

NICHE DIFFERENCES AND THEIR RELATION TO SPECIES' TRAITS IN *CIRSIUM VULGARE* AND *CIRSIUM ERIOPHORUM*

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Abstract: We investigated two congeners that are biologically very similar but show differences in large- and small-scale distribution. *Cirsium vulgare* is a widespread species in Britain and Europe, whilst *C. eriophorum* is of much more restricted distribution generally restricted to soils over limestone. At the small spatial scale of tens of metres, however, *C. vulgare* again appears to show differences in niche occupancy, being present in agriculturally-improved grasslands where *C. eriophorum* is typically lacking. We investigated niche differences in the two species using field data, and also compared plant performance under a range of different experimental conditions. The results shed light on the ecology of the two species and, more widely, on the use of species' traits to make predictions about community assembly. The view that the two *Cirsium* species show niche differences is supported, and this is consistent with trait differences between *C. eriophorum* and *C. vulgare*. These differences are, however, only revealed by close examination. When attempting to link trait differences with differences in habitat or niche occupancy, the selection of traits for examination must be based on a detailed knowledge of the species in the field.

INTRODUCTION

It has long been clear to ecologists that communities of organisms are not just random collections of species (e.g. RAUNKIAER 1934), and for many years attempts have been made to model the way in which a particular community arises from the welter of possible species combinations (e.g. DIAMOND 1975). Predictive models of potentially great utility have been based on the view that the environment filters species on the basis of their attributes (e.g. VAN DER VALK 1981, WEIHER & KEDDY 1995). Community composition from the local species pool can, to some extent, be predicted on the basis of fairly crudely quantified published data such as Ellenberg (ELLENBERG et al. 1991) values (TOFTS & SILVERTOWN 2000), but it is unclear how much better the predictions would be if more extensive trait data were available. We investigated selected traits of two similar *Cirsium* species and examined the extent to which trait differences appear to be linked to differences in small-scale distribution. We address the issue of small-scale distribution here, because it is particularly relevant in the attempts to model community assembly rather than large-scale geographical distribution.

Approximately sixty species of *Cirsium* are reported in Europe (TUTIN et al. 1976), including some very abundant species which infest the sward in commercially-managed grasslands and others which are much more restricted in distribution. They therefore provide excellent study material when investigating links between traits and performance in different habitats or

niches. We compared two morphologically similar *Cirsium* species, *C. vulgare* (SAVI) TEN. and *C. eriophorum* (L.) SCOP. that show differences in both large-scale and small-scale distribution. In the British Isles, *C. vulgare* is ubiquitous except in mountainous parts (KLINKHAMER & DE JONG 1993), being distributed much more widely than *C. eriophorum* which is restricted to calcareous substrates and which seldom occurs further north than the Peak District (TOFTS 1999). At the smaller scale (e.g. over tens of metres), *C. vulgare* again seems to be more widely distributed and generally more frequent. *Cirsium vulgare* is often abundant in heavily-grazed and agriculturally-improved grasslands such as MG6 and MG7 communities (RODWELL 1992) as well as under more traditional management regimes, sometimes with *C. eriophorum* in communities such as CG2 (RODWELL 1992). *Cirsium eriophorum* is usually quite localized in occurrence, although it may occur at high densities in certain sites where it is particularly favoured (TOFTS 1999). *Cirsium vulgare* is known as a problem species in pastures over much of the world, including places where it is not native (e.g. FORCELLA & WOOD 1986, WARDLE et al. 1992). *Cirsium eriophorum* is, however, very rarely recorded as a problem species (TOFTS 1999). These facts suggest that *C. vulgare* has a greater ecological amplitude than *C. eriophorum* quite apart from the more limited edaphic requirements of *C. eriophorum*, but it is unclear whether this apparently greater amplitude can be linked to other biological characteristics of the plants, and comparatively little is known about niche differences between the two species.

