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# Importance of Species Replication in Understanding Plant Invasions into North American Grasslands

## **Abstract**

The global homogenization of the Earth's biota is expected to increase due to the increase in movement of people and goods between regions, and many introduced species are having a negative economic impact. The increase of introduced species can be thought of as a major global change, because ecosystems throughout the world are now impacted by exotics [1, 2]. Grasslands, which cover roughly 25% of the globe, contain perhaps the most disrupted and homogenized communities in the world. Native grasslands have been lost because of land conversion, and native species have been replaced or displaced with introduced grasses and legumes. Many species were intentionally introduced during the early 20th century to prevent erosion or to improve grazing, and many have undoubtedly done so. However, as management objectives for grasslands have expanded to include wildlife habitat, biodiversity, and C sequestration, it has become critical to understand how introduced species are affecting these new objectives as well. For example, Christian and Wilson [3] found that areas in Saskatchewan, Canada, dominated by the introduced forage grass *Agropyron cristatum* are sequestering less C into their soils compared to developing native prairie stands with similar land use histories.

## **Disciplines**

Biodiversity | Ecology and Evolutionary Biology

## **Comments**

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## Importance of species replication in understanding plant invasions into North American grasslands

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### Introduction

The global homogenization of the Earth's biota is expected to increase due to the increase in movement of people and goods between regions, and many introduced species are having a negative economic impact. The increase of introduced species can be thought of as a major global change, because ecosystems throughout the world are now impacted by exotics [1, 2]. Grasslands, which cover roughly 25% of the globe, contain perhaps the most disrupted and homogenized communities in the world. Native grasslands have been lost because of land conversion, and native species have been replaced or displaced with introduced grasses and legumes. Many species were intentionally introduced during the early 20th century to prevent erosion or to improve grazing, and many have undoubtedly done so. However, as management objectives for grasslands have expanded to include wildlife habitat, biodiversity, and C sequestration, it has become critical to understand how introduced species are affecting these new objectives as well. For example, Christian and Wilson [3] found that areas in Saskatchewan, Canada, dominated by the introduced forage grass *Agropyron cristatum* are sequestering less C into their soils compared to developing native prairie stands with similar land use histories.

Exotic species have been planted or have spread to become common or even the dominant species in many grasslands in the US. For example, the grasses *Bromus inermis* and *Agropyron cristatum* are dominant grasses in much of the Northern Plains region (e.g., [3, 4]), species of the genus *Centaurea* dominate some Rocky Mountain grasslands [5, 6], exotic annuals dominate California (e.g., [7]), *Agropyron desertorum* dominates much of the inter-mountain west (e.g., [8–10]), and the grass *Bothriochloa ischaemum* dominates most central Texas grasslands [11]. The spread of these species has occurred within a very short time span. For example, it is stated in the 1979 Flora of Texas that *Bothriochloa ischaemum* was 'not persisting except in cultivation or along roadsides'. The spreading of exotic species, their impact on native communities, and the global homogenization of the flora and fauna makes this an important global issue [1, 12–14].

Several comprehensive reviews exist on invasive plant species [15–21]. Rather than providing another overview of the topic, I will focus on a smaller aspect of the issue, i.e., whether invasive-species conclusions based on single species pairs would differ from conclusions based on means from multiple invasive and native species. I test this hypothesis with a literature review and with data from a common garden experiment.

*Are there differences in growth characteristics between natives and exotics?*

Two important predictions have been made about exotic species: 1) introduced species have higher growth rates than do natives and 2) introduced species are more tolerant to grazing than are native species, at least in regions where plants evolved with low intensities of grazing. Introduced species are predicted to have higher growth rates because they 1) have been ‘released’ from their natural enemies (pathogens or herbivores), 2) are able to shift allocation of resources from secondary compounds to growth (reviewed in [22]), or 3) have undergone rapid evolution for high growth rate and increased competitive ability (e.g., [23]). A factor that is seldom mentioned is the possibility that people consciously selected fast growing species (out of a wide distribution of possible species and genotypes) to introduce. Whatever the mechanism, exotics are predicted to have a higher rate of above-ground growth than natives when grown under common conditions.

