ABSTRACT

Populations of two submersed species, common water-starwort (Callitriche stagnalis Scop.) and curled pondweed (Potamogeton crispus L.), growing in drainage channels in the Solway Drainage Area of north-western England, responded differently to stress and disturbance produced by cutting, dredging and shade in a field experiment. Although the survival strategy of both plants is essentially similar (competitive-disturbance tolerator), the results suggested that starwort was the more competitive of the two species, while curled pondweed tolerated disturbance better. Shade stress was also better tolerated by curled pondweed. Submerged weed management regimes in use in the Solway Drainage Area depend heavily on cutting and dredging; these disturbance-based control methods probably have a low efficacy against disturbance-tolerant species, and may promote their dominance in the channel system.

Key words: submersed macrophytes, plant survival strategies, aquatic weed control, C. stagnalis, P. crispus, common water-starwort, curled pondweed.

INTRODUCTION

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

Starwort is widespread in shallow, disturbed freshwater systems, including small rivers, streams and man-made channels, in northern Europe (Soubly 1974, Eaton et al. 1981, Nevesold et al., 1983, Haslam 1987, Murphy et al. 1990a). The established-phase strategy of starwort was given by Grime et al. (1988) as intermediate between ruderal (= disturbance-tolerant, D) and competitive ruderal (CD). Starwort is a plant which produces a rosette of floating leaves, with the rest of its photosynthetic canopy at or just below the surface (Smithorpe 1967), a competitive trait in submerged macrophytes (Murphy et al., 1990b). In drainage channels in Great Britain, C. stagnalis, together with the closely-related long-stemmed water starwort Callitriche palustris Kut., were the indicators for a functional vegetation type characterised by high tolerance of disturbance (Sabatinii and Murphy 1995). Similarly, in Dutch drainage channel systems, Pot (1993) observed that C. platycarpa was a dominant in submerged vegetation types that experienced regular disturbance from weed control by mowing bucket or cutting boat, repeated up to five times per year.

The established-phase strategy of curled pondweed was designated (using traits characteristic of lake populations of the species) as competitive disturbance-tolerant (CD) by Murphy et al. (1990b). The shade adaptation of curled pondweed is well documented (Nichols and Shaw 1986). This species causes weed problems both in its native European range (Murphy et al. 1990a) and as an introduced species in temperate regions of North America (Nichols and Shaw 1986, Anderson 1999, Steward 1990).

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

SITE DESCRIPTIONS

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

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

Site 2 (Low Level) had a width of 0.8 m and average depth of 0.2 m during summer 1993, with a thick, ochreous sediment, less mobile than that of Site 1. Average conductivity was 0.553 mS cm⁻¹, mean pH 6.8, and mean k 3.97 m⁻¹. The standard weed control regime was one-two manual clearances per summer. At the outset high-density beds of starwort, closely intermixed with beds of curled pondweed, were present throughout, with a much higher probability of interspecific competition effects than in Site 1. Emergent vegetation was absent.

METHODS

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

T1: Low shade stress (LSH): white geotextile material, producing on average 58.6 ± 4.4% attenuation of photosynthetically-active radiation (PAR) at water surface: measured in the centre of the treatment plot, using a two-sensor SKYE SKP210 PAR meter linked to a SKYE Datahog SRH 2540 logger. Taking into account the value of k, and depth of water, light attenuation at the channel bed in Site 1 was calculated as 80.5% of above-barrier incident PAR, and in Site 2, 72.6%.

T2: High shade stress (HSH): black geotextile material, producing on average 91.0 ± 1.5% PAR attenuation, measured as above. Light attenuation at the channel bed was between 96 and 98% of above-barrier incident PAR in both sites.

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


T5: Untreated (UNT).

