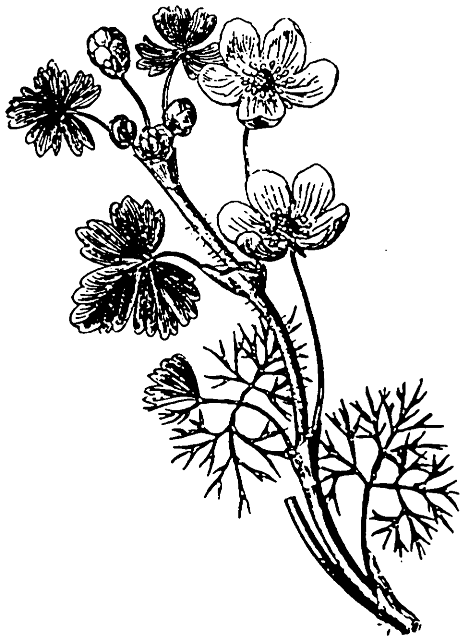
THE ECOLOGICAL STRATEGIES OF AQUATIC *RANUNCULUS* SPECIES



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

by

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Preface

Declaration

I hereby declare that this thesis is composed of work carried out by myself unless otherwise acknowledged and cited and that the thesis is of my own composition. The research was carried out in the period April 1989 to December 1991. This dissertation has not in whole or in part been previously presented for any other degree.

Terminology

Nomenclature of mosses follows Smith (1978) and of vascular plants follows Clapham, Tutin and Moore (1987), with the exception of *Ranunculus* subgenus *Batrachium*, which follows Webster (1988b).

The frontispiece is taken from a drawing of *Ranunculus aquatilis* in Johns (1894)

Acknowledgements

The work described in this thesis would not have been possible without the help of many people. I an indebted to Professor Richard Codgell for the use of the facilities of Glasgow University Department of Botany and for Professor A.D. Berrie for the use of the facilities of the Institute of Freshwater Ecology River Laboratory. The work was financed by the U.K. Natural Environmental Research Council.

Many of the staff at the River Lab have given me practical assistance with the work based there. I would particularly like to thank Bill Beaumont, Hugh Dawson, Brian Dear, Mike Furse, Paul Henville, Mike Ladle, Di Morton, Val Palmer, Graham Richards, Stan Shinn, Sue Smith and Stuart Welton. I would also like to thank Jean Lishman and the other staff at Ferry House for helping with the plant chemical analysis.

Likewise the work based in Glasgow could not have been carried out without the help of people there. I am grateful to Aileen Adams, Magdi Ali, Jim Dickson, Hugh Flowers, Jeremy Hills, Sue Marrs, Jim McGonegal and Ian Pulford for the practical help and useful discussions as well as the support and encouragement that they have given me. The experiment carried out in the Mouse Water (Chapter Four) was carried out jointly between myself and Magdi Ali.

The survey work was made considerably pleasanter by the hospitality given by friends. I would like to thank Tim Bennett, Eileen Butt, Gordon & Pat Doughty, Andrew & Jo Eddleston, Conrad & Sonia Hicks, Terry & Anne Mart, Andy Parsons, David Spink & Lynne Smith, Martin & Jean Tullett, Mark & Helen Wilson and Lyndsey Wood. I should like to pay tribute to the mechanics of the Automobile Association, without whom the final survey would never have been completed. I am also grateful to all the riparian owners who gave permission for work on their land and for the Nature Conservancy Council for permission to work on National Nature Reserves and Sites of Special Scientific Interest. I should like to acknowledge the help I have received from the Clyde and Forth River Purification Boards and from the National Rivers Authority (particularly Elaine Axeford, Liz Chalk and Ed Mycock). Jane Smart (Biological Records Centre) also provided me with invaluable information.

My parents, Neville & Iris Spink, have not only provided hospitality during survey and experimental work but have acted as field assistants on several occasions. I would like to acknowledge not only their help in that but also to express my gratitude for the help, encouragement and support they have given me over the years.

It is a customary duty to acknowledge the help given by supervisors. In this case it is also a pleasure. Derek Westlake has always given me sound and wise advice and I am particularly grateful for his continuing and unpaid assistance following his 'retirement'. As for Kevin Murphy, I simply could not have asked for a better supervisor.

Abstract

A survey involving repeated visits to 56 river sites with a variety of Batrachian *Ranunculus* species was carried out. Analysis of the data using CANOCO suggested that the following measured environmental variables were the most important in determining the plant community composition; pH, sediment nitrogen, phosphate and potassium concentration, shade, water velocity, water phosphate concentration and elevation. In addition, management by cutting and grazing and poaching by cattle were important variables. Chemical analysis of plant and sediment samples revealed significant positive correlations between the concentrations of *Ranunculus* shoot tissue phosphate and water phosphate, *Ranunculus* phosphate and sediment phosphate, and *Ranunculus* nitrogen and water nitrate. A series of transplant trials were carried out to determine to what extent it was possible for *Ranunculus* species to survive outside of the conditions in which they were found in the survey.

Three of the stresses identified in the survey were further investigated in experimental work; shade, low water velocity and eutrophication. A field experiment was carried out on a tributary of the River Frome (a chalk stream dominated by *Ranunculus penicillatus* subsp. *pseudofluitans*). The change in community composition in shaded plots compared with unshaded plots was measured during the growing season. The following season the experiment was repeated, but with the additional stress of reduced water velocity. During the first season the *Ranunculus* cover was much less in the shaded plots, and the cover of other members of the plant community was also significantly less in the shaded plots. During the season with reduced water velocity *Elodea canadensis* rather than *R. penicillatus* subsp. *pseudofluitans* became the dominant species, and the community reacted in a similar way to the shade stress. There was less total plant growth (more visible substrate) in the low velocity (increased stress) season and a higher species diversity.

The effects of elevated phosphate concentration were investigated in an experiment in a pair of artificial recirculating rivers. One of the rivers had the phosphate input raised from 40 $\mu gP\ l^{-1}$ to 200 $\mu gP\ l^{-1}$, which resulted in prolific filamentous algal growth. *R. penicillatus* subsp. *pseudofluitans* and *Potamogeton pectinatus* plants showed a reduction in

growth in the elevated phosphate (presumably due to shading from the algae), and where *Ranunculus* and *Potamogeton* plants were grown next to each other, the *Ranunculus* root biomass was significantly reduced.

Several experiments were carried out on the effects of disturbance on *Ranunculus penicillatus* subsp. *pseudofluitans*. *Ranunculus* clumps were cut repeatedly in the River Rye. It was discovered that after the first and second cuts, the shoots showed increased growth but after the third cut they showed decreased growth. By contrast, in two experiments carried out in polluted sites (Gogar Burn and the headwaters of the River Hull), there was no evidence for an increase in growth after a single cut. *Ranunculus* species are associated both with particular current velocities and particular sediment particle sizes. Does this correlation with sediment imply that the sediment causes the distribution, or is sediment texture itself simply a reflection of current velocity? An experiment in the Mouse Water found no correlation between *Ranunculus* growth and sediment particle size, suggesting that current velocity is the primary determinant.

Throughout the thesis the data were interpreted in terms of C-S-R strategy theory. A greenhouse shading experiment ranked four *Ranunculus* taxa in terms of their stress-tolerance (*R. hederaceus* > *R.circinatus* > *R. penicillatus* subsp. *pseudofluitans* > *R. fluitans*). The data from the survey were used to devise integrated indices of stress and disturbance for each site surveyed, and this was then used to determine the importance of stress and disturbance in the habitats occupied by the various *Ranunculus* species, and by implication the importance of stress and disturbance in the strategy of those species, i.e. the C-S-R strategy of each species. A further survey was carried out of 57 river sites with *Ranunculus* species present, and various morphological attributes were measured on the plants. These attributes were then regressed against the strategy of the plant in order to determine which traits are associated with a particular strategy. Stress-tolerant species tend to have floating leaves, lack divided submerged leaves, and tend to have small, weak shoots. Disturbance-tolerant species lack floating leaves and have large, strong shoots. Competitive taxa tend to have long submerged leaves, and lack floating leaves.

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1. INTRODUCTION

"Water Crow-foot hath tender branches trailing far abroad, whereupon grow leaves under the water most finely cut and jagged like those of Cammomill. Those above the water are somewhat round, indented about the edges, in form not unlike the tender leaves of the mallow but lesser: among which do grow the floures, small, and white of colour, made of five little leaves, with some yellowness in the middle like the floures of the straw-berry, and of a sweet smell: after which these come round rough and prickly knaps like those of the field Crowfoot. The roots be very small hairy strings."

Gerard (1633)

1.1 Riverine *Ranunculus* Species

Ranunculus subgenus *Batrachium* (DC.) A. Gray species are the dominant plants of many British streams and rivers, especially in lowland streams subjected to regular cutting. Their flowers are similar in appearance to meadow buttercups (*R. repens, R. acris*), except that their petals are white rather than yellow. Some *Ranunculus* plants growing in rivers may reach a length of several metres, causing problems for navigation and sometimes increasing the risk of flooding (see for example Murphy *et al.* 1990). Dawson (1989) has estimated that the cost of aquatic plant management in the U.K. could be as high as £100 million, with a large proportion of this being devoted to the control of *R. fluitans* and *R. penicillatus*.

The plants appear to have little current or historical positive medicinal or agricultural uses although Pultney (1798) described how farmers in Hampshire fed cattle, horses and pigs on '*R. fluitans*' from the River Avon, in some cases the *Ranunculus* forming almost the entire diet of the animals. The cattle were reported to find it so palatable that they had to be restrained to eating 11 - 14 kg each day. Cattle in Dorset still graze *R. penicillatus* when given the opportunity (pers. obsv.) and a local farmer has described how when his cattle are let into a field adjacent to the River Frome for the first time in the Spring they ignore the fresh grass and instead eat the *R. penicillatus* in the river.

Along with the majority of aquatic plants, *Ranunculus* species tend to be dismissed as 'water weeds', though as well as the common name of Water Crowfoot, Lodewort and Rams Foot have been historically used as names for the subgenus (Gerard 1633). Grigson (1955) reports a number of regional names including Bacon and Eggs (Somerset), Cow-Weed (Hampshire), Eel Weed (Donegal), Rait, Pickerel Weed (East Anglia - a pickerel is a young pike), and Rawheads (Shropshire). Scots Gaelic names include *fleann uissage* (water-follower) and *lion na h'aibhue* (the river flax) (Cameron 1883).

The taxonomy of the group is difficult and complex due to extreme phenotypic plasticity together with morphological reduction (Webster 1984). Over 300 synonyms have been applied to the taxa in the group and it was not until Cook's 1966 monograph that the situation began to be resolved (although it is still far from clear: Webster 1991). As Babington (1855) put it 'the great difficulty of the subject necessarily weighs heavily on the mind'. More recently Wiegleb (1988) wrote that 'in *Batrachium*... all kinds of hybrids, intermediates and mysterious forms occur which should not puzzle the observer'. The taxonomic uncertainly has led to it being quite unclear which species are being referred to in some earlier ecological work, with associated imprecision in distribution maps, etc.

Like much of the rest of ecological science, it can be argued that studies on the ecology of freshwater aquatic macrophytes have suffered from too many isolated observations and not enough interpretation of the data to give broad theoretical theories (Harris 1985). It is possible that plant strategy theory (Grime 1979) may provide a suitable framework to enable it to be posssible to come to an understanding of the ecology of the sub-genus.

The various ecological studies that have been made concerning the British riverine Batrachian *Ranunculus* species are reviewed below, with the exception of those observations and experiments particularly relevant to work described in chapters later on in this thesis, which are dealt with in the introduction to those chapters. This introductory chapter then concludes with an outline of plant strategy theory, particularly as it has been applied to aquatic communities.

1.1.1 *Ranunculus omiophyllus* Ten. and *Ranunculus hederaceus* L.

These two species are distinct from the rest of the sub-genus due to the absence of submerged, dissected leaves (Cook 1963). It is thought that they have evolved from amphibious ancestors and have lost the ability to develop submerged divided leaves (Cook 1966b, 1970). *R. hederaceus*, as the name implies, has leaves shaped somewhat like the ivy, with the lobes widest at the base, whereas *R. omiophyllus* has more rounded lobes which are narrowest at the base. Although the leaf shapes are fairly distinct (Fig. 1.1), they can be quite variable (Pearsall 1929) which has given rise

Figure 1.1

Shape of floating leaves in Batrachian *Ranunculus* species.

All drawings are life-size. Further details of the sites from which the plants were taken may be found in Appendices A & B

1. *R. peltatus* from River Bourne

2. *R. peltatus* from Eddleston Water

3. *R. baudotii* from Twyn y Pnrhy (intermediate leaf)

4. *R. baudotii* from Twyn y Pnrhy

5. *R. omiophyllus* from River Fowey

6. *R. omiophyllus* from Craigend Burn

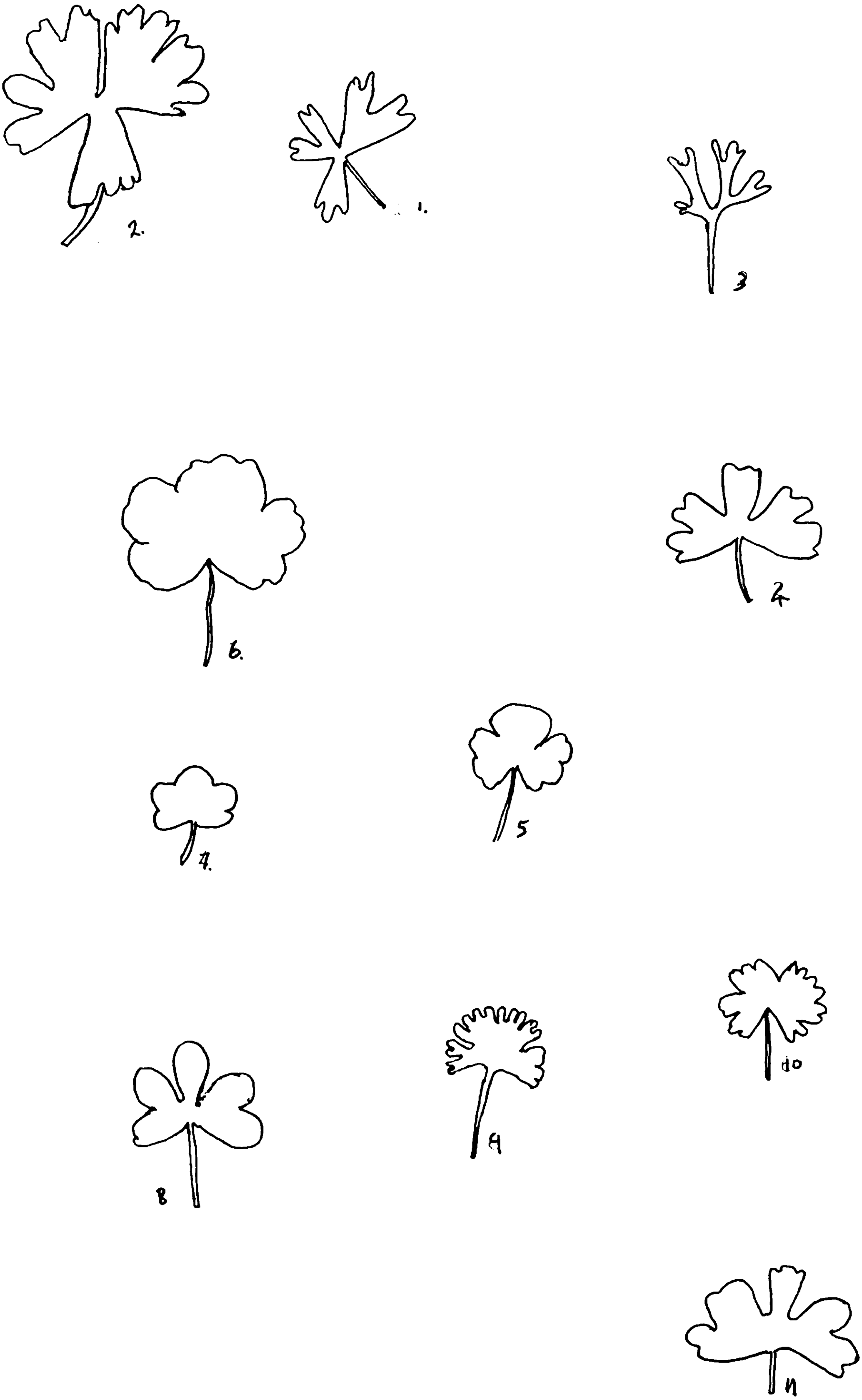
7. *R. hederaceus* from Craigleith Burn

8. *R. penicillatus* subsp. *penicillatus* from River Torridge

9. *R. aquatilis* from pond at Harome, North Yorkshire. National Grid Reference SE 643 806

10. *R. aquatilis* above site.

11. *R. penicillatus* subsp. *penicillatus* from River Torridge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to problems of identification in the past (Babington 1855), though the leaves do retain the characteristic form of each species (Cook 1966a).

When in flower there is no problem distinguishing between the two species; *R. omiophyllus* has petals which are at least twice as long as the (often recurved) sepals, whereas the petals in *R. hederaceus* are much smaller (usually 2.5-3.5 mm) (Holmes 1979; Webster 1988b).

R. hederaceus grows throughout the British Isles with the exception of part of the central and northern Scottish Highlands and a somewhat scattered distribution in southern and eastern England (Biological Records Centre, personal communication 1991; Perring & Walters 1976). The common name, Mud Crowfoot, reflects its habitat in that it tends to be found in wet mud at the edges of pools, ditches, etc (Webster 1988b). A recent study in The Netherlands has shown that *R. hederaceus* is less common there but occupies similar habitats to those it is found in in Britain. It appears to be in decline due to changes in the hydrological stability of its sites rather than actual habitat destruction (van Diggelen & Klooker 1990).

R. omiophyllus has a more Western distribution than *R. hederaceus*; in a recent phytogeographical study Arts & Den Hartog (1990) described it as a characteristic Atlantic species. In Britain it is only found in regions where the mean August rainfall is greater than 75 mm (Webster 1988) and so it is less common than *R. hederaceus* and is absent from much of Scotland, Ireland and eastern England (Biological Records Centre, personal communication 1991; Perring & Walters 1976).

Salisbury (1934) considered that *R. hederaceus* grows in mineral waters whereas *R. omiophyllus* is 'invariably' found in more peaty waters, and this is still thought to be a good generalisation (Webster 1988b). Newbold and Palmer (1979) have ranked all the British aquatic species according to the nutrient ('trophic') status of the waters in which they grow. By this ranking *R. omiophyllus* has a trophic rank of 19 (oligotrophic) and *R. hederaceus* has a trophic rank of 150 (eutrophic).

In Britain *R. omiophyllus* appears to be a calcifuge (Clapham, Tutin & Moore 1987), but Cook (1966a) has observed it growing on a calcareous substrate in Italy. In cultivation British material of *R. omiophyllus* and *R. hederaceus* grows equally well on calcareus and non-calcareus substrates (Cook 1966b). Both tend to grow in somewhat open and disturbed habitats (Webster 1988). Occasionally the two species grow together (Salisbury 1934; see Mill Lawn Brook in Appendix A), but they do not hybridize (Cook 1970). *R. omiophyllus* forms a natural hybrid with *R. peltatus* (Webster 1984, 1986; see Avon Water in Appendix A), known at *R. hiltonii* Groves & Groves after Mr T. Hilton who discovered it in 1896 (Groves & Groves 1901). This plant is highly unusual as it overwinters in the heterophyllous state. It is also a British endemic (Stace 1991). *R. omiophyllus* also forms a natural hybrid with *R. tripartitus* (*R.* × *novae-forestae* S. Webster) (Webster, 1990) which to a large extent replaces the parent species in the New Forest (Cook 1975).

1.1.2 *Ranunculus aquatilis* L.

Linnaeus (1762) recognised just two species in what is now the sub-genus *Batrachium; R. hederaceus* and *R. aquatilis*. As recently as 1951 Willis described the other taxa as 'so-called species', preferring to keep *R. aquatilis* to include the whole sub-genus. Although this position finds little support today, the decision as to how to separate the various taxa, and at what hierarchical level the separations should lie would appear to be far from settled, in spite of recent photochemical and morphological studies (Webster 1984, 1991). In this thesis the nomenclature and classification of Webster (1988b) is followed.

R. aquatilis sensu stricto has a number of characteristics that enable it to be distinguished from other members of the sub-genus. It has both dissected and floating leaves, the latter tending to have rather more crenate (i.e. less rounded) lobes than *R. peltatus* *(Fig. 1.1)* - which it otherwise closely resembles. However in flower it is easily distinguished by the circular shape of the nectar pit (though this characteristic must be used with care as the shape undergoes a developmental sequence, so that it is only reliable on mature petals). *R. aquatilis* also forms intermediate leaves with a proximal capillary portion (see Fig 1.1). In common with all the species with dissected leaves it also grows in a

Figure 1.2

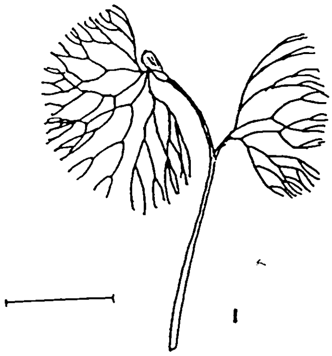
Shape of dissected leaves in Batrachian *Ranunculus* species.

In drawing 1 the scale bar represents 10 mm, the other drawings are life-size. Further details of the sites from which the plants were taken may be found in Appendices A & B

1. *R. circinatus* from Old Bedford River; sample drawn after being grown in cultivation in the greenhouse at Glasgow University Botany Department.

2. *R. penicillatus* subsp. *pseudofluitans* var. *pseudofluitans* from the West Sussex Rother showing obconical shape.

3. *R. fluitans* from Hay-on-Wye



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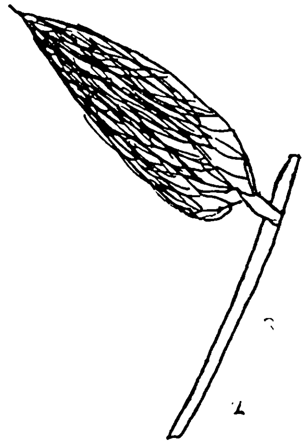

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terrestrial form, in which it is indistinguishable from the other species, even when in flower (Webster 1988b).

R. aquatilis has been used in a variety of studies on the mechanisms underlying the control of heterophylly (for example Askenasy 1870, Bostrack & Millington 1962, Davis and Heywood 1963; Cook 1969). Nielsen & Sand-Jensen (1989) found that it had an intermediate photosynthetic rate compared with thirteen other aquatic species studied (4.92 mg O_2g^{-1} h^{-1} at pH 8.3) though a higher than average dark respiration rate (1.20 mg O_2g^{-1} h^{-1}). It was found to have one of the highest laboratory growth rates of the species studied (0.097 day^{-1}). This growth rate is very similar to that found in field experiments (0.092 day^{-1}) by Nørgaard (1989) for *R. peltatus*.

Litav & Agami (1976) & Agami *et al.* (1976) found that it was one of the species that disappeared from the River Yarkon over a 25-30 year period, during which time a variety of pollutants (especially detergents) increased in concentration in the river.

R. aquatilis is found in scattered localities throughout much of the British Isles and is the commonest species that grows in still water (Butcher 1960) but it is absent from much of Scotland and Ireland (Biological Records Centre, personal communication 1991; Perring & Walters 1976).

Crowder *et al.* (1977) found that it grows over a wide range of substrate-types, although Haslam (1978) found it tended to grow on harder rock-types than *R. peltatus*. Especially in the lowlands, it is more commonly found in ponds than streams. It is frequently found in farm ponds (Pip 1979, Webster 1988b), but if these are very enriched it is displaced by other species. It appears to be able to tolerate a moderate amount of disturbance in the form of drought and grazing (NCC 1989). Newbold and Palmer (1979) placed it at trophic rank 70.

The National Vegetation Classification of Aquatic Communities (NCC 1988) found that *R. aquatilis* was most frequently associated with *Callitriche* species (especially *C. stagnalis* and *C. obtusangula*) and *Glyceria fluitans*. It grows in very similar habitats to *R. peltatus* - Cook (1966a) reports that the two species do not grow together, although natural hybrids have been reported (Stace 1991) and *R. trichophyllus* is found growing intermingled with both of them.

R. aquatilis forms several natural hybrids (Cook 1975, Webster 1990, Stace 1991). It hybridises with *R. fluitans* (*R.* ×*bachii* Wirtgen), *R. baudotii* (*R.* ×*lambertii* A. Felix), *R. trichophyllus* (*R.* ×*lutzii* A. Felix), *R. peltatus* (*R.* × *virzionensis* A. Felix) and *R. tripartitus* (no name).

1.1.3 *Ranunculus peltatus* Schrank

R. peltatus is morphologically and ecologically similar to *R. aquatilis*, especially when not flowering (although Butcher (1960) considered it to be quite different physiologically). When in flower, any confusion which arises is more likely to be with *R. penicillatus* subsp. *penicillatus* as it has similarly sized petals and the same shaped nectary pit as well as similar floating leaves. The most reliable character to separate them is that in *R. peltatus* the dissected leaves are distinctly shorter than the internodes, whereas they are longer in *R.* subsp *penicillatus* (Webster 1984; Holmes pers. comm. 1991).

R. peltatus has a similar distribution in the British Isles to *R. aquatilis*, but it is found in a greater number of localities (Biological Records Centre, personal communication 1991).

Although it has a closely similar carbon extraction capacity to *R. aquatilis* (Madsen & Sand-Jensen 1991), *R. peltatus* seems to be a little more stress-tolerant than *R. aquatilis*, growing in a little deeper water (Holmes 1979) and with the widest physical range of habitats amongst the sub-genus (Haslam 1978). It has a lower trophic rank than *R. aquatilis* (48; Newbold and Palmer 1979). However, Monschau-Dusenhausen (1982) found that it was the most pollution-sensitive species of a range of aquatic macrophytes.

It can tolerate greater fluctuating levels of water and is the most frequent *Ranunculus* species in reservoirs (Grime, Hodgson & Hunt 1988). Arts *et al.* (1990) found that it was found in waters in The Netherlands

Plate 1

Ranunculus peltatus

River Bourne at Idmiston, Wiltshire. Site Number 55 in 1990 Survey (see Appendix A for details). Photograph taken on 1st May 1990, 28 mm lens. Magnification × 1.7

with a mean pH of 6.8 and a mean alkalinity of 0.7 (meq l^{-1}). At pH values of less than 5.7 damage occurred to the plants. Dawson & Kern-Hansen (1979) showed that there was a linear relationship between the amount of artificial shading applied to a *R. peltatus* community and its standing crop.

Cook (1966a) described it as being characteristic of temporary or disturbed habitats, and Ladle & Bass (1981) have described how *R. peltatus* displaced *R.* var. *pseudofluitans* when a chalk stream suffered severe disturbance as it dried up in a period of drought. The colonization of *R. peltatus* was by means of seedlings germinating on the dry stream bed. *R. peltatus* is frequently found at the head of winterbournes (see in Appendix A the Rivers Bourne & Wylye). Valane *et al.* (1982) have shown that *R. peltatus* has a lower degree of intercellular structural adaptation to being submerged than *R. baudotii*. *R. peltatus* has epidermal cells overlaying chloroplast cells (a characteristic of terrestrial plants) and the ultrastructure of its chloroplasts are more similar to those normally found in land plants than aquatics.

Cook (1966a) stated that as the water 'matures' in a pond *R. peltatus* (as well as *R. aquatilis* and *R. trichophyllus*) is replaced by rhizomatous species such as *Potamogeton pectinatus* and *P. crispus*. However if the water is susceptible to regular disturbance *R. peltatus* can persist (NCC 1988). The species is susceptible to frost if not submerged but can withstand being frozen in ice (Cook 1966a).

Natural hybrids are formed with *R. omiophyllus* and *R. baudotii* (Webster 1986), *R. trichophyllus*, *R. aquatilis* (Stace 1991), and with *R. fluitans* (= *R.* × *kelchoensis* S. Webster; Kelso Water Crowfoot) (Webster 1990, Stace 1991) which has spread extensively along the River Welland (Cook 1975). It is possible that *R.* × *kelchoensis* is the taxon that gave rise to *R. penicillatus* subsp. *penicillatus*. (Stace 1991)

Babington (1855) considered *R. peltatus* ('*R. floribundus*') to be 'the most beautiful of our species; its large white flowers being so numerous as to cover the places that it inhabits with a sheet of bloom' (Plate 1).

1.1.4 *Ranunculus baudotii* Godron

R. baudotii is an uncommon species, occurring at only 170 sites in Britain. It is named after the botanist de Baudot of Saarburg (Barnhart 1965).

R. baudotii can be difficult to distinguish from *R. aquatilis* (Blackmore 1985), but although it has similar morphology its distribution is heavily influenced by the fact that (as Babington (1855) put it) it 'appears to delight in slightly brackish water'. Thus it is always found in coastal habitats, with the exception of a few inland records from Cambridgeshire brick pits (Biological Records Centre, personal communication 1991; Perring & Walters 1976). The most reliable character to distinguish it from *R. aquatilis* or other taxa is the shape of the receptacle which elongates in fruit. Other corroborative characteristics are the lunate nectar pit, blue-tipped sepals and winged fruits. The latter two of these characters do not always occur. *R. baudotii* shows considerable phenotypic plasticity. Another characteristic which is not constant is the formation of floating leaves, some populations (sometimes called 'form marinus' which has occasionally ben elevated to specific rank; see Moss 1914) do not form these leaves; for example the *R. baudotii* at the site at Worth Matravers, Dorset (Appendix A). Luther (1947) considered 'form marinus' to be a locally induced habitat form.

Although only found in brackish water, Cook (1966a) showed that it will grow with no loss of vigour in cultivation in fresh water. Cook (1966a) has reported it growing naturally at a site which is covered by the sea at high tide, and in cultivation it will survive in 100% sea water. Kautsky (1991) has found it in sites of up to 1% salinity. Van Viersen & Verhoeven (1983) came to the conclusion that *R. baudotii* was apparently not as salt tolerant as *Zannichellia pedunculata* or *Potamogeton pectinatus*.

Although in the UK it normally grows in shallow water of less than 0.3 m depth (Cook 1966a) it is found in deeper water occasionally (for example at 0.54m at Porth Oer, Gwynedd, see Appendix B) and Kautsky (1991) has recorded it growing at 3 m depth near Stockholm, Sweden. Kiørboe (1980) has observed a standing crop of 3.5 g dry weight *R. baudotii* m^{-2} in a water depth of 0.6 m in a Fiord in Denmark. It has a trophic rank of 133 (Newbold and Palmer 1979).

R. baudotii is characteristic of open and disturbed habitats (Webster 1988b). In view of this and its preference for shallow water it is significant that Van Viersen & Verhoeven (1983) considered its ability to survive desiccation as a decisive factor in its ecology. Kiørboe (1980) has reported wildfowl grazing on *R. baudotii* but concluded that because most of the grazing occurred outside of the plants' main growing season, the damage done would be negligible. The main wildfowl were *Cygnus olor, Anas platyrhynchos, A. penelope* and *Fulica atra*. Crivelli (1983) has described a negative effect of carp (*Cyprinus carpio*) on *R. baudotii*, which appeared to be caused more by uprooting than by an increase in turbidity or actually eating the plants. Reproduction of *R. baudotii* appears to be mainly by vegetative means (axillary buds) (Kautsky 1990).

Kautsky (1991) has shown that in an experimental situation *R. baudotii* grows better in a 50/50 mix of sand and mud than either pure mud or sand. In a de Wit replacement competition experiment Kautsky (1991) found that the effects of interspecific competition between *R. baudotii* and *Potamogeton filiformis* were less than the effects of intraspecific competition when *R. baudotii* was grown in monoculture. When *R. baudotii* was grown with *P. pectinatus* there was greater interspecific than intraspecific competition.

The National Vegetational Classification of Aquatic Communities (NCC 1988) described vegetation dominated by stands of *R. baudotii* but found there was no other species constantly associated with it. In standing or sluggish brackish waters *Ceratophyllum submersum* and *Potamogeton pectinatus* are associated with *R. baudotii* (see Van Viersen and Verhoeven 1983), and as the waters become more saline *Zannichellia* and *Ruppia spiralis* become more frequent. These communities appear to be in decline, so that the 170 sites referred to above may be an over-estimate.

R. baudotii forms natural hybrids with *R. aquatilis*, *R. peltatus* and *R. trichophyllus* (*R.* × *segretii* A. Felix) which is sporadic in occurrence (Cook 1975, Stace 1991).

1.1.5 *Ranunculus trichophyllus* Chaix

R. trichophyllus (as with all the species below) forms no floating leaves, just submerged, dissected leaves (hence the name, which means 'hair-like' Gledhill 1989). It may be distinguished from the other species which do not form floating leaves by its small (< 7mm) petals and lunate nectary pit (although *R. circinatus* has those characteristics its distinctive leaf-shape makes confusion unlikely). However, when it is not in flower it may easily be confused with *R. aquatilis* (Holmes 1979). Several of the sites visited in Lothian (see Appendix B), whilst carrying out the work described in this thesis, had old records of *R. trichophyllus* populations, but turned out to have floating-leaved species present.

R. trichophyllus is found in sites scattered throughout the British Isles, but with a pronounced south-easterly bias (Biological Records Centre, personal communication 1991; Perring & Walters 1976). On a global scale it is probably the most widely distributed Batrachian *Ranunculus* species (Drew 1936, Cook 1966a). It grows from sea-level to 2500 m in the Alps (Arber 1920). It has a trophic rank of 75 (Newbold and Palmer 1979). All the populations in Britain may be assigned to subspecies *trichophyllus* (Cook 1966a).

In temporary waters it behaves as an annual, but if conditions allow it to persist, it grows as a perennial (Holmes 1979). *R. trichophyllus* is more frequently found in eutrophic than oligotrophic waters (Cook 1966a). It is rarely found in swift currents (Holmes 1979) and is the only riverine *Ranunculus* species that has not been included in any of the work described in this thesis.

In spite of its wide distribution, relatively few studies appear to have been carried out on this species. Pond (1905) found that it grew better when rooted than when suspended in tap water. Dale and Miller (1978) observed that it decreased in abundance in a lake that was subjected to sewage and mining discharges over a thirty year period. Murphy & Pearce (1987) described the use of diquat alginate to control the growth *R. trichophyllus* in a Scottish loch used as a salmonid fishery. Lorch and Ottow (1988) have described the bacteria and diatoms that are epiphytic upon *R. trichophyllus*.

R. trichophyllus forms hybrids with *R. baudotii*, *R.aquatilis*, *R. peltatus*, and *R. circinatus* (Stace 1991). *R. trichophyllus* × *circinatus* is known as *R.* × *gluckii* A. Felix and is only found in some artificial pools in West Suffolk - it is rare as the parents are not often found together (Cook 1966a, 1975).

1.1.6 *Ranunculus circinatus* Sibth.

R. circinatus is instantly recognisable by its distinctive fan-shaped leaves, with radiating dividing spokes in one plane (Fig. 1.2). 'Circinatus' literally means 'curled round' (Gledhill 1989).

It has two distinct growth states; in the winter it is prostrate and branching and in the summer erect and simple. The winter state may persist in the summer if the plants are stressed. Both states can co-exist in the same individual (Cook 1966a).

The species does not grow in either fast currents or base-poor waters (Holmes 1979) and is thus virtually absent from upland regions of Britain (Biological Records Centre, personal communication 1991; Perring & Walters 1976). It is usually found in deep water - Luther (1951) recorded it at 5 m deep in Finland. Although it can behave as an annual (Salisbury 1960) it normally has a perennial life-history (Cook 1966a).

R. circinatus is usually found in relatively nutrient rich waters (Holmes 1979), and has a tropic rank of 98 (Newbold & Palmer 1979). It has occasionally been recorded in brackish waters (Olsen 1950) and waters with saline incursions (personal observation 1990, see Old Bedford River site in Appendix B). In a survey of Welsh lakes Seddon (1972) found *R. circinatus* in lakes with a conductivity of > 10 mS m^{-1} and a hardness ratio of >2.5. Bernatowicz (1965) observed the expansion of the range of a *R. circinatus* population in a Polish lake following cutting of the *Phragmites* stand in which it was growing.

Forsberg (1964) found that *R. circinatus* was unable to root in the soft sediments of a Swedish lake, in common with other macrophytes. In a survey of soft-water lakes in The Netherlands Arts & Leuven (1988) found *R. circinatus* occurring in a plant communities characterised by the absence of isoetids and the presence of *Fontinalis antipyretica*. This is a little surprising as although *F. antipyretica* is often found in rivers and lakes it is usually associated with shallow water (Watson 1955) - though it is sometimes found in deeper water, e.g. in the Frome in Dorset.

R. circinatus forms a hybrid with *R. fluitans* which grows in the Berwickshire Blackadder (Cook 1975).

1.1.7 *Ranunculus penicillatus* (Dumort.) Bab.

This taxon has been surrounded by what Holmes (1980) described as 'understandable confusion'. It was not until 1966 that Cook was able to show that it is a collection of segmental amphiploids resulting from hybridization (i.e. speciation has resulted from polyploidy occurring after hybridization). It is believed to have been formed as a result of hybridization of *R. fluitans* with *R. aquatilis*, *R. trichophyllus* and possibly *R. peltatus* (Stace 1975). Taxonomic opinion is still unresolved as to whether taxa within *penicillatus* should be divided from each other at the species level (Haslam & Wolseley 1981; Murrell and Sell 1990), subspecies (Webster 1988a, Stace 1991) or variety (Holmes 1980; Clapham Tutin & Moore 1987). In his 1855 monograph on the Batrachian *Ranunculi* of Britain, Babington observed that 'we have no good definition of a species... and that it is hard or even impossible to apply those which we possess'. One wonders if he might come to the same conclusion with *penicillatus* today, certainly modern biochemical techniques that have proved so useful in separating other taxa have as yet proved inadequate (Webster 1991).

R. penicillatus subsp. *penicillatus* is separated from *R. penicillatus* subsp. *pseudofluitans* (=*R. calcareus*) by the formation of floating laminar leaves in the former. Together with the disjunct distribution and differing ecology, Webster (1988a) considered this difference too great to allow separation only at the varietal level, but as this is the only difference she does not consider that the taxa merit specific rank. As there is morphological and geographical continuity between var. *pseudofluitans* and var. *vertumnus* Webster (1988a) assigned these two to varieties within the subspecies *pseudofluitans*.

Among the 'unfortunate circumstances' (Webster 1988a) surrounding the nomenclature of the group is the widespread use of the term *R. calcareus* for *R. penicillatus* subsp. *pseudofluitans*. Webster (1988a) has convincingly shown that *pseudofluitans* is the earliest epithet to be applied to this taxon, and its use is adopted in this thesis (this term is also used in the most recent British Flora, Stace 1991).

R. penicillatus* subsp. *penicillatus

As indicated above *R. penicillatus* subsp. *penicillatus* is separated from subsp. *pseudofluitans* by the presence of laminar leaves, which it forms after flowering (Holmes 1980). 'Penicillatus' refers to the shape of the dissected leaves and means brush-like (Gledhill 1989). *R. penicillatus* may be confused with *R. peltatus* when flowering; *R. peltatus* has capillary leaves that are usually shorter than the internodes and they tend to be more rigid than *R. penicillatus* (Webster 1988b).

R. penicillatus subsp. *penicillatus* is confined to 41 sites in the west of England and Wales and 25 scattered localities in Ireland (Biological Records Centre, personal communication 1991; Perring & Walters 1976). Palmer & Newbold (1983) identified the taxon as in need of protection. In Britain it is found mostly in base-poor fast flowing rivers where *R. fluitans* is absent or rare (Holmes 1980) but in Ireland it is found in more calcareus habitats (Webster 1988a). It has a trophic rank of 69 (Newbold and Palmer 1979). Decamps (1985) found that its germination was slightly depressed in waters with a high calcium content.

In a survey of macrophytes in the River Suir in Ireland, Caffrey (1985) placed *R. penicillatus* subsp. *penicillatus* in the group most sensitive to pollution. In a survey of 52 Irish rivers Caffrey (1990b) showed that *R.*

penicillatus subsp. *penicillatus* was associated with communities at relatively shallow depths, low conductivities and moderate flow-rates.

R. penicillatus subsp. *pseudofluitans* var. *pseudofluitans* (Syme) S.Webster

R. penicillatus subsp. *pseudofluitans* var. *pseudofluitans* (= *R. calcareus*, referred to below as var. *pseudofluitans*) is by far the most abundant Batrachian *Ranunculus* species in Britain, dominating and forming extensive stands in many stretches of rivers and streams (Plate Two). However, it is probably less common than previously (Grime *et al.* 1988). As with the rest of the group, it is a morphologically plastic species. Some populations have leaves as long as those of *R. fluitans* (up to 385 mm; the 'holmes' morphotype, Webster 1984), but these are always divided at least five times and the flowers have a densely hairy receptacle (Webster 1988a). Separation from var. *vertumnus* is discussed under that taxon. The variety *pseudofluitans* may occasionally be confused with *R. trichophyllus*; when in flower the species can be separated by the shape of the nectary pit (lunate in *R. trichophyllus*, pear-shaped in *R. penicillatus*, Webster 1988b).

Variety *pseudofluitans* is found in rivers and streams throughout England and Wales, though it is sparse in Scotland and absent from Ireland except for one possible site in Derry (Webster 1988a). It has a wider ecological amplitude in terms of calcium requirement than its alternative name of *R. calcareus* would imply. However, it is usually found in base-rich rivers, with alkalinities greater than 100 mg l^{-1} $CaCO_3$ and a high conductivity (Webster 1988a). Holmes (1983) recorded var. *pseudofluitans* in all four of his types of river communities, and Newbold & Palmer (1979) considered var. *pseudofluitans* to be distributed in waters of a trophic status from mesotrophic to eutrophic (trophic rank 99). Merry *et al.* (1981) also found var. *pseudofluitans* to be present in sites with a wide range of conductivity, pH, calcium and altitude values. The overlap of its habitat requirements (ecological niche) with other Batrachian *Ranunculus* species is illustrated by the fact that Géhu and Meriaux (1983) place it in the same phytosociological community as *R. fluitans*.

Due to its importance in lowland rivers, especially chalk streams, a considerable amount of work (including some early physiological studies) has been carried out on this taxon. Studies concerning the effects of shading are reviewed in the introduction to Chapter Three and those concerning the response of the plant to cutting are reviewed in Chapter Four.

One of the factors that appears to determine the maximum standing crop formed by the plant is the rate of water flow in the spring; there is a positive correlation between these two factors in the River Wye over several years (Edwards & Brooker 1982). Other studies have found similar results. For example in a survey of river sites dominated by *Ranunculus* species in northern England and Scotland, Spink *et al.* (1990) found discharge to be an important factor for determining community type. However particularly in chalk streams where discharge is less variable and cutting is frequent other factors such as the cuttng regime, turbidity and insolation may be more important than discharge (Westlake & Dawson 1982).

Marshall and Westlake (1990) measured the water velocities around and within var. *pseudofluitans* clumps. and found that although the water in a stream had a velocity of more than 0.5 m s^{-1} the current velocity inside the *Ranunculus* clump was less than 0.1 m s^{-1}. In still or slow waters one of the most important limiting factors for plant growth is the availability of carbon (either as bicarbonate or as dissolved carbon dioxide) (Black *et al.* 1981; Hough & Fornwall 1988). Westlake (1966) showed that the rate of photosynthesis in var. *pseudofluitans* was primarily limited by the rate of diffusion of carbon dioxide to the plant's leaves, which in turn is determined by the rate of flow of the water (faster flows reduce boundary layer resistance).

Var. *pseudofluitans* shows a marked increase in growth with increase in water velocity (Westlake 1967) and Ham *et al.* (1981) found that the increase in area of var. *pseudofluitans* in the spring in the River Lambourn (a chalk stream in southern England) was correlated with the mean discharge at that time. Percentage cover was lowest in March and the area then rapidly increased to reach a maximum in early summer. During August and September (after flowering) the plants declined (peak

Plate 2

Ranunculus penicillatus subsp. *pseudofluitans* var. *pseudofluitans*.

River Frome Mill Stream at East Stoke, Dorset. National Grid Reference SY 870 867. Site of experiment described in Chapter Three.

Photograph taken on 15 May 1989. 50 mm lens with polarizing filter, Magnification × 1.7

biomass is about a month after flowering, Dawson 1976) and continued to be washed-out during the winter (some above-ground material usually remains and photosynthesis occurs, Sculthorpe 1967). This phenology has been observed in many other studies (Ladle & Casey 1971, Ladle & Bass 1981, Wright *et al.* 1982, Ham *et al.* 1982, Spink *et al.* 1990).

In the light of the above it would appear unlikely that increased nutrient (NPK) supply has caused these growths, contrary to the opinion of many anglers. Large *Ranunculus* standing crops have been observed in rivers before the advent of artificial fertilisers (Hutton 1930) and the concentration of major plant nutrients in chalk streams where var. *pseudofluitans* is dominant is far greater than the nutrient requirements of the plant (Ladle & Casey, 1971). Casey & Downing (1976) found that on the whole there was no correlation between nutrient concentrations in var. *pseudofluitans* shoots taken from eight sites and the water chemistry, with the exception of phosphorus (the *Ranunculus* appearing to exhibit luxury consumption of very high phosphorus concentrations in the water). However during periods of rapid growth in small streams measurable amounts of nutrients are removed from the water (Casey & Westlake, 1974), indicating that nutrients may limit growth at particular sites and times of the year.

The growth of *R. penicillatus* subsp. *pseudofluitans* in many rivers is so abundant as to have a very significant impact on the ecology of the river. Westlake *et al.* (1972) recorded a biomass of 630 g dry weight m^{-2} in a chalk stream dominated by var. *pseudofluitans*. Although this is at the upper end of the productivity recorded for submerged plants in temperate regions it is still considerably less than the maximum productivity of emergent or some terrestrial plants (Westlake 1975). The 'world record' for a submerged macrophyte standing crop is claimed to be 3518 g dry weight m^{-2} of *Lagriosiphon major* in New Zealand (Clayton 1982). More typical values of 130-260 g m^{-2} were measured by Westlake (1968) in the River Frome. The growth of var. *pseudofluitans* can be very variable from one year to the next; Edwards & Brooker (1982) found eight times as much growth in 1977 as in 1976.

If a large growth occurs and then decays due to drought conditions this can cause almost complete deoxygenation of the river in combination with other factors (Edwards & Brooker, 1982). After the var. *pseudofluitans* was cut in a stream in Dorset, Westlake (1968) found that the night minimum oxygen concentration was raised from 40-60% saturation to 60-75% and the day maximum was lowered from 130-160% to 90-100%. The growth of var. *pseudofluitans* stands can lead to increased water depth with an increased risk of flooding. In many lowland rivers this has led to long-term management by cutting one or more times each summer (see for example Westlake & Dawson 1982).

If var. *pseudofluitans* is introduced to a suitable river it can rapidly grow to dominate the flora (Holmes & Whitton 1977a, 1977b). However if the conditions change to make the river less suitable, the cover of var. *pseudofluitans* will decrease. Ladle & Bass (1981) described how following a drought *R. peltatus* competitively replaced var. *pseudofluitans* in a winterbourne in Dorset. Var. *pseudofluitans* has since re-established itself (personal observation 1989-90). Brookes (1986) observed the effects of sedimentation on var. *pseudofluitans*. In the River Wylye sedimentation had little effect as the sediment remained in suspension, but in Wallop Brook the sediment was deposited onto the plant clumps, the *Ranunculus* appeared to be unable to vary its rooting level in response to this and a year later the *Ranunculus* cover was only 5% of that expected. In natural conditions var. *pseudofluitans* clumps act as sediment traps with a consequent build up of sediment around its roots, so that (in contrast to *R. fluitans*), var. *pseudofluitans* clumps are rarely in the same place one year as they were the previous year (Westlake 1968, 1973, Casey & Westlake 1974, Furse 1977). The tendency of *R. penicillatus* subsp. *pseudofluitans* clumps to move with time is also caused by the effects of competition with species such as *Berula erecta* and *Nasturtium officinale*. Sedimentation may also be another way that water flow rates influence the growth of var. *pseudofluitans* as Ham *et al.* (1981) found a negative correlation between discharge and sedimentation rates in a chalk stream.

Several studies have been carried out which describe the invertebrate communities associated with var. *pseudofluitans*; see for example Gunn (1985). The epiphytic bacteria associated with var. *pseudofluitans* have been detailed by Hossell & Baker (1979) and Baker & Orr (1986). Protozoa associated with var. *pseudofluitans* in chalk streams have been described by Baldock *et al.* (1983).

R. penicillatus subsp. *pseudofluitans* var. *vertumnus* C.D.K. Cook

This taxon is separated from var. *pseudofluitans* by having leaves usually shorter than the internodes, 30 - 70 mm long (in summer) and with many (100-400(900)) divergent segments (Webster 1988a). Whereas var. *pseudofluitans* leaves are obconical (Figure 1.2), var. *vertumnus* leaves are globose. The variety was newly described by Cook (1966a). 'Vertumnus' is derived from the Latin *vertere* (to change). Vertumnus was a Roman agricultural god who assumed various disguises and was venerated with the god of the River Tiber, the course of which he was supposed to have altered.

Within the British Isles it only occurs in 41 sites in England and one site in Wales (Biological Records Centre, personal communication 1991). Cook (1966a) states that it requires clear rather than flowing water; 16% of its records are from canals (Webster 1988a). It is not found in rivers subject to frequent flooding (Cook 1966a).

Presumably as a consequence of the rarity of the taxa, little experimental work has been carried out on it. Fox & Murphy (1986) showed that the herbicide diquat alginate was effective in killing back var. *vertumnus* plants so completely in a small river in northern England that the root stock did not re-grow at all later in the season.

1.1.8 *Ranunculus fluitans* Lam

R. fluitans is the largest of the *Ranunculus* species, frequently 2-4 m long and sometimes up to 7 m (Schenck 1885). As well as its size making identification clear, no other species has leaves more than 80 mm and four times divided. It also has a glabrous or pilose receptacle. 'Fluitans' means floating on water (Gledhill 1989).

R. fluitans is found in rivers throughout much of Britain, but is virtually absent from Ireland and Western Scotland (Biological Records Centre, personal communication 1991; Perring & Walters 1976). It is found in 'rivers with a decided current' (Pearsall 1929), which Butcher (1933) quantified to being between 0.4 and 1.0 ms^{-1}. Cook (1966a, 1967) reports that it is occasionally found in stationary waters, where it rarely flowers. Haslam (1978) found that it appeared to tolerate spates better than consistently fast flows and that deeper water (often > 1.0 m) is preferred. *R. fluitans* is most often found in the lower reaches of a river (Haslam 1982), for example Holmes & Whitton (1981) only recorded *R. fluitans* at the most downstream of their sampling sites on the River Tees, and Dethiox (1982) found that *R. fluitans* grows in broader and deeper rivers than *R. penicillatus*.

R. fluitans tends to be less common in limestone areas (Cook 1966a), though it does grow in chalk streams (for example the River Rye in Yorkshire, Appendices A & B) and Decamps (1985) found that it had a higher germination rate in water from a river with a high calcium content than from a river with a low calcium content. It has a trophic rank of 45 (Newbold and Palmer 1979).

The nature of the substrate appears to be important in limiting the distribution of *R. fluitans*. In the River Wye there is a close correlation between the occurrence of *R. fluitans* and the presence of old fords and collapsed bridges (Brian 1983). Cook (1966a) carried out transplant experiments which indicated that its absence from limestone streams appeared to be due to the lack of stable smooth pebbles on the river bed rather than calcium concentration. This limitation may be due to the fact that *R. fluitans* (like *R. circinatus*, see above) has a winter and a summer mode of growth. In the summer *R. fluitans* has a very rapid growth rate, and is able to flower but does not root, whereas in the winter it is slower growing but is able to root (Cook 1966a), so that a clump will tend to remain in the same place in the river bed for several years (Cook 1966, pers. obsv. 1989-1991 in River Rye, Yorkshire). This growth-form may not be constant for all populations as Whitton & Buckmaster (1970) reported that *R. fluitans* clumps in the River Wear and the River Tees do change their size, shape and position quite rapidly.

Several studies have been carried out to ascertain the effects of pollution on *R. fluitans*. Cook (1966a) stated that it was fairly tolerant of pollution, as long as the water remained clear, and attributed the decline in this species in the English Midlands to pollution causing increased turbidity in the water in those sites. Harding (1979, 1980) noted that *R. fluitans* was replaced by *Potamogeton pectinatus* in conditions of increased salinity and nutrient supply. Whitton & Buckmaster (1970) observed that although *R. fluitans* was abundant in the relatively unpolluted River Tees it was much scarcer in the nearby River Wear which had suffered toxic discharges from the coal and coke industries for a number of years. Some *R. fluitans* was transplanted into the Wear, but few plants grew. However following that survey, the pollution ceased and on re-surveying the river Holmes & Whitton (1977) found that *R. fluitans* had increased both its range and abundance. Janauer (1981, 1982) has qunatified the uptake and storage of chemical compounds by *R. fluitans* shoots.

Workers in Continental Europe have found *R. fluitans* populations there to be rather less susceptible to pollution damage. Ska & Vander Borght (1986) found that there was a positive correlation between increased algal blooms, *R. fluitans* growth and increased eutrophication in the River Semois. *R. fluitans* in Germany has been found to be less susceptible to experimentally elevated ammonium concentrations than other species (Von Glänzer *et al.* (1977). Eichenberger & Weilmann (1982) grew *R. fluitans* from the River Rhine in artificial rivers. They found that elevating the phosphorous concentration to 300 $\mu g PO_4$-P l^{-1} had little effect, as did adding domestic sewage from Zürich, but the two added in combination caused a significant increase in growth. It is thought that increased domestic sewage discharges to rivers such as the Rhine may be causing increased growth of *R. fluitans* at those sites. Monschau-Dusenhausen (1982) found *R. fluitans* to be associated with polluted sites. The differences observed in the effects of pollution on *R. fluitans* in Britain and the rest of Europe may either be due to genetically different populations or (probably more likely), the different nature of the pollutants studied.

In the above study Eichenberger and Weilmann (1982) found that herbivory by the crustacean *Gammarus* sp. had a 'devastating' effect on the *R.* -

fluitans grown in their artificial rivers, devouring stout plants in a couple of days. A similar effect has been observed on *R. penicillatus* subsp. *pseudofluitans* growing in the artificial rivers described in Chapter 3 (pers. obsv. 1989). Although Eichenberger & Weilmann (1982) concluded that *Gammarus* may play a role in limiting the distribution of *R. fluitans*, Harrod (1964) found that *Gammarus* rarely occurred on *R. fluitans*, even though it was present on other plants in the same river (the Test, in Hampshire). She found that *R. fluitans* had a fairly varied flora (which was attributed to the divided leaves), with *Simulium ornatum* larvae particularly abundant.

R. fluitans often grows in a monoculture (NCC 1988), but it does grow with *R. penicillatus* - both subsp. *penicillatus* and *pseudofluitans* and both var. *pseudofluitans* and var. *vertumnus* (Appendix A & B). *Callitriche stagnalis* and *Potamogeton pectinatus* are occasionally associated with *R. fluitans* (NCC 1988).

R. fluitans forms a number of hybrids. *R. fluitans* × *R. peltatus* (*R.* × *kelchoensis* S. Webster; Kelso Water Crowfoot) is only currently known from two sites in the UK (Biological Records Centre, personal communication 1991) and *R. fluitans* × *R. circinatus* is also rare.

R × bachii Wirtgen (Wirtgen's Water Crowfoot) is a persistent hybrid of streams, and is known for certain from one current site (but six sites where it is thought to be extinct; Biological Records Centre, personal communication 1991. However it is difficult to separate from *R. penicillatus* subsp. *pseudofluitans* and some records for the latter may refer to *R.* × *bachii*, so *R.* × *bachii* may be quite widespread (Cook 1975, Stace 1991). Parentage of this hybrid is is *R. fluitans* × *R. aquatilis* and × *R. trichophyllus* (Cook 1966, Webster 1990a) and it is thought that *R.* × *bachii* may be the taxon that gave rise to *R. penicillatus* subsp. *pseudofluitans* (Stace 1991).

1.2. Plant Strategy Theory

1.2.1 The Development of the Concept of Strategy

The term 'strategy' is coming into increasing use in plant ecology. Some workers claim that use of the concept has 'more than any other, allowed ecology to begin its escape from a morass of parochial and undigested observations' (Grime, 1985), whereas others regard the use of such concepts more as a symptom of 'post-Darwinian Victorian optimism' (Harper, 1982), considering that ecological information is best gained from studies of stands of single species rather than a broad comparative approach to the ecology of a large number of species within a flora.

Some workers (e.g. Stebbins, 1951) consider the term to be too open to teleological interpretations and prefer expressions such as a 'set of traits'. However, as long as 'strategy' is careful defined, this difficulty is, to a large extent, overcome. Here the term is defined (after Grime, 1979) as *a grouping of similar or analogous genetic characteristics which recurs widely among species or populations and causes them to exhibit similarities in ecology.* It should be noted that some authors (e.g. Lloyd, 1984) use the term in a rather different sense.

Mac Leod (1894; cited in Herny & Stepèruere 1985) was one of the first biologists to attempt this broad grouping of plant ecologies. He said that plants fell into two categories; proletarians and capitalists, their strategy being determined by the amount of capital (i.e. resources) they accumulated. Ramenskii (1938) used a three-strategy model; violents, patients and explerents (opportunists) which he said were equivalent to lions, camels and jackals. The two-strategy model was further developed by Hutchinson (1959) and then by MacArthur and Wilson (1967) and Pianka (1970) with the theory of 'r' and 'K' selection. r-selected organisms are typically colonists. They have short life-spans and early on in their life-history devote a large proportion of their resources to reproduction. K-selected organisms occur later on in a successional sere when resources are more limited. Reproduction is delayed and they will dominate the part of the habitat they occupy. During (1979) used a similar approach to describe bryophyte strategies.

There are two major problems with the two-strategy model. The first is that it fails to recognise a type of strategy described as 'beyond K-selection' (Greenslade, 1972a, b), adversity selection (Greenslade, 1983), or S-selection (Grime, 1974). This is not a problem if the frequency and intensity of disturbance are correlated (Shipley *et al.* 1989), but otherwise a third strategy is found to be necessary. The characteristics of this strategy are described below. The other major problem is that in the two-strategy model the strategies of juvenile organisms are not separated from those of the adults. Grime (1979) suggests that the selection forces and 'design constraints' which determine the strategy of juvenile organisms are different from those acting on the adult population, leading to distinctive regenerative strategies.

1.2.2 The C-S-R Model

There are essentially two types of environmental factors which act upon plants to reduce their biomass. *Stress* may be defined as any factor which reduces the rate of accumulation of biomass (i.e. photosynthetic production) and includes shortages of light, water and minerals. *Disturbance* is any factor which actually destroys biomass and includes grazing, trampling, and fire-damage (Grime, 1974). A habitat may be subjected to any combination of high and low stress and disturbance as shown in Table 1, below. Grime (1974; 1977) proposed the hypothesis that plants conform to one of three primary strategies depending on the combination of stress and disturbance in the environment to which it is adapted.

Table 1. The relationship between environmental factors and primary plant strategies (After Grime, 1977)

Intensity of disturbance	Intensity of stress	
	Low	High
Low	Competitors	Stress-tolerators
High	Ruderals	(*)

*Environmental conditions too hostile to allow any viable strategy

The different primary strategies may be outlined as follows (Grime, 1977; 1979). Plants which grow in habitats which are relatively undisturbed and are not particularly resource-limited may be described as *competitors*. Competition is defined here (after Grime, 1979) as *the tendency of neighbouring plants to utilize the same photon of light, ion of a mineral nutrient, molecule of water, or unit of space*. Plants with a high competitive ability characteristically have a high dense monolayer canopy of leaves and extensive spread above and below ground. There is a fairly rapid turn-over of leaves and roots; well-defined peaks of leaf production corresponding with periods of maximum potential productivity; and photosynthesis and nutrient uptake is strongly seasonal. Large quantities of litter are formed, which is often seasonal. Competitors have a rapid potential relative growth rate and rapidly respond to stress with changes in root-shoot ratio and leaf area ratio. This strategy is equivalent to the K strategy of MacArthur & Wilson (1967). Examples of competitors are *Arrhenatherum elatius, Urtica dioica* and *Galium aparine*.

Stress tolerant plants grow in habitats in which one or more of the resources needed for plant growth are limiting, but there is little disturbance. The leaves are often reduced, evergreen, and have a long life-span, as does the whole plant. The plants have little or no morphological response to changes in stress. Capture of resources is opportunistic and often uncoupled from vegetative growth; the plants will continue to grow very slowly (with a small potential relative growth rate) even if resources do become available. However, the plants exhibit strong physiological acclimation to seasonal variation in temperature, light and water supply. Stress tolerant plants include most lichens, *Sedum acre*, and *Thymus drucei*.

Plants which grow in habitats which are productive but subject to disturbance are *ruderals*. They have a high relative growth rate, but if subjected to stress, rapidly divert resources into reproductive structures. Their uptake of nutrients is opportunistic, and unlike the previous two strategies they do not store any photosynthate (except in seeds, or other propagules). This strategy is equivalent to MacArthur & Wilson's r-strategy (1967). The typical ruderal plant is an arable 'weed' such as *Capsella bursa-pastoris, Stellaria media* and *Plantago major*.

As well as the three primary strategies, Grime (1979) described four secondary, or intermediate strategies; Competitive ruderals, stress-tolerant ruderals, stress-tolerant competitors and C-S-R strategists.

An important feature of the C-S-R strategy model is the uncoupling of juvenile from adult strategies (Grime, 1979; Grime *et al.*, 1981). Grime (1979) identified five regenerative strategies; vegetative expansion, seasonal regeneration in vegetation gaps, regeneration involving a persistent seed bank, a persistent seedling bank and numerous small seeds or spores.

1.2.3 The Triangular Model

Figure 2.3 illustrates a graphical model describing the relation of the adult strategies to stress, disturbance and competition. Individual plant species were plotted on the triangle using two criteria (Grime, 1974).

(1) R_{max} (potential maximum rate of growth), measured in standard conditions represents an increase in the ability to cope with disturbance and

(2) a morphology index which represents competitive ability.

This ordination was found to be unsatisfactory (Grime, 1979), due a lack of 'subtlety'. Grime, Hodgson & Hunt (1988) classified some common 'marker species' into one of the primary or secondary strategies using a dichotomous key based on life-history, morphology and phenology. Marker species were common species that could be classified unequivocally.

A large number of 1 m^2 vegetation samples were then surveyed, and the frequency of occurrence of the marker species in the samples were then used to ordinate them. Thus a vegetation sample with competitive marker species occurring in it would be defined as a competitive habitat.

Finally species other than the marker species could be plotted onto the triangle using by the percentage occurrence of that species in the above vegetation samples. For example a species that occurred in mostly competitive habitats would be defined as a competitor.

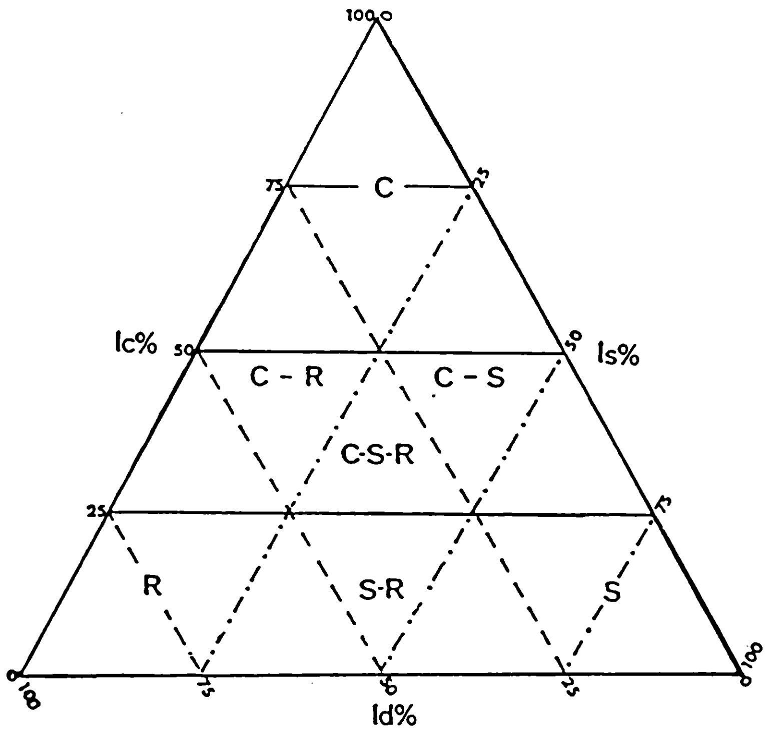


Figure 2.3. Model describing the various equilibria between stress, disturbance and competition, and the relation of the primary and secondary strategies to those factors. C = competitor, S = Stress-tolerator, R = Ruderal. $I_{c,s,d}$ represent relative importance of competition, stress & disturbance.

1.2.4 Problems with Strategy Theory

Four major potential problems have been aired;

1. Whether the theory can be applied to species other than those in herbaceous terrestrial vegetation.
2. Problems with the triangular ordination
3. Semantic problems
4. Whether it is possible to understand the natural world by applying general concepts or whether there is simply a variety of special cases.

1. If the theory is to have widespread ecological relevance, it must be applicable to groups of organisms other than the (predominantly herbaceous) terrestrial angiosperms upon which the majority of the work is based. It is true that attempts have been made to apply it to marine algae (Raven, 1981; Shepherd, 1982; Coesel, 1982; Dring, 1982), freshwater algae (Sandgren, 1988), bryophytes (Rincorn & Grime 1989 a,b; Grime *et al.* 1990), fungi (Pugh, 1980; Cooke & Raynor, 1984, Grime 1988, Pugh & Boddy, 1988), corals (Rosen, 1981) and invertebrates (Greenslade, 1972a, b; 1983; Lee, 1985). There has been somewhat mixed success in transferring Grime's theories to other life-forms. It has been, on the whole successful, but as might be expected, it has not been possible to apply the theory to some groups, for example vertebrates. Some workers have found difficulty in applying the theory to aquatic systems (see below), and the model has had to be adapted to other fit life-forms, for example, it has not been possible to apply the model to fungal taxa, as any one species exhibits different strategies at different stages in its life history (Pugh & Boddy, 1988).

2. Loehle (1988) discussed some problems with the geometry of the triangular ordination. The triangle essentially represents a three dimensional plot of three axes (x,y,z), on which are plotted the importance of stress, competition and disturbance, reduced to two dimensions. It assumes that all the points plotted lie on the plane connecting the points (1,0,0), (0,1,0), and (0,0,1), and it is this plane which is equal to Grime's triangle. This assumption is valid so long as the three components sum to 1·00; if that is not the case then the ordination involves distortion because the points will lie either above or below the plane. Grime (1985) states that the three traits do compensate

for each other (i.e. if for example stress-tolerance decreases by 0·3 then the sum of competitiveness and disturbance-tolerance must necessarily increase by 0·3). Although it is likely that this is the case, Loehle (1988) argues that it is better not to impose this on the data.

A similar distortion would also be caused by either by any strategies or by any environmental factors (depending on which was being plotted) other than competition, stress and disturbance (Menges & Waller, 1983); this may be especially significant in other environments than terrestrial ones. Kautsky, (1988) has postulated a fourth primary strategy for aquatic plants and Pugh and Boddy (1988) have described an apparently high stress plus high disturbance strategy for some fungi.

Tilman (1987, 1988) considers that it is not possible to have a general stress-tolerant strategy because the nature of resources above and below ground are fundamentally different, leading to different strategies, with different stresses favouring different species.

Loehle (1988) cites three examples which he claims represent strategies above or below the 'plane' represented by Grime's triangle. He refers to plants that persist in a stand due to their competitors being heavily grazed and argues that such species are low in competitive ability without necessarily being higher in the other two traits. The grazing is a disturbance pressure and so one would expect such species to exhibit relatively high proportion of ruderal traits. Loehle's second example is that of plants transplanted outside their natural range. However if these plants exhibited a strategy inappropriate to the transplant site they would not survive and thus would not have a viable strategy. His final example is of a pioneer conifer which is both stress and disturbance-tolerant (fire-resistance) which he claims lies above the triangle. Although further studies would be needed to clarify this point, it would appear that the conifer species simply shows a S-D strategy.

Grubb (1985) also cites examples of species which may survive in conditions of both high stress and high disturbance. For example *Elymus flavescens* is found growing on droughted sand dunes which are unstable and therefore subject to disturbance. As with the above examples, this is difficult to assess with no means of seeing just how severe the disturbance is. However the presence of *Elymus* itself stabilises the dune system.

A second potential problem that Loehle (1988) identifies is that there is a geometrical distortion involved in deriving the triangle from rectangular Cartesian coordinates. Although this is a valid criticism of Grime's earlier (1974) method, the ordination method described above as used by Grime *et al.* (1988) is not derived from rectangular coordinates and so does not involve that distortion.

3. Harper (1982), (and in Grime, 1978) argues strongly that the terms strategy, stress, and competition are used in such a variety of ways (and hence with such a lack of precision) that their use is best dispensed with. 'Stress' is commonly used to indicate both a stimulus and a response. He cited Pickering (1961) as saying that he is 'never quite sure what it means'. Many workers (e.g. Levitt 1972) use 'stress' in a general sense to refer to "any factor potentially unfavourable to living organisms". Grubb (1985) also rejects the term stress. He considers that Levitt's usage is too general to be sustainable and that Grime's usage only contains a sub-set of Levitt's meaning and is inadequate. Grubb (1985) does consider the term disturbance to be useful, but he asserts that as disturbance differs in frequency, intensity and extent it in inadequate to consider it on a single axis. This is the basis of Kautsky's fourth strategy of 'biomass storer', which is discussed below.

Chapleau *et al.* (1980) considered that the term strategy was difficult to dissociate from an 'omnipresent allusion of purposefulness', and Grubb (1985) preferred to write of plants specifically suited to their habitats.

Similar discussion has arisen over the term 'competitor'. Pigott (1980) and Grubb (1985) asserted that the term 'competitor' applied to plants in habitats with low stress, implies that competition is not important in stressed habitats. Although Thompson & Grime (1988) made it clear that they agree with Quinn & Dunham (1983) that competition is important in stressed habitats, this has still led to some confusion over terminology (Tilman, 1987). The competition axis implies that competition is less important in heavily stressed sites, not that it has no importance.

However, these semantic arguments are really an arguments for the precise definition of ecological terms and henceforth only using the terms in the defined sense (as was argued by Tansley (1935)).

4. Grubb (1985) argues that there is no such thing as a stress-tolerator, just shade-tolerators, or drought-tolerators or plants adapted to conditions of low nutrients. The specific attributes required to survive in these particular conditions out weigh any general attributes required to survive in conditions of low productivity. This approach underlines the difference in attitude between those biologists who feel that it is possible to understand the natural world with the help of broad principles and those who feel that nature is so varied that such broad theories are more of a hindrance than a help to understanding and predicting how vegetation works.

There are many difficulties with points of detail in evolutionary theory, but this has not prevented its general acceptance or usefulness. The general nature of evolutionary theory has led to Popper (1972) denying that it is a scientific theory, and some of the arguments against strategy theory follow a similar line of argument. For example Menges & Waller (1983) raise the possibility that strategy theory is too broad and simplistic to be predictive.

Referring to his theory of r- and K-strategies, MacArthur (1968) said that 'the very short-sighted will always find discrepancies and be able to say that there is no generality, only a spectrum of special cases'. Even if examples were to be found where the sum of C+S+R traits was not equal to unity this would not invalidate the general assumption that C+R+S=1 so long as it could be shown that it continued to remain true for the bulk of vegetation.

Some of the arguments used against the triangular ordination fall into the same category of attempting to understand plant ecology purely in terms of detail rather than seeking to look at a broader picture. It must always be clearly borne in mind that any graphical representation of data is a method of visually picturing a particular interpretation of that data. Strategy theory is a broad conceptual approach to understanding how vegetation works and as such one would not expect it to accurately describe the minutia of every particular circumstance. Likewise a graphical representation of the strategy of a particular plant species or habitat must be designed to give a clear and accurate visual impression of that strategy, rather than a picture which may possibly have more mathematical precision but which fails to convey the ecological information.

A number of tests of predictions of strategy theory have recently been carried out. One major difference between the C-S-R theory and the r-K theory (MacArthur & Wilson 1967) is that whereas r-K selection couples juvenile with adult strategies, C-S-R strategies in the adult are predicted to be uncoupled from the five juvenile strategies. Shipley *et al.* (1989) found that there was no association between a range of adult and juvenile plant traits in 25 species of emergent wetland plants. Similarly Grime *et al.* (1987) carried out a multivariate cluster analysis on traits in 273 terrestrial plant species and found strong evidence for the uncoupling of regenerative and adult strategies. That same study also found that the traits formed clusters which were consistent with the C-S-R model of primary strategies.

C-S-R theory also predicts that there should be a predictive relationship between environmental gradients and plant traits and strategies. A number of studies have reported data consistent with that prediction. Bryant *et al.* (1989) have shown that there is a correlation between palatability of woody plants and their relative growth rate. Grime & Hunt (1975) demonstrated a correlation between relative growth rate and soil fertility. Shipley *et al.* (1989) found trends along environmental gradients of soil fertility for wetland plants to exhibit competitive traits and along a water depth gradient for plants to exhibit stress-tolerant traits. Gaudet & Keddy (1988) have shown that there is a predictive relationship between competitive ability and a suite of plant traits such as biomass.

Campbell has recently carried out a series of experimental tests of strategy theory. Campbell & Grime (1989) found that a competitive species was better able than a stress-tolerant species to exploit a sustained nutrient supply, which is consistent with the results obtained by Mahmoud & Grime (1976). However Campbell & Grime (1989) also found that the stress-tolerant species was better able to exploit short pulses of nutrient supply. Campbell (1888) also showed that fast-growing competitive species displayed the greatest reduction in growth in response to nutrient supply, whereas slow-growing stress-tolerant species were better able to grow and extract nutrients at very low concentrations. His results are consistent with those of Shipley & Keddy (1988) who found that species whose relative growth rate was highest in more fertile conditions had their relative growth rate most depressed in the less fertile conditions and that this relationship held on a proportional basis. Campbell (1988) also found (utilising stress and disturbance gradients) that competition was greatest in low stress low disturbance conditions but that it still occurred in conditions of high stress or high disturbance. This is in line with the results obtained by Gurevitch & Unnasch (1989) who experimentally demonstrated that the effects of competition due to *Dactylis glomerata* (strategy C-S-R to C; Grime *et al.* 1988) were increased with fertilisation. Day *et al.* (1988) examined fertility and disturbance gradients in a mire adjacent to the River Ottowa. They found that at high fertility and low disturbance *Typha* appeared to competitively exclude other species (whereas at sites with lower fertility it was unable to exclude other species) and that the least fertile sites had species with stress-tolerant traits (*sensu* Grime 1979). However other authors (e.g. Gurevitch *et al.* 1990) have found no apparent change in the effects of competition with changing levels of fertilisation.

The real test of the theory is whether it succeeds in letting 'ecology escape from a morass of parochial and undigested observations' as was claimed by Grime (1985). Does strategy theory provide a broad theoretical framework for ecology, enabling ecological data to be placed in a coherent scheme? It is clear that within the terrestrial herbaceous flora of the Sheffield region the theory has fulfilled expectations (Grime, Hodgson & Hunt, 1988), and also that it can usefully be used to predict the effects of management changes on plant communities (Grime, 1980). What is less clear is how useful the theory will prove to be when applied to different areas. Tilman (1987) thought that the differences between himself and Grime were due to their working on different habitats. One area in which the C-S-R model has been applied with only limited success (so far) is that of aquatic (particularly lotic) vegetation.

1.2.5 Plant Strategy Theory as Applied to Aquatic Vegetation

Grime, Hodgson & Hunt (1988) stated that it is has not been possible to include aquatic species within their autecological accounts because criteria for dealing with those species were not available. Several of the questions applied in the dichotomous key used to classify 'marker species' are not appropriate; aquatic plants cannot be geophytes and the shoot height is frequently determined by the height of the water column. The morphological index used by Grime (1979) would seem to be inappropriate as it is unlikely that (for example) *Ranunculus* species with laminar leaves necessarily have a greater competitive ability than those without laminar leaves. The use of the R_{max} value has been criticised because Van Andel & Jagar (1981) have shown that it shows considerable ontogenetic drift and thus can not be taken as a constant for a species (which lends some weight to the argument that strategy theory is best applied at a population rather than a species level (Verhoeven *et al.*, 1982)).

In spite of these difficulties a number of workers have applied the strategy approach to aquatic vegetation. Boston (1986) concluded that C-S-R theory can 'equally well be applied to aquatic plants' and Lepš *et al.* (1982) declared that 'our results can be explained completely by means of Grime's theory'. Raven (1981) successfully applied the theory to marine macrophytes. He found that stress tolerant species had an increased emphasis on efficiency of use and (especially) retention of resources as well as defence against herbivores and parasites. By contrast species growing in sites with high disturbance were associated with an emphasis on increased rate of metabolism and reproduction.