Several studies have reviewed papers that compared growth rates and competitive abilities between native and exotic plant species (e.g., [24, 25]). Daehler [24], in a literature review, compared natives and exotics for 9 growth related traits, 4 spread related traits, and 3 “composite” traits. He found few differences between natives and exotics. Among the growth related traits, only leaf construction costs and leaf area were significantly different in exotic species. Spread related traits were not significantly different between natives and exotics, except for survival rate, which was higher in natives. Phenotypic plasticity was significantly greater in exotics, and growth generally responded more to nutrients in exotic than in native species. This provides an important link to theory developed by Burke and Grime [26] and Davis et al. [27] that predicts that invasions will be most likely to occur when unused resource pulses occur. Daehler [24] did not analyze tolerance to grazing or clipping, although many of the cited papers contained data on this variable. Daehler concluded that the major difference between exotics and natives is that the former can more rapidly adjust to the fluctuating conditions of disturbed sites. However, Vilá and Weiner [25] found in a meta-analysis that exotics had a higher overall growth rate than natives. They went on to note that differences between natives and exotics may have been influenced by biased choices of investigators, who may have compared highly invasive exotics with “well behaved” native species in at least some cases [25]. The differing conclusions between Daehler [24] and Vilá and Weiner [25], and the large variation in out-

Table 1. Studies that compared native and exotic species (from [24])

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*Studies that replicated both native and exotic species*

- Baars R, Kelly D (1996) Survival and growth responses of native and introduced vines in New Zealand to light availability. *New Zealand J Bot* 34: 389–400
- Baruch Z, Goldstein G (1999) Leaf construction cost, nutrient concentration, and net CO<sub>2</sub> assimilation of native and invasive species in Hawaii. *Oecologia* 121: 183–192
- Blaney CS, Kotanen PM (2001a) Effects of fungal pathogens on seeds of native and exotic plants: A test using congeneric pairs. *J Appl Ecol* 38: 1104–1113
- Blaney CS, Kotanen PM (2001b) Post-dispersal losses to seed predators: An experimental comparison of native and exotic old field plants. *Can J Bot* 79: 284–292
- Frenot Y, Gloaguen JC (1994) Reproductive performance of native and alien colonizing phanerogams on a glacier foreland, Iles Kerguelen. *Polar Biol* 14: 473–481
- Glenn E, Tanner R, Mendez S, Kehret T, Moore D (1998) Growth rates, salt tolerance and water use characteristics of native and invasive riparian plants from the delta of the Colorado River, Mexico. *J Arid Environ* 40: 281–294
- Maillet J, Lopez GC (2000) What criteria are relevant for predicting the invasive capacity of a new agricultural weed? The case of invasive American species in France. *Weed Res* 40:11–26
- Pattison RR, Goldstein G, Ares A (1998) Growth, biomass allocation and photosynthesis of invasive and native Hawaiian rainforest species. *Oecologia* 117: 449–459
- Radho TS, Majer JD, Yates C (2001) Impact of fire on leaf nutrients, arthropod fauna and herbivory of native and exotic eucalypts in Kings Park, Perth, Western Australia. *Aust Ecol* 26: 500–506
- Smith MD, Knapp AK (2001) Physiological and morphological traits of exotic, invasive exotic, and native plant species in tallgrass prairie. *Int J Pl Sci* 162: 785–792

*Studies that replicated native species but not exotics*

- Black RA, Richards JH, Manwaring JH (1994) Nutrient uptake from enriched soil microsites by three great basin perennials. *Ecology* 75: 110–122
- Cleverly JR, Smith SD, Sala A, Devitt DA (1997) Invasive capacity of *Tamarix ramosissima* in a Mojave Desert floodplain: The role of drought. *Oecologia* 111: 12–18
- Horn P, Prach K (1994) Aerial biomass of *Reynoutria japonica* and its comparison with that of native species. *Preslia* 66: 345–348
- Marler MJ, Zabinski CA, Wojtowicz T, Callaway RM (1999) Mycorrhizae and fine root dynamics of *Centaurea maculosa* and native bunchgrasses in western Montana. *Northwest Sci* 73: 217–224
- Nagel JM, Griffin KL (2001) Construction cost and invasive potential: comparing *Lythrum salicaria* (Lythraceae) with co-occurring native species along pond banks. *Am J Bot* 88: 2252–2258
- Nernberg D, Dale MRT (1997) Competition of five native prairie grasses with *Bromus inermis* under three moisture regimes. *Can J Bot* 75: 2140–2145
- Woo I, Zedler JB (2002) Can nutrients alone shift a sedge meadow towards dominance by the invasive *Typha × glauca*. *Wetlands* 22: 509–521
- Yamashita N, Ishida A, Kushima H, Tanaka N (2000) Acclimation to sudden increase in light favoring an invasive over native trees in subtropical islands, Japan. *Oecologia* 125: 412–419

*Studies that replicated exotic species but not natives*

- Fan J, Harris W (1996) Effects of soil fertility level and cutting frequency on interference among *Hieracium pilosella*, *H. praealtum*, *Rumex acetosella*, and *Festuca novae-zelandiae*. *New Zealand J Agric Res* 39: 1–32
- McDowell CR, Moll EJ (1981) Studies of seed germination and seedling competition in *Virgilia oroboides* (Berg.) Salter, *Albizia lophantha* (Willd.) Benth. and *Acacia longifolia* (Andr.) Willd. *J South Afr Bot* 47: 653–685
- Virgona JM, Bowcher A (2000) Effects of grazing interval on basal cover of four perennial grasses in a summer-dry environment. *Aust J Exp Agric* 40: 299–311
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Table 1. (Continued)

