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Mineral nutrient mobilization by plants from rock: influence of rock type and arbuscular mycorrhiza

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Abstract Rock colonization by plant roots and their associated microbiota is one of the major drivers of mineral weathering, nutrient cycling, soil formation and ecosystem stability. Yet the mechanisms of bio-uptake of lithogenic elements from rocks with differential nutrient availabilities and limitations are yet to be established. Here we present results from a mesocosm experiment that examined lithogenic element dissolution and uptake (P, K, Ca, Mg, Mn, Fe, Na, Ti, Al and Si) in *Bouteloua dactyloides* (buffalo grass) grown on four different granular porous media (basalt, rhyolite, granite and schist) comprised of primary mineral assemblages as influenced by arbuscular mycorrhiza (AM; *Rhizophagus irregularis*). Our results demonstrated that nutrient mobilization (chemical denudation + plant uptake) in such oligotrophic systems is governed by nutrient supply in the parent material, nutrient availability in pore water solution, and plant physiology. Overall, total major lithogenic element mobilization in planted columns (with and without AM) exceeded abiotic controls in all substrates. Differences in total mobilization among substrates occurred as follows: Fe, Na, Ti and Al reached high values in planted treatments in basalt, P and Mn in rhyolite, Ca and K in granite and K in schist, suggesting enhanced dissolution of primary minerals in the presence of plants. Element biomass enrichment of Mn, Fe, Ti and Al appeared to be higher in basalt than the rest of the substrates; however, high Al availability limited Ca and Mg uptake and plant growth in this rock media. Presence of mycorrhiza enhanced shoot biomass in rhyolite due to increased P uptake, and increased concentrations and total uptake of lithogenic elements in plants in all rocks but granite. As expected, AM significantly increased plant root concentrations of P, K, Ca, Mn, Fe, Ti, Al in basalt, and Mn shoot concentrations in rhyolite, as well as root total uptake of K, Ca, Mg, Mn, Fe, Na, Ti, Al and Si in basalt. At the same time, AM decreased Ca, Ti and Al concentrations in shoots grown in rhyolite, a possible protection mechanism against Al toxicity. The importance of AM in nutrient uptake is also reinforced by positive correlations between AM infection rate and P, Ca and Mn total uptake across all substrates. Moreover, total mobilization of Ca, Mg and Mn in rhyolite, was significantly higher in the AM versus non-AM treatment, contrary to K, Ca, Mg, Na

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and Si in schist. Our work demonstrates how mineral weathering and associated nutrient release is promoted by plant processes, further enhanced by plant associated with symbiotic AM, and yet more pronounced in basalt and rhyolite compared to granite and schist.

Keywords Buffalo grass · Major elements mobilization · Rocks · Arbuscular mycorrhiza · Incipient weathering · Soil formation

Introduction

Colonization of rocks by plants and their associated root microbiota plays an essential role in rock weathering and incipient soil formation (Bashan et al. 2006; Taylor et al. 2009; Verboom and Pate 2013). As an example, Puente et al. (2004a, b) and Lopez et al. (2009) demonstrated that bare rocks, where plants were grown in association with rhizoplane bacteria, released a significant amount of nutrients, which facilitated plant growth and soil formation. During incipient soil formation, biota growth and nutrient acquisition is initially limited by chemical dissolution of primary minerals (Mapelli et al. 2012; Taylor et al. 2009) from fresh rock substrate. Primary minerals contain most of the nutrients that plants require for normal growth and development (Harley and Gilkes 2000), but they are not readily accessible to organisms because they are bound within crystalline mineral structures. Chemical weathering is facilitated through plant production of carbonic and organic acids, including chelating agents that attack rock primary minerals (Brantley et al. 2011; Chorover et al. 2007; Dontsova et al. 2014). Plants are geochemical pumps that move nutrients from rocks/soil into their tissues to use them for their metabolism, store them temporarily, and return them to the soil via litterfall and biomass decomposition that allows nutrient recycling (Amundson et al. 2007).

Plant roots enhance the rate of chemical weathering of rock and soil formation by increasing substrate porosity and altering local rhizosphere conditions relative to bulk soil. This occurs through multiple mechanisms including: (i) fine roots directly modifying the pH by excreting protons or hydroxide ions to maintain charge balance during mineral nutrient ion uptake; (ii) roots and rhizosphere microbes releasing CO_2 by respiration that upon dissolution in water increases carbonic acid concentration; (iii) modifying the redox conditions in the rhizosphere; (iv) exuding organic acids, including amino acids and phytosiderophores, that can form stable complexes with polyvalent metals (e.g. Fe and Mn); and by (v) absorption of nutrients at the interface of roots and mineral particles (Harley and Gilkes 2000; Hinsinger et al. 2003, 2005, 2009). These various processes likely contribute differentially to mobilization and/or uptake of different elements from mineral media, with potentially important—but as yet poorly resolved—consequences for plant nutrition and soil formation in oligotrophic environments comprising newly exposed rock, where growth is constrained by nutrient availability. Understanding plant strategies to obtain nutrients in adequate supply to fulfill physiological needs is essential in the face of continuous environmental changes that can affect ecosystems functioning and availability of nutrients in soil.

Another mechanism that plants employ to increase their access to nutrients is root association with bacteria and mycorrhizal fungi that can be important bio-weathering agents (Bonneville et al. 2011; Calvaruso et al. 2013; Quirk et al. 2012). Mycorrhizal fungi live in symbiosis with plant roots, supplying host plants with P and lithogenic metals in exchange for photosynthetic carbon compounds that they use for energy and growth. There are several types of mycorrhizae, but the most common are ectomycorrhizae (ECM) and vesicular arbuscular mycorrhizae (AM). The role of mycorrhizal fungi, especially ECM has been previously addressed in studies of mineral dissolution (Balogh-Brunstad et al. 2008; Bonneville et al. 2011; Landeweert et al. 2001; Marschner 2002). Laboratory and field studies provide evidence that ECM fungi are able to extract key nutrients such as P, K, Ca, Mg, and Fe from apatite, biotite, feldspars and other silicates, promoting plant growth under nutrient-limited conditions (Hoffland et al. 2003; Rosling et al. 2004). Conversely, studies pertaining to the influence and quantitative importance of AM on bio-weathering, nutrient mobilization, element cycling, plant nutrition/stoichiometry and soil formation in oligotrophic environments are extremely limited (Bashan et al. 2007; Arocena et al. 2012; Koele et al. 2014).

The present study seeks direct and indirect insight into biological weathering of different classes of rock substrates; specifically, we evaluated the role AM

plays in plant nutrient uptake during incipient soil formation from parent rock focusing on mineral weathering, element mobilization, geochemical cycling of elements, and plant nutrition. Plant growth and nutrient acquisition were measured over 124 days in ground substrate of equivalent particle size distribution from four distinct, yet widespread parent materials (basalt, rhyolite, granite and schist). Although several studies have addressed the role of plants in basalt weathering (Akter and Akagi 2005, 2010) and some other reported the role of lichens and bacteria on granite weathering (Hall et al. 2005; Song et al. 2010) this is the first study to our knowledge that compares biological weathering potential of different substrates under controlled environmental conditions.

We hypothesized that plant roots and symbiotic mycorrhiza would increase weathering relative to abiotic controls, and that rock composition and pore water chemistry would influence plant nutrient uptake, resulting in greatest plant biomass and bulk elemental uptake on basalt, a rock type that is more susceptible to weathering and elemental release (Olsson-Francis et al. 2012). We also predicted that significant deviation from rock substrate stoichiometry by enhanced dissolution of certain elements and elevated nutrient uptake rates would occur in the presence of AM, because of its facilitation of root function and plant establishment on bare rock. Additionally, we postulated that these AM effects would be amplified on rocks with the lowest nutrient availability (e.g. rhyolite, granite and schist).

