

Soil phosphorous is the primary factor
determining species-specific plant growth
depending on soil acidity in island ecosystems
with severe erosion

Hata, Kenji

Hiradate, Syuntaro

Kachi, Naoki

<https://hdl.handle.net/2324/7330426>

出版情報 : Scientific Reports. 13 (1), 2023-07-27. Springer
バージョン :
権利関係 : Creative Commons Attribution 4.0 International





OPEN

Soil phosphorous is the primary factor determining species-specific plant growth depending on soil acidity in island ecosystems with severe erosion

Kenji Hata^{1,2}✉, Syuntaro Hiradate³ & Naoki Kachi²

Disturbances caused by invasive ungulates alter soil environments markedly and can prevent ecosystem recovery even after eradication of the ungulates. On oceanic islands, overgrazing and trampling by feral goats has caused vegetation degradation and soil erosion, which can alter soil chemistry. To understand the effects of the changes on plant performance, we conducted a laboratory experiment to assess herbaceous species growth under various soil conditions with phosphorous, nutrients, and acidity. Subsoil was collected from Nakodo-jima in the northwest Pacific. Six herbaceous species dominating the island were grown in soils with three levels of added CaCO_3 and P_2O_5 and two levels of added KNO_3 . After 4 weeks of growth, the total dry plant weight was significantly lower with no added P_2O_5 , regardless of the addition of KNO_3 . Three species weighed more under P_2O_5 and KNO_3 addition in high-pH soil, whereas the remaining three weighed less. Our results indicated that herbaceous species growth is limited primarily by phosphorous availability; the limitation is dependent on soil pH, and the trend of dependency differs among species. This implies that ecosystems with extreme disturbances cannot recover without improving the soil chemistry.

Ongoing climate change and anthropogenic impacts are degrading ecosystems in many biomes globally. Natural ecosystems can recover to the original state after being disturbed by natural and anthropogenic events; this is called “resilience”¹. However, if the disturbances exceed a threshold of resilience, the original state cannot be recovered². The disturbances that cause irreversible changes are called “extreme events”. To promote the recovery of ecosystems that have undergone extreme modification, and to prevent extreme degradation, it is essential to understand the mechanisms of ecosystem resilience, as well as the environmental and anthropogenic factors that limit recovery.

The ecosystems of many oceanic islands are vulnerable to disturbances by invasive species³. Invasive ungulates have disturbed many oceanic island ecosystems^{3–5}, which can cause terrestrial ecosystems to shift irreversibly. For example, overgrazing and trampling by feral goats, pigs, and sheep naturalized on islands have severely damaged the vegetation and soil environments on many island ecosystems^{3,6,7}. As well as the direct effects of herbivory and digging^{8,9}, overgrazing and trampling indirectly lead to soil erosion via vegetation degradation^{8,10–12}. Conversely, in some instances, grazing and trampling by wildlife affect the plant cover and species composition but not the ecosystem functions¹³, suggesting that the effects of invasive ungulates are highly context dependent.

On Nakodo-jima (27°37′–27°38′N, 142°10′–142°11′E), a northwestern Pacific Ocean island, feral goats have inflicted significant harm on the ecosystem (refer to supplementary Fig. S1, online). These goats became naturalized after 1945, and their subsequent overgrazing and trampling for several decades led to serious vegetation degradation and soil erosion¹⁴. Although the island’s goat population was eradicated between 1997 and 1999¹⁵, the vegetation has yet to recover and soil erosion persists in certain areas¹⁶. This implies that the ecosystems experienced extreme disturbances surpassing their resilience threshold. It is likely that these ecosystems cannot

¹College of Commerce, Nihon University, 5-2-1 Kinuta, Setagaya-ku, Tokyo 157-8570, Japan. ²Department of Biological Sciences, Graduate School of Science, Tokyo Metropolitan University, 1-1 Minami-Osawa, Hachioji, Tokyo, 192-0397, Japan. ³Department of Agro-Environmental Sciences, Faculty of Agriculture, Kyushu University, 744 Moto-oka, Nishi-Ku, Fukuoka, 819-0395, Japan. ✉email: hata.kenji@nihon-u.ac.jp

recover without additional human intervention, even after goat eradication. To preserve and restore these ecosystems, understanding the processes and mechanisms behind the loss of ecosystem functions is crucial¹⁷.

The lack of ecosystem recovery after goat eradication is related to changes in soil chemistry with vegetation loss and soil erosion. Vegetation loss leads to exposed surface soil, promoting erosion that later alters the chemistry of the soil¹⁸. Loss of surface soil exposes the deeper subsoil layer, which is typically nutrient poor and highly acidic¹⁹. Hata et al. suggested that bare ground exposed by goat disturbance limits the primary production of herbaceous vegetation due to increased soil acidity²⁰.

These studies suggested that changes in soil chemistry due to soil erosion limit plant performance, although this hypothesis was based on correlations in field surveys and has not been tested experimentally. To evaluate this hypothesis, it is necessary to quantify the effects of multiple soil chemical factors on plant growth because limitations to plant growth resulting from the chemistry of soil are the product of not only singular effects but also interactive effects among multiple chemical stressors. For example, soil pH and available phosphorus (P) interact such that the amount of available P is low in soils with a low pH, because labile P in soil combines with Fe^{3+} and Al^{3+} , which are unavailable forms for plants²¹. Furthermore, available P can be converted to unavailable forms via combination with calcium carbonate in neutral to subalkaline soils²². Soil pH-related differences in nutrient availability originate from various P retention mechanisms in soils, which are influenced by the balances of non-labile, labile and solution P as well as their dynamics^{23,24}. Thus, the extent to which P limits plant growth is dependent on soil pH; the extent of dependency can differ among species and soil environments.

To evaluate the impact of extreme changes in soil chemistry related to soil erosion on plant growth, we conducted laboratory experiments using subsoil collected from a layer exposed to severe soil erosion on Nakodo-jima. This soil has notably low nutrient levels and high acidity. Indeed, Bray-II P and pH (H_2O) were significantly lower in soil of eroded areas than in less disturbed forests, with $< 20 \text{ mg P}_2\text{O}_5 \text{ } 100 \text{ g}^{-1}$ and < 5 ¹⁹. Additionally, sites with low vegetation coverage ($< 13\%$) experienced $2 \text{ cm}^2 \text{ yr}^{-1}$ soil loss and Bray-II P and exchangeable acidity values of $< 20 \text{ mg P}_2\text{O}_5 \text{ } 100 \text{ g}^{-1}$ and $> 40 \text{ me kg}^{-1}$ respectively¹⁸.