*Studies that did not replicate exotic or native species*

- Aptekar R, Rejmanek M (2000) The effect of sea-water submergence on rhizome bud viability of the introduced *Ammophila arenaria* and the native *Leymus mollis* in California. *J Coastal Conser* 6: 107–111
- Arenas F, Fernandez C, Rico J, Fernandez E, Haya D (1995) Growth and reproductive strategies of *Sargassum muticum* (Yendo) Fensholt and *Cystoseira nodicaulis* (Whit.) Roberts. *Scientia Maritima* 59(Suppl. 1): 1–8
- Baruch Z, Bilbao B (1999) Effects of fire and defoliation on the life history of native and invader C<sub>4</sub> grasses in a neotropical savanna. *Oecologia* 119: 510–520
- Baruch Z (1996) Ecophysiological aspects of the invasion by African grasses and their impact on biodiversity and function of neotropical savannas. In: OT Solbrig, E Medina, JF Silva (eds.): *Biodiversity and savanna ecosystem processes*. Springer-Verlag, Berlin, 79–93
- Caldwell MM, Richards JH, Johnson DA, Nowak RS, Dzurec RS (1981) Coping with herbivory: photosynthetic capacity and resource allocation in two semiarid *Agropyron* bunchgrasses. *Oecologia* 50: 14–24
- Callaway JC, Josselyn MN (1992) The introduction and spread of smooth cordgrass (*Spartina alterniflora*) in South San Francisco Bay. *Estuaries* 15: 218–226
- Carino DA, Daehler CC (2002) Can inconspicuous legumes facilitate alien grass invasions? Partridge peas and fountain grass in Hawaii. *Ecography* 25: 33–41
- Cross JR (1981) The establishment of *Rhododendron ponticum* in the Killarney oakwoods. *J Ecol* 69: 807–824
- Goergen E, Daehler CC (2001a) Inflorescence damage by insects and fungi in native pili grass (*Heteropogon contortus*) versus alien fountain grass (*Pennisetum setaceum*) in Hawaii. *Pacific Sci* 55: 129–136
- Goergen E, Daehler CC (2001b) Reproductive ecology of a native Hawaiian grass (*Heteropogon contortus*; Poaceae) versus its invasive alien competitor (*Pennisetum setaceum*; Poaceae). *Int J Pl Sci* 162: 317–326
- Goergen E, Daehler CC (2002) Factors affecting seedling recruitment in an invasive grass (*Pennisetum setaceum*) and a native grass (*Heteropogon contortus*) in the Hawaiian Islands. *Plant Ecol* 161: 147–156
- Greenberg CH, Smith LM, Levey DJ (2001) Fruit fate, seed germination and growth of an invasive vine—an experimental test of “sit and wait” strategy. *Biol Inv* 3: 363–372
- Gross EM, Johnson RL, Hairston NG Jr (2001) Experimental evidence for changes in submersed macrophyte species composition caused by the herbivore *Acentria ephemerella* (Lepidoptera). *Oecologia* 127: 105–114
- Herron GJ, Sheley RL, Maxwell BD, Jacobsen JS (2001) Influence of nutrient availability on the interaction between spotted knapweed and bluebunch wheatgrass. *Restor Ecol* 9: 326–331
- Holmgren M, Aviles R, Sierralta L, Segura AM, Fuentes ER (2000) Why have European herbs so successfully invaded the Chilean matorral? Effects of herbivory, soil nutrients, and fire. *J Arid Env* 44: 197–211
- Honig MA, Cowling RM, Richardson DM (1992) The invasive potential of Australian *Banksias* in South African fynbos: A comparison of the reproductive potential of *Banksia ericifolia* and *Leucadendron lauroleum*. *Aust J Ecol* 17: 305–314
- Hueneke LF, Thomson JK (1995) Potential interference between a threatened endemic thistle and an invasive nonnative plant. *Conser Biol* 9: 416–425
- Kuhn NL, Zedler JB (1997) Differential effects of salinity and soil saturation on native and exotic plants of a coastal salt marsh. *Estuaries* 20: 391–403
- Larson KC (2000) Circumnutation behavior of an exotic honeysuckle vine and its native congener: Influence on clonal mobility. *Am J Bot* 7: 533–538
- Lesica P, Miles S (1999) Russian olive invasion into cottonwood forests along a regulated river in north-central Montana. *Can J Bot* 77: 1077–1083

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Table 1. (Continued)

