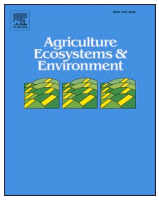
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Global change drivers alter weed performance and threaten forage production in an Andean agroecosystem

Anna M. Visscher [a,b,*], Steven Vanek [c], Jhon Huaraca [d], Jamelith Mendoza [d], Raul Ccanto [d], Katherin Meza [c,d], Edgar Olivera [d], Steven J. Fonte [c]

[a] Soil Biology Group, Wageningen University, Wageningen University & Research, P.O. Box 47, Wageningen 6700 AA, the Netherlands
[b] Faculty of Agricultural, Environmental and Food Sciences, Free University of Bozen-Bolzano, Piazza Università, 5, Bolzano 39100, Italy
[c] Department of Soil and Crop Sciences, Colorado State University, Fort Collins, CO 80523, USA
[d] Grupo Yanapai, Pje. Cordobez N. 117, Mollotingo – El Tambo, Huancayo, Peru

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ABSTRACT

Climate change and other global drivers threaten the long-term sustainability of production systems in the Andean highlands. Impacts on forage production and weed competition have important implications for farmer livelihoods but have received only limited attention. This study examines the impact of key global change drivers on the performance of the common forage, *Lolium multiflorum*, grown in competition with two important weeds of the region (*Rumex acetosella* or *Pennisetum clandestinum*). Forage-weed mixtures were grown in field mesocosms at different elevations, as a proxy for climate (3520 and 3740 m a.s.l.) and under contrasting nutrient management strategies (manure vs. synthetic fertilizer) to reflect a trend of increasing fertilizer use in the region. The findings indicate that warming conditions negatively impacted *L. multiflorum* performance, while manure inputs increased overall biomass production by 27 % relative to synthetic fertilizer. Meanwhile the impacts of amendments on weed-crop competition were plant-specific. For instance, *R. acetosella* competed better with organic manure nutrients, whereas *P. clandestinum* performed better at warmer sites amended with synthetic fertilizer. Findings from this study suggest that climate warming may exacerbate weed pressures, threatening crop production and food security in Andean landscapes. Additionally, continued reliance on traditional nutrient management, instead of synthetic fertilizers, may help support forage productivity and resilience under changing climate conditions.

1. Introduction

Numerous global challenges threaten the sustainability of agricultural systems around the world and emphasize the need for urgent actions to transform the ways in which farmlands are managed (Fischer and Connor, 2018; Pulleman et al., 2022). In particular, climate change can have variable and potentially severe effects on agricultural production and food security (Parry, 2019). Higher temperatures can result in more frequent and severe storms and drought, as well as an increased prevalence of pests and disease, further reducing yields or interfering with fallow periods (Dangles et al., 2013; Tito et al., 2018; Raza et al., 2019). The tropical Andean region is especially vulnerable to the effects of climate change due to its rugged mountainous terrain, high susceptibility to erosion, and wide array of endemic species (Vuille and Bradley, 2000; Bush et al., 2010; Anderson et al., 2011). Higher elevations in this region are expected to face marked temperature increases and alterations in the timing and amount of precipitation (Urrutia and Vuille, 2009, Challinor et al., 2014), which threaten crop yields and farmer livelihoods in these rural Andean communities (Perez et al., 2010; Fiebig-Wittmaack et al., 2012; Tito et al., 2018; Visscher et al., 2024). Much of this region is dominated by indigenous communities where farming has occurred for hundreds or thousands of years, and have deep-rooted cultural, social, and economic connections to the land. Global warming poses a considerable threat to these communities, potentially displacing them and eroding their traditional ways of life (Boillat and Berkes, 2013; Rolando et al., 2017).

In addition to global warming, the intensification of agricultural management, via increased reliance on agrochemical inputs and mechanized tillage, among other factors, undermine long-term soil health and fertility. Andean farmers have traditionally relied on organic

* Corresponding author at: Soil Biology Group, Wageningen University, Wageningen University & Research, P.O. Box 47, Wageningen 6700 AA, the Netherlands.
E-mail address: anna.visscher@wur.nl (A.M. Visscher).

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nutrients inputs, such as animal manure, to maintain soil health, but synthetic fertilizers are becoming more common (Fonte et al., 2012; Caulfield et al., 2019; Visscher et al., 2020). Synthetic fertilizers provide nutrients in a form that is more immediately available to plants and are easier to transport, making them attractive to many farmers (Bulluck et al., 2002). However, synthetic fertilizers are especially prone to loss through leaching, runoff, and gaseous emissions (Kumar et al., 2019) and can lead to long-term soil degradation (Drinkwater and Snapp, 2022). On the other hand, organic inputs provide sustained nutrient release and retention, improve soil structure, and support biological activity, but often show a slower growth response (Geisseler and Scow, 2014). The benefits of organic nutrient sources for soil health and improved plant nutrition (via offering a balanced supply of macro and micronutrients) may also contribute to cropping system resilience in the face of climate change (Visscher et al., 2024), but this remains poorly understood.

Traditional Andean fallows, where a sequence of crops is followed by multiple years of unseeded (largely native) vegetation, have long been used to support soil health and productivity (Pestalozzi, 2000; Fonte et al., 2012). These fallows are characterized by high plant diversity of mostly native perennial grasses and legumes, which are crucial for restoring soil organic matter and providing multiple ecosystem services (de Valença et al., 2017; Manning et al., 2018). However, shortening or complete elimination of these fallow periods with cropping system intensification threatens long-term soil health and the provision of forage in many highland Andean communities. More recently, farmers have begun to integrate multi-purpose, forage-based fallows into their crop rotations, where highly productive perennial forage species are planted for a 2–5 yr period that allows both forage production and soil fertility restoration (Vanek et al., 2020; Meza et al., 2022). However, climate change threatens to not only alter the growth and performance of the planted forages (Yates et al., 2019), but also the distribution of undesirable species (i.e., weeds) within Andean crop rotations. For instance, smallholders have observed significant changes, with the grass *Pennisetum clandestinum* and the forb *Rumex acetosella* emerging as pervasive noxious weeds. These species have created substantial challenges for farmers, complicating field preparations and increasing the burden of weeding activities (Vanek et al., 2020; Visscher et al., 2023).

