# Freshwater Biology

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# ECOLOGY AND MANAGEMENT OF WATER PLANTS IN LOWLAND STREAMS

F. H. DAWSON

## Introduction

The common water plants of lowland streams are characterised by similarity in forms but variety in their taxonomy. The less common species have greater variation in both but are less important to the broad processes, interactions and management of the lowland stream ecosystem. Studies of the growth and seasonal cycles of a member of the commonest genus (*Ranunculus penicillatus* var. *calcareus* (R. W. Butcher) C. D. K. Cook, herein called *R. calcareus*) in a lowland stream (Dawson 1979a) introduced the possibility of improving traditional weed control or introducing new techniques and reducing cuts, with additional benefits to the stream ecosystem.

Lowland streams, which have fairly rapid flows of nutrient-rich water and substrata of sand or gravel, are typically vegetated by herbaceous perennials which grow almost completely submerged, except for the flowers. As an example, plants of *Ranunculus* spp. (Water Crowfoot) grow for much of the year, producing flexible main stems that can achieve a length of 4 m. These bear elongated leaves divided into many fine pliant filaments. In the spring stems become hollow and more buoyant to bear white flowers above the surface.

The growth of these water plants is vigorous in unshaded sections, particularly during spring and summer, and can raise the stream water level by up to 0·7 m. This may raise soil water-tables and increase the risk of summer flooding. Empirical management of these plants has been undertaken for centuries by maintaining channels free of plants, primarily to improve drainage of low lying land, but also to facilitate the use of the water in water-meadows or water-mills and to improve fisheries. In more recent decades a more rationalized approach has started which has led to changes in the form of river channels and in the techniques of plant management.

The commonly-used method of control, cutting the plants in spring and summer, has proved to be only a short-term solution (Dawson 1979a). Cutting leads almost immediately to further rapid, synchronised growth (Fig. 1, see standard annual cut line) because plants are released from the progressively poorer growth conditions and the self-imposed burden of high biomass, which lead to the natural collapse of undisturbed populations by the late summer (Fig. 1, see 'natural line'; see also Ham et al. 1982). Following removal by cutting, however, the remaining rooted parts do not die back but often continue to grow during autumn; this increases the probability of high over-wintering biomasses and thus higher biomasses earlier in the subsequent year. One study, discussed earlier (Dawson 1979a), showed that following the cessation of cutting, the maximum biomass of *Ranunculus* declined over four years to about half of that previously found when plants were regularly removed as part of a 'weed-cutting' programme ('the four-year effect'). Hence it was proposed that if plant management was only used in reaches where flow was obviously restricted, the remainder of the river would maintain a tolerable biomass without cutting. Nevertheless a significant risk of occasional floods would probably remain during late summer.

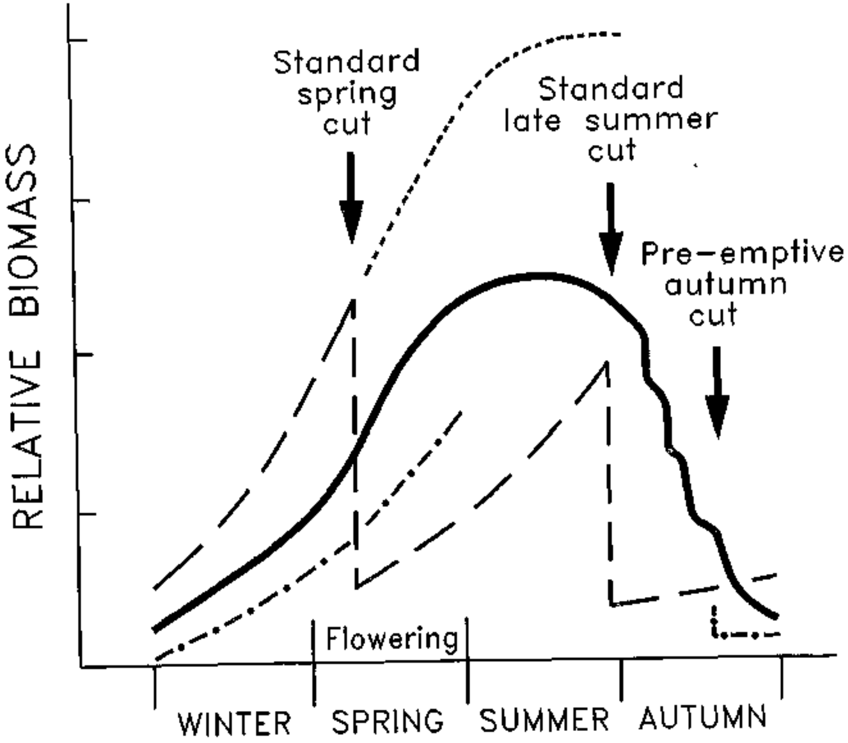


FIG. 1. Comparisons of the seasonal changes in biomass in small lowland rivers resulting from different cutting regimes; (a) the natural unmanaged biomass (solid line); (b) the standard annual spring and late summer cuts (long-dashed line); (c) no cut in the first year following a series of standard cuts (short-dashed line); (d) the first pre-emptive autumn cut (dash & dot line—in late summer this may merge with the natural line or be truncated by a cut). (Based on data from Dawson 1979a and Westlake & Dawson 1986).