Rørslett, Berge & Johansen (1986), Rørslett (1988), Murphy, Rørslett & Springuel (1989) and Springuel, Ali & Murphy (1990) have applied the strategy concept to lake vegetation by using a specifically aquatic set of 'survival traits' specific to freshwater macrophytes to classify plants as competitors, stress-tolerators or disturbance-tolerators (and also combinations of those strategies). Springuel & Murphy (1991) have used the same approach to classify vegetation in the River Nile. Although this approach has produced apparently satisfactory results the appropriateness of some of the 'survival traits' is open to question.

Wilson & Keddy (1985, 1986a, b) were able to test some specific predictions of Grime (1973, 1977) on lake species. They found that species found on nutrient poor shores had low competitive abilities whilst those on sheltered nutrient rich shores had high competitive abilities. However Wilson & Keddy (1991) report that competition appeared to have little effect on aquatic macrophytes. Boston *et al.* (1989) have attempted to relate aquatic plant strategies to physiological characteristics. They found that whereas some traits of aquatic plants correspond closely with equivalent traits in terrestrial plants there are some adaptations giving rise to strategy traits specifically associated with the aquatic environment (especially those associated with carbon acquisition). Svedäng (1990) presents data which seem to indicate that *Juncus bulbosus* exhibits a stress-tolerant strategy (although she does not use C-S-R terminology) and concludes that the primary limiting resource is free CO_2. The plant appears to time its growth when competition for CO_2 from other species is at a minimum - perhaps in a way analogous to that in which vernal woodland species avoid competition for light in the spring.

Wiegleb and Brux (1991) have shown that in the aquatic genus *Potamogeton* there is no coupling between adult and regenerative strategies, which is consistent with Grime's approach. However Brux *et al.* (1987) and Wiegleb & Brux (1991) also argue that *Potamogeton* has 'special properties' making it impossible to apply strategy theory directly to the genus. Other workers have also argued that the theory cannot be transferred quite so easily to aquatic vegetation. Kautsky (1988) proposed that it is necessary to split the stress-tolerant strategy into two strategies; 'stunted' and 'biomass storer'. The 'biomass storer' corresponds to plants exploiting conditions of high stress and low disturbance whereas the stunted strategy occurs when higher conditions of disturbance occur (though in very high stress and disturbance conditions there is no viable strategy). Examples of 'stunted' species include *Ruppia spiralis, Tolypella nidifica* and *Chara fragilis*. Farmer and Spence (1986) considered that isoetids are found in conditions of both high disturbance and high stress. They considered that isoetids do not fit Grime's criteria for ruderals as ruderals are adapted to surviving disturbance by a life-cycle whereby they grow quickly in-between periods of disturbance. Isoetids are exposed to conditions of prolonged disturbance which may involve traits similar to those involved in surviving stress. Although this raises the question of whether a different set of strategy traits is required for a high frequency as opposed to a high intensity of disturbance (a question which will be discussed later in this thesis), the real problem is ascertaining whether these species are growing in conditions of high stress plus high disturbance (with the need for a new strategy type) or in conditions of moderate to high stress and moderate disturbance. Farmer & Spence (1986) point out that the problem may have arisen due to 'attempting to classify macrophytes using ideas developed in an exclusively terrestrial setting'. This indicates that the nature of the adaptations shown by aquatic plants to stress and disturbance is, as yet, poorly understood, and emphasises the necessity of deriving an objectively defined set of criteria to classify aquatic plants into strategy-types.

Verhoeven *et al.* (1982) considered that it was unhelpful to generalize plant traits into a few main strategies, because of the great variability that they observed in aquatic plant characteristics and environmental conditions. Van Vierssen (1982) concluded that none of the characteristics of *Zannichellia* that were observed fitted into any of the primary strategies of Grime (1974, 1979). Jacobs (1981) and Van Wijk (1983, 1988) raised similar objections arising from work on *Zannichellia* and *Potamogeton*.

From the above work, it would appear that it is possible to apply strategy theory to aquatic vegetation, but that it is necessary to use different criteria to determine the strategy of a particular species, and the possibility that some aquatic plants may occur in high stress and high disturbance environments must not be ignored. Murphy *et al.* (1988) have described some criteria which may be used to classify the strategies of lake macrophytes. In flowing waters it is likely that a different set of stresses and disturbances will be important, leading to a different set of ecological adaptations in plant species. In order to assign river species to a particular strategy it must therefore be necessary first to show just what environmental conditions reduce and destroy biomass, then what set of adaptive traits river plants have evolved to cope with those environmental conditions, and finally to use that information as a basis for determining the strategies exhibited in plant species present in river communities. If that were achieved it might then prove possible to use that information to predict the response of river vegetation to changes in stress and disturbance such as a change in the management régime.

The following chapter presents the results of extensive surveys of riverine *Ranunculus* communities, leading to a classification of the community types present and correlations between those community types and environmental variables. This, together with transplant experiments, is used to generate hypotheses as to which stresses and disturbances appear to be important in shaping the plant communities. The results of experimental testing of these hypotheses are discussed in chapters three to five. Chapter six is a consideration of what strategies the individual *Ranunculus* species exhibit and the changes that may be necessary to apply the terrestrial strategy criteria to aquatic species. The conclusions from the preceding chapters are brought together and discussed in the final chapter.

2. WHICH STRESS AND DISTURBANCE FACTORS ARE IMPORTANT IN SHAPING RIVERINE *RANUNCULUS* COMMUNITIES?

"The Froom waters were... rapid as the shadow of a cloud, with pebbly shallows that prattled to the sky all day long. There [in Blackmore Vale] the water-flower was the lily; the crowfoot here"

Thomas Hardy (1902)

Tess of the D'Urbervilles

2.1 Introduction

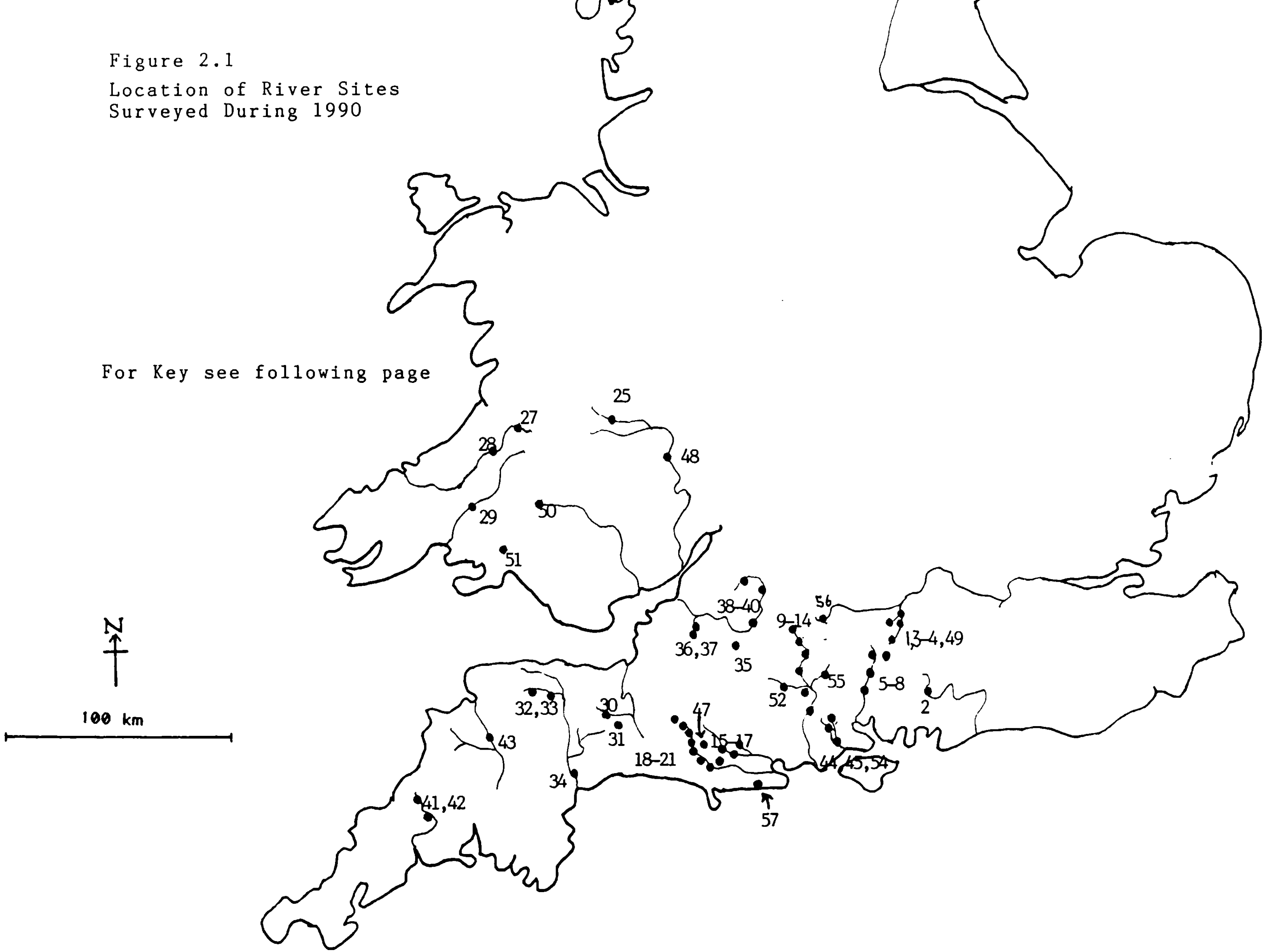
A basic ecological observation is that certain species tend to be associated with certain environmental conditions. Such observations do not prove that those particular conditions have caused the presence of one species rather than another, but they do give rise to hypotheses which can act as working models to be tested experimentally. These hypotheses may be framed in terms of specific factors (for example, plant community composition may change with increasing shade, as in the data below), or in more general terms (for example a species may be associated with sites that have a high intensity of stresses but a low intensity of disturbances).

Hypotheses regarding factors influencing the growth and development of riverine *Ranunculus* species were generated following analysis of the extensive survey of river sites undertaken in 1990. The survey indicated the main plant communities and also provided indications of the stresses and disturbances which appeared to be important in determining the plant community composition. Concentrations of major nutrients were measured in the sediments and in the *Ranunculus* tissue, and correlations calculated, which indicated which nutrients may be limiting plant growth.

Several surveys of British river vegetation have been published previously, notably those of Butcher (1933), Haslam (1978, 1982, 1987), Holmes (1983), and Holmes & Newbold (1984). The survey described below differs from previous work in its emphasis on Batrachian *Ranunculus* species (in particular the identification of *Ranunculus* taxa to variety level) and the measurement of a larger number of environmental variables that was possible in some of the earlier work. In addition more sophisticated statistical techniques for the analysis of such surveys have been developed recently, and these have been applied to the data obtained.

Figure 2.1
Location of River Sites
Surveyed During 1990

For Key see following page



Key to Figure 2.1: River Sites Surveyed During 1990

Site №	Site	National Grid Reference
1	River Whitewater (Surrey) at Risely	SU741 635
2	River Rother (West Sussex) at Maidenmarsh	SU 782 233
3	River Loddon at Wildmoor	SU 692 559
4	River Loddon at Old Basing	SU 660 528
5	River Itchen at Brambridge House	SU 462 225
6	River Itchen at Winchester	SU 486 296
7	River Itchen at Chiland	SU 523 325
8	Candover Brook at Abbotsbury	SU 569 335
9	River Ebble at Odstock	SU 147 096
10	Salisbury Avon at Upavon	SU 136 550
11	Salisbury Avon at Netheravon	SU 150 485
12	Salisbury Avon at Middle Woodsford	SU 120 361
13	Salisbury Avon at Woodgreen	SU 163 174
15	Bere Stream at Bere Heath	SY 857 928
16	River Piddle at Hyde	SY 865 906
17	River Piddle at Affpuddle	SY 806 938
18	River Frome at Lower Brockhampton	SY 721 904
19	River Frome at Moreton	SY 806 895
20	River Cerne at Cowden	SY 678 936
22	River Frome at Notton	SY 610 959
21	River Frome at Frampton	SY 623 944
23	River Frome at Maiden Newton	SY 597 977
24	River Sydling Water near Sydling Saint Nicholas	ST 635 003
25	River Lugg at Mortimer's Cross	SO 427 637
26	River Rye near East Newton	SE 644 805
27	River Teifi at Cors Carron	SN 684 628
28	River Teifi at Altyblata	SN 523 454
29	River Gwendraeth Fach at Llangeiderne	SN 460 139
30	River Tone at Waterrow	ST 052 254
31	Hillfarrance Brook at Hillfarrance	ST 157 248
32	River Exe at Oakford Bridge	SS 919 219
33	River Exe at Exebridge	SS 930 245

Site №	Site	National Grid Reference
34	River Exe at Bamford Speke	SX 929 984
35	Cam Brook at Carlingcott	ST 695 586
36	River Chew at Compton Dando	ST 647 648
37	River Chew at Publow	ST 623 642
38	Bristol Avon at Easton Grey	ST 881 875
39	Bristol Avon at Lacock Abbey	ST 922 681
40	Bristol Avon at Great Summerford	ST 965 831
41	River Fowey at Golitha Woods	SX 228 687
42	River Fowey at Codda	SX 182 785
43	River Torridge at Hele Bridge	SS 542 064
44	River Lymington River at Ivy wood	SU 316 023
45	River Mill Lawn Brook at Mill Lawn House	SU 224 035
46	River Frome at Lewell Mill	SY 739 901
47	Waterston Stream at Druce	SY 742 952
48	River Wye at Hay	SO 238 426
49	River Loddon at Twyford	SU 782 761
50	River Swansea Water at Downstream Usk Reservoir	SN 820 271
51	Swansea Canal at Pontardwe	SN 728 047
52	River Wylye at Codford Saint Mary	ST 970 405
54	Avon Water (New Forest) at Holmsley Bog	SU 016 223
55	River Bourne at Idmiston	SU 195 378
56	River Kennet at Lockeridge	SU 150 683
57	Unnamed stream near Worth Matravers	SU 957 772

As well as the surveys, a series of transplant experiments was carried out. Holmes and Whitton (1977a, b) have shown that sometimes a particular *Ranunculus* species is not present at a site due to a historical lack of viable propagules reaching that site rather than to the unsuitability of the site. *Ranunculus* species were transplanted into rivers which had no indigenous *Ranunculus* in order to ascertain whether it was possible for that species to survive in the conditions in that river.

2.2 Methods

2.2.1 Survey

During August 1989 a large number of river sites was visited to select some suitable for work during the following year. These initial sites were selected chiefly from sites previously studied by I.F.E. River Lab staff and also by reference to the literature (including Haslam 1987, 1982; Holmes 1983) and from 1:50 000 O.S. maps.

Selection criteria for the 56 sites selected were accessibility, wadability and presence of a *Ranunculus* species. The sites were selected to encompass a number of different *Ranunculus* taxa, as wide a geographical and altitudinal spread as possible and a variety of stresses and disturbances (such as pollution, flow-rates, and management regimes). Where possible, sites were chosen that had National Rivers Authority discharge and/or chemical data available. The geographical locations of the sites are shown in Figure 2.1. and full details of the sites are given in Appendix A.

Although the sites were selected to be as representative of riverine *Ranunculus* habitats as possible there were some possible elements of bias. The location of the IFE River Laboratory in southern England meant that the sites did not cover the whole of Britain, and so had a southerly bias. A consequence of the distribution of these sites is that quite a large proportion had *R. penicillatus* subsp. *pseudofluitans* present, reflecting the dominance of this plant in rivers and streams in southern England. However, care was taken to ensure that other taxa were adequately represented. During 1991 the survey described in Chapter 6 was carried out in Northern England and Wales and Scotland. The results of these two surveys are compared in section 2.4. The other possible bias was that it was not possible to survey rivers that were too deep to wade (i.e. > 1.2 m). *R. fluitans* is sometimes found in rivers at greater depths.

During May to October 1990 the sites were visited four times. Sites 13, 52, 54, 55, 56 and 57 (see Figure 2.1) were visited fewer times for various reasons, for example the site at Woodgreen on the Salisbury Avon had been destroyed by bulldozers just before the final visit. Making several visits rather than just one ensured that it was possible to find the *Ranunculus* in flower on at least one occasion at virtually all the sites, which made taxonomic identification much more reliable. In addition the four visits enabled a much more complete picture of the phenology of the plant community and the seasonal variation in the environmental variables measured to emerge. A site was delineated by the extent of a relatively uniform habitat type (e.g. riffle, pool) within a 100 m stretch.

On each occasion the abundance of plant species was measured. Plants which had at least part of their above-ground parts submerged were included in the species list. The percentage frequency of each species was estimated by the frequency of dominance of that species in 50 samples; at each sample point the dominant species in a 0.5 × 0.5 m quadrat was noted, a random distance in a random direction upstream (subjectively selected) was then moved and the process repeated fifty times. Species not included using this technique were recorded as present. Most species were identified on site, but some (such as mosses) were taken back to the laboratory.

The following environmental variables were measured:

a) Water nitrate concentration (measured using Merckoquant nitrate test strips; range 5 - 50 mg l^{-1} as nitrate-nitrogen, accuracy ± 2.5 mg l^{-1})

Water pH (measured using B.D.H. indicator strips, accuracy ± 0.1 pH units)

b) Water (soluble) phosphate concentration (measured using Aquamerck phosphate test kit; range 0.25 - 3 mg l^{-1} soluble phosphate-phosphorus, accuracy ± 0.125 mg l^{-1})

The method of measuring the light attenation co-effcient can give rise to innacuracies due to varying height of the water column (caused by wave action, etc) and scatter of light in the water column, as well as the sampling regime possibly missing some occasions on which the water might have been more turbid. In the analysis of the data, light does not come out as being a particularly important limiting factor of these communities. It is possible that this was due to the above innacuracies.

c) Water depth (at *Ranunculus* clumps)

d) Flow rate (at *Ranunculus* clumps, measured using either an Ott propeller meter or a C.I.D. electromagnetic current velocity meter)

e) Discharge (calculated from flow rate and depth measurements taken at intervals across the river).

f) Cross-sectional area of river

g) Light attenuation co-efficient (calculated from measurements taken with a Licor P.A.R. meter).

h) Percentage shade (estimated)

i) Elevation above mean sea level (from O.S. map)

j) Maximum number of flowers per unit area

k) *Ranunculus* tissue chemical concentrations (method in Appendix C)

l) Sediment chemical concentrations (method in Appendix C)

The management regime (whether cut, grazed, etc.), and the adjacent land use (urban, woodland, etc) were categorized by observations and information from landowners (where available). Sediment and plant samples were taken for chemical analysis during the last visit. At least five samples were taken from each site, which were pooled for analysis. Plant material was stored in polythene bags and sediments in polypropylene bottles in a cooled insulated box. As soon as possible (normally within 36 h) the samples were dried at 95°C. The dried samples were stored in glass bottles. They were analysed for carbon, total nitrogen, and ammonium acetate extractable phosphorous, potassium and calcium. Analytical methods are given in Appendix C. In addition, some regions of the National Rivers Authority provided data.

Herbarium specimens were taken of *Ranunculus* species at all sites to enable verification of taxonomy.

The plant communities were classified using the computer program TWINSPAN (Hill 1979b). TWINSPAN has become a standard method for community classification. The program takes the site-species data and divides it into two groups, the sites in each group being more similar to each other (in terms of their species present) than they are to the sites in the other group. This process is repeated a number of times, resulting in a hierarchical classification, with a number of groups of sites as the product. Indicator species for each group are also produced. The species are not simply treated as present/absent but the abundance is taken into account with each species being divided up into five 'pseudospecies', one pseudospecies for each point of an abundance scale of one to five. If a species is present at abundance three it is treated as three pseudospecies (at abundance one, two and three). The program also groups species in terms of the sites they occur in, but these data were not used here.

Each of the four visits to each site was treated as a separate site for the purposes of this classification. The site-species data from the survey described in Chapter Six was also classified using TWINSPAN. In addition the data from the two surveys were combined and analysed with TWINSPAN. In order to do that only the data from the second out of the four site visits from the 1990 survey were included - that being the one at the same time of year as the 1991 survey.

DECORANA (Hill 1979a; Hill & Gauch 1980), was until recently the standard method for ordination of survey data. However the more recent computer program CANOCO (Ter Braak 1985, 1986, 1989) offers a number of advantages over DECORANA. In particular there are some improvements to the fundamental alogrithms employed and the program allows direct (rather than indirect) correlation of environmental axes with site-species data (Ter Braak 1985).

In common with other ordination programs, CANOCO extracts, from data consisting of the abundance of species at a number of sites, the dominant pattern of variation in community composition. This pattern of variation may then be correlated with the variation in environmental variables. CANOCO provides a number of options to carry out this analysis.

Indirect methods such as correspondence analysis (CA) or detrended correspondence analysis (DCA; e.g. DECORANA) first derive the axes of variation in community composition. Axis one represents the principal axis of variation, the second the secondary axis and so on. It may be inferred that the gradient in community composition along an axis is caused by an environmental gradient. 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). If the analysis is detrended then linear dependence between axes is removed (Hill and Gauch 1980).

Direct methods such as (detrended) canonical correspondence analysis take the environmental data into account when deriving the axes. Thus the species composition is related directly to the environmental variables. This method has the advantages that it can account for variation not related to the first few axes of DCA (which may be substantial) and can enable one to see the effects on species composition due to environmental variables other than those strongly correlated with the first few axes (Carleton 1984; Ter Braak 1986).

Correlation between *Ranunculus* tissue nutrient concentrations and water and sediment concentrations were carried out using the computer program MINITAB (Ryan *et al.* 1985) to carry out linear regressions and calculate Spearman's correlation coefficients (r).

2.2.2 Transplant Studies

In January 1990 a variety of *Ranunculus* species were transplanted from several sites to other sites, and at the same time controls were carried out (i.e. the plants were planted back into the sites from which they were originally taken). The *Ranunculus* plants were placed in 15 cm pots containing sediment from the sites to which the plants were being transplanted into. The roots were not 'pot bound' by the end of the experiment. The pots also contained some 4" nails sealed in polythene to enable location with a metal detector (Scope VLF.TR 770). The surrounding vegetation was cleared away from the pots (approximately 1 m diameter) to limit competition. The pots may have stabalised the rooting medium, and hence that may have been a possible bias to the results. After six months the pots were examined to assess the growth and survival of the transplants. The geographical location of the sites is shown in Figure 2.2. A summary of the transplant experiments is shown in Table 2.1 and details are given in the text below.

Figure 2.2 Location of Transplant Sites

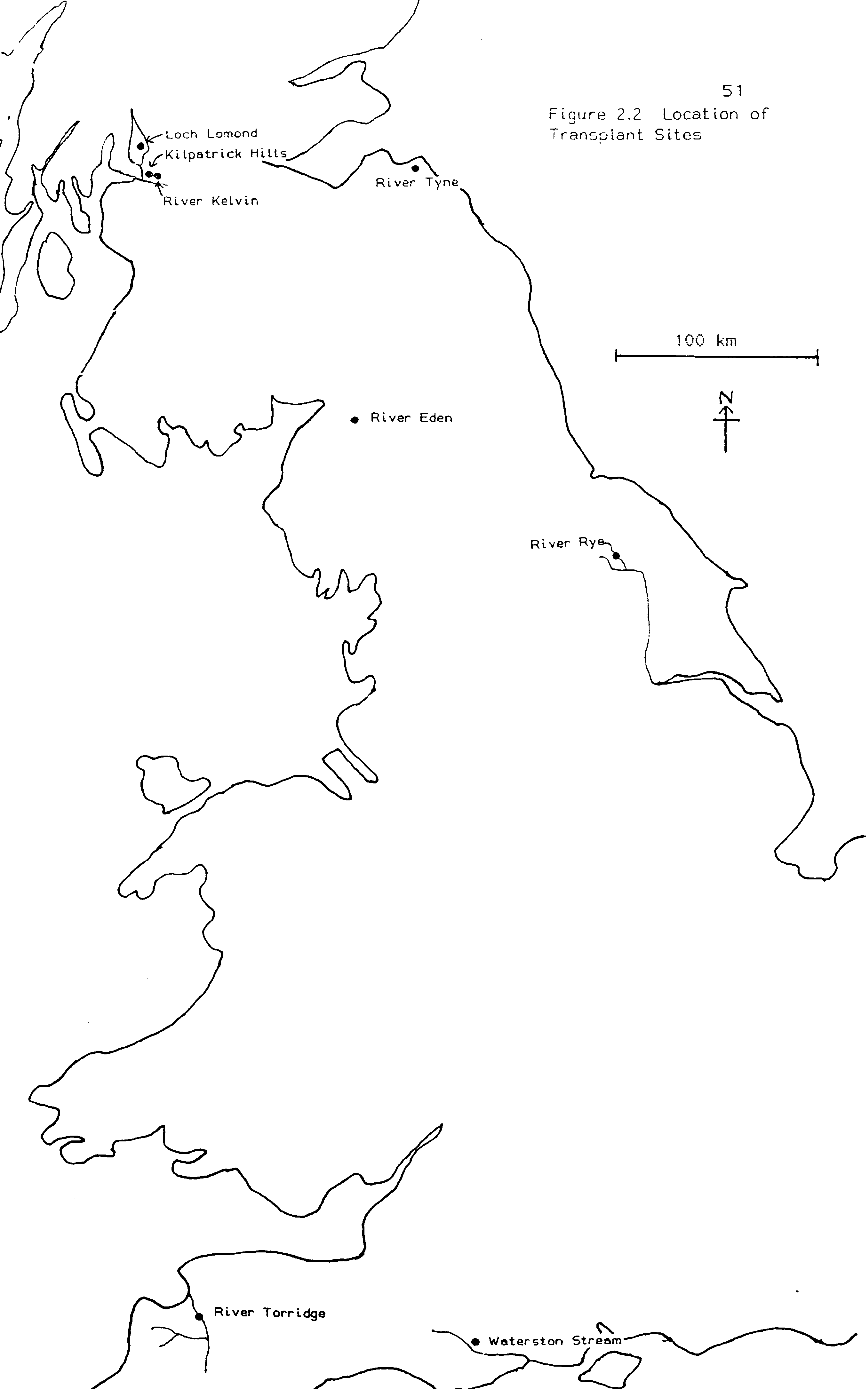


Table 2.1 Summary of Transplant Experiments

Species	Source	To
R. fluitans	River Rye	River Rye Loch Lomond River Kelvin Kilpatrick Hills
R. penicillatus subsp. *pseudofluitans*	River Rye	River Rye River Tyne (Lothian) Loch Lomond Kilpatrick Hills
R. aquatilis	Pond	Pond River Rye
R. penicillatus subsp. *penicillatus*	River Torridge	River Eden Waterston Stream

R. fluitans plants were taken from the River Rye (a moderately sized, relatively unpolluted river with a high alkalinity (115 mg l^{-1}; Personal Communication National Rivers Authority 1989; Appendix A)) near Rye House Fish Farm in North Yorkshire (National Grid Reference SE 632 820). As well as control transplants back to the Rye, *R. fluitans* was planted in Loch Lomond (in the Central Region of Scotland) near Rowardennan (National Grid Reference NS 375 958). In addition to not being a river and therefore lacking unidirectional flow, Loch Lomond has a much lower alkalinity (and lower concentrations of most major ions) than the River Rye. *R. fluitans* was also transplanted into the River Kelvin in the University of Glasgow Garscube Estate in Glasgow (National Grid Reference NS 552 703. At this point the River Kelvin is grossly polluted with a high phosphate concentration (up to 2 mg l^{-1}; Best 1986).

The final site to which *R. fluitans* was transplanted was a small unnamed burn on the Kilpatrick Hills just outside Glasgow (National Grid Reference NS 468 738). This has a much lower flow rate and discharge than the Rye, as well as being relatively acidic and nutrient poor (it is fed from run-off from upland moorland).

R. penicillatus subsp. *pseudofluitans* var. *pseudofluitans* plants were also taken from the River Rye, but a little further downstream from Rye House, near Nunnington (National Grid Reference SE 642804) and transplanted to the River Tyne at East Linton in Lothian (National Grid Reference NT 593 772). This is a similar sized river to the Rye, but with with a much greater phosphate loading and lower alkalinity. *R. penicillatus* subsp. *pseudofluitans* was also planted in Loch Lomond and the burn on the Kilpatrick Hills.

R. aquatilis was taken from a pond adjacent to the River Rye between Nunnington and Rye House (National Grid Reference SE 638 809) and (as well as a control replanted in the pond) was placed in the River Rye near Nunnington (National Grid Reference SE 644 805).

R. penicillatus subsp. *penicillatus* was taken from the River Torridge near Hele Bridge in Devon (National Grid Reference SS 542 064) This is a relatively acidic river pH 6.8, (Appendix A) with a low alkalinity. This transplant was carried out on 2nd March 1990. The *R. penicillatus* was transplanted to the Waterston Stream at the IFE Experimental Stream near Puddletown in Dorset (National Grid Reference SY 739 902). This is a typical chalk stream with a high pH and alkalinity (Ladle & Bass 1981). It was not possible to plant the control transplant at the same time as the River Torridge was extremely turbid (due to heavy rain upstream) and quite deep. For logistical reasons the *R. penicillatus* subsp. *penicillatus* control transplant could not be carried out at the same site from which the plants were originally taken, but was carried out in the River Eden near Warwick Bridge (National Grid Reference NY 472 565) on 21 June 1991.

2.3 Results

2.3.1 TWINSPAN Classification

The hierarchical classification of the sites for the two surveys and the combined data are shown is Figures 2.3, 2.4 and 2.5. The number of sites at any point in the classification is given by 'n= '. The indicator species for the community are indicated where appropriate, with a superscript denoting the abundance. This is on a scale of 1 to 5 where 1 = 0-20%, 2 = 21-40%, 3=41-60%, 4=61-80% and 5=81-100%.

The major communities identified are shown by a capital letter in bold type, and the sites present in that group are listed in capitals. Site names refer to names given in the appendices. If all or most of the sites in a single river system are in the same group the name of the river is listed rather than all the sites. -A to -D after the site names in Figure 2.3 refer to each of the four visits. Where these are all classified together in the same group no suffix is given.

Communities Identified in the 1990 Survey (see Fig. 2.3)

Group A

This group of just two sites was split off from the bulk of the others at the first division, with the moss *Polytrichum commune* as an indicator species. *R. omiophyllus* is also present at both sites. Both receive disturbance from horses and are fairly acidic sites.

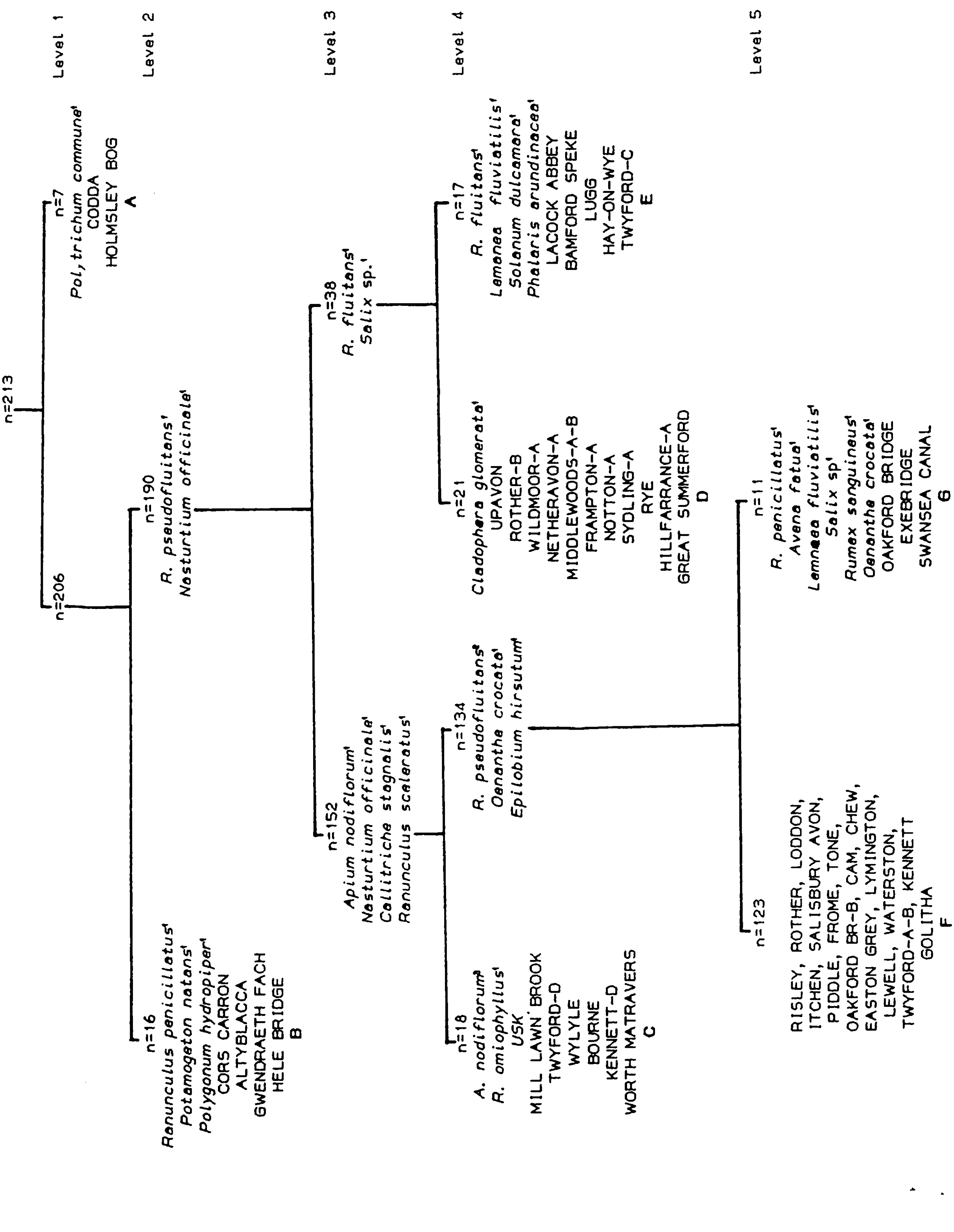
Group B

Although the two subspecies of *R. penicillatus* are closely related taxonomically they have a very distinct ecology and this is reflected by their division at level 2. Not all the *R. penicillatus* subsp. *penicillatus* sites are included in group B (some being in group G), the sites in group B being a little more species rich with e.g. *Potamogeton natans* present.

Group C

These sites are characterised by high disturbance from the Welsh upland site near Usk reservoir to several winterbourne sites. The River Loddon at Twyford was almost dried-up on the last visit, which accounts for its inclusion in with winterbournes, but it is worth noting here that it was grossly polluted and perhaps as a result of that it is the only site that was classified in three different communities after different site visits.

Figure 2.3. TWINSPAN Classification of Communities surveyed during 1990. *R. penicillatus* subsp. *penicillatus* has been abbreviated to *R. penicillatus* and *R. penicillatus* subsp. *pseudofluitans* has been abbreviated to *R. pseudofluitans*. For further details see text



Group D

This group is predominantly composed of the first visit *R. penicillatus* subsp. *pseudofluitans* sites in chalk streams and rivers. It is interesting to note that all the site visits to the River Rye in northern England are classified in the same group as the spring visits to the more southern sites.

Group E

These are relatively large rivers with *R. fluitans* as an indicator species.

Group F

This is a large (n=123) but relatively homogeneous group of sites. If a further division is carried out only four sites are split off. These sites mostly represent typical chalk streams dominated by *R. penicillatus* subsp. *pseudofluitans*, though it does contain some other sites, e.g. the River Lymington (*R. peltatus*) in the New Forest.

Group G

The final group contains the upstream River Exe sites which are (somewhat surprisingly) placed with the Swansea Canal. The canal is disused and has a slight throughflow. The point of similarity may lie with the bank vegetation (heavily shaded by trees). Although the Swansea Canal has rich bank vegetation at the water level the submerged and emergent vegetation of all the sites in Group G is species poor.

Communities Identified in the 1991 Survey (see Fig. 2.4)

Group A

This group contains the majority of the *R. fluitans* sites.

Group B

The *R. baudotii* sites are placed with a *R. hederaceus* site. All are small muddy streams.

Group C

Although *R. peltatus* is an indicator species for these sites it is not found in the Irt or Uggie (*R. penicillatus* subsp. *pseudofluitans* being present at these sites). This is interesting in view of the fact that the ecological range of these two species overlaps and their position in a stream will change according to the conditions prevailing in a particular year (Ladle & Bass 1981).

Group D

This is a group of rivers and streams dominated by *R. penicillatus* subsp. *pseudofluitans* with typical associated flora.

Group E

Although showing close affinity to Group D, these sites are quite varied, ranging from a small stream just a few metres before it runs into the sea at Porth Mendwy in Wales to one of the largest sites covered in this survey, the River Spey at Garmouth in northern Scotland.

Group F

These are the two *R. circinatus* sites covered in this survey.

Group G

Like Group E this is a very varied group of sites with *R. peltatus*, *R. omiophyllus*, *R. aquatilis* and *R. hederaceus* present. As noted in Chapter One *R. aquatilis* and *R. peltatus* have similar ecologies, as do *R. omiophyllus* and *R. hederaceus*.

Group H

This is a small group of just two sites, with *R. aquatilis* as an indicator species.

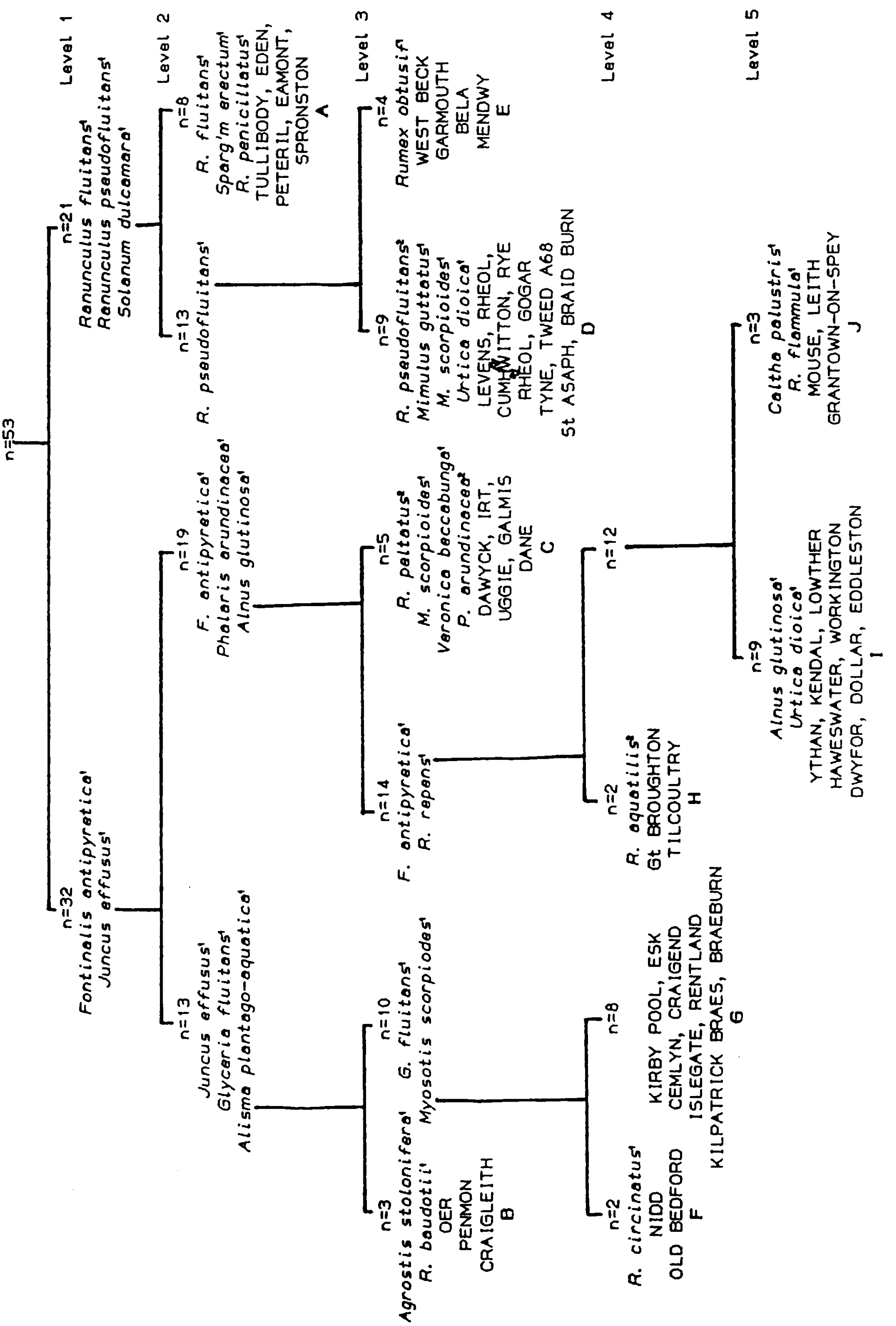
Group I

This group represents sites with a variety of *Ranunculus* species, but all are quite large rivers, moderately fast-flowing and with a low alkalinity.

Group J

A group of relatively species poor sites, apparently classified together on the basis of a similar emergent/bank vegetation.

Figure 2.4. TWINSPAN Classification of Communities surveyed during 1991. R. penicillatus subsp. *penicillatus* has been abbreviated to *R. penicillatus* and *R. penicillatus* subsp. *pseudofluitans* has been abbreviated to *R. pseudofluitans*. *Rumex obtusif* = *Rumex obtusifolius*. For further details see text



Combined Data from 1990 and 1991 Surveys (see Fig. 2.5)

Group A

This group has *R. omiophyllus* as an indicator species. Like Group A of the 1990 survey, they are all fairly highly disturbed.

Group B

This just contains one site, a New Forest stream with three Batrachian *Ranunculus* species present.

Group C

The majority of these sites have *R. peltatus* present demonstrating the ecological amplitude of this species; Braeburn is a small acidic stream running through a disused reservoir, the River Bourne is a winterbourne with a high nutrient and calcium input and *R. peltatus* grows where Rentland Burn joins a large reservoir, the site being one of the deepest surveyed.

Group D

These two sites are separated from Group C by the presence of large quantities of algal species.

Group E

These are all *R. fluitans* sites, the ones in the Petteril also containing *R. penicillatus* subsp. *pseudofluitans* var. vertumnus.

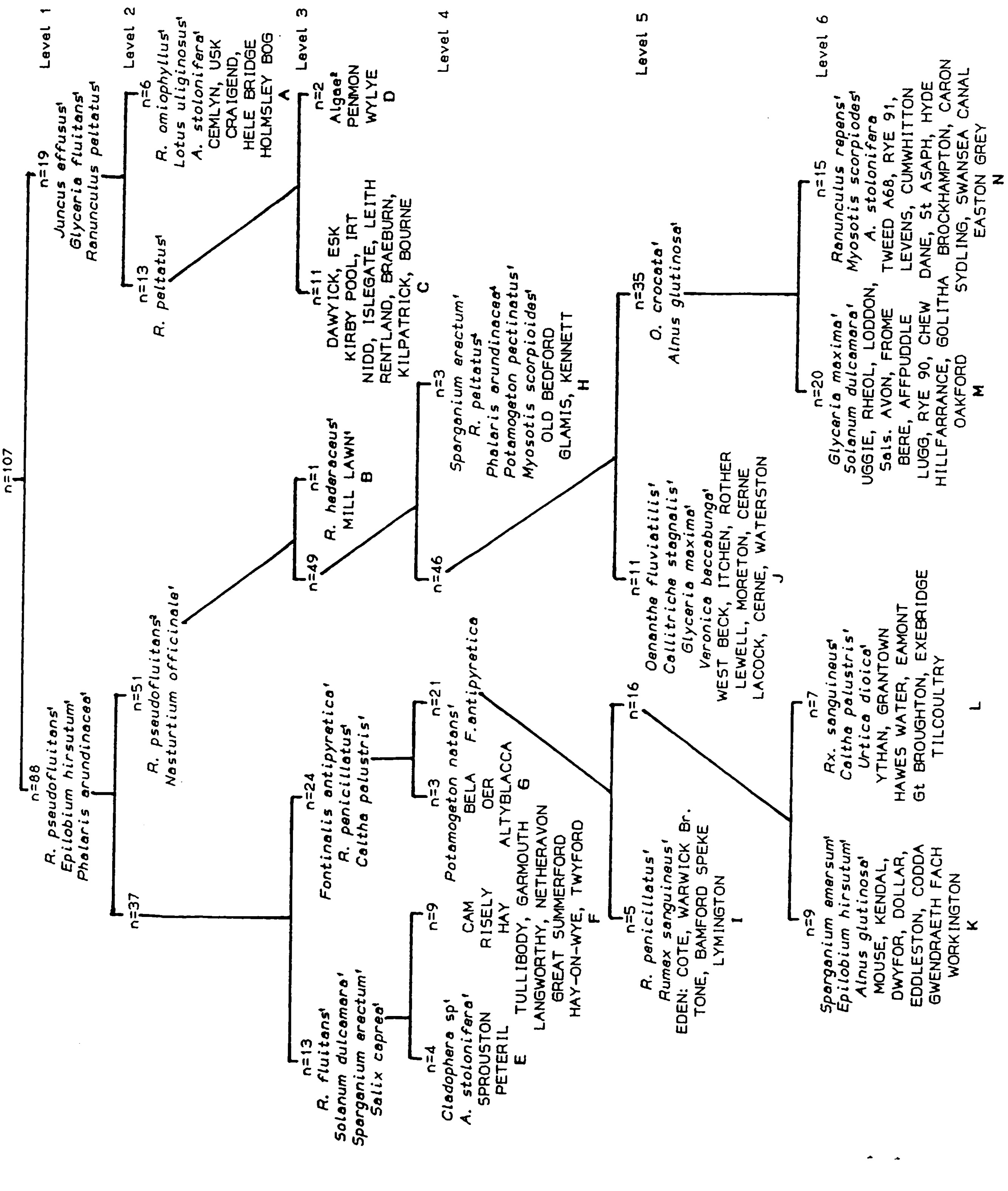
Group F

This is closely related to the above group, containing mostly moderately large rivers. Although at Level 3 *R. fluitans* was an indicator for this group there are a number of *R. penicillatus* subsp. *pseudofluitans* var. pseudofluitans sites, showing the overlap in habitats occupied by these species.

Group G

A small group of sites with *Potamogeton natans* present.

Figure 2.5. TWINSPAN Classification of combined data from communities surveyed during 1990 and 1991. R. penicillatus subsp. *penicillatus* has been abbreviated to *R. penicillatus* and *R. penicillatus* subsp. *pseudofluitans* has been abbreviated to *R. pseudofluitans*. For further details see text



Group H

Although *R. peltatus* is an indicator for this group it is not present at all the sites and extensive stands of *Phalaris arundinacea* are more characteristic.

Group I

Again the *Ranunculus* species is not present at all the sites in this group. The sites are composed of relatively large and relatively acidic rivers.

Group J

A group of chalk stream sites, separated from the others (groups M & N) by species such as *Callitriche stagnalis* and *Veronica beccabunga*.

Group K

Many of these sites experience stress, especially from pollution.

Group L

Group L is composed of relatively large and acidic rivers with a variety of *Ranunculus* species.

Groups M & N

These groups are mostly chalk streams and rivers. They are very closely related (the River Rye is classified in Group M one year and N the next). On the whole Group M appears to have more emergent marginal vegetation. They are dominated by *R. penicillatus* subsp. *pseudofluitans*.

2.3.2 CANOCO Ordination

The ordination diagrams produced by CCA and DCCA of the survey carried out in 1991 are shown in Figures 2.6 and 2.7. Environmental variables are represented by arrows. The direction of the arrow represents the increasing gradient of that variable, e.g. in Figure 2.6 species plotted at the right hand side of the diagram are associated with sites with low pH values whereas species plotted at the left hand side of the diagram mostly occur in sites with high pH values.

The length of the arrow represents the importance of that variable, e.g in Figure 2.6 pH is a more important variable than discharge. The length is derived from the eigen value of the axes (i.e. how much of the variation in the data is explained by the axis) and the interset correlation of that variable with the axes.

If two arrows run in the same direction those variables will have a high correlation with each other (e.g. in Figure 2.6 sites with a low sediment nitrogen concentration will tend to have a low sediment potassium concentration (as one might expect). As height above sea level increases, so the water of the upstream section of the river tends to get shallower. In some cases the correlation is most likely to be simply coincidental, for example it is not easy to see why water phosphate concentration and shade should increase concomitantly (although one might speculate that the decrease in plant growth caused by shading causes less phosphate uptake and so a higher phosphate concentration in the water, and there tends to be less urban development in rural areas).

Ordination diagrams have been drawn for both CCA and DCCA. If these are similar it may be inferred that the two axes are not dependent on each other (Ter Braak 1986): the magnitude and relative positions of the arrows and centroids are similar in Figures 2.6 & 2.7.

As a large proportion of sites in this survey were *R. penicillatus* subsp. *pseudofluitans* communities, DCCA analysis was carried out on these sites alone. The ordination diagram from that is shown in Figure 2.8.

Figures 2.6–2.8 Ordination Diagrams for Canonical Correspondence Analysis for River Surveys. For explanation see text.

<u>Key</u>

SPECIES SCORES

fluitans	*Ranunculus fluitans*
pseudofluitans	*Ranunculus penicillatus* subsp. *pseudofluitans* var. *pseudofluitans*
penicillatus	*Ranunculus penicillatus* subsp. *penicillatus*
aquatilis	*Ranunculus aquatilis*
peltatus	*Ranunculus peltatus*
hederaceus	*Ranunculus hederaceus*
omiophyllus	*Ranunculus omiophyllus*
helmsii	*Ranunculus helmsii* (*R. omiophyllus* × *peltatus*)
Elodea c	*Elodea canadensis*
Elodea n	*Elodea nuttallii*
Fontinalis	*Fontinalis antipyretica*
M.alt	*Myriophyllum alterniflorum* [a]
M.spic	*Myriophyllum spicatum*
P.natans	*Potamogeton natans*

ENVIRONMENTAL VARIABLES (arrows)

V	Velocity (at *Ranunculus* clump)
Q	Discharge
sQ^{a}/sV	Standard deviation velocity/discharge (a measure of how spatey the river is)
PO4	Water soluble phosphate concentration
S	Shade
E	Elevation above mean sea level
P	Sediment extractable-phosphate
K	Sediment extractable-potassium
N	Sediment total nitrogen
H	Water depth (at *Ranunculus* clump).
A	Cross sectional area
Ca	Sediment extractable-calcium

pH	Water pH
NO	Water nitrate

NOMINAL VARIABLES

Land Use;

Wood	Woodland
URB	Urban[b]
ARBLE	Arable[b]
MEADOW	Unimproved pasture
IMPR	Improved pasture[b]

Management;

UNMAN	Unmanaged
CUT1	Cut most years, but not this[a,c]
CUT2	Cut this year[b]
GRAZE	Subject to grazing/poaching
CUT+G	Subject to cutting and grazing/poaching

Variables with superscripts (a,b,c) would be superimposed on the diagrams, so to aid clarity they have been ommited;

[a]Same value as *R. penicillatus* subsp. *pseudofluitans* on the CCA diagram (Figure 2.6)

[b]Same value as URB on the DCCA diagram (Figure 2.7)

[c]Same value as CUT1 on the DCCA diagram (Figure 2.8)

Figure 2.6 Ordination Diagram for Canonical Correspondence Analysis for River Surveys

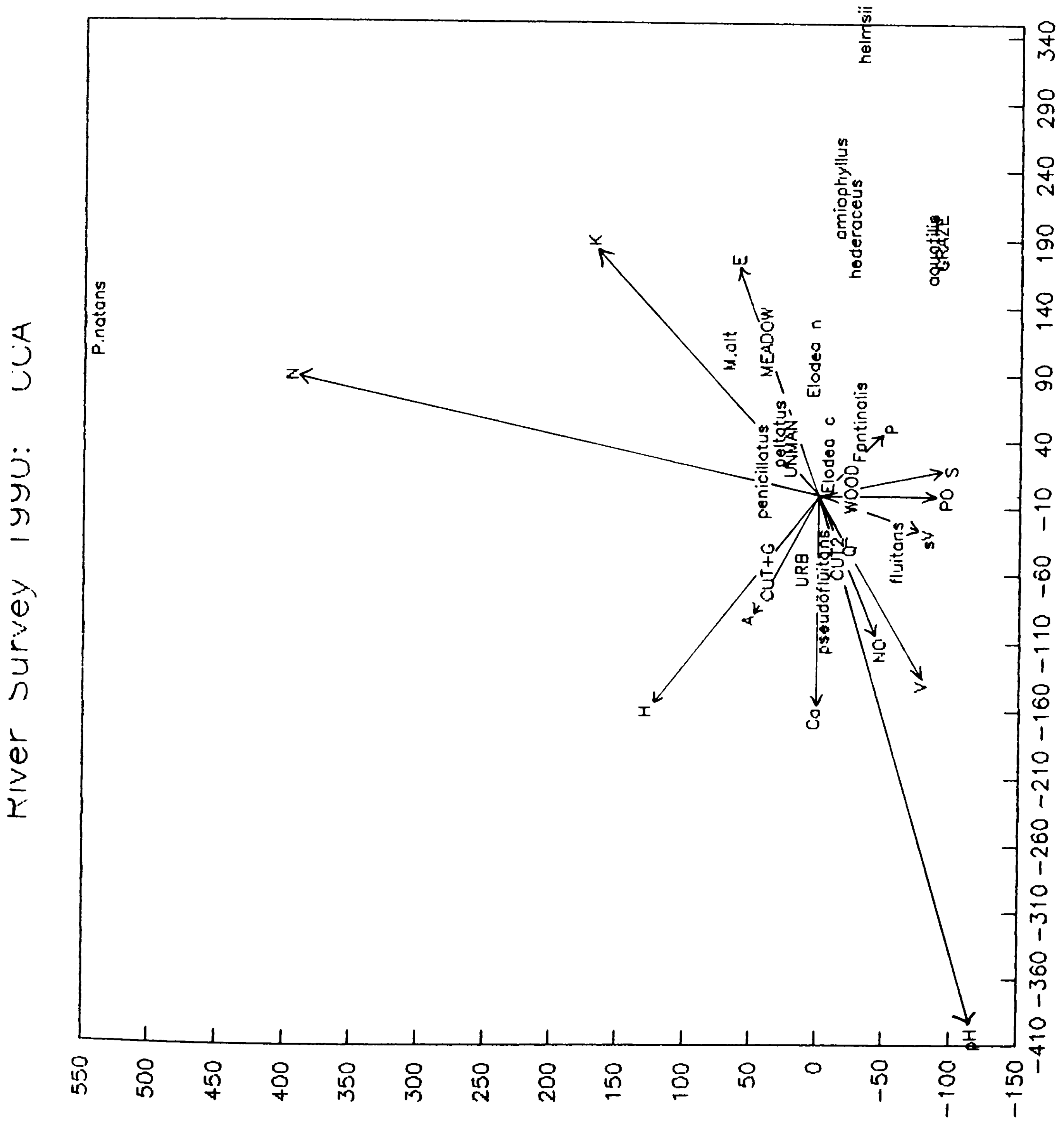
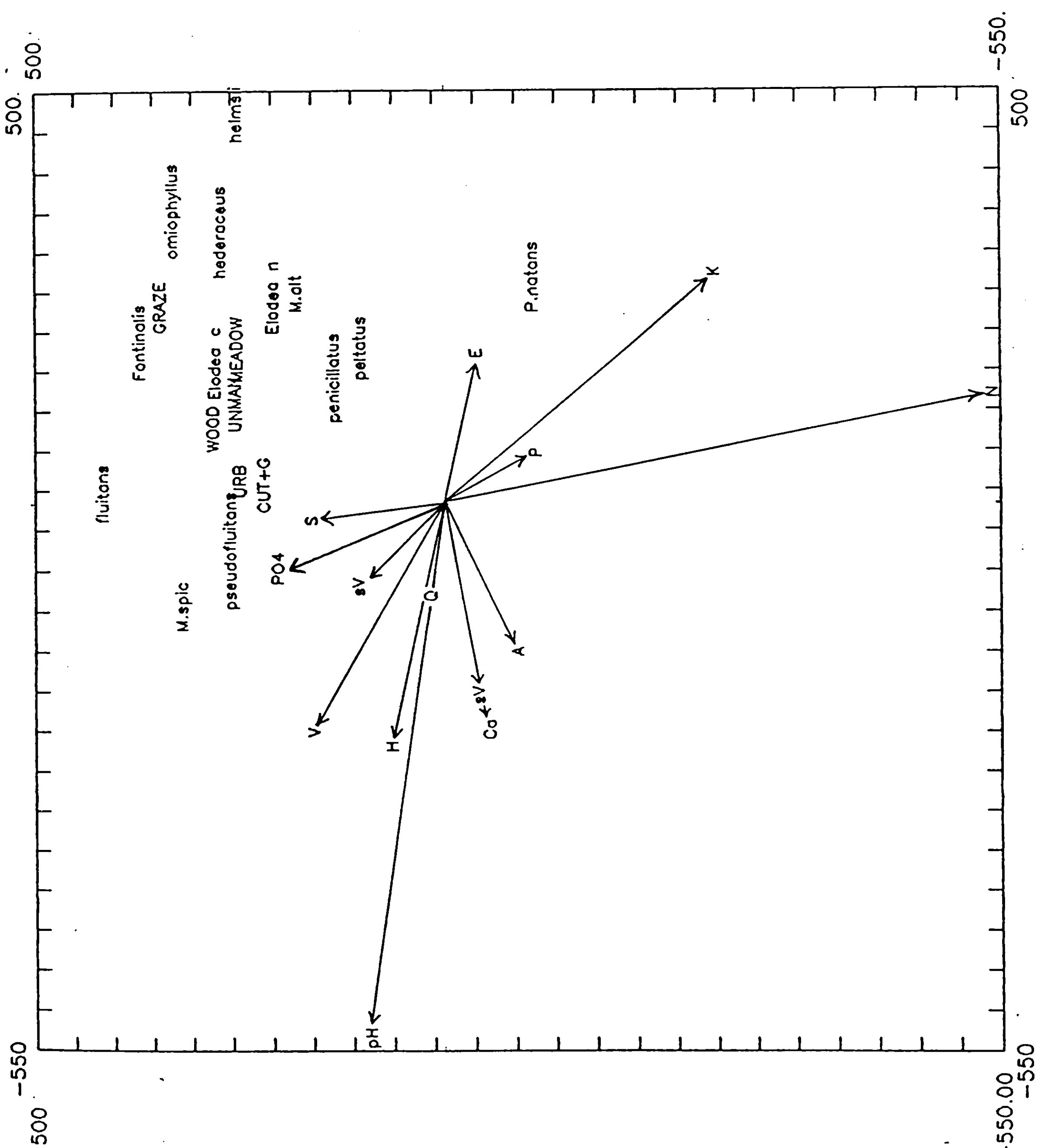


Figure 2.7. Ordination Diagram for Detrended Canonical Correspondence Analysis for River Surveys. For explanation see text. For key see text to Figure 2.6



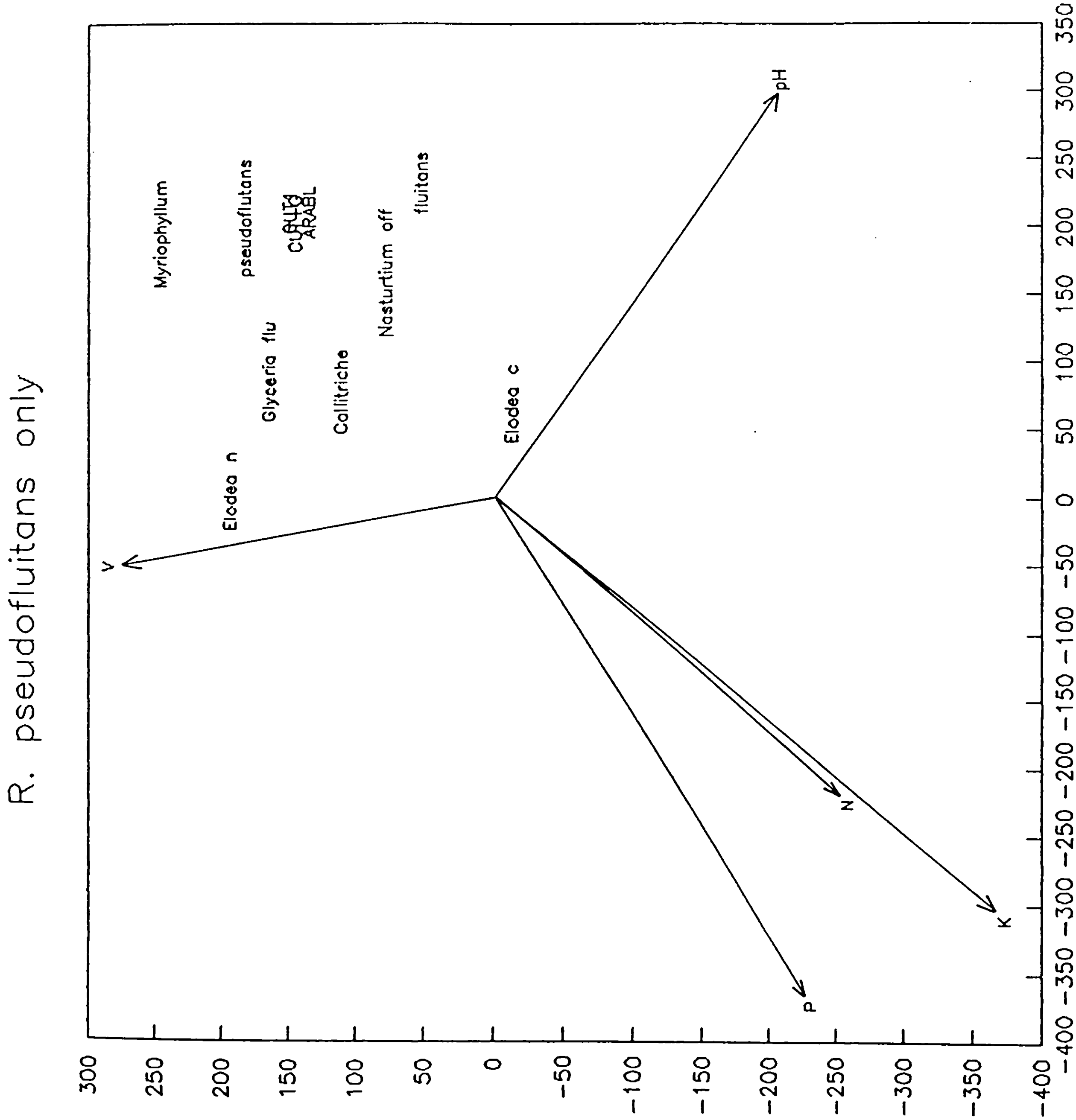


Figure 2.8 Ordination Diagram for Detrended Canonical Correspondence Analysis for River Surveys for sites with *R. penicillatus* subsp. *pseudofluitans*. For explanation see text. For key see text to Figure 2.6.

Species are plotted on the diagram using the species scores. The point at which the species is plotted represents the 'centroid' of distribution of that species, i.e. the point at which the species is most abundant on the diagram. As with DECORANA plots, the closer species (and sites if plotted) are to each other, the more similar they are (in this case in terms of environmental variables as well as species composition). Species plotted are Batrachian *Ranunculus* species and those that are important indicator species in the TWINSPAN classification. If a perpendicular line is dropped from species points to an environmental arrow the species may be ranked in terms of its occurrence along that environmental gradient.

Nominal variables such as classes of land-use and management are represented on the ordination diagram by centroids rather than arrows. The closer a species is plotted to the centroid, the more likely it is to be found in a site associated with that factor. *Ranunculus penicillatus* var. *calcareus* seems to be particularly associated with streams subjected to cutting whereas *R. hederaceus* and *R. omiophyllus* are more strongly associated with sites subjected to grazing.

The importance of these nominal variables in predicting species composition, as with the other environmental variables, may be assessed by the distance away from the axis. However the arrows and centroids are drawn to a different scale (the values for the arrows have been divided by 2.00). The relative importance of nominal and quantitative variables must be assessed with care when interpreting the diagram, and should be compared with the correlation coefficients given in Table 2.1.

Table 2.1 Correlation Coefficients between Environmental Variables and DCCA Axes. Levels of significance are represented as follows; * = $p \leq 0.05$, ** = $p \leq 0.01$, ***= $p \leq 0.01$. Eigen values represent the percentage variation in the data accounted for by that axis.

Variable	Axis 1	Axis 2	Axis 3	Axis 4
Velocity	** -0.257	* 0.212	* -0.215	0.021
Height	** -0.320	-0.180	0.005	* -0.212
Discharge	-0.065	0.076	*0.029	0.144
Area	-0.162	-0.055	0.012	0.132
σ of Velocity	-0.039	0.178	-0.043	0.127
σ of Discharge	* -0.222	-0.010	-0.019	0.124
Nitrate in water	-0.206	0.028	* 0.233	* -0.245
Shade	0.066	** 0.256	***-0.341	-0.160
Elevation	** 0.302	0.062	-0.071	-0.064
Phosphate in water	-0.001	** 0.295	** -0.231	** 0.258
pH	***-0.738	0.071	*** 0.360	-0.112
Sediment nitrogen	0.177	***-0.550	* 0.203	0.006
Sediment phosphate	0.139	-0.041	** 0.317	* -0.201
Sediment calcium	** -0.278	-0.033	*** 0.490	* -0.212
Sediment potassium	*** 0.393	** -0.254	* 0.235	0.015
Unimproved pasture	*** 0.421	-0.064	0.174	** 0.260
Improved pasture	** -0.251	0.037	-0.189	-0.015
Arable	-0.084	-0.049	0.138	0.117
Woodland	0.051	0.149	-0.165	** -0.285
Urban	-0.179	-0.066	0.111	-0.040
Unmanaged	** 0.294	-0.091	-0.246	0.067
Cut most years	***-0.373	0.001	0.092	-0.116
Cut inc this yr	**-0.248	0.029	0.300	-0.070
Grazed/poached	*** 0.471	** 0.246	-0.002	0.121
Cut and grazed	-0.187	-0.191	-0.067	0.001
Eigen value	.571	.468	.306	.218

The object of this analysis was to form hypotheses as to which environmental variables are important in determining the distribution and ecology of Batrachian *Ranunculus* species, which could then be tested by the transplant studies described in this chapter and in the experimental work described in later chapters. In summary, the measured environmental variables can be placed into three classes;

1. Variables primarily responsible for community composition
   - pH and sediment calcium
   - Sediment nitrogen
   - Sediment potassium
   - Management and land use

2. Variables still important, but less than the above
   - Water height
   - Water velocity
   - Water phosphate concentration
   - Shade
   - Elevation

3. Variables of lesser importance.
   - All other measured variables.

On the ordination diagram for the *R. penicillatus* subsp. *pseudofluitans* sites (Figure 2.8) only the most important environmental variables are shown. These are;

- Sediment potassium
- Sediment phosphate
- Sediment nitrogen
- pH
- Water velocity

The ordination diagrams will be discussed further in section 2.4 below.

2.3.3 Correlations between tissue chemical concentrations and chemical concentrations of sediment and water.

In Table 2.2 below the tissue N, P and K concentrations from the *Ranunculus* plants at the sites in the 1990 survey are correlated with the peak nitrate and phosphate concentrations measured in the water at those sites and with the nitrogen, potassium and phosphorus measured in the sediment at those sites.

The table shows r^2 values (equivalent to the percentage variation explained by the data). Levels of significance are represented as follows; * = $p \leq 0.05$, ** = $p \leq 0.01$, ***= $p \leq 0.01$.

Table 2.2 Chemical Correlations from Survey Data

R^2 (%)	*Ranunculus*		Sediment			Water	
	P	K	N	P	K	N	P
N	0.9	20.3**	2.2	0.3	4.4	10.7*	0.2
P-Plant		3.0	0.3	16.2**	0	10.0*	47.7***
K			0.3	0.2	0.1	0.1	1
N				9.4	40.5***	3.1	3.2
P-Sedm't					2.9	11.6*	13.3**
K						0.1	3.8
N-Water							13.5**

The strongest correlation is the positive correlation between phosphorus concentration in *Ranunculus* tissue and in the water. The *Ranunculus* phosphorus concentration is also positively correlated with the phosphorus in the sediment and nitrate in the water. *Ranunculus* tissue nitrogen concentration is negatively correlated with nitrate in the water.

2.3.3 Results of Transplants

R. fluitans

The control transplants were washed out in a severe storm in the River Rye which followed shortly after they were planted there. The control was repeated at the same site the following year. Unfortunately it proved impossible to find either the pots or plants again, it is likely that they were removed by another storm.

All the *R. fluitans* planted in Loch Lomond died, as did the plants in the burn on the Kilpatrick Hills. In the River Kelvin all but one of the pots got washed away, but in the remaining pot the plants grew well. This transplant was repeated the following year (1990) and this time all the pots survived and all the plants are still growing healthily at the time of writing (October 1991).

R. penicillatus* subsp. *pseudofluitans* var. *pseudofluitans

The controls for this species were also washed away, as were the pots placed in the River Tyne in Lothian. The *R. penicillatus* subsp. *pseudofluitans* planted in the small burn on the Kilpatrick Hills is still growing well at the time of writing.

On 6th August 1990 it was found that eight out of ten (one was missing) of the *R. penicillatus* subsp. *pseudofluitans* pots in Loch Lomond still had *Ranunculus* growing. However the plants were small and spindly. They were removed on that date.

R. aquatilis

All the controls survived in the pond. Only three pots in the River Rye were found. These still had *R. aquatilis* growing in them. Unfortunately sediment had accumulated near to where these pots were placed so that they were in an area of still water out of the main current.

R. penicillatus* subsp. *penicillatus

The controls were still growing well on 14 August 1991. The transplants showed quite a dramatic response to being placed in the chalk stream. In less than three weeks they had all shrivelled and died.

2.4 Discussion

The TWINSPAN classification of the sites surveyed during the 1990 survey produced relatively homogenous, intuitively natural groups. By contrast the 1991 survey produced several groups composed of sites that were apparently quite dissimilar. This is probably primarily a reflection of the more accurate picture produced by four visits to each site compared with just one visit for the latter survey. Interestingly when the two data sets were combined, TWINSPAN did not separate the two from each other but produced groups of sites which contained samples from each survey. This indicates that the potential bias in the 1990 survey due to the southern distribution of sites is almost certainly not important.

Probably the most similar survey to the ones reported here is that of Holmes 1983 (see also Holmes and Newbold 1984) and it is instructive to compare the results of the two. There are some similarities. In the 1990 survey Group E corresponds to Holmes's group B4 and Group F corresponds group A3 (and to some extent A4). However there are probably more differences than similarities. This is for a variety of reasons. Holmes' classification was based on a restricted check-list of submerged species, excluding the emergent and bank species which were included as part of the community in the classification and ordination described in this chapter. The sites used were not identical (about half of the sites used in these surveys were at or close to sites used by Holmes 1983). Because of the restriction of the surveys described here to sites with Batrachian *Ranunculus* species present only a particular sub-set of Holmes's 1055 sites were surveyed (e.g. none of the sites in his Group D were covered).

Another, rather more interesting reason, is that it appears that in the decade since Holmes carried out his survey the vegetation at some of the sites has changed. When selecting sites during August 1989 several of Holmes's sites at which a *Ranunculus* species was present during his surveys no longer supported *Ranunculus*. It is not possible to tell whether this is a part of a long-term trend or simply due to fluctuating populations. The unusually dry weather causing low flow-rates may have been a factor.

The results of the DCCA ordination produced by CANOCO are broadly in line with what might be expected from previous work on Batrachian *Ranunculus* species (see Chapter One). *R. fluitans* (the species found in large rivers) is associated with high water velocities whereas *R. peltatus* (the species found in winterbournes) is associated with low velocities. *R. penicillatus* subsp. *pseudofluitans* is associated with management by cutting, whereas *R. omiophyllus* and *R. hederaceus* are found in streams subjected to grazing. These species are found in shallower streams than *R. penicillatus* subsp. *pseudofluitans*. *R. penicillatus* subsp. *pseudofluitans* is found in streams with a higher pH than *R. penicillatus* subsp. *penicillatus*. *R. aquatilis* and *R. peltatus* have close ecological niches whereas *R. penicillatus* subsp. *penicillatus* and *R. omiophyllus* grow in quite different conditions.

These correlations, of course, only suggest hypotheses, the relationships they describe are not necessarily causal. The use of transplant studies provides supporting evidence for the hypothesised relationships. If plants die when moved from one set of conditions to another it may reasonably be inferred that the conditions in the transplant site have caused the death of the plants. The survival of the control plants replaced in the original sites indicates that it is unlikely that the removal of the plants was the cause of death. However as several conditions will have been changed simultaneously the interpretation of such results has to be cautious (Mesters 1990). In some ways the most interesting results are when transplants survive in conditions in which they are not naturally found.

The failure of *R. fluitans* to survive when transplanted to sites with low flow-rates greatly strengthens the hypothesis that its confinement to rivers reflects a requirement for flowing waters. Likewise the sudden death of *R. penicillatus* subsp. *penicillatus* when placed in a chalk stream implies that a physiological limit is inherent in its total absence from calcareous sites. The death of *R. penicillatus* subsp. *penicillatus* when transplanted to a chalk stream was also observed by Webster (1984).

In spite of its previous name of *R. calcareus*, *R. penicillatus* subsp. *pseudofluitans* is sometimes found in relatively acidic streams (e.g. Mill Lawn Brook in the New Forest, see Appendix A). It is known that even within a single river *R. penicillatus* subsp. *pseudofluitans* has distinct genotypes (Dawson 1980). Could it be that its relatively wide ecological tolerance in terms of water pH and velocity was a reflection of many different genetic races rather than phenotypical plasticity? The survival of a population from a chalk river in the small acidic stream near Glasgow (pH 6.1) appears to imply not. Although the plants in this stream were still thriving in October 1991, there was also a thriving population of *Callitriche stagnalis*, which is growing over the *Ranunculus* and shading it. In time the *Callitriche* may competitively displace the *Ranunculus*, which may point to why *R. penicillatus* subsp. *pseudofluitans* is rarely found naturally growing in small acidic streams.

British workers have found that *R. fluitans* appears to be adversely affected by pollution (e.g. Harding 1980), whereas workers in continental Europe have observed increased growth with sewage pollution (e.g. Ska & Vander Borght 1986). The DCCA ordination associated *R. fluitans* with the highest water phosphate and nitrate concentrations (and dose). The River Kelvin in Glasgow not only has a high phosphate loading but is subject to a variety of industrial effluents. The survival of the *R. fluitans* transplants there implies that at the sites where it is absent this is not because the pollution is too great, but that another factor (such as competition from e.g. *Potamogeton pectinatus*) must be involved.

The ordination indicates that water and sediment composition are important factors. This is borne out by the correlations between the plant tissue and environmental chemical concentrations. The tissue nitrogen/water nitrate correlation is barely significant and is in any case negative (Figure 2.9). Likewise the association between tissue phosphate and water nitrate has a very low r^2 value. Of more interest are the significant correlations with tissue phosphate and water and sediment phosphate. Recent work (e.g. Chambers *et al.* 1989; Barko *et al.* 1991) suggests that sediment rather than water is the primary source for phosphate for river macrophytes and Barko & Smart (1980) have shown that macrophytes can derive their phosphate exclusively from sediments in certain circumstances. Conversely Waisel *et al.* (1990) found that even though most phosphate was concentrated in the sediment, more was taken up by the shoots than the roots. The correlative data presented in this chapter are a reminder that both water and sediments can be an important source for phosphate and neither can be ignored if a full understanding is to be gained. It is likely that different sources will be important in different circumstances. Peltier & Welch (1970) found that there was no relationship between nitrate and phosphate concentrations in plants in a reservoir whereas they found that the growth of river plants was related both to nutrients in the water and in the sediments (Peltier and Welch 1969).

In terrestrial plants, low soil nutrient concentrations are thought to be the most important stress (J.P. Grime pers. comm. 1991; Grime *et al.* 1988). Tilman (1988) considers a major problem with Grime's approach to be the difference between plants that are nutrient stressed, and so respond by changes in their below-ground parts (with a concomitant trade-off in the shoot biomass), and those that are shaded and so adapt their shoots. This he feels to be in contradiction with the concept of a general stress-tolerant strategy to both light and nutrient stress. The data discussed in this chapter suggest that in Batrachian *Ranunculus* species both nutrients and light are intercepted to some extent by the shoots, and so increased shoot growth would harvest both more light and more nutrients, avoiding the need for trade-off.