Materials and methods

Experimental setting and plant species

The mesocosm experiment was conducted for a period of 4 months using the environmental controls available within the Desert Biome at the Biosphere 2 research facility at the University of Arizona (UA), where day/night temperatures were constrained to 22 and 10 °C, respectively, relative humidity averaged 46 %, and a natural photoperiod was utilized to support plant growth. Plants and rocks were held in plexiglass columns (30/5 cm) embedded in six sealed/sterile plexiglass mesocosms (168.9 cm length × 96.04 cm height × 75.3 cm width; Patent application no. 61/982,318, Docket no. UA 14-092-P, U.S Patent and Trademark Office; Fig. 1), where filtered air (Gem guardian, AC4850CAPT Digital 3-in-1 Hepa Air Purifier System) was pumped through each volume at a rate of 0.5–1 L s^{-1}. Within each enclosure, plants received ultrapure (18 MΩ-m) water each 2 weeks for the first month and once per month thereafter. Watering was by drip/syringe irrigation system at a rate of 4 mL s^{-1} with a total of 100–120 mL $column^{-1}$ added each time, which brought rock profiles to near-field capacity.

Buffalo grass (*Bouteloua dactyloides*), a western American perennial shortgrass, was selected as a model species because it has shown good potential for growth in nutrient-poor environments (Solis-Dominguez et al. 2012). Triplicate columns of three treatments (plants with and without mycorrhiza and abiotic controls) per each rock were used. Buffalo grass seeds were surface sterilized by immersion for 5 min in 95 % ethanol, then rinsed with sterile ultrapure water, soaked for 5 min in 2 % sodium hypochlorite solution, rinsed three times with sterile distilled water, soaked for 3 min in 0.1 % sodium thiosulfate solution and then rinsed a final time. The effectiveness of the surface sterilization procedure was confirmed by placing sterilized seeds on R2A agar plates and monitoring microbial growth. After sterilization, seeds were soaked in sterile water and pre-germinated before planting them in columns. Twenty pre-germinated seeds were then planted in each column at a 20 mm depth below the surface.

Porous rock media preparation

We compared grass growth and nutrient dynamics across four porous rock media types. Material used for replicated mesocosms were generated from (i) basalt, (ii) rhyolite, (iii) granite and (iv) schist rock samples. Igneous (mafic basalt, felsic rhyolite and granite) and metamorphic (schist) rocks with different chemical composition were selected for this experiment because they are also the subject of inter-disciplinary earth science projects currently underway in the Catalina–Jemez Critical Zone Observatory (http://criticalzone.org/catalina-jemez/) and the Landscape Evolution Observatory at UA's Biosphere 2 (LEO, http://leo.b2science.org/). Findings from this laboratory-based research on element cycling, weathering rates, plant growth and incipient soil formation will be applied to help interpret the field and 'macrocosm' scale studies being conducted at the CZO and LEO, respectively. Basalt was collected from Merriam Crater (Flagstaff,

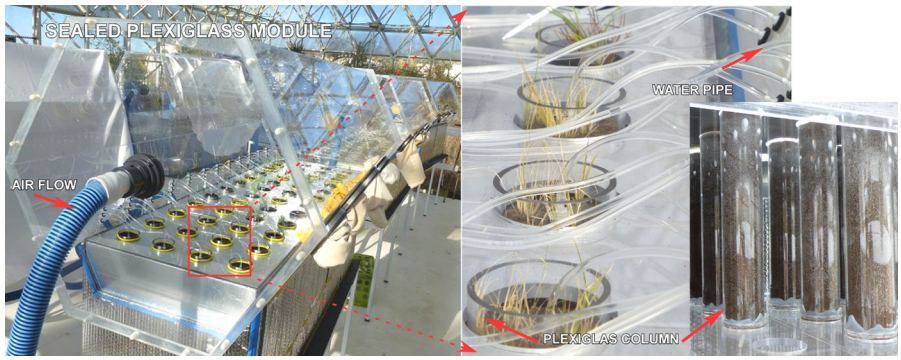


Fig. 1 Enclosed environments (plexiglass modules/mesocosms) with buffalo grass growing on different rock types in a column experiment at Biosphere 2 research facility, University of Arizona

AZ, USA), rhyolite from Valles Caldera National Preserve (Jemez Springs, NM, USA), granite from W. Santa Catalina Mountains and schist from E. Santa Catalina Mountains (Coronado National Forest, Tucson, AZ, USA).

Toward the goal of decreasing uncontrolled variability in the experiments, all rocks were treated before introduction into the mesocosms. Weathered rock surfaces were first removed via pneumatic chisel to reveal unweathered cores that were then crushed, and sieved to obtain the 250–500 μm fraction. This fraction was then cleaned on a water table, and sterilized for 3 days at 121 °C to remove any native or contaminant microbial cells. Based on prior work pertaining to the dissolution kinetics of basalt bearing minerals (Calvaruso et al. 2013), we assumed that mineral structure was not altered by autoclaving.

Average basalt mass in the experimental columns was 690 ± 6 g, bulk density (ρ_b) was 1.32 ± 0.03 g cm^{-3} and porosity (calculated from the water mass required to yield saturation) was 0.33 ± 0.007. Rhyolite columns comprised a rock mass of 690 ± 10 g, a ρ_b of 1.24 ± 0.02 g cm^{-3} and a porosity of 0.35 ± 0.01. Granite columns contained 640 ± 8 g of rock, ρ_b was 1.34 ± 0.003 g cm^{-3}, and porosity was 0.32 ± 0.008. Schist columns contained 480 ± 5 g of rock, ρ_b was 1.04 ± 0.02 g cm^{-3}, and porosity was 0.43 ± 0.01.

Mineralogical and lithogenic element analyses

Wavelength dispersive X-ray spectroscopy (CAMECA SX100 electron microprobe) and synchrotron X-ray diffraction (XRD) analyses were used to identify and quantify chemical and mineral composition by mass of studied ground rock material. Microprobe allowed full qualitative and quantitative analysis of all elements through point analyses, line analyses, and x-rap maps. Crystalline mineral composition of each rock was determined by synchrotron-based X-ray diffraction (XRD) analysis, conducted on the bulk column material on beam line 11-3 at Stanford synchrotron radiation lightsource (SSRL). Quantitative analysis of minerals was performed using the Rietveld module included in the X'Pert High Score Plus software (PANalytical B.V., Almelo, Netherlands) (see Perdrial et al. 2011 for details).

Total elemental concentrations in the rock samples were determined by subjecting the unweathered granular rock samples to lithium metaborate fusion, followed by inductively coupled plasma mass spectrometric (ICP-MS) and optical emission spectrometry (ICP-OES) analyses (Activation Laboratories, Ontario, Canada).

Porous rock microbial inoculum

All experimental columns were inoculated with a native microbial consortium isolated from fresh basalt collected at the field site (Flagstaff, Arizona). This inoculum was prepared by mixing 1.0 g of fresh basalt with 95 mL of sterile ultrapure water. The mixture was vortexed for 2 min to separate rock particles and bath sonicated (VWR Aquasonic 250D model; 120 V, 4 A, 40 Hz) for 2 min to further release bacteria to suspension. A 90 mL aliquot of this inoculum, containing 1.43 × 10^5 CFU mL^{-1} heterotrophic bacteria, was filtered through a 25 μm sieve to remove native

AM fungi, and then mixed with the porous media which was placed into the plexiglass columns under sterile conditions. Inoculum solution added to abiotic controls was sterilized prior to addition.

AM inoculation, root colonization assessment and biomass harvesting

For the mycorrhizal treatment, we used *Rhizophagus irregularis*, a common mycorrhizal fungus, readily found in symbiotic association with grass plants in soil environments (Eskandari and Danesh 2010). An inoculum consisting of sterile spores of *R. irregularis* suspended in an aqueous solution (Premier Tech Biotechnologies, CA) was used across all AM treatments. 1 mL of solution containing approximately 400 spores was added to each column with germinated seeds.

