

EFFECTS OF NUTRIENT ENRICHMENT ON THE AUCHENORRHYNCHA (HOMOPTERA) IN CONTRASTING GRASSLAND COMMUNITIES

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SUMMARY

(1) Auchenorrhyncha were sampled from control, fertilizer- and sludge-treated plots within agricultural and fourth-year old-field communities.

(2) Nutrient enrichment significantly increased net primary productivity in both plant communities.

(3) Functional plant community properties (e.g. net primary production) were more robust indicators of nutrient enrichment than were structural properties (e.g. plant species diversity).

(4) Nutrient-enriched plots generally exhibited higher Auchenorrhyncha population densities than control plots in both community types; differences were more frequent in the more mature old-field community.

(5) There were significant differences in Auchenorrhyncha species richness only in the nutrient-enriched plots in the old-field community.

(6) Changes in Auchenorrhyncha density and diversity were attributed to changes in plant composition, productivity and probably plant quality and vegetational architecture.

(7) Auchenorrhyncha within the more mature old-field community exhibited a greater response to nutrient subsidy than within the agricultural community; these differences were attributed to plant–insect life-history characteristics.

INTRODUCTION

Numerous studies have investigated the effects of nutrient enrichment on the community or ecosystem levels of biological organization (Hurd *et al.* 1971; Hurd & Wolf 1974; Olechowicz 1976; Grant, French & Swift 1977; Kirchner 1977; Prestidge 1982a). The need for such research has long been recognized (Barrett, van Dyne & Odum 1976; Barrett 1978). Only a few studies have attempted to evaluate contrasting types of nutrient enrichment on different community types (e.g. Anderson & Barrett 1982; Maly & Barrett 1984). None of these studies, however, focused on the effects of different types of nutrient enrichment on insects within contrasting grassland communities.

The major objective of this investigation was to determine the effects of contrasting types of nutrient enrichment on the Auchenorrhyncha in replicate wheat and fourth-year old-field communities. The Auchenorrhyncha was selected for analysis because (a) it represents a dominant group of insect herbivores in various grassland habitats (Whittaker 1969; Morris 1971; Waloff & Solomon 1973; Hawkins *et al.* 1979; Waloff 1974, 1975, 1980); (b) their abundance appears to be related to plant productivity (Hurd *et al.* 1971;

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Hurd & Wolf 1974), vegetational architecture (Andrzejewska 1965; Morris 1971, 1973; Lawton 1978; Waloff 1980; Prestidge & McNeill 1982), and plant nutritional status, e.g. food quality (Andrzejewska 1976; Prestidge & McNeill 1982; Prestidge 1982a); (c) their diversity is apparently related to vegetational architecture (Evans & Murdoch 1968; Murdoch, Evans & Peterson 1972; Denno 1977; Lawton 1978; Tallamy & Denno 1979) and plant nutritional status (Lawton 1978; Prestidge & McNeill 1982); and (d) some Auchenorrhyncha may be relatively host-specific (Whitcomb 1957; Waloff & Solomon 1973; Waloff 1980).

MATERIALS AND METHODS

This study was conducted at the Miami University Ecology Research Center, near Oxford, Ohio. The study areas consisted of a 0.8-ha old-field (perennial grassland meadow) and a 0.8-ha agricultural field (annual wheat field), each enclosed within a 20-gauge galvanized steel enclosure wall. Each field (community type) was subdivided into eight 0.1-ha grids. Enclosures of this type have been described (Barrett 1968; Bulan & Barrett 1971; Suttman & Barrett 1979).

Experimental design and treatment procedures

Plots in the agricultural field were ploughed and disc harrowed and a commercial fertilizer (12-12-12; N-P-K) was applied at 336 kg ha⁻¹ on 24 October 1977. Winter wheat (*Triticum aestivum* L. 'Ranger') was sown at 68 kg ha⁻¹ on 25 October 1977. On 8 April 1978, the community was sown with red clover (*Trifolium pratense* L. 'Logan') at 17 kg ha⁻¹.

