

Impact of altitude on the performance and anthocyanin concentration in five varieties of purple corn in the Peruvian Amazon

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Abstract

Purple corn (*Zea mays* L.) is known for its high anthocyanin content and its agricultural relevance in the Andean-Amazonian region. This study analyzed the impact of the altitudinal gradient (672; 2,437 and 2,892 meters above sea level) on agronomic performance and anthocyanin content in five varieties of purple corn grown in the Amazonas region, Peru. A completely randomized block design with three replications was applied, evaluating morphological, agronomic characteristics, and anthocyanin content in different plant tissues. The results revealed significant differences in vegetative development, with taller plants at low altitude (144.7 ± 21.6 cm) compared to mid-altitude (86.4 ± 35.4 cm). Anthocyanin accumulation showed clear tissue-specific fragmentation, with significantly higher concentrations in the husk (6.3 ± 3.4 mg g⁻¹) and bracts (7.8 ± 3.5 mg g⁻¹) at high altitude ($p < 0.001$). Although grain yield showed no significant differences between altitudes ($p=0.612$), a trend towards higher yields was observed at lower altitudes (633.3 kg ha⁻¹). The varieties showed specific adaptations: 'INIA 615' excelled in yield at low altitude ($1,201.5$ kg ha⁻¹), while 'Sintético MM' performed better at high altitude ($1,381.3$ kg ha⁻¹). These findings suggest an adaptive trade-off between yield and anthocyanin synthesis, providing valuable information to optimize production according to specific goals and environmental conditions.

Keywords: adaptation; agronomic traits; altitudinal gradient; genotype by environment interaction; phenolic compound; yield stability

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Introduction

Anthocyanins, natural pigments belonging to the flavonoid family, have emerged as bioactive compounds of growing interest in biomedical and nutritional research due to their potent antioxidant properties and multiple health benefits for humans (Monroy *et al.*, 2020). These molecules play a crucial role in the prevention of chronic diseases such as cardiovascular diseases, type 2 diabetes, and certain types of cancer, primarily due to their ability to neutralize free radicals and reduce oxidative stress (Rabanal-Atalaya and Medina-Hoyos, 2021a; Sadowska-Bartosz and Bartosz, 2024). Furthermore, recent studies have shown that anthocyanins possess significant anti-inflammatory (Kowalczyk *et al.*, 2024), antidiabetic (Kozłowska and Nitsch-Osuch, 2024) and anticancer (Bharathy and Thanikachalam, 2025), properties, which have generated growing interest in their study and utilization in human nutrition (Lu *et al.*, 2024).

In the agricultural field, anthocyanins are present in various plant species, with purple corn (*Zea mays* L.), being one of the most notable, an endemic variety of the Andean and Amazonian regions of Latin America that contains some of the highest concentrations of these bioactive compounds (Medina-Hoyos *et al.*, 2020; Rabanal-Atalaya and Medina-Hoyos, 2021a). The Peruvian Amazon, with its rich biodiversity and variability in environmental conditions, constitutes a unique setting for investigate how environmental factors influence both the yield and anthocyanin concentration in this crop, even when it is the same variety (Ranilla *et al.*, 2021). Research has shown that specific environmental factors, such as altitudinal gradients, temperature, and rainfall patterns, can significantly modulate the synthesis and accumulation of these bioactive pigments (Cai *et al.*, 2023). In addition to its traditional role in Amazonian cuisine, purple corn has become a strategic resource for the food and pharmaceutical industries, thanks to its remarkable phytochemical profile and scientifically supported functional properties, which have driven its increased value in the international market (Cristianini and Guillén Sánchez, 2020; Roy and Rhim, 2021).

In this context, the current research employs a systematic approach to understand how the interaction of environmental factors influences the synthesis and accumulation of anthocyanins in different varieties of purple corn (Cai *et al.*, 2023). This understanding is key to improving agricultural practices and promoting the sustainable development of this valuable phyto-genetic resource. Specifically, this study aims to evaluate how altitude affects agronomic performance and anthocyanin content in five varieties of purple corn grown in three representative locations within the Amazonas region, Peru.

Materials and Methods

Study area

The study was conducted in 2023 at three locations in the Amazonas Department, Peru, strategically chosen to represent three distinct altitudinal categories. According to the altitudinal classification, the areas were categorized as: high altitude (>2,500 meters above sea level), mid-altitude (1,500 - 2,500 meters above sea level), and low altitude (<1,500 meters above sea level) (Vélez and Rueda, 2023).

