BIOLOGICAL WEED CONTROL VIA NUTRIENT COMPETITION: POTASSIUM LIMITATION OF DANDELIONS

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Abstract. Weedy plants are often controlled by the application of herbicides. Here we explore an alternative method of control. We suggest that the abundance of an undesired plant species (here dandelions: *Taraxacum officinale*) may be controlled by modifying interspecific competition via changes in resource supply rates. This hypothesis is supported by several lines of evidence. First, analyses of effects of different patterns of fertilization on plant-species abundances in the 140-yr-old Park Grass Experiment at Rothamsted, England, show that *Taraxacum* abundances were highly dependent on potassium fertilization and on liming, but not on addition of other nutrients. Potassium fertilization led to a 17- to 20-fold increase in *Taraxacum* abundances in the classical Park Grass data, and to a 4- to 7-fold increase in the modern data. Liming led to a 2- to 3-fold increase for classical data and to a 3- to 4-fold increase for modern data.

Second, in a greenhouse study in Minnesota, *Taraxacum* had a higher requirement for potassium and had its biomass more limited by potassium than any of five common grass species of Park Grass. This suggests that *Taraxacum* may be a poorer competitor for potassium than these grasses, but this mechanism has not yet been tested. Third, in a series of Minnesota lawns that had not received fertilizer or herbicides, both *Taraxacum* density and abundance were significantly positively correlated with its tissue potassium levels.

This demonstration that desired and weedy plant species can differ in their resource requirements suggests that adjustments in resource supply rates may determine the outcome of interspecific competition, allowing desired species to competitively control weedy species. In particular, for soils with low potassium levels, the use of potassium-free lawn fertilizer is predicted to decrease *Taraxacum* because of competition from grasses like *Festuca rubra.*

Key words: Agrostis tenuis; Alopecurus pratensis; *biological control of pests via competition;* Dactylis glomerata; *dandelions,* Taraxacum officinale; Festuca rubra; *herbicides and fertilizer; interspecific competition, resource-dependent; lawns; Park Grass Experiment, Rothamsted, UK; plant competition; potassium fertilization and dandelion abundance.*

INTRODUCTION

Although most biological control programs have used herbivores, parasites, predators, or pathogens as control agents (e.g., DelFosse 1985, 1990; DeBach and Rosen 1991, McEvoy et al. 1991), interspecific competitors also may exert biological control on a pest species (e.g., Richards 1989, Kuo et al. 1992, McCarty and Murphy 1994, Angonin et al. 1996, Jornsgard et al. 1996, Lemerle et al. 1996). Studies of the mechanisms of interspecific competition for resources (e.g., Tilman 1982, 1990, 1994) suggest several potential, but untested, mechanisms for competitive control of a pest species. First, in an ecosystem in which many species are limited by and compete for the same single resource, all that should be required, in theory, for competitive control of a pest species would be the introduction of a desired species that is a superior com-

petitor for the limiting resource (i.e., a lower "R*" in the terminology of Tilman [1982]) but that has no other compromising traits. Second, it might be that a desired species is a superior competitor to a problem species but is in low abundance or absent from a habitat because of low rates of propagule production or poor dispersal ability (e.g., Horn and MacArthur 1972, Tilman 1994). In this case, control might be achievable by regularly adding propagules of the superior competitor to the habitat. Third, the competitive abilities of species might depend on the amounts and ratios of various limiting resources (e.g., Warren and Johnston 1964, Thurston 1969, Tilman 1980, 1982, Grover 1997) or on physical factors, such as soil pH or temperature. Changes in resource ratios or physical factors could then competitively favor one species over another. The appropriate adjustment of resource supply rates or environmental conditions might allow desired species to suppress undesired ones. This third possibility is addressed in this paper.

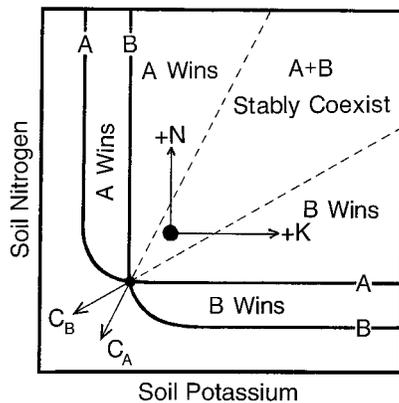The underlying theory of resource competition has

FIG. 1. Diagram illustrating competition for potassium and nitrogen between two plant species, using the graphical approach of Tilman (1982), where additional details can be found. The solid curves labeled ''A'' and ''B'' are resource-dependent zero net-growth isoclines for Species A and B. These show the soil solution concentrations of nitrate and potassium at which the growth of a species exactly balances all sources of loss and mortality to that species. C_A and C_B are vectors that show the amounts of N and K consumed by Species A and B. These define the regions in which one or the other species is the competitive winner, or in which the species stably coexist. Note that Species B is similar to *Taraxacum officinale* and dominates habitats with relatively high K but low N, whereas Species A is similar to *Festuca rubra* and dominates habitats with relatively low K but high N.

been developed elsewhere (e.g., Tilman 1980, 1982), and will only be briefly summarized here. Its predictions can be illustrated by a hypothetical case in which a desired plant species (Species A) is an inferior competitor for soil nitrogen but a superior competitor for soil potassium, and an undesired competing species (Species B) has the reverse traits (Fig. 1). The undesired species would competitively dominate habitats with low soil N:K ratios and the desired species would dominate those with high soil N:K ratios. They would coexist at intermediate ratios (Fig. 1). The relative abundances of the species would depend on the N:K resource ratios supplied by the soil. Starting from a habitat in which N and K levels allowed both species to coexist (the large dot in Fig. 1), fertilization with sufficient N (represented by the arrow labeled ''+N'') would allow the desired species, Species A, to competitively displace Species B. This occurs because N addition would cause both species to be limited by K, and Species A is the superior competitor for K. Note that the habitat created by the addition of N is one in which Species B can survive at high density in the absence of Species A. Species B is not directly impacted by the addition of N, but is driven to local extinction by competition with species A. The addition of N increases the abundance of Species A, increasing its consumption of K, driving K levels below that required for the survival of Species B. Similarly, addition of sufficient K would competitively favor Species B over Species A. Thus, if species differ in their require-

ments for two limiting nutrients, changes in nutrient availability can modify the outcome of interspecific competition.