Reviews of different aspects of plant growth and growth-controlling factors have emphasised the importance of light (Dawson 1981b, 1986; Dawson & Pitlo 1988). There is no universal solution to the control of excessive growth of macrophytes but knowledge of the biology of plants and their environmental interactions leads to general principles which can be applied to each problem area and can be used to modify current methods or to develop new or innovative techniques.

The general principles derived include:

(1) Light at the plant surface is needed for growth ('no light, no growth').
(2) Nutrient supply affects the balance between the large plants and algae in different ways, depending on the depth and turnover rate of the water.
(3) Growth continues until the resources of light, nutrient or space are fully utilised.
(4) The growth and distribution of biomass influences the environment; the horizontal and vertical distribution in flowing water influences hydraulic resistance.
(5) Plants have numerous roles in the ecosystem, as sources of energy, as diverse habitats and as part of the landscape.
(6) It is essential to isolate the reasons for controlling aquatic plants at specific sites and monitor results.

Specific suggestions to be considered were:

(a) Changes in extent or timing of cutting methods.
(b) Manipulations of the plants' environment (such as changes in incident light, nutrients or water turbidity).
(c) Manipulations of the profile of water bodies to change the quantity or species composition of plant communities.

These reviews summarised progress in the application of ecological knowledge to the management of water plants. Some ideas presented may appear fanciful or of limited, albeit locally beneficial use, but combined manipulations of the biological and physical environment can produce economic improvement or solutions, to problems of aquatic plant management, or to problems consequential upon their presence, e.g. habitats for pathogen hosts. Much of the experimental work has been carried out in rivers dominated by *Ranunculus calcareus* but the understanding derived is being extended to the management of water plants in general.

## The significance of seasonal growth

The seasonal behaviour of water plants has important consequences for their management in addition to those already considered (above, and Dawson 1979a). Flowering marks the time of change in growth habit from the exclusive formation of leaves and stems, towards flower and seed production and also precedes preparations for food storage by roots and rhizomes for the next season's growth (Dawson 1980a). In *R. calcareus* flowering involves the formation of hollow buoyant stems of larger diameter, upon which the flowers are borne aerially; such stems are more vulnerable to damage and loss. Flowering signals the start of the decline in the rate of growth as the accumulation of biomass begins to reduce the net photosynthesis of the stand. The maximum biomass coincides with the end of flowering. Thus flowering can be regarded as an indicator of the timing of the seasonal cycle and the probable adaptation of plants to the average environmental conditions of that reach of the river. It was observed that flowering started earlier upstream in rivers, particularly at spring-fed sites, where the water is then usually clearer and relatively warmer than at downstream sites. On the R. Piddle, Dorset there was a progressive downstream delay of the start of flowering resulting in a difference of 2–3 months between source and river mouth only 40 km apart (Fig. 2; Dawson 1980a). This ecocline, with a genetically fixed internal or endogenous rhythm, was confirmed by experimental transplants and by culturing plants in different day-lengths in artificially illuminated channels.

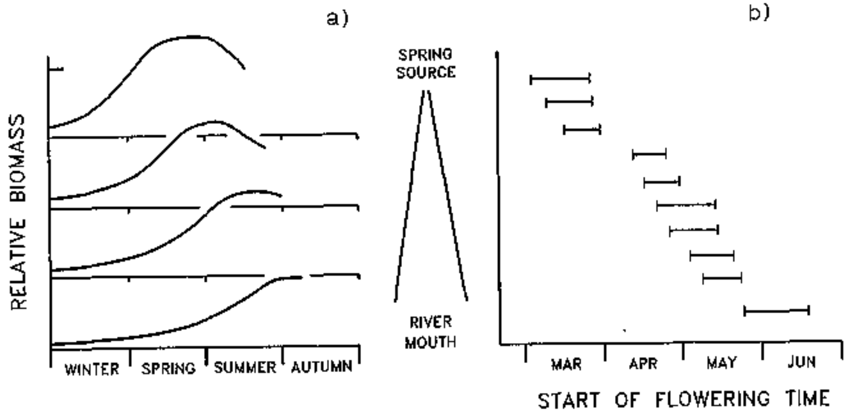


FIG. 2. *Ranunculus calcareus*: downstream differences in flowering and biomass from source to mouth along the River Piddle, Dorset. (a) diagrammatic seasonal changes in biomass, (b) the time of the start of flowering. (After Dawson 1980a.)

