Seedling resistance to herbivory as a predictor of relative abundance in a synthesised prairie community

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In a laboratory experiment seedlings of 24 perennial herbaceous prairie species were offered to the omnivorous cricket *Acheta domestica* in an extended feeding trial. Leaf damage was monitored daily allowing an index of palatability to be calculated for each plant species.

The index of palatability successfully predicted relative abundance within the same set of species in an independently-conducted study involving community assembly from seed in low-fertility plots.

These results support the hypothesis that resistance to herbivory may be an important component of plant fitness in unproductive vegetation. However, the correlation between palatability and community composition may be interpreted as a positive association between traits that lead to high competitive ability and herbivory resistance.

There is a need to establish whether the success of the dominant grasses at Cedar Creek arises from their superior ability to capture nitrogen from low external concentrations or is, rather, due to their superior ability to minimise nitrogen loss to herbivores.

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It is widely recognised that admission of species into plant communities is frequently controlled by events occurring during seedling establishment. There is also general agreement that herbivores are a major cause of seedling mortalities (Crawley 1983) and many studies have focussed upon the role of herbivores in modifying plant succession (Brown and Gange 1992, Davidson 1993, Hulme 1996). In order to understand more precisely and with greater generality where and how seedling herbivory modulates plant community composition various research methods have been employed. These vary from seedling demographics in permanent quadrats (Sarukhán and Harper 1973, Hanley et al. 1995) to herbivory trials with leaf discs and captive animals in the laboratory (Grime et al. 1968). Each approach has strengths and weaknesses. Field studies in natural vegetation embrace reality but usually leave unanswered many of the questions relating to underlying mechanisms and generality of the phenomena observed. Tissue feeding trials, on the other hand, provide broad comparisons across many plant species and herbivores and allow some penetration to control mechanisms but they are executed in conditions that are only weakly-related to the circumstances in which seedling mortalities affect community composition in the field.

The experiment described in this paper seeks a course between these two contrasted approaches by conducting an extended feeding trial in the laboratory using seedlings of 24 grassland species. Features of the experiment were the recording of herbivore damage on a

daily basis and the use of controls which were not subjected to herbivory. In contrast to a tissue test this approach enabled recognition of species in which recovery from damage occurs, either by mobilisation of seed reserves or development of adult defensive traits. The most important feature of the experiment, however, was its relationship to an existing experiment at Cedar Creek Natural History Area, Minnesota (CCNHA) in which the same set of species had been sown together in field plots (Tilman et al. 1996). This provided an opportunity to test the value of palatability indices as predictors of community composition by reference to an independently-conducted study of community assembly. The feeding trial forms part of a larger programme in which screening procedures have been used to characterise the 24 grassland species and further results will be reported in due course.

On the basis of previous research into the mechanisms structuring plant communities occupying infertile soils, two rather different hypotheses can be made with respect to the patterns likely to emerge in the herbivory trial. From screening experiments on plant species from fertile and infertile habitats (Grime et al. 1968, 1996) and from experiments in which plant communities have been allowed to assemble on low fertility soil in the presence and absence of invertebrate herbivores (Fraser and Grime 1999, Buckland and Grime 2000) we would predict that the success of species in the Cedar Creek plots would be correlated with the ability to resist the attentions of the experimental herbivores. As a corollary we would expect that susceptibility to herbivory would be observed in the species that declined in importance in the course of the field experiment. In previous investigations at Cedar Creek however the importance of herbivory has rarely been invoked. Rather, a variety of comparative studies (Gleeson and Tilman 1990, Tilman 1990) and studies of interspecific competition (Tilman and Wedin 1991, Wilson and Tilman 1991, Wedin and Tilman 1993) showed that the dominant grasses, mainly C_4, that prevail in the natural grassland and in sown unfertilised plots at this site were superior competitors for nitrogen because of greater root mass and lower tissue nitrogen. The ability to conserve nitrogen by resisting losses to herbivores was not considered important because of extremely low rates of tissue loss to herbivory in the natural and experimental communities.

Materials and methods

Herbivory study

All work relating to the herbivory experiment was undertaken in greenhouse facilities at Tapton Experimental Garden, Sheffield during the period April to June 1999. No supplemental heating was provided,

except for 3 days in June during a cold spell. The experiment itself was conducted over 3 weeks commencing 26th May 1999 and involved the 24 perennial prairie/savannah species listed in Table 1.

Twenty four cavity insert trays, each containing 24 cells of dimensions 51 mm length × 50 mm width × 52 mm depth, were filled with Levington F1 fine structure, low nutrient compost and allowed to stand in 362 × 212 × 56 mm plastic trays. The cells were then saturated with tap water, which filled the trays to a depth of approximately 15 mm. In a random draw each cell was allocated one of the species. Using information gained during previous studies, a staggered programme of seed sowing began on 20th April 1999 with the aim of synchronising germination across the species. Several seeds were sown directly into each cell and seedlings were subsequently thinned, as necessary, to leave one individual per cell. This procedure was successful and only one species, the forb *Euphorbia corollata*, produced insufficient individuals resulting in omission of this species from all analyses. The bulk of germination occurred at the beginning of May and seedlings were grown for a further three weeks. No nutrients were added and cells were watered as necessary to avoid any possibility of droughting.

