RESTORATION ECOLOGY
The Journal of the Society for Ecological Restoration

RESEARCH ARTICLE

Ungulate responses to the addition of silicate rock powder in acidified oak (*Quercus robur*) forests at the Veluwe, the Netherlands

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Abstract

Introduction: Addition of silicate rock powder (SRP) is an increasingly used measure to restore vegetation and fauna on acidified mineral-poor soils in protected areas. In theory, however, the positive effects of SRP addition on vegetation may be offset by grazing and browsing ungulates attracted to higher-quality forage.
Objectives: This study aimed to determine whether SRP addition to acidified old oak (*Quercus robur*) forests attracts foraging ungulates in the short term.
Methods: We measured wildlife activity within an SRP-addition experiment established at nine *Quercus robur* forests at the Veluwe, the Netherlands, 3 years after SRP application. Each site had three 0.5-ha plots: one with addition of volcanic SRP, one with addition of metamorphic SRP, and one control. We used camera trapping to quantify foraging by four ungulate species: wild boar (*Sus scrofa*), red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), and European fallow deer (*Dama dama*).
Results: While SRP addition increased mineral concentrations in tree leaves within 3 years after treatment, we found no significant differences between treatments in the frequency and duration of ungulate foraging.
Conclusion: Our study yields no evidence for the attraction of foraging ungulates to oak forests treated with SRP within 3 years after application.

Implications for Practice: Old pedunculate oak forests on sandy podzolic soils in Europe are highly sensitive to soil acidification due to deposition of reactive atmospheric nitrogen, resulting in impoverishment of protected vegetation and fauna. A restoration intervention that is increasingly used to mitigate these negative effects is the application of silicate minerals in the form of SRP. However, SRP-treated plots in heathland systems appeared to attract foraging ungulates shortly after treatment, presumably because of higher forage quality. This has raised concerns that ungulates may offset positive effects of SRP addition on tree recruitment in forests. Our study, however, yielded no evidence for foraging ungulates being attracted to SRP-treated plots in old oak forests in the Netherlands 3 years after treatment. Delayed effects remain possible, highlighting the need for long-term monitoring to capture the full impacts of SRP addition.

Key words: camera trapping, *Cervus elaphus*, herbivory, pedunculate oak, red deer, soil restoration, *Sus scrofa*, tree recruitment, wild boar

Introduction

Soil acidification is a major environmental problem worldwide, with acid rain, nitrogen deposition and increased levels of atmospheric CO_2 as major causes (van Breemen et al. 1984; Rice & Herman 2012; Tian & Niu 2015). Soil acidification can result in both the leaching of important base cations, such

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Author contributions: MJW, HS, JJV designed and established the rock powder experiment; MJMH, PAJ conceived and designed the wildlife survey; MJMH conducted the survey; MJMH, SH, PAJ analyzed the data; PAJ supervised the survey; MJMH, PAJ wrote the manuscript; all authors commented and edited the manuscript.

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doi: 10.1111/rec.70321
Supporting information at:
http://onlinelibrary.wiley.com/doi/10.1111/rec.70321/suppinfo

as magnesium, potassium, and calcium, loss of the buffering capacity, and mobilization of heavy metals (e.g., Al) which can be toxic (Blume et al. 2016). Nutrient imbalances in the soil caused by soil acidification can negatively affect the abundance of soil organisms (Bünemann et al. 2006) and the growth, health and nutrient content of vegetation (Pabian et al. 2012a, 2012b). A persistent cause of soil acidification is increased nitrogen deposition from traffic, industry and intensive agriculture (Elser 2011; Holtgrieve et al. 2011; Stokstad 2019; Penuelas et al. 2020; van der Maas et al. 2021).