It is a common ecological approach to look for a positive significant correlation between input of a particular element and the concentration of that element in plant tissues (see for example Spink 1988). If they are correlated then it can be postulated that the element is limiting, and experimental work can be carried out to test that hypothesis. A number of such studies have been carried out in freshwater ecosystems. Ho (1979) found a positive correlation between water phosphate concentrations and tissue phosphate in *Potamogeton pectinatus* in Forfar Loch, Scotland. Nichols and Keeney (1976) carried out a study on *Myriophyllum spicatum* from a range of sites and found that the tissue nitrogen was proportional to the nitrogen concentration in the sediment (the nitrate concentration in the water was about the same in all their sites). Barko and Smart (1986a, b) found that macrophyte growth and nutrient accumulation were highly correlated with sediment nutrient densities (concentration/sediment volume). Casey & Downing (1976) measured the tissue phosphate concentrations in *R. penicillatus* subsp. *pseudofluitans* at eight sites and found a possitive correlation with water phosphate at only one of the eight sites, where the water phosphate concentration was highest.

The 1990 surveys showed a significant positive correlation between *Ranunculus* tissue phosphate concentration and sediment phosphate and (particularly) between tissue phosphate and water concentration. The DCCA ordination diagram (Figure 2.7) suggests that not only is the phosphorus important but also sediment nitrogen and potassium are important factors.

Conclusions

As has been stated above, the main goal of a survey such as that described here is to generate hypotheses which may then be tested. The DCCA diagram suggested that pH is one of the most important environmental factors for these communities. It is not clear whether hydrogen ion concentration *per se* is the important factor or whether this is an indicator for a combination of other factors such as calcium concentration and alkalinity. The importance of this complex of factors, particularly for *R. penicillatus* subsp. *penicillatus* has been confirmed by the transplant experiment described in this chapter.

The ordination indicated that sediment nutrient composition is also extremely important. There is already an extensive literature on this subject (recently reviewed in Barko *et al.* 1991) and so it was felt that this was not a priority for experimental work. However there is a relative paucity of field experiments examining the effect of enhanced phosphate concentrations in water on macrophytes and the results of three such experiments are presented in chapters three and five: both the DCCA ordination and the *Ranunculus* tissue correlations suggest this is an important factor.

Water height and shade were also important factors. Peñuelas (1988a, b) has shown that the main effect of water height is to increase shading (rather than hydrostatic pressure). It is well established that *Ranunculus* species are associated with clear waters (Haslam 1987) and that light stress is important for these communities (see for example Westlake 1966, Dawson 1981). Use of shade (particularly by trees) is becoming an established management technique for riverine *Ranunculus* communities (Dawson & Kern-Hansen 1979). Although considerable work has been carried out on the effects of shade on *R. penicillatus* subsp. *pseudofluitans* there are two specific areas that require further study. The different responses of different *Ranunculus* species to shade has yet to be investigated and such a study is reported in chapter six. An experimental investigation of the interaction of shade with another stress, low current velocity, is described in chapter two. The rate of flow of a river was another factor highlighted by the DCCA ordination as being important in affecting *Ranunculus* communities. As well as the experiment just mentioned, this environmental factor is (indirectly) examined in an experiment described in chapter four.

The management regime applied to the streams (in particular the cutting regime) is also significantly associated with the *Ranunculus* communities. As with shading this is an area which has received extensive study, particularly the effects of cutting on *R. penicillatus* subsp. *pseudofluitans* (see for example Westlake & Dawson 1982, 1986). Two questions are examined in this thesis; is the response of *Ranunculus* to cutting altered when the plant is heavily stressed, and what is the response of *Ranunculus* to an increased frequency of disturbance by cutting? These questions are examined in chapters four and five.

As outlined above, the survey described in this chapter has suggested particular stresses and disturbances which appear to be influential in determining the growth and distribution of riverine *Ranunculus* species in Britain. These stresses and disturbances are experimentally investigated in the following chapters.

3. The Response of *Ranunculus* to Stress

The degree in which vitality is sometimes retained by plants, under conditions aparently the most unfavourable, for a period to which it is difficult to assign a limit, is one of the most interesting and curious circumstances in their economy.

William Carpenter (1847)

3.1 Introduction

'Stress' is a word which has a variety of meanings to different ecologists. Levitt (1972, 1980) used the term to describe any factor which is potentially unfavourable to plants, and this is probably the most common usage. As outlined in Chapter One the concept is used in a more restrictive sense here; stress is defined as a factor which reduces the rate of accumulation of biomass of a plant (Grime 1979).

Three stresses likely to be important in limiting the growth and distribution of *Ranunculus* communities were shade, low water velocity and eutrophication (see Chapter Two). Although Hynes (1969) argued that 'eutrophication' can not really be applied to running waters because it had connotations of the evolution of the environment, the term is widespread in littoral studies and is consistent with its original usage (Weber 1907). Here the term is used simply to denote the changes that occur with increasing nutrient supply.

Shade

Spence (1976) pointed out that all but the clearest and shallowest of waters may be regarded as a shade habitat. Butcher (1927) noted that *R. penicillatus* subsp. *pseudofluitans* was absent from shady portions of the River Itchen. Haslam (1987) has shown that *Ranunculus* species are closely associated with clear waters. Grillas and Duncan (1986) showed that the distribution of *R. baudotii* (together with some other *Ranunculus* species) could be explained by light attenuation by the water column which limited the extension of *Ranunculus* into deeper water. These results are consistent with work on other species (see for example Denny 1972, Barko *et al.* 1982, Titus & Adams 1979, Spence & Chrystal 1970a, b). The distribution of plants with water depth is due mainly to light attenuation rather than the effects of increased pressure, at least at depths less than about 10 m (Bodkin *et al.* 1980, Dale 1981, 1984, Spence 1982, Peñuelas 1988a, b) .

Owens and Edwards (1961) measured the biomass of *R. penicillatus* subsp. *pseudofluitans* in a chalk stream in both shaded and unshaded sites and concluded that solar irradiation was the main factor determining the distribution of macrophytes at that site. Ham *et al.* (1981), Ham *et al.* (1982), and Wright *et al.* (1982) have compared a *R. penicillatus* subsp. *pseudofluitans*-dominated community growing in a shady portion of a chalk river in southern England with a similar unshaded site on the same river. The biomass of the *Ranunculus* was less in the shaded site, but other species (*Berula erecta, Callitriche stagnalis* and *C. obtusangula*) were not affected to the same extent, and had equal or higher biomass in the shade. It appeared that in the stressed site the importance of competition was reduced and the *Ranunculus* was not able to competitively dominate the site as it did in the less stressed, unshaded site.

Field observations and experiments have indicated that in sites where *Ranunculus* grows vigorously, self-shading is important in limiting growth (Dawson 1973, 1976). As well as a leaf being shaded by the leaf above it, shading due to epiphytic algae is thought to be important (Sand-Jensen 1977, Ham *et al.* 1982, Sand-Jensen & Borum 1991). Brookes (1986) has shown that increased sedimentation loads can reduce *R. penicillatus* subsp. *pseudofluitans* growth (though this is due to abrasion as well as shading).

A series of field experiments has been carried out to investigate the effects of natural and artificial shade on *R. penicillatus* subsp. *pseudofluitans* and *R. peltatus* (Dawson 1978, Dawson & Kern-Hansen 1979, Dawson 1981a, Dawson & Hallows 1983). These have shown that reducing the light available to *Ranunculus* leads to a proportional decrease in *Ranunculus* biomass and a concomitant increase in species diversity at those sites. This has led to the recommendation that effective management of streams dominated by *Ranunculus* is best achieved by manipulating the bank vegetation (either by letting emergent species grow up in the case of small streams, or by planting trees on the south bank) to shade the submerged vegetation (Dawson & Kern-Hansen 1979). It has been argued that the use of shade as a means of weed control may select for less vigorous plants, as opposed to management by cutting which may select for more vigorous plants, and so it may prove a more efficient technique in the long term (Dawson 1988).

Although the work described above has been extensive, there are still some aspects in need of further investigation. The differential effect of shade on different Batrachian *Ranunculus* species has not previously been investigated: the results of a series of greenhouse experiments on four *Ranunculus* species of contrasting ecology are presented in Chapter Six. Although the interaction between low light stress and other stresses has been investigated for other macrophyte species (e.g. Hough & Fornwall 1988), the experiments on the effects of shade on *Ranunculus* have tended to look at that factor in isolation. The shade experiment described in this chapter was designed to look at the effects of low light stress in combination with the stress caused by low water velocity. In addition, previous studies have not measured the whole plant community, for the duration of the growing season (as opposed to simply harvesting at the end of the year), in experimentally controlled conditions.

Low Water Velocity

"The chief factor which governs the distribution of larger plants in running water is current" (Butcher 1933). As outlined in Chapter One, some species such as *R. hederaceus* are associated with still or slow-flowing water whilst for example *R. fluitans* is associated with larger rivers. The period of most rapid seasonal growth of *R. penicillatus* subsp. *pseudofluitans* is normally at the time of greatest discharge (Edwards and Brooker 1982, Ham *et al.* 1981) although on occasions an inverse relationship of *Ranunculus* growth with discharge has been measured (Brooker *et al.* 1978). Chambers *et al.* (1990) found that the biomass of several riverine *Potamogeton* species was strongly positively correlated with velocity (but only weakly with discharge).

Very fast velocities act as a disturbance, removing plant biomass (Haslam 1982), whereas low water velocities act as a stress. At low water velocities the boundary layer resistance round a leaf is increased, limiting the uptake of nutrients and carbon (Westlake 1966, 1967, Smith & Walker 1980, Wheeler 1980, Black *et al.* 1981, Madsen 1984, Hough & Fornwall 1988, Madsen & Sand-Jensen 1991). Even at relatively high water velocities, carbon depletion at the leaf surface is not necessarily prevented (Raven *et al.* 1982) and in any case the velocity at the centre of a clump is much less than the velocity of the stream itself (Marshall & Westlake 1990). Changes in water velocity will also affect the habit of the plant, so that at higher velocities the plant will become more streamlined (Dawson & Robinson 1984, Dawson 1988).

Water velocity also has indirect effects on plant growth. The velocity affects the sediment particle size of the river bed (Minnikin 1926, Butcher 1927, Tansley 1939), which influences the ability of at least some *Ranunculus* species to establish propagules (Cook 1966a). This is investigated further in the experiment described in section 4.2. Of course, as well as the flow of the river affecting the growth of the plants, macrophyte growth in rivers will in turn affect the flow of the river causing a reduction of flow, an increase of water depth, and an increase in sedimentation rate (Westlake *et al.* 1972, Gregg & Rose 1982, Dawson & Robinson 1984).

Eutrophication

Macrophyte species tend to be associated with particular nutrient conditions (Newbold & Palmer 1979, Holmes & Newbold 1984). In streams where there is an inflow of polluted water, species such as *R. fluitans* and *R. penicillatus* are often replaced by *Potamogeton pectinatus* (e.g. Harding 1979, 1980). It would appear likely that the concentrations of the pollutants are not in themselves sufficient to eliminate the *Ranunculus*, but that the competitive balance between *Ranunculus* and *Potamogeton pectinatus* is tipped in favour of the *Potamogeton*. There are cases of pollution being intense enough to destroy *Ranunculus* outright; in 1970 untreated sewage was discharged into the River Ray, and not only *Ranunculus*, but *Cladophora* was completely destroyed (Hawkes 1978). Petersen and Brown (1979) report that macrophytes are rarely found in waters with a soluble phosphate concentration of greater than 10 $\mu g\ P\ l^{-1}$ and Twilley *et al.* (1985) concluded that soluble phosphate concentrations of greater than 20 $\mu g\ P\ l^{-1}$ can give rise to the exclusion of macrophytes in estuaries. Both these concentrations are considerably lower than phosphate concentrations at which apparently healthy macrophytes were found during the 1990 survey (Chapter Three).

Such circumstantial evidence certainly clearly demonstrates that increasing eutrophication leads to a decrease in abundance of all *Ranunculus* species (and that there is a differential effect between species). From the above observations it would appear that at intermediate levels of nutrient concentrations the relative growth rate of *Ranunculus* compared with e.g. *Potamogeton pectinatus* is decreased. At higher concentrations *Ranunculus* cannot survive even in the absence of competition from other macrophytes. The mechanism for this is not clear: is it a direct effect due to the increased nutrient concentrations decreasing the growth of *Ranunculus*; or is it an indirect effect due to increased growth rate of competitor species (other macrophytes and/or algae)?

There has been an ongoing debate concerning the relative roles of roots and shoots in the uptake of nutrients in macrophytes (reviewed by Sculthorpe 1967, Denny 1980, Smart & Barko 1985, Agami & Waisel 1986, Barko *et al.* 1986, and Barko *et al.* 1991). That debate is of relevance here because if macrophytes obtain their nutrients solely or mainly *via* the substrate it is less likely that water nutrient concentrations will have a major direct effect on macrophyte growth and survival.

Early workers came to the conclusion that sediment was the main source of nutrients (e.g. Pearsall 1920) on the basis of correlations obtained between nutrient concentrations in plant tissue and sediments, but not between plant tissue and water. Pond (1905) found that *R. trichophyllus* plants grew better when rooted than when suspended in tap water and better when rooted in mud than in sand. Experimental work in the last decade has largely confirmed the view that sediments tend to be the more important source for N & P (see for example Barko & Smart 1980, Carignan & Kalff 1980, Barko 1982, Anderson & Kalff 1986, Chambers *et al.* 1989). Many Batrachian *Ranunculus* species have been found to be infected with vesicular-arbuscular mycorrhizas, which increase the efficiency of phosphorus uptake from the sediments (Clayton & Bagyaraj 1984, Tanner & Clayton 1985a, b).

However, that is not to say that the shoots have no role in nutrient uptake. Non-rooted species such as *Ceratophyllum demersum* clearly successfully rely entirely on their shoots for nutrient supply. Cut-shoot experiments (e.g. Normann 1967, Kussatz *et al.* 1984) show that shoots are capable of nutrient uptake. At least some *Ranunculus* species have substrate inducible nitrate reductase activity in their leaves (Melzer

1980, Melzer & Exler 1982), indicating that nitrate is taken up *via* the leaves.

In Chapter Two it was shown that *Ranunculus* tissue phosphorus content was correlated with both water and sediment phosphate. This is in line with the consensus that has developed that both roots and shoots have importance in nutrient uptake (see for example Bristow & Whitcome 1971, Denny 1972, 1980, Waisel *et al.* 1990, Barko *et al.* 1991) and so it is not unreasonable to look for effects on plant growth caused by water chemistry.

Casey & Downing (1976) have shown that the tissue nutrient concentrations of *R. penicillatus* subsp. *pseudofluitans* in chalk streams are frequently in excess of limiting concentrations (Gerloff & Krombholz 1966) and are thus exhibiting luxury uptake (Chapin 1980) in streams where the throughputs are many times the total nutrients in the biomass (Casey & Westlake 1974). However there are many reported cases of increased 'weed' growth with increasing eutrophication (e.g. Thomes 1970, Vander Borght *et al.* 1982, Ska & Vander Borght 1986, Caffrey 1990b). Carr 1988 and Carr & Goulder 1990 have shown that *R. penicillatus* subsp. *pseudofluitans* shoots from a eutrophic sites have a greater growth potential than shoots upstream of the source of eutrophication. The ability of competitive macrophyte species (i.e. species which capture resources efficiently, Grime 1979) to extract nutrients from eutrophic waters is used as a managment tool to reduce nutrient concentrations (see e.g. Beltman 1990, Nichols 1991, Tripathi & Shukla 1991).

These data indicate that in the cases where eutrophication appears to have a negative effect on the more competitive *Ranunculus* species such as *R. fluitans* (see Chapter Six) this must be due to one of two reasons. One possibility is that the increased nutrient supply increases the growth of other macrophyte and algal species even more than the growth of *Ranunculus* (in other words there is a reduction of nutrient stress leading to increased effects of competition, including an increase in light stress to the macrophytes if algal blooms occur). Alternatively the concentrations may be supra-optimal for the growth of that species, i.e. there is direct toxicity.

There is a paucity of data on direct negative effects of elevated nutrient concentrations on aquatic macrophytes. Fox (1987) has shown that *Ranunculus* leaves appear to be more susceptible to the herbicide diquat in N and P enriched waters. Forsberg (1965) has demonstrated phosphorus toxicity in *Chara globularis*, though his results have been contradicted by later studies (Blindon 1988).

There is considerably more data on wetland and terrestrial plants indicating that a supra-optimal nutrient supply can decrease growth, especially for species associated with low nutrient-status sites. For example Studholme (1989) has shown a decrease in *Sphagnum cuspidatum* growth with supra-optimal nitrogen and sulphur supply. Spink (1988) found a decrease in *Narthecium ossifragum* growth with high nitrogen supply. Berdowski & Zelinga (1987) showed that *Calluna vulgaris* to have an increased susceptibility to infection by *Lochmaea suturalis* (the heather beetle) when subjected to a high nitrogen supply. Aronsson (1980) has shown that *Pinus sylvestris* trees with a high tissue nitrogen content are more susceptible to frost damage than normal.

The majority of authors ascribe the negative effects of eutrophication on macrophyte growth to competition from algae. It is well established that eutrophication gives increased algal production (e.g. Butcher 1947, Owens 1970, Carrick & Lowe 1989) and that macrophyte production is reduced in turbid waters (e.g. Robel 1961). A number of studies have concluded that macrophyte decline associated with eutrophication has been brought about by shading from increased algal growth (e.g. Mulligan & Baranowski 1969, Mulligan *et al.* 1976, Phillips *et al.* 1978, Twilley *et al.* 1985, Hough *et al.* 1989, Daldorph & Thomas 1991, and Sand-Jensen & Borum 1991). There is some evidence that other factors such as competition for nutrients may be important (Hogetsu *et al.* 1960). Phillips (1976) has shown that a dense bed of *Ceratophyllum demersum* can remove 0.1 g N m^{-2} day^{-1} and 0.02 g P m^{-2} day^{-1}. As the macrophytes decline the alleopathic substances secreted by them also decline, removing limits to growth on the phytoplankton and resulting in a form of positive feedback (Phillips *et al.* 1978, Hootsmans 1991).

Although some studies have been carried out in rivers these have tended to be relatively slow-flowing and it is not clear how relevant these are to rapidly flowing streams. In these systems (in Britain at least) shading from algae tends to be from epiphytic algae and mats of filamentous taxa such as *Cladophora* and *Vaucheria*, rather than phytoplankton blooms, because the residence time of the water in such rivers is too short for a true phytoplankton bloom to develop (Westlake *et al.* 1972). Epiphytic algae and algal mats will clearly affect the macrophyte community in a different way than phytoplankton. For example, the seasonal phenology of the algae will be different (Macan & Worthington 1951, Marker & Casey 1982). Phillips *et al.* (1978) have shown that in the Norfolk Broads in England epiphytic algal growth preceded macrophyte decline, which was only then followed by increased phytoplankon growth.

The second experiment described in this chapter was designed to elucidate the effects of eutrophication (in the form of increased phosphate supply) on the growth and competitive ability of *R. penicillatus* subsp. *pseudofluitans*.

3.2 The response of a *Ranunculus penicillatus* subsp. *pseudofluitans* community to Shading and Low Velocity

3.2.1 Methods

The experiment was carried out at the East Stoke mill stream (National Grid Reference SY 870 867), a branch of the River Frome in Dorset, England. This is a typical chalk stream, dominated by *Ranunculus penicillatus* subsp. *pseudofluitans*. Its management has followed the traditional pattern of cutting when the *Ranunculus* growth elevates the water level sufficiently to present a risk of flooding, normally in early summer (Westlake 1968, Westlake *et al.* 1972, Westlake & Dawson 1982). For the duration of this experiment cutting in the mill stream was discontinued. However, in September 1990 one of the plots was accidentally cut during management operations upstream; the data from this plot were analysed as missing values for September and October 1990. The discharge through the stream was controlled using sluice-gates downstream of the plots which altered the amount of water which flowed down the mill stream from the main river.

Eight plots were established in the mill stream. Each plot was 4 m × the width of the stream, which was about 10 m, including marginal emergent vegetation. There was a 4 m 'buffer zone' between each plot. The plots were delineated with permanent stakes at each corner. In June 1990 an electric fence was placed on the north side of the plots to exclude cattle.

During April - October 1989 and April - October 1990 the vegetation in each plot was mapped at approximately monthly intervals using a method adapted from the rectangle method of Wright *et al.* (1981). The percentage cover value derived was equal to the area in which a species was dominant (i.e. occupying more than 50% of a 1 × 0.5 m quadrat). Full details are given in Appendix C. A value for species richness in each plot was calculated on the basis of the mean number of species per square meter, excluding areas with no vegetation. The velocity and depth profile were measured at a fixed point every month. Discharge was continually monitored at the National Rivers Authority gauging weir downstream of the plots. Solar irradiance was continually measured on the roof of the I.F.E. River Lab adjacent to the stream and water

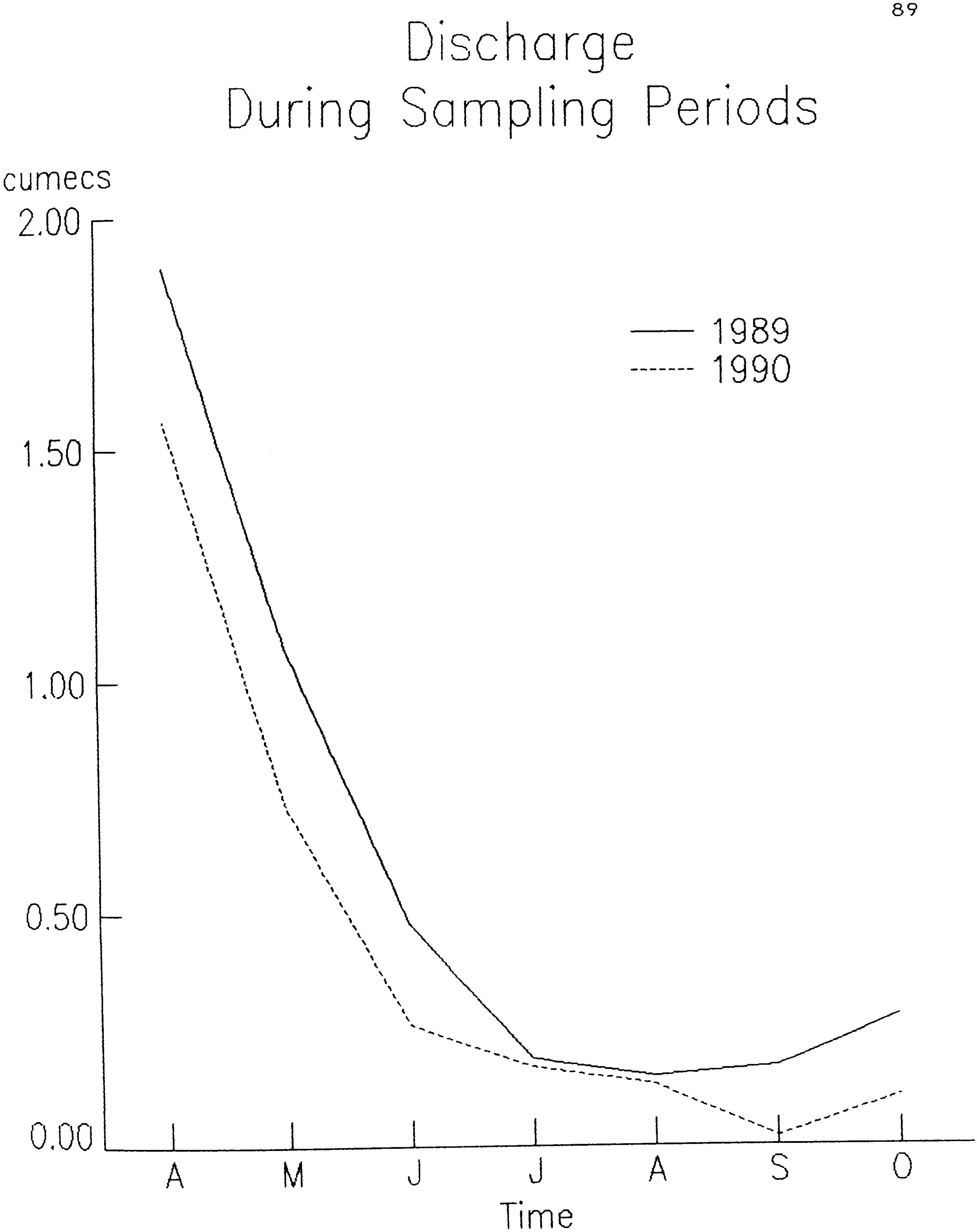


Figure 3.1 Discharge in mill stream at East Stoke April 1989 to October 1989, April 1990 to October 1990. Data from NRA gauging weir

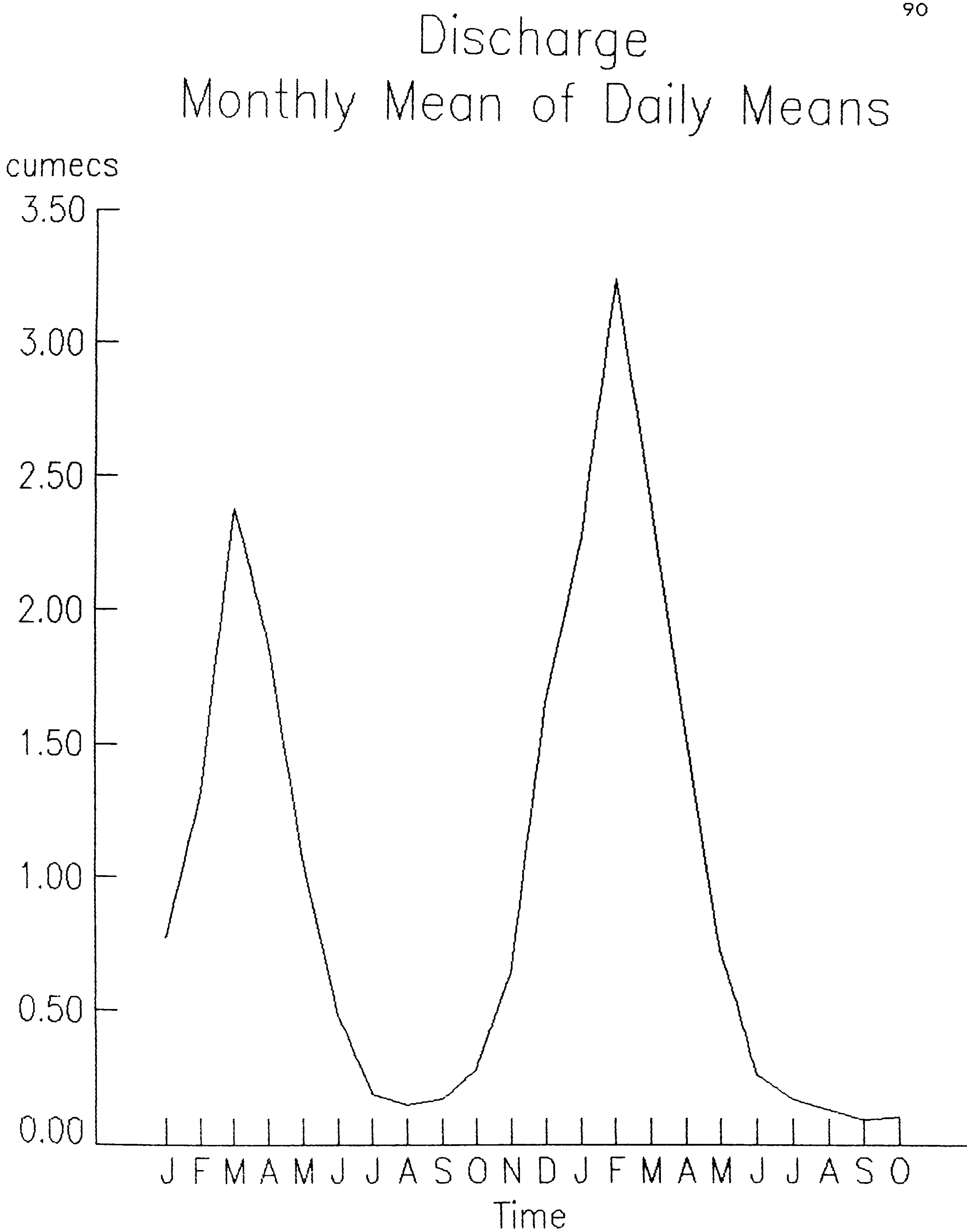


Figure 3.2 Discharge in mill stream at East Stoke April 1989 to October 1990. Data from NRA gauging weir

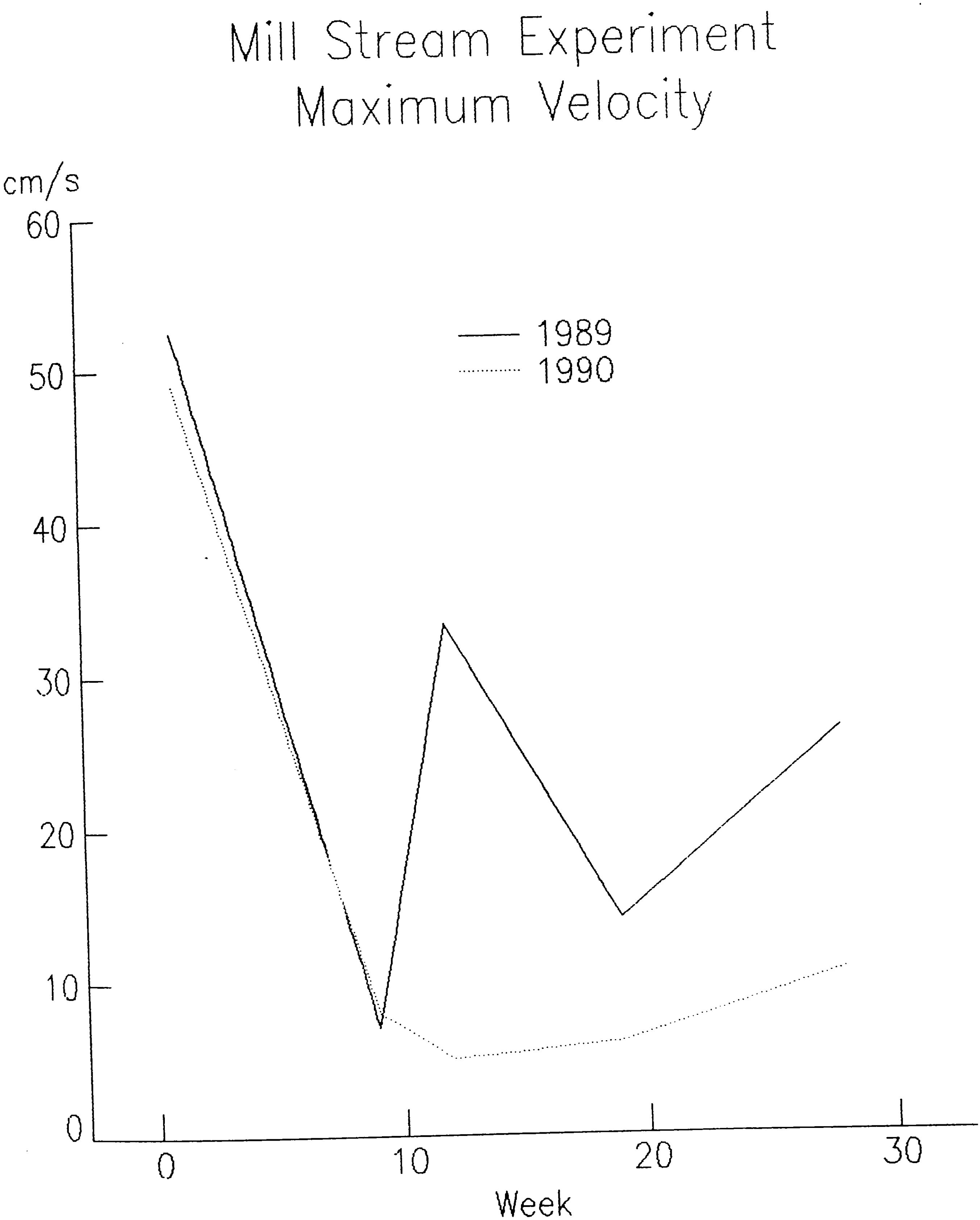


Figure 3.3 Velocity measured in mill stream at East Stoke during 1989 and 1990 growing seasons. 'Week' refers to time after vegetation cover measurements, i.e. week of the experiment.

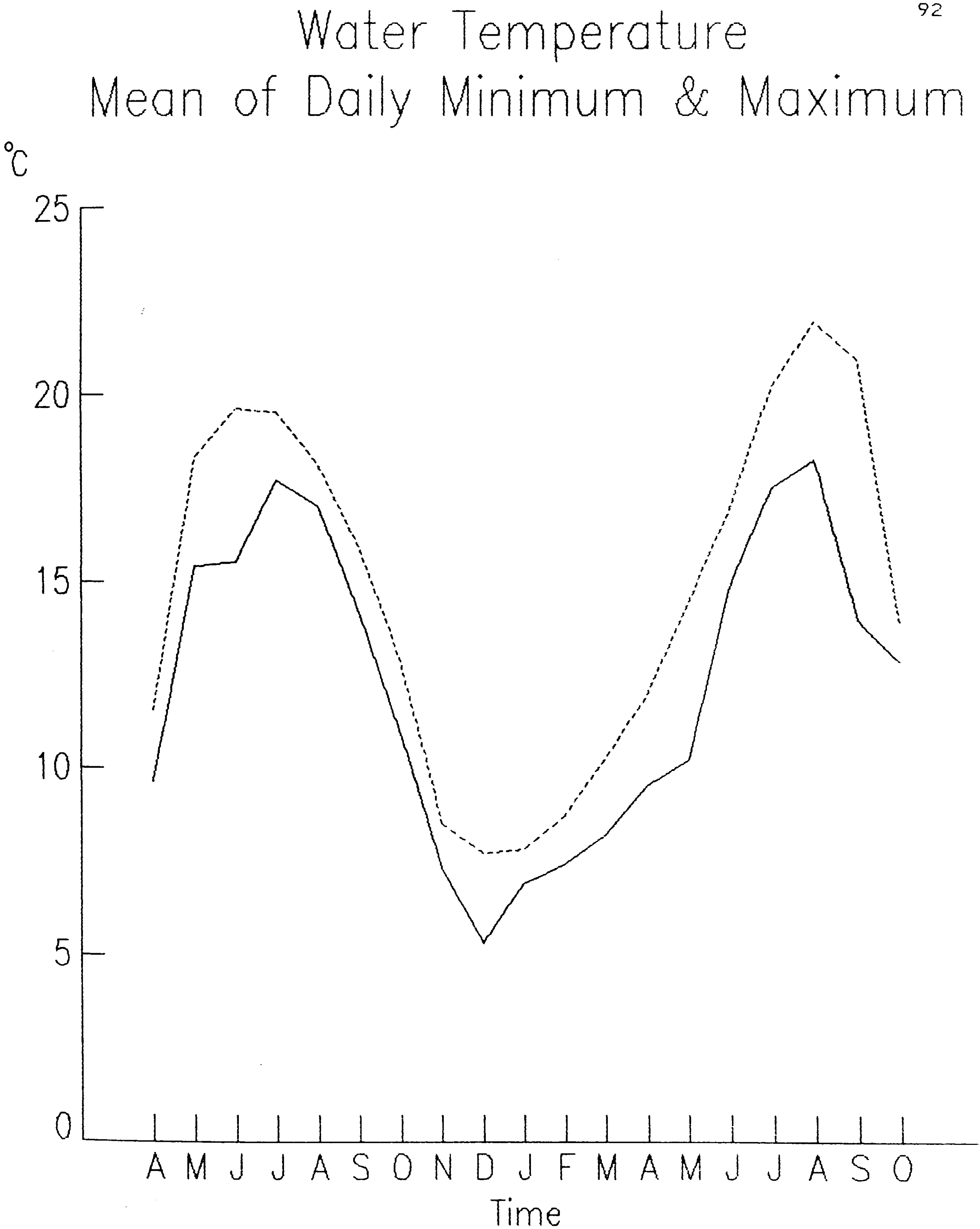


Figure 3.4 Water temperature in mill stream at East Stoke April 1989 to October 1990. Data from IFE Fish Counter 500 m upstream of experiment. Data plotted are mean monthly values derived from daily minima and maxima.

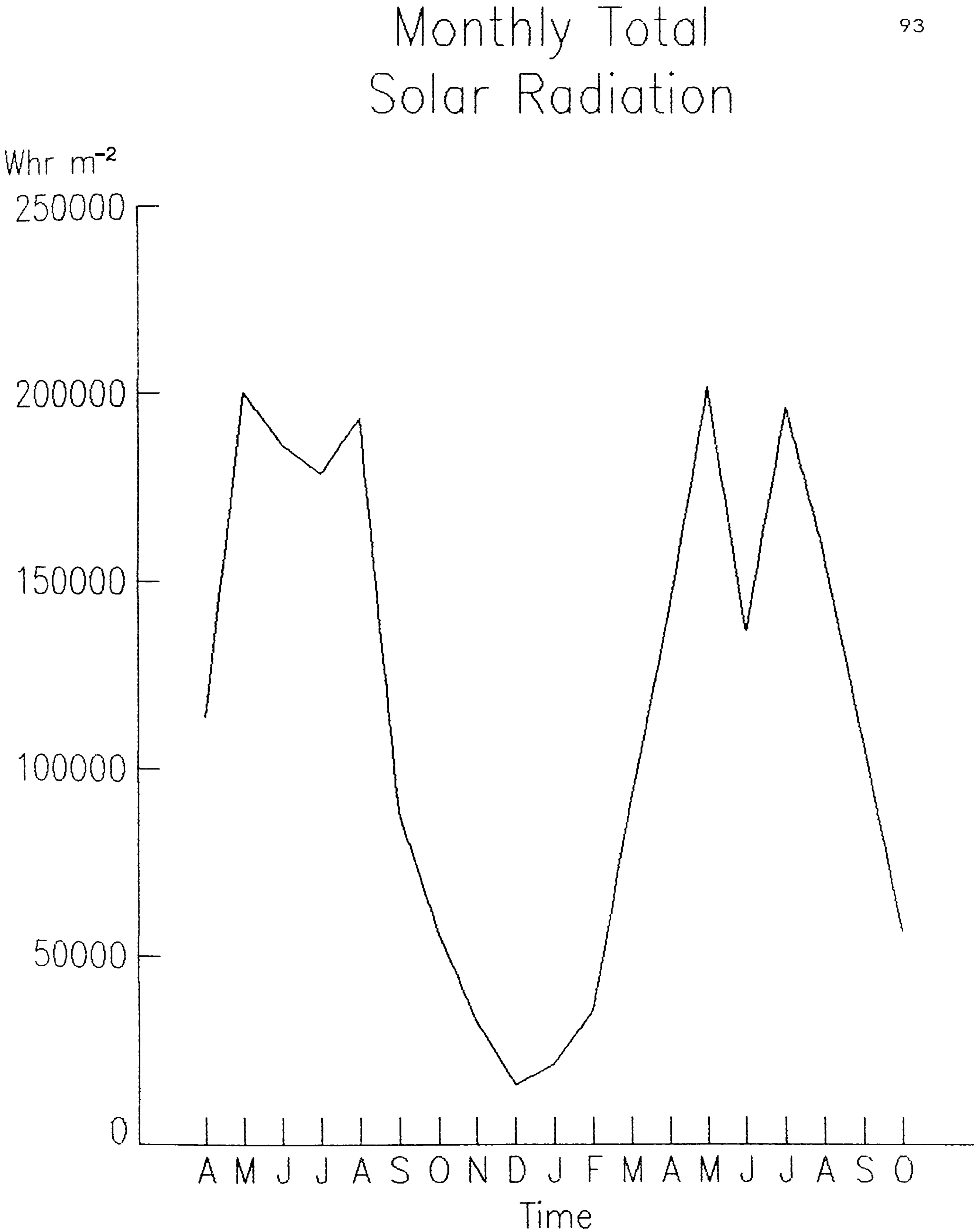


Figure 3.5 Solar Irradiance at mill stream at East Stoke April 1989 - October 1990. Data plotted are monthly totals derived from daily totals measured on the roof of the IFE River Lab adjacent to the experiment.

temperature was continually recorded at the I.F.E. fish counter upstream of the plots.

On 7th June 1989 half of the plots (selected randomly) had shading placed over them. A sturdy wooden framework was built over the plots and shading material was fixed onto the framework. 'Typar 3267' (a type of superbonded polypropylene) was used as the shading material (Cooke & Gorman 1980, Dawson & Hallows 1983). 'Typar' is manufactured by Dupont Ltd. and was supplied by the Iron and Steel Company, Ltd., Nuneaton. The material reduced incident photosynthetically active radiation to the water surface by 61-76% (the greater figure being directly under a wooden strut). When tested in a Unicam SP8000 scanning spectrophotometer it was found to have a linear absorbance of light from 380 to > 750 nm. On a very hot day (13 July 1989, when it was 33° C in the shade) there was no measurable difference in the surface water temperature in the shaded compared with the unshaded plots (21° C). The shading was removed for the winter on 19th October 1989 in order to reduce the potential for damage by winter floods and mimic the effect of shading by deciduous trees. it was replaced on 30th May 1990.

On 30th March 1990 the discharge of the stream was reduced. Although the severe drought during 1989 meant that the velocity in the 'fast' year was not as great as had originally been intended, there was still a substantial difference between the two years (see Figure 3.1). During the winter between the two experimental growing seasons there were storms which gave rise to floods which completely washed out the vegetation in the stream (Figure 3.2). This meant that the plant community at the start of the 1990 measurements was quite different from the community composition at the beginning of the experiment. The implications of this are discussed in section 3.2.3.

At the end of the experiment on 25th and 26th October 1990 all the submerged plant material was removed from the plots and weighed. The plants were cut at the surface of the sediment and placed into baskets holding approximately ½ m^3 which were suspended for exactly five minutes to let the water drain off. A sub-sample of each basket was removed and dried at 95° C to enable an estimate of the dry weight of each basket to be calculated. The plants were sorted by species; however virtually all the biomass was composed of *Elodea nuttallii* at this date. Whilst the plants were being removed from the stream the flow was completely stopped so that no plant material was lost downstream.

3.2.2 Results

Analysis of variance was carried out on the species cover, exposed substrate and species richness. In 1989 *R. penicillatus* subsp. *pseudofluitans*, *Lemna* spp, *Nasturtium officinale* (=*Rorippa nasturtium-aquaticum* (L.) Hayek, Watercress), and *Apium nodiflorum* were sufficiently abundant for analysis. In 1990 *R. penicillatus* subsp. *pseudofluitans*, *Lemna* spp, *Elodea nuttallii* and *Potamogeton pectinatus* were abundant. A split-plot design was used (with time as the sub-plot factor), and the data were analysed using the GENSTAT 5 computer program. Where necessary the data were normalised by a $\log_{10}$ transformation (Little & Hills 1978). The results are summarised in Table 3.1. and in Figures 3.4. - 3.11. Least significant differences were calculated from the standard error of difference of the mean and bars on the figures show L.S.D. between shaded and unshaded values.

Table 3.1 Summary of the Effects on Species Cover of Shading in Mill Stream Experiment

Levels of significance are as follows; n.s.=p>0.05, *=p<0.05, **=p<0.01, ***=p<0.001

Variate	Shade	Date	Shade×Date	$\log_{10}$ Transformed?
1989 (High Velocity)				
Ranunculus	***	***	n.s.	
Nasturtium	n.s.	***	n.s.	✓
Apium	*	**	n.s.	✓
Lemna	n.s.	***	n.s.	
Substrate exposed	***	***	n.s.	
Species Richness	*	***	*	✓
1990 (Low Velocity)				
Ranunculus	n.s.	*	n.s.	
Elodea	*	***	n.s.	✓
Potamogeton	*	**	n.s.	✓
Lemna	n.s.	*	n.s.	
Substrate exposed	***	***	n.s.	
Species Richness	n.s.	*	n.s.	

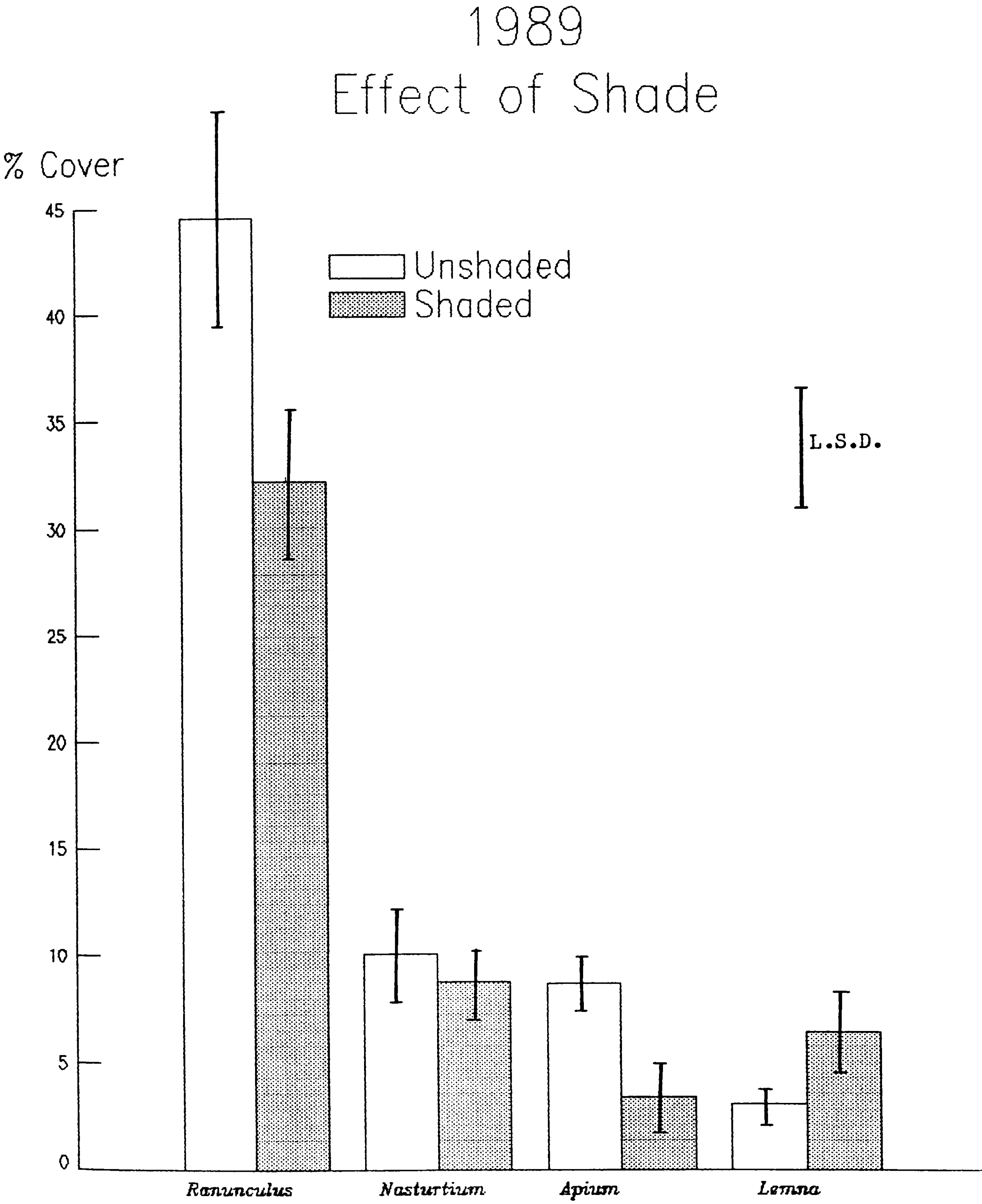


Figure 3.6 Effects of shade on average plant species cover during growing season in year with relatively swift current. Bars on histograms represents ± 1 s.e., separate bar represents Least Significant Difference (P<0.05)

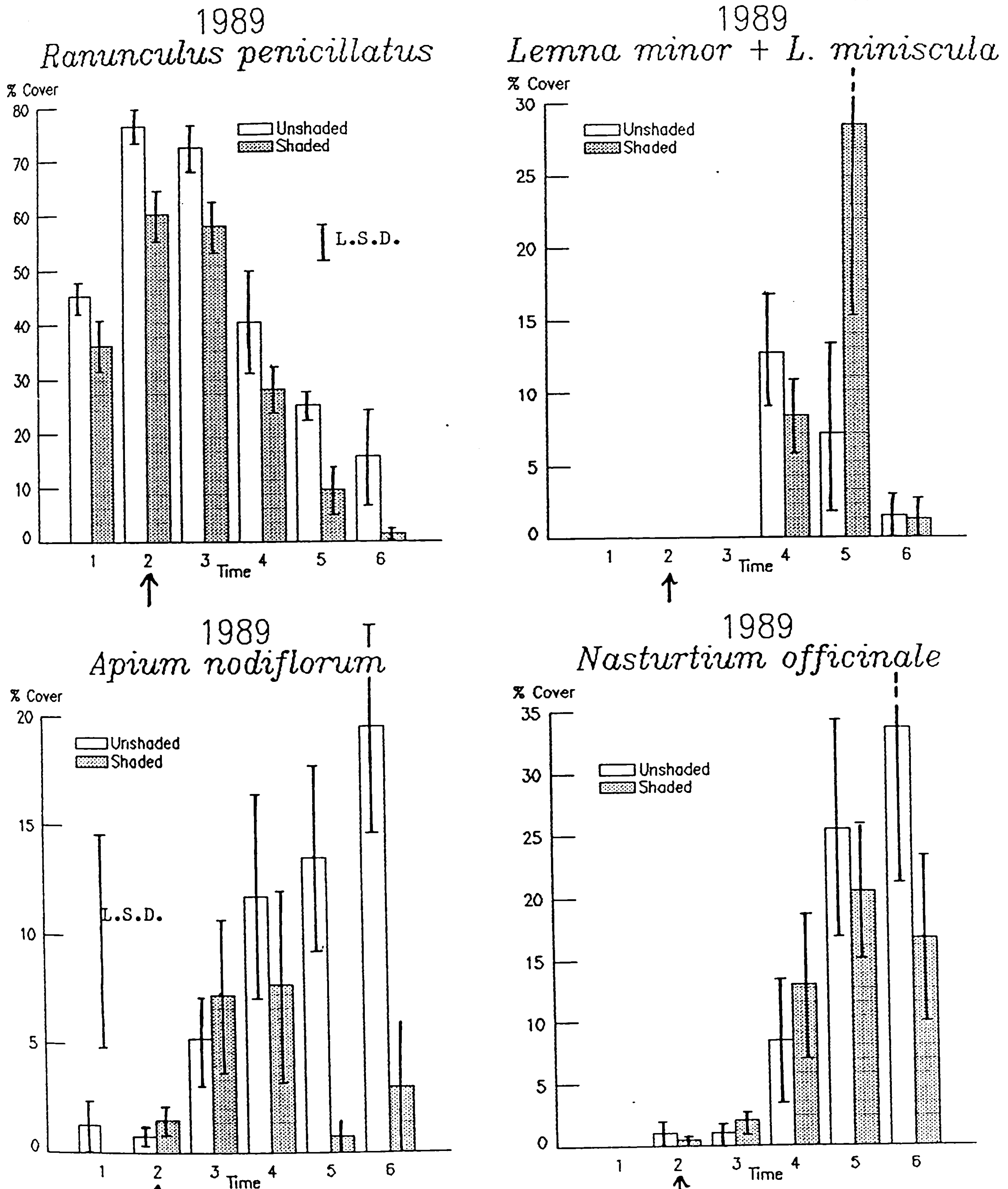


Figure 3.7 Effect of Shade on individual species during year with relatively swift current. Bars on histograms represents ± 1 s.e., separate bar represents Least Significant Difference (P<0.05). Shading was applied on 7th June (arrow). 1=27 April, 2=6 June, 3=10 July, 4=2 August, 5=30 August, 6=18 October

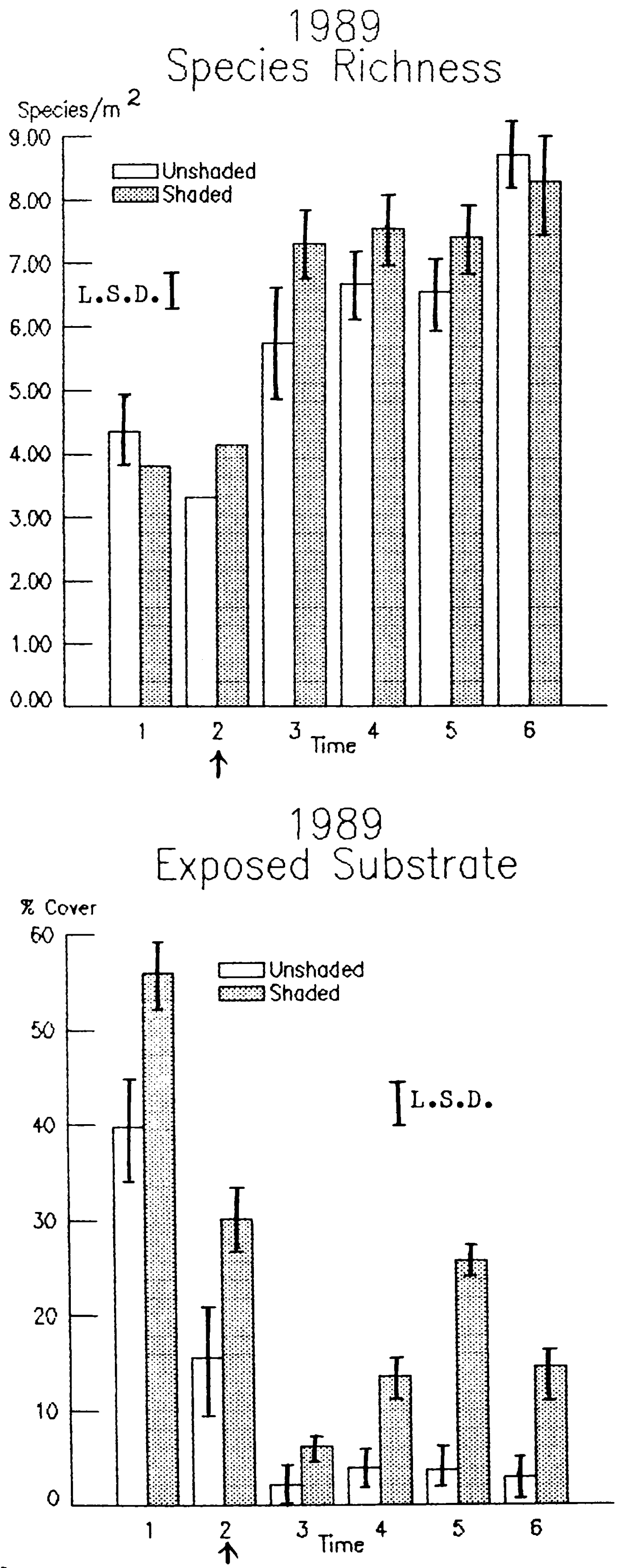


Figure 3.8. Effect shade on unvegetated substrate and species richness in year with relatively swift current. Bars on histograms represents ± 1 s.e., separate bar represents Least Significant Difference ($P<0.05$). Shading was applied on 7th June 1989 (arrow). 1=27 April, 2=6 June, 3=10 July, 4=2 August, 5=30 August, 6=18 October

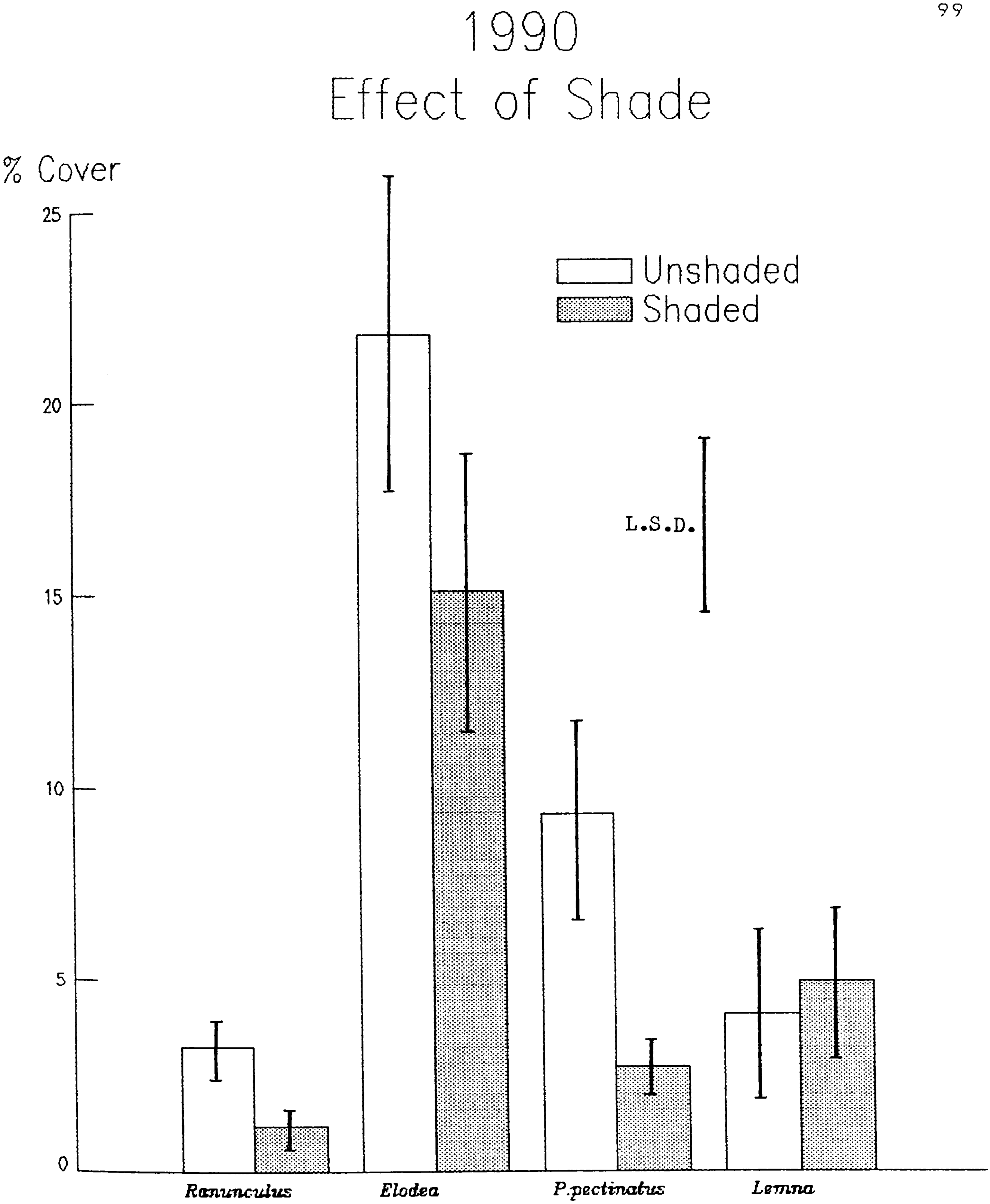


Figure 3.9. Effects of shade on average plant species cover during growing season in year with relatively slow current. Bars on histograms represents ± 1 s.e., separate bar represents Least Significant Difference (P<0.05) .

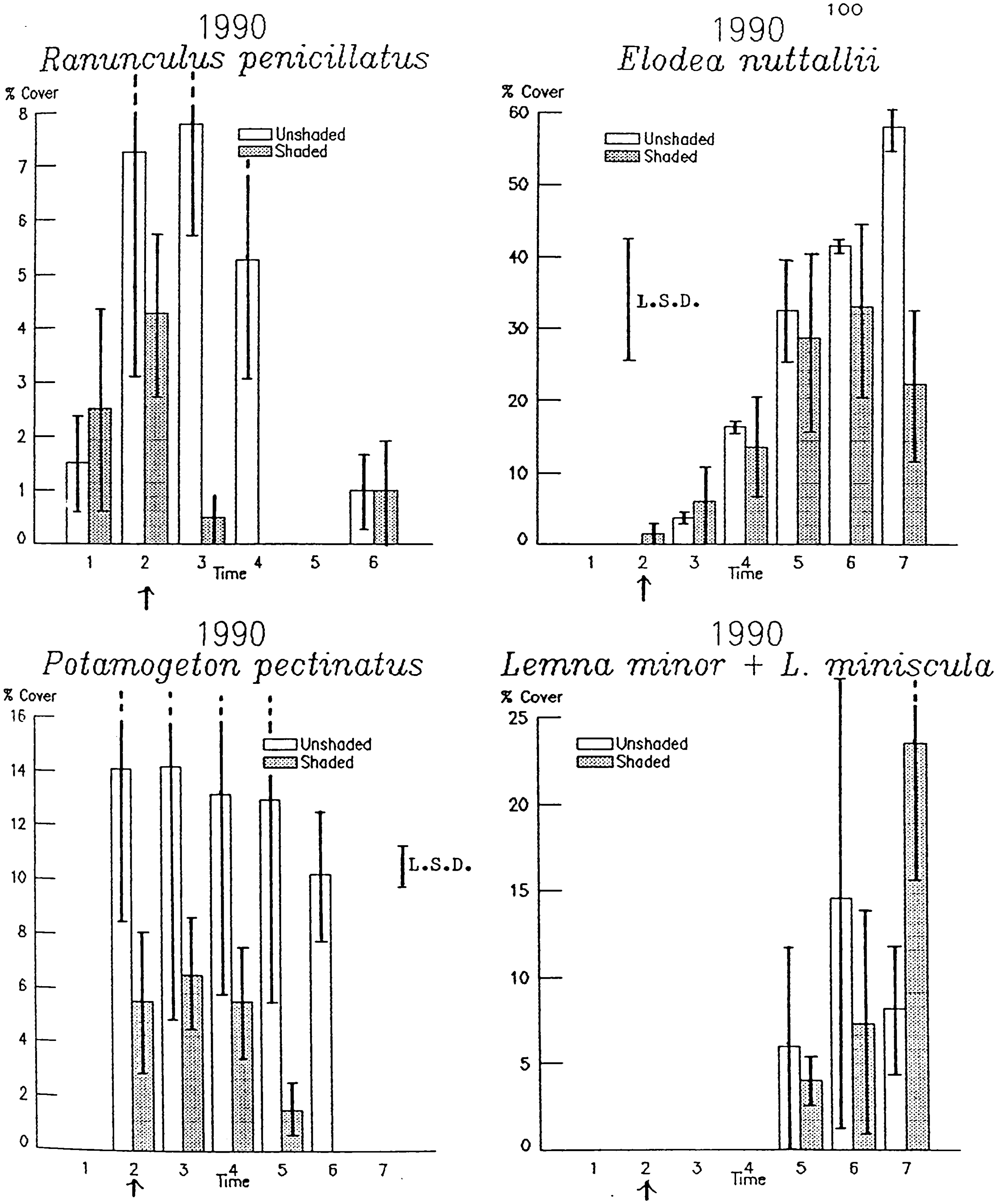


Figure 3.10. Effects of shade on individual species during year with relatively swift current. Bars on histograms represent ± 1 s.e., separate bar represents least significant difference ($P<0.05$). Shading was applied on 30 May 1990 (arrow). 1=26 April, 2=1 June, 3=30 June, 4=19 July, 5=30 August, 6=25 September, 7=24 October

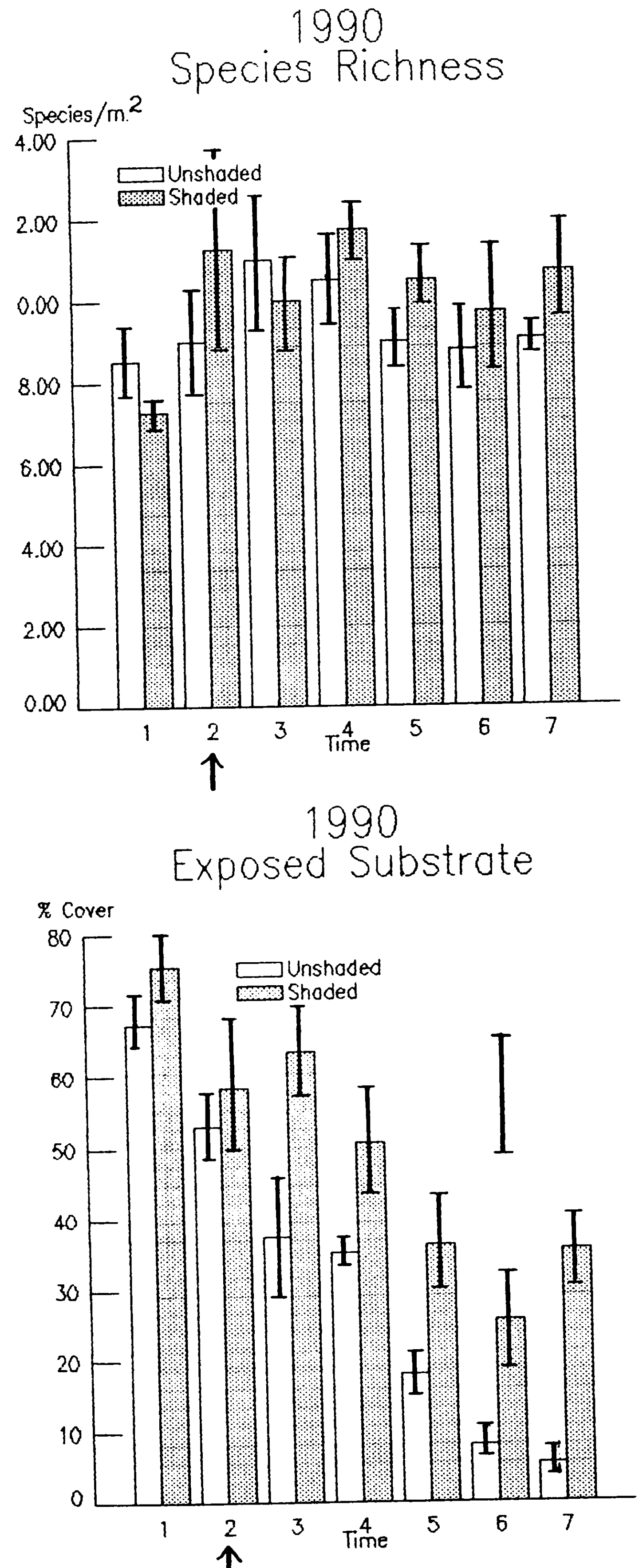
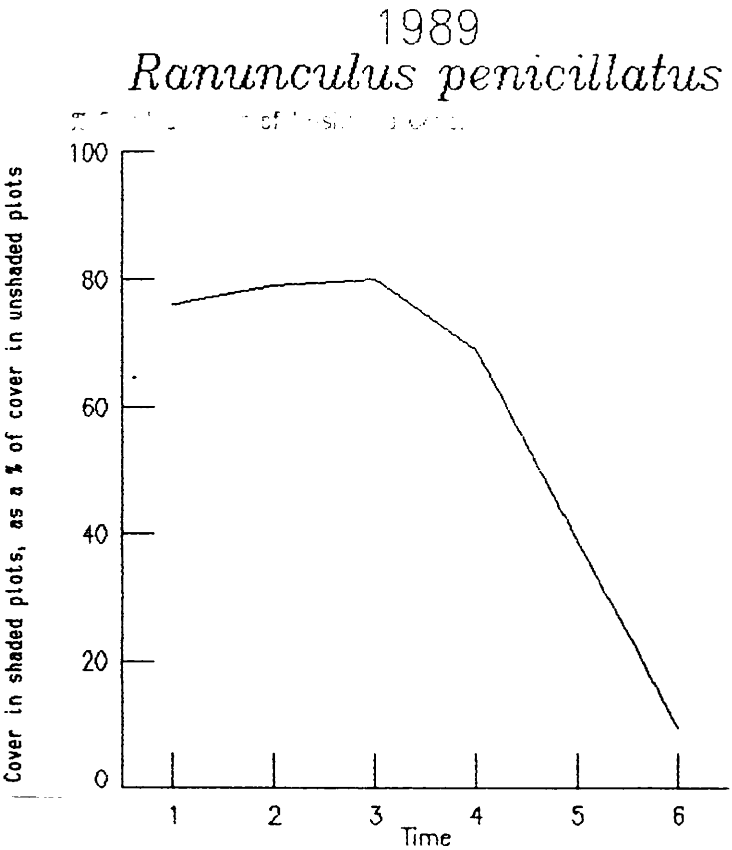


Figure 3.11 Effects of shade on unvegetated substrate and species richness during year with relatively slow current. Bars on histograms represents ± 1 s.e., separate bar represents Least Significant Difference ($P < 0.05$). Shade was applied on 30 May 1990 (arrow). 1=26 April, 2=1 June, 3=30 June, 4=19 July, 5=30 August, 6=25 September, 7=24 October

As can been seen from Figure 3.6, during 1989 the cover was significantly less in the shaded plots for *R. penicillatus* subsp. *pseudofluitans* and *Apium nodiflorum*. However, although Figure 3.12 (below) shows that there was a clear trend for an increasing effect on *Ranunculus* following the application of shading this was not statistically significant. By the final measurement the *Ranunculus* cover was ten times greater in the unshaded plot compared with the shaded. The cover of all the various plant species was very variable from one plot to another (as would be expected in a natural community) and to a large extent this variability has masked some of the effects of the shading.

Figure 3.8 shows that the plant cover was sufficiently reduced in the shaded plots to give rise to significantly more exposed (unvegetated) substrate. The diversity of the plant community was significantly greater in the shaded plots (Figure 3.8). One would expect an increase in stress to reduce the vigour of the more competitive species leading to an increase in species richness (Grime 1973a, b). Interestingly the final measurement in October shows that there was no significant difference between the plots, perhaps indicating that as the vegetation began to die back, competitive pressures were lessened allowing more species to be established, particularly in the unshaded plots.

Figure 3.9 summarises the vegetation cover in 1990. The abundance of *Ranunculus* was much less than the previous year and there was no significant difference between the average cover in the treatments (Figure 3.9). However examination of each month's data is more revealing (Figure 3.10). The month before the shading was applied there was slightly more *Ranunculus* in the 'shaded' plots but by the date the shading was put on, the *Ranunculus* in the unshaded plots had grown rapidly so that the situation was reversed. There was no significant difference between the plots on either of these dates. The next two sampling occasions show a rapid decrease of *Ranunculus* cover (Figure 3.10) in the shaded plots, such that in June it was dominant in only one quadrat, and in July in no quadrats, in the shade compared with relatively higher cover in the unshaded plots. After that date the *Ranunculus* was only present in very small quantities in both treatments.



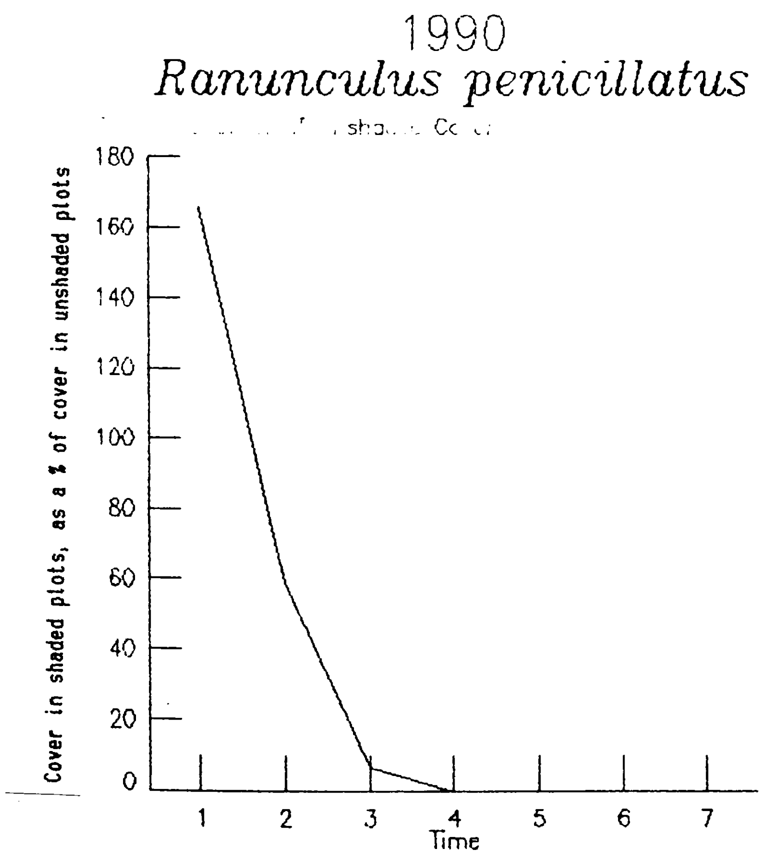


Figure 3.12. Effects of shade on reduction in *R. penicillatus* subsp. *pseudofluitans* cover. In 1989 shading was applied on the 7th June, in 1990 shading was applied on 30th May (indicated by arrows). Note - different scales. Dates are as Figures 3.7 and 3.10. In 1990, for samples 5-7 there was insufficient *Ranunculus* present to compare.

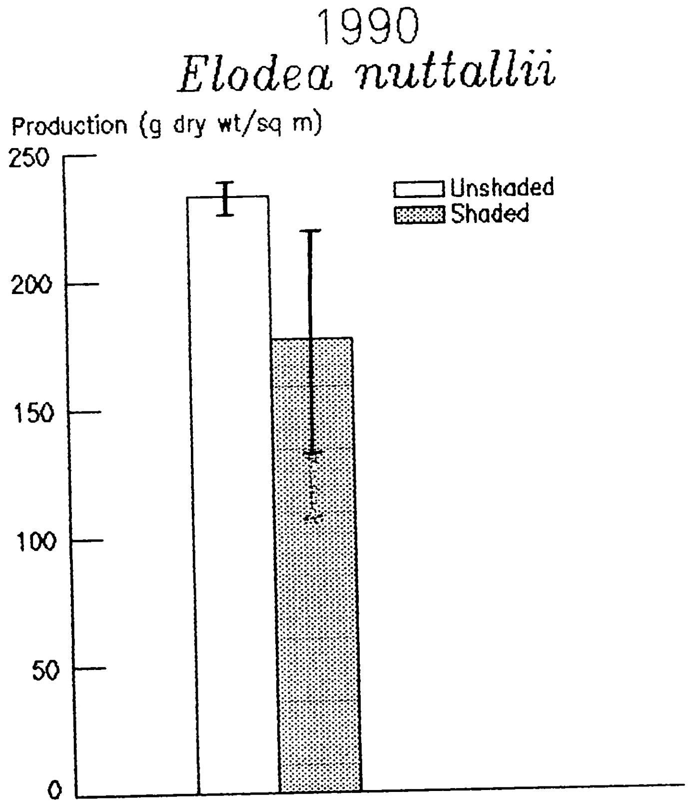
The place of *Ranunculus* as the dominant species in 1989 was taken by *Elodea nuttallii* in 1990. This responded to the shade in a broadly similar way to the *Ranunculus* in 1989 (Figure 3.8). Before the shading was applied there was a slightly higher amount of *Elodea* in the unshaded plots (not statistically different) but whereas the *Elodea* in the unshaded plots continued to grow throughout the season until it covered an average of nearly 60% of the plot, in the shaded plots it only covered 23%.

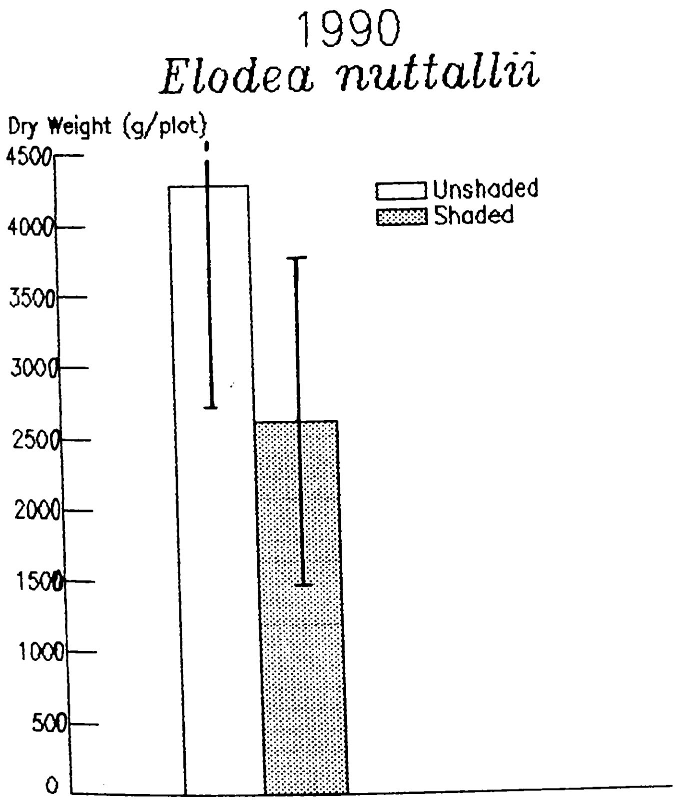
Potamogeton pectinatus showed a similar pattern of growth, reaching a much higher cover value in the unshaded plots, and also declining more rapidly in the shaded plots.

Lemna minor and *Lemna miniscula* showed no significant changes in cover in either year as a result of the shade treatment (Figure 3.4, 3.8). However, the mean value of the shaded cover of *Lemna* is greater than the unshaded in both years. The data showed great variability both between plots and between sampling dates (for both years), including two occasions when the *Lemna* cover in the shaded plots was greater than in the unshaded plots.