Treatment plots comprised a 5 m stretch of channel, with intervening 5 m stretches left untreated as separators. Shade barriers used material stretched over a wooden frame 5 m long and the width of the channel, supported on wooden corner posts driven into the bank so that the material was positioned approximately 1 m above water surface. Above-sediment weed standing crop samples were collected using a Lambourn sampler (Hiley et al. 1981) to remove all vegetation from 25 × 20 cm sample subplots, located in randomly-chosen beds of the target species within each treatment plot. In the laboratory samples were oven-dried at 90°C prior to weighing. Sampling was undertaken on two occasions, 2 and 3 months after the experiment was set up, respectively in August and September 1993. Physico-chemical, management history and species differences ruled out direct statistical comparisons between channels of the effects of treatment on starwort (Hurlbert 1984). Standing stock was assessed as the product of the standing crop in 

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crop data were initially analysed separately for each site, using ANOVA with mean separation by Tukey’s test. There were no significant differences between sampling dates, so samples from the two visits were pooled for final analysis, to result in within-treatment replication of n = 6 for each site. Use of the term ‘significant’ in the results and discussion below implies means different at P ≤ 0.05 from Tukey’s test.

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

RESULTS AND DISCUSSION

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

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

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

Curled pondweed, in the presence of competitor starwort plants, showed a standing crop response to stress and disturbance quite different from that of starwort. Shade (LSH or HSH) had no significant effect. Disturbance increased the standing crop of curled pondweed compared to untreated control, significantly so for CUT plots, which experienced a three-fold increase (Figure 2).

For both species, treatments had no significant effects on any of the traits measured in either Site 1 or Site 2. However, individual starwort plants from Site 2 (Table 1) were overall significantly longer (LEN), and significantly heavier (WST, WLE) than plants from Site 1, perhaps reflecting the more intense disturbance-history of Site 1. The trait data also show that curled pondweed plants were significantly longer, heavier, and had a higher LA than starwort plants (Table 1).

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In our study, low shade stress (LSH treatments) produced none of the typically-observed morphological responses of young submersed plants to shade (e.g. Vermaat and Hoitmans 1991; Tobbiesen and Snow 1984). The likely explanation is that shade stress produced by LSH treatments was not strong enough to produce such responses. The average sub-surface (0 m) PAR recorded in unshaded channels in northwest England during the course of this study, was 345 µE m⁻² s⁻¹ (range 48-960 µE m⁻² s⁻¹). Even though the low shade treatment reduced these incident light values by a further 39%, it is probable that plants, with foliage at or close to the sur-

![Figure 1. Standing crop of Callitriche stagnalis in August-September 1993 in Site 1 (mean ± SE; n = 6 samples). Treatments labeled with different letters (a-c) are significantly different (Tukey h.s.d. test, P < 0.05).](image1)

![Figure 2. Standing crop of Callitriche stagnalis and Potamogeton crispus in August-September 1993 in Site 2 (mean ± SE; n = 6 samples). Treatments labeled with different letters for each individual species (a-b; A-B) are significantly different (Tukey h.s.d. test; P < 0.05).](image2)

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face, rarely experienced shade stress from light levels as low as the 20 - 200 µM s⁻¹ normalised as necessary to produce morphological trait changes.

In North European populations of curled pondweed and starwort, the established-phase of the life cycle is in early to mid summer (Scotter et al. 1977; van Vierssen 1990). Our results demonstrated how phenology may be affected by management disturbance: removal of standing crop produced a strong regrowth response in curled pondweed in mid summer (Scotter et al. 1977; van Vierssen 1990). Our results showed no such recovery (Figure 1 and 2).

The results of the experiment support the designation of starwort populations present in the Solway drainage system by the effects of the present weed control treatments, but was much more tolerant of disturbance when competition from starwort was reduced by management treatments. It is possible that in the crowded conditions and shallow waters of the Site 2, populations of starwort may out-compete curled pondweed by overgrowing the deeper-water foliage of the latter. While the shade adaptation of curled pondweed may permit it to survive such conditions at reduced standing crop, it is only when the abundance of its competitor is reduced that curled pondweed can develop a large standing crop.

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

There were measurable differences in disturbance-tolerance between the two species: curled pondweed being the better disturbance-tolerator under the field conditions of the experiment. The starwort populations present in the experimental channels were better competitors than curled pondweed. It is quite likely that the less-competitive curled pondweed is maintained and encouraged in the Solway DA system by the effects of the present weed control regime in reducing competition from starwort.

ACKNOWLEDGEMENTS

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LITERATURE CITED


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* LEN = above-sediment length of plant (cm); WST = individual stem weight (g); WLE = weight of leaves per stem; LA = leaf area per leaf (cm²). Data are means ± standard error, with value of n given in brackets.