An ecosystem that is particularly affected by nitrogen-driven soil acidification are old pedunculate oak (*Quercus robur*) forests on sandy podzolic soils in Europe. These forests are protected under European Natura 2000 law as "Acidophilous oak woods with *Quercus robur* on sandy plains" (habitat code H9190) because of their high conservation value (Mölder et al. 2019). Their vitality, however, has been declining for decades (Thomas et al. 2002), driven primarily by acidifying (SO_x, NO_x, NH_y) and eutrophying (NO_x, NH_y) deposition (Skidmore et al. 2024), in interaction with biotic factors (e.g., pathogens, infestation by insects and herbivory) and abiotic factors (e.g., drought stress) (Thomas et al. 2002). Soils have lost their buffering capacity as the base cations leach out (Krug & Frink 1983, Tian & Niu 2015), which ultimately causes increased tree mortality, and impoverishment of the understory vegetation and fauna. Herbs and flowers are being replaced by homogenous vegetation mainly consisting of tall grasses (Bobbink et al. 2010), which reduces food quality and quantity available to the local fauna (Nijssen et al. 2017).

One restoration intervention that is increasingly used to mitigate these negative effects is the application of silicate minerals in the form of silicate rock powder (SRP), extracted from stone quarries. SRP is rich in Ca, Mg, and other base-providing minerals. Application of SRP reduces soil acidity and partly restores the soil buffer capacity (Vogels et al. 2018; Jansone et al. 2020; Swoboda et al. 2021; van der Bauwhede et al. 2024), and possibly increases soil microbial activity, enhances decomposition rates, and increases nutrient availability for plants (Martikainen et al. 1989; Bloem et al. 2022). SRP addition seems effective in combatting acidification of the soil in these forests and is an experimental component of the restoration strategy for this habitat type (Hommel et al. 2020). Experiments have shown that SRP addition reduces the N content in the soil and leaves and increases levels of K, Ca, and Mg in acidified forests (Aarnio et al. 1995; Aarnio et al. 2003; Pabian et al. 2012a; de Vries et al. 2019). Although effects of SRP addition may take more than 10 years to fully express (Moore et al. 2012; Court et al. 2017), they can emerge already within few years after application. For example, SRP addition improved topsoil chemistry in Dutch forest areas just 3 years after application and increased base cation concentration in leaves, indicating that the nutrient uptake by vegetation starts soon after the treatment (de Vries et al. 2019).

Forest managers have expressed concerns that in forests, positive effects of SRP addition may be offset by increased herbivore activity (Den Ouden et al. 2020), because improved elemental content of plants can make this more palatable to grazing and browsing ungulates. Ungulates are known to forage selectively to meet their high needs of P, Ca, and Mg to produce antlers, horns and bones (French et al. 1956; Tajchman et al. 2018) and during the weaning period (Tajchman et al. 2018). That SRP addition indeed attracts ungulates is suggested by a study in the Netherlands in which elevated levels of grazing by cattle were observed in experimentally treated heathland plots 3 years after addition of SRP (Weijters et al. 2018). It is thus conceivable that herbivores are attracted to forest stands that have undergone SRP addition or liming and increase their foraging time in these stands (Pabian et al. 2012a; Weijters et al. 2018).

The aim of this study was to determine whether SRP addition to acidified pedunculate oak forests elevates levels of foraging by ungulates 3 years after treatment, like seen in heathland by Weijters et al. (2018). Our approach was to compare the levels of foraging between plots of oak forest 3 years after experimental addition with two types of SRP applied to nine different old oak forest sites in the Veluwe, the Netherlands. We tested the hypotheses that ungulates (1) forage SRP-treated plots more often (higher number of foraging events) than untreated control plots and (2) spend more time foraging in these plots.

