



Drivers of growth and establishment of the invasive plant *Rumex acetosella* within Andean fallow systems

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ABSTRACT

Intensification of crop rotations and associated agricultural practices are reducing the capacity of traditional fallows to restore soil fertility and provide forage in Andean cropping systems. While the implementation of improved fallows offers great promise to enhance forage provision and maintain soil productivity, effects of these practices on the establishment of problematic weeds, including non-native plant species, remain poorly understood. To address this knowledge gap, we studied: i) how biotic and abiotic environmental factors influence the establishment and productivity of weeds in traditional fallows; and ii) to what extent improved fallows can help control weedy vegetation in smallholder rotations of the high Andes. Specifically, in this research, we focused on the invasive plant species *Rumex acetosella* L., which is a common concern of farmers throughout the central Peruvian Andes. We leveraged a multi-site, participatory research trial established in 2017 across eight communities in the region to understand the main drivers of *R. acetosella* presence and productivity. We used a total of 82 sites, each with paired treatments of traditional fallow (control with natural revegetation) and improved fallow (seeded with *Vicia sativa* L. and *Avena sativa* L.). Prior to treatment establishment we measured soil texture, pH, soil organic matter content as well as exchangeable macro-nutrients. Vegetation data was recorded in each treatment and divided into four categories: 1) *A. sativa*, 2) *V. sativa*, 3) *R. acetosella*, and 4) other weeds, and weighed to determine the relative biomass contribution of each. From these data, we calculated an index for *R. acetosella* pressure, weed pressure, and forage productivity. Our findings indicate that improved fallows greatly suppress weedy vegetation relative to unmanaged controls, including the invasive *R. acetosella*. Multivariate analyses suggested that *R. acetosella* abundance was associated with the presence of other non-planted weeds and predictors of soil fertility. The mean *R. acetosella* index in improved fallows was significantly lower compared to traditional fallows. We found *R. acetosella* biomass to be greater at lower productivity sites, i.e., those at higher elevations with cooler climates and sites with less fertile soils. Our findings indicate that if the fallow portion of a rotation is kept productive via adequate soil fertility inputs, the biomass of weeds, including the alien *R. acetosella*, is dramatically reduced.

1. Introduction

Around the world, smallholder farmers have used vegetated fallows as a traditional soil management strategy to restore fertility after multiple years of cropping (Sanchez, 1999; Zerbe, 2022). In the Andes,

intensification of crop rotations and other agricultural practices are reducing the implementation and duration of traditional fallows, a land-use system traditionally based on the natural establishment of spontaneous vegetation mainly deriving from native species present in the soil seed bank (Vanek et al., 2020). Traditional fallows historically

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represent one of the main soil management practices to restore soil fertility in the region, while also providing key forage resources in these mixed crop-livestock systems (Pestalozzi, 2000; Fonte et al., 2012). This fallow phase of the rotation typically lasts from 1 to 15 years, depending on elevation and land-use intensity. Improved forage-based fallows, in which more productive annual and perennial forages are seeded into this fallow phase, offer great potential for enhancing forage provision while suppressing weeds within multifunctional Andean agroecosystems (Rolando et al., 2017; Vanek et al., 2020). Improved fallows often include well-adapted, fast-growing species to rapidly cover soils and protect them against erosion (Sarmiento, 2000). Given that improved fallows are often implemented for shorter durations than traditional fallows, legumes are often included to support N accumulation for building soil organic matter (SOM) and overall soil fertility (Pestalozzi, 2000; Sarmiento and Bottner, 2002; Fornara and Tilman, 2008).

Plant diversity in traditional Andean fallows is typically high (de Valença et al., 2017). This diversity important to ensure the provision of multiple ecosystem functions and services (Manning et al., 2018; Meza et al., 2022). Preserving traditional practices is crucial in maintaining biodiversity (Bonari et al., 2017). However, invasive plants are threatening the long-term viability of these systems (Pauchard et al., 2009). It is expected that climate change will facilitate a great shift in vegetation, weed pressure, and distribution at higher elevations due to changes in temperature and humidity as well as greater frequency of extreme weather events (IPCC, 2007). For instance, persistent changes in climatic conditions could accelerate the life cycle of weeds by increasing the weeds' seed dispersal or vegetative propagation, which opens niches for weeds to colonise new terrains (Singh et al., 2011). Furthermore, with warming, the potential habitats of many plant species, including weeds and alien species, are moving to higher elevations that would have previously been too cold (Gottfried et al., 2012).

Across much of the tropical Andes, the herb *Rumex acetosella* L. is a common invasive alien species that is causing problems for farmers throughout the region, especially at higher elevations (Sarmiento et al., 2003; Vanek et al., 2020). Analyses of the vertical stratification of fossil pollen revealed this species was first introduced into the Andean landscape with the settlement of European colonists (Huber and Markgraf, 2003). This species is a vigorous perennial dioecious herb, wind-pollinated, that occupies a wide variety of habitats, but being especially common to grasslands, pastures, and disturbed lands (Leuschner and Ellenberg, 2017). Farmers often note that *R. acetosella* inhibits the growth of other less competitive native species and can dominate soil cover in the first year following disturbance, hence reducing the overall plant diversity within traditional fallows. While *R. acetosella* is sometimes grazed by livestock, it has little forage value, and is thus highly undesirable for farmers. Additionally, *R. acetosella* is difficult to control as it reproduces via clonal propagation and seed dispersal (Huber and Markgraf, 2003), which strongly complicates field preparations and weeding activities of smallholder farmers (Bentley et al., 2005).

Biological invasions are one of the most important drivers of biodiversity loss and ecosystem degradation worldwide (Seebens et al., 2017; Lazzaro et al., 2020). The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) ranked alien species fifth amongst direct drivers of biodiversity loss, after changes in land use, direct exploitation of organisms, climate change, and pollution (Bronzizio et al., 2019). Alien species are those whose presence in an ecosystem is attributed to anthropogenic impact (Richardson et al., 2000; Pyšek et al., 2004; Essl et al., 2018). The establishment and spread of invasive species can impact multiple ecosystem properties such as community composition and biotic interactions (Vilà and Hulme, 2017). Furthermore, alien species can impose costly management interventions to reduce their spread, hence impacting socio-economic aspects of an ecosystem (Bacher et al., 2018). The magnitude and impacts of biological invasions are shaped by both direct and indirect drivers (Pyšek et al., 2020). Direct drivers of biological invasions are both natural and

anthropogenic and affect species physiology, behaviour, and demography. On the other hand, indirect drivers are processes that influence the magnitude, direction, and rate of direct drivers (e.g. economic, governance, technological, and cultural processes; Pyšek et al., 2012). The growing number of alien species becoming established around the world highlights an urgent need for prevention, early detection, and to understand direct and indirect drivers of these organisms to enhance their control (Seebens et al., 2017; Pyšek et al., 2020).

