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An experimental study of the effects of pH and nitrogen on grassland vegetation

D. Tilman (*) and H. Olff (**)

(*) *Department of Ecology, Evolution and Behavior, 318 Church Street S.E., University of Minnesota, Minneapolis, MN 55455, USA*

(**) *Department of Plant Biology, University of Groningen, P.O. Box 14, 9750 AA Haren, Netherlands*

Abstract

The response of plant species to a full-factorial experimental manipulation of soil pH and soil N in a Minnesota old field is compared to patterns observed in a chronosequence of old fields. *Agropyron repens* reached its greatest relative abundance in low pH but high N treatments. *Schizachyrium scoparium* was less affected by N, but was most abundant at low pH. *Poa pratensis* had its greatest relative abundance in high N and high pH treatments. Total biomass and species richness were also influenced by the treatments. Thus, the common plant species were differentiated in their responses to pH and N manipulations. However, these pH and N responses did not explain the patterns observed in the old field chronosequence unless the differential colonization abilities of the species and the relationships between soil pH, soil N and successional age were considered.

Keywords: pH, nitrogen, *Agropyron repens*, *Schizachyrium scoparium*, *Poa pratensis*, *Solidago nemoralis*, *Achillea millefolia*, succession.

Résumé

La réponse d'espèces végétales à une expérimentation multifactorielle sur le pH et le N du sol d'une friche du Minnesota est comparée à ce qu'on observe sur une chronoséquence de friches. *Argopyron repens* atteint son taux d'abondance le plus élevé pour des traitements à pH bas mais N élevé. *Schizachyrium scoparium* est moins sensible au N mais très abondant à pH bas. *Poa pratensis* a son plus fort taux d'abondance relative pour des traitements à N et pH élevés. La biomasse totale et la richesse spécifique sont également influencées par ces traitements. Les réponses des espèces végétales communes aux manipulations de pH et de N sont donc différentielles. Néanmoins, ces réponses n'expliquent pas à elles seules ce qu'on observe sur les chronoséquences de friches; il faut prendre en considération les capacités différentielles de colonisation des espèces ainsi que les relations entre pH du sol, N du sol et âge de la succession.

INTRODUCTION

The composition, successional dynamics and diversity of vegetation are influenced by, and influence, soil characteristics (e. g. CROCKER & MAJOR, 1955; ELLENBERG,

1953; papers in RORISON, 1969; GRUBB *et al.*, 1969; WILLIAMS, 1978; WEDIN & TILMAN, 1990). Often, one or a few soil nutrients limit plant growth and influence vegetation composition (e. g., MILTON, 1934; WILLIS, 1963; SPECHT, 1963; THURSTON, 1969; SHAVER & CHAPIN, 1980; TILMAN, 1982). However, other soil factors, such as pH and redox potential, also influence plant communities (GRUBB *et al.*, 1969; WILLIAMS, 1978; ARMSTRONG, 1982; TILMAN, 1982) and may affect nutrient availability in complex ways (BARBER, 1984). Thus, a more complete understanding of the effects of edaphic factors on vegetation may require the experimental manipulation of both nutrients and other soil factors, such as pH.

The pH gradient imposed on the nutrient addition plots in the Rothamsted Park Grass Experiments suggests that plant species are differentiated along both nutrient and pH gradients (WILLIAMS, 1978). Experimental studies in a variety of fields at Cedar Creek Natural History Area (CCNHA; TILMAN, 1987), Minnesota, have shown that soil nitrogen is the major nutrient limiting plant growth and determining the composition and diversity of successional grasslands (TILMAN, 1987, 1988, 1990). However, soil pH varies widely both within and among these fields (pH ranges from 4.8 to 6.4 in successional fields and is as low as 3.9 in oak savannah) and pH and soil N are weakly correlated (INOUYE *et al.*, 1987). Furthermore, the abundances of dominant plant species at CCNHA are correlated with soil pH (see Discussion), and seem to be influenced by a tradeoff between colonization rates and competitive ability (GLEESON & TILMAN, 1990; TILMAN, 1990).

Thus, to study the combined effects of nitrogen supply and pH, and to determine if our species were differentiated with respect to both of these variables, we established a full factorial experiment in which both soil pH and the rate of nitrogen supply were experimentally manipulated in an old field. We compared the experimental results with patterns observed in a further analysis of the survey of the soils and vegetation of CCNHA old fields performed by INOUYE *et al.* (1987).

METHODS

Study Area: The experiment was performed at Cedar Creek Natural History Area, Minnesota, USA (45°24'N. 93°12'W), using the existing vegetation of a field dominated by the native prairie grass *Schizachyrium scoparium* (little bluestem), and containing other native prairie species as well as *Poa pratensis*, *Agropyron repens* and other introduced European pasture and weedy species (TILMAN, 1987). This field, called "Field B" (TILMAN, 1987) was last farmed, to soybeans, in 1957, and thus had been abandoned from agriculture for 27 years when this work began in 1984. The annual *in situ* rate of N mineralization in its soil was 3.4 g-N m^{-2} yr^{-1} (PASTOR *et al.*, 1987), and the average total N content of its sandplain soil was 378 mg-N per kg-soil (TILMAN, 1987). Addition of various nutrients singly and in combination demonstrated that N was the most important limiting nutrient in this field (TILMAN, 1987, 1988).