By manipulating soil nutrient levels and pH, we assessed the effects of essential soil nutrients and pH on the initial growth of herbaceous species, focusing specifically on available P. Phosphorus inputs in ecosystems primarily originate from rock weathering; hence, even minor losses in P cannot be easily replenished²⁵. Isolated island ecosystems likely have even more limited P inputs^{26,27}. Given this and the relationship between P availability and pH, we anticipated that the impact of soil erosion would be most pronounced on P availability compared to other nutrient elements such as nitrogen (N) and potassium (K). Indeed, Hiradate et al. suggested correlations among vegetation degradation caused by feral goats, available P, soil pH, and vegetation status in Nakodo-jima during goat invasion and subsequent eradication¹⁹.

We tested three predictions: first, the initial growth of plants will increase with the addition of available P and other nutrient elements; second, the magnitude of this growth increase will be dependent on soil pH; and third, the extent of dependency on nutrient elements and soil pH will differ among species. We compared the biomasses of six herbaceous species grown on the subsoil across various phosphorus pentoxide (P_2O_5), potassium nitrate (KNO_3), and calcium carbonate (CaCO_3) treatments; N and K are two other major essential macronutrients for plant growth. The KNO_3 treatment was included to determine whether plant growth was limited by factors other than P, N and K. We hypothesized that plant growth is limited primarily by available P. If plant growth under sufficient available P is limited secondarily by the availabilities of N and K, the addition of N and K should enhance plant growth. The six study species (three Poaceae and three Asteraceae, Table 1) are non-native species but comprise a large proportion of the herbaceous vegetation (i.e., dominant species) that was disturbed by goats and recovered after goat eradication in the Ogasawara (Bonin) Islands, including Nakodo-jima. Based on our results, we discuss the restoration of ecosystems whose functions have been lost as a result of severe disturbances following ungulate eradication.

Results

Over the 4-week experiment, out of 162 seedlings per species (3 P_2O_5 levels \times 3 KNO_3 levels \times 2 CaCO_3 levels \times 9 replicates), five *Paspalum dilatatum*, one *Sporobolus diander*, six *Bidens pilosa*, and nine *Emilia sonchifolia* seedlings died. All of the *Paspalum scrobiculatum* and *Symphytotrichum subulatum* seedlings survived the entire study.

The ranges of total dry plant weights at the end of the experiment were $0.010\text{--}0.332 \text{ g pot}^{-1}$ for *P. dilatatum*, $0.012\text{--}0.496 \text{ g pot}^{-1}$ for *P. scrobiculatum*, $0.002\text{--}0.112 \text{ g pot}^{-1}$ for *S. diander*, $0.025\text{--}0.377 \text{ g pot}^{-1}$ for *B. pilosa*, $0.003\text{--}0.330 \text{ g pot}^{-1}$ for *E. sonchifolia*, and $0.0008\text{--}0.082 \text{ g pot}^{-1}$ for *S. subulatum*. In preliminary experiments, we

Species		Family	Experiment period
<i>Paspalum dilatatum</i>	PasDil	Poaceae	2016/01/11–2016/02/10
<i>Paspalum scrobiculatum</i>	PasScr	Poaceae	2016/04/12–2016/05/16
<i>Sporobolus diander</i>	SpoDia	Poaceae	2016/10/13–2016/11/11
<i>Bidens pilosa</i>	BidPil	Asteraceae	2016/08/01–2016/08/31
<i>Emilia sonchifolia</i>	EmiSon	Asteraceae	2016/08/15–2016/09/17
<i>Symphytotrichum subulatum</i>	SymSub	Asteraceae	2016/09/08–2016/10/11

Table 1. The six herbaceous species used in the laboratory experiments and experimental durations. Life forms, phenologies, and seed morphologies of the species are presented in Supplementary Table S1.

confirmed that addition of CaCO_3 increased soil pH (Fig. 1a), whereas addition of P_2O_5 increased the amount of available P in the soil (Fig. 1b).

For all the investigated species, the total dry weights were significantly affected by the addition of P_2O_5 (Table 2). Seedlings were significantly smaller in the treatments without P_2O_5 addition than in those with P_2O_5 addition, regardless of the addition of CaCO_3 or KNO_3 (Fig. 2). We found a significant interaction effect between P_2O_5 and KNO_3 additions for all species (Table 2), indicating that the growth response to KNO_3 addition was dependent on the addition of P_2O_5 . The total dry weights increased with the addition of both KNO_3 and P_2O_5 , but not with the addition of KNO_3 alone (Fig. 2).

The effect of CaCO_3 addition on total dry seedling weights was dependent on P_2O_5 and KNO_3 additions. There was evidence of a significant effect of CaCO_3 addition for all species, as well as evidence of interactions between CaCO_3 and P_2O_5 and between CaCO_3 and KNO_3 (Table 2). In agreement with these findings, the investigated species were roughly classified into two types according to their treatment responses. Type 1 included *P. dilatatum*, *P. scrobiculatum*, and *E. sonchifolia* and type 2 included *S. diander*, *B. pilosa*, and *S. subulatum*. For type 1 species, total dry seedling weight considerably increased with the addition of P_2O_5 and KNO_3 when no or little of CaCO_3 was added (Fig. 2a–c). For type 2 species, total dry weight substantially increased with the addition of P_2O_5 and KNO_3 in the presence of high CaCO_3 addition (Fig. 2d–f). Type 2 species were further classified into two types (Type 2a: *S. diander* and *B. pilosa*; Type 2b: *S. subulatum*) according to their treatment responses, especially to changes in the amounts of CaCO_3 . Compared with Type 2a (*S. diander* and *B. pilosa*), Type 2b (*S. subulatum*) appeared to be more affected by CaCO_3 .

Discussion

Limitation of plant growth on changing soil chemistry. Our results indicated that the initial growth of herbaceous species will be limited in soils whose chemistry has been affected by severe erosion (i.e., surface soil loss and exposed subsoil), in agreement with the relationship between herbaceous species and soil chemistry found in this study¹⁸. Surface soil loss due to vegetation degradation exposes the deeper subsoil below, which on Nakodo-jima is highly acidic and nutrient poor¹⁹. Few plants occur at these sites¹⁸, likely because of limited

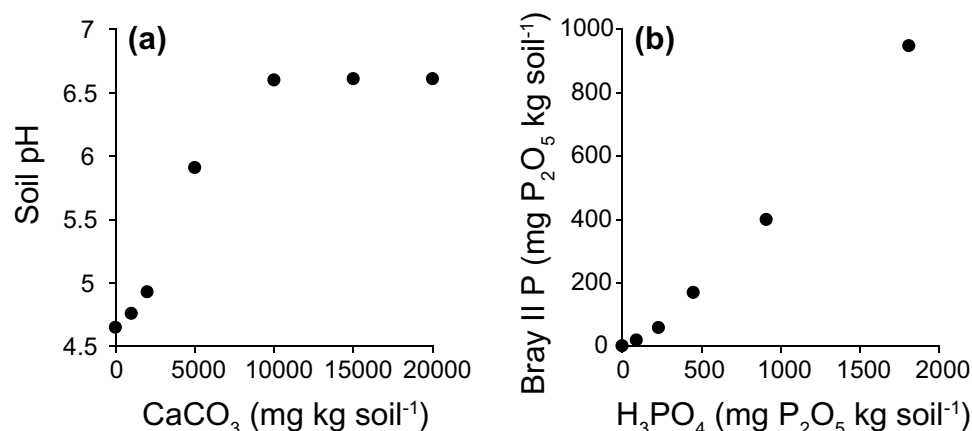


Figure 1. Relationships (a) between soil pH and the amount of CaCO_3 added, and (b) between soil-available phosphorus (Bray-II P) and the amount of P_2O_5 added.