This paper combines experiments and field sampling. Our approach concentrates on the potentially crucial phase of establishment rather than on the later stages of growth. This arises from the observation (TOFTS, unpubl. data) that damage to young plants of *C. eriophorum* and to a lesser extent *C. vulgare* was observed in sheep-grazed pastures, but little evidence of damage was observed in older plants which are well-protected by sharp spines. Field observations and a study of the literature also suggested other factors which may influence establishment. We investigated experimentally four hypotheses suggested by informal observations that may account for the apparently narrower niche of *Cirsium eriophorum* compared with *C. vulgare* within sites where the soils appear suitable for both species:

(i) *C. eriophorum* has a lower growth rate soon after germination in comparison with *C. vulgare* (GRIME & HUNT 1975) and is, therefore, more likely to be ousted by competitive species typical of agriculturally-improved situations;

(iia) *C. eriophorum* is less able than *C. vulgare* to tolerate the intense grazing to which agricultural grasslands are subject;

(iib) the early leaves of *C. eriophorum* are more erect in habit than those of *C. vulgare*, and grazing to a particular sward height results in correspondingly greater loss of biomass for *C. eriophorum*; and

(iii) *C. eriophorum* is less able than *C. vulgare* to tolerate or utilize the relatively high levels of nutrients prevalent in many agricultural grasslands.

The potential importance of leaf differences in relation to defoliation is very great (e.g. GIVNISH 1987, DIAZ et al. 1992), as leaves or their functional analogues are the primary sites of photosynthesis in green plants. In experiment 1, hypotheses (i), (iia) and (iii) are examined. Experiment 2 is designed to examine hypothesis (iib), but also allows hypotheses (i) and (iia) to be investigated.

We use quadrat data to investigate whether the communities in which *C. vulgare* grows tend to be composed of more competitive species (hypothesis (i)), and species indicative of more nutrient rich conditions (hypothesis (iii)).

METHODS

Experiment 1

Seeds of *C. eriophorum* and *C. vulgare* were sown into plug trays filled with John Innes seed compost on 4 April 1997 and watered as required. The seed mass of *C. eriophorum* (7.9–10.3 mg, TOFTS 1999) is conspicuously greater than that of *C. vulgare* (2.4–4.5 mg in one population of plants quoted by KLINKHAMER & DE JONG 1993). The experiment was run in an unheated greenhouse at the Open University, Milton Keynes. On 20 April, 40 plugs of each species at the same stage of development (2 true leaves) were removed and re-potted into 9 cm pots filled with John Innes No. 2 compost and arranged into 5 blocks of 16 pots (8 pots of each species) and watered. On 23 April, the following experimental treatments were imposed: (i) simulated grazing – plants were either cut back to the cotyledons (simulated grazing) or allowed to grow unhindered, and (ii) nutrient level – plants were either watered as required with 25 ml tap water or 25 ml NPK fertilizer solution which contained 0.21 g N, 0.07 g P and 0.34 g K. This level of fertilizer application was chosen on the basis of information provided by Phostrogen Ltd., in order to provide an excess of nutrients as may be found in agriculturally-improved grasslands. No attempt was made to reproduce a particular field situation, because even if it were possible to create nutrient levels which were identical in both field and greenhouse conditions, many other variables affecting the rate of nutrient uptake would be different. Instead, the objective was to create a distinct contrast in nutrient levels compared with the tap water treatment in order to test the hypothesis that, under conditions of high nutrient status, *Cirsium vulgare* grows comparatively more rapidly than *C. eriophorum*. A 2 × 2 × 2 (species × grazing × fertilizer) factorial design was adopted with two replicates in each of five blocks. On average, plants were watered or fertilized approximately three times per week. This was continued until 19 May at which time the plants were harvested, had the soil washed from their roots and were then oven-dried for 48 hours at 80 °C (further drying resulted in no further detectable weight loss). Total dry weight was used as the dependent variable in a factorial analysis of variance.

Hypothesis (i) suggests that a main species effect will be observed, with *C. vulgare* having the higher biomass. Hypothesis (iia) suggests that a species × cutting interaction will be observed, with *C. eriophorum* biomass being disproportionately reduced by cutting. Hypothesis (iii) suggests that a species × fertilizer interaction will be observed, with *C. eriophorum* accumulating relatively less extra biomass when fertilized than *C. vulgare*.

