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REGULAR ARTICLE

Plant-induced changes in soil nutrient dynamics by native and invasive grass species

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Abstract Alteration of soil nutrient dynamics has recently garnered more attention as both a cause and an effect of plant invasion. This project examines how nutrient dynamics are affected by native (*Elymus elymoides*, *Pseudoroegneria spicata*, and *Vulpia microstachys*) and invasive (*Aegilops triuncialis*, *Agropyron cristatum*, *Bromus tectorum*, and *Taeniatherum caput-medusae)* grass species. This research questions whether natives and invasives differ in their effects on nutrient dynamics. A greenhouse study was conducted using two field-collected soils. Effects on nutrient dynamics were compared using an integrated index that evaluates the total nutrients in soil and in plant tissue compared to an unplanted control. With this index, we evaluated whether soil nutrients increased or decreased as a result of plant growth, controlling for plant uptake. We found no consistent support for our hypothesis that invasive grass species as a group influence nutrient dynamics differently than native grass species as a group. Our results indicate species-specific effects on nutrient dynamics. Alteration of nutrient dynamics is not a trait shared by all of the invasive grass species in our study. However, alteration of nutrient dynamics may be a mechanism by which some individual species increase their invasive potential.

Keywords Plant invasion · nutrient dynamics · *Bromus tectorum* · *Taeniatherum caput-medsae* · Nitrogen budget

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Introduction

An invasive species is non-native and able to spread over a considerable area into natural, non-disturbed sites (Richardson et al. 2000). One of the underappreciated impacts after plant invasion is alteration of nutrient cycling (Levine et al. 2004; Strayer et al. 2006). Plant species differ in their capabilities for nutrient uptake and soil nutrient mining, and these differences can affect ecosystem nutrient cycling (Ehrenfeld 2003). For example, if an invasive species has a unique effect on soil nutrients compared with native species, an alteration of endemic nutrient cycles may occur (Ehrenfeld 2003). The ability of a species to alter abiotic features of their ecosystem has been termed ecosystem engineering (Jones et al. 1994). If an invasive plant species has the ability to ecosystem engineer (i.e. alter nutrient dynamics) enough to disrupt population dynamics of native vegetation (Cuddington et al. 2009), then that ecosystem engineering ability may contribute to the invasive potential of the invasive species and increase the negative impact of that invasion.

The understanding that soil nutrients affect plant growth has been established in scientific literature since the work of Liebig in the mid 1800's (Marschner 2003). However, how plant growth affects soil nutrients has more recently begun to be investigated. Several different types of mechanisms by which plants influence soil nutrient dynamics exist, of which the most direct is nutrient uptake. Nutrient requirements, and thus nutrient uptake, differ among plant species. For example, nitrogen (N) requirements for agriculture crops range from 2 to 5% of the plant's dry weight and phosphorus (P) requirements from 0.3 to 0.5% (Marschner 2003). Thus, species identity will affect soil nutrient dynamics through species-specific nutrient requirements. However, typically less than 1% by weight of soil nutrients are readily available for plant uptake (Jenny 1980), requiring plants to utilize nutrient acquisition strategies such as scavenging and mining (Lambers et al. 2008). Scavenging is achieved by morphological changes to roots such as rapid root growth (Hodge 2003; Larigauderie and Richards 1994), localized root proliferation (Hodge 2003; Jackson and Caldwell 1989), and development of symbiotic relationships (Ehrenfeld et al. 2005, Lambers et al. 2008). Soil mining is defined as accessing more recalcitrant forms of nutrients in soil and is achieved by plant roots inducing biochemical changes in soil that increase availability of nutrients in solution (Lambers et al. 2008). Roots (and associated rhizosphere community) mine nutrients through changes in pH (Ehrenfeld et al. 2005, Hinsinger et al. 2003) and through the exudation of enzymes, chelators, siderophores, and organic acids (Ehrenfeld et al. 2005, Hinsinger et al. 2003; Lambers et al. 2008; Marschner 2003). Mining moves nutrients from unavailable pools to soil solution where they become available for plant uptake. The reverse of mining is nutrient immobilization whereby plants decrease the amount of extractable nutrients in soil, after accounting for plant uptake (Kuzyakov 2002). Immobilization can be achieved by two pathways: through stimulating microbial uptake that removes nutrients from solution, and through chemical precipitation of a nutrient out of soil solution.