In 1975, the old-field plots were ploughed and disc harrowed and each was sown with a homogeneous mixture of grasses, consisting of 6.8 kg fescue (*Festuca elatior* L.), 11.3 kg Kentucky bluegrass (*Poa pratensis* L.) and 4.5 kg ryegrass (*Lolium perenne* L.) (Stueck & Barrett 1978). The field had been left undisturbed since 1975 and was in its fourth year of secondary succession when this investigation was initiated.

In each community type, three replicate plots were treated with dried sewage sludge, three replicate plots were treated with commercial fertilizer and two were left as untreated controls. A completely randomized research design was established in each community type (Hurlbert 1984).

The sewage sludge used was Milorganite, a heat-dried, activated (undigested) municipal sludge with a dry, granular texture (Anderson 1959). Nutrient composition is 6-2-0 (N-P-K). Sludge was applied at 1792 kg ha⁻¹, conforming to standard N-fertilizing rates (Shea & Stockton 1975). In order to supply the same level of nutrient subsidy, three replicate plots in each community type were treated with a commercial urea-phosphate fertilizer (34-11-0; N-P-K). The fertilizer was applied at 314 kg ha⁻¹; no inert filler was used. Thus, each sludge and fertilizer treatment consisted of an equivalent 6-2-0 (N-P-K) application rate. Sludge and fertilizer were applied monthly from May to September.

Vegetation sampling

Four vegetation samples per plot were taken monthly from April to October; see Taylor (1979) for details. Each 0.25 m² sample included all living and dead plant matter, plus ground litter. Sample areas were chosen using a system of coordinates and a table of random numbers. Live plants were sorted to species, dried at 80 °C for 48 h and weighed

to the nearest g. Net primary production ($\text{g m}^{-2} \text{ year}^{-1}$) was estimated by summing the peak production values for each species in each plot (Malone 1968).

Auchenorrhyncha sampling

Auchenorrhyncha populations were sampled using the vacuum method described by Barrett (1968) with modifications modelled after techniques used by Teraguchi, Teraguchi & Upchurch (1977). Sample sites were also located by a system of coordinates and a table of random numbers. A 0.062 m^2 polyethylene cylinder fitted with a nylon organdy sleeve was placed over the standing vegetation to prevent insects from escaping while the hose of the vacuum-type sampler swept them into a nylon organdy collection bag. Vegetation was then clipped to ground level beneath the cylinder and any remaining surface insects were removed.

Three samples were collected from each 0.1-ha plot within both plant communities on eight sampling dates from May to October 1978. Thus, on each sampling date, nine fertilizer-treated samples, nine sludge-treated samples and six control samples were collected from each plant community. Insects collected were killed with carbon tetrachloride, stored in plastic bags, with vegetation and litter, and frozen until sorting, identification and weighing were completed. The primary taxonomic keys used for identification and host associations were: Metcalf (1923); Osborn (1938, 1940); DeLong (1948); Oman (1949); Beirne (1956); Young (1959); Kramer (1973) and Hamilton (1979). Individuals were separated into species; when identification to species was not possible, individuals were assigned a code number and treated as 'kinds' in the calculation of species diversity and apportionment indices.

Auchenorrhyncha analyses

The following parameters were used to determine the effects of fertilizer and sludge treatments on adult Auchenorrhyncha community structure.

Density. The number of individuals m^{-2} was calculated. Values for each treatment were averaged for each sampling date.

Species diversity. Two measures of diversity were calculated for the Auchenorrhyncha in both the old-field and wheat plant communities. Species diversity per unit area was used to calculate species richness (variety) values. Richness values were computed for each plot and averaged per treatment for each sampling date.

The evenness index of Pielou (1966), $e = H'/\ln S$, where H' is the Shannon-Weiner index (Shannon & Weaver 1963) and S is the total number of species, was used to calculate Auchenorrhyncha species apportionment values. Apportionment values were computed for each plot and averaged per treatment for each sampling date.

