RANUNCULUS CALCAREUS AND ITS ROLE IN LOWLAND STREAMS

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Introduction

Ranunculus calcareus is the species of water crowfoot which occurs most widely in the clear, nutrient-rich waters of chalk streams. These plants are herbaceous perennials and grow almost completely submerged in lowland streams of up to two metres depth with a moderately fast flow. The main stems may grow up to 4 m long and at regular intervals they bear leaves which are divided into many fine filaments. During the spring the stems enlarge, become more buoyant and bear white flowers above the water surface, although dispersal seems to be by vegetative means. The species of water crowfoot show considerable morphological variation in response to environmental conditions and this poses serious difficulties in identifying and distinguishing the species (Cook 1966). The plants are capable of vigorous growth in spring and summer and can dominate open sections of stream to such an extent that they raise the water level considerably, sometimes causing water-logging of adjacent land and increasing the risk of summer flooding. Such luxuriant growth also interferes with sport fishing and has led to the well-established method of plant removal by cutting. Plant growth and water level changes have been further accentuated by the decline in the use of water for water-meadows and for milling, resulting in a decrease in the number of serviceable hatches and sluices.

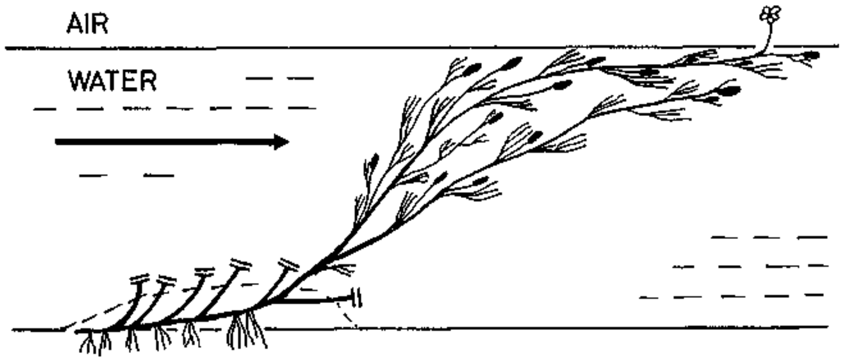

FIG. 1. A lateral diagrammatic view of the organization of stems, leaves and flowers of a typical plant of *R. calcareus*. The basal region of the plant is generally buried in silt (below dashed line). Only one of the many main stems is drawn together with its associated lateral branches; short double lines indicate stems not drawn. Leaves are shown with three filaments only instead of the normal 50-150. The growth of the lateral stems, which also bear flowers, is partially suppressed by the main stem apices, and this gives an obconical outline to solitary plants growing in flowing water when viewed from the surface. (Modified from Dawson 1976a).

The seasonal changes in biomass of RANUNCULUS CALCAREUS

The study of the biomass of *R. calcareus* showed that the typical growth-cycle starts in the autumn or winter, but the biomass increases rapidly only in the late winter and spring, reaching a maximum by summer (Dawson 1976a). Flowering occurs during spring or summer and is significant because the stems produced after its initiation, apart from being more buoyant, are more brittle and more easily damaged and lost. The maximum biomass achieved may be limited by a combination of factors, but self-shading is probably the most important, since this begins to decrease the net photosynthesis of the stand when the biomass is only about one third of the maximum (Westlake 1966). Another factor limiting the increase in biomass may be the decrease in water velocity which produces a progressive increase in hydraulic drag and reduces the supply of dissolved carbon dioxide and mineral nutrients to the plants (Westlake 1967). The respiration rate of the plant is increased during photosynthesis (Dawson 1973 and in prep.) and may be further increased by a reduction in the rate of removal of oxygen. This reduces the gain in biomass which represents the balance of the relatively large scale processes of photosynthesis and respiration. Respiration is continuous throughout day and night, while photosynthesis only occurs during daylight and then may exceed respiration for only around two-thirds of this period. Thus any factor influencing photosynthesis even slightly can produce a significant effect on the gain in biomass (Westlake 1966).