On 26th May 1999 each replicate, containing one individual per species, was enclosed in a plastic container (570 × 450 × 255 mm) hereafter referred to as an insectory. The most abundant generalist herbivores that have access to the biodiversity experiment at Cedar Creek are grasshoppers from the order orthoptera (Ritchie 2000, J. Haarstad pers. comm.). Although not found on the experimental site at CCNHA, it was decided that the herbivory experiment should utilise another orthopteran species, the house cricket *Acheta domestica*, for three specific reasons:

(i) As an omnivore it was expected to have a less-defined range of feeding preferences compared to many generalist herbivores and, as such, was considered to be an ideal species for the feeding trial.
(ii) It was easier to identify damage, and particularly the comparative rates of damage, to individual plants caused by chewing insects rather than, say, sucking insects.
(iii) A ready supply of house crickets was available at the Univ. of Sheffield and Cedar Creek grasshoppers were not available.

Prior to the experiment, the crickets had been fed on a cereal-based rodent food and only recently emerged adult males of approximately equal age and size were used. Twelve randomly selected and located replicates were chosen to each receive six individual crickets whilst the remaining twelve acted as controls. Vials of drinking water were placed inside all insectories which were then covered with a clear perspex or glass lid to ensure the crickets could not escape.

Table 1. Biomass comparisons of seedlings of 24 perennial prairie savannah species grown in the presence and absence of omnivores. Mean (i) leaf and (ii) shoot biomass of individual seedlings after 3 weeks exposure to the cricket *Acheta domestica* (cols a) and controls (cols b). T-tests measure the statistical significance of differences between the two weights (cols c). The ratio of above-ground biomass (crickets present) to the above-ground biomass (crickets absent) is (i) leaf weight index and (ii) shoot weight index (col d). N is the number of replicates and s.e. is the standard error.

(i) LEAVES		a			b			c				d
		CRICKETS PRESENT dry weight			CRICKETS ABSENT dry weight							
Species	Func group	N	(g)	s.e	N	(g)	s.e.	t test	df	p value		Leaf weight index
Achillea millefolium	Forb	12	0.194	0.015	12	0.252	0.0231	−2.21	22	0.038	*	0.77
Agropyron smithii	C_3 grass	11	0.054	0.011	12	0.077	0.0105	−1.52	21	0.143	NS	0.71
Andropogon gerardi	C_4 grass	12	0.141	0.009	12	0.137	0.0169	0.19	22	0.848	NS	1.03
Anemone cylindrica	Forb	11	0.029	0.007	12	0.040	0.0040	−1.53	21	0.141	NS	0.72
Asclepias tuberosa	Forb	8	0.055	0.013	6	0.050	0.0158	0.30	12	0.771	NS	1.11
Aster azureus	Forb	12	0.146	0.016	12	0.116	0.0071	1.82	22	0.082	NS	1.26
Astragalus canadensis	Legume	12	0.061	0.011	12	0.106	0.0139	−2.69	22	0.014	*	0.57
Bouteloua gracilis	C_4 grass	12	0.053	0.009	12	0.072	0.0096	−1.51	22	0.146	NS	0.73
Buchloe dactyloides	C_4 grass	12	0.032	0.012	12	0.046	0.0084	−1.05	22	0.304	NS	0.69
Coreopsis palmata	Forb	12	0.057	0.005	12	0.063	0.0049	−0.83	22	0.416	NS	0.91
Elymus canadensis	C_3 grass	12	0.095	0.008	12	0.115	0.0125	−1.42	22	0.171	NS	0.82
Koeleria cristata	C_3 grass	12	0.020	0.005	12	0.027	0.0036	−1.24	22	0.227	NS	0.74
Lespedeza capitata	Legume	12	0.083	0.009	12	0.065	0.0062	1.76	22	0.092	NS	1.28
Liatris aspera	Forb	12	0.060	0.012	12	0.073	0.0122	−0.79	22	0.436	NS	0.82
Panicum virgatum	C_4 grass	12	0.038	0.011	11	0.069	0.0151	−1.69	21	0.106	NS	0.56
Petalostemum purpureum	Legume	12	0.033	0.003	12	0.040	0.0035	−1.51	22	0.146	NS	0.84
Poa pratensis	C_3 grass	12	0.034	0.009	12	0.081	0.0075	−4.11	22	0.000	***	0.42
Rudbeckia hirta	Forb	12	0.167	0.012	12	0.237	0.0165	−3.57	22	0.002	**	0.71
Schizachyrium scoparium	C_4 grass	12	0.063	0.007	12	0.070	0.0107	−0.60	22	0.555	NS	0.89
Solidago nemoralis	Forb	12	0.086	0.012	12	0.120	0.0099	−2.35	22	0.028	*	0.72
Sorghastrum nutans	C_4 grass	12	0.078	0.015	12	0.076	0.0072	0.13	22	0.901	NS	1.03
Sporobolus cryptandrus	C_4 grass	12	0.058	0.014	12	0.084	0.0169	−1.25	22	0.224	NS	0.69
Vicia villosa	Legume	12	0.097	0.015	12	0.234	0.0398	−3.36	22	0.003	**	0.41
Euphorbia corollata	Forb	Excluded due to insufficient seed germination										