Numerous fertilization experiments in both natural vegetation and in agricultural fields have shown that the relative abundances of plant species are highly dependent on the ratios of supply of limiting soil resources (e.g., Milton 1947, Willis 1963, Thurston 1969, Tilman 1982, 1987, Bakker 1989). This supports the hypothesis that selective fertilization might allow competitive control of some undesired species (e.g., Kuo et al. 1992, Angonin et al. 1996, Jornsgard et al. 1996), which we explore for control of dandelion in grasslands and lawns. We also discuss more general effects of selective fertilization on the relative abundances of grasses and forbs.

Dandelion (*Taraxacum officinale*) is a common lawn weed often controlled via herbicides (e.g., McCarty and Murphy 1994). One trait that makes it an abundant weed is its ability to rapidly colonize disturbed sites (Solbrig and Simpson 1974), which results from copious production of well-dispersed seeds. However, *Taraxacum* also may compete with other plant species for soil nutrients, water, and/or light. In this paper we show that the long-term fertilization experiments in the Park Grass Experiment of Rothamsted, England, suggest that competition for soil potassium (K) may be a critical additional factor determining *Taraxacum* abundances. We then test this hypothesis via greenhouse studies, performed at the University of Minnesota, of the K requirements of *Taraxacum* and five grass species common at Rothamsted, and via a survey of *Taraxacum* abundances on residential lawns in Minnesota.

METHODS

Park Grass experiment

We analyzed the classical data from the Park Grass fertilization experiment on permanent grassland, as reported by Lawes and Gilbert (1863, 1880), Warren and Johnston (1964), Thurston (1969), and Williams (1978). We also analyzed as-yet-unpublished data gathered in 1991, 1992, and 1993 by M. J. Crawley and co-workers. The Park Grass experiment was established in 1856 at what is now the Rothamsted Experiment Station, Harpenden, Hertfordshire, England. Plots were laid out on a 4-ha area of grassland that had been grazed and mown for hay for several hundred years prior to its establishment. The vegetation in each plot continued to be mown, removed, and weighed twice each year (in June and late autumn) after establishment of the experiment, but the plots were not grazed, except briefly before 1875. Grasslands in this region revert to closed-canopy forest if they are not grazed or mown.

Originally 20 plots, ranging in size from 0.05 to 0.2 ha (see Tilman et al. 1994: Fig. 1) received either no nutrient additions, or various amounts and combina-

tions of inorganic N, P, K, and Na plus Mg, or farmyard manure. In 1903 plots were split, with half of each plot limed (2.24×10^3 kg CaO/ha every fourth year) and half unlimed. In 1965 each of these was split again to create four liming-treatment subplots, with three of these limed with the goal of having pH levels of ~5, 6, or 7. The fourth was unlimed. Because of this change in the liming treatment, the 1914–1976 data (for subplots receiving the classical liming treatment) and the 1991–1993 data (for the modern liming treatments) were analyzed separately. A few of the original treatments have been changed through the years (Warren and Johnston 1964), or plots subdivided into smaller plots for other studies, and are not analyzed here.

Nitrogen is applied either as ammonium sulphate or as sodium nitrate. Ammonium sulphate is added to supply either 0, 48 (called ''N1'' below), 96 (''N2''), or 144 (''N3'') kg N·ha^{-1}·yr^{-1} and sodium nitrate to supply 0, 48 (''N*1''), or 96 (''N*2'') kg N·ha^{-1}·yr^{-1}. Potassium is supplied as potassium sulphate to give either 0 or 225 (''K'') kg K·ha^{-1}·yr^{-1}. Phosphorus is added as superphosphate to give 0 or 35 (''P'') kg P·ha^{-1}·yr^{-1}. Sodium and magnesium are added together as their sulphates to give either 0 or 15 (''Na'') and 10 (''Mg'') kg·ha^{-1}·yr^{-1} of each element.

Vegetation in each subplot has been sampled periodically since 1856. Samples were sorted to species, dried, and weighed. The 1914 sample was the first taken after the liming treatment was imposed in 1903. Using the summary data tables in Williams (1978) for the period from 1914 to 1976, we calculated the average relative abundance of *Taraxacum officinale* for each plot during the period. We used these averages in our analyses. For 1965 to 1976, we only used data from the two portions of each plot that still received the classical liming treatment. We similarly used the average of data gathered in 1991, 1992, and 1993 for *Taraxacum,* but with the expanded liming levels. Thus, data were split into two categories: ''classical'' data gathered before 1976, and ''modern'' data acquired from 1991 to 1993.

For the classical data, the unlimed and limed subplots of Plots 1 (N1); 2 (control), 3 (control); 4/1 (P), 4/2 (N2 and P), 7 (P, K, Na, and Mg); 8 (P, Na, and Mg), 9 (N2, P, K, Na, and Mg); 10 (N2, P, Na, and Mg), 11/1 (N3, P, K, Na, and Mg), 11/2 (N3, P, K, Na, Mg, and Si); 12 (control); 14 (N2*, P, K, Na, and Mg), 16 (N1*, P, K, Na, and Mg); 17 (N1*); and 18 (N2, K, Na, and Mg) were used, for a total of 32 subplots. For the modern data, all four liming treatments within Plots 1, 2, 3, 4/1, 4/2, 7, 8, 9, 10, 11/1, 11/2, 12, 14, 15, 16, 17, and 18 were used, for a total of 68 subplots. Plot 15 was not included in the classical data because it was fertilized with NaNO, at the high rate from 1858 to 1875, at which time it was switched to and has remained as P K Na Mg. Smaller subsets of these treatments were used in more focused analyses. We did not distinguish between the form of N added (NH$_4$SO$_4$ or NaNO$_3$), but did distinguish among rates of N addition.

