



Original Articles

Decade-long unsustainable vegetation management practices increase macronutrient losses from the plant-soil system in the Taklamakan Desert

Akash Tariq^{a,b,c,*}, Corina Graciano^{d,1}, Jordi Sardans^{e,f,1}, Abd Ullah^{a,b,c}, Fanjiang Zeng^{a,b,c,*}, Ihteram Ullah^g, Zeeshan Ahmed^{a,b,c}, Sikandar Ali^b, Dhafer A. Al-Bakre^h, Zhihao Zhang^{a,b,c}, Yanfu Baiⁱ, Weiqi Wang^{j,k}, Josep Peñuelas^{e,f}

^a Xinjiang Key Laboratory of Desert Plant Roots Ecology and Vegetation Restoration, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Urumqi 830011, China

^b State Key Laboratory of Desert and Oasis Ecology, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Urumqi 830011, China

^c Cele National Station of Observation and Research for Desert-Grassland Ecosystems, Cele 848300, China

^d Instituto de Fisiología Vegetal, Consejo Nacional de Investigaciones Científicas y Técnicas, Universidad Nacional de La Plata, Buenos Aires, Argentina

^e CSIC, Global Ecology Unit, CREAM-CSIC-UAB, Bellaterra 08193, Barcelona, Catalonia, Spain

^f CREAM, Cerdanyola del Vallès 08193, Barcelona, Catalonia, Spain

^g Department of Plant Breeding & Genetics, Gomal University, Dera Ismail Khan, Pakistan

^h Department of Biology, College of Science, University of Tabuk, Tabuk, Saudi Arabia

ⁱ College of Grassland Science and Technology, Sichuan Agricultural University, Chengdu 611130, China

^j Key Laboratory of Humid Subtropical Eco-Geographical Process, Ministry of Education, Fujian Normal University, Fuzhou 350007, China

^k Institute of Geography, Fujian Normal University, Fuzhou 350007, China

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ABSTRACT

Arid ecosystems are characterized by low availability and mobility of soil nutrients and slow geochemical cycles. Management of native vegetation in such ecosystems for fuel, livestock grazing, and other agricultural activities (burning and cutting) may threaten semi-natural communities due to the changes in nutrient cycles and soil fertility. *Alhagi sparsifolia* is a dominant perennial legume in the Taklamakan Desert of northwestern China and has been used as fodder for livestock and plays a crucial ecological role in stabilizing dunes in the oasis-desert ecotone. We evaluated the effects of long-term (12 years) burning and cutting of plant biomass on the mineral nutrition of *A. sparsifolia* and associated soils at two depths (0–50 and 50–100 cm) in the field conditions following the block design experiment. We found that burning effects tended to be restricted to the topsoil (0–50 cm), and the concentration of many micro- and macronutrients was increased. Burning was associated with a decrease in plant nitrogen (N) and phosphorus (P) concentration, whereas concentrations of other micro- and macronutrients increased; overall, burning reduced foliar stocks of N, P, and potassium (K). Annual cutting elicited smaller increases in soil mineral (total sulfur, total P, calcium, magnesium, and available P and K) concentrations than burning, and soil enzymatic activities increased. There were contrasting response patterns of leaf N and P concentration and macro- and micronutrients between the two management approaches. Burning and cutting reduced leaf N and P concentrations, while changes in root and shoot N and P concentrations depended on treatments. Thus, burning and cutting of *A. sparsifolia* impact organ nutrient stoichiometry (increased losses of macronutrients from arid plant-soil ecosystems) and nutritional quality (for feeding livestock), particularly due to predicted rises in extreme climatic events under climate change that are expected to increase risks of soil erosion, however, impacts on native trophic webs remain unclear.

* Corresponding authors at: Xinjiang Key Laboratory of Desert Plant Roots Ecology and Vegetation Restoration, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Urumqi 830011, China.

E-mail addresses: akash.malik786@mailsucas.ac.cn (A. Tariq), zengfj@ms.xjb.ac.cn (F. Zeng).

¹ Indicates equal contribution.

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1. Introduction

Globally, hyper-arid, arid, and semi-arid landscapes represent almost a third of the terrestrial surface and host just under a fifth of the human population that practices livestock production as a key source of food, fuel, and fiber (Maestre et al., 2021; Karatassiou et al., 2022). Geochemical cycles are inherently slow in arid ecosystems, such as deserts, and consequently, the availability and mobility of nutrients in soils are similarly low (Delgado-Baquerizo et al., 2013). Thus, the ongoing removal of plant biomass, which reduces soil nutrient content (Wang et al., 2022), may impact nutrient cycles and carbon (C) losses in arid ecosystems as a result of the effects of soil compaction and changes in nutrient inputs (Munjonji et al., 2020). For example, the long-term annual removal of plants from natural grasslands has been shown to cause significant losses in soil fertility, with consequences for ecosystem structure and functionality (Abdalla et al., 2021). While arid ecosystem soil and vegetation dynamics are a function of the natural fires that are a feature of these environments, those initiated by human activity may lead to additional effects on vegetation growth and soil fertility, and contribute to land degradation (Kong et al., 2003), depending on soil and climatic conditions and plant species composition (Conant et al., 2017). For example, fire reduces inputs of C, nitrogen (N), phosphorous (P), and sulfur (S) to soils due to the combustion of plant biomass and litter and stable organic matter that negatively affects soil aggregation (Abdalla et al., 2021) and impacts N cycling (Mora et al., 2021). On the other hand, the removal of aboveground biomass increases the levels of aridity and erosion through greater exposure to the actions of sunlight and wind, respectively (Gonzalez-Perez et al., 2004; González-Pelayo et al., 2006). While intense and frequent burning events tend to reduce soil content of mineral nutrients through losses in soil organic matter and effects of leaching (Michelsen et al. 2004), these impacts may be lower following fires that occur during the spring for ecosystems dominated by plants, such as phreatophytes, that accumulate belowground biomass and nutrients in the soil during the fall (Li et al., 2014).

The effects of harvesting and burning vegetation vary among species

and ecosystems (Alhamad et al., 2012). For example, the growth of *Molinia caerulea* (Brys et al., 2005) and *Pinus sylvestris* (Hancock et al., 2009) are stimulated post-burning, whereas that of *Hypericum perforatum* (Clark and Wilson 2001) and *Salix caroliniana* (Lee et al., 2005) is suppressed. Moreover, the growth of *Trifolium repens* in upland meadows is stimulated following cutting (Gaisler et al., 2004), while the regeneration of *Rhizophora mucronata* in mangroves is reduced following harvest (Walters, 2005); while harvesting inhibits the regeneration capacity of plants in tropical forests (Pearce et al., 2003), and survival of trees in semiarid caatinga is largely unaffected (Figueirôa et al., 2006).