The interaction of the hydrographic cycle with the seasonal cycle of growth and decline of *R. calcareus* was studied on a small chalk stream, and the effects of the biomass on water flow and level were quantified in terms of changes in the Chezy-Manning hydraulic coefficient (Dawson 1978a). The discharge cycle typically starts with a rapid rise in the autumn or winter following the seasonal increase in precipitation, and reaches a maximum in late winter before gradually decreasing to reach a low level in late summer. In late winter and spring the plant imposes an increasing restriction to water flow as growth becomes more rapid in the increasing light levels. This increase in hydraulic drag results in a progressive decrease in velocity and an increase in water depth (Fig. 2). Coincident with this increase there is often a significant seasonal decrease in discharge and this ameliorates what would otherwise be severe increases in water level. The maximum biomass occurs in summer and coincides with the lowest discharges and water velocities. The high biomass on this small stream may result in an increase in the mean water depth to around 40 cm, four times that of the plant-free section. The increase in water depth in larger chalk streams and rivers can be up to 80 cm but depends upon local

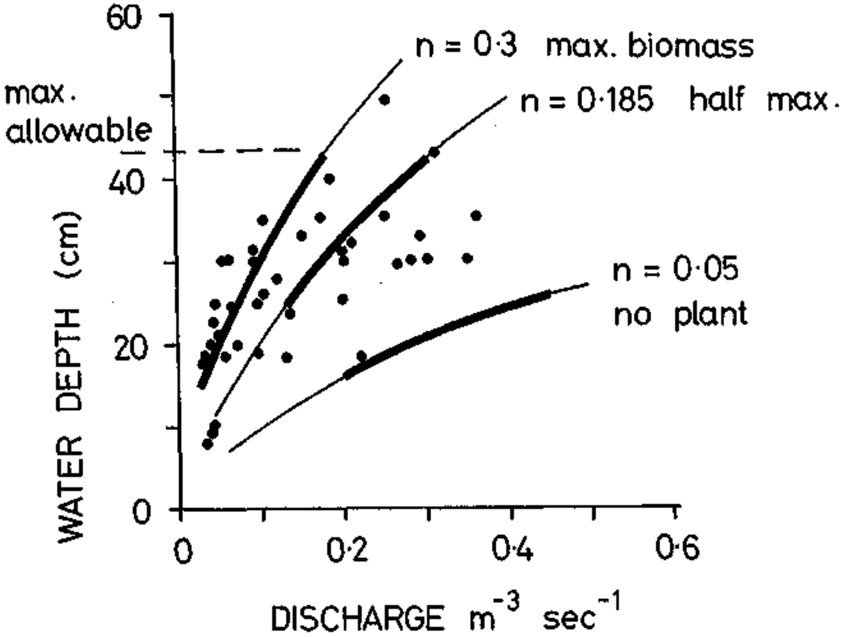

FIG. 2. The relationship between water-depth and discharge at different plant biomasses together with the values of Chezy-Manning hydraulic coefficient 'n', during the growth season in an open unshaded section of stream, the Bere Stream at Bere Regis, Dorset. The thick lines represent normal background relationship whereas the extended thin lines represent the effects of abnormally high or low discharges. The maximum allowable depth is represented by the broken line and is the water level at which plant removal is considered essential as small areas of adjacent land are water-logged. Management by plant removal is typically undertaken when half the maximum biomass is achieved before the risk of flooding becomes too high.

conditions. The accumulation of sediments during the growth season can also make the increase in water-level more pronounced (Ladle & Casey 1971). A linear relationship between biomass and the Chezy-Manning hydraulic coefficient was demonstrated for *R. calcareus* despite some differences in the relationship between seasons (Dawson 1978a). The values for the hydraulic coefficient were however about three to five times higher than those normally considered for use in channel maintenance and redesign, and meant that flooding was inevitable unless direct management was undertaken.

The monitoring of the biomass of *R. calcareus* continued on one shallow stream site, to confirm the growth cycle in this previously managed site, but within four years the maximum biomass was reduced to half of that previously found, although the cover at the stream surface was similar in each year (Dawson 1976a). To judge biomass from cover, therefore, can be misleading and can at worst lead to a significant error if interconversion is attempted. Observations on a number of individual plants indicated that the reduction in maximum biomass probably resulted partly from a release from the influence of cutting which had previously synchronized regrowth and partly from a smaller overwintering biomass. The latter resulted from suppression of regrowth, in the late summer and autumn, by the moribund and dying plant material of the current season overlying the shoots which initiate the following season's growth. During the four seasons without management, the dominance of *R. calcareus* was maintained and there were no changes in the physical environment that would account for the observed change in maximum biomass.