After 4 months, plants were harvested and separated into above and below-ground structures. All rock particulate matter was removed from the root surface by carefully washing the plants in sterile ultrapure water. Particle removal was further confirmed by microscopic examination of the roots. Dry plant biomass for all columns was obtained by oven-drying at 70 °C for 3 days. Root fragments were stained to determine mycorrhizal infection rate in each column. Specifically, random subsamples of approximately 0.05 g of fresh roots, were cut into 1 cm pieces, boiled and cleared in 10 % KOH for 15 min at 90 °C, neutralized by 10 % HCl for 2 min, and stained with 0.05 % trypan blue for 10 min at 90 °C. Root colonization percentages by AM were determined by placing 30 segments of stained roots on microscope slides and recording the number of segments with any infection with the use of a compound microscope (after Phillips and Hayman 1970).

Plant versus solution concentrations of rock-derived elements

Pore water solution and plants were analyzed for major element concentrations (P, K, Ca, Mg, Mn, Fe, Na, Ti, Al and Si) by inductively coupled plasma mass spectrometry (ICP-MS, Perkin Elmer, Elan DRC-II) in the University of Arizona's Laboratory for Emerging Contaminants (ALEC). Solution samples collected after each watering event were centrifuged at 4600 rpm for 30 min, their supernatant was removed, diluted with ultra-pure water, acidified with trace metal grade nitric acid, and stored for ICP-MS analysis. The pH of collected solution samples was also measured.

To determine elemental concentrations in plant tissues, samples of shoot (~3 mg) and root (~4.5 mg) were microwave-digested (CEM MARS 6) using a 1:1 mixture of 70 % nitric acid (Aristar-plus- BDH) and 30 % hydrogen peroxide (J.T. Baker's Ultrex). The analyses followed standard procedures and QA/QC protocols. Certified reference material (apple leaves, CRM 1515), as well as procedural blanks were included in each digestion batch. Additionally, several samples were analyzed in triplicate to assess analytical precision. Coefficients of variation (% CV) among such replicates were less than 5 %, with relative standard deviations (% RSD) among measurements of the same sample being less than 3 %. All reagents were of ultra-pure quality (Aristar grade). Stock standard solutions were Merck Certificate AA standards. Ultra-pure water was used in all samples, standard solutions, and dilutions as appropriate. Element uptake in roots was quantified as element mass per unit dry root mass, which includes both root-absorbed and -adsorbed contributions.

In order to determine the effect of plants and/or fungi on relative differences in nutrient mobilization from minerals into plant tissues, here termed enrichment, element concentrations in plant tissues were normalized to their concentrations in solution to enable direct comparisons. Values above unity were considered enriched.

Element mobilization from rock was estimated in each experimental column by summing total chemical denudation in leachate and total element uptake into plant tissue. This approach enabled estimation of the contribution of plants to total element mobilization when compared to the abiotic controls.

Statistical analysis

Significant differences in plant dry biomass, plant element concentrations (μg g^{-1}), element concentrations normalized by solution concentrations (μg g^{-1}),total element mobilization (chemical denudation + plant uptake) from substrates and total uptake in plants (μg $plant^{-1}$) were determined and compared among rock types and/or treatments (AM vs. non-AM) using multivariate (MANOVA) or one-way analysis of variance ANOVA. In the case of significance, the Tukey post hoc tests were used to compare groups' means.

The Pearson product moment correlation coefficient (r) was used to examine the relationship between colonization rate and total element content in plants. All statistical analyses were performed using the software SPSS 15.0 package for Windows.

Results

Rock mineral and element content

Microprobe and quantitative (Q-)XRD analyses showed that basalt particles used in this study consisted of glass ~44.8 %, andesine 26.3 %, pyroxene (augite) 11.5 %, olivine (forsterite) 11.3 %, and minor phases (defined as minerals under 2 %) including labradorite 1.9 %, titanomagnetite 1.9 %, fayalite 0.3 %, chromite and apatite. Rhyolite particles contained feldspars (oligoclase 36 %, sanidine 22.3 % and anorthoclase 16.4 %), quartz 16.9 %, zeolite (faujasite) 4.9 % and minor minerals (e.g. titanomagnetite 1.5 %, apatite, hematite, zircon, titanite, ilmenite). Granite particles contained quartz 20.4 %, feldspars (oligoclase 22.1 %, albite 20.3 %, and sanidine 19 %), titanite 8.2 %, biotite 8 %, and minor minerals (muscovite, ilmenite, chlorite, hematite/magnetite, apatite, and garnet). Schist particles comprised quartz 46.3 %, phengite mica 44.2 %, biotite 7.5 %, and minor minerals: hematite, ilmenite, oligoclase, andesine, zircon, and xenotine.

Among the elements discussed in this study, Si was present at the highest mass concentration, and P and Mn at lowest mass concentration (Table 1). Mafic basalt was richer in P, Ca, Mg, Fe, Mn and Ti compared to the other more felsic rocks studied here. Several elements (e.g. Na and Si) showed high concentration in rhyolite and granite, while P concentration in these felsic igneous rock types was relatively low. Potassium and Al had high concentrations in schist (Table 1).

Plant growth on rock

Plants developed a higher root than shoot biomass during growth in all studied rocks (Fig. 2). Total biomass per plant, root biomass, as well as root to shoot ratio were higher in rhyolite than in the other substrates (ANOVA, $F_{total} = 3.68$, $P = 0.03$; $F_{root} = 4.89$, $P = 0.01$; $F_{root/shoot} = 8.52$, $P = 0.001$). There was positive correlation between P uptake (μg) per plant and biomass (g) per plant in rhyolite (Pearson correlation, $r = 0.96$, $N = 6$, $P = 0.003$). Mycorrhiza increased significantly aboveground biomass of buffalo grass growing in rhyolite (one way ANOVA, $F = 12.92$, $P = 0.04$) indicating a clear growth stimulation in this rock type. Generally, grasses infected with AM in rhyolite showed higher shoot, root, total biomass and root/shoot ratio when compared to mycorrhizal plants on the other mineral substrates (one way ANOVA, $F_{shoot} = 5.48$, $P = 0.04$; $F_{root} = 8.25$, $P = 0.02$; $F_{total} = 8.12$, $P = 0.02$; $F_{root/shoot} = 5.48$, $P = 0.04$) (Fig. 2). This is also supported by a slightly higher colonization rate (mean ± SE) in rhyolite (60 ± 10 %) than in basalt (52 ± 11 %) or schist (20 ± 5 %). In granite, grasses did not get infected and so this treatment effect is not further discussed.

Nutrient partitioning in plants

Variations in plant element concentrations between above and belowground biomass were observed for each rock type, regardless of treatment (Fig. 3). Generally, P, K, Ca and Si showed higher concentration in shoots, whereas Na, Fe and Al exhibited higher root concentration. Buffalo grass responded to inoculation with AM by increasing element (e.g. P, K, Ca, Mn, Fe, Ti and Al) concentration in roots grown in basalt (one way ANOVA, $F_P = 13.18$, $P = 0.02$; $F_K = 9.27$, $P = 0.04$; $F_{Ca} = 12.59$, $P = 0.04$; $F_{Mn} = 45.95$, $P = 0.002$; $F_{Fe} = 10.29$, $P = 0.03$; $F_{Ti} = 14.26$, $P = 0.02$; $F_{Al} = 10.23$, $P = 0.03$), and Mn concentration in plant shoots in rhyolite ($F_{Mn} = 10.45$, $P = 0.03$). Moreover, AM stimulated K, Ca, Mn, Fe, Na, Ti, Al and Si total uptake in plant roots in basalt (Table S1). However, AM also significantly decreased Ca, Ti and Al concentrations (one way ANOVA, $F_{Ca} = 7.75$, $P = 0.05$; $F_{Ti} = 10.38$, $P = 0.03$; $F_{Al} = 12.92$, $P = 0.02$) in plant shoots in rhyolite (Fig. 3). Colonization rate was positively correlated to total nutrient uptake of P, Ca and Mn in buffalo grass across all rock media (Fig. 4).