Statistical analyses

Data were tested for significance ($P \leq 0.05$) using an analysis of variance (Barr *et al.* 1976). If the treatment effect was significant, individual means were compared using Duncan's new multiple range test (Duncan 1955). Duncan's tests were performed for each sampling date within the agricultural and the old-field communities.

TABLE 1. Plant species composition and annual net primary production (NPP) in $\text{g m}^{-2} \text{ year}^{-1}$ in each of the treatments of the wheat and old-field communities

Species	Wheat field		
	Fertilizer	Sludge	Control
<i>Aster pilosus</i> Willd.	*	*	*
<i>Erigeron annuus</i> (L.) Pers.	*	*	*
<i>Daucus carota</i> L.	*	*	*
<i>Trifolium pratense</i> L.	14	38	110
<i>Triticum aestivum</i> L.	536	326	364
<i>Ambrosia artemisiifolia</i> L.	877	456	151
<i>Cirsium arvense</i> (L.) Scop.	48	52	89
<i>Polygonum pennsylvanicum</i> L.	14	10	*
<i>Setaria faberii</i> Herrm.	*	*	*
<i>Chenopodium album</i> L.	56	5	6
<i>Phleum pratense</i> L.	10	—	—
<i>Dactylis glomerata</i> L.	8	8	*
<i>Melilotus officinalis</i> (L.) Lam.	5	18	26
Total	1568	913	746
	Old-field		
	Fertilizer	Sludge	Control
<i>Festuca elatior</i> L.	350	177	125
<i>Poa pratensis</i> L.	120	100	75
<i>Solidago canadensis</i> L.	120	112	21
<i>Ambrosia artemisiifolia</i> L.	*	*	*
<i>Barbarea vulgaris</i> R. Br.	*	*	*
<i>Setaria faberii</i> Herrm.	11	13	*
<i>Oenothera biennis</i> L.	*	*	*
<i>Phalaris arundinacea</i> L.	270	200	119
<i>Melilotus officinalis</i> (L.) Lam.	55	*	9
<i>Phleum pratense</i> L.	15	6	—
Total	941	608	349

* NPP < 5 $\text{g m}^{-2} \text{ year}^{-1}$.

Data adapted from Taylor (1979).

RESULTS

Vegetation response

Annual net primary production (NPP) values for the fertilizer, sludge, and control treatments within the wheat field were 1568, 913 and 746 $\text{g m}^{-2} \text{ year}^{-1}$, respectively. Annual NPP values for fertilizer, sludge, and control treatments within the old-field community were 941, 608 and 349 $\text{g m}^{-2} \text{ year}^{-1}$, respectively (Table 1).

There were significant differences in NPP in the wheat fields and old-fields between control and nutrient-enriched treatments. However, the increase was greater and occurred earlier in the fertilizer-treated plots than in the sludge-treated plots (Taylor 1979; Anderson & Barrett 1982). The sludge-type nutrient subsidy was apparently in a less available form than the fertilizer (Moberg, Waddington & Duich 1970; Waddington, Moberg & Duich 1972). NPP peaked in early July in the wheat field, corresponding to wheat maturation. Weedy annuals became established after the wheat matured. The fertilizer- and sludge-treated wheat fields reached a second peak in mid-August, mainly because of production of ragweed (*Ambrosia artemisiifolia* L.). Ragweed comprised 56% of total NPP in the fertilized wheat field; wheat accounted for 34%. No other species accounted for > 5% of the annual NPP.

Ragweed comprised 50% of NPP, wheat 36%, Canada thistle (*Cirsium arvense* (L.)