The perennial semi-shrub (1–1.5-m high) legume and phreatophyte *Alhagi sparsifolia*, which is characterized by a deep root system (20-m long) (Thomas et al., 2008), produces shoots in spring and flowers in summer with autumn-ripening fruit and reproduces via asexual clones. All these traits are consistent with its proven adaptation to growth in salinized and arid regions across its native range of Xinjiang, north-western China (Li et al., 2012). It is mainly found in Central and Eastern Asia (Fig. 1) and is planted to mitigate desertification (GBIF, 2021) by stabilizing mobile sand and reducing soil erosion to maintain ecosystem services (provisional, regulatory, and supporting) (Gao et al., 2022). Due to a well-developed root system and stiff stalks, the branches swing with the airflow, and the wind-sand flow encounters considerable settlement and accumulation (Tariq et al., 2022a,b). Feng et al. (2016) reported an indirect relationship between the vegetation cover of *A. sparsifolia* and the wind speed and the more fine-grained matter in the sand material accumulated. Moreover, densely distributed sparse leaves of *A. sparsifolia* in the aboveground branches have important spatial occupancy ability, and the area of wind protection on the surface is large. Therefore, *A. sparsifolia* plays a crucial role in wind damping, sand fixation, and soil erosion (Han et al., 2013). *A. sparsifolia* provides a range of socio-economic services, including as an essential source of forage for livestock, due to its high protein content (Li et al., 2021a,b) and as a traditional medicine to treat gastrointestinal, fever, toothache, and enteritis problems (Wei et al., 2021). However, intensive grazing, cutting, and burning to clear large areas of *A. sparsifolia* in desert

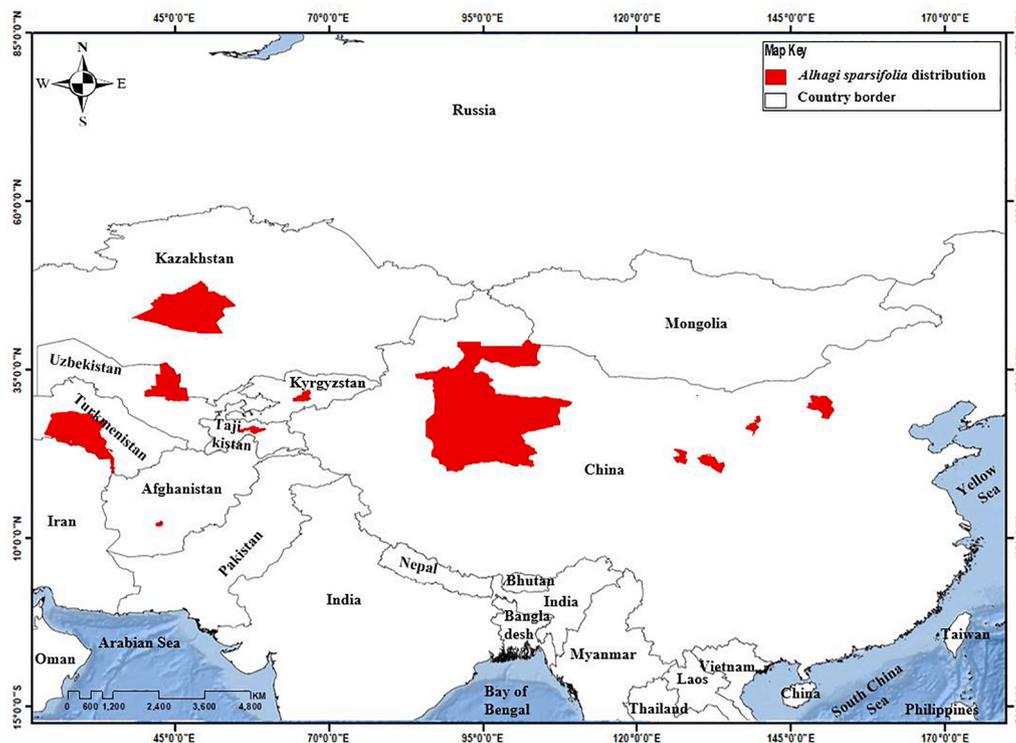


Fig. 1. Distribution of *Alhagi sparsifolia* in Central and Eastern Asia. This map is designed based on the spatial data available in the species database (<https://www.gbif.org/>).

ecotones for agricultural land expansion (Li et al., 2012) threatens its native population. These anthropogenic disturbances are likely to affect associated biogeochemical processes due to a decrease in soil input and accumulation of plant biomass and organic matter, respectively, which lead to reduced soil fertility (Tariq et al., 2022a,b).

Plants obtain most of the mineral nutrients required for growth from the soil, and levels of soil chemical fertility have been shown to determine plant nutritional status (Marschner, 1995), as indicated by the concentration of mineral nutrients in plant tissues (Haase and Rose, 1995), including leaf organs that require high levels of nutrient content to support photosynthetic processes and organs, and shoots and roots that supply reserves of nutrients to leaves (Yin et al., 2021). Thus, understanding the impacts of long-term harvesting and burning on the mineral nutrition of *A. sparsifolia* may indicate their effects on arid ecosystem function and nutrient cycling and be used to inform the sustainable management of *A. sparsifolia* populations. Therefore, this study aimed to evaluate the effects of a reduction in soil chemical fertility by burning and harvesting over 12 years on the leaf, shoot, and root mineral nutrition of *A. sparsifolia*, by testing the following hypotheses: 1) vegetation burning reduces C, N, and P nutrient availability in the topsoil and increases the availability of other minerals, due to disturbance of aggregates and oxidation of organic matter; 2) vegetation removal by cutting reduces soil nutrient and mineral concentration to a lesser extent than burning; and, 3) changes in soil nutrient availability from burning and cutting affect nutrient concentration of plant tissues and stocks. The present research will provide baseline information for designing sustainable management practices to reduce pressure on the *A. sparsifolia* population and to halt desertification and land degradation problems.

2. Material and methods

2.1. Study site

The study site was located within a long-term experiment in an oasis-desert ecotone, near the Cele Research Station of the Chinese Academy of Sciences, between the southern edge of the Taklamakan Desert and the northern edge of the Kunlun Mountains (37°00'56"N, 80°43'81"E), where annual average precipitation is 35 mm, with a potential annual evaporation rate of 2600 mm, and temperatures range between -23.98 and 41.98 °C in winter and summer, respectively (Zhang et al., 2020). The 5–10-km-wide belt of natural vegetation in the foreland, which serves as a source of livestock feed and fuel, is sparse (average cover: 5–20 %), dominated by shrub and sub-shrub species, such as *A. sparsifolia* and *Tamarix ramosissima* (Zeng et al., 2008). As observed from a well 500 m southeast of the experimental site, the water table is 17-m deep; soils are uniform across the study site, dominated by silt (>87 %).

2.2. Experimental design and sampling

The long-term experiment was established in 1983 across an area of c. 200 ha to test the ecosystem effects of vegetation management and disturbance. Here, we included spring cutting (SC) and burning (SB) treatments that commenced in 2010 to represent traditional low-intensity management of *A. sparsifolia* and clearance of *A. sparsifolia* in preparation for the cultivation of crops, such as cotton and maize, respectively. The untreated control (CK) plot was excluded from grazing and management activities with the help of fences. Species composition of the experimental treatments tended to be homogeneous and dominated by *A. sparsifolia*; aboveground biomass of *A. sparsifolia* was either cut at ground level using a hoe, following local traditional practice (SC) or burned to a depth of 5 cm, using controlled burning (SB), annually in April.

