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Traditional soil fertility management ameliorates climate change impacts on traditional Andean crops within smallholder farming systems

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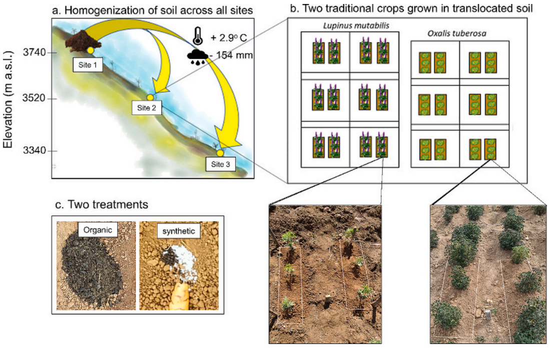
HIGHLIGHTS

- Traditional crops were tested across elevations as a proxy for climate warming.
- *Lupinus mutabilis and Oxalis tuberosa* mature faster at lower, warmer elevations.
- Growth of *Oxalis tuberosa* declined at the lowest elevation.
- *Oxalis tuberosa* performed better with manure vs. synthetic inputs at all elevations.
- Elevation and nutrient management had minimal impact on *Lupinus mutabilis* growth.

GRAPHICAL ABSTRACT



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ABSTRACT

Global changes, particularly rising temperatures, threaten food security in smallholder mountain communities by impacting the suitability of cultivation areas for many crops. Land-use intensification, associated with agrochemical use and tillage, threatens soil health and overall agroecosystem resilience. In the Andean region, farmers often cultivate crops at multiple elevations. Warming climates have led to a shift in cultivation upslope, but this is not feasible in many areas. Traditional soil fertility management practices together with a focus on traditional (orphan) crops offers promise to cope with rapid climate warming in the region. To understand the impacts of warming and changing nutrient management, we established two side-by-side experiments using the traditional Andean crops *Oxalis tuberosa* (Oca) and *Lupinus mutabilis* (Tarwi) at three elevations, each with two fertility treatments (organic and synthetic). Soil and climate data (i.e., temperature and precipitation) were collected throughout the growing season, and crop performance was evaluated through impacts on yield and other growth metrics (e.g., biomass, pest incidence). We used two-way ANOVA to assess the influence of site (elevation) and management type (organic vs. synthetic) on crop performance. Results indicated that warmer climates (i.e., lowest elevation) negatively impact the production and performance of *O. tuberosa*, but that

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organic fertilization (sheep manure) can help maintain crop yield and biomass production in warmer conditions relatively to synthetic nutrient inputs. In contrast, *L. mutabilis* showed accelerated growth in warmer conditions, but grain yield and biomass production were not significantly affected by site and showed no interaction with nutrient management. Our findings highlight that climate warming represents a serious threat to small-scale crop production in the Peruvian Andes and could cause severe declines in the production of locally important crops. Additionally, the continued reliance on traditional crops with organic inputs, instead of synthetic fertilizers, may help support agricultural productivity and resilience under climate change.

1. Introduction

Climate change has been shown to have variable and potentially severe consequences for agricultural production and food security around the globe (Rosenzweig and Parry, 1994; Parry, 2019). The tropical Andean region is considered to be particularly vulnerable to the impacts of climate warming due to its rugged mountain environments that harbour a wide variety of endemic plant species and other organisms (Vuille and Bradley, 2000; Bush et al., 2010; Anderson et al., 2011; Challinor et al., 2014). Additionally, higher elevations are thought to experience more pronounced temperature increases and changes in precipitation patterns (Urrutia and Vuille, 2009which can lead to crop yield reductions and food insecurity in rural Andean communities (Perez et al., 2010; Fiebig-Wittmaack et al., 2012; Tito et al., 2018). Much of the Andes is home to indigenous communities who have lived in the region for many generations and have developed deep cultural, social, and economic ties to the land and its resources. Thus, climate warming is of great concern in the Andean region as it threatens to displace these communities and erode their traditional ways of life (Boillat and Berkes, 2013; Rolando et al., 2017). Increasing temperatures can lead to increased frequency and severity of drought, as well as higher incidence of pests and disease, further reducing crop yields (Dangles et al., 2013; Tito et al., 2018; Raza et al., 2019). Additionally, changes in the timing of the rainy season can also disrupt the time of crop planting and harvest, with important implications for crop performance and the stability of production (Urrutia and Vuille, 2009). Accordingly, the understanding of the likely impacts of climate warming on traditional cropping systems is crucial to developing farming strategies that can help farmers to adapt to changing conditions and to ensure food security for rural communities. In the absences of clear adaptation strategies, local Andean farmers could face significant economic losses, potentially up to \$2300 ha^{-1} annually (Tito et al., 2018). Management strategies to mitigate these impacts currently include shifting the cultivation of crops to higher elevations or latitudes (Skarbø and van der Molen, 2016) and the promotion of traditional ecological knowledge and farmer skills (Berkes et al., 2000). Other options include transitioning to crops and varieties that are more resilient to droughts and high temperatures, adjusting planting dates, and implementing water-efficient irrigation systems (Korres et al., 2016; Raza et al., 2019).

Along with climate warming, other global drivers (e.g., shifting market demands, labour availability, land tenure, and access to synthetic agrochemicals) are leading to the intensification of land-use and high-input management throughout the Andes (Wiegers et al., 1999; Vanek et al., 2020). For example, while Andean farmers have long relied on organic nutrient sources such as animal manure to maintain soil health and agricultural productivity, the use of synthetic fertilizers to meet crop nutrient demands is becoming more common in many areas (Fonte et al., 2012; Caulfield et al., 2019; Visscher et al., 2020). Despite the many benefits of organic inputs such as manure for soil health (Rayne and Aula, 2020), synthetic fertilizers typically release nutrients more quickly and are easier to transport than manure, and thus are more attractive to farmers in many ways (Bulluck III et al., 2002). Nonetheless, synthetic fertilizers may have negative consequences for the environment, such as increased greenhouse gas emissions and pollution of water resources (Kumar et al., 2019; Zerbe, 2022). Additionally, synthetic fertilizers may lead to soil degradation, soil organic matter decline, and reduced productivity in the long-term, especially when used to fully replace organic nutrient sources (Drinkwater and Snapp, 2022). Organic inputs typically result in a more sustained nutrient release, but slower growth response. The relative effectiveness of organic inputs vs. synthetic fertilizers in the short term often depends on soil conditions and climate related effects (Geisseler and Scow, 2014). For instance, in areas with heavy rainfall and/or coarse texture soils, synthetic fertilizers may be especially prone to loss via leaching, runoff and/or gaseous loses, thus reducing their effectiveness. Organic inputs are typically less susceptible to such losses and can provide numerous benefits to soil structure, nutrient retention, and soil biological activity (Bulluck III et al., 2002; Murphy et al., 2016). These soil health benefits can support improved plant resistance against pests and diseases and enhance the overall resilience of agricultural system to multiple environmental stresses associated with climate warming (Sharma and Chetani, 2017); however, the potential for organic nutrient management strategies to mitigate the effects of climate change remain poorly understood.