Methods

Study Area

The study was conducted at the Veluwe, the largest protected land area in the Netherlands (coordinates: 52.140336; 5.824105) with a total area of approximately 130,000 ha. Annual precipitation averages around 960 mm, temperature averages 11–12°C (KNMI, Deelen Airport). The Veluwe has a long history of intense use by humans, including agricultural clearances, wood-cutting, sod-cutting and grazing that degraded the area by the end of the Middle Ages (Buis 1985). Like elsewhere across Northwestern Europe, this produced a degraded drift sand landscape, known as the 'European Aeolian Sand Belt' (Koster 2009). Nowadays, the Veluwe consists of a patchwork of remnants of old deciduous forest, heathland, drift sand, cropland and young, mostly coniferous forest (van den Burg et al. 2015; den Ouden et al. 2020).

Oak forests (*Quercus robur* and *Q. petreae*) are native to the Veluwe. These forests have a long history of exploitation for fuel wood, boar feed and timber (Buis 1985). Many oak forests were coppiced for firewood and bark for leather tanning (Buis 1985; Rövekamp & Maes 2002). Between 1900 and 1940, when coppicing ceased, many oak coppices transformed into high forests (Bijlsma et al. 2019). The old oak forests remaining at the Veluwe today include forest remnants dating back to before 1850 (Buiteveld & Koelewijn 2006; Hommel et al. 2020). These forests are considered valuable because they harbor many tree species of autochthonous origin (Rövekamp & Maes 2002) and often support a higher biodiversity, and are protected under the Natura 2000 habitat directive as "acidophilous oak woods with *Quercus robur* on

Figure 1. Large mammal species in the old oak forest of the Veluwe, photographed by camera traps in this study. (A) Female red deer with young; (B) fallow deer; (C) young wild boar; (D) male red deer; (E) male roe deer; (F) male red deer.

sandy plains (habitat code H9190)." The Veluwe is considered a stronghold of this habitat type (Bijlsma et al. 2009). The Veluwe is also home to a variety of mammalian herbivores and omnivores, including roe deer (*Capreolus capreolus*), European fallow deer (*Dama dama*), red deer (*Cervus elaphus*), rabbits and hares (Leporidae), murids (Muridae), and omnivore species such as wild boar (*Sus scrofa*) (Fig. 1). These ungulates at the Veluwe have a strong influence on tree recruitment and understory vegetation (den Ouden et al. 2020).

Experimental Design

The study was conducted within an existing experimental setup to assess the impacts of SRP addition on old oak forests. The experiment includes nine old oak forests across the Veluwe that together can be considered representative for this system (Table S1; Fig. 2). All forests had canopies dominated by pedunculate oak (*Quercus robur*); five had a dominant undergrowth of European blueberry (*Vaccinium myrtillus*). Each forest site had three experimental plots of 70 × 70 m (0.5 ha) that had a similar soil structure, elevation and vegetation. Three treatments had been randomly assigned and applied during February–April 2020: (1) spreading of volcanic SRP (*Eifelgold*, 10 t/ha), (2) spreading of heteromorphic SRP (Soilfeed, 10 t/ha), and (3) a control. *Soilfeed* and *Eifelgold* both contain Ca, K, P and Mg in variable concentrations; Eifelgold contains three times more Mg and P than *Soilfeed* (Bloem et al. 2022) (Table S2). At the time of our study, leaves of oak trees already showed increased concentrations of Ca and K in both SRP addition treatments, and elevated Mg concentrations in the Eifelgold treatment (Sitters et al. 2023), indicating that SRP resulted in increased elemental uptake by the vegetation.

Camera Trapping

Plot visitation and foraging by ungulates was measured with wildlife camera traps from late March to early July of 2023, that is, during the early growing season (Didion et al. 2009). In each of the 27 plots, we deployed two camera traps (Reconyx

