Andean maize in Argentina: physiological effects related with altitude, genetic variation, management practices and possible avenues to improve yield

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Abstract

In the Argentinean Andean region, maize is a main staple being cropped up to 3,900 m above sea level (masl). Yields are limited by the sharp decrease in temperature associated with altitude but also by a lack of management and breeding technologies to underpin traditional practices. In this review we discuss: (i) the main physiological changes of increasing altitude using experimental reports up to 2,650 m above sea level plus own experiments up to 3,300 masl; (ii) available genetic diversity within local races; (iii) maize cropping systems based on literature and own data from 23 surveys; and (iv) possible avenues for improving yield. Among physiological traits, major penalties are associated with delayed phenology reducing light capture, and low temperatures inhibiting photosynthesis and kernel growth rate. As a result, yields can be reduced up to 85% at 3,300 masl compared with 2,300 masl in contrast to increases at lower latitudes. Local races are characterized by a high genetic diversity that is aiming to be preserved by both *in situ* and *ex situ* conservation initiatives. However, little is known about phenotypic variation, impairing the exploitation of these genetic resources in breeding programs. Breeding strategies could consider tillering ability (to buffer stand heterogeneity) and photosynthetic recovery rates from chilling as important target traits, whereas plant density management could overcome penalties related with delayed plantings and phenology. Water availability is currently insufficient, especially at higher altitudes where most farmers rely on water from thaw, and climate change projections suggest this will worsen; thus improving water use efficiency also deserves further work.

Introduction

The Northwest of Argentina (NWA) comprises different agroecological regions that extend from −22 up to −30 degrees in latitude. Within this territory, there are around 14 million hectares spanning from 1,000 up to more than 4,000 m above sea level (masl) usually known as the Andean highlands of Argentina[1]. Here, approximately 60,000 farms, mostly being produced by smallholders,[2] struggle with the limits of agricultural possibilities. While crops are usually irrigated and fertilized with animal manure (Fig. 1), the sharp decrease in temperature (T) associated with increased altitude (0.55 °C for every 100 m[3]), imposes the major environmental limitation. Among the main crops (maize, potatoes and beans, https://datos.magyp.gob.ar/), maize (a crop with C_4 photosynthetic metabolism) has the greatest sensitivity to low T and thus, to increasing altitudes. The lack of specific management strategies associated with the altitudinal gradient together with no formal breeding programs further limit attainable yields in these environments. Not surprisingly, in the NWA, average income in the agriculture sector is the lowest of the country and poverty rates are the highest[4].

Regarding the maize crop, the altitudinal gradient appears as a key factor for decision-making[5]. However, scientific information needed to understand the physiological responses of the maize crop to increasing altitudes is scarce and has mostly been obtained at lower latitudes than those of the NWA (Table 1). Whereas many previous works found a yield increase in response to higher altitudes, this cannot be easily extrapolated to the NWA because the lower thermal regime associated with increased latitude is likely to reduce positive crop responses to a much shorter altitudinal range. Moreover, except for the three variables 'physically tied to meters above sea level' (T, atmospheric pressure and clear-sky turbidity[3]) other altitude-related changes will vary between geographical regions. In the NWA higher altitudes are also associated with increased solar radiation, especially within the range of UV wavelengths[6]. This increased UV interplaying with low temperatures within the genetic framework of the native races of the NWA has not been explored.

Research on crop management strategies or breeding approaches for these high altitude environments could contribute to improving yields and with this, farmer's livelihood, while also supporting the survival of these cropping systems and the cultural and genetic diversity associated with

them. In this review, we provide a critical analysis of the literature on the subject, and propose some working hypothesis, vacancy areas and perspectives. Different sections address: (i) the main physiological effects of increasing altitude in maize crops; (ii) available genetic diversity within races of the NWA; (iii) maize cropping systems in the NWA; and (iv) possible avenues for improving yields including management practices and target traits for breeding.
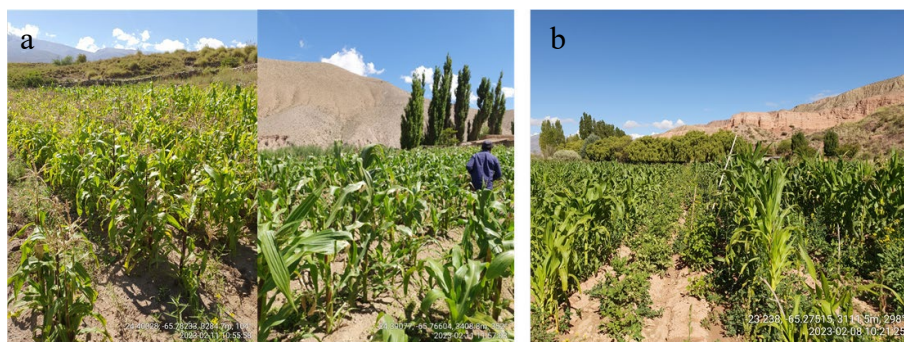

Fig. 1   Maize plots in farmer's fields located at very high altitude environments (> 3,000 masl). Usually, the crop is fertilized with goat manure and irrigated by furrow throughout the growing season following weekly turns organized by the community. Weeds are manually controlled, and pest incidence is overall very low. Sowing is done manually leading to significant stand heterogeneity (a), and furrows are placed against the slope when appropriate (a, left). (b) Intercropping is also a usual practice. Geographical coordinates, altitude and date are indicated in the right corner of each image.

