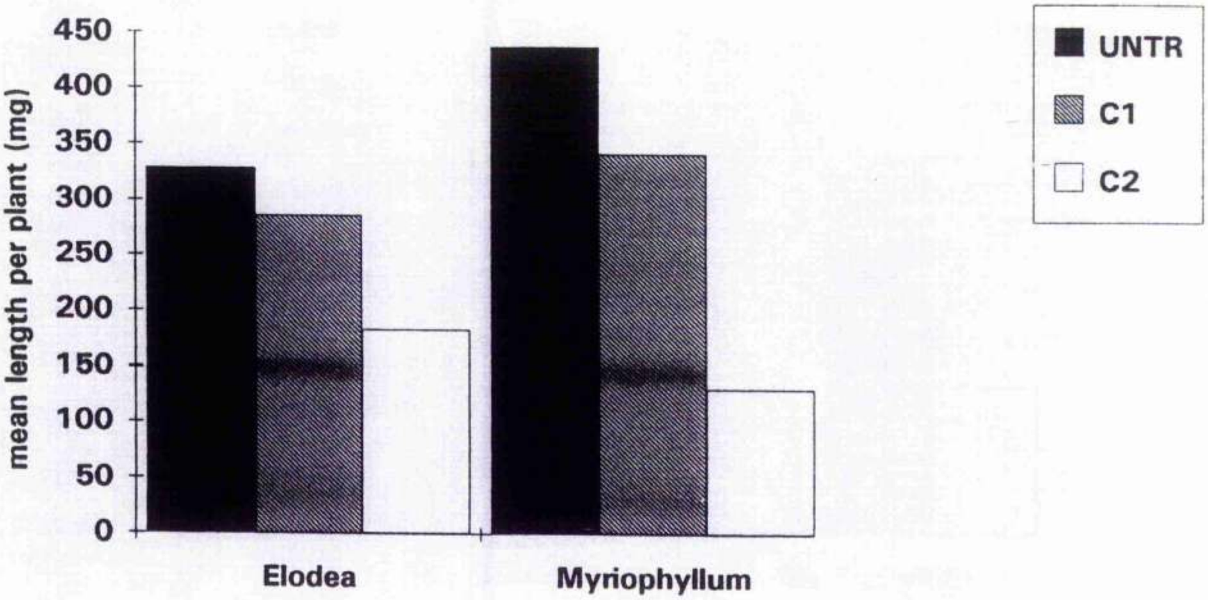
Fig. 1. Effects of stress caused by shade on (a) length, and (b) biomass per plant of *Elodea canadensis* and *Myriophyllum spicatum.*

Fig. 2. Effects of disturbance caused by cutting on (a) length, and (b) biomass per plant of *Elodea canadensis* and *Myriophyllum spicatum.*

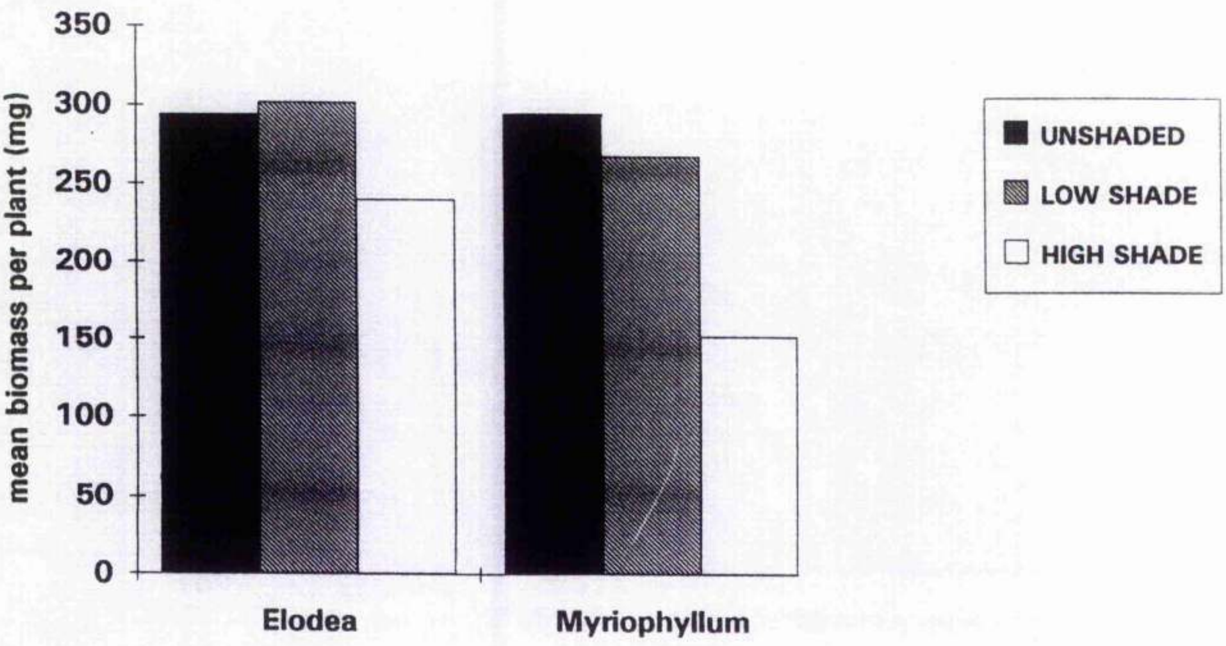
Fig. 3. Effects of interspecific competition on (a) length, and (b) biomass per plant of *Elodea canadensis* and *Myriophyllum spicatum*, grown in pure and mixed culture.