Because the Rothamsted experiment was established before modern statistics, it has little replication, and not all possible combinations of factors were tested. Despite this, we believe that this uniquely long-term study may generate valuable hypotheses. To do so, we mainly focus on treatment means, but we have used the tools of modern statistics, especially ANOVA and contrasts of means, as one way to test for the plausibility that resultant patterns might be attributable to treatments. We place little faith on the level of statistical significance attached to any given analysis, but rather look for consistencies among the classical and modern data and for consistencies when data are grouped and analyzed in different ways. The hypotheses we generated from analyses of the Park Grass data were then tested in a greenhouse experiment and in observations in Minnesota lawns.

Two different methods of data classification were used for generating mean plant abundances in response to treatments, and for ANOVAs. For the first, all plots were classified as receiving or not receiving K, as receiving or not receiving lime, as receiving or not receiving nitrogen, and as receiving or not receiving phosphorus. However, the experiment did not include many of the possible combinations of these four factors, and this imbalance was ignored. For the second method, plots were grouped into those receiving no K but some other combination of N and P (''X''), and those receiving K and that same combination (''X + K''). This held N and P constant to better determine the effect of K. In particular, it compared treatments that received P with those that received P and K, those receiving N with those receiving N and K, and those receiving P and N with those receiving P, N, and K, with 6 treatments being in the group that received K and 6 in the matched group that received no K. Plots receiving the N3 level of nitrogen were excluded because none lacked K, but N1 and N2 were treated interchangeably, and Na and Mg were ignored. Because each plot had sections with and without lime (classical data) or at one of four levels of liming (modern data), lime was also a variable in these exploratory analyses.

Greenhouse experiment

To test the effects of K on plant growth and tissue chemistry, we grew *Taraxacum officinale* and five common Park Grass grasses (*Agrostis tenuis, Alopecurus pratensis, Dactylis glomerata, Festuca rubra,* and *Poa pratensis*) from seed in a greenhouse receiving supplemental light from sodium vapor lamps. Each 10 × 10 × 13 cm pot was filled with a commercial sterilized low-nutrient soil mixture, seeded to have about 200 seedlings per pot, watered daily, and allowed to grow for 2 wk before nutrient treatments were begun. Nutrient treatments consisted of a weekly addition to each pot of either (a) 50 mL of deionized water (the control,

called the "H₂O" treatment), or (b) 50 mL of a nutritionally complete mineral solution (0.0006 mol NH_4NO_3/L, 0.0003 mol NH_4HPO_4/L, 0.0008 mol $Ca(NO_3)_2/L$, 0.0002 mol $MgSO_4/L$, 0.0005 mol $KHCO_3/L$, and Fe-EDTA chelated trace metals; called the "complete mineral solution" treatment) or (c) 50 mL of this same solution but without K (called the "no-K solution" treatment). There were 10 replicate pots for each species at each nutrient treatment, for a total of 180 pots. Pot position was randomized. After 9 wk of growth, aboveground biomass was clipped, dried, and weighed. It was then ground and analyzed for K, Ca, Mg, and P using inductively coupled plasma spectroscopy (ICP) and for N using a Carlo-Erba C-N analyzer. ANOVA determined the effect of species and nutrient treatment on biomass and on tissue chemical composition.

Lawn studies

In August 1996 we sampled 19 lawns in Hennepin, Isanti, Anoka, and Crow Wing counties of central and north-central Minnesota to determine the relationship between *Taraxacum* abundance and *Taraxacum* tissue K concentration. We sampled all lawns that we could find that were certified by their owners as free of herbicides, fertilizer, and hand weeding of *Taraxacum* for at least the past 7 yr. Each lawn was divided into three approximately equal areas. For each area, the sampling site was "randomly" chosen by tossing a ball about 3 to 8 m behind the investigator, and placing a 1 × 1 m grid centered on the ball. All *Taraxacum* individuals were counted within the grid to give plant density (number/m²). Cardboard cutouts of various areas were used as a guide to visually estimate the percentage of each grid covered by *Taraxacum* leaves (percentage cover). *Taraxacum* leaves in each plot were then harvested, dried, ground, ashed, and analyzed for K, Ca, Mg, and P content via inductively coupled plasma spectroscopy.

RESULTS

Park Grass

Using either the classical data or the modern data, comparisons of average *Taraxacum* relative abundances for plots classified as receiving either K or no K, N or no N, P or no P, and lime or no lime showed that the largest differences occur for K (Fig. 2), with K leading to a 20-fold increase in *Taraxacum* abundance in the classical data and a 4-fold increase in the modern data. Lime led to a 3-fold increase in *Taraxacum* in the classical data and to a 4-fold increase in the modern data. ANOVAs and contrasts supported these observations. The overall ANOVAs had $F_{6,24} = 7.10$, $P = 0.0002$ (classical) and $F_{8,48} = 4.87$, $P = 0.0002$ (modern). Analysis of treatment effects showed that the K treatment had the highest F and lowest P values (classical: $F_{1,24} = 25.6$, $P < 0.0001$; modern:
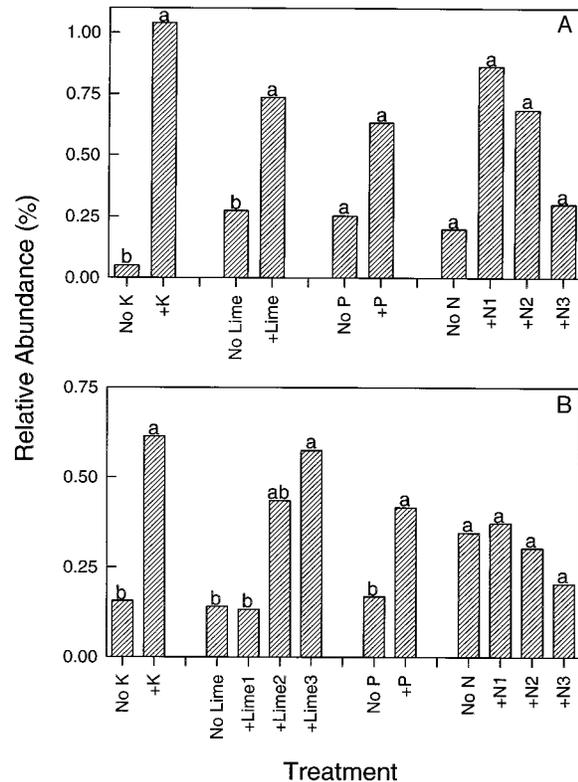