Table 1.   Changes in different traits in response to increasing altitude based on available literature. When more than one season was available, average change across seasons is considered; when several adaptation groups were tested, the response of the highland-adapted group is reported (or the best-performing genotype). Relative values for the responses are approximate as most of the results are based on figures.

| Trait	Location	Latitude	Altitudinal range	Response to increased altitude	References
Phenology and canopy development					
Days to tasseling	East-African countries	8°–(−13)°	352 vs 1913	Increase (+27 d)	Darrah and Penny[37]
Days to tasseling	East-African countries	8°–(−13)°	1210 vs 1913	Increase (+27 d)	Darrah[80]
Crop cycle length	Kenya	0–1°	1268 vs 2250	Increase (80 d)	Cooper[13]
Crop cycle length	Mexico	19°	600 vs 2050	Increase (69 d)	Pace[27]
Crop cycle length	Mexico	19–21°	60 vs 2650	Increase (58 d)	Jiang et al.[8]
Thermal time	Kenya	0–1°	1268 vs 2250	Unchanged	Cooper[13]
Thermal time	Mexico	19–21°	60 vs 2650	Decrease	Jiang et al.[8]
Final leaf number	Kenya	0–1°	1268 vs 2250	Decrease (-2 leaves)	Cooper[13]
Final leaf number	Mexico	19–21°	800 vs 2240	Decrease	Lafitte & Edmeades[14]
Final leaf number	Mexico	19–21°	60 vs 2650	Increase (2,4 leaves)	Jiang et al.[8]
Leaf size	Kenya	0–1°	1268 vs 2250	Increase, then decrease	Cooper[13]
Leaf size	Mexico	19–21°	800 vs 2240	Increase, then decrease	Lafitte & Edmeades[14]
Canopy senescence	Mexico	19–21°	800 vs 2240	Delayed	Lafitte & Edmeades[14]
Canopy senescence	Southafrica	(−29)°	420 vs 1620	Accelerated	Wilson et al.[35]
Biomass and yield					
Biomass	Southafrica	(−29)°	420 vs 1620	Unchanged	Wilson et al.[35]
Biomass	Mexico	19–21°	800 vs 2240	Similar	Lafitte & Edmeades[14]
Biomass	Mexico	19–21°	60 vs 2240	Increase (+ 147%)	Jiang et al.[8]
Yield	Kenya	0°	1525 vs 2593	Unchanged	Arkel[81]
Yield	East-African countries	8°–(−13)°	352 vs 1913	Increase (+ 60%)	Darrah & Penny[37]
Yield	East-African countries	8°–(−13)°	1210 vs 1913	Increase (+ 18%)	Darrah[80]
Yield	Kenya	0–1°	1268 vs 2250	Increase (+ 82%)	Cooper[13]
Yield	Mexico	16°	1500 vs 2150	Increase (+ 300%)	Mercer et al.[38]
Yield	Mexico	19–21°	60 vs 2240	Increase (+ 155%)	Jiang et al.[8]
Yield	Mexico	19°	1850 vs 2400	Increase (+ 800%)	Pace[27]
Prolificy	Kenya	0–1°	1268 vs 2250	Increase (+ 58%)	Cooper[13]
Grain number	Mexico	19°	1850 vs 2400	Increase (+ 83%)	Pace[27]
Grain number	Southafrica	(−29)°	420 vs 1620	Unchanged	Wilson et al.[35]
Grain number	Kenya	0–1°	1268 vs 2250	Increase (+ 48%)	Cooper[13]
1000 grain weight (primary cob)	Kenya	0–1°	1268 vs 2250	Increase (+ 25%)	Cooper[13]
1000 grain weight	Mexico	19°	1850 vs 2400	Increase (+ 64%)	Pace[27]
1000 grain weight	Mexico	19–21°	60 vs 2240	Increase (+ 9%)	Jiang et al.[13]
1000 grain weight	Mexico	19°	600 vs 2050	Increase (400%)	Pace[27]
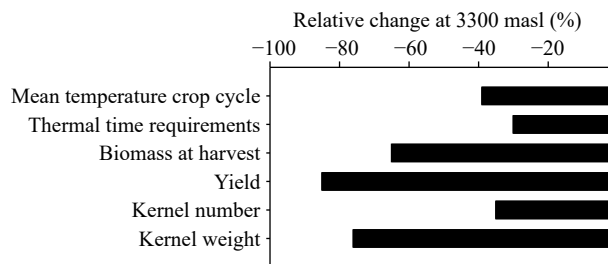
Fig. 2 Relative change for different factors or crop parameters measured at 3300 masl compared with 2300 masl during experiments carried out at two high altitude sites of Argentina: Hornillos (2,300 masl, Jujuy) and El Rosal (3,300 masl, Salta) during 2021−22 (calculated from absolute values in Salve et al.[9]).

Phenological and physiological effects of increased altitude in maize

Phenology and canopy development

Decreasing T with altitude impose a shortening of the growing cycle, since sowing dates must be delayed to avoid late spring frosts killing the crop. This implies a concomitant decrease in radiation capture which is further worsened by delayed development, since lower average temperatures extend the chronological duration of the phenological stages[7]. Differences in crop cycle length of up to 80 d between sites differing in 1,000 m of altitude have been reported (Table 1). Nonetheless, thermal time requirements to achieve a particular phenological stage usually decrease with higher altitudes[8,9] partially compensating for the phenological delay (Fig. 2). This is related with a shortening of the plastochron (thermal time between the initiation of successive leaf primordia) and the phyllocron (thermal time interval between the appearance of successive leaf tips) after exposure to low T[10−12] and also to increased solar radiation[11]. Moreover, final leaf number is usually reduced[13,14] (Table 1). The outcome is a delayed phenological development partially compensated for by decreased thermal time requirements.