While a number of studies have examined how global warming and soil degradation will influence the distribution of weeds, including invasive plants, and associated management challenges, very little is known about the Andean highlands. To help address this research gap, we focused on *R. acetosella* during the fallow phase of crop rotations and answer the following two research questions: i) How do direct environmental drivers (soil, climatic, and biotic) influence the establishment and productivity of *R. acetosella* and weedy vegetation?; ii) To what extent can improved fallows control weedy vegetation in rotational smallholder systems in the high Andes? Specifically, we hypothesized that *R. acetosella* (and other weeds) is more abundant in degraded soils and at higher elevations. Such factors might result influencing *R. acetosella* success. We anticipated that improved fallows could help control weeds early in the fallow period by outcompeting *R. acetosella* and other weeds. Results of this study will help the scientific community and local farmers to identify the niche in which *R. acetosella* develops in the Andean region, while also providing insight for controlling undesirable plant species for farmers in the area, via the practice of improved fallows.

2. Material and methods

2.1. Site description

This study is part of a set of on-farm participatory field trials established in October and November of 2017 within eight communities across three different regions of the central Peruvian Andes (Fig. 1). The communities were Cruzccasa, Jacaspampa, and Urubamba in the region of Ayacucho (13.17°S, 74.22°W), Pacchomolinos, Pomavilca, and Santa Cruz de Paccho in the region of Huancavelica (12.79°S, 74.98°W), and Tiso and Huahuanca in the Junín region (11.16°S, 75.99°W; Table 1). The landscapes in all the regions considered are characterised by a mosaic of land-uses (pasture, cropping lands, scattered trees, hedgerows, and patches of forests) and a mountainous topography with elevations ranging from 3300 to 4300 m a.s.l. Andean communities are typically comprised of two distinct production zones with different cropping systems. Within the lower-middle elevation zone (3300 – 3800 m a.s.l.) it is common to have 3–5 years of cropping (e.g., potatoes, maize, faba beans, barley) followed by an unseeded fallow phase of 2–3 years. At higher elevations (>3800 m a.s.l.) longer rotations are more common, with one or two cropping seasons (typically with potatoes) followed by 7–15 years of unseeded, traditional fallow (Pestalozzi, 2000; Vanek et al., 2020). Livestock, such as sheep, llamas, alpacas, horses, and cows are important in most communities and provide a source of food, manure, and traction. Livestock typically graze on traditional fallows within the communities and are supplemented with forage crops to enrich their basal grazing diet. Additional description of land uses and socioeconomic aspects of the communities can be found in Caulfield et al. (2021).

Soils in the communities are mainly derived from non-calcareous sedimentary rocks (ORSTOM, 1978) and are largely acidic to very acidic (pH < 5.5). Soil organic matter generally increases with elevation, ranging from 1% to 9% organic carbon. While climates are broadly similar, the communities in Ayacucho have a dry-winter subtropical highland climate, while those in Junín and Huancavelica are somewhat higher in elevation and have a tundra climate according to the Köppen–Geiger climate classification system (Peel et al., 2007). Precipitation in all regions occurs almost exclusively from October to April,

with approximately 900 mm yr^{-1} (WorldClim, 2022). Mean annual temperature varies slightly by region (Junin 14.4°C , Huancavelica 15.9°C , and Ayacucho 19.8°C). Precipitation and temperature between the two elevation zones differ, being slightly colder and rainier at higher elevation zones across the regions.

2.2. Species of interest

Rumex acetosella L. was domesticated as a crop in Neolithic European settlements, hence its origin is Europe (Euro+Med, 2006-2023). *R. acetosella* is a perennial species of the Polygonaceae family and can grow about 20 cm tall. In Europe, *R. acetosella* is naturally present in nutrient poor grasslands (Leuschner and Ellenberg, 2017). Within Andean ecosystems it is commonly perceived as a problematic weed by smallholder farmers as it tends to invade fallows (Figs. S1 and S2). In the Andes, extensive logging activities and fires of the colonists might have contributed to the rapid expansion of *R. acetosella* since it has strong affinity for disturbed soils and is only moderately shade tolerant (Lamb et al., 2003). *R. acetosella* can establish itself rapidly via clonal propagation and by seed dispersal. *R. acetosella* produces seeds also after fire disturbance (Huber and Markgraf, 2003). The expansion of *R. acetosella* into remote areas, such as the Andes, could have been promoted by grazing of ruminants, owned by the ancestors of the original inhabitants of these areas (Huber and Markgraf, 2003).

2.3. Multi-site experimental design and management

The research trial utilized here was designed using a participatory planning process in 2017 that relied on previous trials in Junin and Huancavelica (Vanek et al., 2020), as well as a farmer learning process to examine the importance of combining different plant groups (annual vs. perennial, legumes vs. grasses) in the design of promising forage mixes that contribute to soil health (Meza et al., 2022). A group of participating farmers in each community selected the three-five forage treatments (mixtures of different plant groups) in each community, thus these treatments varied between communities. At the same time, consistent control treatments were maintained across all trials/communities – these were: traditional unmanaged fallow (TF) and seeding of *Avena sativa* L. (oat) and *Vicia sativa* L. (vetch) for an improved fallow (IF). In this study, we focused only on TF and IF treatments because of their standardized implementation across all fields. In total, 82 trials (out of 108 originally established) were selected for analysis, as some fields experienced issues with trial management or data collection. For all trials, five to seven treatments, including TF and IF, were randomly allocated to contiguous experimental plots ($5 \times 5 \text{ m}$) on each farm. The fields were selected based on their planned entry into the fallow phase in 2017, following 2–5 years of continuous crop production (depending on production zone). While soils on most farms were not disturbed since harvest of the most recent crop (typically in May 2017), several farmers (5) opted for light soil preparation using local tillage methods (i.e., Andean foot plow). However, there were no