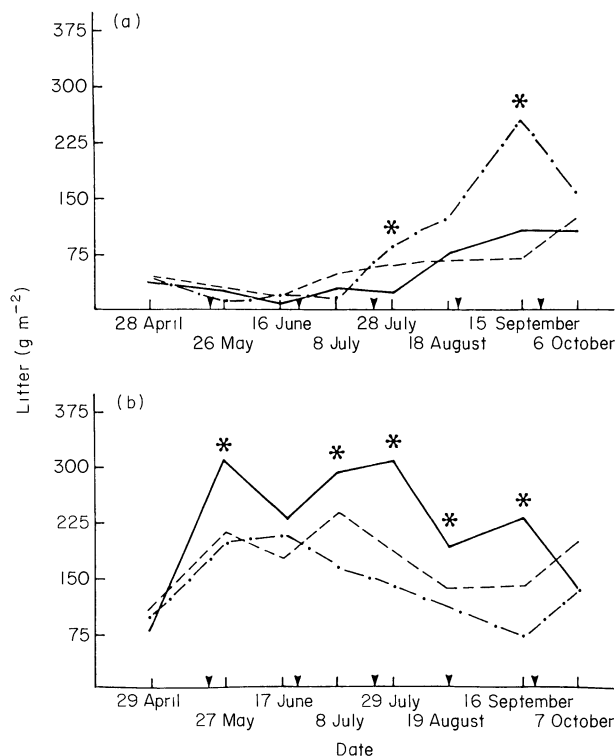


FIG. 1. Seasonal accumulation of litter during 1978 in (a) wheat and (b) old-fields; * significant difference ($P \leq 0.05$) using Duncan's new multiple range test. Data adapted from Taylor (1979); (— · — · —) fertilizer, (---) sludge, (—) control, (▼) nutrient application.

Scop.) 6%, and red clover 4% in the sludge-treated wheat fields. Ragweed comprised only 20% of NPP, wheat 49%, and red clover 15% in the control plots.

NPP values in the old-field are summarized in Table 1. Estimates of net annual primary productivity for the dominant species were higher in the fertilizer-treated plots than in the sludge-treated or control plots in the old-field. Nutrient enrichment enhanced NPP of the grasses, namely fescue, Kentucky bluegrass, giant foxtail (*Setaria faberii* Herrm.), reed canary grass (*Phalaris arundinacea* L.) and timothy (*Phleum pratense* L.), between treatments in the old-field (Table 1). Estimates of annual NPP for goldenrod (*Solidago canadensis* L.) in nutrient-enriched plots significantly increased, compared with control plots, in the fourth-year old-field. Control plots in the old-field community were mainly dominated by fescue and reed canary grass.

Litter production in the wheat field followed a different seasonal trend from the old-field community (Fig. 1). No significant differences were found between treatments until 28 July, when both sludge and fertilizer treatments were significantly greater than the control. Litter in the fertilizer-treated plots was significantly greater than in the sludge-treated or control plots on 15 September.

Litter values peaked early in the old-field community for all treatments (Fig. 1). Litter production in the control plots was significantly greater than in both the sludge and

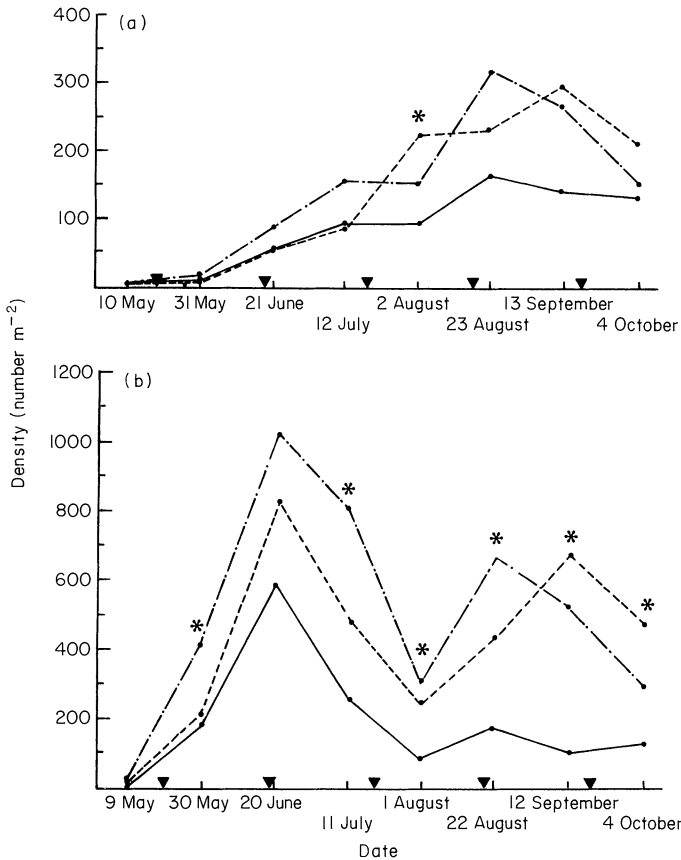
Nutrient-enriched grassland *Auchenorrhyncha*