These observations are apparently at variance with the statement above, that vegetative growth is the main method of spread of the plant. However this merely emphasises the strength of the environmental selection pressures, which initially created the ecotypes which flower progressively later down the river, but now prevent the growth of fragments of these ecotypes drifting downstream, at downstream sites.

Aquatic plants are an important source of easily-available organic material to drive the aquatic ecosystem. Their wholesale removal from the water during normal management in spring and summer, depletes the system of valuable aquatic plant material. In addition such removal concentrates the local settlement and prevents the seasonal retention of much of the terrestrial input, which is no longer broken down and used as food within the river system throughout the year (Dawson 1980b).

## The significance of stand structure

The growth of submerged plants, and particularly their maximum biomass, results from the interaction of the plant, its physiological condition and potential growth form or habit, with the physical and chemical conditions of its environment, particularly light, nutrients and water flow. Some of these interactions, particularly those between biomass and light, and biomass and hydraulic resistance, have been introduced previously (Dawson 1979a). Studies have now been extended to cover broader aspects of light, stand structure, hydraulic resistance and the plants' physiological responses to temperature and dissolved oxygen. The effects of these factors are difficult to separate, for they interact to produce not only the biomass at a particular time and its seasonal variation, but also the form of the plant stand within the constraints of the habitat, through interactions within the plant stand and with the general riverine environment.

### *The stand and its environment*

As the growth habit or architecture of the individual plant stand develops, several environmental interactions are involved. As plants grow they increase the hydraulic resistance to water flow and slow the mean velocity of the water, increasing water depth. In addition, as the growing season progresses, the rate of discharge and water velocity typically decrease, whilst the ambient temperature of the water rises (Dawson & Robinson 1984). Additionally, the bulk of the plant stand progressively develops its own internal microclimate during the growing season. For example, the average water velocity within the stand may fall to one tenth of the external velocities (Marshall & Westlake, in press), or the surface water temperature within stands may rise by 2–4°C. By the time of maximum biomass it is likely that the majority of the plant material is not exposed to the general flowing water environment.

Although more research is required to understand the nature of the internal environment of plant stands and the consequential effects on metabolism and seasonal changes in biomass, some data on the plants responses—particularly those of respiration to water velocity, water temperature and dissolved oxygen—have already been obtained (Dawson, Westlake & Williams 1981). Such study was aided by the development of a programmable metabolic chamber with partial recirculation of water to allow the use of realistic water flows on whole plant stems. Results confirmed previous work at low velocities, and added knowledge of both the metabolic relationships at higher velocities around developing plants and of the dissolved oxygen variation within plant stands; the behaviour of the latter was found to be contrary to that often assumed in many mathematical analyses of stream oxygen data.

A better understanding of the internal environment of plant stands, as their biomass becomes progressively denser during the second half of the growing season, will help in evaluating current proposals for modifying management practices. For example, selective cutting involves severe cutting in some areas while others are left uncut to suffer the disadvantage of high biomass and substantial deterioration in conditions for their growth (Fig. 6).

### *The stand and its hydraulic resistance*

Knowledge of the resistance to water flow resulting from the seasonal growth of water plants has been extended from shallow streams (Dawson 1979a) to larger vegetated rivers, typical of the managed rivers of lowland areas (Fig. 3; Dawson & Robinson 1984). The previous results for small streams gave values of hydraulic resistance coefficients (e.g. the 'n' parameter of Manning) far higher than those currently in use for the hydraulic design of channels. In the larger rivers the values obtained were three times those in normal use. Increasing velocities were shown to markedly decrease the resistance coefficient, so that rivers with weed-beds have mechanisms that reduce the effect of discharge on water level (Dawson & Robinson 1984, Westlake & Dawson 1988). It was proposed that higher values of the resistance coefficient should be introduced in preference to those of the normal design procedures, in which resistance values for substrata without vegetation are used to design channels to carry winter flows; and hence weed cutting has to be accepted as a normal practice to alleviate summer flooding.

Preliminary investigations of the nature of vegetative roughness were attempted by determining the drag and associated forces acting upon plants, *in situ*, using a simple tensiometer. The force acting upon a plant increased exponentially with water velocity but varied with plant size and species, and with season through variation in stand structure. Several parameters relating size to drag were measured, because it was difficult to define precisely the