This paper examines nutrient dynamics (differential nutrient uptake, changes in soil nutrient content, and mining abilities) of seven uncultivated grass species found in the Great Basin region of the western United States. Much of the Great Basin is undergoing rapid invasion of grass species in what was previously shrubland with an understory of perennial grass species (Hemstrom et al. 2002; Humphrey and Schupp 2004; Wisdom and Chambers 2009). The grass species in this study include 4 invasive (*Aegilops triuncialis*, *Agropyron cristatum*, *Bromus tectorum*, and *Taeniatherum caput-medusae*) and 3 native (*Elymus elymoides*, *Pseudoroegneria spicata*, and *Vulpia microstachys*) species. The groups of native and invasive species include both annual (*A. triuncialis*, *B. tectorum*, *T. caput-medusae*, and *V. microstachys*) and perennial (*A. cristatum*, *E. elymoides,* and *P. spicata*) species. *Aegilops triuncialis* is reported to have been introduced into California in 1914 and has become a very common invader in northern California grasslands (Dyer 2004). *Aegilops triuncialis* has recently been found just within the Great Basin in northern Nevada (E. Leger, personal communication). Because of its extreme invasive potential in California and recent discovery in the Great Basin, *A. triuncialis* is included in this project as a potential invader into the Great Basin. *Agropyron cristatum* is a non-native perennial grass species commonly used for restoration projects in the Great Basin but is considered invasive in the neighboring Great Plains of the United States (Christian and Wilson 1999) and fits a strict definition of an invasive (non-native and able to spread a considerable area into natural, non-disturbed sites; Richardson et al. 2000) within the Great Basin. The invasive *B. tectorum* was introduced in the late 1800's (Pellant et al. 2004), and currently millions of hectares of the land in the Great Basin are at moderate to high risk of *B. tectorum* invasion (Bradley and Mustard 2005). *Taeniatherum caput-medusae* invasion into the Great Basin has a similar history to *B. tectorum* invasion except that *T. caput-medusae* prefers soils with more clay content (Young 1992), which resulted in a less continuous range than *B. tectorum*. *Elymus elymoides* is a widespread, native perennial grass species that, at some life stages, confers resistance to annual grass invasion (Humphrey and Schupp 2004). *Pseudoroegneria spicata* also is a widely distributed, native perennial grass species but is generally not considered competitive with invasive grass species (Blank 2010). The final grass included in this project, *Vulpia microstachys*, is one of the few native annual grass species within the Great Basin. Although *V. microstachys* is found throughout the western United States

(USDA, NRCS. 2010), it has small stature and is not a dominant feature on the landscape.

The goal of this project was to assess how plants influence nutrient dynamics and whether invasive grass species as a group influence nutrients differently, either in direction or in magnitude, than native grass species. Nutrients examined were N, P, K, Ca, Mg, Fe, and Mn. In order to elucidate mechanisms by which plants may influence nutrient dynamics, we examined species-specific differences in nutrient uptake, soil nutrient content, and nutrient mining or immobilization. Our hypothesis was: invasive plants will have a different effect on nutrient dynamics than native plants. This difference is expected to be manifest as increased nutrient uptake by invasives, decreased extractable soil nutrients after growth by invasives, and a larger mining effect induced by invasive grass species.

Methods

Two soils were collected from natural sagebrush steppe areas outside Reno, NV USA. These soils were chosen as typical soils of the Great Basin. Initial soil characteristics are shown in Table 1. The first soil is classified as a Durinodic Xeric Haplargid by United States Department of Agriculture (USDA) Natural Resources Conservation Service (NRCS) and is hereafter referred to as the Sandy loam. Vegetation at the Sandy loam site was a diverse mix of shrubs, grasses, and forbs including: *Artemisia tridentata*, *E. elymoides*, *Achnatherum hymenoides*, *B. tectorum*, *A. cristatum*, and *Lupinus argenteus*. However, soil was collected from unvegetated areas to minimize any soil legacy effects from individual species in the native vegetation. The second soil is classified as an Aridic Haploxerert (USDA, NRCS) and is hereafter referred to as the Clay soil. The only vegetation at the Clay soil site was sparse *Artemisia tridentata* with ample interspace. Again, soil was collected from unvegetated areas. For both soil types, only the most biologically active (top 20 cm) soil was collected (Boone et al. 1999), homogenized, and stored for 14 days until it was potted in deepot 40 containers (656 ml volume, 6.4×25 cm tubes commercially available from Stuewe & Sons, Inc. Corvallis, OR, USA) in a glasshouse in Reno, NV USA. Each pot was randomly assigned a grass species or an unplanted control. The unplanted control was included to account for any background effects of experimental conditions (soil being placed in pot in the glasshouse and being watered) on soil nutrients.