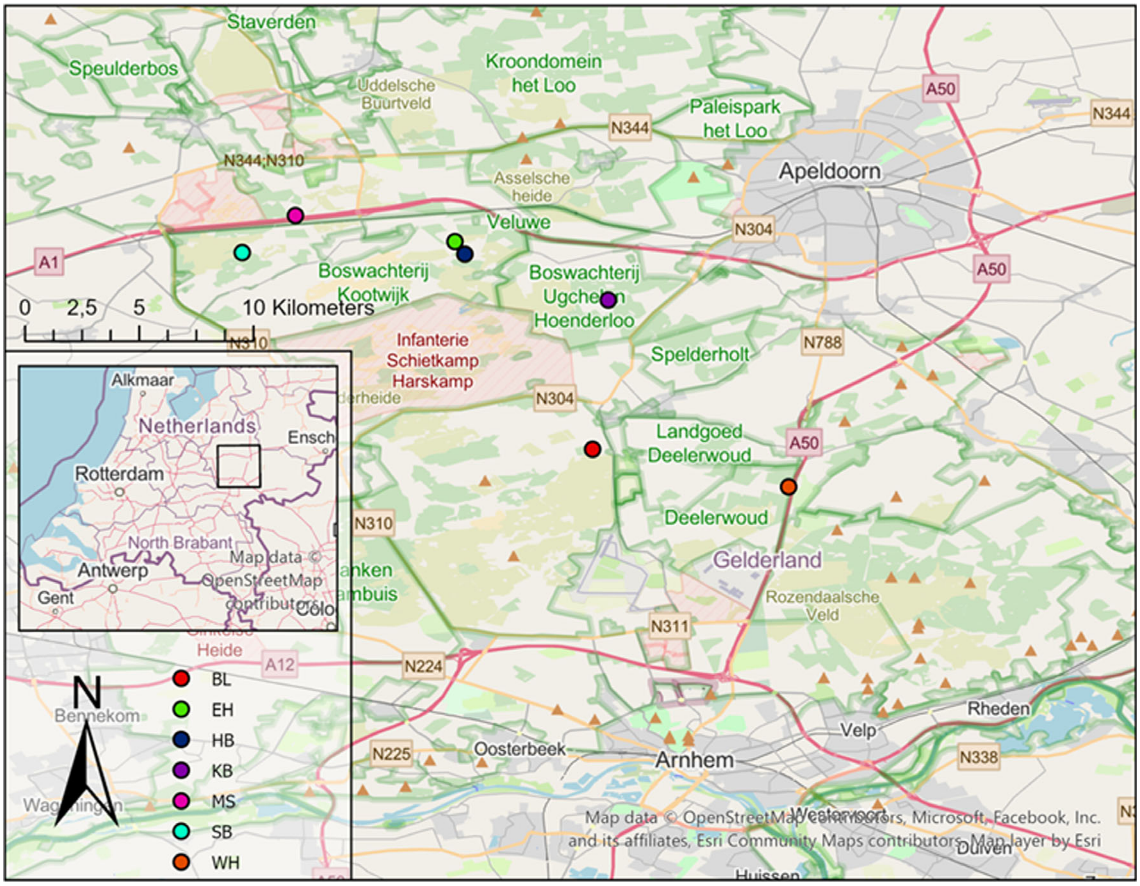

Figure 2. Location of the nine experimental sites at the Veluwe. WH and SB both contain two locations: WH North and WH South and SB North and SB South.

hyperfire 2, Reconyx Inc., Wisconsin, USA) in 5 rounds of 3 weeks, yielding 10 deployments and approximately 210 days of sampling effort per plot. Deployments were adjacent to 10 different oak trees, scattered across the plots, that had been selected and marked for monitoring leaf chemistry in a companion study. The cameras were set up in motion-trigger mode, with a 10-picture rapid-fire upon each trigger and without delay between subsequent triggers. A time-lapse photograph was taken every 12 hours at 12:00 and 24:00 hours to quantify possible camera failure. Cameras were mounted on trees that offered a clear line of sight of at least 10 m northward. The cameras were mounted with the lens 50 cm off the ground. Short vegetation that blocked the view of the sensor was pruned down. A walk test was performed to check if the cameras were properly set up. The maximum detection distance usually exceeded 10 m.