The vulnerability of staple crops such as maize, wheat and rice to climate warming is becoming more apparent (Mabhaudhi et al., 2019), posing a significant threat to global food security. Diversification of our food systems offers great promise to increase the resilience of agricultural production (Kremen and Merenlender, 2018). Less studied crops, often referred to as orphan crops, are those that have been traditionally grown and consumed by local communities but have been overlooked by mainstream agriculture due to reasons such as low yield, poor marketability, and lack of research and development (Dawson et al., 2007; Tadele, 2019). There is a growing recognition that these crops are often more resilient to climate change and can play a significant role in food security, nutrition, and biodiversity conservation (Padulosi et al., 2002; Bvenura and Afolayan, 2015). Furthermore, orphan crops often have unique nutritional and health benefits (i.e., vitamins, minerals, and antioxidants), which can help address malnutrition and diet-related diseases (Kumar and Bhalothia, 2020). The high Andean region is known for its rich biodiversity and cultural heritage, which includes traditional crops such as *Chenopodium quinoa* Willd. (quinoa), *Amaranthus caudatus* L. (amaranth), *Oxalis tuberosa* Molina (oca), and *Lupinus mutabilis* Sweet (tarwi; Jacobsen et al., 2003). With rapidly growing impacts of climate warming, the cultivation of traditional Andean crops may play an important role in building resilient and sustainable local food systems. However, realizing the full potential of Andean crops, requires increased investment in research and supportive policies and market linkages. While extensive research has focused on the vulnerability of staple crops like maize, wheat, and rice to climate change, there remains a significant knowledge gap concerning the resilience and adaptability of traditional crops under changing climatic and soil fertility conditions.

In light of the complex challenges posed by climate warming and other global drivers, this study aims to examine the effect of increasing temperatures on two understudied, locally important crops in the Andes, *Oxalis tuberosa* and *Lupinus mutabilis*. Additionally, we sought to understand how changes in climate interact with altered soil fertility management (synthetic fertilizer vs. traditional manure inputs). To address these questions, we set up a field study to capitalize on an elevational gradient that reflects potential shifts in future climate warming. This approach offers a valuable means to study how climate and other factors influence the distribution and performance of different species (Tito et al., 2020). In our experiment, *O. tuberosa* and *L. mutabilis* were planted at different elevations (and thus temperatures) to simulate future climatic scenarios for the tropical Andes, where temperatures are expected to rise approximately 0.3 °C per decade (Vuille and Bradley, 2000). At each elevation we tested the effect of manure vs. synthetic fertilizer on the growth and performance of these crops. We hypothesize that: i) the productivity of traditional crops declines at lower elevations, due to increasing temperature and associated stress related to drought and/or pest pressure; ii) organic inputs better support crop performance (i.e., yield, biomass production, pest resistance) under warmer climatic conditions than synthetic fertilizer, since organic inputs can better support multiple soil functions related to nutrient provision, water dynamics and pest regulation. By focusing on these understudied yet locally significant crops in the Andean region, this study has broader implications for agricultural policies and practices that could enhance climate resilience and food security in vulnerable high-altitude communities.

2. Materials and methods

2.1. Study area

This study was conducted in the central Peruvian Andes, in the community of Quilcas, near the city of Huancayo, in the Junín region (11°56.252′S, 75°15.554′W). Land management in the community is divided into a low-mid elevation zone (3200–3800 m a.s.l.), where most of the population lives and where most agricultural production takes place, and a high elevation zone (> 3800 m a.s.l.) mainly used for grazing and low intensity production of potato landraces. The dominant soils in this mountainous region are classified as Inceptisols (USDA taxonomy) with neutral to acidic pH and texture ranging from loamy to clayey loams. Mean annual precipitation averages approximately at 700 mm, with most rain falling from September to April. Average monthly temperatures vary between 12 and 16 °C in July and November respectively (Garcia, 2011). Decreasing roughly 0.7 °C with every 100 m gain in elevation (Table 1; Fig. S1).

The range of elevations and associated climatic variability in the region allows local farmers (~4000 inhabitants) to cultivate a wide range of crops and crop varieties. Local farmers typically cultivate several small (<1 ha) plots of land, located at different elevations. These plots typically involve a complex 5–7-years crop rotation, consisting of potato (*Solanum tuberosum* L.), followed by Andean tubers (e.g., *O. tuberosa*), legumes (e.g., *Vicia faba* L. and *L. mutabilis*), corn (*Zea mays* L.), and/or forages (*Lolium multiflorum* Lam. and *Trifolium pratense* L.), followed by a 2–3-years traditional fallow (Vanek et al., 2020). Production is mainly for home consumption, but some crops and animal products are sold at local markets.

From the traditional Andean crops cultivated in the Quilcas community, we chose *O. tuberosa* and L. *mutabilis* in consultation with smallholder and local stakeholders. *L. mutabilis*, or Andean lupine (locally known as tarwi), is a tall, fibrous legume typically grown for its grain and grows in a range from 1500 up to 3800 m a.s.l. (Tapia Nuñez, 2015), while *O. tuberosa*, locally known as oca, is a small tuber that grows well from altitudes of 2800 up to 4000 m a.s.l. (Moscoe et al., 2017; Moscoe and Emshwiller, 2016). *L. mutabilis* and *O. tuberosa* are generally grown using only organic nutrient sources (e.g., sheep manure), usually without mechanized tillage and with limited use of agrochemicals. Such small-scale and low-input agriculture is typical for most of the Andean regions of Peru (Halloy et al., 2005). Nevertheless, the use of synthetic fertilizers and mechanized tillage (where plot size is large enough) is becoming more common (Fonte et al., 2012; Caulfield et al., 2019).

2.2. Experimental design and management

In September 2021, we installed two side by side experiments using the crops *O. tuberosa* and *L. mutabilis*, each grown at three elevations (3340, 3520, and 3740 m; Fig. 1). The elevational gradient used in this experiment was designed to simulate warming climate conditions in the study area for the next ~50 to 100 years based on increases of 1.6 °C and 2.9 °C (Vuille and Bradley, 2000). Each site was selected to have a similar slope (7–9 %), aspect (260–276 W), and management history. At each of the three elevations, two fertility treatments were applied – one using local (dried) sheep manure as a nutrient source (hereafter referred to as 'organic' treatment) and another based on synthetic fertilizer inputs ('synthetic' treatment, details below). These two treatments were randomly applied to small plots (~2.5 m × 3 m) and replicated three times at each elevation, for a total of 18 plots per crop (Fig. 2). To minimize the effect of potential soil differences between elevations, we collected soil from a common site at 3700 m.a.s.l. (located near the highest experimental site) and transferred this 'reference soil' to plots at each of the three elevation sites. After being collected from a depth of 0–20 cm, the reference soil was carefully blended using shovels and then transported by truck to the three sites. Soil was applied to two microplots, located in the center rows of each replicate plot (Figs. 1 and 2). Microplots were created by excavating small rectangular pits (0.45 m × 1.05 m for L. *mutabilis* or 0.35 m × 1.05 m for *O. tuberosa*) to a depth of

Table 1
Site characteristics for the three experimental sites along an elevational gradient in the community of Quilcas, Junin region, Peru.