Explanatory variable	d.f	(a) PasDil		(b) PasScr		(c) EmiSon		(d) SpoDia		(e) BidPil		(f) SymSub	
		χ^2		χ^2		χ^2		χ^2		χ^2		χ^2	
CaCO_3	2	157.9	***	382.6	***	292.1	***	9.9	**	158.1	***	172.5	***
P_2O_5	2	1848.9	***	5670.8	***	2481.4	***	2008.8	***	1969.8	***	1619.8	***
KNO_3	1	577.1	***	953.2	***	321.3	***	34.6	***	109.0	***	32.3	***
$\text{CaCO}_3 \times \text{P}_2\text{O}_5$	4	62.8	***	163.4	***	125.5	***	10.3	*	8.5	n.s.	59.1	***
$\text{CaCO}_3 \times \text{KNO}_3$	2	42.0	***	113.1	***	0.4	n.s.	12.5	**	0.9	n.s.	19.9	***
$\text{P}_2\text{O}_5 \times \text{KNO}_3$	2	235.9	***	461.1	***	115.4	***	43.9	***	165.9	***	20.7	***
$\text{CaCO}_3 \times \text{P}_2\text{O}_5 \times \text{KNO}_3$	4	39.2	***	43.6	***	22.1	***	5.0	n.s.	5.0	n.s.	23.9	***

Table 2. Effects of treatments (CO_3 , P_2O_5 , and KNO_3 addition and their interactions) on total dry plant weight, as tested by generalized linear mixed models (GLMMs). Degrees of freedom (d.f) and Chi-square values (χ^2) are shown for explanatory variables. (a) PasDil, *Paspalum dilatatum*; (b) PasScr, *Paspalum scrobiculatum*; (c) EmiSon, *Emilia sonchifolia*; (d) SpoDia, *Sporobolus diander*; (e) BidPil, *Bidens pilosa*; (f) SymSub, *Symphyotrichum subulatum*. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, n.s. = not significant.

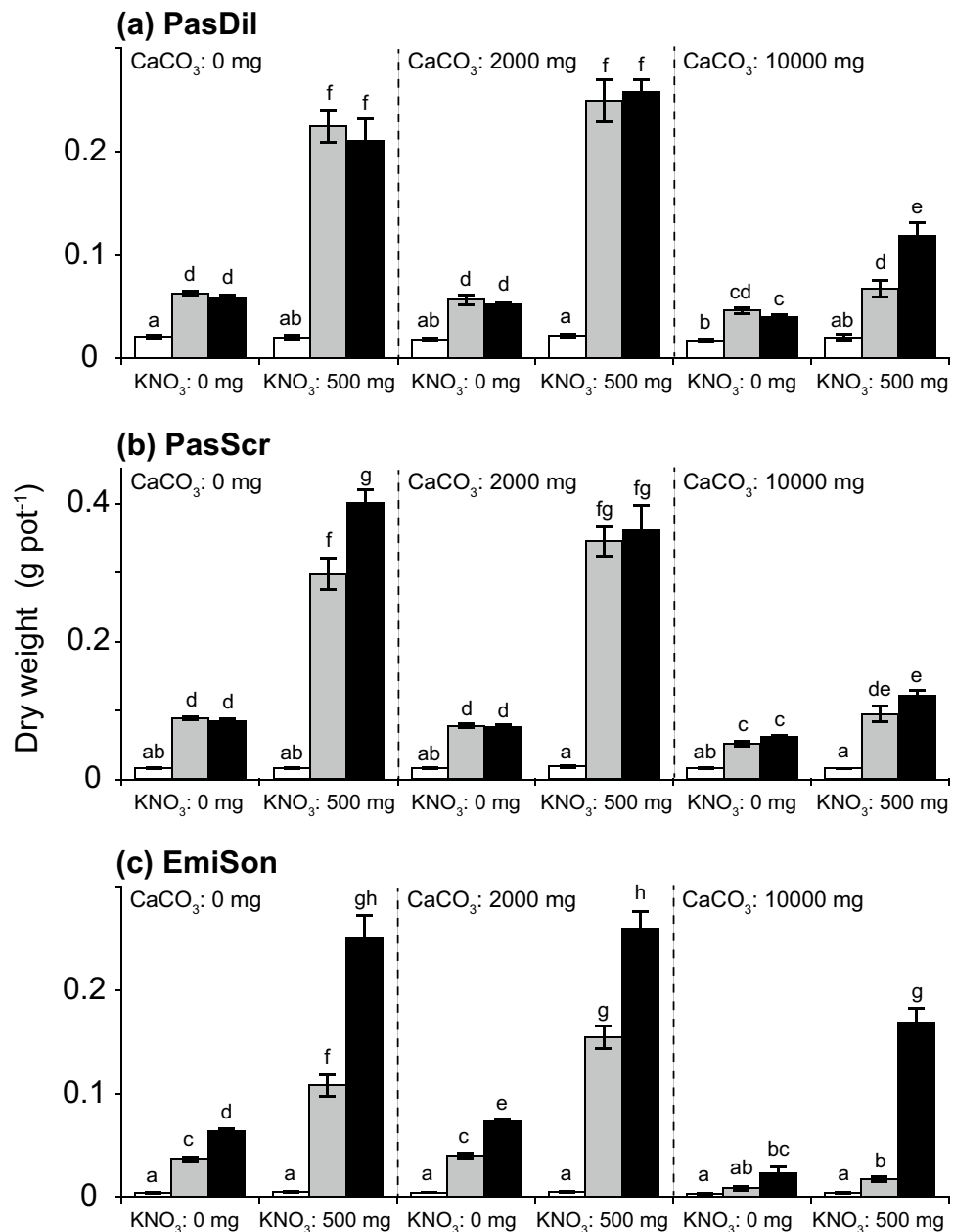


Figure 2. Total dry weights (g pot^{-1}) of investigated species under 18 combinations of three treatments ($3 \times 3 \times 2$). White, gray, and black bars represent 0, 250, and 500 $\text{mg P}_2\text{O}_5 \text{ kg soil}^{-1}$ concentrations, respectively. Mean values (columns) and standard errors (bars) are shown. Letters indicate significant differences ($p < 0.05$) among treatments based on Holm's multiple comparison method after generalized linear mixed model (GLMM) analyses. (a) PasDil, *Paspalum dilatatum*; (b) PasScr, *Paspalum scrobiculatum*; (c) EmiSon, *Emilia sonchifolia*; (d) SpoDia, *Sporobolus diander*; (e) BidPil, *Bidens pilosa*; (f) SymSub, *Symphyotrichum subulatum*.

seed or propagule dispersal^{28,29} or poor plant growth and survival. Our results suggested that it is unlikely that herbaceous species can survive or thrive at sites that have experienced heavy soil erosion, even following goat eradication and assuming sufficient seed or propagule dispersal.