FIG. 2. Mean relative abundance (percentage of total living plant biomass) of *Taraxacum* in the Park Grass Experiment (UK) in response to various nutrient treatments, with (A) being the classical (1914–1976) data and (B) being the modern (1991–1993) data. The contrasts shown compare all plots that received a given nutrient with all those that did not receive it, but they do not control for other nutrients that a plot may or may not have received. Within a given grouping, means that share the same lowercase letter do not differ "significantly" ($P > 0.05$) based on Duncan's multiple-range test, but this must be cautiously interpreted given the lack of replication and the incompleteness of the design of the Park Grass Experiment.

$F_{1,48} = 16.7$, $P = 0.0002$). The other treatments either had high P values ($P > 0.05$ for the classical phosphorus treatment and for the modern nitrogen treatment), or were weak ($0.05 > P > 0.04$ for classical nitrogen and lime treatments and for modern phosphorus treatment), except that the classical lime treatment was stronger ($P = 0.009$). Contrasts using Duncan's multiple-range test (see Fig. 2) supported there being K and lime effects for the classical data, and supported there being K, lime, and P effects for the modern data. Thus, both visual examination of the data and statistical analyses suggest consistent effects of K and lime on *Taraxacum* abundances, but no consistent effects of other treatments.

Our second analyses classified the data so as to determine the effect of K or lime addition on *Taraxacum* abundance when other nutrients were held constant. The analyses compared matched sets of plots that received a particular combination of N and P ("X") but
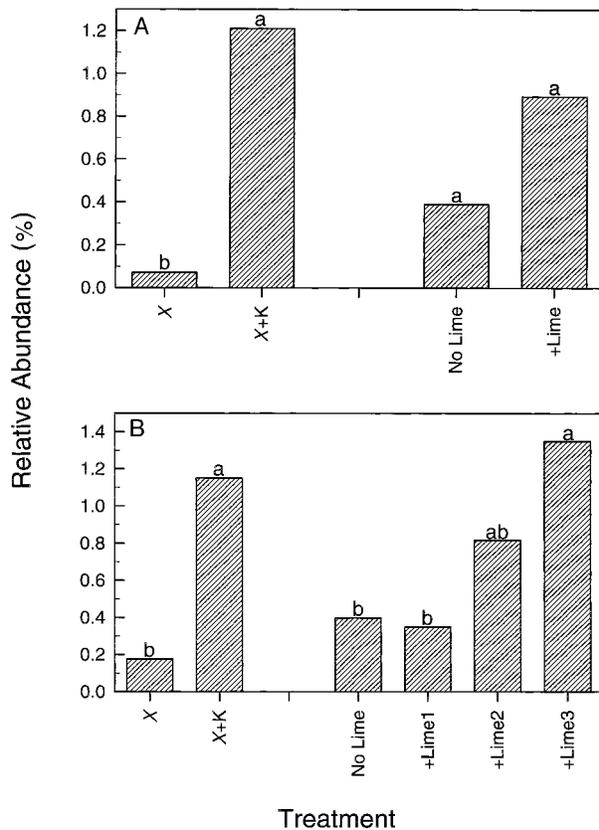
FIG. 3. Mean relative abundance of *Taraxacum* in Park Grass when comparing matched sets of plots that all received the same background set of nutrients (''*X*'') but either did or did not receive K or lime. (A) Classical data and (B) modern data. Statistical tests are as in Fig. 2.

no K with those that received that same combination but with K (''*X* + K''). Comparing means for the classical data, the addition of K gave a 17-fold increase in *Taraxacum* relative abundance and the addition of lime a 2.3-fold increase (Fig. 3). The modern data were similarly grouped, with K leading to a 6.6-fold increase in *Taraxacum* relative abundance and lime to a 3.4-fold increase. Both ANOVAs supported these trends (for overall effects of treatments in the classical data: $F_{3,20} = 8.19$, $P = 0.0009$; for modern data: $F_{7,49} = 4.98$, $P = 0.0003$), with the effects attributable to K having $P < 0.001$ in both cases, but with effects attributable to lime being much less certain (classical: $P = 0.07$; modern: $P = 0.01$). Neither ANOVA suggested the existence of a K × lime interaction.

Greenhouse

For the greenhouse experiment, ANOVA determined the effects of nutrient treatment (complete mineral solution, no K, control) and species on aboveground plant tissue K. The overall ANOVA was highly significant ($F = 201.6$, $P = 0.0001$). Species ($F = 200.83$, $P = 0.0001$), treatment ($F = 1149.08$, $P = 0.0001$), and the species × treatment interaction ($F = 12.56$, $P =$

0.0001) were also significant. *Taraxacum* aboveground tissue had a significantly higher K content in the no-K treatment, the complete mineral treatment, and the water treatment than any of the other species (Fig. 4A). *Poa pratensis* had the next highest K content for all three treatments, whereas *Festuca rubra* and *Agrostis tenuis* had the lowest tissue K contents.