Despite considerable focus on global warming and other global change drivers, limited information exists on how they affect the performance and competitiveness of undesirable species and invasive species, particularly in forage-based systems of the Andean highlands. The establishment and spread of invasive species can impact multiple ecosystem functions, including productivity, water dynamics, and erosion control (Vilà and Hulme, 2017). Furthermore, invasive species can impose costly management interventions to control their spread and competition with crops, hence impacting farm economics and livelihoods (Bacher et al., 2018). Thus, there is an urgent need to understand how various global change drivers influence weed performance and competition with crops (Howden et al., 2007). Elucidating future changes and factors that are likely to influence weed dynamics and associated impacts on crop performance is key to developing effective strategies to manage weeds and minimize their negative impacts in cropping systems.

In light of the complex challenges posed by climate warming and other global drivers, this study focuses on three prevalent species in the Andean fallow systems: *Lolium multiflorum* a commonly planted C3 forage grass in the region, as well as two common weedy species, *P Pennisetum clandestinum* (a C4 grass) and *Rumex acetosella* (a C3 forb). The weedy species were chosen not only for their prevalence and potential impact in the study region, but also for their distinct growth forms and physiologies that likely mediate their response to changing environmental conditions. This study sought to answer the following research questions: i) how do changing climatic conditions influence competition between two important Andean weed species and forage crops, and ii) how do shifting nutrient management strategies affect this competition across distinct climates. It is hypothesized that under warmer conditions, weeds (*P. clandestinum* and *R. acetosella*) will gain a competitive edge over the forage species (*L. multiflorum*), as invasive species often demonstrate superior fitness and adaptability, enabling them to thrive in changing ecosystems (Yates et al., 2019; Chandregowda et al., 2023). This is especially true to *P. clandestinum*, as C4 plants are known to be more tolerant of warming conditions (Edwards et al., 2001). Furthermore, it is predicted that a shift towards synthetic fertilizers will favor weed performance in warmer environments compared to fertilization with organic manure, since weeds are often fast growing early colonizing species that are able to rapidly exploit soil resources such as added nutrients (Little et al., 2021) and outcompete crops. To test these hypotheses, a mesocosm experiment was established in two distinct climates along an elevational gradient and with two different fertilization strategies (organic using sheep manure versus synthetic fertilizers). The mesocosms were designed to evaluate competition between *L. multiflorum* and the two local recognized weed species (*P. clandestinum* and *R. acetosella*) across these different environmental and management contexts. By investigating the impact of key global drivers on the competition between forage crops and weeds in the Andean highlands, this research provides insights into adaptive farming strategies and weed management.

2. Materials and method

2.1. Study area

This study was conducted in the community of Quilcas, near the city of Huancayo, in the Junín region of Peru (11.931S, 75.251 W). Soils in this mountainous landscape are largely classified as Inceptisols (USDA taxonomy), with neutral to acidic pH and texture ranging from loamy to clay-loamy (Garcia., 2011). Precipitation averages approximately 700 mm yr^{-1}, falling mainly between September and April. Average monthly temperatures vary between 12 °C and 16 °C. Farming in the region typically occurs across a range of elevations and consists of mixed crop-livestock systems, with complex, multi-year rotations. Within the lower-middle elevation zone (3200 – 3800 m) it is common to have 3–5 years of cropping (e.g., potatoes, maize, faba beans, barley) followed by an unseeded, natural fallow for 2–3 years. At higher elevations (>3800 m) longer rotations are more common, with one or two cropping seasons (typically dominated by potato) 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.

2.2. Species of interest

This study focused on the common forage crop *L. multiflorum* (Italian rye grass) and two invasive species, *R. acetosella* (sheep sorrel) and *P. clandestinum* (Kikuyu grass), which are sources of major concern for farmers throughout the central Andean region (Visscher et al., 2023). *Lolium multiflorum* is an annual to biennial poaceous species, and is a highly competitive and rapidly growing plant, capable of producing large quantities of seed and commonly reaching a height of up to 40 cm (Hubbard et al., 1968). The species is widely planted across and performs best within areas with high rainfall and neutral to alkaline soils. *L. multiflorum* is native to lowland habitats in Central Europe, North-west Africa and Southwest Asia and is highly adaptable due to a high degree of phenotypic plasticity (Beddows, 1973).

The low-growing perennial species *P. clandestinum* (Poaceae) spreads through both belowground rhizomes and seed dispersal, generally reaching a hight of about 15 cm (Parker, 2008). The species is native to highlands of eastern Africa but has been widely introduced across the world for forage use. It is unclear when the species was first introduced

in Peru, but it has proved to be quite invasive, since *P. clandestinum* is highly tolerant of mowing and grazing and often invades natural areas with resultant loss of biodiversity. This species is also known for tolerating a wide variety of climatic conditions, being a species with a drought-tolerant C4 photosynthesis strategy that also is able to tolerate cool conditions (Wilen and Holt, 1996)

Rumex acetosella is a perennial in the Polygonaceae family, reproducing by relatively shallow, extensive slender roots and seed (Huber and Markgraf, 2003). Multiple stems can appear from a single crown and grow upright, reaching 15–40 cm in height (Clements, 2013). Originating from Europe, *R. acetosella* was once domesticated in Neolithic European settlements for human consumption (Euro Med, 2006. Holm et al. (1997) listed *R. acetosella* as one of the world's most problematic weeds, infesting over 70 countries worldwide. The species is naturally present in nutrient poor grasslands (Leuschner and Ellenberg, 2017). In the Andes, land use change and associated disturbance (e.g., logging, tillage, grazing) activities may have contributed to the rapid expansion of *R. acetosella* since it has a strong affinity for disturbed soils and is only moderately shade tolerant (Llambí et al., 2003). Local farmers commonly identify this species as a widespread, highly invasive and problematic weed (Visscher et al., 2023)

2.3. Experimental design and management

In October 2021 a mesocosm experiment was installed to examine the impacts of climate, nutrient management, and weed pressure on forage growth and performance. Sites at two different elevations (3520 and 3740 m a.s.l.; Fig. 1), were used as a proxy for warming climate conditions in the study area (central Peru) for the next ~50 years based on increases of 1.6 °C (Vuille and Bradley, 2000). At each elevation *L. multiflorum* grew under two different fertilization strategies (traditional Andean/organic, using sheep manure vs. agrochemical/agro-industrial, with synthetic fertilizer inputs) and with one of two common weed species *P. clandestinum or R. acetosella)*, in a full factorial design. Each treatment was randomly assigned to mesocosms at each elevation, with six replicates per treatment per elevation.