The initial growth and survival at heavily eroded sites are most likely related to soil deficiencies in nutrients, especially available P. The reduced biomass observed in seedlings that did not receive P_2O_5 additions, regardless of CaCO_3 and KNO_3 additions (Fig. 2), suggested that available P is the primary limiting factor for initial growth in the degraded soil systems on Nakodo-jima. Indeed, the amount of soil-available P recorded at eroded sites on Nakodo-jima [$29.72 \pm 9.85 \text{ mg P}_2\text{O}_5 \text{ kg soil}^{-1}$ (Bray-II P), Hata et al.¹⁸], would be insufficient for the establishment of many herbaceous species^{30,31}. Evidence of P limitation was also shown in the above- and below-ground biomass allocations in seedlings. The shoot:root ratios of all species, excluding *B. pilosa*, tended to be lower in treatments without P_2O_5 addition (see Supplementary Fig. S2 online), indicating that a P deficiency may be related to an

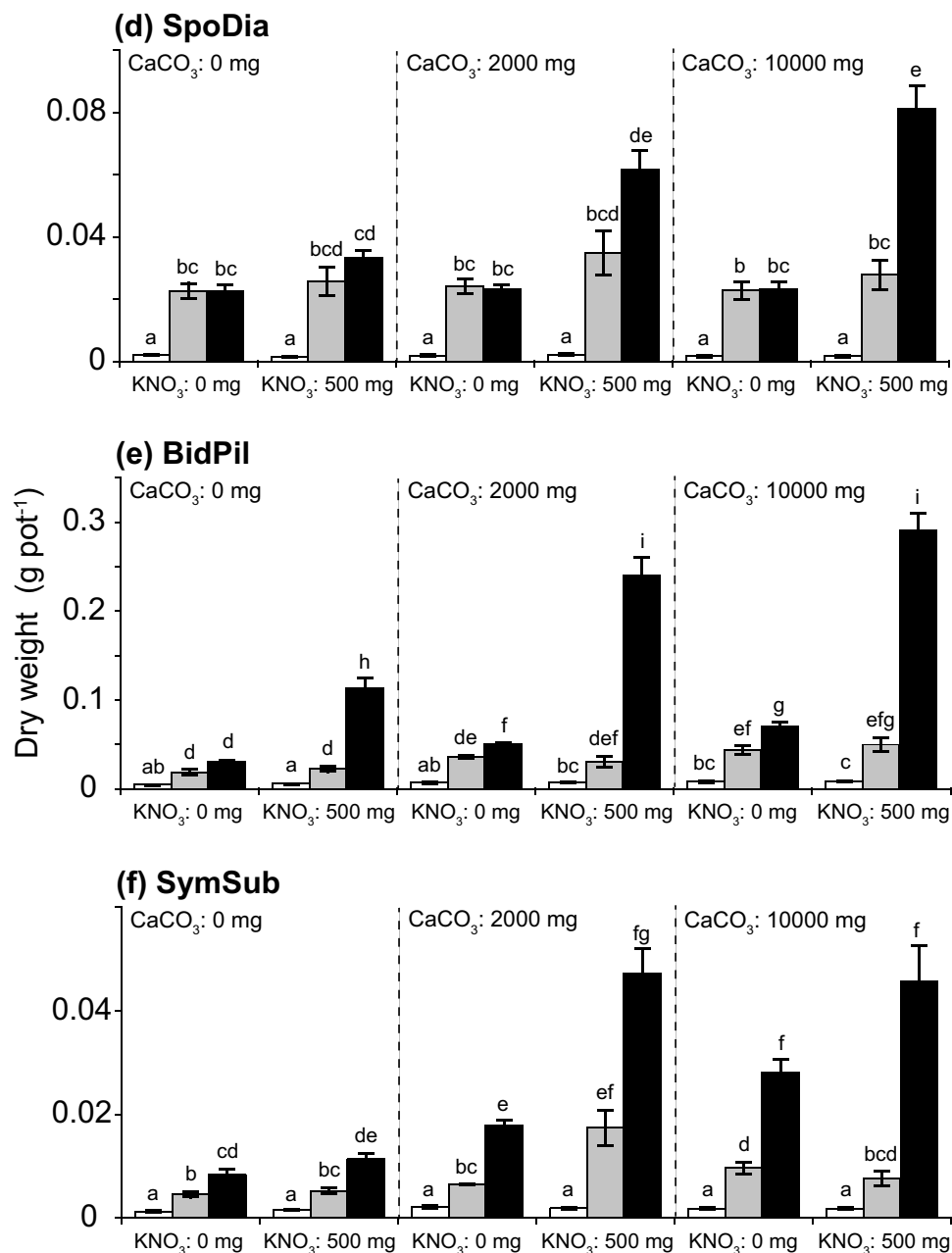


Figure 2. (continued)

increase in root biomass in an effort to acquire P from the soil^{32,33}. However, the significant interaction between the addition of P₂O₅ and KNO₃ (Table 2) demonstrated that N and K can also have substantial effects on plant growth in denuded soils when P availability is adequate (Fig. 2). This may be explained by the interaction between available P and N in soils, as available N increases with the addition of P³⁴.

Significant interactions between CaCO₃ and P₂O₅ and between CaCO₃ and KNO₃ additions (Table 2) indicated that the effect on plant growth caused by the addition of N, K and P was dependent on soil pH, which was consistent with our second prediction. This dependency, in part, is explained by the relationship between soil nutrient availability and pH. Available P is typically low in low pH soils because labile P forms stable complexes with Fe³⁺ and Al³⁺, which are unavailable forms for plant uptake^{21,35}. These unavailable forms of P dissolve and become available to plants as soil pH approaches neutral. This was exemplified in the response of type 2 species in our study, growth increased in *S. diander*, *S. subulatum*, and *B. pilosa* with nutrient addition when soil pH was relatively high (Fig. 2d–f). However, type 1 species displayed the opposite response (Fig. 2a–c), suggesting that the addition of P, N and K has minimal impact in neutral pH soil. This result may be associated with growth limitations caused by reduced supplies of heavy metals such as Fe, Zn, or Cu under mildly acid and neutral pH conditions^{35,36}.