ANOVA revealed highly significant effects of species ($F = 132.4$, $P < 0.0001$) and nutrient treatment ($F = 299.01$, $P < 0.0001$) on total plant biomass per pot, and a highly significant interaction ($F = 4.29$, $P < 0.0001$). Of the six species grown in the greenhouse, only *Taraxacum, Festuca,* and *Dactylis* had significantly less biomass in the no-K treatment compared to the complete mineral treatment. Their biomasses in the no-K treatment were reduced to 81%, 84%, and 92%, respectively, of their biomasses in the complete mineral
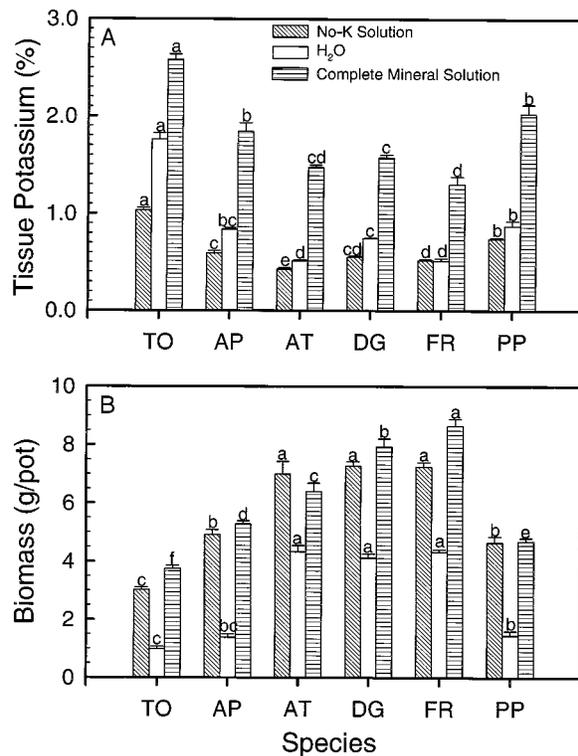

FIG. 4. Results of the greenhouse growth study for *Taraxacum officinale* (TO), *Alopecurus pratensis* (AP), *Agrostis tenuis* (AT), *Dactylis glomerata* (DG), *Festuca rubra* (FR), and *Poa pratensis* (PP). Contrasts, based on Duncan's multiple-range test, were performed to compare the responses of the six species to a given nutrient treatment; separate contrasts were performed for each of the three nutrient treatments. For a given nutrient treatment, species that share the same lower-case letter do not differ significantly in their mean responses, whereas those that do not share a letter do differ significantly ($P < 0.05$). Note that contrasts that compare the response of a given species to the three nutrient treatments are not shown. (A) Effects of greenhouse nutrient-addition treatments on aboveground plant tissue K. (B) Effects of nutrient-addition treatments on mean aboveground living biomass at time of harvest.
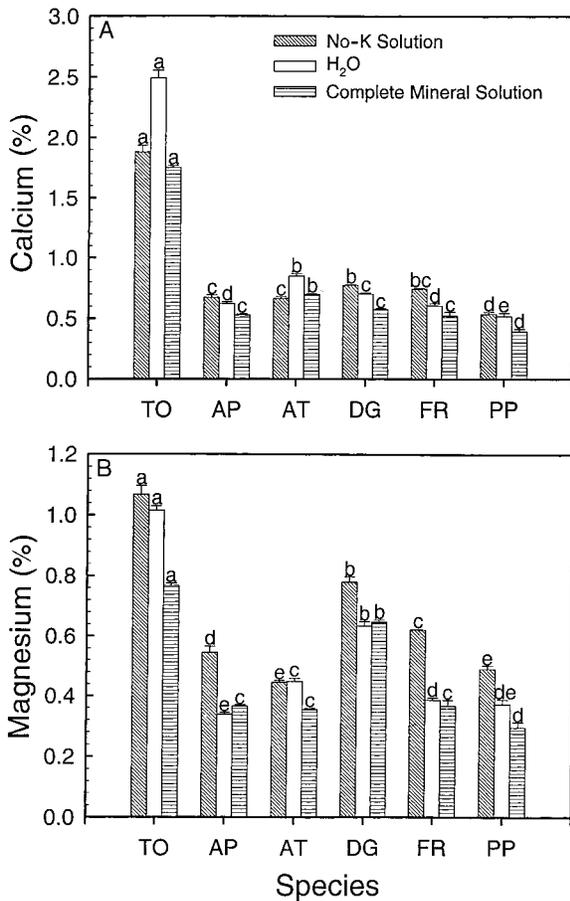
FIG. 5. Further results of the greenhouse study shown as in Fig. 4, except for effects of treatments on aboveground plant tissue calcium (A) and magnesium (B). Contrasts are as in Fig. 4.
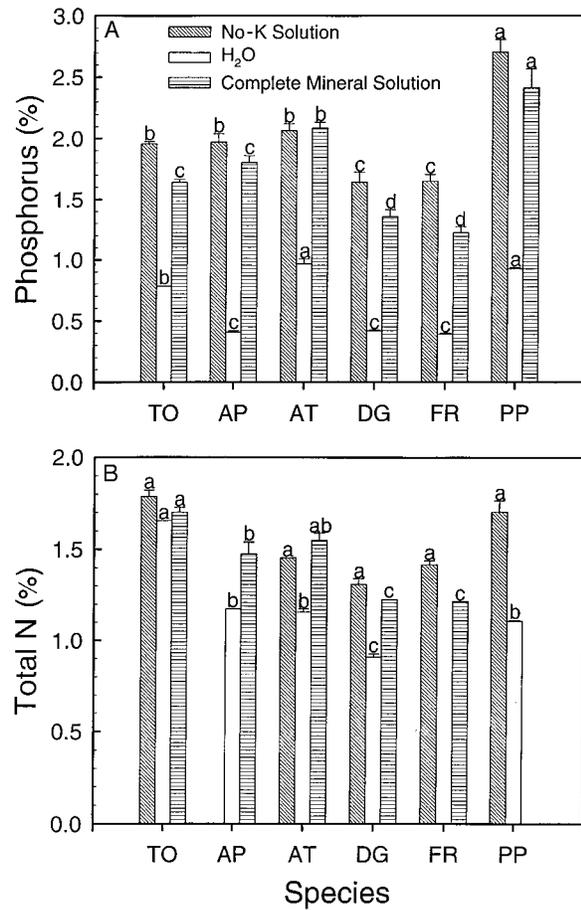
FIG. 6. Further results of the greenhouse study shown as in Fig. 4, except for effects of treatments on aboveground plant tissue phosphorus (A) and nitrogen (B). There was insufficient *Taraxacum* tissue to measure N for some cases.