Canopy development will be determined not only by the rate of leaf initiation and appearance, but also by the rate of cell division and expansion in leaf tissues defining final leaf size. Available evidence shows that individual leaf size can increase with altitude in early-developed leaves as a result of prolonged duration of leaf expansion whereas for middle-positioned and apical leaves, the opposite trend is observed (larger size with decreasing altitude, Table 1). Here, the effect of low temperatures reducing cell division and expansion rates[15,16] likely play the major role over leaf size. Consistent with this, unpublished data of our group shows that epidermal cell size can decrease by 33% between sites differing in 1,000 m in altitude. Thus, there seems to be interplay between prolonged duration of leaf expansion increasing leaf size and low night T reducing leaf size, the former effect being more important in leaves developed under the cooler temperatures of the early spring. Further work exploring genetic variation for leaf expansion rate under low T could help to identify traits contributing to overcome the delayed phenology with a better ability to sustain cell expansion under low T.

Anatomical and biochemical leaf traits

Many anatomical and biochemical traits can be affected by the increased altitude. Our own data show a decrease in specific leaf area (the ratio between leaf area and leaf weight, an estimator of the thickness and/or density of the leaf tissue) in plants developed at 3,300 masl compared with the same cultivar grown at 2,300 masl[17]. This is consistent with low T decreasing specific leaf area due to limited cell expansion and increased leaf sugar accumulation[12]. Low temperatures also induce other changes in leaf composition, such as increased lipid unsaturation, which has been related with improved germination and seedling growth under chilling[18].

Regarding chlorophyll and nitrogen (N) content, these are usually decreased in maize grown under low temperatures (e.g., at 14/12 °C[19]; at 15/13 °C[20]; at 15 °C[21]). However, these evidences are based on experiments carried out in controlled environments, with low temperatures always above 10 °C (not representative of the thermal amplitude of the highlands, not strongly affecting specific leaf area and, nor chlorophyll or N content per area basis). Our own data shows that leaves from high altitude environments are capable of achieving very high values of chlorophyll and N content compared with leaves developed 1,000 m below[17]. Additionally, other factors could be taking part: increased UV-B radiation is reported to increase both chlorophyll[22,23] and leaf protein concentration[24]. Pigment composition is also likely to be modified, with higher chl a/chl b (probably evidencing a lower antenna complex in the photosystems) and carotenoid/total chl relationships (reflecting a higher photoprotection capacity) with increasing altitude (personal observations), which has also been reported as result of chilling treatments[12]. Thus, well supplied crops could theoretically compensate part of the reduction in leaf area index through increased photosynthetic activity associated with a thicker mesophyll and higher leaf protein content although further work is needed to assess the consistency of these changes in leaf traits.

Stomatal conductance, photosynthetic rates and instantaneous water use efficiency

Increased altitude results in changes in several environmental factors that influence stomatal conductance and photosynthesis. Stomatal limitations for photosynthesis could take place in the high altitude environments of the NWA given the lower CO_2 partial pressure[3] combined with, usually, a high vapour pressure deficit[25] promoting stomatal closure[26]. However, evidence is not conclusive, with stomatal conductance decreasing (between 1,850 and 2,400 masl[27]), being maintained (between 2,300 and 3,300 masl) or even increasing at higher altitudes (between 600 and 2,050 masl[27]). Changes in stomatal density could be playing a role here, since stomatal density usually increases with altitude as a result of decreased cell size, whereas stomatal index is maintained or slightly decreased[27]. Our own data also supports non major stomatal limitations for photosynthesis; daily measurements show that highest photosynthetic rates (in the afternoon) co-occur with lowest Gs, implying that, at least during the major part of the day, photosynthesis is not limited by Gs[17].

Regarding the higher radiation intensity with altitude[6] this could increase photosynthetic rates considering that at the leaf level, maize photosynthesis saturates above 2,000 μmoles photons m^{-2} s^{-1}[28]. Consistent with this, maximum photosynthetic rates were achieved at 2,050 masl compared with 600 masl in highland-adapted maize races of Mexico[27]. However, at the same time, low night temperatures (< 10 °C) can reduce maize photosynthesis up to 30%, especially during the early

morning[29,30], chlorophyll fluorescence parameters such as electron transport rate (ETR) being directly affected[30]. Our own data indicates that higher photosynthetic rates can be achieved at a high altitude site (3,300 masl compared with 2,300 masl) but recovery rates from night chilling can also be rather long. We have measured 37% higher photosynthetic rates at maximum irradiance in the afternoon compared with the morning, with minimum night temperatures of 8 °C[17]. Further work manipulating night temperature could help to dissect specific night chilling effects from those related with low morning temperatures *per se*.

Altogether, these effects may have consequences over photosynthetic (instantaneous) water use efficiency (i.e., the quotient between photosynthesis and transpiration rate) and water availability, a critical issue in this irrigated cropping systems. Instantaneous water use efficiency is reported to be lower in a common garden at 2,050 masl compared with 600 masl in Mexico[27]. This trend may be accentuated in higher altitudes at high latitude environments as the NWA, where cooler nights further depress photosynthetic performance during the early (and even midday) hours of the day (T around 6–10 °C at dawn; personal observations). In this scenario, improving stomatal regulation seems necessary as maximum stomatal conductance is achieved in the morning, despite the low photosynthetic rates (determining lower intrinsic water use efficiency, i.e. the quotient between photosynthesis and stomatal conductance). Further work could also consider exploring stomatal sensitivity to abscisic acid, which can be partially reduced[31] or even completely lost[32] under cold temperatures in warm-climate species explaining extremely low relative water content detected in maize leaves after chilling treatments[33].

