Rapid foliar uptake of inorganic and amino acid nitrogen in three dryland plant species

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Research Article

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Abstract

Background and aims

Dryland primary production is often nitrogen (N) limited due in part to spatiotemporal decoupling of soil nutrient availability and plant uptake. Our aim is to quantify inorganic and organic N uptake at daily timescales to compare short-term nutrient acquisition patterns among dryland plant species.

Methods

We assessed N uptake in three commonly co-occurring perennial plant species from a Chihuahuan Desert grassland (a C_4 grass, C_3 grass, and C_3 subshrub). In the greenhouse, we applied ^{15}N-ammonium, nitrate, or glutamate tracers to plant roots and quantified uptake and recovery in leaves after 12, 24, and 48 h.

Results

Plants took up inorganic and amino acid N to leaves as rapidly as 12 h following application, and uptake more than doubled between 24 and 48 h. Inorganic N uptake was 3-4x higher than glutamate in all three species, and plants took up ammonium and nitrate at 2-3x faster rates overall. On average, *Bouteloua eriopoda* had the highest inorganic N recovery and uptake rates, while *Gutierrezia sarothrae* had the highest glutamate uptake over time. *Achnatherum hymenoides* uptake was ~50% lower than the other two species after 48 h.

Conclusion

Plants showed similar patterns of short-term foliar uptake and recovery indicating a lack of niche partitioning by N form among the three dryland species measured. Our results suggest that soil inorganic N, particularly nitrate, may comprise a greater proportion of plant N nutrition than amino acid-N and may be more widely exploited following a precipitation pulse in this habitat.

Abbreviations

N – nitrogen, NH_4^+ – ammonium, NO_3^- – nitrate, glu – glutamate, dw – dry weight

Introduction

In dryland ecosystems, aboveground primary production is constrained by the episodic availability of soil water and nitrogen (N) for plant uptake (Hooper and Johnson 1999;

47 Reichmann et al. 2013; Yahdjian 2011). The amount and forms of plant-available soil N are
48 restricted by low organic matter inputs (Hou et al. 2021; Stursova et al. 2006), high gaseous N
49 losses (Homyak et al. 2016; Leitner et al. 2017; Whitford and Duval 2019), and seasonal soil
50 moisture fluctuations which impact rates of soil N cycling processes (Austin et al. 2004; Hartley
51 et al. 2007; Lajtha and Schlesinger 1986; Reynolds et al. 2003). Additionally, microbial N
52 transformations (e.g., mineralization and nitrification) can happen within minutes following soil
53 rewetting (Jackson et al. 1989; Krichels et al. 2022), and bioavailable sources of N can be
54 depleted or lost to the atmosphere within < 24 hours of a precipitation event if plant uptake is
55 decoupled from microbial release (Brown et al. 2022; Collins et al. 2008; Schimel and Bennett
56 2004). Thus, knowing when and how rapidly different plants acquire different soil N forms for
57 growth is important to understanding patterns of N availability and loss in dryland soils (Homyak
58 et al. 2016).

59 Numerous studies indicate that roots of both mycorrhizal and non-mycorrhizal plants can
60 acquire multiple forms of soil N, including inorganic compounds such as nitrate (NO_3^-) and
61 ammonium (NH_4^+), as well as dissolved organic N forms like amino acids, peptides, and proteins
62 (Daly et al. 2021; Farrell et al. 2013; Hill and Jones 2019; Smith and Chalk 2021; Warren 2014;
63 Wilkinson et al. 2015). For agricultural plant species, N uptake and recovery are well detailed
64 and have been previously reviewed (Engels and Marschner 1995; Farzadfar et al. 2021; Glass
65 2003; Smith and Chalk 2020; Vidal et al. 2020), but these rates are difficult to compare with
66 dryland species since most agroecosystem-based experiments use irrigated crop plants and often
67 apply N fertilizers to soils at higher concentrations than what would be found in natural systems
68 (Farzadfar et al. 2021; Jones et al. 2009). In non-cultivated plant communities, plant uptake of
69 free amino acids can be significantly greater than inorganic N from soils (Bueno et al. 2019; Hill

et al. 2011; Li et al. 2016; Näsholm and Persson 2001), and soil organic N can make up a significant portion of plant nutrition in seasonally N-limited arctic, boreal and alpine ecosystems (Lipson and Näsholm 2001; Miller and Bowman 2003; Näsholm et al. 2009; Schimel and Chapin 1996). Compared to these more mesic habitats, there is limited information on the concentrations and relative contribution of soil organic N to dryland plant N nutrition. Few comparative studies of dryland plants have generally found higher recovery and 1.5-5x greater rates of inorganic N uptake compared to amino acids like glycine (Aanderud and Bledsoe 2009; Jin and Evans 2010; Ouyang et al. 2016; Yang et al. 2022; Zhuang et al. 2020), although experimental methods and species vary. Understanding the limitations on soil N availability as well as the patterns of dryland plant N uptake may ultimately expand our knowledge of how resource-limited plants adapt different strategies for acquiring soil N and contribute to a better understanding of N cycling processes and ecosystem functioning in drylands.

In addition to gaining a more complete picture of the dryland N cycle, another reason to understand plant N uptake patterns is the potential for resource partitioning, or complementary uptake of different chemical N forms by different species, which has been suggested as one way for plants to maximize resource capture and species diversity in soils with limited N resources (Bueno et al. 2019; Gherardi et al. 2013; Kahmen et al. 2006; McKane et al. 2002). However, there is mixed evidence to support this phenomenon in drylands. Several soil-based dryland experiments found low relative uptake of amino acid-N tracers into plant tissues compared to inorganic N, which was attributed to strong microbial competition for organic N rather than niche specialization among species (Chen et al. 2015; Huygens et al. 2016; Jin and Evans 2010; Ouyang et al. 2016). An alternate understanding of resource use by N-limited plants is that co-occurring species exhibit niche plasticity – rather than specialization – and can take up multiple

forms of N from shared soil pools wherever and whenever they are available (Ashton et al. 2010; Chalk and Smith 2021; Chesson et al. 2004). Differences in dryland plant uptake of NH_4^+, NO_3^-, and amino acid-N are more likely to be driven by individual growth strategies and competition for spatiotemporally variable local N sources than by species-specific "preferences" for N (Hong et al. 2017; James and Richards 2007; James et al. 2009; Patrick et al. 2009; Stahl et al. 2011), and it is possible that dryland plant species may exhibit resource use plasticity, but more comparative studies of N uptake dynamics among species with different growth strategies are needed, especially if soil water and nutrient uptake are asynchronous following a moisture pulse to these systems (BassiriRad and Caldwell 1992; Gebauer and Ehleringer 2000).

To explore dryland plant N uptake capabilities, we here investigate the timing of root-to-leaf N uptake in 2 perennial grasses and 1 subshrub species from a semiarid grassland-shrubland transition zone in the Northern Chihuahuan Desert. We conducted a greenhouse experiment to compare N uptake of ^{15}N-labeled ammonium (NH_4^+), nitrate (NO_3^-), and glutamate (an amino acid) over 12 to 48 hours. Our study examined three main questions: **(1)** How rapidly do these dryland plants take up available soil N? Based on prior studies, we predicted that 24 h would be sufficient for observing foliar ^{15}N uptake as other studies have documented increased photosynthetic response, leaf transpiration, and root proliferation within 24 h following natural and experimental precipitation events in drylands (Gebauer et al. 2002; Lauenroth et al. 1987; Sala and Lauenroth 1982; Thomey et al. 2011). Prior experiments have also observed that 48 h (2 days) is a reasonable measured limit after which evapotranspiration and soil diffusion rates (and thus root N influx) decline in dryland grassland communities (Ivans et al. 2003; James and Richards 2006; Kurc and Small 2004). **(2)** Does leaf N uptake differ among inorganic and amino acid N forms? We hypothesized that N uptake patterns would reflect the plant-available soil N

116 pool in this habitat, which is dominated by ammonium over nitrate in the uppermost layers where
117 plant roots are located (Adelizzi et al. 2022; Brown et al. 2022; Kurc and Small 2004), and that
118 both NH_4^+ and NO_3^- would be taken up at greater rates than glutamate based on our review of
119 past comparative studies which demonstrated greater inorganic versus amino acid N uptake
120 (Bueno et al. 2019; Kuster et al. 2016; Thornton and Robinson 2005; Yang et al. 2022; Zhuang et
121 al. 2020). **(3)** Do plant species differ in the rate or form of short-term N uptake? We expected
122 that individuals of all three species in this study would ultimately transport similar amounts of
123 ^{15}N to leaves within 12 – 48 h based on evidence from prior dryland ^{15}N tracer experiments that
124 reported recovery of NH_4^+, NO_3^-, and amino acid-N forms in leaves of similar perennial grass
125 and woody shrub/subshrub species < 72 h following application of water and N (Aanderud and
126 Bledsoe 2009; BassiriRad et al. 1999; Carvajal Janke and Coe 2021; Ivans et al. 2003; James et
127 al. 2008; Zhuang et al. 2015; Zhuang et al. 2020). Finally, much of the key background literature
128 comparing inorganic and organic N uptake among different plant functional types comes from
129 studies performed in non-dryland ecosystems such as temperate grasslands (Bardgett et al. 2003;
130 Näsholm et al. 2000; Näsholm et al. 2009; Weigelt et al. 2003; Wilkinson et al. 2015) and tundra
131 ecosystems (Ashton et al. 2008; Ashton et al. 2010; McKane et al. 2002; Miller and Bowman
132 2003; Miller et al. 2007; Näsholm et al. 2009). Thus, to add context to the methods and results of
133 our study, we also compiled published data from experiments that specifically measured N
134 uptake in dryland plant species.
135
136 **Materials and Methods**
137 *Site description*

We studied two grassland locations within the Sevilleta National Wildlife Refuge (SNWR) in central New Mexico, USA. Mean annual precipitation at the SNWR is ~250 mm, with two distinct growing seasons: C_3 shrubs and forbs in the spring, and C_4 grasses during the summer monsoon (July-September) when more than half of annual precipitation occurs (Pennington and Collins 2007; Notaro et al. 2010). Soil pH is basic (8-8.5; Stursova et al. 2006). Atmospheric N deposition occurs at an average rate of 0.2 g m^{-2} yr^{-1} at this site, with over half (57%) deposited as NH_4^+ (Báez et al. 2007). Previous N fertilization experiments indicated that N can be limiting to primary productivity in grasslands at this site (Báez et al. 2007; Collins et al. 2010; Muldavin et al. 2008).