Table 1 Initial soil characteristics for the Sandy loam and the Clay soil

Property	Sandy loam	Clay soil
texture		
% sand	83	47
% silt	2	4
% clay	15	49
pH	5.51	5.87
Mineral N mg pot^{-1}	2.49	1.23
P mg pot^{-1}	33.06	30.31
K mg pot^{-1}	3.25	12.31
Ca mg pot^{-1}	4.03	2.74
Mg mg pot^{-1}	2.34	1.82
Fe mg pot^{-1}	4.51	6.75
Mn mg pot^{-1}	5.33	13.51
weight mg pot^{-1}	650	570

The difference in weight pot^{-1} is due to inherent differences in soil bulk density.

Several seeds were planted in each tube but only the first emergent was allowed to grow. The experimental design included 5 replicates of each of the 7 plant species and the unplanted control in each of the soil types. The glasshouse had diurnal temperature fluctuations between 7°C and 24°C with ambient light. Careful and attentive watering maintained soils near field capacity without allowing any leaching or water to drain out of the pots. Planting occurred on January 28, 2009 and harvest occurred on April 18, 2009 for a total of 80 days of growth. Pots were periodically rearranged in the greenhouse to compensate for any environmental variation. Soils were sampled before and after plant growth, and above-ground tissue was collected at harvest. After the aboveground biomass was removed, the soil in each tube was homogenized before sampling. Due to the small size of the grasses, most roots were very fine and were not removed from the soil. Soil homogenization was specifically done to avoid sampling just rhizosphere soil. Sampling just rhizosphere soil might have produced more significant results but would not reflect effects of plants on bulk soil. Because our goal was to examine how plants affect the bulk soil, soils were homogenized.

Plant and extractable soil nutrients were determined by the same methods as Blank (2010) and expressed as content (i.e. amount nutrient per pot or per plant), not as concentration (i.e. amount per unit weight of plant or of soil). Briefly, plant tissue was dry ashed at 550°C and solubilized in 1 N HCl. Phosphorus was quantified using the molybdenum-blue procedure. Calcium, magnesium, potassium, iron and manganese were quantified by atomic absorption/emission spectroscopy. Total N was determined for both soil and plant tissue via combustion (LECO TruSpec CN). Soil nutrients were extracted from fresh soil samples using the following standard procedures: KCl-extractable NO_3 and NH_4; ammonium acetate extractable Ca, Mg, K; Fe, and Mn via DTPA extraction; and bicarbonate extraction for extractable P. Soil NO_3 and NH_4 values were converted to total mineral N.

Plant tissue nutrient content was used as a measure of nutrient uptake. Extractable soil nutrients were evaluated to assess effects on extractable soil nutrient content. An integrated index was used to evaluate *P*lant-induced *C*hanges in soil *N*utrients (PCN). This index evaluates the difference between total extractable nutrients per pot in the planted pots (defined as the sum of extractable soil nutrient content and plant nutrient content at the end of the growing season) and total extractable soil nutrients in the unplanted pots (*sensu* Hallsby 1995). This was done individually for each nutrient with a paired design (i.e. planted pots were compared with the unplanted pot with the same replicate). The equation used was:

$$\mathrm{PCN} = \left(\mathrm{Nutr}_{\,planted\ soil} + \mathrm{Nutr}_{\,plant}\right) - \mathrm{Nutr}_{\,unplanted\ soil}$$

where Nutr = a given extractable nutrient.

A value for PCN greater than zero indicates that more nutrients were extractable after the growing season due to plant growth, and thus mining took place. A value for PCN less than zero indicates that nutrients were less extractable after the growing season due to plant growth, and thus immobilization took place. Note that unplanted pots account for effects of experimental conditions on soil nutrients in the absence of any current plant influence.