These varied responses to soil pH could be related to species-specific tolerances to soil acidity and/or limitations regarding available nutrients^{37–39}. Besides the previously mentioned limitation of available P in low pH soil^{21,35}, there are also evidences that available P is lower in near neutral pH soil^{22,23}. The diverse responses to soil pH suggests that there are multiple dynamic mechanisms among P reactions (non-labile, labile and solution) in soil depending on pH. These mechanisms are related to soil environmental factors such as anion exchange, precipitation of Ca, Al, and Fe phosphates, and ligand exchange²⁴. Taking these mechanisms into account, further investigation of plant responses to available nutrients, as well as plant uptake under various soil environments, will contribute to a better understanding of the factors limiting plant establishment in severely eroded soil environments.

Conclusion and implications for the restoration of extremely altered ecosystems. We demonstrated that extremely altered soil chemistry, caused by severe soil erosion resulting from vegetation degradation induced by feral goats, limits the initial growth of herbaceous species. Therefore, disturbances that dramatically alter the soil environment (e.g., disturbance caused by invasive ungulates) may prevent the re-establishment of plants even after the stressor (i.e., feral goats) is removed. Furthermore, our experiment successfully quantified the interactive effects of multiple soil chemistries on plant performance and highlighted the importance of these effects. Indeed, some of the interactions were stronger than single effect (Table 2), suggesting that the dependency of soil pH on nutrient availability can influence the re-establishment of plants. The findings contribute to our understanding of the processes underlying ecosystem function loss and will aid predictions of the recovery of ecosystems with anthropogenically and naturally altered soil chemistry.

Limited or no natural recovery in heavily disturbed ecosystems following invasive species eradication suggests that the altered functional states of ecosystems changed by disturbances are irreversible. In the case of Nakodo-jima, ecosystem function has been lost in goat-disturbed soils. Given that the ecosystem is not resilient to this loss and therefore cannot return naturally to its pre-disturbance state (i.e., historical condition), Nakodo-jima is considered a “novel ecosystem”⁴⁰. Management is therefore necessary to increase stability in this novel ecosystem⁴¹. Management actions that could stabilize or restore the soil environment and allow for plant re-establishment include soil control dams, fertilizer application, and/or soil amendments in eroded soils. Additionally, biochar can be an effective tool for the improvement of P availability in soil⁴², which could enhance plant growth via alteration of mycorrhizal activities⁴³.

In the context of anthropogenic fertilization of soils with low nutrient levels and strong acidity, our results could help identify the fertilizer combinations that can affect the establishment of herbaceous species. For example, the addition of P, N, and K, which are usually included in commercial fertilizers, can promote the establishment of plant species like type 1 in this study (*P. dilatatum*, *P. scrobiculatum*, and *E. sonchifolia*), which have higher growth rates in soils with lower pH. Conversely, it is necessary to supply P, N, K, and CaCO₃ for plant species like type 2 (*S. diander*, *S. subulatum*, and *B. pilosa*), which grow better in soils with higher pH.

As well as anthropogenic fertilization, soils in disturbed ecosystems on oceanic islands can be fertilized naturally by seabird nesting via the deposition of feces, eggshells, and carcasses^{44–46}. Seabird nesting typically decreases in the presence of invasive mammals because of predation⁴⁷ and trampling⁷, but often recovers following invasive species eradication^{48,49}. Indeed, the populations of several dominant seabird species on Nakodo-jima have increased since goat eradication⁵⁰, and higher soil nutrient concentrations were detected at sites with seabird nesting following eradication^{16,20}. Seabird population recovery has been shown to alter soil pH as well as soil nutrients, although these effects are likely to be species-specific⁵¹. In addition, the species composition of seabird communities that recover after goat eradication can differ from those before eradication⁵². Thus, seabird recovery following invasive ungulates eradication cannot always promote plant growth by altering soil chemistry. A comprehensive understanding of species-specific growth responses to altered soil chemistry both before and after the introduction of invasive species will enable more effective and practical plant and ecosystem management and restoration practices.

The use of non-native herbaceous species instead of native ones was related to the observation that only few native herbaceous species were able to recover after goat eradication on the island. It is less likely that native herbaceous species can re-establish on the island after goat eradication because of the lack of seed and propagule supplies. A top priority for ecosystem restoration should be the protection of soil environments to prevent further loss of ecosystem functions of soil. Although the restoration of ecosystems degraded by invasive ungulates ideally should be conducted using native species that were present before degradation, this can be difficult in some situations, such as an island ecosystem with loss of ecosystem functions. In these situations, the first priority should be restoration of ecosystem functions (e.g., stabilization of soil environments in this study) regardless of native or non-native species rather than the biotic compositions of the original communities⁵³. If non-native species are used for ecosystem restoration, the second priority should involve evaluating how the establishment of non-native species can alter the ecosystem functions and how the alteration can affect the subsequent establishment of native species.

Methods

Soil collection site. The soil samples used in the laboratory experiments were collected from a grassland area on Nakodo-jima (27°37'–27°38'N, 142°10'–142°11'E, 1.37 km²) in the Ogasawara (Bonin) Islands, a subtropical archipelago in the northwestern Pacific Ocean (Supplementary Fig. S1 online). The mean precipitation and annual temperature on Chichi-jima, the largest island, were 1305 mm and 23.3 °C, respectively, during 1995–2014 (Japan Meteorological Agency, Tokyo, Japan).

Many areas of Nakodo-jima were likely forested before the introduction of goats¹⁴. Goats became naturalized on Nakodo-jima by 1945⁵⁴. They had access to most areas of the island and severely damaged the native vegetation

through grazing and trampling^{14,54}. Goat grazing on tree and shrub seedlings hindered native forest regeneration after the death of canopy trees¹⁴. This lack of regeneration led to a shift from forested to grassland areas. The grassland vegetation was roughly classified into two types; one dominated by *P. dilatatum* and *P. scrobiculatum*, and the others dominated by *Zoysia tenuifolia*¹⁴.

Grasslands dominated by *P. dilatatum* and *P. scrobiculatum* experienced continued grazing and trampling, resulting in grassland loss and surface soil exposure until the early 1990s⁵⁴. Exposed surface soils were then subjected to erosion by wind and rain. Consequently, areas of forest and grassland decreased, while areas of bare ground increased. For instance, the proportion of forest area declined from 14.6% in 1968 to 8.6% in 1991⁵⁴. This is in agreement with the re-survey of aerial photos between 1978 and 1991, which showed a decrease of forests and grasslands and an increase of bare ground areas^{54,55}.

Feral goats were eradicated from the archipelago between 1997 and 1999¹⁴. After eradication, the natural recovery of herbaceous vegetation, which was dominated by non-native species rather than native species, was patchy (i.e., it occurred at some sites but not others)⁵⁵. In 2012, many areas of bare soil still remained⁵⁶.