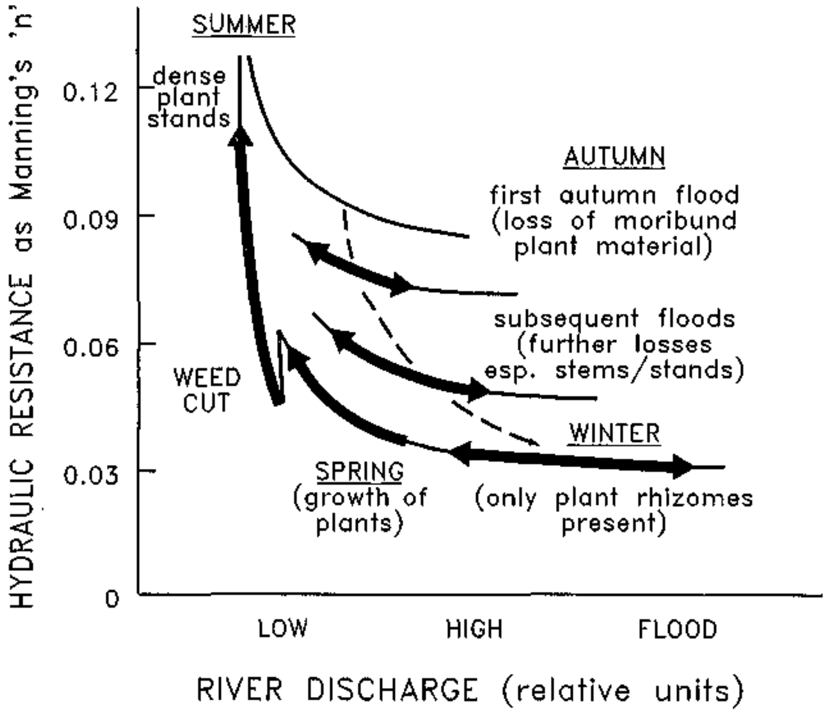


FIG. 3. Typical seasonal relationships between hydraulic roughness and discharge for a lowland river, River Frome, Dorset. 1–1·5 m in depth, dense summer stands of attached fluviatile macrophytes, predominantly *Ranunculus calcareus*, thin lines indicate ranges of discharge values, thick lines indicate the predominant values. (After Dawson 1988.)

area presented to water flow (the 'drag form'). However when biomass was used as an index of plant population in a calculation of the numbers of plants and their individual resistance, for a section of river, this accounted for more than half the hydraulic resistance.

Several factors are important for understanding the nature of roughness of aquatic plant stands. These are: water velocity and turbulence; the species, with its associated seasonal changes including stem-length, angle, and buoyancy (response to flowering); the distribution of stems within stands; the distribution of stands, and the accumulation of associated sediment (Dawson & Robinson 1984; Dawson & Charlton 1988; Pitlo & Dawson 1989). The nature of hydraulic roughness is more variable than is generally considered. Thus the commonly used concept of vertical and flexible rods (cf. reeds) is inappropriate for many species of river vegetation. Flume studies have shown

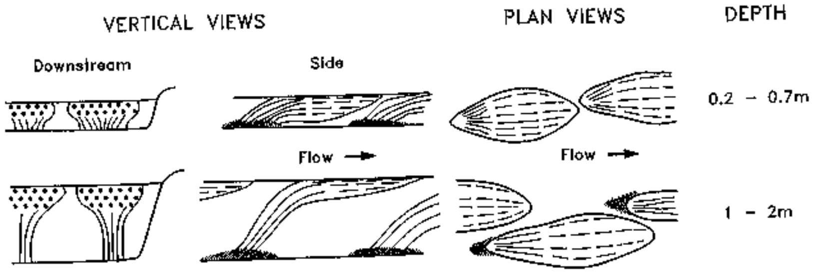


FIG. 4. Typical stand forms of *Ranunculus calcareus* growing amongst others in shallow and deep water of a river. The density of lines and large dots represents stem density from side and in section; fine dots represent typical accumulation of river silt. (After Dawson & Robinson 1984.)

that the forces acting upon oblique stems are considerably less than vertical ones (Dawson & Robinson 1984). Similarly the nature and combination of plant stands can produce effects which vary from sub-surface tube-like flow in deeper water (without the commonly-assumed velocity-depth vertical profile) to between-plant flow in shallow streams, giving a pseudo-braided effect within the channel (Fig. 4; Marshall & Westlake, in press). Nevertheless, despite the complex relationship of water plants to flow, it is apparent that plants of faster water are adapted, or are selected, for their ability to keep a low drag profile consistent with the water power acting upon them at their selected site. Changes in the biomass and form of individual plant stands, resulting from modifications of plant management techniques, have already shown possibilities for decreased vegetative hydraulic resistance (Westlake & Dawson 1986, 1988).

## Assessment of current river management

### *The cost of traditional plant management in watercourses*

A current estimate of total cost for aquatic plant control in flowing waters in England and Wales (undertaken for the Water Research Centre) is between £M45–75 per annum although it could be as high as £M100:

'main' rivers, by Regional Water Authorities, £M8;
streams, by groups or individuals, £M8;
Internal Drainage Board (IDB) channels ('drains'), *c.* £M22;
farm drains within IDB areas, £M17;
farm drains outside IDBs, £M17;
canals (of 0·5 Mm in length), <£M1.