Ratios of (Ca + Mg) to Al in plants and solution were used to assess the effect of Al presence on nutrient uptake and plant growth. Lower ratios in plant uptake and leaching solution were observed in basalt and schist compared to rhyolite and/or granite. Mycorrhiza increased Al leaching in basalt and schist

Table 1 Total major and minor element concentrations (μg g^{-1}) in porous rock media used in experiments

Element	Conc.	Basalt	Rhyolite	Granite	Schist	ANOVA F (*P*)
P	Mean (%)	0.28	0.04	0.04	0.02	103,384 (**)
	SD	0.0007	0.0005	0.0005	0.0002	
K	Mean (%)	0.61	3.73	3.45	5.58	1128 (**)
	SD	0.002	0.1	0.09	0.09	
Ca	Mean (%)	6.52	0.74	1.69	0.09	43,891 (**)
	SD	0.03	0.02	0.02	0.004	
Mg	Mean (%)	6.50	0.13	0.49	1.72	5862 (**)
	SD	0.10	0.006	0.03	0.05	
Mn	Mean (%)	0.15	0.04	0.03	0.05	7273 (**)
	SD	0.0004	0.0001	0.002	0.0005	
Fe	Mean (%)	8.94	1.88	1.94	3.40	3313 (**)
	SD	0.11	0.09	0.05	0.06	
Na	Mean (%)	2.15	3.41	2.80	0.22	764 (**)
	SD	0.02	0.12	0.07	0.002	
Ti	Mean (ppm)	9862	2249	2561	2919	3002 (**)
	SD	140	72	78	70	
Al	Mean (ppm)	79,067	76,802	78,521	93,454	24 (*)
	SD	781	3871	5	2094	
Si	Mean (%)	21.13	33.20	33.10	30.20	165 (**)
	SD	0.05	0.6	0.9	0.7	

Significance by one way ANOVA test is given at $P < 0.0001$ (**) and at $P < 0.01$(*) levels

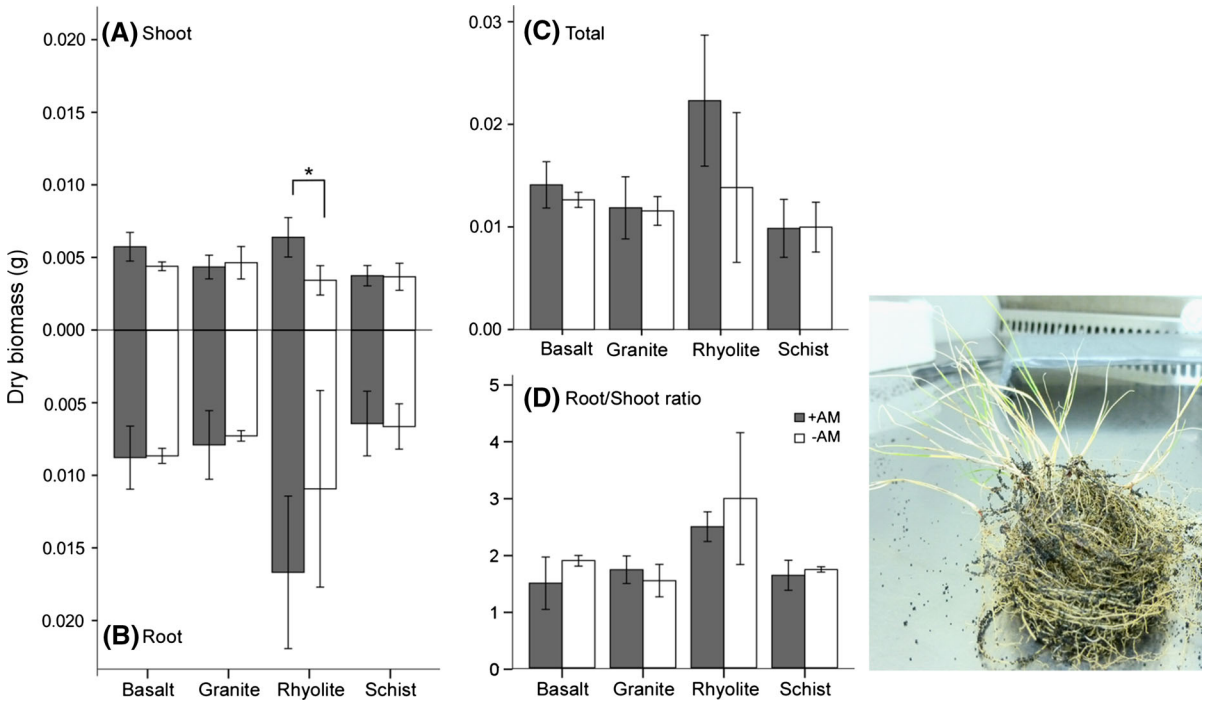


Fig. 2 Effect of *R. irregularis* myccorhiza inoculation on buffalo grass shoot (**a**), root (**b**) and total (**c**) biomass accumulated per plant in four rock types after 4 months. Symbol "asterisk" shows significant differences identified by one way ANOVA at $P < 0.05$ level. *Plotted values* represent mean ± SE; N = 3 per treatment

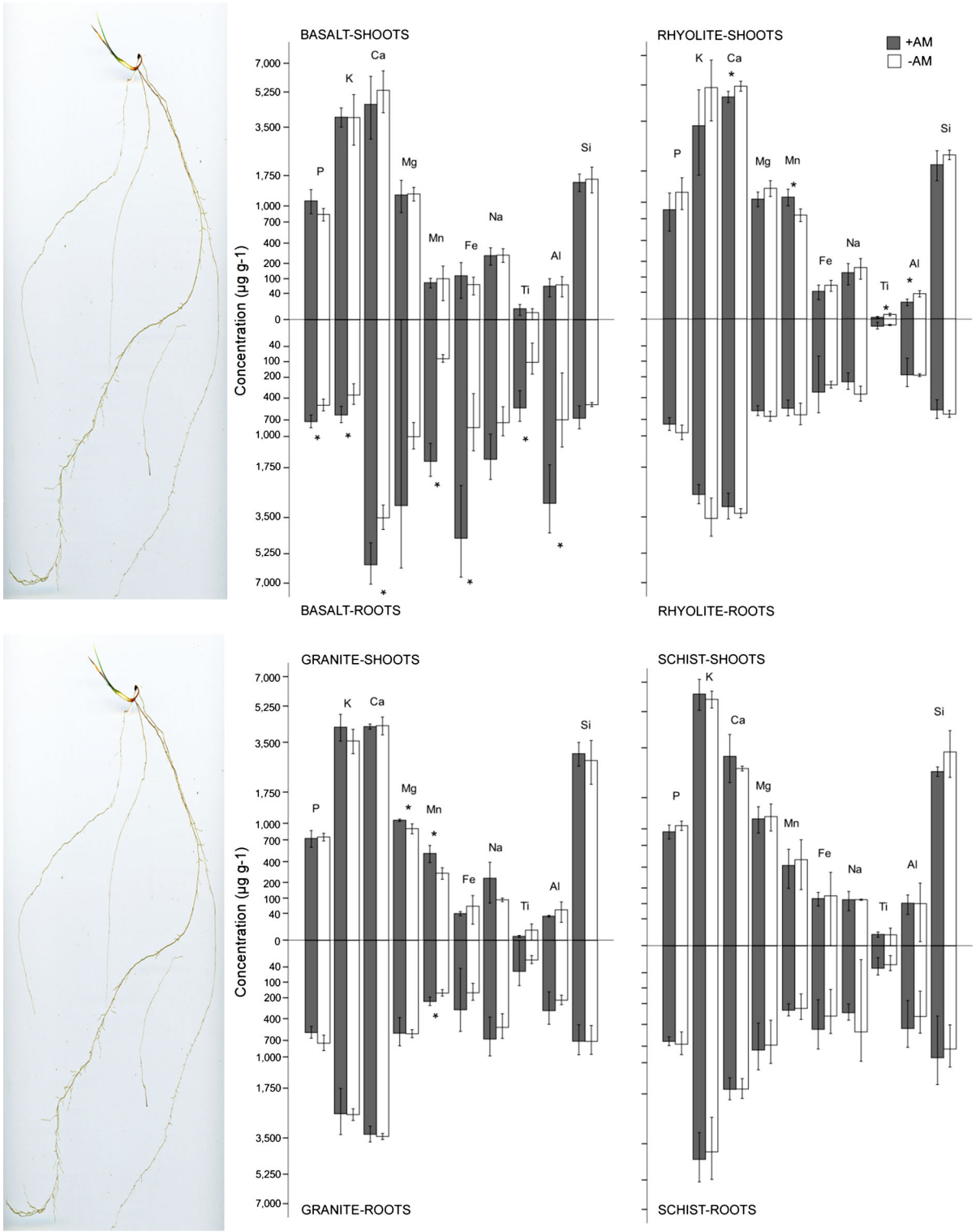


Fig. 3 Mycorrhizal effect on nutrient fractionation in above and below ground organs of buffalo grass, on each studied rock. An exponential scale was used with the exponent = 0.4. *Values* represent mean ± SE