Images were processed in the camera-trapping platform Agouti (www.agouti.eu; Casaer et al. 2019). The footage was linked to the corresponding plot ID, corresponding tree, the distance of the walk test and the camera height. Agouti grouped images into sequences with a cut-off time of 120 seconds. Artificial Intelligence was used for the classification of sequences by species (Western Europe species model version 4a), and sequences for which this failed were annotated manually. Species, number of individuals and behavior were recorded. For all ungulate observation sequences, classifications were validated, and the behavior was manually scored as foraging, standing, walking/running, and resting. The data were exported from Agouti in camtrapdp format (Bubnicki et al. 2023).

Data preparation and analysis were done in R (version 4.3.1). Observations were filtered to include only foraging animals of the species of interest: wild boars (*Sus scrofa*), red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), and fallow deer (*Dama dama*). Then we calculated the total number of foraging events and foraging seconds per species per tree.

Data Analyses

To assess whether the number of foraging events and the foraging time differed between treatments, we fitted general linear mixed models (GLMMs) using the glmmtmb package (Brooks et al. 2017), with a negative binomial type 2 distribution for the foraging events, and a Tweedie distribution for the foraging time. Both these distributions are well-suited for nonnormal count or count-related continuous data with random effects (Bolker et al. 2009). Treatment was included as a fixed effect, and site and tree (nested structure) were included as random effects. To account for the small difference in sampling effort between the deployments, we included the log of the effort as an offset. To improve the convergence of the models, we

Table 1. Number of individuals observed per species by treatment for each of the nine forests. C = control, E = Eifelgold and S = Soilfeed.

Forest	*Treatment*	*Wild Boar*	*Fallow Deer*	*Red Deer*	*Roe Deer*
Hoog Baarlo	C	49	0	121	48
	S	100	0	146	94
	E	54	0	88	65
Woeste Hoeve North	C	7	63	27	1
	S	34	99	70	6
	E	5	45	48	1
Woeste Hoeve South	C	9	45	58	4
	S	13	102	104	9
	E	14	98	120	8
Keulerbosch	C	17	0	2	14
	S	50	0	11	12
	E	23	0	11	9
Eikenheg	C	108	6	43	32
	S	72	13	20	30
	E	39	3	30	23
Heidensberg	C	52	4	25	18
	S	95	4	16	49
	E	101	2	13	32
Stroesebergen North	C	480	0	35	69
	S	296	0	8	28
	E	578	0	19	100
Stroesebergen South	C	283	0	25	25
	S	231	0	22	30
	E	113	0	0	19
Maanschoten	C	156	0	27	55
	S	87	0	22	48
	E	161	0	41	60
Total		3,234	484	1,152	889

used the L-BFGS-B optimization method (Byrd et al. 1995; Zhu et al. 1997). Model validation was performed using the DHARMa package (Hartig 2022) to assess residual dispersion, zero inflation, and overall model fit.

Results

Of the 270 deployments, 269 were successful. Deployment duration averaged 21.9 days (± 4.57 SD). A total of 3,987 animal observations of the species of interest were obtained, showing 6,466 individuals (Tables 1 & S4). The number of observed animals per day ranged almost 10-fold between locations, from 15.4 at Stroesebergen North to 1.6 observations per day at Keulerbosch (Fig. 3; Table S3). Wild boar was the most frequently observed species, with a total record of 3,234 individuals. Of the cervids, red deer was the most observed species with 1,152 individuals observed across all the locations. Fallow deer were observed in just four locations (Fig. 3; Table 1).

Significant differences in foraging events between the treatment plots and the control were found for none of the ungulate species, neither in terms of the number of foraging events nor in terms of the duration of those events. Neither the *Eifelgold* treatment nor the *Soilfeed* treatment showed significant differences compared with the control (GLMM; Table 2). Inclusion of all foraging events—also non-foraging—yielded a similar pattern (not shown).