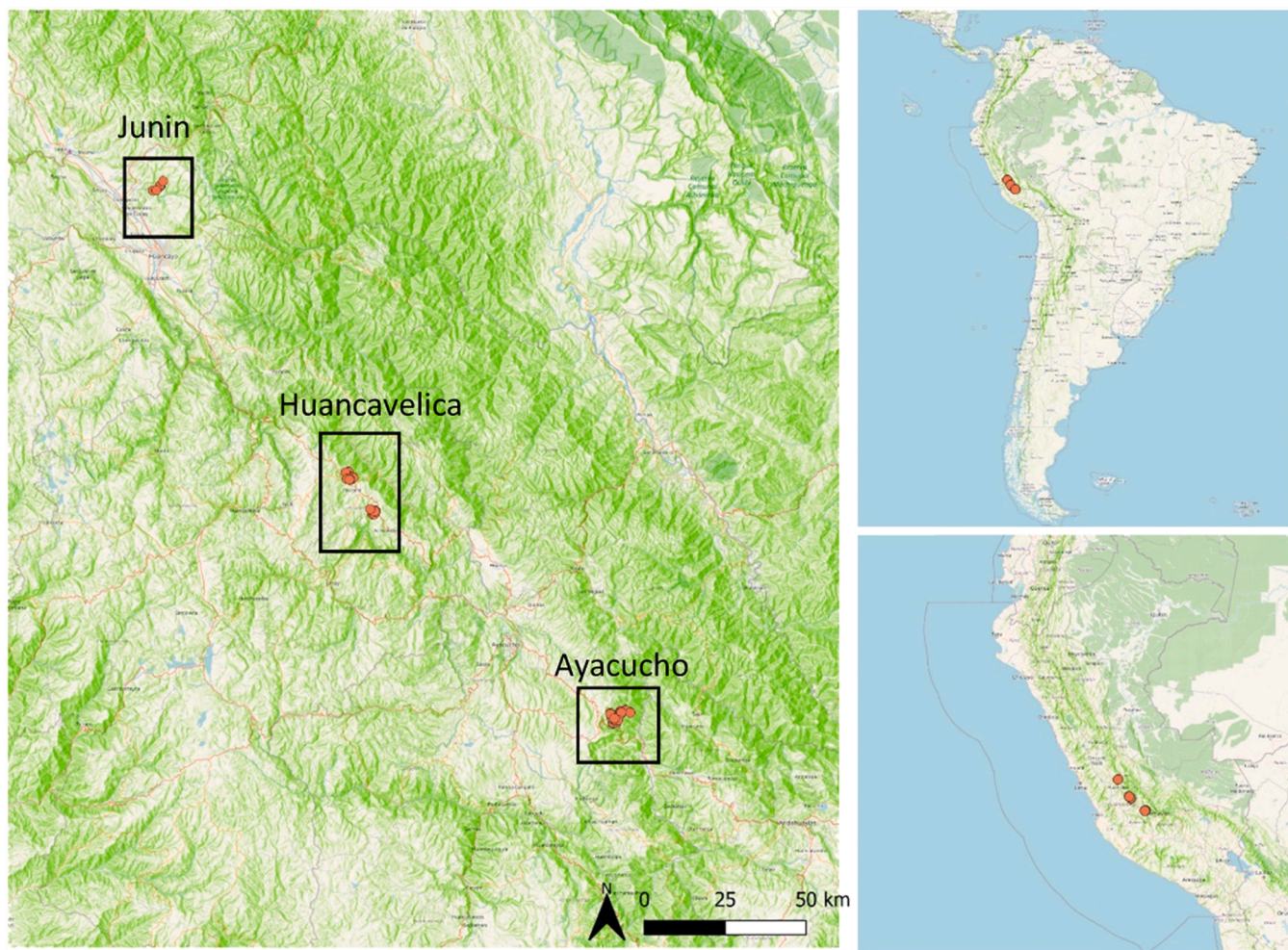


Fig. 1. Map showing the location of fields with participatory trials in three regions of central Peru. Trials were established in September 2017 with both traditional fallow and improved fallow plots in the central Peruvian Andes ($n = 82$).

obvious impacts of this soil preparation on biomass production or plant establishment and these fields were included in the 82 selected for analyses. Across all sites, IF was seeded at a rate of 70 kg ha⁻¹. *A. sativa* and 30 kg ha⁻¹ *V. sativa* in late October or November 2017 by broadcasting the seed and light raking. No soil amendments were applied to any of the fields, following typical management of fallows in the region and no grazing occurred prior to biomass harvest in April 2018. Most fields relied on natural precipitation, except for ten fields that were occasionally furrow irrigation, using a traditional canal system.

2.4. Vegetation, soil, and climatic data

Vegetation data was recorded in each treatment in April 2018, using two quadrats (0.80 × 0.80 m) per plot. The quadrats were placed at the top left and bottom right corner of each plot, at least 1 m from the border to avoid the edge effect. Percentage cover of different non-seeded fallow components (*A. sativa*, *V. sativa*, *R. acetosella*, and other weeds) and seeded components were estimated visually. All plants within each quadrat were then cut to a height of 5 cm, separated into planted grasses, planted legumes, *R. acetosella*, and other weeds and the fresh biomass of each component recorded. Biomass of other species were further separated into grasses and non-grasses species. A subsample for each component (~250 g) was weighed and then dried at 60 °C to calculate dry biomass of all vegetation components. Individual components were then summed to calculate the mean dry biomass yield (g m⁻²) for each treatment. Finally, a *R. acetosella* index was calculated by dividing the *R. acetosella* biomass by the total biomass in each plot. Similarly, weed pressure was estimated for the IF treatment by dividing the other (non-planted) species by the total biomass (seeded + unseeded species).