Biomass accumulation and yield

Most of the available evidence indicates that biomass accumulation during the vegetative period is reduced at higher altitude environments[13,27]. Our own experiments in the NWA (Hornillos, 2,300 masl) show that by the beginning of the critical period, leaf area index can be around 2[34], far below 4, the approximate value considered critical for optimizing light interception in maize. After achieving maximum leaf area index, biomass accumulation will be related to photosynthetic rates (see earlier section) and canopy senescence, apart from sink strength regulating both processes. A delay in canopy senescence was observed in an environment at 2,240 masl compared with another at 800 masl in Mexico, likely as a result of lower temperatures which, in any case, remained above 16 °C[14]. Similarly, leaf area duration was almost doubled in a site at 1,200 masl compared with another one at 400 masl with average T during the reproductive period above 20 °C[35]. This contributed to the similar biomass accumulation achieved at harvest between sites at different altitudes[14]. However, with increasing latitudes and altitudes, seasonal T will be much lower, possibly promoting rather than delaying canopy senescence, but further work is needed to properly assess it in the context of high altitude environments where changes in light quality could also play a role. In the core productive region of Argentina, temperatures < 20.8 °C during the reproductive period can accelerate senescence rates of maize cropped without water or nutrient limitations[36]. Highland adapted races may have higher tolerance to low temperatures in terms of canopy senescence promotion, but the occurrence of much lower temperatures would have in the end, the same effect.

Our own registers at 3,300 masl show T < 10 °C during the reproductive period, and biomass accumulation at harvest being 65% lower than that achieved at 2,300 masl[9] (Fig. 2).

Regarding yield, in the highlands of some African countries[13,37] and Mexico[27,38] higher yields, grain number in the main ear and higher prolificy were achieved with increasing altitude (Table 1). This is consistent with lower temperatures extending the duration of the critical period, with a concomitant increase in light interception that strongly correlates with grain number in maize[39]. As occurs with the critical period, lower temperatures also extend the duration of the grain filling period, contributing to higher average grain weights with increasing altitudes in low-latitude environments[8,13,37]. However, below certain thresholds, low temperatures (e.g., 15 °C) during the lag phase (before active biomass accumulation) can substantially affect sink strength and subsequent grain filling rates[40]. Moderately low minimum T (< 20.7 °C) and high daily thermal amplitude (> 7 °C) also reduce kernel growth rate[41] whereas dry matter mobilization from vegetative parts is reduced when ear T drops below 16 °C[42]. In the NWA at 2,300 masl, 26% interannual variation in yield was related to low temperatures during the grain filling likely reducing kernel growth rate since biomass at harvest was not negatively affected[17]. Between sites at 2,300 and 3,300 masl yields can be reduced by 87% mainly because of a reduced grain weight related with early frosts arresting grain filling[9] (Fig. 2). Thus, unlike low-latitude highlands (v.g. mountains in tropical and equatorial areas), in the highlands of the NWA, lower temperatures during the reproductive stage strongly reduce yields, by accelerating canopy senescence, reducing kernel growth rates and directly arresting grain filling when early frosts take place. Further work is needed to understand the relative importance of each of these processes.

Genotypic variation in maize races of the NWA

Origins and characterization of Andean maize races of the NWA

Given the multiple physiological effects produced by increased altitude, many adaptations are likely to be found in highland maize races. High genetic diversity in this region is associated with maize domestication history. First archaeological registers of maize were found in Mexico 9,000 years back from present[43]. From there, the crop expanded to further latitudes, mainly through the Andes Mountains, arriving to the Peruvian-Bolivian plateau by 4,000–3,500 years back[44], which became an important centre of maize diversification. Evidence based on microsatellite differentiation shows that, among 194 populations collected throughout Latin America, populations from Andean origin are markedly different[44]. In Argentina, earliest registers of maize have been dated 3500 years back from present[45], with highest genetic diversity being found in the NWA[46,47], the southernmost extreme of the Andean diversification centre.

In the NWA, maize races have been identified according to utilitarian criteria as ear and kernel characteristics, especially endosperm type, number of rows in the ear and kernel size, shape and colour[48]. Under these criteria, a race can be defined as '*any group of populations with an enough number of distinctive traits in common that self-reproduce through panmitic reproduction within the populations and occupy specific areas*'[49]. At

Table 2. Characterization of main maize races cropped in high altitude environments from the Northwest of Argentina based on races defined by Cámara Hernández et al.[]. The criteria we followed for grouping races was based on the different traits indicated in columns.

Group	Representative races	Cycle length	Plant size	Ear traits	Endosperm	Uses
'Capias'	'Capia' ('blanco'/ 'variegado'/ 'rosado'/ 'amarillo'/ 'marrón'), 'Cuzco', 'Chulpi' and 'Culli'	Long	Tall plants	Big ears, 16–20 number of rows, large kernels, wide variety of colours	Floury (dextrinous in the Chulpi race)	Typical food and drinks: 'Capias', 'Mote', 'Tamal', 'Tijtincha', Äpi'and 'Chicha morada'
'Cristalinos'	'Morocho', 'Calchachí', 'Cristalino Blanco', 'Cristalino Amarillo' (or 'chico'), and 'Amarillo de Ocho' (or 'grande').	Medium	Medium plants	Crystalline endosperm, yellow or white color	Crystalline (flint)	Typical food: 'Locro', 'Mazamorra', 'Humita' and 'Chicha'
'Reventadores'	'Pisingallo', 'Perlita'	Short	Medium plants	Small kernels, pointed shape, popped	Crystalline (flint)	Pop-corn and typical food and drinks ('chilcan', 'ulpada' and 'miskopitapi').
'Altiplano'	'Bola blanca' and 'altiplano'	Short	Small plants	Small and round ears with small kernels. Irregular kernel row arrangement	Floury or crystalline	Grain or forage