Discussion

In this study, we tested the hypothesis that SRP addition in forests attracts wild ungulates, potentially interfering with tree recruitment. We used camera traps to compare wildlife activity between treatments in SRP addition experiments in nine oak forests across the Veluwe, the Netherlands. Despite evidence of increased concentrations of Ca, K, and Mg in tree leaves (Sitters et al. 2023), we found no evidence of preferential use of treated plots by ungulates.

None of the three ungulate species showed a significant difference between the number of foraging events or the duration of the foraging events between the treatments and the control. This was unexpected given the importance of these elements in ungulate diet (French et al. 1956; Tajchman et al. 2018), and given responses seen in an earlier study in heathland (Weijters et al. 2018). Several earlier studies only considered the effects of measures aimed at reducing forest soil acidification on wildlife other than ungulates. For example, Pabian and colleagues (Pabian & Brittingham 2007; Pabian et al. 2012b) found that the abundance of snails and birds increased after liming, which only increases the availability of Ca and Mg but can lower soil acidity very effectively. Snails require Ca for their shells, high acidity degrades shells, and birds in turn feed on snails to acquire Ca for their eggs (Graveland et al. 1994; Graveland & vanderWal 1996). These dependencies, however, were more direct and related specifically to Ca.

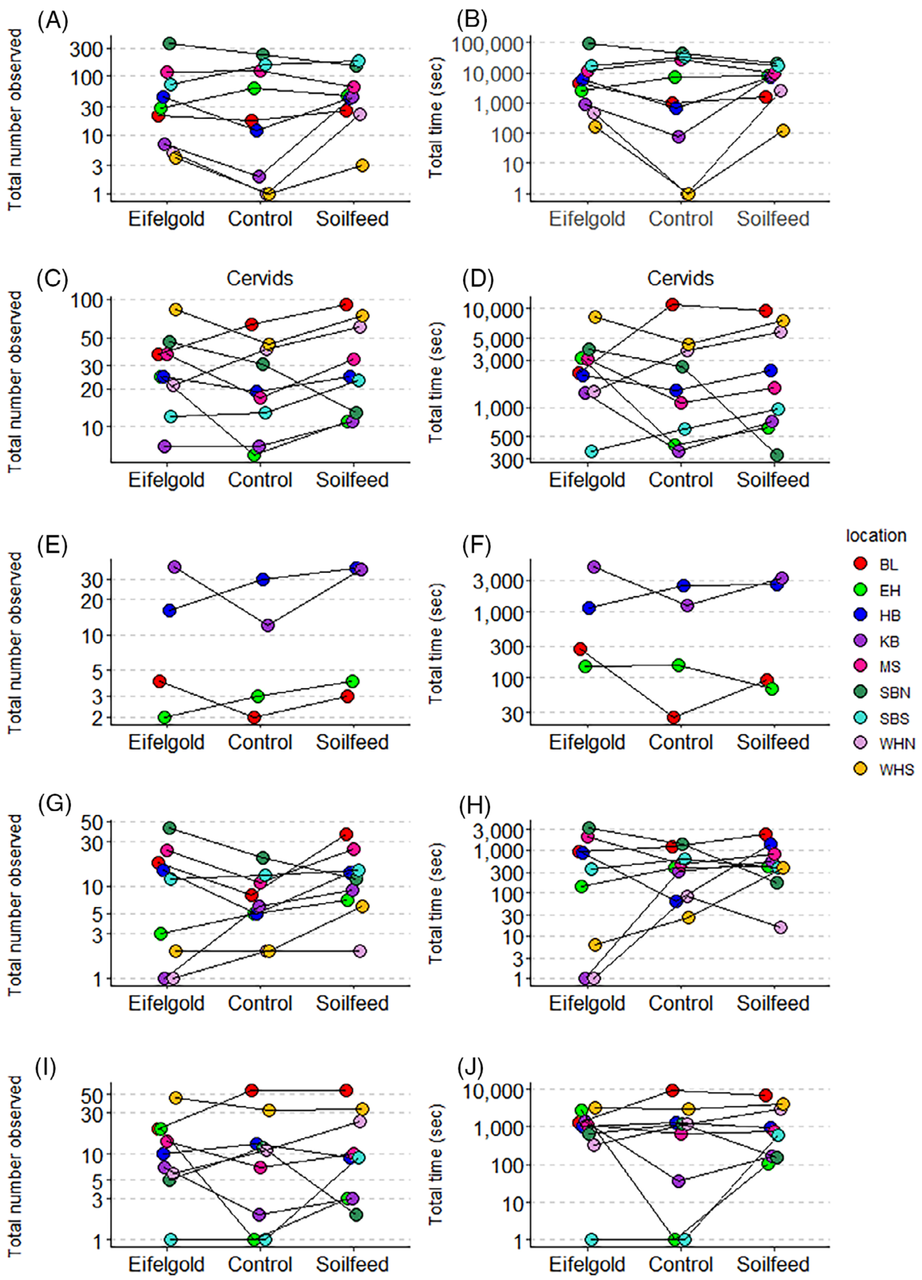

Figure 3. Number of foraging individuals between experimental plots with the addition of two types of SRP and control plots, in nine acidified oak forests across the Veluwe, the Netherlands. Shown are the relationships between the total number of foraging events and treatment (left column) and between the total foraging time and treatment (right column). (A, B) Wild boar; (C, D) Cervids grouped; (E, F) Fallow deer; (G, H) Roe deer; and (I, J) Red deer.