FIG. 2. Seasonal abundance of adult *Auchenorrhyncha* during 1978 in (a) wheat and (b) old-fields; * significant difference ($P \leq 0.05$) using Duncan's new multiple range test; (---) fertilizer, (-.-.-) sludge, (—) control, (▼) nutrient application.

fertilizer treatments on 27 May and significantly greater than in the fertilizer treatment from 8 July to 16 September.

Auchenorrhyncha population density

Wheat field nutrient-enriched plots generally exhibited higher *Auchenorrhyncha* densities than control plots (Fig. 2). However, the only significant difference was found on 2 August, when sludge values were greater than control values. All treatments peaked later in the growing season in the wheat field.

Relative abundance (percentage of total *Auchenorrhyncha* density) of the ten most common species on 23 August in the wheat field are summarized in Table 2. *Pissonotus flabellatus* (Ball), *Amblycellus curtisii* (Fitch), *Empoasca* sp. 5 (Walsh), and *Philaenus spumarius* (L.) were the most abundant species in the fertilizer-treated plots, whereas, *Liburniella ornata* (Stål), *Planicephalus flavacostatus* (Van Duzee), and *Philaenus spumarius* were the most abundant species in the sludge-treated plots. The most abundant species in the control plots were *Aceratagallia sanguinolenta* (Provancher), *Endria inimica* (Say) and *Philaenus spumarius*.

TABLE 3. Relative abundance (percentage of total Auchenorrhyncha density) of the ten most common species observed during peak densities on 20 June in each treatment of the old-field

	Fertilizer	Sludge	Control*
Cicadellidae			
	<i>Amblycellus curtisii</i> (Fitch)	0.3	<i>Amblycellus curtisii</i> (Fitch)
	<i>Aphrodes fuscifaciata</i> (Goeze)	1.0	<i>Aphrodes fuscifaciata</i> (Goeze)
	<i>Athysanus argentatus</i> (Fab.)	8.7	<i>Athysanus argentatus</i> (Fab.)
	<i>Doratura stylata</i> (Sahlberg)	52.0	<i>Doratura stylata</i> (Sahlberg)
	<i>Endria inimica</i> (Say)	0.2	<i>Draeculacephala antica</i> (Walker)
	<i>Forcipata loca</i> (DeL. & Cald.)	1.9	<i>Forcipata loca</i> (DeL. & Cald.)
	<i>Latalus sayi</i> (Fitch)	23.7	<i>Latalus sayi</i> (Fitch)
	<i>Psammnotetix lividellus</i> (Zetterstedt)	5.2	<i>Psammnotetix lividellus</i> (Zetterstedt)
Cercopidae			
	<i>Philaenus spumarius</i> (L.)	1.6	<i>Philaenus spumarius</i> (L.)
Delphacidae			
	<i>Delphacodes campestris</i> (Van Duzee)	4.8	<i>Delphacodes campestris</i> (Van Duzee)

* Only eight species captured for this treatment on this sampling date.

Old-field nutrient-enriched plots consistently had higher Auchenorrhyncha densities than control plots (Fig. 2). A significant difference was detected on 30 May, when fertilizer plots had greater densities than sludge or control plots. Densities on fertilizer plots were significantly greater than on control plots from 11 July to 22 August. Densities on fertilizer and sludge plots were greater than on control plots on 12 September; only sludge plots had greater densities than control plots on 4 October. All treatment types exhibited peak densities early in the growing season, on 20 June.