In 2010, we established three replicate 20 × 20-m of each treatment plot (three for cutting, three for burning, and three for control)

separated by 200 m. Plant (leaf, shoot, and root) and soil (0–50 and 50–100 cm horizons) samples were collected on 21 October 2021 from three randomly selected *A. sparsifolia* of each treatment plot. The samples were combined to comprise a single composite sample. To maintain the root integrity, we washed away any soil with the help of running water after removing the above-ground parts. Then the above-ground organ samples were classified and oven-dried at 60 °C for 72 h to determine biomass. Using ball mill, we milled the plant organ samples into a fine powder (<0.15 mm) for their elemental analysis. Soil samples were air-dried and passed through a 0.25-mm sieve because the washed soil cannot be used for analyzing soil nutrients.

2.3. Plant nutrient concentration and aboveground nutrient content

Following digestion in concentrated sulfuric acid (H₂SO₄), leaf and root N and P concentrations were determined using a Kjeldahl Nitrogen Analyzer (K1160, Jinan Hanon Instruments Co. Ltd., China) and an inductively coupled plasma optical emission spectrometer (iCAP 6300, Thermo Elemental, USA), respectively. Samples of leaf and root material were soaked overnight in nitric acid (HNO₃) and HF-HNO₃-H₂O₂ that was then tested for potassium (K), calcium (Ca), S, magnesium (Mg), copper (Cu), zinc (Zn), lead (Pb), cadmium (Cd), cobalt (Co), nickel (Ni), iron (Fe), and sodium (Na) concentrations using an inductively coupled plasma optical emission spectrometer (iCAP 6300, Thermo Elemental, USA). Nitrate (NO₃⁻) concentration was determined from 0.2 g of frozen leaf material in 5 mL of deionized water and ammonium (NH₄⁺) concentration was determined from 0.2 g of frozen leaf material homogenized in 2 mL of 10 % HCl; the supernatants were analyzed using a quantitative colorimetric method (Tang, 1999). Organic carbon (OC) was determined by a wet-oxidation technique described by Shaw (1979). At the end of the experiment, we randomly harvested the aboveground parts of treated and untreated plants to calculate the plot aboveground biomass of *A. sparsifolia*. With the obtained leaf and shoot N, P, K, S, and NO₃⁻ and NH₄⁺ concentrations we obtained the total amount of these chemicals stored in aboveground biomass.

2.4. Soil bio-physicochemical properties

Soil total N (TN) concentrations were determined following micro-Kjeldahl digestion (KDN-102C, Shanghai, China), and soil total P (TP) concentrations were determined using molybdenum blue colorimetric analysis using a visible spectrophotometer (UV-1200, Shanghai, China), following Na₂CO₃ oxidation; soil total K (TK) concentrations were measured using a flame photometer (FP6400A, Shanghai, China), after Na₂CO₃ oxidation (Yang et al., 2008). Soil available N (AN) concentrations were determined using the alkaline hydrolysis diffusion method (Yang et al., 2008), soil available P (AP) was extracted using 0.5-mol/L Na₂CO₃ (pH 8.5), and concentration was analyzed as for TP, and soil available K (AK) concentrations were determined from extracts of 1 mol/L ammonium acetate (NH₄Ac, pH 7.0) via flame photometry (FP640: INASA). Concentrations of trace elements (Ca, S, Mg, Cu, Zn, Pb, Cd, Co, Ni, Fe, and Na) in clear solutions were determined using inductively coupled plasma mass spectrometry (ICP-MS) (PerkinElmer, SCIEX ELAN-9000; PerkinElmer SCIEX, Concord, ON, Canada).

Soil organic C (SOC) concentrations were determined using the K₂Cr₂O₇-H₂SO₄ oxidation method. Dissolved organic N (DON) was determined using a modified method described by Ge et al. (2010), where fresh soil samples, equivalent to 3 g oven-dried weight, were extracted using 30 mL of distilled water in a 50-mL polypropylene centrifuge tube that was shaken for 30 min at 300 rpm and 20 °C; then, the mixture was centrifuged at 4500 rpm for 15 min before passing through a 0.45-µm filter. The filtrate was analyzed using an automated TOC Analyzer (Elemental Liquid TOC II, Elementar, Germany).

To separate light fraction organic N (LFON), we added 30 mL of 1.7 g cm⁻³ NaI to a 50-mL polypropylene centrifuge tube containing 15 g of air-dried soil; after shaking for 1 h at 180 rpm, the tubes were

centrifuged at 4500 rpm for 15 min, and the supernatant was filtered to collect low density ($<1.7 \text{ g cm}^{-3}$) components that were transferred to a dish, using 0.05 mol/L of CaCl_2 and distilled water, and oven-dried at 50°C for 48 h (Gregorich and Ellert, 1993; Yang et al., 2012). Particulate organic N (PON) was separated from 10 g of air-dried soil by shaking in 30 mL of 5 g/L sodium hexametaphosphate for 16 h; the separated soil was then passed through a $53\text{-}\mu\text{m}$ sieve, and the material remaining on the screen was dried at 50°C for 48 h and weighed. Then, the PON concentration of TN was determined using the Kjeldahl digestion procedure (Bremner and Mulvaney, 1982).

We extracted NH_4^+ using 2 M KCl and analyzed concentration using the phenate method (APHA, 1985); NO_3^- concentrations were analyzed using the phenol disulphonic acid method after extraction using CaSO_4 (Jackson, 1958). Soil pH was measured at a soil:water ratio of 1:2.5 (w/v) using a pH meter (PHSJ-6L, INESA Scientific Instrument Co. Ltd., China), and electrical conductivity (EC) was measured at a soil: water ratio of 1:5 (w/v) using an EC meter (DDSJ-319L, INESA Scientific Instrument Co. Ltd., China).

Soil microbial biomass N (MBN) and P (MBP) concentrations were measured using the chloroform fumigation-extraction method (Turner et al., 2014). Soil *N*-acetyl- β -glucosaminidase (NAG) activity ($\text{nmol MU g}^{-1} \text{ soil h}^{-1}$) was determined as the rate of release of 4-methylumbelliferone (MU) from the MU-labeled fluorescent substrate (4-MU-*N*-acetyl- β -glucosaminide) (Marx et al., 2001). An aqueous soil suspension (soil: water = 1:100, with 1 mM NaN_3 to prevent microbial activity) was incubated in a 200- μM substrate solution, and a 0.2-M acetate buffer (pH5.0) for 1.5 h at 30°C ; the reaction was stopped using 1 M NaOH and the released MU was determined immediately using a fluorimetric microplate reader (Tecan Infinite 200 PRO, TECAN Group Ltd., Mannedorf, Switzerland), with excitation at 360 nm and emission at 450 nm. We analyzed protease activity based on the determination of released tyrosine ($\mu\text{g tyrosine g}^{-1} \text{ soil h}^{-1}$) after incubation of soil with sodium caseinate and 0.1 M Tris (hydroxymethyl) amino methane buffer (pH8.1) for 2 h at 50°C (Zubair et al., 2021); the reaction was terminated using trichloroacetic acid (TCA) solution, and the released tyrosine was spectrophotometrically determined using the Folin-Ciocalteu reagent. Soil urease activity was determined according to the method described by Guan et al. (1986), where 2 g of fresh soil was incubated at 37°C for 24 h in a dissolution containing 20% urea and citric acid buffer (pH 6.7), to which sodium phenol and hypochlorite were added, and subsequent release of $\text{NH}_4^+\text{-N}$ was quantified using colorimetry at 578 nm; distilled water was used as a control substrate.