The lack of observed differences was unlikely an artifact of our experimental design. Our design controlled for differences in habitat properties with treatments replicated across sites. Our sampling effort—around eight camera months per plot—was fairly high, and all sites had a good number of captures. In fact, the sites with the highest capture rates showed the smallest differences between treatments. The proximity of the three treatment plots within each forest site was also advantageous as this gave animals a discrete choice between the alternative treatments. The problem of animals walking through and between plots was accounted for by focusing on animals displaying foraging behavior. Also, the SRP dose (10 tons ha^{-1}) was well chosen. It was similar to previous SRP addition projects at the Veluwe, based on expert judgment and model calculation of the acidification model VSD+ (de Vries et al. 2019), and representative of management interventions in this ecosystem.

There are several potential ecological explanations for the lack of ungulate responses. The most plausible is that any chemical responses of the understory vegetation were too small for ungulates to detect or to induce preference. It is possible that

Table 2. GLMM comparisons of foraging by ungulates between treated and control plots in the old oak forests at the Veluwe, in terms of the number and duration of foraging events. Values shown are model coefficients for comparisons with control plots. None of the differences were statistically significant at $p = 0.05$ note that estimates are not back transformed.

	Number of Foraging Events		*Total Visit Duration in Seconds*	
	Eifelgold	*Soilfeed*	*Eifelgold*	*Soilfeed*
Wild boar	$\beta = 0.583$, SE $= 0.852$, $Z = 0.684$	$\beta = 0.954$, SE $= 0.851$, $Z = 1.122$	$\beta = 0.687$, SE $= 1.082$, $Z = 0.635$	$\beta = 0.997$, SE $= 1.08$, $Z = 0.923$
Cervids	$\beta = 0.268$, SE $= 0.348$, $Z = 0.77$	$\beta = 0.353$, SE $= 0.348$, $Z = 1.015$	$\beta = 0.225$, SE $= 0.463$, $Z = 0.485$	$\beta = 0.199$, SE $= 0.466$, $Z = 0.429$
Fallow deer	$\beta = 0.149$, SE $= 1.635$, $Z = 0.091$	$\beta = 0.457$, SE $= 1.627$, $Z = 0.281$	$\beta = 0.583$, SE $= 0.852$, $Z = 0.684$	$\beta = 0.382$, SE $= 1.776$, $Z = 0.215$
Roe deer	$\beta = 0.223$, SE $= 0.566$, $Z = 0.394$	$\beta = 0.635$, SE $= 0.55$, $Z = 1.154$	$\beta = 0.185$, SE $= 0.759$, $Z = 0.243$	$\beta = 0.531$, SE $= 0.741$, $Z = 0.717$
Red deer	$\beta = 0.235$, SE $= 0.594$, $Z = 0.396$	$\beta = 0.277$, SE $= 0.594$, $Z = 0.467$	$\beta = 0.197$, SE $= 0.665$, $Z = 0.296$	$\beta = 0.277$, SE $= 0.665$, $Z = 0.419$