Old field survey: In 1983, INOUYE *et al.*, (1987) surveyed the soils and vegetation of 22 Cedar Creek old fields that had been abandoned from agriculture from 1 to 56 yr. We briefly describe their methods because we further analyze their data for the five species abundant in the experiments described below. A soil sample (analyzed for total N and pH) and a vegetation sample (percent cover of all species in a 0.5×1.0 m quadrant centered on the soil sample) were collected at 25 points spaced at 1.5 m intervals along each of four parallel transects per field, with the transects being 25 m apart. Two fields had six transects, giving a total of 2300 sampling points. The old field colonization patterns of the five abundant species were determined by graphing the frequency of occurrence of each species in an old field (fraction of plots in which it was present) against field age. Spearman rank correlation coefficients were used to test for significant trends.

Because a species can only respond to pH and N if it is present, the response of the percent cover of a species to N and pH was computed only for the cases when it was present in a plot. The 2300 sampling points were assigned to 10 classes of total N, ranging from 300 to 1200 mg kg^{-1} (class width 100) and 12 classes for pH, ranging from 5.1 to 6.2 (class width .1). This yielded a total of 120 possible cells (12 pH classes × 14 N classes), which represent the combined variation in pH and total N. The mean cover of each species was computed for each cell, but only if there were at least five plots in which a species was present in that cell.

Experimental Design: The experiment had a completely randomized full factorial design with 4 levels for pH and 3 levels for N, giving 12 combinations of pH and soil N. Each combination was randomly assigned to four different 4 × 4 m plots, giving a total of 48 plots. The nitrogen treatments were established by adding either 0.0 (control), 5.4, or 17.0 g m^{-2} yr^{-1} of N. This was manually sprinkled over each plot in two equal doses each year (early May, late June) as NH_4NO_3. The plots receiving N also received a mixture of other nutrients (P, K, Ca, Mg, S and trace metals; TILMAN, 1987) to assure that N remained the only limiting nutrient. The lowest pH treatment received 1.0 kg S and 4.0 kg $FeSO_4$ per plot. The next pH level, the control, received nothing to modify its pH. The third pH level, a moderately elevated pH, received 1.0 kg of $Ca(OH)_2$ per plot, and the fourth pH level received 2.0 kg of $Ca(OH)_2$ per plot. The treatments began in spring, 1984. Nutrients have been added ·each year since then. Soil pH was periodically measured, and additional amounts of the appropriate compound added to maintain pH levels, which were fairly stable. The vegetation in plots was not sampled before manipulation. However, the replicated and randomized control plots should represent initial conditions in this field because the vegetational composition of control plots in this field is fairly stable (TILMAN, 1987).

Sampling and analysis of the experiment: Vegetation in each plot was sampled in July 1987 by clipping a 10 × 300 cm strip at the soil surface in the same relative position in each of the 48 plots. The sampling was repeated, but in a different position, in July 1989. Each sample was sorted to living tissue and litter. Living tissue was sorted to species. Samples were then dried to a constant mass and weighed. Soils were sampled for pH, moisture content and extractable N in July 1987. A 1:1 mixture of soil with distilled water was used for pH measurement. For measurement of extractable N, a 2.5 cm diameter by 15 cm long soil core was collected from each plot. About 40 g of a homogenized subsample of this soil was immediately placed in 70 ml of 2 M KCl, shaken for 1 hr, and allowed to settle overnight at 2-4°C. The supernatant was analyzed on a Technicon Autoanalyzer for NH_4^+ and NO_3^-. The rest of the soil sample was dried to constant mass to determine soil moisture content. A Lambda Instruments integrating meter (integration time of 10 seconds) equipped with a 1 m long photosynthetically active radiation (PAR) sensor measured light intensity above the vegetation and at the soil surface in each plot. Data on light penetration are expressed as the proportion of incident PAR that reached the soil surface.

The effects of the N and pH treatments on total above-ground living biomass, on the abundances of dominant species, and on soil characteristics and light were determined using two-way analysis of variance with Student-Newman-Keuls contrasts among treatment means. Although a total of 33 species were observed in the 48 plots, many of these occurred in only a few plots, and thus had insufficient data for analysis. We analyzed data only for those five species that occurred in at least 4 different treatment combinations and that each comprised at least 1% of total plant biomass, averaged over all 48 plots, in either 1987 or 1989.

RESULTS

Manipulation of pH and N

The mean pH in 1987 of the 4 pH treatment levels was 4.23 (level 1), 5.70 (level 2), 6.44 (level 3), and 6.72 (level 4). ANOVA of measured soil pH with the pH level and the N level as factors revealed a highly significant effect of the pH manipulation on actual soil pH, no effect of the N treatment on actual soil pH,

TABLE I. — F *values for two-way analyses of variance for the effect of experimental treatments* (4 pH *levels,* 3 N *levels) on soil characteristics, light penetration, total plant biomass, species richness, and the relative biomass (biomass/total plot biomass) of the most abundant plant species in 1987 and 1989. Only species which occurred in more than* 3 *treatment combinations and represented more than* 1% *of the total biomass for that year were analysed in these ANOVA's.*

Variable	ANOVA F-values for:		
	pH[1]	N[2]	pH × N[3]
Soil pH in 1987	67.99***	1.84ns	0.34ns
Soil moisture content (%) 1987	0.93ns	4.14*	2.36ns
Extractable NH_4^+ 1987	5.32**	4.34*	1.03ns
Extractable NO_3^- (g.m^{-2}) 1987	1.59ns	16.80***	2.71*
Percent NO_3^- of $NH_4^+ + NO_3^-$ 1987	4.74**	43.15***	5.51***
Total extractable N 1987	3.34*	10.03***	1.32ns
Fraction light on soil 1987	4.41*	29.03**	0.83ns
Total aboveground living biomass (g.m^{-2}) 1987	10.49***	19.30***	1.82ns
Total aboveground living biomass (g.m^{-2}) 1989	1.22ns	35.10***	0.68ns
Number of species.plot^{-1} 1987	5.77**	12.28***	1.97ns
Number of species.plot^{-1} 1989	3.86*	5.32**	2.76*
Poa pratensis 1987	3.49*	6.33**	0.22ns
Poa pratensis 1989	1.05ns	6.54**	0.15ns
Schizachyrium scoparius 1987	2.85*	1.63ns	0.60ns
Schizachyrium scoparius 1989	4.33*	2.65ns	0.66ns

[1] 3,35 d.f.; [2] 2,35 d.f.; [3] 6,35 d.f..