Climate and soil factors	Measurement unit	Site 1	Site 2	Site 3
Latitude	-	11° 55′ 55”	11° 55′ 51”	11° 55′ 13”
Longitude	-	75° 15′ 25”	75° 14′ 34”	75° 14′ 11”
Elevation	m a.s.l.	3340	3520	3740
Slope	o	7	8.5	9
Aspect	-	263 W	276 W	260 W
Temperature[a]	°C year^{-1}*	12.60	10.97	9.73
Temperature range	°C year^{-1}	5.62–26.46	3.55–24.77	3.03–25.71
Precipitation[b]	mm	584.4	630.9	738.4
Soil moisture content[c]	g water g dry soil^{-1}	0.14	0.18	0.25
Soil moisture content range	g water g dry soil^{-1}	0.04–0.29	0.05–0.31	0.10–0.56
Organic Matter[d]	g kg^{-1}	23.5	34.9	44.3
pH	1:1	5.1	4.4	4.3
Available P	mg kg^{-1}	10.2	6.8	5.7
Available K	mg kg^{-1}	192	126	143
Texture (sand/silt/clay)	%	44/30/26	40/34/26	44/30/26

[a] Mean daily temperature measured over growing season.
[b] Precipitation was measured from October 2021 until June 2022 (8 months).
[c] Mean weekly soil moisture content measured over growing season.
[d] Soil data corresponds to samples taken from 0 to 10 cm layer at each site.

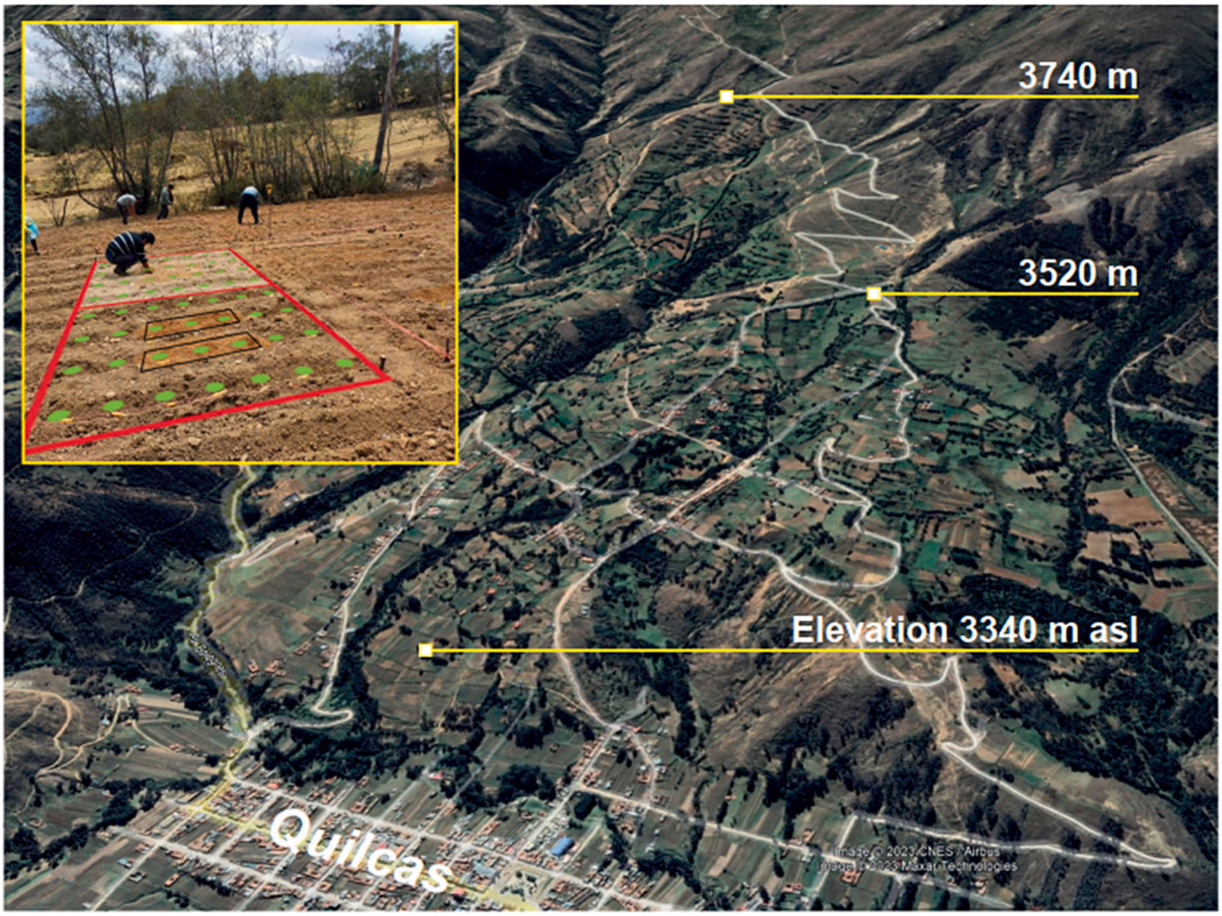

Fig. 1. Visual representation of the Quilcas mountainside experiment, which aimed to evaluate the performance of two traditional Andean crops, *Lupinus mutabilis* and *Oxalis tuberosa*, under warming conditions. The satellite image indicates the locations of the experimental sites, while the black rectangles visible in the close-up photo (upper left) indicate the micro-plots filled with reference soil. This soil was transferred from 3700 m a.s.l. to lower elevations to ensure that growth conditions were similar across all sites.

20 cm and filling them with homogenized reference soil. Each soil pit with translocated reference soil had three plants growing in it, totalling six plants per small plot, hence a total of 36 plants per species per elevation (Fig. 2). The remaining areas of the plots were prepared and sown using the same management as the micro-plot but employing the local soil present at the experimental site.

During the design, implementation, and maintenance of the experiment, we tried to follow as closely as possible the agronomic practices employed by local farmers. The local soil in the study plots, surrounding each micro-plots, was thoroughly mixed and turned to a depth of 20 cm and mounded up before planting. A single landrace of *O. tuberosa (‘amarillio’)* and a variety of L. *mutabilis* (‘*Andenes* INIA’) were obtained from local vendors in Quilcas and used across all three elevations. For the cultivation of *O. tuberosa*, vegetative propagules were used, while L. *mutabilis* was planted from seed, reflecting traditional cultivation methods within the community. Both *O. tuberosa* and L. *mutabilis* have a rich history of cultivation in the region. Their adaptability range, based on both traditional knowledge and scientific investigations (Moscoe et al., 2017; Gulisano et al., 2019), has shown resilience to various environmental stressors. While our study did not incorporate landrace and cultivar diversity as a variable, we acknowledge its significance and potential impact, particularly in the context of climate change. *O. tuberosa* seeds were sown (one small tuber per hole) at 40 cm spacing within rows, and 70 cm between rows (i.e., 28 plants per plot). Half of the *O. tuberosa* plots were amended with synthetic fertilizer at time of planting, at a rate of 60 kg N ha^{-1}, 20 kg P ha^{-1}, and 28 kg K ha^{-1} (using a mix of diammonium phosphate, potassium chloride, and urea) based on local recommendations (Table 2). Additions of sheep manure in the organic treatment were based on N content of the manure and the assumption that 50 % of the N would become available over the course of the growing season (132 kg N/ 66 kg P/ 118.7 kg K ha^{-1}). *L. mutabilis* was planted (three seeds per hole) at a spacing of 35 cm within rows, and 70 cm between rows (i.e., 28 plants per plot). Plots were amended with fertilizer (2.9 kg N/ 16 kg P/ 21 kg K ha^{-1}) or sheep manure (70.4 kg N/ 35.2 kg P/ 63.1 kg K ha^{-1}) based on the recommendations for P rather than N, since L. *mutabilis* is a legume and not typically fertilized with N, again assuming that 50 % of the P would become available over the growing season. In all cases, synthetic fertilizer was applied in small holes next to the plant to prevent damage to seeds and tubers, while manure was mixed with the soil covering the seeds and tubers.