Species descriptions

We sampled three species within the SNWR: *Bouteloua eriopoda* (Torr.) Torr. (black grama), *Achnatherum hymenoides* (Roem. & Schult.) Barkworth (Indian ricegrass), and *Gutierrezia sarothrae* (Pursh) Britton & Rusby (broom snakeweed). These plants overlap within grassland ecotones at SNWR, where graminoids and sub-shrubs make up >75% and 13% of ANPP, respectively (Muldavin et al. 2008; Peters and Yao 2012; Thomey et al. 2014). These three species also differ in physiology and phenology, and thus may have distinct growth demands and nutrient acquisition strategies. Among the two perennial grass species, *B. eriopoda* is a long-lived, stoloniferous C_4 grass with fibrous, finely divided roots concentrated in the upper 5 – 10 cm of soils (Burnett et al. 2012; Gibbens and Lenz 2001; Kurc and Small 2004), and *Achnatherum hymenoides*, an early-season C_3 bunchgrass, grows fibrous roots up to 0.8 – 1.5 m below the soil surface (DeFalco et al. 2007; Reynolds and Fraley 1989; Yoder et al. 2000). *G. sarothrae* is a woody, perennial C_3 subshrub with a taproot extending as far as 1–2 m below the

161 soil surface that allows for rapid subsoil water uptake (Gibbens and Lenz 2001; Wan et al. 1995).
162 Within Chihuahuan Desert grasslands at SNWR, *B. eriopoda* is considered a foundation species
163 and has exhibited negative growth responses to experimental drought and N fertilization
164 treatments (Collins et al. 2010; Ladwig et al. 2012). *A. hymenoides* reaches the southernmost
165 limits of its range in mixed grasslands at SNWR (Muldavin et al. 2008) and has not shown strong
166 responses in aboveground cover or foliar N content in N fertilization experiments from the
167 Colorado Plateau (Osborne et al. 2022; Petersen et al. 2004; Phillips et al. 2021). *G. sarothrae* is
168 a sub-dominant species found throughout *B. eriopoda*-dominated grasslands that has shown
169 marginal cover increases in response to N fertilization at 2 g N m^{-2} yr^{-1} (Collins et al. 2010;
170 Ladwig et al. 2012; Muldavin et al. 2008; Thomey et al. 2014). In this habitat, belowground
171 resource competition during the growing season is likely highest in the uppermost 10 – 20 cm of
172 soils where extensive intermixing of grass and shrub roots can occur (Caldwell et al. 1991;
173 Casper and Jackson 1997; Gibbens and Lenz 2001; Kurc and Small 2004; Ogle and Reynolds
174 2004; Thomey et al. 2011).
175
176 *Plant collection*
177 On February 3rd, 2017, we collected 25 individuals of *B. eriopoda,* 75 individuals of *G.*
178 *sarothrae* from a Chihuahuan Desert grassland site (34.338 N, -106.735 W; 1605 m), and 25
179 individuals of *A. hymenoides* from a Great Plains/Chihuahuan Desert grassland ecotone site
180 (34.404 N, -106.683 W; 1560 m) within the SNWR. We sampled prior to the start of the spring
181 growing season while plants were still senescent to reduce transplant shock. We selected
182 vegetative individuals < 30 cm in height to better facilitate individual growth in pots, and we
183 attempted to extract the major roots of each plant up to ~20 cm below the soil surface. Any

loosely attached rhizosphere soil was gently shaken from roots prior to potting. Immediately following field collection, we transplanted plants into D40L Deepots (7 x 25 cm, 656 mL, Stuewe & Sons, Tangent, OR, USA) using a 1:1 mixture of sand and Metro-Mix® (SunGro, Agawam MA, USA). Each individual *B. eriopoda* and *A. hymenoides* bunchgrass was split into three different pots so that genetically identical individuals would receive an addition of each ^{15}N tracer (see section below), and grasses were trimmed to the crown to remove past season leaves.

Greenhouse set-up

We divided up the total individuals of each species to be maintained in greenhouses at the University of New Mexico (150 pots) and the University of Texas at El Paso (75 pots). Plants in both greenhouses had identical supplemental overhead lighting (10 h light, 14 h dark) and were hand-watered to soil water holding capacity 1-3 times per week for ~6 weeks following harvest to stimulate growth. Of the total plants collected (N = 225 individuals), 60 of *B. eriopoda*, 63 of *A. hymenoides* and 42 of *G. sarothrae* (N = 165) plants survived to tracer application (see next section). We positioned pots in trays > 20 cm apart so that no leaves touched between individuals. Prior to tracer application, we removed each individual from their pot and gently wrapped aluminum foil around all roots and soils below the stem to better constrain the contents of the pot while accessing the roots. A small opening was left at the bottom of each aluminum wrap for water to drain, and wrapped plants were placed back in their respective pots. One day prior to tracer application, we watered all pots to free drainage and collected green leaf samples to measure natural abundance of stable isotopes for each species.

^{15}N tracer application

Plants were randomly selected to receive one of three ^{15}N-labelled isotopic tracers (all at 98 atom % ^{15}N): i) ammonium chloride ($^{15}NH_4Cl$); ii) potassium nitrate ($K^{15}NO_3$); or iii) L-glutamic acid ($HO_2C(CH_2)_2CH(^{15}NH)CO_2H$; Sigma-Aldrich, Inc., St. Louis MO, USA). Each solid ^{15}N tracer was mixed into 25 mL of Milli-Q® purified water (MilliporeSigma, Burlington, MA, USA) to create three aqueous solutions at the following concentrations: 0.057 *M* $^{15}NH_4Cl$, 0.057 *M* ^{15}N-glutamate (both 0.43 mg ^{15}N per plant), or 0.048 *M* of $K^{15}NO_3$ (0.36 mg ^{15}N per plant). While the latter was added at a slightly lower solution concentration (due to a minor miscalculation), the mass of ^{15}N detected in leaves indicated that the total amount of $^{15}NO_3^-$ added per plant (0.36 mg) was enough to exceed the detection limits for each species. We chose these ^{15}N solution concentrations to enable detection of plant uptake and allocation without significantly exceeding background soil inorganic N concentrations measured in unamended soils at this site (Table S3). Each individual plant received only one type of ^{15}N tracer to avoid the potentially inhibitory effects of combining chemical N forms (Miller et al. 2007; Thornton and Robinson 2005).

All ^{15}N tracer solutions were applied to roots and rhizosphere soils between 8:00 – 9:00 AM. Immediately prior to tracer application, we securely covered aboveground stems and leaves with a sealable plastic bag to prevent ^{15}N solutions from inadvertently contacting leaf surfaces. We then removed each plant from its pot, opened the aluminum foil wrap to access the roots, and applied 0.5 mL of ^{15}N tracer solution directly to the outer surface of all visible roots and soils using a 2.5 mL glass atomizer bottle. The aluminum foil wrap was then re-secured around the roots to keep the soils in place before reinserting into pots, and the aboveground plastic bag was removed and discarded.

Sample collection and processing

We collected 5 leaves from each plant at 12, 24, and 48 hours post-application in order to capture two day/night cycles when plant stomata would be open to facilitate transpiration-driven water movement from roots to leaves. This timescale was chosen based on prior dryland experiments that reported N recovery in leaves of similar species within 24 – 48 hours following application of aqueous ^{15}N tracer solutions to soils (Adelizzi et al. 2022; BassiriRad et al. 1999; Green et al. 2008; Ivans et al. 2003; James and Richards 2006). For some individuals, we could not harvest sufficient leaf material at every time point (0, 12, 24, and 48 h) due to poor aboveground condition and/or small size of leaves. At the end of the experiment, we clipped all shoots, rinsed roots clean from soil using tap water, and separated above- and belowground biomass for drying. All plant samples were dried for 3 d at 60 °C and then weighed to the nearest 0.1 mg following collection.