The high-altitude location was situated in Cohecham (2,892 meters above sea level), in the Conila district, Luya province, where temperatures range from 10 to 18 °C. The topographical conditions and cultivation system used at the altitudinal locations are illustrated (Figure 1). These conditions are typical of high-Andean ecosystems, where low temperatures and high UV radiation significantly impact the biosynthesis of secondary metabolites. The mid-altitude location, Paclas (2,437 meters above sea level), located in the San Jerónimo district, Luya province, represents a transition zone with temperatures ranging from 11 to 24 °C, conditions that have proven favorable for various Andean crops. The low-altitude zone, represented by El Aserradero (672 meters above sea level) in the Jamalca district, Utcubamba province, shows typical

characteristics of the Amazon region, with temperatures fluctuating between 16 and 33 °C (Table 1), creating a significant contrast for crop evaluation.



Figure 1. Panoramic view of purple corn (*Zea mays* L.) cultivation on terraced slopes typical of high-altitude locations in the Peruvian Amazon

The photograph shows the topographical challenges and adaptation of the crop to steep terrain conditions at approximately 2,800 m.a.s.l. (meters above sea level), demonstrating the environmental context of the altitudinal gradient study

Table 1. Geographical and climatic characteristics of the experimental locations categorized by altitude in the Amazonas department, Peru

Altitudinal category	Province	District	Locations	Geographic coordinates	Altitude (m.a.s.l.)	Average temperature (°C)
High (>2,500 m a.s.l.)	Luya	Conila	Cohechán	6°59'37" S, 78°6'31" O	2,892	10 a 18
Mid (1,500 - 2,500 m a.s.l.)	Luya	San Jerónimo	Paclas	6°03'35" S, 77°58'28" O	2,437	11 a 24
Low (<1,500 m a.s.l.)	Utcubamba	Jamalca	Aserradero	5°56'30" S, 77°54'50" O	672	16 a 33

Plant material and experimental design

Five purple corn (*Zea mays* L.) cultivars were evaluated: one native variety ('Canteño') and four improved varieties ('INIA-601', 'INIA 615', 'PMV 581', and 'Sintético MM'), whose phenotypic characteristics and genetic origin are detailed below (Table 2).

Table 2. Characteristics of the varieties planted for study

Variety	Native / Improved	Description
'Canteño'	Native variety	Derived from the Cuzco race, it is earlier maturing and is cultivated in many areas of the Peruvian Sierra, especially in the highlands between 1,800 and 2,500 meters above sea level (Medina-Hoyos <i>et al.</i> , 2020).
'INIA-601'	Improved variety	Originating from the Cajabamba experimental substation of INIA, formed with 256 progenies: 108 from the Morado Caráz variety and 148 from the local Negro de Purubamba variety, it adapts to the northern highlands between 2,490 and 3,175 meters above sea level (Medina-Hoyos <i>et al.</i> , 2020).
'INIA 615'	Improved variety	'INIA 615': An improved variety by INIA, selected through recurrent selection from half-siblings of 36 collections of Kulli race cultivars over nine cycles (Medina-Hoyos <i>et al.</i> , 2020).
'PMV 581'	Improved variety	Improved variety by the National Agrarian University La Molina, obtained from the Morado de Caraz variety, adapted to the coast and lower highlands, with resistance to rust and cercospora. Its vegetative period is intermediate, with medium-sized ears of 15 to 20 cm, elongated, and high pigment content (Medina-Hoyos <i>et al.</i> , 2020).
'Sintético MM'	Improved variety	A synthetic variety derived from 'INIA-601', this cultivar is being selected by the Baños del Inca Experimental Station of INIA, using a selection of S1 progenies (Medina-Hoyos <i>et al.</i> , 2020).

The experiment was conducted using a Randomized Complete Block Design (RCBD) with three replications. Each experimental unit consisted of five rows, each 5.5 meters long, with 0.8 meters spacing between rows and 0.5 meters between plants, establishing a target population density of 75,000 plants per hectare (Figure 2). The effective evaluation area comprised the three central rows, from which ten plants per experimental unit were systematically selected for biometric measurements.



Figure 2. Early vegetative stage of purple corn (*Zea mays* L.) experimental plots showing the systematic planting arrangement with 0.8 m spacing between rows and 0.5 m between plants at one of the study locations in the Peruvian Amazon

The photograph illustrates the field design used in the completely randomized block design with three replications

Agronomic management

Fertilization was carried out through the localized application of island guano (50 g per plant). Weed control was performed manually, adapted to the crop's phenology in each location: In El Aserradero, weeding was carried out 15 and 30 days after sowing (DAS); in Paclas, at 30 and 60 DAS; and in Cohechán, at 37 and 90 DAS. Fertilizer application was performed during the first weed control in each location.