Relative abundance (percentage of total Auchenorrhyncha density) of the ten most common species observed during peak densities in the old-field appears in Table 3. *Athysanus argentatus* (Fab.), *Doratura stylata* (Sahlberg) and *Latalus sayi* (Fitch) were the most abundant species in each of the treatments in this community type. *D. stylata* was the most abundant species in both fertilizer- and sludge-treated plots, with 52.0% and 57.7% of the total Auchenorrhyncha density, respectively. *L. sayi* was the most abundant species in the control plots, with 42.9% of the total Auchenorrhyncha density, whereas only 29.2% of the density was represented by *D. stylata*.

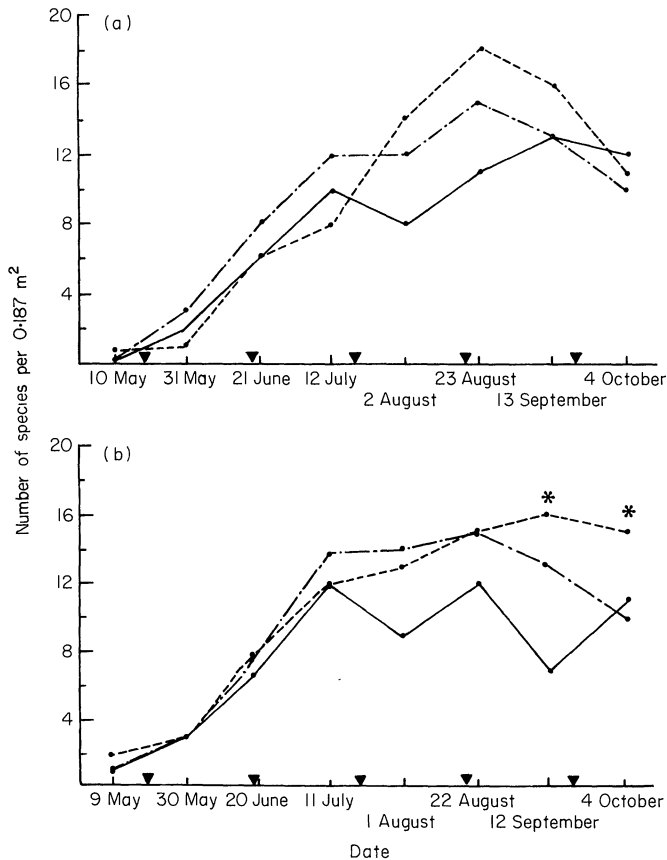


FIG. 3. Seasonal trends in mean number of adult species of Auchenorrhyncha during 1978 in (a) the wheat and (b) old-fields; * significant difference ($P \leq 0.05$) using Duncan's new multiple range test; (.....) fertilizer, (---) sludge, (—) control, (▼) nutrient application.

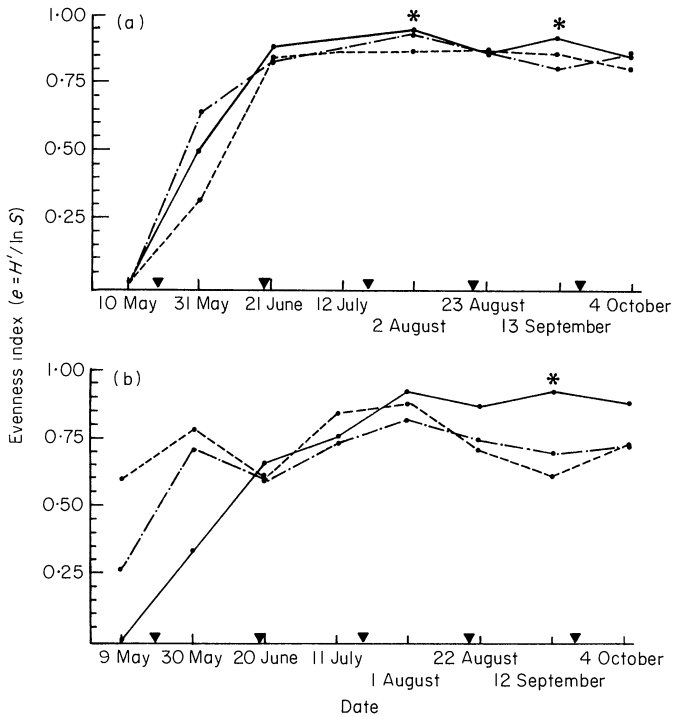
Nutrient-enriched grassland *Auchenorrhyncha*