Leaf samples from each time point were ground for 24 to 32 h in 1.5 mL plastic scintillation vials using stir bars to homogenize tissue. Approximately 4.5 mg of ground leaf material was packed in aluminum capsules (CE Elantech, Lakewood, NJ) for ^{15}N analysis. Samples were analyzed at the Center for Stable Isotopes (University of New Mexico) on an ECS 4010 Elemental Analyzer and a Delta V Isotope Ratio Mass Spectrometer (Thermo Fisher Scientific, Waltham, MA, USA), at the University of California-Davis Stable Isotope Facility using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK), or at the EaSI Lab in the Department of Geological Sciences at the University of Texas at El Paso, in which samples were combusted using a PyroCube® (Elementar, Langenselbold, Germany), followed by isotope analysis with a continuous-flow isotope ratio mass spectrometer (IsoPrime GeovisION, Elementar,

253 Langenselbold, Germany). Samples were sent to different facilities to increase data turnaround
254 time, and facility location had no significant influence on isotope values because standards sent
255 to each facility did not significantly differ in nitrogen content ($N = 17$; $P = 0.18$) among
256 facilities.
257
258 *Response variables*
259 Nitrogen isotope ratios were expressed in δ notation (‰) using atmospheric N_2 as the
260 standard (Mariotti 1983). Leaf samples collected prior to ^{15}N tracer addition (Time 0) were used
261 to calculate natural abundance or background $\delta^{15}N$ values for each species (*B. eriopoda*, *A.*
262 *hymenoides*, and *G. sarothrae*) at each greenhouse location where plants were grown (see Table
263 1). We used the average $\delta^{15}N$ natural abundance values to estimate six "enrichment cutoff"
264 values by fitting a kernel density function to each set (one set per species × location; Warren and
265 Silverman 1987) and selecting the 99.9th percentile as the cutoff value. We chose a conservative
266 threshold for the cutoff estimate to be certain that the ^{15}N tracers we applied at the roots had
267 indeed been assimilated into aboveground tissues. We considered post-addition samples with
268 $\delta^{15}N$ values above the respective species cutoff value to be "enriched", and those with $\delta^{15}N$
269 values equal to or below the species cutoff as "unenriched". For our analyses, we used a subset
270 of 220 enriched leaf samples out of the total 278 collected, excluding 23 Time 0 samples (leaves
271 collected prior to ^{15}N tracer addition) and 35 non-Time 0 samples that were unenriched, or had
272 enrichment values below their respective species cutoff value.
273 For enriched samples only, we first determined the total mass of all N (M_{sample}) in leaves
274 using the following equation:
275 $$M_{sample} = \%N_{plant} \times adw_{plant}$$

where $\%N_{plant}$ is the average %N across all leaf samples of the same plant, and adw_{plant} is the total aboveground dry weight (dw) of all leaf samples plus the final harvested biomass from the plant (mg). We then determined the proportion of ^{15}N measured in each leaf sample (F) using the following equation:

$$F = \frac{R}{(1+R)}$$

where R = sample $\delta^{15}N$ value converted to atom %. We then calculated the total mass of ^{15}N in each post-addition sample ($M_{labeled}$) using the following equation (Robinson 2001):

$$M_{labeled} = M_{sample} \times F$$

We did the same for all leaves collected at Time 0 to calculate the total mass of ^{15}N in each natural abundance sample ($M_{background}$). We then subtracted $M_{background}$ (mg) from $M_{labeled}$ (mg) to determine *leaf N uptake*, or the total mass of ^{15}N recovered in leaves in excess of natural abundance (mg ^{15}N per g leaf dw). We converted this value to µg and then to µmol ^{15}N by dividing it by the atomic mass of N (14.0067 u) for ease of comparison with other studies.

To answer Question 1, we calculated the mean N uptake rate (µmol ^{15}N per g dw per h) by dividing leaf N uptake by time (h) since tracer addition for each sample, and then averaged values across samples in each tracer, species, or tracer × species group to determine the speeds at which plants took up applied ^{15}N to leaves (Table 3, Table S1). For individuals that were sampled at all three post-addition time points, we also calculated percent (%) N recovery per plant using the following equation:

$$\%\text{ N recovery} = \frac{\text{Total mass of } ^{15}\text{N recovered in leaves}}{\text{Total mass of } ^{15}\text{N applied to plant}} \times 100$$

where the total mass of ^{15}N recovered in leaves equals the cumulative sum of leaf N uptake from all samples collected from the same plant (mg), and the total amount of ^{15}N applied equals 0.43

298 mg (or 0.36 mg for plants given $K^{15}NO_3$). We also calculated the percentage of leaf samples
299 enriched for each ^{15}N tracer × species group by dividing the total number of enriched samples by
300 the total number of samples collected at each time point and multiplying by 100.
301
302 *Analysis*
303 We performed all statistical analyses in R version 4.2.2 (R Core Team 2022). To answer
304 Questions 2 and 3, a linear mixed-effects (lme) model was fit by maximum likelihood using the
305 'lmer' function in the *lme4* package version 1.1-27 (Bates et al. 2015) to compare leaf N uptake
306 among different ^{15}N tracers and plant species over time. Response data were log-transformed in
307 order to improve the normality of residuals. The full lme model included ^{15}N tracer (3 levels:
308 NH_4^+, NO_3^-, or glutamate), plant species (3 levels: *B. eriopoda, A. hymenoides,* or *G. sarothrae*),
309 and time point (3 levels: 12, 24, or 48 h) as categorical fixed effects, and plant genotype (n = 58;
310 nested within plant species), and pot ID (n = 86; nested within plant species and genotype) as
311 random effects to account for repeated measures of the same plant genotype and individual.
312 The significance of main effects and interactions was assessed via analysis of deviance
313 Type II tests using the 'Anova' function in the *car* package version 3.0–10 (Fox et al. 2012).
314 Results were visualized using the *visreg* package version 2.7.0 (Breheny and Burchett 2017) and
315 the amount of variance explained by our whole model was substantial (marginal R^2 = 0.29,
316 conditional R^2 = 0.88; see Table S2). We checked model fit by performing a backwards model
317 selection process where terms were sequentially removed and compared the reduced models to
318 the full model using analysis of variance (ANOVA) via the 'anova' function in the R *stats*
319 package version 4.2.2 (R Core Team 2022) and the Akaike Information Criterion (AIC). The
320 final model included all 3 fixed effects but removed the random effect of plant genotype, which

obtained statistically similar results to the full model (LRT: $X^2 = 1.0$, $P = 0.32$) with a slightly smaller AIC value. Including time as a categorical vs. continuous variable did not significantly affect model fit (LRT: $X^2 = 8.7$, $P = 0.47$), and results using categorical time are reported below to allow for nonlinear change through time. We checked the normality of model residuals via a Kolmogorov-Smirnov test using the 'km.test' function in the *R stats* package version 4.2.2 (R Core Team 2022), which indicated that the residuals were normally distributed ($D = 0.08$, $P = 0.13$). We assessed homogeneity of variance across groups by performing a Levene's test on model residuals using the 'leveneTest' function in the *car* package version 3.0–10 (Fox et al. 2012) and found that the assumption of equal variances was met for tracer ($F = 0.71$, $P = 0.49$), species ($F = 0.40$, $P = 0.67$), and timepoint ($F = 0.77$, $P = 0.46$). We also checked the final model for uniformity, over- and under-dispersion, outliers, and zero inflation (none detected) of fitted vs. simulated residuals using tests within the *DHARMa* package version 0.4.5 (Hartig 2022). *Post hoc* pairwise comparisons of treatment means for main effects and interactions among ^{15}N tracer × time, species × time, and ^{15}N tracer × species × time were performed in the *emmeans* package version 1.6.1 (Lenth, 2021). *P* values were adjusted for multiplicity using the Tukey method for comparing a family of 3 estimates, and all pairwise comparisons of means used the Kenward-Roger degrees-of-freedom method and a 0.95 confidence level.

Literature search and review

To help place our results in context and compare broader trends of plant N uptake in dryland habitats, we compiled existing data from 30 experiments in 28 published studies that quantified uptake of inorganic and/or organic ^{15}N tracers in uncultivated dryland plant species. We used a combination of Google Scholar (https://scholar.google.com) and Connected Papers

344 (https://www.connectedpapers.com) to search for publications that included more than one
345 chemical N form and/or plant species from dryland ecosystems only. We derived study data
346 directly from main text data tables and figures and supplementary materials as necessary, using
347 ImageJ (Schindelin et al. 2012) to determine values from graphical data. We report values from
348 20 soil-based experiments from field (n = 16), greenhouse (n = 2), and growth chamber (n = 2)
349 settings, and 10 laboratory assay experiments in which plant N uptake was quantified via
350 depletion of assay solutions by either roots of "intact" plants (those still connected to
351 aboveground tissues) or excised roots only. For experiments that measured plant N uptake from
352 soils, the application of ^{15}N tracer solutions occurred either at the soil surface (i.e., to biological
353 soil crust patches, or to the entire plot surface in a simulated rainfall event) or in the upper ~10
354 cm of soils, where solutions were injected directly into the soil at one or more points surrounding
355 a target plant. In studies that applied N at multiple soil depths (e.g., 0-5 cm and 5-10 cm), we
356 averaged values across depth. In solution-based experiments where solutions of varying N
357 concentrations were used, we reported the median concentration (i.e., if solutions ranged from 0
358 to 1000 μM ^{15}N, we reported results from plants in 500 μM solutions only). Details on the
359 chemical form and concentration of N added were simplified by converting concentrations to
360 similar molar (M) units where possible. In studies that featured other experimental manipulations
361 (e.g., elevated CO_2, drought or warming treatments, etc.), we reported data from non-treated
362 control or ambient conditions only and averaged across technical replicates, if applicable. In
363 some studies, the authors combined results from NH_4^+ and NO_3^- applications although they were
364 applied to plants separately, and this is noted in Table 5.
365 We grouped data based on the most common N uptake responses measured across
366 studies: (i) percent N recovery, or the percentage (%) of ^{15}N recovered in plant tissues out of the