Soils were sampled in September 2017 in all farmer fields, immediately prior to treatment establishment, to understand the influence of initial soil properties on the vegetation growth and establishment. At each farm, 10–15 soil sub-samples (0–20 cm depth) were collected from each field using a 2.5 cm diameter soil corer, and one composite sample per field was sent for analysis at the soil lab at La Molina University, in Lima. Soils were analysed for soil texture, pH (1:1 water:soil), soil organic matter (SOM; Walkley and Black, 1934), permanganate-oxidizable C (POXC; Weil et al., 2003), available phosphorus (P; Olsen extraction); exchangeable potassium (K), calcium (Ca) and magnesium (Mg; ammonium acetate extraction) following methods outlined by Estefan et al. (2013). Climate data for each field, including mean (T_{mean}), maximum (T_{max}) and minimum (T_{min}) annual temperature (derived from monthly averages for each category), total annual precipitation (Precip) and seasonality-related indicators (Precip_{seas}; Temp_{seas}), were derived from WorldClim at 1 km resolution (Fick and Hijmans, 2017). Topographic data, including elevation (m) and slope (°) were obtained at each trial site using a GPS to measure elevation and a clinometer to measure slope.

2.5. Statistical analysis

For the purpose of the analysis, we grouped plots with TF and IF based on the presence of *R. acetosella* in the arable field sites: i) *R. acetosella* present in plots (RP); ii) *R. acetosella* not present at site (RNP); iii) *R. acetosella* potentially suppressed (RPS). A plot was considered RPS if *R. acetosella* was present at the site (i.e., observed in one of the other experimental plots not considered in our analysis), but not in the two treatment plots considered for this study. The three variables *R. acetosella* index, weed pressure and forage production (i.e., *A. sativa* + *V. sativa* biomass) were considered separately for the control plots (TF; n = 82) and *A. sativa* - *V. sativa* plots (IF; n = 82), except when testing for differences between treatments. Response variables were log transformed to meet assumptions of homoscedasticity and normality. Normality was tested using a combination of the Anderson-Darling normality test and residual by fit plots were checked for homogeneity of variance.

A one-way ANOVA was performed to compare *R. acetosella* index in the TF vs. IF. Other one-way ANOVAs with Tukey tests were carried out to understand how *R. acetosella* establishment is influenced by the different biotic and abiotic environmental response variables in the TF plots. In this case, we compared environmental variables between different categories of *R. acetosella* presence (RP, RPS, and RNP). Simple linear regression was used to investigate the influence of the different individual environmental predictors on weed pressure and forage production within the IF plots.

Using a variation partitioning approach (Borcard et al., 1992; Legendre, 2008), we separated the variance explained by the environment into three distinct sets of predictors (soil, biotic, and climate). Prior to the variation partitioning analysis, we minimized multicollinearity by performing a Principal Component Analysis (PCA) separately for each set of predictors, extracting the first axis of each PCA (PC1 site scores) to use as an explanatory variable in subsequent analyses, for a total of three PCs (PC1 soil, PC2 biotic, PC3 climate). Additionally, all environmental properties together with the *R. acetosella* index, were included in a PCA to relate *R. acetosella* to different environmental predictors. This PCA was conducted with a sub-set of the data from the TF plots, including only the plots with *R. acetosella* present (RP; n = 41). We focused on RP plots to understand the effects of biotic and abiotic environmental features on *R. acetosella* growth. PC1, PC2, and PC3 were plotted as explanatory variables against the *R. acetosella* index to further study the interactions between the variables. Each principal component (PC) was then interpreted according to the magnitude of their eigenvalues.

Data input for the variation partitioning was derived from the TF plots where *R. acetosella* was present (n = 41) and IF plots where weed pressure and forage production were estimated (n = 82). The outputs obtained allowed us to distinguish: i) the portion of total variation in the *R. acetosella* index; ii) the portion of total variance in the weed pressure index; and iii) the forage production as a dependent variable. The variance was partitioned into: a) pure effect of soil; b) pure effect of

Table 1

Site information for 82 experimental research sites (each with traditional and improved fallow plots) across three regions within the central Peruvian Andes.

Community	Cruzccasca	Jacaspampa	Urubamba	Paccho- molinos	Pomavilca	Santa Cruz de Paccho	Tiso	Huahuanca
Region	Ayacucho	Ayacucho	Ayacucho	Huancavelica	Huancavelica	Huancavelica	Junín	Junín
District	Ocros	Ocros	Ocros	Acobamba	Acobamba	Paucara	San Pedro de Saños	Ingenio
Location	13°24'S 73°24'W	13°24'S 73°24'W	13°24'S 73°24'W	12°51'S 74°34'W	12°51'S 74°34'W	12°43'S 74°40'W	11°57'S 75°15'W	11°53'S 75°15'W
Elevation (m a.s.l.)	3360–3545	3372–3677	3396–3562	3864–4056	3704–3890	4018–4230	3965–4059	3396–3562
Annual temperature (°C)	11.8	11.1	11.9	7.8	8.8	6.8	6.6	10.9
Precipitation (mm y ⁻¹)	901	904	909	865	866	863	867	846
Slope (°)	0–40	15–45	8–40	4–25	6–25	8–20	2–24	7–14
Soil texture								
Sand (%)	34–62	30–60	24–62	36–60	36–62	32–62	36–60	32–42
Silt (%)	16–32	24–40	24–44	30–36	20–32	26–40	24–46	34–38
Clay (%)	22–38	12–40	14–36	10–32	14–34	8–28	14–24	24–30
Number of fields	12	17	9	8	14	7	13	2

climatic predictors; c) pure effect of other weeds present; (d + e + f) partial shared effects of two/three sets of predictors; (o) total shared effect of all variables considered along with unexplained variation. The partitioning was based on the adjusted R^2 statistic (Peres-Neto et al., 2006). We used 999 permutations were used to assess the significance of constraints. Variation partitioning was performed using the 'vegan' library using R version 3.4.4 (Development Core Team, 2022). All the other analyses were carried out using JMP pro 15.0 software (SAS Institute, 2021).

3. Results

3.1. Vegetation and forage productivity in traditional and improved Andean fallows

Total mean biomass within the IF was 7300.5 kg ha⁻¹ vs. 2653.8 kg ha⁻¹ in the TF plots. Mean biomass of non-planted species was 578.6 kg ha⁻¹ in the IF plots, for an average weed index of 0.079. When examining the presence of *R. acetosella*, this species showed a significantly lower proportion of the total biomass in IF (0.03) compared to TF (0.24; $p < 0.001$; Fig. 2a and 2 b).