The summer biomass of submerged macrophytes at sites dominated by *R. calcareus* varies from 200-520 g dry weight m^{-2} of stream but with considerable local variation (Dawson 1973*b*). Westlake (1968) found a mean midsummer biomass of 200 g m^{-2} in a 43 km section of the River Frome, a large managed chalk stream in Dorset. Subsequent sampling by divers demonstrated that there is an inverse logarithmic relationship between the biomass obtained by sampling from 5-m-wide belt transects and the mean water depth (Dawson 1976a). The biomass at midsummer, immediately prior to weed removal, ranged from approximately 250 g dry wt m^{-2} in water 0·5 m deep to 25 g m^{-2} in water 2·75 m deep. The average depth of the water was 1 m and the mean biomass was again about 200 g m^{-2}. Other experiments, undertaken in Denmark on a very similar species, *R. peltatus*, indicate that the growth strategy of this species enables plants rooted in slightly deeper waters to achieve a similar maximum biomass to those rooted in shallower areas. This depends on the plants approaching the water surface sufficiently early in the growth season to have time left to rapidly increase their biomass (Dawson & Kern-Hansen 1978). Provided that the nutrient and inorganic carbon supply is sufficient the maximum is determined by the balance between the photosynthesis in the available light and respiration which is primarily dependent on temperature. These experiments suggest that the maximum biomass in natural unmanaged streams is more related to surface area and the light available to the plant than to depth of water alone. Nevertheless a logarithmic relationship between plant biomass and depth can still be demonstrated in deeper water, as such areas are more influenced by hydrological regime and thus may have increased turbidity for longer periods, particularly over winter. Any increase in the duration of high turbidity reduces the period suitable for plant growth and the maximum biomass may not be achieved.

In shallow streams in which the midsummer water depths may reach 0·7 m, the maximum biomass of *R. calcareus* can also vary by a factor of up to two if there is competition with marginal emergent plants such as watercress, *Rorippa nasturtium-aquaticum* (L.) Hayek. These two plants can be seasonally codominant and can interact so that the biomass of *R. calcareus* influences the success and biomass of *Rorippa nasturtium-aquaticum* by providing suitable sites for its overgrowth. The *Rorippa nasturtium-aquaticum* in turn regulates the *R. calcareus* in the following season by determining the time of regrowth and thus the biomass achieved by flowering time. The flowering time regulates the maximum biomass by diverting the energies of the plants from vegetative into reproductive growth. The overlying control for *Rorippa nasturtium-aquaticum* lies with the timing of the autumnal increase in discharge which washes out the major part of the biomass. The timing can vary by up to 4 months. If the autumnal increase in flow is regularly early, this can produce a stream with more *R. calcareus*, or if it is regularly late can produce one dominated by *Rorippa nasturtium-aquaticum* (Dawson et al. 1978).

The annual production of RANUNCULUS CALCAREUS

The annual production of *R. calcareus* was determined by correcting the annual maximum biomass for losses occurring up to the time at which the maximum was reached, and considering any changes in the quantity of material carried over from previous seasons, e.g. in the form of rhizomes. The latter were about 0.005 of the maximum biomass (Dawson 1976a). The losses were determined in two ways. The first method involved labelling studies on the individual stems and leaves in order to follow their length of life and their rate of loss. The second method was to install 5-mm mesh screens which were operated continuously over three growing seasons to collect all the plant material lost from a section of stream 160 m long, dominated by *R. calcareus*. The labelling study suggested that half the biomass was lost before the maximum was achieved. However only one-tenth of the maximum biomass was actually lost from the study section of stream, as determined from collections on the screens, because many stems lost from individual plants were retained on other plants almost immediately downstream and many of these pieces remained viable. When both *in situ* decomposition of leaf fall and stem loss from *R. calcareus* in the section were allowed for, the annual production was estimated to be about 1·2 times the maximum biomass in this section of stream.