Experiment 2

On 2 June 1997, seeds of *C. vulgare* and *C. eriophorum* were sown as described in experiment 1, and 18 plants of each species at the same stage of development (three true leaves showing) were planted into 9 cm pots on 11 July 1997. The pots were completely filled with John Innes No. 2 compost, thus leaving no projecting pot rim, and were watered as required. The experimental arrangement used three pots of each species randomly arranged in each of six blocks. On 18 July the following treatments were imposed randomly on each of the two species in each block (i) uncut, (ii) leaves cut to a height of 2 cm above the soil surface, and (iii) leaves cut to a height of 4 cm above the soil surface. Cutting was undertaken at intervals of approximately 10 days (resulting in five harvests), and was continued until 28 August. All cut material was dried and weighed as described above, and on 28 August all plants were removed from their pots, roots washed and dried. Beyond examining the cumulative

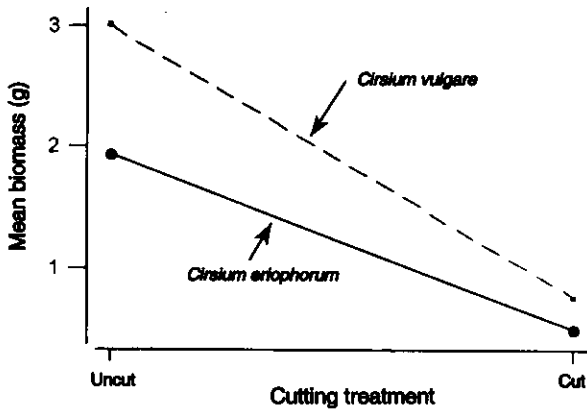


Fig. 1. Interaction between species and cutting in experiment 1.

selected on the basis of either personal knowledge or a study of the appropriate county flora. Each site was initially walked to determine the extent of grassland plant communities and then a systematic search was made for the study species. When one of the study species was located, a 2×2 m quadrat was centred on it and the presence of all the vascular plants was recorded. Up to three quadrats per species were recorded for each site, subject to the constraint that they were at least 10 m distant from one another. Once quadrats had been recorded for one species, every effort was made to locate populations of the congener in order that a within site comparison might be made. In total, 22 quadrats were recorded for *C. vulgare* and 21 for *C. eriophorum*. Most sites supported both species. Competitiveness (C-value) of a plant in the scheme of GRIME *et al.* (1988) was converted to a numerical value. Plants which are classed wholly as competitors were given a competitiveness score of 12. Plants exhibiting intermediate strategies were given intermediate values as appropriate. Thus a CR plant would be given a C-value of 6, and a CSR plant a C-value of 4. Similarly, the Ellenberg N (nitrogen) value (ELLENBERG *et al.* 1991) of the plants recorded in each quadrat was used to give an indication of the nutrient status of the soils in each quadrat. The Ellenberg values have proved to be useful predictors of plant requirements/tolerances in Britain (THOMPSON *et al.* 1993). In both cases, the values for the target species (either *C. vulgare* or *C. eriophorum*) were omitted from the analysis, and the environment of each quadrat was categorized on the basis of the other species present.

RESULTS

Experiment 1

The analysis of final biomass (square root transformed) is given in Tab. 2. Statistically significant effects were identified for species and cutting and the interaction between species and cutting, as well as fertility. The results (back transformed) for species and cutting are shown in Fig. 1. When cut, the final biomass of *C. eriophorum* averaged 0.49 g compared with *C. vulgare* at 0.75 g. When uncut, the corresponding values were 1.95 g and 3.02 g respectively. The species \times cutting interaction indicated that *C. eriophorum* was in fact

loss of biomass for the two species, three additional analyses were performed: (i) ANOVA on the final biomass values of the plants, (ii) ANOVA on the proportion of final total biomass (in relation to the uncut control) for the two cutting heights, and (iii) ANOVA on the amount of biomass removed during the course of cutting.

Field sampling

Quadrat data were obtained for both study species from a variety of sites in southern and central Britain (Tab. 1). All sites supported at least moderately basic grassland and were

Table 1. Vegetation sampling sites, with Ordnance Survey grid reference.