To determine whether mining or immobilization effect is significant, PCN values were compared to zero. To include all dependent variables in one analysis and minimize the probability of a Type I Error, MANOVA was used. Differences in plant nutrient content, soil nutrients, and PCN were evaluated: (1) between natives and invasives using Hotelling's trace (a multivariate statistic for comparing between two groups, Quinn and Keough 2003); and (2) among species using Wilk's lambda (a multivariate statistic for comparing among more than two groups). The following transformations were performed to meet the assumption of normality: soil N, soil Mg, plant Mn, and plant Fe were log transformed, and soil Mn was square root transformed. The following planned contrasts were performed to account for difference in life form (annual and perennial): perennial invasive/annual invasive; perennial native/annual native; invasive perennial/native perennial; and invasive annual/native annual. Significance was evaluated at $\alpha \leq 0.05$. Statistical analysis was conducted in PASW Statistics 18 (PASW for Windows, Rel. 18.0.0. 2009. Chicago: SPSS Inc.).

Results

Although volumetrically equivalent, full pots of the Sandy loam were heavier than full pots of the Clay soil due to inherent differences in bulk density. Results were similar when extractable soil nutrients were calculated as soil nutrient concentration (mg nutrient g $soil^{-1}$) as when calculated as soil nutrient content (mg nutrient pot^{-1}). We used soil nutrient content to evaluate the effects of species on nutrients within each pot. Soil type significantly affected plant tissue nutrients ($p<0.001$) and extractable soil nutrients after plant growth ($p\leq0.001$). No effect of plant species on soil pH was found ($p=0.254$). Further analysis was conducted separately for each soil type.

Across all variables, multivariate analyses indicated no significant differences between native grass species and invasive grass species in plant nutrient content (Sandy loam $p=0.112$; Clay soil $p=0.132$); soil nutrients (Sandy loam $p=0.419$; Clay soil $p=0.541$); and PCN (Sandy loam $p=0.308$; Clay soil $p=0.079$) (Table 2). No consistent confounding effect of life form (i.e., perennials and annuals) was found. The planned contrasts found no significant differences in plant nutrient content, extractable soil nutrients or PCN between native perennials and invasive perennials in either soil type. No significant differences

Table 2 Mean values ± 1 SE for plant tissue nutrient content (mg/plant for N and μg/plant for the rest of the nutrients); soil content (mg/pot), and *P*lant induced *C*hanges in soil *N*utrients (PCN, units are mg, see text for explanation and formula)

		N	P	K	Ca	Mg	Fe	Mn
Sandy loam								
Plant content	native	4.90±0.23	1.09±0.06	8.11±0.74	1.77±0.17	0.41±0.04	0.13±0.02	0.03±0.01
	non-native	4.42±0.22	1.42±0.13	8.12±0.56	2.41±0.29	0.53±0.05	0.19±0.03	0.16±0.01
Soil content	native	0.07±0.01	31.32±2.79	12.71±0.94	1.03±0.38	1.85±0.11	6.65±0.18	4.21±0.11
	non-native	0.09±0.02	29.97±3.07	10.83±0.89	2.31±0.67	1.85±0.21	7.19±0.22	4.42±0.13
PCN	native	4.51±0.23[a]	2.04±4.12	9.21±1.09[a]	−3.74±1.28[a]	−1.11±0.31[a]	−0.60±0.21[a]	−0.12±0.11
	non-native	3.85±0.29[a]	1.03±3.15	7.34±1.34[a]	−1.84±0.88[a]	−0.98±0.26[a]	−0.001±0.22	0.12±0.16
Clay soil								
Plant content	native	1.63±0.22	0.31±0.02	2.24±0.20	0.81±0.07	0.19±0.02	0.09±0.01	0.01±0.002
	non-native	1.44±0.09	0.45±0.04	2.29±0.22	0.76±0.65	0.30±0.04	0.08±0.10	0.02±0.003
Soil content	native	0.02±0.002	37.78±3.15	6.80±2.34	1.95±0.55	1.54±0.29	4.18±0.28	8.38±0.55
	non-native	0.02±0.002	34.31±3.10	5.67±1.70	2.14±0.35	1.56±0.17	4.66±0.18	8.39±0.35
PCN	native	1.52±0.22[a]	−1.51±4.38	6.40±2.47[a]	−1.67±0.85	−1.15±0.42[a]	−0.21±0.29	−0.90±0.64
	non-native	1.17±0.08[a]	−0.21±3.70	0.84±2.34	−2.59±0.87[a]	−1.26±0.33[a]	−1.28±0.35[a]	1.59±0.68[a]

Values for PCN indicated with a [a] are significantly different than zero. Significance was determined at $p<0.05$.

