Temperature and functional traits influence differences in nitrogen uptake capacity between native and invasive grasses

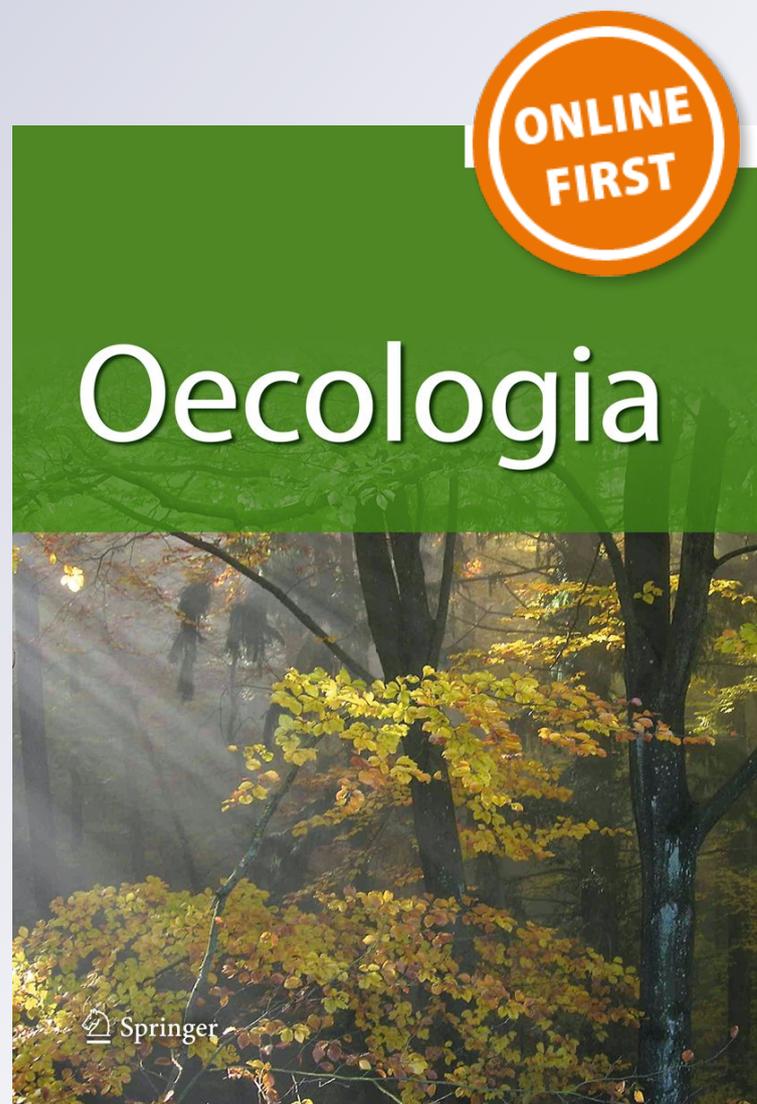## A. Joshua Leffler, Jeremy J. James & Thomas A. Monaco

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Temperature and functional traits influence differences in nitrogen uptake capacity between native and invasive grasses

**A. Joshua Leffler · Jeremy J. James ·
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Abstract Performance differences between native and exotic invasive plants are often considered static, but invasive grasses may achieve growth advantages in western North America shrublands and steppe under only optimal growing conditions. We examine differences in N uptake and several morphological variables that influence uptake at temperatures between 5 and 25 °C. We contrast two native perennial grasses in western North America: *Elymus elymoides* and *Pseudoroegneria spicata*; two invasive annual grasses: *Bromus tectorum* and *Taeniatherum caput-medusae*; and one highly selected non-native perennial grass: *Agropyron cristatum*. The influence of temperature on N uptake is poorly characterized, yet these invasive annual grasses are known to germinate in warm soils in the autumn, and both experience cool soils during the short growing season following snowmelt in the spring. To further explore the influence of temperature on the correlation between morphological variables and N uptake, our data are applied to a previously published path model and one proposed here. Differences in N uptake between native and invasive grasses were small at the lowest temperature, but were large at the highest temperature. At lower temperatures, uptake of N by annuals and perennials was correlated with leaf N and mass. At higher temperatures, uptake by annuals was correlated only with these leaf traits, but uptake by perennials was correlated with these leaf traits as well as root N and mass. Consequently, our results imply that annual grasses face fewer morphological constraints on N uptake than perennial grasses, and annual grasses may gain further advantage in warmer temperature conditions or during more frequent warm periods.

Keywords Cheatgrass · Exotic species · Medusahead · Specific absorption rate

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Introduction

The invasion and dominance of exotic annual plant species is often attributed to their ability to exploit resources either before, or to a greater extent than native species (Tilman 1985; Knapp 1996; Verdú and Traveset 2005; Chambers et al. 2007). Many invasive species have high specific leaf area (SLA) or specific root length (SRL), traits that promote rapid carbon and nitrogen acquisition, respectively (Grotkopp et al. 2002; Pyšek and Richardson 2007; Osone et al. 2008; James et al. 2009). Rapid resource acquisition can occur in these species because little biomass is dedicated to structural tissue (Westoby 1998) and respiration is primarily directed at growth rather than maintenance (Lambers and Poorter 1992). Rapid uptake of N by annuals can lead to soil conditions that are not favorable for the

establishment or persistence of longer-lived species (Wedin and Tilman 1993). Consequently, N uptake by exotic annual grasses can impact community assembly and facilitate invasion (Tilman 1985; Fargione et al. 2003).

Morphological traits such as SLA, considered 'acquisitive' on the tissue economics spectrum (Wright et al. 2004; Díaz et al. 2004), allow rapid uptake only under optimal growth conditions (Westoby 1998) such as high soil N availability (James 2008). Enzymatic processes such as N uptake are temperature dependent (Miller and Cramer 2004; Warren 2009); a species morphologically suited for rapid uptake may not achieve rapid uptake at suboptimal temperatures. While many root and leaf traits are correlated with N uptake (James 2008; James et al. 2009), the degree to which temperature changes the correlation of N uptake with traits such as SRL, R_M, SLA, and L_M (Table 1) is unknown. Furthermore, growth temperature can influence community assembly and invasion (Mooney 1976; Tilman 2004; McGill et al. 2006; Sandel and Dangremond 2011) because species differ in their temperature optima (Mooney 1980; Atkin and Tjoelker 2003).