total amount applied; (ii) N uptake rate, or the amount of ^{15}N in excess of natural abundance per gram plant dry weight (dw) per unit time, most often expressed as micromoles ^{15}N per gram root dw per hour; and (iii) aboveground plant $\delta^{15}N$ values following isotopic tracer application, expressed as permille (‰). Note that $\delta^{15}N$ values alone are not directly comparable among different studies without additional information about the total mass of the elemental N pool in those study systems (Currie 2007). If the amount of foliar ^{15}N recovery by mass (excess N) was the only result reported, we converted values to micromoles ^{15}N for ease of comparison and divided these values by the time since application to calculate rates of N uptake per hour. In one case, we include N uptake rates measured in terms of soil surface area (e.g., milligrams N per square meter per hour) instead of by plant mass (Jackson et al. 1989). For studies using more than one N form, we also calculated two unitless ratios to compare proportional N uptake and recovery among chemical forms (NH_4^+ vs. NO_3^- and inorganic vs. organic N) regardless of addition amount. For studies that included at least one inorganic and one organic form, we divided inorganic N values (averaged across both NH_4^+ and NO_3^- when applicable) by those from amino acid-N to calculate the inorganic:organic ratio.

Results

How rapidly do these dryland plants take up available N?

Rapid N transport from roots to leaves occurred within 12 h of tracer application (mean ± SE leaf uptake at 12 h = 0.27 ± 0.05 μmol ^{15}N g^{-1} dw) and more than doubled between 24 h (mean ± SE = 0.34 ± 0.07 μmol ^{15}N g^{-1} dw) and 48 h (mean ± SE = 0.86 ± 0.13 μmol ^{15}N g^{-1} dw) across all ^{15}N tracers and species (time point main effect: $X^2 = 215.94$, $P < 0.001$; pairwise comparisons of 12 vs. 24 h: $t = -4.71$, $P < 0.001$, and 24 vs. 48 h: $t = -10.13$, $P < 0.001$; Table 2,

Fig. 1). Overall minimum and maximum rates of N uptake ranged from 0.002 to 0.045 μmol ^{15}N g^{-1} dw h^{-1} over the course of the experiment, and mean N uptake rates were ultimately similar across 48 h for all species and tracer types (mean ± SE = 0.017 ± 0.002 μmol ^{15}N g^{-1} dw h^{-1}; Table 3), matching our statistical model results which did not find a significant difference in the three-way interaction of ^{15}N tracer × Species × Time: $X^2 = 2.73$, $P = 0.950$; Table 2). Mean percent N recovery after 48 h was 6.0 ± 1.1% across all plant individuals, which was ~6x higher at the conclusion of the experiment versus after 12 h post-application (mean ± SE = 1.0 ± 0.2%; Table 4).

Does leaf N uptake differ among inorganic and amino acid N forms?

On average across species, plants took up 3-4x more of the two inorganic N forms (NH_4^+ and NO_3^-) than the amino acid glutamate (^{15}N tracer main effect: $X^2 = 19.05$, $P < 0.001$; pairwise comparisons of glu vs NH_4^+: $t = 2.74$, $P = 0.021$; vs NO_3^- $t = -4.39$, $P < 0.001$) from roots to leaves (Table 2). Across all species and timepoints, plants given NO_3^- had the highest leaf N uptake on average (mean ± SE = 0.70 ± 0.11 μmol ^{15}N g^{-1} dw), followed by NH_4^+ (mean ± SE = 0.53 ± 0.09 μmol ^{15}N g^{-1} dw), and then glutamate (mean ± SE = 0.19 ± 0.04 μmol ^{15}N g^{-1} dw; Table 3). Plants took up 2-3x more NH_4^+ than glutamate after 12 and 48 h on average (pairwise comparison of NH_4^+ vs. glu at 12 h: $t = 2.84$, $P = 0.014$; 24 h: $t = 1.73$, $P = 0.198$; and 48h: $t = 2.81$, $P = 0.017$), and 3-4x more NO_3^- than glutamate at every post-application time point (pairwise comparisons of glu vs. NO_3^- at 12 h: $t = -4.68$, $P < 0.001$; 24 h: $t = -3.73$, $P < 0.001$; and 48 h: $t = -3.44$, $P = 0.002$; Table 3, Fig. 2a). Similarly, plants transported NO_3^- 3x faster and NH_4^+ 2x faster (mean rate for both inorganic N forms = 0.02 μmol ^{15}N g^{-1} dw h^{-1}) than glutamate, which moved at an average rate of 0.01 μmol ^{15}N g^{-1} dw h^{-1} across all species (Table

413 3, Fig. 1). Plants given inorganic N also had 2-4x higher percent N recovery than those given
414 glutamate and mean ± SE and maximum N recovery, respectively, for each tracer type were
415 NH_4^+: 5.1 ± 1.2% and 16%; NO_3^-: 8.6 ± 2.2% and 48%; and glu: 2.2 ± 0.6% and 9% at the
416 conclusion of the experiment (Table 4). The overall highest percent N recoveries were from
417 individuals given NO_3^- at the roots.
418
419 *Do plant species differ in the rate or form of N uptake?*
420 According to our model, plant species alone was not a significant predictor of the amount
421 of leaf N uptake (species main effect: $X^2 = 3.25$, $P = 0.197$) when averaged across ^{15}N tracers and
422 time (Table 2). However, some species-level differences emerged over time (species × time: $X^2 =$
423 17.53, $P = 0.002$), and N uptake for each species doubled on average across all tracer types
424 between 24 and 48 h (pairwise comparisons of 24 h vs. 48 h: *B. eriopoda*: $t = -6.74$, $P < 0.001$;
425 *A. hymenoides*: $t = -5.14$, $P < 0.001$; and *G. sarothrae*: $t = -5.56$, $P < 0.001$; Table 3, Fig. 2b).
426 Overall, *B. eriopoda* N uptake increased the most over time with 3.4x higher uptake after 48 h
427 compared to 12 h post-application (Table 3). Across all tracer types, *B. eriopoda* also had ~2-3x
428 greater percent N recovery than *A. hymenoides* and *G. sarothrae*, and overall mean and
429 maximum N recovery, respectively, for each species were *B. eriopoda*: 12.2 ± 4.6% and 48%; *A.*
430 *hymenoides*: 3.9 ± 0.8% and 15%; and *G. sarothrae*: 5.4 ± 1.2% and 23% (Table 4). Differential
431 uptake among species were also apparent at individual time points. For example, *B. eriopoda* and
432 *G. sarothrae* individuals had similar N uptake amounts after 12 h, but *B. eriopoda* tended to take
433 up 1-1.5x more N (across all tracer types) after 24 and 48 h than *G. sarothrae* (Fig. 2b), and *A.*
434 *hymenoides* took up 1-2x less N than the other two species at 12, 24, and 48 h post-application
435 (Fig. 2b). *B. eriopoda* and *G. sarothrae* also had marginally faster N uptake rates (mean value =

436 0.02 μmol ^{15}N g^{-1} dw h^{-1}) than *A. hymenoides*, which had a mean rate of 0.01 μmol ^{15}N g^{-1} dw h^{-1}
437 across all tracers (Table 3). Although the interactive effects of N form and species were not
438 considered significant predictors of N uptake in our model (^{15}N tracer × species $P = 0.774$; Table
439 2), *B. eriopoda* plants given NO_3^- had the overall fastest uptake rates (0.04 ± 0.01 μmol ^{15}N g^{-1}
440 dw h^{-1}) and *G. sarothrae* plants took up glutamate ~2x faster than the other two species. The
441 three-way interaction of ^{15}N tracer × species × time was also not significant in our model ($P =$
442 0.950; Table 2), however *G. sarothrae* took up 2.5-5x more glutamate than *B. eriopoda* and 1.6-
443 2.5x more glutamate than *A. hymenoides* at each time point, and the two grass species took up
444 similar amounts of NH_4^+ and glutamate over time (Table S1). Overall, each of the three species
445 followed a similar pattern of NO_3^- > NH_4^+ > glutamate uptake over time (Fig. 1; see Table S1).
446 While we did not statistically compare the percentage (%) of leaf samples that were
447 enriched for each ^{15}N tracer × species group over time (top of each panel in Fig. 1; see Fig. S1),
448 we also note some patterns that emerged among species. For *G. sarothrae*, plants had 100% of
449 leaves enriched at nearly every timepoint across all N tracer types, except for plants given NO_3^-
450 after 12 and 48 h, which both had 90% of samples enriched. The percent of leaves enriched for
451 *B. eriopoda* plants given NO_3^- also decreased from 86% to 78% between 12 and 24 h, but then
452 increased to 100% after 48 h. This seemingly anomalous pattern is likely due to the fact that
453 most plants do not assimilate root N into all leaves in a consistent pattern (Tegeder and
454 Masclaux-Daubresse 2018), and that we collected a different set of leaves from each individual
455 at each time point to account for this potential variation in leaf N uptake. *B. eriopoda* plants
456 given glutamate also had the overall lowest percentage of leaves enriched (13%) after 12 h, and
457 only 67% enriched after 48 h, which was ~40% lower than *B. eriopoda* plants given NH_4^+ and
458 NO_3^- which had 91% and 100% leaf enrichment after 48 h, respectively. At each time point, *A.*