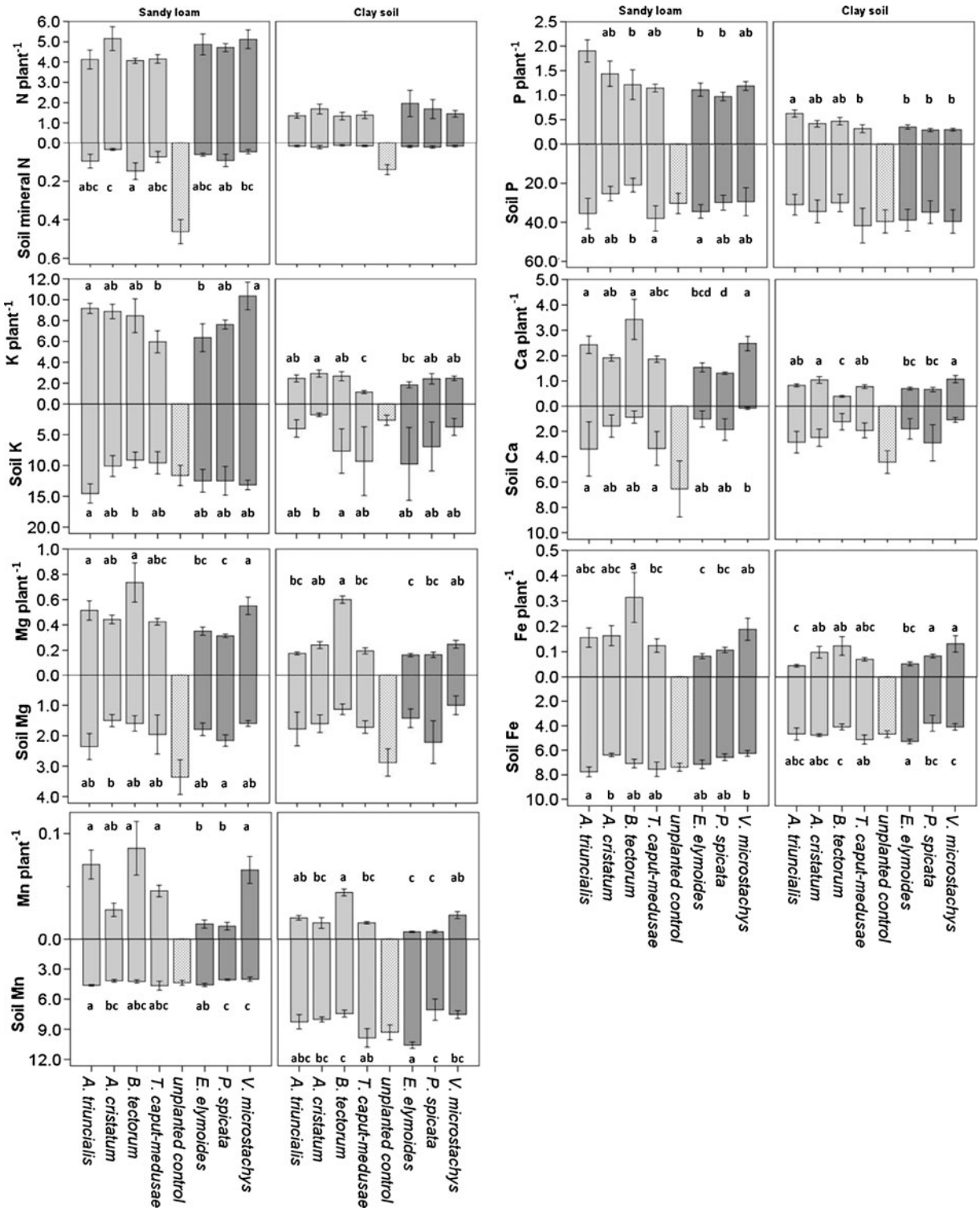
were found between native annuals and invasive annuals for plant nutrient content (in the Sandy loam), extractable soil nutrients, and PCN. However in the Clay soil, plant nutrient contents were significantly different between native annuals and invasive annuals ($p=0.014$), specifically in Ca plant^{-1} ($p=0.001$).