Three quarters of this control is either manual or mechanical, and although chemical control has increased, it is probably not increasing any further. Two significant areas, streams (i.e. 'non-main' river) and farm ditches outside IDBs, were identified as not previously included in the national cost. A comprehensive survey of all aquatic plant control needs to be undertaken in order to give context to further research, because the only previous survey is over 20 years old and was acknowledged to have been selective. It is clear that relatively large resources are spent on aquatic plant control by independent and often uncoordinated groups, but that significant economic and ecological benefits could be derived through general improvements in techniques, at the cooperative level.

### *Channelization and plant growth*

A regional survey of England and Wales using data from official records and from drainage engineers, indicated that a total of 8500 km of major or capital works schemes were undertaken between 1930 and 1980 with an additional 35500 km being maintained (Brookes et al. 1983). This river channelization has been undertaken to reduce or alleviate flooding, to drain agricultural land, and to reduce or prevent erosion. Effects similar to channelization may also occur by regular and intensive plant management. Channelization can have a range of impacts on river morphology and aquatic vegetation. Particular attention has been focussed on prediction of the consequences for the channel further downstream following the release of sediment during construction and from erosional adjustments to the channel resulting from increased flows through the section in both vegetated and unvegetated rivers (Brookes 1983). Such data have been applied in work for British Petroleum with regard to the crossing of rivers by pipelines.

### *Traditional management of river plants*

A long-term study of the effort expended on cutting and removing water plants, dominated by *R. calcareus*, from 50 km of the R. Frome, Dorset, allowed some interpretation of the year-to-year changes of biomass (Westlake & Dawson 1982). Despite some changes in technique, it was clear that the weight of weed removed is due to the interaction of three factors of similar importance—environmental growth-controlling factors, the initial biomass present, and the river engineer's decisions on the timing and extent of the cuts. Environmental effects, such as incident light, water temperature and discharge, directly influence the plants' metabolism. Growth is also indirectly affected by increases in discharge which increase water turbidity and reduce underwater light, and modify the form of individual plant stands. The initial biomass is determined by the previous cut, usually in spring or late summer. The engineer's decision on the timing of the spring cut is influenced by his judgement of the flood risk to adjacent agricultural crops, observation of the plant cover (which is not a good measure of standing crop) and the discharges prevailing in the spring. Completion of the cut at upstream areas before the 'mayfly' hatch for sport fishing is also an important consideration.

The economics of weed cutting needs to take account of several biological, agricultural and economic factors, but there has been little quantitative work carried out on any of these, particularly the loss in value of crops that are being protected from flooding. Much weed cutting may have become necessary through the over-zealous removal of bankside vegetation and the construction of elaborate drainage schemes. As costs are increasing rapidly, the time is now ripe for examining the economics of the restoration of self-balancing river-channels.

### *Adverse effects of river plant management*

Although effects of management are normally valued by their benefits, there are detrimental effects, not only on the fauna (Mills 1981; Dawson 1984), but on the physical environment and on the plant communities. For example, when the physical environments of several small streams of similar size and discharge were compared, it was found that previously managed streams which were left unmanaged had a wider, more extreme range, of both dissolved oxygen and water temperature (Dawson, Kern-Hansen & Westlake 1981; Dawson & Henville 1985). The morphological changes associated with the management of streams tended to create stress within the system because the system is modified to cope with winter flooding rather than allowing the channel to become naturally adjusted, by flood erosion. The biomass levels at which management normally occurred coincided with the maximum biomasses found in unmanaged streams. Thus lack of management did not cause flooding and the fauna did not suffer the destabilizing effects of plant removal.

## Improvements to plant management techniques

### *No cutting*

The initial proposal for improving management for both economic and ecological reasons was to avoid cutting wherever possible. It has been shown for other problem species that reductions of biomass can thus be achieved even more rapidly than the four years required for *R. calcareus* (Dawson & Kern-Hansen 1979). Further analysis of the data on the 'four-year' effect of *R. calcareus* was undertaken to find which aspect was amenable to further experimentation. The effect was attributed to (a) the late summer suppression of growth as plant biomass declined naturally, (b) the consequent low biomass in winter which reduced the potential for growth in the next season, and (c) to the encouragement of plants adapted to maintaining a presence rather than those with capacity for more rapid re-growth (Fig. 1). The seasonal changes in biomass indicated that growth was exponential up to half the maximum biomass (*c.* 150–200 g dry wt $m^{-2}$), after which self-shading and interaction between plants progressively occurred; this relationship requires direct confirmation by culturing the plant under controlled conditions (particularly of water velocity). The significance of the exponential growth rate as obtained from the field data (Dawson 1979a) is that a low initial biomass is expected to reduce seasonal maximum biomasses at flowering time, and could therefore be utilised as a management technique.