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- Li Y, Norland M (2001) The role of soil fertility in invasion of Brazilian pepper (*Schinus terebinthifolius*) in Everglades National Park, Florida. *Soil Sci* 166:400–405
- Luken JO, Kuddes LM, Tholemeier TC, Haller DM (1997) Comparative responses of *Lonicera maackii* (amur honeysuckle) and *Lindera benzoin* (spicebush) to increased light. *Am Midl Natur* 138: 331–343
- Marco DE, Paez SA (2000) Invasion of *Gleditsia triacanthos* in *Lithraea ternifolia* montane forests of Central Argentina. *Environ Manage* 26: 409–419
- Mesleard F, Ham LT, Boy V, Van Wijck C, Grillas P (1993) Competition between an introduced and an indigenous species: The case of *Paspalum paspalodes* (Michx) Scribn. and *Aeluropus litoralis* (Gouan) in the Camargue (southern France). *Oecologia* 94: 204–209
- Pavlik BM (1983a) Nutrient and productivity relations of the dune grass *Ammophila arenaria* and *Elymus mollis*. I. Blade photosynthesis and nitrogen use efficiency in the laboratory and field. *Oecologia* 57: 227–232
- Pavlik BM (1983b) Nutrient and productivity relations of the dune grass *Ammophila arenaria* and *Elymus mollis*. II. Growth and patterns of dry matter and nitrogen allocation as influenced by nitrogen supply. *Oecologia* 57: 233–238
- Pyke DA (1986) Demographic responses of *Bromus tectorum* and seedlings of *Agropyron spicatum* to grazing by small mammals: occurrence. *J Ecol* 74: 739–754
- Sallabanks R (1993) Fruiting plant attractiveness to avian seed dispersers: native versus invasive *Crataegus* in western Oregon. *Madroño* 40: 108–116
- Schierenbeck KA, Mack RN, Sharitz RR (1994) Effects of herbivory on growth and biomass allocation in native and introduced species of *Lonicera*. *Ecology* 75: 1661–1672
- Shafroth PB, Auble GT, Scott ML (1995) Germination and establishment of the native plains cottonwood (*Populus deltoides* Marshall subsp. *monilifera*) and the exotic Russian-olive (*Elaeagnus angustifolia* L.). *Conser Biol* 9: 1169–1175
- Sher AA, Marshall DL, Gilbert SA (2000) Competition between native *Populus deltoides* and invasive *Tamarix ramosissima* and the implications for reestablishing flooding disturbance. *Conser Biol* 14: 1744–1754
- Simoes M, Baruch Z (1991) Responses to simulated herbivory and water stress in two tropical C<sub>4</sub> grasses. *Oecologia* 88: 173–180
- Smith MA, Bell DT, Loneragan WA (1999) Comparative seed germination ecology of *Austrostipa compressa* and *Ehrharta calycina* (Poaceae) in a Western Australian Banksia woodlands. *Aust J Ecol* 24: 35–42
- Smith RGB, Brock MA (1996) Coexistence of *Juncus articulatus* L. and *Glyceria australis* C.E. Hubb. in a temporary shallow wetland in Australia. *Hydrobiologia* 340: 147–151
- Vila M, D'Antonio CM (1998a) Fruit choice and seed dispersal of invasive versus noninvasive *Carpobrotus* (Aizoaceae) in coastal California. *Ecology* 79: 1053–1060
- Vila M, D'Antonio CM (1998b) Fitness of invasive *Carpobrotus* (Aizoaceae) hybrids in coastal California. *Ecoscience* 5: 191–199
- Williams DG, Black RA (1994) Drought response of a native and introduced Hawaiian grass. *Oecologia* 97: 512–519
- Witkowski ETF (1991) Growth and competition between seedlings of *Protea repens* (L.) L. and the alien invasive, *Acacia saligna* (Labill.) Wendl. in relation to nutrient availability. *Func Ecol* 5: 101–110
- Zedler JB, Paling E, McComb A (1990) Differential responses to salinity help explain the replacement of native *Juncus kraussii* by *Typha orientalis* in Western Australian salt marshes. *Aust J Ecol* 15: 57–72
- Studies included in Daehler (2003) that confound differences in lifespan (annual or perennial) and native or exotic origin (and did not replicate species)*
- Claassen VP, Marler M (1998) Annual and perennial grass growth on nitrogen-depleted decomposed granite. *Restor Ecol* 6: 175–180
- Zink TA, Allen MF (1998) The effects of organic amendments on the restoration of a disturbed coastal sage scrub habitat. *Restor Ecol* 6: 52–58
-

comes among studies, suggests that differences in sampling design (e.g., vote counting *versus* meta-analysis) might have affected the conclusions reached.