When *O. tuberosa* plants attained a height of 10–15 cm, soil was mounded up around the base of all plants in each plot (∼ 2 kg dry weight from the corresponding local or reference soil). This same procedure was repeated when plants were 30–35 cm in height. This technique, known as hilling, is commonly employed by local farmers to facilitate plant development and support tuber growth. In the *O. tuberosa* trial no synthetic pesticides were applied. *L. mutabilis* plants that germinated on the reference soil were thinned to just one plant per hole when plants attained a height of 10–15 cm. L. *mutabilis* in the plots was affected by several insects and pathogens including *Feltia subterranea* F. (cutworm), *Apion* sp. (weevil), *Frankliniella* spp. (thrips), *Ascochyta* sp. and *Pharma lupini* (fungi causing stem burn), and *Uromyces lupini* Berk. & M.A. Curtis (fungi causing leaf rust). Therefore, insecticides (thiamethoxam and lambda-cyhalothrin) and fungicides (fosetyl-aluminium and

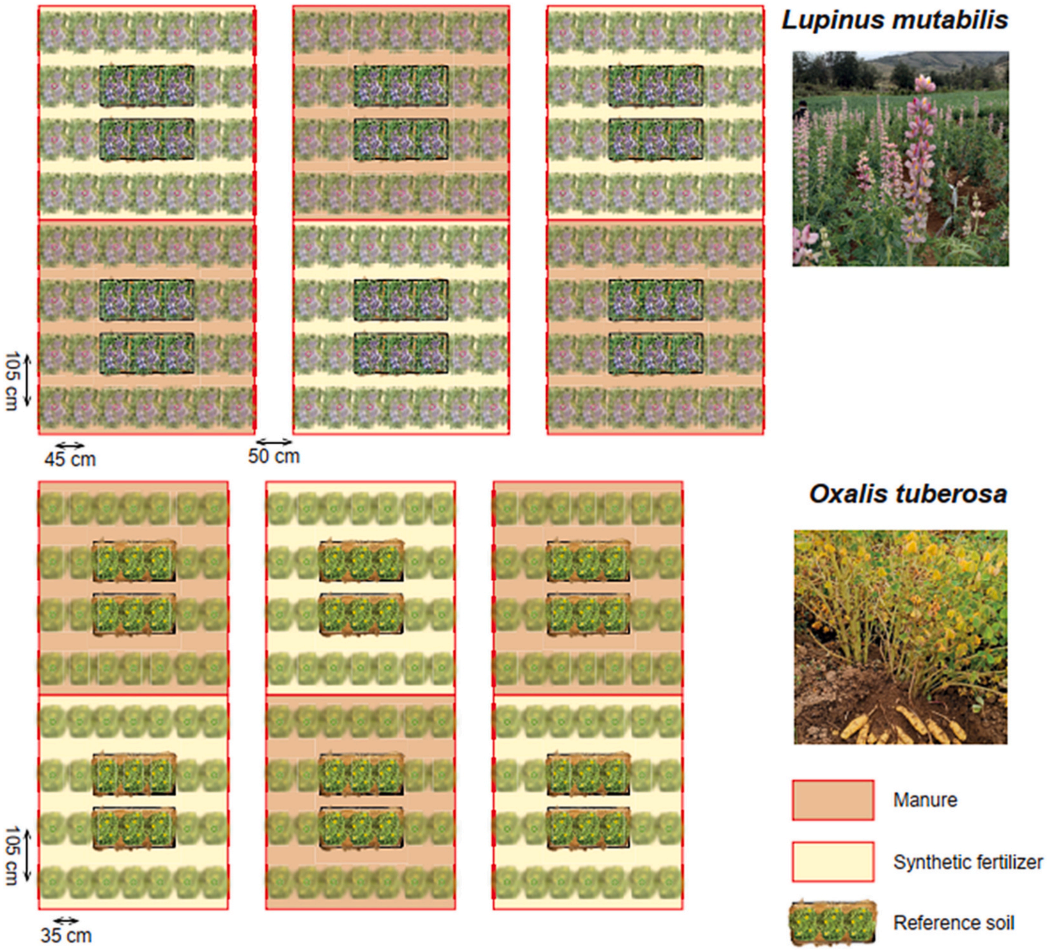

Fig. 2. The two side-by-side experiments conducted in this study involved the use of *Oxalis tuberosa* and *Lupinus mutabilis* crops, each grown at three elevations (3340, 3520, and 3740 m a.s.l.) representing a climatic gradient. At each experimental site (3340, 3520, 3740 m a.s.l.), a total of 12 small plots were established, with six plots designated for L. *mutabilis* and six for *O. tuberosa*. Each plot was either amended with manure or synthetic fertilizer. Inside each plot, six plants were grown on reference soil, resulting in a total of 36 plants per species at each experimental site.

Table 2
Input rates for organic and synthetic nutrient treatments applied to crops *Oxalis tuberosa* and *Lupinus mutabilis* within the trial.

Nutrient application rates[a,b,c]	Unit	Nutrients		
		N	P	K
Organic *O. tuberosa*	kg ha^{-1}	132	66.0	118.7
Synthetic *O. tuberosa*	kg ha^{-1}	60	20	28
Organic L. *mutabilis*	kg ha^{-1}	70.4	35.2	63.1
Synthetic L. *mutabilis*	kg ha^{-1}	2.9	16	21

[a] Diammonium phosphate contains 18 % N.

[b] Note: manure application for L. *mutabilis* plants were based on P needs and for oca plants on N needs.

[c] Sheep manure (2.48 % N/ 1.24 % P/ 2.23 % K).

tebuconazole) were applied as needed with a backpack sprayer (equivalent application rate across all elevations) and in accordance with local recommendations.

2.3. Environmental data collection and field monitoring

To characterize soils at each site, 15 sub-samples were collected with a shovel to a depth of 10 cm and composited at the time of planting. Samples from the local soil and reference soil were air-dried upon return to the lab and sent to the Soil and Plant Laboratory at La Molina University (Lima, Peru) for analysis. Soil analyses included texture by hydrometer method (Bouyoucos, 1962), total soil organic matter (SOM; Walkley-Black) available phosphorus (Olsen extraction), available potassium (ammonium acetate extraction), and pH (1:1 water:soil), according to methods outlined in Estefan et al. (2013). Results from the soil analysis can be found in Table 1.

To monitor climatic data, we installed a weather station (HOBO Rain Gauge Data Logger RG3) and two temperature sensors (iButton DS1921G-F5) at each elevation. Each weather station (logging precipitation and temperature) was 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 (Fig. S1). Soil moisture content (1–8 cm depth) was measured weekly over the growing season by collecting a composite soil sample (~ 250 g) from a sub-set of representative treatment plots at each research site. Upon return to the lab, a sub-sample of this soil was oven-dried at 60 °C to determine gravimetric moisture content.