FIG. 4. Seasonal trends in mean evenness values of adult *Auchenorrhyncha* during 1978 in (a) the wheat and (b) old-fields; *significant difference ($P \leq 0.05$) using Duncan's new multiple range test; (---) fertilizer, (-.-) sludge, (—) control, (▼) nutrient application.

Auchenorrhyncha species diversity

Effects of nutrient enrichment on the mean number of *Auchenorrhyncha* species per unit area per community type are summarized in Fig. 3. No significant differences between treatments were detected in the wheat field on any sampling date. Old-field nutrient-enriched plots, however, had significantly higher values for species diversity per unit area on 12 September and 4 October. On 12 September, sludge- and fertilizer-treated plots had significantly higher diversity values than control plots; sludge plots exhibited a significantly higher value than fertilizer or control plots on 4 October.

Effects of treatment on Pielou's species evenness are depicted in Fig. 4. Interestingly, the *Auchenorrhyncha* in both plant communities responded to the effects of nutrient enrichment late in the growing season. Control and fertilizer-treated plots had significantly higher mean apportionment values than sludge-treated plots on 2 August. Control plots exhibited a significantly higher mean apportionment value than the fertilizer plots on 13 September. A significant difference was detected in the old-field treatments on 12 September, when control plots had a significantly higher mean apportionment value than either fertilizer- or sludge-treated plots.

DISCUSSION

Mature communities are hypothesized to be more stable than younger (e.g. agricultural) communities (Odum 1969). In the present study, we hypothesized that nutrient

enrichment would act as a perturbation which would destabilize Auchenorrhyncha communities (Odum 1969; Woodwell 1970; Rosenzweig 1971; Andrzejewska 1976; Prestidge 1982a,b; Prestidge & McNeill 1982, 1983).

Interestingly, the Auchenorrhyncha in the more mature old-field community exhibited more significant differences in density and species richness between treatments than the agricultural community. These differences, however, could not be attributed to plant species diversity. For example, Shannon–Weiner plant diversity values (H') for the fertilizer, sludge and control plots were 1.66, 1.61 and 1.63, respectively, for the old-field community (see Anderson & Barrett (1982) for details). Taylor (1979) noted that the effects of nutrient enrichment on plant community biomass and species richness were significantly greater in the annual (wheat) community than in the more mature (old-field) community. We found that the Auchenorrhyncha (a primary consumer trophic guild) responded quite differently from the producer trophic level.

Differences in plant community composition, however, may account for the observed differences in Auchenorrhyncha density and diversity (Whittaker 1976). For example, the wheat field was mainly dominated by wheat and the summer annual ragweed, whereas the old-field community was dominated by several grass species and perennial goldenrod.

The increased productivity of several grass species (e.g. fescue, Kentucky bluegrass, reed canary grass and timothy) may have been partly responsible for this Auchenorrhyncha response to nutrient enrichment in the old-field community. Many species of Auchenorrhyncha have, for example, been shown to be closely associated with the phenologies of their host-plants (Waloff & Solomon 1973; Waloff 1980). Closer examination of the Auchenorrhyncha in the old-field during peak densities revealed that the cicadellids *Athysanus argentatus*, *Doratura stylata* and *Latalus sayi* were the dominant species in all three treatment types; *D. stylata* comprised > 50% of the individuals in each of the nutrient-enriched treatments. Byers & Jung (1979) also found *D. stylata* to be more abundant on fertilized than on unfertilized plots. All three species are abundant in grassland habitats and use grasses as hosts (DeLong 1948; Beirne 1956).