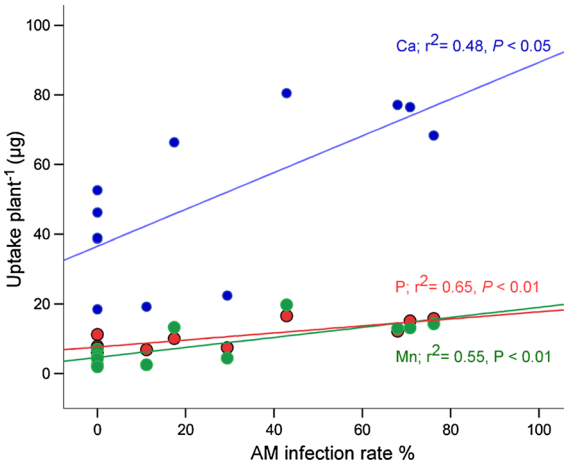


Fig. 4 Relationships between total uptake per plant of P, Ca and Mn and the infection rate in mycorrhizal grasses. Each *data* point represents an experimental column (N = 3 per rock)

solutions and decreased significantly plant uptake of nutrients (i.e., Ca and Mg) in basalt (Table S2).

Total element mobilization and distribution between plant biomass and solution

Mass balance analysis of the column experiment demonstrated that P, K, Mn, Fe, Ti and Al were among the elements that had a greater fraction of the total mobilized amount accumulated in plant tissues (Fig. 5). Element concentrations in plants and in pore water solutions were positively correlated for several elements: P, K, Ca, Na and Al (Pearson correlations: $r_P = 0.41$, $P < 0.01$; $r_K = 0.37$, $P < 0.05$; $r_{Ca} = 0.30$, $P < 0.05$; $r_{Na} = 0.45$, $P < 0.01$; $r_{Al} = 0.32$, $P < 0.05$). Significant differences in total element mobilization in planted treatments occurred among rock substrates. For example, Mg, Fe, Na, Ti and Al total amounts mobilized in the planted treatments in basalt were higher than in the other rock media, as were P, Mn and Si total amounts mobilized in rhyolite, K and Ca in granite and K in schist (Table S3).

One way ANOVA showed that plants contributed significantly to total elemental mobilization from substrate, compared to abiotic controls. Specifically, P, Ca and Mg total mobilization by plants (AM or non-AM treatments) was higher than in abiotic controls in basalt, as well as P, K, Ca, Mg, Mn, Na and Si in rhyolite, and P, K, Ca, Mg and Mn in granite. Potassium amount mobilized by non-AM plants was higher than in control treatment, while Ca and Na exhibited lower total mobilization in AM plants versus controls in schist (Fig. 5). The Tukey post hoc test revealed that AM increased the total amount mobilized of metabolically critical elements (Ca, Mg and Mn) in rhyolite relative to the non-AM treatment. Although, AM increased total mobilization of several elements (Mn, Fe, Ti and Al) compared to plants without mycorrhizal colonization in all substrates, this increase was not statistically significant. On the other hand, AM decreased total mobilization of non-essential elements (Na and Si) in rhyolite, as well as K, Mg, Na and Si in schist compared to non-AM planted systems.

Pore water solution pH decreased significantly in the planted columns of basalt, rhyolite and granite and increased in the schist relative to abiotic controls (one way ANOVA, $F_{basalt} = 7.29$, $P < 0.01$; $F_{rhyolite} = 3.35$, $P < 0.05$; $F_{granite} = 3.35$, $P < 0.05$; $F_{schist} = 6.58$, $P < 0.01$) (Fig. 5). Significant pH differences among AM versus non-AM treatments were not detected.

Element enrichment in biomass

The main pathway for nutrient uptake by both plant roots and fungal mycelium is through absorption from solution. Element concentrations in plants normalized to mean values for solution were significantly influenced by rock composition (MANOVA, $F = 7.57$, $P < 0.001$), and rock by treatment interaction ($F = 2.14$, $P = 0.02$). Manganese, Fe, Ti and Al were the most plant-enriched elements in all substrates, reaching highest values in basalt and lowest in schist (Fig. 6). Mycorrhiza enhanced enrichment of several elements (one way ANOVA, $F_{Mn} = 18.52$, $P < 0.05$; $F_{Ti} = 8.35$, $P < 0.05$; $F_{Al} = 12.08$, $P < 0.05$) in basalt and Ca ($F = 11.51$, $P < 0.05$) in schist, but it decreased plant enrichment relative to solution of Ca ($F = 11.48$, $P < 0.05$) and Mg ($F = 23.48$, $P < 0.05$) in rhyolite (Fig. 6).

Discussion

Rock type effect on biomass accumulation and lithogenic element stoichiometry in biomass

Despite the apparent inhospitability of the rock environment, buffalo grass germinated and

established in all substrates using pure water without any addition of nutrient solution. However, buffalo grass grown in porous rock media in our study recorded ca. 10–25 times lower total biomass than the same grass species growing in soil environments (Moffet 2003), indicating the oligotrophic nature of our substrates. For all rocks, belowground exceeded aboveground biomass, consistent with the grass physiological attributes (Weaver 1954) and with low nutrient availability promoting biomass allocation to roots (Göransson 2001).

Plant growth was significantly higher in rhyolite than in other rocks, despite basalt having higher concentrations of all major lithogenic nutrient elements except for K (Table 1). Root to shoot ratio, root and total biomass were also higher in rhyolite than in the other substrates (Fig. 2). Field studies documented higher plant capacity to colonize rhyolite containing high amounts of Si, K and Na than other volcanic rocks rich in Ca, Mg, Mn, Fe, Ti and Al (Lopez et al. 2009) perhaps indicating the critical importance of K availability for rock colonization by plants.