least 44 maize races have been identified in Argentina[50], and 18 of these have been found exclusively in the NWA[51]. These can be classified into four main groups according to different traits, namely 'capias', 'pisingallos', 'altiplano' and 'cristalinos', with a trend towards smaller plants and shorter cycle lengths in those races better adapted to extreme high-altitude environments (Table 2).

However, genetic studies of 30 maize accessions from the NWA indicate that genetic affinities are not in accordance with racial assignments[5]. This inconsistency is probably related with the combined effect of a high number of races cropped seasonally per farm and a small plot size (usually few long rows per race) resulting in extensive cross-pollination, intensified by seed exchange practices (further discussed in the "Maize crop management and seed exchange practices" section). In any case, this genetic heterogeneity is typical of traditional agroecosystems and highly contrasting with the much more genetically homogenous modern varieties, with positive outcomes such as increased resilience to environmental stress[52]. Different initiatives exist to preserve the genetic resources represented by Andean maize races. *Ex situ* preservation in Argentina is currently relying on REDGEN of INTA ('Network of plant genetic resources'), with Andean maize races being conserved at the Germplasm Bank of Pergamino[53]. *In situ* preservation is being promoted by national projects (mostly related to INTA) and also international initiatives (as those associated with the International Treaty on Plant Genetic Resources for Food and Agriculture, FAO-TIRFAA[54]).

Genotypic and phenotypic variation in highland-adapted maize races

The altitudinal gradient seems to shape the genetic characteristics of the races[55]. Rivas et al.[5] identified three main genetic clusters (inferred ancestral population) for 30 maize accessions of the NWA, with a mean altitude of the collection site of 1,684, 2,584 and 2,745 masl. Similarly, Mexican races seem to be grouped by altitude according to isozyme analyses[56]. Accessions collected from higher altitudes have reduced genetic variability (up to 2,950 masl[5]), higher proportion of chromosomes B and lower content of A-DNA and A heterochromatin (up to 3,900 masl[55]). This could evidence the stronger selection pressure of the environment reducing the survival and concomitant contribution to genetic variability of other races better adapted to lower altitudes.

Despite many works highlighting the importance of genetic diversity within Andean maize races[46,47,5], little is known on how this variability translates into different phenotypes. Evaluation of phenotypic traits in 15 accessions representing different races in an experiment at 2,300 masl resulted in highest variability found for days to silking, followed by yield per plant and prolificy[47]. By contrast, another work evaluating 30 maize accessions at 2,300 masl identified highest variability for tillering ability followed by number of secondary branches on tassel and tassel peduncle length[5]. Other traits more easily related with yield (such as prolificy and kernel number per row) showed a low coefficient of variation[5]. In both works, maize accessions represented different landraces and were collected across an altitudinal gradient spanning from 326 to 3209 masl[47] or from 1,120 to 2,950 masl[5] and tested at 2,300 masl. Thus, it is not possible to discern between phenotypic variability related with (i) intrinsic characteristics of the races, (ii) constitutive highland-adaptations, and (iii) specific acclimation to the altitude of the experimental site. Further work characterizing maize accessions from the NWA could consider these three sources of phenotypic variation in order to identify traits potentially useful for breeding.
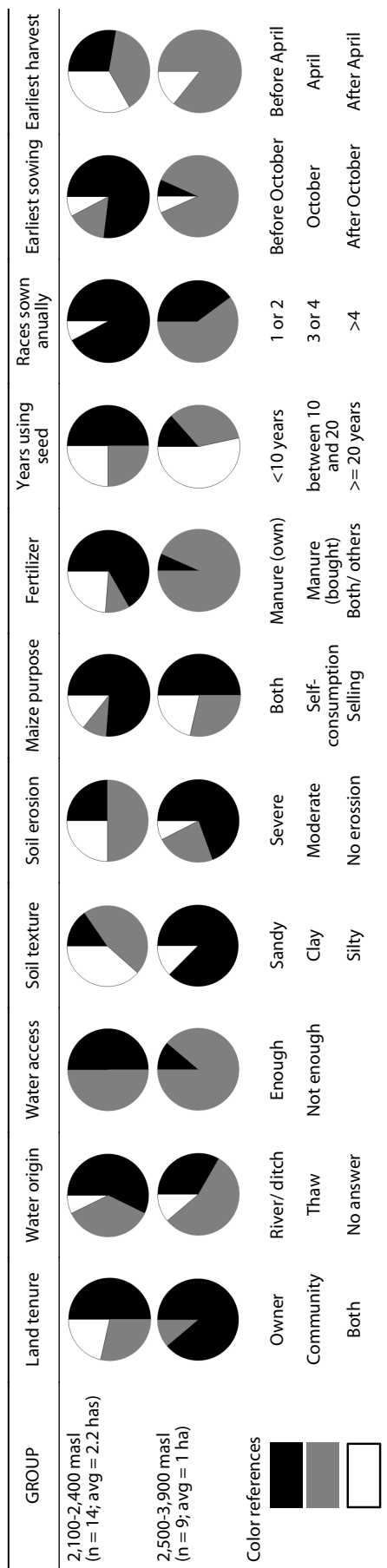
Regarding yield, highland-adaptations in other regions do account for yield improvements in several works[27,37,38] and this is mainly related with higher grain number[27] . Highland adapted races from Mexico are also capable to sustain grain filling at lower temperatures than mid or lowland races[57]. Whether this also occurs in highland-adapted maize races of the NWA deserves further work. Additionally, many works agree on that highland-adaptation penalizes the crop performance under mid and lowland environments[14,27,38]. While different traits could account for these penalties, phenological development is likely to play a major role, with usually highland races having shorter cycles[8] related with lower total leaf number[5,14] that reduce yields when the environmental window allows a slower developmental rate.