Phenotypic characterization of L. *mutabilis* plants (grown on the reference soil) was carried out weekly over the entire growing season, to assess the plants' growth height, days to first emergence (when 80 % of plants reached 2 cm), days to first flower, days to full flowering (when 67 % of plants had at least one open flower), days until first pod, number of pods on central stem and number of secondary and tertiary stems with pods. Given that *O. tuberosa* is a tuber, aboveground characteristics were not closely monitored during the growing season, and only plant height was measured weekly until senescence.

2.4. Final field evaluation and yield

In early May of 2022, *O. tuberosa* plants were harvested by first cutting all vegetative material at 1 cm above the soil surface to assess aboveground biomass. Total fresh biomass was recorded in the field and a sub-sample of ~200 g was taken to the lab and dried at 60 °C to determine biomass on a dry weight basis. Within each microplot containing the reference soil we first harvested the six *O. tuberosa* plants by carefully removing all tubers manually for each plant. We then harvested the rest of the tubers in each 2.5 × 3 m plot, from the local soil. All *O. tuberosa* tubers harvested were assigned to one of three categories: 1) high-value commercial ($>$ 12 g), 2) non-commercial ($<$ 12 g), and 3) those damaged mechanically (i.e., during harvest) or by blight, insects or rotting. Pest pressure was mainly due to weevil (*Premnotrypes suturicallus* Kuschel, 1956 and *Premnotrypes piercei* Alcalá, 1979) and late blight (*Phytophthora infestans* (Mont.) De Bary). Each category of *O. tuberosa* tubers was subsequently counted and weighed (separately for each plant) using a field scale. Ten representative *O. tuberosa* tubers per plant were dried at 60^o C to determine dry weight. Only high-value commercial and non-commercial tubers are considered in our evaluation of total yield. We further estimated the percentage of commercial, non-commercial, and damaged tubers. Harvest index was calculated dividing the dry weight aboveground biomass by the dry weight of the belowground tuber biomass.

L. mutabilis plants were harvested at the end of May 2022. It is important to note that L. *mutabilis* plants are indeterminate, hence plants continued to produce pods even when the central or secondary branches were already mature and dry. Immediately prior to harvest, we evaluated all six plants in the reference soil microplot and six representative plants in the surrounding plot for plant height as well as number of secondary and tertiary stems. Within each plot, we first harvested the six plants grown in the reference soil microplot by cutting each plant at 1 cm above the soil surface and removing all physiologically mature pods from each plant. Each pod was further sorted into damaged and undamaged pods. Flowers and pods that were not fully formed from the tertiary stems were grouped together with stems and leaves and considered as non-grain fresh biomass. All aboveground plant components were weighed in the field. Then the physiologically mature pods, as well as a sub-sample of fresh biomass, were returned to the lab and dried at 60^o C. Pods of each plant were peeled to determine 10-seed, 50-seed weight, and number and weight of damaged seeds (in 100 seeds). For each L. *mutabilis* plant, we calculated harvest index by dividing total grain yield by total dry matter plant biomass (including pods).

2.5. Statistical analysis

To understand how site (i.e., locations at 3340, 3520, 3740 m a.s.l.; treated as a categorical variable) and management type (organic vs. synthetic nutrient inputs) influenced crop performance, two-way ANOVAs were conducted separately for each crop, considering all plants that reached the reproductive phase (i.e., producing flowers, fruits, and seeds) in the reference soil of each plot ($n = 18$). Predictor variables in this model included site/elevation, fertility management treatment, and the site x fertility management interaction. Where needed, (natural) log or square root transformations were applied to response variables (i.e., yield or harvest index) to meet assumptions of homoscedasticity and normality. All analyses were carried out using the JMP pro 15.0 software (SAS Institute, 2022).

3. Results

3.1. Site variation in climate and soils

Mean daily temperature differed by 2.9 °C between the highest (3740 m) and lowest (3340 m) elevations (Table 1), while growing season precipitation (October 2021 and June 2022) decreased from 738 mm at the highest site to just 584 mm at the lowest elevation. Soil analyses revealed that local soils varied strongly across sites, especially SOM, which increased from 17.1 g kg^{-1} at the lower elevation up to 44.3 g kg^{-1} at the highest elevation. Soil quality indicators (i.e., SOM, pH, available P and K) of the reference soil did not differ significantly between the different research sites.

3.2. Effects of temperature and management on Oxalis tuberosa

Overall survival rate for *O. tuberosa* (oca) plants was 99 % in the microplots, with no significant differences between treatments or sites (Table 3). Total tuber yield was strongly affected by site such that at the middle elevation produced the highest yield (6.8 kg m^{-2}) and the lowest site yielded the least (3.5 kg m^{-2}; $p = 0.006$). Comparable trends were observed when dividing this into commercial ($p = 0.004$) and non-commercial yield ($p = 0.007$), representing 43.6 and 24.7 % of the total belowground biomass, respectively (Table 3). Additionally, total yields were roughly double in plots receiving organic vs. synthetic nutrient inputs ($p = 0.003$), with similar trends observed for both commercial yield ($p < 0.001$) and non-commercial yield ($p = 0.001$). Beyond the total amount produced, commercial tubers represented a

Table 3
Indicators of the performance of *Oxalis tuberosa* grown in microplots (with reference soil). Values represent the treatment mean, with standard errors presented underneath each mean in parentheses. *P*-values are provided for two-way ANOVA examining the effects site/elevation (E), management type (M) and their interaction, with significant effects ($P \leq 0.05$) in bold. All data was collected at harvest, in May 2022, in the community of Quilcas, Junin region, Peru.

Indicator	Unit	Site 1 (3340 m)		Site 2 (3520 m)		Site 3 (3740 m)		P-values		
		Organic	Synthetic	Organic	Synthetic	Organic	Synthetic	Elevation (E)	Management (M)	E x M
Survival rate	%	100	100	100	100	94.4	100	0.397	0.337	0.397
		(0.00)	(0.00)	(0.00)	(0.00)	(5.56)	(0.00)			
Days until first flower	N	103	132	103	119	124	142	**0.016**	**0.002**	0.581
		(5.00)	(13.00)	(5.00)	(0.00)	(5.33)	(4.04)			
Total AG plant biomass	kg m^{-2}	2.3	1.1	2.5	2.1	2.3	1.5	0.070	**0.035**	0.522
		(0.27)	(0.31)	(0.23)	(0.12)	(0.24)	(0.07)			
Yield	kg m^{-2}	4.7	2.4	9.1	4.5	6.5	3.4	**0.006**	**0.003**	0.342
		(0.74)	(0.56)	(0.92)	(0.09)	(1.03)	(0.32)			
Commercial yield	kg m^{-2}	3.1	1.1	6.5	2.8	4.6	2.2	**0.004**	**<0.001**	0.344
		(0.62)	(0.43)	(0.82)	(0.19)	(0.92)	(0.16)			
Non-commercial yield	kg m^{-2}	1.7	1.1	2.5	1.7	1.8	1.3	**0.007**	**0.001**	0.634
		(0.15)	(0.17)	(0.17)	(0.11)	(0.27)	(0.24)			
Proportion commercial tubers	%	38.7	31.6	65.5	32.5	56.4	37.0	**0.002**	**<0.001**	**0.007**
		(3.90)	(3.52)	(3.05)	(0.81)	(3.15)	(1.81)			
Proportion non-commercial tubers	%	22.2	35.3	25.6	21.3	21.6	22.4	0.153	0.275	0.064
		(0.96)	(5.03)	(1.46)	(3.63)	(3.28)	(4.10)			
Proportion damaged tubers	%	39.1	33.1	8.9	46.2	22.0	40.6	0.099	**<0.001**	**<0.001**
		(3.05)	(1.65)	(3.35)	(4.04)	(2.52)	(5.67)			