The most extensive plant invasion in North America is the replacement of native perennial plant communities in the Great Basin by exotic annual grasses (D'Antonio and Vitousek 1992; Chambers et al. 2007). The invasive annual grass *Bromus tectorum* (cheatgrass) forms monocultures over millions of hectares in this region (Bradley and Mustard 2006). While plant growth in this cold desert is primarily in the spring (Caldwell 1985), *B. tectorum* can emerge in the autumn and continue to grow at low soil temperatures over winter (Harris and Wilson 1970). Consequently, when newly germinated perennials emerge in the spring, they face competition with larger annuals capable of rapidly drying soils and depleting soil N (Knapp 1996; Leffler et al. 2005; Chambers et al. 2007; Blank 2010; Ryel et al. 2010). Another exotic annual grass, *Taeniatherum caput-medusae* (medusahead), has a similar life history (Young 1992) and is widespread in the northern Great Basin.

Here, we examine root and shoot morphological traits and N uptake under various temperature conditions in several perennial and invasive annual grasses in the Great Basin. Our goals are to determine (1) if temperature has a different influence on N uptake by perennial and invasive annual grasses, (2) which root or leaf traits are most predictive of N uptake in these species, and (3) if predictive traits are the same regardless of temperature. We address these questions using measurements of shoot and root morphology and N uptake with plants raised in growth chambers. We subjected our data to path analysis, which allows independent assessment of the importance of variables that are correlated with each other. Two path models are evaluated: the first (Fig. 1a), published in James (2008), links N uptake to root length and root mass, while the second (Fig. 1b) links N uptake to leaf and root traits. We use these models to determine the relative importance of root and leaf traits in N uptake at different temperatures and discuss how our temperature-based experiments refine the current understanding of annual grass invasion and persistence in the Great Basin of western North America.

Materials and methods

Study species

Five common grasses were selected to address questions regarding N uptake by annual and perennial grasses. Three

Table 1 Path analysis model parameters, abbreviations, units, and indication if the parameter was log-transformed prior to analysis

Parameter	Abbreviation	Unit	Log-transform
Plant nitrogen uptake	PNU	µg N h^{-1}	Y
Mass-specific absorption rate	SAR_M	µg N g^{-1} root h^{-1}	Y
Area-specific absorption rate	SAR_A	µg N cm^{-2} root h^{-1}	Y
Length-specific absorption rate	SAR_L	µg N m^{-1} root h^{-1}	Y
Root length	R_L	cm	N
Root mass	R_M	g	Y
Leaf mass	L_M	g	Y
Leaf N concentration	$L_{[N]}$	mg leaf N g^{-1} leaf	Y
Root N concentration	$R_{[N]}$	mg root N g^{-1} root	N
Total leaf N	L_N	mg	N
Total root N	R_N	mg	N
Specific root length	SRL	cm root mg^{-1} root	Y
Specific leaf area	SLA	cm^2 leaf g^{-1} leaf	Y
Root weight ratio	RWR	g root g^{-1} plant	Y
Leaf N ratio	LNR	g leaf N g^{-1} plant N	N

(a) James (2008) path model

(b) N model
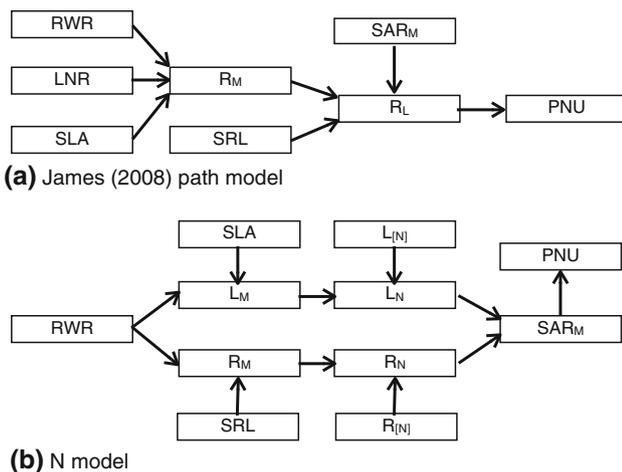
Fig. 1 Models used in path analysis. Parameter abbreviations are shown in Table 1. Model **a** attributes plant N uptake rate (PNU) primarily to root length and the morphological factors contributing to root length variation (James 2008). Model **b** attributes PNU to physiological processes involved in mass-specific absorption rate, which are constrained by morphological factors

of the grasses were cultivars of perennial species found throughout the Great Basin and commonly used in remediation of lands invaded by annual grasses. Two of the perennial grasses were native to this region, including Rattlesnake bottlebrush squirreltail germplasm [*Elymus elymoides* (Raf.) Sweezey ssp. *elymoides*] and Anatone bluebunch wheatgrass germplasm [*Pseudoroegneria spicata* (Pursh) A. Löve ssp. *spicata*]. *Elymus elymoides* was selected because it is a short-lived perennial that can naturally establish in annual-dominated ecosystems (Hironaka and Tisdale 1963; Hironaka and Sindelar 1973) while *P. spicata* is a long-lived perennial grass. The third perennial grass was Hycrest II crested wheatgrass [*Agropyron cristatum* (L.) Gaertn.], a widely planted non-native grass developed from several populations in central Asia. *Agropyron cristatum* was chosen for its vigorous growth and evidence that various cultivars of *A. cristatum* are largely resistant to invasion by annual grasses (Davies 2010; Fansler and Mangold 2011). Seeds of the two invasive annual grasses described above [*Bromus tectorum* L. and *Taeniatherum caput-medusae* (L.) Nevski] were collected from populations in northern Utah, USA. The three perennial grasses were certified as pure and were obtained from local seed producers.