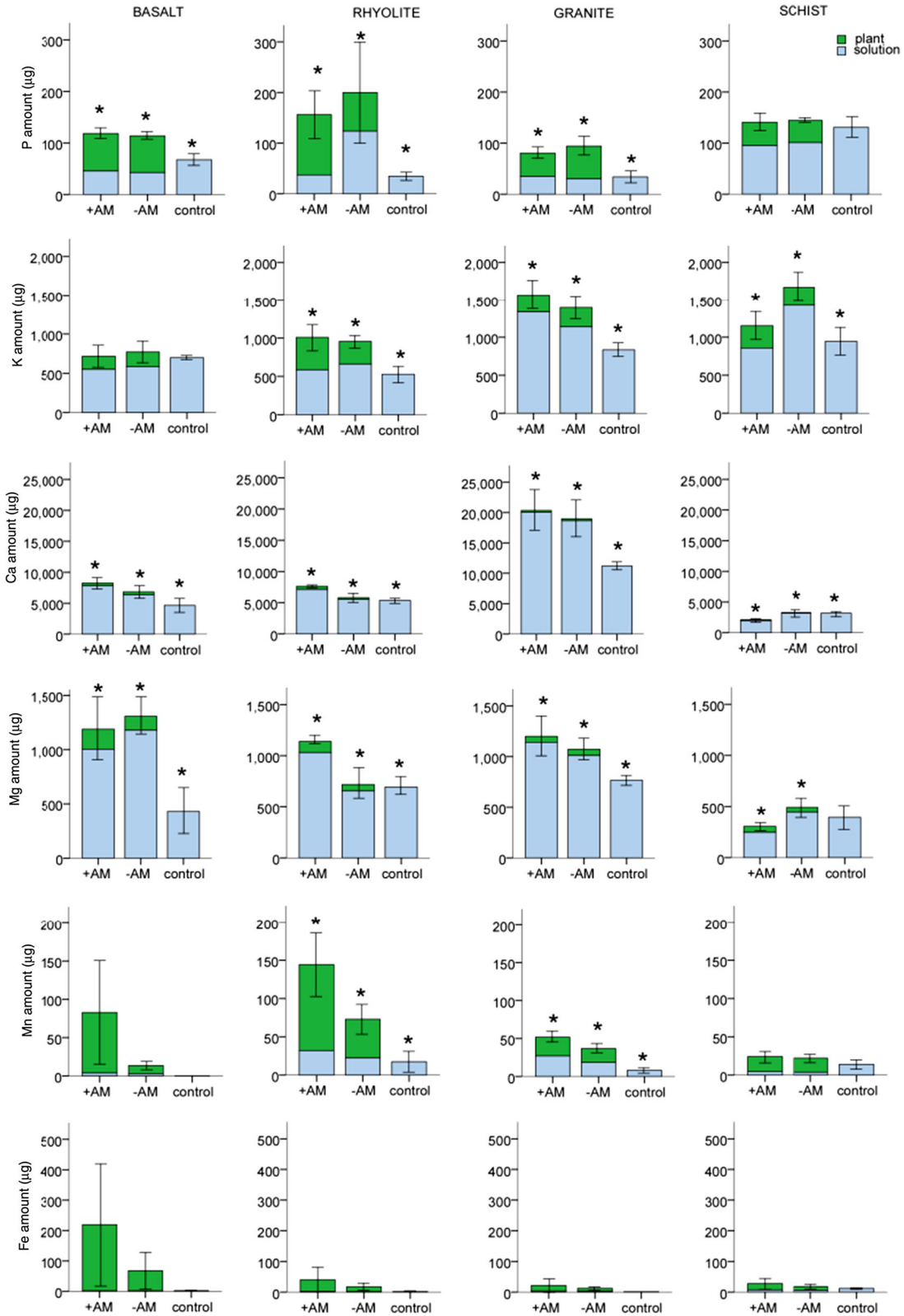
Though rock nutrient concentrations exhibited high variability (Table 1), concentrations in the plants varied much less across the rock treatments (Fig. 3). For example, some of the highest differences in element concentrations in plants among rocks were recorded for K which reached 1.5 times higher concentration in plant shoots grown in schist than in the other substrates; Mn concentration was 2–10 times higher in buffalo grass shoots grown in rhyolite, and Fe, Na, Ti and Al were ca. eight times higher concentrations in roots established on basalt than in the other rocks (Fig. 3). The concentrations of macronutrients (P, K, Ca and Mg) in buffalo grass from our study were 3–6 times lower relative to previously reported values for grasses (Thompson et al. 1997; Whitehead 2000), again indicating nutrient limitations associated with oligotrophic, primary mineral-dominated conditions during initial rock colonization by plants.

Differences in element concentration in different plant tissues among substrates were element specific (Fig. 3). Several lithogenic elements displayed higher concentrations in the shoots (e.g. P, K, Ca and Si), and others in the roots (e.g. Fe, Na and Al) of buffalo grass (Fig. 3), similar to other studies on grasses (El-Nashaar et al. 2009). The differences may be attributed partly to the functions of each element, and partly to whether the element is susceptible to being bound by the root tissue. It is likely, for example, that Al and Fe hydrolysis and polymerization in the root zone may lead to Al and Fe (oxy) hydroxide plaque formation on the root surface.

Fig. 5 Mass balance, showing significant differences (one way ANOVA, $P < 0.05$) in total element mobilization (mean ± SE) in planted columns relative to abiotic controls in the four rock substrates. Pore water solution pH values for each treatment are also presented

Enhanced weathering by buffalo grass and AM

Nutrient availability is a crucial factor affecting rock colonizers (Lopez et al. 2009) and plants influence nutrient availability through enhancement of mineral dissolution. A considerably higher total mobilization (soluble loss + plant uptake) of Mg, Fe, Na, Ti and Al was observed in the presence of plants in basalt, P, Mn and Si in rhyolite, K and Ca in granite, and K in schist (Table S3). Increase in lithogenic element mobilization was rock specific, but not directly related to the total concentration of these elements in the rocks (Table 1). For example, among elements that were significantly mobilized by the plants, although Mg, Fe, and Al were present in basalt in higher concentrations than in other rocks, the same is not true for Ti. Similarly, P and Mn were effectively mobilized by plants in rhyolite but were present there in smaller concentrations than in other rocks. Therefore, we can assume that these differences in element mobilization may be related to dissolution kinetics of minerals specific to different rock types. For example, glass and olivine present in basalt are more kinetically susceptible to weathering than quartz and K-feldspars from rhyolite and granite (Wilson 2004), so Mg, Fe, Na, Ti and Al in basalt might have been mobilized by plants through preferential dissolution of basaltic glass and olivine. Similarly, a higher mobilization of P in rhyolite relative to the other rock types (Table S3) may be related to preferential dissolution of apatite, and can be scored as a factor responsible for the observed increase in plant growth in this porous rock medium (Fig. 2). More K was mobilized in granite and schist than basalt and/or rhyolite (Fig. 5) most likely due to biotite dissolution and high plant nutrient


BASALT
RHYOLITE
GRANITE
SCHIST
plant
solution
P amount (µg)
K amount (µg)
Ca amount (µg)
Mg amount (µg)
Mn amount (µg)
Fe amount (µg)
+AM
-AM
control