In early September 2021, soil was collected to a depth of 20 cm from a field adjacent to the high elevation site (at 3700 m a.s.l.) in the first year of traditional fallow, after a 3–5-year crop sequence. All soil was passed through a 5 mm sieve to remove rocks and large organic debris, and then thoroughly mixed to homogenize material. Three representative subsamples (each approx. 2 kg) of the soil were collected, air-dried, passed through a 2 mm sieve, and sent to the Plant Nutrient Lab at La Molina University (Lime, Peru) for analysis of physical and chemical properties. The soil had a low to moderate SOM content (18.3 g kg^{-1}), with a clay loam texture, and an acidic pH of 4.0.

Mesocosms were constructed from 10 cm diameter PVC pipe cut into 40 cm long sections, with a cap affixed to the bottom. Each mesocosm was filled with approximately 3 kg of a soil-sand mixture (3:1 soil:sand ratio by volume, to ensure adequate drainage), with drainage holes at the base (~ 3 mm in diameter). At both sites, mesocosms were filled with soil from the high elevation field described above to simulate warming of the same soil. In order to help regulate temperature and humidity and reflect ambient conditions of the surrounding soil, the

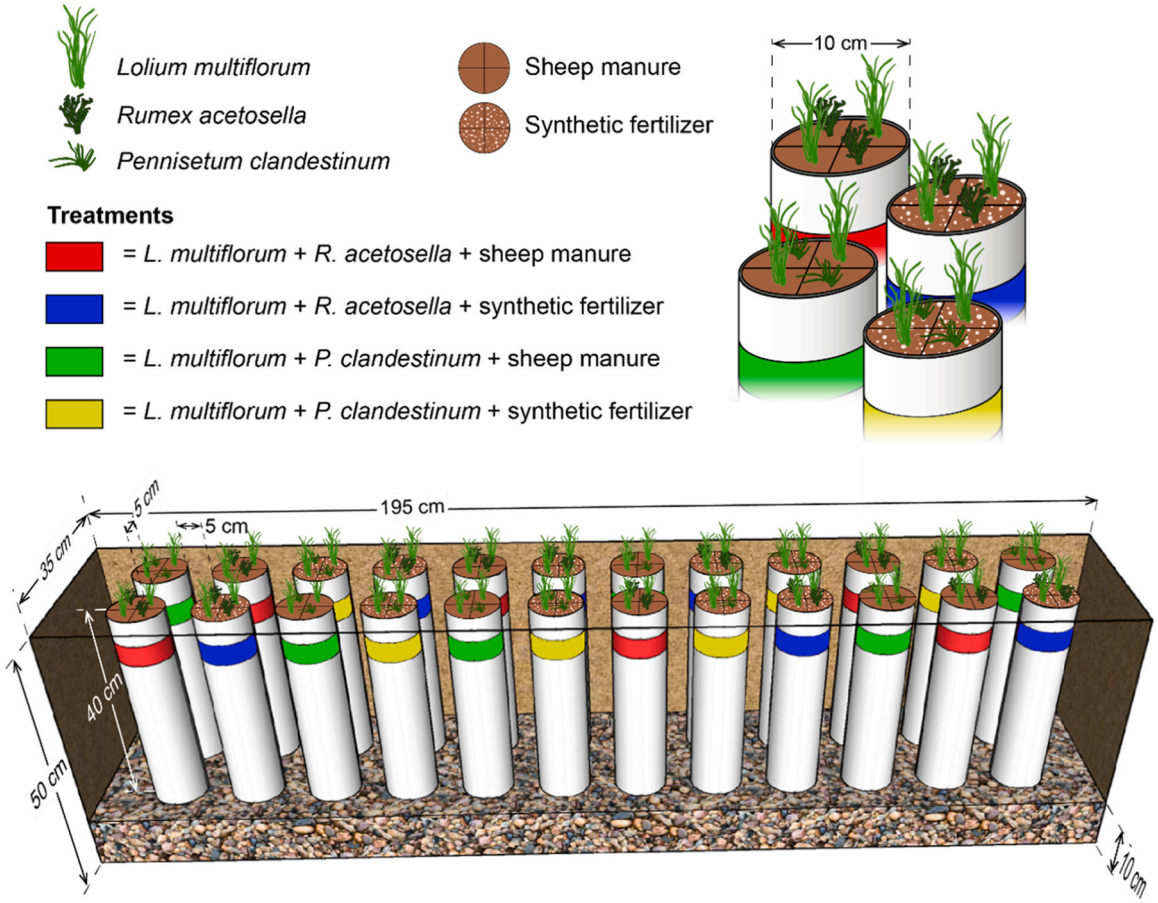


Fig. 1. Layout of our mesocosm experiment where the forage crop *Lolium multiflorum* and common Andean weeds (*Rumex acetosella* or *Pennisetum clandestinum*) were grown. The experiment was conducted at two elevations (3520 and 3740 m a.s.l.). At each elevation, PVC cylinders were filled with a soil-sand mixture. The mesocosms were placed in backfilled trenches to maintain natural soil and climate conditions, with a rock layer at the bottom for drainage. Soil management treatments include sheep manure application (organic) or synthetic fertilizer application (synthetic). Trials were established in the community of Quilcas in the Junín region of Peru in September 2021 and harvested in May 2022. The treatments were applied in a full factorial design at each site, with six replicates per treatment.

mesocosms were placed in trenches (~ 2 m long, with a rock layer at the bottom for drainage) and spaced 15 cm from each other. Trenches were backfilled with soil, such that the soil surface in each mesocosm was level to the surrounding ground. At the beginning of October 2021, *L. multiflorum* seeds were sown into mesocosms at slightly higher density (six per mesocosm) than needed, covered with a thin layer of sand, and were thinned to the desired density (two seedlings per mesocosm) 4 weeks after germination. At the same time, two identical fresh rhizome cuttings of either *P. clandestinum or R. acetosella* were planted into the mesocosm a few days after germination. In several cases of poor germination of *L. multiflorum* seeds or establishment of the rhizome cuttings, a separate set of *L. multiflorum* seeds were pre-germinated and weed rhizome cuttings propagated in the laboratory, and these seedlings were used as needed in the first few weeks of the experiment to achieve the desired densities in several mesocosms with missing plants. No plants were replaced after 10 weeks.