Growth conditions, experimental treatments,
and measurements

Plants were grown in pots (4×21 cm 'cone-tainers'; Ray Leach, Canby, OR, USA) for the duration of the experiment. Pots were filled with a 1:1 mixture of a coarse and fine growth medium (Turface MVP and Greens Grade;

Profile Products, Buffalo Grove, IL, USA) holding ca. 0.5 g H_2O g^{-1} medium. The medium was rinsed with tap water several times before use to insure no nutrients were adsorbed to the particle surface. Three to five seeds of a single species were added to a pot and kept moist with periodic watering. Ten days following emergence, pots were transferred to growth chambers at constant temperature and a 14/10 h day/night cycle. Photosynthetic flux density inside the chambers was about 900 μmol m^{-2} s^{-1} above the uppermost leaves. After several days of growth, seedlings were thinned to two individuals per pot.

Plants were kept in four growth chambers at either 5, 10, 15, or 25 °C. Each week, plants and temperature conditions were rotated among chambers to minimize chamber effects. Chambers contained 20 pots of each species and temperature was recorded every 15 min (model Watchdog B101; Spectrum Technologies, Plainfield, IL, USA). While target temperatures were achieved at night, the daytime was 2–3 °C warmer than intended (8.0/4.9, 13.1/9.9, 18.1/14.9, and 28.6/24.8 °C day/night, respectively). Pots were maintained near saturation daily with an NH_4^+-free nutrient solution containing 0.20 g l^{-1} KNO_3, 0.21 g l^{-1} $Ca(NO_3)_2$, 0.06 g l^{-1} NaH_2PO_4, 0.12 g l^{-1} $MgSO_4$, and 0.3 g l^{-1} of a complete micronutrient fertilizer (J.R. Peters, Allentown, PA, USA).

We measured acquisition of NO_3^- by incubating roots in a $K^{15}NO_3$ solution (BassiriRad et al. 1993). Nitrate was chosen for this study because unlike NH_4^+, its uptake is not limited by soil properties, but is closely tied to uptake capacity (BassiriRad et al. 1993; Miller and Cramer 2004). In addition, high autumn $[NO_3^-]$ is common in annual-invaded systems in the Great Basin (Booth et al. 2003; Blank and Sforza 2007). Assays began with the 25 °C treatment 5 weeks following germination. Plants in other treatments were measured in 1-week intervals. We separated samples among several weeks to account for slower development of individuals in the colder treatments and to minimize differential pot effects among treatments. Ten pots of each species were randomly selected for measurement. Individual plants were removed from the pots and washed of growth medium. Plants from eight of the pots were placed in eight flasks, each containing 250 ml of 1 mM 60 atom % $K^{15}NO_3$ and 0.5 mM $CaSO_4$. Plants from the remaining two pots were treated as controls and placed in flasks of $K^{14}NO_3$. After a 2-h incubation at the same temperature as during growth, plants were removed from assay flasks and immersed in a chilled 50 mM KCl solution to stop NO_3^- acquisition. Plants were then washed five times in distilled water, and roots and shoots were stored frozen. Upon thawing, surface area of leaf tissue was measured with a leaf area meter (model 3100; Li-Cor, Lincoln, NB, USA) and root images were obtained with a flatbed scanner and analyzed for length and surface area

using the software package WinRhizo (v. 2005b; Regent Instruments, Quebec, QC, Canada). Root and shoot tissue was dried at 75 °C for at least 48 h, weighed, and ground to a fine powder using a shaker mill (model 2000; SPEX CertiPrep, Metuchen, NJ, USA). Tissue samples were analyzed for $[^{15}N]$ at the University of California, Davis Stable Isotope Facility. Excess ^{15}N in labeled compared to control root and shoot tissues were combined and NO_3^- acquisition is expressed as PNU, SAR_M, SAR_A, or SAR_L (Table 1). While this method quantifies NO_3^- uptake, it cannot fully account for NO_3^- efflux which may also vary with environmental conditions and among species (Scheurwater et al. 1999).

Statistical analysis

We analyzed differences in N uptake among species and treatments with two-way fixed-effect ANOVA using PROC GLM in SAS (v. 9.2; SAS Institute, Cary, NC, USA). Two analyses were performed, the first contained all species, while in the second, the annual grasses were combined, and the perennial grasses were combined to examine differences between the two life forms. *Agropyron cristatum* was omitted from this second analysis because it is a non-native perennial that has undergone multiple population crosses during its development.

The correspondence of morphological and physiological variables (Table 1) with PNU was assessed with two path analysis models (Fig. 1) using PROC CALIS. The first was based on relationships between root structure and growth rate (James 2008). Because we did not measure RGR in this study, an alternative path model was tested based on the physiology of N uptake as an active process (Miller and Cramer 2004) and consequently correlated with L_N and R_N (Table 1). For both path models, three separate analyses were performed. The first included all five species (full analysis); the second included only the annuals, while the third included only the perennials (excluding *A. cristatum*). All parameters were determined with maximum-likelihood estimation and significance was assessed with confidence intervals. Several of the variables were log-transformed for normality (Table 1). Each analysis included all temperature conditions.

Variables that were significant in the second path model with all species were examined for differences between invasive annuals and native perennials (excluding *A. cristatum*) using effect size statistics. We used the standardized mean difference (Hedges' g) as a test statistic and 95 % confidence intervals about g were determined from the non-central t-distribution using Package MBESS within the R Statistical Computing Language (R Development Core Team 2005). Effect size was computed first for all

temperature treatments, second for the 5 °C treatment, and finally for the 25 °C treatment.

Results

Species differed in their capacity to acquire N and temperature had a significant influence on N uptake (Table 2). We observed a significant species by temperature interaction for PNU and SAR_M. This interaction is evident in the distinction between *E. elymoides,* which maintained low uptake regardless of temperature, and *T. caput-medusae,* which responded to higher temperatures with a considerable increase in uptake capacity (Fig. 2; Online Resource 1, multiple comparisons). At 5 °C, all species except *E. elymoides* had statistically similar SAR_M, but at 25 °C, differences among species were evident (Fig. 2). We observed the same interaction between invasive annuals and native perennial grasses (Table 2). At 5 °C, SAR_M of perennials was 82 % of SAR_M by annuals; at 25 °C SAR_M by perennials was 51 % of SAR_M by annuals (Fig. 2). Of the three perennial grasses, only *A. cristatum* had SAR_M near that of the annual grasses; *A. cristatum* and *B. tectorum* had similar SAR_M, but SAR_M of *T. caput-medusae* exceeded SAR_M of *A. cristatum*, especially at high temperatures. Throughout the study, SAR_M, SAR_L, SAR_A, and PNU were highly correlated (Table 3). SAR_M is reported throughout the paper for comparison with other studies. Figures of morphological differences among species and temperature conditions are shown in Online Resource 2.