<i>Cirsium vulgare</i>	<i>Cirsium eriophorum</i>
Aston Upthorpe, Berks. SU5483	Aston Tyrold, Berks. SU5585
Cam Long Down, Glos. ST7799	Aston Upthorpe, Berks. SU5483
Cherhill Down, Wilts. SU0569	Cam Long Down, Glos. ST7799
Crickley Hill, Glos. SO9316	Cherhill Down, Wilts. SU0569
Farmoor, Oxon. SP4607	Crickley Hill, Glos. SO9316
Hassop Mines, Derbys. SK2273	Farmoor, Oxon. SP4607
Knap Hill, Wilts. SU1263	Hassop Mines, Derbys. SK2273
Ousel Meadows, Bucks. SP8937	Knap Hill, Wilts. SU1263
Winstone, Glos. SO9709	Sharnbrook, Beds. TL0060
	Winstone, Glos. SO9709

significantly less affected by cutting than *C. vulgare* although this result was small in magnitude (see Fig. 1). Fertilizer addition resulted in a significant increase in biomass (1.67 g vs. 1.08 g, averaged across treatments and back transformed).

Experiment 2

The cumulative amount of biomass removed for both thistle species under the two cutting regimes is shown in Figs. 2–3. When a simulated sward height of 2 cm was maintained, *Cirsium eriophorum* initially lost significantly more biomass than *C. vulgare*. By the end of the experiment, however, no significant differences remained. When a simulated sward height of 4 cm was maintained, no significant differences were identified.

Tab. 3 shows the effects of species and cutting height on final biomass (square root transformed). The results with regard to species identity indicate that *C. vulgare* had a significantly greater final biomass than *C. eriophorum* (5.94 g vs. 2.24 g, averaged over all cutting treatments and back transformed). Cutting height also had the expected effect, with final biomass being greatest in uncut plants, intermediate in those cut to 4 cm and least in those cut to 2 cm (means averaged over species and back transformed: 5.99 g, 3.94 g and 2.27 g respectively). There was no evidence of an interaction between species and cutting height.

An analysis of the proportion of final biomass (expressed as a proportion of the biomass of the uncut control, and log transformed) is given in Tab. 4. The proportion of biomass compared with the control was significantly lower in the case of *C. eriophorum* (30.5% of the control value for *C. eriophorum* vs. 69.9% for *C. vulgare*, back transformed). The effect of cutting height was also statistically significant, with a 2 cm cutting reducing the proportion compared with 4 cm cutting as expected (34.8% vs. 61.3% respectively, back transformed).

The ANOVA for total biomass removed is given in Tab. 5. There was no significant difference between the two species in the amount of biomass removed. More surprisingly, no significant difference was detected between the two cutting heights by the end of the experiment.

Field sampling

The distribution of C-values for *C. vulgare* and *C. eriophorum* quadrats are shown in Figs. 4–5. The differences between species are not significant ($P = 0.420$, Mann-Whitney U-test).

Table 2. ANOVA for final biomass, experiment 1. The dependent variable is square root transformed total plant biomass. Bonferroni corrected 5% cut-off point at $P = 0.0064$.

Treatment	d.f.	Sum of squares	Mean square	<i>F</i>	Significance
Species S	1	1.2927	1.2927	78.24	0.000
Cutting C	1	12.3702	12.3702	748.74	0.000
Fertility F	1	0.2062	0.2062	12.48	0.001
Block B	4	0.1167	0.0292	1.77	0.146
S × C	1	0.1430	0.1430	8.65	0.004
S × F	1	0.0003	0.0003	0.02	0.901
C × F	1	0.0263	0.0263	1.59	0.211
S × C × F	1	0.0163	0.0163	0.99	0.324
Error	68	1.1235	0.0165		
Total	79	15.2951			

Table 3. ANOVA for final biomass square root transformed. Bonferroni corrected 5% cut-off point at $P = 0.0127$.