Evaluation of agronomic characteristics

Phenological and morphological parameters analyzed, included days to, 50% male flowering (80-90 DAS) and female flowering (90-120 DAS), plant height (PH, measured from the soil surface to the insertion point of the flag leaf), and ear insertion height (EI). The plant development and morphological characteristics evaluated are shown (Figure 3). Both measurements were taken in centimeters using a measuring tape, 20 days before harvest, near the end of the crop cycle. Agronomic variables were quantified, such as root lodging (number of uprooted plants), stem lodging (number of plants with broken or bent stems that remained viable), total number of plants and ears harvested, incidence of rot, field weight (g), and moisture content (%) using the G610i moisture tester. The qualitative evaluation was conducted by an assessor who rated the plant and ear appearance using an ordinal scale from 1 to 5, where 1 represents highly desirable characteristics and 5 represents highly undesirable characteristics, according to the criteria established by the International Maize and Wheat Improvement Center (CIMMYT) (CIMMYT, 2023).



Figure 3. Purple corn (*Zea mays* L.) plants at advanced vegetative stage showing typical plant architecture and development under Amazonian conditions
The photograph demonstrates the morphological characteristics evaluated including plant height and ear insertion height across the experimental plots

The photographs were taken after harvest, separating the husk and cob from the grain in each experimental field (Figure 4).



Figure 4. Representative photographs of bracts and cobs of the five varieties of purple corn (*Zea mays* L.) evaluated after harvest

Grain yield determination

Grain yield was calculated after adjusting the grain weight to a standard commercial moisture content of 14% (Mulvaney and Devkota, 2020), using the following formula:

$GY = FW \times \left(\frac{10000}{EPA} \times \frac{(100 - \%H)}{86} \right) \times ID$	(1)
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Where:

RGN = grain yield in kg ha⁻¹;

PC = field weight (kg);

%H = grain moisture percentage;

86 = moisture correction coefficient for 14% (Halvorson *et al.*, 2020);

AEP = effective plot area (17.6 m²);

ID = threshing index, determined using a random sample of ten ears per experimental unit.

Anthocyanin content analysis

Anthocyanin content was evaluated in three anatomical structures (bracts, cob, and grain) using a modified differential pH method (Chen *et al.*, 2024). Samples were ground to obtain uniform particles smaller than 250 μm were obtained, followed by extraction with 1N HCl, filtration, and pH adjustment (Resende and Franca, 2022; Taghavi *et al.*, 2023). Spectrophotometric quantification was performed at 510 nm, and the results expressed as milligrams of cyanidin-3-glucoside equivalent per gram of dry sample, according to the following equation (Khamphan *et al.*, 2020):

$\text{Anthocyanins (mg/100g)} = \frac{RA \times DF \times V \times 100}{\epsilon \times L \times W}$	(2)
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Where:

A = absorbance at 510 nm,

FD = total dilution factor (30),

V = total extract volume in mL (10),

ϵ = molar extinction coefficient of cyanidin-3-glucoside (26,900 L/mol-cm),

L = path length (1 cm), y

W = sample weight in grams (0.5).

The results were expressed as milligrams of cyanidin-3-glucoside equivalent per 100 grams of dry sample (Khamphasan *et al.*, 2020), and the values were converted to mg g^{-1} statistical analysis.

Statistical analysis

The data were analyzed using SPSS version 29.0. Normality and homogeneity of variances were checked using the Shapiro-Wilk and Levene tests, respectively. A two-way analysis of variance (ANOVA) was conducted to compare, genotype, and their interaction on the morphological, agronomic, and biochemical variables among the different altitudes. A post-hoc analysis was performed using the Bonferroni test. For categorical variables, such as plant and ear appearance, the Chi-square test was used. The figures were created using GraphPad Prism 10.4.2 (Prism 10.4.2). The statistical significance adopted was $p \leq 0.05$.

Results

The study was conducted in three locations of the Peruvian Amazon representing an altitudinal gradient: Cohechán (2,892 m.a.s.l.), Paclas (2,437 m.a.s.l.), and El Aserradero (672 m.a.s.l.). A randomized complete block design with three replications was used, evaluating five varieties of purple corn in experimental plots of 88 m² each. A total of 552 plants were harvested, yielding 382 commercially acceptable ears and 58 ears showing signs of rot. The total weight of the grain obtained from the commercial ears was 3,962.8 g (3.963 kg), with an average moisture content that varied significantly ($p=0.022$) among locations, being lowest in Paclas (8.97%) and highest in El Aserradero (14.8%). Additionally, El Aserradero (low altitude) had the earliest vegetative cycle, with male and female flowering occurring at 57 and 72 days after sowing (DAS), respectively. In contrast, Paclas (medium altitude) presented an intermediate cycle, reaching male flowering at 108 DAS and female flowering at 129 DAS. Cohechán (high altitude) had the latest cycle, requiring 126 DAS for male flowering and 147 DAS for female flowering, showing a significant gradient in phenological development among the three locations analyzed.