### *Problems with generalizing from studies of exotic-native pairs*

Most land managers deal with large multi-species communities that contain multiple exotic species (salt marsh dominated by *Spartina* spp is the exception, e.g., [28]). They are commonly interested in knowing, in general, how all of the exotic species in their area are affecting community and ecosystem processes. The literature that compares exotic and native species growth characteristics (e.g., [24, 25]) is highly relevant to these management issues. However, because species are not replicated in most comparisons of native and exotic species within a given site, results may not provide the best information for management. Results and conclusions will be as highly variable as the variation among species. As any basic statistics book will explain, a greater number of replicates will lead to more precise estimates that approach the actual mean. Using few or no replicates may be leading to the widely varying results, with some results falling well above the actual mean and some falling well below the actual mean. Among-species variation in morphological or physiological traits is enormous among both native and exotic species. Picking one species out of a large distribution will give much greater weight to outlier species and lead to widely varying conclusions among studies. Thus, I hypothesize that conclusions about exotic-native differences by Daehler [24] may have been different if species had been replicated within sites.

Another, but less common problem with exotic-native species comparisons is that growth form (e.g., annual *versus* perennial) is sometimes confounded with native-exotic status [29, 30]. In many cases, the objective of the researcher is to test hypotheses associated with how to restore native species dominance [29, 30]. In these cases, researchers sometimes choose a perennial native species to compare to an annual exotic. In this case, annual-perennial (i.e., successional stage) and native-exotic status are confounded. This makes sense in the context of restoration ecology, but it makes less sense in comparisons of natives to exotics (Tab. 1).

### **Literature review of native and exotic species comparisons**

Here, I analyze data from papers cited in the review by Daehler [24] as well as a few more recent studies, and break down the analysis into two data sets: those that compare a single pair of native and exotic species and those that replicate either native or exotic species, or both (Tab. 1). My prediction is that studies that replicate species within their study areas will give a more accurate estimate of the overall effect of exotic species, and will be less variable than studies that use single pairs within sites. Furthermore, I analyze a variable that

was not measured by Daehler [24], but that is important to grazed grasslands: tolerance to either real or simulated defoliation by grazers. There are few studies with replicated species responses to grazing or clipping, so this variable was analyzed with the combined data set (pooling replicated and non-replicated studies).

A total of 61 studies were analyzed. Of those 61 studies, only 10 replicated both native and exotic species (16%). Seven studies replicated natives only and 3 replicated exotics only, for another 16%. Most studies (41 out of 61, 67%) did not replicate either species type, i.e., they compared a single exotic species to a single native species (Tab. 1).

I found that results differed between studies that did and did not replicate native and exotic species (Fig. 1). I used a vote count technique [24] and classified studies into categories of 1) exotic mean > native mean, 2) no significant difference between exotic and native species means and 3) native mean > exotic mean. In contrast to Daehler [24], who classified studies as exotic = native if any of the natives equaled the exotic (which biases the results towards

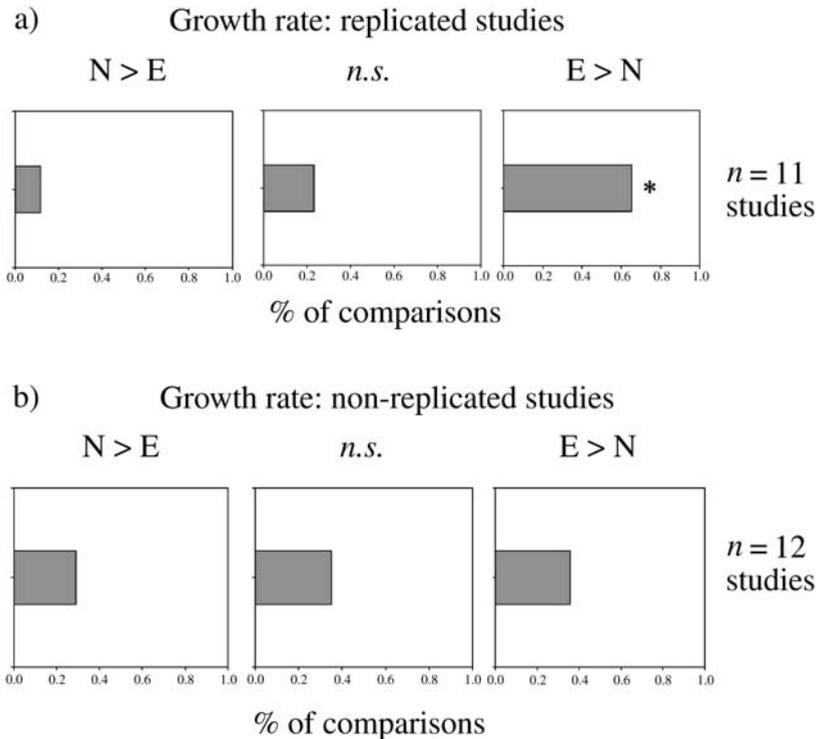


Figure 1. Proportion of studies cited by Daehler [24] that found higher growth rates in exotics than natives (E > N), no significant difference (n.s.), or higher rates in natives than exotics (N > E) among studies that replicated either native or exotic species identity, or both (a) or among studies that did not replicate species (b).