treatment (Fig. 4B). For both the no-K and the complete mineral treatments, *Taraxacum* had significantly lower biomass than all other species, and *Agrostis tenuis, Dactylis glomerata,* and *Festuca rubra* had the greatest biomasses.

The effects of treatment and species on plant calcium, magnesium, phosphorus, and nitrogen content were each analyzed separately by ANOVA. The overall ANOVA was highly significant ($P < 0.001$) for each. The effects of species and treatment were also significant for each element. *Taraxacum* had markedly higher calcium content, for all three nutrient treatments, than the other species (Fig. 5A). It also had higher magnesium content than the other species (Fig. 5B). However, there were no such clear differences between *Taraxacum* and the other species for either tissue phosphorus or tissue nitrogen (Fig. 6). *Taraxacum* tissue phosphorus was in the mid-range of the values for the six species.

Minnesota lawns

Using the average values for each of the 19 lawns, *Taraxacum* percentage cover was significantly posi-

tively correlated with *Taraxacum* tissue K concentration (Pearson $r = 0.53$, $P = 0.02$, $N = 19$; Fig. 7A). Similarly, *Taraxacum* density (plants/m²) was significantly correlated with tissue K ($r = 0.51$, $P = 0.03$, $N = 19$; Fig. 7B). However, simple correlations between *Taraxacum* cover and either tissue Ca, or tissue Mg, or tissue P were never significant ($P > 0.05$ in all cases). Similarly, simple correlations between *Taraxacum* density and either tissue Ca or tissue Mg were not significant ($P > 0.05$), but *Taraxacum* density was correlated with tissue P ($r = 0.54$, $P = 0.02$, $N = 19$).

DISCUSSION

Each spring the Rothamsted plots present an interesting visual mosaic. Some plots are yellow with dandelion blooms, but are bordered by plots where dandelions are almost absent despite the heavy dandelion seed-rain they receive annually. Our analyses suggest that a critical difference between these plots was the addition of potassium. The low densities of *Taraxacum* in plots that received no K, despite annual inputs of *Taraxacum* seed, and their high densities in plots that
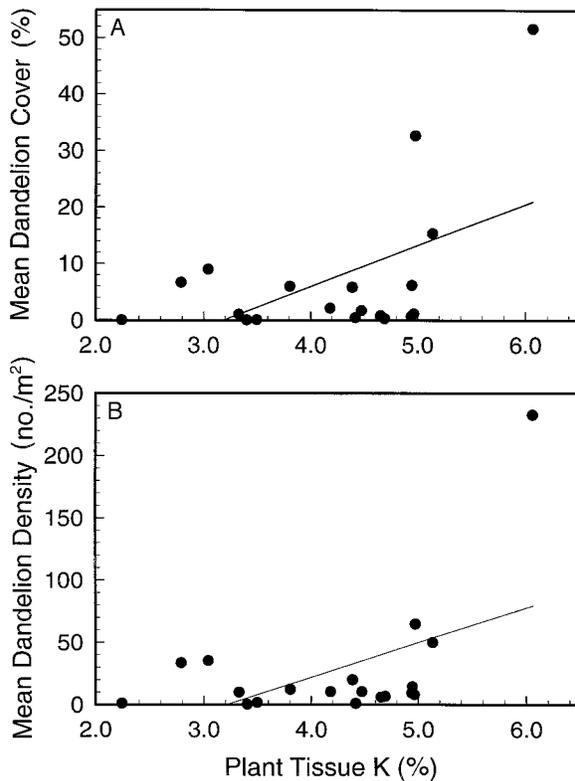
FIG. 7. Results of a dandelion survey of 19 Minnesota (USA) lawns that had not been fertilized or treated with herbicides for at least the past 7 yr. (A) Mean dandelion cover, visually estimated, vs. dandelion tissue K. The correlation is significant at $P < 0.05$. (B) Mean dandelion density vs. dandelion tissue K. The correlation is significant at $P < 0.05$.

received K, suggest that *Taraxacum* may be a poor competitor for K compared to other Park Grass plant species. If this were so, on low-K soils *Taraxacum* would be held at low densities by species that are superior K competitors and that, presumably, reduce soil solution concentrations of K to a level at which dandelions do not grow well. Addition of K should free *Taraxacum* from the constraint of competing for K by making some resource other than K limiting to both dandelions and their competitors. *Taraxacum* increased in abundance when K was added, as would be expected if it was a poor K competitor. Thus, *Taraxacum* behaved much as does Species B of Fig. 1. *Festuca rubra* behaved like Species A.