2.5. Statistical analysis

We used cluster analyses to test for similarity in the measured soil biochemical properties, and plant organ nutrient concentration across treatments, based on standardized data and Euclidian distance, and relationships between soil properties and treatment were explored using principal components analysis (PCA). After checking data for normality and homoscedasticity, we tested for the main effects of treatment and soil depth on soil bio-physicochemical properties and the main effect of treatment on plant organ nutrient concentrations and content in aboveground organs using two-way and one-way analysis of variance (ANOVA), respectively, with a comparison of means using Tukey tests ($p < 0.05$). Relationships between plant organ TN, NO_3^- , and NH_4^+ concentrations and availability of nutrients related to the N biocycle (NO_3^- , NH_4^+ , PON, TN, SOC, AN, DON, MBN, protease activity, urease activity, NAG activity, and LFON) at the two soil depths were tested using stepwise linear multiple regression at $p < 0.05$. All analyses were conducted using InfoStar Software (Di Rienzo et al., 2020).

3. Results

Cutting and burning changed many chemical soil concentrations differentially in upper (0–50 cm) and deeper (50–100 cm) soil, as an

interaction between soil depth and treatment was observed in TN, TP, TS, Mg, SOC, Fe, Zn, Ni, Co, Na, Cd, LFON, DON, MBN, MBP, Protease, Urease, NO_3^- , NH_4^+ , AP and AK concentrations (Tables S1, S2, S3, and S4). Few concentrations changed with treatment and soil depth, but no interaction occurred: Ca, Cu, Pb, NAG, and AN concentrations. K concentration was similar in the three treatments and both soil depths. Cluster analysis showed separation of soil biochemical composition at depths of 0–50 and 50–100 cm among treatments, where composition in the upper 0–50 cm layer following burning was most distinct (Fig. 2).

Similarly, PCA showed separation of soil biochemical composition following cutting in the 50–100-cm layer and burning in the 0–50-cm layer along PC1 and separation of the untreated controls and following burning in the 50–100-cm layer from the cutting treatment at the two soil depths and burning in the 0–50 cm soil along PC2 (Fig. 3). The biochemical composition of soils following cutting was positively associated with NAG and protease activity and concentration of TP and LFON, while the composition of soils following burning was associated with high levels of concentration of SOC, AP, TK, and TN; the biochemical composition of unmanaged soils was positively associated with urease activity and negatively associated with TS and AK.

Cluster analysis of plant organ mineral concentrations showed separation of leaves, regardless of treatment, from roots and shoots; root and shoot in cutting plants were separated from unmanaged and burning plants (Fig. 4). There were treatment effects on plant organ mineral concentration, where vegetation burning and cutting reduced leaf N and Ca concentrations and increased shoot N concentration, decreased P concentration across all organ types, and decreased root and shoot Ca concentration, while the concentration of K, S, and Na increased in leaf and shoot material and decreased in root material; vegetation cutting led to an increase in root N concentration while burning led to an increase in shoot and root concentration of Ca (Fig. 5). The concentrations of Mg and micronutrients (Cu, Zn, Fe, Co, and Ni) in shoots, leaves, and roots were affected by burning and/or cutting with respect to control (Table S5).

Given the decreases in leaf N concentration following vegetation cutting and burning, our analyses showed that burning decreased the concentration of NO_3^- in aboveground organs and an increase in root material, and an increase in NH_4^+ concentration of leaf material, and a decrease in root material; across all organ types, vegetation cutting led to decreases in NO_3^- concentration and increases in NH_4^+ concentration (Fig. 6).

The mineral concentration of leaf material was related to soil and plant organs (Table 1). Leaf N concentrations were positively related to soil Ni concentration in the 50–100-cm layer and root TS concentration and negatively related to PON in the upper soil layer; leaf P concentrations were positively related to root TP concentration and negatively related to MBP in the upper soil layer; leaf K concentrations were positively related to Fe concentration of the upper soil layer and leaf material, and negatively related to Co concentration of the upper soil layer; leaf S concentrations were positively related to soil TK and MBP concentration of the upper soil layer and PON concentration of the deeper soil layer, and leaf NH_4^+ and Cu concentration; leaf Ca concentrations were positively related to Ca concentration of the upper soil layer and Ni and TP concentration of the deeper soil layer and negatively related to root Mg and Cu concentration; and, leaf Na concentrations were positively related to leaf NH_4^+ concentration and negatively related to root TN concentration.

Except for leaf NO_3^- concentration that was negatively related to shoot TN concentration, the concentrations of ions related to N nutrition in plant tissues (N, NO_3^- , NH_4^+) were associated with concentrations in the soil: enzyme activities (urease and/or protease) and different inorganic and organic N forms (NH_4^+ , NO_3^- , DON, SOC, and/or MBN) (Table 2). Analysis of plant traits in year 12 of the experiment, combining nutrient concentrations with plant biomass, showed a decrease in leaf N, P, and K stocks and P of aboveground plant biomass following long-term vegetation burning and cutting management

Soil traits (Average linkage)

Distance: Euclidean

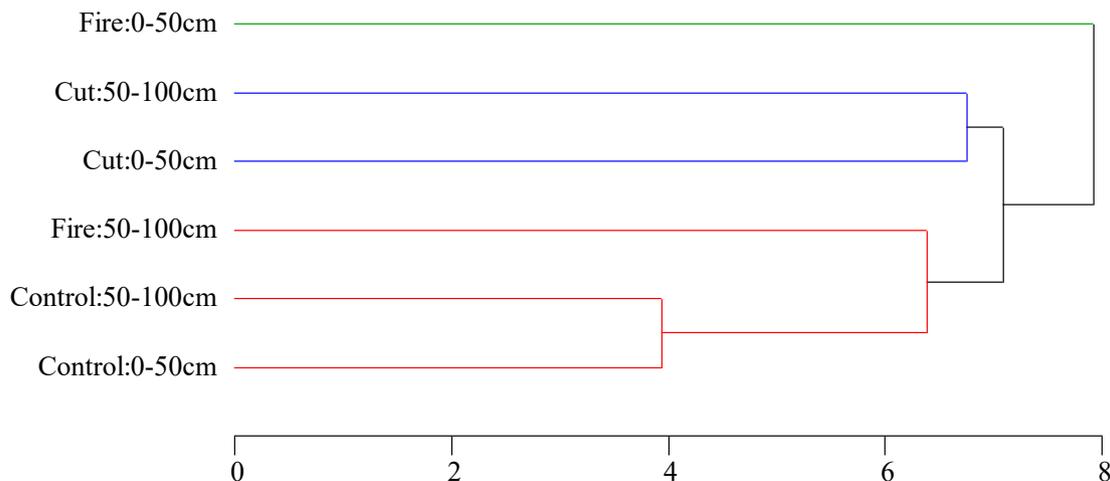


Fig. 2. Cluster analysis of soil biochemical properties across treatments in the upper (0–50 cm) and deeper (50–100 cm) layers. Biochemical factors comprised NO_3^- , NH_4^+ , PON, TN, TK, TP, TS, SOC, AN, AP, AK, Ca, Mg, Cu, Zn, Pb, Cd, Co, Ni, Fe, Na, DON, MBN, MBP, protease, urease, NAG, and LFON.