Mesocosms were fertilized by amending with synthetic fertilizer (80 kg N, 26 kg P, 37 K kg ha^{-1}), or sheep manure. Input rates were based on typical nutrient input rates of forage-based fallows within the region and standardized by N input, assuming that 50 % of the applied manure N would become available over the growing season. This approach led to roughly equivalent amounts of available N in both treatments (80 kg N ha^{-1}), but somewhat higher inputs of available P and K in the manure treatment (36.3 kg P and 74.9 K kg ha^{-1}). Both manure and synthetic fertilizers were incorporated to a depth of 10 cm at the start of the experiment. The mesocosms were monitored weekly and were watered uniformly within each site as needed during periods of insufficient rainfall. Mesocosms received no other inputs (e.g., pesticides) and were weeded regularly to limit the growth of undesired species. All plants were trimmed back to 1 cm after 110 days to simulate typical management of forage crops in the region.

Weather stations were installed (HOBO Rain Gauge Data Logger RG3) at both elevations to monitor precipitation and temperature. Sensors were installed on a pole at a height of 2 m in conditions of full sun and remained in the field from September 2021 until early June 2022 (Table 1).

2.4. Plant harvest and data collection

Mesocosms in all treatments were harvested 237 days after establishment, in April 2022 (end of the raining season) when most (80 %) of the *L. multiforum* had reached flowering stage. At harvest plant height, number of stems, and survival rate of *L. multiforum* and the corresponding weed species in each container were evaluated. Mesocosms were then destructively sampled to assess above- and belowground biomass. Plants and soil were removed from the mesocosms and deposited onto a tray. Soil was removed from plant roots by gently breaking apart large aggregates. Roots were then rinsed with water on top of sieves (0.5 mm) to capture fragments that were broken during the root washing. Biomass (above and belowground) was separated by species and the aboveground portion separated into stems, leaves and flowers. All plant components were dried at 60 °C, and weighed separately for each mesocosm. Root to shoot ratios for all species were calculated. Additionally, a weed index for each mesocosm was calculated dividing the weed biomass by the total biomass in each mesocosm.

Table 1
Climate and topographic information for the two experimental sites in Quilcas, Junin region, Peru.

Climatic features	Unit	Lower elevation	Higher elevation
Elevation	m asl	3520	3740
Slope	°	8.5	9
Aspect	-	276W	260W
Temperature[a]	°C *	10.97	9.73
Temperature range	°C	3.55 – 24.77	3.03 – 25.71
Precipitation[b]	mm	630.9	738.4
Soil moisture content[c]	g water g dry $soil^{-1}$	0.18	0.25
Soil moisture content range	g water g dry $soil^{-1}$	0.05 – 0.31	0.10 – 0.56

[a] Mean daily temperature measured over the growing season
[b] Precipitation was measured from October 2021 until June 2022 (8 months)
[c] Mean weekly soil moisture content measured over the growing season

2.5. Statistical analysis

To understand the effect of site (elevation), weed species and nutrient management on the performance of *L. multiflorum*, three-way ANOVA were used with site, nutrient management type and weed species, and all two-way interactions as fixed explanatory variables. The performance of *R. acetosella* and *P. clandestinum* were examined separately for each species using a two-way ANOVA with site and nutrient management and their interaction as categorical explanatory variables. Where interactions were significant, estimated means were compared using Tukey tests. To meet ANOVA assumptions of homoscedasticity and normality, square root transformation and natural log transformations were applied as needed. All analysis were carried out using the JMP pro 15.0 software (SAS Institute, 2022).

3. Results

3.1. Elevation, weed competition, and management impacts on L. multiflorum performance. and weed growth

The survival rate of *L. multiflorum* over the growing season was 100 %. Performance of *L. multiflorum* was influenced by elevation ($p = 0.032$), such that aboveground biomass was 37 % greater at the higher elevation compared to the lower elevation. The total biomass of *L. multiflorum* (above and belowground) was 27 % greater when grown with manure vs. synthetic inputs (Fig. 2), but was not influenced by weed species present. The performance of *L. multiflorum* showed several marginally significant trends ($p < 0.10$; Table 2). In line with findings for total biomass, both aboveground and belowground of *L. multiflorum* exhibited a marginally significant response to management (Table 2), where organic inputs increase aboveground growth by 18 % ($p = 0.078$) and root biomass by 30 % ($p = 0.056$) compared to synthetic treatments. An marginally significant interaction between elevation and management ($p = 0.081$) indicates that the difference in belowground biomass between organic and synthetic management was more pronounced at lower elevations. Furthermore, the root:shoot ratio showed a marginally significant effect of elevation ($p = 0.055$), with plants at lower elevations tending to allocate more biomass to roots. An additional interaction between elevation and management ($p = 0.052$) revealed that the root:shoot ratio was higher under organic management at lower elevations (Table 2).

We observed a strong effect of elevation on the number of stems ($p = 0.033$; Table 2) and plant height ($p = 0.008$), such that plant height and number of stems counted for *L. multiflorum* were 14–18 % greater at the upper elevation compared to the lower elevation, regardless of management strategy. We further note that the number stems for *L. multiflorum* differed depending on the weed species present in the mesocosm ($p = 0.048$), such that the number of stems was 12 % lower when grown with *R. acetosella* compared to *P. clandestinum*.