Our objective to compare the effects of natives and invasives implicitly relies on the assumption that the species within each group induce similar changes in nutrient dynamics, i.e. all natives behave similarly and all invasives behave similarly. When we analyze species individually in order to evaluate this assumption, we found significant species-specific differences in plant nutrient content (Sandy loam $p=0.001$; Clay soil $p<0.001$), extractable soil nutrients (Sandy loam $p=0.005$; Clay soil $p<0.001$), and PCN (Sandy loam $p=0.02$; Clay soil $p<0.001$). Much of the between species variation is found within the groups of natives and invasives (Fig. 1). Natives *E. elymoides* and *P. spicata* often had similar plant nutrient content but native *V. microstachys* tended to have higher plant content of K, Ca, Mg, Fe, and Mn (Sandy loam $p=0.073$; Clay soil $p=0.414$). Among the group of invasive species, we also found large variation in plant nutrient content. *Taeniatherum caput-medusae* tissue had very low content of K and P whereas *B. tectorum* had very high contents of Ca, Mg, Fe, and Mn.

Comparison of soil nutrient content also revealed no consistency within groups. Among the group of natives, extractable soil Fe and Mn were much higher in *E. elymoides* soil and K, Mg, and Ca were much lower in *V. microstachys* soil than the soils of other natives. Among the invasive species, extractable soil P, K, Ca, Mg, and Fe were much lower in *B. tectorum* soil and P, K, and Mn were much higher in *T. caput-medusae* soils than in the soils of other invasives (Fig. 1). Within group differences were especially evident for the integrated index of PCN among the invasive grass species (Fig. 2). Invasives produced opposing effects on P, K, Fe, and Mn, with some species mining and some species immobilizing nutrients. Within the group of natives, *E. elymoides* mined soil Mn and Fe in the Clay soil whereas the other natives induced immobilization (Fig. 2).

Discussion

We found limited significant differences between the effects on nutrient dynamics induced by invasives, as a group, and natives, as a group (Table 2). Other studies have yet to find a characteristic shared by all non-native invasive plants (Alpert et al. 2000), and the ability to alter nutrient dynamics is no exception. Despite the limited significance differences between natives and



invasives, interesting and unexpected trends did emerge (Table 2). Invasive grass species did have higher nutrient uptake for most soil nutrients (excluding N) than native grass species. However, the higher uptake did not translate to lower extractable soil nutrients after plant growth by invasives. The integrated index of PCN

◀ **Fig. 1** Plant tissue (*top panels*) and extractable soil nutrients after plant growth (*bottom panels*) by plant species in the Sandy loam and the Clay soil. Invasives (*light bars*) are grouped on the left of the unplanted control and natives (*dark bars*) are grouped on the right. *Bars* indicated with the different letters are significantly different from each other within each soil type. Soil and plant nutrients are not compared with each other. Panels with no letters have no pairwise significant difference. *Error bars* indicate 1 SE. Units for nutrient plant^{-1} are mg plant^{-1} for N and μg plant^{-1} for all other nutrients. Units for soil nutrients are mg pot^{-1}

revealed the surprising result that native grass species often had larger PCN values than invasive grass species.

For alteration of nutrient dynamics to be a general invasive trait, all the invasive grass species should induce similar changes in nutrient dynamics, and these changes also should differ from those induced by all native grass species. However, the results of this project indicate species-specific differences in nutrient dynamics. We found species-specific differences in plant uptake, extractable soil nutrients after plant growth, and PCN. These results are concordant with other published studies (Blank and Young 2004; Johnson et al. 2007; Kourtev et al. 2003; Markham et al. 2009; and Vanderhoeven et al. 2005) and meta-analysis (Ehrenfeld 2003). Accumulating evidence indicates that whereas every plant species does not affect every soil nutrient uniquely, some plant species do affect some soil nutrients in a significantly different manner. A good illustration of this species-specific difference is the relationship of *A. cristatum*