Treatment	d.f.	Sum of squares	Mean square	<i>F</i>	Significance
Species S	1	7.9787	7.97	52.35	0.000
Cutting height H	2	4.8468	2.4234	15.90	0.000
Block	5	0.9077	0.1815	1.19	0.342
S × H	2	0.6944	0.3472	2.28	0.123
Error	25	3.8102	0.1524		
Total	35	18.2378			

Table 4. ANOVA for proportion of final biomass in relation to uncut control, and log transformed. Bonferroni corrected 5% cut-off point at $P = 0.0127$.

Treatment	d.f.	Sum of squares	Mean square	<i>F</i>	Significance
Species S	1	4.1357	4.1357	18.77	0.001
Cutting height H	1	1.9132	1.9132	8.68	0.010
Block	5	2.4693	0.4939	2.24	0.104
S × H	1	0.0158	0.0158	0.07	0.792
Error	15	3.3056	0.2204		
Total	23	11.8396			

Table 5. ANOVA for biomass removed during the course of experiment 2. Bonferroni corrected 5% cut-off point at $P = 0.0127$.

Treatment	d.f.	Sum of squares	Mean square	<i>F</i>	Significance
Species S	1	0.0379	0.0379	0.18	0.678
Cutting height H	1	0.4315	0.4315	2.03	0.174
Block	5	1.2641	0.2528	1.19	0.359
S × H	1	0.4061	0.4061	1.91	0.187
Error	15	3.1827	0.2122		
Total	23	5.3223			

The distribution of N-values for *C. vulgare* and *C. eriophorum* quadrats are shown in Figs. 6–7. The differences between species are just significant ($P = 0.049$, Mann-Whitney U-test) and in the expected direction, with *C. vulgare* being characterized by presence in communities of species with higher N-values.

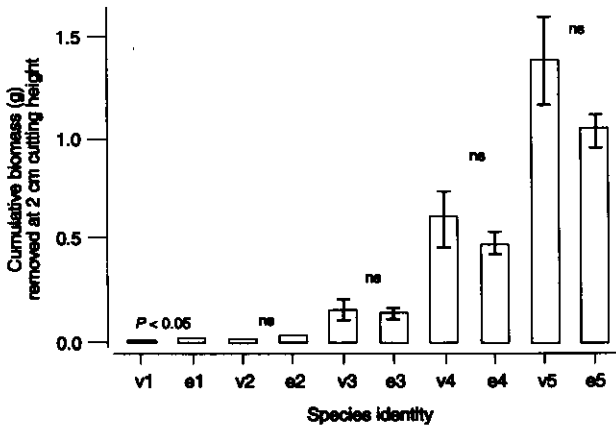


Fig. 2. Cumulative biomass removed at 2 cm cutting height. Species identity: v – *C. vulgare*, e – *C. eriophorum*, harvest number – 1–5 (t-test).

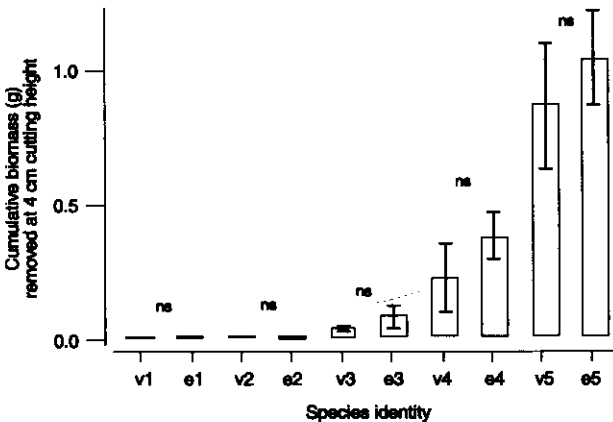


Fig. 3. Cumulative biomass removed at 4 cm cutting height. Species identity: v – *C. vulgare*, e – *C. eriophorum*, harvest number – 1–5 (t-test).