(ns) not significant; * $p < .05$; ** $p < .01$; *** $p < .001$.

and no significant interaction (table I). Thus, the pH treatments resulted in the desired pH gradient, with pH being statistically independent of the rate of N addition.

Total extractable soil N ($NO_3^- + NH_4^+$) was significantly higher in the high N treatment than in the two lower N treatments (table II), but the two lower N treatments did not differ significantly from each other. Total extractable N also depended on pH (tables I and II), with the lowest values, for a given N treatment, being in the intermediate pH plots. There was no significant N treatment by pH treatment effect on total extractable soil N (tables I et II).

Extractable soil NH_4^+ and extractable NO_3^- responded differently to the treatments (tables I and II). NO_3^- increased significantly with the rate of N addition, was independent of the pH treatment, but had a significant pH treatment by N treatment interaction (table I). NH_4^+ had significant N treatment and pH treatment effects, but no interaction (table I). The percent NO_3^- of the total extractable soil N depended significantly on the N treatment, the pH treatment, and their interaction (table I). The highest percent NO_3^- occurred in the three highest pH treatments at the highest N treatment. In contrast, for the lowest pH treatment, the three different N treatments did not differ significantly in their percent NO_3^- or their NO_3^- concentration, but did differ significantly in their NH_4^+ concentrations (table II).

In both 1987 and 1989, total above-ground biomass was significantly different between the N treatments, but was only significantly dependent on pH in 1987

TABLE II. – Mean values (with s.d.) per treatment combination of several soil characteristics, light penetration through the vegetation, total biomass and species richness in 1987 and 1989. The pH treatments were established by addition of sulfur or $CaCO_3$ (see Methods). The N treatments refer to the $g\ m^{-2}\ y^{-1}$ of N added, with no N added to the control. Means with the same letter were not significantly different (p>0.05) between pH treatments. Means with the same underlining indicate non-significant (p>0.05) differences between N treatments within each pH treatment. Contrasts were computed using the Student-Neumann-Keuls test after two-way analysis of variance.

pH Trtm: N Trtm:	pH 1			pH 2			pH 3			pH 4		
	Control	5.4	17	Control	5.4	17	Control	5.4	17	Control	5.4	17
pH 1987	4.10^a (.51)	4.72^a (.49)	4.31^a (.56)	5.39^b (.54)	5.69^b (.31)	6.03^b (.53)	6.27^c (.62)	6.46^c (.40)	6.58^c (.36)	6.62^c (.48)	6.90^c (.17)	6.70^c (.45)
Moisture 1987 (%)	9.39^a (1.63)	14.78^a (4.25)	10.99^a (1.56)	10.17^a (1.62)	11.38^a (0.93)	10.63^b (2.93)	12.02^a (0.49)	10.89^a (1.14)	10.10^a (0.82)	10.17^a (1.00)	11.26^a (.53)	10.24^a (0.97)
NH$_4^+$ 1987 (g.m^{-2})	2.13^a (0.64)	9.69^a (0.72)	8.95^a (7.56)	1.01^b (0.22)	1.86^a (0.52)	3.80^b (2.00)	1.39^b (0.37)	1.33^b (0.30)	2.80^b (0.52)	1.71^b (0.48)	3.46^b (1.32)	5.15^b (0.61)
NO$_3^-$ 1987 (g.m^{-2})	0.11^a (0.06)	0.99^a (0.66)	0.84^a (0.65)	0.10^a (0.06)	0.12^a (0.03)	4.69^b (4.15)	0.11^a (0.04)	0.19^a (0.11)	1.72^a (1.09)	0.10^a (0.02)	0.11^a (0.01)	4.85^b (3.06)
% NO$_3^-$ 1987	4.80^a (2.14)	10.29^a (3.05)	9.14^a (1.80)	8.95^a (3.20)	6.47^a (2.15)	52.63^c (19.05)	7.26^a (2.23)	12.56^a (7.17)	35.13^b (17.77)	5.59^a (0.52)	3.27^a (1.10)	45.21^{bc} (18.20)
NH$_4^+$+NO$_3^-$ 1987 (g.m^{-2})	2.24^a (0.67)	10.69^a (9.27)	9.80^a (8.21)	1.11^{bc} (0.27)	1.98^{bc} (0.53)	8.50^{bc} (5.26)	1.30^a (0.39)	1.52^c (0.32)	4.53^c (1.37)	1.81^{bc} (0.49)	3.56^{bc} (1.32)	10.01^{bc} (2.71)
Frac light on soil 1987	0.71^a (0.07)	0.18^a (0.11)	0.38^a (0.35)	0.50^b (0.29)	0.08^b (0.05)	0.13^b (0.06)	0.47^b (0.14)	0.06^b (0.06)	0.19^b (0.09)	0.39^b (0.08)	0.07^b (0.03)	0.21^b (0.13)
Total Biom. 1987 (g.m^{-2})	76.86^a (14.62)	124.41^a (41.70)	108.78^b (65.62)	95.56^b (64.08)	260.53^b (78.71)	306.39^b (58.80)	131.41^b (58.35)	221.70^b (35.89)	253.80^b (89.13)	133.23^b (30.72)	237.65^b (54.17)	236.92^b (59.47)
Total Biom. 1989 (g.m^{-2})	114.50^a (43.84)	239.38^a (96.34)	241.80^a (18.28)	64.08^a (20.47)	212.39^a (18.05)	224.56^a (85.84)	65.94^a (11.56)	228.44^a (40.05)	207.08^a (83.18)	128.12^a (37.25)	199.11^a (61.25)	241.25^a (30.25)
No. Species.plot^{-1} 1987	2.4^a (0.6)	3.5^a (1.7)	3.0^a (1.2)	7.8^b (3.4)	5.0^b (1.6)	3.8^b (0.9)	10.3^b (1.3)	5.3^b (1.5)	3.5^b (1.0)	7.3^b (2.1)	6.5^b (2.9)	5.0^b (1.8)
No. Species.plot^{-1} 1989	3.0^{bc} (2.0)	3.5^{abc} (1.7)	2.3^c (1.3)	6.3^a (2.2)	3.5^{abc} (1.9)	2.5^{bc} (0.6)	6.0^{ab} (1.4)	2.8^{abc} (0.9)	3.3^{abc} (1.3)	5.0^{abc} (0)	4.0^{abc} (1.2)	5.5^{abc} (2.5)