### *Early or pre-emptive cutting*

The above interpretation was, coincidentally, linked with the observations of a local river engineer who commented that light autumn dredging, with minimal disturbance to the stable river bed, suppressed plant growth for many months. Together these observations led to trials of a weed-cut late in the year to reduce overwintering biomass and thus 'pre-empt' growth in the subsequent season (Fig. 1, see 'pre-emptive' line). This has been shown to be

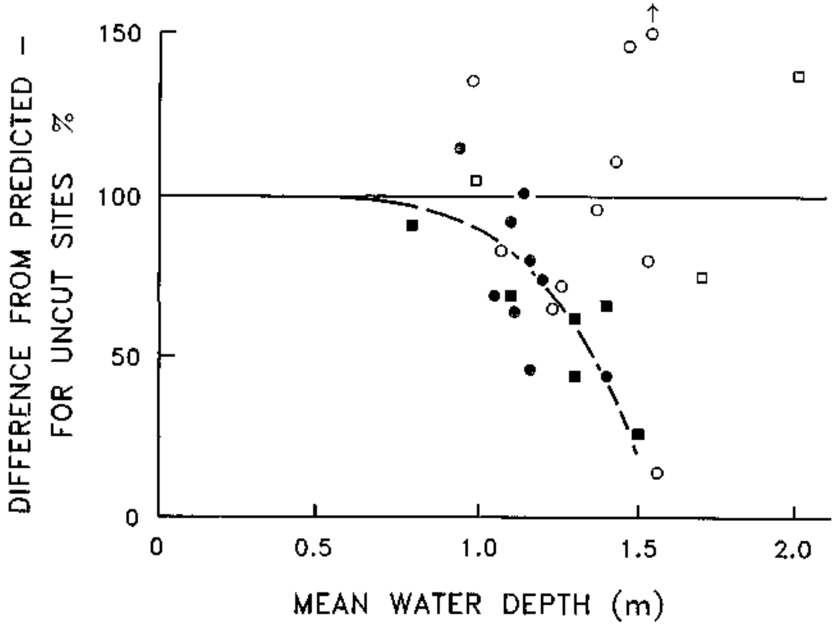


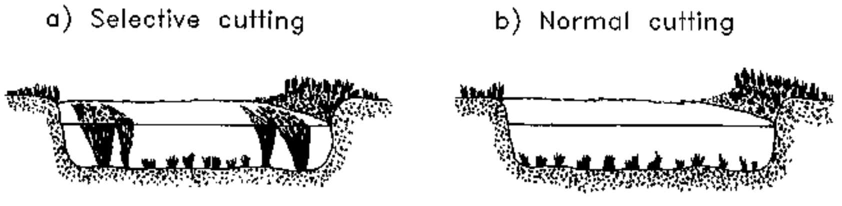
FIG. 5. Effect of depth on reduction of spring biomass after autumn cut. Spring biomasses of individual transects, plotted as percentages of the biomass predicted at that depth (by curves fitted to biomass/depth data from uncut transects for each year). Open symbols and solid line, uncut transects. Closed symbols and dashed line, autumn cut transects. Squares 1984/85. Circles 1985/86. (From Westlake & Dawson, 1986.)

an economically advantageous improvement to accepted weed cutting practices (Westlake & Dawson 1986). When pre-emptive cutting, called locally 'close autumn weed cutting', was tested over three years for the Wessex Water Authority in the River Frome, it indicated that the biomass in the lower river was on average 28% lower than expected at normal cutting time. Direct assessment of plant biomass, and measurements of water level changes related to the resistance to flow offered by plants, confirmed the effect (Westlake & Dawson 1986, 1988). Detailed study of the relationship of spring plant biomass to water depth, in autumn-cut and autumn-uncut sections, indicates that the benefit of autumn cutting may be limited to water deeper than 0·7 m, or to only the lower half of this 50 km river (Fig. 5; Westlake & Dawson 1986). Although the experiment required spring cutting to proceed as previously, it became progressively less necessary, and almost ceased in the third year.

Immediate benefits of pre-emptive control included reductions in the weed removed, and consequential reductions in the logistic problems of time and labour needed and in the need for a further summer cut. A decrease in spring flooding gave an agricultural benefit. Ecological benefits accrued through the reduction in the need for a spring cut, the encouragement of less vigorously growing plants and the 'four-year effect', an increase in the numbers of large plants, and a change in their form. Such changes in the structure of individual plant stands require investigation. It has been observed that few, larger plants have less hydraulic resistance than many, small ones (Dawson & Robinson 1984; Westlake & Dawson, 1988). Also their removal and capture on weed removal booms may well be more effective (when cutting control is necessary). These benefits were only demonstrated for one dominant plant, *Ranunculus calcareus,* and other species may act in a different manner or indeed be selected for, by this change in management.