(ii) SHOOTS		a			b			c				d
		CRICKETS PRESENT dry weight			CRICKETS ABSENT dry weight							
Species	Func group	N	(g)	s.e	N	(g)	s.e.	t test	df	p value		Shoot weight index
Achillea millefolium	Forb	12	0.209	0.017	12	0.276	0.024	−2.38	22	0.026	*	0.76
Agropyron smithii	C_3 grass	11	0.119	0.021	12	0.155	0.021	−1.27	21	0.218	NS	0.77
Andropogon gerardi	C_4 grass	12	0.234	0.015	12	0.233	0.026	0.05	22	0.962	NS	1.01
Anemone cylindrica	Forb	11	0.031	0.007	12	0.042	0.004	−1.54	21	0.14	NS	0.72
Asclepias tuberosa	Forb	8	0.083	0.018	6	0.073	0.022	0.36	12	0.727	NS	1.13
Aster azureus	Forb	12	0.154	0.017	12	0.122	0.007	1.84	22	0.08	NS	1.26
Astragalus canadensis	Legume	12	0.081	0.014	12	0.131	0.017	−2.37	22	0.027	*	0.61
Bouteloua gracilis	C_4 grass	12	0.079	0.014	12	0.106	0.015	−1.37	22	0.185	NS	0.74
Buchloe dactyloides	C_4 grass	12	0.046	0.016	12	0.067	0.012	−1.09	22	0.288	NS	0.68
Coreopsis palmata	Forb	12	0.118	0.006	12	0.122	0.010	−0.33	22	0.743	NS	0.97
Elymus canadensis	C_3 grass	12	0.162	0.014	12	0.193	0.022	−1.19	22	0.247	NS	0.84
Koeleria cristata	C_3 grass	12	0.025	0.006	12	0.034	0.005	−1.35	22	0.19	NS	0.72
Lespedeza capitata	Legume	12	0.116	0.012	12	0.090	0.009	1.8	22	0.086	NS	1.28
Liatris aspera	Forb	12	0.064	0.012	12	0.079	0.013	−0.93	22	0.361	NS	0.80
Panicum virgatum	C_4 grass	12	0.063	0.019	11	0.120	0.029	−1.74	21	0.096	NS	0.53
Petalostemum purpureum	Legume	12	0.070	0.005	12	0.078	0.006	−1.03	22	0.314	NS	0.90
Poa pratensis	C_3 grass	12	0.051	0.013	12	0.116	0.011	−3.96	22	0.001	***	0.44
Rudbeckia hirta	Forb	12	0.320	0.030	12	0.425	0.030	−2.59	22	0.017	*	0.75
Schizachyrium scoparium	C_4 grass	12	0.113	0.013	12	0.121	0.018	−0.35	22	0.73	NS	0.94
Solidago nemoralis	Forb	12	0.092	0.012	12	0.128	0.010	−2.39	22	0.026	*	0.72
Sorghastrum nutans	C_4 grass	12	0.134	0.024	12	0.129	0.014	0.18	22	0.861	NS	1.04
Sporobolus cryptandrus	C_4 grass	12	0.104	0.026	12	0.173	0.050	−1.28	22	0.212	NS	0.60
Vicia villosa	Legume	12	0.338	0.056	12	0.520	0.083	−1.89	22	0.072	NS	0.65
Euphorbia corollata	Forb	Excluded due to insufficient seed germination										

Inserting a small bowl of silica crystals in each insectory rectified excessive humidity and condensation observed at the outset of the experiment. Netting was used to shade the insectories during hot weather allowing temperatures to be maintained at less than 35°C. Daily censuses of the crickets were undertaken and dead or missing individuals replaced as necessary. Monitoring of damage caused by the crickets to individual plants commenced 27th May 1999 with a daily assessment using a categorical scoring system to derive a cumulative palatability index (PI), which effectively measured the resistance of seedlings of different species to herbivory. Scores were allocated as follows:

0 = all cotyledons and leaves undamaged
0.5 = cotyledons only damaged
1 = less than 50% of leaf material consumed
2 = more than 50% of leaf material consumed
3 = 100% of leaf material consumed and/or plant dead

On 16th June 1999 the decision was made to stop the experiment when the supply of equal-aged crickets was exhausted. A full harvest of all above ground plant material was subsequently undertaken. Stems and leaves were separated, dried for 5 days at 60°C and then weighed. The resulting data were used to derive an index measuring the depression of above-ground biomass calculated from the ratio of mean biomass (crickets present) to mean biomass (crickets absent). This index, which can be calculated separately for leaf, stem and shoot components, sought to quantify the proportion of material lost to herbivory in individual species. Further measurements of all individual plant heights and numbers of leaves were taken at both the start and finish of the experiment to provide a simple quantitative assessment of plant size.