The first path model (Fig. 1a) suggests the importance of SAR_M, R_L, R_M, and SRL in determining PNU (Fig. 3). The strongest relationship (partial $r < 0.82$) for the full, annual, and perennial analyses was between SAR_M and R_L. Root length, however, was a much stronger predictor of PNU in perennials than in annuals (partial $r = 0.59$ vs. 0.10, respectively). Overall, the strongest morphological predictor of PNU was R_M, although SRL was also important.

The second path model demonstrates the significance of L_N, $L_{[N]}$, and L_M in predicting SAR_M (Fig. 4) and suggests that leaf physiological processes are important in determining PNU. For the full, annual, and perennial analyses, partial r exceeded 0.91 between SAR_M and PNU. The pathway through R_N, was significant, but less so than the pathway through L_N (full analysis partial $r = 0.28$ and 0.49, respectively); the R_N pathway was more important for perennials (partial $r = 0.22$) than annuals (partial $r = 0.06$). Overall the strongest morphological predictor of PNU was L_M.

Many of the variables that were significant predictors of PNU were different between annual and perennial grasses regardless of temperature condition. Large effect sizes ($g > 0.8$) were observed in SAR_M and SRL, but L_N, R_N,

Table 2 Two-way ANOVA examining differences among species (*Sp*) and temperature (*Temp*) treatments

Effect	Full analysis			Annual versus perennial analysis		
	df	F	P	df	F	P
PNU						
Sp	4	75.5	<0.001	1	143	<0.001
Temp	3	281	<0.001	3	158	<0.001
Sp × temp	12	9.45	<0.001	3	4.86	0.003
SAR_M						
Sp	4	51.38	<0.001	1	169	<0.001
Temp	3	104	<0.001	3	100	<0.001
Sp × temp	12	9.77	<0.001	3	16.2	<0.001

The 'full analysis' compares all species while the 'annual versus perennial model' treats *B. tectorum* and *T. caput-medusae* as annuals, and *P. spicata* and *E. elymoides* as perennials and determines if they are different from each other. This model excludes *A. cristatum,* which has been highly modified by artificial selection
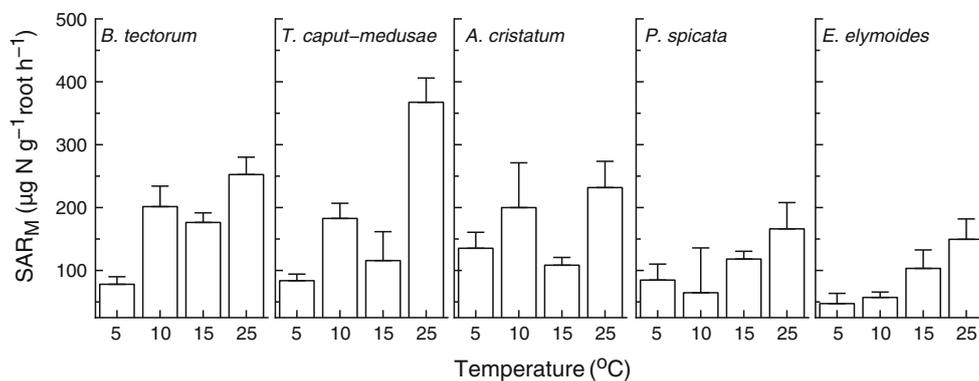
Fig. 2 Mass specific absorption rate (SAR_M) of NO_3^- for each species at all temperature conditions examined. *Open bars* represent the mean SAR_M with *whiskers* indicating the 95 % confidence interval. See Online Resource 1 for multiple comparisons among species and temperature conditions

Table 3 Pearson correlation coefficients; *P*-values for uptake variables

|	SAR_M	SAR_L	SAR_A
PNU	0.908; <0.001	0.892; <0.001	0.947; <0.001
SAR_M		0.825; <0.001	0.902; <0.001
SAR_L			0.966; <0.001

$n = 156$ for each correlation

L_M and R_M were also significantly greater in annuals compared to perennials (Fig. 5, upper panel). Annuals were 90, 47, 34, 32, 29, and 32 % greater than perennials in SAR_M, SRL, L_N, R_N, L_M, and R_M, respectively (Table 4). Annuals and perennials were similar in $R_{[N]}$ and RWR. $L_{[N]}$ was only marginally greater in annuals (Fig. 5, upper panel).

Differences between annual and perennial grasses were temperature dependent (Fig. 5, lower two panels). For most variables, the effect size was greater at 25 °C (mean $g = 1.27$) than at 5 °C (mean $g = 0.31$). The difference between annuals and perennials for R_N and SRL was not significant at 5 °C, but at 25 °C, annuals had higher values than perennials for these two variables. This difference has important implications for interpretation of the path models at low and high temperatures. At 5 °C, since R_N is 'downstream' in the path model, and not significantly different between annuals and perennials, all 'upstream' variables are also not important at this temperature. Consequently, at 5 °C, only leaf traits are important for distinguishing PNU between annuals and perennials, whereas at 25 °C, both leaf and root traits are important.