our assessment happened too early after SRP addition to expect effects—model calculations indicate that the SRP addition may take 10–15 years to reach its full effects (de Vries et al. 2017). Elevated levels of Ca, K and Mg had been measured in the foliage of the trees in the canopy and in the year prior to sampling (Sitters et al. 2023), but this does not necessarily imply a meaningful increase in the understory vegetation that can be selected by ungulates.

A second possible explanation is that the ungulates in this study did not experience a limitation for the observed increased elements (i.e., Ca, Mg, or K), resulting in no selective feeding behavior for these elements. For the Veluwe region, deficiencies of Na, P and Ca are reported for ungulates, but not for K or Mg (Groot Bruinderink et al. 2000). Foraging may have been steered geared towards elements that did not increase in our study sites, for example, P and Na. This explanation cannot, however, explain the lack of foraging selection for increased Ca in the SRP-treated plots.

A third possibility is that understory vegetation cover was too sparse to induce preferential feeding. A fourth is that food abundance and quality are relatively high during our assessment, the early growing season, allowing less selective foraging behavior. William et al. (2018), for example, found that female roe deer are less selective under high-resource conditions. Fifth, inter- and intra-specific competition and human disturbance may have constrained the expression of feeding preferences (Gaynor et al. 2018; Zini et al. 2023). We consider this less plausible because treatment plots within forests were not far apart, hence were likely effected by the same disturbances. Finally, the mineral uptake by the ungulates may already have been sufficient due to artificial mineral licks. We rule out this explanation because mineral licks were ample only at one site (Hoog Baarlo). They were entirely absent at the two sites at Woeste Hoeve (Natuurmonumenten 2023, personal communication) and scarce in the six remaining sites.

Overall, we found no evidence for attraction of feeding ungulates to oak forests with SRP addition, at least not within 3 years after treatment. The lack of observed differences is likely due to a combination of limited improvement of forage attractiveness, lack of meaningful increases in the elements that are likely to be deficient in the studied ungulates, and high ambient food availability. We cannot rule out that SRP addition still increases browsing by deer and rooting by wild boar during fall and winter, when the feeding behavior and nutritional needs of the animal might differ. This can be tested by repeating this study in those seasons. More importantly, we cannot rule out that ungulates will show responses later, for example, after a decade, when the effect of SRP on addition on soil and vegetation has fully expressed. This can be tested by repeating the study after another 10 years.

Acknowledgments

We thank A. van der Schaaf, L. R. Dijkhuis, and S. He for field assistance; Y. Liefting and the Wildlife Ecology and Conservation Group of Wageningen University for providing the camera traps and all other materials; the Agouti initiative for hosting the project; L. Krul (Stichting Het Nationale Park De Hoge Veluwe), A. ten Hoedt (Natuurmonumenten), and D. Goudkuil (Staatsbosbeheer) for granting permits; the province of Gelderland and the Wildlife Ecology and Conservation group of Wageningen University for providing funding.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. General information on the nine study sites.
Table S2. Composition of the used silicate rock powder with micro-wave destruction in mmol/kg dry material.
Table S3. Overview of the start and end dates, the total number of days, total number of observations and the observations per day (total number of observations/total number of days).
Table S4. Number of animals observed per location.

Coordinating Editor: Stephen Murphy

Received: 20 May, 2025; First decision: 8 August, 2025; Revised: 23 November, 2025; Accepted: 30 December, 2025