CCNHA biodiversity experiment

In this study we use results from a biodiversity experiment, begun in 1994, in which 80 mm of topsoil was initially removed from an area sufficient to mark out 147 plots, each 3×3 m (Tilman et al. 1996). Plant communities containing 1, 2, 4, 6, 8, 12 or 24 species were then synthesised on bare ground using 90 g of seed per plot, sub-divided by the number of species sown. Fencing was erected at the outset to prevent the two principle mammalian herbivores (deer and pocket gophers) from gaining access to the site. In the intervening period communities have been allowed to develop, with on-going management restricted to the removal of weeds and watering as necessary to prevent plant losses due to drought. Measures of species composition, within the plots, have been conducted each year beginning in 1995 and involve assessments of plant cover or an above-ground biomass harvest in July each year.

Only results from the plots containing 24 species have been used in this paper.
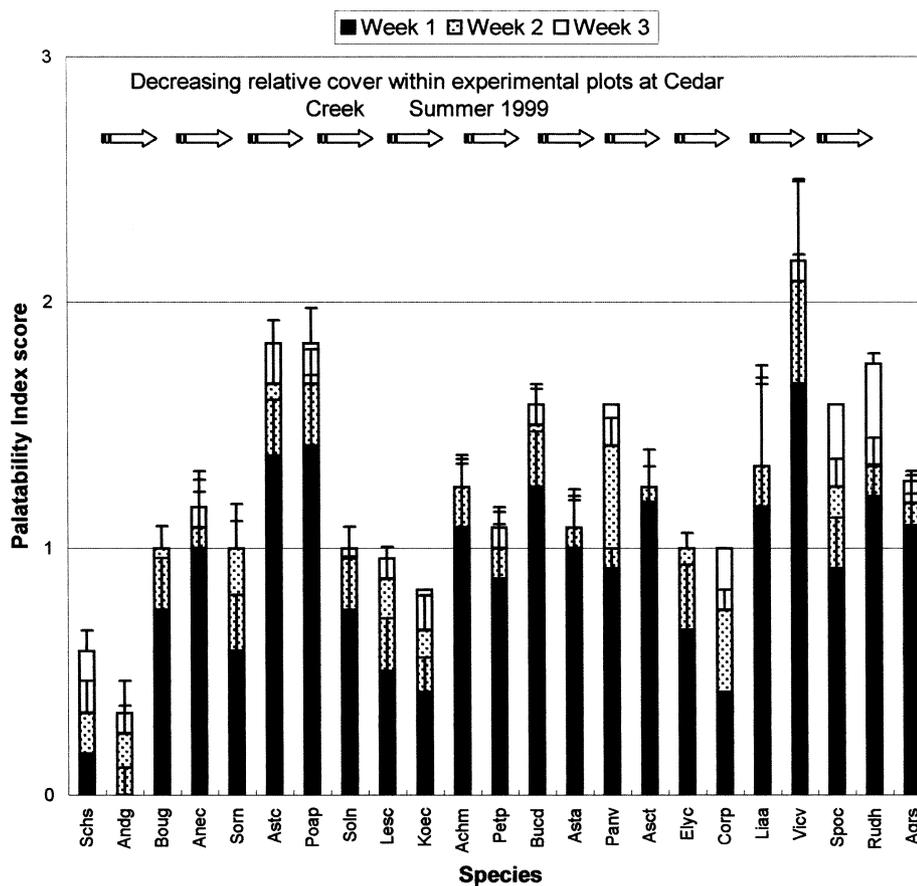
Results

Relative palatability of the twenty-four species

The crickets clearly preferred certain species and this selective feeding resulted in different temporal patterns of attack and varying PI scores (Fig. 1). Over the course of the experiment 15 species were attacked at a roughly constant rate. The remaining 8 species appeared to reach a critical stage of development beyond which the intensity of herbivore attack declined resulting in at least 1 week where there was no increase in the palatability index, although there were no obvious physical changes in the appearance of the plants which might explain this decline in consumption. Legumes were consistently attacked throughout the experiment whilst the C_4 grasses were always least preferred (Fig. 2).