3.2. Elevation and management impacts on the growth and performance of weed species

The survival rate of *R. acetosella* differed between elevations ($p < 0.001$; Table 3) and management type ($p < 0.001$), such that *R. acetosella* experienced 40 % higher survival in organic vs. synthetically amended mesocosms, and 40 % higher survival at the higher elevation compared to the lower elevation. The survival rate of

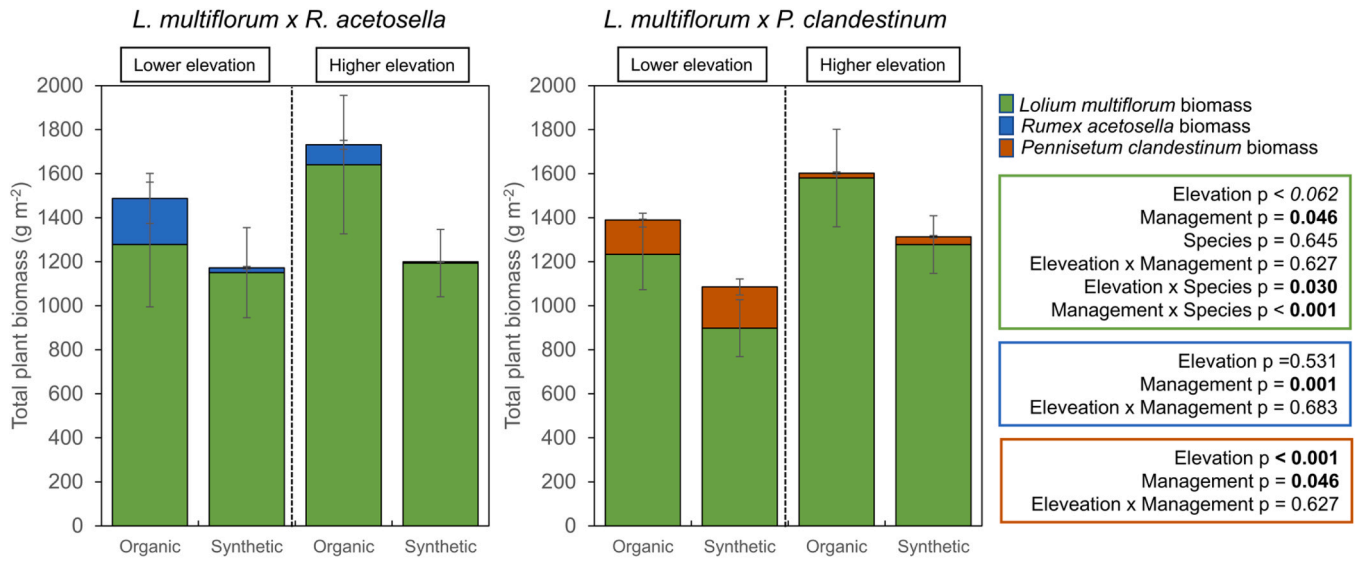


Fig. 2. Total biomass (above- and belowground) recovered in mesocosms including both the forage crop *Lolium multiflorum* and the common Andean weeds (*Rumex acetosella* or *Pennistum clandestinum*). Trials were installed at two elevations (3520 and 3740 m a.s.l.). Bars represent the mean ± standard error. Soil management treatments are sheep manure (organic) or fertilizer application (synthetic). Trials were established in the community of Quilcas in the Junín region of Peru in September of 2021 and harvested in May of 2022. P-values for elevation, nutrient management and weed species and their interactions are presented to the right of the figure.

P. clandestinum was 26 % higher at the lower elevation compared to the higher elevation ($p = 0.013$; Table 4).

Above- and belowground biomass of *R. acetosella* plants was roughly an order of magnitude higher in mesocosms amended with manure vs. those receiving synthetic inputs ($p < 0.001$; Table 3). Neither elevation nor the elevation by management interaction influenced the biomass production of *R. acetosella*. Root to shoot ratio was influenced by management type ($p = 0.003$), such that mesocosms receiving synthetic inputs had 3–4 times higher ratios than mesocosms receiving manure, even as their total biomass was much lower. *R. acetosella* plants in mesocosms amended with manure demonstrated significantly higher plant height ($p < 0.001$).

P. clandestinum plants demonstrated higher above- and belowground biomass ($p < 0.001$), as well as higher root to shoot ratio ($p = 0.013$) at the lower vs. higher elevation site (Table 4). Belowground biomass of *P. clandestinum* was 25 % higher in synthetically fertilized mesocosms vs. those receiving manure ($p = 0.045$). *P. clandestinum* plants in mesocosms at the lower elevation were also significantly taller ($p < 0.001$)

3.3. Treatment and elevation impacts on weed index

The weed index (weed to total biomass ratio) was three times higher, on average, at the lower elevation compared to the higher elevation ($p < 0.001$; Fig. 3). However, this difference was more pronounced for *P. clandestinum* than for *R. acetosella* (elevation x species interaction, $p = 0.030$). Mesocosms amended with manure had a 42 % higher weed index compared to those receiving fertilizer ($p = 0.001$), while the weed index for *P. clandestinum* was, on average, 46 % higher than that observed for *R. acetosella* ($p = 0.004$). However, the effects of species and nutrient management interacted ($p < 0.001$) suggesting that manure best supported *R. acetosella* growth, while *P. clandestinum* grew better in synthetically fertilized mesocosms (Fig. 3).

4. Discussion

4.1. Climate impacts on forage productivity and weed competition

In this study, elevation was used as a proxy for climate and found to be an important driver of the growth and performance of *L. multiflorum*, such that aboveground biomass, number of stems, and plant height were all greater at the upper elevation. This suggests that the cooler climate provides a more favourable environment for *L. multiflorum* growth and that continued warming in this region may have adverse effects on forage production, especially since *L. multiflorum* is one of the most commonly planted forage crops in the region. The marginally significant increase of root:shoot ratio of *L. multiflorum* at the lower elevation, suggests that the plants invest relatively more in roots in the warmer climate, which may be associated with increased water stress. Environmental stressors such as water or nutrient limitation can cause plants to invest more in root development to enhance resource uptake, potentially reducing leaf elongation and increasing the root:shoot ratio. For example, Chandregowda et al. (2023), working in southeastern Australia also found perennial grasses to increase root biomass allocation under drought conditions, indicating a shift in plant resources towards enhancing water uptake and ensuring survival. Similar to the response of *L. multiflorum* observed here, drought stress is known to cause increased belowground investment for a number of crops, often at the expense of shoot growth Basu et al. (2016).