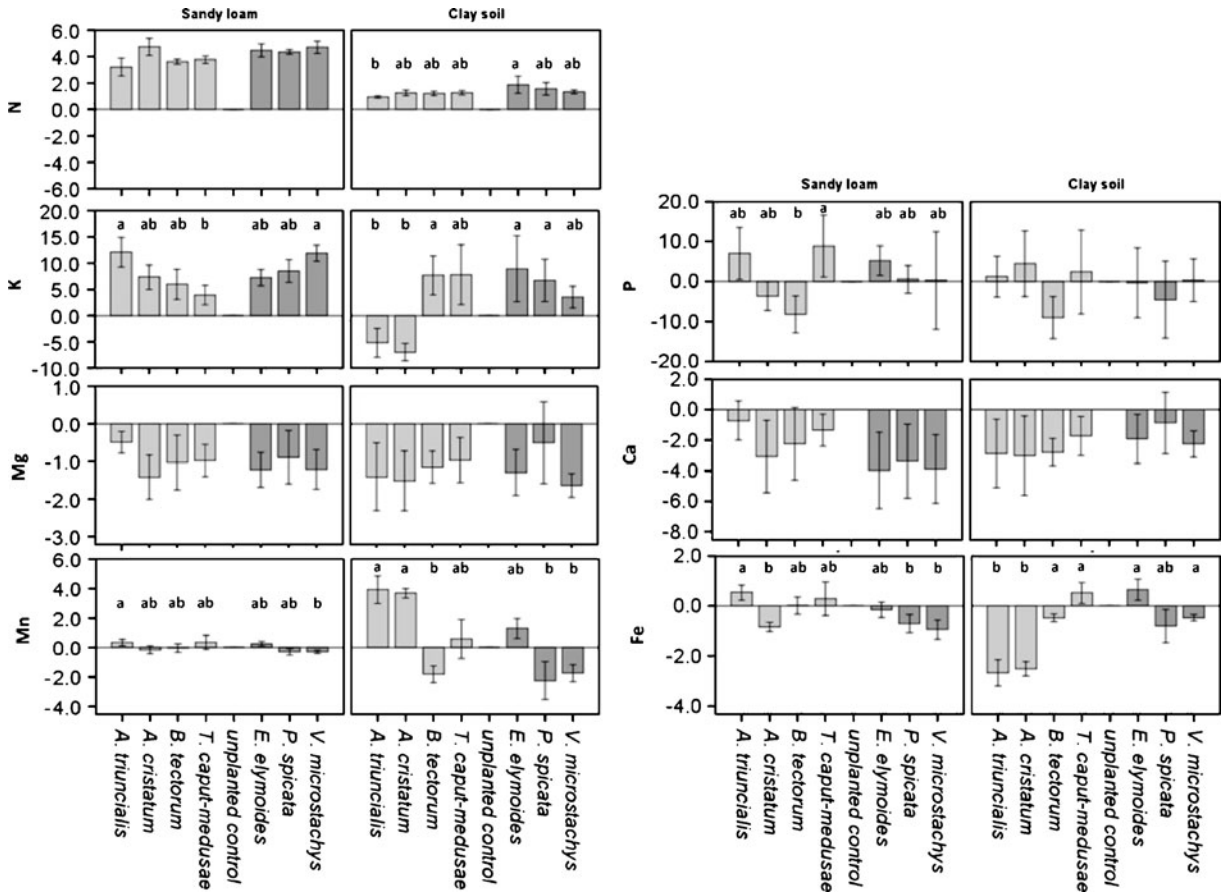


Fig. 2 Plant induced Changes in soil Nutrients (PCN, units are mg, see text for explanation and formula) by plant species. A value greater than 0 indicates mining of nutrients and a value less than 0 indicates immobilization of nutrients (see text for definitions). *Error bars* indicate 1 SE. *Bars* not indicated with the same letter are significantly different from each other within each soil type. Panels with no letters have significant no pairwise differences. Invasives (*light bars*) are grouped on the left and natives (*dark bars*) are on the right of the unplanted control

with K. In the Clay soil, *A. cristatum* had both significantly more plant uptake of K and significantly immobilized K in the soil compared to other species. This alteration of K (an essential macronutrient) may relate to one mechanism by which increasing *A. cristatum* densities decrease native grass species (Heidinga and Wilson 2002). Two individual species, *B. tectorum* and *V. microstachys*, stand out by consistently having very high plant uptake of many nutrients compared with all other species for the former and among other natives for the latter.

Our calculation of PCN is an effective way to evaluate soil nutrient mining and immobilization. By examining the combination of aboveground biomass and changes in extractable soil nutrients, in relation to the unplanted control, better insight of how species may affect nutrient cycles can be gained. Four of the nutrients (P, Mn, Fe, and K in the Clay soil) included in this study had species-specific trends in the direction of change: some species increased availability of (mined) the nutrient while other species decreased availability of (immobilized) the nutrient (Fig. 2). In the Sandy loam, *A. triuncialis* mined Fe whereas other species either produced no effect (*B. tectorum*, *T. caput-medusae* and *E. elymoides*) or immobilized Fe (*A. cristatum*, *P. spicata* and *V. microstachys*). Although this project is the first to examine soil nutrient dynamics for most of the species included, *B. tectorum* and *T. caput-medusae* have been previously examined, and our species-specific results agree with trends in other studies (Blank et al. 2002; Blank and Sforza 2007; Blank and Young 2004). We found an increase in extractable soil N and decrease of soil Ca, Mg, and Mn compared with other species in at least one soil type due to *B. tectorum*; these trends were also found by Blank et al. (2002) and Blank and Young (2004). The tendency of *T. caput-medusae* to decrease soil N, Ca, and Mg and increase soil Mn and Fe in this study agree with other studies (Blank and Sforza 2007).