From a total of 271 individual plants which were initially exposed to the crickets, 31 had suffered no damage by the end of the experiment and 24 had been completely defoliated or had died. There were 10 species with one or more individuals in the "no damage" category. These included 8 grass species which together accounted for 90% of the undamaged specimens. Particularly resistant species were *Andropogon gerardi* (66.6% of plants undamaged), *Schizachyrium scoparium* and *Koeleria cristata* (both 42%), *Sorghastrum nutans* (33.3%) and *Bouteloua gracilis* (25%). Thirteen species had one or more individuals which suffered total defoliation and, in some cases, death. These included 8 grasses, 3 forbs and 2 legumes with the most susceptible species being *Poa pratensis* (33.3%), *Buchloe dactyloides* and *Panicum virgatum* (both 25%). Six grass species, one forb but no legumes had individuals in both of the extreme categories.

The legume, *Vicia villosa*, recorded the highest mean leaf weight loss (59%) whilst another legume, *Lespedeza capitata*, registered a gain in mean leaf weight of 28% when losses to herbivory were calculated by reference to the yield of control plants (Table 1). The average leaf weight loss across all species was 23.4%. Ranking of the species revealed that the six species which recorded statistically significant losses in leaf biomass due to herbivory featured in the top ten in terms of control plants' leaf biomass suggesting that losses to herbivores may have been partially size-dependant. However four species recorded gains in leaf biomass but these were not statistically significant and did not occupy a consistent position in the range of sizes represented by the species investigated. These species did, however, comprise four of the five species which appeared to become relatively unpalatable following an initial period of

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Fig. 1. Intensity of herbivore damage per species after 1, 2 and 3 weeks. The palatability index reflects the mean cumulative assessment of leaf damage (see text). Species are ordered from highest mean relative cover in 1999 within the maximum diversity experimental plots at Cedar Creek Natural History Area, Minnesota, USA. For full list of species' names see Table 1. Bars indicate plus one standard error.

susceptibility to attack (Fig. 1). There was no overall difference in mean leaf biomass loss between monocots and dicots (mean depression of above-ground biomass$_{Leaf}$ both 0.76). Similar results emerged in mean losses of shoot biomass caused by herbivory (Table 1).

Palatability and performance in the synthesised communities

Having first ranked each species in each plot according to cover, Spearman Rank Correlation analyses were used to test for similarity between all possible pairs of plots. 10.9% of all possible combinations differed in 1995 reducing thereafter to just 1.8% by 1999, pointing to the development of consistent hierarchies across the communities. Over this period there has been a gradual change in ranks amongst the species of intermediate and lesser dominance with the result that the cover estimate in 1999 shows a plant community which differs significantly, in terms of relative abundance, from that seen in the first year. The most substantial changes involve forbs and legumes with declines in *Rudbeckia hirta*, *Achillea millefolium* and *Vicia villosa* offset by expansions in *Astragalus canadensis*, *Petalostemum purpureum* and *Anemone cylindrica*.

Although there was a weak positive correlation between PI and relative abundance in the first year of the experiment, 1995, this became both negative and significant from 1996 onwards (Fig. 3). In particular, just six of the least palatable species (*Andropogon gerardi*, *Schizachyrium scoparium*, *Bouteloua gracilis*, *Sorghastrum nutans*, *Koeleria cristata* and *Lespedeza capitata* each recording a PI of one or less) collectively accounted for relative cover of 36% in 1995, 67% in 1996, 64% in 1997, 66% in 1998 and 63% in 1999. Palatable species became increasingly associated with low abundance, although there was some variability amongst the most palatable species which individually accounted for between zero and 5% of mean relative cover in each year. The correlations were particularly pronounced amongst the monocots, whilst the dicots have always recorded a non-significant relationship between abundance and resistance to herbivory.

Discussion

In order to achieve generality and predictive power in ecological research it is necessary to discover phenomena of wide geographical and taxonomic scope. It was with this objective in mind that this investigation was