While the two weed species present did not have large absolute impacts on the growth and performance of *L. multiflorum* in this experiment, they might in a more field-based context. The weed index offers valuable insights on how climate may influence competitive interactions between agricultural crops and weeds. Overall, a higher weed index was observed at the lower elevation, suggesting that competition with weeds may in part explain the reduced performance of *L. multiflorum*. This largely supports the first hypothesis that a warmer climate will support the competitive ability of weeds, since many invasive species have evolved to grow and exploit resources quickly and are adaptable to a variety of conditions (Finch et al., 2021). At the same time, an elevation by species interaction indicates that this trend was much more pronounced in mesocosms with *P. clandestinum* than those with *R. acetosella*. Thus, findings from this study indicate that both weed species, but especially *P. clandestinum* may become more problematic in the region with continued warming. In agreement with our findings, Tungate et al. (2007) found that increased temperatures bolster weed competitiveness in the southern United States, but that the impacts of warming vary depending on the weed species in question. It should be noted that *P. clandestinum* appears to be particularly adaptable to change, as was

Table 2
Indicators of the performance of forage crop *Lolium multiflorum* (n = 48) planted together with common weeds in the Andes (*Rumex acetosella* or *Pennistum clandestinum*). The experiment was established in September 2021 at two elevations and harvested in May 2022 along an elevation gradient in Quilcas, Junin region, Peru. Values represent means, with standard errors provided beneath each mean in parentheses. Soil management treatments are sheep manure (organic) vs. synthetic fertilizer application (synthetic). P-values are provided for the effects of elevation (E), management type (M), weed species (S) and their interaction, with significant effects ($P \leq 0.05$) in bold font and marginal significant effects in italics ($P \leq 0.10$).

		Lower elevation				Higher elevation				*p*-values					
		Organic		Synthetic		Organic		Synthetic							
Indicator	Unit	*R. acetosella*	*P. clandestinum*	*R. acetosella*	*P. clandestinum*	*R. acetosella*	*P. clandestinum*	*R. acetosella*	*P. clandestinum*	Elevation (E)	Management (M)	Species (S)	E x M	E x S	M x S	E x M x S
Aboveground biomass	g m^{-2}	800	767	807	592	1207	1198	757	913	**0.032**	*0.078*	0.840	0.263	0.434	0.973	0.973
		(229)	(10)	(171)	(108)	(257)	(208)	(172)	(103)							
Belowground biomass	g m^{-2}	478	466	343	306	434	382	437	365	0.884	*0.056*	0.279	*0.081*	0.636	0.772	0.977
		(80)	(64)	(39)	(48)	(84)	(241)	(41)	(42)							
Root:shoot ratio	-	0.82	0.61	0.50	0.59	0.45	0.40	0.73	0.42	*0.055*	0.873	0.279	*0.052*	0.310	0.933	0.115
		(0.23)	(0.05)	(0.08)	(0.11)	(0.11)	(0.10)	(0.15)	(0.05)							
Plant height	cm	52.3	52.1	51.3	53.2	57.8	66.7	57.8	65.1	**0.008**	0.854	0.223	0.961	0.256	0.912	0.7334
		(2.98)	(5.77)	(4.56)	(4.25)	(8.53)	(4.76)	(1.41)	(2.59)							
Stems	No. $plant^{-1}$	53	54	52	55	57	67	53	66	**0.033**	0.755	**0.048**	0.676	0.142	0.764	0.966
		(2.72)	(5.57)	(4.92)	(4.68)	(8.51)	(4.13)	(1.67)	(1.83)							

evidenced by a more than five-fold increase in total biomass at the lower elevation. *Pennisetum clandestinum* is highly tolerant of mowing, which allows it to invade natural areas, leading to a significant loss of biodiversity. Its adaptability to a wide range of climatic conditions, combined with a drought-resistant C4 photosynthesis mechanism facilitating water use and nutrient use efficiency (Edwards et al., 2001), further enhances its invasive potential (Wilen and Holt, 1996). While *R. acetosella* demonstrated a less dramatic shift in biomass and root: shoot ratio between elevations, the relative performance of *R. acetosella* at the lower elevation was still greater than that observed for *L. multiflorum*. The distinct species responses highlight the pivotal role of environmental conditions, particularly temperature, in determining the growth and competitiveness of specific weed species and crops that they are in competition with.

Plants can modify their traits in response to environmental conditions, which provides them with competitive advantages through behaviours like avoiding or confronting neighbours. The plasticity of key functional traits, such as height and leaf area, is essential for species coexistence and adaptation to varying abiotic and biotic stressors (Novoplansky, 2009; Teughels et al., 1995; Pérez-Ramos et al., 2019). In this study, the lower survival and reduced growth of *P. clandestinum*, a species native to tropical East Africa, at higher elevations suggest it may be less suited to the cooler, wetter conditions, or may be outcompeted by *L. multiflorum*. In contrast, the higher survival of *R. acetosella*, a European species, at these elevations may be due to its adaptation to lower temperatures and increased moisture, which enhance its competitive fitness in these environments (Visscher et al., 2023). Nonetheless, the findings show that *R. acetosella* exhibits enhanced competitiveness under warming conditions when grown alongside forage crops. However, it appears to be outperformed by superior forage crops at higher elevations. This finding largely aligns with Visscher et al. (2023), who reported that the competitiveness of *R. acetosella* strongly depends on soil health and the growth and performance of other species – i.e., *R. acetosella* competes better in less productive sites where seeded forages grow less vigorously. A 13 % increase was observed in stem count and an 18 % increase in plant height for *L. multiflorum* at higher elevations, suggesting notable phenotypic plasticity in response to environmental variation. This suggests that increased tillering may contribute to its competitive advantage at higher elevations. Past research has shown that tillering in grasses, including *L. multiflorum*, enhances competitive ability by increasing shoot density and resource acquisition, allowing for better adaptation to environmental variability (Doust, 2007). The increase in height and stem count at higher elevations may be attributed to reduced competition (Bebre et al., 2021). In the context of the Andes, the findings presented here suggest that *L. multiflorum*, a species native to Europe, exhibits phenotypic plasticity at higher elevations that could confer a competitive advantage, enabling it to adapt and thrive in this landscape where elevation and soil nutrient factors are varying. This adaptability, along with its European origin and cooler climate adaptations, may be key factors in shaping plant community structure and could have implications for agricultural management in high-elevation Andean ecosystems.