459 *hymenoides* plants given glutamate also tended to have ~10-20% lower leaf enrichment
460 compared to those given inorganic N tracers, and *A. hymenoides* individuals given NO_3^- were
461 100% enriched at every time point.
462
463 *Literature review*
464 All of the 30 dryland N uptake experiments we found included at least one form of
465 inorganic N (NH_4^+ and/or NO_3^-). Nine experiments only compared both inorganic N forms
466 (NH_4^+ *and* NO_3^-), 11 experiments only used one inorganic form (NH_4^+ *or* NO_3^-), 3 experiments
467 used a combined inorganic form (NH_4NO_3), and 7 studies compared at least one inorganic N
468 form with an organic amino acid form (see Table S4 for study details). Percent N recovery
469 results reported from 8 soil-based experiments were the simplest response to compare across
470 studies with different methodologies, and we found that percent recovery of NH_4^+ ranged from
471 1.2% to 73.5% (median = 12.5%) and of NO_3^- ranged from 0.8% to 85.1% (median = 30.8%;
472 Table 5) across 7 studies that injected each tracer individually into soils surrounding plants. One
473 study used $^{15}NH_4{}^{15}NO_3$ and found 0.3% to 6.7% recovery in two subshrub species from 8 – 48 h
474 (James and Richards 2006). In experiments that compared inorganic and organic N uptake, ^{15}N-
475 glycine was the most widely used amino acid, and percent recovery of glycine ranged from 0.6%
476 to 41.6% (median = 7.8%) across 6 studies. One experiment applied ^{13}C-^{15}N-glutamate to
477 biocrust soil patches < 1 m away from perennial bunchgrass tussocks (Aanderud and Bledsoe
478 2009; Green et al. 2008) and found 0.2% to 0.4% N recovery in leaves between 1 and 4 d
479 following application (Table 5). Results from studies measuring both inorganic and organic N
480 uptake consistently found greater percent recovery of NO_3^- compared to amino acid-N, and

similar or lower percent recovery of NH_4^+ compared to amino acid-N recovery. Overall, all reported studies that compared inorganic and organic N forms had recovery ratios > 1 (Table 5).

Prior dryland studies that quantified N uptake rates per unit time were primarily laboratory assay experiments which measured inorganic N depletion from nutrient solutions of known concentrations within a range of ~0.5 to 4 hours (see Table S4). The 10 solution-based experiments that we reviewed documented the highest uptake rates overall, ranging from 4.6 to 25.2 μmol ^{15}N g^{-1} dw h^{-1} for NH_4^+ (median = 9.8), and 2.1 to 17.8 μmol ^{15}N g^{-1} dw h^{-1} for NO_3^- (median = 5.9; Table S5). One study (James et al. 2009) combined results from both inorganic forms, and these rates ranged from 1.6 to 9.1 μmol ^{15}N g^{-1} dw h^{-1} (median = 7.3). We only found one dryland experiment that measured organic N uptake from solution of an aquatic plant species (Schiller et al. 1998), but it was not included due to differences in physiology and habitat. For soil-based experiments, regardless of the N addition method, inorganic N uptake rates were much lower than those measured in solution-based experiments, with values ranging from 0.002 to 2.1 μmol ^{15}N g^{-1} dw h^{-1} for NH_4^+ (median = 0.20) and from 0.05 to 14.9 μmol ^{15}N g^{-1} dw h^{-1} for NO_3^- (median = 0.42; Table S5). Foliar uptake rates of amino acid-N from soils were reported from ^{15}N-glycine in 4 studies (Jin and Evans 2010; Ouyang et al. 2016; Yang et al. 2022; Zhuang et al. 2020) and ranged from 0.01 to 1.98 μmol ^{15}N g^{-1} dw h^{-1} (median = 0.19). Results from 6 field-based experiments that only reported leaf $\delta^{15}N$ values at more than one timepoint indicate that overall, foliar $\delta^{15}N$ enrichment from NH_4^+, NO_3^-, or NH_4NO_3 increased significantly over time (> 48 h) following water and ^{15}N tracer application (Table S5).

Discussion

503 Our experiment resulted in three main findings: 1) dryland plants transported all sources
504 of available nitrogen to leaves as rapidly as 12 h following ^{15}N tracer application to roots; 2)
505 plants given NH_4^+ and NO_3^- took up 3-4x more N to leaves and had 2-4x higher percent N
506 recovery than those given glutamate; 3) each of the three plant species took up inorganic N
507 sources 2-3x faster than glutamate, with a similar pattern of $NO_3^- > NH_4^+ >$ glutamate uptake
508 over time.
509
510 *How rapidly do these dryland plants take up available soil N?*
511 Overall, these results indicate that tracer amounts of ^{15}N can be translocated from roots to
512 aboveground shoots on the scale of 12 to 48 hours in wild-harvested plants of *B. eriopoda*, *A.*
513 *hymenoides*, and *G. sarothrae* under non-water-limiting conditions. We observed the highest N
514 recovery 48 h following tracer application, and mean N uptake rates more than doubled between
515 24 and 48 h, suggesting that these plants may continue to take up available inorganic and/or
516 organic N within several days of a pulse event until nutrient supply and soil moisture decline.
517 We found less N recovery compared to some other soil-based dryland experiments, which could
518 be due to the relatively lower concentrations and solution amounts (0.5 mL) that we used in
519 order to reflect realistic soil nutrient availability at the roots of plants in this ecosystem. We
520 intentionally used tracer amounts of N so as not to exceed background soil levels, which could
521 likely disrupt plant-soil-microbial feedbacks responsible for growth responses and N cycling
522 processes under otherwise natural conditions (Knops et al. 2002; Reynolds et al. 2003).
523 However, these results matched with other dryland experiments that found < 20 % inorganic N
524 recovery and < 5% amino acid-N recovery within 24 to 48 hours of N and water application
525 (James and Richards 2006; Wang et al. 2016; Zhuang et al. 2020), including one field study in

526 the same Chihuahuan Desert grassland where some of our plants were collected (Green et al.
527 2008). On average, the N uptake rates we measured were comparable to several other soil-based
528 experiments that quantified N uptake by roots of intact plants within < 24 to 72 hours (Booth et
529 al. 2003; James et al. 2008; Ouyang et al. 2016), although they were much lower than those
530 measured in solution-based experiments where roots were removed from soils. For example, in
531 one hydroponic experiment, *Bouteloua eriopoda* uptake of NO_3^- after 4 h was 30.98 μmol ^{15}N g^{-1}
532 dw h^{-1} (BassiriRad et al. 1997), which was more than 600x the highest NO_3^- uptake rate we
533 measured from this species (~ 0.05 μmol ^{15}N g^{-1} dw h^{-1}). In a different experiment, NH_4^+ uptake
534 by *A. hymenoides* plants was measured up to 5.6 μmol ^{15}N g^{-1} dw h^{-1} after 30 minutes (Yoder et
535 al. 2000), which was ~250x the highest N uptake rate we measured for *A. hymenoides* in our
536 study (~0.02 μmol ^{15}N g^{-1} dw h^{-1}). We did not find any background reference values for *G.*
537 *sarothrae*, and we believe that our study is the first to document N uptake rates for this species.
538 These solution-based experiments provide valuable insight into potential short-term nutrient
539 uptake kinetics at timescales ranging from minutes to hours; however, they may not capture
540 realistic rates of N uptake from within the soil matrix nor reflect the complexity of rhizosphere
541 interactions (Jilling et al. 2018; Schmidt et al. 2013; Warren 2006). For example, some root-
542 associated mycorrhizae mediate acquisition and biochemical transformation of inorganic and
543 organic soil N before root transfer occurs (Govindarajulu et al. 2005; Leigh et al. 2009; Moe
544 2013). Excluding the influence of fungi and other microbes would not accurately capture the
545 feedbacks that regulate root N uptake in soils under more natural conditions, and could
546 ultimately alter the rate and form(s) by which N enters into internal plant uptake pathways over
547 the course of hours to days (Dijkstra et al. 2010; Kuypers et al. 2018; Näsholm et al. 2009; Wen
548 et al. 2022). In our experiment, we did not remove all soils attached to fine roots or rhizosheaths