(table I). In both years, total biomass increased with the rate of N addition (table II, figs. 1 and 2). Total biomass was significantly lower on the lowest pH treatment in 1987, but not in 1989 (table II).

The five most abundant species differed in their responses to the various combinations of pH and N (figs. 1 and 2, table I). *Agropyron repens* was absent from the three lowest pH levels for the plots that received no added N, and was increasingly abundant at higher rates of N addition at the lower pH levels. Thus its greatest response to the gradient, in both 1987 and 1989, occurred in low pH but high N plots. In contrast, the relative abundance of *Schizachyrium scoparium* was independent of N level but was significantly dependent on pH level in both years, with significantly greater relative abundance at low pH (figs. 1 and 2, table I). *Poa pratensis* was rare in the low N, low pH combinations, and much more dominant in the high N, high pH combinations both years (figs. 1 and 2). The two forb species had less distinct patterns. *Solidago nemoralis*, a rosette-forming goldenrod, reached its peak abundance at intermediate pH on the lowest N level, rarely occurred in the two higher N levels, and had no clear pH response when at the higher N levels (figs. 1 and 2). *Achillea millefolium* seemed to reach its peak abundance at intermediate pH and high N in 1987, but was absent from most plots in 1989.

In both 1987 and 1989, species richness (the total number of all species of vascular plants observed in a given plot) depended on both the N treatment and the pH treatment (table I). Species richness tended to be highest at intermediate pH and to decline with increases in the rate of N addition during both years (figs. 1 and 2). There was a significant N × pH interactive effect for species richness in 1989, but not in 1987.

Old field survey

Although the total N content of the soil significantly increased with field age in the successional sequence (fig. 3; INOUYE et al., 1987), soil pH was independent of field age (fig. 3). However, the between-field variance in pH decreased with field age, with much greater pH variation between early successional fields than between later successional fields (fig. 3). Thus, during succession, the fields changed from having low N but variable pH to higher N with relatively low but similar pH.

All species but *Achillea* had their frequency of occurrence significantly dependent on field age (fig. 4). These data suggest that *Agropyron* is a rapid colonist of abandoned fields, that *Poa* is the next most rapid colonist, and that *Schizachyrium* and *Solidago* are much slower colonists.