Herbivory by functional group - day 7

Herbivory by functional group - day 14
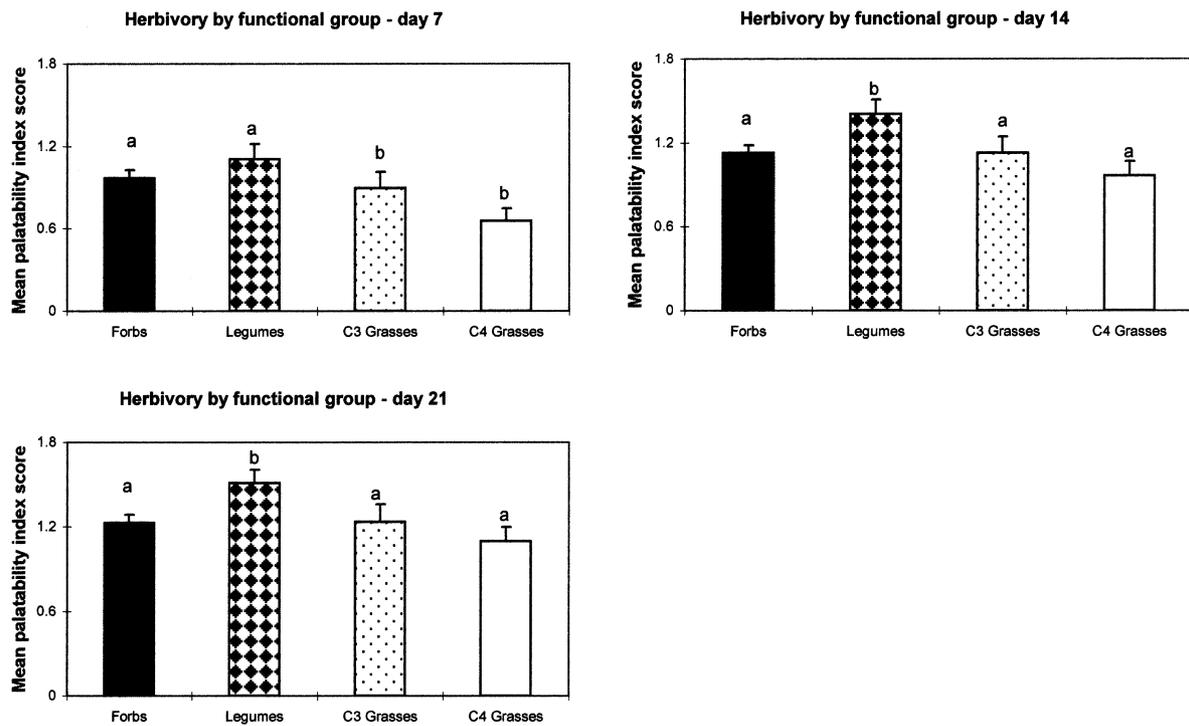

Herbivory by functional group - day 21

Fig. 2. A comparison of Leaf damage inflicted by the cricket, *Acheta domestica*, compared on 4 functional groups of plant species. The palatability index reflects the mean cumulative assessment of leaf damage (see text). For forbs n = 8; legumes n = 4; C_3 grasses n = 4; C_4 grasses n = 7. Bars indicate plus one standard error. ANOVA has been used to detect differences in means after (a) 7 days (F = 4.49, d.f. = 3, 267, p < 0.01) (b) 14 days (F = 3.52, d.f. = 3, 267, p < 0.05) and (c) 21 days (F = 3.04, d.f. = 3, 267, p < 0.05). Groups with a different letter are statistically significant using Tukeys HSD (p < 0.05).

designed to permit interaction between datasets from two experiments conducted independently on two widely separated continents. The attributes that we measured and that some of us expected, on the basis of previous investigations to have the greatest power to predict abundance in a plant community assembling on infertile soil, included much-investigated traits such as relative growth rate (Grime and Hunt 1975), specific leaf area (Poorter and Remkes 1990, Lambers and Poorter 1992, Reich et al. 1992, Cornelissen et al. 1996) and leaf dry matter content (Wilson et al. 1999). However, we did not measure other traits, such as R* values for soil nitrate (Tilman and Wedin 1991) and dispersal ability, that others of us expected to have the greatest ability to predict relative abundance. Nonetheless, it is of interest that, of the traits we did measure, an assay of resistance to herbivory emerged as a significant factor.

This result seems to have two interesting but alternative interpretations. The first is that relative abundances of species may be controlled by generalist herbivores. In the feeding trial, involving equal-aged seedlings, crickets selectively differentiated between twenty-three different prairie/savannah species to produce a hierarchy of palatability consistent across twelve replicates. After the first year of the experiment, the resulting index of palatability proved to be the single most successful

trait, of those measured, in predicting relative cover values achieved by the same species when sown together to form communities within plots at CCNHA. In the first year, it is suggested that there was a release of nutrients following removal of previous vegetation from the site at the start of the experiment, promoting early dominance by the comparatively fast-growing and short-lived *Rudbeckia hirta* (which accounted for 32% of mean relative cover in 1995) and another forb, *Achillea millefolium* (mean relative cover 11%) which is known to prosper on more fertile sites in the UK (Grime et al. 1988). Thereafter it is evident that the least palatable species proved to be the most dominant in terms of cover. Four of these species are C_4 grasses, supporting studies by Caswell and Reed (1975, 1976) who found that *Melanoplus confusus* and other species of grasshoppers were capable of digesting C_3 grass material, but were unable to digest totally the thick-walled bundle sheath cells of C_4 grasses. This is, perhaps, of some relevance when it is considered that the index of palatability successfully predicts relative abundance of the C_3 and C_4 monocots, but is unable to differentiate amongst the dicots. Amongst the seven species, which each represented less than 2% cover in the plots in 1999, six were highly palatable to the crickets in the herbivory experiment, suggesting that failure in the plots may have been precipitated by the

actions of herbivores. In particular the early dominants (*Rudbeckia hirta* and *Achillea millefolium*), which were both comparatively palatable, have shown the most precipitous declines through the course of the experiment to date leading to speculation that high biomass losses may have become unsustainable in an environment of declining fertility.