549 prior to potting the field-collected plants, and it is possible that these types of plant-microbe
550 interactions were preserved. Ultimately, our results support our hypothesis and confirm that 24 h
551 following water and N application is a realistic study period for observing foliar uptake of
552 different N forms from roots and rhizosphere soils in this plant community.
553
554 *Does leaf N uptake differ among inorganic and amino acid N forms?*
555 We found significantly greater uptake of NO_3^- and NH_4^+ versus glutamate, an amino acid
556 form, which was transported 3-4x slower from roots to leaves than either inorganic form within
557 48 hours of application. These findings are consistent with prior studies in which dryland shrub,
558 grass, and herbaceous species acquired more NO_3^- than dissolved organic N from glycine after
559 24 to 48 h (Zhuang et al. 2020, Jin and Evans, 2010) but contrast with the conclusions of another
560 where a forb species had higher glutamate uptake after 24 h than either NO_3^- or NH_4^+ (Zhuang et
561 al. 2015). Information about organic N concentrations and retention in dryland soils is limited,
562 because soil amino acid-N pools can be highly dynamic with a half-life of < 1 h in some
563 locations (Chen et al. 2015; Daly et al. 2021; Lipson and Näsholm 2001; Owen and Jones 2001).
564 On a shorter timescale than our study, a previous field experiment evaluating amino acid uptake
565 in *Bouteloua gracilis* found that ~50% of applied alanine was recovered in microbial biomass
566 and only 0-1% in plant tissues after 3 h, which they hypothesized was due to rapid fungal uptake
567 and immobilization (Chen et al. 2015). The significantly slower rates of glutamate uptake we
568 observed could possibly be due to this type of short-term microbial competition, since we did not
569 sterilize nor fertilize potting soils during the experiment, and active rhizosphere microbes may
570 have immobilized glutamate-N before it could be transported across root cell membranes (Jones
571 et al. 2005). It is also possible that glutamate applied to rhizosphere soils was converted into

572 inorganic N forms by these microbes (Rothstein 2014) and using double-labelled (^{13}C and ^{15}N)
573 tracers could provide further insight into the uptake of intact amino acid-N once it reaches the
574 roots of these species.
575 Background soil N pool sizes are also an important consideration for making accurate
576 comparisons of plant N uptake across and within ecosystems. In other ecosystems where organic
577 N has been found to comprise a greater portion of plant N nutrition (Lipson and Näsholm 2001;
578 Näsholm et al. 2009), plants generally acquire N from mixed pools where soil organic matter is
579 high and mineral and organic N cycling are biologically coupled (Boudsocq et al. 2012; Vidal et
580 al. 2020). In these systems, seasonal availability and the ability of plant roots and their
581 mycorrhizal associates to access mineral-bound proteins may be the primary limitation to uptake
582 (Raab 1999). However, dryland soils have lower levels of organic matter, high pH and high
583 oxidative enzyme activity compared to those in more mesic systems, and potentially greater
584 decoupling of N cycling processes (Stursova et al. 2006). Thus, although our results demonstrate
585 that these plant species are capable of taking up amino acid-N from glutamate when added as a
586 single N source to roots, soil organic N may not be a consistent source for plant N nutrition in
587 this habitat (Stursova and Sinsabaugh 2008). N from amino acids like glutamate could
588 potentially meet a portion of these species' N demands if encountered by plant roots or root-
589 associated microbes, but further details on the concentrations and distribution of soil organic N at
590 this site are still needed to clarify these findings.
591 Among the two inorganic N forms applied, we expected that plants given NH_4^+ would
592 have the highest N uptake based on background measurements of soil N pools at the SNWR (see
593 Table S3), but we found consistently higher NO_3^- vs. NH_4^+ uptake across species over time,
594 although the differences were not statistically significant at $P < 0.05$. From our review of other

595 dryland studies, NO_3^- uptake tends to be higher than NH_4^+ when both were added to soil-based,
596 intact plant systems (NH_4^+: NO_3^- ratio < 1.00), while NH_4^+ uptake tends to be higher than NO_3^- in
597 solution-based experiments where N was consistently provided to roots in nutrient solutions
598 (NH_4^+: NO_3^- ratio > 1.00). These trends may be attributable to solubility of the two mineral
599 forms: NO_3^- is negatively charged and has a much higher soil diffusion rate (effective soil
600 diffusion coefficient = 2.82×10^{-1} cm^2 d^{-1} (Owen & Jones, 2001) than NH_4^+, which can be
601 sorbed to soil particles and becomes less accessible to roots and microbes as soil moisture
602 declines (Wang and Macko 2011). Additionally, while NO_3^- is more energy intensive for plants
603 to assimilate, it can be stored in plant tissues unlike NH_4^+, which can be phytotoxic if it
604 accumulates in cells (Britto and Kronzucker 2002; Engels and Marschner 1995; Moreau et al.
605 2019). Our results indicate that these grassland species can take up multiple inorganic and
606 organic forms of N locally within 24 h of N reaching the roots, and the clear patterns of greater
607 inorganic N uptake versus glutamate observed across species offer partial support for our
608 hypothesis of $NH_4^+ > NO_3^- >$ glutamate uptake.
609
610 *Do plant species differ in the rate or form of N uptake?*
611 In our experiment, we did not observe statistically significant differences in N uptake at P
612 < 0.05 among the three plant species tested. However, there were a few distinguishable patterns
613 over the 48 h timespan that could likely be attributed to differences in life history strategies and
614 physiology. *B. eriopoda* plants had the overall highest rates of N uptake and recovery in our
615 experiment, which might be expected for a dominant species that forms large monospecific
616 patches at SNWR compared to the other two subdominant C_3 species in our study (Kurc and
617 Small 2004). The lowest amount of mean N uptake was observed in *A. hymenoides* individuals,

618 which had ~50% lower uptake than the other two species after 48 h. This cold desert grass
619 species reaches the southernmost limits of its range at the SNWR where we sampled (Muldavin
620 2002), and it is possible that plants required a different set of environmental conditions to break
621 winter dormancy and/or were experiencing stress when transplanted into the greenhouse.
622 Although the percentage of samples enriched for each species × tracer group do not equate to the
623 amount of N uptake by mass, they indicated that *G. sarothrae* leaves were 100% N-enriched at
624 every timepoint in contrast to the two grass species, particularly noticeable for plants given
625 glutamate at 12 h following application (Fig. 1). *G. sarothrae*, a ruderal subshrub, also had
626 higher glutamate uptake than the two grasses at each time point and took up glutamate twice as
627 fast as the other species overall. In the greenhouse pots, *G. sarothrae* individuals had 3-4x higher
628 mean aboveground biomass than either *B. eriopoda* or *A. hymenoides* (data not shown), and
629 potentially greater photosynthetic demands may have driven root uptake in this woody species
630 compared to the two perennial grass species, which could explain the higher percentages of
631 leaves enriched for nearly all N forms for *G. sarothrae*.
632 Plants in resource-limited habitats may also adopt different belowground strategies to
633 increase the solubility and mobilization of mineral and organic N forms to roots, such as altering
634 root architecture and foraging behaviors (Forde and Walch-Liu 2009; Jumpponen et al. 2002), or
635 exuding carbon from roots to boost local microbial activity and enzyme production in the
636 rhizosphere (Ladwig et al. 2015). Shallow-rooted dryland grasses can have greater radial root
637 spread to capture soil water from small rain events (Sala and Lauenroth 1982; Thomey et al.
638 2014), whereas woody plants can extend lateral and vertical roots to access water and/or
639 nutrients in deeper soil layers (Lee and Lauenroth 1994; Wan et al. 1995). While these
640 adaptations could also allow coexisting plants to partition resources based on soil depth, the

641 similarities in N uptake observed among *B. eriopoda*, *A. hymenoides* and *G. sarothrae* indicate
642 that rather than specializing in a certain chemical N form to avoid competing for the same
643 limiting resource, these species may employ similarly flexible strategies for acquiring whichever
644 soil N source is most available when growth conditions are favorable (Ashton et al. 2008; Chalk
645 and Smith 2021; Stahl et al. 2011).

646 While our study quantifies baseline information about relative N uptake in intact plants
647 once soil moisture limitation is lifted, inter- and intra-species competition for shared soil
648 nutrients are nuanced and likely more complex than what we were able to measure in a single
649 study. In the greenhouse, roots were constrained to 25 cm depth and had limited lateral spread,
650 pots were watered to field capacity prior to N additions, and individuals were evenly spaced in
651 the greenhouse to receive equal amounts of light and water. These growth alterations, as well as
652 removing individuals from direct competition for local resources, may have muted species-
653 specific N uptake responses that might be more clearly observed under field conditions during
654 their respective growing seasons (James and Richards 2007; Miller et al. 2007). Under non-
655 water-limiting conditions, our hypothesis was supported as N uptake did not statistically differ
656 among the three species. However, BassiriRad et al. 1999 observed species-level differences in
657 $^{15}NO_3^-$ uptake of two Chihuahuan Desert shrub species in watered vs. unwatered treatments,
658 which supports that co-occurring plants in this system may have differential nutrient uptake
659 responses under more limited soil moisture conditions. In future experiments tracing inorganic or
660 organic N uptake in these species, we may expect that any divergence from rapid (24 to 48 h)
661 root to leaf uptake could be due to other physical, biological, or competitive interactions when N
662 is applied directly to roots or rhizosphere soils.