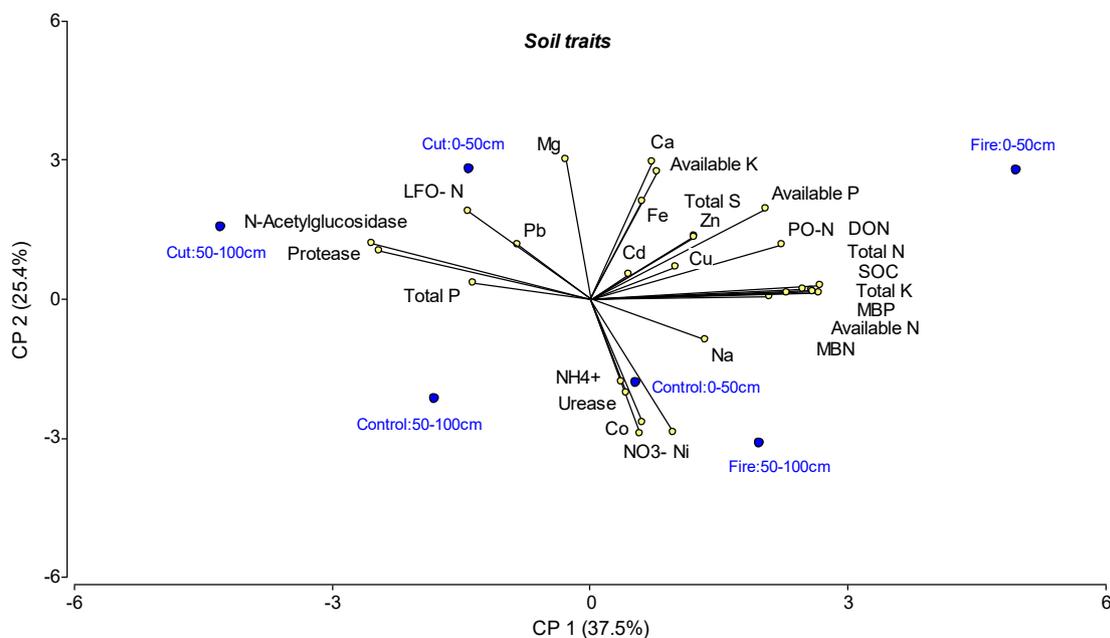


Fig. 3. Principal components analysis of the soil biochemical factors across treatments included in the cluster analysis (Fig. 1). Data included in the analysis (Tables S1–4) are grouped by treatment and soil depth (blue circles).

(Fig. 7).

4. Discussion

4.1. Effects of vegetation burning and cutting on soil biochemical properties

Effects on biochemical properties in the upper soil layer were greater following the annual burning of vegetation than following annual removal by cutting. Under burn temperatures higher than 180 °C, volatilization of N and C occurs, resulting in losses of organic matter from topsoil (Allen et al., 2011). In contrast, under lower temperatures,

increases in extractable-N in upper soils have been reported (Li et al., 2014; Daryanto et al., 2019), as indicated in this study, given the increases in the concentration of SOC and soil TS and TN (Fig. 3, Table S1). Understanding of the behavior and availability of micronutrients following fire events is limited (Tulau and McInnes-Clarke, 2015). Nevertheless, and as expected, there were differences in the effect of burning on soil concentration of cations, as there were decreases in soil concentrations of Na and Cu and increases in Fe (Table S2) due to contrasting volatilization temperatures concerning nutrients related to organic matter; for example, K, mineral P, Ca, Mg, and Na require higher temperatures for volatilization than N, S, and organic P, and their losses under lower-temperature burning tend to be minimal in the absence of

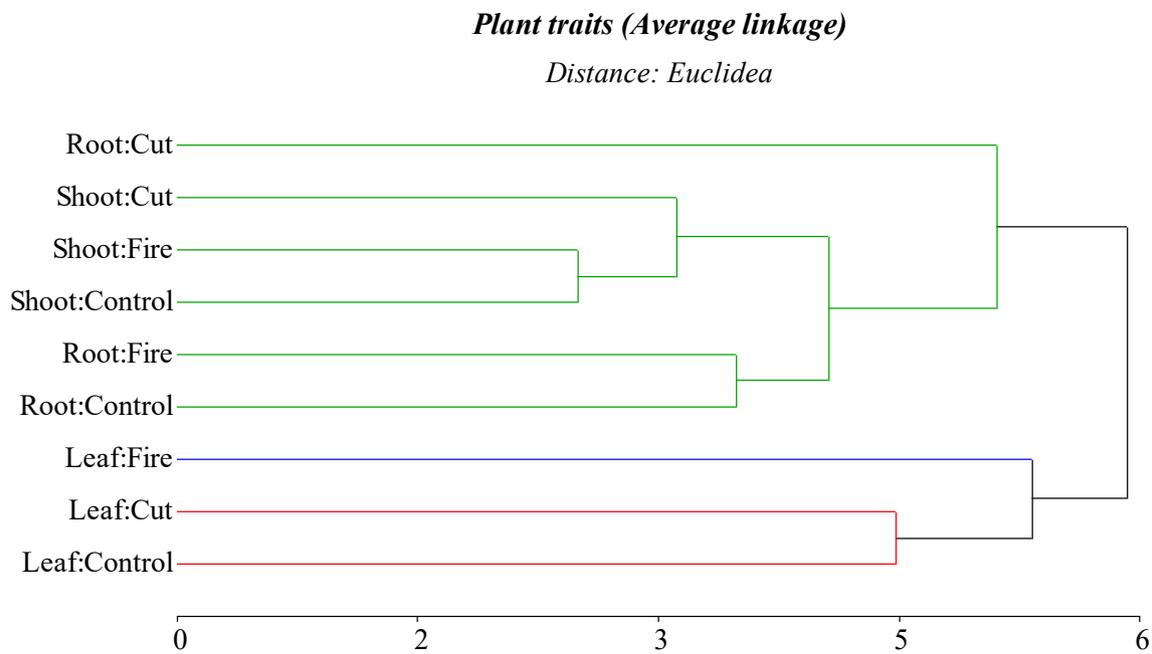


Fig. 4. Cluster analysis of plant organ mineral concentration across treatments. The factors comprised TN, TP, TK, TS, Cu, Zn, Fe, Ca, Mg, organic C, Na, Cd, Co, Ni, NH_4^+ , and NO_3^- .

subsequent erosion events, such as precipitation (Tulau and McInnes-Clarke, 2015).