The second interpretation is that the community is structured by competition for soil nitrogen, and that the ability to compete for nitrogen is inversely correlated with palatability. The soils at CCNHA are infertile, containing low levels of nitrogen (Tilman 1983, 1984). In previous investigations at the site (Tilman 1984, 1987, Tilman and Wedin 1991, Wilson and

Tilman 1991) it has been concluded that the dominant plant species owe their success to their superior ability to compete for nitrogen. Indeed, the plant species that attained greatest abundance in the 24 species biodiversity plots, *Schizachyrium scoparium* and *Andropogon gerardi*, were the two best nitrogen competitors identified in a series of long-term competition experiments (Tilman and Wedin 1991, Wedin and Tilman 1993). This suggests that one explanation for the apparent predictive ability of the palatability index is that the same plant traits that make plants be good competitors for nitrogen also make them have low palatability to a generalist herbivore. For instance, good nitrogen competitors tend to have lower tissue N (low protein) and
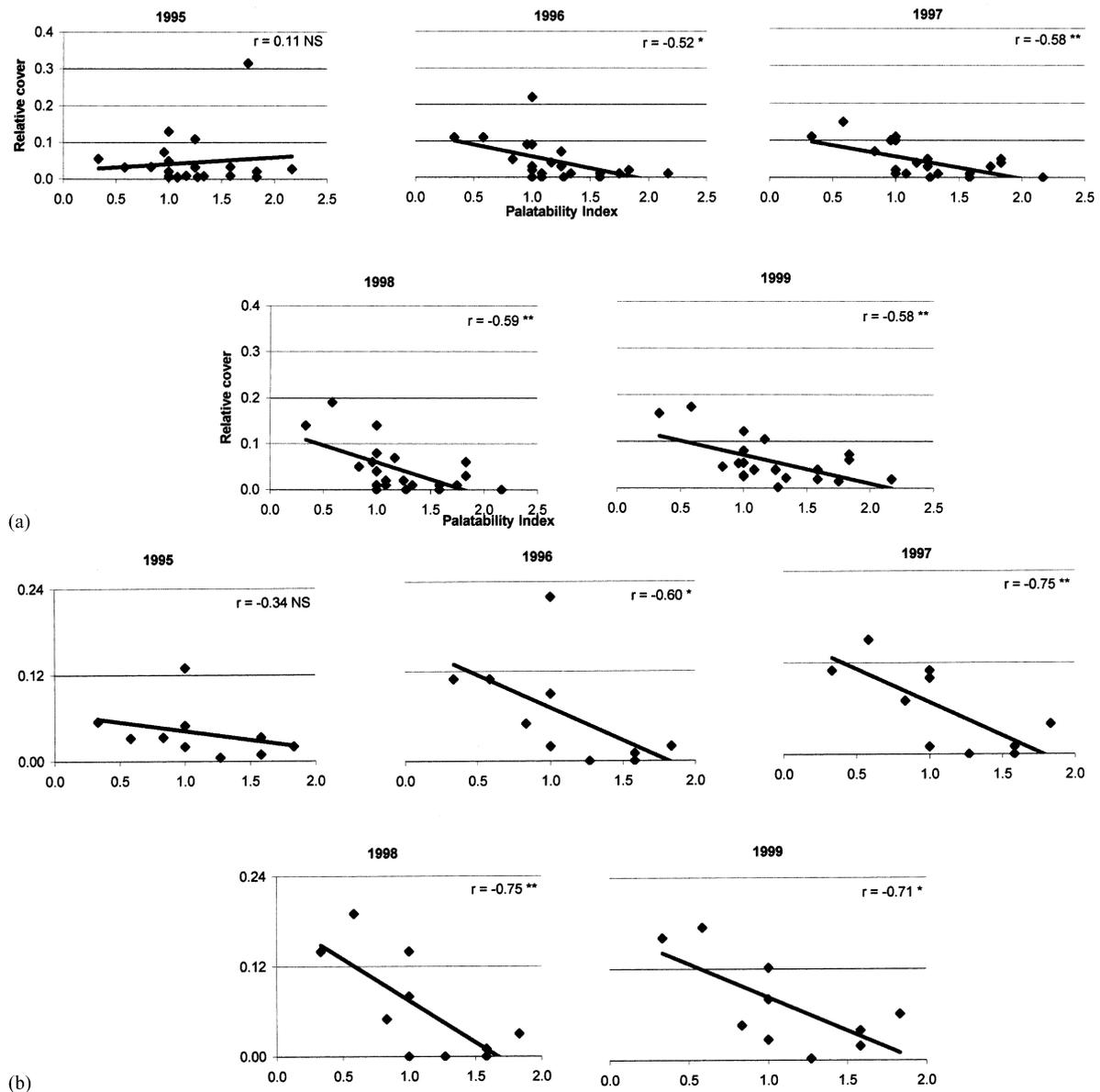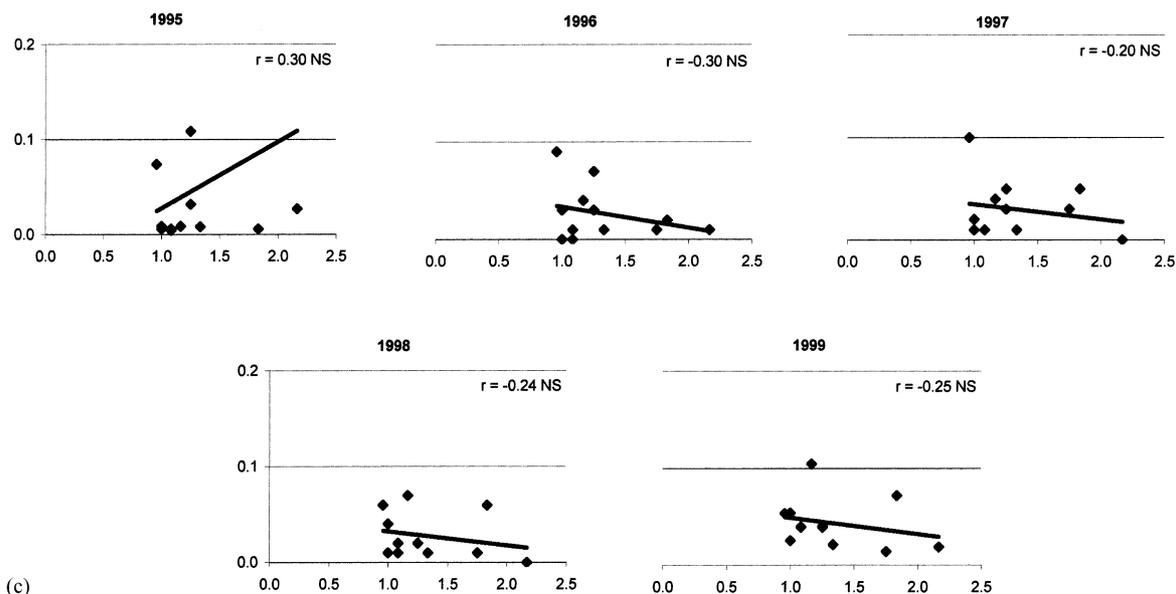