Plants of all three grassland species opportunistically took up all forms of available N within 48 h following application of ^{15}N tracers to roots and rhizosphere soils. Our results confirm the occurrence of rapid N uptake in these grassland species once water limitation is lifted, lending support to the concept of serial resource limitation in this dryland ecosystem. Although average percent recovery and root-to-leaf N uptake rates were lower than those measured in some prior experiments, overall we were able to detect a consistent trend across species that showed significantly higher uptake of inorganic N sources (NH_4^+ and NO_3^-) versus an organic amino acid form (glutamate). Since we did not observe significant differences in N uptake by species, the similar uptake pattern and rates indicate that they may have similar capacity for exploiting inorganic soil N sources and suggests they may compete for the same plant-available N pools (e.g., inorganic N and amino acid-N in excess of microbial demand) in their shared habitat. From our review of published N uptake experiments, we can conclude that inorganic N, particularly NO_3^-, is generally taken up at faster rates than amino acid-N in dryland studies that included both inorganic organic N uptake, and this pattern appears to be consistent across different plant species and habitats. We also observed a wide range of methods for testing different N forms and plant species, and greater standardization of N application and sample collection methods may facilitate more effective comparisons of short-term uptake among studies and habitats. Assessing nutrient uptake patterns in dryland-adapted plants will improve our understanding of their responses to current and predicted environmental changes, and how asynchronous water and N availability may influence biotic interactions and nutrient retention in these globally important communities. As increasing N deposition and changing climate variables shift the balance of N inputs to dryland soils (Báez et al., 2007; Ramond et al., 2022),

685 interpreting short-term responses of individuals and the effects on plant community dynamics
686 will be key to preventing N losses from these ecosystems.
687
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696
697 **Author Contributions**
698 ES conceived of study, CC, ES and GC collected and analyzed data with assistance from ADN.
699 CC wrote the manuscript and ES, GC, and ADN contributed to writing and editing. ADN
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Statements and Declarations

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Competing Interests

The authors declare that there are no conflicts of interest.

Data Availability

All data presented in this study will be archived in the Environmental Data Initiative (EDI) Repository (https://portal.edirepository.org/nis/home.jsp) under the Sevilleta Long-Term Ecological Research site upon publication.

Tables and Figures

Table 1. Leaf natural abundance ± standard error and calculated enrichment cutoff $\delta^{15}N$ values (permille, ‰) for three plant species (*B. eriopoda*, *A. hymenoides*, and *G. sarothrae*) maintained at two different greenhouse locations at the University of New Mexico (UNM) or University of Texas at El Paso (UTEP). For *G. sarothrae*, natural abundance $\delta^{15}N$ values were only measured from plants at UNM, so one cutoff value was applied for that species.

Plant Species	Institution	Natural Abundance (‰)	Enrichment Cutoff (‰)
Bouteloua eriopoda	UNM	1.90 ± 1.01	8.63
	UTEP	1.47 ± 0.36	2.74
Achnatherum hymenoides	UNM	0.25 ± 0.83	5.15
	UTEP	-0.17 ± 1.17	4.25
Gutierrezia sarothrae	UNM	-1.30 ± 0.29	-0.06

Table 2. Results from generalized linear mixed effects ANOVA model testing for main and interacting effects of ^{15}N tracer type (ammonium, nitrate, and glutamate), plant species (*B. eriopoda, A. hymenoides*, and *G. sarothrae*) and time (12, 24, and 48h post-application) on leaf N uptake. Significant predictors ($P < 0.05$, Type II Wald Chi-square tests) are bolded.

		Leaf N Uptake	
Predictors	df	X^2	P
^{15}N Tracer	2	**19.05**	**< 0.001**
Species	2	3.25	0.197
Time	2	**215.94**	**< 0.001**
^{15}N Tracer × Species	4	1.79	0.774
^{15}N Tracer × Time	4	**14.94**	**0.005**
Species × Time	4	**17.53**	**0.002**
^{15}N Tracer × Species × Time	8	2.73	0.950

Table 3. Leaf N uptake (μmol ^{15}N per g plant dw) and N uptake rate (μmol ^{15}N per g dw per h) for ^{15}N-enriched samples only (N = 220). Mean ± standard error (SE) values are averaged across n samples for each ^{15}N tracer or plant species level, and overall mean is averaged across the 3 post-addition time points (12, 24, and 48 h). Significant predictors ($P < 0.050$, Type II Wald tests) are bolded; superscript letters indicate significant *post hoc* differences among levels ($P < 0.05$).

			Leaf N Uptake (μmol ^{15}N g^{-1} plant dw)				
	Levels	n	12	24	48	Overall Mean	N Uptake Rate
^{15}N Tracer	Ammonium[a]	83	0.23 ± 0.07	0.26 ± 0.06	0.99 ± 0.20	0.53 ± 0.09	0.017 ± 0.002
	Nitrate[a]	83	0.41 ± 0.10	0.59 ± 0.17	1.13 ± 0.27	0.70 ± 0.11	0.027 ± 0.004
	Glutamate[b]	54	0.10 ± 0.04	0.13 ± 0.03	0.32 ± 0.09	0.19 ± 0.04	0.006 ± 0.001
Species	*B. eriopoda*[c]	57	0.34 ± 0.17	0.53 ± 0.23	1.16 ± 0.33	0.73 ± 0.16	0.024 ± 0.005
	A. hymenoides[c]	88	0.20 ± 0.07	0.26 ± 0.07	0.51 ± 0.10	0.33 ± 0.05	0.012 ± 0.002
	G. sarothrae[c]	75	0.33 ± 0.08	0.31 ± 0.06	1.01 ± 0.23	0.56 ± 0.09	0.020 ± 0.003

Table 4. Percent (%) N recovery of NH_4^+, NO_3^-, and glutamate in leaves of *B. eriopoda*, *A. hymenoides*, and *G. sarothrae* plants over 48 h. Mean and standard error (SE) values are averaged for species × ^{15}N tracer combination across the 3 post-addition time points for ^{15}N-enriched samples only (N = 220).

	B. eriopoda		*A. hymenoides*		*G. sarothrae*	
^{15}N Tracer	Mean	Max	Mean	Max	Mean	Max
NH_4^+	3.79 ± 1.28	15.85	2.00 ± 0.52	10.22	1.81 ± 0.61	15.85
NO_3^-	8.36 ± 3.42	47.96	2.91 ± 0.85	15.00	4.72 ± 1.00	23.44

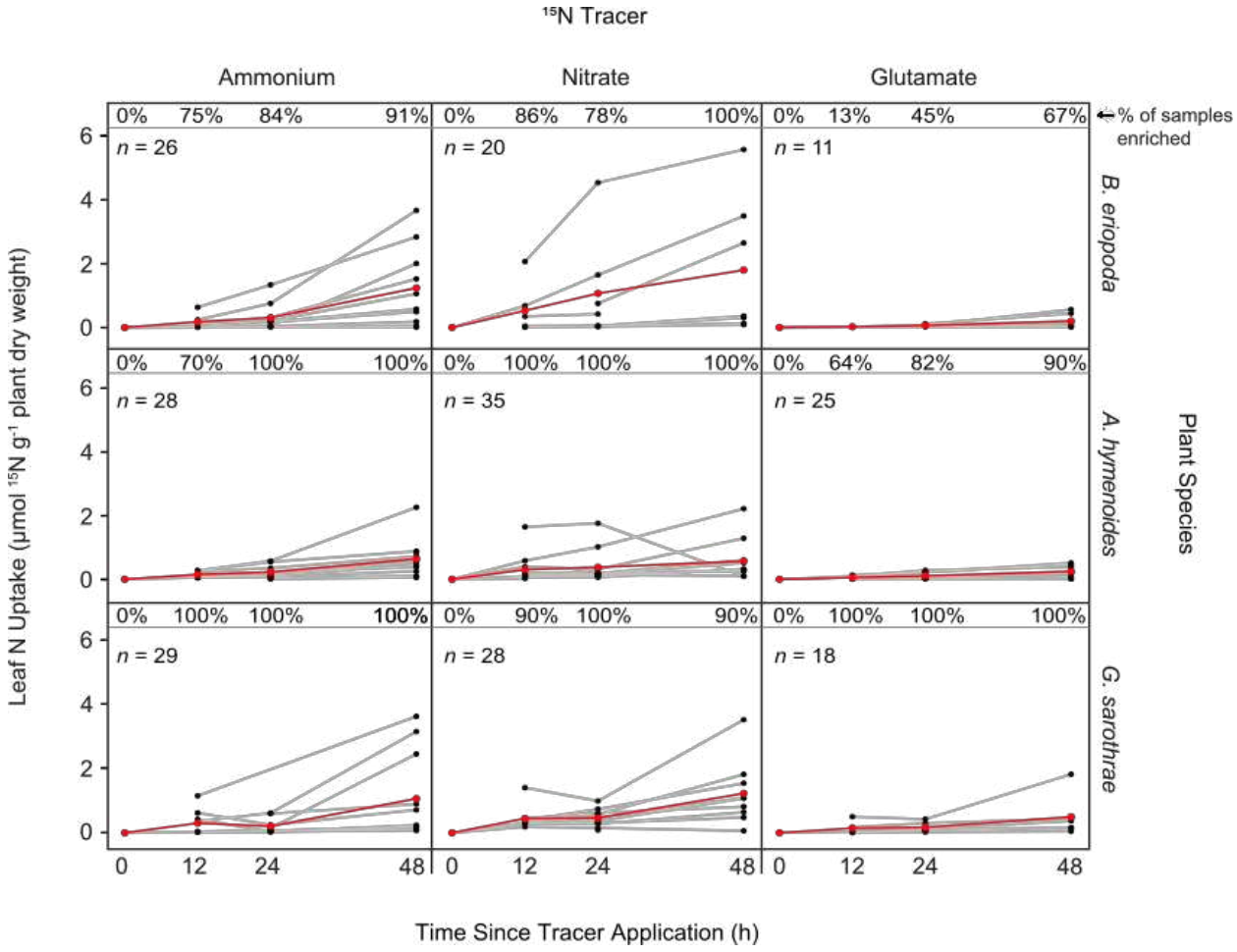
Glu	0.85 ± 0.28	2.16	0.76 ± 0.19	2.70	1.42 ± 0.45	9.12

Table 5. Percent (%) N Recovery results from published studies measuring soil inorganic and organic N uptake in dryland plant species. Values are reported as percent (%) of applied ^{15}N recovered in plant shoots. The ratio of NH_4^+:NO_3^- recovery represents %NH_4^+ recovery divided by %NO_3^- recovery (unitless). The ratio of inorganic:organic N recovery represents the average % recovery of NH_4^+ and NO_3^- (if both forms were applied in the study) divided by the % amino acid recovery (unitless). Data are from control (no treatment) plots only. An "--" indicates that the variable was not measured in the study. An "NA" indicates that the variable could not be determined or calculated based on the data provided in the study. An "*" indicates that the study reported combined results from $^{15}NH_4$ and $^{15}NO_3^-$ treatments; an "**" indicates the study added ammonium nitrate ($^{15}NH_4{}^{15}NO_3$).