Discussion

We observed species-specific responses to temperature for N uptake. Differences among species in ability to acquire N are well documented (Chapin et al. 1986; Warren 2009) and can arise directly from specialization on N-form (McKane et al. 2002; Aanderud and Bledsoe 2009), root
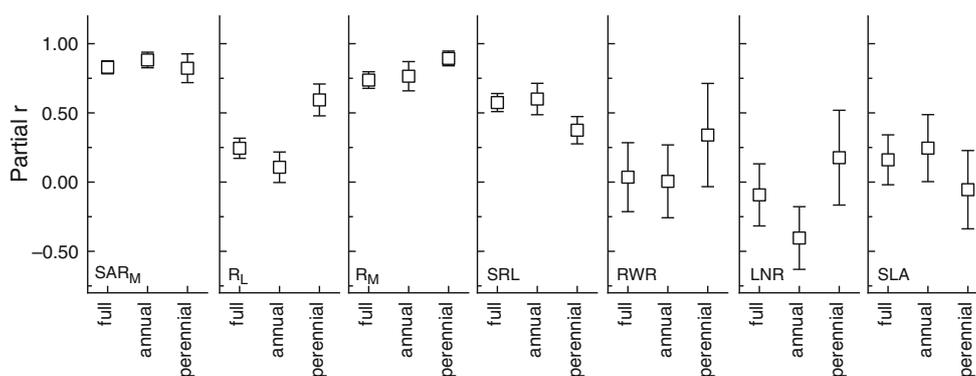
Fig. 3 Partial correlation coefficients for path model A in Fig. 1. *Whiskers* indicate 95 % confidence interval about the estimated coefficient; *whiskers* that overlap 0 are not significant predictors in the model. The *x*-axis indicates which analysis is reported: *full* analysis of all species, all temperatures; *annual* analysis of *B. tectorum* and *T. caput-medusae*, all temperatures; *perennial* analysis of *P. spicata* and *E. elymoides*, all temperatures
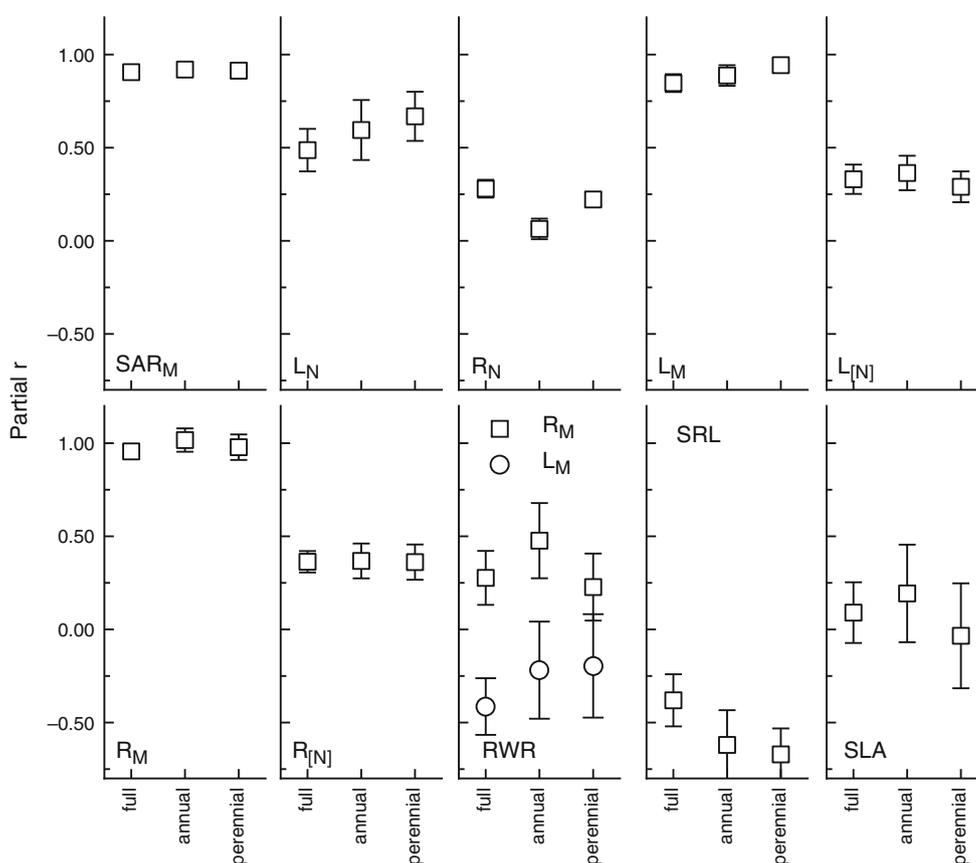
Fig. 4 Legend as in Fig. 3 but pertaining to path model B in Fig. 1. For RWR, *squares* indicate partial correlation with R_M, *circles* indicate partial correlation with L_M, see Fig. 1

tissue density or surface area (Comas et al. 2002), density of uptake proteins (Glass et al. 2001), differences in biomass allocation to root tissue (Agren and Franklin 2003), coordination of nitrogen acquisition and RGR (Rodgers and Barneix 1988), or species differences in transpiration rate influencing mass flow of ions in soils (Warren 2009). Sensitivity of N acquisition to temperature has been demonstrated previously for *B. tectorum* (Leffler et al. 2011), but not for *T. caput-medusae*, which was the most sensitive in this study. Of the species examined here, all but *E. elymoides* had the same N acquisition at 5 °C (Fig. 2), despite previous studies suggesting many of these species differ in root elongation at low temperatures (Harris and Wilson 1970; Eissenstat and Caldwell 1987). Our findings
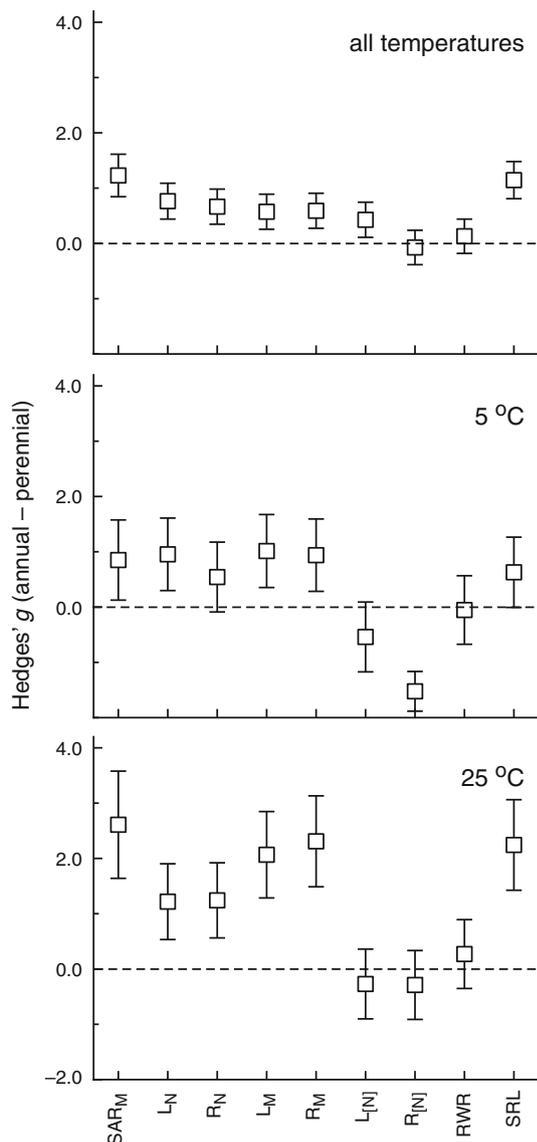
Fig. 5 Effect size of the standardized mean difference between invasive annuals (*B. tectorum* and *T. caput-medusae*) and native perennials (*P. spicata* and *E. elymoides*) in traits that were significant from path model B. *Points* indicate Hedges' *g* and *whiskers* indicate the 95 % confidence interval for this statistic. *Whiskers* that overlap 0 indicate that trait does not differ between invasive annual and native perennial species. Differences were calculated for all temperature conditions combined, or for only 5 °C, and only for 25 °C