not finding overall differences), I based differences on the means for all native or exotic species. I only had enough data to test for above-ground growth rate variables because of the small number of studies that replicated species. In 11 studies that replicated either native or exotic species or both (Fig. 1a), I found a significant difference among outcomes (chi-squared exact test,  $\chi^2 = 6.3$ , 2 d.f.,  $P < 0.05$ ). Majority of studies (65%) found that exotic species had higher growth rates than natives (Fig. 1). Only 12% of studies found that native species had higher growth rates than exotics. Thus, this analysis supports the hypothesis that growth rate overall is higher in exotics than it is in natives. When I analyzed the data set that included studies that did not replicate species (Fig. 1b), I found no significant difference among the three outcomes (chi-squared exact test,  $\chi^2 = 0.1$ , 2 d.f.,  $P > 0.10$ ), which does not support the hypothesis that exotics differ from natives. Taken together, the difference between these two data sets suggests that conclusions about exotic species may change depending on whether species are replicated within groups. If multiple species were used, the (correct?) generalization reached was that exotics had higher growth rates than natives. If un-replicated species pairs were used, the (incorrect?) generalization is that there was no overall effect. This result is not entirely surprising. By using species pairs, one is less likely to find a difference between natives and exotics because of the very high variability among species. Replicating species leads to a more precise estimate of mean differences between native and exotic species within sites, which is an important variable to managers.

### *Grazing tolerance in exotic species*

Many plant species were introduced into North and South America, Australasia and elsewhere to improve grazing lands. In many cases, introductions were made of species that tolerate grazing well. For example, grasses from East Africa were introduced to many places because they evolved with large populations of grazing mammals [31, 32]. Tolerance is defined as having a smaller reduction (or even an increase) in relative growth rate due to compensatory growth after grazing or simulated grazing (i.e., clipping) [33–35]. An intolerant plant would have larger reductions in relative growth rate. A few influential early studies found that a native species was less tolerant of defoliation than an invading exotic species [8, 32]. Again, both of these studies used only a single native and exotic species. Based on these studies, the authors concluded that an exotic *Agropyron* (now *Pseudogneria* sp.) species was spreading in grazed grasslands of the inter-mountain western USA and an African grass was spreading across South America due their greater tolerance to grazing [8, 32].

I reviewed studies cited by Daehler [24] that included data on grazing or clipping tolerance in exotic and native species. By including several studies in my analysis, I could test the generality of the hypotheses of Caldwell et al. [8]

and Simoes and Baruch [32]. I found that out of seven studies, all but one found support for the hypothesis that exotics are more tolerant of grazing or clipping than native species (Fig. 2). Support of the hypothesis was found by Caldwell et al. [8], Pyke [10], Fan and Harris [36], Simoes and Baruch [32], Schierenbeck et al. [37], and Holmgren et al. [38]. Only one study [39] reported inconsistent results, with exotics being more tolerant to grazing only in situations where water availability was high. Thus, the overall data set seemed to support the hypothesis that exotics have higher grazing tolerance than natives. The higher tolerance of exotics to grazing may be important in their spread in grasslands, which could be due to the commonness of grazing by native and domestic animals throughout grasslands of the world. The processes underlying this phenomenon deserve much further research.

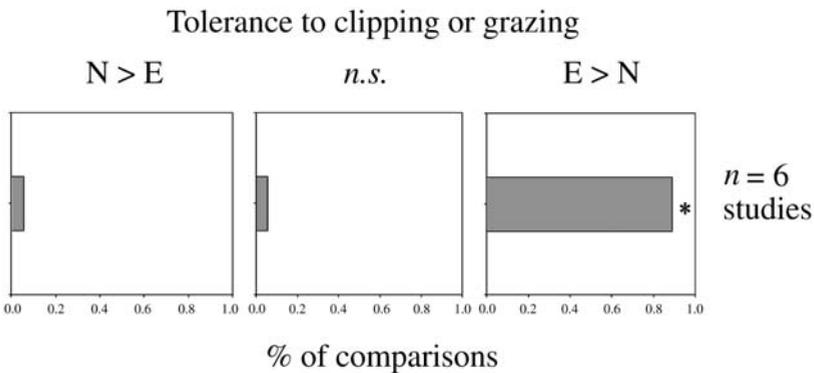


Figure 2. Proportion of studies cited by Daehler [24] that found higher tolerance to grazing or clipping in exotics than natives ( $E > N$ ), no significant difference (*n.s.*), or higher rates in natives than exotics ( $N > E$ ). Studies that either did or did not replicate species were combined due to small sample sizes.