The hypothesis that *Taraxacum* can be held in check on low-K soils because it is a poor competitor for K compared to at least some grass species requires that a resource other than K also be limiting in Park Grass. Analyses of changes in total plot biomass and in the abundances of individual grass species show that N, P, or K are all limiting to the common grass species at Park Grass, and light may also limit some species (Tilman 1982, Tilman et al. 1994). When there are multiple limiting resources, addition of one resource changes

the ratio of that resource relative to others. Such changes in resource ratios are expected to cause changes in the relative abundances of competitors (Fig. 1; Tilman 1982). The responses of *Taraxacum* to K and N addition are consistent with the hypothesis that *Taraxacum* is an inferior K competitor but a superior N competitor compared to several grass species (see Fig. 1). Alternatively, *Taraxacum* may be an inferior competitor for K (and perhaps Ca and Mg), but a superior competitor for open sites (see Horn and MacArthur 1972, Tilman 1994) compared to several common grass species. This would be consistent with its high allocation to seed, the high dispersal ability of its seed, and other weedy traits (Solbrig and Simpson 1974). In total, the difference between the response of *Taraxacum* to K addition and the responses of other species suggests the existence of an interspecific trade-off in which *Taraxacum* is a poor competitor for K, but a superior competitor for another limiting factor.

Plant species that have higher tissue concentrations of a limiting nutrient often have higher requirements (i.e., R* values [Tilman 1982]) for that resource and can be inferior competitors for it (e.g., Tilman and Wedin 1991*a, b*, Wedin and Tilman 1993). Of the six species grown, *Taraxacum* had the highest requirement for K, as measured by tissue K concentrations, in all three greenhouse treatments. Its production of biomass was significantly inhibited by the no-K treatment compared to the complete mineral treatment, whereas only two of the five grass species were so inhibited by no K. These traits are consistent with *Taraxacum* being a poor competitor for K compared to most of the grasses that are dominant at Rothamsted, but competition experiments will be required to test this hypothesis. Our observations on Minnesota lawns also support the role of K in regulating *Taraxacum* abundance. *Taraxacum* had significantly greater plant density and cover in lawns in which it had higher tissue concentrations of K. *Taraxacum* also had the highest requirements (nutrient content in aboveground biomass) for calcium and magnesium, and may be a poor competitor for these as well. The effect of liming on *Taraxacum* abundance in Park Grass may have been to overcome Ca limitation, but liming may also have increased K availability. Further work is needed to test among these possibilities.

These results lend credence to the hypothesis that the density of a weedy species can be controlled via adjustments to the ratios of supply of limiting resources. Such control would require, at a minimum, that a weedy species be an inferior competitor for a limiting resource compared to a desired species and that the ratios of limiting resources could be adjusted to cause both the weedy species and the desired species to be limited by that resource. Such adjustments might be best achieved by not adding the resource for which the weedy species is an inferior competitor but by adding one or more other limiting resources. Interestingly, fertilization with just NH_4SO_4 at Park Grass (Plot 1,

unlimed) led to an amazingly lawn-like vegetation that was 62% *Agrostis tenuis* (bent grass), 29% *Festuca rubra* (red fescue), 5% other perennial grasses, and that had no *Taraxacum* and only 4% of biomass from other forbs (based on 1939–1973 averages calculated from Williams 1978). Similarly, Zahnley and Duley (1934) found that fertilization of lawns with NH_4SO_4 favored lawngrasses and caused marked reductions in *Taraxacum.* This further supports the hypothesis that fertilization with nutrients other than K (and, perhaps Ca) suppresses *Taraxacum.* Soil acidification caused by ammonium sulfate fertilization (e.g., Tilman 1982, Tilman et al. 1994) may also have played a role in this dominance by grasses.

Similarly, the three Park Grass control (unfertilized) plots contained 47% grass biomass (and thus 53% of biomass from legumes and other forbs), whereas the 10 plots that received nitrogen had 93.7% grass biomass, based on the most recent year reported by Williams (1978). Thus, at Park Grass N addition favored grasses over forbs, in general, with grass species diversity and the identity of the dominant grass species depending on soil pH (Tilman 1982) and on the other nutrients added. This suggests that these pasture and lawn grasses are poorer N competitors than pasture forbs but are better competitors than forbs for other resources, such as K, Ca, open sites, and/or light, that become more limiting when N is added. In contrast, the bunchgrasses of North American tallgrass prairie are strong competitors for N (Tilman and Wedin 1991*b*, Wedin and Tilman 1993), and lose to European forbs and European pasture grasses when N is added (Tilman 1987, 1996, Wedin and Tilman 1996).

High *Taraxacum* densities are a major reason why herbicides such as 2,4-D are applied to many lawns. Such lawns are also often fertilized with a mixture of N, P, and K. Our work suggests that removal of K from lawn fertilizer should decrease *Taraxacum* densities, all else being equal. However, for grazed pastures, K may be needed to meet nutrition requirements of livestock. Because some grass species used in lawns may have relatively high requirements for K, competitive control of dandelions in lawns would require that alternative lawn grasses, which have low K requirements, be used. In our study, *Agrostis tenuis* (bent grass) and *Festuca rubra* (red fescue) had the lowest tissue K concentration when grown on low K soils, suggesting that they may be the better K competitors of these five grass species. This, though, has not been tested experimentally. *Poa pratensis* (Kentucky bluegrass), which is a common grass used for many north temperate lawns, had the highest tissue K concentration of the five grass species, and was exceeded only by *Taraxacum.* Thus, *Poa pratensis* may provide poor competitive control of *Taraxacum* via competition for potassium.

Experimental studies on lawns are an essential next step in testing this hypothesis, as are controlled studies of K (and perhaps Ca) competitive abilities of these and other lawn species. Other Rothamsted plots in which wheat has been grown continuously since 1843 have shown that the composition of the agricultural weed community depends on the availability of soil nutrients. This suggests that there may be additional opportunities for competitive control of particular weedy species by appropriate control of nutrient ratios.