grasses is likely responsible for lower SAR_M (Lambers and Poorter 1992; Ryser and Eek 2000; Comas et al. 2002). We hypothesize that low plasticity in N uptake among temperatures in the perennial grasses is a consequence of the predictable springtime pulse of water and nutrients in Great Basin shrublands (Ryel et al. 2010). High plasticity is typically associated with unpredictable environments (Droste et al. 2010); however, the root zone of grasses reliably saturates even in poor snowfall years (Ryel et al. 2010), and this pulse occurs when soils are cool (Caldwell 1985). A previous study with younger plants found low absolute N uptake capacity and low plasticity with respect to temperature in *T. caput-medusae* (Leffler et al. 2011). This difference may be caused by lower soil N availability or inadequate induction of N uptake by younger plants in the previous study.

Despite *A. cristatum* being a perennial grass, under all temperature conditions it had the same or greater SAR_M as the annual *B. tectorum*. This exotic grass was developed by artificial selection from numerous populations in central Asia (Wang and Jensen 2009). Plantings throughout the Intermountain West are largely resistant to invasion by annual grasses even following moderate disturbance (Davies 2010; Fansler and Mangold 2011). Because breeding efforts involved selection for early and rapid emergence, productivity, and seed production, our results suggests that these efforts may have inadvertently selected for high SAR_M. Future experiments should explore the possibility that high SAR_M in *A. cristatum* contributes to the long-term stability of plantings in heavily disturbed regions (Fansler and Mangold 2011).

Regardless of the path model we explored, SAR_M was the best predictor of PNU. James (2008) concluded SAR_L had little influence on N capture at different levels of N availability; however, James (2008) measured long-term rather than instantaneous uptake and examined the influence of N availability on N capture. James (2008) suggested R_L as a significant predictor of PNU. Here, the first path model (Fig. 1a) demonstrated that R_L was only marginally important in describing PNU by annuals, but R_L was a significant predictor of PNU by perennials (Fig. 3). Consequently, PNU by annuals was not limited by R_L and it remains unexplained in this model. R_L in perennials further corresponded with SRL while RWR and SLA were not predictors of PNU, consistent with the conclusions of James (2008), but not others (Garnier et al. 1995).

The second path model (Fig. 1b) illustrates the importance of L_N over R_N in predicting SAR_M. R_N was a significant predictor of SAR_M in perennials but not in annuals, but our data indicate that L_N was highly predictive of SAR_M in both groups. Therefore, R_N, a function of root mass and density of NO_3^- transport proteins (Glass et al. 2001), may limit N uptake by perennials. Conversely,

of similar uptake among species at low temperature are compatible with different root elongation rates since these species also differ in nitrogen productivity (Garnier et al. 1995; James 2008).

The largest distinction in N uptake capacity was between native perennial grasses and invasive annuals. As previously observed, SAR_M in perennials was lower and less plastic in response to temperature than in annuals (BassiriRad et al. 1993, 1999; Leffler et al. 2011). Greater investment in long-lived leaves and roots by perennial

Table 4 Mean (standard deviation) and sample size for annuals (*B. tectorum* and *T. caput-medusae*), perennials (*E. elymoides* and *P. spicata*), and *A. cristatum* among all temperature conditions

	Annuals		Perennials		*A. cristatum*	
	Mean (SD)	n	Mean (SD)	n	Mean (SD)	n
SAR_M	187 (95.7)	62	98.7 (48.8)	62	169 (78.0)	32
L_N	20.0 (6.44)	80	14.9 (6.86)	77	23.6 (9.71)	39
R_N	6.37 (2.37)	81	4.86 (2.19)	80	5.40 (1.58)	40
L_M	0.564 (0.239)	81	0.436 (0.215)	78	0.799 (0.306)	40
$L_{[N]}$	37.9 (7.70)	79	34.8 (5.70)	77	31.8 (9.26)	39
R_M	0.318 (0.141)	80	0.241 (0.120)	80	0.310 (0.121)	40
$R_{[N]}$	20.9 (3.42)	80	21.2 (4.66)	79	18.6 (3.68)	40
RWR	0.361 (0.042)	81	0.356 (0.054)	79	0.283 (0.075)	40
SRL	8.89 (3.47)	80	6.043 (1.45)	79	6.36 (1.43)	39

See also Online Resource 2 for additional figures

uptake of N in annuals and perennials is related to L_N, which has been linked to photosynthetic capacity (Evans 1989). High L_N and rapid uptake allow rapid growth (Eissenstat 1991; Ryser and Eek 2000; Comas et al. 2002), which may lead to size asymmetric competition, early resource acquisition (Wedin and Tilman 1993), and possibly facilitate invasion (Grotkopp et al. 2002; Pyšek and Richardson 2007; James et al. 2009).