In the old field survey, the response of the percent cover of *Agropyron* to total N and pH, given that it was present in a plot, showed that *Agropyron* had its lowest percent cover in the low pH classes with low total N (fig. 5). Its high percent cover in high pH classes might reflect its early successional status because early successional fields often have higher pH (fig. 3 A). The high cover of *Agropyron* in experimental plots with low pH, high total N (figs. 1, 2), can not be ascribed to its colonization dynamics and could therefore be a result of resource-dependent interactions with other species.
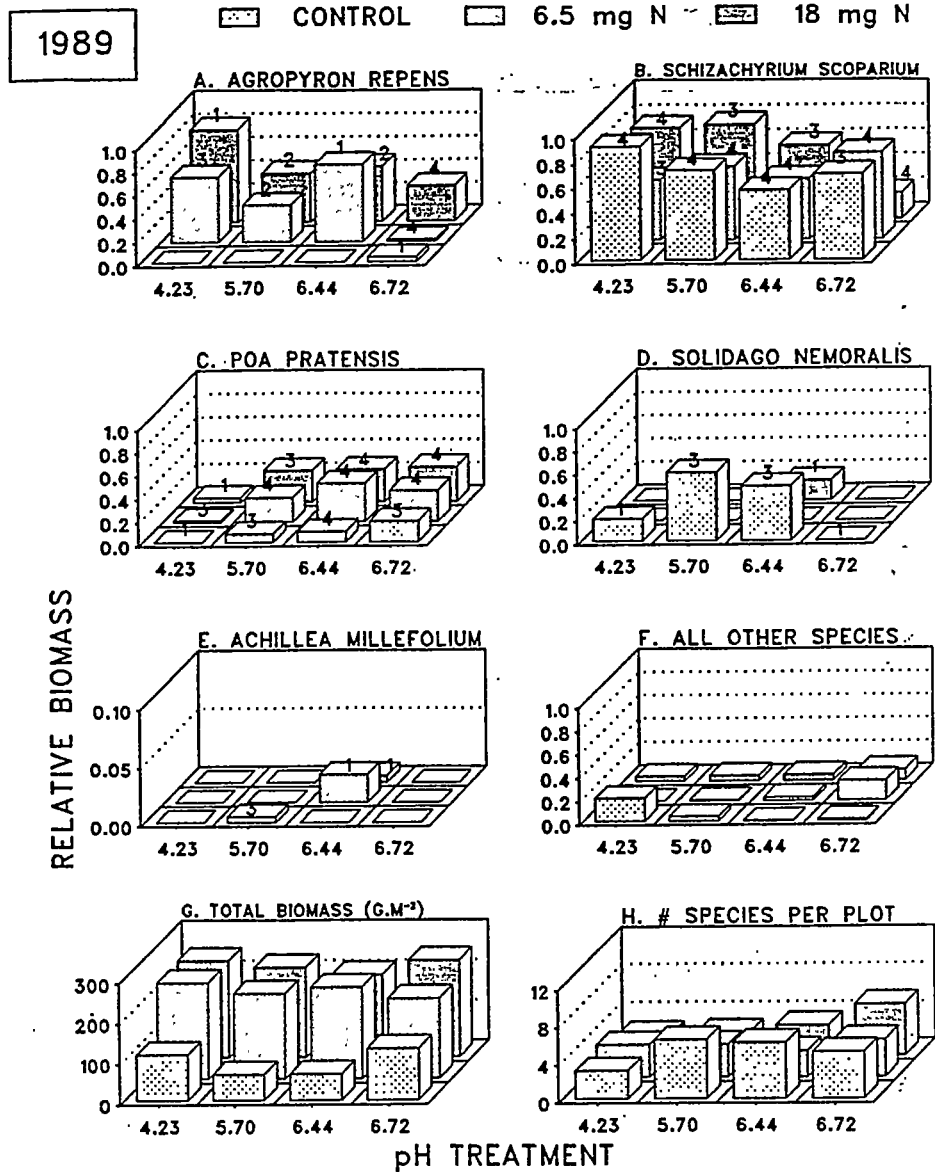
Fig. 1. — The 1987 results for the full-factorial pH and N experiment. (A-F) Relative biomass of the five most abundant species, and of all other species combined in each of the treatment combinations. Relative biomass was calculated separately for each plot in each treatment combination by dividing the aboveground biomass of a species by the total aboveground biomass in that plot. Plots in which a given species did not occur were excluded from analysis of that species response. The integer shown at the top of each bar in parts A-E gives the number of replicates (maximum=4) in which a given species was present for each of the treatment combinations. (G) Total aboveground biomass (gm) in each treatment combination. (H) Species richness per plot, for each treatment combination.
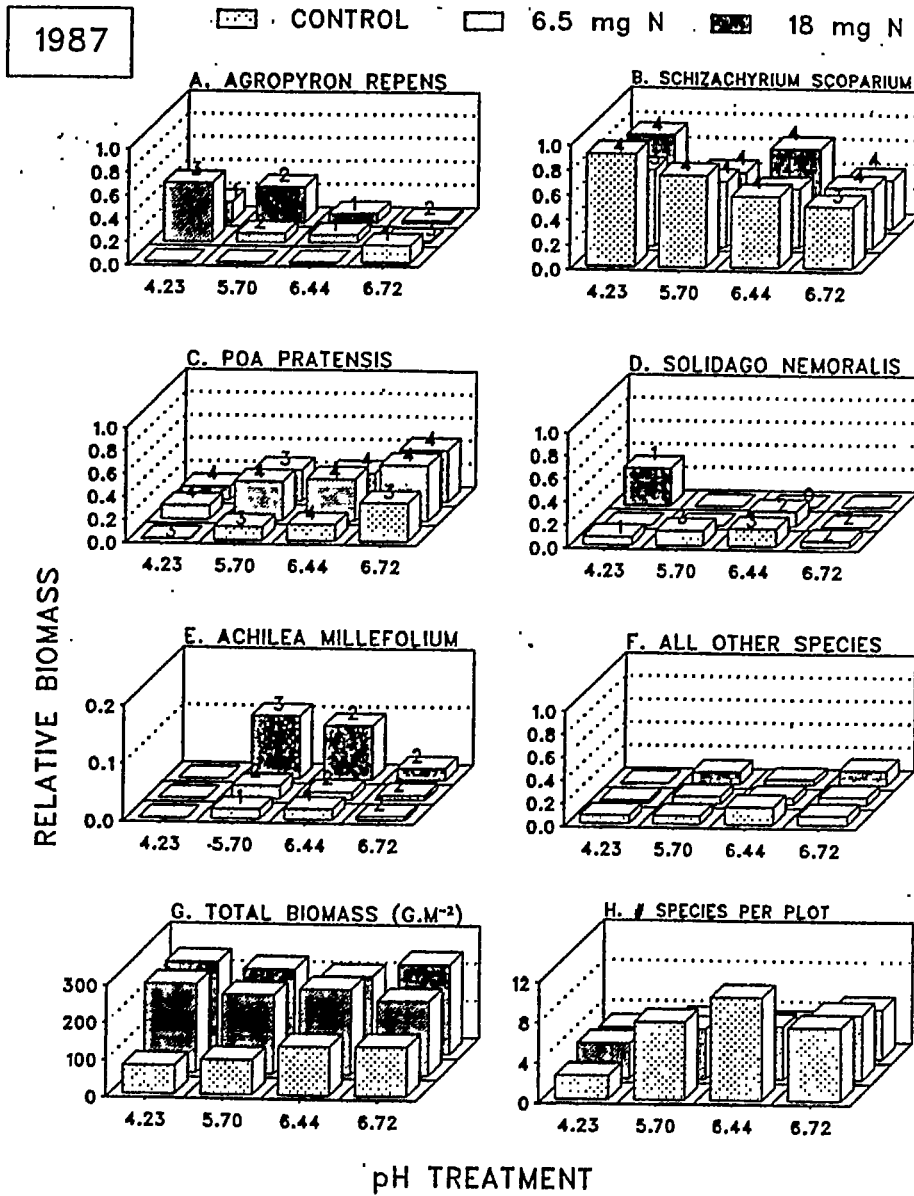
Fig. 2. — The 1989 results for the full factorial pH and N experiment. See figure 1 for details.