LITERATURE CITED

Angonin, C., J.-P. Caussanel, and J.-M. Meynard. 1996. Competition between winter wheat and *Veronica hederifolia*: influence of weed density and the amount and timing of nitrogen application. Weed Research **36**:175–187.

Bakker, J. P. 1989. *Nature management by grazing and cutting.* Kluwer Academic Publishers, Dordrecht, The Netherlands.

DeBach, P., and D. Rosen. 1991. *Biological control by natural enemies.* Cambridge University Press, Cambridge, UK.

Delfosse, E. S. 1985. Proceedings of the VI International Symposium on Biological Control of Weeds. University of British Columbia, Vancouver, British Columbia, Canada, 19–25 August 1984. Agriculture Canada, Ottawa, Ontario, Canada.

———. 1990. Proceedings of the VII International Symposium on Biological Control of Weeds. Rome, Italy, 1988. CSIRO Publications, East Melbourne, Victoria, Australia.

Grover, J. P. 1997. Resource competition. Chapman & Hall, London, UK.

Horn, H. S., and R. H. MacArthur. 1972. Competition among fugitive species in a harlequin environment. Ecology **53**: 749–752.

Jornsgard, B., K. Rasmussen, J. Hill, and L. J. Christiansen. 1996. Influence of nitrogen on competition between cereals and their natural weed populations. Weed Research **36**:461–470.

Kuo, S., S. E. Brauen, and E. J. Jellum. 1992. Phosphorus availability in some acid soils influences bentgrass and annual bluegrass growth. HortScience **27**:370.

Lawes, J. B., and J. H. Gilbert. 1863. The effect of different manures on the mixed herbage of grassland. Journal of the Royal Agricultural Society of England **24**(Part I):1–36.

Lawes, J., and J. Gilbert, 1880. Agricultural, botanical and chemical results of experiments on the mixed herbage of permanent meadow, conducted for many years in succession on the same land. I. Philosophical Transactions of the Royal Society **171**:289–416.

Lemerle, D., B. Verbeck, R. D. Cousens, and N. E. Coombes. 1996. The potential for selecting wheat varieties strongly competitive against weeds. Weed Research **36**:505–514.

McCarty, L. B., and T. R. Murphy. 1994. Control of turfgrass weeds. Pages 209–248 *in* A. J. Turgeon, D. M. Kral, and M. K. Viney, editors. Turf weeds and their control. American Society of Agronomy, and Crop Science Society of America, Madison, Wisconsin, USA.

McEvoy, P., C. Cox, and E. Coombs. 1991. Successful biological control of ragwort, *Senecio jacobaea,* by introduced insects in Oregon. Ecological Applications **1**:430–442.

Milton, W. 1947. The yield, botanical and chemical composition of natural hill herbage under manuring, controlled grazing and hay conditions. I. Yield and botanical section. Journal of Ecology **35**:65–89.

Richards, M. C. 1989. Crop competitiveness as an aid to weed control. Proceedings 1989 Brighton Crop Protection Conference—Weeds. **2**:573–578.

Solbrig, O. T., and B. B. Simpson. 1974. Components of regulation of a population of dandelions in Michigan. Journal of Ecology **62**:473–486.

Thurston, J. 1969. The effect of liming and fertilizers on the botanical composition of permanent grassland, and on the yield of hay. Pages 3–10 *in* I. Rorison, editor. Ecological aspects of the mineral nutrition of plants. Blackwell Scientific, Oxford, UK.

Tilman, D. 1980. Resources: a graphical–mechanistic approach to competition and predation. American Naturalist **116**:362–393.

———. 1982. Resource competition and community structure. Monographs in population biology. Princeton University Press, Princeton, New Jersey, USA.

———. 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. Ecological Monographs **57**:189–214.

———. 1990. Mechanisms of plant competition for nutrients: the elements of a predictive theory of competition. Pages 117–141 *in* J. Grace and D. Tilman, editors. Perspectives on plant competition. Academic Press, New York, New York, USA.

———. 1994. Competition and biodiversity in spatially structured habitats. Ecology **75**:2–16.

———. 1996. Biodiversity: population versus ecosystem stability. Ecology **77**:350–363.

Tilman, D., M. E. Dodd, J. Silvertown, P. R. Poulton, A. E. Johnston, and M. J. Crawley. 1994. The Park Grass Experiment: insights from the most long-term ecological study. Pages 287–303 *in* R. A. Leigh and A. E. Johnston, editors. Long-term experiments in agricultural and ecological sciences. CAB International, Wallingford, Oxfordshire, UK.

Tilman, D., and D. Wedin. 1991*a*. Plant traits and resource reduction for five grasses growing on a nitrogen gradient. Ecology **72**:685–700.

Tilman, D., and D. Wedin. 1991*b*. Dynamics of nitrogen competition between successional grasses. Ecology **72**: 1038–1049.

Warren, R. G., and A. E. Johnston. 1964. The Park Grass Experiment. Pages 240–262 *in* Rothamsted Experimental Station, Report for 1963. Rothamsted Experimental Station, Harpenden, Hertfordshire, UK.

Wedin, D., and D. Tilman. 1993. Competition among grasses along a nitrogen gradient: initial conditions and mechanisms of competition. Ecological Monographs **63**:199–229.

Wedin, D. A., and D. Tilman. 1996. Influence of nitrogen loading and species composition on the carbon balance of grasslands. Science **274**:1720–1723.

Williams, E. D. 1978. Botanical composition of the Park Grass plots at Rothamsted 1856–1976. Rothamsted Experimental Station, Harpenden, Hertfordshire, UK.

Willis, A. 1963. Braunton Burrows: the effects on the vegetation of the addition of mineral nutrients to the dune soils. Journal of Ecology **51**:353–374.

Zahnley, J. W., and F. L. Duley. 1934. The effect of nitrogenous fertilizers on the growth of lawn grasses. Journal of the American Society of Agronomy **26**:231–234.