Differences between annuals and perennials were temperature dependent. The best predictor of PNU, SAR_M, was only marginally different between annuals and perennials at 5 °C (Fig. 5). Additionally, because R_N is similar in annuals and perennials at low temperatures, the root component of the model is not important at low temperatures. Accordingly, during much of the cool growing season, N uptake by annual and perennial grasses appears to be a function of accumulated aboveground biomass and N. During warm periods, however, N uptake by perennials is potentially limited by belowground biomass and N accumulation, while annuals do not face a similar constraint. Hence, this interpretation suggests that, under warm conditions, annuals face fewer constraints on N uptake than perennials.

Our results contribute to a more complete understanding of how annual grasses exclude native perennials in the Great Basin. Previous work has suggested that annual grasses are capable of rapid root elongation even at low temperatures (Harris and Wilson 1970). Here, we suggest similar N uptake capacity between annuals and perennials at low temperatures, but greater uptake capacity by annuals at high temperatures. Our assessment of greater differences in N uptake under warmer temperatures provides an explanation of how annual grass germination in the fall, when soils are warm and NO_3^- is available (Booth et al. 2003; Blank and Sforza 2007), improves their likelihood of colonization. While these grasses can achieve rapid N

uptake following fall germination, they remain small (Leffler et al. 2011). During the winter and spring, annual grasses continue to grow at low temperatures (Harris and Wilson 1970) and have a large root system relative to perennials that emerge following snowmelt. When temperatures warm as the spring progresses, annuals rapidly exploit soil N because they face fewer constraints than perennials, i.e., they have accumulated more biomass and N belowground. However, if established perennial grasses become active following fall rains, they may be capable of preventing germinating annuals from accessing soil N despite lower N uptake capacity of perennials (Beckstead and Augspurger 2004; Prevéy et al. 2010). Consequently, maintenance of a healthy perennial flora is necessary to prevent annual invasion in these systems, and annuals need to be controlled if perennials are to be restored (Davies 2010).

Our interpretation of the interaction between species and temperature not only suggests how temperature might influence the species composition of a community but it also has clear implications for a warming climate. Here, N uptake of native perennial grasses and invasive annual grasses are both suppressed by low temperatures, but increasing temperatures would have a greater influence on annual grass performance. In a warming world, annual grasses may gain further advantage (D'Antonio and Vitousek 1992; Dukes and Mooney 1999; Sandel and Dangremond 2011) through changes in the length of the frost-free season, winter precipitation, and/or fire frequency (Abatzoglou and Kolden 2011). Our results suggest changes in the nitrogen cycle (Booth et al. 2003) through more rapid N uptake by annual grasses may be another threat to already vulnerable sagebrush ecosystems (Bradley 2010).

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References

Aanderud ZT, Bledsoe CS (2009) Preferences for N-15-ammonium, N-15-nitrate, and N-15-glycine differ among dominant exotic and subordinate native grasses from a California oak woodland. Environ Exp Bot 65:205–209

Abatzoglou JT, Kolden CA (2011) Climate change in western US deserts: potential for increased wildfire and invasive annual grasses. Rangel Ecol Manag 64:471–478

Agren GI, Franklin O (2003) Root : shoot ratios, optimization and nitrogen productivity. Ann Bot 92:795–800

Atkin OK, Tjoelker MG (2003) Thermal acclimation and the dynamic response of plant respiration to temperature. Trends Plant Sci 8:343–351

BassiriRad H, Caldwell MM, Bilbrough C (1993) Effects of soil temperature and nitrogen status on kinetics of $^{15}NO_3^-$ uptake by roots of field-grown *Agropyron desertorum*. New Phytol 123:485–489

BassiriRad H, Tremmel DC, Virginia RA, Reynolds JF, de Soyza AG, Brunell MH (1999) Short-term patterns in water and nitrogen acquisition by two desert shrubs following a simulated summer rain. Plant Ecol 145:27–36

Beckstead J, Augspurger CK (2004) An experimental test of resistance to cheatgrass invasion: limiting resources at different life stages. Biol Invasions 6:417–432

Blank RR (2010) Intraspecific and interspecific pair-wise seedling competition between exotic annual grasses and native perennials: plant-soil relationships. Plant Soil 326:331–343

Blank RR, Sforza R (2007) Plant-soil relationships of the invasive annual grass *Taeniatherum caput-medusae*. Plant Soil 298:7–19

Booth MS, Stark JM, Caldwell MM (2003) Inorganic N turnover and availability in annual- and perennial-dominated soils in a northern Utah shrub-steppe ecosystem. Biogeochemistry 66:311–330

Bradley BA (2010) Assessing ecosystem threats from global and regional change: hierarchical modeling of risk to sagebrush ecosystems from climate change, land use and invasive species in Nevada, USA. Ecography 33:198–208

Bradley BA, Mustard JF (2006) Characterizing the landscape dynamics of an invasive plant and risk of invasion using remote sensing. Ecol Appl 16:1132–1147

Caldwell M (1985) Cold desert. In: Chabot BF, Mooney HA (eds) Physiological ecology of North American Plant Communities. Chapman and Hall, New York, pp 198–212

Chambers JC, Roundy BA, Blank RR, Meyer SE, Whittaker A (2007) What makes great basin sagebrush ecosystems invasible by *Bromus tectorum*? Ecol Monogr 77:117–145

Chapin FS III, Van Cleve K, Tryon PR (1986) Relationship of ion absorption to growth rate in taiga trees. Oecologia 69:238–242

Comas LH, Bouma TJ, Eissenstat DM (2002) Linking root traits to potential growth rate in six temperate tree species. Oecologia 132:34–43

D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annu Rev Ecol Syst 23:63–87

Davies KW (2010) Revegetation of medusahead-invaded sagebrush steppe. Rangel Ecol Manag 63:564–571

Díaz S et al (2004) The plant traits that drive ecosystems: evidence from three continents. J Veg Sci 15:295–304

Droste T, Flory SL, Clay K (2010) Variation for phenotypic plasticity among populations of an invasive exotic grass. Plant Ecol 207:297–306

Dukes JS, Mooney HA (1999) Does global change increase the success of biological invaders. Trends Ecol Evol 14:135–139

Eissenstat DM (1991) On the relationship between specific root length and rate of root proliferation: a field study using citrus rootstocks. New Phytol 118:63–68