Fig. 3.

Fig. 3. Palatability as a predictor of relative cover in synthesised plots at Cedar Creek Natural History Area, Minnesota, USA. Results are shown for years 1995 to 1999 for (a) all species; (b) monocots alone; and (c) dicots alone. Trendlines have been fitted and correlation coefficients (r) shown (NS p > 0.05; * p < 0.05; ** p < 0.01).

tougher, more long-lived tissues, both of which would likely reduce palatability. Indeed, there is evidence, based on visual surveys of subplots sprayed weekly with insecticide, suggesting that herbivory has been insignificant within the plots (D. Tilman, pers. comm.). In addition, insect herbivory has not generally been found to be a dominant factor structuring plant communities at Cedar Creek. An herbivore exclusion experiment performed in three different grassland fields (Tilman 1990) found no significant effects of herbivores. In another field experiment at CCNHA Ritchie and Tilman (1992) did report a change in the relative abundance of grassland species at low fertility within cages to which grasshoppers had been added compared to cages in which grasshoppers were excluded and concluded that this was an indirect effect of herbivory mediated through herbivore effects upon concentrations of soil nitrate. However, the grasshopper densities used in this experiment were comparable to densities during outbreaks. Thus, nitrogen competition, not herbivory, might drive the pattern reported in Fig. 3.

Evidence from other low fertility sites suggests that the vegetation in such circumstances is often dominated by species which contain nutrient-poor, physically-resistant tissue and, in some cases, also defensive secondary compounds (Bryant et al. 1983, Coley et al. 1985, Naiman et al. 1986, Brown and Heske 1990) whose primary role is suspected to involve defence against herbivores. In their studies of insect herbivory and community regulation, Carson and Root (1999, 2000) found that insects, even at non-outbreak levels, might play a significant role. It is also perhaps significant that

in experimental studies measuring plant relative abundance at different fertility levels it has been found that, in the absence of herbivores, the ranking of species remains unaffected by fertility treatment (Donald 1958, Mahmoud and Grime 1976, Fraser and Grime 1998, 1999, Buckland and Grime 2000). In the investigation reported here there is circumstantial evidence that similar mechanisms may be occurring on the highly infertile soils at CCNHA. Experiments at this site involving the synthesis of plant communities in the presence and absence of the resident herbivores may be expected to provide an adequate test of this hypothesis.

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