The exposed substrate (Figure 3.9) showed a similar pattern in 1990 to the previous year. There was significantly more exposed substrate in the shaded plots. The ratio between the two treatments was considerably greater at the end of the season compared with the measurements taken before the shading was applied, when there was no significant difference between treatments. However, unlike the previous year, the shade had no significant effect on the species diversity of the plant community.

After the final cover measurement, the submerged plants (nearly all *Elodea*) were removed from the stream and weighed. There was no significant difference (t-test) between treatments for total above ground fresh weight, dry weight or biomass production (i.e. dry weight per area of *Elodea*) (Figure 3.13). Regressing the dry weight measurements against cover values, there is a significant correlation for the full data set ($r=0.86$, $p<0.01$), and for the unshaded data ($r=0.93$, $p<0.05$), but not for shaded data alone ($r=0.33$, $p>0.5$).





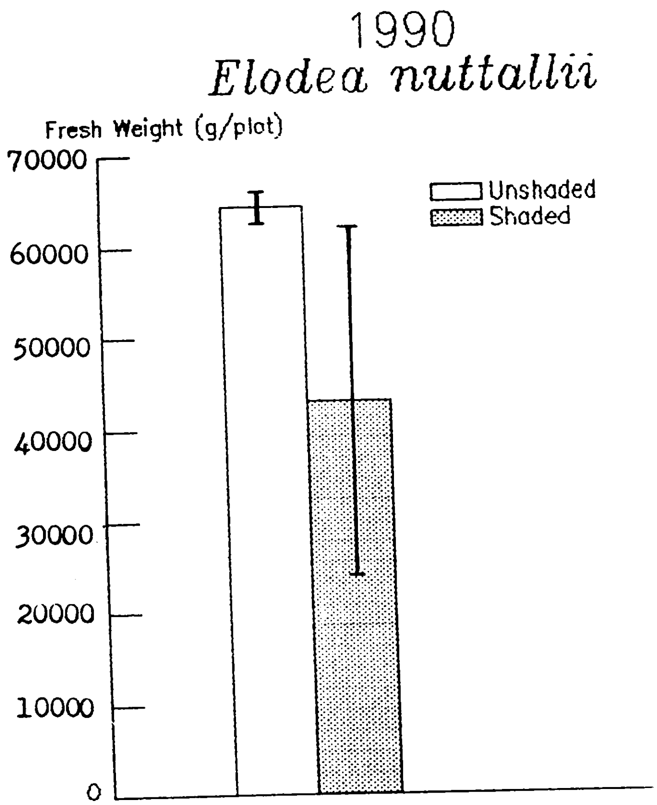


Figure 3.13. Effects of shade on *Elodea nuttallii* biomass. Dry weight was calculated from sub-samples. Bars on histograms represents ± 1 s.e.

3.2.3 Discussion

One of the predictions of Strategy Theory is that stress tolerant species will show little change in their growth compared with species that do not have stress-tolerance as a major part of their strategy. These data indicate that certain species such as *R. penicillatus* show a relatively large difference in cover between the shaded (stressed) and unshaded treatments - in 1989 the percentage of the plot over which *Ranunculus* was dominant was reduced by a maximum of 90.4%, and in 1990 by 100% (Figure 3.12).

It might be argued that as the shade×date treatment interaction was not significant (i.e. the effect of shade did not on average significantly increase with time), the significant effect of shade could be just due to differences before the shading was applied. In 1990 this was certainly not the case as the shaded plot started with a greater *Ranunculus* cover than the unshaded plot. This initial sample is probably the reason why there is no significant difference for the average cover throughout the season, though it may be that there really was no effect due to shade either due to the greater effect of flow stress on the small amount of *Ranunculus* in 1990. In 1989 although the effect of shade×date is not statistically significant, Figure 3.12 does show a quite clear and unambiguous trend.

Table 3.1 shows that for *Apium,* and exposed substrate in 1989 and *Elodea, Potamogeton* and exposed substrate in 1990 there was a significant effect of shade, but that the effect does not vary with time. Nevertheless, as with the 1989 data, there is for all these variables, a clear suggestion of a trend for the effect of shade to increase during the growing season, especially after the shading was applied (Figures 3.5, 3.8, and 3.10). The fact that the trend is consistently in the same direction for all the variables makes it likely that it is a real effect.

For *Nasturtium officinale* there was no evidence for any effect of shade on cover. This may be simply due the large variability in the data (Figures 3.5 and 3.8), or it may indicate that it is tolerant of the stress produced by shade. However Grime *et al.* (1988) identified this species as a competitive ruderal (with an almost identical triangular ordination to *Apium nodiflorum*), the lack of stress-tolerance being based on its absence from unproductive habitats (Howard and Lyon 1952). This indicates that the apparent lack of response to shade is probably an artifact of the large variability of the data rather than actual shade tolerance.

Lemna minor (the other species showing no statistically significant effect of shade) is also identified by Grime *et al.* (1988) as a competitive ruderal. Figures 3.5 and 3.8 show that the data are very variable with some samples showing much greater cover in the shaded plots. *Lemna* is not rooted in the substrate and what these data probably indicate is that what is being measured is not the cover of plants that have grown under shade or in the open, but what plants have happened to drift into a particular plot in the period before the vegetation was mapped.

Little mention has been made so far regarding the significance of differences observed between the vegetation in 1989 and 1990. There was an important and intended difference in treatment between these two growing seasons; in 1990 the velocity and discharge were considerably less than that of 1989 and so an additional stress was applied to the stream. Although there were eight plots in each year, these can not be regarded as true replicates as they were not statistically independent of each other (Hurlbert 1984). If it could be assumed that the years were, in every respect other than the treatment, exactly the same as each other, then a comparison might have been possible. This was certainly not the case.

The storms which preceded the 1990 growing season meant that the plant community at the start of the two years was quite different, and so some of the differences between 1989 and 1990 were probably due to that. For example some *Potamogeton pectinatus* tubers may have got carried into the plots by the current and the greater growth of *Potamogeton pectinatus* in the second year may have been a consequence of that. The lower *Ranunculus* cover in 1990 compared with 1989 was probably due to the removal of its rootstock during the winter storms (disturbance) - rather than an effect of low velocity stress.

However the same may not be true of *Elodea nuttallii*. There was no *Elodea* present in the plots in April 1990 and at the beginning of August there was about the same amount present in both years (*c.* 5%). Thereafter the two years showed a quite different pattern. In 1989 the *Elodea* remained present as a minor component of the vegetation whereas in 1990 the *Elodea* rapidly increased its cover to nearly 60%, becoming the dominant species (Figure 3.13). The DCCA ordination (Figures 2.7 and 2.8) indicated that *Elodea* is associated with habitats with a lower current velocity than *R. penicillatus* subsp. *pseudofluitans*, as was also found by Bilby (1977). Taking all those factors into account, it is possible that the dominance of *Elodea* in 1990 was a direct result of the lower water velocity in that year. However, it is equally possible that its rapid growth in 1990 was a reflection of the lack of competition from *Ranunculus* - there was much more exposed substrate in July-August 1990 than 1989, which was the time when the *Elodea* came to dominate the community.

It is possible that the substantially greater amount of exposed substrate present throughout most of 1990 (Figures 3.9 and 3.16) was itself a result of the stress imposed by the low water velocity. One would expect the total amount of plant growth to be determined by the overall limits to growth (stress) rather than by the initial make-up of the community. This indicates that the low water velocity did provide an additional stress to the community during the growing season of 1990.

In 1989 the average species richness was 6.18, in 1990 it was 9.79 species per m^2 with vegetation. In general, as stress increases so the importance of competition decreases, decreasing competitive exclusion and so increasing species diversity (Grime 1973a, b, 1979). It is likely that these data are an example of that effect.

Most of the above discussion is based on measurements of plant cover, with the assumption that this will be related to the biomass of the plants. At the end of the experiment the submerged plants were removed from the stream and weighed. It was found that the biomass was significantly correlated with the cover both for the whole data-set and for the unshaded plots on their own. However there was no such correlation for the shaded plots.

Wright *et al.* (1982) have recorded a significant correlation between biomass and macrophyte cover at a shaded chalk stream, but not at an unshaded site on the same stream. This is because if the site has near to 100% cover, any further growth will be underneath the leaves already covering the site, and an unshaded site is more likely to have to have 100% cover (as shown by the exposed substrate data from this chapter). It should be emphasised that any discrepancy between cover and biomass will tend to understate the effects of shade as the unshaded plots may have a greater biomass than is implied by the cover. However it should also be borne in mind that the lack of correlation between biomass and cover on unshaded plots is based on only three points, all of which have rather similar values of cover and biomass so that too much should not be made of this result.

This experiment has demonstrated some of the difficulties of working with an actual stream rather than in an artificial environment. The vagaries of the weather meant that any differences between the two years may not have been due to the treatment and so a comparison between the slow and relatively fast velocity treatments has to be tentative. The variation in the species composition from one plot to another meant that statistical comparison between shade treatments did not give such clear-cut results as one might have hoped for.

Nevertheless some conclusions may be drawn. Several of the species (including *R. penicillatus*) showed a marked reduction in growth when subjected to shade. This indicates that, as one might expect in this relatively productive habitat, stress tolerance is not an important feature of the vegetation. The results obtained (in particular the reduction in total vegetation cover in the year with low water velocity) were consistent with the hypothesis that low water velocity is an important stress in rivers and streams. There was evidence for an increase in species diversity with increasing stress which indicates that the competitive element of the strategy of many chalk stream species may play a role in limiting the establishment and survival of other, less competitive species.

3.3 The Effects of Eutrophication on the Competitive Balance between *Ranunculus penicillatus* subsp. *pseudofluitans* and *Potamogeton pectinatus*

3.3.1 Methods

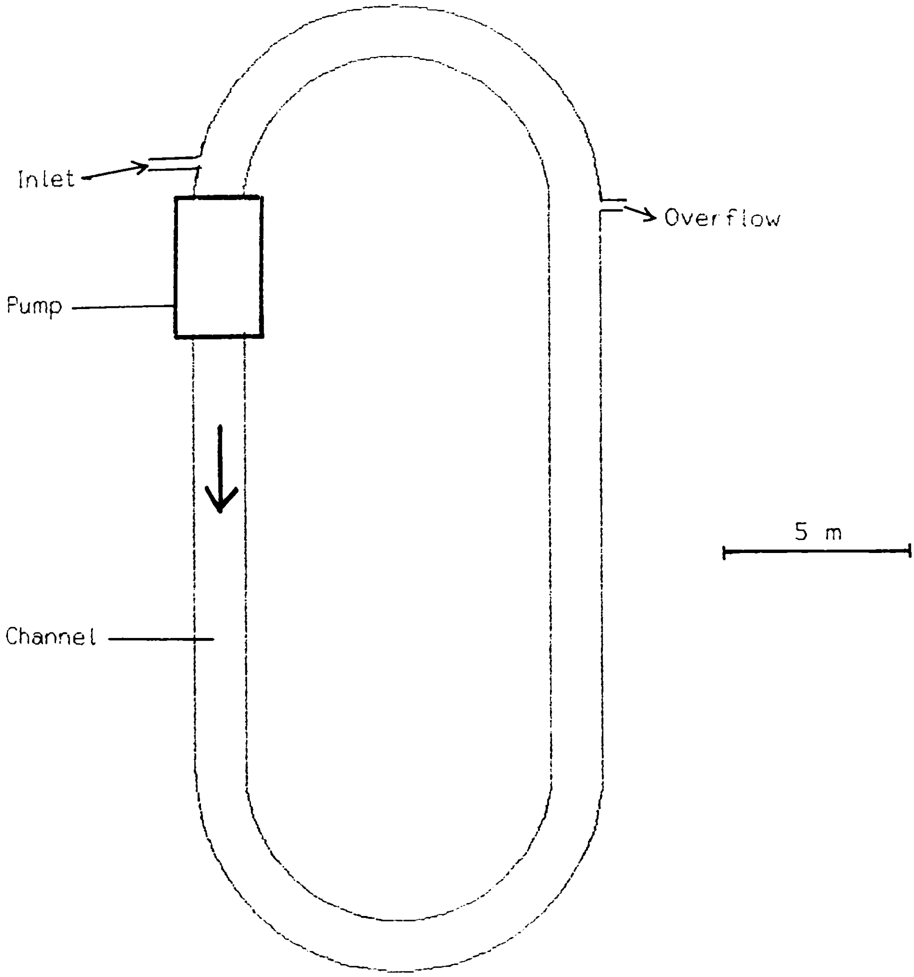
The experiment was carried out in two artificial recirculating rivers at the Waterston Experimental Station of the Institute of Freshwater Ecology. Each artificial river consists of a 53 m long race-track shaped fibreglass channel, incorporating an Archimedes screw pump to circulate the water. The water velocity was, on average 25 cm s^{-1}, with no significant difference in velocity between the two channels. The channels were both filled with water to a depth of 0.4 m above the gravel surface. They have a trapezoid cross-section, and the base was filled with gravel to a depth of 0.4 meters (see Figure 3.14, and for further details Ladle *et al.* 1977). The structure is partially buried in a disused watercress bed containing groundwater at a constant 10° C which helps to stabilise the water temperature in the channels.

The channels were continuously topped-up with groundwater from a borehole. This water supply has a constant chemical composition which is similar to the source of many chalk streams (Marker & Casey 1982, Casey & Newton 1973, Westlake *et al.* 1972). The input was adjusted to 0.17 l s^{-1} which is equal to 100 m^3 $week^{-1}$. The volume of each channel is *c.* 60 m^3 (*c.* 50 m^3 when full of gravel) (Fox, 1987), giving a turnover time of *ca.* 3 - 4 days.

Bullhead fish (*Cottus gobio*) were electro-fished from a nearby stream (the Waterston Stream at National Grid Reference ST 745 950) and placed in the channels to prevent large fluctuations in invertebrate populations. Details of the normal seasonal cycle of algae in the channels are given by Marker *et al.* (1982), Marker *et al.* (1984) and Marker *et al.* (1986).

The concentrations of ions in the borehole water are indicated by the arrow on the ordinate of Figures 3.15 to 3.18. The borehole water contains adequate concentrations of all the ions necessary for plant growth, with the exception of iron (Marker & Casey, 1982), so iron was

Plan View of Channel



Cross Section of Channel

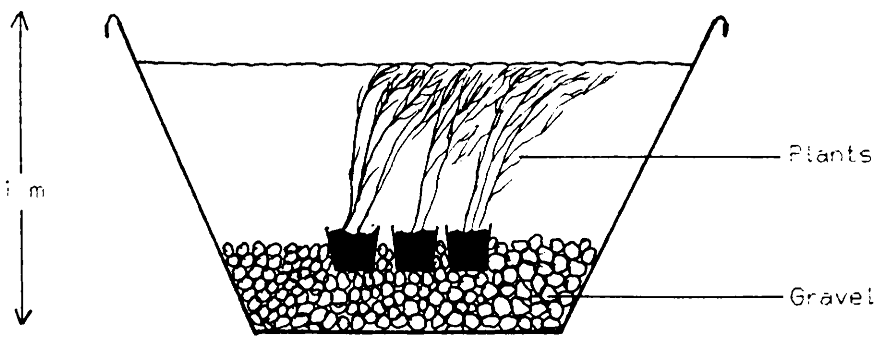


Figure 3.14. Artificial Recirculating River: Plan and Cross Section

added (as $FeCl_3$) together with ethylenediaminetetraacetic acid (EDTA; in order to make the iron available to the plants). The iron chloride and EDTA were continuously added from a 40 l vat using a peristaltic pump at a rate and concentration that was equivalent to 3 mg l^{-1} $FeCl_3$ (1 mg l^{-1} Fe^{3+}) and 1 mg l^{-1} EDTA in the borehole water.

In one channel (the control) no other additional chemicals were added. In the other one phosphate was added as H_3PO_4. This is the form in which phosphate is added to commercial watercress beds (pers. comm. S. Rothwell 1989). The concentration of PO_4-P in the borehole water is a constant 40 μgP l^{-1}. This was increased by 160 μgP l^{-1} to 200 μgP l^{-1}. The data from the river surveys described in Chapter 2 & Appendix A indicate that this value is in excess of what would normally be expected for rivers in the Frome river system (see also Casey & Clarke, 1986), but is by no means unrealistic; for example 200 - 750 μgP l^{-1} was measured in the River Itchen (a river with abundant *R. penicillatus* subsp. *pseudofluitans*) in July 1990 (Appendix A). The phosphate was continuously added by a peristaltic pump from a 60 l vat.

On 31 March 1990 *R. penicillatus* subsp. *pseudofluitans* and *Potamogeton pectinatus* plants were planted in the two channels. The plants were planted in six inch pots filled with sediment from the Waterston Stream adjacent to the channels (N.G.R. ST 740 953). Chemical composition of the sediment is given in Appendix A (see also Cumbus, Robinson & Clare 1980). The *Ranunculus* plants were taken from the same stream, and five *Ranunculus* plants were placed in each pot. The plants were selected to be approximately 0.3 m in length. Five pots were placed next to each other (buried in the gravel in the bottom of the channel) to make a group (simulating the 'clump' growth-form of *Ranunculus* in natural conditions) and ten groups of plots were put at 3 m intervals in each channel.

Half of the groups (randomly selected) also had four *Potamogeton pectinatus* plants in the same pots as the *Ranunculus*. The *Potamogeton pectinatus* plants had been grown as a clone in artificial channels at the Waterston Experimental Station. This culture was derived from plants originally taken from the River Frome (N.G.R. SY 866 867). The fresh weight of all the plants was measured before planting out to ensure that there was no initial difference between treatments.

Before the plants were planted, water was pumped for several hours between the two channels (in both direction, consecutively) to ensure that the initial algal populations were similar for both channels.

The concentrations of the major elements in the water were analysed approximately weekly; these data are shown in Figures 3.15 - 3.18. As would be expected, the phosphate concentrations are much higher in the channel which had extra phosphate added. Except at the very beginning (before the plants had been planted) and for a short period towards the end the phosphate concentration in the channel with added phosphate was less than the input concentration. It is notable that when the phosphate concentration showed a marked increase, the silica concentration also dramatically increased. This may indicate that algal growth may have become limited by another factor (such as a trace element) and so may have ceased to consume phosphate and silica.

In general the concentrations of most of the elements (and the conductivity) were lower in the channel with added phosphate. This would be expected because the increased phosphate would allow greater phytoplankton and macrophyte growth, which in turn would deplete the other elements. The calcium concentration and hydrogen ion concentration were lower in both channels than the input water. This is probably due to the release of carbon dioxide from solution as the water was aerated in the screw pump, which would cause a shift in pH and a consequent change in calcium carbonate solubility. It is also likely that there was some co-precipitation of calcium carbonate with the added phosphate; see House *et al.* (1986) and House, Casey & Smith (1986).

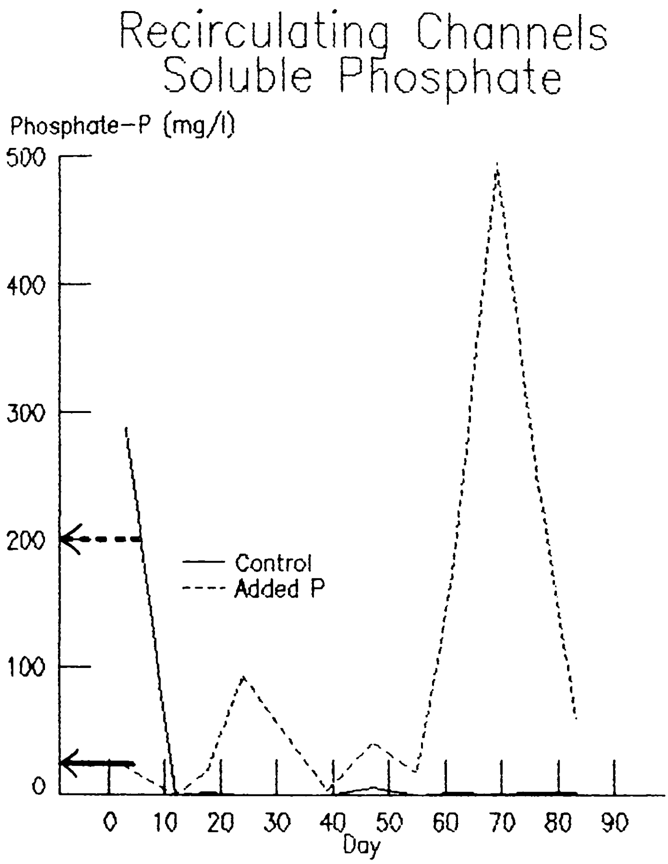
For many of the elements analysed, the concentrations rose and fell in concert in the two channels. This may be demonstrated by correlating the values in the two channels against each other (Table 3.2); potassium, nitrate, pH, magnesium, sodium and conductivity are positively correlated. This emphasises the fact that the conditions in the two channels were essentially similar, aside from the effect of the phosphate treatment.

Table 3.2 Correlation Co-efficients for elements in Recirculating Channels

Element	R	Significance
Soluble Phosphate	-.19	n.s.
Total Phosphate	-.19	n.s.
Potassium	0.73	**
Sulphate	0.11	n.s.
Nitrate	0.71	*
Silica	0.27	n.s.
pH	0.67	*
Calcium	0.46	n.s.
Magnesium	0.69	*
Sodium	0.76	**
Alkalinity	0.51	n.s.
Conductivity	0.76	**

Not significant = n.s.; $p < 0.05$ = *; $p < 0.01$ = **

On 12 July 1990 the plants were removed from the channels, and then dried (95°C), weighed and the tissue concentrations of phosphorous, nitrogen, carbon and potassium were measured (methods in Appendix C). An estimate was also made of the weight of the algae (*Cladophora glomerata*) in the channels. A rigid polypropylene container (*c.* 20 l) was carefully placed in the channel and allowed to fill with water plus algae. The container was removed from the channel, the volume of water was determined and the weight of algae used to estimate the total weight in the total volume of the channel (nine replicates).



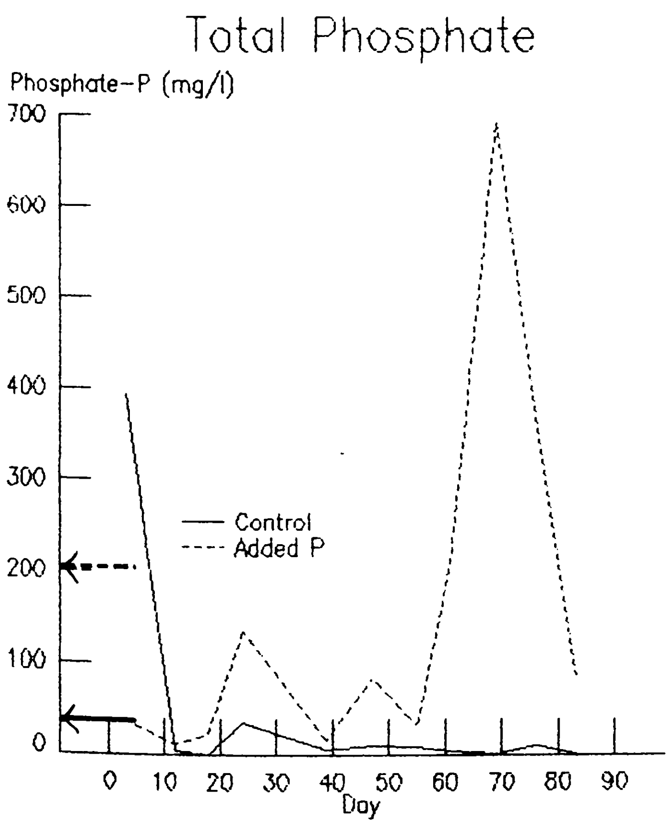
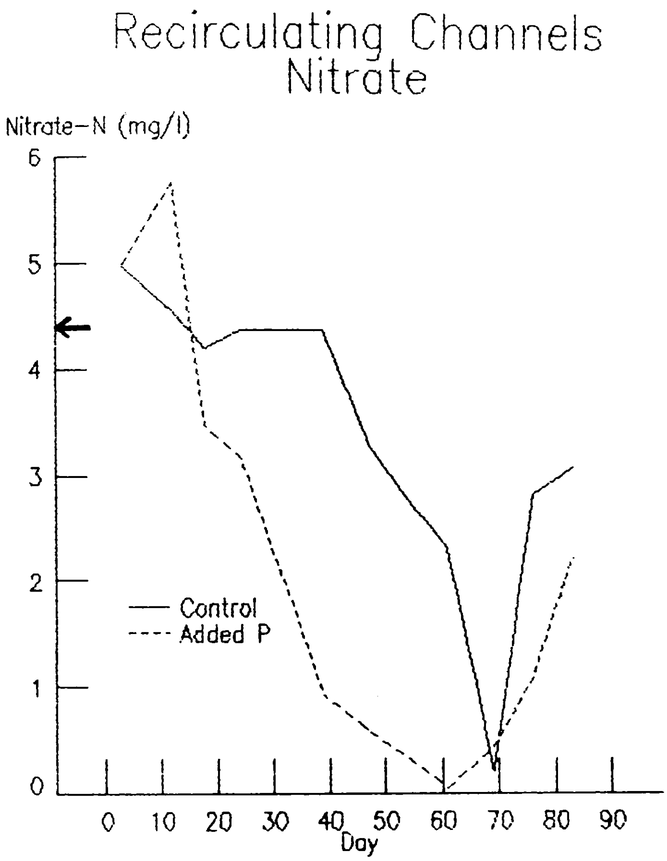


Figure 3.15. Phosphorus concentrations (filtered samples) in recirculating channels. Day 0 = 20 April, Day 90 = 18 July 1990. The solid arrow represents the input concentration in the control channel, the dotted arrow the concentration in the channel with added phosphate.



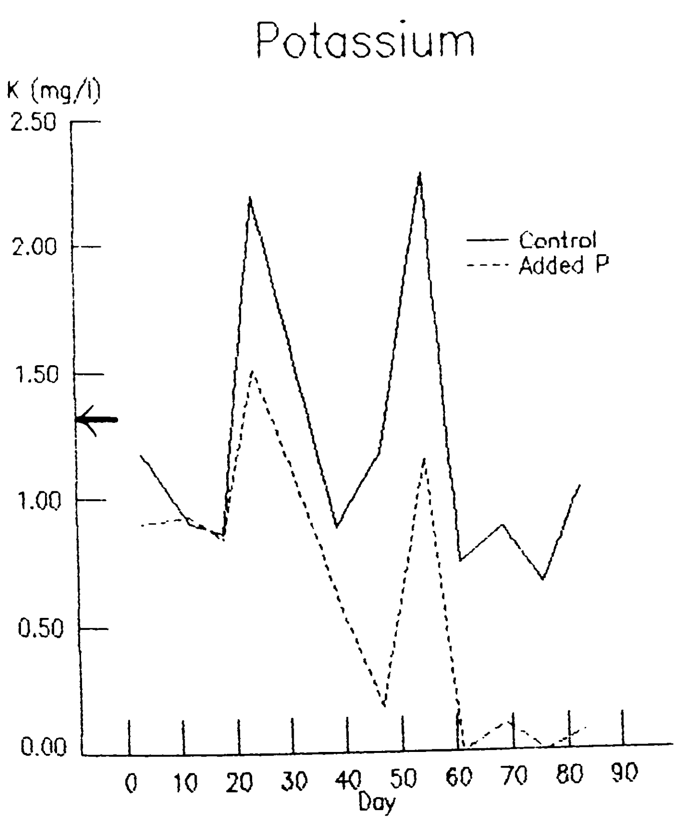


Figure 3.16. Nitrate and potassium concentrations in recirculating channels. Day 0 = 20 April, Day 90 = 18 July 1990. The arrow represents the concentration of the input water from the borehole.

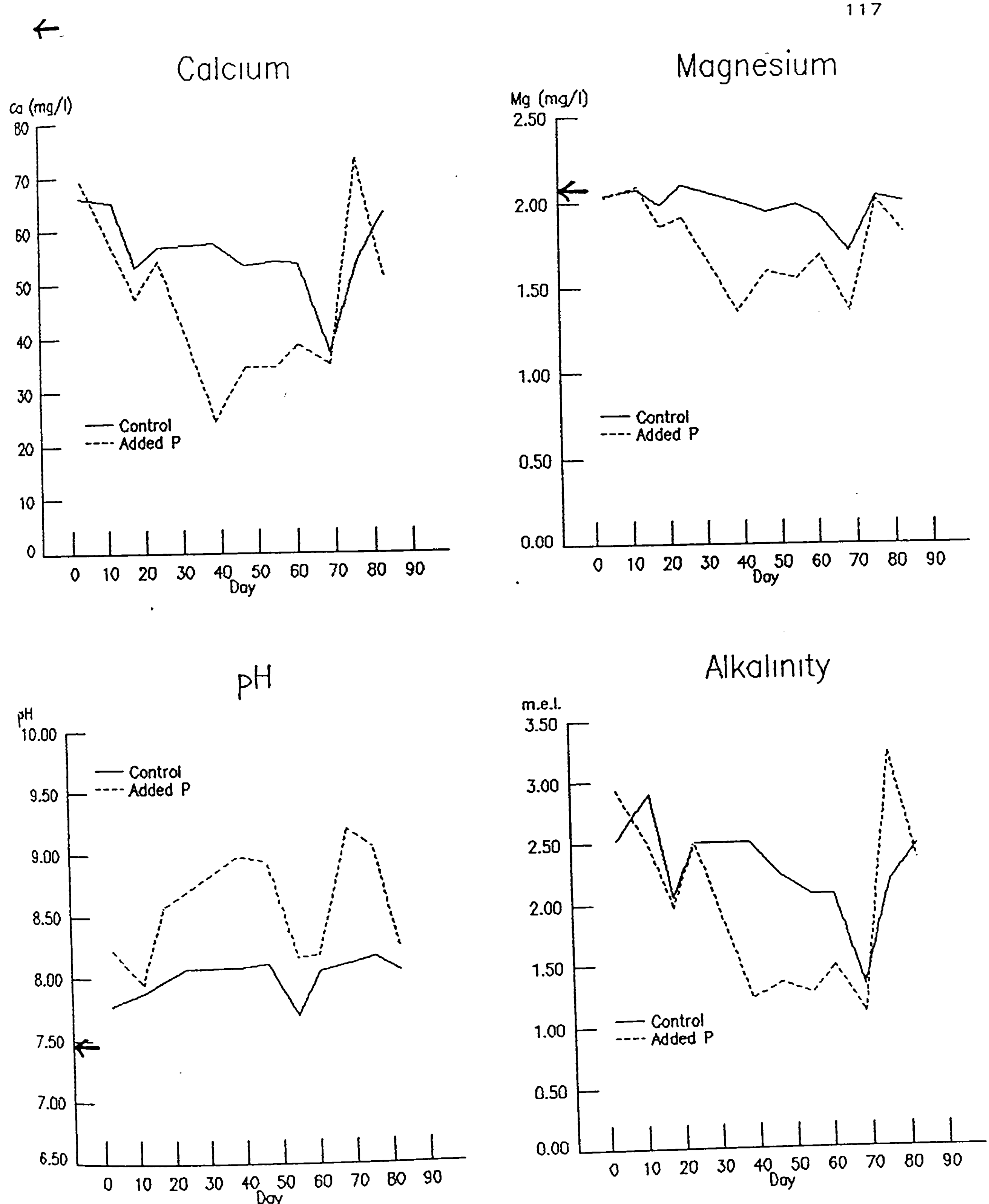


Figure 3.17. Calcium and magnesium concentrations, pH and alkalinity as HCO_3^-) in recirculating channels. Day 0 = 20 April, Day 90 = 18 July 1990. The arrow represents the concentration of the input water from the borehole (alkalinity 4.5 m.e.l.).

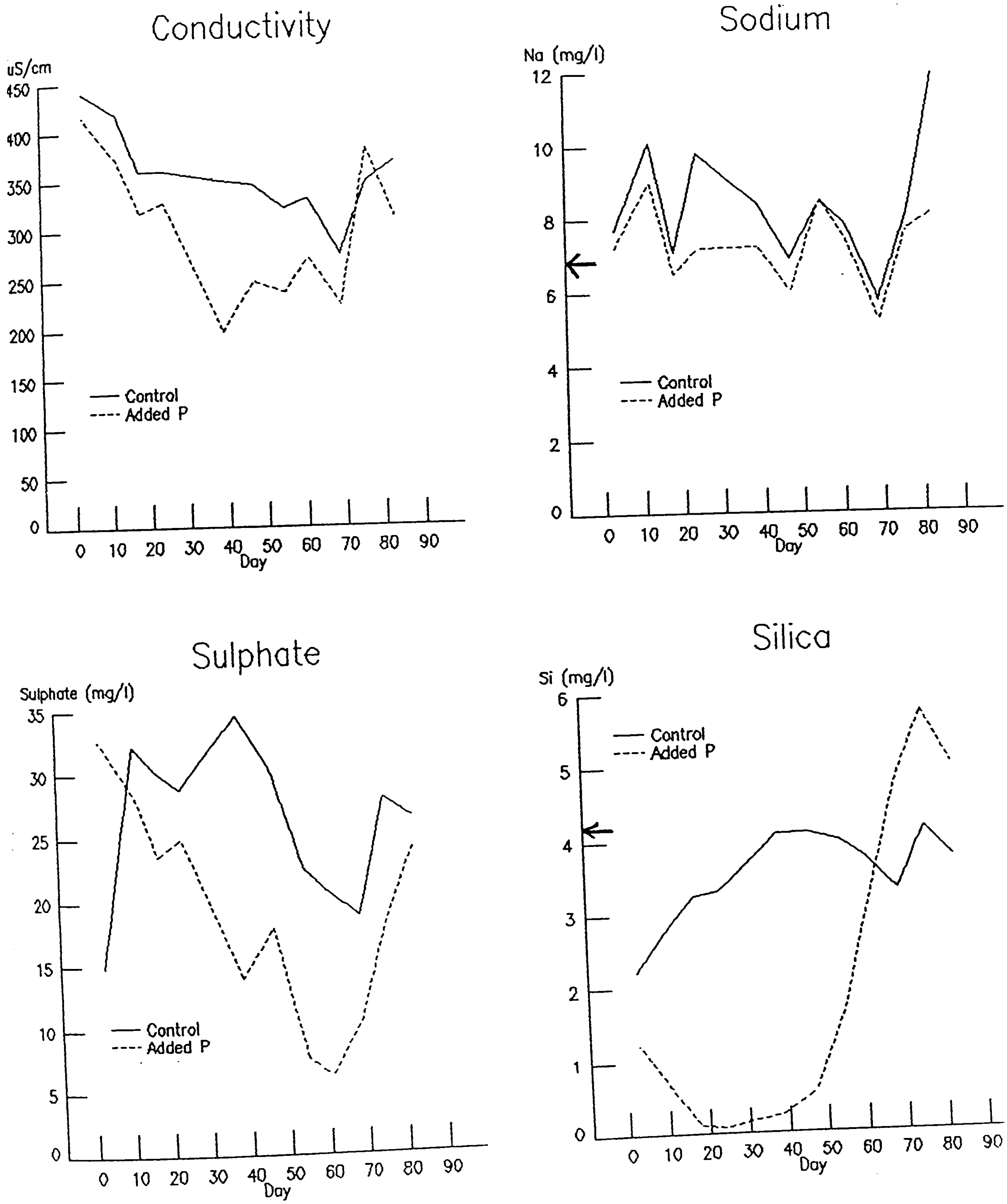


Figure 3.18. Conductivity and sulphate, sodium and silica concentrations in recirculating channels. Day 0 = 20 April, Day 90 = 18 July 1990. The arrow represents the concentration of the input water from the borehole.

Results

Results of the experiment are shown in Figures 3.19 to 3.36. Analysis of variance of the data was carried out using the Genstat 5 computer program; the results of which are summarised in Table 3.4 and 3.5 below. The amount of algae growing in the two channels is shown in Table 3.2.

Table 3.2 Estimated Algal Biomass in the Eutrophication/Competition Experiment

Channel	Fresh Weight	Dry Weight
Control	Undetectable	Undetectable
Added Phosphate	770 kg	23 kg

In summary, the channel with added phosphate had less *Ranunculus* shoot biomass, the root to shoot ratio was increased and there was a greater concentration (but not amount) of major nutrients in the shoots. There was no effect on the root biomass, but this was decreased in the pots with *Potamogeton pectinatus* present.

The *Potamogeton pectinatus* root and shoot biomass was reduced in the channel with added phosphate (though the ratio remained unaltered) and there were reduced levels of major nutrients.

Table 3.4 Summary of Analysis of Variance for *Ranunculus* in Eutrophication/Competition Experiment.

Variate	Source	Significance
Shoot Dry Weight	Competition	n.s.
	Channel	***
	Interaction	n.s.
Root Dry Weight	Competition	*
	Channel	n.s.
	Interaction	n.s.
Root/Shoot Ratio	Competition	n.s.
	Channel	***
	Interaction	n.s.
C/N Ratio	Competition	n.s.
	Channel	***
	Interaction	n.s.
Nitrogen concentration	Competition	n.s.
	Channel	***
	Interaction	n.s.
Phosphate concentration	Competition	n.s.
	Channel	***
	Interaction	n.s.
Potassium concentration	Competition	n.s.
	Channel	***
	Interaction	n.s.
Nitrogen amount	Competition	n.s.
	Channel	***
	Interaction	n.s.

Variate	Source	Significance
Phosphate	Competition	n.s.
amount	Channel	n.s.
	Interaction	n.s.
Potassium	Competition	n.s.
amount	Channel	n.s.
	Interaction	n.s.

'Competition' indicates the effects of *Potamogeton pectinatus* plants on the *Ranunculus* plants, 'Channel' indicates the difference between the control channel and the one with added phosphate. Nutrient values refer to levels in shoot tissue. Levels of significance as follows: n.s. = not significant, * = 95%, ** = 99%, *** = 99.9%.

Table 3.5. Summary of Analysis of Variance for *Potamogeton pectinatus* in Eutrophication/Competition Experiment.

Variate	Source	Significance
Shoot Dry Weight	Channel	**
Root Dry Weight	Channel	*
Root/Shoot Ratio	Channel	n.s.
C/N Ratio	Channel	***
Nitrogen concentration	Channel	**
Phosphate conc.	Channel	***
Potassium conc.	Channel	*
Nitrogen amount	Channel	*
Phosphate amount	Channel	n.s.
Potassium amount	Channel	*

As no *Potamogeton pectinatus* plants were grown separate from *Ranunculus* plants, (due to a shortage of *Potamogeton* plants at the start of the experiment) the effects of *Ranunculus* competition on *Potamogeton* could not be assessed. Notation as for Table 3.4.

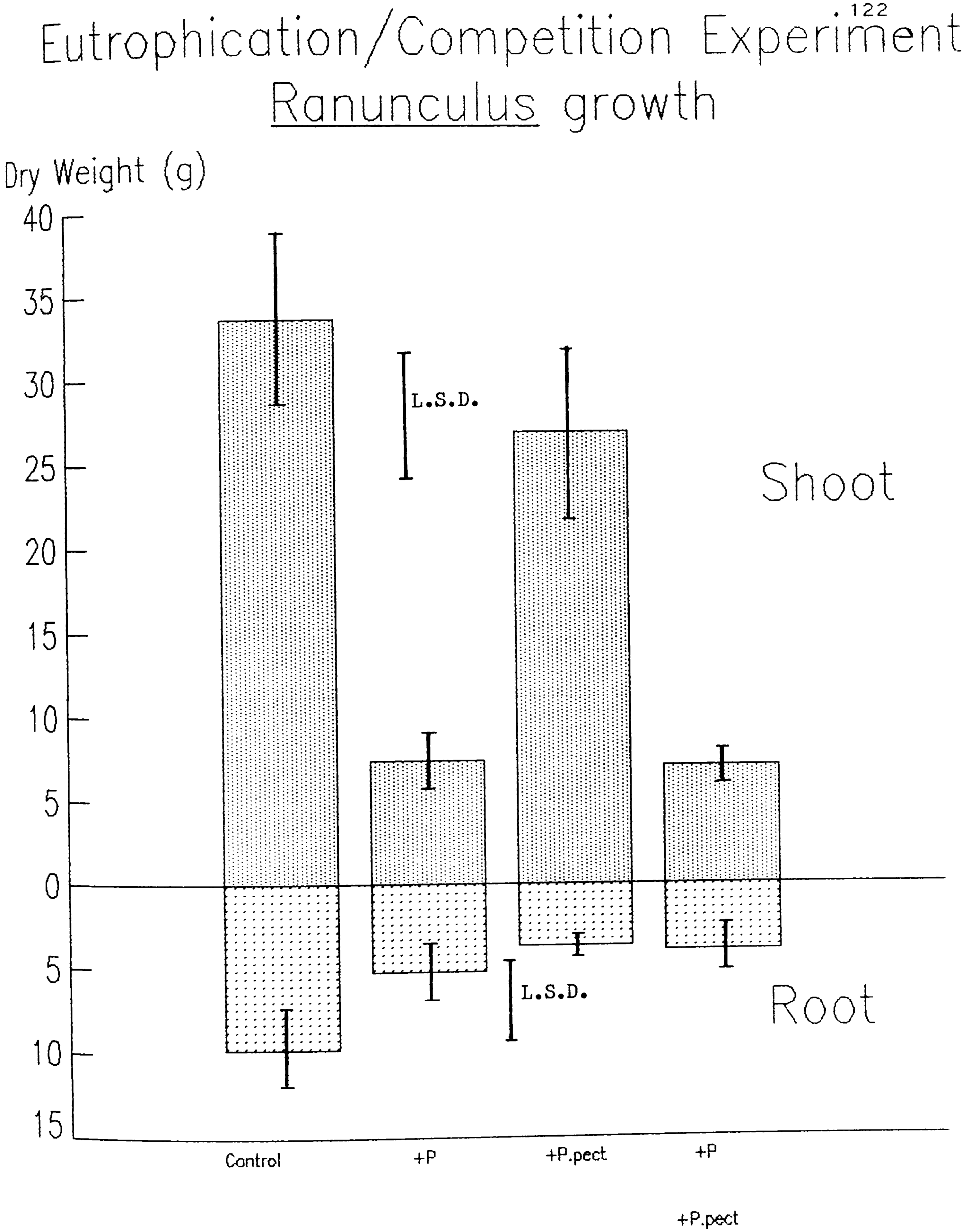


Figure 3.19. Effect of channel with added phosphate (+P) and presence of *Potamogeton pectinatus* (+P.pect) on *R. penicillatus* subsp. *pseudofluitans* growth. Bars on histograms represent ± 1 s.e., separate bars represent least significant difference ($p<0.05$)

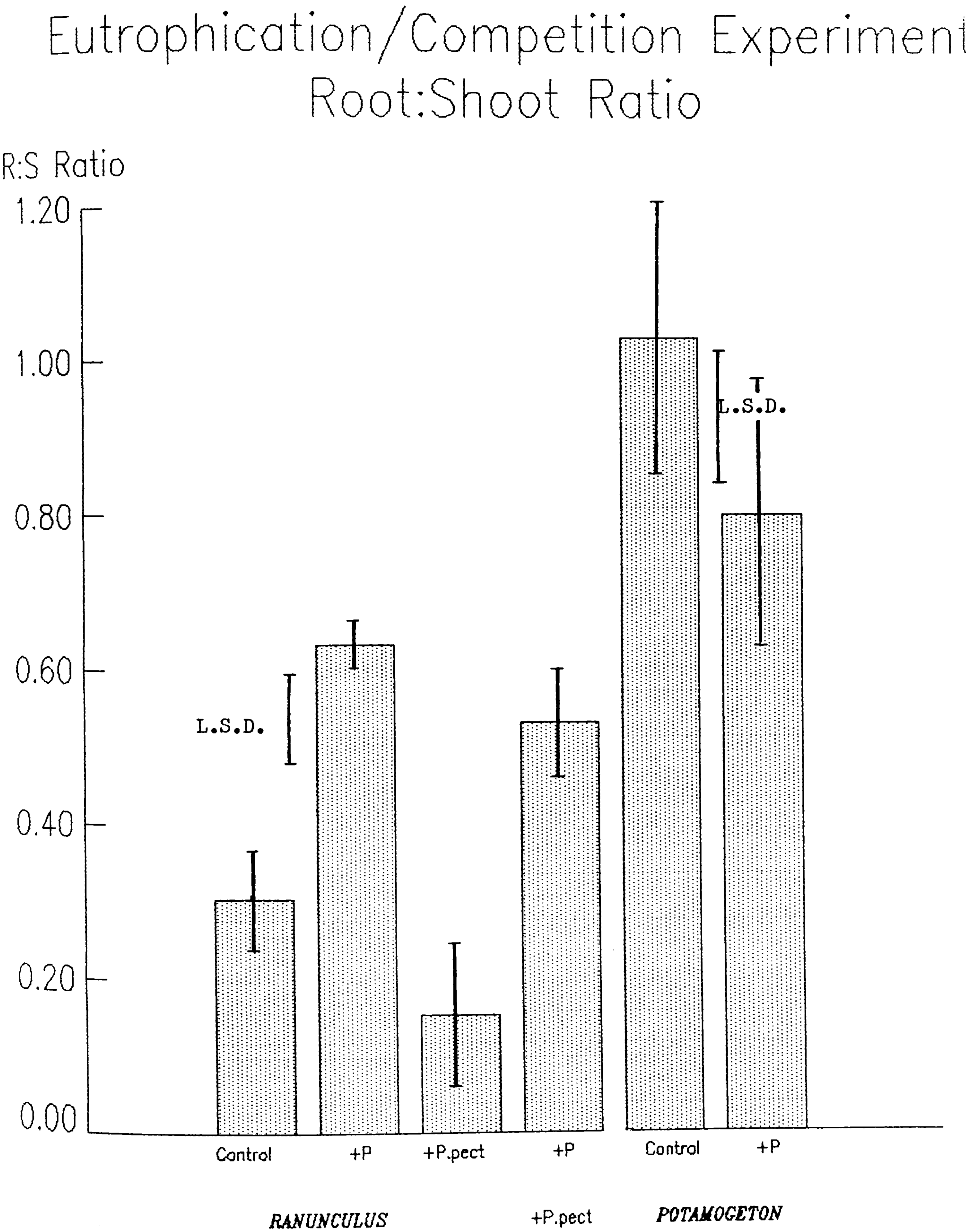


Figure 3.20. Effect of channel with added phosphate (+P) and presence of *P. pectinatus* (+P.pect) on *R. penicillatus* subsp. *pseudofluitans* and *P. pectinatus* root/shoot ratio. Bars on histograms represent ± 1 s.e., separate bars represent least significant difference ($p<0.05$)

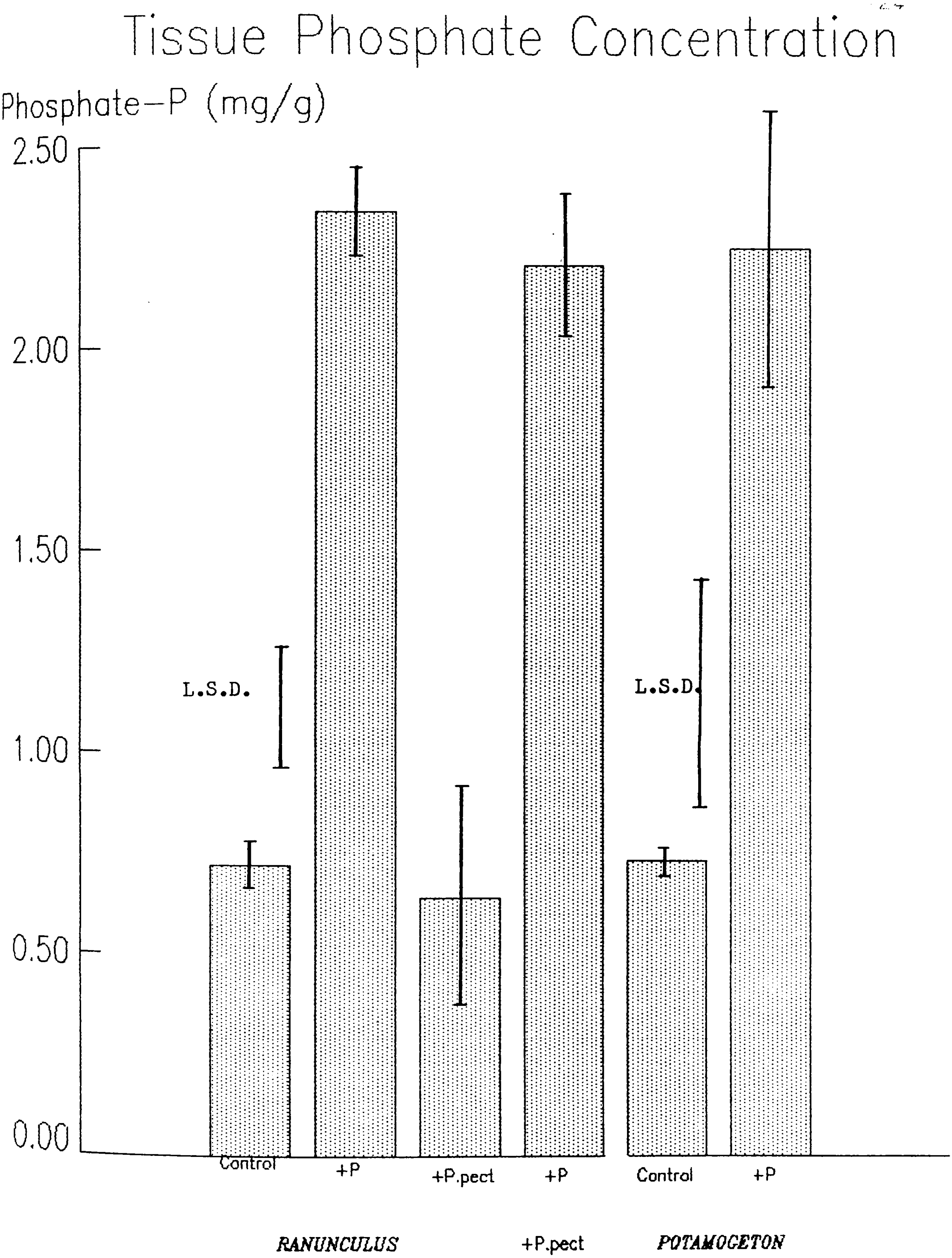


Figure 3.21. Effect of channel with added phosphate (+P) and presence of *Potamogeton pectinatus (+P.pect)* on *R. penicillatus* subsp. *pseudofluitans* and *P. pectinatus* shoot tissue phosphate concentration. Separate bars represent least significant difference ($p < 0.05$), bars on histograms represent ± 1 s.e..

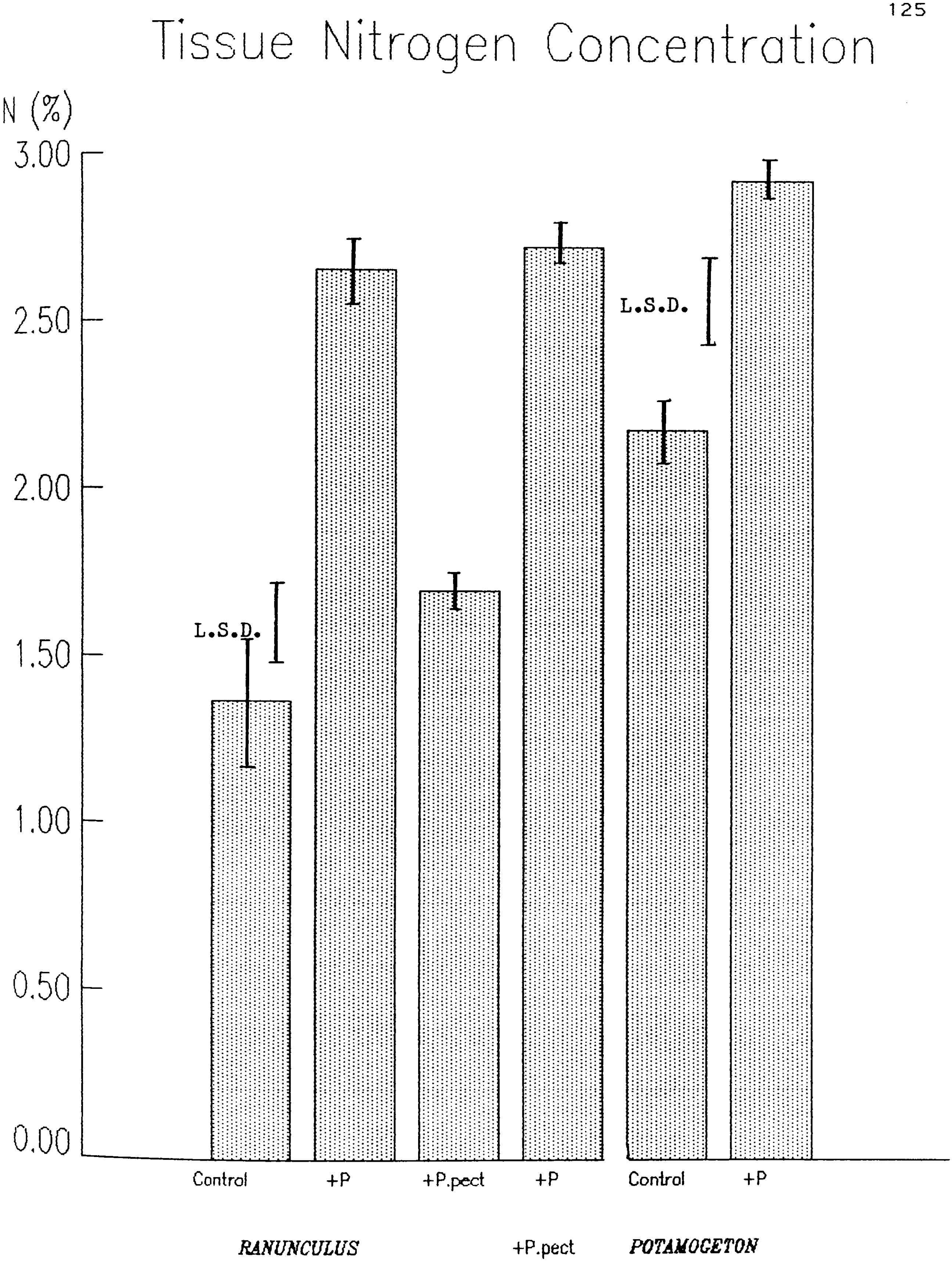


Figure 3.22. Effect of channel with added phosphate (+P) and presence of *Potamogeton pectinatus (+P.pect)* on *R. penicillatus* subsp. *pseudofluitans* and *P. pectinatus* shoot tissue nitrate concentration. Separate bars represent least significant difference ($p < 0.05$), bars on histograms represent ± 1 s.e..

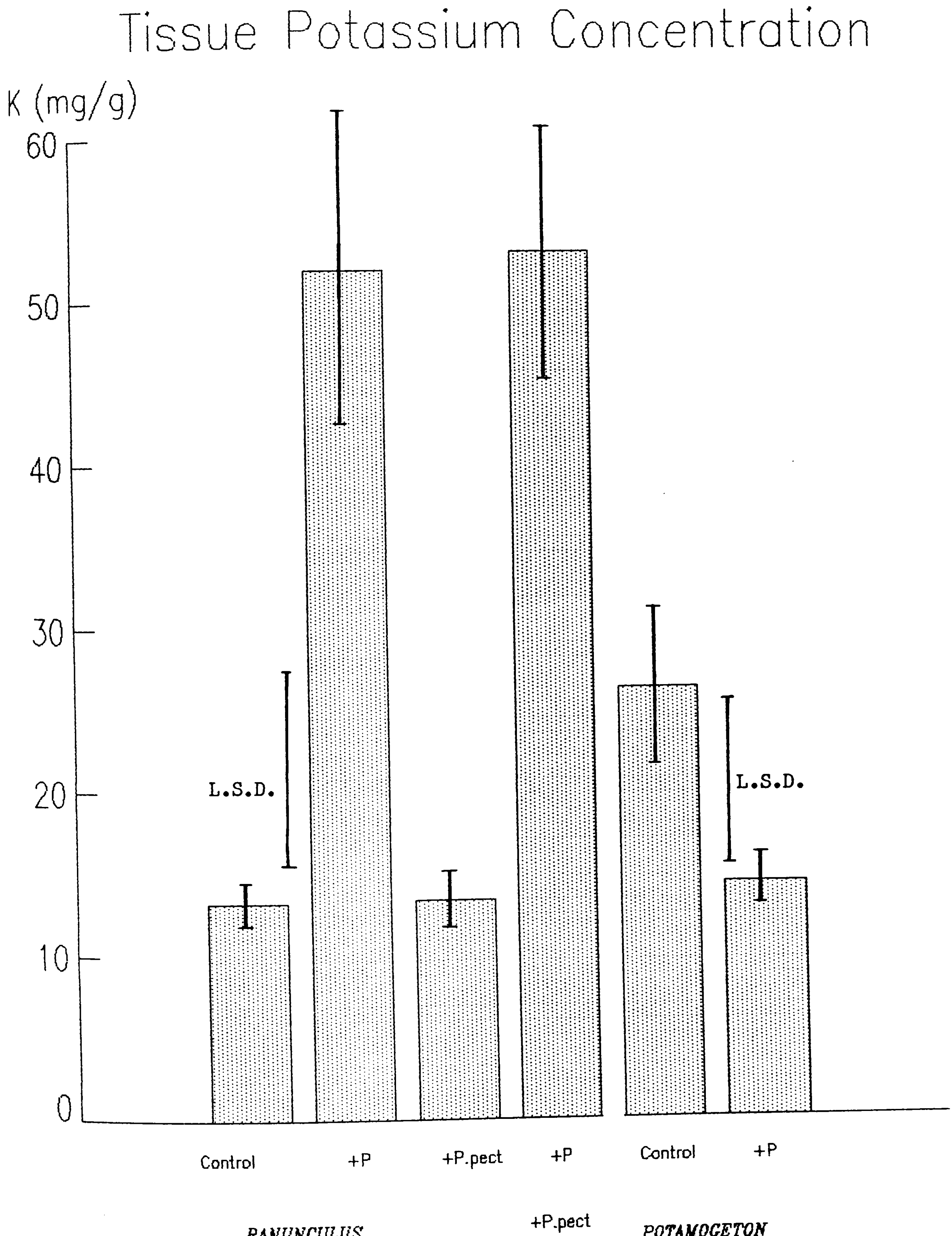


Figure 3.23. Effect of channel with added phosphate (+P) and presence of *Potamogeton pectinatus* (*+P.pect*) on *R. penicillatus* subsp. *pseudofluitans* and *P. pectinatus* shoot tissue potassium concentration. Separate bars represent least significant difference ($p<0.05$), bars on histograms represent ± 1 s.e..

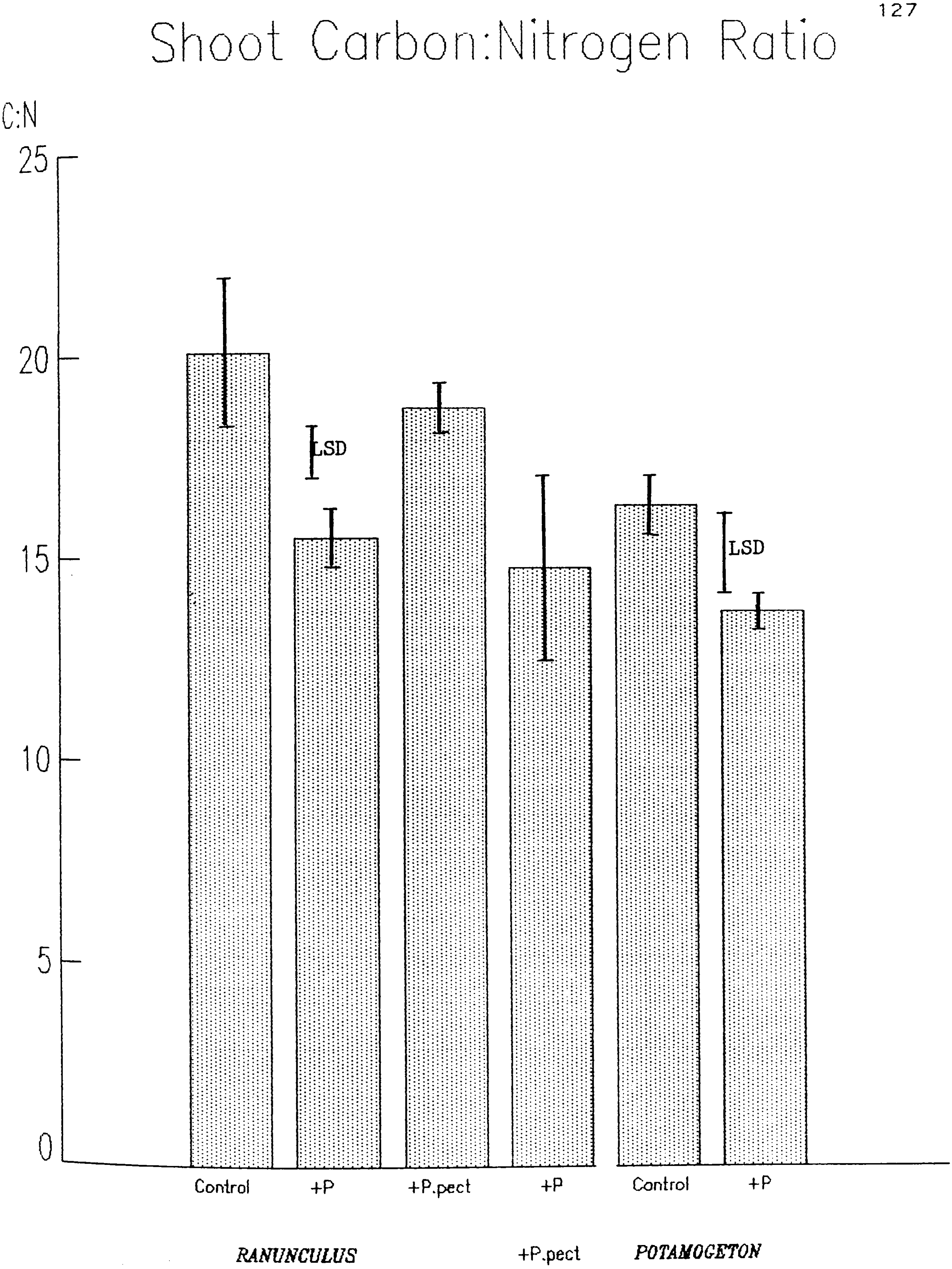


Figure 3.24. Effect of channel with added phosphate (+P) and presence of *Potamogeton pectinatus (+P.pect)* on *R. penicillatus* subsp. *pseudofluitans* and *P. pectinatus* shoot carbon:nitrogen ratio. Separate bars represent least significant difference ($p \leqslant 0.05$), bars on histograms represent ± 1 s.e..

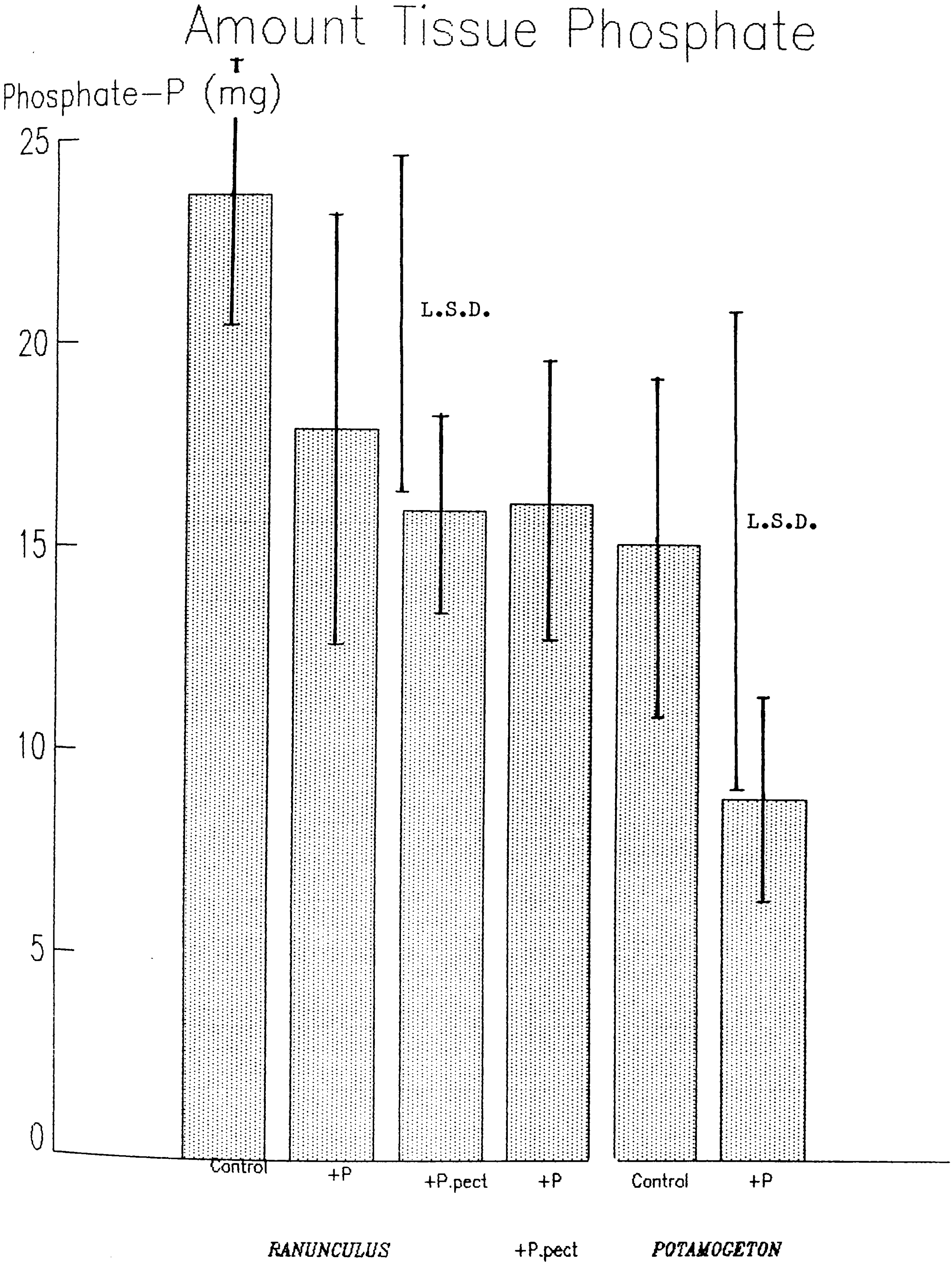


Figure 3.25. Effect of channel with added phosphate (+P) and presence of *Potamogeton pectinatus* (+P.pect) on *R. penicillatus* subsp. *pseudofluitans* and *P. pectinatus* amount of tissue phosphate (concentration × dry weight). Separate bars represent least significant difference ($p<0.05$), bars on histograms represent ± 1 s.e..

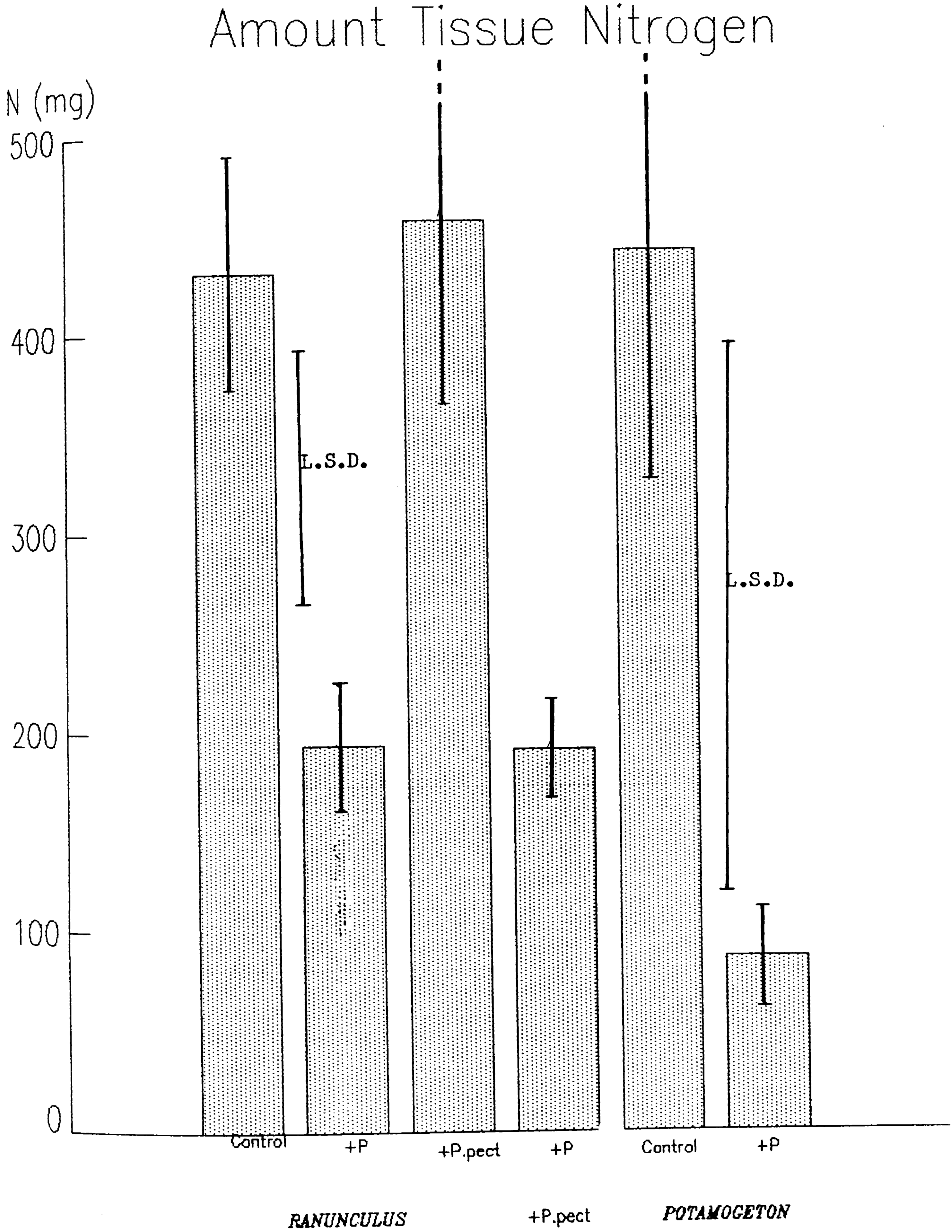


Figure 3.26. Effect of channel with added phosphate (+P) and presence of *Potamogeton pectinatus* (+P.pect) on *R. penicillatus* subsp. *pseudofluitans* and *P. pectinatus* amount of tissue nitrogen (concentration × dry weight). Separate bars represent least significant difference ($p<0.05$), bars on histograms represent ± 1 s.e..

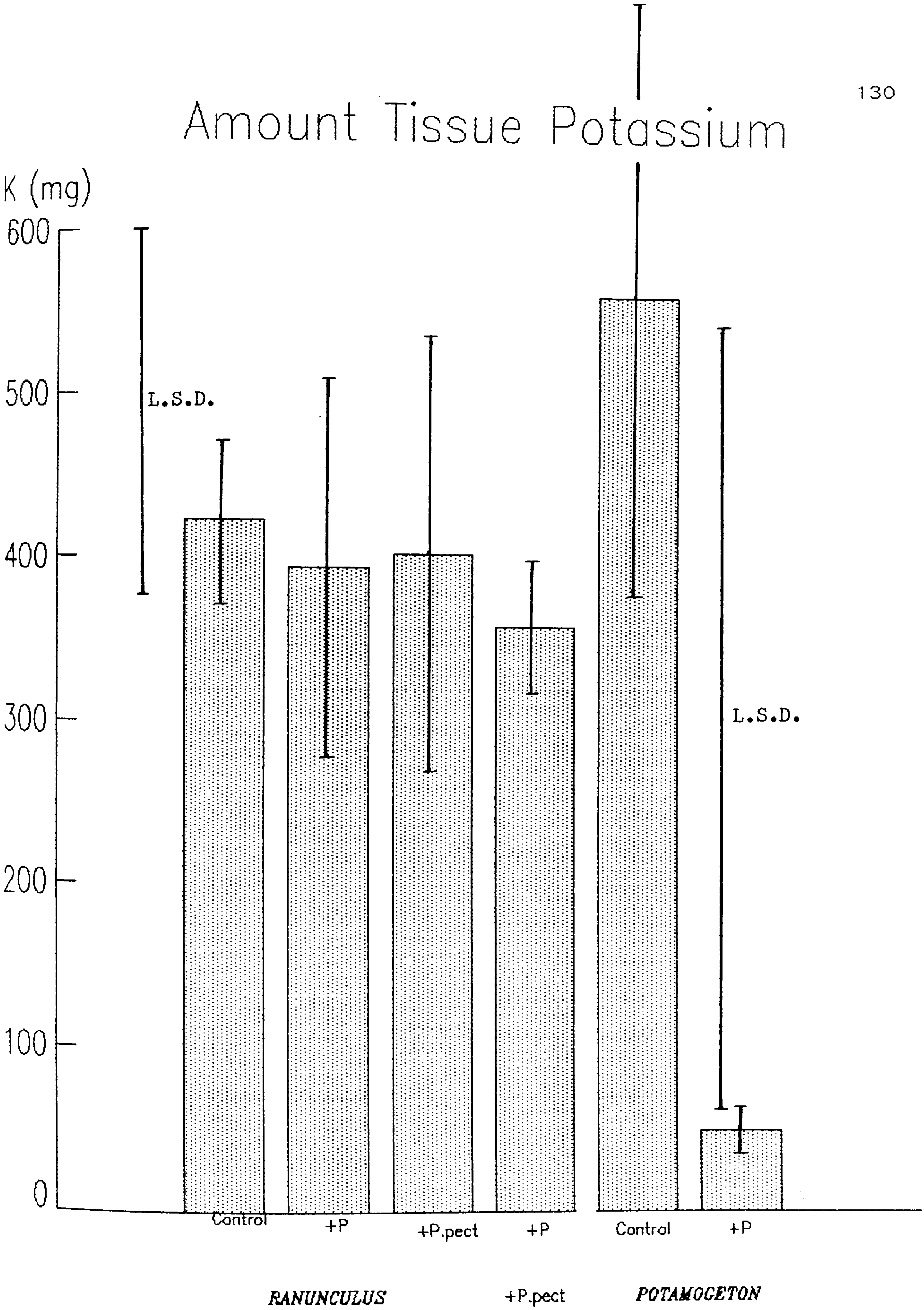


Figure 3.27. Effect of channel with added phosphate (+P) and presence of *Potamogeton pectinatus (+P.pect)* on *R. penicillatus* subsp. *pseudofluitans* and *P. pectinatus* amount of tissue potassium (concentration × dry weight). Separate bars represent least significant difference ($p \leq 0.05$), bars on histograms represent ± 1 s.e..

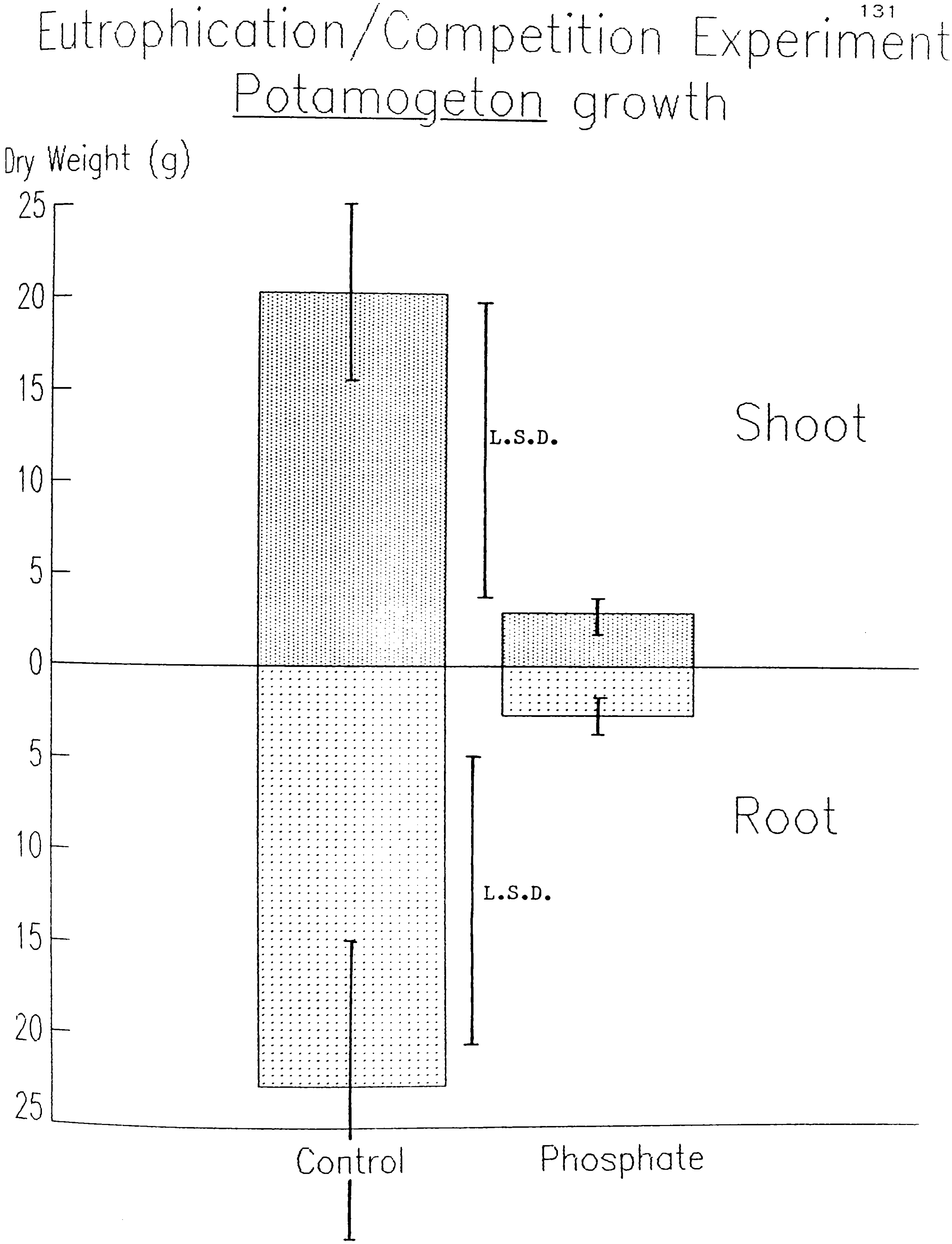


Figure 3.28. Effect of added phosphate (+P) on *Potamogeton* growth. Separate bars represent least significant difference ($p \leq 0.05$), bars on histograms represent ± 1 s.e..