Rumex acetosella was present in 41 TF plots and had an average biomass of 895.2 kg ha⁻¹. In 29 plots, *R. acetosella* was absent (RNP), while in 12 fields *R. acetosella* was observed in an adjacent plot but did not occur in the TF treatment (RPS). The proportion of total biomass belonging to other non-planted species was significantly higher in TF plots where *R. acetosella* was classified as either RNP or RPS ($p < 0.001$; Table 2). Total biomass was generally higher in RPS plots vs. RP plots, but this difference was only marginally significant ($p = 0.060$, if $\alpha = 0.10$; Table 2). The weed index in the 82 IF plots significantly reduced ($p < 0.001$) with the increased presence of planted forage crops (Table 3). Forage productivity (i.e., combined biomass of *A. sativa* and *V. sativa*) within IF plots averaged 6721.9 kg ha⁻¹ across all sites.

3.2. Identifying driving factors of *Rumex acetosella* performance in an Andean landscape

One-way ANOVA comparing the different biotic and abiotic environmental features and *R. acetosella* categories (Table 2) indicated that climatic variables, such as mean annual temperature ($p = 0.025$), temperature and precipitation seasonality ($p = 0.045$; $p = 0.027$, respectively) and elevation ($p = 0.006$), were important drivers in *R. acetosella* occurrence within traditional Andean fallows. The main differences were found between RP and RNP, with RP plots generally being higher and cooler compared to RNP plots. Soil variables appeared to differ less between the *R. acetosella* categories, except for a marginally significant difference in P availability ($p = 0.090$, if $\alpha = 0.10$), where RP plots were generally lowest in available P and the RNP plots had the highest values (Table 2).

Biotic and abiotic environmental features (Tables 2 and 3) were also examined using PCA to understand which of them were most associated with the *R. acetosella* index (i.e., proportion of total plant biomass) within TF plots where *R. acetosella* occurred (RP; Fig. S3 and Tables S1 and S2). PC1 explained 42.6% of the variance and was mainly associated with climatic features such as elevation (-0.97 score), mean annual temperature (0.95 score), precipitation seasonality (0.95 score), precipitation (0.89 score), temperature seasonality (0.94 score). PC2 explained 19.1% of the variance and was mainly associated indicators of soil productivity such as the presence of other non-planted species (0.82), available soil P (0.74), K (0.38), SOM (0.38), and pH (0.38). Linear regression showed that both PC1 ($p = 0.024$, $R^2 = 0.13$) and PC2 ($p < 0.001$, $R^2 = 0.61$) were both negatively correlated with the *R. acetosella* index within TF (Fig. 3a and 3b), such that the proportion of *R. acetosella* tended to increase with elevation and cooler temperatures (associated with PC1) and decreased with soil fertility and overall biomass production (associated with PC2). Similar results were obtained

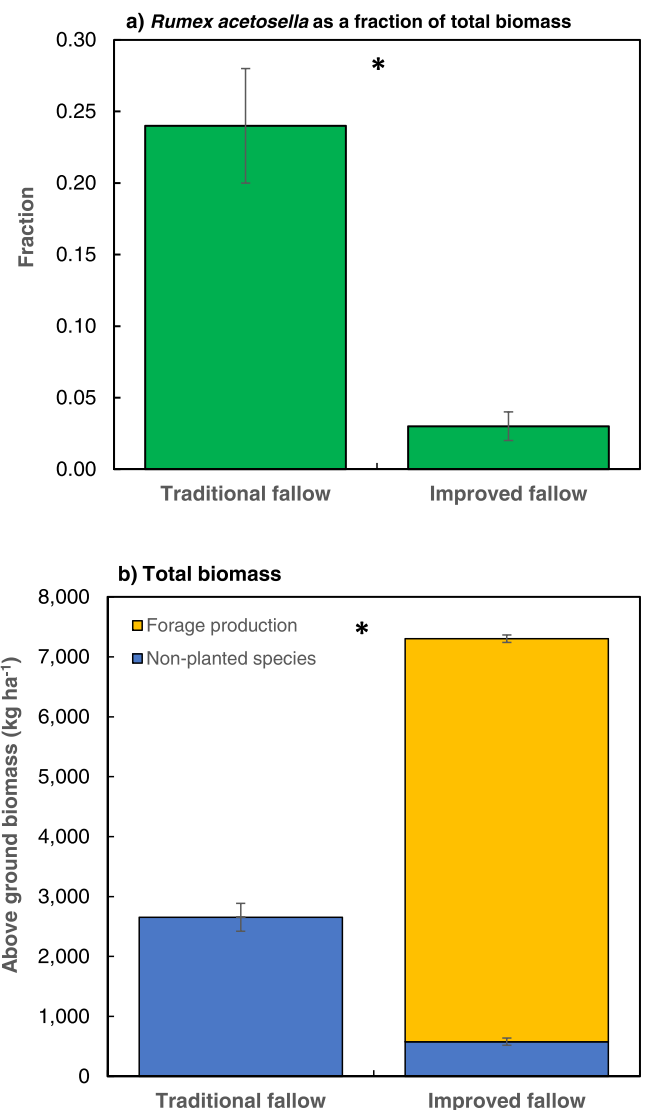


Fig. 2. Mean values for (a) *Rumex acetosella* index and (b) total biomass within traditional and improved fallow plots (separated by forage production and non-planted species) present across 82 sites in a participatory field trial in the central Peruvian Andes. The asterisk indicates a significant difference according to one-way ANOVA.

when we performed the PCA and included TF plots where *R. acetosella* was considered as suppressed, or potentially suppressed (RPS; $n = 53$ for RP + RPS plots).

Results of variation partitioning for the *R. acetosella* index showed that 'pure biotic' and 'pure soil' factors explained a significant degree of variance (10.1%, $p = 0.014$; 14.7%, $p = 0.022$, respectively; Fig. 4a). Nonetheless, partially shared effects (combinations) of all sets of predictors explained the largest portion of the total variation. Within the traditional fallows, *R. acetosella* responded weakly to climate variables. The partitioning indicated 45% of the variance was unexplained.