Eissenstat DM, Caldwell MM (1987) Characteristics of successful competitors: an evaluation of potential growth rate in two cold desert tussock grasses. Oecologia 71:167–173

Evans JR (1989) Photosynthesis and nitrogen relationships in leaves of C_3 plants. Oecologia 78:9–19

Fansler VA, Mangold JM (2011) Restoring native plants to crested wheatgrass stands. Restor Ecol 19:16–23

Fargione J, Brown CS, Tilman D (2003) Community assembly and invasion: an experimental test of neutral versus niche processes. Proc Natl Acad Sci USA 100:8916–8920

Garnier E, Gobin O, Poorter H (1995) Nitrogen productivity depends on photosynthetic nitrogen use efficiency and on nitrogen allocation within the plant. Ann Bot 76:667–672

Glass ADM, Brito DT, Kaiser BN et al (2001) Nitrogen transport in plants, with an emphasis on the regulation of fluxes to match plant demand. J Plant Nutr Soil Sci-Zeitschrift Fur Pflanzernernahrung Und Bodenkunde 164:199–207

Grotkopp E, Rejmánek M, Rost TL (2002) Toward a causal explanation of plant invasiveness: seedling growth and life-history strategies of 29 pine (Pinus) species. Am Nat 159:396–419

Harris GA, Wilson AM (1970) Competition for moisture among seedlings of annual and perennial grasses as influenced by root elongation at low temperature. Ecology 51:530–534

Hironaka M, Sindelar BW (1973) Reproductive success of squirreltail in medusahead infested ranges. J Range Manag 26:219–221

Hironaka M, Tisdale EW (1963) Secondary succession in annual vegetation in Southern Idaho. Ecology 44:810–812

James JJ (2008) Leaf nitrogen productivity as a mechanism driving the success of invasive annual grasses under low and high nitrogen supply. J Arid Environ 72:1775–1784

James JJ, Mangold JM, Sheley RL, Svejcar T (2009) Root plasticity of native and invasive Great Basin species in response to soil nitrogen heterogeneity. Plant Ecol 202:211–220

Knapp PA (1996) Cheatgrass (*Bromus tectorum* L) dominance in the Great Basin Desert. Glob Environ Change 6:37–52

Lambers H, Poorter H (1992) Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. Adv Ecol Res 23:187–261

Leffler AJ, Peek MS, Ryel RJ, Ivans CY, Caldwell MM (2005) Hydraulic redistribution through the root systems of senesced plants. Ecology 86:633–642

Leffler AJ, Monaco TA, James JJ (2011) Nitrogen acquisition by annual and perennial grass seedlings: testing the role of performance and plasticity to explain plant invasion. Plant Ecol 212:1601–1611

McGill BJ, Enquist BJ, Weiher E, Westoby M (2006) Rebuilding community ecology from functional traits. Trends Ecol Evol 21:178–185

McKane RB et al (2002) Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. Nature 415:68–71

Miller AJ, Cramer MD (2004) Root nitrogen acquisition and assimilation. Plant Soil 274:1–36

Mooney HA (1976) Some contribution of physiological ecology to plant population biology. Syst Bot 1:269–283

Mooney HA (1980) Photosynthetic plasticity of populations of *Heliotropium curassavicum* L. originating from differing thermal regimes. Oecologia 45:372–376

Osone Y, Ishida A, Tateno M (2008) Correlation between relative growth rate and specific leaf area requires associations of specific leaf area with nitrogen absorption rate of roots. New Phytol 179:417–427

Prevéy JS, Germino MJ, Huntly NJ, Inouye RS (2010) Exotic plants increase and native plants decrease with loss of foundation species in sagebrush steppe. Plant Ecol 207:39–51

Pyšek P, Richardson DM (2007) Traits associated with invasive alien plants: where do we stand? In: Nentwig W (ed) Biological invasions, vol 193. Springer, Berlin, pp 97–125

R Development Core Team (2005) R: A language and environment for statistical computing, reference index version 2.10.1. R Foundation for Statistical Computing, Vienna, Austria

Rodgers CO, Barneix AJ (1988) Cultivar differences in the rate of nitrate uptake by intact wheat plants as related to growth rate. Physiol Plant 72:121–126

Ryel RJ, Leffler AJ, Ivans C, Peek MS, Caldwell MM (2010) Functional differences in water-use patterns of contrasting life forms in Great Basin steppelands. Vadose Zone J 9:548–560

Ryser P, Eek L (2000) Consequences of phenotypic plasticity versus interspecific differences in leaf and root traits for acquisition of aboveground and belowground resources. Am J Bot 87:402–411

Sandel B, Dangremond EM (2011) Climate change and the invasion of California by grasses. Glob Change Biol 18:277–289

Scheurwater I et al (1999) Relatively large nitrate efflux can account for the high specific respiratory costs for nitrate transport in slow-growing grass species. Plant and Soil 215:123–134

Tilman D (1985) The resource-ratio hypothesis of plant succession. Am Nat 125:827–852

Tilman D (2004) Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. Proc Natl Acad Sci USA 101:10854–10861

Verdú M, Traveset A (2005) Early emergence enhances plant fitness: a phylogenetically controlled meta-analysis. Ecology 86:1385–1394

Wang R, Jensen KB (2009) Chapter 3: Wheatgrass and wildryes. In: Singh RJ (ed) Genetic resources, chromosome engineering, and crop improvement. Forage crops, vol 5, CRC Press, Boca Raton, FL, pp 41–79

Warren CR (2009) Why does temperature affect relative uptake rates of nitrate, ammonium and glycine: a test with *Eucalyptus pauciflora*. Soil Biol Biochem 41:778–784

Wedin D, Tilman D (1993) Competition among grasses along a nitrogen gradient: initial conditions and mechanisms of competition. Ecol Monogr 63:199–229

Westoby M (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. Plant Soil 199:213–227

Wright IJ et al (2004) The worldwide leaf economics spectrum. Nature 428:821–827

Young JA (1992) Ecology and management of medusahead (*Taeniatherum caput-medusae* ssp. Asperum [Simk.] Melderis). Gt Basin Nat 52:245–252