Soil collection method. To obtain soil with low nutrient levels and pH, a sample was collected from the subsoil layer (5–80 cm depth, B-layer) in an area with grassland cover on Nakodo-jima in July 2013. Soil was collected at one site only because our objective was to evaluate plant growth in response to nutrient addition and increased pH for soil with extremely low nutrient levels and low pH, rather than to evaluate relationships between plant growth and soil chemistry. Grassland had a total coverage of approximately 80% and it was mainly composed of *P. dilatatum* and *P. scrobiculatum* (Hata, K. personal observation). We collected approximately 300 kg raw-weighted soil from > 10 locations in one area within a ~ 5-m radius range and mixed the sample.

The collected soil was frozen at $-30\text{ }^{\circ}\text{C}$ in a deep freezer for 48 h to reduce the effects of soil microbes. The sample was thoroughly mixed and sieved through a 5-mm mesh; visible plant residues in the soil sample were carefully removed using tweezers. Soil was air-dried within the Tokyo Metropolitan University Ogasawara Field Research Station in Chichi-jima between July 30 and November 14. The air temperature in the station ranged approximately from 25 to 35 $^{\circ}\text{C}$. The air-dried soil was then stored in sealed polyethylene bags in an environment without direct sunlight until the experiments began (Table 1). The soil pH and available P of the sample were estimated as 4.56 ± 0.07 and $29.72 \pm 9.85\text{ mg P}_2\text{O}_5\text{ kg soil}^{-1}$ (Bray II P) (mean \pm standard error), respectively, and were determined according to the method of Hata et al.¹⁸. The sieved and air-dried soil had a very low total carbon level (0.84%, see Supplementary Table S2 online) such that the effects of soil microbes on soil mineralization would be small.

Study species and collection of the seeds. The initial growth of six herbaceous species (*Paspalum dilatatum*, *Paspalum scrobiculatum*, *Sporobolus diander*, *Bidens pilosa*, *Emilia sonchifolia*, and *Symphyotrichum subulatum*) was evaluated in this study (Table 1). All six species are non-native but have been dominant herbaceous species in grasslands on Nakodo-jima since goat eradication, where native herbaceous species are not dominant²⁰. These species are also dominant around soil sample collection sites. Seeds from each species were collected from grasslands around the sampling site and similar grasslands on Nakodo-jima in July 2015 and 2016. Seeds were stored in sealed containers with silica gel at the Plant Ecology Laboratory, Tokyo Metropolitan University, Hachioji, Japan (35 $^{\circ}$ 37' N, 138 $^{\circ}$ 22' E), until the experimental trials began.

Laboratory experiments. Laboratory experiments were conducted in a temperature-controlled chamber (Koito-toron KG-50-HLA, Koito Manufacturing, Tokyo, Japan) at the Tokyo Metropolitan University. The chamber temperature was maintained at 25 $^{\circ}\text{C}$ during the day (16 h) and 18 $^{\circ}\text{C}$ at night (8 h), which is roughly similar to the field conditions on Nakodo-jima. The light intensity in the chamber was $\sim 650\text{ }\mu\text{mol m}^{-2}\text{ s}^{-1}$.

In a randomized block design, the experiment included 18 treatments derived from combinations of three concentrations of CaCO_3 (0, 2,000, and 10,000 mg kg soil⁻¹), three concentrations of P_2O_5 (0, 250, and 500 mg kg soil⁻¹), and two concentrations of KNO_3 (0 and 500 mg kg soil⁻¹). We conducted nine replications (blocks) per treatment. The concentrations of P_2O_5 were determined based on vegetated soil value on Nakodo-jima (mean value; 202 mg kg soil⁻¹, Hiradate et al.¹⁹). The concentration of KNO_3 was approximately equivalent to 80 kg N ha⁻¹, which falls within the standard fertilization range in cultivated areas in Japan⁵⁷.

We added powdered CaCO_3 , a 10,000 ppm solution of H_3PO_4 (as P_2O_5), and powdered KNO_3 to the air-dried soil and mixed them well in a polyethylene bag for each respective treatment. For the plant growth experiment, each pot contained air-dried soil equivalent to 40 g oven-dried soil. We mixed 162 soil samples (18 treatments \times 9 replicates per treatment) and filled polypropylene pots (50 cc) for each of the six study species. The pots were placed in the chamber using a randomized block design.

We sowed more than 1000 seeds from each species on a 50 \times 35 \times 8 cm plastic tray filled with vermiculite and stored in the chamber until germination. The tray was watered without sterilization using a spray bottle every 1–2 days, ensuring that the vermiculite did not dry out. We transplanted cotyledon-stage seedlings into the treatment pots filled with soil and nutrients. If a planted seedling died within 1 week of transplanting, we replaced it with a new transplant. Pots were watered every 1–2 days, providing sufficient water and minimizing limitations on plant growth.

Four weeks after transplanting, planted seedlings were divided into shoot and root portions and dried at 70 $^{\circ}\text{C}$ for 72 h. Shoot and root dry weights were measured separately. The laboratory experiment was conducted from October 2015 to November 2016 (Table 1).

Statistical analyses. All statistical analyses were performed using R ver. 4.1.2.⁵⁸. Generalized linear mixed models (GLMMs) were applied using the *glmer* package, wherein the response variable was the total dry weights

of plants, with a gamma distribution and a log link function. Each of the six species was analyzed separately. Seven factors (CaCO_3 , P_2O_5 , and KNO_3 concentrations and four interactions among them, see Table 2) were used as explanatory variables. Blocks ($n=9$) were treated as a random effect. After the GLMMs, all possible pairwise combinations of treatments were investigated, again using treatments as the explanatory variables and blocks as a random effect. The resulting p -values were adjusted using Holm's method⁵⁹.

Research involving plants. We obtained appropriate permission to collect the seeds of plants used in this study from the Ministry of Environment in Japan and the Department of National Forests in the Ogasawara Islands, Tokyo Metropolitan Government. We collected the seeds of plant species in compliance with relevant guidelines and legislation of the Ministry of Environment, Japan.

Data availability

All data generated or analyzed in this article are included in supplementary information files as follows: (1) Hata_et_al_supplementary_fig_table_r3_20230721 (PDF file)*. (2) Hata_et_al_supplementary_dataset_fig_2_r1_20230309 (xlsx file). (3) Hata_et_al_supplementary_dataset_fig_3_tabel_2_r1_20230309 (xlsx file). (4) Hata_et_al_supplementary_dataset_fig_s2_r1_20230309 (xlsx file).