DISCUSSION

It is well known that the distribution of *C. eriophorum* in Britain and over most of its range reflects the presence of basic soils. It is, however, equally clear that *C. vulgare* can grow well on basic soils and thus it is necessary to consider more than soil pH to explain small-scale differences in distribution. This is evident from published information about the two species (KLINKHAMER & DE JONG 1993, TOFTS 1999), and was also confirmed during the present field study where there was in fact a slightly (although not significantly) higher median Ellenberg R-value (reflecting higher soil pH) in quadrats supporting *C. vulgare* compared with *C. eriophorum* (results not reported in full here).

In the introduction, four hypotheses were offered which may (at least partly) account for the small-scale distributional differences between *Cirsium eriophorum* and *C. vulgare*. The results of the field sampling support the view that there are niche differences between the two *Cirsium* species, at least in terms of soil nutrient status, with

C. eriophorum being characteristic of a less nutrient-enriched environment. Although this effect was only just significant, the test was a comparatively insensitive one and we regard the effect as biologically meaningful. The findings of the experiments support three of the hypotheses (at least in part) but not the other. The hypothesis that *C. eriophorum* has a lower growth rate than *C. vulgare* shortly after germination was strongly supported by both experiments. There is evidence (GRIME et al. 1997) of a “decoupling” between attributes relating to the regenerative and mature phases of plant growth, and there are many instances of regenerative attributes playing a key role in the organization of plant communities (e.g. see review by GRUBB 1977, THOMPSON et al. 1996, ERIKSSON & JACOBSSON 1998). It is, therefore, possible that the characteristics of plants soon after germination revealed over a short-term experiment may have a substantial bearing on their presence or absence over the long term in plant communities. In the present case, the result was in accordance with our

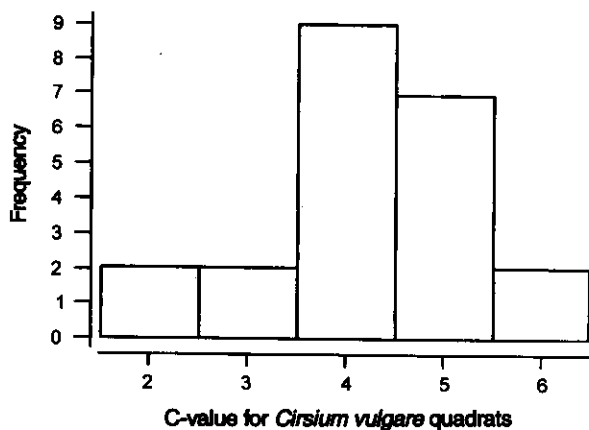


Fig. 4. Distribution of C-values for quadrats containing *Cirsium vulgare*.

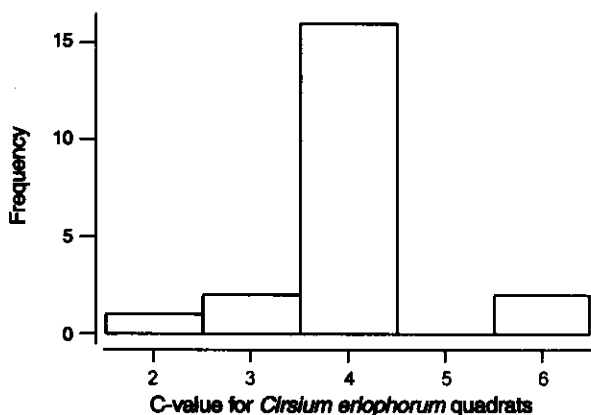


Fig. 5. Distribution of C-values for quadrats containing *Cirsium eriophorum*.

hypothesis. There is strong evidence to suggest that *C. vulgare* accumulates biomass more rapidly than *C. eriophorum* in the early stages after germination, and does so under a range of different conditions (different degrees of defoliation and different nutrient regimes). This characteristic is likely to confer benefits in grasslands subject to modern agricultural practices, and to result in a broader niche occupancy. It is important to bear in mind that our experiments here only address the early stages of growth in species which are monocarpic perennials. There are, therefore, many other potential trait differences which may manifest themselves later in the life cycle. The establishment phase is, however, of fundamental importance in shaping the composition of many plant communities and traits linked to the establishment phase may, therefore, be revealing, even if they only act over a comparatively short period of time.