We found that burning vegetation affected soil biology, as indicated by impacts on soil concentration of N forms and enzymes; for example, we found reductions in NAG and urease activities, increases in protease activity, and concentration of MBN and DON in the upper soil layer (Table S3). In arid ecosystems, biocrusts, which comprise non-vascular photoautotrophs, including lichens, mosses, and cyanobacteria, stabilize the soil surface and have been shown to respond positively to the removal of plant biomass for firewood (Li et al., 2021a,b). Soils beneath biocrusts contain increased TN, AN, and N-transformation rates, along with higher MBN concentration, likely due to increased microbial activity (Sosa-Quintero et al., 2022), indicating that fire-stimulated biocrusts may affect the biogeochemical nutrient cycling, as observed in our results. Water leached through the biocrust layer may transport NH_4^+ , NO_3^- , biogenic P, and a wide variety of metabolites (Young et al., 2022), as indicated by our finding of increased soil concentration of NO_3^- and NH_4^+ in the deep soil layer, following burning (Table S4), likely due to inputs of N-rich ashes (Mora et al., 2021).

We expected direct and indirect effects of vegetation removal by cutting on microorganisms and found decreased levels of SOC concentration in the deep soil layer (Table S1), supporting findings of increased SOC concentration following the exclusion of grazing in semiarid grassland (Li et al., 2022). Biomass removal reduces soil fertility in many ecosystems (Munjonji et al., 2020; Abdalla et al., 2021; Wang et al., 2022), but cutting *A. sparsifolia* repeatedly over 12 years did not reduce the availability of N in the upper layer as expected and increased soil concentration of S, P, Ca, Mg, AP, and AK. We analyzed extracellular enzymatic activity as a surrogate measure of the activity of microorganisms that rely on the degradation of polymeric substrates (Burns et al., 2013) and found increased activities of NAG and protease following cutting and lower activities following burning, whereas urease activity, which facilitates the release of NH_4^+ , was reduced by both types of vegetation management (Table S4). Thus, burning led to an accumulation and leaching of NO_3^- and NH_4^+ to the deep soil layers, along with decreases in the availability of NO_3^- in the upper soil layer due to reduced levels of nitrification and increased availability of nutrients and minerals in the topsoil, except for TP.

In brief, we found smaller effects on soil mineral concentrations of vegetation removal by cutting than by burning. Thus, our study shows that burning enhances medium–long term soil availability of some nutrients and reduces stocks of N, P, and K in some aboveground plant, and highlights the need for additional studies to determine overall responses by the plant-soil system to the management of vegetation by burning, including the global capacity to retain nutrients.

4.2. Relationship between soil nutrient concentrations and *A. sparsifolia* nutrition

Cluster analysis showed that impacts on *A. sparsifolia* leaf nutrition of vegetation management by burning were greater than by cutting. In contrast, impacts on root nutrition were the reverse, and shoots were least affected by the two management treatments. Changes in soil nutrient concentrations elicit greater effects on *A. sparsifolia* leaf, shoot, and root nutrient stoichiometry than changes in climate (Luo et al., 2021). Across plant organs, we found that nutrient concentration is greatest in leaf material, and we found that leaf N and P concentrations reduced following vegetation burning and cutting, despite increased soil availability of N forms and P, indicating N-concentration of *A. sparsifolia* is not soil N-limited. It is possible that N limitation in *A. sparsifolia* is associated with low soil biological activity; given that the species is a legume and fixes N (Li et al., 2022) and the reduced levels of leaf, shoot, and root P concentration following burning indicate low levels of P-uptake, despite its pyromineralization. These results contrast with previous research that showed increases in the proportion of P relative to C and N in plant tissues following burning (Pellegriani et al., 2015). Nevertheless, our results showed that vegetation burning and cutting lead to lower accumulations of N, P, and K in leaf material and of P in aboveground biomass, indicating that these types of vegetation management reduce leaf nutritional quality, with potential implications for grazing livestock, water use efficiency (WUE) capacity of photosynthetic plant tissues (Waraich et al., 2010; Wang et al., 2018; Turcios et al., 2021) and, together with the partial trend for increased soil nutrient concentration, long-term losses of macronutrients from the plant-soil system in arid ecosystems, particularly under predicted increases in soil erosion events under climate change (Lioubimtseva et al., 2005).

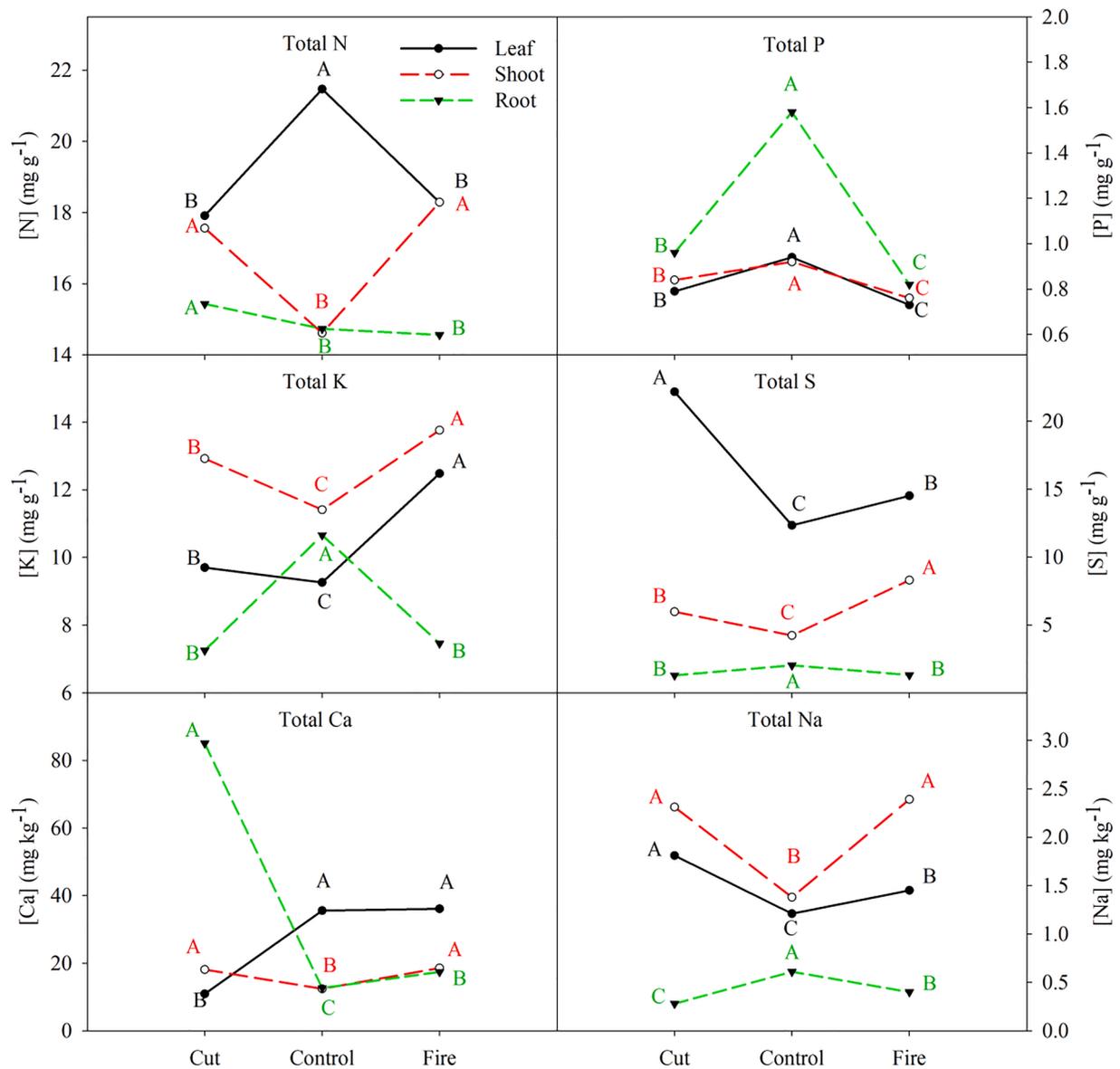


Fig. 5. Analysis of treatment differences in plant organ mineral concentration. Black lines: leaf material; red lines. shoot material; green lines. root material; different letters indicate differences at $p < 0.05$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