Schizachyrium colonized the successional sequence during the later stages (fig. 4) when only situations of lower pH but higher total N occurred (fig. 3), and had its highest cover at intermediate total N classes (fig. 5).
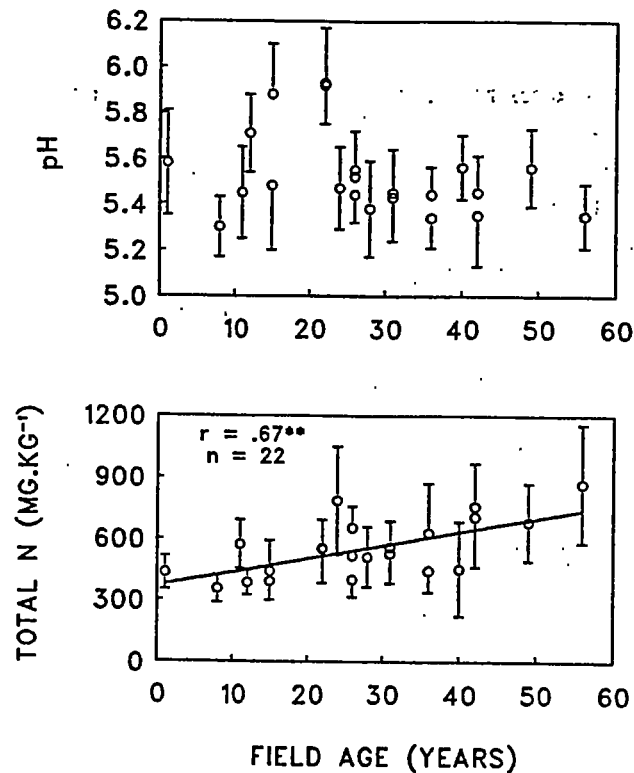
Fig. 3. — Soil pH and soil total N for a chronosequence of 22 old fields sampled in 1983 (see INOUYE *et al.*, 1987 for details). Each data point represents the mean of a variable in each field. Standard errors illustrate the range of variation within each field. Total N is expressed as mg of N per kg of dry soil.

In the old field survey, *Poa* showed no response to pH, occurred over the entire range of variation in pH, and increased in cover at higher levels of total N (fig. 5). Because *Poa* also increased in frequency with successional age (fig. 4), these data cannot determine if this is simply a colonization effect, or a result of a competitive advantage of *Poa* at higher total N levels. *Achillea* only occurred in low pH, low total N classes (fig. 5), which is not a result of its colonization dynamics, since its frequency of occurrence did not depend on field age (fig. 4). *Solidago* occurred at low pH and intermediate total N (fig. 5), which could just reflect its late successional status (fig. 4) and the successional trends in soil N and pH.

DISCUSSION

The experimental manipulation of both soil pH and the rate of nitrogen addition affected the total biomass, species richness and species composition of
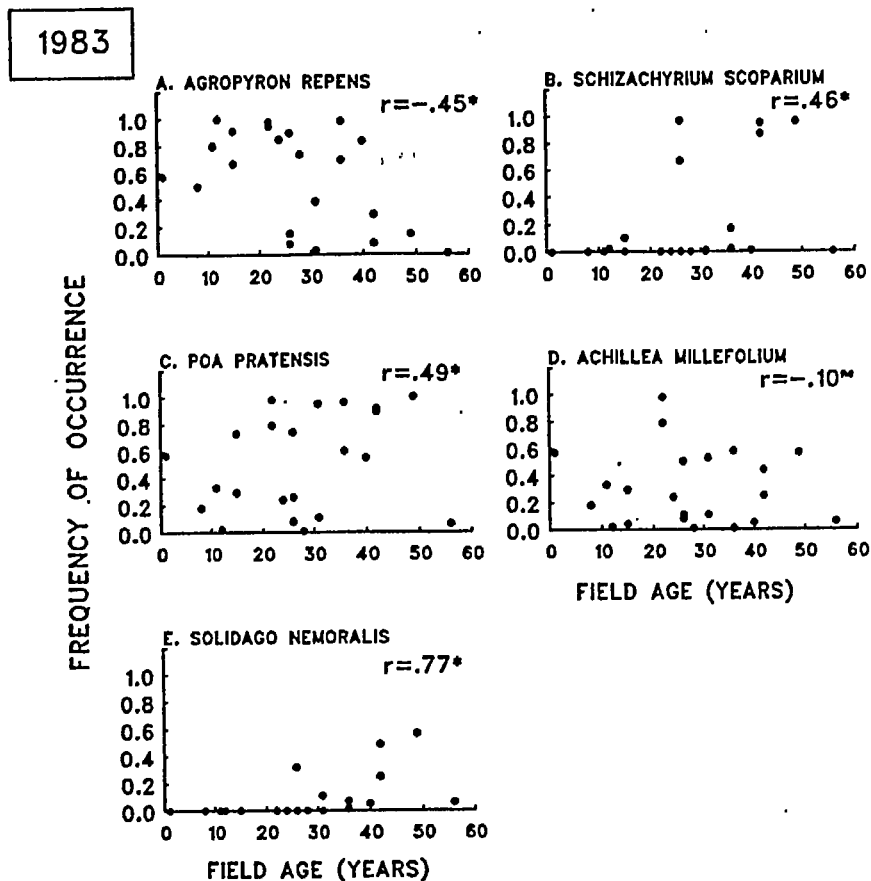
171