D. stylata inhabits the root and litter zones of its host-plants (Beirne 1956). Therefore, the absence of this cicadellid species in the wheat field and its abundance in the old-field may in part be due to the significant accumulation of litter in the old-field plots. Increased productivity of fescue, Kentucky bluegrass, and reed canary grass in the old-field plots also appears to have contributed to the high densities of *D. stylata* in the old-field community.

Auchenorrhyncha densities exhibited a greater frequency of significant differences following nutrient enrichment in the old-field than in the wheat field. In general, nutrient enrichment resulted in increased Auchenorrhyncha densities in both community types. Olechowicz (1976, 1977) and Andrzejewska (1976) obtained similar results in studies on the effects of fertilizer application on insect communities in meadow ecosystems. It appears that increased densities of adult arthropods in fertilized fields may be attributed to an increase in plant production (Hurd *et al.* 1971; Hurd & Wolf 1974; Kirchner 1977), resulting in an increase in the available food and vegetation for phytophagous insects (Prestidge & McNeill 1982). The nutrient subsidy also probably resulted in increased food quality for the Auchenorrhyncha in terms of protein or nitrogen content (Prestidge 1982a, b; Prestidge & McNeill 1982, 1983).

Further, it has been demonstrated that grassland Auchenorrhyncha populations are affected by nutrient cycles in host-plants (McNeill & Southwood 1978; Waloff 1980). Prestidge (1982a,b) demonstrated that different grassland Auchenorrhyncha species

would be affected by nutrient enrichment or herbage quality. Although herbage quality was not measured in our study, we contend that food quality increased because of nutrient subsidy.

The Auchenorrhyncha density peaked late in the growing season in the wheat field. The cicadellid species of the *Empoasca* spp. complex, *Amblycellus curtisii* and *Planicephalus flavocostatus* along with the delphacid species *Pissonotus flabellatus* and *Liburniella ornata* were dominant in the wheat field nutrient-enriched plots during this time. Peak densities of the Auchenorrhyncha in the nutrient-enriched plots were attributed to the establishment of weedy annuals following wheat maturation and to an increase in litter production. The cicadellids *Aceratagallia sanguinolenta* and *Endria inimica* and the cercopid *Philaenus spumarius* were the most abundant in the control plots. This response was primarily attributed to the establishment of grasses, legumes and herbaceous weedy annuals after wheat maturation. These findings further illustrate the importance of small-scale disturbances (e.g. Armesto & Pickett 1985) in the enhancement of plant-insect coexistence, which is often highly dependent on life-history characteristics.

Evans & Murdoch (1968) found that arthropod species diversity peaked in mid-summer followed by a gradual decline in autumn. These changes have been correlated with changes in standing crop biomass (Hurd *et al.* 1971; Hurd & Wolf 1974; Kirchner 1977) and plant species diversity (Murdoch, Evans & Peterson 1972). Auchenorrhyncha species diversity (richness) increased early in the growing season, with peak values in late August and mid-September, especially in nutrient-enriched plots. Nutrient-enriched plots in the old-field community contained significantly more Auchenorrhyncha species in mid-September. Auchenorrhyncha species apportionment in nutrient-enriched plots, however, was significantly less than in control plots, indicating dominance of a few leaf hopper species. *Forcipata loca* (DeL. & Cald.), *Amblycellus curtisii*, and *Latalus sayi* accounted for 68% of the individuals caught in the fertilizer plots on 13 September, whereas *Forcipata loca*, *Draeculacephala antica* (Walker) and *Delphacodes campestris* (Van Duzee) accounted for 69% of the individuals caught in the sludge plots at this time.

In summary, it appears that increased plant productivity or other related factors (e.g. herbage quality or vegetational architecture), not increased plant diversity, influenced Auchenorrhyncha density and species richness, especially in the old-field community. Thus, it appears that changes in plant composition, productivity and, probably, quality and vegetational architecture are clear indicators of phytophagous insect community response to such a perturbation as nutrient enrichment.

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