3.3.3 Discussion

The addition of phosphate to one channel clearly had the effect of causing a great increase in algal growth in that channel; ¾ tonne is a lot of algae. This would undoubtedly have had the effect of reducing the quantity of light available to the macrophytes and so would be a significant cause of stress (S. Marrs Unpublished Data 1991). However as the algal population was filamentous rather than phytoplankton, there was no significant difference in extinction coefficient (measured as described in Chapter Two) between the two channels (Figure 3.39). It is possible that phytoplankton growth was at least in part inhibited by allopathic secretions by the macrophytes (Hootsmans & Vermaat 1991). These results are similar to those described by Howard-Williams (1981). He found that when a *Potamogeton pectinatus* community was enriched with nitrate and phosphate a dense filamentous algal population developed, but there was little planktonic algae.

The ten pots in each channel were not ten true replicates but 'pseudoreplicates' as they were not statistically independent (Hurlbert 1984). As only two channels were available for this experiment it was not possible to fully replicate the treatment. The statistical comparisons are therefore comparisons between the two channels rather than between the two treatments. The 'competition' treatment was fully replicated and so does not have the same statistical problems.

The question therefore arises as to whether it is a reasonable assumption that the differences observed between the channels were due to the phosphate treatment or due to another factor. There are a number of reasons why it is likely that the differences were caused by the addition of phosphate. The major measured differences between the channels were the relatively high phosphate concentration and large algal growth in the channel with the added phosphate. Both of these effects were clearly directly caused by the treatment. Conversely the concentrations of many of the other chemical elements rose and fell in concert during the growing season (Figures 3.15 - 3.18, Table 3.2). This indicates that it is likely that external factors acting on the channels had similar effects to each channel. However, although it is likely that the effects on the plants observed were due to the treatment, the possibility that it was due to another factor can not be excluded.

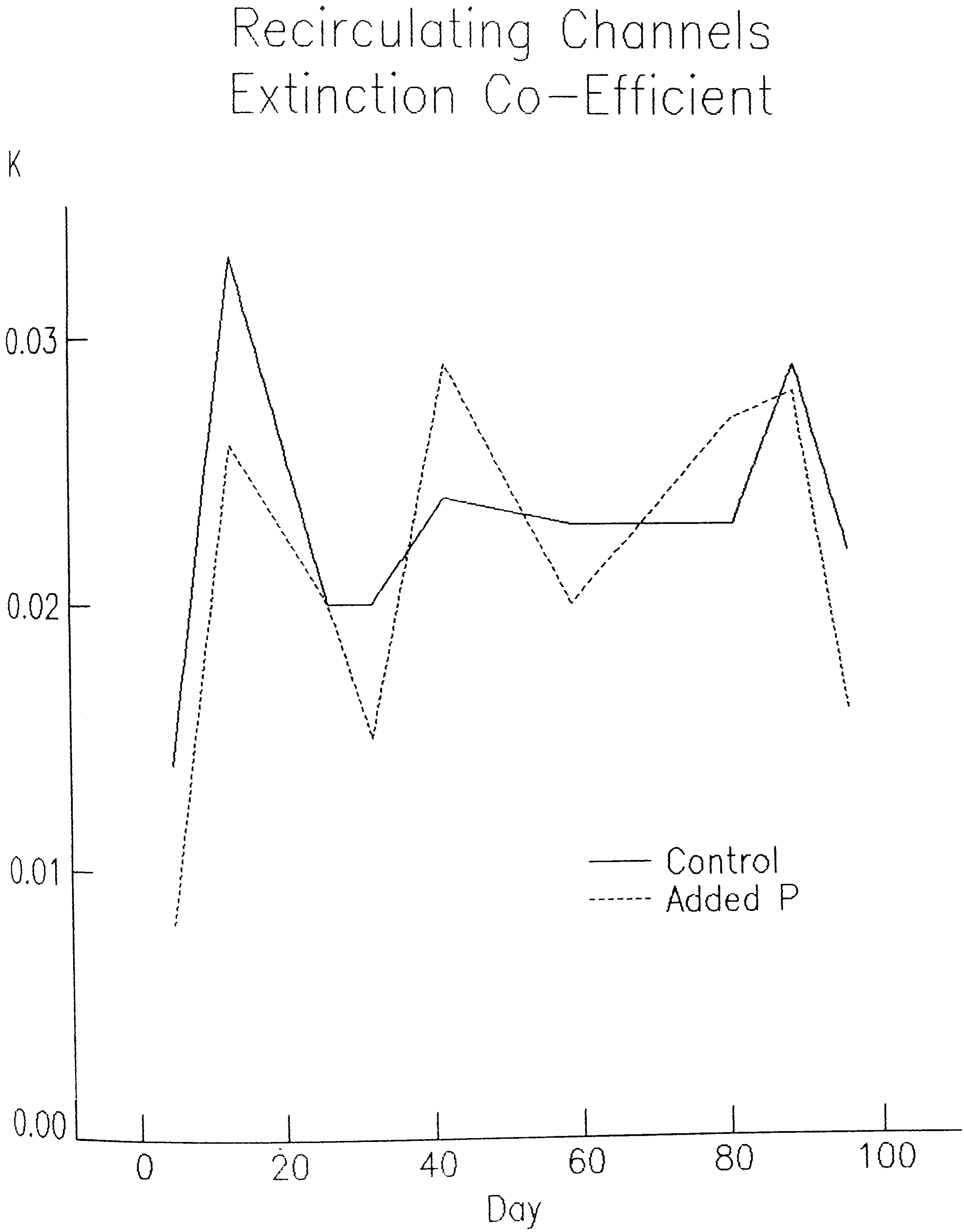


Figure 3.39. Extinction co-efficient in control channel and channel with added phosphate. Day 0 = 31 March 1990, Day 100 = 9 July 1990.

The data indicate that in the channel with the increased phosphate treatment the *Ranunculus* responded with a reduction in shoot growth rate (but no change in the root growth rate). Conversely, the competition from the *Potamogeton* did not cause any reduction in shoot biomass, but it did cause a significant reduction in root growth.

It is unlikely that the effects of *Ranunculus* growth measured here were mainly due to direct effects of phosphorus toxicity (though the possibility of this having a less important contributory effect should not be disregarded). Several of the *R. penicillatus* subsp. *pseudofluitans* communities surveyed in 1990 (Chapter Two, Appendix A) had apparently healthy *Ranunculus* plants growing in phosphate concentrations in excess of that measured in the high phosphate channel in this experiment. It is more likely that the reduced growth in both *Ranunculus* and *Potamogeton pectinatus* was caused by shading which was caused by the increased filamentous algae growth. This effect is consistent with the hypothesis proposed by Phillips *et al.* (1978) to explain the disappearance of aquatic macrophytes from the Norfolk Broads.

As one would expect, the tissue phosphate concentrations of both the *Ranunculus* and the *Potamogeton pectinatus* were increased in the high phosphate channel (Figure 3.21). Even in the control channel the tissue phosphate concentrations were considerably higher than the critical concentrations thought to be necessary for growth (Gerloff & Krumbholz 1966, Gerloff & Westlake 1980). The concentration of phosphate in the water of the control channel was very low (Figure 3.15), indicating that virtually all the phosphate was either taken up by the plants or removed by co-precipitation with calcium carbonate.

In the *Ranunculus* plants the concentrations of nitrogen and potassium were increased in the high phosphate channel, as was the nitrogen concentration in the *Potamogeton pectinatus* plants (Figure 3.34). Both potassium and nitrate concentrations were lower in the water of the high phosphate channel (Figures 3.15 and 3.16), presumably due to increased uptake by the increased algal growth, and so one might have expected the concentrations of these elements to be lower in the plant tissues. Although the concentrations of tissue nitrogen and potassium were higher in the high phosphate channel, the actual total amount of the element in the shoots (concentration × dry weight) was lower in the high phosphate channel (Figure 3.25, Figure 3.26). Thus the apparent increase of potassium and nitrogen uptake was in reality a result of the reduced growth in the high phosphate channel, the actual total amount taken up in the high phosphate channel was less for both the *Ranunculus* and the *Potamogeton pectinatus*. As the sediment concentrations of nitrogen and potassium were identical in both channels these data indicate that the concentration of these elements in the water is a significant factor, demonstrating that for both *Potamogeton pectinatus* and *R. penicillatus* subsp. *pseudofluitans*, shoots as well as roots are an important pathway for nutrient (N, P and K) uptake. The concentration of elements in the water was controlled not only by the inputs but also by the uptake by the filamentous algae. Agami & Reddy (1990) have shown translocation of nutrients between roots and shoots in macrophytes subjected to eutrophication.

A prediction of strategy theory is that as stress is increased, so the importance of competition in that habitat is decreased (Chapter One). Thus one might predict that the effect of *Potamogeton pectinatus* on *Ranunculus* would be less in the channel with added phosphate than in the control channel, i.e. there would be a significant 'interaction' effect between the two factors in the analysis of variance. No such response was observed (Table 3.3, Figure 3.19). However this is likely to be due to the general lack of effects due to competition. There was no effect on any of the tissue elements measured, nor did competition have any effect on shoot growth. There was a small effect on root growth (but not on root to shoot ratio). Thus as competition had little effect on the *Ranunculus* plants in the time-scale of the experiment, one would not expect to see a significant difference in the effects of competition in the control channel compared with the stressed channel.

Potamogeton pectinatus is a common macrophyte throughout the world and is of considerable importance as a wildfowl food. It is considered to be the most important food plant for ducks in the U.S. (Martin & Uhler 1939). Because of its economic importance a considerable quantity of research has been carried out on this macrophyte which has been comprehensively reviewed in Van Wijk 1988a, b; 1989a, b and Van Wijk *et al.* 1988. A sufficiently detailed understanding of its biology has been arrived at to enable a computer model of its ecology to have been written (Van Vierssen & Hootsmans 1990, Hootsmans & Vermaat 1991).

Van Wijk (1989c) has discussed the strategy that *Potamogeton pectinatus* exhibits. He considered that it was difficult to fit it into any of Grime's strategies, partly because of the inadequate information for placing aquatic plants into strategy-types and partly because the species is very variable, so that different populations apparently exhibit different strategies (Verhoeven *et al.* 1982, Van Wijk 1988b). The former problem is one of the central questions that this thesis is attempting to answer and will be addressed in Chapter Six. Hootsmans & Vermaat (1991) have shown that *Potamogeton pectinatus* shows great variability both in terms of phenotypic plasticity and in genotypic differences between populations. However Grime (1979) identifies a plastic morphological response to stress as itself an indicator of a competitive strategy. A number of other characteristics of the biology of *Potamogeton pectinatus* suggest that it has a strongly competitive strategy. It is frequently found in very productive eutrophic habitats (Van Wijk 1989a). It can form an extensive dense canopy (Van Wijk 1988a). It shows little physiological acclimation to changes in light intensity, responding instead with changes in biomass (Hootsmans & Vermaat 1991). The species shows a strong seasonal variation in phenology and photosynthesis (Van Wijk 1988a). All these characteristics are identified by Grime (1977, 1979) as being associated with a competitive strategy. However its tolerance of wildfowl grazing shows that it has some disturbance tolerance and populations from brackish habits show stress-tolerance to salinity (Van Wijk *et al.* 1988).

From the above characteristics it might be expected that *Potamogeton pectinatus* would be a more competitive (and so less stress-tolerant) plant than *Ranunculus penicillatus* - the data from this experiment go some way towards confirming that. A competitive plant responds to stress with relatively large changes in growth rate (Grime 1977, 1979), whereas a more stress-tolerant plant will show a smaller change. The *Potamogeton* shoot biomass was seven times smaller in the added phosphate ('stress') treatment (Figure 3.28), whereas the *Ranunculus* shoot was only 4.4 times smaller (Figure 3.19). In addition there was a significant biomass reduction in the shoot and root of the *Potamogeton*, whereas there was only a significant reduction in the shoot of the *Ranunculus*.

In several chalk streams dominated by *R. penicillatus* subsp. *pseudofluitans*, the water phosphate concentrations have increased over the past few decades. For example, the River Itchen at Winchester (Site number 6, Chapter Two and Appendix A) has shown a three-fold increase in phosphate concentration during the period 1979 - 1989 (National Rivers Authority, unpublished data). The results from this experiment indicate that if the concentration of phosphate continues to increase it is likely that there may be a decline in macrophytes and an increase in filamentous algae.

In the recirculating channels the algae could not get washed away downstream and so this may have led to more algal accumulation than would occur naturally in a fast-flowing river (though during the 1990 survey described in Chapter Two, algal populations apparently as dense as that in this experiment were observed in some chalk rivers). In situations where algae may not grow so abundantly (for example, if silica was limiting) it would be useful to predict what changes might occur in the balance between the species making up the macrophyte community. The data from this experiment support the hypothesis that *Potamogeton pectinatus* is more of a competitive taxon than *R. penicillatus* subsp. *pseudofluitans*, and so it is likely that if there was a situation of increased nutrient supply without the stress caused by competition from filamentous algae, the *Potamogeton* would forage nutrients more efficiently than the *Ranunculus*, show a greater plasticity in its growth response, and so out-compete the *Ranunculus*. Indeed there is evidence to suggest that this has already happened in some organically polluted rivers (see e.g. Caffrey 1990b).

4. The Response of *Ranunculus* to Disturbance

THE WATER CROWFOOT

O' small-feac'd flow'r that now does bloom
To stud wi' white the shallow Frome,
An' leave the clote to spread his flow'r
On darksome pools o' stwoneless Stour,
When sof'ly-rizen airs do cool
The water in the sheenen pool,
The beds o' snow-white buds do gleam
So feair upon the sky-blue stream,
As whitest clouds, a-hangen high
Avore the blueness o' the sky;
An' there, at hand, the thin-heair'd cows,
In airy sheades o' withy boughs,
Or up bezide the mossy rails,
Do stan' an' zwing their heavy tails,
The while the ripplen stream do flow
Below the dousty bridge's bow;
An' quiv'ren water-gleams do mock
The weaves, upon the sheaded rock;
An' up athirt the copen stwone
The laitren bwoy do lean alone,
A-watchen, wi' a stedvast look,
The vallen waters in the brook,
The while the zand o' time do run
An' leave his errand still undone.
An'd oh! as long's thy buds would gleam
Above the softly-sliden stream,
While sparklen zummer-brooks do run
Below the lofty-climen zun,
I only wish that thou could'st stay
Vor noo man's harm, an' all men's jay.
But no, the waterman 'ull weade
Thy water wi' his deadly bleade,
To slay thee even in thy bloom,
Fair small-feaced flower o' the Frome.

William Barnes
Poems of Rural Life in the Dorset Dialect
2nd collection, London 1847

4.1 Introduction

The 'deadly blade' of the waterman that William Barnes describes in the above poem has been the traditional mode of management of chalk streams dominated by *R. penicillatus* subsp. *pseudofluitans* in England for centuries (Westlake & Dawson 1982). The cost of the operation is considerable (estimated at £100 M annually for the U.K., Dawson 1989) but is necessary in order to prevent flooding of the surrounding land and for fisheries management. In the past flooding was a part of the management regime of the grassland, but few water meadows now remain, so that management is now more necessary than ever. Cutting by hand has been largely replaced by mechanised methods (weed-cutting boats and cutting-arms mounted on mechanical diggers) as well as some use of the herbicide diquat-alginate (Fox & Murphy 1986, Barrett *et al.* 1989). Management of aquatic vegetation by applying disturbance is carried out in many different countries; examples may be cited from The Netherlands (Van Strien *et al.* 1991), Poland (Bernatowicz 1965), the United States (Haller *et al.* 1991) and Ireland (Caffrey 1990b) amongst others (see Pieterse & Murphy 1990).

Different macrophyte species have different responses to disturbance by cutting (e.g. Middleton 1990). In consequence many years of cutting might be expected to select for those species which are more tolerant of disturbance. Several workers have shown that *R. penicillatus* subsp. *pseudofluitans* is preferentially encouraged by the traditional cutting regime (e.g. Soulsby 1974, Furse 1977, Ham, Wright & Berrie 1982). Some studies have shown that if the intensity of disturbance is increased the importance of competition is apparently decreased (eg. Bailey 1988, Day *et al.* 1988). Bernatowicz (1965) observed that when vegetation dominated by *Phragmites australis* was cut (i.e. disturbance to the habitat was increased), *Ranunculus circinatus* was able to invade that area, as it was no longer competitively excluded.

The increased growth observed in some *Ranunculus* species after cutting is not purely due to a reduction in competition from other species. In a dense weed bed the centre of a *Ranunculus* clump receives little light due to self-shading from upper leaves and there is a slow supply rate of carbon and nutrients due to the reduced current velocity. After the plant has been cut, the remaining stems are no longer limited by these factors and they show exponential growth (Westlake 1968b; Ham, Wright & Berrie 1982). This has led to the development of different management techniques which do not stimulate growth, such as cutting at the end of the growing season which produces a smaller initial biomass and so there is less growth in the following season (Westlake & Dawson 1986) or the use of bankside trees for shading (Dawson & Kern-Hansen 1979).

Cutting is not the only disturbance to which macrophyte communities are subjected. Grazing by waterfowl may be important for some *Ranunculus* communities (see for example Kiørboe 1980), and although fish rarely graze macrophytes directly, their activities may result in the destruction of macrophyte beds through disturbance of sediments and associated increased turbidity of the water (see for example Crivelli 1983, Carpenter & McCreary 1985). There in an ongoing debate as to the importance of grazing by invertebrates (Reavell 1980, Gregory 1983, Sheldon 1987, Sand-Jensen & Madsen 1989, Brönmark 1990). Do they graze the macrophytes or just the periphyton? The consensus which appears to be emerging is that the importance of invertebrate grazing has been underestimated in the past and that at least in some habitats it is an important disturbance (Lodger 1991).

Vegetation near the bank may be subject to trampling and grazing and both floating and submerged vegetation may be disturbed by boat traffic (Eaton 1986, Murphy 1980, Murphy & Eaton 1983). In some rivers ice formation affects the macrophyte community (Nichols *et al.* 1989) whereas in warmer climates streams may dry out in the summer with a resultant destruction of biomass by severe drought (see for example Ladle & Bass 1981). In rivers regulated by dams there are considerable fluctuations in water level which can be an important disturbance pressure (see e.g. Springuel *et al.* 1990). Van Diggelen & Klooker (1990) have shown that an increase in fluctuation of the water levels of Dutch streams has been responsible for the decrease in abundance of *R. hederaceus* - a species with low disturbance tolerance (Chapter Six). Severe spates can markedly change the vegetation of a stream (Bilby 1977). At low values, current velocity can be a stress (see Chapter Three), whereas a high water current velocity acts as a disturbance, removing biomass. Clonal species that reproduce through fragmentation have weaker stems than species that spread through seeds (Brewer and Parker 1990), and those that grow in turbulent water also have stronger stems (Haslam 1978, Brewer and Parker 1990). Species which are found in rivers with faster velocities tend to have a lower hydraulic resistance due to their growth form (Dawson & Robinson 1984, Dawson 1988, Pitlo & Dawson 1990). Water velocity does not just affect macrophytes directly but determines the nature and extent of sedimentation (Dawson 1988). *Ranunculus* species have been found in many studies to be strongly correlated with particular sediment types (Haslam 1978, Brian 1983, Purseglove 1989), though Edwards & Owens (1960) found no correlation between species present and substratum type.

Two questions are explored in this chapter. Firstly, although it is known that disturbance by cutting increases the growth rate of *R. penicillatus* subsp. *pseudofluitans*, it is not clear whether or not this positive response continue to occur as the intensity of disturbance is increased. Secondly, although most studies show *Ranunculus* species to be strongly correlated with sediment type there is no experimental evidence to show whether this is due to the effect of sediment *per se*, or whether it is a reflection of the association of particular sediment particle sizes with particular water velocities.

4.2 Effects of Repeated Cutting on *Ranunculus* Growth

4.2.1. Methods

The experiment was carried out the River Rye near East Newton in North Yorkshire (NGR SE 642803). The Rye is a limestone river in the north of England. Anecdotal evidence suggests that *Ranunculus* species were either absent or much less abundant fifty years ago (A. Storey, pers comm. 1989). Parts of the upland area of the North York Moors form a significant proportion of its catchment area and there is consequently considerable seasonal variation in flow rates (National Rivers Authority unpublished data 1988). In 1757 Rev. John Wesley reported in his journal that the Rye near to this site had no above-ground flow in July of that year, which he described as 'the hottest I ever knew in England' (Wesley 1757). Such low flow-rates have not been observed in recent years. *R. penicillatus* subsp. *pseudofluitans* and *R. fluitans* grow at this site - other species and environmental conditions are described in Appendix A (Site 26).

R. penicillatus subsp. *pseudofluitans* characteristically grows in clumps, i.e. several genetically identical plants not physically connected but rooted at approximately the same place in the river bed. The site was visited four times (22 March. 28 April, 8 June and 31 July 1990). The area and volume occupied by each clump was estimated on each occasion, and the biomass was measured for the cut clumps on the first three occasions, and for both clumps after the final cut. Area was estimated from the length × width of the clump and volume was estimated from the area × height of the clump. Although the biomass of the cut plants could be directly measured, the biomass of the uncut clumps obviously had to be estimated. Figures 4.1 and 4.2 show the biomass of all the cut clumps regressed against the volume and against the area of the clumps. Although the volume of the clump is a statistically significant predictor of the biomass (r^2=33%, P<0.001), the clump area gives a better correlation (r^2=50%). This is probably because the height of a clump is as heavily influenced by the water depth at the time of measurement as well as by as the actual quantity of plant material present. Accordingly the results discussed below are presented on a clump area basis.

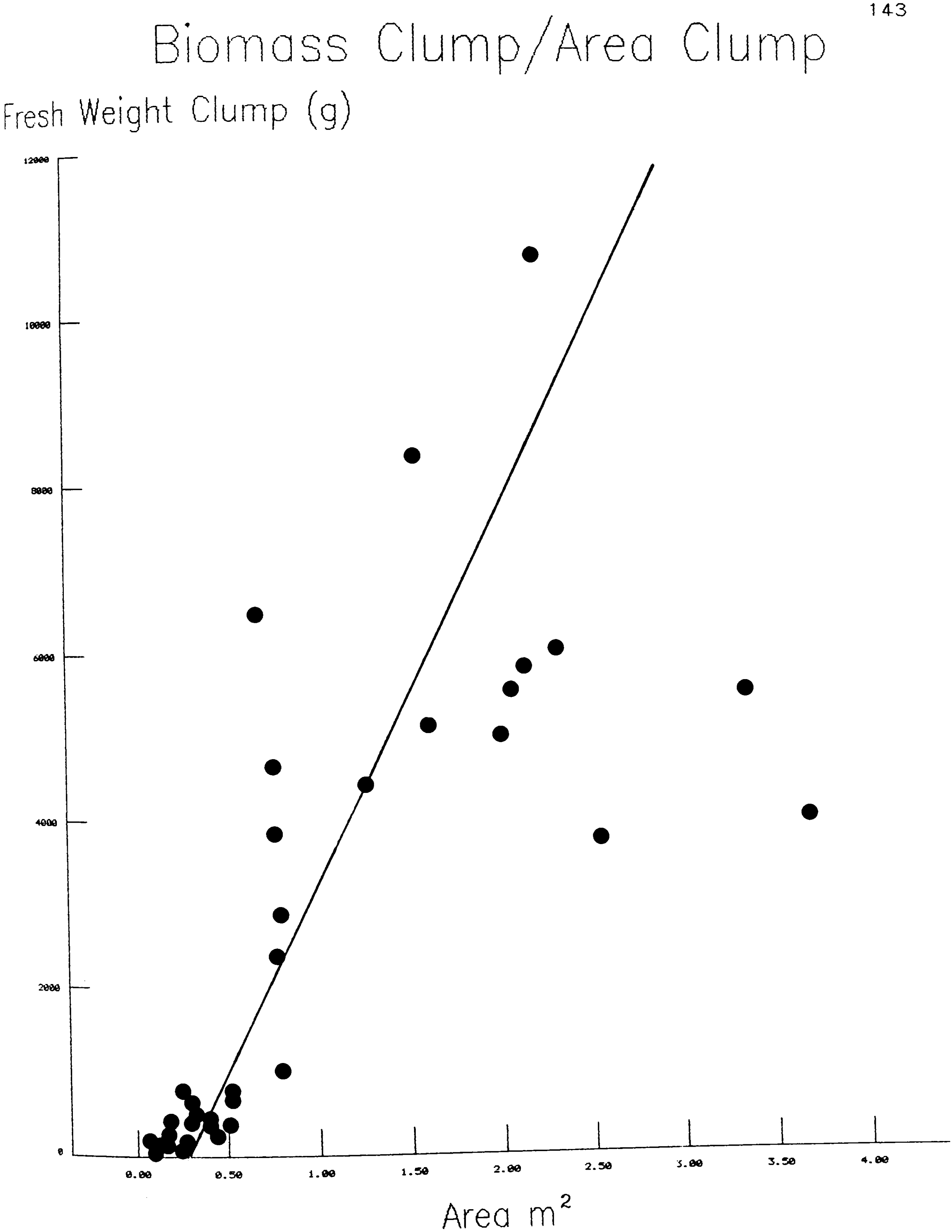


Figure 4.1 Fresh weight of *R. penicillatus* subsp. *pseudofluitans* clump regressed against the area of the clump. The line is the line of best fit. r^2=49.8%, P<0.001.

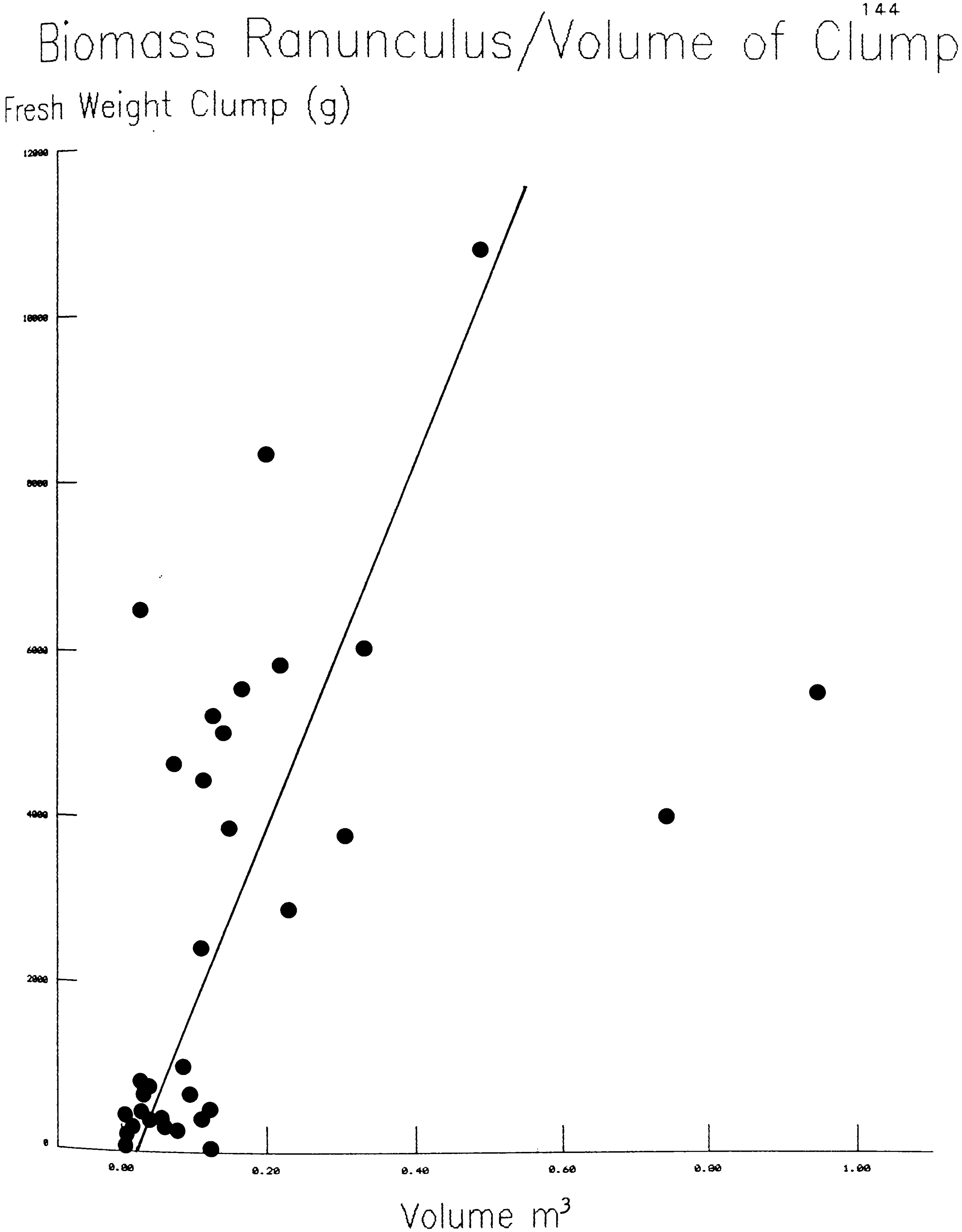


Figure 4.2 Fresh weight of *R. penicillatus* subsp. *pseudofluitans* clump regressed against the volume of the clump. The line is the line of best fit. $r^2 = 33.1\%$, $P < 0.001$.

Statistical analysis was carried out using the computer program Minitab. Differences between mean values for the paired clumps were evaluated using a paired t-test.

4.2.2 Results

Figure 4.3 shows the mean area of the cut and uncut clumps during the experiment and the production (i.e. fresh weight per unit area, strictly the yield) of the cut clumps during the experiment is shown in Figure 4.4. There was no significant difference between the area covered by the two sets of clumps before the experiment. After the first cut, the cut *Ranunculus* showed a slight stimulation of growth, but this was insufficient to make up the difference by the time of the second cut. However, following the second cut, the *Ranunculus* that had been cut showed a marked stimulation in growth so that by the third cut its area was slightly greater than the uncut clumps (statistically, the difference is not significant).

Conversely, after the third cut there was no stimulation of growth, so that by the time of the final cut the average area covered by the cut clumps was only 58% of the area covered by the uncut clumps, and the difference in biomass between the treatments is highly significant ($T=3.35$, $P=0.012$). In the period up to the third cut, the cut clumps were increasing their area at approximately twice the rate of the uncut clumps, whereas following the third cut the two sets of clumps were increasing their area at the same rate (0.04 m^2 day^{-1}).

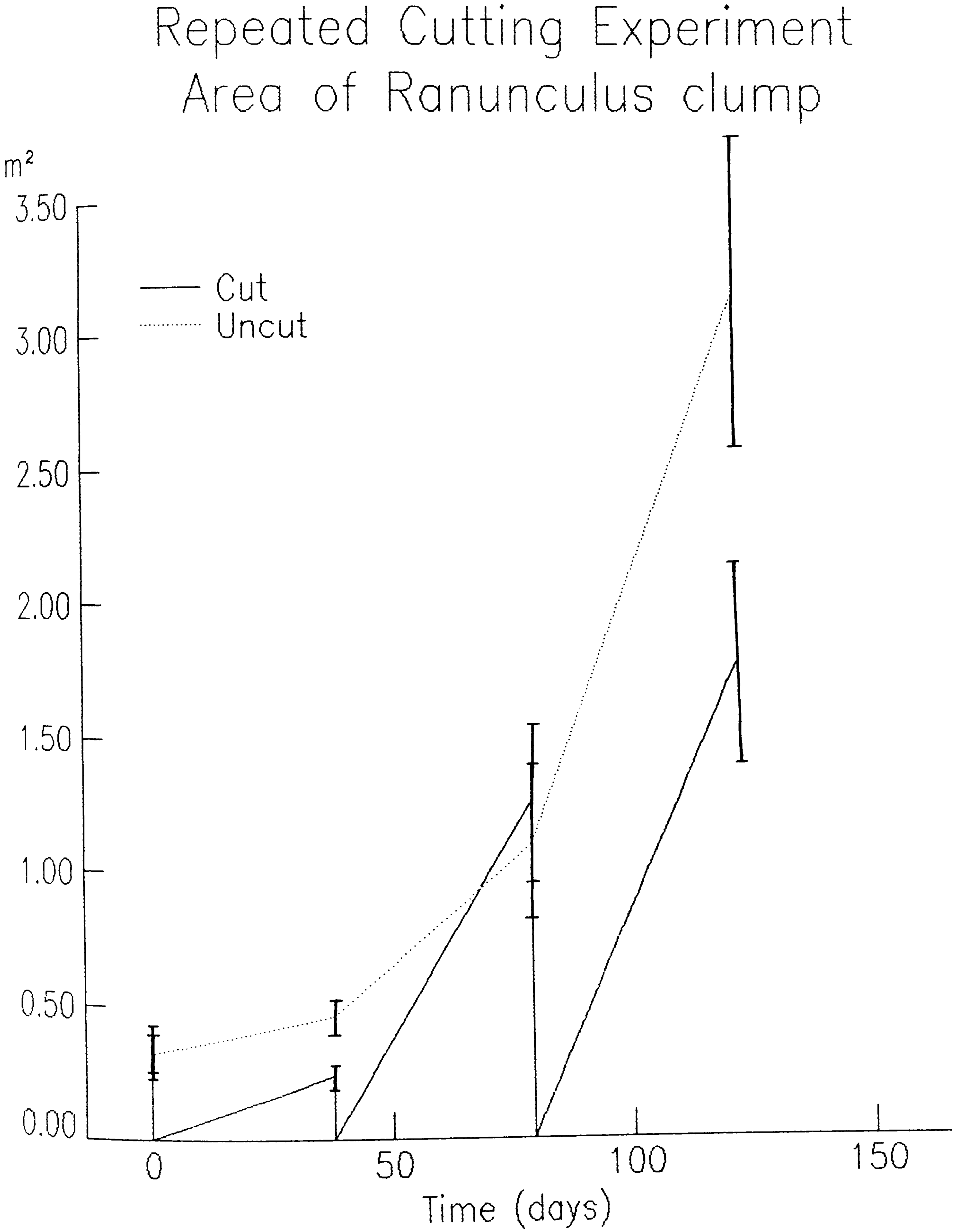


Figure 4.3. Mean area occupied by cut and uncut *R. penicillatus* subsp. *pseudofluitans* clumps. Bars represent ± 1 standard error.

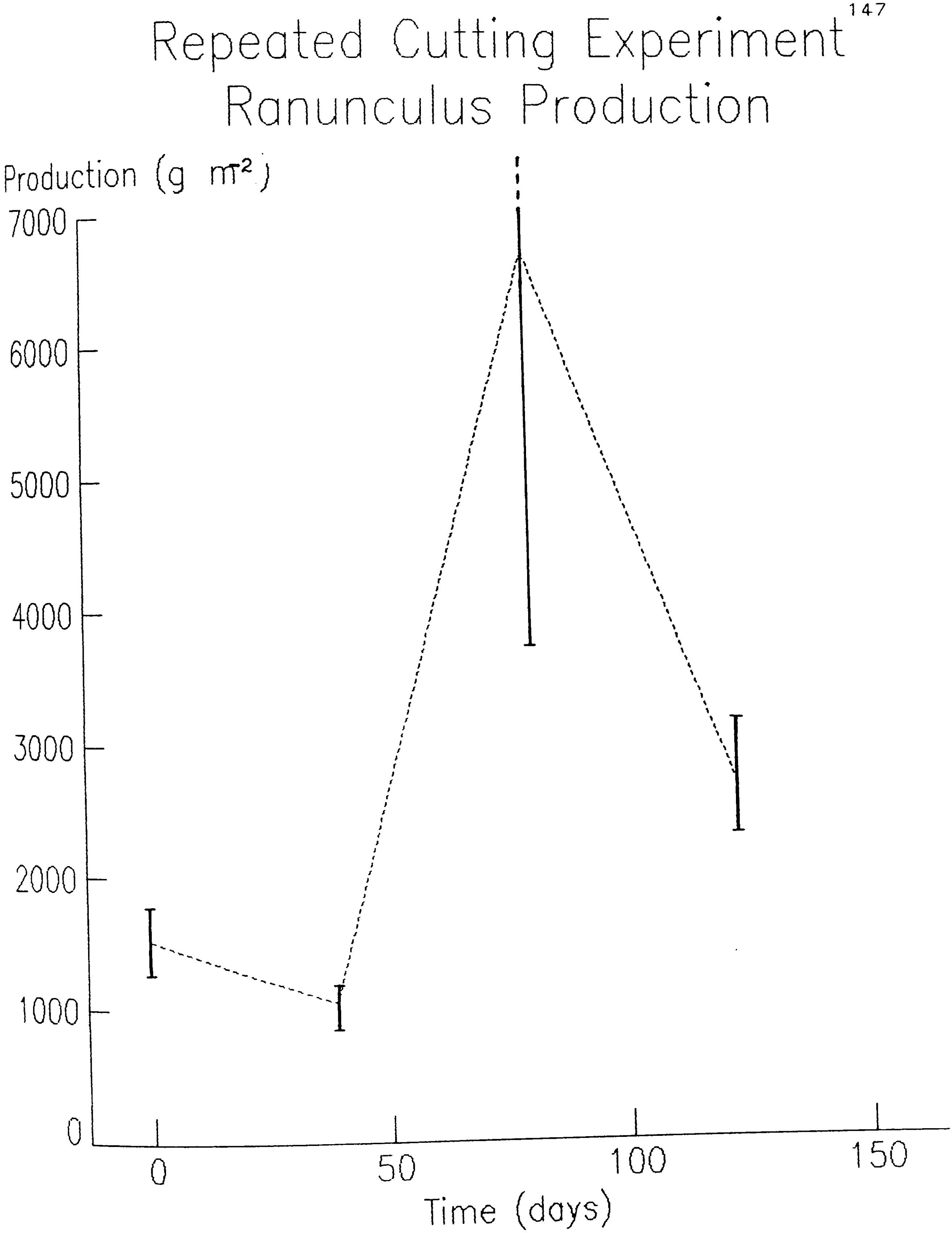


Figure 4.4. Production (g fresh weight m^{-2}) of cut *R. penicillatus* subsp. *pseudofluitans* clumps. Bars represent ± 1 standard error.

4.2.3 Discussion

Ham *et al.* 1982 showed that *Ranunculus* responds to cutting with increased growth, probably due to the increased rate of resource supply (particularly carbon) caused by the increase of water velocity brought about by the removal of the plants and also a decrease in self-shading. These data are in agreement with their findings and provide a more accurate picture of the effect of cutting on *R. penicillatus* subsp. *pseudofluitans* growth due to measuring the growth of individual clumps. They also suggest that if the intensity of disturbance is increased beyond a critical point the *Ranunculus* is no longer able to respond with increased growth, but instead shows decreased growth. This may be due to some factor such as an exhaustion of stored carbohydrate, or it may be that some other mechanism may be responsible.

In June and July *Ranunculus* growth rates tend to start to decrease, following the onset of flowering (Westlake *et al.* 1970, Dawson 1976). The results here are not due to that, because the comparison is between the relative growth rates of the cut and the uncut clumps, and because if a *Ranunculus* clump is cut as it comes into flower this normally delays recession rather than advances it. In many chalk streams, growth at this time of year is frequently slowed by the stress due to low current velocity, in this case the velocity was in excess of 0.5 m s^{-1} at the time of the final harvest. However the possibility that the exact results obtained were in part due to the date of the cut can not be excluded.

Within the terms of plant strategy theory, the results indicate that although disturbance-tolerance is an important part of the strategy of *Ranunculus penicillatus* subsp. *pseudofluitans*, it is only tolerant of a certain intensity of disturbance.

4.3 The Effect of Sediment Particle Size on *Ranunculus* Growth

4.3.1 Methods

The experiment was carried out in the River Mouse in Lanarkshire at Shortshill (National Grid Reference NS 935 486). The Mouse rises in the the Pentland Hills in Lothian and so has a strong limestone influence (pH 7.8, Fox 1987). Most of the catchment is farmland and there have been occasional problems with organic pollution. The site is upstream of the Dippol which contaminates the river with mine spoilheap effluent. A full plant species list is given in Appendix B.

On 15th April 1991 approximately 40 kg of sediment was removed from the river (adjacent to a *Ranunculus* clump), dried at 95° C and weighed. The sediment was sorted into different sized particles using sieves. Living material (roots etc) was removed. These were then combined to form five types of sediment (Table 4.1).

Table 4.1. Composition of Experimental Sediments

Treatment	Composition
Control	Same Composition as original sediment.
	Gravel 56%, Coarse Sand 38%, Fine Sand 5%, Silt 1%
Fine Sand	Gravel 20%, Coarse Sand 19%, **Fine Sand 60%**, Silt 1%
Coarse Sand	Gravel 14%, **Coarse Sand 80%**, Fine Sand 5%, Silt 1%
Gravel	**Gravel 80%**, Coarse Sand 14%, Fine Sand 5%, Silt 1%
Silt	Gravel 0%, Coarse Sand 75%, Fine Sand 10%, **Silt 15%**

The particle sizes were defined as follows; Gravel > 2mm, Coarse sand 2-0.18 mm, Fine Sand 0.18-0.035 mm, Silt < 0.35 mm.

The proportion of silt was kept constant for all but the silt treatment, as this fraction contributes most of the available nutrients (Etherington 1982), so if an effect was observed that could be due to different silt proportions it would not be possible to determine if that was due to physical or chemical causes.

On 27th May 1991 the sediments were transfered to 9 cm pots. Three shoots of *R. penicillatus* subsp. *pseudofluitans*, 300 mm in length were also placed in each pot. Gravel and stones were placed on top of the sediment in the pots to prevent it being washed out by the current. The pots were placed in the River Mouse, the tops level with the river bed. Four replicate pots were used for each sediment type. To ensure that there was no difference between treatments the *Ranunculus* shoots were all pooled before planting out. Ten shoots from this pool were taken back to be weighed and dried to assess the growth during the experiment.

After 92 days, on 27th August 1991, the pots were removed from the stream. All but two pots were retrieved. In 22% of the pots the plants had failed to be established. The plants were washed, divided into root and shoot, dried at 95°, and weighed. The data obtained were assessed by single factor analysis of variance using the computer program Genstat 5 (Lane *et al.* 1987).

4.3.2 Results

The plants had increased their shoot biomass by approximately four times in the 92 day growth period. Figures 4.5 - 4.9 show the effect of the different sediment particle sizes on the various parameters measured.

For all the parameters measured, there was no significant difference between any of the sediment types. This was the case whether the data were analysed per pot (as in Figures 4.5 - 4.9) or per shoot and whether the pots with no plants in were treated as having a value of zero (as in Figures 4.5 - 4.9) or as missing values. The treatments had no effect on either the establishment or the growth of the *Ranunculus* plants.

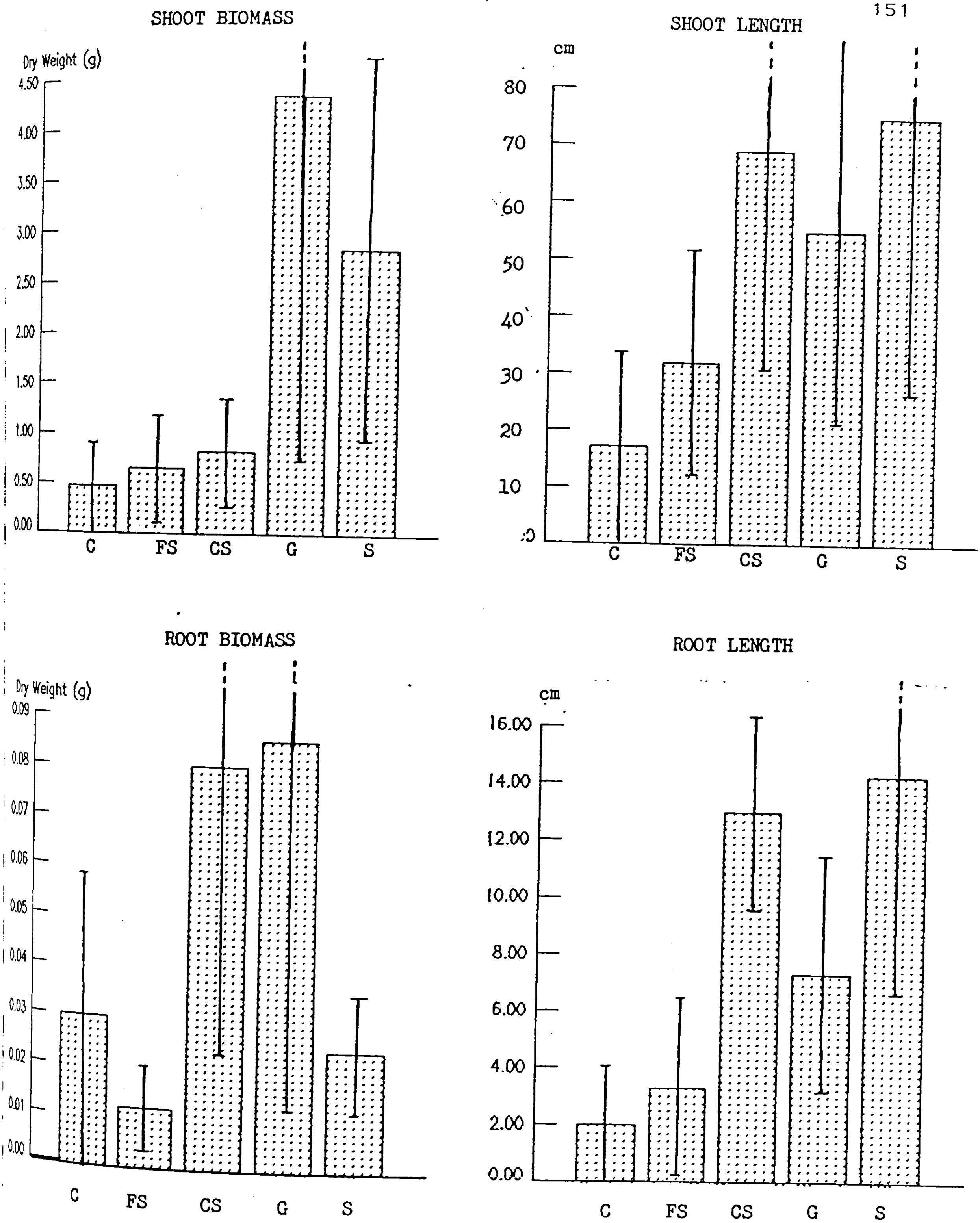


Figure 4.5 Effect of sediment particle size on dry weight (g/pot) of *R. penicillatus* subsp. *pseudofluitans* and length of shoot and root. Bars represent ± 1 standard error.
C = Control, FS = Fine Sand, CS = Coarse Sand, G = Gravel, S = Silt

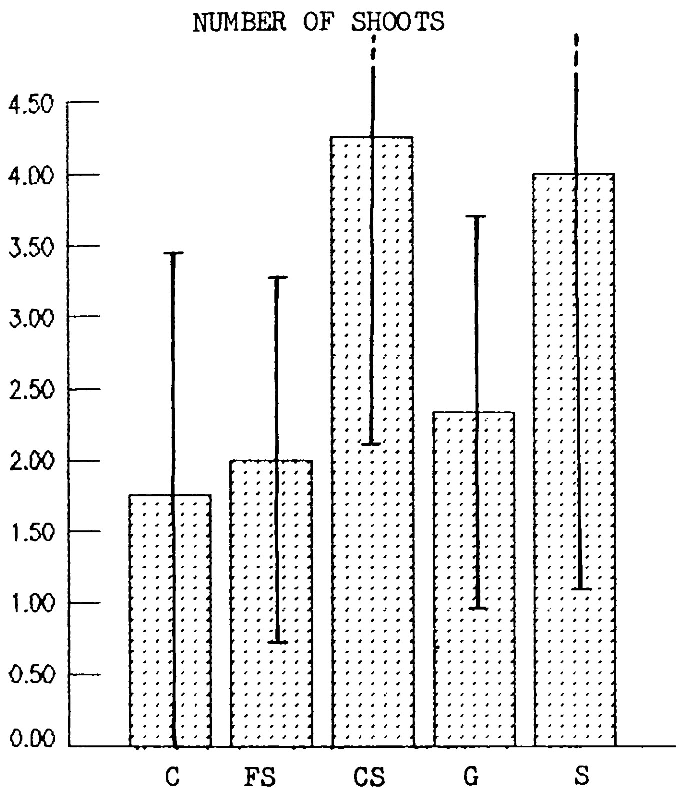


Figure 4.6. Effect of sediment particle size on mean number of *R. penicillatus* subsp. *pseudofluitans* shoots per pot. Bars represent ± 1 standard error.
C = Control, FS = Fine Sand, CS = Coarse Sand, G = Gravel, S = Silt

4.3.3 Discussion

The analysis of variance revealed that the variation within treatments (particle sizes) was greater than the variation between treatments. This indicates either that the treatments made no difference to the growth of the *Ranunculus* plants, or that the variability between different plants (presumably caused by variation in conditions at different places in the river bed) masked the effects of the treatments. Figure 4.5 shows that the mean value of the shoots in the sediment predominantly composed of gravel was greater than the values for the other treatments. However, if the raw data is examined this is seen to be entirely due to one particularly large value. For all the sediment types, if the data is carefully examined, it can be seen that the analysis of variance gives a true picture; the particle size made no difference to the growth of the plants.

However, *Ranunculus* species are clearly associated with particular sediment particle sizes (Haslam 1978, Brian 1983, Pursglove 1989). Caffrey (1990a) found that physical factors (including both flow-rate and substrate type) showed a stronger correlation with the distribution of *R. penicillatus* subsp. *penicillatus* communities in Ireland than chemical factors. Other workers have found similar correlations between sediment particle size and distribution of other macrophyte species (see, for example, Ali 1992). These data contrast with those of Edwards and Owens (1960) who found no correlation between sediment particle size and plant species.

Although such surveys indicate what factors are probably important, they do not indicate either whether a particular factor itself is causing the distribution of the species (as opposed to a second factor correlated with and causing the observed factor), or in what way the factor may influence the growth distribution of a species.

Sediment particle size may influence the distribution of species in one of four ways;

1. As a result of available nutrients being associated with fine sediments.

2. Indirectly, as a result of the texture of a river bed being determined by the velocity of the water current (Minnikin 1926, Butcher 1927, Haslam 1978), i.e. it may not be the sediment itself that influences the growth but the factor that causes the deposition of particular particle sizes. This is analogous to the distribution of some lake species which are associated with particular sediment particle sizes due to exposure to wave energy (see e.g. Keddy 1982, Weisner 1987).

3. The growth of the plant may not be affected, but its initial establishment and subsequent ability to stay in that place may be affected by the sediment particle size.

4. Directly; the particle size may have a direct physical effect on the growth of the plants.

The influence of the first factor was deliberately excluded from this experiment (all bar one of the treatments had the same proportion of the finest grade of sediment). Sediment nutrient concentrations undoubtedly influence *Ranunculus* growth and distribution (see Chapter Two), and could act in combination with the other factors associated with sediment particle size. Some experimental *Ranunculus* plants had rooted in the sediment outside the pots, and so towards the end of the experiment the artificial sediment would not have been their only source of nutrients.

Previous work has not shown whether the fourth factor (i.e. a direct physical effect of particle size) was of importance. These data indicate that, for this species at least, there is no direct effect on growth.

Cook (1966a) concluded from transplant experiments that the association of *R. fluitans* with particular substrates was due to an inability to become established and remain rooted in particular substrate types. *R. fluitans* has a different mode of root growth from the species studied here. Although a number of plants became uprooted from pots in the experiment described here, there was no significant difference in the number of shoots per pot at the end of the experiment between any of the sediment types (in fact the greatest loss of plants was from the control sediment with the same composition as that in which the *Ranunculus* was growing in the river). This indicates that for *R. penicillatus* subsp. *pseudofluitans*, in the relatively moderate flow conditions found in the River Mouse, sediment particle size probably does not influence whether a plant becomes uprooted. It is not possible to tell from these data if sediment particle size would influence the initial establishment of an unrooted fragment of *Ranunculus*. Caution must be exercised when extrapolating these data to other species and in other conditions. However, these data certainly provide no support for the hypothesis that the main effect of particle size is its influence on the ability of macrophyte species to establish and remain rooted in a particular place.

In a survey of Irish river sites Caffrey (1990a) found that water velocity was one of the most important determinants for *R. penicillatus* communities, and velocity was also shown to be an important factor in the survey described in Chapter Two of this thesis. The experiment described in Chapter Three indicated that very low velocities can act as a stress to stream communities. At high velocities it may be hypothesised that the current is an important disturbance factor and that the correlation between *Ranunculus* distribution and particular sediment types is due to the effect of velocity on sediment type. The data from the experiment described in this chapter are consistent with that hypothesis.

4.3.4 Conclusions

High water velocities have a direct effect on macrophyte growth, removing pieces of the shoot and uprooting whole plants, perhaps especially plants in sediments with particular textures. They also have an indirect effect on the sediments, larger particles being found in faster flows. The majority of *Ranunculus* species are associated both with intermediate flow-rates and intermediate sediment particle sizes (Haslam 1978). The data from this experiment indicate that the correlation with particular particle sizes is not a direct effect of the particles themselves, but is more likely to be the influence of disturbance caused by high water velocities.

5. THE RESPONSE OF *RANUNCULUS PENICILLATUS* SUBSP. *PSEUDOFLUITANS* TO STRESS COMBINED WITH DISTURBANCE

5.1 Introduction

One of the fundamental assumptions of strategy theory is that a habitat with severe stress together with severe disturbance will be too harsh for the survival of living organisms (Grime 1977, 1979). Areas with no vegetation frequently fall into just that category, for example some paths that suffer from both stress from nutrient deficiency and disturbance from trampling. Either factor on its own is not sufficient to prevent growth - such paths can sometimes recover if fertilised (Tallis & Yalden 1983) and there is vegetation present in the undisturbed area adjacent to the path.

A number of authors have argued that some organisms do exhibit a high stress, high disturbance strategy, as detailed in Chapter One (Farmer & Spence, 1986, Kautsky 1988, Loehle 1988, Pugh & Boddy 1988). With the exception of the examples cited by Loehle (which, as outlined in Chapter One, are arguably not examples of high stress plus high disturbance), the examples are drawn from organisms other than terrestrial plants. This probably illustrates the necessity to derive different criteria for placing aquatic plants, fungi, etc in strategy types. These problems illustrate the difficulty of proof from inductive reasoning from a multitude of examples - no matter how many examples can be produced of species and habitats which do not exhibit a high stress plus high disturbance strategy, there is always the possibility of another example which may fit into a high stress/disturbance category.

An alternative approach is to attempt experimental manipulation of plant communities. Campbell (1988) found that under artificial gradients of stress and disturbance the vegetation behaved consistently in respect to the predictions of strategy theory, including the elimination of vegetation in the high stress plus high disturbance treatment.

In this chapter the effects of high stress together with severe disturbance are investigated in two field experiments on riverine *Ranunculus* communities. *R. penicillatus* subsp. *pseudofluitans* has the largest ecological amplitude of the sub-genus *Batrachium* (Chapter One) and was selected for this study - if any taxon were to exhibit tolerance of high intensities of stress and disturbance it probably would be that one.

Both experiments investigate the effects of disturbance in the form of cutting to *Ranunculus* plants in stressed habitats. In both cases the stress is in the form of pollution; in the first experiment it is moderately severe and in the second the pollutants are at higher concentrations. The methods and results of the two experiments are described consecutively and then the results of both are discussed together.

5.2 Methods and Results

5.2.1 Experiment One (Gogar Burn): Site Description

The experiment was carried out in a moderate to highly polluted stream near Edinburgh (Gogar Burn at Suntrap; NGR NT 171706). Gogar Burn has a mean phosphate concentration of 0.1 mgP l^{-1}, a mean ammonium concentration of 0.26 mgN l^{-1}, and a conductivity of 470 µS cm^{-1}. The stream has an average flow rate of 0.44 m^3 s^{-1} (Forth River Purification Board 1986-89, unpublished data) and is 1-2 m in width by 0.2-0.5 m deep.

Methods

Ten pairs of similar-sized clumps of *R. penicillatus* subsp. *pseudofluitans* were selected. The area occupied by and height of the clumps was measured on 13 March 1990, and then one half of each pair was cut, removing the entire above-ground biomass. As Figure 5.1 shows, there was no significant difference in the size of the clumps before cutting. After 148 days on the 8th August 1990 eight of the ten clumps were found again and their area, volume and biomass were measured. The amount of plant material was too great to permit dry weights to be measured, so fresh weights were measured after centrifuging at 1400 r.p.m. for approximately one minute (as was the plant material from the initial cut in March).

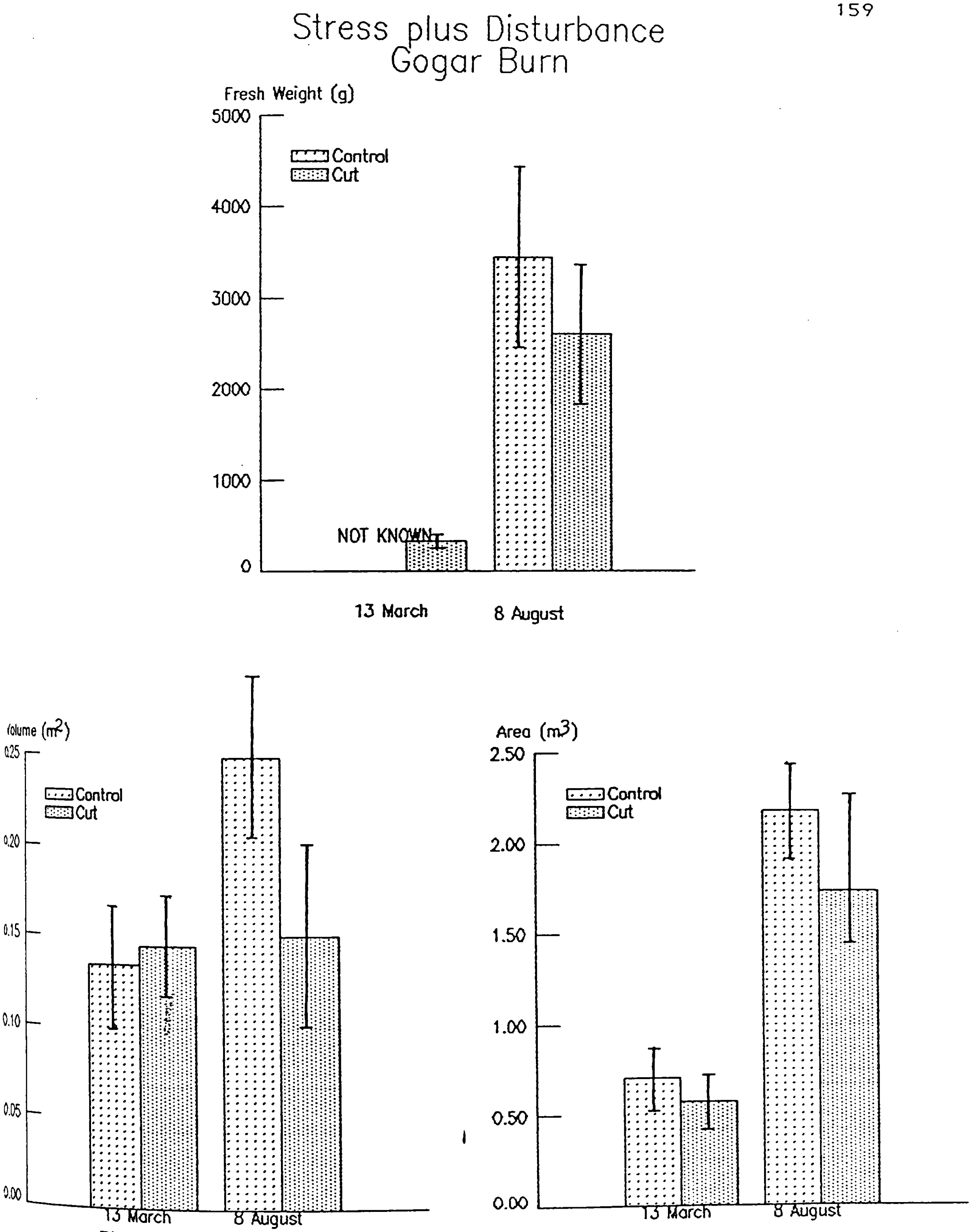


Figure 5.1. Effect of cutting on biomass, volume and area of clumps of R. penicillatus subsp. *pseudofluitans* in Gogar Burn on 13 March and 8th August 1990. Bars represent ± 1 standard error. The fresh weight of the uncut clumps could not be weighed on 13 March (for obvious reasons).

Results

The cut clumps showed an increase in biomass during the growing season in excess of seven times. There was no significant difference (paired t-test) between the clumps that had been cut and those left uncut, in the area, volume or fresh weight of the clumps (Figures 5.1, 5.2, 5.3). However it is notable that the mean values for the cut plants, for all three parameters measured, are less than that of the uncut (control) clumps.

5.2.2 Experiment Two (West Beck): Site Description

The West Beck is part of the headwaters of the River Hull in Humberside, which is designated as a Site of Special Scientific Interest by English Nature (previously NCC), as 'the most northerly chalk stream system in Britain' (NCC 1988). The experimental site was at Wansford, immediately downstream of the discharge from Wansford Trout Farm (National Grid Reference TA 053 563). The flow is somewhat greater than at Gogar Burn (mean 1.02 m^3 s^{-1}, NRA Unpublished Data 1989), and the stream is about 5 m wide and 0.5 - 1.0 m deep.

The invertebrate fauna of the stream has been described by Whithead (1955). In the past decade the vegetation at this site has been studied both by the National Rivers Authority (previously Yorkshire Water Authority) and Hull University (Carr 1988, Carr & Goulder 1990). In some years the site was dominated by *R. penicillatus* subsp. *pseudofluitans*, whilst in others the macrophytes were smothered by a dense cover of the green filamentous alga *Vaucheria*. The plant species present in 1991 are given in Appendix B. Wansford Trout Farm consistently exceeds its discharge limits in regard to phosphate, and was successfully prosecuted for this by Golden Hill Anglers in 1991. The water and sediment chemical composition at the Wansford site are shown in Table 5.1.

Table 5.1 Water and Sediment Chemical Composition of West Beck at Wansford.

	Element	Carr (1988)	YWA 1984-86, 1982
WATER	PO_4-P	0.048-0.107	0.076
(mg l^{-1})	NH_4-N	0.426	0.152
	NO_3-N	4.49	7.2
	NO_2-N	0.096	0.081
	pH	7.7	8.0
SEDIMENT	C	3.77	
(%)	N	0.37	
	C/N	7.43	
	Organic		15.14
	Total P		0.01-0.3

YWA data are unpublished data from the Yorkshire Water Authority (now the Yorkshire Region of the National Rivers Authority).

Carr (1988) found that orthophosphate and alkaline phosphatase activity concentrations increased downstream of the fish farm outfall. Algae (*Selenastrum cupricornutum*) grew faster in water from downstream of the fish farm, compared with growth in water from upstream of the fish farm. Experiments were also carried out on *Ranunculus* shoots.

Shoots from downstream of the farm demonstrated greater extension growth when cultured in the laboratory, compared with shoots from upstream. *Ranunculus* shoots from downstream showed greater extension growth when grown in upstream water than shoots from upstream. The downstream shoots had higher concentrations of tissue phosphorus and nitrogen. This implies that the shoots from downstream of the fish farm were able to take up enhanced phosphate (and nitrogen) and, when not shaded by algae, utilise the nutrients for growth (Carr 1988, Carr & Goulder 1990). However, these data must be interpreted with caution as the upstream and downstream sites had experienced a differential cutting regime prior to the experiment which could provide an alternative explanation for the differential growth.

Methods

On the 3rd June 1991 *R. penicillatus* subsp. *pseudofluitans* plants were taken from a ditch about 100 m south of the West Beck (National Grid Reference TA 049567), cut to 33 cm length and pooled in a tank. Three shoots were placed in each of twenty 9 cm pots, which were then filled with sediment from the experimental site. Ten pots were placed in the river as they were, and ten had the shoots cut level with the top of the pot. The pots were buried so that the top of the pot was level with the river bed. A similar procedure was carried out upstream of the fish farm but these pots were apparently removed from the river before the end of the experiment.

After 70 days on 13 August 1991 the pots from the downstream site were removed from the river, the number of shoots and the length of the roots and shoots were measured on site, and the plants were taken back the laboratory to be dried at 95° C and weighed.

Results

Only 13 pots (65%) were found in August, and in 54% of those the plants had failed to grow or remain rooted, presumably due to the polluted nature of the site. The plants that had grown showed an average increase in shoot length of 475%. The effects of cutting on shoot and root length, biomass, and number of shoots are shown in Figures 5.2 and 5.3. The biomass and number of shoots (Figure 5.2) is calculated both taking the pots which had no plants in as zero values (i.e. assuming the lack of survival was an effect of the pollution) and taking those data to be missing values and excluding them from the calculation (i.e. assuming the lack of survival was due to another factor).

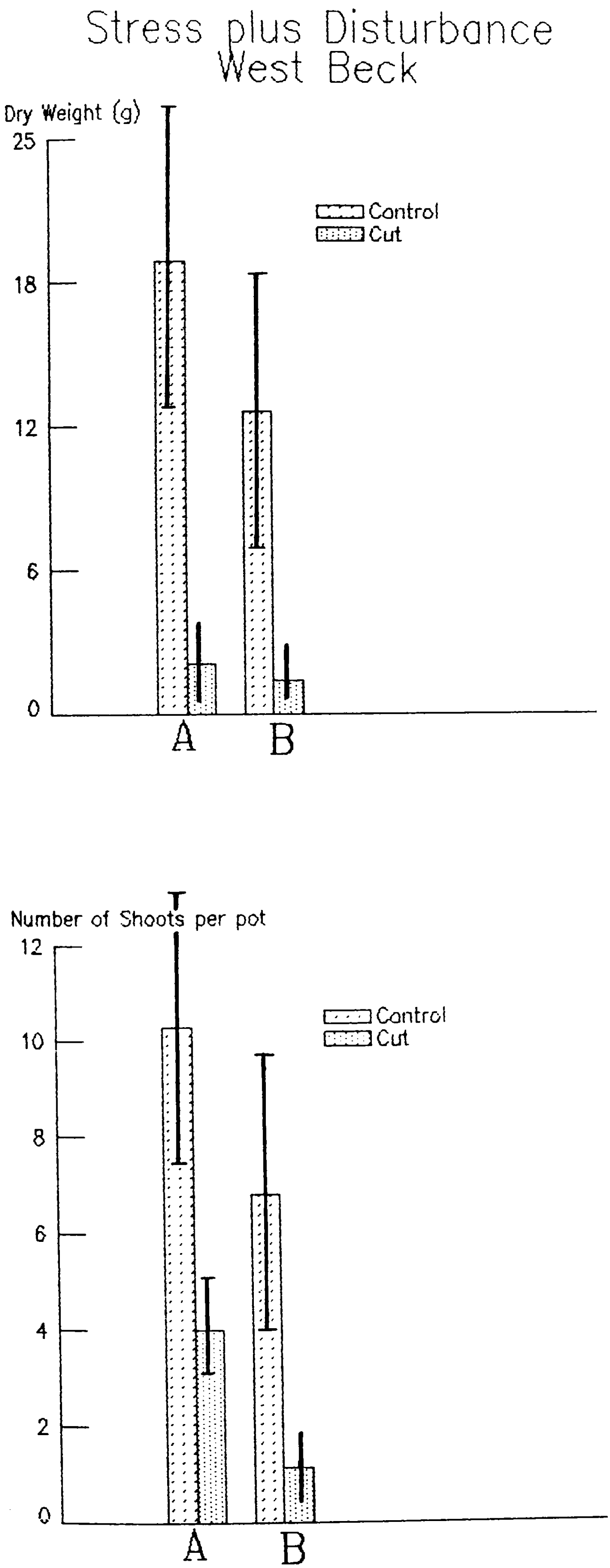


Figure 5.2. Dry weight and number of shoots of control (uncut) and cut *R. penicillatus* subsp. *pseudofluitans* plants after 70 days in the West Beck. 'A' represents the biomass if the plots with no plants in are excluded from the analysis (control n=4, cut n=2), 'B' if these are taken as zero values (control n=6, cut n=7). Bars represent ± 1 standard error.

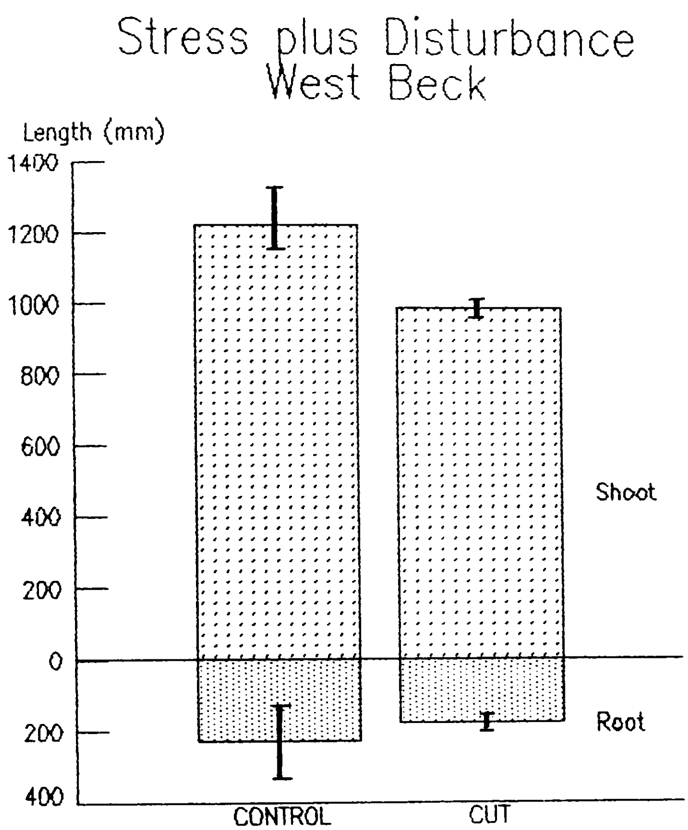


Figure 5.3. Length of control (uncut) and cut *R. penicillatus* subsp. *pseudofluitans* shoots and roots after 70 days in the West Beck. Bars represent ± 1 standard error.

Although the mean values of the cut shoots was less than the uncut (control) shoots for all the parameters measured, the difference was not statistically significant (t-test). However, this is almost certainly due to the fact that only two pots containing plants were recovered, in the cut treatment. This is particularly evident in the dry weight data. Every single one of the control dry weights was at least twice as large as the largest cut dry weight and if the pots with no plants in are taken to be true zero values then t=2.36, p=0.06. As the 95% significance level is essentially arbitrary, 94% may be taken to be close enough to indicate a real effect, particularly bearing in mind the fact that the mean dry weight of the uncut plants was over twenty times greater than the dry weight of the cut plants.

5.3 Discussion

When *R. penicillatus* subsp. *pseudofluitans* is cut in a 'healthy' chalk stream it responds with an increase in growth (Ham, Wright & Berrie 1982, Chapter 4). The data presented in this chapter show that in moderately polluted streams this disturbance-tolerance is lost, and when more severely stressed the cut plants not only fail to make up the growth of the undisturbed plants but show a reduction in growth.

In the West Beck the *Ranunculus* plants were stressed by a dense covering of *Vaucheria* algae and shading from other macrophytes (indigenous *R. penicillatus* subsp. *pseudofluitans*, *Callitriche stagnalis* and *Nasturtium officinale*). Further downstream *Ranunculus* is to a large extent replaced by *Potamogeton pectinatus* (see Chapter Three). The sediment there has a higher phosphorus concentration (the higher value given in Table 5.1), probably because the experimental site was until relatively recently upstream of the fish farm outflow.

In Gogar Burn the exact nature of the stress from pollution is less clear as there was no extensive development of filamentous algae observed. *Ranunculus* is able to take up and concentrate toxic heavy metals (Dietz 1972, Mesters 1990) and a variety of other substances including radionucleotides (Sculthorpe 1967). The effect of the pollution on the *Ranunculus* in Gogar Burn is more likely to have been due to other pollutants than direct phosphorus toxicity, as the concentration of phosphate was not that great (0.1 mg l^{-1}). Another strong possibility is that there was shading due to algal growth between March and August, and so stress from that source occurred but was not observed.

These experimental data conclusively demonstrate that *R. penicillatus* subsp. *pseudofluitans* cannot survive in conditions of both high stress and high disturbance. The disturbance was not particularly intense (only one cut, at the time of maximum growth rate) and the taxon has been found in more stressed conditions than either in West Beck of Gogar Burn. However when these two factors were applied together, the *Ranunculus* failed to demonstrate its normal positive response to cutting in Gogar Burn and showed a decrease in growth in the West Beck (though these were cuttings rather than established plants). These data strongly support the hypothesis that there is a trade-off between disturbance-tolerance and stress-tolerance, if one is increased the other appears to be decreased; the plant only has a finite quantity of resources.

The fact that *R. penicillatus* subsp. *pseudofluitans* fails to demonstrate a high stress/disturbance strategy does not necessarily exclude the possibility that another species may demonstrate such a strategy. Further work would have to be carried out on other species that exhibit a large ecological amplitude and thus may be exposed to high intensities of stress and disturbance simultaneously. These data certainly show that the case for a high stress/high disturbance strategy remains unproven, and support the argument on theoretical grounds that such a strategy is impossible (Grime 1979, Grime *et al.* 1988).

6. WHAT STRATEGY DO *RANUNCULUS* SPECIES EXHIBIT?

"The actual phenomena of vegetation are complicated enough... Nevertheless, it is clear that the complex of interactions between plants and their environment does lead to a certain degree of order in the arrangement of characters of the resulting vegetation. The human mind is irresistibly impelled to express this order in some systematic form [which] is indispensable as a framework into which to fit our investigations on the concrete phenomena of vegetation"

A.G. Tansley (1920)

6.1 Introduction

It is claimed that strategy theory provides exactly the sort of framework into which to fit ecological observations that Tansley described as 'indispensable' in the above quotation. It could well be argued that much contemporary ecological research consists of studies that succeed in providing answers to particular questions, but it is difficult to extrapolate the results of those studies to other, wider problems (Harris 1985). This is in part due to the lack of a general unified theory into which new data may be placed.

How far strategy theory succeeds in such an aim was discussed in Chapter One. It was concluded that the theory was now sufficiently far developed as applied to terrestrial vegetation to enable it to act as just such a broad conceptual framework, but that when applied to aquatic vegetation it was at a much more primitive stage. The central aim of the work described in this thesis has been to attempt to apply strategy theory to riverine *Ranunculus* communities, with the hope that the results gained from such a study would have wider applicability to other riverine communities.

The previous chapters have described studies designed to investigate the fundamental environmental forces acting on Batrachian *Ranunculus* communities - stress and disturbance. Species with different strategies will react to stress or disturbance in different ways. For example a stress tolerant species will respond to stress by physiological acclimation but little in the way of morphological adaptation, whereas a more competitive species will show larger morphological changes when stress occurs. Thus the degree of stress tolerance that a species (or population) exhibits may be ascertained by measuring its response to experimentally applied stress. Such a series of experiments is described in this chapter (section 6.2), and the results are used to rank four *Ranunculus* species in terms of their stress-tolerance.