Received: 27 May 2022; Accepted: 17 July 2023

Published online: 27 July 2023

References

- Mori, A. S. Ecosystem management based on natural disturbances: Hierarchical context and non-equilibrium paradigm. *J. Appl. Ecol.* **48**, 280–292 (2011).
- Whisenant, S. *Repairing Damaged Wildlands: A Process-Oriented, Landscape-Scale Approach* (Cambridge University Press, 1999). <https://doi.org/10.1017/CBO9780511612565>.
- Loope, L. L., Hamman, O. & Stone, C. P. Comparative conservation biology of oceanic archipelagoes. *Bioscience* **38**, 272–282 (1988).
- Courchamp, F., Chapuis, J. L. & Pascal, M. Mammal invaders on islands: Impact, control and control impact. *Biol. Rev.* **78**, 347–383 (2003).
- Leopold, C. R. & Hess, S. C. Conversion of native terrestrial ecosystems in Hawai'i to novel grazing systems: A review. *Biol. Invasions* **19**, 161–177 (2017).
- Coblentz, B. E. The effects of feral goats (*Capra hircus*) on island ecosystems. *Biol. Conserv.* **13**, 279–286 (1978).
- Gizicki, Z. S., Tamez, V., Galanopoulou, A. P., Avramidis, P. & Foufopoulos, J. Long-term effects of feral goats (*Capra hircus*) on Mediterranean island communities: Results from whole island manipulations. *Biol. Invas.* **20**, 1537–1552 (2018).
- Dunkell, D. O., Bruland, G. L., Evensen, C. I. & Litton, C. M. Runoff, sediment transport, and effects of feral pig (*Sus scrofa*) exclusion in a forested Hawaiian watershed. *Pac. Sci.* **65**, 175–194 (2011).
- Long, M. S. *et al.* Impact of nonnative feral pig removal on soil structure and nutrient availability in Hawaiian tropical montane wet forests. *Biol. Invas.* **19**, 749–763 (2017).
- Yong-Zhong, S., Yu-Lin, L., Jian-Yuan, C. & Wen-Zhi, Z. Influences of continuous grazing and livestock exclusion on soil properties in a degraded sandy grassland, Inner Mongolia, northern China. *Catena* **59**, 267–278 (2005).
- Cole, R. J., Litton, C. M., Koontz, M. J. & Loh, R. K. Vegetation recovery 16 years after feral pig removal from a wet Hawaiian forest. *Biotropica* **44**, 463–471 (2012).
- Strauch, A. M., Bruland, G. L., MacKenzie, R. A. & Giardina, C. P. Soil and hydrological responses to wild pig (*Sus scrofa*) exclusion from native and strawberry guava (*Psidium cattleianum*)-invaded tropical montane wet forests. *Geoderma* **279**, 53–60 (2016).
- Ibañez-Alvarez, M. *et al.* Ungulates alter plant cover without consistent effect on soil ecosystem functioning. *Agr. Ecosyst. Environ.* **326**, 107796 (2022).
- Shimizu, Y. Vegetation of Mukojima Island Group in the Bonin (Ogasawara) Islands with reference to the ecology of *Ardisia* dominant forest and the influence of feral goats. *Komazawa Geogr.* **29**, 9–58 (1993) (in Japanese).
- Sato, N. Recent control of invasive alien animals in the Bonin Islands. *Glob. Environ. Res.* **23**, 9–19 (2019).
- Hata, K., Kohri, M., Morita, S., Hiradate, S. & Kachi, N. Fine-scale distribution of aboveground biomass of herbaceous vegetation and soil nutrients on an oceanic island after goat eradication are correlated with grazing damage and seabird nesting. *Pac. Conserv. Biol.* **20**, 344–353 (2014).
- Kremen, C. Managing ecosystem services: What do we need to know about their ecology?. *Ecol. Lett.* **8**, 468–479 (2005).
- Hata, K., Osawa, T., Hiradate, S. & Kachi, N. Soil erosion alters soil chemical properties and limits grassland plant establishment on an oceanic island even after goat eradication. *Restor. Ecol.* **27**, 333–342 (2019).
- Hiradate, S. *et al.* Effects of soil erosion and seabird activities on chemical properties of surface soils on an oceanic island in Ogasawara Islands Japan. *Catena* **133**, 495–502 (2015).
- Hata, K., Kohri, M., Morita, S., Hiradate, S. & Kachi, N. Complex interrelationships among aboveground biomass, soil chemical properties, and events caused by feral goats and their eradication in a grassland ecosystem of an island. *Ecosystems* **17**, 1082–1094 (2014).
- Bardgett, R. *The Biology of Soil: A Community and Ecosystem Approach* 256 (Oxford University Press, 2005).
- Gerdol, R., Marchesini, R. & Iacumin, P. Bedrock geology interacts with altitude in affecting leaf growth and foliar nutrient status of mountain vascular plants. *J. Plant Ecol.* **10**, 839–850 (2017).
- Barrow, N. J. The effects of pH on phosphate uptake from the soil. *Plant Soil* **410**, 401–410 (2017).
- Penn, C. J. & Camberato, J. J. A critical review on soil chemical processes that control how soil pH affects phosphorus availability to plants. *Agriculture* **9**, 120 (2019).
- Vitousek, P. M., Porder, S., Houlton, B. Z. & Chadwick, O. A. Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen–phosphorus interactions. *Ecol. Appl.* **20**, 5–15 (2010).
- Vitousek, P. M. Oceanic islands as model systems for ecological studies. *J. Biogeogr.* **29**, 573–582 (2002).
- Wardle, D. A. Islands as model systems for understanding how species affect ecosystem properties. *J. Biogeogr.* **29**, 583–591 (2002).
- Weerasinghe, U. R., Akiko, S., Palitha, J. & Seiki, T. The role of the soil seed bank in vegetation recovery on an oceanic island severely damaged by introduced goats. *Appl. Veg. Sci.* **11**, 355–364 (2008).
- Bellingham, P. J., Wiser, S. K., Wright, A. E., Cameron, E. K. & Forester, L. J. Disperser communities and legacies of goat grazing determine forest succession on the remote Three Kings Islands New Zealand. *Biol. Conserv.* **143**, 926–938 (2010).
- Plenchette, C., Fortin, J. A. & Furlan, V. Growth responses of several plant species to mycorrhizae in a soil of moderate P-fertility: I. Mycorrhizal dependency under field conditions. *Plant Soil* **70**, 199–209 (1983).