### An experimental example on the importance of replication

In an ongoing experiment in the Texas Blackland Prairie region [40], we are comparing growth characteristics of the common exotic and native  $C_4$  grasses in the region. Plants are being compared in common garden monoculture plots, as well as in 2, 4, and 8 species mixtures. Small equal-sized transplants were planted into monoculture  $1\text{ m}^2$  plots (96 transplants per plot) in spring 2001 within three blocks (block term,  $F_{1,15} = 2.4$ ,  $P = 0.143$ ) and allowed to grow for two growing seasons before harvest. Plots were weeded when necessary. An estimate of average difference between exotics and natives is possible because species identity is replicated, with 3 exotic and 5 native species being represented (Fig. 3). A fixed effects model (that uses plots as the error term) is appropriate here because we have all the major native and exotic species in this system, and therefore, the choice of species would not change if we were to

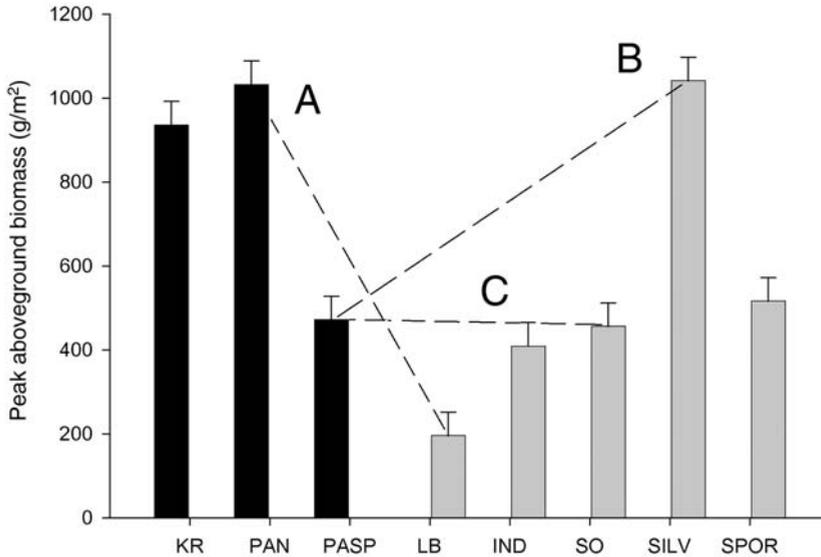


Figure 3. Peak biomass of exotic and native  $C_4$  grass species grown in a common garden through two growing seasons. Exotic species, which are denoted by black bars, are KR = King ranch bluestem, *Bothriochloa ischaemum*, PAN = Kleingrass, *Panicum coloratum*, and PASP = Dallisgrass, *Paspalum dilatatum*. Native species, which are denoted by gray bars, are LB = little bluestem, *Schizachyrium scoparium*, IND = indian grass, *Sorghastrum nutans*, SO = side-oats grama, *Bouteloua curtipendula*, SILV = silver bluestem, *Bothriochloa laguroides*, and SPOR = tall dropseed, *Sporobolus asper*. A, B, and C denotes the varying results that would have been found if species were not replicated and conclusions were based on comparisons of single exotic-native species pairs.

conduct the experiment a second time. Thus, we are attempting to determine if exotics differ from natives, but only at this site. Mean aboveground productivity (peak biomass) was  $813 \text{ g/m}^2$  for exotics and  $524 \text{ g/m}^2$  for natives, and this represents a highly significant difference ( $F_{1,15} = 49.1$ ,  $P < 0.001$ ). This represents a 55% increase in growth overall in exotics over natives. There was also a large amount of variation among species within native-exotic type ( $F_{6,15} = 29.8$ ,  $P < 0.001$ ). In order to compare our overall results with what would have been found if we had not replicated species, we back selected several species pairs to point out how variable results could have been. A, B and C in Figure 3 denote single species pairs, which might have been chosen for comparison. In scenario A, if these two species were pre-chosen for comparison, we would have made the correct qualitative generalization (exotic > native), but would have hugely overestimated the difference, i.e., a 428% increase in growth in the exotic. If the species pair in scenario B had been used, an incorrect generalization would have been reached: that exotic species had a 55% decrease in growth compared to the native species due the use of a non-representative native species, *Bothriochloa laguroides*. In scenario C, virtually no difference (3%) would have been found between the exotic and native species.

Thus, widely different conclusions would have been reached at this site if we had not replicated species in this study. By including the major native and exotic species from this system in our design, we were able to more accurately estimate the overall impact of exotic species in this system. Exotic species ecology will greatly benefit by developing a more community-level approach that replicates species [24].