Previous workers (e.g. Murphy *et al.* 1990) have assessed which strategies aquatic plants exhibit by using morphological and life-history traits which were selected *a priori*. The traits were subjectively selected by analogy with the traits used to define the strategies exhibited by terrestrial plants. The problem with such an approach is that, with a different set of stresses and disturbances present in aquatic environments, aquatic plants are likely to have evolved responses to stress and disturbance different from those of terrestrial plants. It is therefore necessary to have an objective method for deciding what traits are associated with a particular strategy by aquatic species. The studies described in this chapter attempt to follow just such an objective procedure. The strategy exhibited by each of the *Ranunculus* species was determined not by *a priori* subjectively-selected morphological and life history traits, but on the basis of the habitats in which the plants are found, i.e. if a particular species is generally found in a stressed ' [illegible] habitat it is by definition defined as a stress-tolerator. Data from the survey described in Chapter Two together with information from the literature are used to determine the combinations of stress and disturbance associated with the occurrence of each Batrachian *Ranunculus* species in river habitats (section 6.3)

In 1991 a further survey of 57 river sites was carried out to discover which traits are associated with the particular strategies exhibited by *Ranunculus* species (section 6.4). As these traits were selected objectively, they can be applied to other riverine species with confidence.

6.2 The Response of a range of *Ranunculus* species to experimentally imposed stress

6.2.1 Methods

Four Batrachian *Ranunculus* species (*R. fluitans*, *R. penicillatus* subsp. *pseudofluitans*, *R. hederaceus* and *R. circinatus*) were grown in consecutive experiments in the greenhouse at Glasgow University Botany Department. The growth of the plants was compared in two treatments; a control treatment in which the plants were exposed to full light and a stress treatment in which the plants were shaded.

The experimental set-up was essentially the same for all four species, with a few differing points of detail which are given below. The shading was supplied by four layers of muslin stapled to a wooden framework placed on top of the tanks in which the plants were growing. The cloth reduced the P.A.R. transmission by 37%; there was no preferential absorption of any wavelengths of light between at least 350 - 750 nm (tested using a Unicam SP8000 scanning spectrophotometer). With the exception of the *R. fluitans* experiment (which was carried out during the summer), natural light was supplemented by mercury vapour artificial lighting, providing 35 W m^{-2} for 16 h. At midday on a sunny day in November 1990 the total light falling on the tanks had a mean value of 228 ± 13 W m^{-2}. There was no measurable difference in water temperature between shaded and unshaded tanks.

The plants were grown in black polypropylene tanks, which measured 0.41 × 0.27 × 0.30 m, with the exception of the *R. fluitans* plants which were grown in larger polypropylene tanks (0.6 m × 0.4 m diameter). The plants were grown in sediment collected from Cumwhitton Beck in Cumbria (National Grid Reference NY 506 523) which was mixed 2 parts sediment to 1 part garden soil. A large quantity of growing medium was made up at the beginning of the series of experiments so that the same sediment composition could be used throughout.

The water in the tanks had air vigorously bubbled into it. This has been shown to encourage plant growth by increasing carbon supply (Robson 1974) and it appears to reduce epiphytic algal growth, perhaps by slowing the rate at which the algae becomes attached to the leaves. Certainly stagnant water will quickly develop a much larger algal population.

The plants were weighed before planting to ensure that there was no significant difference between the treatments. After the plants were planted out in the tanks they were left unshaded for a few days to become acclimatised to the greenhouse conditions. Then after the shading was applied they were grown for a further 50 days before harvesting. The roots and shoots were separated, dried at 95°C and weighed.

The *R. penicillatus* subsp. *pseudofluitans* plants were taken from Cumwhitton Beck in Cumbria (National Grid Reference NY 506 523; Site № 29 in Appendix B and Figure 6.4.1) on 13 December 1989. They were planted out on 15th December and the shading was applied on 18th December. 25g fresh weight of *Ranunculus* was planted in seed trays in each of 12 tanks (6 replicates of each treatment). The plants were harvested on 13 February 1990. As well as fresh and dry weights, measurements of leaf and internode length were also made. The *Ranunculus* flowered during this experiment, and the number of flowers in each tank was recorded.

R. hederaceus plants were taken from a muddy track crossed by Braeburn near Craigleith Cottage in Strathclyde (National Grid Reference NS 471 738; Site 51 in Appendix B and Figure 6.4.1) on 21st January 1991. The plants were planted out on 24th January and shading was applied on 15th February. Six pots each containing one plant were placed in each of ten tanks (five per treatment). The plants were harvested on 4th April.

The *R. circinatus* was taken from the Old Bedford River at Welches Dam in Cambridgeshire (National Grid Reference TL 471 858; Site 12 in Appendix B and Figure 6.4.1) on 15th April 1991. They were planted out on 22 April, the shading was applied on 1 March and they were harvested on 4th July. There were five pots per tank, each with one plant, and there were four replicate tanks for both treatments.

R. fluitans was taken from the River Eden at Warwick Bridge in Cumbria (National Grid Reference NY 473 565; Site 31 in Appendix B and Figure 6.4.1) on 23 May 1991. They were planted out on 24 May, the shading was applied on 16th June and the plants were harvested on 5 August. One plant of 0.5 m length was placed in each pot, and there were four pots per tank, and four replicate tanks for each treatment.

6.2.2 Results

The shading decreased the growth of the species of *Ranunculus*, i.e. it acted as a stress. The different species showed a differential response, with some species showing a greater reduction than others. The effects on shoot and root biomass are shown in Figures 6.2.1 and 6.2.2. In some cases (particularly *R. circinatus*) only a very small root biomass was measured and so these data (and the root to shoot ratio, Figure 6.2.3) must be interpreted with caution. The best indicator of the response of the plants to the applied stress is probably shoot biomass. These data are summarised in Table 6.2.1.

Table 6.2.1 Ratio Unshaded:Shaded Shoot Biomass.

Species	Ratio
R. fluitans	6.06
R. penicillatus	4.78
R. circinatus	3.85
R. hederaceus	2.50

Some morphological measurements were also made, but these could not be comparative due to the differences between the leaf form of different species (floating and submerged). The measurements are shown for *R. penicillatus* subsp. *pseudofluitans* in Figure 6.2.4. These show that shade reduced the (submerged) leaf length and internode length, but the ratio remained unaltered (the relative length of leaf length to internode length is an important taxonomic character in the group, see Chapter One). Although fewer plants in the shaded tanks flowered, this was not a significant difference. The area of unshaded *R. hederaceus* (floating) leaves was 2.5 times greater than that of the shaded leaves. The leaf length of unshaded *R. fluitans* (submerged) leaves was 1.47 times greater than the shaded leaves whilst the shoot length was only 1.17 times greater.

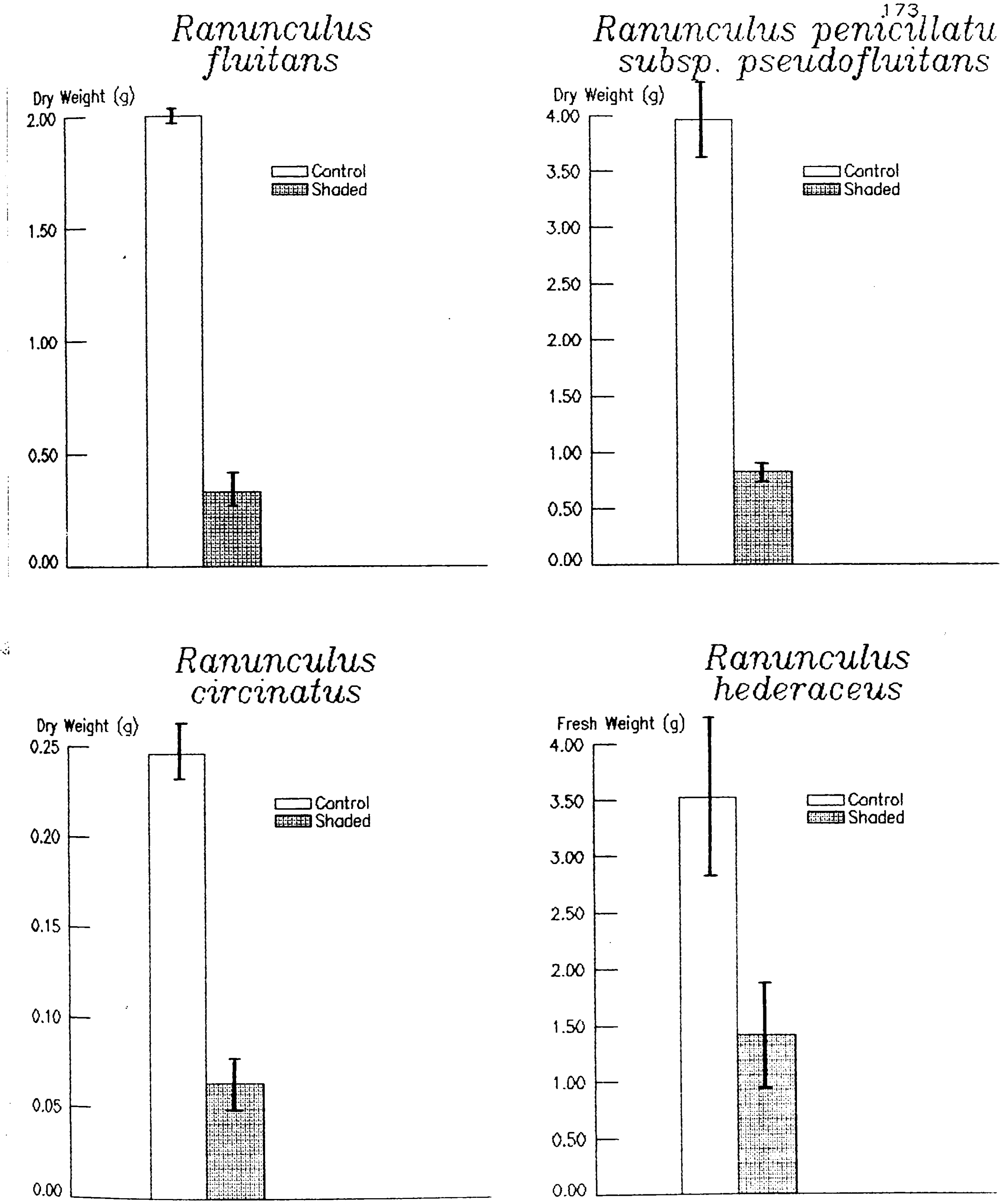


Figure 6.2.1 Effect of shading on shoot biomass of Batrachian *Ranunculus* species in greenhouse experiment. Bars represent ± 1 standard error. For details see text.

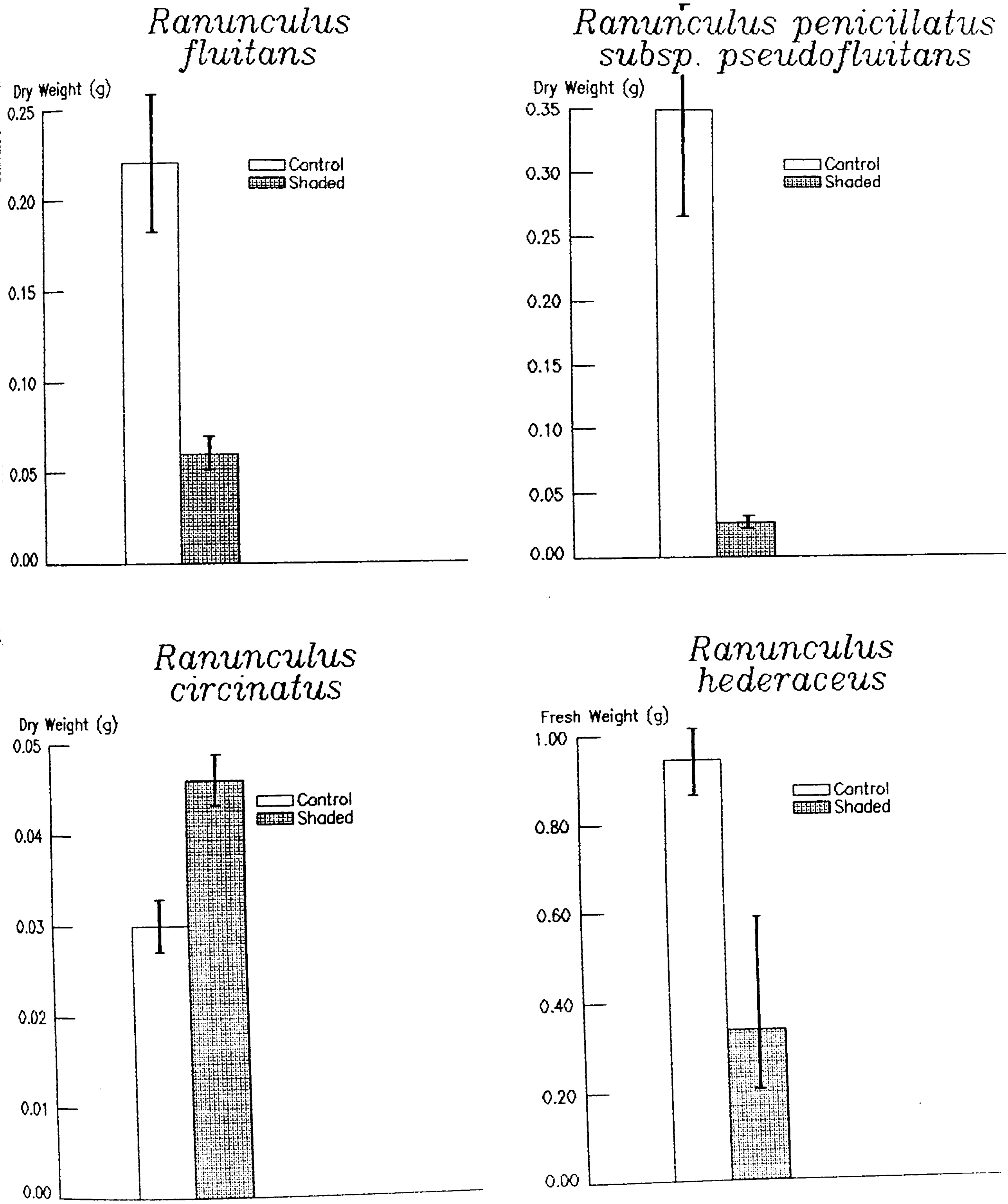


Figure 6.2.2 Effect of shading on root biomass of Batrachian *Ranunculus* species in greenhouse experiment. Bars represent ± 1 standard error. For details see text.

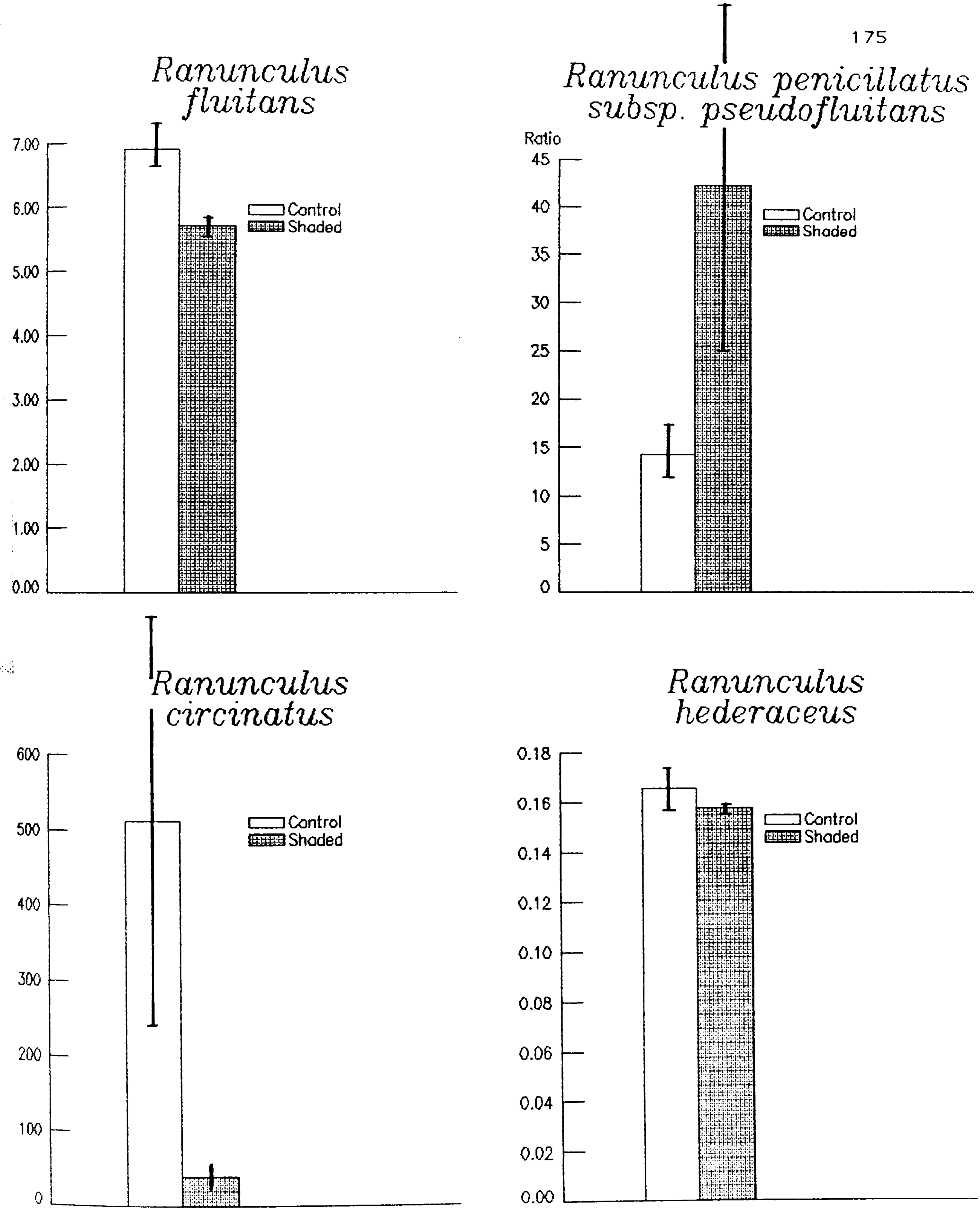


Figure 6.2.3 Effect of shading on shoot to root ratio of Batrachian *Ranunculus* species in greenhouse experiment. Bars represent ± 1 standard error. Note different scales for different graphs. For details see text.

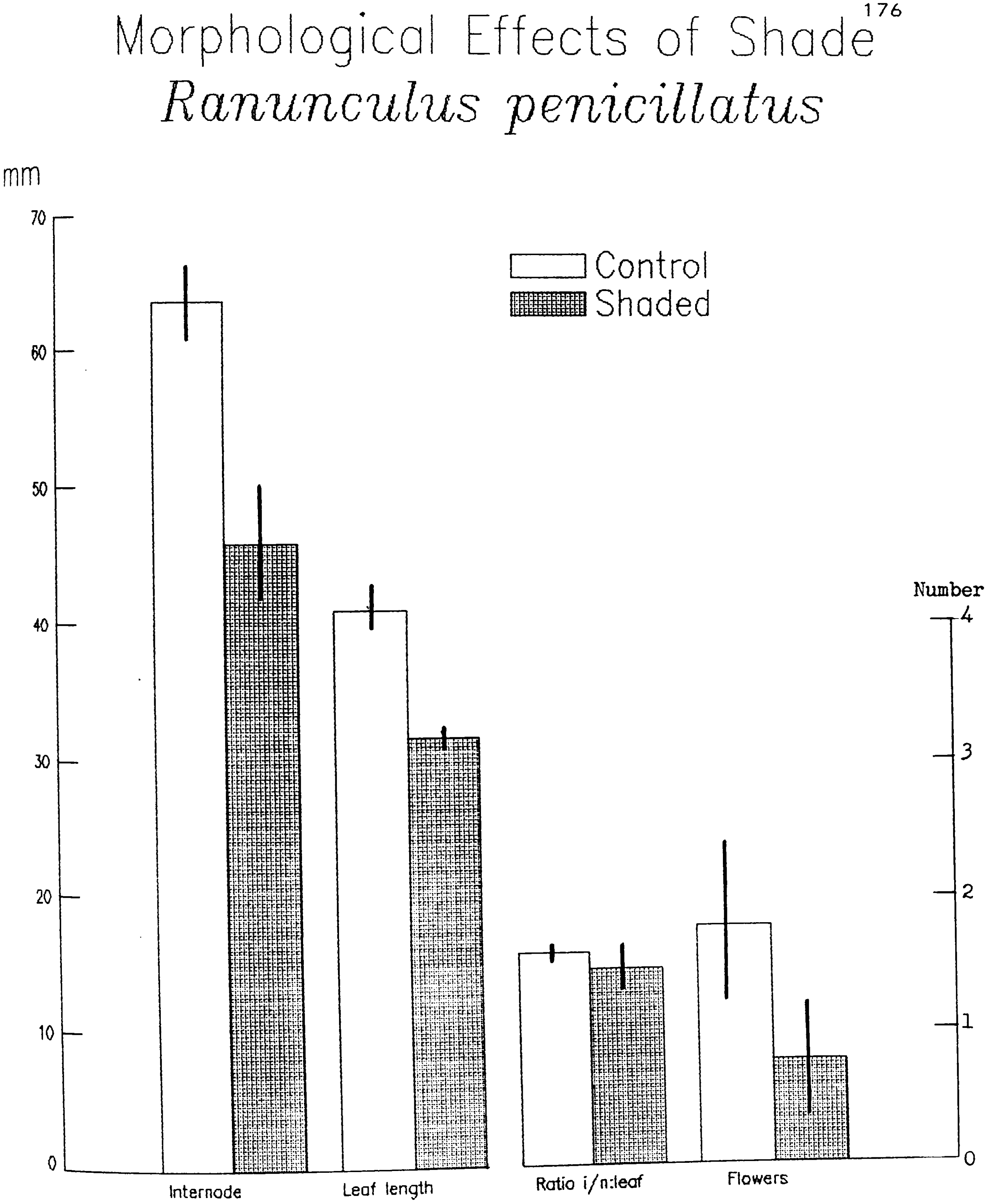


Figure 6.2.1 Effect of shading on morphological characters of Batrachian *Ranunculus* species in greenhouse experiment. The ratio and number of flower have been multiplied by 10. Bars represent ± 1 standard error. For details see text.

6.2.3 Discussion

Although the experimental design of each of the series of experiments was not precisely the same, they were sufficiently similar to enable broad comparisons to take place. From the reduction in shoot biomass, the taxa may be ranked in terms of their morphological response to shading stress;

R. fluitans > *R. penicillatus* subsp. *pseudofluitans* > *R. circinatus* > *R. hederaceus*.

Grime (1979) has asserted that stress-tolerators will respond to stress by physiological acclimation rather than morphological changes, whereas competitors respond to stress by morphological changes. That implies that the above ranking may also serve as an (inverse) ranking for stress-tolerance. As will be seen in the following section, this is the same ranking as that obtained by seeing how stress-tolerant are the habitats in which the taxa are found. This suggests both that it is likely to be a meaningful ranking, and that such a technique may usefully be used as a screening procedure to rank a wide range of species in terms of their stress tolerance.

6.3 How stressed and disturbed are the habitats in which riverine *Ranunculus* species occur?

6.3.1 Methods

The survey of river sites carried out during 1990, which was described in Chapter Two, revealed which stresses and disturbances were important in shaping riverine *Ranunculus* communities. The analysis of the data in that chapter did not make it possible to describe the sites in general terms of stress and disturbance.

In this chapter the data from that survey are re-analysed using an integrated index of stress and of disturbance for each site. The indices were calculated on the basis of a score derived from the number of stress or disturbance factors that exceeded a threshold value. The factors were selected according to which variables the initial DCCA analysis had revealed as the most important. The threshold values are given in Table 6.3.1.

Table 6.3.1 Threshold Values for Integrated Indices of Stress and Disturbance

Disturbance		Stress	
Velocity	≥50	Sediment nitrogen	u/d
σ discharge	≥0.5	Sediment potassium	≤ 40
Cut (score 1, 2)		Shade	≥ 50%
Grazed/poached		Water Phosphate	u/d
Winterbourne (score 2)		pH	≤ 6.0
		Velocity	= 0

u/d = undetectable

Factors for which no value are given are qualitative, and score is based on presence/absence.

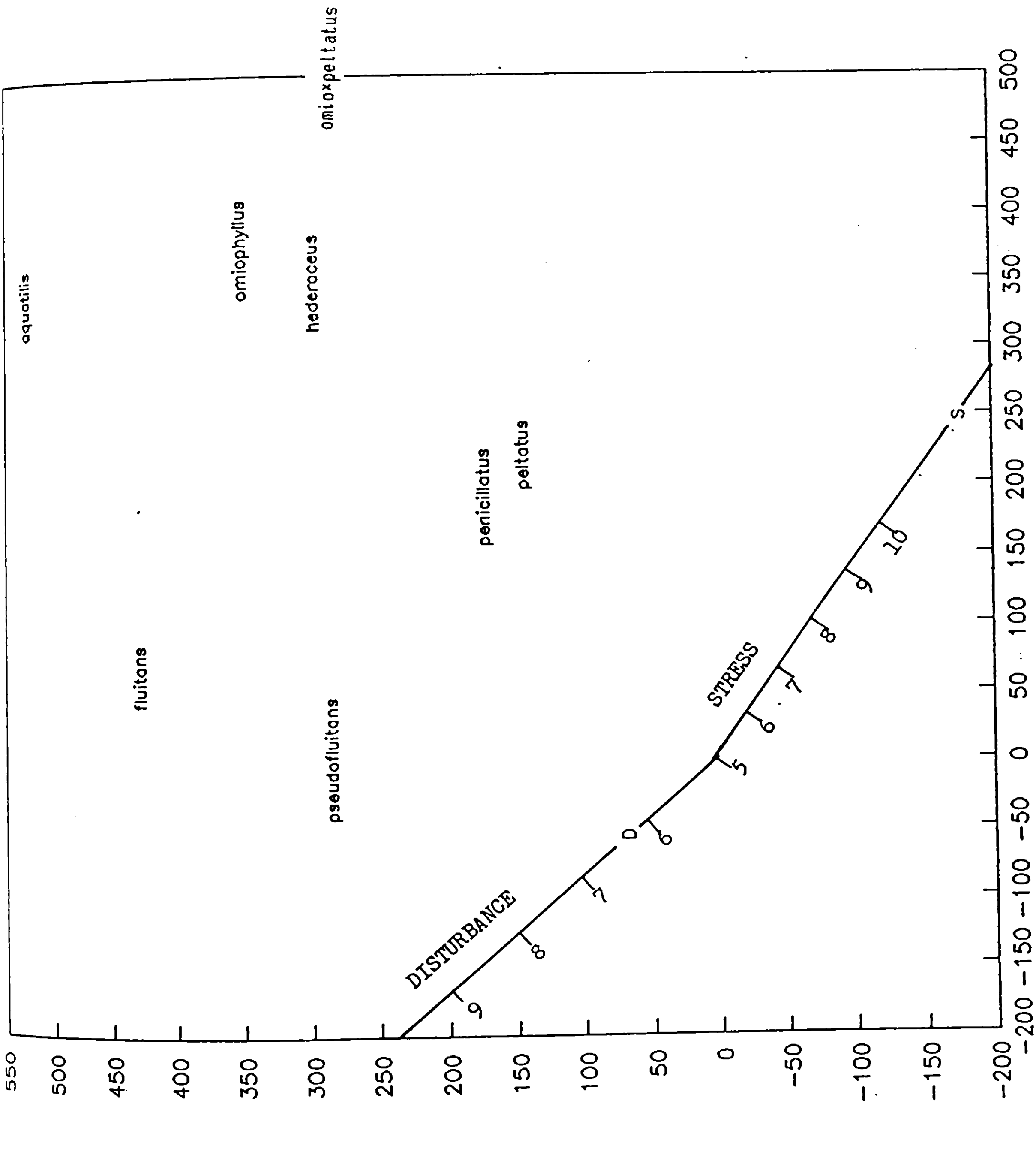


Figure 6.3.1 DCCA Ordination of 1990 River Surveys with *Ranunculus* species plotted in relation to integrated indices of stress and disturbance. For details see text.

Those indices were then used as 'passive' environmental variables in the DCCA analysis with Canoco, i.e. they did not influence the formation of the ordination axes, but were then plotted on the DCCA plot in the same way as the rest of the environmental variables (Figure 6.3.1). The *Ranunculus* species were then ranked in terms of their stress- and disturbance-tolerance according to their position along the axes of stress and disturbance.

6.3.2. Results

If a perpendicular line is dropped from the position of the taxa in Figure 6.3.1 to the axes of stress and disturbance, the taxa may be ranked from the least to greatest stress/disturbance in the habitats they grow in as follows (axis score in brackets);

Stress

R. fluitans (1)

R. penicillatus subsp. *pseudofluitans* (2)

R. aquatilis (5)

R. penicillatus subsp. *penicillatus* (6)

R. peltatus (7.5)

R. hederaceus (8.5)

R. omiophyllus (8.5)

R. omiophyllus×peltatus (11)

Disturbance

R. omiophyllus×peltatus (4)

R. peltatus (5)

R. penicillatus subsp. *penicillatus* (5)

R. hederaceus (5)

R. omiophyllus (5.)

R. penicillatus subsp. *pseudofluitans* (8)

R. aquatilis (7.5)

R. fluitans (8.5)

6.3.3 Discussion

If the data from the above section together with the data for the greenhouse experiments described in section 6.2 are taken together then a reasonable picture of the stress- and disturbance-tolerance of the *Ranunculus* taxa can be obtained. This is not a complete picture as there are not data in the above work for all the species, and some sites may not be representative of the ecological range of the species, especially *R. aquatilis* and the hybrid taxon *R. helmsii* which are based on a single site. These deficiencies may be overcome to some extent by reference to the information in the published literature regarding which habitats the taxa grow in (reviewed in Chapter One, where the references to the statements below regarding habitat may be found), and the greenhouse experimental data (Section 6.2).

Taking all this information into account, the habitat and thus the strategy of each taxon is described in turn in the following account. These are summarised in the form of a score for stress and disturbance. For taxa such as *R. penicillatus* subsp. *pseudofluitans* the scores are simply the scores from the stress and disturbance axes. For taxa which were either not covered or have an inadequate number of sites in the 1990 survey both the greenhouse experiment, and information from the literature were used to derive a score by comparison with the other species. For example *the score for R. penicillatus* subsp. *pseudofluitans* var. *vertumnus* is based on the fact that is is found growing with *R. fluitans* and *R. penicillatus* subsp. *pseudofluitans* var. *pseudofluitans*, and so will have similar scores, but is not found in the most stressed or disturbed sites where those species grow.

The scores are then used to provisionally place the species on a triangular ordination. From the method of derivation of the scores, it may be assumed that the position is fairly accurate for those species present in a large proportion of sites in the 1990 survey, with their scores directly derived from the stress and disturbance axes. The position of the other species may be regarded as more approximate, especially for those species for which their ecology is little understood.

R. fluitans

The ordination places this species as having both the highest disturbance-tolerance and lowest stress-tolerance of the Batrachian *Ranunculus* species and this is consistent both with the greenhouse experimental data (which denotes *R. fluitans* as the least stress-tolerant species) and the habitats the species are found in: large fast-flowing rivers, sometimes managed by cutting, rarely shaded or otherwise stressed.

Stress: 1

Disturbance: 8.5

R. penicillatus subsp. *pseudofluitans* var. *pseudofluitans*

As has been shown in experimental work throughout this thesis, this taxon has a high disturbance-tolerance but a low tolerance of stress. This is bourne out by the habitats it is found in as represented by the ordination.

Stress: 2

Disturbance: 8

R. penicillatus subsp. *penicillatus*

This species is associated with moderate stress and disturbance on the ordination axes. The stress score from the ordination is probably an over-estimate as although its sites tend to have a high score due to a low pH (i.e. low carbon supply) and low nutrient concentrations, they are usually in swift streams, so that although the concentration of resources in the water at its sites is low, the rate of supply is relatively high.

Stress: 5

Disturbance: 5

R. penicillatus subsp. *pseudofluitans* var. *vertumnus*

This taxon is sometimes found growing with both *R. penicillatus* subsp. *pseudofluitans* var. *pseudofluitans* and *R. fluitans*. These sites tend to be in shallow fast-flowing unmanaged rivers and streams, though it is sometimes found in still waters. Although the lack of data makes conclusions hard to draw with any certainty it appears that this taxon has slightly lower or similar stress-tolerance and disturbance-tolerance than either *R. fluitans* or *R. penicillatus* subsp. *pseudofluitans* var.

pseudofluitans.
Stress: 2.5
Disturbance: 6

R. hederaceus

This was the most stress-tolerant species in the greenhouse experiment, perhaps indicating that its score on the stress axis in the ordination as a slight underestimate. It is found in habitats with a slow or stationary current, frequently acidic and often in muddy water (shading). However its sediments tend to be fairly nutrient rich. It had a moderate score on the disturbance axis of the ordination reflecting its occurrence in habitats with moderate disturbance; some poaching and a tendency for the water level to be relatively variable.
Stress: 9
Disturbance: 5

R. omiophyllus

This species had closely similar stress and disturbance scores on the ordination axes to the above species, and the two species are sometimes found growing together. There is some evidence that it is found in slightly more nutrient deficient habitats and so it is probably slightly more stress-tolerant.
Stress: 9.5
Disturbance: 5

R. peltatus

R. peltatus has a moderate disturbance score on the ordination axis. This is probably an underestimation as the main disturbance was drought and this was frequently very severe in *R. peltatus* sites. *R. peltatus* is also the Batrachian *Ranunculus* species most frequently associated with reservoirs (which have large fluctuation in water level) and it is found in a wide physical range of habitats (which were under-represented in the 1990 survey). The sites in the 1990 survey were probably more stressed than many of the sites the species is found in, and so it should have a lower score on the stress axis.
Stress: 5
Disturbance: 7

R. aquatilis

This species is found in similar habitats to *R. peltatus*, and it has similar scores on the ordination axes. There is some evidence that it is a little less stress-tolerant (as is implied by the ordination) as it is found in shallower water and tends to be associated with richer sediments. It is probably also less disturbance-tolerant as it is not usually found in winterbournes or reservoirs.

Stress: 4.5

Disturbance: 6

R. baudotii

Although this species was present at one of the sites surveyed during 1990 (site 57) no sediment sample was taken from that site and so it was not possible to include it in the ordination. It is found in relatively open and disturbed sites, often associated with grazing by wildfowl - probably a little more disturbed than *R. omiophyllus* or *R. hederaceus*. The species is usually found in still waters, and is usually strongly associated with high salinity concentrations, which indicate a high degree of stress tolerance.

Stress: 8

Disturbance: 6

R. circinatus

R. circinatus was the other species which was not plotted on the ordination. It clearly has a high degree of stress tolerance, growing in the deepest water of any Batrachian *Ranunculus* species, the water is often very slow flowing and sometimes it has saline incursions. In the greenhouse experiment *R. circinatus* was more stress-tolerant than *R. penicillatus* subsp. *pseudofluitans* but less so than *R. hederaceus*. It is not normally associated with high levels of disturbance; as well as being found in low current velocities it is not normally grazed or cut and is usually found in habitats with a constant water level - it is thus given a lower disturbance value than any other species.

Stress: 8

Disturbance: 2

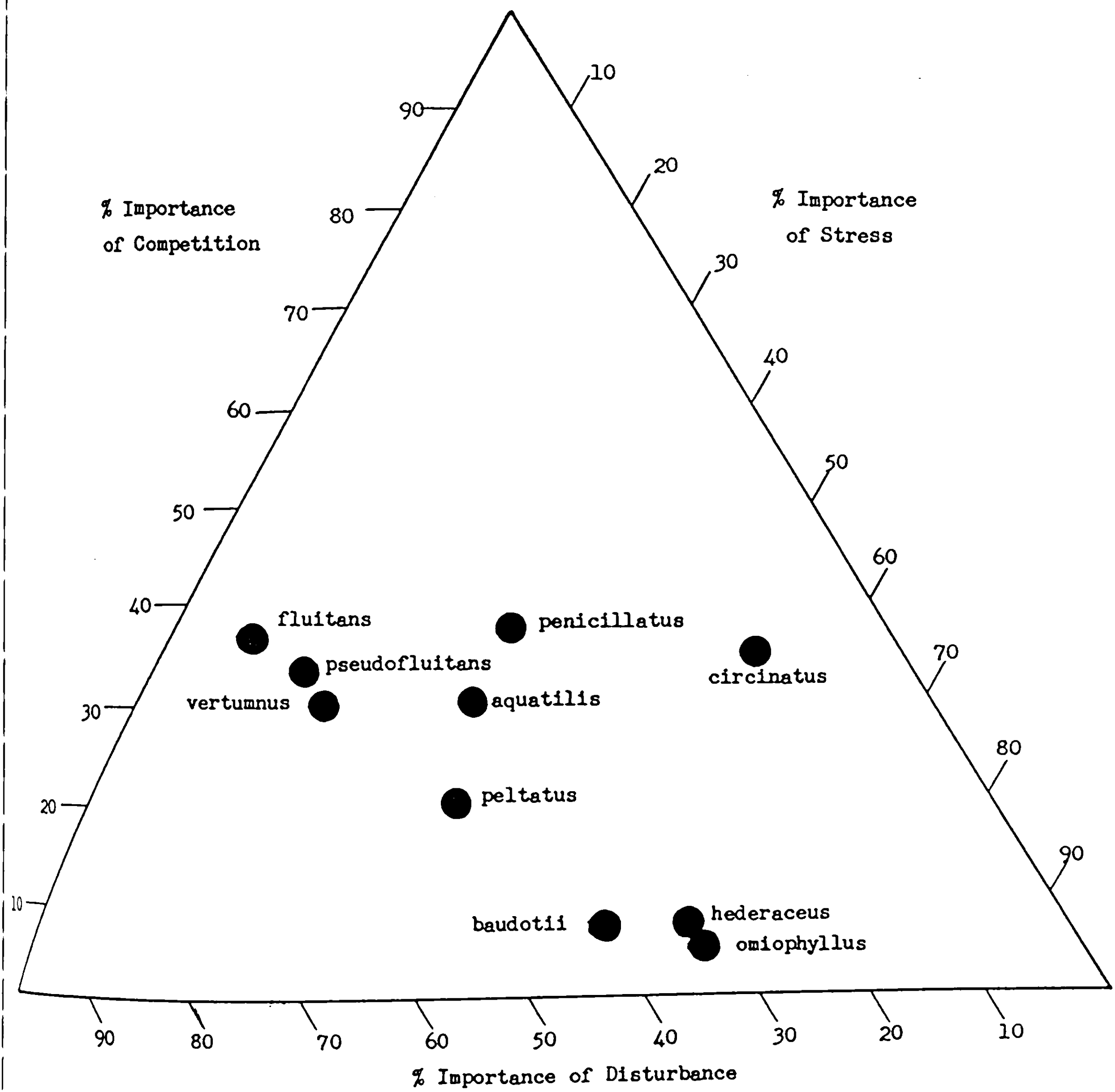


Figure 6.3.2. Provisional triangular ordination of Batrachian *Ranunculus* taxa derived from the amount of stress and disturbance in the riverine habitats that the plants grow in. For details see text.

In order to place the species on the triangle it was assumed that there was a trade-off between stress-tolerance, disturbance-tolerance and competitiveness (Grime 1974, Grime *et al.* 1988), i.e. as one increased the others decreased. The scores for competitiveness are derived entirely from the other two scores. The values used to plot the triangle are shown in Table 6.3.2, below - they are percentages derived directly from the scores, assuming a maximum possible score of 15.

The triangular ordination gives a picture of the ecology of the taxa which is mostly consistent with what might be predicted. Species which are found growing together or in similar habitats are placed near to each other on the triangle. There are two unexpected results. Firstly, even the large dominant species such as *R. fluitans* and *R. penicillatus* do not come out as being particularly competitive. However if the standing crop that these species attain in British rivers is considered (the largest standing crop in the experiment in the River Rye was 565 g dry weight m^{-2}, *cf.* 630 g dry weight m^{-2} measured by Westlake *et al.* 1972), this is quite low by terrestrial standards; Al-Mufti *et al.* 1977 found that competitive dominance occurred in terrestrial herbaceous vegetation at a standing crop biomasses of greater than about 750 g m^{-2}. This underlines the fact that all submerged habitats are to some degree stressed compared with terrestrial habitats by virtue of the shading and limits to carbon supply caused by the aquatic medium (Spence 1976, Black *et al.* 1981). More productive aquatic habitats tend to be dominated by algae rather than macrophytes (see Chapter 3).

The other unexpected feature of the triangular ordination is that no species come out as being strongly disturbance-tolerant, in spite of the positive response to cutting exhibited by *R. penicillatus* and the predilection of *R. peltatus* to grow in winterbournes and reservoirs. It is difficult to judge whether these habitats are severely disturbed compared with terrestrial habitats; is the cutting of a chalk stream a more severe disturbance than the defoliation of a *Quercus* tree by *Tortrix* caterpillars or the regular grazing of a meadow? However it is interesting to note that the Canoco ordination implies that disturbance is less important than stress (the arrow for the integrated index is smaller). It is equally possible that the failure to categorise any of the *Ranunculus* species as purely ruderals demonstrates an inadequacy of the ordination procedure, perhaps due to the fact that the integrated disturbance index was based on factors such as management some of which were less easy to quantify than the factors used in the stress index.

6.3.4 Conclusions

Table 6.3.2 Strategies of Batrachian *Ranunculus* species

	Importance of factor (%)			
Species/variety	S	D	C	Description
hederaceus	60	33	7	Stress-tolerator, with some ruderal characteristics
omiophyllus	63	33	3	Stress-tolerator, with some ruderal characteristics
baudotii	53	40	7	Stress-tolerator, with some ruderal characteristics
circinatus	53	13	33	Stress-tolerator, with a degree of competitiveness
aquatilis	30	40	30	C-S-R strategist
peltatus	33	47	20	C-S-R strategist /stress-tolerant ruderal
penicillatus	30	33	37	C-S-R strategist
vertumnus	17	53	30	Competitive-ruderal
pseudofluitans	13	53	33	Competitive-ruderal
fluitans	7	56	37	Competitive-ruderal

6.4 Which morphological attributes are associated with stress-tolerance, disturbance-tolerance and competitiveness in riverine *Ranunculus* Species?

6.4.1 Methods

In section 6.3 the strategies of the Batrachian *Ranunculus* species were defined. This was done on the basis of the habitat they occupied rather than their physical traits as it is not known which traits are associated with which strategies in aquatic plants (Grime *et al.* 1988). During 1991 an extensive survey of river sites with *Ranunculus* species present was carried out in order to determine which morphological features are associated with the various strategies exhibited with the plants.

57 sites were visited in the early summer of 1991, and twenty traits were measured on the *Ranunculus* species present. Details of the sites are given in Appendix B, and their geographical location is shown in Figure 6.4.1. The following traits were measured;

Biomass of individual shoot
Biomass of clump
Biomass of shoots rooted in 0.01 m^2
Height of canopy above river bed
Height of water above river bed
Proportion of above two
Area of canopy
Maximum shoot length
Length of submerged leaves
Width of submerged leaves when lying naturally in the water
Thickness of submerged leaves when segments pressed together
Number of divisions of submerged leaves
Length of floating leaves
Width of floating leaves
Thickness of floating leaves
Internode length
Stem thickness
Force required to break stem
Number of flowers per 0.25 m^2

Number of macrophyte species at that site (listed in Appendix B, site defined as in 1990 survey, Chapter One)).

Figure 6.4.1 Location of River Sites surveyed during 1991

The site number refers to the number on the Figure and the number in Appendix B.

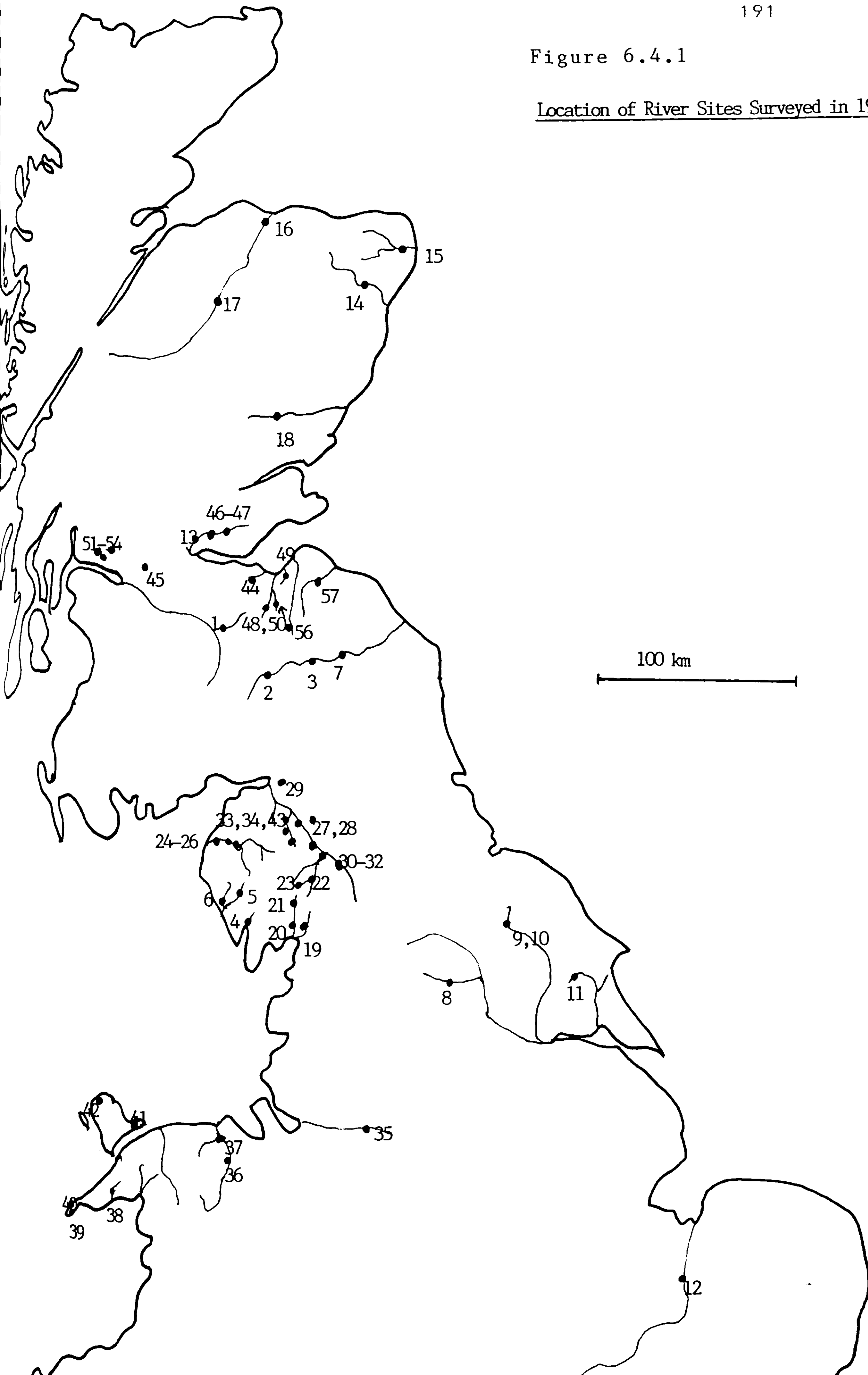
Site	Site №	National Grid Reference
River Mouse at Shortshill	1, 55	NS 935 486
River Tweed at Dawyck	2	NT 165 355
River Tweed where crossed by the A68	3	NT573 347
Kirkby Pool near Broughton in Furness	4	NY 232 862
River Esk (tributary of) at Hinning House		5 SD 123 973
River Irt at Holmrook	6	SD 082 995
River Tweed at Sprouston	7	NT 75 35
River Nidd at Pateley Bridge	8	SE 158 655
River Rye at Nunnington	9, 10	SE 642 804
River Hull (West Beck) at Wansford Bridge	11	TA 065 559
Old Bedford River at Welches Dam	12	TL 471 858
River Devon at Tilbody Bridge	13	NS 857 959
River Ythan at Ellon	14	NJ 955 302
River Uggie at Inverugie	15	NK 100 480
River Spey near Garmouth	16	NJ 344 610
River Spey at Grantown-on-Spey	17	NJ 035 268
Dean Water at Glamis	18	NO 38 48
River Bela at Whasatt	19	SD 512 801
River Kent at Levens	20	NY 495 852
River Kent at Kendal	21	SD 518 915
River Lowther at Bampton	22	NY 518 181
Haweswater Beck at Noddaw Bridge	23	NY 510 160
River Derwent at Iselgate	24	NY 165 334
River Derwent at Great Broughton	25	NY 082 313
River Derwent at Workington	26	NY 009 292
River Eamont at Broughton Castle	27	NY 538 291

Figure 6.4.1 Contd.

Site	Site №	National Grid Reference
River Eden at Langworthy	28	NY 565 333
Cumwhitton Beck at Cumwhitton	29	NY 506 523
River Eden near Cote House	30	NY 475 430
River Eden at Warwick Bridge	31, 32	NY 473 565
River Peteril near Newbiggin Hall	33	NY 435 512
River Peteril at Southwaite	34	NY 452 450
River Dane at Forge Mill	35	SJ 849 637
River Clwyd at Rhewl	36	SJ 119 099
River Clwyd at Llanerch	37	SJ 060 719
River Dwyfor at Ty-Cerrig	38	SH 496 424
Unnamed Stream at Porth Mendwy	39	SH 163 256
Naud Eiddan at Porth Oer	40	SH 168 308
Unnamed stream at Trwyn y Penrhyn	41	SH 628 802
Unnamed stream at Cemlyn	42	SH 333 930
River Peteril at Kitchen Hill	43	NY 498 342
Gogar Burn at Suntrap	44	NT 171 706
Craigend Burn at Craigend Muir (near Stepps)	45	NS 663 676
River Devon at Tilcoultry	46	NS 962 939
River Devon at Dollar	47	NS 968 969
Water of Leith at West Cairns	48	NT 087 600
Braid Burn in Edinburgh	49	NT 277 770
Rentland Burn upstream of Loganlea Resrv.	50	NT 190 620
Muddy track crossed by Braeburn, near Craigleith cottage	51	NS 471 738
Braeburn in Braeburn Reservoir (disused)	52, 53	NS 474 373
Unnamed burn by the Kilpatrick Braes	54	NS 467 742
Eddleston Water at Milkieston	56	NT 237 457
River Tyne at East Linton	57	NT 592 773

Figure 6.4.1

Location of River Sites Surveyed in 1991



All measurements were carried out on site, details of methods are given in Appendix B, the mean values for each species for each of the variates are given there as well.

Analysis of the data was carried out by stepwise multiple regression using Genstat 5. Each site was assigned a value for competitiveness, d-tolerance and s-tolerance according to the values for the *Ranunculus* species present at that site (given in Table 6.3.2), so that for example all the *R. aquatilis* sites had a C value of 30%, a S value of 40% and a D value of 30%, representing the strategy of that species. Thus, for the purposes of this analysis the assumption has been made that all the populations of one species in this survey will have a similar strategy. These strategy values were then regressed against the traits. Traits were added in a stepwise fashion until the t value indicated that the addition was not significant.

6.4.2 Results

The traits are listed in order of their importance.

Stress Tolerance

The following variates were found to be significant predictors of stress-tolerance;

Trait	r	t
Thickness floating leaves	35.90	4.6
Number of divisions submerged leaves	-3.74	-5.8
Force to break	-0.01	-3.9
Biomass shoot	-0.59	-2.65

69% of the variance was accounted for.

The data indicate that stress-tolerant *Ranunculus* species tend to have floating leaves (i.e. positive thickness floating leaves) and not to have submerged leaves (i.e. divisions zero). They also tend to have weaker and smaller shoots.

Disturbance Tolerance

The following variates were found to be significant predictors of disturbance-tolerance;

Trait	r	t
Width floating leaves	-3.91	-2.96
Force to break	0.06	2.65
Number of divisions submerged leaves	1.33	2.58
Biomass shoot	0.40	2.24

41% of the variance was accounted for.

The data indicate that *Ranunculus* species with floating leaves do not tend to be disturbance-tolerance. A tough stem is a characteristic of toleration of disturbance, and a larger shoot also confers tolerance of disturbance pressures.

Competitiveness

The following variates were found to be significant predictors of competitiveness;

Trait	r	t
Number of divisions submerged lvs	2.18	6.2
Thickness floating leaves	-23.17	-4.34
Length submerged leaves	0.036	3.04

57.7 of the variance was accounted for.

The data indicate that competitive species tend to have submerged leaves and not have floating leaves. More competitive species will tend to have larger submerged leaves - both more divided and longer.

6.4.2 Discussion

The regression indicated that by far the most important factor for stress tolerance is the thickness of the floating leaves. The least stress-tolerant species have no floating leaves, and the most stress-tolerant species have thicker leaves than the intermediate species (a summary of the data is in Appendix B). This feature is consistent with the two stresses that are most important for the above-ground parts of the plant; shading and low water velocity. Submerged leaves are shaded by the water column above them and by self-shading, and so particularly in low light intensities floating leaves will confer a selective advantage. At low water velocities carbon supply is limiting to photosynthesis in submerged leaves, whereas floating leaves can obtain their carbon from the atmosphere.

The other factors were statistically less important. The number of divisions in the submerged leaves can been seen as simply the reciprocal of the importance of floating leaves. The data showed that stress-tolerant plants also tended to be small plants. Stress-tolerant terrestrial plants also tend to have small shoots, though they do show a diversity of growth forms (Grime 1979, Grime *et al.* 1988). It is likely that the negative correlation with the force required to break the stem is a feature of smaller plants being stress-tolerators.

The regression with disturbance tolerance only accounts for forty percent of the variance. This indicates that there were probably attributes other than those measured, which are disturbance-tolerant traits. As with stress-tolerance, floating leaves are an important trait. At high water velocities the broad lamina of a floating leaf is less able to withstand the force of the water than a dissected leaf (Sculthorpe 1967). The fact that this trait is positively linked to stress tolerance and negatively linked with disturbance tolerance may be a reflection of the fact that water velocities are a stress at low values and a disturbance at high values.

The force required to break the stem might be expected to be correlated with disturbance tolerance, though whether the correlation is positive or negative is harder to predict. Does toleration occur through fragmentation when disturbed and so lead to dispersal and propagation, or do the plants resist breakage in high water velocities (See Brewer & Palmer 1990)? These data indicate that the latter is more important for these species. It may well be that sufficient fragments will be dispersed even if the plant is very resistant to breakage and that additional fragments will not be particularly advantageous, whereas the ability to withstand high water velocities without too much disturbance damage occurring may be very important particularly for the plants which grow in larger rivers (the ones which are most disturbance-tolerant, Figure 6.3.2).

The other two factors (number of leaf divisions and shoot biomass) are likely to be consequent upon the two factors discussed above, though it may be that if some biomass is destroyed (for example by cutting) a larger plant will be better able to grow again than a smaller plant, due to underground carbohydrate reserves, and so a large shoot biomass may confer a selective advantage in its own right to a plant growing in a disturbed habitat (assuming a constant root:shoot ratio).

Submerged leaves rather than floating leaves are correlated with competitiveness. This may in part be due to the role that these leaves play in stress and disturbance tolerance, though from the above data one might have expected plants growing in the absence of stress and disturbance to have both floating and submerged leaves. However it may be also be the case that a multiple layered canopy is more effective than a monolayer for suppressing competitors in this ecosystem. This is contrary to what is found in terrestrial plants (Grime *et al.* 1988), but it may be that the lower layers of leaves act in a similar manner to leaf litter in a productive terrestrial habitat, shading other species.

These data also show that competitive species tend to have longer submerged leaves than less competitive species. This may be because a larger leaf will confer a selective advantage in shading-out competitors, or it may be that larger (and more divided leaves) will be better placed to extract nutrients from the flowing water in a productive system. None of the species here came out on the ordination diagram as being very strongly competitive. Only 58% of the variance was accounted for and it may be that strongly competitive riverine plants will have traits such as an emergent morphology that are not represented within the group of species studied.

Of equal interest to the traits that are correlated with certain strategies are the traits which are apparently of no selective advantage for growing in particular combinations of stress and disturbance. It might have been expected that stress-tolerators would have small clumps (either in terms of biomass or of area), as well as small shoots, but this does not appear to be the case. Neither are stress-tolerators particularly associated with growing in deep water. It is particularly surprising that competitive plants don't appear to be particularly large - either in terms of big clumps or big shoots. All the *Ranunculus* species have a similar number of other species associated with them; there is no evidence from the data that higher levels of species diversity are associated with intermediate levels of stress/disturbance.

It is always difficult to draw firm conclusions from negative evidence, so it may be that the lack of correlations with some of the traits which were measured is of little significance, and is simply a consequence of a relatively small data-set. Some of these data may point to wider conclusions, however. The lack of correlation between competitiveness and size of clump or shoot serves as a reminder that competitiveness (the ability to acquire resources) is not the same thing as dominance (occupying a large proportion of the habitat). *R. peltatus* (a C-S-R Strategist) is clearly dominant in some sites covered in this survey, at Rentland Burn (site № 50) it has stems 1.5 m long and is virtually the only submerged species for several hundred square meters.

The above discussion shows that there is a probable biological mechanism for a selective advantage being conferred by the traits which were correlated with stress, disturbance and competition, and so it is likely that that these attributes are true strategy traits conferring a selective advantage in particular environmental conditions, rather than a statistical artifact simply caused by inter-correlations of factors related to each other by a third factor or by coincidence. That is not to say that these are necessarily the most important traits. There are many other factors which could have been measured if repeated visits were made or measurements carried out in the laboratory.

Studies of the physiological acclimation to shade and other stresses, the changes in above-ground biomass through the seasons, the reproductive biology and a larger number of replicates particularly of some of the under-represented species, together with environmental measurements at the sites would all have provided useful additional information which might have revealed other traits to be as important. Other morphological measurements such as biomass density (Duarte & Kalff 1990) might have provided additional information. However the measurements that were made did account for a large proportion of the variation in the data, and demonstrated unequivocally that substantially useful data concerning strategy traits can be gathered from measurements made on site at just one site visit.

The data indicated at least some of the strategy traits that have conferred a selective advantage on the Batrachian *Ranunculus* species in rivers in habitats with different combinations of stress and disturbance. The question then arises as to how widely applicable are these conclusions; do other riverine species share the same traits, or must one carry out a similar process for other groups of species? That question will be examined in the General Discussion (Chapter Seven).

7. GENERAL DISCUSSION

It is with much diffidence that I venture to attempt the elucidation of the Batrachian Ranunculi of Britain, for the great difficulty of the subject necessarily presses heavily on the mind. Also it cannot be otherwise than disheartening to feel, that however successful I may be in my own estimation, and even in that of my friends... it is certain that several of the most eminent of the botanists of Britain will consider that I have been wasting my time and retarding rather than advancing science.

C.C. Babington (1855)

This discussion is divided into three broad areas. Firstly the merits and demerits of the methods described here are discussed. Secondly the implications for the results presented here for understanding the ecology of riverine *Ranunculus* species, and river plant ecology in general are discussed. Finally the implications of the results for C-S-R strategy theory are examined.

7.1 Techniques

It is an underappreciated fact that advances in science have frequently occurred as a result of the availability of a new piece of technology or new methodology (Mooney 1991). The structure of DNA was unknown until the development of x-ray crystalography - without that machine there would quite possibly have been no molecular biology. The science of ecology would be very different today if the atomic-absorption spectrophotometer had never been invented or if digital computers were not available. Thus the methods used are of importance and are worthy of consideration.

The aquatic environment presents unique sampling problems. These are frequently sidestepped by using plant cover to form an estimate of the amount of plant material growing beneath the water surface (standing crop). In two of the experiments described in this thesis (those carried out in the Frome Mill Stream and the River Rye) and both surveys, the area of *Ranunculus* clumps was used as an estimate of standing crop. When the *Ranunculus* was cut, the area of the clump was regressed against the biomass of the clump, and they were normally found to be correlated. However this did not hold for the unshaded clumps in the Mill Stream and the best correlation only accounted for 50% of the variation. This indicates that although equating cover with biomass may be a reasonable estimate, it is not precise, particularly in very productive situations. If it is not possible to confirm the accuracy of cover measurements they should only be used in situations where the biomass density (Duarte & Kalff 1990) is likely to be constant.

In the analysis of survey data it is normal to indicate an estimate of the frequency or abundance of the species surveyed when carrying out multivariate analysis. Programs such as TWINSPAN treat the abundance value as five 'pseudospecies' rather than as continuous variables, so any imprecision in the abundance values will be of little importance. However indirect and direct gradient analysis (e.g. DECORANA, CANOCO) treat 23% cover of *Ranunculus aquatilis* in one site as being equal to 23% cover of *Ranunculus aquatilis* in another site, so that if these two values do not represent the same standing crop of *R. aquatilis* serious distortions may arise. If the goal of the survey is simply to generate hypotheses for further testing then it is not particularly significant if a weak hypothesis is generated - further experimental work should show its inadequacies. However if it is hoped to demonstrate a cause and effect relationship the distortion may be more important.

It has become standard practice to evaluate survey data by means of multivariate analysis of community and environmental data. This is often done by deriving the major axes of community variation using techniques such as correspondence analysis (e.g. DECORANA) and then (indirectly) correlating the measured environmental variables with those axes. In the past few years it has become possible to use direct gradient analysis (i.e. the environmental data are taken into account when deriving the ordination axes) by using programmes such as CANOCO. There is as yet, a scarcity of published data of analysis of British ecosystems using CANOCO. The analysis presented here demonstrates that it is a powerful yet easy to use package. It enables a large number of environmental variables to be examined and assessed simultaneously and produces a clear diagram to aid interpretation of the data. This is of great value in generating hypotheses - the goal of much survey work.

Another common technique used in this thesis was the use of transplants. These were used both to discover if the absence of a species from a particular habitat was due to a lack of suitable propagules reaching those sites or whether it was outside the ecological niche of that species, and the technique was used to place plants in habitats for experimental work where there were not any suitable plants already *in situ*. As with any field work, a quantity of data was lost through damage caused by vandalism and storms. The data gained from straight-forward transplants was of somewhat limited value, but in the experimental work (in the River Mouse and the West Beck) the relatively uniform nature of the transplanted plants compared with indigenous vegetation made it possible to draw conclusions that would almost certainly have been masked by the variability of the data if indigenous vegetation had been used.

This indicates the value of working using a spectrum of approaches from fully controlled laboratory studies through field experiments through to extensive surveys. Each type of study has it merits and limitations and it is important to use it appropriately (Campbell *et al.* 1991, Grace 1991). For example surveys have shown that *Ranunculus* species are associated with particular sediment particle sizes (Haslam 1978), and so it might be assumed that there was a causal relationship. However the controlled field experiment in the River Mouse demonstrated that particle size *per se* does not affect *R. penicillatus* subsp. *pseudofluitans* growth, implying that a third factor such as water current velocity is responsible for the distribution of both particular particle sizes and particular *Ranunculus* species.

As can be seen from all the experiments described in this thesis, one of the main problems of field experiments is that the natural variation in conditions within a river will tend to produce very variable results, which can mask the effects of the treatments. It is not always possible to carry out laboratory experiments in constant conditions, either because the effect of a treatment on a whole plant community is being investigated (e.g. the experiment in the Frome Mill Stream) or because it might be difficult to ascertain whether the plants might respond quite differently to a treatment in the conditions of a greenhouses compared with field conditions. A compromise between these two extremes is to design an artificial habitat which is ideally as uniform as in laboratory conditions, but with those conditions closely similar to those found in the field. The I.F.E. artificial recirculating rivers used in the experiment described in Chapter Three come close to this ideal, and it would have been impossible to carry out that experiment either in the field or in the laboratory. The artificial rivers too had their problems, chiefly that that size of the channels excluded the possibility of the provision of sufficient replicate channels to enable adequate statistical comparisons to be carried out.

However, laboratory studies also have their place within a purely ecological project. As the experiment in Chapter Six demonstrates, laboratory growth experiments can be valuable in providing uniform conditions in which to screen a variety of plant species to see the differential effect of the same treatment in the same conditions on the growth of those plants. The ecological relevance of such data lies not so much in the results from individual species (which may have behaved sufficiently differently from how they would in the field to make extrapolation difficult) but in the comparative difference between species; if one species is more shade-tolerant than another in the laboratory, it is likely to be more shade-tolerant in the field as well.

Many ecological studies focus on the ecology of an individual species, or of a particular community (e.g. part of a lake), or a group of similar plants (e.g. isoetids), usually within a relatively limited geographical area (e.g the English Lake District). The terms of reference for this study were somewhat different, looking at a group of species that was related taxonomically but that were not closely similar morphologically and in a wide variety of different rivers. This had some disadvantages in that in some ways it was too restricted (e.g. no emergents could be included) and in some ways it was rather too open (studying ten taxa for a limited period of time inevitably meant that not all could be studied in the same depth). However such an approach also has its advantages. There was no bias in selecting the species to be studied (particularly in terms of their strategy traits). Variation between species that was simply due to differing evolutionary histories was reduced. Studying rivers throughout virtually the whole of Britain meant that a much fuller and more representative picture was obtained than if a smaller region had been chosen. Studying a taxonomically related group of taxa proved to be profitable, and it would be useful to carry out similar work with e.g. *Potamogeton*.

The two surveys carried out in 1990 and 1991 demonstrated some of the merits and demerits of either making one or several site visits as part of a survey. The survey involving several visits to each site certainly obtained far more information both about the composition of the plant community and the environmental factors affecting that community. Clearly, the extra data obtained from repeated visits can be an advantage. However the 1991 survey indicated that substantial useful information can be gained from one site visit. Although it is clear that additional potential strategy traits could have been assessed (for example phenological patterns) by repeated visits, sufficient information was obtained to enable some of the main traits to be pinpointed - the primary goal of the survey.

The one major novel technique described in this thesis was placing the species on the ordination triangle by means of multivariate analysis of an integrated index of stress and of disturbance to discover how stressed and disturbed the habitats are in which the plants are found. The index itself was devised objectively using multivariate analysis to determine which stresses and disturbances were the most important in shaping community composition. Grime *et al.* (1988) define the stress and disturbance of habitats in terms of marker species (themselves defined by strategy traits) rather than by directly measuring the environmental forces. The use of CANOCO enabled the use of marker species to be bypassed. For the taxa which were adequately represented in the survey on which the ordination was based, the amount of stress and disturbance in the habitats in which the plants are found (and therefore the strategy of that taxon) could be assessed with confidence. For the other species for which there was less survey data, it proved possible to derive an apparently reasonable triangular ordination in relation to the former species. The limited results described in this thesis show that the use of this technique has the potential to be fruitful with other species and in other ecosystems.

7.2 River Ecology

Public concern about the 'health' of British rivers has never been higher. Recently published National River Authority data demonstrating that pollution has significantly increased in rivers in England and Wales over the last five years has been reported prominently in national newspapers (e.g. the editorial in *The Guardian* 18 December 1991). Major nutrient concentrations are increasing in many rivers (Casey & Clarke 1979, 1986), with associated effects on the biota. Although the effects on some groups such as the invertebrate fauna are relatively well understood (Wright *et al.* 1984) the functioning of the river macrophyte community has had considerably less work carried out upon it. In order to ensure that management of rivers achieves the desired objective it is necessary to understand both the underlying ecological mechanisms of the community and the detailed response of individual species to changes in their environment. It is hoped that the application of strategy theory may contribute towards achieving an overall understanding of the functioning of those plant communities. Some of the specific results obtained for the experimental work described in this thesis are also of value in furthering the understanding of the autecology of individual taxa.

The survey described in Chapter Two suggested that management by cutting, pH, sediment nitrogen, sediment and water phosphate, water height and velocity, shade and site elevation were probably the main factors affecting the plant communities in the sites surveyed. Many of these factors are changing as a result of anthropogenic influences. The effects of some of these are better understood than others. In a recent review of the affects of acidic deposition on aquatic habitats (Nikolaidis *et al.* 1989) 147 papers were reviewed but not one dealt specifically with the effects of decreasing pH on river macrophytes. More research has been carried out on the effects of pollutants (heavy metals, elevated nutrient concentrations, etc), see for example Haslam (1990).

The results from the experiment carried out in the artificial rivers described in Chapter Three indicate that increasing phosphate concentrations in *Ranunculus* rivers has differential effects on the plant species present. Where conditions are suitable for algal growth problems can arise from growth of genera such as *Cladophora* or *Vaucheria*. This has often been assumed to have been caused by increased phosphorus and other nutrient concentrations, but experimental studies such as the one reported here are rare and often fail to give consistent information on the role of phosphorus. The data presented here unequivocally demonstrate that there can be a causal relationship between eutrophication in rivers and enhanced growth of filamentous algal populations.

The study also provided indirect evidence for the sort of changes that might occur if conditions were unsuitable for algal growth. The *Potamogeton pectinatus* plants showed larger changes in biomass with stress than the *Ranunculus penicillatus* subsp. *pseudofluitans* plants. -

This implies that if the algae had not shaded the macrophytes the *Potamogeton pectinatus* plants would have overgrown the *Ranunculus*. I.e. in more productive (less stressed) conditions the competitive interaction between the macrophytes would have become more important and the more competitive *Potamogeton* plants would have competitively dominated the *Ranunculus*. Again this is something which observations have suggested may occur in eutrophic sites (e.g. Butcher (1933) observed *Potamogeton pectinatus* entering the River Lark downstream of a sewage plant), but there has been a lack of experimental studies to back up these observationally derived conclusions.

Practical implications follow from these data. If macrophyte vegetation and so the whole community structure, rather than just invertebrate populations, is affected by increased phosphorus discharges there is an even greater imperative for provision of adequate sewage treatment plants. In lake ecosystems reduction in phosphate inputs has not always led to the anticipated recovery of macrophyte vegetation due to high phosphorus concentrations in the sediments (e.g. in the English Norfolk Broads, Wheeler & Giller 1982). In the West Beck (see Chapter Five) the sediment total phosphorus concentration is as high as 3 $mgP\ g^{-1}$ and the *R. penicillatus* subsp. *pseudofluitans* plants are frequently overgrown with *Vaucheria* and/or *Potamogeton pectinatus*. The *Ranunculus* population shows great variability from one year to the next, apparently in response to competition from *Vaucheria* and *Potamogeton pectinatus*. The reason that the sediment is so phosphorus rich is high phosphate discharges from the adjacent fish farm.

If these discharges were to cease what would happen to the vegetation? The filamentous algae derive their nutrients from the water rather than from the sediments (they are not rooted) and so it is likely that they would decrease. In the Norfolk Broads reduction in phosphate inputs have not resulted in a concomitant reduction in algal populations because the water phosphate concentrations have remained high due to P exchange between the water and sediments. However in fast-flowing rivers, phosphate which diffused from the sediments to the water would be rapidly diluted by water from upstream of the enriched sediment. The results from the artificial river experiment suggest that in a stream such as the West Beck, if the phosphate inputs were decreased then this would lead to a decrease in the growth of *Vaucheria* but an increase in the growth of *P. pectinatus* which would still receive a high phosphate supply *via* its roots and would no longer be shaded by filamentous algal growth. If, after a few years, the macrophytes began to reduce the phosphate pool in the sediments, then the less competitive *Ranunculus* may begin to recover.

The stress caused by shade and low water velocity was investigated in the field experiment in the Frome mill stream described in Chapter Three. It is already well established that shade can have a large effect on productive *Ranunculus* communities (Dawson 1978, Dawson & Hallows 1973) and that this can be a useful management technique (Dawson & Kern-Hansen 1979). Dawson (1988) has suggested that such management may select for 'less vigorous' plants. This concept may be clarified by examining it in the light of strategy theory. Stressing a plant community may select for stress-tolerant plants. These will have a number of characteristics (traits) in common, including a relatively slow growth rate. Management by cutting (disturbance) will select for plants with ruderal traits, including a rapid growth rate (Grime *et al.* 1988). The data from the Mill Stream experiment (Chapter Three) also shows that the application of stress to productive streams leads to a lower total vegetation cover (the major aim of the traditional management by cutting) and an increase in species diversity (a major aim of modern management for conservation). These data are consistent with the assumption made by strategy theory that as stress increases so competition (though it still occurs) becomes less important.

The data from the artificial recirculating river implied that competition between the macrophytes was not a very important factor in that situation. Wilson & Keddy (1991) came to the conclusion that competition had little effect on aquatic macrophytes. There are a multitude of approaches to studying the effects of competition in macrophyte communities, and different authors reach different conclusions regarding the importance of competition (McCreary 1991). As discussed in Chapter Six, river macrophyte communities in Britain do not exceed the productivity at which terrestrial competitive dominance occurs (750 g dry weight m^{-2}), and even the most productive Batrachian *Ranunculus* species do not come out on the triangular ordination as being very competitive.

If the nutrient concentrations in a river with a large macrophyte standing crop are increased then the macrophytes appear to be insufficiently competitive to take advantage of the enhanced productivity, and instead algal populations come to dominate the ecosystem. This implies that *Cladophora* and *Vaucheria* occupy the Competitor strategy niche in aquatic systems.

Although competition may not be very important in chalk streams dominated by *Ranunculus*, there can be no doubt that for several *Ranunculus* species, disturbance plays a major role in shaping the community. *R. penicillatus* subsp. *pseudofluitans* and *R. fluitans* plants are traditionally managed by cutting and are often subjected to grazing and poaching by cattle. They are also both associated with fast flowing rivers. *R. peltatus* is associated with reservoirs (fluctuating water levels) and winterbournes. Although it is well established that *R. penicillatus* subsp. *pseudofluitans* responds positively to disturbance in the form of cutting (Westlake 1968b, Soulsby 1974, Ham Wright & Berrie 1982), the response is still incompletely quantified.

The experiments described in Chapters Four and Five provide further data detailing the response of *Ranunculus* to cutting. The effect of stress (by definition) is to decrease the growth rate of a plant, and the data here indicate that if stressed *Ranunculus penicillatus* subsp. *pseudofluitans* is disturbed by cutting then it no longer increases its growth rate when cut. Likewise, the normal increase in growth which is clearly shown after the first two cuts of *R. penicillatus* subsp. *pseudofluitans* in the experiment in the Rye (Chapter Four) no longer occurs following the third cut. Thus, as might be predicted, there are limits to disturbance-tolerance even of disturbant-tolerant communities.

This too has implications for management. It might be assumed that because a community is disturbance-tolerant it can therefore recover from severely damaging operations such as poorly planned construction works or over-dredging or inappropriate use of herbicide. These data demonstrate that no such assumption can be made, and that careful consideration of the effects on the whole plant community must occur before such potentially damaging impacts proceed. The data also imply that when conditions change in a river it may no longer be appropriate just to continue a particular management regime simply because the river has 'always' been managed that way. If a river becomes polluted then continuing the annual 'weed' cut may result in a severe reduction in *Ranunculus* growth and a consequent subsequent increase in algal populations.

The results from the experiment in the River Mouse (Chapter Four) show that management practices leading to a change in sedimentation will not necessarily have the results that may be expected. Changes in the total sediment load will affect the plant community (Brookes 1986), but if the nature of the sediment is changed this may not have such substantial effects unless the chemical composition of the sediment is altered. *Ranunculus* species are correlated with particular sediment types (Haslam 1978) and for some species there may be a direct effect due to their rooting ability (e.g. *R. fluitans*, Brian 1983). However the data presented in Chapter Four imply that the correlation with sediment particle size is an indirect effect of current velocity. This emphasises the importance of not automatically treating correlations as indications of cause and effect, but carrying out experimental verification of hypotheses suggested by those correlations.

7.3 C-S-R Strategy Theory

In his paper *Pattern and process in the plant community*, Watt (1947) declared that 'it is our primary business to understand'. If an understanding is to be reached of how the plant community functions then it is insufficient to treat ecological data as a series of disconnected observations. A coherent theoretical framework must be generated to integrate disparate observations. The nature of that theoretical framework must depend on the hierarchical level at which the data are examined; ecology examines aspects of the living world ranging from the biochemical level to the biosphere. At the levels of the community, population and individual, strategy theory provides a useful paradigm within which to attempt an understanding of how the system functions. Throughout this thesis, C-S-R strategy theory has been utilised to aid the interpretation of the observations and experimental data which has been presented. In this final section of this chapter the theory itself will be examined and the bearing that the data herein presented has on strategy theory will be discussed.

One problem with using strategy theory to understand the ecology of Batrachian *Ranunculus* species is that the theory has hitherto not been systematically applied to riverine plant communities. Hence the strategy of the species is not known (Grime *et al.* 1988), and cannot be derived from the morphological or life history traits of the species as the appropriate criteria are not available for aquatic macrophytes (Grime *et al.* 1988).

The data presented in Chapter Six go a little way towards alleviating that problem. The *Ranunculus* species studied were categorised in terms of their competitiveness, stress-tolerance and disturbance-tolerance; not by using morphological traits, but by determining the combination of stress and disturbance in the habitats with which the plants were associated.

Having provisionally defined the strategy exhibited by the taxa, this information was then used to determine some of the morphological traits associated with each primary strategy. The data indicated that the stress-tolerant species tended to have small shoots with floating leaves, whereas disturbance-tolerant and competitive species tended to have submerged leaves. Disturbance-tolerant species tended to have large shoots and competitive species tended to have long leaves.