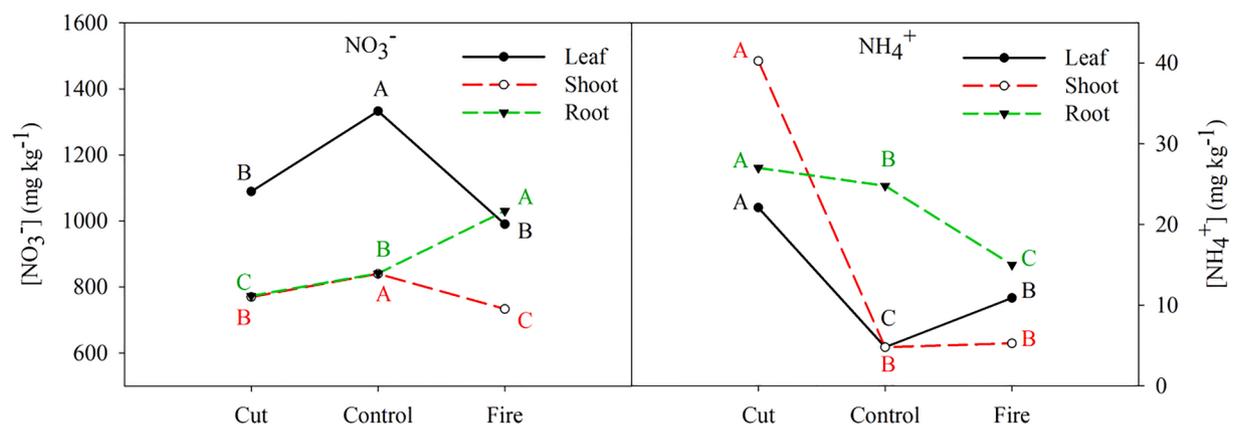


Fig. 6. Treatment differences in plant organ concentration of nitrate (NO₃⁻) and ammonium (NH₄⁺). Black lines. leaf material; red lines. shoot material; green lines. root material; different letters indicate differences at $p < 0.05$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1Stepwise multiple regression analysis of the relationships between leaf nutrient concentration and soil and plant organ nutrient concentration at $p < 0.05$ ($n = 9$).

Dependent variable		Independent variable coefficients		Adjusted R ²	Weighted MSE
Leaf nutrient concentration	Coefficient	Soil nutrient concentration	Plant organ nutrient concentration		
N	4.08	Ni (50–100 cm): 0.59PON (0–50 cm): -5.40	Root TS: 4.59	1.00	0.04
P	0.69	MBP (0–50 cm) -0.08	Root TP: 0.24	1.00	<0.01
K	8.11	Co (0–50 cm): -1.19Fe (0–50 cm): 0.28	Leaf Fe: 0.65	1.00	0.01
S	-11.12	TK (0–50 cm): 0.83PON (50–100 cm): 8.30MBP (0–50 cm): 0.64	Leaf NH ₄ ⁺ : 0.23 Leaf Cu: 1.10	1.00	<0.01
Ca	17.86	Ni (50–100 cm): 0.91Ca (0–50 cm): 0.16TP (50–100 cm): 6.62	Root Mg: -2.54 Root Cu: -0.72	1.00	0.04
Na	2.36		Leaf NH ₄ ⁺ :0.04 Root TN: -0.09	0.99	<0.01

Table 2Stepwise multiple regression analysis of the relationships between leaf organ nutrient concentration and factors associated with soil and plant N-biocyling at $p < 0.05$ ($n = 9$).

Dependent variable	coefficient	Independent variable coefficients		Adjusted R ²	Weighted MSE
		Soil concentration	Plant organ nutrient concentration		
Leaf N	12.82	Urease (0–50 cm): 11.17 NH ₄ ⁺ (0–50 cm):1.66		0.99	0.06
Leaf NO ₃ ⁻	2631.90		-88.85 Shoot TN	0.92	3904.60
Leaf NH ₄ ⁺	29.43	Urease (50–100 cm): -68.26Protease (50–100 cm): 0.50		1.00	0.87
Shoot N	16.60	Urease (0–50 cm): -7.69DON (0–50 cm): 0.63		0.99	0.12
Shoot NO ₃ ⁻	629.75	NO ₃ ⁻ (0–50 cm): 13.88		0.94	251.96
Shoot NH ₄ ⁺	165.13	SOC (50–100 cm): -89.12		0.93	36.87
Root N	16.87	MBN (50–100 cm): -0.37		0.85	0.06
Root NO ₃ ⁻	1221.87	Protease (0–50 cm): -45.32		0.97	798.90
Root NH ₄ ⁺	5.88	Protease (0–50 cm): 2.18		0.99	0.70

The distribution of nutrients among plant organs varied following the vegetation management, where burning and cutting increased shoot N concentration and cutting increased root N concentration, consistent with responses of subalpine grassland plants subjected to increased grazing pressure (Lin et al., 2022) and possibly due to repeated losses in leaf material, as observed in grazed perennial plants that developed physiological and morphological responses (Song et al., 2020). We found that plant concentration of P decreased following burning, and there was a greater concentration of NH₄⁺, likely due to lower soil and tissue availability of NO₃⁻, although NH₄⁺ uptake did not affect NO₃⁻ availability. In contrast, cutting increased the N concentration of shoots and roots, the organs that persist after the management event. Although cutting and burning in spring removes aboveground biomass of *A. sparsifolia*, including flower buds, the principal reproduction method is by clonal spread of belowground tillers (Li et al., 2022); therefore, the increases in shoot and root N indicate investment in rhizome growth.

Plant uptake of N tends to be as NO₃⁻ and NH₄⁺, where protease and urease release NH₄⁺ from organic compounds. Our finding of increased protease activity in the upper soil layers following cutting (Table S3) may have been due to greater root concentration of NH₄⁺, given there were no effects on soil NH₄⁺ concentrations (Table S4). In contrast, decreases in root NO₃⁻ were consistent with decreases in soil NO₃⁻ concentrations (Table S4). We found that plant tissue concentration of N, NO₃⁻, and NH₄⁺ was driven by soil chemical traits rather than plant tissue traits and soil urease activity positively affected leaf N concentration and negatively affected leaf NH₄⁺ concentration, indicating that soil urease activity is a greater driver of leaf N nutrition than soil TN and AN concentration. These results demonstrate that the role of extracellular soil enzymes in plant nutrition requires further research (Burns et al., 2013).