3.3. Environmental drivers of weed pressure and forage production in improved fallows

When examining the IF plots, linear regression showed a significant effect of forage biomass production (seeded vegetation) on weed pressure ($p = 0.001$), with greater forage production significantly decreasing the biomass of non-planted species (Table 3). Abiotic factors related to soil fertility or climate did not show any direct effects on the

Table 2

Biotic and abiotic environmental characteristics for traditional fallow plots (n = 82) separated into three *Rumex acetosella* categories: 1) *R. acetosella* present (RP), 2) *R. acetosella* potentially suppressed (RPS), and 3) *R. acetosella* not present (RNP). The trend of the correlation for weed presence with the environmental variables are indicated (+ indicates an increase in weediness and - indicates a decrease). P-values are provided for one-way ANOVAs examining differences between *R. acetosella* categories, with significant effects in bold ($p \leq 0.05$). Standard errors are in parentheses and in italics below each mean. Lower case letters indicate difference between categories as indicated by the Tukey post-hoc analysis.

Factors	Indicator ^a	Unit	Rumex acetosella presence			p-values	Trend	
			RNP	RP	RPS			
Biotic	Total biomass	kg ha ⁻¹	2872.86 (287.93)	2177.92 (313.41)	3750.01 (875.60)	0.06	[-]	
	Weed biomass (no <i>R. acetosella</i>)	kg ha ⁻¹	2872.86 (287.93)	a 1282.73 (274.15)	b 3750.01 (875.60)	a < .001	[-]	
Abiotic Soil	pH		5.07 (0.15)	4.87 (0.11)	5.19 (0.22)	0.346	[-]	
	SOM	%	5.03 (0.48)	5.43 (0.38)	6.22 (1.08)	0.435	[-]	
	P	mg kg ⁻¹	32.55 (6.40)	18.85 (2.22)	27.88 (9.21)	0.090	[-]	
	K	mg kg ⁻¹	307.34 (77.04)	237.76 (31.71)	300.75 (74.48)	0.598	[-]	
	CEC	cmol kg ⁻¹	18.63 (0.89)	19.50 (0.61)	19.17 (1.41)	0.358	[+]	
	POXC	mg kg ⁻¹	694.41 (47.20)	753.32 (40.50)	826.58 (102.82)	0.713	[-]	
	Clay	%	24.90 (1.38)	21.95 (1.14)	25.50 (2.43)	0.173	[-]	
	Climate	Tmax	°C	18.25 (0.48)	a 16.71 (0.31)	b 17.7 (0.790)	ab 0.029	[-]
		Tmin	°C	2.21 (0.35)	a 1.05 (0.23)	b 1.85 (0.55)	ab 0.019	[-]
		Tmean	°C	10.07 (0.41)	a 8.73 (0.27)	b 9.61 (0.67)	ab 0.025	[-]
Monthly temperature seasonality		stdv*100 ^b	96.9 (2.19)	a 89.95 (1.69)	b 95.21 (4.05)	ab 0.045	[-]	
Precipitation		mm y ⁻¹	887.86 (4.0)	878.09 (3.1)	886.53 (6.8)	0.136	[-]	
Monthly precipitation seasonality		CV	74.860 (1.47)	a 69.82 (1.08)	b 72.67 (2.59)	ab 0.027	[-]	
Elevation		m a.s.l.	3628 (48.33)	b 3824 (36.73)	a 3732 (62.90)	ab 0.006	[+]	

^a SOM, Soil Organic Matter; P, Available P; K, Available K; CEC, Cation Exchange Capacity; POXC, Permanganate Oxidizable Carbon; Tmax, Average Annual Maximum Temperature; Tmin, Average Annual Minimum Temperature; Tmean, Average Mean Annual Temperature.

^b Mean monthly temperature seasonality is calculated using the standard deviation (stdv) of the mean monthly temperature (O'Donnell and Ignizio, 2012)

weed proportion of total biomass. In contrast, linear regressions showed that key indicators of soil fertility, available P (P_{olsen} ; avg. 25.0 mg kg⁻¹) and K (avg. 271.8 mg kg⁻¹), had a significant positive correlation with forage production within improved fallows. Results of variation partitioning for the weed proportion of total biomass showed that the overall biomass production (pure biotic) explained a significant degree of variance (23.1%, $p < .001$; Fig. 4b). The partitioning showed 81.9% of the variance as unexplained. Pure climatic and soil features, or their interactions did not influence the pressure of non-planted species within improved fallow systems. Variation partitioning on forage production, indicated 96% of the variance was unexplained (Fig. 4c). The pure effect of soil explained a significant degree of variance after the hypothesis acceptance level was set at $\alpha < 0.10$ (7.4%, $p = 0.084$).

4. Discussion

4.1. Performance of non-planted species within improved fallow systems

Our findings indicate that improved fallows can reduce the growth and establishment of the invasive plant species *R. acetosella* to a fraction of that observed in traditional fallow plots, indicating that improved fallows offer a promising option for controlling invasive species and other weeds in this environment. When examining the improved fallow plots, we found that increased forage productivity was directly linked to a reduction in weed pressure. Our findings further suggest a relationship with soil fertility, such that the productivity of the forage crops, and

their ability to outcompete weeds, within improved fallow systems depends mainly on soil variables. However, we urge caution in interpreting this result, as variation partitioning indicated that most of the variance remained unexplained when analysing forage production matrices. Nonetheless, the variance explained by the 'pure soil' partitioning was significant (at $\alpha < 0.10$) and is further supported by results of linear regression, where only soil macronutrients (i.e., available soil P and K) appear to significantly influence forage production in improved fallow systems, while other potentially important environmental drivers play a lesser role.

Previous research indicates that if fallows would decrease in length, so in general do subsequent crop yields and species diversity within the plots, and hence the ability of fallows to support a broader range of ecosystem functions such as weed suppression and restoration of soil fertility (Buresh and Cooper, 1999; Pestalozzi, 2000; Fonte et al., 2012). Our findings are in accordance with related literature on cover crops demonstrating their effectiveness in suppressing invasive species and other weeds and for improving soil fertility (Teasdale, 1996; Sturm et al., 2018; Haramoto and Pearce, 2019). *A. sativa*-*V. sativa* mixtures, both annual species, have been widely used as a short-term agroecological option to obtain important farmer objectives such as forage production and soil conservation (Dhima et al., 2007; Finney and Kaye, 2017). Compared to other types of seed mixtures for improved fallow systems, the better performance of *A. sativa* and *V. sativa* largely corresponds to their faster growth rate, which is a common trait among annual species (Meza, 2022). A faster growth rate likely translates into

Table 3

Relationships of the environmental characteristics with weed pressure and forage productivity within improved fallow plots in the central Peruvian highlands. The trend of the correlation for weed presence with the environmental variables are indicated (+ indicates an increase in weediness and - indicates a decrease). P-values are provided for regression examining the effect of biotic and abiotic factors on weed presence in improved fallows (n = 82), with significant effects in bold ($p \leq 0.05$). Standard errors are written in italics between brackets.