The question arises as to how relevant this might be to other riverine species. If the genus *Potamogeton* is examined, species such as *P. natans* and *P. polygonifolius* with floating leaves are not associated with disturbed sites and species such as *P. pectinatus* and *P. filiformis* with thread-like submerged leaves are often associated with fairly productive (competitive) sites (Haslam *et al.* 1975). However the genus *Potamogeton* also illustrates some of the limitations of extrapolating this data to other riverine species. The genus contains morphological characters not present in *Batrachium*. Several *Potamogeton* species have submerged broad leaves (unlike any *Ranunculus* species). These leaves are not tolerant of the disturbance caused by swift currents, but present a large lamina for photosynthesis in shaded conditions.

The most productive riverine species tend to have an emergent morphology. It might be predicted that this morphology would be associated with competitiveness, but this prediction cannot be tested from the Batrachian *Ranunculus* data set.

It is clear that in order to accurately determine which morphological (and other) traits are associated with particular strategies then it will be necessary to carry out measurements similar to those described in Chapter Six for a larger sample of species and traits. However, it would appear that the most efficient way of classifying riverine species in terms of their strategy might not be to derive a dichotomous key based on strategy traits (as used by Grime *et al.* 1988 for their marker species), but to use the procedure described in Section 6.2 to define the strategy of the taxa in terms of the stress and disturbance of their habitats.

Until such data becomes available it is possible to use the information from Chapter Six to assess the strategies shown by taxa other than Batrachian *Ranunculus* species. Some traits are likely to be widely relevant. Any species with broad floating leaves is unlikely to be disturbance-tolerant, and if a large force is required to fracture the plant then that probably indicates a degree of disturbance-tolerance. Likewise, taxa with small shoots are likely to be stress-tolerators. In addition, the *Ranunculus* taxa may be used as marker species to indicate particular strategies, particularly for those *Ranunculus* taxa which were placed on the triangular ordination primarily by utilising the survey data rather than by reference to the literature. Thus species growing at sites with *R. fluitans* or *R. penicillatus* subsp. *pseudofluitans* are likely to be disturbance-tolerant competitors, species associated with *R. aquatilis* or *R. peltatus* may be C-S-R strategists and species found with *R. hederaceus* or *R. omiophyllus* will be likely to be stress-tolerators.

However, caution must be exercised when considering whether a species is growing with a particular *Ranunculus* species. A Twinspan classification may place two species in the same group because they occur at the same sites, but that does not necessarily indicate that they are occupying a similar niche. The stresses and disturbances experienced by a plant growing near the bank a short distance from a *Ranunculus* clump in the middle of a swift stream may be considerably different from the stresses and disturbances acting on the *Ranunculus* clump.

Riverine species exhibit different strategy traits from terrestrial species because they have experienced different stresses and disturbances and so evolved specific responses to those selective pressures. As with terrestrial systems, interpreting the environment in term of stress, disturbance and competition is not without its problems (Grubb 1985, Tilman 1987). A single environmental factor such as water velocity can act as a stress, limiting plant production at low values, but at high values it can act as a disturbance, removing biomass. The derivation of the integrated indices of stress and disturbance (Chapter Six) showed that this is not necessarily a problem and does not prevent clear interpretation of the data.

It has also been argued that because a particular level of a disturbance (or stress) may disturb some plants but not others, it is not sensible to use such a broad term (Menges & Waller 1983). However, as the strategy trait data from Chapter Six show, the basis of a disturbance-tolerant strategy may lie precisely in the ability to avoid biomass destruction (e.g. though stronger stems) rather than just the ability to recover effectively from disturbance.

However the interpretation of the artificial river experiment (Chapter Three) indicated that on occasions analysis in terms of stress, disturbance and competition can be quite complex. The *Ranunculus* plants were stressed by shading from *Cladophora* in the high phosphate channel. The *Ranunculus* was also possibly stressed by the algae by other factors such as competition for carbon. Although they experienced stress, this was in effect due to increased competition. The increased phosphate reduced nutrient stress for the algae, which then competed for another resource (light) with the macrophytes. If two individuals attempt to acquire the same resources they are competing for it. Once that resource has been captured the species that failed to capture it is then stressed (resource limited), and because the more competitive species will have used that resource to increase its uptake of further resources, the less competitive species is likely to be further stressed. If it has a competitive strategy (such as the *P. pectinatus*) it will show a large reduction in growth as it fails to capture resources, if it is less competitive (such as the *Ranunculus*) it will show a smaller reduction in growth and be able to tolerate the stress caused by competition. For that reason C-strategists have been referred to as competitors rather than competition-tolerators throughout this thesis.

This analysis in terms of fundamental attributes such as growth rate leads to two further conclusions. Firstly, it makes the argument more persuasive that there is a trade-off between different strategies; such that as stress tolerance increases, competitiveness and disturbance-tolerance decreases. If stress tolerance was purely a matter of a morphological trait such as possessing floating leaves then it might be hard to see why a trade-off must necessarily occur. However if, fundamentally stress-tolerance is tied-up with low growth rates (instantaneously expressed as small shoots), and the other strategies require a rapid growth rate then it is clearer why an increase in one must involve a decrease in the other. If there is a trade-off between different strategies then this further reinforces the conclusion that a high stress plus high disturbance strategy is non-viable (Chapter Five).

Secondly, it helps resolve the argument as to whether there is any such thing as a general stress-tolerant strategy, or whether there are simply a variety of adaptations for shade, low nutrient levels, low water velocity, etc (see e.g. Grubb 1985, Grace 1991). Tilman (1988) has made a similar argument for in effect two strategies to respond to above- and below-ground stresses (shade and nutrient limitations). That discussion is less relevant in the present context as aquatic plants are able to take up nutrients through their shoots (Chapter Three), but it is still denying the existence of a general stress-tolerant strategy.

It is clear that there are specific adaptations to these different stresses - the very fact that the terrestrial criteria for assigning strategies to plants can not be applied directly to aquatic species demonstrates that. However the data in Chapter Six also demonstrate that it is possible to describe stress-tolerance in general terms. The integrated stress index defined species associated with deep water, slow current and low nutrient supply as being stress-tolerators, and the regression against morphological traits showed that there were certain traits (such as a small size and floating leaves) which these species all tended to have in common. The same line of argument may also be applied to competitive and disturbance-tolerant taxa.

In terrestrial systems it is likely that the fundamental stress is nutrient deficiency (Grime *et al.* 1988), and so it might be argued that the reason for a common stress-tolerant strategy in such habitats is a response to a common stress. In aquatic systems both shade (Spence 1976) and carbon supply (caused by low pH and low current velocity; Madsen & Sand-Jensen 1991) are important additional stresses. The survey described in Chapter Two indicated that although nutrient supply is very important in determining the distribution of riverine *Ranunculus* communities these other factors are also important stresses. Chapter Six contains evidence that there does appear to be a general strategy for stress-tolerance in spite of the variety of stresses. Likewise different species are exposed to different disturbances (high water velocity, cutting, grazing, drought in winterbournes and fluctuating water-levels) and yet appear to exhibit a general disturbance-tolerant strategy in addition to the specific adaptations associated with specific disturbances.

Grubb (1985) and Miller (1982) have discussed the question of whether increasing the frequency of disturbance has a similar effect to increasing the intensity of disturbance. Will a continuous, but low level of biomass removal (e.g. high current velocity) lead to a selective pressure for the same attributes as an infrequent but severe disturbance (e.g. management by cutting). Some authors (e.g. Grubb 1985, Farmer & Spence 1986) consider that the former will lead to attributes similar to those of stress tolerance. Miller (1982) argued that frequent small disturbances favour competitive species and that the size of individual disturbance events affects the community organisation independently of the frequency of disturbance. Miller (1982) has used the concept of the rate of disturbance (intensity×frequency) to combine the two aspects. He defines the disturbance rate as being equal to the sum of the magnitude of all the disturbance events in a given area per unit time.

Whilst it is clear that plants may show specific adaptations to either high frequencies or high intensities of disturbance, that does not necessarily imply that there can not be a general strategy that plants may show if they are to be suited to disturbed sites. The potential to exhibit a high growth rate in response to biomass removal (and attributes associated with that trait), will be of value whether or not the biomass is removed frequently or in large quantities. If the plant does not show a large growth rate, its biomass will decrease, leading ultimately not to a successful strategy but to death.

As with the above discussion on stress-tolerance the question is whether there is such a thing as a general disturbance-tolerant strategy or whether different types of disturbance require different strategies if the plant is to survive. Some of the data presented in this thesis imply that the former hypothesis is more likely to be correct, i.e. there is such a thing as a D-tolerant strategy, not separate strategies for frequent and for intense disturbance. The species subjected to a variety of disturbance-pressures, both frequent and intense, appeared to have certain traits (such as a large strong shoot) in common (Chapter Six). *Ranunculus penicillatus* subsp. *pseudofluitans* is associated both with certain sediment particle sizes and with fast-flowing rivers. The experiment in Chapter Four indicated that the flow rate rather than the particle size was more probably causing the distribution of this taxon. This taxon is also strongly associated with rivers and streams managed by cutting. Thus the same taxon thrives in situations of low intensity, high frequency disturbance (fast flows) and low frequency high intensity disturbance (cutting). In order to further clarify this situation, it would be informative to compare the results of an experiment whereby the same biomass was removed from *Ranunculus* plants as in the repeated cutting experiment described in Chapter Four, but at a lower intensity and higher frequency (e.g. the shoot tips removed each day).

Another area of contemporary discussion concerning strategy theory concerns the taxonomic level at which the theory may be applied. Is it possible to speak of a strategy for a species (as in the autecological accounts in Grime *et al.* 1988), or is it necessary to consider every population as exhibiting a differing strategy (Verhoeven *et al.* 1982, Van Wijk 1989c)? The Batrachian *Ranunculus* species with their complex and poorly understood taxonomy, bring this debate into sharp focus. It is clear that if all three taxa placed in *Ranunculus* penicillatus were regarded as having the same strategy, this would lead to a considerable loss of data. Although they are in a similar area of the triangular ordination (Figure 6.3.2), there are important differences in their ecology and strategy. Subspecies *penicillatus* has floating leaves (identified in the strategy trait data as an important indicator for strategy type), whereas subspecies *pseudofluitans* lacks floating leaves. Each variety is associated with particular environmental stresses and disturbances (Chapter Two, Chapter Six).

The root of the problem is that there is not always a very great convergence between ecologically similar and taxonomically similar groups (see Wayne & Bazzaz 1991). A species such as *Potamogeton pectinatus* contains several different ecotypes, which can not be reliably taxonomically separated but undoubtedly exhibit differing ecologies (Van Wijk *et al.*, 1988); workers on that taxon have concluded that the whole species does not have a single strategy (Van Wijk 1989c). However, confusion has also arisen from assuming that if a species is morphologically plastic it necessarily exhibits a different strategy with each morphotype. Such plasticity is itself a strategy trait (associated with competitiveness, Grime 1979). Conversely a species such as *Ranunculus fluitans* shows little variation between populations and so it seems reasonable to apply the label of disturbance-tolerant competitor to the whole species.

The data presented in Chapter Six suggest that for most Batrachian *Ranunculus* species, the whole species has essentially the same strategy. However for *R. penicillatus*, in which the different varieties/sub-species have markedly different ecologies, each has a distinct strategy. The conclusion suggested is that a single strategy is most appropriately applied to a single ecotype, which may or may not correspond to a taxonomic division. In some cases a whole species will have essentially the same ecological strategy, in others different populations will have separate ecologies and so strategies.

Although it can be argued that the goal of ecology is to understand the ecosystem (Watt 1947), if strategy theory really furthers understanding of the plant community then it should be possible to use the theory to predict the effects of management (or other) changes to the community (Grime 1980). Some workers argue that prediction is the ultimate aim of ecological science (Peters 1991).

A number of changes to British rivers may be postulated as being likely to occur in the next few decades. If ecological science has succeeded in understanding the river ecosystem then it should be possible to predict the effects of these changes.

In many chalk streams the water nutrient concentrations will undoubtedly continue to increase as nitrate and phosphate is percolated through the chalk aquifer (Casey & Clarke 1985, 1986). As the data in Chapter Three indicates, this will lead to a change in vegetation type towards more competitive vegetation; either competitive macrophytes such as *Potamogeton pectinatus*, or filamentous algae such as *Cladophora* and *Vaucheria*. Strategy theory suggests that if it is not possible to reduce nutrient levels to their historic concentration, then increasing disturbance (e.g. cutting *P. pectinatus* plants, treating algae with herbicides) may result in a less competitive vegetation with a lower biomass and higher species diversity.

Many stretches of rivers which have historically showed continuous flow throughout the year have recently become winterbournes due to increased water abstraction and recent low rainfall (e.g. the River Wylye, Appendix A). Strategy theory would identify that as an increase in both stress and disturbance; winterbournes are associated with C-S-R strategists such as *R. peltatus*. In sites currently occupied by species with a low disturbance tolerance (such as *R. hederaceus*) these species might be expected to become extinct at that site (as has occurred in some streams in the Netherlands, Van Diggelen & Klooker 1990). In sites currently occupied by species with a low stress-tolerance (such as *R. penicillatus* subsp. *pseudofluitans*) one might expect their replacement by species with more stress-tolerance such as *R. peltatus* (as has been recorded in the Waterston stream, Ladle & Bass 1981).

In some rivers such as the River Rye (Chapter Four, Appendix A) there is anecdotal evidence that *Ranunculus* species have colonized the river relatively recently. Management by cutting the *Ranunculus* clumps at their peak biomass has been instituted. Strategy theory (and the data from Chapter Four) would predict that this would lead to more rather than less growth of disturbance-tolerant taxa such as *R. penicillatus* subsp. *pseudofluitans* and *R. fluitans*, and that either the timing of the cut should be altered (Westlake & Dawson 1986) or management should be through increasing stress, e.g. by encouraging overhanging trees (Dawson & Kern-Hansen 1979). It is also not clear that the *Ranunculus* biomass is sufficiently large to be a real problem in the Rye, and it may be that management is not actually necessary at such sites.

The management of river ecosystems subjected to changing patterns of stress and disturbance is a complex subject, currently determined as much by following modified forms of traditional practice as by a thorough understanding of how the ecosystem functions. Traditional management regimes may no longer always be appropriate when conditions change in the river (due to pollution, abstraction, etc), and when management aims to satisfy not just the aims of one party (e.g. the landowner) but resolve the potential conflict between many groups (farmers, conservationists, anglers and other recreational users, industry, etc). This thesis has attempted to show that if river management is to be based on an understanding of how the ecosystem works then C-S-R strategy theory can provide a valuable aid to understanding, and so prediction.

APPENDIX A

SURVEY OF RIVER SITES 1990

List of Sites

Site numbers refer to Figure 2.1

Site №	Site	National Grid Reference
54	Avon Water (New Forest) at Holmsley Bog	SU 016 223
15	Bere Stream at Bere Heath	SY 857 928
55	River Bourne at Idmiston	SU 195 378
38	Bristol Avon at Easton Grey	ST 881 875
40	Bristol Avon at Great Summerford	ST 965 831
39	Bristol Avon at Lacock Abbey	ST 922 681
35	Cam Brook at Carlingcott	ST 695 586
8	Candover Brook at Abbotsbury	SU 569 335
20	River Cerne at Cowden	SY 678 936
36	River Chew at Compton Dando	ST 647 648
37	River Chew at Publow	ST 623 642
9	River Ebble at Odstock	SU 147 096
34	River Exe at Bamford Speke	SX 929 984
33	River Exe at Exebridge	SS 930 245
32	River Exe at Oakford Bridge	SS 919 219
42	River Fowey at Codda	SX 182 785
41	River Fowey at Golitha Woods	SX 228 687
21	River Frome at Frampton	SY 623 944
46	River Frome at Lewell Mill	SY 739 901
18	River Frome at Lower Brockhampton	SY 721 904
23	River Frome at Maiden Newton	SY 597 977
19	River Frome at Moreton	SY 806 895
22	River Frome at Notton	SY 610 959
29	River Gwendraeth Fach at Llangeiderne	SN 460 139
31	Hillfarrance Brook at Hillfarrance	ST 157 248
5	River Itchen at Brambridge House	SU 462 225
7	River Itchen at Chiland	SU 523 325
6	River Itchen at Winchester	SU 486 296
56	River Kennet at Lockeridge	SU 150 683
4	River Loddon at Old Basing	SU 660 528
49	River Loddon at Twyford	SU 782 761
3	River Loddon at Wildmoor	SU 692 559

Site №	Site	National Grid Reference
25	River Lugg at Mortimer's Cross	SO 427 637
44	Lymington River at Ivy wood	SU 316 023
45	Mill Lawn Brook at Mill Lawn House	SU 224 035
17	River Piddle at Affpuddle	SY 806 938
16	River Piddle at Hyde	SY 865 906
26	River Rye at East Newton	SE 644 805
12	River Salisbury Avon at Middle Woodsford	SU 120 361
11	River Salisbury Avon at Netheravon	SU 150 485
10	River Salisbury Avon at Upavon	SU 136 550
13	River Salisbury Avon at Woodgreen	SU 163 174
1	River Surrey Whitewater at Risely	SU 741 635
51	Swansea Canal at Pontardwe	SN 728 047
50	Swansea Water at Downstream Usk Reservoir	SN 820 271
24	Sydling Water at Sydling Saint Nicholas	ST 635 003
28	River Teifi at Altyblata	SN 523 454
27	River Teifi at Cors Carron	SN 684 628
30	River Tone at Waterrow	ST 052 254
43	River Torridge at Hele Bridge	SS 542 064
57	Unnamed steram near Worth Matravers	SY 957 773
47	Waterston Stream at Druce	SY 742 952
2	West Sussex Rother at Maidenmarsh	SU 782 233
48	River Wye at Hay	SO 238 426
52	River Wylye at Codford Saint Mary	ST 970 405

Details of the chemical measurements below are given in section 2.2 and Appendix C. Sediment and plant N is total nitrogen, otherwise concentrations are ammonium acetate-extractable values. 'P' is phosphate-phosphorus. Zero indicates below the level of detectability. Blanks indicate data not available for that site - normally for sites where data: from other sites nearby could form a reliable basis for estimating the data from that site.

References are not intended to be comprehensive, but an indication of some of the previous work carried out at these sites. They are listed by the first site in a particular river. Celtic river names are from Muir & Muir (1986).

Avon Water (New Forest) at Holmsley Bog Site № 54

Site Details:
National Grid Reference: SU 016 223
Height above mean sea level: 40 m
Estimated percentage shade: 0%
Land Use Code: 1
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 4
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity (cm s^{-1})	Discharge (m^3 s^{-1})	Area (m^2)	Height (cm)
8.5.1990	0	0	0.72	14
13.6.1990	20	.00084	.042	9.7
5.9.1990	11	.014	.126	16
S.D.	10	0.37		

Extinction Coefficient (K)
5.4 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
8.5.1990	0	0
13.6.1990	0	0
5.9.1990	0	0

Mean pH: 6.07

Plant & Sediment Composition (September 1990):
No samples taken (rare taxon)

Biological Data:

Maximum Number of flowers per 0·25 m^2
70

Plant species present: 19
Polytrichum commune, Sphagnum auriculatum, Cardamine pratensis, Eleocharis sp, *Galium palustre, Glyceria fluitans, Juncus effusus, Myosotis scorpioides, Myrica gale, Potamogeton polygonifolius, Ranunculus helmsii, Ranunculus omiophyllus, Ranunculus flammula, Ranunculus sceleratus, Hydrocotyle vulgaris, Hypericum elodes, Elatine* sp, *Eriophorum angustifolium, Lotus uliginosus*

Notes
'Avon' is from the Celtic *abona* which means river or water

References
Webster 1984, 1986

Bere Stream at Bere Heath

Site № 15

Site Details:
National Grid Reference: SY 857 928
Height above mean sea level: 25 m
Estimated percentage shade: 0%
Land Use Code: 2
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 3
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity (cm s^{-1})	Discharge (m^3 s^{-1})	Area (m^2)	Height (cm)
20.4.1990	37	1.97	1.83	31
5.6.1990	0	.46	3.35	44
6.7.1990	0	.196	3.4	43
24.9.1990	42	.32	.95	20
S.D.	22.9	.83		

Extinction Coefficient (K)
2 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
20.4.1990	10	
5.6.1990	10	0
6.7.1990	45	0
24.9.1990	10	0

Mean pH: 7.5

Plant & Sediment Composition (September 1990):

Sed N %	Sed P µg g^{-1}	Sed K µg g^{-1}	Sed Ca mg g^{-1}
.04	3.95	50	4.54

	Plant N %	Plant P mg g^{-1}	Plant K mg g^{-1}
	2.05	3.2	37

Biological Data:

Maximum Number of flowers per 0·25 m^2
80

Plant species present: 21
Apium nodiflorum, Carex acutiformis, Catabrosa aquatica, Glyceria fluitans, Juncus effusus, Oenanthe crocata, Phalaris arundinacea, Ranunculus calcareus, Ranunculus sceleratus, Sparganium emersum, S. erectum, Veronica anagallis-aquatica, Rumex sanguineus, Myosotis scorpioides, Senecio squalidis, Nasturtium officinale, Ranunculus acris, Lemna minor, Mentha aquatica, Galium aparine, Pulicaria dysentrica

References
This stream is owned and managed by the Institute of Freshwater Ecology and several studies have been carried out including Crisp *et al.* (1982), Ladle & Casey 1971, Dawson 1981.

River Bourne at Idmiston

Site № 55

Site Details:
National Grid Reference: SU 195 378
Height above mean sea level: 70 m
Estimated percentage shade: 0%
Land Use Code: 1
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 1
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity ($cm\ s^{-1}$)	Discharge ($m^3\ s^{-1}$)	Area (m^2)	Height (cm)
9.5.1990	11	.11	.0088	12
14.6.1990	16	.8	.05	3.5
5.9.1990	0	0	0	0
S.D.	8.19	0.43		

Extinction Coefficient (K)
5.86 (mean value)

Chemical Data:

	Nitrate ($mgN\ l^{-1}$)	Phosphate ($mgP\ l^{-1}$)
9.5.1990	25	0
14.6.1990	40	0

Mean pH: 7

Plant & Sediment Composition (September 1990):

Sed N %	Sed P $\mu g\ g^{-1}$	Sed K $\mu g\ g^{-1}$	Sed Ca $mg\ g^{-1}$
.06	5.56	70	5.76

	Plant N %	Plant P $mg\ g^{-1}$	Plant K $mg\ g^{-1}$
	2.16	4.85	67.42

Biological Data:

Maximum Number of flowers per 0·25 m^2
288

Plant species present: 19
Alopecurus geniculatus, Apium nodiflorum, Cardamine hirsuta, Catabrosa aquatica, Chenopodium album, Glyceria declinata, Myosotis scorpioides, Polygonum hydropiper, Poa annua, Poa trivialis, Ranunculus peltatus, Ranunculus sceleratus, Ranunculus repens, Urtica dioica, Veronica beccabunga, Rosa sp, Rubus fructicosus, Rumex sanguineus, Juncus inflexus

Bristol Avon at Easton Grey

Site № 38

Site Details:
National Grid Reference: ST 881 875
Height above mean sea level: 80 m
Estimated percentage shade: 50%
Land Use Code: 4
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 1
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity (cm s^{-1})	Discharge (m^3 s^{-1})	Area (m^2)	Height (cm)
9.4.1990	37	.2	.82	17
10.5.1990	14	.16	.64	10
15.6.1990	39	.23	.88	14
7.9.1990	35	.075	.71	19
S.D.	11.6	0.07		

Extinction Coefficient (K)
3.28 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
9.4.1990	18	
10.5.1990	25	.5
15.6.1990	25	1
7.9.1990	10	.7

Mean pH: 6.8

Plant & Sediment Composition (September 1990):

Sed N %	Sed P µg g^{-1}	Sed K µg g^{-1}	Sed Ca µg g^{-1}
.03	13.7	53	4.38

Plant N %	Plant P mg g^{-1}	Plant K mg g^{-1}
4.53	5.82	46.33

Biological Data:

Maximum Number of flowers per 0·25 m^2
0

Plant species present: 15
Apium nodiflorum, Callitriche stagnalis, Callitriche obtusangula, Caltha palustris, Elodea canadensis, Epilobium hirsutum, Nasturtium officinale, Mentha aquatica, Phalaris arundinacea, Polygonum hydropiper, Ranunculus penicillatus subsp. *pseudofluitans, Solanum dulcamara, Sparganium emersum, Rubus fructicosus, Veronica anagallis-aquatica*

Notes
'Avon' is from the Celtic *abona* which means river or water.

Bristol Avon at Great Summerford

Site № 40

Site Details:

National Grid Reference: ST 965 831
Height above mean sea level: 55 m
Estimated percentage shade: 0%
Land Use Code: 2
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 3
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity (cm s^{-1})	Discharge (m^3 s^{-1})	Area (m^2)	Height (cm)
9.4.1990	44	1.75	3.19	17
10.5.1990	53			19
15.6.1990	39			15
7.9.1990	27			15
S.D.	10.84			

Extinction Coefficient (K)
2.63 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
9.4.1990	10	
10.5.1990	20	1
15.6.1990	20	3
7.9.1990	10	2.5

Mean pH: 7.7

Plant & Sediment Composition (September 1990):

Sed N %	Sed P µg g^{-1}	Sed K µg g^{-1}	Sed Ca mg g^{-1}
0.13		44	4.23

	Plant N %	Plant P mg g^{-1}	Plant K mg g^{-1}
	3.43	6.14	29.27

Biological Data:

Maximum Number of flowers per 0·25 m^2
33

Plant species present: 12
Enteromorpha, *Fontinalis antipyretica*, *Glyceria maxima*, *Phalaris arundinacea*, *Ranunculus penicillatus* subsp. *pseudofluitans*, *Salix spp*, *Veronica anagallis-aquatica*, *Sparganium erectum*, *Epilobium hirsutum*, *Apium nodiflorum*, *Lemna minor*, *Brassica oleracea*

Bristol Avon at Lacock Abbey — Site № 39

Site Details:
National Grid Reference: ST 922 681
Height above mean sea level: 45 m
Estimated percentage shade: 20%
Land Use Code: 1
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 3
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity (cm s^{-1})	Discharge (m^3 s^{-1})	Area (m^2)	Height (cm)
6.4.1990	45	2.03	4.375	29
10.5.1990	29	1.24	3.89	23
15.6.1990	25	0.82	2.84	15
7.9.1990	39	1.41	3.47	22
S.D.	9.15	0.59		

Extinction Coefficient (K)
3.46 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
6.4.1990	15	
10.5.1990	12	>3
15.6.1990	20	>3
7.9.1990	10	>3

Mean pH: 7.7

Plant & Sediment Composition (September 1990):

Sed N %	Sed P µg g^{-1}	Sed K µg g^{-1}	Sed Ca mg g^{-1}
0.01	8.23	51	5.85

	Plant N %	Plant P mg g^{-1}	Plant K mg g^{-1}
	2.06	4.44	15

Biological Data:

Maximum Number of flowers per 0·25 m^2
70

Plant species present: 14
Fontinalis antipyretica, *Ranunculus penicillatus* subsp. *pseudofluitans*, *Ranunculus fluitans*, *Scirpus lacustris*, *Solanum dulcamara*, *Sparganium erectum*, *S. minimum*, *S. emersum*, *Symphytum officinale*, *Epilobium hirsutum*, *Phalaris arundinacea*, *Salix* sp, *Poa trivialis*, *Urtica dioica*

Cam Brook at Carlingcott

Site № 35

Site Details:
National Grid Reference: ST 695 586
Height above mean sea level: 60 m
Estimated percentage shade: 0%
Land Use Code: 4
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 1
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity ($cm\ s^{-1}$)	Discharge ($m^3\ s^{-1}$)	Area (m^2)	Height (cm)
9.4.1990	18	.24	.9	22
10.5.1990	20	.12	.58	23
15.6.1990	20	.13	.93	26
8.9.1990	20	.11	.63	25
S.D.	1	.06		

Extinction Coefficient (K)
2.9 (mean value)

Chemical Data:

	Nitrate ($mgN\ l^{-1}$)	Phosphate ($mgP\ l^{-1}$)
9.4.1990	0	
10.5.1990	10	>3
15.6.1990	40	>3
8.9.1990	20	>3

Mean pH: 7.3

Plant & Sediment Composition (September 1990):

Sed N %	Sed P $\mu g\ g^{-1}$	Sed K $\mu g\ g^{-1}$	Sed Ca $mg\ g^{-1}$
.03	3.03	162	6.29

	Plant N %	Plant P $mg\ g^{-1}$	Plant K $mg\ g^{-1}$
	3.43	7.94	20

Biological Data:

Maximum Number of flowers per 0·25 m^2
42

Plant species present: 21
Fontinalis antipyretica, Epilobium hirsutum, Glyceria maxima, Myososton aquaticum, Oenanthe crocata, Petasites hybridus, Ranunculus penicillatus subsp. *pseudofluitans, Sparganium minimum, S. erectum, S. emersum, Ranunculus sceleratus, Scrophularia aquatica, Urtica dioica, Rumex obtusifolius, Symphytum officinale, Elymus repens, Solanum dulcamara, Callitriche stagnalis, Callitriche obtusangula, Arctium lappa, Brassica oleracea*

Notes
A domestic sewage outfall was just adjacent to this site.

Candover Brook at Abbotsbury

Site № 8

Site Details:
National Grid Reference: SU 569 335
Height above mean sea level: 60 m
Estimated percentage shade: 30%
Land Use Code: 3
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 3
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity ($cm\ s^{-1}$)	Discharge ($m^3\ s^{-1}$)	Area (m^2)	Height (cm)
23.4.1990	38	.45	1.35	26
14.5.1990	14	.19	1.29	22
7.7.1990	66	.65	1.37	30
26.9.1990	20	.27	1.63	42
S.D.	23.3	.2		

Extinction Coefficient (K)
.57 (mean value)

Chemical Data:

	Nitrate ($mgN\ l^{-1}$)	Phosphate ($mgP\ l^{-1}$)
23.4.1990	15	
14.5.1990	12	0
7.7.1990	20	0
26.9.1990	20	0

Mean pH: 7.7

Plant & Sediment Composition (September 1990):

Sed N %	Sed P $\mu g\ g^{-1}$	Sed K $\mu g\ g^{-1}$	Sed Ca $mg\ g^{-1}$
0	1.78	80	4.02

Plant N %	Plant P $mg\ g^{-1}$	Plant K $mg\ g^{-1}$
2.15	2.75	17.8

Biological Data:

Maximum Number of flowers per 0·25 m^2
0

Plant species present: 19
Fontinalis antipyretica, Apium nodiflorum, Callitriche obtusangula, Elodea canadensis, Glyceria fluitans, Nasturtium officinale, Petasites hybridus, Lolium perenne, Ranunculus penicillatus subsp. *pseudofluitans, Salix fragilis, Veronica anagallis-aquatica, Arrhenatherum elatius, Corylus avellena, Fraxinus excelsior, Rubus fructicosus, Ulmus glabra, Solanum dulcamara, Urtica dioica, Callitriche stagnalis*

Reference
Soulsby (1974)

River Cerne at Cowden

Site № 20

Site Details:
National Grid Reference: SY 678 936
Height above mean sea level: 155 m
Estimated percentage shade: 60%
Land Use Code: 2
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 1
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity (cm s^{-1})	Discharge (m^3 s^{-1})	Area (m^2)	Height (cm)
17.4.1990	75	.46	.71	18
4.5.1990	70	.37	.68	13
6.7.1990	40	.18	.52	13
24.9.1990	53	.15	.35	21
S.D.	16.1	.15		

Extinction Coefficient (K)
2.7 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
17.4.1990	15	
4.5.1990	15	.4
6.7.1990	20	.5
24.9.1990	0	0

Mean pH: 7.9

Plant & Sediment Composition (September 1990):

Sed N %	Sed P µg g^{-1}	Sed K µg g^{-1}	Sed Ca mg g^{-1}
.05	2.12	26	3.49

	Plant N %	Plant P mg g^{-1}	Plant K mg g^{-1}
	3.59	2.94	42.67

Biological Data:

Maximum Number of flowers per 0·25 m^2
12

Plant species present: 23
Epilobium hirsutum, Glyceria fluitans, Phalaris arundinacea, Ranunculus penicillatus subsp. *pseudofluitans, Arrhenatherum elatius, Filipendula ulmaria, Rubus fructicosus, Catabrosa aquatica, Glyceria maxima, Hedera helix, Mentha aquatica, Nasturtium officinale, Oenanthe crocata, Solanum dulcamara, Sparganium emersum, S. erectum, Urtica dioica, Symphytum officinale, Myosotis scorpioides, Bryonia cretica, Myriophyllum spicatum, Veronica anagallis-aquatica, Veronica beccabunga*

Notes
'Cerne' is derived from the Celtic *carn* which means stony river.

River Chew at Compton Dando — Site № 36

Site Details:
National Grid Reference: ST 647 648
Height above mean sea level: 22 m
Estimated percentage shade: 50%
Land Use Code: 4
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 1
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity (cm s^{-1})	Discharge (m^3 s^{-1})	Area (m^2)	Height (cm)
9.4.1990	68	.78	1.29	17
10.5.1990	55	.43	.9	17
15.6.1990	32	.35	.96	13
7.9.1990	57	.38	.74	19
S.D.	15.1	.2		

Extinction Coefficient (K)
3.71 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
9.4.1990	10	
10.5.1990	20	1
15.6.1990	10	1.3
7.9.1990	0	2

Mean pH: 7.5

Plant & Sediment Composition (September 1990):

Sed N %	Sed P µg g^{-1}	Sed K µg g^{-1}	Sed Ca mg g^{-1}
0.01	10	see next site (№ 37)	

Plant N %	Plant P mg g^{-1}	Plant K mg g^{-1}
4.95	see next site (№ 37)	

Biological Data:

Maximum Number of flowers per 0·25 m^2
15

Plant species present: 30
Amblystegium riparium, Liverworts (not determined), *Fontinalis antipyretica*, *Equisetum fluviatile*, *Alnus glutinosa*, *Apium nodiflorum*, *Epilobium hirsutum*, *Holcus lanatus*, *Oenanthe crocata*, *Phalaris arundinacea*, *Petasites hybridus*, *Ranunculus penicillatus* subsp. *pseudofluitans*, *Solanum dulcamara*, *Salix* sp, *Urtica dioica*, *Veronica beccabunga*, *Arctium lappa*, *Bryonia cretica*, *Humulus lupulus*, *Impatiens capensis*, *Rubus fructicosus*, *Symphytum officinale*, *Polygonum amphibium*, *Eupatorium cannabinum*, *Calystegia sepium*, *Nasturtium officinale*, *Helianthus annuus*, *Scrophularia aquatica*, *Acer psuedoplatanus*, *Cardamine hirsuta*

River Chew at Publow

Site № 37

Site Details:
National Grid Reference: ST 623 642
Height above mean sea level: 30 m
Estimated percentage shade: 30%
Land Use Code: 2
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 1
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity (cm s^{-1})	Discharge (m^3 s^{-1})	Area (m^2)	Height (cm)
9.4.1990	44	.46	1.56	19
10.5.1990	31	.4	1.34	21
15.6.1990	28	.43	1.43	17
7.9.1990	46	.51	1.3	17
S.D.	9.07	.05		

Extinction Coefficient (K)
3.2 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
9.4.1990	3	
10.5.1990	15	1.2
15.6.1990	10	1
7.9.1990	0	2

Mean pH: 7.5

Plant & Sediment Composition (September 1990):

Sed N %	Sed P µg g^{-1}	Sed K µg g^{-1}	Sed Ca mg g^{-1}
0.01	10	53	3.69

Plant N %	Plant P mg g^{-1}	Plant K mg g^{-1}
4.93	6.54	70.67

Biological Data:

Maximum Number of flowers per 0·25 m^2
27

Plant species present: 24
Fontinalis antipyretica, Agrostis stolonifera, Apium nodiflorum, Glyceria fluitans, Oenanthe crocata, Phalaris arundinacea, Petasites hybridus, Ranunculus penicillatus subsp. *pseudofluitans, Ranunculus sceleratus, Arctium lappa, Avena fatua, Rubus fructicosus, Rumex obtusifolius, Rumex sanguineus, Silene dioica, Trifolium repens, Viburnum opulus, Poa trivialis, Sparganium minimum, Sparganium emersum, Salix* spp, *Glechoma hereracea, Lemna minor, Mentha aquatica*

River Ebble at Odstock

Site № 9

Site Details:
National Grid Reference: SU 147 096
Height above mean sea level: 45 m
Estimated percentage shade: 5%
Land Use Code: 2
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 5
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity ($cm\ s^{-1}$)	Discharge ($m^3\ s^{-1}$)	Area (m^2)	Height (cm)
5.4.1990	51	1.34	2.59	26
8.5.1990	32	.6	1.84	19
13.6.1990	30	.45	1.51	18
6.9.1990	15	.18	1.31	15
S.D.	14.7	.5		

Extinction Coefficient (K)
3.4 (mean value)

Chemical Data:

	Nitrate ($mgN\ l^{-1}$)	Phosphate ($mgP\ l^{-1}$)
5.4.1990	15	
8.5.1990	20	0
13.6.1990	15	0
6.9.1990	10	0

Mean pH: 7.7

Plant & Sediment Composition (September 1990):

Sed N %	Sed P $\mu g\ g^{-1}$	Sed K $\mu g\ g^{-1}$	Sed Ca $mg\ g^{-1}$

No sample taken - see Salisbury Avon data.

Plant N %	Plant P $mg\ g^{-1}$	Plant K $mg\ g^{-1}$
2.2	1.69	33.67

Biological Data:

Maximum Number of flowers per 0·25 m^2
27

Plant species present: 18
Apium nodiflorum, Cornus sanguinea, Glyceria maxima, Phalaris arundinacea, Ranunculus penicillatus subsp. *pseudofluitans, Rubusructicosus, Glyceria fluitans, Poa trivialis, Mentha aquatica, Myosotis scorpioides, Oenanthe crocata, Potamogeton pectinatus, Ranunculus sceleratus, Solanum dulcamara, Veronica anagallis-aquatica, Veronica beccabunga, Rumex sanguineus, Urtica dioica*

River Exe at Bamford Speke

Site № 34

Site Details:
National Grid Reference: SX 929 984
Height above mean sea level: 12 m
Estimated percentage shade: 0%
Land Use Code: 1
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 1
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity (cm s^{-1})	Discharge (m^3 s^{-1})	Area (m^2)	Height (cm)
2.4.1990	176	7.12		50
3.5.1990	70	3.8	6	41
21.6.1990	37	3.01	6.6	48
3.9.1990	55	2.34	4.72	36
S.D.	62.5	2.12		

Extinction Coefficient (K)
2.94 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
3.5.1990	5	.6
21.6.1990	0	.6
3.9.1990	0	0

Mean pH: 6.8

Plant & Sediment Composition (September 1990):

Sed N %	Sed P µg g^{-1}	Sed K µg g^{-1}	Sed Ca mg g^{-1}
No sample taken - see other Exe sites			

Plant N %	Plant P mg g^{-1}	Plant K mg g^{-1}
3.93	7.43	41.50

Biological Data:

Maximum Number of flowers per 0·25 m^2
110

Plant species present: 19
Agrostis stolonifera, Phalaris arundinacea, Ranunculus fluitans, Salix spp, *Sparganium emersum, Rumex sanguineus, Elodea nuttallii, Rorippa sylvestris, Ranunculus sceleratus, Stachys palustris, Dactylis glomerata, Lycopus europaeus, Oenanthe fluviatilis, Poa trivialis, Solanum dulcamara, Myosotis scorpioides, Polygonum amphibium, Alnus glutinosa,*

Notes
'Exe' is derived from the Celtic *isca* which means water.

River Exe at Exebridge

Site № 33

Site Details:

National Grid Reference: SS 930 245
Height above mean sea level: 110 m
Estimated percentage shade: 5%
Land Use Code: 1
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 1
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity (cm s^{-1})	Discharge (m^3 s^{-1})	Area (m^2)	Height (cm)
3.4.1990	43			
4.5.1990	36			30
22.6.1990	57			29
4.9.1990	53	1.76	3.9	20
S.D.	9.54			27

Extinction Coefficient (K)
2.87 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
3.4.1990	0	
4.5.1990	0	0
22.6.1990	0	0
4.9.1990	0	0

Mean pH: 6.7

Plant & Sediment Composition (September 1990):

Sed N %	Sed P µg g^{-1}	Sed K µg g^{-1}	Sed Ca mg g^{-1}
0.02	0	28	0.41

Plant N %	Plant P mg g^{-1}	Plant K mg g^{-1}
3.97	3.66	28.67

Biological Data:

Maximum Number of flowers per 0·25 m^2
0

Plant species present: 19
Fontinalis antipyretica, Agrostis stolonifera, Apium nodiflorum, Epilobium hirsutum, Myriophyllum alterniflorum, Nasturtium officinale, Oenanthe crocata, Poa trivialis, Ranunculus penicillatus var *penicillatus, Salix* sp, *Avena fatua, Rumex sanguineus, Calystegia sepium, Impatiens glandulifera, Phalaris arundinacea, Petasites hybridus, Callitriche obtusangula, Alnus glutinosa, Polygonum hydropiper*

River Exe at Oakford Bridge

Site № 32

Site Details:
National Grid Reference: SS 919 219
Height above mean sea level: 100 m
Estimated percentage shade: 0%
Land Use Code: 1
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 1
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity (cm s^{-1})	Discharge (m^3 s^{-1})	Area (m^2)	Height (cm)
3.4.1990	9			
4.5.1990	24			13
22.6.1990	28	2	5	17
4.9.1990	6	.81	3.6	4
S.D.	18.9	.84		

Extinction Coefficient (K)
1.29 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
3.4.1990	0	
4.5.1990	0	0
22.6.1990	0	0
4.9.1990	0	0

Mean pH: 6.7

Plant & Sediment Composition (September 1990):

Sed N %	Sed P µg g^{-1}	Sed K µg g^{-1}	Sed Ca mg g^{-1}

No samples taken (see previous site)

Plant N %	Plant P mg g^{-1}	Plant K mg g^{-1}

No samples taken (see previous site)

Biological Data:

Maximum Number of flowers per 0·25 m^2
0

Plant species present: 18
Lemanea fluvlatilis, Fontinalis antipyretica, Agrostis stolonifera, Callitriche obtusangula, Callitriche stagnalis, Oenanthe crocata, Phalaris arundinacea, Ranunculus penicillatus var *penicillatus, Urtica dioica, Filipendula ulmaria, Rumex sanguineus, Caltha palustris, Lemna minor, Polygonum hydropiper, Elodea nuttallii, Myosotis scorpioides, Potentilla anserina*

River Fowey at Codda

Site № 42

Site Details:
National Grid Reference: SX 182 785
Height above mean sea level: 260 m
Estimated percentage shade: 15%
Land Use Code: 1
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 1
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity (cm s^{-1})	Discharge (m^3 s^{-1})	Area (m^2)	Height (cm)
2.4.1990	0	.02	.18	20
3.5.1990	0			6
21.6.1990	0	.0047	.078	6
3.9.1990	0	.017	.16	11
S.D.		.0079		

Extinction Coefficient (K)
1.28 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
2.4.1990	0	
3.5.1990	0	0
21.6.1990	0	0
3.9.1990	0	0

Mean pH: 5.5

Plant & Sediment Composition (September 1990):

Sed N %	Sed P µg g^{-1}	Sed K µg g^{-1}	Sed Ca mg g^{-1}
0.02	1.78	50.5	0.27

Plant N %	Plant P mg g^{-1}	Plant K mg g^{-1}
4.38	1.54	36

Biological Data:

Maximum Number of flowers per 0·25 m^2
14

Plant species present: 31
Clinclidotus fontinaloides, Hyocomium amoricum, Hygrohypnum luridum, Fontinalis squamosa, Liverworts (not determined), *Polytrichum commune, Alnus glutinosa, Agrostis stolonifera, Callitriche stagnalis, Eleocharis sp, Galium palustre, Glyceria fluitans, Juncus bulbosus, Juncus effusus, Myosotis scorpioides, Potamogeton natans, Ranunculus ficaria, Ranunculus flammula, Ranunculus omiophyllus, Ranunculus sceleratus, Viola palustris, Digitalis purpurea, Rubus fructicosus, Rumex sanguineus, Trichophorum cespitosum, Lotus uliginosus, Pinguicola vulgaris, Rumex acetosa, Prunus spinosa, Cytisus scoparius, Stachys palustris*

River Fowey at Golitha Woods Site № 41

Site Details:
National Grid Reference: SX 228 687
Height above mean sea level: 190 m
Estimated percentage shade: 95%
Land Use Code: 4
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 1
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity (cm s^{-1})	Discharge (m^3 s^{-1})	Area (m^2)	Height (cm)
2.4.1990	51	0.63	2.26	20
3.5.1990	23			10
21.6.1990	55	0.55	1.56	14
3.9.1990	39	0.3	1.02	11
S.D.	14.4	0.2		

Extinction Coefficient (K)
1.07 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
2.4.1990	0	
3.5.1990	0	0
21.6.1990	0	0
3.9.1990	0	0

Mean pH: 6.0

Plant & Sediment Composition (September 1990):

Sed N %	Sed P µg g^{-1}	Sed K µg g^{-1}	Sed Ca mg g^{-1}
	1.42	42	0.27

	Plant N %	Plant P mg g^{-1}	Plant K mg g^{-1}
	3.71	5.18	84

Biological Data:

Maximum Number of flowers per 0·25 m^2
0

Plant species present: 15
Amblystegium riparium, Brachythecium rivulare, Eurhynchium praelongum, Fontinalis antipyretica, Mnium hornum, Dryopteris felix-mas, Callitriche stagnalis, Oenanthe crocata, Oenanthe fluviatilis, Ranunculus penicillatus subsp. *pseudofluitans Ranunculus sceleratus, Fagus sylvatica, Potamogeton natans, Sparganium emersum, Hedera helix*

Notes
This site is part of the Golitha Woods National Nature Reserve.

River Frome at Frampton — Site № 21

Site Details:
National Grid Reference: SY 623 944
Height above mean sea level: 85 m
Estimated percentage shade: 30%
Land Use Code: 2
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 2
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity (cm s^{-1})	Discharge (m^3 s^{-1})	Area (m^2)	Height (cm)
17.4.1990	23	Discharge intermediate		27
4.6.1990	31	between Notton & Maiden Newton		27
6.7.1990	17	Too deep to measure here		28
21.9.1990	28			31
S.D.	6.13			

Extinction Coefficient (K)
1.5 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
17.4.1990	30	
4.6.1990	15	0
6.7.1990	15	0
21.9.1990	0	.5

Mean pH: 7.7

Plant & Sediment Composition (September 1990):

Sed N %	Sed P µg g^{-1}	Sed K µg g^{-1}	Sed Ca mg g^{-1}
0.03	4.9	8	2.8

	Plant N %	Plant P mg g^{-1}	Plant K mg g^{-1}
	3.47	3.7	47.67

Biological Data:

Maximum Number of flowers per 0·25 m^2
35

Plant species present: 26
Fontinalis antipyretica, Alnus glutinosa, Apium nodiflorum, Calystegia sepium, Carex riparia, Circium arvense, Epilobium hirsutum, Hedera helix, Nasturtium officinale, Oenanthe crocata, Potamogeton crispus, Potamogeton pectinatus, Ranunculus penicillatus subsp. *pseudofluitans, Solanum dulcamara, Sparganium minimum, S. erectum, Salix spp, Galium mollugo, Rumex obtusifolius, Sambucus nigra, Stachys sylvatica, Lemna minor, Veronica anagallis-aquatica, Hedera helix, Impatiens glandulifera, Symphytum officinale*

Notes
'Frome' is derived from the Celtic *fram-* which means fair river

References
A large number of studies have been carried out on the River Frome. These include; Casey & Clarke (1979, 1986), Casey & Newton (1973), Crisp *et al.* (1982), Hossell & Baker (1979), Westlake (1968), Westlake *et al.* (1972), Westlake & Dawson (1982).

River Frome at Lewell Mill

Site № 46

Site Details:
National Grid Reference: SY 739 901
Height above mean sea level: 45 m
Estimated percentage shade: 0%
Land Use Code: 2
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 5
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity (cm s^{-1})	Discharge (m^3 s^{-1})	Area (m^2)	Height (cm)
17.4.1990	55	1.74	3.17	44
4.6.1990	22	1.105	4.6	38
6.7.1990	15	0.62	3.96	38
20.9.1990	14	0.5	3.49	28
S.D.	19.3	0.56		

Extinction Coefficient (K)
1.99 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
17.4.1990	5	
4.6.1990	8	0
6.7.1990	20	.8
20.9.1990	0	0

Mean pH: 7.4

Plant & Sediment Composition (September 1990):

Sed N %	Sed P µg g^{-1}	Sed K µg g^{-1}	Sed Ca mg g^{-1}
0	5	17	4.83

	Plant N %	Plant P mg g^{-1}	Plant K mg g^{-1}
	3.24		

Biological Data:

Maximum Number of flowers per 0·25 m^2

Plant species present: 20
Cladophora, Fontinalis antipyretica, Apium nodiflorum, Callitriche stagnalis, C. platycarpa, Elodea nuttallii, Glyceria maxima, Glyceria fluitans, Ranunculus penicillatus subsp. *pseudofluitans, Sparganium emersum, Veronica beccabunga, Juncus effusus, Lemna minor, L. miniscula, Nasturtium officinale, Oenanthe fluviatile, Phalaris arundinacea, Poa annua, Ranunculus sceleratus, Myriophyllum spicatum*

River Frome at Lower Brockhampton

Site № 18

Site Details:
National Grid Reference: SY 721 904
Height above mean sea level: 48 m
Estimated percentage shade: 30%
Land Use Code: 2
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 3
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity (cm s^{-1})	Discharge (m^3 s^{-1})	Area (m^2)	Height (cm)
17.4.1990	21	.44	3.22	38
4.6.1990	9	.28	3.54	36
6.7.1990	10	.43	2.91	45
24.9.1990	0	.022	3	15
S.D.	8.6	.19		

Extinction Coefficient (K)
2.74 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
17.4.1990	10	
4.6.1990	15	0
6.7.1990	30	0
24.9.1990	0	0

Mean pH: 7.3

Plant & Sediment Composition (September 1990):

Sed N %	Sed P µg g^{-1}	Sed K µg g^{-1}	Sed Ca mg g^{-1}
0.24	4.89	201	5.31

	Plant N %	Plant P mg g^{-1}	Plant K mg g^{-1}
	2.81	4.05	60

Biological Data:

Maximum Number of flowers per 0·25 m^2
10

Plant species present: 23
Alnus glutinosa, Apium nodiflorum, Epilobium hirsutum, Glyceria maxima, Nasturtium officinale, Oenanthe fluviatilis, Oenanthe crocata, Petasites hybridus, Phalaris arundinacea, Ranunculus penicillatus subsp. *pseudofluitans, Veronica anagallis-aquatilis, Fraxinus excelsior, Callitriche platycarpa, C. stagnalis, C. obtusangula, Lemna minor, Lemna miniscula, Myosotis scorpioides, Elodea canadensis, Glyceria fluitans, Solanum dulcamara, Symphytum officinale, Valeriana dioica*

River Frome at Maiden Newton

Site № 23

Site Details:
National Grid Reference: SY 597 977
Height above mean sea level: 95 m
Estimated percentage shade: 5%
Land Use Code: 1
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 3
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity ($cm\ s^{-1}$)	Discharge ($m^3\ s^{-1}$)	Area (m^2)	Height (cm)
18.4.1990	16	.136	.69	18
4.6.1990	0	.11	.7	26
5.7.1990	26	.18	.91	35
21.9.1990	21	.07	.56	28
S.D.	11.3	.05		

Extinction Coefficient (K)
2.02 (mean value)

Chemical Data:

	Nitrate ($mgN\ l^{-1}$)	Phosphate ($mgP\ l^{-1}$)
18.4.1990	20	
4.6.1990	15	.5
5.7.1990	15	.75
21.9.1990	0	0

Mean pH: 7.5

Plant & Sediment Composition (September 1990):

Sed N %	Sed P $\mu g\ g^{-1}$	Sed K $\mu g\ g^{-1}$	Sed Ca $mg\ g^{-1}$
No sample taken - see other Frome sites			

	Plant N %	Plant P $mg\ g^{-1}$	Plant K $mg\ g^{-1}$
No sample taken - see other Frome sites			

Biological Data:

Maximum Number of flowers per 0·25 m²
76

Plant species present: 26
Agrostis stolonifera, Alnus glutinosa, Callitriche platycarpa, Callitriche stagnalis, Juncus articulatus, Juncus bulbosus, Oenanthe crocata, Ranunculus penicillatus subsp. *pseudofluitans, Glyceria plicata, Catabrosa aquatica, Epilobium hirsutum, Nasturtium officinale, Ranunculus sceleratus, Veronica anagallis-aquatica, Veronica beccabunga, Sambucus nigra, Glyceria maxima, Polygonum hydropiper, Pulicaria dysentrica, Urtica dioica, Arrhenatherum elatius, Bromus erectus, Filipendula ulmaria, Rumex sanguineus, Circium arvense, Equisetum fluviatile*

River Frome at Moreton

Site № 19

Site Details:
National Grid Reference: SY 806 895
Height above mean sea level: 25 m
Estimated percentage shade: 30%
Land Use Code: 2
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 2
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity (cm s^{-1})	Discharge (m^3 s^{-1})	Area (m^2)	Height (cm)
17.4.1990	30	See Lewell Mill		28
4.5.1990	43			22
6.7.1990	50			20
21.9.1990	40			13
S.D.	8.3			

Extinction Coefficient (K)
2.6 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
17.4.1990	20	
4.5.1990	20	.6
6.7.1990	20	.6
21.9.1990	10	.6

Mean pH: 7.6

Plant & Sediment Composition (September 1990):

Sed N %	Sed P µg g^{-1}	Sed K µg g^{-1}	Sed Ca mg g^{-1}
No sample taken - see other Frome sites			

Plant N %	Plant P mg g^{-1}	Plant K mg g^{-1}
No sample taken - see other Frome sites		

Biological Data:

Maximum Number of flowers per 0·25 m^2
0

Plant species present: 13
Glyceria maxima, *Ranunculus penicillatus* subsp. *pseudofluitans*, *Carex acuta*, *Fontinalis antipyretica*, *Veronica anagallis-aquatica*, *Rumex sanguineus*, *Eupatorium cannabinum*, *Lemna minor*, *Nasturtium officinale*, *Polygonum hydropiper*, *Scrophularia aquatica*, *Urtica dioica*, *Poa annua*

River Frome at Notton

Site № 22

Site Details:
National Grid Reference: SY 610 959
Height above mean sea level: 87 m
Estimated percentage shade: 0%
Land Use Code: 2
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 3
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity (cm s^{-1})	Discharge (m^3 s^{-1})	Area (m^2)	Height (cm)
18.4.1990	62	1.46	1.39	43
4.6.1990	31	.64	2.13	44
6.7.1990	36	.65	2.01	41
21.9.1990	17	.3	1.64	28
S.D.	18.8	.49		

Extinction Coefficient (K)
1.52 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
18.4.1990	2	
4.6.1990	20	0
6.7.1990	10	0
21.9.1990	0	.5

Mean pH: 8

Plant & Sediment Composition (September 1990):

Sed N %	Sed P µg g^{-1}	Sed K µg g^{-1}	Sed Ca mg g^{-1}
0.03	2.79	8	2.79

	Plant N %	Plant P mg g^{-1}	Plant K mg g^{-1}
	2.76	2.56	29.27

Biological Data:

Maximum Number of flowers per 0·25 m^2
0

Plant species present: 19
Fontinalis antipyretica, Circium arvense, Epilobium hirsutum, Myriophyllum spicatum, Phalaris arundinacea, Ranunculus penicillatus subsp. *pseudofluitans, Sparganium emersum, S. minimum, Rumex obtusifolius, Glyceria maxima, Sparganium angustifolium, Veronica anagallis-aquatica, Glyceria declinata, Apium nodiflorum, Urtica dioica, Arrhenatherum elatius Lemna minor, L. triscula, Galium mollugo*

River Gwendraeth Fach at Llangeiderne

Site № 29

Site Details:
National Grid Reference: SN 460 139
Height above mean sea level: 45 m
Estimated percentage shade: 0%
Land Use Code: 2
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 5
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity (cm s^{-1})	Discharge (m^3 s^{-1})	Area (m^2)	Height (cm)
10.4.1990	26	.34	1.44	32
16.5.1990	28	.32	1.57	19
27.6.1990	86	.51	.71	21
19.9.1990	61	.37	.6	18
S.D.	28.7	.09		

Extinction Coefficient (K)
1.8 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
10.4.1990	0	
16.5.1990	0	0
27.6.1990	10	.6
19.9.1990	0	0

Mean pH: 7.2

Plant & Sediment Composition (September 1990):

Sed N %	Sed P µg g^{-1}	Sed K µg g^{-1}	Sed Ca mg g^{-1}
0.02	3.5	79	2.76

Plant N %	Plant P mg g^{-1}	Plant K mg g^{-1}
5.1	3.66	107

Biological Data:

Maximum Number of flowers per 0·25 m^2
30

Plant species present: 20
Fontinalis antipyretica, Apium nodiflorum, Glyceria maxima, Juncus bulbosus, Oenanthe crocata, Phalaris arundinacea, Polygonum hydropiper, Potamogeton natans, Ranunculus penicillatus var *penicillatus, Sparganium erectum, S. emersum, S. minimum, Rumex sanguineus, Callitriche hamulata, Callitriche stagnalis, Epilobium hirsutum, Glyceria fluitans, Circium arvense, Ranunculus sceleratus, Urtica dioica*

Hillfarrance Brook at Hillfarrance Site № 31

Site Details:
National Grid Reference: ST 157 248
Height above mean sea level: 35 m
Estimated percentage shade: 0%
Land Use Code: 2
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 2
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity (cm s^{-1})	Discharge (m^3 s^{-1})	Area (m^2)	Height (cm)
3.4.1990	61	.79	1.25	25
22.6.1990	35	.32	.79	22
4.9.1990	30	.23	.47	20
S.D.	16.6	.3		

Extinction Coefficient (K)
3.57 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
4.5.1990	30	0.8
22.6.1990	45	1.4
4.9.1990	20	2

Mean pH: 7.2

Plant & Sediment Composition (September 1990):

Sed N %	Sed P µg g^{-1}	Sed K µg g^{-1}	Sed Ca mg g^{-1}
0	6.85	24	2.79

	Plant N %	Plant P mg g^{-1}	Plant K mg g^{-1}
	3.6	4.82	18.5

Biological Data:

Maximum Number of flowers per 0·25 m^2
10

Plant species present: 23
Fontinalis antipyretica, Phalaris arundinacea, Ranunculus penicillatus subsp. *pseudofluitans, Alnus glutinosa, Apium nodiflorum, Oenanthe crocata, Epilobium hirsutum, Circium arvense, Poa trivialis, Scrophularia aquatica, Solanum dulcamara, Sparganium emersum, S. erectum, Urtica dioica, Filipendula ulmaria, Rumex obtusifolius, Rumex sanguineus, Glyceria fluitans, G. declinata, Glechoma hederacea, Calystegia sepium, Cardamine hirsuta, Circium arvense*

River Itchen at Brambridge House — Site № 5

Site Details:
National Grid Reference: SU 462 225
Height above mean sea level: 15 m
Estimated percentage shade: 0%
Land Use Code: 4
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 1
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity (cm s^{-1})	Discharge (m^3 s^{-1})	Area (m^2)	Height (cm)
23.4.1990	67	3.99	6.18	35
14.5.1990	40	3.16	5.43	28
2.7.1990	54	2.64	5.03	34
26.9.1990	41	2.01	4.48	34
S.D.	12.7	0.61		

Extinction Coefficient (K)
2.4 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
23.4.1990	10	
14.5.1990	20	0
2.7.1990	50	.2
26.9.1990	8	0

Mean pH: 7.4

Plant & Sediment Composition (September 1990):

Sed N %	Sed P µg g^{-1}	Sed K µg g^{-1}	Sed Ca mg g^{-1}
0.01	See other Itchen samples		

	Plant N %	Plant P mg g^{-1}	Plant K mg g^{-1}
	3.66	2.99	59.5

Biological Data:

Maximum Number of flowers per 0·25 m^2
0

Plant species present: 21
Fontinalis antipyretica, Apium nodiflorum, Carex acutiformis, Oenanthe crocata, O. fluviatilis, Ranunculus penicillatus subsp. *pseudofluitans, Fraxinus excelsior, Rubus fructicosus, Epilobium hirsutum, Glyceria maxima, Nasturtium officinale, Scrophularia aquatica, Solanum dulcamara, Veronica beccabunga, Eupatorium cannabinum, Petasites hybridus, Impatiens glandulifera, Veronica anagallis-aquatica, Filipendula ulmaria, Lemna minor, L. miniscula*

References
Butcher (1927)

River Itchen at Chiland

Site № 7

Site Details:
National Grid Reference: SU 523 325
Height above mean sea level: 45 m
Estimated percentage shade: 5%
Land Use Code: 5
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 3
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity (cm s^{-1})	Discharge (m^3 s^{-1})	Area (m^2)	Height (cm)
23.4.1990	129	3.91	4.47	56
14.5.1990	71	3.49	4.68	34
2.7.1990	57	2.58	4.66	50
26.9.1990	40	2.22	5.23	58
S.D.	38.6	0.78		

Extinction Coefficient (K)
1.71 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
23.4.1990	10	
14.5.1990	10	0
2.7.1990	20	0
26.9.1990	0	0

Mean pH: 7.3

Plant & Sediment Composition (September 1990):

Sed N %	Sed P µg g^{-1}	Sed K µg g^{-1}	Sed Ca mg g^{-1}
0.12	11.85	54.3	6.23

	Plant N %	Plant P mg g^{-1}	Plant K mg g^{-1}
	4.56	5.1	54.67

Biological Data:

Maximum Number of flowers per 0·25 m^2
0

Plant species present: 22
Fontinalis antipyretica, Agrostis stolonifera, Apium nodiflorum, Nasturtium officinale, Phalaris arundinacea, Phragmites australis, Ranunculus penicillatus subsp. *pseudofluitans, Sparganium emersum, Sparganium minimum, Epilobium hirsutum, Callitriche stagnalis, Callitriche obtusangula, Callitriche platycarpa, Veronica anagallis-aquatica, Veronica beccabunga, Poa trivialis, Petasites hybridus, Ranunculus sceleratus, Scirpus lacustris, Scrophularia aquatica, Solanum dulcamara, Fraxinus excelsior*

River Itchen at Winchester

Site № 6

Site Details:
National Grid Reference: SU 486 296
Height above mean sea level: 50 m
Estimated percentage shade: 15%
Land Use Code: 5
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 3
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity (cm s^{-1})	Discharge (m^3 s^{-1})	Area (m^2)	Height (cm)
23.4.1990	70	5.33	7.59	62
14.5.1990	60	4.57	7.1	63
2.7.1990	58	3.66	6.25	70
26.9.1990	46	2.53	5.61	70
S.D.	9.85	1.21		

Extinction Coefficient (K)
1.7 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
23.4.1990	5	
14.5.1990	10	1.2
2.7.1990	30	.75
26.9.1990	10	0

Mean pH: 7.3

Plant & Sediment Composition (September 1990):

Sed N %	Sed P µg g^{-1}	Sed K µg g^{-1}	Sed Ca mg g^{-1}
0.01	3.41		4.83

Plant N %	Plant P mg g^{-1}	Plant K mg g^{-1}
3.41	5.21	60

Biological Data:

Maximum Number of flowers per 0·25 m^2
0

Plant species present: 9
Fontinalis antipyretica, Apium nodiflorum, Callitriche platycarpa, Callitriche stagnalis, Oenanthe fluviatilis, Ranunculus penicillatus subsp. *pseudofluitans, Sparganium minimum, Sparganium emersum, Elodea canadensis*

Notes
The low number of species is probably due to the iron banks of the river as it passes through the city.

River Kennet at Lockeridge

Site № 56

Site Details:
National Grid Reference: SU 150 683
Height above mean sea level: 130 m
Estimated percentage shade: 5%
Land Use Code: 3
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 1
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity (cm s^{-1})	Discharge (m^3 s^{-1})	Area (m^2)	Height (cm)
9.5.1990	21	.051	.982	30
14.6.1990	11	.002	.00017	16.
5.9.1990	0	0	0	0
S.D.	10.5	0.03		

Extinction Coefficient (K)
5.28 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
9.5.1990	8	0
14.6.1990	12	0

Mean pH: 7.73

Plant & Sediment Composition (September 1990):

Sed N %	Sed P µg g^{-1}	Sed K µg g^{-1}	Sed Ca mg g^{-1}
0.10	17.7	93	5.07

Plant N %	Plant P mg g^{-1}	Plant K mg g^{-1}
3.79	2.49	42.5

Biological Data:

Maximum Number of flowers per 0·25 m^2
86

Plant species present: 22
Fontinalis antipyretica, Agrostis stolonifera, Apium nodiflorum, Epilobium hirsutum, Nasturtium officinale, Phalaris arundinacea, Polygonum amphibium, Ranunculus peltatus, Solanum dulcamara, Sparganium erectum, Urtica dioica, Veronica anagallis-aquatica, Veronica beccabunga, Filipendula ulmaria, Rumex sanguineus, Rumex obtusifolius, Symphytum officinale, Myosotis scorpioides, Chenopodium album, Mentha aquatica, Salix sp, *Matricaria matricaria*

Note
This site is a winterbourne and was dried up by the last visit. 'Kennet' is derived from the Celtic *cunetio* which means regal or holy.

River Loddon at Old Basing

Site № 4

Site Details:
National Grid Reference: SU 660 528
Height above mean sea level: 75 m
Estimated percentage shade: 10%
Land Use Code: 4
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 3
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity ($cm\ s^{-1}$)	Discharge ($m^3\ s^{-1}$)	Area (m^2)	Height (cm)
25.4.1990	27	.46	1.92	25
13.5.1990	21	.42	1.95	24
4.7.1990	25	.56	2.35	29
28.9.1990	16	.24	1.36	26
S.D.	4.68	.07		

Extinction Coefficient (K)
2.5 (mean value)

Chemical Data:

	Nitrate ($mgN\ l^{-1}$)	Phosphate ($mgP\ l^{-1}$)
25.4.1990	15	
13.5.1990	20	0
4.7.1990	15	0
28.9.1990	10	0

Mean pH: 7

Plant & Sediment Composition (September 1990):

Sed N %	Sed P $\mu g\ g^{-1}$	Sed K $\mu g\ g^{-1}$	Sed Ca $mg\ g^{-1}$
0.13	3.52	56	6.21

Plant N %	Plant P $mg\ g^{-1}$	Plant K $mg\ g^{-1}$
2.25	2.63	33.4

Biological Data:

Maximum Number of flowers per 0·25 m^2
30

Plant species present: 25
Apium nodiflorum, Callitriche platycarpa, Callitriche stagnalis, Callitriche obtusangula, Lemna minor, Carex acutiformis, Carex riparia, Epilobium hirsutum, Phalaris arundinacea, Ranunculus penicillatus subsp. *pseudofluitans, Veronica anagallis-aquatica, Veronica beccabunga, Filipendula ulmaria, Rumex sanguineus, Ranunculus sceleratus, Agrostis stolonifera, Glyceria maxima, Myosotis scorpioides, Petasites hybridus, Solanum dulcamara, Arrhenatherum elatius, Aesculus hippocastanum, Stachys sylvatica, Phragmites australis, Scrophularia aquatica*

Notes
This site is upstream of the sewage works that affect the other sites on the Loddon

River Loddon at Twyford

Site № 49

Site Details:
National Grid Reference: SU 782 761
Height above mean sea level: 40 m
Estimated percentage shade: 20%
Land Use Code: 2
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 4
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity (cm s^{-1})	Discharge (m^3 s^{-1})	Area (m^2)	Height (cm)
25.4.1990	35	.078	.27	12
15.5.1990	19	.008	.08	8
4.7.1990	17	.0085	.058	2.4
28.9.1990	0	0	0	0
S.D.	14.3	0.004		

Extinction Coefficient (K)
3.8 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
25.4.1990	20	
15.5.1990	25	>3
4.7.1990	30	>3
28.9.1990		

Mean pH: 7.1

Plant & Sediment Composition (September 1990):

Sed N %	Sed P µg g^{-1}	Sed K µg g^{-1}	Sed Ca mg g^{-1}
No sample taken			

Plant N %	Plant P mg g^{-1}	Plant K mg g^{-1}
No sample taken		

Biological Data:

Maximum Number of flowers per 0·25 m^2
0

Plant species present: 23
Apium nodiflorum, Glyceria maxima, Oenanthe crocata, Phalaris arundinacea, Ranunculus fluitans, Sparganium emersum, S. erectum, Urtica dioica, Veronica anagallis-aquatica, Veronica beccabunga, Rumex sanguineus, Myosotis scorpioides, Brassica oleracea, Solanum dulcamara, Alnus glutinosa, Impatiens glandulifera, Epilobium hirsutum, Lemna minor, Salix sp, *Mentha aquatica, Polygonum hydropiper, Poa trivialis, Silene alba*

Notes
On the last visit the river consisted of pools which were not joined. ID of the *Ranunculus* uncertain.

River Loddon at Wildmoor

Site № 3

Site Details:
National Grid Reference: SU 692 559
Height above mean sea level: 50 m
Estimated percentage shade: 0%
Land Use Code: 3
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 3
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity (cm s^{-1})	Discharge (m^3 s^{-1})	Area (m^2)	Height (cm)
25.4.1990	24	1.01	3.83	44
15.5.1990	23	.8	3.53	48
4.7.1990	30	.5	3.5	55
28.9.1990	33	.7	3.7	57
S.D.	4.8	.75		

Extinction Coefficient (K)
3.13 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
25.4.1990	25	
15.5.1990	25	>3
4.7.1990	50	>3
28.9.1990	40	>3

Mean pH: 7.5

Plant & Sediment Composition (September 1990):

Sed N %	Sed P µg g^{-1}	Sed K µg g^{-1}	Sed Ca mg g^{-1}
0.03	3.27	36	4.88

	Plant N %	Plant P mg g^{-1}	Plant K mg g^{-1}
		10.53	58

Biological Data:

Maximum Number of flowers per 0·25 m^2
0

Plant species present: 25
Carex riparia, *Glyceria maxima*, *Myriophyllum spicatum*, *Phalaris arundinacea*, *Ranunculus penicillatus* subsp. *pseudofluitans*, *Sparganium erectum*, *Salix spp*, *Sambucus nigra*, *Callitriche stagnalis*, *C. obtusangula*, *Elodea canadensis*, *Epilobium hirsutum*, *Galium palustre*, *Lemna minor*, *Mentha aquatica*, *Myosotis scorpioides*, *Scirpus lacustris*, *Urtica dioica*, *Rubus fructicosus*, *Nasturtium officinale*, *Scrophularia aquatica*, *Sambucus nigra*, *Solanum dulcamara*, *Veronica anagallis-aquatica*, *Juncus effusus*,

River Lugg at Mortimer's Cross

Site № 25

Site Details:
National Grid Reference: SO 427 637
Height above mean sea level: 90 m
Estimated percentage shade: 0%
Land Use Code: 2
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 1
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity ($cm\ s^{-1}$)	Discharge ($m^3\ s^{-1}$)	Area (m^2)	Height (cm)
11.4.1990	70	2.12	3.39	22
16.5.1990	61	1.5	2.5	10
25.6.1990	48	.86	1.85	21
18.9.1990	76	.78	1.73	19
S.D.	12.2	.63		

Extinction Coefficient (K)
2.6 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
11.4.1990	15	
16.5.1990	15	0
25.6.1990	20	0
18.9.1990	10	0

Mean pH: 7.5

Plant & Sediment Composition (September 1990):

Sed N %	Sed P $\mu g\ g^{-1}$	Sed K $\mu g\ g^{-1}$	Sed Ca $mg\ g^{-1}$
0	0.03	60	4.45

	Plant N %	Plant P $mg\ g^{-1}$	Plant K $mg\ g^{-1}$
	1.63	1.45	21.93

Biological Data:

Maximum Number of flowers per 0·25 m^2
1

Plant species present: 23
Amblystegium riparium, Lemanea fluviatilis, Fontinalis antipyretica, Leskea polycarpa, Isothecium myosuroides, Callitriche platycarpa, Glyceria maxima, Oenanthe crocata, Phalaris arundinacea, Ranunculus penicillatus subsp. *pseudofluitans, Ranunculus fluitans, Sparganium erectum, Veronica anagallis-aquatica, Veronica beccabunga, Rumex obtusifolius, Rumex sanguineus, Symphytum officinale, Impatiens glandulifera, Myosotis scorpioides, Mentha aquatica, Elodea canadensis, Epilobium hirsutum, Calystegia sepium*

References
Brooker *et al.* (1978), Barfield *et al.* (1983), and Brian (1983)

Lymington River at Ivy wood — Site № 44

Site Details:
National Grid Reference: SU 316 023
Height above mean sea level: 8 m
Estimated percentage shade: 40%
Land Use Code: 4
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 1
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity (cm s^{-1})	Discharge (m^3 s^{-1})	Area (m^2)	Height (cm)
5.4.1990	25	.47	1.23	16
8.5.1990	5	.2	1.48	17
13.6.1990	1	.16	1.07	14
6.9.1990	26	.12	.45	14.5
S.D.				

Extinction Coefficient (K)
2.63 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
5.4.1990	0	
8.5.1990	0	1.4
13.6.1990	0	.7
6.9.1990	2	>3

Mean pH: 6.2

Plant & Sediment Composition (September 1990):

Sed N %	Sed P µg g^{-1}	Sed K µg g^{-1}	Sed Ca mg g^{-1}
0	8.5	37.5	0.55

Plant N %	Plant P mg g^{-1}	Plant K mg g^{-1}
3.07	9.88	36

Biological Data:

Maximum Number of flowers per 0·25 m^2
34

Plant species present: 30
Athryum felix-femina, Agrostis stolonifera, Alisma lanceolatum, Apium nodiflorum, Bidens tripartita, Callitriche hamulata, Callitriche stagnalis, Callitriche obtusangula, Cardamine hirsuta, Elodea canadensis, Elodea nuttallii, Glyceria maxima, Juncus articulatus, Mentha aquatica, Lychnis floc-cocci, Myosotis scorpioides, Oenanthe fluviatilis, Polygonum hydropiper, Ranunculus flammula, Ranunculus peltatus, Ranunculus sceleratus, Rosa sp, *Scrophularia aquatica, Sparganium emersum, Sparganium minimum, Urtica dioica, Veronica beccabunga Rubus fructicosus, Rumex sanguineus, Valeriana dioica*

Notes
'Lym' is derived from the Celtic *leamhan* which means elm.