31. Plenchette, C., Fortin, J. A. & Furlan, V. Growth responses of several plant species to mycorrhizae in a soil of moderate P-fertility: II. Soil fumigation induced stunting of plants corrected by reintroduction of the wild endomycorrhizal flora. *Plant Soil* **70**, 211–217 (1983).
32. Abdolzadeh, A., Wang, X., Veneklaas, E. J. & Lambers, H. Effects of phosphorus supply on growth, phosphate concentration and cluster-root formation in three *Lupinus* species. *Ann. Bot.* **105**, 365–374 (2009).
33. Ma, Q., Zhang, F., Rengel, Z. & Shen, J. Localized application of NH_4^+ -N plus P at the seedling and later growth stages enhances nutrient uptake and maize yield by inducing lateral root proliferation. *Plant Soil* **372**, 65–80 (2013).
34. Crews, T. E., Farrington, H. & Vitousek, P. M. Changes in asymbiotic, heterotrophic nitrogen fixation on leaf litter of *Metrosideros polymorpha* with long-term ecosystem development in Hawaii. *Ecosystems* **3**, 386–395 (2000).
35. Hiradate, S., Ma, J. F. & Matsumoto, H. Strategies of plants to adapt to mineral stresses in problem soils. *Adv. Agron.* **96**, 65–132 (2007).
36. Brady, N. C., Weil, R. R. & Weil, R. R. *The Nature and Properties of Soils* 662–710 (Prentice Hall, 2008).
37. Wheeler, D. M., Edmeades, D. C., Christie, R. A. & Gardner, R. Effect of aluminum on the growth of 34 plant species: A summary of results obtained in low ionic strength solution culture. *Plant Soil* **146**, 61–66 (1992).
38. Osaki, M., Watanabe, T. & Tadano, T. Beneficial effect of aluminum on growth of plants adapted to low pH soils. *Soil Sci. Plant Nutr.* **433**, 551–563 (1997).
39. Kochian, L. V., Hoekenga, O. A. & Piñeros, M. A. How do crop plants tolerate acid soils? Mechanisms of aluminum tolerance and phosphorous efficiency. *Annu. Rev. Plant Biol.* **55**, 459–493 (2004).
40. Hobbs, R. J., Higgs, E. & Harris, J. A. Novel ecosystems: Implications for conservation and restoration. *Tre. Ecol. Evol.* **24**, 599–605 (2009).
41. Hallett, L. M. *et al.* Do we practice what we preach? Goal setting for ecological restoration. *Restor. Ecol.* **21**, 312–319 (2013).
42. Zhang, H. *et al.* Roles of biochar in improving phosphorus availability in soils: A phosphate adsorbent and a source of available phosphorus. *Geoderma* **276**, 1–6 (2016).
43. Solaiman, Z. M., Abbott, L. K. & Murphy, D. V. Biochar phosphorus concentration dictates mycorrhizal colonisation, plant growth and soil phosphorus cycling. *Sci. Rep.* **9**, 5062 (2019).
44. Anderson, W. B. & Polis, G. A. Nutrient fluxes from water to land: seabirds affect plant nutrient status on Gulf of California islands. *Oecologia* **118**, 324–332 (1999).
45. Fukami, T. *et al.* Above- and below-ground impacts of introduced predators in seabird-dominated island ecosystems. *Ecol. Lett.* **9**, 1299–1307 (2006).
46. Morita, S. *et al.* Unusually high levels of bio-available phosphate in the soils of Ogasawara Islands, Japan: Putative influence of seabirds. *Geoderma* **160**, 155–164 (2010).
47. Towns, D. R. *et al.* Impacts of introduced predators on seabirds. In *Seabird Islands: Ecology, Invasion, and Restoration* (eds Mulder, C. P. H. *et al.*) 56–90 (Oxford University Press, 2011). <https://doi.org/10.1093/acprof:osobl/9780199735693.003.0003>.
48. Jones, H. P. Seabird islands take mere decades to recover following rat eradication. *Ecol. Appl.* **20**, 2075–2080 (2010).
49. Brodier, S. *et al.* Responses of seabirds to the rabbit eradication on Ile Verte, sub-Antarctic Kerguelen Archipelago. *Anim. Conserv.* **14**, 459–465 (2011).
50. Suzuki, H., Horikoshi, K., Sasaki, T. & Kawakami, K. Rapid increase in seabird breeding population after feral goat eradication on Mukojima, Ogasawara Islands Japan. *Jpn. J. Ornithol.* **68**, 273–287 (2019).
51. Mulder, C. P. H. *et al.* Impacts of Seabirds on plant and soil properties. In *Seabird Islands: Ecology, Invasion, and Restoration* (eds Mulder, C. P. H. *et al.*) 135–176 (Oxford University Press, 2011). <https://doi.org/10.1093/acprof:osobl/9780199735693.003.0005>.
52. Kawakami, K. & Horikoshi, K. Recovery or change Differences between in seabird fauna in island ecosystems before alien mammal disturbance and after alien mammal eradication. *Restor. Ecol.* **30**, e13579 (2022).
53. Hallett, L. M. *et al.* Towards a conceptual framework for novel ecosystems. In *Novel Ecosystems: Intervening in the New Ecological World Order* (eds Hobbs, R. J. *et al.*) 16–28 (Wiley-Blackwell, 2013).
54. Japan Wildlife Research Center. *Report on the Urgent Research About Damage of Feral Goats on Plants and Animals in the Ogasawara Islands* (Japan Wildlife Research Center, 1992) (In Japanese).
55. Hata, K., Suzuki, J. I. & Kachi, N. Vegetation changes between 1978, 1991 and 2003 in the Nakoudojima island that had been disturbed by feral goats. In *Restoring the Oceanic Island Ecosystem* (eds Kawakami, K. & Okochi, I.) 85–91 (Springer, 2010).
56. Osawa, T., Hata, K. & Kachi, N. Eradication of feral goats enhances expansion of the invasive shrub *Leucaena leucocephala* on Nakoudo-jima, an oceanic island. *Weed Res.* **56**, 168–178 (2016).
57. Mishima, S. I. Quantitative evaluation of environmental risk associated with nitrogen flow in agricultural production and mitigation plan for 2 typical prefectures in Japan. *Soil Sci. Plant Nutr.* **47**, 511–518 (2001).
58. R Development Core Team. in *R: a language and environment for statistical computing*. (R Foundation for Statistical Computing, 2022). Available from <http://www.r-project.org/index.html>.
59. Holm, S. A simple sequentially rejective multiple test procedure. *Scandinavian J. Stat.* **6**, 65–70 (1979).

Acknowledgements

We express our gratitude to the Ministry of Environment and the Department of National Forests in the Ogasawara Islands for granting us permission to conduct this study. We appreciate Drs. Kazuto Kawakami, Katsuhiko Yoshida, and Takeshi Osawa for providing insightful comments on the discussion. Dr. Takeshi Osawa, Dr. Yuki Murakami, Mr. Yamato Unno, and Ms. Ai Takaoka assisted with soil sampling. This study was conducted using the Tokyo Metropolitan University Ogasawara Field Research Station on Chichi-jima Island. We also thank two anonymous reviewers and the Managing Editor for their valuable comments, which greatly improved this manuscript. This work was partially supported by Japan Society for the Promotion of Science KAKENHI Grants (Nos. 25241025, 16H01794 and 17K00648).

Author contributions

K.H., S.H., and N.K. conceptualized and designed the study; K.H. and S.H. collected soil for the experiments, while S.H. analyzed the soil chemistry, K.H. carried out laboratory experiments and analyzed the data. Finally, K.H., S.H., and N.K. collaborated on writing the paper.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1038/s41598-023-38934-9>.

Correspondence and requests for materials should be addressed to K.H.

Reprints and permissions information is available at www.nature.com/reprints.

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.



Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

© The Author(s) 2023