Shoot and leaf K, S, and Na concentrations increased following

vegetation burning and cutting, and leaf macronutrient concentration was related to soil and plant tissue mineral concentration; for example, soil Ni concentration positively affected leaf concentration of N and Ca. The impacts of burning management on these relationships between plant and soil nutrient concentration need to be explored further, given we found that soil Co, which increased following burning, negatively affected leaf K concentrations and Ni, which decreased, positively affected leaf N and Ca concentration, indicating that effects of burning on plant nutrition may be mediated by micronutrients that are essential for grazing livestock tissue health (Munyati, 2018).

Overall, our results provide evidence for changes in soil nutrient availability due to vegetation burning and cutting, which lead to reductions in plant tissue concentrations of N and P and increases in the concentration of other macro and micronutrients. Decreased leaf N and P concentration reduced leaf stocks of N, P, and K, increased root N content, and decreased root P, K, S, and Na content, indicating that soil and plant micronutrient concentrations are relevant to plant macronutrient nutrition.

5. Conclusions

Annual spring burning of arid ecosystem vegetation over 12 years was found to affect the biochemical properties of the topsoil, where biological activity and N and P nutrition of *A. sparsifolia* were reduced, and soil concentrations of many micro- and macro-nutrients increased. Overall, long-term fire management of *A. sparsifolia* reduced plant foliar stocks of N, P, and K. Vegetation management by cutting led to smaller impacts than by burning, where soil enzymatic activity increased; however, plant nutrition was negatively affected, with reduced leaf N and P content and increased concentrations of some macro and micro-nutrients. Responses of soil and plant nutrients varied between burning

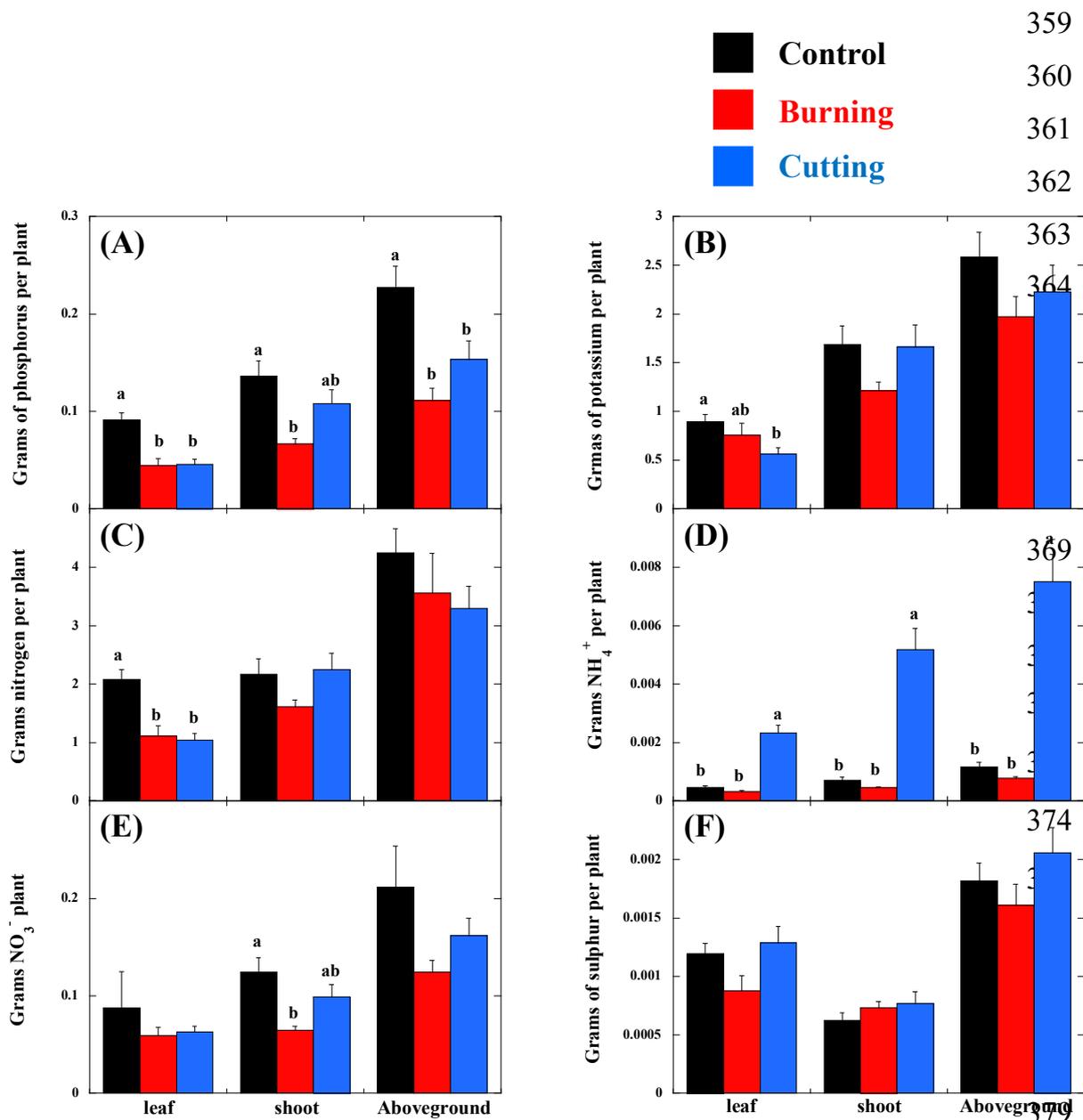


Fig. 7. Differences in mineral content of leaf and shoot material and total aboveground biomass following annual cutting and burning for 12 years.

and cutting treatments. Given the impacts on *A. sparsifolia* mineral nutrition of effects of the two management approaches on soil enzyme activity and availability of micronutrients, there are likely implications for the nutritional quality of this species as a feedstock for livestock, along with impacts on native trophic webs that remain to be studied. Moreover, to reduce the overexploitation of the *A. sparsifolia* population, there is a dire need to adopt effective management strategies such as promoting eco-friendly alternative energy sources to provide sufficient fuel to the farmers, capacity building of the local population, poverty alleviation in these harsh regions, and advanced scientific knowledge and research. Applying these measures is vital to overcome the unsustainable exploitation of natural vegetation that could lead to halting land degradation and livelihood improvement.

CRediT authorship contribution statement

Akash Tariq: Conceptualization, Methodology, Validation, Formal

analysis, Investigation, Visualization, Funding acquisition, Data curation, Project administration, Software, Writing – original draft. **Corina Graciano:** Methodology, Formal analysis, Supervision, Software. **Jordi Sardans:** Methodology, Formal analysis, Supervision, Software, Writing – review & editing. **Abd Ullah:** Investigation, Data curation. **Fanjiang Zeng:** Resources, Supervision, Project administration, Funding acquisition, Conceptualization, Writing – review & editing. **Ihteram Ullah:** Formal analysis. **Zeeshan Ahmed:** Investigation, Data curation. **Sikandar Ali:** Data curation, Writing – review & editing. **Dhafer A. Al-Bakre:** Writing – review & editing. **Zhihao Zhang:** Investigation, Data curation. **Yanfu Bai:** Writing – review & editing. **Weiqli Wang:** Writing – review & editing. **Josep Penuelas:** Supervision, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial

interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All the data related to this research have been included and presented in the paper

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2022.109653>.

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