### **Do exotic species affect species diversity-NPP relationships?**

There has been much recent interest in whether exotic species are lowering species diversity, and in turn, whether lowered species diversity will affect ecosystem process rates. Although 25% of the earth's surface is reported to be grassland, much of it is human-derived grassland, or grassland that assembled from previously farmed areas. Classical succession theory would predict that a high diversity native system would develop in these systems given enough time. However, this has not been the case. Many areas no longer have an adequate seed source of native species, or even if a seed source is available, native species have a multitude of exotic species to contend with during early community development. A few studies have shown that exotic grasslands tend to have lower diversity than do native grasslands, even many years after abandonment from agriculture [3, 11, 41]. However, in many cases, it is unknown whether this low diversity is caused solely by higher resource availabilities due to fertilizer carry-over [42–45], or if part of the effect is due to characteristics of the species themselves. Christian and Wilson [3] found that former Saskatchewan croplands planted with *Agropyron cristatum* had lower species diversity than adjacent unplanted areas even after many years of abandonment. Foster et al. [41] found that 34 species were largely unable to establish from seed in low diversity grassland patches with strong dominance by exotic grasses such as *Bromus inermis* in Kansas. I have found essentially zero seedling emergence in *Bromus inermis* plots within western Iowa (unpublished data). Less interest has been focused on whether exotic species affect species diversity-ecosystem functioning relationships [46, 47].

Although most researchers focus on the individual plant or population levels, invasive species establish and grow in communities. Higher aboveground growth rates by exotic species might lead not only to higher productivity, but to a greater rate of local species extinctions [40]. Loreau and Hector [48] outlined a powerful technique for partitioning the net biodiversity effect (i.e., yield of a plant species in mixtures compared to expectations from monocultures) into a selection and complementarity effect. The overall net biodiversity effect compares yield in mixtures to yield in monocultures. The partitioning method then breaks this overall effect into a selection and complementarity effect. These two effects can hypothetically range from negative to positive, and are combined to account for the net biodiversity effect. The complementarity effect combines the effects of niche differentiation and facilitation [48].

A positive selection effect occurs when species that are highly productive in monoculture are the ones over-yielding in mixture. Taken together, these two processes can increase the growth of mixtures above that which would be expected based on that expected from monocultures [48]. Loreau and Hector [48] used this technique on native species assemblages in Europe and found that the complementarity effect accounted for the higher yields in mixtures. The selection effect varied from negative to positive across sites and was less important than complementarity.

In contrast to the results of Loreau and Hector [48], we have found strong selection effects in native-exotic mixtures that are caused by exotic grasses. Polley et al. [49] found that both the selection and “complementarity” effects were negative in three species mixtures with annuals. The exotic *Lolium perenne* was the most important species in explaining negative selection effects. Wilsey and Polley [40] found a large positive selection effect that increased with species richness; a smaller complementarity effect was found only when mixtures were planted with high evenness. The strong selection effect, especially during the first year, was driven mostly by the exotic grass *Panicum coloratum*. Local species extinctions, which started in the second year of the study, were highest in species with low aboveground growth rates and in plots planted with low species evenness [40]. Taken together, these studies suggest that the dynamics of native-exotic mixtures may differ from mixtures with only native species. However, further research with a greater number of study systems is needed to determine how general this phenomenon is. Further monitoring of our experimental plots over many years will be helpful in determining whether local extinction rates are higher in plots as a function of the proportion of exotic species.

## Conclusions

I found that results from exotic-native comparisons differed depending on whether a single exotic-native species pair was compared or if replicated groups of exotics and native species were compared. Comparing groups of exotics to natives gave more consistent results, and supported the hypothesis that exotic species have higher aboveground growth rates than natives. Comparing single species gave more widely varying results because of the large amount of variation that exists among species. Of course, this variation among species is important and should be taken into account by land managers dealing with a new invasive species. Management plans will have to be somewhat species-specific in these cases. However, if the goal of a manager or policy maker is to develop a comprehensive general management plan for exotic species at a given site, or to develop ecological theories on exotic species effects, studies with replicated species will be highly useful.

There are other problems with studies that focus on native-exotic species pairs. For one, native species are not always picked randomly. Introduced spe-

cies are often selected for research studies because they are highly invasive and problematic in their area [25]. This is not surprising, but it makes it difficult to decide which native species should be chosen for comparison. Should the exotic be compared to an equally aggressive native species, or to a nonaggressive native? These choices have the potential to greatly impact the conclusions that are reached [25]. By focusing on the overall effects (i.e., mean of several species responses) of exotic species, the biases from individual (“outlier”) species are likely to be lessened. Thus, by replicating species, we may be able to increase the predictive power of invasive species ecology.

Finally, in addition to finding mean growth rate was higher in exotics than in natives in monocultures at our study site, we also found that exotic species can have especially large effects on productivity in mixture [40]. The higher growth rate of exotics in mixture [40] is potentially very important because it 1) may partially explain why exotic species are commonly associated with lower species diversity (i.e., exotics are causing diversity loss), and 2) could lead to altered ecosystem process rates. These issues deserve further study.

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