4.2. Nutrient management as driver of forage and weed performance

When examining the effect of nutrient sources on total forage biomass, organic inputs enhanced *L. multiflorum* productivity. This same trend was observed, though only marginally significant, for aboveground and belowground biomass separately. These findings highlight the potential benefits of traditional, organic fertilization practices for enhancing forage production in certain contexts, which could have implications for sustainable livestock production. In a modelling study comparing manure and fertilizer inputs on forage crop productivity, Annicchiarico et al. (2011) found that manure offers a viable substitute for chemical fertilizers without reducing the gross production or sustainability of cropping systems. In a similar study conducted in the same

Table 3
Indicators of the performance of *Rumex acetosella* (n = 20) planted together with *Lolium multiflorum*. The experiment was established in September 2021 at two elevations and harvested in May 2022 along an elevation gradient in Quilcas, Junin region, Peru. Soil management treatments are sheep manure (organic) vs. synthetic fertilizer application (synthetic). Values represent means, with standard errors provided beneath each mean in parentheses. P-values are provided for the effects of elevation (E), management type (M) and their interaction, with significant effects (P ≤ 0.05) in bold font.

		Lower elevation		Higher elevation		*p*-values		
Indicator	**Unit**	**Organic**	**Synthetic**	**Organic**	**Synthetic**	**Elevation (E)**	**Management (M)**	**E x M**
Aboveground biomass	g m^{-2}	112.4 (70.52)	1.2 (0.91)	56.8 (15.17)	1.27 (0.21)	0.804	**<.001**	0.815
Belowground biomass	g m^{-2}	96.8 (43.04)	8.2 (6.96)	33.3 (7.47)	4.6 (1.49)	0.204	**<.001**	0.533
Root:shoot ratio	-	2.09 (0.84)	5.58 (1.48)	0.68 (0.12)	4.36 (1.27)	0.101	**0.003**	0.718
Plant height	cm	24.8 (3.99)	8.5 (3.50)	24.3 (1.88)	11.1 (1.46)	0.377	**<.001**	0.552
Survival rate*	%	75 (11.18)	50 (0.00)	100 (0.00)	75 (11.18)	**<.001**	**<.001**	0.095

* For the analysis of this indicator the four mesocosms where R. acetosella did not survive were also included (n = 24), survival rate was measured at the ned of the season after initial replant.

Table 4
Indicators of the performance of *Pennistum clandestinum* (n = 24) planted together with *Lolium multiflorum*. The experiment was established in September 2021 at two elevations and harvested in May 2022 along an elevation gradient in Quilcas, Junin region, Peru. Soil management treatments are sheep manure (organic) vs. synthetic fertilizer application (synthetic). Values represent means, with standard errors provided beneath each mean in parentheses. P-values are provided for the effects of elevation (E), management type (M) and their interaction, with significant effects (P ≤ 0.05) in bold font.

		Lower elevation		Higher elevation		*p*-values		
Indicator	**Unit**	**Organic**	**Synthetic**	**Organic**	**Synthetic**	**Elevation (E)**	**Management (M)**	**E x M**
Aboveground biomass	g m^{-2}	26.7 (5.92)	24.7 (5.68)	8.71 (3.85)	7.23 (1.66)	**0.001**	0.940	0.682
Belowground biomass	g m^{-2}	129.6 (28.08)	162.4 (31.63)	12.5 (2.47)	27.7 (6.13)	**<.001**	**0.045**	0.236
Root:shoot ratio	-	6.31 (1.51)	7.73 (1.34)	3.23 (1.70)	4.72 (1.36)	**0.013**	0.156	0.675
Plant height	cm	10.3 (1.56)	9.3 (0.66)	5.2 (0.76)	5.3 (0.81)	**<.001**	0.685	0.571
Survival rate	%	100 (0.00)	100 (0.00)	75 (11.18)	83 (10.54)	**0.013**	0.594	0.594

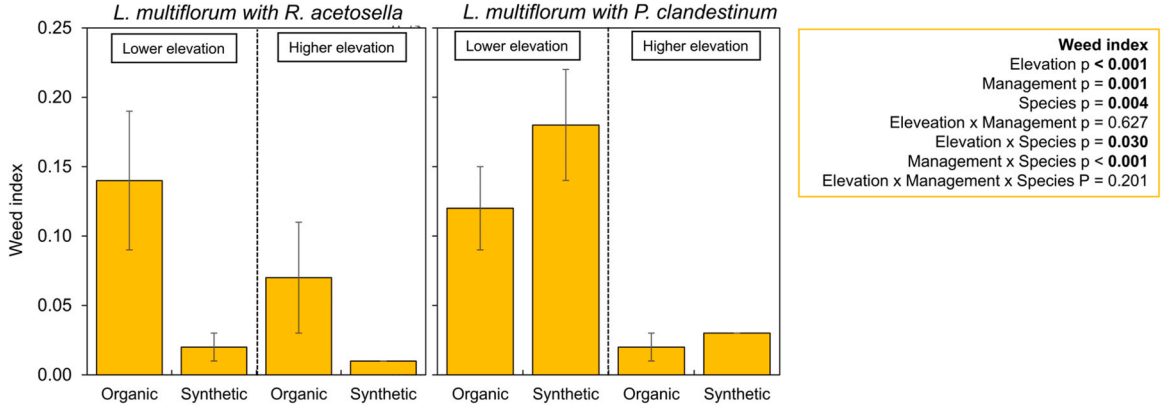


Fig. 3. Mean weed index (i.e., weed biomass as a proportion of total biomass) in mesocosms including both the forage crop *Lolium multiflorum* and the common Andean weeds (*Rumex acetosella* or *Pennisetum clandestinum*). Trials were installed at two elevations (3520 and 3740 m a.s.l.). Bars represent the mean ± standard error. Soil management treatments are sheep manure (organic) or synthetic fertilizer application (conventional). Trials were established in the community of Quilcas in the Junín region of Peru in September of 2021 and harvested in May of 2022. P-values for elevation, nutrient management and weed species and their interactions are presented to the right of the figure.

region, Visscher et al. (2024) found organic soil nutrient inputs to better support the performance of traditional Andean crops under the impact of climate change. Specifically, they observed that the tuber, *Oxalis tuberosa* (Oca), performed better with manure compared to synthetic inputs across a range of elevations, which largely aligns with this study's findings. This suggests that with warming climates becoming more common in the mountain landscapes of the Andes, organic fertilizer may better support plant performance compared to synthetic fertilizers, at least for some important crops. Additionally, it is worth considering that crops like Oca, which have experienced less breeding selection under higher input, fertilizer-based systems, might be better adapted to organic nutrient sources. However, to provide more precise

recommendations for farmers on how to amend their crops, more plant-specific research is necessary to address continuing knowledge gaps in this area.