The fragmentation of RANUNCULUS CALCAREUS

The breakdown, fragmentation and downstream movement of *R. calcareus* following the maximum biomass was also studied (Dawson 1976a). After the maximum biomass the shoots became increasingly moribund, and three quarters of this material fragmented away within three

months of the maximum being achieved. The remainder was lost from the study section at the beginning of the autumnal increase in discharge. An organic budget which included the import, accumulation and export of fine suspended material for this section of stream confirmed that the greater part of the plant material was broken down and utilized *in situ* (Dawson 1973 and in press). This demonstrates that if fragmentation is a guide to the 'usefulness' of materials, then this aquatic plant is very 'useful' to the ecosystem. In managed sections of stream the greater part of such plant material is cut, collected and removed to the bank or swept downstream to the sea. This material, which may amount to two-thirds of the plant production, is thus lost to the ecosystem (Dawson 1976a).

A comparison was made of the fragmentation and breakdown of these aquatic plants with typical chalk-stream terrestrial inputs by considering a similar-sized reach of wooded chalk stream. The time required for fragmentation of the submerged macrophyte *R. calcareus* was about half that for terrestrial litter, mainly *Salix viminalis* L., which was about three months (Dawson 1973 and in press). Marginal emergent plants were rarely found being transported downstream, and normally fragmented rapidly *in situ*. The time taken for fragmentation of the various materials varied with their structure, composition and the time for which they were retained in an environment suitable for breakdown near their site of origin. Overriding this was the timing of the major autumnal increase in discharge. Thus, in a year of early autumn rain, terrestrial leaves were mainly whole when they were transported downstream but in a year of late rain, fragments of leaves predominated. The combination of the above factors, which affect fragmentation, resulted in the observed ratio of aquatic to terrestrial materials found on the move downstream.

The presence of submerged macrophytes, predominantly *R. calcareus*, greatly retarded the downstream passage of terrestrial litter and this resulted in a substantial increase in fragmentation of litter near to the site of origin (Dawson 1973a and in prep.). The submerged plants of *R. calcareus* retained material which had been brought into movement by the autumnal increase in discharge, and which would, in the absence of plants, have continued downstream to accumulate in areas of slow flow or to be lost to the sea. Such movements can occur when plants are absent as a result of either dense shade or excessive weed removal activities. The plant population also aided fragmentation of leaf material by holding it dispersed amongst the shoots of the plant rather than allowing it to accumulate on the stream bed in a thick layer, where near anaerobic conditions can occur. The latter would tend to discourage fragmentation by invertebrate populations.

The studies on the production and fragmentation of submerged aquatic and terrestrial inputs show that both have a fairly similar potential input of useful organic material to stream ecosystems (Dawson 1976b), but that problems can occur in areas dominated by one or the other. In open unshaded areas macrophyte growths often have to be reduced by man, whereas in the densely wooded areas they are almost absent and this reduces the amount and availability of food and cover for fish.

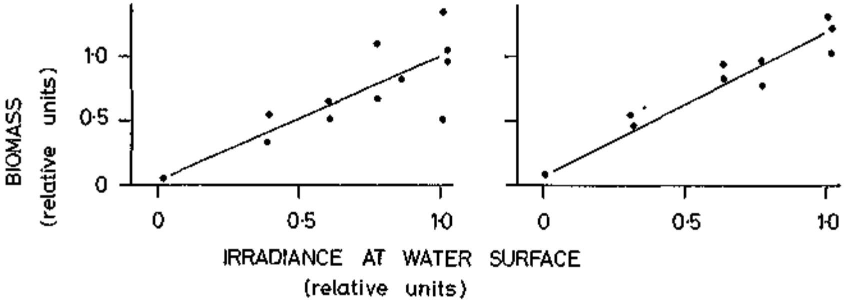

FIG. 3. The relationship between the irradiance at the water surface and the biomass of submerged aquatic plants: (l.) single species (*Ranunculus peltatus*) and (r.) two species (*Elodea canadensis* and *Potamogeton crispus*) at the time of the maximum, in artificially shaded sections of stream. The biomass is expressed as a proportion of that in adjacent sections of stream. The irradiance is also expressed as a proportion of that reaching an adjacent and unshaded section of stream (from Dawson & Kern-Hansen, in press).