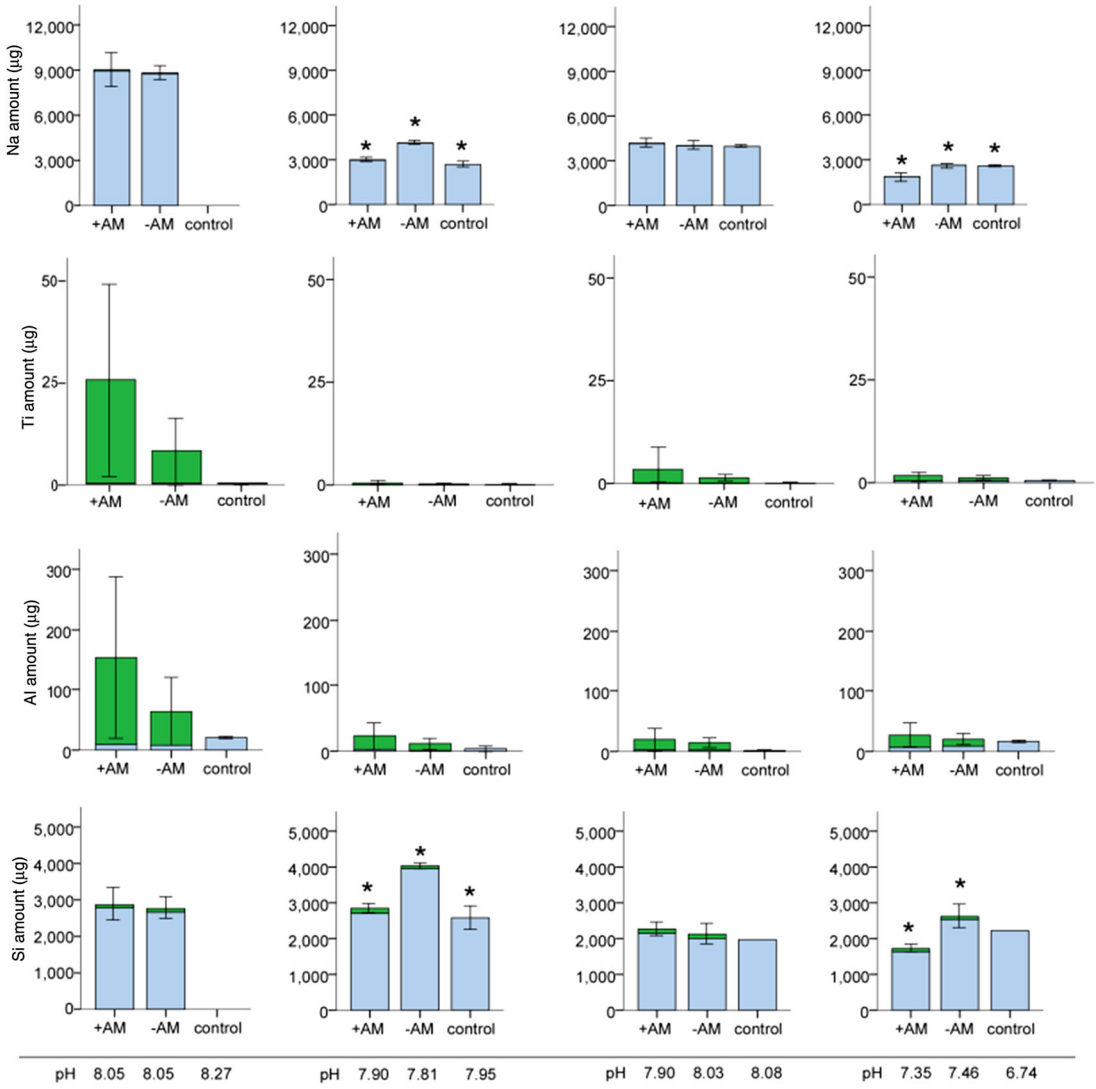


Fig. 5 continued

demand. For some elements (P, K, Mn, Fe, Ti and Al), the majority of mobilized mass was sequestered in the plant biomass due to active uptake (likely for nutrients, such as P and K) or preferential dissolution of minerals containing Mn, Fe, Ti, and Al. Mycorrhiza influenced total mobilization of lithogenic elements in our study, by increasing mobilization of important nutrients such as Ca, Mg and Mn in rhyolite and decreasing K, Ca, Mg, Na and Si mobilization in schist, as well as Na and Si in rhyolite, when compared to the non-AM treatment (Fig. 5). The trends were not consistent across elements and rocks.

Mycorrhiza effects on plant growth and element enrichment in biomass

Arbuscular mycorrhiza symbiosis promoted plant shoot growth in rhyolite (Fig. 2), as a result of the increase in P uptake, and significantly impacted concentrations of elements in shoots and roots (Fig. 3). Contrary to our expectation that AM impact would be most pronounced in rhyolite, granite and schist, because of lower nutrient concentrations in these rocks, the largest effects were observed in basalt. Basalt dissolution seems to be cost- effective for AM,

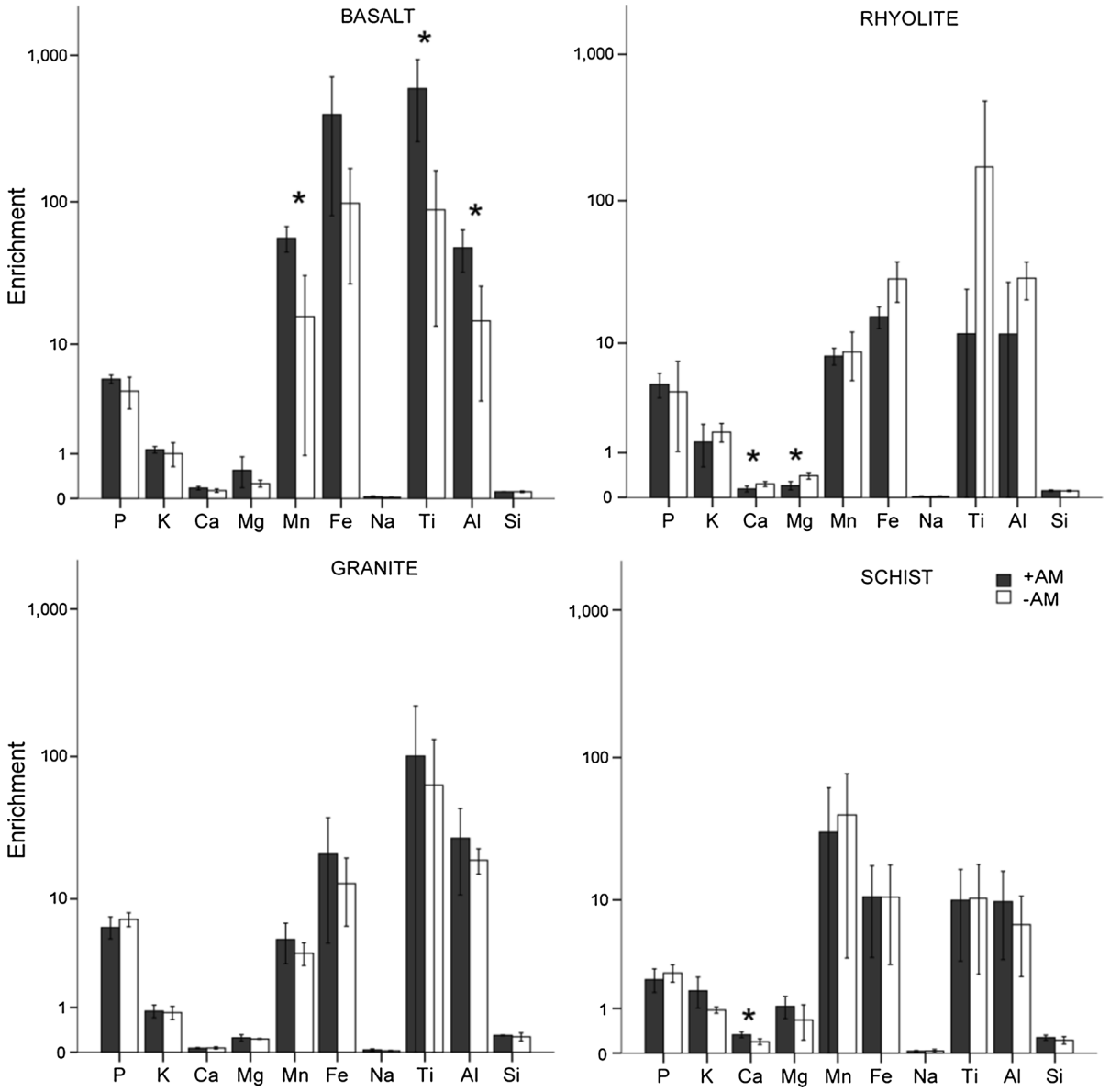


Fig. 6 Plant element enrichment ratios for treatments with and without mycorrhizal fungi, growing on different mineral media. Enrichment was quantified by normalizing plant concentration (μg g^{-1} biomass) to pore water solution concentrations (μg g^{-1} solution). *Values* represent mean ± SE

since minerals can be more easily accessed and nutrients can be more readily made available for plant uptake. It is also possible that less available nutrients in other rocks can take longer to dissolve, so differences between treatmentswith and without AM are smaller and less significant.

Mycorrhiza increased concentrations of P, K, Ca, Mn, Fe, Ti and Al in root biomass of plants grown in basalt, and Mn in shoot biomass of plants grown in rhyolite (Fig. 3). At the same time the opposite effect, decrease in Ca, Ti and Al concentrations was observed in shoots of plants growing in rhyolite. It has been shown that AM plays a significant role in Fe^{3+}- mineral weathering through the excretion of siderophores or low molecular chelators, and Fe^{3+}- specific ligands which increase Fe solubility (Haselwandter 1995). Iron uptake increase due to mycorrhiza in the roots grown in basalt (Fig. 3) might be the result of hyphae, but also the

increase of root Fe^{3+} chelate reductase activity as suggested by Wang and Xia (2009). Positive effects of AM on Fe uptake have been previously observed in grass plants (Miransari et al. 2009).