significantly higher proportion of the total belowground biomass produced at the middle (49.0 %) and highest (46.7 %) elevations compared to the lowest site (35.2 %; $p = 0.002$). However, a significant interaction with management ($p = 0.007$) indicated that this effect was more pronounced in plots with organic nutrient sources (Table 3). The proportion of damaged tubers was overall higher in synthetic (40.0 %) vs. organically (23.3 %) managed plots ($p < 0.001$), but a significant interaction ($p < 0.001$) indicated that this trend was only evident at higher elevations. Total aboveground biomass of *O. tuberosa* plants was not influenced by elevation, but a significant management effect ($p = 0.035$) indicates that aboveground plant biomass was generally higher in organic (2.4 kg m^{-2}) vs synthetic (1.6 kg m^{-2}) managed plots. Interestingly, harvest index decreased with warming temperatures, from high to low elevations, ($p < 0.001$), but a significant interaction effect with management ($p = 0.026$) indicated that this trend was more pronounced with synthetic vs. organic nutrient amendments (Fig. 3). Phenotypic traits of *O. tuberosa* plants were also influenced by both elevation and fertilizer management. For instance, elevation significantly influenced the number of days until the first flower appeared ($p = 0.016$), such that plants at the highest elevation took an average of 133 days to reach inflorescence compared to just 118 days and 111 days at the lowest and middle sites, respectively. Also, a significant management effect ($p = 0.002$) indicates that inflorescence is delayed for synthetic managed plots.

3.3. *Effects of temperature and management on Lupinus mutabilis*

Survival rate was somewhat lower for L. *mutabilis* (83 %) than *O. tuberosa*, but there were no significant differences observed between elevations (temperature) or management treatments (Table 4). Grain yield averaged 524.2 g m^{-2} across all plots and did not differ between elevations or fertilizer treatments. While total aboveground plant biomass was not significantly influenced by elevation, the highest elevations generally had more secondary stems per plant compared to the lower elevation sites ($p < 0.043$). The harvest index ($p = 0.016$) was a 30 % higher at the lowest elevation (0.42) compared to the highest elevation (0.32, Fig. 3). Furthermore, harvest index was generally higher in organic vs. synthetic managed plots ($p = 0.037$). The proportion of damaged grains per plant were significantly influenced by elevation ($p = 0.023$; Table 4), such that the lowest rate was at the highest elevation. At the same time, the proportion of damaged pods was significantly higher ($p = 0.042$) in organically managed plots (3.2 %) compared to plots receiving synthetic nutrient inputs (1.0 %). We further observed a strong effect of elevation on certain phenotypic traits of L. *mutabilis*. For example, the appearance of the first pods was much later at the highest elevation (159 days) compared to the low (119 days) and middle (125 days) elevation plots ($p < 0.001$). Plants were also significantly taller ($p < 0.001$) at the middle (144 cm) and high (126 cm) elevations compared to the lowest elevation (92 cm).

4. Discussion

4.1. *Effects on Oxalis tuberosa*

For *O. tuberosa,* production declined by 30–50 % percent when plants were grown at the lowest elevation (relative to the middle and high elevations). Production further declined with synthetic fertilizer inputs, resulting in a 60 % reduction in commercial yield compared to organically fertilized plots at this same elevation. Hence, warmer climate conditions and a shift towards synthetic fertilizer appears to negatively impact the production and performance of *O. tuberosa.* We suspect that the elevated temperature and decreased water availability, due to lower precipitation and higher evapotranspiration, negatively impacted tuber production at the lowest site. Nonetheless, yields observed at the lowest elevation were within the range of expected yields for *O. tuberosa* in the region (INIA, 2023). It is also important to consider the inherent genetic variation and adaptive capacity of traditional crop like *O. tuberosa*. While we only considered one variety in our study, the diversity within and among landraces can play an important role in buffering the impacts of climate change, as different genotypes likely exhibit varying levels of resilience to changing environmental conditions (Brush, 1995). While *O. tuberosa* is commonly grown at altitudes ranging from 2800 to 4000

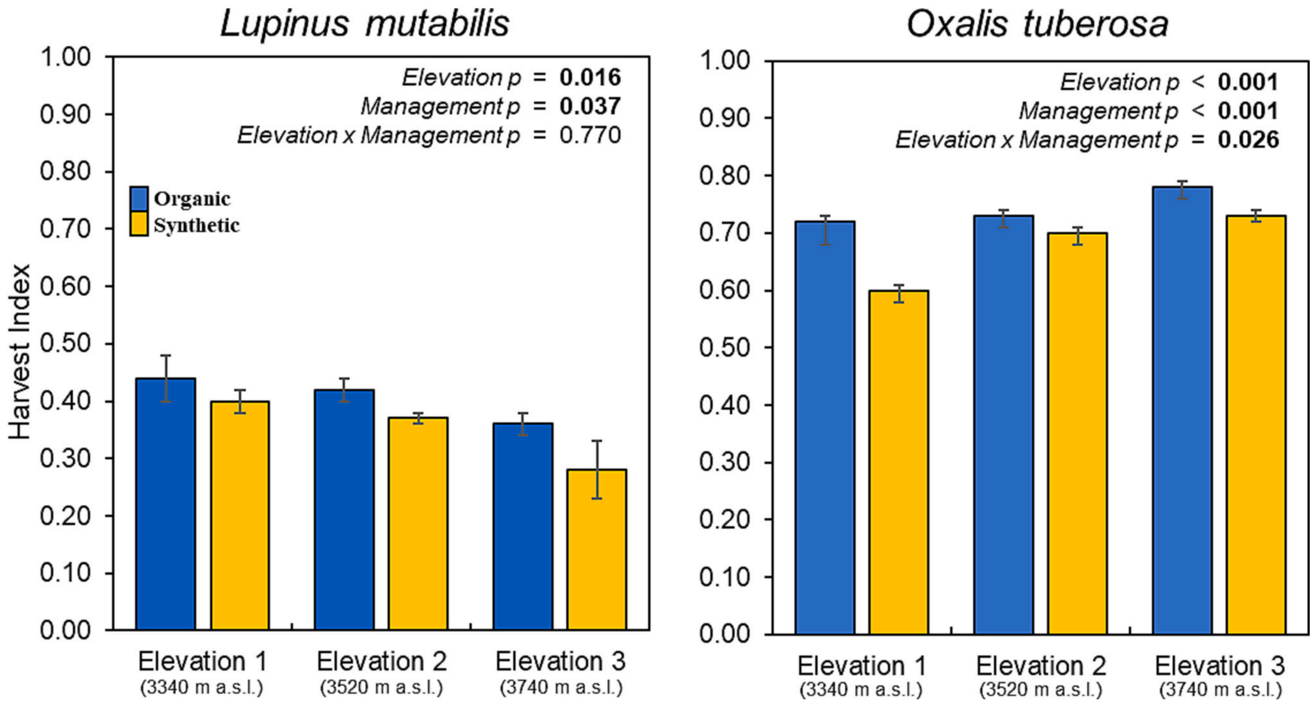

Fig. 3. Mean harvest index of two traditional Andean crops (*Lupinus mutabilis* and *Oxalis tuberosa*) grown at three elevations (x-axis). Bars are mean ± standard error. Soil management treatments are sheep manure application (organic) and synthetic fertilizer application (synthetic). Two-factor ANOVA *p*-values for elevation, management and their interaction are shown for each variable. Bolded values are significant.