While organic inputs generally increase the growth of *L. multiflorum,* the effect on weed species development depended on the species. For instance, the competitive ability of *R. acetosella* improved with organic inputs, likely because the manure could have provided essential micronutrients that favor *R. acetosella* for growth, while *P. clandestinum* was relatively less sensitive to the type of nutrient input. In this study, manure was mutually beneficial for both the crop and the weed. Organic nutrient sources typically provide a balance of essential nutrients such as N, P, and K, as well as with other important macro- and micronutrients (Fe, Zn, Cu, Mn, B, Mo; Shaji et al., 2021). Decomposing manure tends to release nutrients slowly which can ensure that forage crop and weeds at both elevations have a consistent supply of nutrients (Zhang et al., 2020). Furthermore, organic matter addition can help to buffer against acidity, support P availability, improve disease resistance (Rosskopf et al., 2020; Mutai et al., 2024), and may increase water capture (i.e., infiltration) and retention, which can be crucial for yields within rain-fed systems (Sharma and Chetani, 2017, Bulluck et al., 2002).

The significant management by species interaction observed for the weed index further emphasizes the importance of considering different management strategies for specific weed species. Soil amendments to annual cropping systems can benefit weeds as well as crops, sometimes decreasing or eliminating the benefits of fertilization (Little et al., 2021). For instance, in this study the weed index was higher under *R. acetosella* when amended organically, while *P. clandestinum* appeared to be more competitive when synthetic fertilizers were applied. The interplay between fertility management and integrated weed management remains an important topic. In a comprehensive review Little et al. (2021) synthesized findings from recent studies and reported that the type of nutrient source (e.g., synthetic vs. organic) can have varying impacts on weed-crop competition and overall crop yield, even within the same plant family. They listed numerous studies where increased nutrient inputs (organic and synthetic) boosted not only the biomass of the primary crop under consideration but also enhanced the competitive ability of certain weed species. In this study, organic inputs benefited both the crop and the weed *R. acetosella*, highlighting the complexity of nutrient dynamics and the need for context-specific management strategies. For instance, smallholders may need to consider alternative organic weed control measures, such as mechanical removal or the use of organic herbicides, to help mitigate the growth of *R. acetosella* if they continue to rely on traditional nutrient management strategies. Additionally, there is inherent uncertainty associated with nutrient availability in organic or manure treatments, which can influence the degree to which these inputs affect crop and weed growth dynamics. Hence, nutrient source and rate effects on weed competitiveness is species but also context dependent (Blackshaw, 2008).

This study's findings highlight several areas of uncertainty, particularly concerning the specific mechanisms by which elevation and associated microclimatic factors influence weed dynamics and crop-weed interactions. The study was limited to two elevations, which restricts understanding of the broader range of conditions present in the Andean region. It is also noted that, while the mesocosm setup provided valuable control over experimental variables, it may have introduced certain biases by not fully replicating the complexity of natural field conditions, such as microclimatic variations and biotic interactions. Despite these potential limitations, the findings remain robust, with the observed effects of organic inputs on crop-weed dynamics likely reflecting key processes in real-world agricultural systems. Future research could address this limitation by incorporating more study sites at varying elevations and conducting multi-year trials across diverse Andean microclimates. This would provide a more comprehensive understanding of how these factors interact and threaten agricultural systems in the region, leading to more robust and generalizable findings.

5. Conclusions

It was hypothesized that increasing temperatures along the elevation gradient would confer a competitive advantage to weeds over the forage species considered here. Indeed, the findings indicate that *L. multiflorum* exhibits reduced biomass in warmer conditions, and that competition from weeds generally increased at the lower elevation (warmer) site, raising concerns about global warming and associated impacts on forage production and related management challenges. Our findings align with previous findings that temperature and soil moisture significantly influence plant resource allocation, such that *L. multiflorum* invests relatively more belowground at lower elevations to cope with water stress. Species-specific responses to warming highlight the need for targeted weed management. In particular, *P. clandestinum* competes better under warming conditions, posing a threat to crop production in Andean agroecosystems. Conversely, *R. acetosella* seems to better survive at higher elevations, indicating that weed management must be tailored to climate-specific conditions. Nutrient management further complicates weed dynamics. Organic inputs enhance *L. multiflorum* productivity, especially at higher elevations, but also benefit weeds like *R. acetosella*. This emphasizes the importance of appropriate nutrient sources and the need to plant competitive crops to manage weed pressure. At the same time, the findings of this study suggest that continued reliance on traditional nutrient management, instead of synthetic fertilizers, may help support forage productivity and resilience under changing climate conditions. For Andean smallholders and smallholder farmers globally, the implications are significant; as climate change progresses, warming conditions may exacerbate weed pressures, threatening crop production and food security. Effective weed management strategies and adaptive agricultural practices will be essential to mitigate these impacts and sustain agricultural productivity.

CRediT authorship contribution statement

Huaraca Jhon: Writing – review & editing, Project administration, Investigation. **Vanek Steven:** Writing – review & editing, Visualization, Supervision, Conceptualization. **Visscher Anna M.:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Olivera Edgar:** Writing – original draft, Project administration, Investigation. **Meza Katherin:** Writing – review & editing, Methodology, Investigation. **Ccanto Raul:** Writing – review & editing, Methodology, Investigation. **Mendoza Jamelith:** Project administration, Investigation. **Fonte Steven J.:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

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.

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Data Availability

Data will be made available on request.

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