Fig. 4. — Frequency of occurrence of five plant species in old fields of different ages, based on the 1983 chronosequence. Frequency was calculated by dividing the number of plots in which a species was present by the total number of plots sampled in a given field. Pearson correlation coefficients (r) are shown for the relationship between frequency of occurrence and field age in the chronosequence.

this old field. Each of the common species responded to the treatments in a different manner. For plots that received no added nitrogen, the results show that the common species are differentiated in their response to soil pH. *Schizachyrium scoparium*, which is a native prairie bunchgrass, dominated the lowest pH plots and decreased in abundance as pH increased. *Poa pratensis* consistently increased in relative abundance from low to high pH for the lowest N level. *Agropyron repens* was quite rare in these plots. *Solidago. nemoralis* seemed to reach its peak abundance at intermediate pH on the unfertilized plots. The species were also differentiated in their response to added N, with *Agropyron* increasing with added N at low pH, *Poa* increasing with added N at high pH, and *Schizachyrium* unaffected by N. A more long-term N addition experiment performed in this and
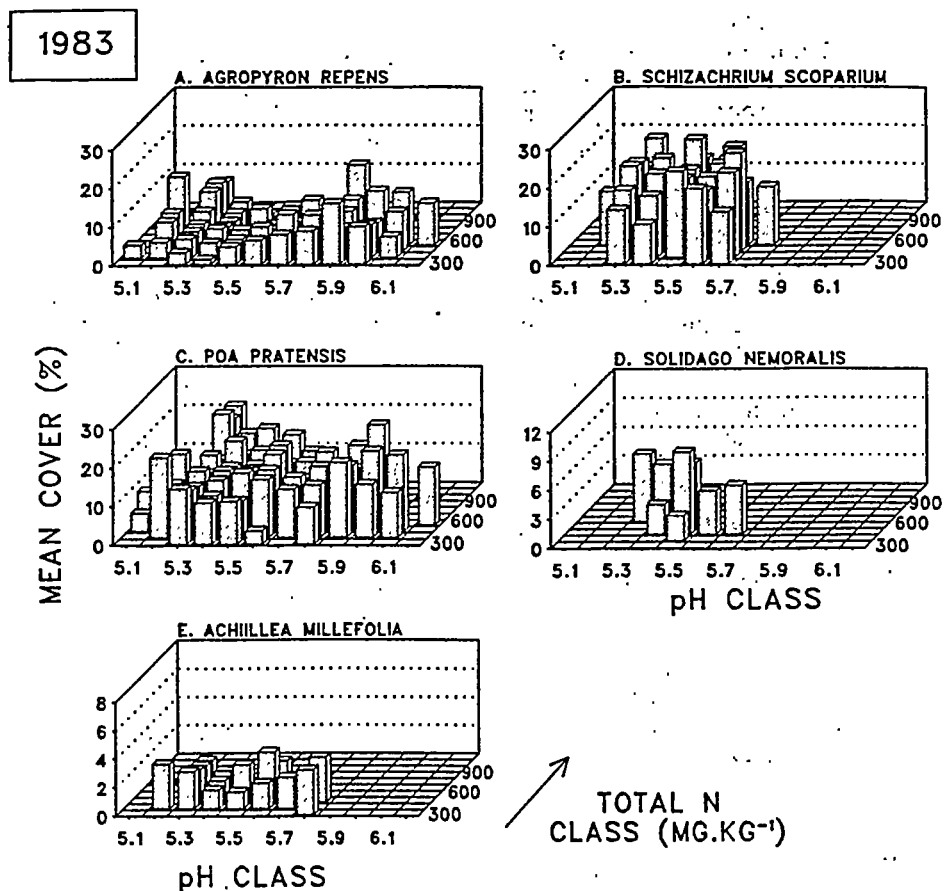
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Fig. 5. — The N and pH dependence of the mean cover of five species in the 1983 survey of a chronosequence of old fields. For this analysis, the 2300 plots sampled in the 22 old fields were assigned to a soil pH and a soil total N class. Average percent cover for a species in each of these classes was calculated using data for all plots in which the species was present. Results are shown only for cases in which there were at least five such plots per class.

other fields at natural (control) pH levels has shown sharp differentiation of these three species, with *Schizachyrium* dominating unfertilized plots, *Poa* dominating plots receiving intermediate rates of N addition, and *Agropyron* dominating plots receiving high rates of N addition (TILMAN, 1990). This suggests that *Agropyron* may begin displacing *Schizachyrium* from the lower pH but high N plots once it colonizes these plots (INOUYE & TILMAN, 1988), and that *Poa* may continue displacing *Schizachyrium* from the intermediate N and higher pH plots. .