### *Further refinements to cutting regimes*

Many are possible; for example, the selective cutting of particular parts of the channel which could be ecologically as well as economically beneficial (Dawson 1986). Selective cutting of the central area of a river in a sinuous or less regular manner, could reduce weed cutting effort and provide bank-protection by the remaining marginal bands of aquatic vegetation (Fig. 6). Uncut plants remaining would be at a physiological disadvantage because of self-shading and through the reduction of water levels, which, in turn, would reduce water flows and thus limit the supply of inorganic carbon and nutrient supplies. Conversely the remaining shoots and roots of the cut central plants would be exposed to higher than normal velocities which is also likely to restrict their growth. Within-channel water capacity would also be increased during summer and thus this technique is likely to facilitate the passage of floods.



a) Selective cutting

b) Normal cutting

FIG. 6. Comparison of plant management by (a) selective and (b) normal 'clear' cutting techniques in a river.

## Alternatives to the traditional techniques of river plant management

### *Shading by bankside vegetation*

Observations of the plant biomass of open and shaded sections of streams, combined with the study showing the equal importance of terrestrial and aquatic organic material to the stream system, led to the proposal that some shade could be a useful alternative to weed cutting (Dawson 1979a & b). Field experiments for the Environment Ministry of Denmark demonstrated that the biomasses of three dominant and problem species of macrophyte were directly proportional to the light reaching the water surface in both artificially and naturally shaded sections of stream (Dawson & Kern-Hansen 1979; Dawson 1981a). These results were refined and led to the development of a proposal for management by 'half-shade', with recommendations for the size of vegetation for streams and rivers of differing size (Dawson & Haslam 1983).

The theme of half-shade has been developed because marginal vegetation along a river bank does provide shade from sunlight, and therefore provides an economical way of controlling the excessive growth of water plants in streams. However excessive shade is just as ecologically undesirable as excessive plant growth. It is likely to limit fish populations by reducing cover and invertebrate food; there are however no direct data on the correlation of fish and plants, for these interrelationships are complex. A further examination of the management of river vegetation developed the theme of the 'riverscape' and included a discussion of the role of trees alongside rivers both from the viewpoints of aesthetics and economic management of lowland rivers (Dawson & Haslam 1983). Data on the transverse distribution of light across rivers under varying degrees of shade, and more detailed data on the degree of shade under the major compass orientations of artificial shade, were given in addition to summarising the best current guidelines. The latter incorporate the principles of half-shade by deciduous marginal vegetation, in which the height of the shade should be equal to the width of the stream when the marginal vegetation is growing on the south bank, or otherwise marginal shade should interrupt 2/3 of the direct light in summer. Marginal vegetation should be intermittent and only occupy 2/3 of the length of one bank. If trees are utilised there should be a planned cycle of planting and cropping to avoid trees falling into the river and to provide economic benefits. 'Fine-tuning' and improvements remain to be made for planting regimes on sinuous rivers or those of varying orientation and on the choice or mixture of vegetation; together with objective studies on the effects of flooding on channels in which half-shade control is operating. Further improvements in the technique of 'half-shade' depend upon the development of a light model which can account not only for direct and coronal sunlight but which incorporates data on average day-to-day changes in diffuse light distribution within the hemisphere.

*Opaque materials*

One short-term solution, designed particularly to control critical areas of streams and rivers, during the growth period required for the development of shade by marginal vegetation, is the use of lightweight opaque material which is both strong for ease of handling and gas-permeable to prevent gas accumulation (Dawson & Hallows 1983). Trials for Du Pont (UK) Ltd, using 'Typar', indicated that the time for optimum control varied from 6 weeks for submerged macrophytes without large rhizomes to 12 weeks for areas of emergent plants with rhizomes. Shorter periods gave some control, but extended periods eradicated plants and required plants to reinvade. The build-up of detritus on the surface of submerged sheets enhanced the shading effect and allowed the use of less optically dense material. A planned cycle of movement of sheets of material was most important to this technique and, in fact, made it economically competitive with other methods (Fig. 7). This material can be applied to a variety of sites currently being managed by techniques which stress the biological system. Recommendations given to British Petroleum for its use at extraction sites adjacent to nature reserves in an area of outstanding natural beauty, should allow this aspect of its efficacy to be tested. The basic problem in application is that it does not give instantaneous results (unlike weed cutting), and therefore has user-resistance. There is also concern by river engineers that material could be lost downstream, be caught on hatches and lead to flooding; this has not occurred in five years of trials in streams.