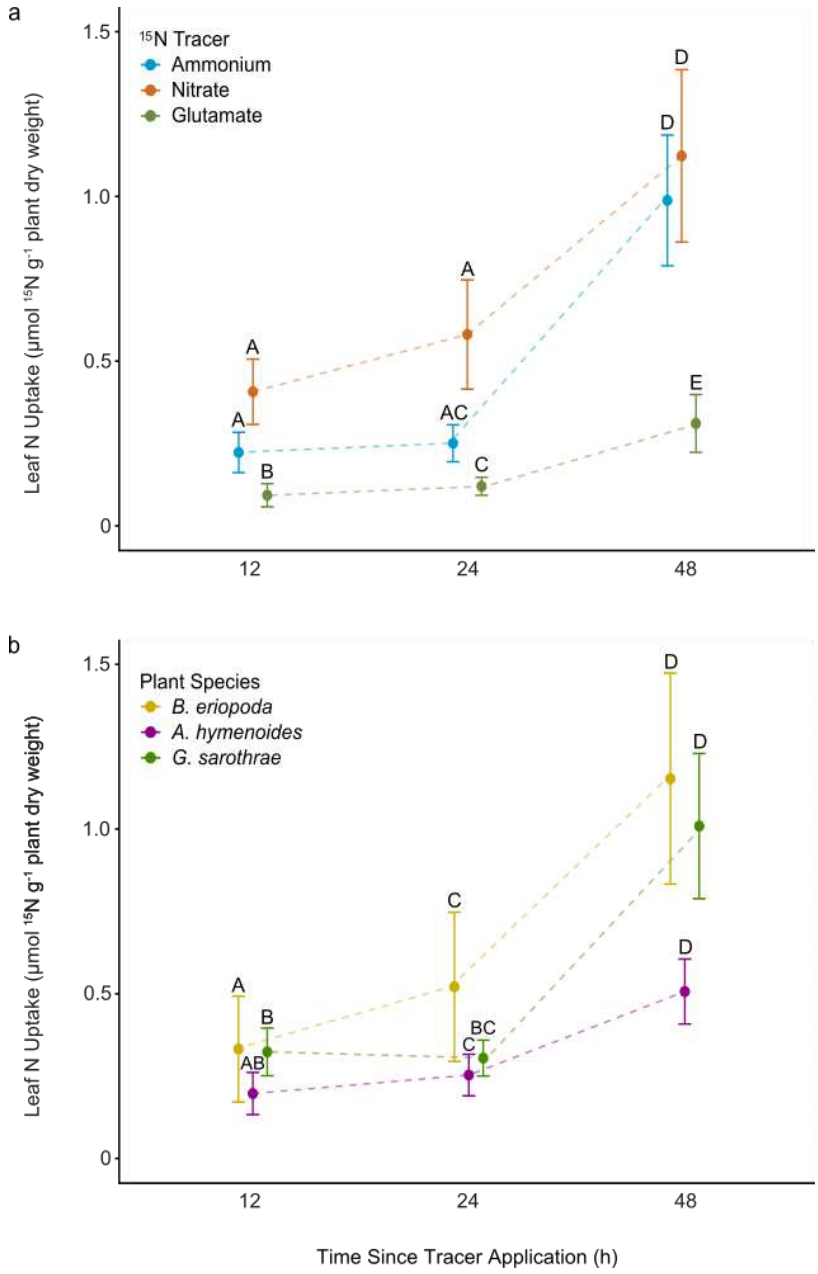
			%N Recovery			Recovery Ratio	
Reference	Plant Species	Time	NH_4^+	NO_3^-	AA	NH_4^+:NO_3^-	Inorg:Org
Jackson, Schimel & Firestone 1989	*Avena barbata, Bromus mollis, Lolium multiflorum*	24 h (Feb)	8.7	19.6	--	0.44	--
		24 h (Apr)	10.7	25.9	--	0.41	--
James & Richards 2006	*Atriplex confertifolia*	8 h	3.8	**	--	NA	--
		12 h	3.1	**	--	NA	--
		24 h	5.3	**	--	NA	--
		48 h	6.7	**	--	NA	--
	Atriplex parryi	8 h	0.3	**	--	NA	--
		12 h	0.3	**	--	NA	--
		24 h	1.9	**	--	NA	--
		48 h	3.3	**	--	NA	--

James et al. 2008	*Bromus tectorum*	72 h	22.0	49.3	--	0.45	--
	Taeniatherum caput-medusae		17.4	43.5	--	0.40	--
	Elymus elymoides		10.2	35.7	--	0.29	--
	Pseudoroegneria spicata		17.0	21.3	--	0.80	--
	Poa secunda		14.9	24.8	--	0.60	--
	Crepis intermedia		20.4	48.7	--	0.42	--
	Lomatium triternatum		20.8	52.8	--	0.39	--
Green et al. 2008	*Bouteloua* spp.	24 h	--	5.1	Glu: 0.2	--	21.11
		4 d	--	9.4	Glu: 0.3	--	28.01
Aanderud & Bledsoe 2009	*Bromus diandrus*	72 h	73.5	51.4	Gly: 38.6	1.43	1.62
	Bromus hordeaceus		48.7	47.4	Gly: 41.6	1.03	1.16
	Elymus glaucus		23.3	52.5	Gly: 29.3	0.44	1.29
	Nassella pulchra		21.8	45.0	Gly: 23.5	0.48	1.42
Wang et al. 2016	*Leymus chinensis*	3 h	1.2	0.9	Gly: 0.6	1.42	1.90
	Stipa grandis	(Aug)	1.3	0.8	Gly: 0.8	1.57	1.39
Zhuang et al. 2020	*Erodium oxyrrhynchum*	24 h (May)	2.7	3.3	Gly: 2.2	0.80	1.35
	Hyalea pulchella		3.4	3.6	Gly: 2.5	0.95	1.41
	Nonea caspica		6.6	5.8	Gly: 3.8	1.15	1.65
	Lactuca undulata		3.4	5.4	Gly: 2.8	0.62	1.60
Yang et al. 2022	*Cleistogenes squarrosa*	3 h	11.1	76.5	Gly: 13.1	0.15	3.34
	Leymus chinensis		8.1	85.1	Gly: 7.8	0.10	6.00
	Stipa grandis		13.9	75.5	Gly: 11.4	0.18	3.91
Present Study	*Achantherum hymenoides*	12 h	0.5	1.2	Glu: 0.2	0.41	4.67
		24 h	1.5	2.7	Glu: 0.6	0.54	3.39

	48 h	4.0	5.0	Glu: 1.6	0.80	2.80
Bouteloua eriopoda	12 h	0.6	2.1	Glu: 0.1	0.28	16.69
	24 h	2.4	7.8	Glu: 0.3	0.31	15.83
	48 h	9.1	18.5	Glu: 2.2	0.49	6.39
Gutierrezia sarothrae	12 h	1.0	1.8	Glu: 0.5	0.56	2.90
	24 h	1.2	3.8	Glu: 1.1	0.33	2.36
	48 h	3.4	8.6	Glu: 2.7	0.40	2.23



1191 **Fig. 1** Leaf N uptake (µmol ^{15}N per g plant dw) over time (h) of ^{15}N-enriched samples only (*N* =
1192 220) collected from individuals of *B. eriopoda*, *A. hymenoides,* and *G. sarothrae* before and after
1193 application of one of three ^{15}N tracers (ammonium, nitrate, or glutamate) to root and rhizosphere
1194 soils. Grey lines connect samples from the same plant individual while red lines show mean N
1195 uptake rates (µg ^{15}N per g plant dw per h) for each tracer and species group. The percentage (%)
1196 of leaf samples considered N-enriched out of the total number of samples (*n*) for each ^{15}N tracer
1197 × species × time point group is displayed at the top of each panel.



1198 **Fig. 2** Mean leaf N uptake ± standard error (µmol ^{15}N per g plant dw) of (a) ^{15}N tracer types
1199 (ammonium, nitrate, glutamate) averaged across species, and (b) plant species (*B. eriopoda*, *A.*
1200 *hymenoides,* and *G. sarothrae*) averaged across tracer types at each time point measured (12, 24,
1201 and 48 h). Letters indicate significant *post hoc* differences ($P < 0.05$) among (a) ^{15}N tracers at
1202 each time point, and across time points for each ^{15}N tracer type; and (b) species at each time
1203 point, and across time points for each species. Values are reported in Table 3.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- 231222CortPlantSoilESM.docx