Maize cropping systems in the NWA

Characteristics of the farming system

Both the available genetic variation within Andean maize races and the characteristics of the farming systems should be considered for planning strategies to improve the crop

Table 3. Own results obtained from surveys to farmers carried out in 2021 as part of a FAO Project (detailed in the text). A total of 23 farmers were interviewed across an altitudinal gradient spanning from 2,100 to 3,900 masl; results were grouped into two groups according to altitude.

GROUP	Land tenure	Water origin	Water access	Soil texture	Soil erosion	Maize purpose	Fertilizer	Years using seed	Races sown anually	Earliest sowing	Earliest harvest
2,100–2,400 masl (n = 14; avg = 2.2 has)											
2,500–3,900 masl (n = 9; avg = 1 ha)											

Color references:

	Land tenure	Water origin	Water access	Soil texture	Soil erosion	Maize purpose	Fertilizer	Years using seed	Races sown anually	Earliest sowing	Earliest harvest
(black)	Owner	River / ditch	Enough	Sandy	Severe	Both	Manure (own)	<10 years	1 or 2	Before October	Before April
(grey)	Community	Thaw	Not enough	Clay	Moderate	Self-consumption	Manure (bought)	between 10 and 20	3 or 4	October	April
(white)	Both	No answer		Silty	No erossion	Selling	Both/ others	>= 20 years	>4	After October	After April

performance in these environments. The vast majority of the establishments in the Andean highlands of Argentina can be classified as Family Agriculture, defined as '*that which is operated by the farm family, with no permanent salaried workers, and with a size limit that varies by macro-regions and provinces*'[4]. Most of the population self-identify with the kolla ethnicity, especially in the provinces of Salta and Jujuy[2]. Cultural identity has been developed not only around ancestral crops, but also around community farming practices and festivities related with cropping seasons. Any attempt to improve the crop performance in these systems should be made in tight collaboration with farmers, to be aware of their priorities, the variety of purposes related with maize production and the labors implied, among others.

Little quantitative information is available to characterize the cropping systems of the NWA, and, as far as we are aware, there are no works comparing cropping system trends across the altitudinal gradient. For this reason, here, we provide information based on our own source of data obtained from surveys conducted as part of the FAO Project funded by the Benefit-sharing Fund of the International Treaty on Plant Genetic Resources for Food and Agriculture[54]. Except when other references are provided, all the information of this section is thus based in these surveys (Table 3). Surveys were carried out in 2021 (from January to April) in different locations of Salta (Santa Victoria Oeste) and Jujuy (Humahuaca, Tilcara and Tumbaya) across an altitudinal range spanning from 2,100 to 3,900 masl. A total of 23 families representing different farm establishments were interviewed and data was divided according to the altitude into two groups: below 2,500 masl (n = 14 farms, hereafter, the mid-altitude group-MA) and above 2,500 masl (n = 9 farms, hereafter, the high-altitude group- HA). All the farmers surveyed were land owners, either exclusively or as part of the community property, whereas the piece of land used annually for agriculture was much lower in the HA group (Table 3). Main crops include maize, faba beans, potatoes, oca (*Oxalis tuberosa*), barley, alfalfa, summer wheat and some also have small orchards for self-consumption in the lowest lands (personal observations).

Weather conditions are characterized by dry climate during most of the year with a rainy season centered during spring and summer[58]. Still, rainfall water is not enough for most of the crops. All the farmers surveyed use irrigation during the summer (mostly furrow), either directly from the river, from ditches, water springs or from thaw origin. Between groups, a larger proportion of irrigation water came from thaw in the HA group, who also reported more frequently insufficient water availability for crop growth (Table 3). Climate change projections studied at lower latitudes, in the Andes mountains of Bolivia and Peru, show that, after a period of increased flow due to the glacier melt disequilibrium, water resources are expected to diminish as a consequence of, both, reduced ice mass and changes in precipitation trends[59,60], with a further effect of warming increasing vapour pressure deficit. Thus, improving water use efficiency turns out to be a key issue in the long term survival of these cropping systems. Regarding soil conditions, all the surveyed fields were characterized by a shallow soil (< 50 cm depth) typical of the NWA[1]. Soil texture was usually dominated by clay in the MA group but was much more sandy in the HA

group. Either moderate or severe erosion processes were observed in both groups of farms (Table 3), which has been related to the topographic characteristics and low soil cover during the dry season[61].

Maize crop management and seed exchange practices

In most of the farms surveyed, maize is used both for self-consumption and for selling, although a higher proportion for self-consumption was reported in the HA group (Table 3). Usually, selling depends on surplus production[53] which may be limited in the HA group not only because of the harsher conditions associated with increased altitude but also because of the smaller piece of land and insufficient water availability (Table 3). Whereas the MA uses their own animal manure for fertilization, most of the farmers in the HA group buy manure from external animals to fertilize. All the farmers surveyed sow manually, usually following contour lines or against the slope which is a usual practice in these environments (Fig. 1). A wider variety in both sowing and harvest date was reported in the MA group, whereas the HA group was mostly limited to sow in October and harvest by April (Table 3). This likely represents the effect of frost occurrence restricting the environmental window for the crop in the HA group. After sowing, common practices include hilling and weeding (Fig. 1).