Table 4

Indicators of the performance of *Lupinus mutabilis* grown in microplots (with reference soil). Values represent the treatment mean, with standard errors presented underneath each mean in parentheses. P-values are provided for two-way ANOVA examining the effects site/elevation (E), management type (M) and their interaction, with significant effects ($P \leq 0.05$) in bold. All data was collected at harvest, in May 2022, in the community of Quilcas, Junin region, Peru.

Indicator	Unit	Site 1 (3340 m)		Site 2 (3520 m)		Site 3 (3740 m)		P-values		
		Organic	Synthetic	Organic	Synthetic	Organic	Synthetic	Elevation (E)	Management (M)	E x M
Survival rate	%	83.3 (9.62)	88.9 (5.56)	94.4 (5.56)	77.8 (14.70)	88.9 (5.56)	66.7 (16.67)	0.673	0.225	0.412
Days until first pod	N	119 (0.00)	119 (0.00)	119 (0.00)	131 (6.49)	156 (0.00)	162 (6.67)	**<0.001**	0.064	0.303
Plant height	cm	88.1 (3.91)	96.9 (9.18)	134.8 (8.05)	154.0 (10.41)	125.4 (6.33)	127.4 (6.21)	**<0.001**	0.134	0.543
Total AG plant biomass	$g\ m^{-2}$	1028.2 (56.32)	1583.3 (153.83)	1382.3 (183.12)	1358.1 (141.10)	1384.0 (270.10)	1538.7 (208.37)	0.697	0.148	0.298
Number of secondary axes	N per plant $^{-1}$	3.6 (0.44)	3.6 (0.28)	4.4 (0.39)	3.5 (0.07)	5.2 (0.59)	4.2 (0.20)	**0.043**	0.061	0.395
Pod weight	$g\ m^{-2}$	605.5 (26.63)	858.7 (93.19)	756.9 (97.34)	679.4 (47.74)	644.9 (137.78)	687.3 (67.62)	0.729	0.322	0.195
Damaged pods	%	2.2 (1.15)	0.5 (0.28)	3.5 (0.90)	0.9 (0.04)	3.8 (2.22)	1.6 (0.90)	0.434	**0.042**	0.972
Grain weight	$g\ m^{-2}$	483.3 (28.29)	688.2 (71.95)	568.1 (75.15)	520.7 (36.29)	472.9 (112.62)	411.9 (58.27)	0.148	0.582	0.141
Damaged grains	%	5.10 (2.41)	1.74 (0.29)	4.66 (0.12)	7.15 (0.93)	1.84 (0.53)	2.19 (1.33)	**0.023**	0.864	0.090

m a.s.l. (Moscoe et al., 2017), research on this crop is sparse and the ideal growing conditions are not well understood. We suspect that the observed decline in production may be attributed to various factors, potentially linked to the warming climate. In addition to the less-favourable water balance, higher temperatures can impact plants in several ways. Firstly, they can impede the synthesis of plant hormones, which are essential for normal plant growth (Waraich et al., 2012). Second, elevated temperatures can accelerate the process of tuber initiation and formation, and as a result, tubers may not receive sufficient carbohydrates (produced by photosynthesis) to support their growth (Ewing and Struik, 1992; Jackson, 1999; Hancock et al., 2014). This can lead to smaller tubers, reduced yield, or even failed tuber development in extreme cases (Hannapel et al., 2017). This idea is supported by an accelerated growth cycle observed at the lower elevation, as *O. tuberosa* plants already started flowering after 119 days. We note that the observed decline in tuber production of *O. tuberosa* is similar to that reported for native potatoes by Tito et al. (2018), who found an 87–97 % reduction in yield due to increased temperature in the southern Andes of Peru. Their study examined both potatoes and maize and found that tubers exhibited a greater susceptibility to climate warming. The decline in tuber production observed within our study was less severe, suggesting that *O. tuberosa* might better maintain its production under warming conditions compared to potatoes. In a global simulation of potato yield under climate change scenarios, Raymundo et al. (2018) predicted that yields of this tuber crop would decrease by the end of the century, and that the impacts of this decline would vary by region. Interestingly, their simulations indicate that potato yields in the rainfed production systems of the Andes may actually increase with warming at higher elevations, suggesting that current production may not always occur at optimal elevations and that potatoes (and other tubers) will likely remain a feasible staple crop in the region in the coming century. However, these simulation results appear to contradict with the study by Tito et al. (2018) and our own findings, thus highlighting the need for further research to better understand climate warming effects on crop production in mountain agroecosystems. It is worth noting that our results suggest that *O. tuberosa* grows best at the middle elevation (3520 m; +1.6 °C), where growing conditions might be optimal for the crop. We suspect that incidence of pests or soil fertility did not influence this result, since there were no significant differences between sites (elevations) within our study for these two factors.

Our findings suggest that the growing use of synthetic fertilizers may have important implications for *O. tuberosa* production, especially in a context of a warming climate. This was especially evident for harvest index, a key parameter of crop performance, where warming conditions reduced the proportion of overall biomass allocated to tuber production more in synthetically fertilized plots than those receiving manure. The apparent negative impacts of synthetic fertilizers may be due to several factors. For example, inorganic fertilizers often emphasize N over other nutrients, which can promote vegetative growth (leaves and stems) at the expense of tuber formation (Kumar et al., 2019). In contrast, organic nutrient sources typically provide a balance of essential nutrients like N, P and K, along with other nutrients (e.g., Fe, Zn, Cu, Mn, B, Mo), which can promote healthy growth and tuber formation (Shaji et al., 2021). At the same time, synthetic fertilizers can disrupt microbial communities in the soil (Bulluck III et al., 2002; Tripathi et al., 2020), which can greatly facilitate growth, while manure is more likely to promote a healthy balance of microorganisms, and thus better support tuber yield (Rayne and Aula, 2020; Pantigoso et al., 2022). Related to this, it has been suggested local landraces and other crops that have not been bred under a regime of high nutrient availability may have a greater ability to recruit rhizosphere communities that allow them to utilize nutrients more efficiently within low-input smallholder systems that are based on organic nutrient inputs (Sangabriel-Conde et al., 2014; Kelly et al., 2022).