Factor	Indicator ^a	Weed pressure			Forage productivity	
		Mean (<i>std.err</i>)	p-value	Trend	p-value	Trend
Biotic	Total biomass (no weeds; Kg ha ⁻¹)	6721.9 (62.21)	< 0.001	[-]	n.d. ^b	n.d.
Abiotic						
Soil	pH	4.98 (0.08)	0.179	[-]	0.170	[+]
	SOM (%)	5.40 (0.29)	0.268	[+]	0.293	[-]
	P (mg kg ⁻¹)	25.02 (2.90)	0.267	[-]	0.032	[+]
	K (mg kg ⁻¹)	271.59 (33.14)	0.827	[+]	0.021	[+]
	CEC (cmol kg ⁻¹)	19.14 (0.48)	0.378	[+]	0.693	[+]
	POXC (mg kg ⁻¹)	743.20 (30.18)	0.804	[+]	0.602	[+]
	Clay (%)	23.51 (0.84)	0.787	[-]	0.399	[+]
Climate						
	Tmax (°C)	17.40 (0.27)	0.516	[+]	0.448	[+]
	Tmin (°C)	1.58 (0.19)	0.687	[+]	0.310	[+]
	Tmean (°C)	9.34 (0.23)	0.600	[+]	0.407	[+]
	Monthly temperature seasonality (stdv*100) ^c	93.18 (1.32)	0.408	[+]	0.516	[+]
	Precipitation (mm y ⁻¹)	882.79 (2.36)	0.390	[+]	0.349	[+]
	Monthly precipitation seasonality (CV)	72.02 (0.87)	0.409	[+]	0.433	[+]
	Elevation (m a.s.l.)	3740.98 (28.20)	0.736	[-]	0.249	[-]

^a SOM, Soil Organic Matter; P, Available P; K, Available K; CEC, Cation Exchange Capacity; POXC, Permanganate Oxidizable Carbon; Tmax, Average Annual Maximum Temperature; Tmin, Average Annual Minimum Temperature; Tmean, Average Mean Annual Temperature.

^b Non defined

^c Mean monthly temperature seasonality is calculated using the standard deviation of the mean monthly temperature (O'Donnell and Ignizio, 2012)

an improved ability to take-up nutrients and rapidly invest energy in leaf area and biomass shortly after emergence and during early growth stages (Franzuebbers, 2015; King and Blesh, 2018). This increased competitive ability combined with an increased seeding rate and more uniform germination (relative to species present the natural seed bank), likely allows for this mixture to outcompete weeds.

4.2. Biotic and soil fertility drivers of *Rumex acetosella*

Our findings demonstrate that distinct biotic, soil, and climatic environmental features influence in different ways, both the distribution of *R. acetosella* in the landscape, and its abundance in a fallows. For example, we found the distribution of *R. acetosella* is mainly influenced by climatic features. Our data confirms that this species typically grows at higher elevations that are cooler and more humid, in agreement with observations by local smallholder farmers. Precipitation seasonality also influences the distribution of *R. acetosella*, such that *R. acetosella* appears to be more often present when there is a more stable monthly precipitation pattern over the year, versus sites that have a more pronounced dry season. When looking at traditional fallows where *R. acetosella* was established, we found that the presence of other non-planted species and predictors of soil fertility were strongly associated with its abundance, such that *R. acetosella* mainly grows on disturbed soils, with lower overall productivity and poor nutrient availability. While we believe that our findings are relatively robust, it is worth noting that legacy effects of past management (e.g., differences in tillage, irrigation,

grazing) likely contributes to some of the unexplained variability observed in weediness and *R. acetosella* productivity in this study.

Studies on secondary succession in the Venezuelan Andes have shown that *R. acetosella* can persist as the most abundant species for up to 9 years after leaving a field fallow (Sarmiento, 2003), although in later successional stages, other species become more abundant. Meanwhile, farmers in our study region suggest that *R. acetosella* does not typically persist so long. In agreement with Sarmiento (2003), the presence of other (non-planted) species at our study sites is inversely correlated with the presence of *R. acetosella*. Also, our findings confirm that *R. acetosella*, like in its native habitat in Europe, appears to act as a pioneer species in the Andean region. Furthermore, we observed throughout the Peruvian Andes, farmers often use *R. acetosella* as an indicator species for soil fertility (indigenous farmers, pers. comm.; Becker et al., 2001), such that when *R. acetosella* disappears from traditional fallows, due to natural succession and/or increasing nutrients in the soil, it is time to plant crops again, so that soil fertility is 'restored'. Hence, we speculate that shortening of the fallow period is likely to increase the abundance of *R. acetosella* in Andean farming systems, unless other measures are taken to control this species or better maintain soil fertility.

We suspect that endozoochorous dispersal (particularly sheep, alpacas, and llamas) has likely contributed to the spread of *R. acetosella* throughout the Andes over the past centuries, as seed remains viable following gut passage and can germinate in deposited manure (Huber and Markgraf, 2003). At the same time, that absence of livestock,