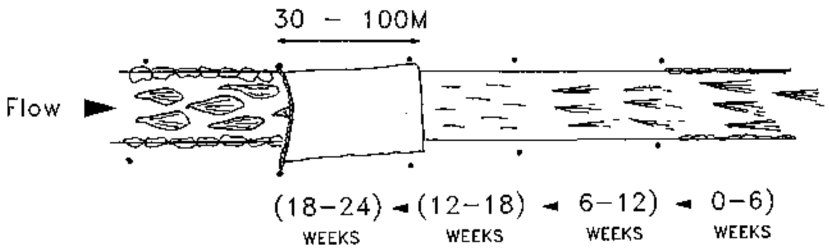


FIG. 7. The planned cycle of upstream movement of a sheet of dark shading fabric for the control of stream water plants. (Longitudinal scale distorted; after Dawson & Hallows 1983).

*Further possibilities*

These have been discussed by Dawson (1979b, 1986). They include other methods of reducing the light reaching the plants, changes in river morphology, changes in cutting patterns and changes in the nutrient status of the river. The latter is not usually applicable to lowland streams, where nutrients are abundant, unless wide control of the catchment is possible.

## Conclusions

Aquatic macrophytes will normally be present in natural waters if light, nutrients and suitable sites are available. Their growth depends primarily upon the intensity and duration of sunlight which they receive but also upon the physical conditions of the water, its movement, temperature, clarity and chemistry (and the absence of growth inhibiting compounds). However, as they grow in response to their environment, their growth produces changes to this environment, creating their typical habitat. Thus as growth proceeds during the season, and stands of plants develop, progressive changes in the environment occur which can adversely restrict further plant growth, e.g. reductions in water velocity with increases in depth or diel extremes in dissolved oxygen. Their growth depends upon the daily balance between photosynthesis and respiration which they can achieve within these environmental conditions and leads to the seasonal cycles of growth, maximum biomass and eventual decline. Sudden or catastrophic changes in the plants' environment, e.g. flood or 'weed cutting' can also affect plant populations, either altering them when the changes are intermittent or perpetuating them when the changes are regular.

When favourable growth conditions prevail, particularly in lowland streams and rivers, dense macrophyte growths occur and, as this is often considered undesirable, reduction in biomass or weed management may be undertaken. Such direct removal of excess plant is rapid and effective but short-term, as the effects of cutting can stimulate synchronised regrowth accentuating the original problem for future years. In the current ecological and economic climate improvements to plant control techniques are more likely to be considered, such as reduced, retimed or selective removal, or the introduction of indirect techniques which moderate biomass through growth-controlling factors.

Control by light is a prime example of such techniques. It is direct in effect, with a good practical chance of success, as opposed to other factors, such as water velocity or nutrient limitation which may have disproportionate or low limiting thresholds. Half-shade provides a generally acceptable solution to weed control, with the presence of some macrophytes to provide readily-available organic material and habitat for animals of all types and age. Other modifications or innovative techniques can be developed, which also reduce rather than eliminate plants. The absence of plants might make rivers hydraulically simpler but, apart from the high cost of continual removal it would be detrimental, with direct effects on the numbers of invertebrates and fish fry expected.

Although the extent of aquatic plant control in the UK is not well quantified there is a market for considerable further improvements in the traditional, alternative and innovative techniques for plant control in a broad spectrum of freshwater habitats. Such changes should seek to reduce ecological stress and management effort, but information is still required on both basic data and cost-benefit analyses of current technique, and biological studies of the problem plants. Emphasis on standard river engineering solutions should, in many cases, be re-examined and account taken of the biological and geomorphological responses of the whole system.

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# FACTORS AFFECTING THE SUSCEPTIBILITY OF SALMONID FISH TO DISEASE

A. D. PICKERING

## Introduction

Outbreaks of disease in fish populations occur when susceptible fish are exposed to potential pathogens under conditions which favour the survival and growth of the infective organism. Changes in the physical and chemical characteristics of the environment can increase the abundance and virulence of pathogenic organisms as can genetic mutation, factors which must have an important influence on the outcome of a situation in which fish are challenged by pathogens in the water. However another influence, namely the *degree of susceptibility* of the host, may also be instrumental in determining whether or not pathogenic challenge results in disease. This aspect of the equation forms the subject for the present review.

Like all vertebrates, fish possess a wide array of defence systems to protect themselves against colonization by disease-causing organisms. Under favourable conditions these systems control pathogen-loading of the fish to such an extent that disease (i.e. an impairment of the normal physiological functioning of the whole, or part, of the body) is absent. However under conditions of stress (Pickering 1981), the defence systems can breakdown and disease may be caused by organisms which, under normal circumstances, are relatively harmless. Stress may take the form of a deleterious change in the environment, which then causes a disturbance of the normal homeostatic mechanisms within the fish, or it may be caused by endogenous physiological processes such as those associated with sexual maturation. Examples of both types of stress are given in this paper.

Studies of the effects of stress on disease resistance are of importance with regard to salmonids because of the value of these fish to man. Salmon and trout require water of high quality and are reared in Britain, almost to the exclusion of all other species, in an expanding aquaculture industry. The