Our study results clearly show that tuber damage from pests (i.e., *Premnotrypes suturicallus*, *P. piercei*, and *Phytophthora infestans*), was higher when synthetic fertilizers were applied. This finding is not surprising, as other studies have suggested that synthetic nutrient inputs can increase the susceptibility of plants to pests and diseases (Huber et al., 2012; Wyckhuys et al., 2017). Organic nutrient sources, on the other hand, can help to promote healthy plant growth by improving soil fertility, structure, and microbial communities, which can reduce susceptibility to pests and diseases (Razdan and Sabitha, 2009). Our study showed that *O. tuberosa* plants receiving synthetic fertilizer were smaller and faster to mature compared to plants that received manure. Decomposing manure tends to release nutrients slowly, which can help ensure that crops have a consistent supply of nutrients. This is in contrast to synthetic fertilizers, where nutrients are typically available immediately, prone to loss, and might not sustain the aboveground biomass growth needed to support adequate tuber development (Shaji et al., 2021; Zhang et al., 2020). Furthermore, organic matter addition can help to buffer against acidity, support P availability and may increase water capture (i.e., infiltration) and retention, which can be crucial for maintaining yields within rain fed systems (Sharma and Chetani, 2017; Bulluck III et al., 2002). It should be noted that the improved performance of *O. tuberosa* in the manure treatments may also be due to the higher overall nutrient input. Manure inputs were based on regional N recommendations and an assumption that half of the manure N would mineralize and become available over the course of the growing season. However, nutrient release from organic inputs is difficult to predict and depends greatly on environmental conditions and so we cannot be certain how much N, P, and K became available over the course of the growing season. Despite this uncertainty, our study warrants some concern regarding the growing use of synthetic fertilizers in the Andean region (and elsewhere) and suggests that organic nutrient sources used in traditional crop management could better support the overall resilience and productivity of *O. tuberosa* in a warming climate.

4.2. Effects on Lupinus mutabilis

Our findings indicate an accelerated growth cycle for L. *mutabalis* with increasing temperature, especially in terms of plant height, days until first pod, and number of secondary stems. At the time of harvest, plants at the lowest elevation were completely dry with mature pods, while experimental plots at the highest elevation were still flowering, and/or even continued to develop secondary and tertiary axes. These findings are not entirely unexpected, as higher temperatures can speed up a plant's growth cycle for several reasons. Warmer temperatures generally increase the rate of photosynthesis (Sage and Kubien, 2007), which increases the activity of enzymes that are involved in growth and development, such that flowers and pods emerge faster (Moore et al., 2021). Evapotranspiration rates also increase, leading to increased water stress that can cause a shift in the plant's priorities, prompting it to allocate resources towards reproduction rather than growth (Vadez et al., 2012). Consequently, plants may develop flowers and fruits more quickly, accelerating the reproductive process. We note that while the accelerated growth cycle and higher temperatures might be beneficial in terms of getting the plant to maturity more quickly, it could also have negative consequences (Lipiec et al., 2013). For example, if a plant is not able to absorb enough water and nutrients to support its accelerated growth, it could suffer deficiencies or be more prone to pests and disease (Rosenzweig et al., 2001). Our findings support this idea, as L. *mutabilis* pods at the lowest altitude contained a greater number of damaged grains. We note that not all pest damage can be attributed solely to increased plant susceptibility, as pests have their own optimal niches and may exert greater pressure depending on environmental conditions (Singh and Emden, 1979; Parsa et al., 2011). For instance, *Apion* beetles may reproduce faster at lower elevations, leading to more significant damage within their preferred habitat (Crawley, 1989).

Grain yield and plant biomass of L. *mutabilis* were not significantly influenced by warmer growing conditions or management practices, while the harvest index (grain yield/total biomass) showed clear elevation and management impacts. One potential reason that warmer temperatures might not directly affect grain yield and biomass production of L. *mutabilis*, is that the plant (or this particular variety) is able to tolerate and adapt to the higher temperatures, withstand droughts, and fix N due to its symbiotic relationship with Rhizobia (Hardy et al., 1997; Gulisano et al., 2019). *L. mutabilis*, like other legumes, is capable of acclimating to changing conditions through a process called hardening (Wahid et al., 2007), where the plant adjusts its physiology and biochemistry to cope with new conditions (Sung et al., 2003). The ability to adapt to higher temperatures could help L. *mutabilis* to maintain its yield and biomass production even under warmer conditions (Gulisano et al., 2019). In our study, the harvest index of L. *mutabilis* was lower for plots receiving synthetic fertilizer compared to those with manure, indicating a nutrient management effect. This result indicates that plant allocation to grain yield is relatively higher when the plants are amended with (sheep) manure. This finding corresponds with the findings of Ramesh et al. (2006), who found that the application of (cattle) manure resulted in higher grain yield of pigeon pea (*Cajanus cajan*) compared to chemical inputs or no amendments. We suspect that greater production is related to the potential benefits of manure to water dynamics and soil biological communities, especially N-fixing bacteria and development of nodules of L. *mutabilis* (Abubakari et al., 2016; Rayne and Aula, 2020). However, due to uncertainty in N, P, and K mineralization for the manure treatment, we may simply be observing the effect of increased nutrient availability and cannot be certain as to the mechanisms involved.

Despite the negative consequences of warming, our research indicates that L. *mutabilis* exhibits a higher tolerance to increasing temperature and drought, compared to *O. tuberosa* and other prevalent Andean crops (Tito et al., 2018; Gulisano et al., 2019). At the same time, we note that L. *mutabilis* can provide a valuable source of protein, and due to its leguminous nature and high biomass production could contribute substantially to soil health and human nutrition in a changing climate. While our findings are of great interest for agroecosystem resilience in the face of key global changes, we emphasize that we only considered impacts on two types of crops in one community and that further research is needed to better understand the potential impact of climate change, combined with evolving nutrient management strategies, on agroecosystem resilience and the livelihoods of smallholder farmers around the world.

5. Conclusions

Climate warming poses a significant threat to smallholder agriculture in the Peruvian Andes and around the world, as it will likely cause declines in production of locally important crops such as *O. tuberosa*, as well as more widespread crops such as potatoes and maize. This study elucidates how key Andean crops, such as *O. tuberosa* and L. *mutabilis*, may react to global changes, with a particular focus on the effects of differing fertilization strategies on these plants. Common strategies to confront climate warming, such as switching to other crops (or varieties) that can better tolerate warmer temperatures and/or pests, can have negative outcomes including the loss of local crops and varieties that communities have adapted to their systems over centuries and that they greatly value and depend on. At the same time, shifting crop production upslope to higher (cooler) elevations may not be a possibility for many communities, where crops are already being cultivated at or near mountain tops. Furthermore, the shift of the production of crops upslope could threaten highly sensitive *Puna* ecosystems in the Andean region, which store large amounts of C in soils (Rolando et al., 2017). Although there is much evidence that 'modern' high-input agriculture can support higher yields of staple crops and contribute to food surpluses in some regions, traditional practices often offer advantages in terms of stability and the provision of ecosystem services (Kremen and Miles, 2012; Altieri and Nicholls, 2017). Our findings suggest that use of organic nutrient sources (e.g., sheep manure) instead of synthetic fertilizers may help support *O. tuberosa* crop growth and productivity in the face of warming conditions and may enhance overall improvement in agroecosystem resilience. At the same time, *L. mutabilis* shows less drastic responses to warming and nutrient inputs, with minimal effects of higher temperatures on grain yield and plant biomass, suggesting that some traditional crops like L. *mutabilis* could play a stabilizing role in food production systems under warming conditions. Our findings emphasize the urgency of understanding climate impacts on crop performance for developing resilient agroecosystems and preventing food insecurity. Our findings suggest that organic fertilization can mitigate climate effects, although this depends on the crop in question. This study's insights into organic fertilization and crop resilience have broad applicability for managing agricultural systems globally in the face of climate change and reinforces the need for focused research on climate-adaptive, crop-specific management.

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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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