Regarding seed exchange practices, all the farmers reproduce their own seed for the following harvest. However, the MA group reported a much higher rate of seed replacement (half of them using the 'same' seed for less than 10 years) whereas in the HA group, half of the farmers interviewed reported to be using the 'same' seed for more than 20 years. This apparently lower seed exchange rate in the HA group is likely reflecting a general lack of adaptation of most of the new seeds acquired by the HA farmers, finally resulting in the farmer keeping its own seed instead of replacing it by a lower-performance accession. We raise this conclusion based on the fact that farmers interviewed are not especially isolated (personal observations), and also because they do crop varieties that must be harvested before maturity (i.e., they need frequent seed supply). While the seed origin is not always clear, many farmers report exchanging seeds with other communities located at higher altitudes (Ferreyra, Salve, personal communication). Seeds originated from higher altitudes are likely to have gone through a process of empirical breeding, being improved for tolerating harsher conditions, but, at the same time, may drag into lower altitudes some yield penalizing traits (e.g., shorter than needed cycles). Further work is needed to characterize seed exchange practices and understand genetic fluxes within maize native races of the NWA.

The total number of maize varieties sown in each group was similar (9-10) with some varieties being sown in both groups of farms ('amarillo', 'blanco', 'kully') whereas other were exclusively mentioned in the MA group ('anaranjado chichero', 'garrapata', 'bolita del altiplano', 'pizancalla', 'gateado', 'capia' and 'híbrido') or in the HA group ('8 rayas', 'diente de caballo', 'costeñito', 'pisincho', 'morocho' and 'chullpi'). Synonymy is also common; the same variety may be named differently according to the region. In some cases, the same variety sown across the altitudinal gradient may be harvested before maturity in higher altitude sites for fresh consumption (known as 'choclo' by local people), before the occurrence of early frosts that arrest grain filling and deteriorate grain quality[62]. The HA group used a higher number of maize varieties per season, most of the farmers using at least three varieties compared with two or less in the MA group (Table 3). This is lower than reported for Caspalá, 3,070 masl (Jujuy), where 6.6 races or 'etnotaxa' are sown annually[62] but higher than reported for the highlands of Mexico, where an average of 1.57−1.42 maize varieties were cropped across a gradient from 2,400 to 1,200 masl[63]. A higher number of races in the HA group could be related with migration habits across altitudinal floors allowing exploitation of different environments[64], with the specific interest of some farmers in preserving seeds that are not easy to acquire[62], and also because this group is less influenced by market preferences towards yellow and white corn (farmers' statements), since most of the production is for personal consumption.

Many authors raise the concern about the decreasing number of races sown annually, due to many factors including changes in culinary practices[62], changes in migratory uses of land[64] and the introduction of improved varieties[53,54], all of these identified as proximate drivers promoting genetic erosion[52]. Moreover, conservation of the genetic identity of the races may not be an easy goal for farmers. The high number of races cropped per farm together with the small size of the plots and the narrow sowing window, is likely to result in extensive cross-pollination. Potential pollen dispersal in maize can reach up to 55 m from the pollen source, although the relative impact on the pollen receptor is usually small, < 0.2%[65]. This process could be larger as altitude increases, because phenological variability between races is restricted (increased overlapping in the reproductive period). Regarding cross-pollination between farms, this may be less important given the distances, although not completely negligible since topography and wind direction can increase potential pollen dispersal[66]. Overall, this highlights the importance of ensuring ex situ conservation of local races by public institutions to avoid progressive genetic erosion[52]. At the same time, in situ conservation could be met by effectively supporting those farmers aiming to practice it and also by market strategies increasing the demand of different maize varieties.

Possible avenues to improve yields: management and breeding

Plant density

Unlike other cereals, in maize, plant density is an important variable defining yield as the crop has lost tillering ability during domestication[67]. A range of optimum plant density for maximizing yield is usually defined for each environment x genotype combination for the core maize productive regions, with usually higher optimum densities in those environments with a higher yield potential[68]. However, this is not always true; e.g., cool environments[69] or late sowings[70,71] may require higher plant densities to maximize yields despite having a lower yield potential than other environments using the same plant densities. This could also be the case of high altitude environments, where increased planting densities bring closer the achievement of a critical leaf area index with positive effects on biomass accumulation and yield[17]. At the same time, detrimental effects associated with barrenness[72] when the minimum threshold for grain fixation is not achieved (plant growth rate per kernel during the critical period[73]) could be attenuated due to the extension of the critical period. Our

own data shows that yield improvements can be met by increasing plant densities 50% more than recommended, with a higher advantage in the lowest yielding environment mostly related with higher grain number[9]. Moreover, within the same location, interannual fluctuations indicate that higher plant densities have a greater impact when lower T during the grain filling are experienced[69]. This could be related with low T reducing kernel growth rates and kernel weight[41], and thus a higher role for kernel number in determining yields. Further work is needed to understand the mechanisms behind these responses.