The hypothesis that *C. eriophorum* was less able to withstand defoliation compared with *C. vulgare* was not supported when absolute biomass loss was

considered (experiment 1), but was supported when proportionate loss (in comparison with uncut controls) was considered (experiment 2). This proportional difference is probably more important biologically than the lack of an absolute difference, because the loss of a given amount of biomass is likely to be more "costly" for the smaller species with lower biomass to begin with (*C. eriophorum*). The hypothesis that *C. eriophorum* suffers a greater absolute loss of biomass when cut back to a fixed height compared with *C. vulgare* was only weakly and partially supported, but as argued above, the proportionately greater loss of biomass is likely to be of more biological importance. Field observations (TOFTS 1999) suggest that *C. vulgare* is better able to tolerate conditions of heavy grazing than *C. eriophorum*, and the experimental results obtained here are consistent with what was observed in the field. Sheep damage to young *C. eriophorum* plants was noted on several occasions in a field experiment (TOFTS & SILVERTOWN, in prep.).

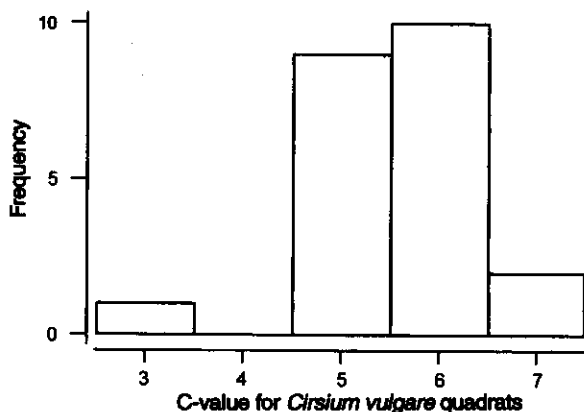


Fig. 6. Distribution of N-values for quadrats containing *Cirsium vulgare*.

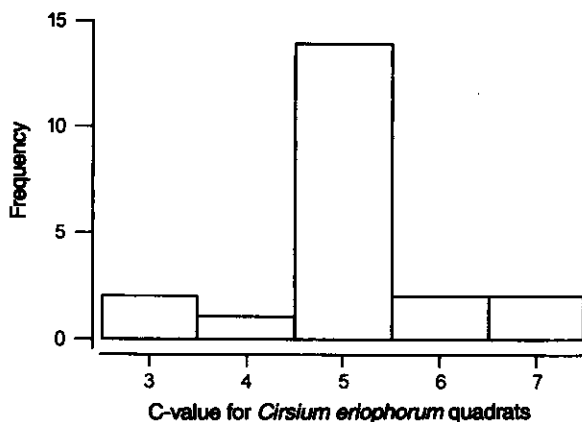


Fig. 7. Distribution of N-values for quadrats containing *Cirsium eriophorum*.

“competitiveness” and seed characteristics. In many communities, however, it will probably be necessary to obtain additional information on many traits before reliable predictions about species presence or abundance can be made, and the choice of which traits to measure should be based on a good knowledge of the species in the field. Even with regard to the tightly circumscribed question examined here, there are additional traits such as palatability and visibility to grazers that must be considered in order to understand the relationship between community composition and defoliation.

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The finding that *C. vulgare* accumulates more biomass at higher nutrient levels is consistent with the findings of other workers (AUSTIN et al. 1985, 1988), but the hypothesis that *C. eriophorum* was less able to tolerate or utilize high levels of nutrients compared with *C. vulgare* was not supported. The fact that the two nutrient regimes applied here were sufficient to reveal significant differences in biomass under the two treatments suggests that they would also have been sufficient to show relative differences in the ability of the two *Cirsium* species to tolerate or assimilate nutrients if this were the case. The species were, however, only examined in isolation rather than in an environment where competition may complicate the relationship between nutrient levels and plant performance, and this limitation must be borne in mind (cf. MCGRAW & CHAPIN 1989).

What are the wider implications of this work for trait-based studies? It is possible to link species presence in or absence from a community to various traits available from published sources (e.g. TOFTS & SILVERTOWN 2000). These include measures of

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