Mill Lawn Brook at Mill Lawn House

Site № 45

Site Details:

National Grid Reference: SU 224 035
Height above mean sea level: 40 m
Estimated percentage shade: 0%
Land Use Code: 1
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 4
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity (cm s^{-1})	Discharge (m^3 s^{-1})	Area (m^2)	Height (cm)
5.4.1990	0	.01	.065	9
8.5.1990	0	.0036	.1175	13
13.6.1990	0	.0056	.12	11
6.9.1990	0	.0034	.12	10
S.D.	0	.003		

Extinction Coefficient (K)
2.6 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
5.4.1990	0	
8.5.1990	8	0
13.6.1990	10	0
6.9.1990	0	0

Mean pH: 6.7

Plant & Sediment Composition (September 1990):

Sed N %	Sed P µg g^{-1}	Sed K µg g^{-1}	Sed Ca mg g^{-1}
0.07		88	0.8

	Plant N %	Plant P mg g^{-1}	Plant K mg g^{-1}
	4.12		104

Biological Data:

Maximum Number of flowers per 0·25 m^2

Plant species present: 17
Apium nodiflorum, Callitriche platycarpa, Cardamine pratensis, Elodea nuttallii, Glyceria declinata, Juncus articulatus, Nasturtium officinale, Ranunculus penicillatus subsp. *pseudofluitans, Ranunculus flammula, Ranunculus hederaceus, Ranunculus omiophyllus, Ranunculus bulbosus, Ranunculus sceleratus, Veronica beccabunga, Lemna minor, Polygonum hydropiper, Elatine* sp

River Piddle at Affpuddle

Site № 17

Site Details:

National Grid Reference: SY 806 938
Height above mean sea level: 35 m
Estimated percentage shade: 0%
Land Use Code: 2
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 5
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity ($cm\ s^{-1}$)	Discharge ($m^3\ s^{-1}$)	Area (m^2)	Height (cm)
18.4.1990	14	.55	3.18	40
5.5.1990	12	.23	2.06	36
6.6.1990	25	.42	1.52	28
24.9.1990	4	.0078	1.5	14
S.D.	8.66	.24		

Extinction Coefficient (K)
1.56 (mean value)

Chemical Data:

	Nitrate ($mgN\ l^{-1}$)	Phosphate ($mgP\ l^{-1}$)
18.4.1990	3	
5.5.1990	50	0
6.6.1990	40	0
24.9.1990	10	0

Mean pH: 7.9

Plant & Sediment Composition (September 1990):

Sed N %	Sed P $\mu g\ g^{-1}$	Sed K $\mu g\ g^{-1}$	Sed Ca $mg\ g^{-1}$
0	4.56	24	4.37

Plant N %	Plant P $mg\ g^{-1}$	Plant K $mg\ g^{-1}$
1.61	See other Piddle site	

Biological Data:

Maximum Number of flowers per 0·25 m^2
17

Plant species present: 20
Agrostis stolonifera, Callitriche platycarpa, C. stagnalis, Glyceria fluitans, Phalaris arundinacea, Ranunculus penicillatus subsp. *pseudofluitans, Ranunculus sceleratus, Ranunculus repens, Sparganium erectum, Veronica anagallis-aquatica, Veronica beccabunga, Crataegus monogyna, Rumex sanguineus, Iris pseudacorus, Mentha aquatica, Lemna minor, Nasturtium officinale, Urtica dioica, Plantago lanceolata, Epilobium hirsutum*

References
Casey & Newton (1973), Dawson (1980), Westlake *et al.* (1972)

River Piddle at Hyde

Site № 16

Site Details:

National Grid Reference: SY 865 906
Height above mean sea level: 20 m
Estimated percentage shade: 40%
Land Use Code: 4
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 1
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity (cm s^{-1})	Discharge (m^3 s^{-1})	Area (m^2)	Height (cm)
20.4.1990	38	1.54	4.2	43
5.6.1990	32	.9	3.53	37
6.6.1990	23	.69	3.53	39
20.9.1990	11	0.28	2.83	29
S.D.	11.7	.53		

Extinction Coefficient (K)
3 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
20.4.1990	0	
5.6.1990	15	0
6.6.1990	25	0
20.9.1990	0	0

Mean pH: 7.6

Plant & Sediment Composition (September 1990):

Sed N %	Sed P µg g^{-1}	Sed K µg g^{-1}	Sed Ca mg g^{-1}
0.03	3.75	24	3.61

Plant N %	Plant P mg g^{-1}	Plant K mg g^{-1}
3.32	3.36	39

Biological Data:

Maximum Number of flowers per 0·25 m^2
0

Plant species present: 19
Fontinalis antipyretica, Apium nodiflorum, Carex acutiformis, Glyceria maxima, Glyceria fluitans, Iris pseudacorus, Oenanthe crocata, Phalaris arundinacea, Ranunculus penicillatus subsp. *pseudofluitans, Corylus avellena, Filipendula ulmaria, Symphytum officinale, Callitriche stagnalis, Calystegia sepium, Epilobium hirsutum, Mentha aquatica, Solanum dulcamara, Veronica anagallis-aquatica, Pulicaria dysentrica*

River Rye at East Newton

Site № 26

Site Details:
National Grid Reference: SE 644 805
Height above mean sea level: 40 m
Estimated percentage shade: 20%
Land Use Code: 3
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 2
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity (cm s^{-1})	Discharge (m^3 s^{-1})	Area (m^2)	Height (cm)
28.5.1990	69	1.38	2.31	25
8.6.1990	65	1.2	1.99	18
31.7.1990	53	.87	1.53	16
13.9.1990	50	.89	1.93	16
S.D.	9.18	.25		

Extinction Coefficient (K)
1.5 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
28.5.1990	0	
8.6.1990	0	0
31.7.1990	0	0
13.9.1990	0	0

Mean pH: 7.6

Plant & Sediment Composition (September 1990):

Sed N %	Sed P µg g^{-1}	Sed K µg g^{-1}	Sed Ca mg g^{-1}
0	0	47	4.24

	Plant N %	Plant P mg g^{-1}	Plant K mg g^{-1}
	4.81	2.5	39.6

Biological Data:

Maximum Number of flowers per 0·25 m^2
33

Plant species present: 18
Agrostis stolonifera, Alopecurus geniculatus, Apium nodiflorum, Alnus glutinosa, Epilobium hirsutum, Galium aparine, Glyceria fluitans, Impatiens glandulifera, Lemna minor, Phalaris arundinacea, Potentilla anserina, Ranunculus penicillatus subsp. *pseudofluitans, Ranunculus fluitans, Rumex obtusifolius, Urtica dioica, Veronica anagallis-aquatica, Veronica beccabunga*

Notes
Anecdotal evidence from anglers indicates that *Ranunculus* has become much more abundant here in the last twenty years or so. This site was used for the experiment described in chapter four.

Salisbury Avon at Middle Woodsford

Site № 12

Site Details:

National Grid Reference: SU 120 361
Height above mean sea level: 60 m
Estimated percentage shade: 10%
Land Use Code: 4
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 2
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity ($cm\ s^{-1}$)	Discharge ($m^3\ s^{-1}$)	Area (m^2)	Height (cm)
6.4.1990	79	3	6	56
9.5.1990	49	2.35	5.83	38
14.6.1990	48	2.24	4.5	30
5.9.1990	19	1.1	5.86	48
S.D.	24.5	.79		

Extinction Coefficient (K)
3.4 (mean value)

Chemical Data:

	Nitrate ($mgN\ l^{-1}$)	Phosphate ($mgP\ l^{-1}$)
6.4.1990	0	
9.5.1990	8	.7
14.6.1990	8	.8
5.9.1990	10	1.5

Mean pH: 7.6

Plant & Sediment Composition (September 1990):

Sed N %	Sed P $\mu g\ g^{-1}$	Sed K $\mu g\ g^{-1}$	Sed Ca $mg\ g^{-1}$
0.11	See other Avon sites		

	Plant N %	Plant P $mg\ g^{-1}$	Plant K $mg\ g^{-1}$
	4.85	4.24	43.5

Biological Data:

Maximum Number of flowers per 0·25 m^2
10

Plant species present: 22
Ranunculus penicillatus subsp. *pseudofluitans, Ranunculus fluitans, Epilobium hirsutum, Solanum dulcamara, Symphytum officinale, Chamaenerion angustifolium, Montia fontana, Myosotis scorpioides, Nasturtium officinale, Ranunculus sceleratus, Scrophularia aquatica, Urtica dioica, Filipendula ulmaria, Galium palustre, Impatiens glandulifera, Impatiens capensis, Mentha aquatica, Polygonum amphibium, Urtica dioica, Epilobium roseum, Lycopus europaeus, Lythrum salicaria*

Notes
'Avon' is from the Celtic *abona* which means river or water.

Salisbury Avon at Netheravon

Site № 11

Site Details:

National Grid Reference: SU 150 485
Height above mean sea level: 90 m
Estimated percentage shade: 5%
Land Use Code: 4
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 2
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity (cm s^{-1})	Discharge (m^3 s^{-1})	Area (m^2)	Height (cm)
6.4.1990	75	2.89	4	25
9.5.1990	47	1.21	2.89	18
14.6.1990	52	1.16	2.3	11
5.9.1990	49	.48	2.28	18
S.D.	13	1.03		

Extinction Coefficient (K)
2.58 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
6.4.1990	12	
9.5.1990	10	.6
14.6.1990	10	.75
5.9.1990	10	.9

Mean pH: 7.5

Plant & Sediment Composition (September 1990):

Sed N %	Sed P µg g^{-1}	Sed K µg g^{-1}	Sed Ca mg g^{-1}
See other Avon sites			

Plant N %	Plant P mg g^{-1}	Plant K mg g^{-1}
4.9	3.28	62

Biological Data:

Maximum Number of flowers per 0·25 m^2
38

Plant species present: 23
Ranunculus penicillatus subsp. *pseudofluitans, Veronica anagallis-aquatica, Arrhenatherum elatius, Apium nodiflorum, Catabrosa aquatica, Epilobium hirsutum, Glyceria maxima, Nasturtium officinale, Phalaris arundinacea, Polygonum hydropiper, Poa trivialis, Symphytum officinale, Berula erecta, Callitriche obtusangula, Callitriche platycarpa, Elodea nuttallii, Lemna minor, Myosotis scorpioides, Potamogeton pectinatus, Solanum dulcamara, Sparganium emersum, Urtica dioica, Veronica beccabunga*

Notes
Subject to periodic high sediment loads from tank crossing upstream.

Salisbury Avon at Upavon

Site № 10

Site Details:
National Grid Reference: SU 136 550
Height above mean sea level: 98 m
Estimated percentage shade: 30%
Land Use Code: 5
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 3
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity (cm s^{-1})	Discharge (m^3 s^{-1})	Area (m^2)	Height (cm)
6.4.1990	35	1.45	3.83	27
9.5.1990	40	1.17	2.99	19
14.6.1990	46	.74	1.92	20
5.9.1990	25	.47	2.44	22
S.D.	8.89	.44		

Extinction Coefficient (K)
2.98 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
6.4.1990	5	
9.5.1990	15	1.3
14.6.1990	30	1.5
5.9.1990	15	1.2

Mean pH: 7.7

Plant & Sediment Composition (September 1990):

Sed N %	Sed P µg g^{-1}	Sed K µg g^{-1}	Sed Ca mg g^{-1}
0.09	0.6	40	4.5

Plant N %	Plant P mg g^{-1}	Plant K mg g^{-1}
4.84	6.16	130

Biological Data:

Maximum Number of flowers per 0·25 m^2
0

Plant species present: 17
Fontinalis antipyretica, Callitriche platycarpa, Hedera helix, Ranunculus fluitans, Salix sp, Sambucus nigra, Ulmus minor, Acer psuedoplatanus, Callitriche stagnalis, Cornus sanguinea, Glechoma hederacea, Lemna minor, Mentha aquatica, Myosotis scorpioides, Myriophyllum spicatum, Phalaris arundinacea, Scrophularia aquatica

Salisbury Avon at Woodgreen

Site № 13

Site Details:
National Grid Reference: SU 163 174
Height above mean sea level: 30 m
Estimated percentage shade: 0%
Land Use Code: 2
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 4
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity ($cm\ s^{-1}$)	Discharge ($m^3\ s^{-1}$)	Area (m^2)	Height (cm)
5.4.1990	97	4.13	3.6	51
8.5.1990	42	.64	1.38	17
13.6.1990	36	.25	1.52	11
S.D.	33.6	2.14		

Extinction Coefficient (K)
2.87 (mean value)

Chemical Data:

	Nitrate ($mgN\ l^{-1}$)	Phosphate ($mgP\ l^{-1}$)
5.4.1990	8	
8.5.1990	15	0
13.6.1990	15	.3

Mean pH: 7.3

Plant & Sediment Composition (September 1990):
No samples taken (see note below)

Biological Data:

Maximum Number of flowers per 0·25 m^2
1

Plant species present: 13
Fontinalis antipyretica, Glyceria maxima, Phalaris arundinacea, Ranunculus penicillatus subsp. *pseudofluitans, Oenanthe crocata, Potamogeton pectinatus, Epilobium hirsutum, Apium nodiflorum, Callitriche stagnalis, Myosotis scorpioides, Sparganium minimum, Veronica anagallis-aquatica, Rumex crispus*

Notes
On the last site visit bulldozers were digging up the site so no data were obtained

River Whitewater (Surrey) at Risely — Site № 1

Site Details:
National Grid Reference: SU 741 635
Height above mean sea level: 47 m
Estimated percentage shade: 10%
Land Use Code: 5
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 1
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity (cm s^{-1})	Discharge (m^3 s^{-1})	Area (m^2)	Height (cm)
25.4.1990	26	1.17	3.92	28
15.5.1990	12	.64	3.11	32
3.7.1990	25	.64	2.56	20
28.9.1990	16	.21	2.37	16
S.D.	6.85	.39		

Extinction Coefficient (K)
2.24 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
25.4.1990	15	
15.5.1990	40	>3
3.7.1990	10	2.5
28.9.1990	50	>3

Mean pH: 7.3

Plant & Sediment Composition (September 1990):

Sed N %	Sed P µg g^{-1}	Sed K µg g^{-1}	Sed Ca mg g^{-1}
0.03	17.08	101	2.6

Plant N %	Plant P mg g^{-1}	Plant K mg g^{-1}
3.02	11.16	42

Biological Data:

Maximum Number of flowers per 0·25 m^2
0

Plant species present: 24
Enteromorpha, Elodea canadensis, Agrostis stolonifera, Alisma plantago-aquatica, Epilobium hirsutum, Holcus lanatus, Nasturtium officinale, Nuphar lutea, Oenanthe fluviatilis, Poa trivialis, Potamogeton nodosus, Potamogeton pectinatus, Ranunculus penicillatus subsp. *pseudofluitans, Ranunculus sceleratus, Scrophularia aquatica, Veronica beccabunga, Rumex sanguineus, Callitriche stagnalis, Sparganium emersum, Sparganium erectum, Urtica dioica, Lemna minor, Lemna miniscula, Polygonum amphibium*

Swansea Canal at Pontardwe — Site № 51

Site Details:
National Grid Reference: SN 728 047
Height above mean sea level: 50 m
Estimated percentage shade: 30%
Land Use Code: 5
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 1
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity (cm s^{-1})	Discharge (m^3 s^{-1})	Area (m^2)	Height (cm)
10.4.1990	9	.081	2.29	43.
16.5.1990	13	.186	1.5	32
27.6.1990	14	.21	1.5	64
19.9.1990	11	.17	1.3	
S.D.	22	.06		

Extinction Coefficient (K)
1.92 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
10.4.1990	0	
16.5.1990	0	0
27.6.1990	0	0
19.9.1990	0	0

Mean pH: 6.9

Plant & Sediment Composition (September 1990):
No samples taken

Biological Data:

Maximum Number of flowers per 0·25 m^2
0

Plant species present: 26
Callitriche stagnalis, Chamaenerion angustifolium, Hedera helix, Holcus lanatus, Oenanthe crocata, Polygonum amphibium, Potamogeton crispus, Poa annua, Plantago major, Petasites hybridus, Ranunculus penicillatus subsp. *pseudofluitans, Ranunculus sceleratus, Ranunculus repens, Salix spp, Arrhenatherum elatius, Avena fatua, Digitalis purpurea, Epilobium roseum, Filipendula ulmaria, Rumex sanguineus, Sonchus asper, Nasturtium officinale, Juncus effusus, Lolium perenne, Trifolium repens*

Notes
Canal disused, some throughflow.

References
Glamorgan Naturalists' Trust & NCC (1982), Hadfield (1960), Pollins (1952, 1960).

Swansea Water downstream of Usk Reservoir — Site № 50

Site Details:
National Grid Reference: SN 820 271
Height above mean sea level: 315 m
Estimated percentage shade: 0%
Land Use Code: 1
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 1
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity (cm s^{-1})	Discharge (m^3 s^{-1})	Area (m^2)	Height (cm)
10.4.1990	10.4	.066	.66	10
16.5.1990	44	.14	.54	12
26.6.1990	21	.086	.6	13
19.9.1990	0	.088	.16	28
S.D.	18.8	.03		

Extinction Coefficient (K)
3.2 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
10.4.1990	0	
16.5.1990	0	0
26.6.1990	0	0
19.9.1990	0	0

Mean pH: 6.7

Plant & Sediment Composition (September 1990):

Sed N %	Sed P µg g^{-1}	Sed K µg g^{-1}	Sed Ca mg g^{-1}
0.02	2	223	0.9

Plant N %	Plant P mg g^{-1}	Plant K mg g^{-1}
2.95	1.37	53

Biological Data:

Maximum Number of flowers per 0·25 m^2
38

Plant species present: 22
Fontinalis squamosa, Calliergon giganteum, Lemanea fluviatilis, Leskea polycarpa, Sphagnum palustre, Agrostis stolonifera, Apium nodiflorum, Callitriche stagnalis, Carex demissa, Elodea canadensis, Juncus effusus, Myriophyllum alterniflorum, Potamogeton polygonifolius, Ranunculus aquatilis, Ranunculus omiophyllus, Ranunculus sceleratus, Veronica beccabunga, Trifolium repens, Lotus uliginosus, Glyceria fluitans, Mentha aquatica, Ranunculus flammula,

Sydling Water near Sydling Saint Nicholas Site № 24

Site Details:
National Grid Reference: ST 635 003
Height above mean sea level: 120 m
Estimated percentage shade: 30%
Land Use Code: 5
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 3
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity (cm s^{-1})	Discharge (m^3 s^{-1})	Area (m^2)	Height (cm)
18.4.1990	27	.16	.64	15
5.6.1990	30	.14	.56	12
5.7.1990	33	.14	.52	15
21.9.1990	20	.065	.22	14
S.D.	5.57	.04		

Extinction Coefficient (K)
2.5 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
18.4.1990	17	
5.6.1990	10	0
5.7.1990	12	0
21.9.1990	0	.6

Mean pH: 7.5

Plant & Sediment Composition (September 1990):

Sed N %	Sed P µg g^{-1}	Sed K µg g^{-1}	Sed Ca mg g^{-1}
0.01	0.37	30	1.48

	Plant N %	Plant P mg g^{-1}	Plant K mg g^{-1}
	4.08	2.56	41

Biological Data:

Maximum Number of flowers per 0·25 m^2
35

Plant species present: 15
Asplenium scolopendrium (=Phyllitis scolopendrium), Nasturtium officinale, Oenanthe crocata, Ranunculus penicillatus subsp. *pseudofluitans, Salix* sp, *Viburnum opulus, Epilobium hirsutum, Glyceria fluitans, Apium nodiflorum, Phalaris arundinacea, Rumex sanguineus, Ranunculus sceleratus, Scrophularia aquatica, Alnus glutinosa, Callitriche obtusangula*

Notes
Sediment is washed down this site every time a vehicle passes the ford just upstream.

Reference
Casey & Westlake (1974)

River Teifi at Altyblacca

Site № 28

Site Details:
National Grid Reference: SN 523 454
Height above mean sea level: 105 m
Estimated percentage shade: 20%
Land Use Code: 2
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 1
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity (cm s^{-1})	Discharge (m^3 s^{-1})	Area (m^2)	Height (cm)
10.4.1990	43			17
16.5.1990	96			25
27.6.1990	86	1.6	1.9	18
19.9.1990	62	1.62	2.7	21
S.D.	23.9	.01		

Extinction Coefficient (K)
1.7 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
10.4.1990	0	
16.5.1990	0	0
27.6.1990	5	0
19.9.1990	0	0

Mean pH: 6.5

Plant & Sediment Composition (September 1990):

Sed N %	Sed P µg g^{-1}	Sed K µg g^{-1}	Sed Ca mg g^{-1}
0	0.62	160	2.42

Plant N %	Plant P mg g^{-1}	Plant K mg g^{-1}
4.03	7.04	87.67

Biological Data:

Maximum Number of flowers per 0·25 m^2
0

Plant species present: 21
Lemanea fluviatilis, Brachythecium rivulare, Hygrohypnum luridum, Ranunculus penicillatus var penicillatus, Alnus glutinosa, Callitriche platycarpa, Elodea canadensis, Glyceria fluitans, Lolium perenne, Oenanthe crocata, Phalaris arundinacea, Polygonum mite, Poa annua, Ranunculus sceleratus, Sparganium erectum, S. minimum, S. emersum, Alisma plantago-aquatica, Cardamine hirsuta, Lemna minor, Myriophyllum alterniflorum

Reference
Currey & Slater (1986)

River Teifi at Cors Carron

Site № 27

Site Details:
National Grid Reference: SN 684 628
Height above mean sea level: 160 m
Estimated percentage shade: 0%
Land Use Code: 1
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 1
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity (cm s^{-1})	Discharge (m^3 s^{-1})	Area (m^2)	Height (cm)
11.4.1990	4.2	.3	6	62
17.5.1990	0	0	6.65	45
26.6.1990	7	.4	4.2	54
18.9.1990	0	0	3	30
S.D.	3.43	.21		

Extinction Coefficient (K)
2.07 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
11.4.1990	0	
17.5.1990	0	0
26.6.1990	0	0
18.9.1990	0	0

Mean pH: 5.8

Plant & Sediment Composition (September 1990):

Sed N %	Sed P µg g^{-1}	Sed K µg g^{-1}	Sed Ca mg g^{-1}
0.87	0	260	4.58

Plant N %	Plant P mg g^{-1}	Plant K mg g^{-1}
1.67		9.6

Biological Data:

Maximum Number of flowers per 0·25 m^2
0

Plant species present: 15
Callitriche hamulata, Callitriche platycarpa, Carex acutiformis, Glyceria fluitans, Iris pseudacorus, Juncus effusus, Nuphar lutea, Phalaris arundinacea, Potamogeton natans, Ranunculus penicillatus var penicillatus (?), Sparganium angustifolium, Alisma plantago-aquatica, Myriophyllum alterniflorum, Polygonum amphibium, Ranunculus sceleratus

Notes
This site is part of the Cors Caron National Nature Reserve.

River Tone at Waterrow

Site № 30

Site Details:
National Grid Reference: ST 052 254
Height above mean sea level: 150 m
Estimated percentage shade: 80%
Land Use Code: 4
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 1
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity (cm s^{-1})	Discharge (m^3 s^{-1})	Area (m^2)	Height (cm)
3.4.1990	35	.15		10
4.5.1990	47			12
22.6.1990	28	.14	.5	12
4.9.1990	39	.117	.35	8
S.D.	7.93	.02		

Extinction Coefficient (K)
3 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
3.4.1990	0	
4.5.1990	8	1.8
22.6.1990	0	0
4.9.1990	0	0

Mean pH: 6.5

Plant & Sediment Composition (September 1990):

Sed N %	Sed P µg g^{-1}	Sed K µg g^{-1}	Sed Ca mg g^{-1}
0.03	2.4	37.5	1.48

	Plant N %	Plant P mg g^{-1}	Plant K mg g^{-1}
No sample taken			

Biological Data:

Maximum Number of flowers per 0·25 m^2
4

Plant species present: 15
Rhynchostegium ripararioides, Acer psuedoplatanus, Agrostis stolonifera, Alnus glutinosa, Carex pseudocyperus, Epilobium hirsutum, Hedera helix, Oenanthe crocata, Phalaris arundinacea, Ranunculus penicillatus subsp. *pseudofluitans, Ranunculus repens, Rubus fructicosus, Cardamine pratensis, Lagriosiphon major, Urtica dioica*

River Torridge at Hele Bridge — Site № 43

Site Details:
National Grid Reference: SS 542 064
Height above mean sea level: 55 m
Estimated percentage shade: 0%
Land Use Code: 3
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 1
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity (cm s^{-1})	Discharge (m^3 s^{-1})	Area (m^2)	Height (cm)
3.4.1990	60			18
3.5.1990	32			16
22.6.1990	51	5.3	9.96	44
4.9.1990	10	.46	3.93	20
S.D.	22	3.4		

Extinction Coefficient (K)
3.6 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
3.4.1990	0	
3.5.1990	0	0
22.6.1990	0	0
4.9.1990	0	0

Mean pH: 6.8

Plant & Sediment Composition (September 1990):

Sed N %	Sed P µg g^{-1}	Sed K µg g^{-1}	Sed Ca mg g^{-1}
0	0.02	85	0.3

Plant N %	Plant P mg g^{-1}	Plant K mg g^{-1}
1.92	3.35	46

Biological Data:

Maximum Number of flowers per 0·25 m^2
0

Plant species present:
Fontinalis antipyretica, Holcus lanatus, Impatiens glandulifera, Juncus effusus, Oenanthe fluviatilis, Phalaris arundinacea, Polygonum hydropiper, Poa annua, Ranunculus penicillatus var *penicillatus, Ranunculus omiophyllus, Rumex sanguineus, Ulmus minor*

Notes
This site was used as the source of the *R. penicillatus* subsp. *penicillatus* transplant.

Unnamed stream at Worth Matravers Site № 57

Site Details:
National Grid Reference:
Height above mean sea level: 10 m
Estimated percentage shade: 0%
Land Use Code: 4
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 1
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity (cm s^{-1})	Discharge (m^3 s^{-1})	Area (m^2)	Height (cm)
16.4.1990	21	.016	.074	20
20.9.1990	25.5	.005	.02	20
S.D.	3.18	.0078		

Extinction Coefficient (K)
2.72 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
16.4.1990	40	
20.9.1990	15	0

Mean pH: 7.95

Plant & Sediment Composition (September 1990):
No samples taken

Biological Data:

Maximum Number of flowers per 0·25 m^2

Plant species present: 18
Cladophora, Equisetum fluviatile, Apium nodiflorum, Callitriche obtusangula, Callitriche stagnalis, Chenopodium album, Glyceria declinata, Myosotis scorpioides, Onosis repens, Ranunculus baudotii, Circium arvense, Juncus articulatus, Nasturtium officinale, Brassica oleracea, Petasites hybridus, Sonchus asper, Plantago coronopus

Waterston Stream near Druce

Site № 47

Site Details:
National Grid Reference: SY 742 952
Height above mean sea level: 70 m
Estimated percentage shade: 10%
Land Use Code: 4
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 3
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity (cm s^{-1})	Discharge (m^3 s^{-1})	Area (m^2)	Height (cm)
18.4.1990	8	.045	.31	24
5.6.1990	42	.015	.21	16.
5.7.1990	0	0	.17	7
21.9.1990	0	0	0	0
S.D.	20	.02		

Extinction Coefficient (K)
1.44 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
18.4.1990	5	
5.6.1990	0	0
5.7.1990	30	0

Mean pH: 7.1

Plant & Sediment Composition (September 1990):

Sed N %	Sed P µg g^{-1}	Sed K µg g^{-1}	Sed Ca mg g^{-1}
0.17	15.04	225	5.62

Plant N %	Plant P mg g^{-1}	Plant K mg g^{-1}
3.26	3.1	45.67

Biological Data:

Maximum Number of flowers per 0·25 m^2
33

Plant species present: 9
Amblystegium riparium, Apium nodiflorum, Nasturtium officinale, Oenanthe crocata, Ranunculus penicillatus subsp. *pseudofluitans, Urtica dioica, Rumex obtusifolius, Sambucus nigra, Symphytum officinale,*

Notes
This stream dried up in years with low rainfall, such as 1990, so that it was dry on the final visit. It runs through the Institute of Freshwater Ecology's Waterston Research Station. *R. penicillatus* subsp. *penicillatus* was transplanted here as part of the transplants described in chapter two

References
Ladle & Bass (1981), Webster (1984)

West Sussex Rother at Maidenmarsh — Site № 2

Site Details:
National Grid Reference: SU 782 233
Height above mean sea level: 50 m
Estimated percentage shade: 10%
Land Use Code: 2
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 1
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity (cm s^{-1})	Discharge (m^3 s^{-1})	Area (m^2)	Height (cm)
25.4.1990	10	.58	1.51	15
14.5.1990	35	.58	1.35	14
2.7.1990	35	.36	.86	17
28.9.1990	0	.24	.79	10
S.D.	14.4	.17		

Extinction Coefficient (K)
2.68 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
25.4.1990	2	
14.5.1990	10	>3
2.7.1990	30	2.5
28.9.1990	10	3.5

Mean pH: 6.9

Plant & Sediment Composition (September 1990):

Sed N %	Sed P µg g^{-1}	Sed K µg g^{-1}	Sed Ca mg g^{-1}
0.02	3.81	54	0.69

Plant N %	Plant P mg g^{-1}	Plant K mg g^{-1}
2.07	6.81	42

Biological Data:

Maximum Number of flowers per 0·25 m^2
0

Plant species present: 19
Agrostis stolonifera, *Alnus glutinosa*, *Glyceria maxima*, *Cardamine hirsuta*, *Impatiens glandulifera*, *Oenanthe crocata*, *Phalaris arundinacea*, *Ranunculus penicillatus* subsp. *pseudofluitans*, *Ranunculus repens*, *Sparganium emersum*, *S. erectum*, *S. minimum*, *Silene alba*, *Apium nodiflorum*, *Lemna minor*, *Myosotis scorpioides*, *Urtica dioica*, *Potamogeton crispus*, *Polygonum hydropiper*.

River Wye at Hay-on-Wye

Site № 48

Site Details:
National Grid Reference: SO 238 426
Height above mean sea level: 75 m
Estimated percentage shade: 10%
Land Use Code: 5
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 1
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity (cm s^{-1})	Discharge (m^3 s^{-1})	Area (m^2)	Height (cm)
11.4.1990	91			30
17.5.1990	109			28
25.6.1990	64			23
18.9.1990	67			14
S.D.	21			

Extinction Coefficient (K)
1.97 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
11.4.1990	0	
17.5.1990	0	0
25.6.1990	0	0
18.9.1990	0	0

Mean pH: 6.6

Plant & Sediment Composition (September 1990):

Sed N %	Sed P µg g^{-1}	Sed K µg g^{-1}	Sed Ca mg g^{-1}
0.01	1.8	76	3.22

	Plant N %	Plant P mg g^{-1}	Plant K mg g^{-1}
	6.65	3.79	37.66

Biological Data:

Maximum Number of flowers per 0·25 m^2
0

Plant species present: 15
Lemanea fluviatilis, Fontinalis antipyretica, Carex riparia, Epilobium hirsutum, Oenanthe crocata, Phalaris arundinacea, Poa trivialis, Ranunculus fluitans, Salix sp, *Mentha aquatica, Alnus glutinosa, Myosotis scorpioides, Lycopus europaeus, Polygonum amphibium, Rorippa sylvestris,*

Notes
Due to the size of the river, it was not possible to measure the discharge; the mean value measured by the NRA is 45.75 m^3 s^{-1}.
'Wye' is derived from the Celtic *wey* which means flowing.

References
Brooker *et al.* (1978), Merry *et al.* (1981), and Edwards & Brooker (1982)

River Wylye at Codford Saint Mary

Site № 52

Site Details:
National Grid Reference: ST 970 405
Height above mean sea level: 95 m
Estimated percentage shade: 0%
Land Use Code: 2
(1=Unimproved pasture, 2=Improved pasture, 3=Arable, 4=Woodland, 5=urban)
Management Code: 4
(1=Unmanaged, 2=Cut in normal year, 3=Cut including this year, 4=Grazing/Poaching, 5=Cut & Grazed)

Physical Data:

	Velocity (cm s^{-1})	Discharge (m^3 s^{-1})	Area (m^2)	Height (cm)
9.5.1990	9	.056	1.577	24
14.6.1990	0	0		16
5.9.1990	0	0	0	0
S.D.	5.19	0.03		

Extinction Coefficient (K)
2.83 (mean value)

Chemical Data:

	Nitrate (mgN l^{-1})	Phosphate (mgP l^{-1})
9.5.1990	5	0
14.6.1990	30	0

Mean pH: 7.2

Plant & Sediment Composition (September 1990):

Sed N %	Sed P µg g^{-1}	Sed K µg g^{-1}	Sed Ca mg g^{-1}
0.41		340	6.21

	Plant N %	Plant P mg g^{-1}	Plant K mg g^{-1}
	2.39	4.62	39.5

Biological Data:

Maximum Number of flowers per 0·25 m^2
28

Plant species present: 15
Cladophora, Alisma plantago-aquatica, Alopecurus geniculatus, Apium nodiflorum, Catabrosa aquatica, Chenopodium album, Glyceria fluitans, Nasturtium officinale, Poa trivialis, Plantago major, Ranunculus peltatus, Ranunculus repens, Ranunculus bulbosus, Veronica anagallis-aquatica, Rumex sanguineus

Notes
This winterbourne was dry on the final visit. Anecdotal evidence from local people indicates that it is only in recent years that the river has been a winterbourne at this site, possibly due to increased abstraction.

APPENDIX B

River Surveys 1991

1. Details of Sites

2. Summary of Strategy Trait Data

3. Methods

Details of Sites Surveyed During 1991

River Mouse at Shortshill Site № 1, 55

National Grid Reference: NS 935 486 Date: 27 May, 11 June

Species: *Agrostis stolonifera, Caltha palustris, Carex acutiformis, Eleogiton* sp., *Filipendula ulmaria, Fontinalis antipyretica, Glyceria declinata, Iris pseudacorus, Phalaris arundinacea,* ***Ranunculus peltatus, R. penicillatus*** **subsp.** ***pseudofluitans****, Sparganium emersum, S. erectum.*

River Tweed at Dawyck Site № 2

National Grid Reference: NT 165 355 Date: 29 April

Species: *Caltha palustris,* Diatoms (unidentified) & other green algae, *Fontinalis antipyretica, Lemanea fluviatilis, Myosotis scorpioides, Phalaris arundinacea,* ***Ranunculus peltatus****, Veronica beccabunga.*

River Tweed where crossed by the A68 Bridge. Site № 3

National Grid Reference: NT573 347 Date: 29 May

Species: *Agrostis stolonifera, Cladophora glomerata, Myosotis scorpioides, Phalaris arundinacea,* ***Ranunculus penicillatus*** **subsp.** ***pseudofluitans***

Kirkby Pool near Broughton in Furness Site № 4

National Grid Reference: NY 232 862 Date: 31 May

Species: *Alisma plantago-aquatica, Callitriche stagnalis, C. palustris, Equisetum fluviatile, Glyceria fluitans, Mentha aquatica, Myosotis scorpioides, Nuphar lutea, Phalaris arundinacea, Potamogeton gramineous, P. natans,* ***Ranunculus peltatus***

River Esk (tributary of) at Hinning House Site № 5

National Grid Reference: SD 123 973 Date: 31 May

Species: *Glyceria fluitans, Juncus effusus,* ***Ranunculus omiophyllus****, R. repens.*

River Irt at Holmrook Site № 6

National Grid Reference: SD 082 995 Date: 31 May

Species: *Alnus glutinosa, Myriophyllum alterniflorum, Oenanthe crocata, Phalaris arundinacea,* ***Ranunculus peltatus****, Rubus fructicosus*

River Tweed at Sprouston Site № 7

National Grid Reference: NT 75 35 Date: 3 June

Agrostis stolonifera, Cladophora glomerata, Lemanea fluviatilis, Phalaris arundinacea, ***Ranunculus fluitans***

River Nidd at Pateley Bridge Site № 8

National Grid Reference: SE 158 655 Date: 4 June

Species: *Alnus glutinosa, Caltha palustris, Glyceria fluitans, Juncus effusus, Luzula sylvestris,* ***Ranunculus circinatus***

River Rye at Nunnington Site № 9, 10

National Grid Reference: SE 642 804 Date: 4 June

Species: *Agrostis stolonifera, Alnus glutinosa, Alopecurus geniculatus, Epilobium cannabinum, Galium aparine, Glyceria fluitans, Impatiens glandulifera, Lemna minor, Nasturtium officinale, Phalaris arundinacea, Polygonum amphibium,* ***Ranunculus fluitans, R. penicillatus*** **subsp.** ***pseudofluitans****, Rumex obtusifolius, Urtica dioica.*

River Hull (West Beck) at Wansford Bridge Site № 11

National Grid Reference: TA 065 559 Date: 4 June

Species: *Callitriche stagnalis, Epilobium hirsutum, Fraxinus excelsior, Glyceria maxima, Nasturtium officinale, Phalaris arundinacea,* ***Ranunculus penicillatus*** **subsp.** ***pseudofluitans,*** Rumex obtusifolius, Scrophularia aquatica, Solanum dulcamara, Veronica beccabunga

Old Bedford River at Welches Dam Site № 12

National Grid Reference: TL 471 858 Date: 6 June

Species: *Alisma plantago-aquatica, Callitriche stagnalis, Chara globularis, Elodea nuttallii, Glyceria maxima, Juncus effusus, Myosotis scorpioides, Myriophyllum spicatum, Potamogeton pectinatus, P. perfoliatus,* ***Ranunculus circinatus****, R. repens, Sparganium emersum, S. erectum, Vaucheria* sp.

River Devon at Tilbody Bridge Site № 13

National Grid Reference: NS 857 959 Date: 10 June

Species: *Glyceria maxima,* Green algae (unidentified), *Impatiens glandulifera, Phalaris arundinacea, Potamogeton polygonifolius,* ***Ranunculus fluitans****, Sparganium erectum, Urtica dioica*

River Ythan at Ellon Site № 14

National Grid Reference: NJ 955 302 Date: 12 June

Species: *Caltha palustris, Fontinalis antipyretica, Glyceria maxima, Iris* *pseudacorus*, *Mentha aquatica*, *Myriophyllum alterniflorum*, *Phalaris arundinacea*, ***Ranunculus fluitans***, *Rumex obtusifolius*, *Sparganium erectum*, *Urtica dioica*.

River Uggie at Inverugie Site № 15

National Grid Reference: NK 100 480 Date: 12 June

Species: *Caltha palustris*, *Equisetum fluviatile*, *Fontinalis antipyretica*, *Phalaris arundinacea*, ***Ranunculus penicillatus* subsp. *pseudofluitans***

River Spey near Garmouth Site № 16

National Grid Reference: NJ 344 610 Date: 12 June

Species: *Myosotis scorpioides*, *Phalaris arundinacea*, ***Ranunculus fluitans***, *Rumex obtusifolius*, *Veronica beccabunga*

River Spey at Grantown-on-Spey Site № 17

National Grid Reference: NJ 035 268 Date: 12 June

Species: *Caltha palustris*, *Fontinalis antipyretica*, *Glyceria fluitans*, *Phalaris arundinacea*, *Ranunculus flammula*, ***R. fluitans***

Dean Water at Glamis Site № 18

National Grid Reference: NO 38 48 Date: 11 June

Species: *Epilobium hirsutum*, *Galium uliginosum*, *Myosotis scorpioides*, *Phalaris arundinacea*, *Potamogeton crispus*, *P. pectinatus*, ***Ranunculus peltatus***, *Sparganium erectum*

River Bela at Whasatt Site № 19

National Grid Reference: SD 512 801 Date: 18 June

Species: *Elodea canadensis*, *Potamogeton lucens*, ***Ranunculus fluitans***, *Rumex obtusifolius*, *Scrophularia aquatica*, *Urtica dioica*

River Kent at Levens Site № 20

National Grid Reference: NY 495 852 Date: 18 June

Species: *Brassica rapa*, *Heracleum mantegazzianum*, *Oenanthe crocata*, *Petasites hybridus*, *Phalaris arundinacea*, ***Ranunculus penicillatus* subsp. *pseudofluitans***, *R. repens*, *Rumex sanguineus*, *Salix cinerea*, *Symphytum officinale*, *Urtica dioica*

River Kent at Kendal Site № 21

National Grid Reference: SD 518 915 Date: 18 June

Species: *Epilobium hirsutum*, *Myriophyllum alterniflorum*, *Oenanthe crocata*, *Phalaris* *arundinacea*, ***Ranunculus penicillatus*** **subsp.** ***pseudofluitans***, *Rubus fructicosus*, *Sparganium emersum*

Site № 22

River Lowther at Bampton

National Grid Reference: NY 518 181 Date: 18 June

Species: *Alnus glutinosa*, *Caltha palustris*, *Epilobium hirsutum*, *Filipendula ulmaria*, *Fontinalis antipyretica*, *Lycopus europaeus*, *Mentha aquatica*, *Myriophyllum alterniflorum*, *Phalaris arundinacea*, ***Ranunculus penicillatus*** **var.** ***penicillatus***, *Ribes rubrum*, *Rumex obtusifolius*, *Salix cinerea*, *Ulmus glabra*, *Urtica dioica*

Site № 23

Haweswater Beck at Noddaw Bridge

National Grid Reference: NY 510 160 Date: 18 June

Species: *Alnus glutinosa*, *Callitriche hamulata*, *Caltha palustris*, *Cardamine pratensis*, *Chrysosplenium oppositifolium*, *Fontinalis antipyretica*, *Glyceria fluitans*, *Juncus effusus*, ***Ranunculus penicillatus*** **subsp.** ***penicillatus***, *Rumex sanguineus*, *Urtica dioica*

Site № 24

River Derwent at Iselgate

National Grid Reference: NY 165 334 Date: 19 June

Species: *Agrostis stolonifera*, *Elodea canadensis*, *Galium palustre*, *GLyceria fluitans*, *Juncus effusus*, *Myriophyllum alterniflorum*, *Phalaris arundinacea*, ***Ranunculus aquatilis***, *Ulmus minor*

Site № 25

River Derwent at Great Broughton

National Grid Reference: NY 082 313 Date: 19 June

Species: *Crataegus monogyna*, *Oenanthe crocata*, *Phalaris arundinacea*, ***Ranunculus aquatilis***, *Urtica dioica*

Site № 26

River Derwent at Workington

National Grid Reference: NY 009 292 Date: 19 June

Species: *Alnus glutinosa*, *Fontinalis antipyretica*, *Iris pseudacorus*, *Oenanthe crocata*, *Phalaris arundinacea*, ***Ranunculus aquatilis***

Site № 27

River Eamont at Broughton Castle

National Grid Reference: NY 538 291 Date: 19 June

Species: *Caltha palustris*, *Phalaris arundinacea*, ***Ranunculus fluitans***, ***R. penicillatus*** **subsp.** ***penicillatus***, *R. repens*, *Sparganium erectum*

River Eden at Langworthy Site № 28

National Grid Reference: NY 565 333 Date: 20 June

Species: *Epilobium hirsutum, Petasites hybridus, Phalaris arundinacea,* ***Ranunculus fluitans, R. penicillatus*** **subsp.** ***penicillatus****, Sparganium erectum, Urtica dioica, Vaucheria* sp.

Cumwhitton Beck at Cumwhitton Site № 29

National Grid Reference: NY 506 523 Date: 20 June

Species: *Apium nodiflorum, Catabrosa aquatica, Filipendula ulmaria, Glyceria fluitans, Heracleum sphondylium, Holcus lanatus, Lemna minor, Myosotis scorpioides, Petasites hybridus, Poa pratensis,* ***Ranunculus penicillatus*** **subsp.** ***pseudofluitans****, R. repens, Rumex sanguineus, Scrophularia aquatica, Veronica anagallis-aquatica*

River Eden near Cote House Site № 30

National Grid Reference: NY 475 430 Date: 20 June

Species: *Agrostis stolonifera, Alnus glutinosa, Fontinalis antipyretica*, unidentified liverworts, *Oenanthe crocata, Phalaris arundinacea,* ***Ranunculus fluitans****, Rumex sanguineus, Urtica dioica*

River Eden at Warwick Bridge Site № 31, 32

National Grid Reference: NY 473 565 Date: 20 June

Species: *Carex acutiformis, Myosotis scorpioides, Phalaris arundinacea,* ***Ranunculus fluitans, R. penicillatus*** **subsp.** ***penicillatus****, Rumex sanguineus, Urtica dioica*

River Peteril near Newbiggin Hall Site № 33

National Grid Reference: NY 435 512 Date: 21 June

Species: *Agrostis stolonifera, Cladophora glomerata, Epilobium hirsutum, Hesperis matronalis, Phalaris arundinacea, Poa pratensis, Ranunculus flammula,* ***R. fluitans, R. penicillatus*** **subsp.** ***pseudofluitans*** **var.** ***vertumnus****, Rumex obtusifolius, Solanum dulcamara, Sparganium erectum*

River Peteril at Southwaite Site № 34

National Grid Reference: NY 452 450 Date: 21 June

Species: *Cladophora glomerata, Lolium perenne, Phalaris arundinacea,* ***Ranunculus fluitans, R. penicillatus*** **subsp.** ***pseudofluitans*** **var.** ***vertumnus****, R. repens, Rumex sanguineus*

River Dane at Forge Mill Site № 35

National Grid Reference: SJ 849 637 Date: 25 June

Species: *Aegopodium podagraria, Agrostis stolonifera, Alnus glutinosa, Apium nodiflorum, Brassica oleracea, Callitriche stagnalis, Catabrosa aquatica, Epilobium hirsutum, Fontinalis antipyretica, Fraxinus excelsior, Impatiens glandulifera, Myosotis scorpioides, Nasturtium officinale, Petasites hybridus, Phalaris arundinacea,* ***Ranunculus peltatus****, Rumex sanguineus, Salix cinerea, S. fragilis, Urtica dioica, Veronica beccabunga*

River Clwyd at Rhewl Site № 36

National Grid Reference: SJ 119 099 Date: 25 June

Species: *Agrostis stolonifera, Epilobium hirsutum, Fontinalis antipyretica, Phalaris arundinacea,* ***Ranunculus penicillatus* subsp. *pseudofluitans****, Rubus fructicosus, Solanum dulcamara, Sparganium erectum, Urtica dioica, Vaucheria* sp.

River Clwyd at Llanerch (near Llanelwy (Saint Asaph)) Site № 37

National Grid Reference: SJ 060 719 Date: 25 June

Species: *Agrostis stolonifera, Alopecurus geniculatus, Circium arvense, Dactylis glomerata, Epilobium hirsutum, Glyceria plicata, Juncus effusus, Mimulus guttatus, Myosotis scorpioides, Oenanthe crocata, Phalaris arundinacea, Polygonum amphibium,* ***Ranunculus penicillatus* subsp. *pseudofluitans****, R. repens, Rumex obtusifolius, Sisymbrium altissimum, Solanum dulcamara, Sparganium erectum, Trifolium repens, Veronica anagallis-aquatica, V. beccabunga*

River Dwyfor at Ty-Cerrig Site № 38

National Grid Reference: SH 496 424 Date: 26 June

Species: *Alnus glutinosa, Callitriche stagnalis, Fontinalis antipyretica, Mentha aquatica, Myriophyllum alterniflorum, Oenanthe crocata, Potamogeton polygonifolius,* ***Ranunculus penicillatus* subsp. *penicillatus****, R. repens, Rubus fructicosus, Salix cinerea*

Unnamed Stream at Porth Mendwy Site № 39

National Grid Reference: SH 163 256 Date: 26 June

Species: *Agrostis stolonifera, Epilobium hirsutum, Equisetum palustre, Filipendula ulmaria, Galium aparine, nasturtium officinale, Oenanthe crocata, Poa pratensis,* ***Ranunculus omiophyllus****, R. repens, Ribes rubrum, Solanum dulcamara*

Nand Eiddan at Porth Oer Site № 40

National Grid Reference: SH 168 308 Date: 26 June

Species: *Agrostis stolonifera, Alisma plantago-aquatica, Glyceria plicata, Iris pseudacorus, Juncus effusus, Oenanthe crocata, Phalaris arundinacea, Poa pratensis, Potamogeton natans,* ***Ranunculus baudotii****, Sparganium erectum*

Unnamed stream at Trwyn y Penrhyn (near Penmon) Site № 41

National Grid Reference: SH 628 802 Date: 27 June

Species: *Agrostis stolonifera*, green algae (unidentified), Juncus effusus, ***Ranunculus baudotii****, Schoenus nigricans*

Unnamed stream at Cemlyn Site № 42

National Grid Reference: SH 333 930 Date: 27 June

Species: *Agrostis stolonifera, Callitriche stagnalis, Glyceria fluitans,* ***Ranunculus hederaceus****, Urtica dioica*

River Peteril at Kitchen Hill Site № 43

National Grid Reference: NY 498 342 Date: 29 June

Species: *Agrostis stolonifera, Myosotis scorpioides, Phalaris arundinacea,* ***Ranunculus fluitans, R. penicillatus*** **subsp.** ***pseudofluitans*** **var.** ***vertumnus****, R. repens, Rhynchostegium riparioides, Solanum dulcamara, Sparganium erectum, Urtica dioica*

Gogar Burn at Suntrap Site № 44

National Grid Reference: NT 171 706 Date: 1 July

Species: *Glyceria fluitans, Myosotis scorpioides, Poa pratensis,* ***Ranunculus penicillatus*** **subsp.** ***pseudofluitans****, R. repens, Urtica dioica, Vaucheria* sp.

Craigend Burn at Craigend Muir (near Stepps) Site № 45

National Grid Reference: NS 663 676 Date: 2 July

Species: *Agrostis stolonifera, Alisma plantago-aquatica, Chamaenerion angustifolium, Galium palustre, Holcus lanatus, Juncus effusus, Myosotis scorpioides, Poa pratensis, Potamogeton natans, P. polygonifolius,* ***Ranunculus omiophyllus****, Sparganium erectum, Urtica dioica*

River Devon at Tilcoultry Site № 46

National Grid Reference: NS 962 939 Date: 3 July

Species: *Agrostis stolonifera, Fontinalis antipyretica, Mimulus guttatus, Myosotis* *scorpioides, Polygonum amphibium,* ***Ranunculus aquatilis****, R. repens, Rumex sanguineus, Sparganium erectum, Urtica dioica*

River Devon at Dollar Site № 47

National Grid Reference: NS 968 969 Date: 3 July

Species: *Alnus glutinosa, Fontinalis antipyretica, Mentha aquatica, Mimulus guttatus, Phalaris arundinacea, Potamogeton crispus,* ***Ranunculus aquatilis***

Water of Leith at West Cairns Site № 48

National Grid Reference: NT 087 600 Date: 5 July

Species: *Agrostis stolonifera, Anthoxanthum odoratum, Caltha palustris, Fontinalis antipyretica, Ranunculus flammula,* ***R. peltatus****, R. repens*

Braid Burn in Edinburgh Site № 49

National Grid Reference: NT 277 770 Date: 7 July

Species: *Elodea canadensis, Epilobium hirsutum, Glyceria plicata, Impatiens glandulifera, Mimulus guttatus, Myosotis scorpioides, Nasturtium officinale, Phalaris arundinacea,* ***Ranunculus penicillatus*** **subsp.** ***pseudofluitans****, R. repens, Urtica dioica, Veronica beccabunga*

Rentland Burn at upstream of Loganlea Reservoir Site № 50

National Grid Reference: NT 190 620 Date: 7 July

Species: *Callitriche stagnalis, Galium palustre, Glyceria fluitans, Juncus effusus, Myosotis scorpioides,* ***Ranunculus peltatus****, Rumex sanguineus, Urtica dioica*

Muddy track crossed by Braeburn, near Craigleith cottage Site № 51

National Grid Reference: NS 471 738 Date: 8 July

Species: Agrostis stolonifera, Glyceria declinata, Holcus lanatus, Juncus effusus, Lotus uliginosum, ***Ranunculus hederaceus****, R. repens, Trifolium repens, Veronica beccabunga*

Braeburn in Braeburn Reservoir (disused) Site № 52, 53

National Grid Reference: NS 474 373 Date: 8 July

Species: *Callitriche stagnalis, Elatine* sp., *Eleogiton* sp., *Equisetum fluviatile, Juncus bulbosus, J. effusus, Myosotis scorpioides, Potamogeton natans, P. polygonifolius,* ***Ranunculus peltatus****, R. hederaceus, R. repens, Trichophorum cespitosum.*

Unnamed burn by the Kilpatrick Braes Site № 54

National Grid Reference: NS 467 742 Date: 8 July

Species: *Callitriche stagnalis, Deschampsia cespitosa, Elatine* sp., *Epilobium parviflorum, Glyceria fluitans, Juncus bufonius, J. effusus, J. inflexus, Lotus uliginosus, Myosotis scorpioides, Nasturtium officinale, Poa pratensis, Ranunculus flammula,* ***R. hederaceus****, R. repens, Rumex acetosella, R. sanguineus*

Eddleston Water at Milkieston Site № 56

National Grid Reference: NT 237 457 Date: 10 July

Species: *Agrostis stolonifera, Alnus glutinosa, Dactylis glomerata, Epilobium cannabinum, Filipendula ulmaria, Fontinalis antipyretica, Mimulus guttatus, Myosotis scorpioides, Phalaris arundinacea,* ***Ranunculus peltatus****, R. repens, Sparganium emersum, Urtica dioica*

River Tyne at East Linton Site № 57

National Grid Reference: NT 592 773 Date: 10 July

Species: Lolium perenne, Mimulus guttatus, Myosotis scorpioides, Petasites hybridus, Phalaris arundinacea, Polygonum amphibium, ***Ranunculus fluitans****, Rumex sanguineus, Salix alba, Sparganium erectum, Vaucheria* sp.

Summary of Strategy Trait Data

Trait (units in text)	psu	pen	ver	flu	pel	aqa	cir	bau	hed	om
Biomass Shoot	11.7	6.3	5.5	11.9	3.7	4	0.43	5	1.45	4.22
Biomass Clump	2891	630	3079	954	1210	328	11	588	3.66	87
Biomass 0.01 m^2	626	174	195	360	265	185	7	45	3.7	87
Height Canopy	14	20	21.7	24	35	30	37	53	6	8
Height Water	21	41	36.7	43	35	52	55	53	6	10
Proportion	77	48	100	56	100	52	60	100	100	100
Area canopy	9232	4645	2800	5312	5519	2228	17k	9500	1080	1000
Max shoot length	130	96	78	185	76	86	56	82	11	19
Length sub lvs	9.3	10.6	2.5	21	5.6	4.8	1.4	3.5	0	0
Width sub lvs	1.9	1.4	1.3	1.3	2.73	1.65	2.5	3.1	0	0
# divisions	6.3	5.4	6	4	5.8	6.7	5	5.5	0	0
Thickness sub lvs	0.98	0.85	0.85	1.2	0.9	0.5	0.4	0.4	0	0
Length flot lvs	0	2.8	0	0	2.1	2.2	0	3	1.55	2.37
Width flot lvs	0	1.55	0	0	1.55	1.5	0	1.5	1.07	1.6
Thickness flot lvs	0	0.33	0	0	0.39	0.25	0	0.4	0.3	0.44
Internode l	10.3	8.1	8.14	13.1	7.16	5	8.6	7.3	3.6	3.2
Stem thickness	2.4	1.69	1.56	2.1	1.75	1.4	0.91	2	3.8	3
Force to break	1490	955	523	1403	675	422	68	623	638	241
# flowers/0.25 m^2	12	6	15	11.4	10	14	17	8	10.3	4
# assoc species	11.5	10.3	9.5	8	10.6	7.6	11	8	10.8	10
# Sites	11	7	4	9	10	5	2	2	4	3

Abbreviations for species used are as follows; psu = *Ranunculus penicillatus* subsp. *pseudofluitans* var. *pseudofluitans*, pen = *R. penicillatus* subsp. *penicillatus*, ver = *R. penicillatus* subsp. *pseudofluitans* var. *vertumns*, flu = *R. fluitans*, pel = *R. peltatus*, aqa = *R. aquatilis*, cir = *R. circinatus*, bau = *R. baudotii*, hed = *R. hederaceus*. om = *R. omiophyllus*.

Methods

All measurements were carried out on site. Biomass measurements are given in g fresh weight. The plants were cut at the level of the river bed. Large plants were wrung out and smaller plants were spun in a manually operated field centrifuge (1400 r.p.m.). They were weighed using a spring balance. The biomass of 0.01 m^2 was weighed by cutting plants growing in a quadrat of that size, it is thus the biomass of plants rooted in that area and not the biomass present in a vertical column above that area.

Length measurements are given in cm, except for thicknesses which are given in mm. Areas are in cm^2 and are calculated on the basis of length × width of a clump. The width of the submerged leaves ('sub lvs') is the width of the leaf when lying naturally in the water, the thickness is the thickness of the leaf when pressed together. Thicknesses were measured using a pair of callipers (accurate to 0.05 mm), other distances with a ruler. '№ divisions' is the number of times the submerged leaves are divided.

The force need to break the stem at its base was measured by placing the stem over a rod attached to a spring balance and exerting a downward force on the stem until it broke. Values are given in g.

The number of associated species is the number of other plant species present at that site. Species which had at least part of their above-ground parts below the water are included.

The values given are arithmetic means of the values from each site. The value for each site was derived from at least five replicate plants/clumps. Each replicate value of a variate such as leaf length were derived from several measurements on each of the five replicate plants, whereas values derived from whole clumps are simply from five replicate clumps.

APPENDIX C

METHODS

1. Digestion of Plant Material

2. Extract of Sediment Samples

3. Analysis of Phosphate in Sediment Extracts

4. Analysis of Nitrogen, Carbon and Hydrogen in Sediment and Plant Samples

5. Analysis of Potassium in Sediment Extracts and Plant Digests

6. Analysis of Calcium in Sediment Extracts

7. Analysis of Phosphorus in Plant Digests

8. Detailed Vegetation Mapping

1. Digestion of Plant Material

Plant material was digested by the wet pressure method described by Adrian (1973) and Adrian and Stevens (1977). This method has the advantage over most other methods (see for example Allen *et al.* 1974) that it can be carried out at 65°C in a waterbath. Three replicates of all samples were digested (except for one or two for which there was not sufficient material available) and subsequently analysed.

0.5 g of dried plant material was placed in 500 ml polypropylene bottles (previously acid-washed; Lewis & Grant 1978). 4 ml concentrated nitric acid plus 2 ml concentrated perchloric acid were placed in the bottles, which were then swirled to soak all the samples with acid. Acid was also placed in bottles containing no plant material, and these blanks were treated exactly the same way as the bottles with plant material. The bottles were loosely capped and stood for 24 hours. If this predigestion stage was not carried out the bottles would burst when heated. The bottles were then heated in a water bath at 65°C for three hours, with the lids screwed on tightly. After cooling, 2 ml of distilled water was added, the bottle lids were replaced and heating was continued for another two hours.

After cooling, approximately 15 ml of distilled water was added to each bottle, and the contents were filtered and made up to 50 ml with distilled water. A sample from the 50 ml was stored in a glass bottle at 4°C for analysis at a later date.

2. Extract of Sediment Samples

5 g of dried sediment was placed in a 250 ml glass bottle. 50 ml of one molar ammonium acetate was added to the bottles. The lid of the bottle was screwed on tightly and the bottle was shaken for 18 hours. This was carried out on a machine which constantly rotated the bottles about an axis. The samples were then filtered and the extracts were retained in polypropylene bottles for analysis. Blanks with no soil in had exactly the same procedure carried out. Three replicates of each sediment sample were extracted.

3. Analysis of Phosphate in Sediment Extracts

Reagent

151 ml Analar concentrated sulphuric acid was added to 500 ml distilled water. After cooling 20 g ammonium molybdate dissolved in 200 ml distilled water was added. 0.4 g potassium antimony tartrate dissolved in 100 ml distilled water was then added and the solution was made up to one litre with distilled water. This was stored in a dark bottle at 4°C until it was needed. Just before use 1.5 g per 100 ml reagent Analar ascorbic acid was added.

Procedure

10 ml of plant extract was pipetted into a 50 ml volumetric flask and diluted to approximately 30 ml. 5 ml of the reagent was added, followed by 5 ml 2.5 molar sulphuric acid. An aliquot of the solution was placed in a test-tube and its absorbance at 880 nm was read in a spectrophotometer after half an hour. The reading was calibrated against phosphate standards in the range 0 - 50 mg P l^{-1}.

4. Analysis of Nitrogen, Carbon and Hydrogen in Sediment and Plant Samples

Measurement of total nitrogen, carbon and hydrogen was carried out by placing approximately 0.5 mg dried soil or plant materials in a Carlo Element Analyser (Model 1106) at the Institute of Freshwater Ecology's Ferry House Laboratory. The samples were atomised and the carbon, hydrogen and nitrogen present determined by gas chromatography.

5. Analysis of Potassium in Sediment Extracts and Plant Digests

This was carried out using an Evans Electro-Selenium Flame Photometer, calibrated against standards made up in solution with the same concentrations of acid or extractant as the samples after dilution, in the range 0 - 50 mg K l^{-1}

6. Analysis of Calcium in Sediment Extracts

This was carried out using a Perkin Elmer 1100B atomic absorption spectrophotometer. The readings were calibrated against calcium standards in the range 0 - 5 mg Ca l^{-1} containing the same concentration of ammonium acetate extractant as in the samples after dilution. The samples and standards contained 0.1_% stannous chloride to reduce interference (Perkin Elmer 110B Operator Manual, 1989).

7. Analysis of Phosphorus in Plant Digests

Phosphorus was measured in the digests using a Technicon auto-analyser. The chemistry was essentially the same as the colorimetric molybdate method described above. Duplicates of each replicate sample were analysed. Zero and 25 mg P l^{-1} standards were made up with the same concentration of acid as in the digests.

8. Detailed Vegetation Mapping

This method is based on the rectangle method of Wright *et al.* (1981). The area to be mapped was divided into 1 × 0.5 m quadrats. This was carried out by stretching two tape measures across the river, with a 1 m space between them. After the vegetation had been mapped between the tape measures, the fist tape was moved to 1 m above the second tape and the procedure repeated. At each 0.5 m interval the vegetation in that quadrat was recorded. The dominant plant species (or substrate, if that was dominant) was recorded, other species present and the type of substrate. The type of substrate (mud, sand or gravel) was determined visually; there was no difficulty determining the type.

The percentage cover of a species was calculated on the basis of the number of quadrats in which the species was dominant. Species richness was defined as the mean number of species present in each 0.5 × 1 m vegetated quadrat.

APPENDIX D

Spink A.J., Murphy K.J. & Westlake D.F. (1990)
The Effect of environmental stress on the growth of
Batrachian *Ranunculus* Species.

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THE EFFECT OF ENVIRONMENTAL STRESS ON THE GROWTH OF BATRACHIAN *RANUNCULUS* SPECIES

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Summary. A field survey of British river sites gave rise to the hypothesis that water velocity and alkalinity are two important factors determining the distribution of Batrachian Ranunculus species. The effects of a third potential stress factor (reduced light intensity) were also investigated in a field experiment.

INTRODUCTION

Environmental constraints may cause a plant to attain less than its potential maximum biomass in one of two ways. The rate of increase of biomass (growth) may be reduced by an environmental constraint: for example shade stress or the shortage of an essential mineral nutrient. In slow-flowing waters, nutrient (especially carbon) supply may become limiting due to leaf boundary layer resistance to diffusion (Westlake, 1967; Smith and Walker, 1980; Black et al., 1981). Such environmental pressures **stress** the plant. Alternatively biomass may actually be destroyed (for example by grazing), and this may be defined as **disturbance** (Grime, 1979). Plant species have evolved different strategies to cope with differing combinations of stress and disturbance (Grime, 1974). A description of these strategies can provide a coherent ecological framework within which the plant community may be studied.

In this study Batrachian Ranunculus communities are examined within the framework provided by plant strategy theory. A survey of river sites generated hypotheses concerning the environmental constraints which might be important in determining the distribution of Ranunculus species: these hypotheses can be experimentally tested.

MATERIALS AND METHODS

a) **Survey.** During 1988 twelve river sites in Scotland and northern England were visited two or three times. The sites were as follows (National Grid Reference in brackets); Gogar Burn (NT 171706), River Gryfe (NS 43969 and NS 433667), Locher Water (NS 4136576), River Irvine (NS 356378), Mouse Water (NS 955482), River Petteril (NY 498342), River Uggie (NK 101481), River Ythan (NJ 957303), River Rye (SE 642803), River Hull (TA 057562), and Cumwhitton Beck (NY 506523). The percentage frequency of each plant species present was recorded in a 100 m stretch for each stream habitat (riffle or pool), to give a total of 52 samples.

b) **Experimental Study.** The effect of stress due to slow water current velocity and low light intensity is being investigated by experimental manipulation of the East Stoke Mill Stream (SY 870867) adjacent to the Institute of Freshwater Ecology River aboratory in Dorset, southern England. The stream was initially dominated by Ranunculus penicillatus var. calcareus (R.W. Butcher) C.D.K. Cook. Eight plots (4 m × width of stream (c. 10 m)) were established in the stream, with a 4 m buffer zone between plots. The vegetation was mapped at approximately monthly intervals, using the rectangle method, adapted from Wright et al. (1981). On 7th June 1989 half of the plots (selected at random) had shading material ('Typar 3267' superbonded polypropylene: Dawson & Hallows, 1983), placed over them supported by a wooden framework. The shading gave a reduction in photosynthetically active radiation of 61 - 76%.

RESULTS

a) Survey.

The data were analysed using the multivariate statistical programs TWINSPAN (Figure 1) and DECORANA (Figure 2) (Hill, 1979a, b; Hill & Gauch, 1980). Percentage frequency data were converted to a simplified abundance scale (1 = 0 - 20%; 2 = 21 - 40%; 3 = 41 - 60%; 4 = 61 - 80%; 5 = 81 - 100%) and the downweighting option was used for rare species in both the ordination and classification analyses. Detrended correspondence analysis (D.C.A.) ordination using DECORANA (Figure 2) revealed that variations in the species composition between sites, as expressed on the first two major axes of the variation, were significantly correlated with two environmental variables. DCA Axis 1 was positively correlated with the alkalinity of the water (37 - 190 mgl^{-1}, R = 0·397, P ≤ 0·01) and DCA Axis 2 was negatively correlated with the mean annual flow (discharge) at the sites (0·44 - 8·8 m^3s^{-1}, R = −0·578, P ≤ 0·001).

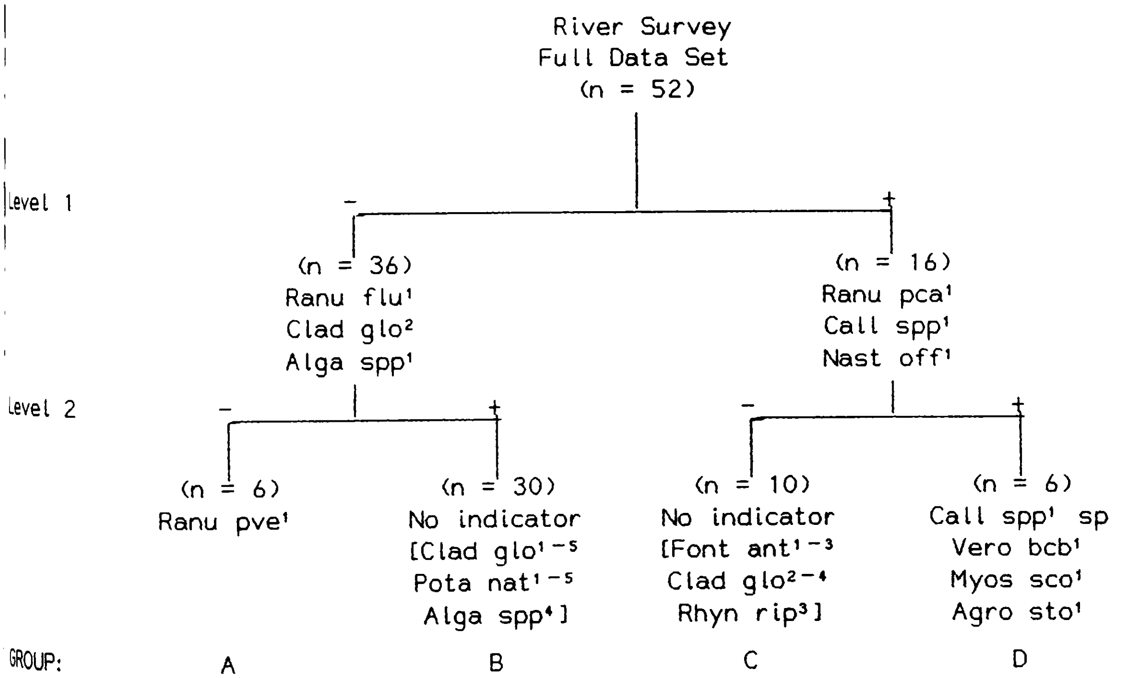

Figure 1. Results of TWINSPAN analysis of sample × species data from northern rivers survey 1988. Hierarchical subdivisions are shown for the first two levels of the sample classification, with indicator species, or (where these are not present), preferential species shown in brackets. The key to the species is as follows; Agro sto = Agrostis stolonifera L.; Alga spp = Algae other than Cladophora glomerata; Call spp = Callitriche spp; Clad glo = Cladophora glomerata L. (Kutz.); Nast off = Nasturtium officinale R. Br.; Ranu flu = Ranunculus fluitans Lam.; Ranu pca = R. penicillatus var. calcareus (R.W. Butcher) C.D.K. Cook; Ranu pve = R. penicillatus var. vertumnus C.D.K. Cook; Myos sco = Myosotis scorpioides L.; Vero bcb = Veronica beccabunga L. Superscript values are abundance scale values for species (see text):

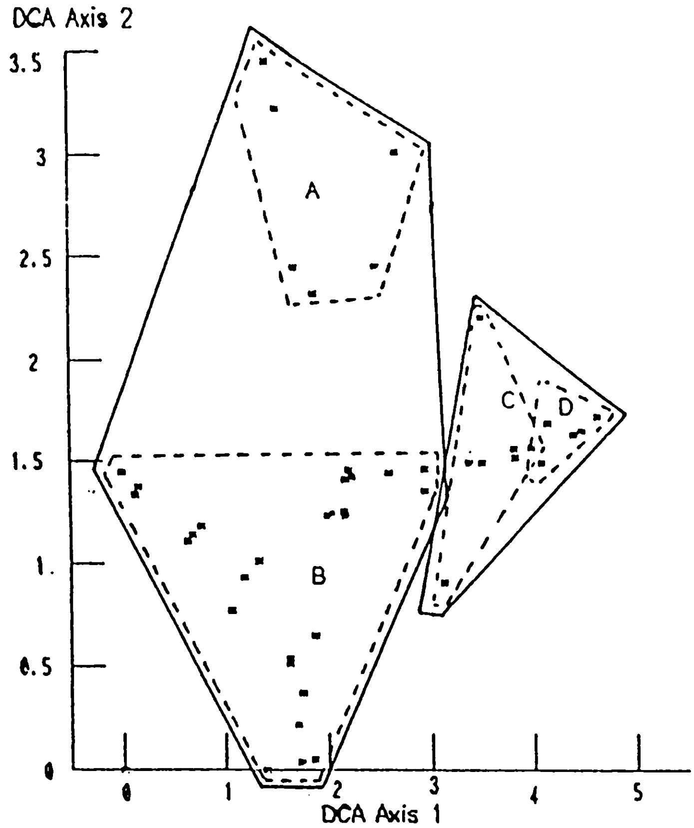

Figure 2. DCA ordination of river surveys, plotting the division of samples by TWINSPAN at Level 1 (———) and Level 2 (- - -) of the classification, into 4 sample groups (A – D: c.f. Figure 1). Axis units are standard deviation of species turnover.

b) Experimental Study.

Analysis of variance was carried out on the species cover data for Ranunculus penicillatus var. calcareus, Lemna spp., Nasturtium officinale and Apium nodiflorum (L.) Lag.. A split-plot design was utilised with species and shade as full factors and time as a sub-factor, following the recommendations of Little & Hills (1978) for analysis of repeatedly-sampled plots. The results are presented in Figure 3. All factors and sub-factors, and the species×time and species×shading interactions were significant at $P \leq 0{\cdot}01$. Orthogonal Least Significant Difference (L.S.D. $P \leq 0{\cdot}05$) for separation of means of the species×shading interaction was calculated (Figure 3a).

In the shaded plots Ranunculus had a significantly lower cover (and so probably biomass (Wright et al., 1982)) than in the unshaded plots. Although the Ranunculus cover was slightly lower in the shaded plot before the shading was applied, this difference was not statistically significant. Figures 3b and 3c show that as well as the expected seasonal variation in cover of Ranunculus (Ham, Wright & Berrie, 1981; Ham et al., 1982) there was a clear trend for the reduction of Ranunculus cover by shade to increase through the growing season. By the final measurement (in October) the cover of shaded Ranunculus was only one tenth that of the unshaded Ranunculus.

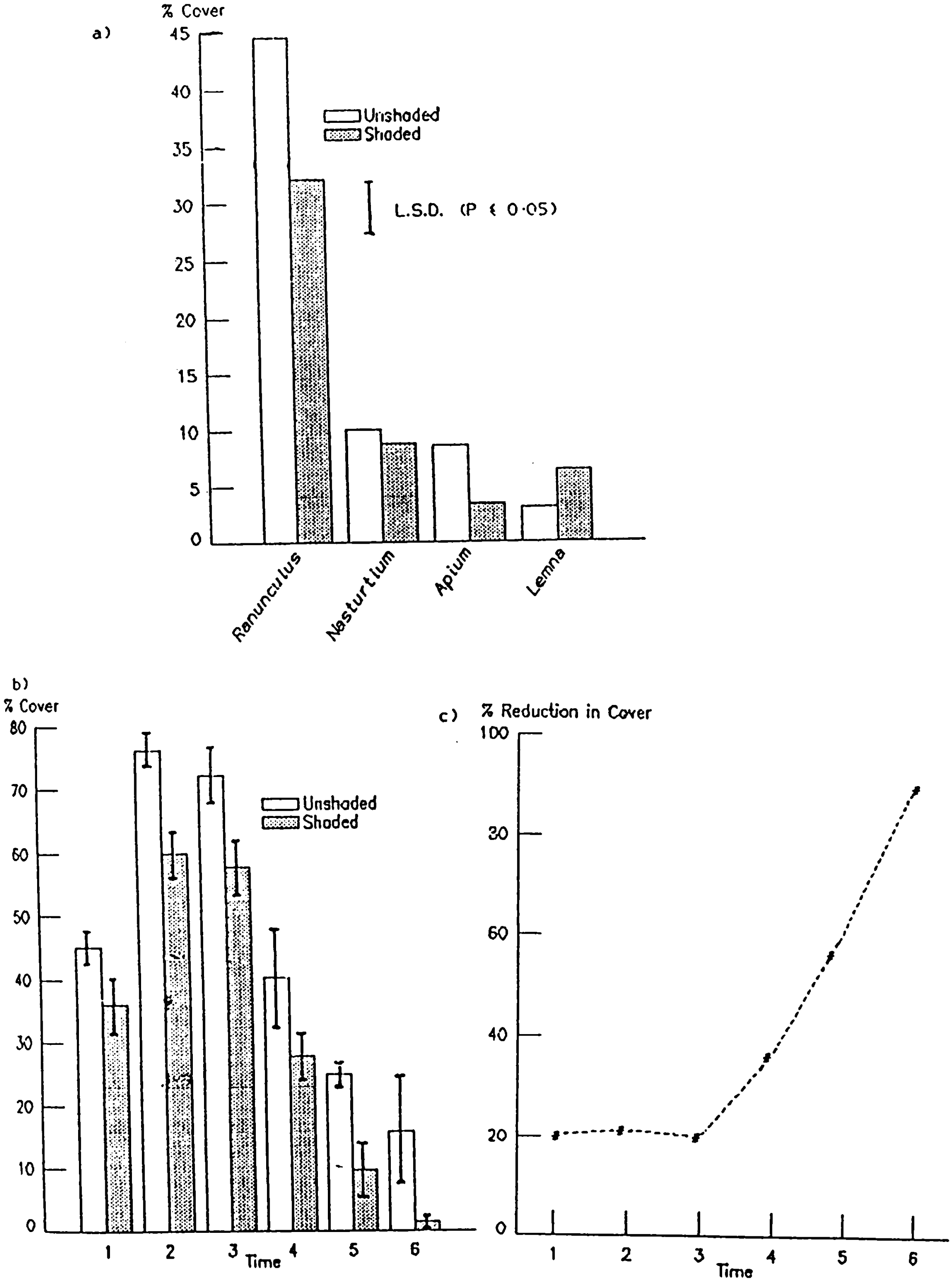

Figure 3. a) Mean cover of each species in the shaded and unshaded plots over 27th April to 18th October 1989.
b) Ranunculus cover in shaded and unshaded plots for each sampling date. Bars represent ± one standard error.
c) Cover of Ranunculus in shaded plots, as a percentage of Ranunculus cover in unshaded plots, for each sampling date.
1 = 27 April, 2 = 6 June, 3 = 10 July, 4 = 2nd August, 5 = 30 August and 6 = 18 October. Shading was applied from 7 June.

DISCUSSION

The results of the survey indicate that the hypothesis that low alkalinity and low flow rate are important stresses limiting the growth of R. penicillatus var. calcareus is worth testing. The effect of alkalinity will be tested in a transplant experiment. R. penicillatus var. calcareus will be transplanted from sites with high to low alkalinity and the effect on growth will be monitored. The interaction between low light levels and slow flow rate (previously shown to limit Ranunculus growth: Westlake 1966; 1967)) will be further examined in a continuation of the study reported here. In 1990 the velocity of the stream will be reduced, so that the effect of low water velocity, and the interaction between the two stresses may be measured. The results obtained so far confirm previous work (Westlake, 1966; Dawson & Kern-Hansen, 1979), in demonstrating that light is an important stress factor, limiting the growth of R. penicillatus var. calcareus.

The approach used here is designed to indicate survival strategies of established phase (adult) Batrachian Ranunculus populations. It is likely that aquatic species will exhibit different strategy traits from terrestrial species but little information is as yet available for most submerged macrophytes (Grime, Hodgson & Hunt, 1988). Although Murphy et al. (1990) and Wilson & Keddy (1985) have successfully applied the plant strategy approach to analysis of lake vegetation, the theory has yet to be successfully applied to lotic species, including Ranunculus penicillatus.

Grime (1979) suggested that plants which show little change in growth rate when shaded are often tolerant of stress, i.e. shade-tolerance is a good general indicator of the stress-tolerance strategy. In the study reported here R. penicillatus var. calcareus showed a rather large difference in its growth rate between shaded and unshaded treatments. This suggests that stress tolerance may play a relatively minor role in the strategy of Ranunculus penicillatus var. calcareus.

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Résumé

Une enquête sur le terrain de sites des rivières britanniques donna naissance à l'hypothèse que la vélocité et l'alcalinité de l'eau sont deux éléments importants dans la détérmination de la distribution de l'espèce Batrachian Ranunculus. Les effects d'un troisième élément potentiel de tension (intensité de lumière reduite) furent étudiés aussi dans une expérience sur le terrain.

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