Increased planting densities also deserve other considerations. Some farmers have stated that increased plant densities are advantageous for facing unexpected late frosts, with upper, more exposed plants, protecting the lowermost plants (farmers' statements), improving plant survival at the stand level although with an erratic plant density outcome. This empirical observation should be tested by quantifying plant survival rates under different planting densities, and complemented with thinning procedures after late frosts period, to reach plant densities within the optimum range. Later on, stand density also modifies the canopy microclimate, with higher densities contributing to conserve heat loss from the soil[74], thus attenuating daily thermal fluctuations and the impact of low night T on subsequent photosynthetic performance. Nonetheless, the high genotypic variability encountered at the population level for these highland open-pollinated races of the NWA[46] could enhance interplant variation (the occurrence of dominant and dominated individuals) especially under high planting densities with a negative impact on yields[75]. Further exploring the potential impacts of increased plant density in high altitude environments is needed for a thorough understanding of crop responses.

Breeding strategies for highlands

Is breeding necessary at all?

A full exploitation of the available genetic diversity lying within Andean maize races depends on the development of breeding programs aimed for these environments. Further, the conservation of this genetic diversity is also dependent to some point on developing specific varieties for the highlands. Otherwise, these environments could be exposed, sooner or later, to the introduction of higher-yielding lowland varieties with much lower genetic diversity, as has been reported to occur in the midlands of Mexico[63]. In Mexico, lowland varieties appear to be as fit as midland varieties when both were tested in midlands[14,38], which is possibly related with a higher input of improved genetics in lowland races[63]. In the highlands of Bolivia, Peru and Ecuador, even after numerous varieties released for these target environments in the last 20 years, yields are 3-times lower than those of dent or semident commercial maize hybrids[76]. This could prompt the thinking that a high yielding genotype could drag that advantage to other environments such as highlands. However, at least for lowlands, evidence indicates that yield potential is not related with tolerance to different types of stress[77].

As described above, low T stress is probably the most important environmental constraint in these high altitude environments. Physiological responses to T are usually characterized by thresholds below or above which, the response changes drastically impairing an extrapolation of genotypic responses across wide altitudinal ranges. Consistent with this, effects of most QTLs important to adaptation gradually changed with T, and broad adaptation is possible only across a moderate range of temperatures[8]. Available evidence for low-latitude highlands show important genotype x environment interaction for the different traits modified by altitude, including yield[14,27,38]. For example, in Mexico, highland-adapted races achieved > 90% lower yields than lowland-adapted groups at 800 masl but up to 60% higher yields at 2,250 masl[14]. This implies that breeding should be carried out considering, at least, different ranges of target altitudes (and, ideally, for each latitudinal range).

Target traits for breeding

A comprehensive characterization of phenotypic variation in NWA maize populations is needed before identifying target traits for breeding. Unfortunately, as far as we are aware, little information is available. In a recent paper, tillering index (number of tillers per main stem) has been identified as highly variable, with a coefficient of variation of 73% among 30 maize accessions collected in the NWA[5]. Tillering improves the crop plasticity to take advantage of unexpected increases in resources during the vegetative period, such as higher than usual rainfall[78]. In these high altitude environments, tillering could also be important to compensate for stand heterogeneity due to occurrence of stresses that compromise plant survival such as very low T or late frosts, and due to manual sowing and seed failure. Moreover, in these highly variable open-pollinated populations, tillering ability could buffer plant hierarchies improving resource use efficiency.

Another potentially important trait for further exploring its variation among the NWA populations is the rate of photosynthetic recovery from night chilling or from chill-induced photoinhibition (see earlier sections). Different works indicate that photosynthetic rates under chilling are not necessarily related to the rates of recovery of the photosynthetic rate once chilling has passed (in maize[33]; in barley[79]). The typically large thermal amplitude of high-altitude environments implies that T rise relatively quickly after the minimum T valley, and thus quick rates of recovery from low T could keep pace with the T increase experienced during the first hours of the day. In other words, recovery rates determine the ability to take advantage of warmer T later in the day. In cool environments, the recovery of photosynthetic rates after a cool night was associated with yield differences[29].

Conclusions

In the mid-latitude highlands of the NWA low T stress (chilling) and related frost occurrence (freezing) are the main constraints for maize production. Delayed plantings and slower phenological development reduce light capture whereas low T during the reproductive period may affect photoassimilate availability, potential grain size and kernel growth rate. Local maize races have been characterized as highly genetically diverse but characterization of phenotypic variation is lacking, and breeding programs are needed for fully exploiting this. Using local germplasm as the main source of genetic variation would be important in preventing genetic erosion, whereas participatory breeding approaches would allow awareness of farmer's goals apart from improved yields (e.g., traditional uses of the grain, other purposes, working labours). Among management strategies, increased plant density could improve light

capture and yield despite a lower yield potential compared with lower latitudes. Cropping systems are threatened by climate change, as many farmers rely on irrigation derived from thaw, and instantaneous water use efficiency is lower than in other environments. Further work is needed to develop management strategies and breeding approaches for these cropping systems in tight collaboration with farmers.

Author contributions

The authors confirm contribution to the paper as follows: study conception and design: Salve D, Ferreyra M, Defacio R, Tambussi E, Antonietta M; data collection: Ferreyra M, Salve D, Lauff D, Maydup ML; analysis and interpretation of results: Ferreyra M, Salve D, Tambussi E, Antonietta M; draft manuscript preparation: Antonietta M, Defacio R, Ferreyra M. All authors reviewed the results and approved the final version of the manuscript.

Data availability

Data sharing not applicable to this article as no datasets were generated during the current study except for information related with surveys to farmers, which is available from the corresponding author on reasonable request.

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Conflict of interest

The authors declare that they have no conflict of interest.

Dates

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