Indirect plant management

The results of a study on the growth rate and requirements of a plant such as *R. calcareus* can be used to explain its distribution and its interactions with other plants; they may also be used as tools to aid in its management in areas where the plant is extremely successful (Dawson 1978b). For instance, certain minimum nutrient levels are required for maximum plant growth, and if they are not available growth is reduced. Some potential factors limiting biomasss, such as reduction in nutrients or inorganic carbon in the stream water, are not practical alternatives for management except in limited areas, whereas reduction of light may be more generally applicable. Indirect methods of plant control through manipulation of these factors have been considered, because direct methods such as cutting, although successfully reducing the biomass of the problem species, may have many undesirable consequences. For example, invertebrate drift (Kern-Hansen 1978) and the mortality of fish fry (Mortensen 1977) are increased, while the rapid synchronized regrowth of submerged plants accentuates the original problem (Dawson 1976a).

Observations of open and densely shaded areas lead to the proposal that partial shading could be a useful alternative to direct management by plant removal, and experiments to determine the actual degree of shading necessary have been undertaken (Dawson & Kern-Hansen in press). The first stage was to demonstrate that the biomasses of three problem species of aquatic plants of lowland streams were directly proportional to the light available at the stream surface, in both artificially and naturally shaded sections of stream, despite the natural gradation of shade (Fig. 3). Analysis of the effects of naturally-occurring biomasses on summer water levels in various situations led to the proposal that half-shade would at least halve the biomass and reduce water heights significantly. In sections managed by cutting regularly the maximum biomass may further decrease after this type of direct management ceases. For the practical application of half-shade conditions as a management technique, the effective height and orientation of marginal vegetation, together with the height of the stream bank, were found to be important in relation to the stream or river width (Fig. 4). Thus, for example, on a stream flowing east-west, half-shade could be produced by marginal herbs on the south bank of a stream 2-3 m in width, but mature trees would be needed if it was a river of 20 m in width. Light penetration of the water affects growth rate and its artificial decrease would be possible, for instance using dyes, but, unlike the use of marginal shade, this is not practical on a large scale. Amongst the other management possibilities is a change in the time of plant removal.

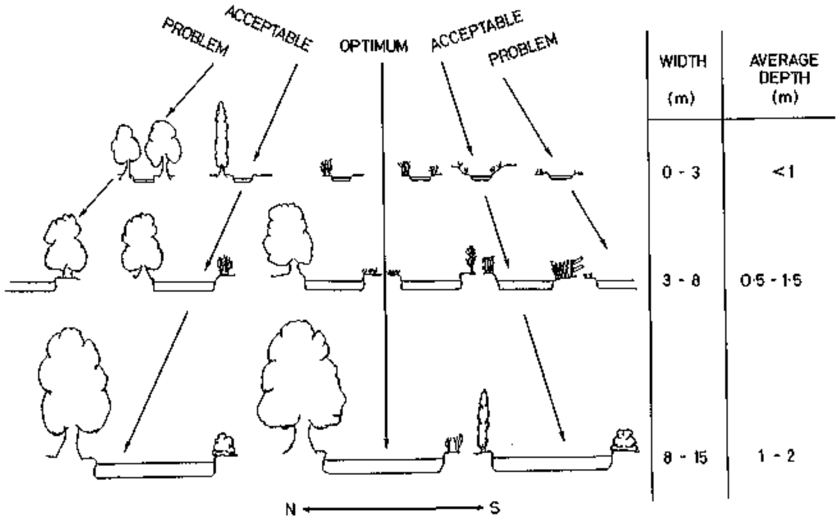

FIG. 4. A diagrammatic representation of the optimum shaded condition for reducing the irradiance to approximately a half on streams and rivers of varying width, together with acceptable and problematic types of marginal vegetation for management (from Dawson & Kern-Hansen, in press). It must be emphasised that river banks with tall grasses or bushes to the south can be considerably shaded in the same way as trees on the north bank can decrease general sky light.

At a subjective level, the optimum biomass reflects the attitude, interest or vocation of the observer, be he fisherman, water engineer, farmer or conservationist. Any rational decision must be based on a balanced consideration of all aspects of the stream ecosystem which must include a true appreciation of the plant, its growth form and cycle, the factors limiting its growth and the spatial and temporal variations of its distribution together with the implications of the method of biomass reduction. On the whole it is considered that streams and rivers should be allowed to return towards their original natural meanderings and channel-form and that management should be indirect, possibly by marginal shading rather than by partial removal of plant material.

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