Other observational (e. g., INOUYE *et al.*, 1987; GLEESON & TILMAN, 1990) and experimental (TILMAN & COWAN, 1989; TILMAN, 1990; TILMAN & WEDIN 1991*a*, 1991*b*) studies have shown that a major cause of the first 50 years of herbaceous

succession at CCNHA is the tradeoff between the colonization ability of a species versus its competitive ability for nitrogen. The early successional species of CCNHA have high allocation to seed or rhizome and are rapid colonists. However, they allocate less to root, and are poorer N competitors than later successional species. None of these previous studies, though, has considered the possible role of soil pH during succession.

When combined with the results of the old field survey, the results of our experiments can help determine how the successional abundances of the common species are influenced by both differences in colonization/dispersal dynamics and by resource- and pH-dependent interactions. *Agropyron* had greater abundance under conditions of low pH but high total N in the old field survey (fig. 5 A) and in the experiment (fig. 2 A), which suggests that it performs best under these conditions. However, it also had high cover at high pH in the old field survey but not in the experiment. Thus, its high cover at high pH in the old fields may not be caused by pH, but could be a spurious correlation that results from its rapid colonization of early successional fields, some of which have higher pH than do any late successional fields. *Schizachyrium* dominated the low pH levels both in the old field survey and in the experiment, suggesting that this species may have an advantage in this situation. *Poa* increased in cover with total N both in the old field survey and in the experiment, but its increase with pH in the experiment was not observed in the old field survey. This may be because it is a slow colonist (fig. 4), and there are few successional fields that still have high pH by the time it is present. Neither *Achillea* nor *Solidago* had much correspondence between their response in the experiment and in the old field survey. Both are copious seed producers, and may specialize on colonization of disturbed sites independent of their pH (PLATT, 1975; PLATT & WEIS, 1977; WERNER & PLATT, 1976).

The three common grasses in this study have been grown both in monoculture and in various pairwise combinations on an experimental N gradient (WEDIN, 1990; WEDIN & TILMAN, 1990; TILMAN, 1990; TILMAN & WEDIN, 1991 a, 1991 b) at one pH. This work showed that *Schizachyrium*, which has high allocation to roots, low tissue N levels, and low allocation to seed and rhizome, is a superior competitor on low N soils compared to either *Poa* or *Agropyron*. *Poa* and *Agropyron* were stronger competitors than *Schizachyrium* on nitrogen rich soils, on which soils the species may have competed for light. These findings suggest that the differentiation we observed in the relative abundance of these species with respect to the rate of N addition (figs. 1 and 2) n .y be causea ·y interspecific competition. Moreover, the differentiation that we have observed in response to soil pH may mean that the ability of these species to compete for N and light depends on soil pH. If so, the trajectory of soil pH values during succession may influence successional dynamics.

However, the actual mechanisms behind the pH effect on relative abundances is difficult to determine with our data. The response may represent a direct effect of pH on plant growth and survival and thus on tolerance or interspecific competition, or may be caused by various direct and indirect effects of pH on nutrient availability (RORISON *et al.*, 1983; ARMSTRONG, 1982; FITTER, 1986) or on the abundances of various mutualistic or pathogenic soil organisms and microorganisms. The observed dominance of *Schizachyrium* on low pH soils may mean that low pH indirectly induced low nutrient availability. Soil pH can affect the activity

of nitrifying bacteria, and thus change the relative availability of NH_4^+ versus NO_3^- (tables I and II; FOCHT, 1974) and may influence N mineralization rates. Thus, changes in plant species composition along the pH gradient could be partially caused by the plants being differentiated in their abilities to compete for ammonia versus nitrate (e. g., FITTER, 1986). Alternatively, plant species may respond directly to pH, and the change in ammonia and nitrate concentrations along the pH gradient could be caused by the plants. Our experiments cannot differentiate among such alternative hypotheses because, despite our direct and independent manipulations of pH and N addition rates, soil pH and extractable N levels became correlated in our experimental plots.

The effect of the treatments on species richness supports the often reported decrease in species richness associated with nutrient addition and increased productivity (see review in TILMAN, 1982). Species richness tended to be lower on low pH soils, and to be highest on low N soils of intermediate pH (fig. 3). Both effects may be related to soil heterogeneity. The addition of nutrients makes a plot be effectively more homogeneous, since the added nutrients tend to swamp any pre-existing spatial heterogeneity in soil nitrogen. More importantly, large nutrient additions eliminate both nutrient heterogeneity and limitation by nutrients, but should drive all plants in a habitat toward being light limited. The best competitor for light may then displace other species, reducing diversity. Similarly, the adjustment of soil pH may reduce preexisting heterogeneity in soil pH. However, in the lowest pH treatment, plots receiving the highest rate of N addition did not have significantly lower species richness than those receiving no N. An alternative cause of the pH effect on species richness may be that there are fewer species present in this habitat that can tolerate acidic soils, and thus decreased pH necessarily leads to decreased diversity, much as DENSLOW (1980) has suggested for other such experimental manipulations.

Our experiment suggests that old field chronosequences can yield spurious correlations between species abundances and soil pH or soil total N, and that it is necessary to consider the differential colonization abilities of species when interpreting correlational data from a chronosequence. We found that both the supply rate of nitrogen, which is the major limiting nutrient in this habitat (TILMAN, 1987), and soil pH have significant effects on the total biomass, species composition, successional dynamics, and diversity of this vegetation. The major species were differentiated in their responses to N and pH. When combined with the previously reported interspecific tradeoff between N competitive ability and colonization ability (TILMAN, 1990), this suggests that successional dynamics may be determined by tradeoffs along three axes (N competition, pH, and colonization).

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