500
450
400
350
300
250
200
150
100
50
0
mean length per plant (mm)
Elodea
Myriophyllum
■ UNSHADED
▨ LOW SHADE
☐ HIGH SHADE

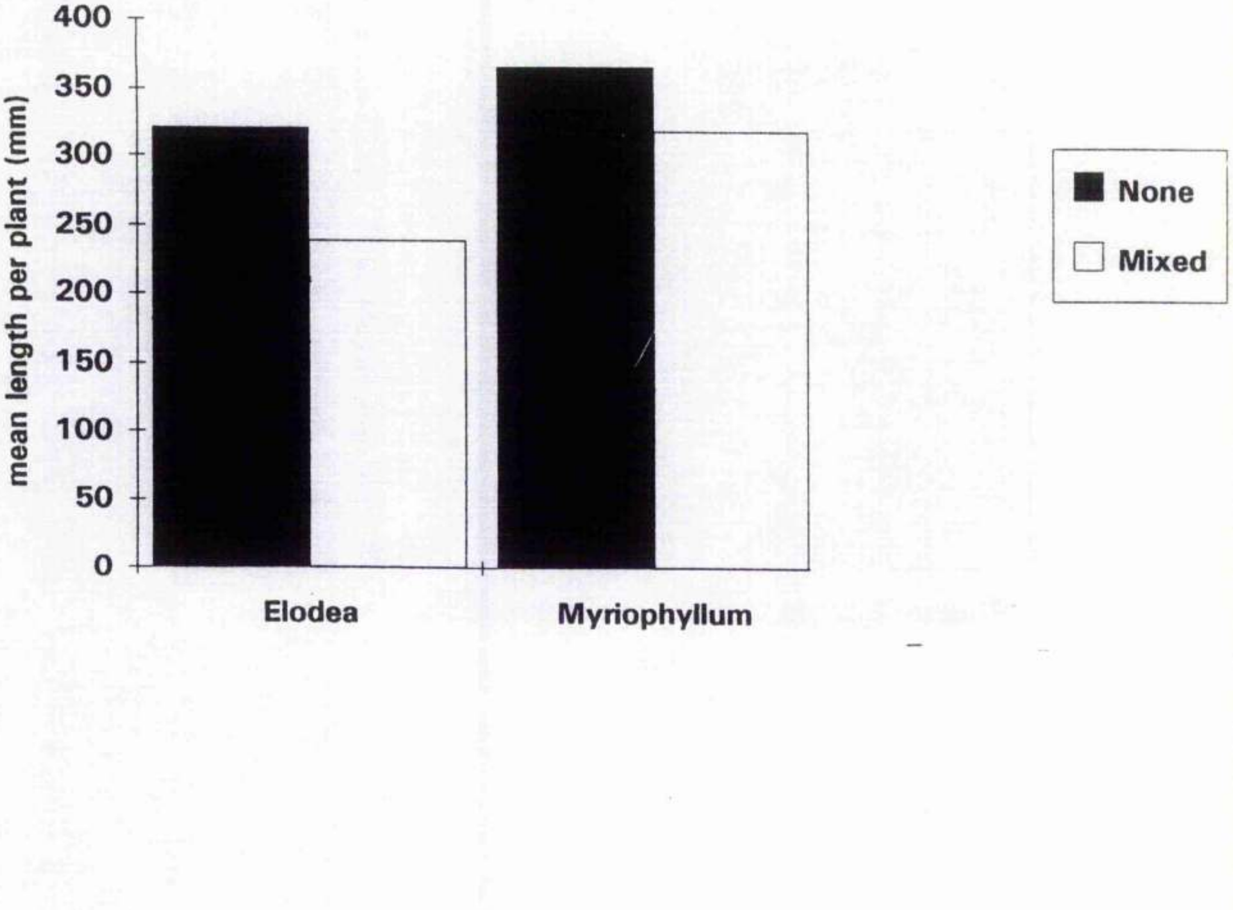

300
250
200
150
100
50
0
mean biomass per plant (mg)
Elodea
Myriophyllum
UNTR
C1
C2



mean length per plant (mg)
450
400
350
300
250
200
150
100
50
0
Elodea
Myriophyllum
UNTR
C1
C2



350
300
250
200
150
100
50
0
mean biomass per plant (mg)
Elodea
Myriophyllum
■ UNSHADED
▨ LOW SHADE
☐ HIGH SHADE



400
350
300
250
200
150
100
50
0
mean length per plant (mm)
Elodea
Myriophyllum
■ None
□ Mixed