This project examines the degree of difference on soil nutrients induced by one individual in a glasshouse situation. Although evaluating per-individual effect is a vital and important step, it is only the first step in evaluating how plant species influence nutrient cycling (Ehrenfeld 2003). Extrapolating from one individual to a plant population may or may not be appropriate as plant nutrient uptake and soil mining change with both intra- and inter-specific neighbors (Blank 2010) and increasing plant density. Further study is needed to examine the threshold relative abundance at which an invasive species can affect stand-level processes of nutrient cycling (Ehrenfeld 2003). Our results lead to the hypothesis that the threshold abundance to influence soil properties will be species-specific. Species that produce larger per-individual effects may need smaller abundances to influence stand level nutrient cycling than species that show smaller per-individual effect. Nonetheless, species with large relative biomass or high conspicuousness may not be the species with the largest effects on soil properties or nutrient cycles (Peltzer et al. 2009) as our results for *V. microstachys* illustrate. Thus examination of many plants present at a site might be necessary to appropriately investigate nutrient dynamics at stand level.

This project provides insight into the changes in nutrient dynamics that occur after one growing season under glasshouse conditions. If these trends in nutrients compound over time and occur under natural conditions, chronic effects and long-term feedbacks may become established (Strayer et al. 2006). For *B. tectorum*, trends in several soil nutrients have been observed to compound and become more pronounced over multiple growing seasons (Blank et al. 2002; and Blank and Young 2004). Our trend of less soil NO_3 in the Sandy loam under *A. cristatum* compared with *B. tectorum* was also found in soils in a field study using monoculture plots of each species that had been established for at least 6 years (Hooker et al. 2008). Changes in nutrient cycling are also caused by differences in plant uptake and litter quality among plant species. Our results show species-specific differences in plant tissue nutrient contents. For example, our result for *B. tectorum* tissue nutrient content agrees with previous studies (Blank and Young 2004; Evans et al. 2001). These differences in plant tissue nutrient content lead directly to differences in litter quality. Previous studies have reported that sites with *B. tectorum* have significantly higher litter than sites without (Evans et al. 2001), and when coupled with our results of high plant nutrient content (Fig. 1) strongly indicates a mechanism by which *B. tectorum* may influence nutrient dynamics. The difference between *B. tectorum* litter and native litter has been observed to alter nutrient cycling at one study site in as little as 2 years (Evans et al. 2001). Thus, our results after one growing season under

glasshouse conditions likely represent effects that occur over multiple years under natural conditions; however this needs to be tested in natural conditions.

Although individual species clearly influence nutrient dynamics, alteration of nutrient dynamics cannot continue in the same direction indefinitely. Although soil nutrient pools can be very large, they are not infinite, and not all of that larger pool can be mined. A rough guideline for the amount of nutrients that can be mined is the amount by which agricultural soils seem to have been depleted of total organic matter over several decades of cultivation, which is on the order of 20% (Mann 1986). Certainly, there is a level of nutrients in the soil beyond which a species cannot mobilize and uptake enough of a nutrient for survival.

Conclusion

This paper provides evidence of species-specific changes induced by plants on nutrient dynamics. We found little support for our hypothesis that invasive grass species, as a group, influence nutrient dynamics differently than native grass species, as a group. Rather, our results strongly point to a more intricate interaction between plant species and nutrient dynamics than is encapsulated in our hypothesis. We only examined changes in nutrients induced by one individual plant in one growing season under glasshouse conditions. Further study is needed to evaluate how changes induced by individuals during one growing season scale up to populations and over multiple growing seasons. Past projects suggest that some of the patterns that we found compound over growing seasons (Blank et al. 2002; Blank and Young 2004; and Hooker et al. 2008) and impact large scale nutrient cycling (Ehrenfeld 2003). Although we found that alteration of nutrient dynamics is not an invasive trait shared by all of the invaders in this study, it may be a mechanism by which individual species increase invasiveness. Alteration of nutrient dynamics is also an impact of invasion by plant species and thus deserves increased attention.

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