Manganese was the element which most consistently increased its concentration in plant tissues in the presence of AM among the rocks in our study (Fig. 3). Similar to Fe, an increased Mn concentration in the presence of AM observed in basalt roots and rhyolite shoots (Fig. 3) could be related to reduction of Mn(IV) to Mn(II) by mycorrhizal roots which led to its higher solubility and uptake, and to the presence of siderophores/phytosiderophores excreted by both fungi and roots (Caris et al. 1998). The fact that in our study Mn had greater translocation to the shoots in the presence versus absence of AM in rhyolite (Fig. 3), supports Mn uptake as Mn^{2+}(aq) in agreement with Kabata-Pendias and Pendias (2000). Mycorrhizal effect on Mn concentrations and plant nutrition is most often controversial in the literature, several studies reporting an increase while some others a decrease in Mn concentrations in plant tissues (Wu et al. 2011; Lehmann and Rillig 2015).

Mycorrhizal roots colonizing basalt accumulated higher concentrations of Al and Ti than non-AM plants (Fig. 3), suggesting that these elements may strongly bind into the root cells. Plant root uptake is often metabolically regulated to exclude and actively excrete Al (Anderson 1988). In this context, it might be considered that Al can accumulate in the hyphae of mycorrhiza colonizing cortical cells of plants, concentrated in polyphosphate granules (Turnau et al. 1993). Therefore, AM hyphae by sequestering the potential toxic elements into the polyphosphate granules might act as "metals filters" for symbiotic plants. Some studies reported a decrease in Al accumulation in mycorrhizal plants (Lux and Cummings 2001). In rhyolite, the effect of AM was also evident at the shoot level, where Ca, Ti and Al concentrations were restricted (Fig. 3) potentially as a defense mechanism against Al toxicity.

Mycorrhiza also enhanced the total uptake of K, Ca, Mg, Mn, Fe, Na, Ti, Al and Si into biomass of roots grown in basalt (Table S1). An increase in root uptake in basalt can be mostly associated with an increase in root exudates in the presence of AM, more specifically organic acids, siderophores and organic ligands with complexing capacity (Klugh and Cumming 2007). High accumulation of non-essential and potential toxic elements (Na, Ti, Al and Si) does not appear to have a negative effect on plant survival; it is likely that buffalo grass is tolerant to potentially stressful levels of elements that are often toxic to other plants.

Overall, there was a significant positive effect of AM inoculation on total plant nutrient uptake of P, Ca and Mn across all rocks (Fig. 4). This is consistent with the most important benefit of AM symbiosis to buffalo grass, i.e., enhancing essential nutrient acquisition. We can conclude that the interaction of AM infection with rock type in our experiment can increase nutrient acquisition into plant biomass in the substrates where elements are more easily available (e.g. basalt).

Mycorrhiza has contributed to enrichment of nutrients from solution into plants in basalt (Mn, Ti and Al) and in schist (Ca), whereas it depressed Ca and Mg enrichment in plants growing in rhyolite (Fig. 6). Similarly, Azcón et al. (1991) reported a buffering effect of AM on Ca and Mg plant uptake in calcareous soils. While Ca and Mn are required for normal plant growth, some non-essential elements (e.g. Ti and Al) can be easily taken up if highly accessible in the substrate (Marschner 2002). The availability of elements and subsequent selectivity was especially high in basalt, a substrate that undergoes rapid weathering kinetics due to its high glass content (Akter and Akagi 2010; Dontsova et al. 2014). Mycorrhizal infection enhanced plant selectivity, probably due to alkaline and acid phosphatases present in intra- and extraradical fungal hyphae that help enhance the solubility and availability of immobile nutrients which are further transported to the plants (Eckardt 2005). Therefore, element selectivity depends not only on nutrient availability but also on the ability of AM to actively colonize the substrates, weather silicate minerals and forage for nutrients.

Ca and Mg to Al ratios as potential indicators of Al inhibitory effect on plant growth

In our study Al reached a high enrichment in the plants irrespective of rock type (Fig. 6).The high Al accumulation in plants developed on basalt (Fig. 6) has raised the concern that high Al uptake can affect plant growth. A lower total biomass, and root to shoot ratio in basalt than in rhyolite supports this view (Fig. 2). Calcium and Mg are elements coupled to structure and

photosynthetic activity and directly related to plant growth (Wright et al. 2005). Lower (Ca + Mg) to Al ratios in plants developed on basalt and schist, than rhyolite and granite, indicated that growth on these two substrates can be limited (Fig. 2) by a lower uptake of Ca and Mg in the presence of Al in excess of growth requirements (Table S2). Especially in acidic conditions, Al availability increases in the form of the trivalent cation (Al^{3+}) which can be toxic to plants by altering their physiological and biochemical processes and consequently their productivity (Mora et al. 2006). Numerous other studies demonstrated that Al interferes with the acquisition of cations in plants by depressing their concentrations in plant tissues (Cumming and Ning 2003; Göransson 2001; Lindberg and Strid 1997; Nichol et al. 1993). Mycorrhiza increased significantly the release to solution of Al in basalt and schist; a high Al concentration in basalt solution affected Ca and Mg uptake in plants grown in basalt (Table S2). However, a decrease in Ca and Mg uptake in the AM treatment was apparently not quantitatively large enough to affect growth of mycorrhizal plants in basalt compared to non-AM plants (Fig. 2) at high Al concentrations.

Conclusions

This study provides evidence of differential rock effects on plant growth, and both, preferential/selective and total lithogenic element uptake in biomass. The weathering budgets of basalt, rhyolite and granite were higher than that of schist. The differences in elemental mass balance among substrates provide evidence of selective dissolution. Buffalo grass was able to grow on rock media without addition of fertilizers. Plant growth was enhanced in rhyolite relative to other rock types, because of the efficient extraction of essential nutrients (e.g. P). Enhanced uptake of several elements (Mn, Fe, Ti and Al) in plant tissue relative to their concentration in water was higher in basalt (Fig. 6) than in the other substrate. However, high Al availability in basalt and schist resulted in imbalances in nutrient acquisition (Ca and Mg; Table S2) and limited plant growth when compared to other substrates such as rhyolite (Fig. 2).

As expected, mass balance analysis demonstrated that plants enhanced rock weathering when compared to abiotic controls. Our results also highlight the strong effects of plant-AM interaction on mineral weathering, nutrient uptake, enrichment and biomass accumulation; these effects varied with rock type. Mycorrhiza increased element preferential uptake in basalt and schist while decreasing element selective uptake in rhyolite. Additionally, AM increased element concentration and total uptake in plant roots in basalt (Fig. 3 and Table S1), and shoot biomass in rhyolite, suggesting that demand for elements by shoots may be influencing the entire weathering process. Overall, plant-AM induced weathering (total mobilization and enrichment in biomass of several elements) of basalt and rhyolite was higher than in the other rocks and this was reflected in enhanced plant growth in rhyolite. Plant-mycorrhiza associations can therefore accelerate soil formation in basaltic or rhyolitic parent rock environments. Moreover, mycorrhizal infection rate was positively correlated with total plant uptake of P, Ca and Mn across all rocks, which indicates fundamental importance of fungi to supply nutrients to host-plants in a variety of nutrient poor systems.

This mesocosm-scale study deepens our understanding of the significance of plant roots and AM in lithogenic nutrient mobilization and use efficiency, and associated plant growth and biological stoichiometry in systems where nutrients are not readily available. Our findings are relevant in the context of incipient biological weathering that accompanies ecosystem colonization of bare rock substrates and soil genesis in environments with similar geochemical substrates.

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