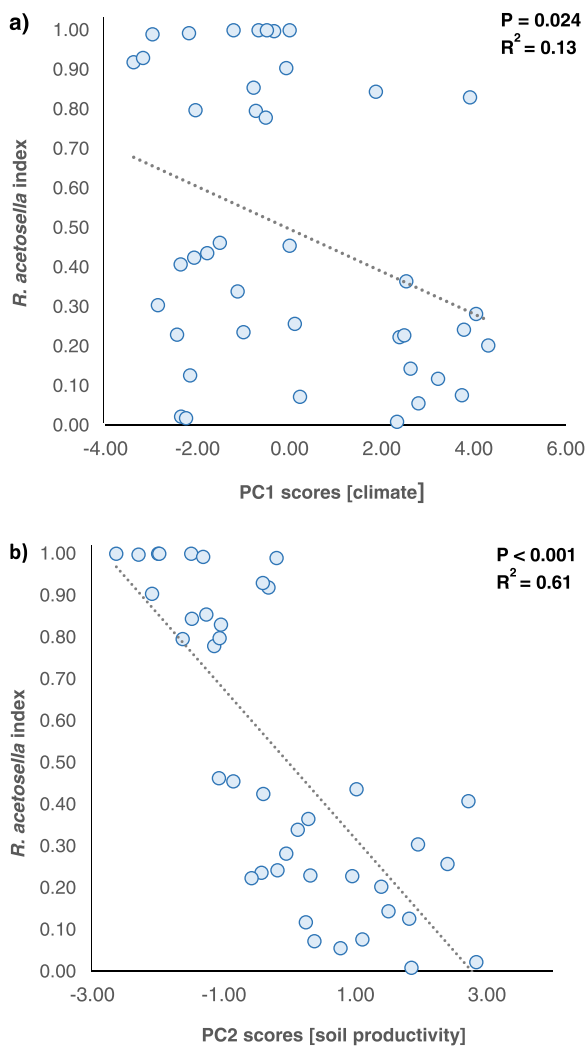


Fig. 3. Scatter plots showing a linear regression between the loadings of a) PC1 (mainly associated with climatic variable) and b) PC 2 (mainly associated with soil and biotic factors; see description Tables 2 and 3) and the *Rumex acetosella* index of traditional fallow plots (n = 41; only RP). PCs are derived from Fig. S3.

specifically the lack of nutrient return in manure inputs, may also have played a role in supporting the spread of *R. acetosella*, especially on less fertile soils. Across much of the Andes, livestock are key to long-term sustainability and soil fertility, and often graze in sectorial (traditional) fallows (Leon-Velarde et al., 2000; Tulachan et al., 2000; Waller, 2007). If livestock numbers decrease, less manure would likely be added to these systems, and this may contribute to reduced soil fertility that can favour *R. acetosella* over other native or alien species. In this case, improved fallows offer a workable option for smallholder farmers to naturally control for the problematic weeds and invasive species, as vegetative suppression by forage growth will also improve soil fertility by increasing manure input to the system via livestock grazing and intentional manure return (in the case of cut forages).

5. Conclusion

Our findings suggest that climatic features mainly influence the presence of *Rumex acetosella*, while soil productivity (biotic and soil features) mainly drives its growth and biomass within traditional fallow systems. In the short-term, with cropping systems and *Rumex acetosella* moving up Andean hillsides towards cooler environments, the undesirable species for farmers will likely become more invasive within cropping fields and pastures. *R. acetosella* is expected to become more abundant within agricultural fields, especially at higher elevations, where it will continue to compete, establish, and grow well. Nonetheless, in the longer-term, temperatures at the mid-high elevations will increase due to global warming, creating a growth environment in which *R. acetosella* may no longer flourish. Improved, forage-based fallows appear to offer a promising agroecological option for smallholder farmers in the high tropical Andes to control *R. acetosella* and other weeds. While the fallow period has historically been considered important to restore soil health, our findings suggest that improved fallows can also help to suppress weeds and support greater forage production for local populations. When focusing solely on weed pressure within improved fallows, we found that forage productivity influenced the suppression of the non-planted species. Hence, in these systems, maintaining productivity of a field, via regular inputs of organic matter and nutrients in a traditional manner, appears to be important for reducing the success of invasive species, and more generally weeds.

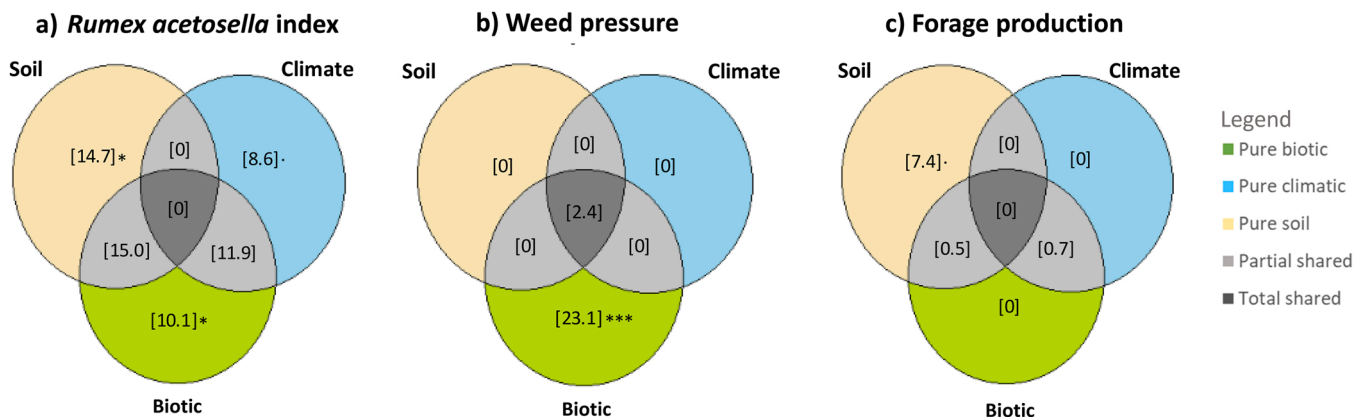


Fig. 4. Biotic versus abiotic drivers of *Rumex acetosella* presence (in traditional fallow plots with RP; n = 41), *weed pressure* and *forage production* (in improved fallow plots; n = 82) within sampled field of three central Andean regions in. Variation partitioning shows: a) the portion of total variation in the *R. acetosella* index; and b) the portion of total variance in the *weed pressure* and c) the portion of total variance in the *forage production* as dependent variable(s), explained by soil, climatic, and biotic predictor sets as independent variable(s). Venn diagram (left) shows: (a) pure effect of soil variables (pure soil), (b) pure effect of climatic variables (pure climatic), (c) pure effect of the biotic factors (pure biotic), (d + e + f) partial shared variation explained by the overlapping effects of two/three sets of factors (partial_shared), (o) total shared effect of all sets of predictors (total shared). Negative values of R^2 (i.e. cases where the explanatory variables explain less variation than a normal random variable) were interpreted as zeros. If a p-value is less than 0.05, it is flagged with one star (*). If a p-value is less than 0.01, it is flagged with two stars (**). If a p-value is less than 0.001, it is flagged with three stars (***). The point indicates which pure effect was marginally significant ($p < 0.10$).

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

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.agee.2023.108446](https://doi.org/10.1016/j.agee.2023.108446).

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