Morphological characteristics and yield components

Plants grown at low altitude (El Aserradero, 672 m.a.s.l.) exhibited pronounced vegetative growth, with an average height of 144.7 ± 21.6 cm and an ear insertion height of 85.0 ± 37.1 cm, significantly higher than in other locations ($p < 0.001$). This site also recorded the highest number of harvested plants (19.5 ± 8.7) and commercial ears (15.7 ± 8.0), significantly outperforming ($p < 0.001$) Cohechán (8.6 ± 4.9 plants; 4.5 ± 5.4 ears) and Paclas (8.7 ± 5.7 plants; 5.2 ± 4.2 ears). However, the low altitude conditions also increased susceptibility to root lodging (3.1 ± 1.3 plants) and stem lodging (6.3 ± 1.2 plants), as well as the incidence of ear rot (2.9 ± 2.5) (Table 3).

Table 3. Morphological characteristics, agronomic features, and anthocyanin content in purple corn grown in three locations of the Peruvian Amazon

Characteristic	High Altitude	Medium Altitude	Low Altitude	p
Morphological Characteristics				
Plant height (cm)	124.2 ± 28.0 b	86.4 ± 35.3 a, c	144.7 ± 21.6 b	<0.001
Ear insertion height (cm)	59.1 ± 17.8 c	48.7 ± 17.6 c	85.0 ± 37.1 a, b	0.001
Agronomic Characteristics				
Root Lodging (No. plants)	1.5 ± 0.7 c	1 ± 0.9 c	3.1 ± 1.3 a, b	<0.001
Stem Lodging (No. plants)	2.2 ± 1.5 c	1.7 ± 1.6 c	6.3 ± 1.2 a, b	<0.001
Harvested plants (N°)	8.6 ± 4.9 c	8.7 ± 5.7 c	19.5 ± 8.7 a, b	<0.001
Harvested ears (N°)	4.5 ± 5.4 c	5.2 ± 4.2 c	15.7 ± 8.0 a, b	<0.001
Rotting ears (N°)	0.5 ± 0.9 c	0.5 ± 0.9 c	2.9 ± 2.5 a, b	<0.001
Field weight (g)	82.3 ± 110.1	66.6 ± 17.1	115.3 ± 62.3	0.278
Moisture (%)	9.1 ± 7.7	9.0 ± 7.6 c	14.8 ± 0.2 b	0.022
Qualitative Aspects *				
Plant appearance, points	3.7 ± 0.8	4.1 ± 0.8 c	3.3 ± 0.9 b	0.026
Optimum (n %)	0 (0%)	0 (0%)	0 (0%)	<0.001
Very good (n %)	0 (0%)	0 (0%)	2 (13.3%)	
Good (n %)	7 (46.7%)	4 (26.7%)	9 (60%)	
Regular (n %)	5 (33.3%)	5 (33.3%)	2 (13.3%)	
Poor (n %)	3 (20%)	6 (40%)	2 (13.3%)	
Ear appearance, points	3.7 ± 1.4	4.3 ± 0.8	3.8 ± 0.7	0.295
Optimum (n %)	1 (6.7%)	0 (0%)	0 (0%)	<0.001
Very good (n %)	1 (6.7%)	0 (0%)	0 (0%)	
Good (n %)	3 (20%)	3 (20%)	5 (33.3%)	
Regular (n %)	5 (33.3%)	5 (33.3%)	8 (53.3%)	
Poor (n %)	5 (33.3%)	7 (46.7%)	2 (13.3%)	
Yield and anthocyanin content				
Grain yield (kg ha ⁻¹)	460.8 ± 562.6	480.3 ± 518.4	633.3 ± 473.2	0.612
Anthocyanins in husk (mg g ⁻¹)	6.3 ± 3.4 b, c	3.1 ± 1.0 a	2.9 ± 0.7 a	<0.001
Anthocyanins in bracts (mg g ⁻¹)	7.8 ± 3.5 b, c	3.7 ± 2.1 a	3.2 ± 1.0 a	<0.001
Anthocyanins in grain (mg g ⁻¹)	2.0 ± 0.3	1.6 ± 0.3	1.7 ± 0.9	0.093

The values are represented as mean ± standard deviation. Cohechán, Paclas, El Aserradero (a, b, c, respectively). Different letters (a, b, c) in the same row indicate significant differences among locations according to the Bonferroni test ($p < 0.05$). *Qualitative evaluation scale: 1=optimal, 2=very good, 3=good, 4=regular, 5=poor

Grain yield and varietal adaptation

The yield showed a notable interaction between genotype and environment. Table 4 shows that 'INIA 615' stood out at low altitude with 1,201.5 kg ha⁻¹, while 'Sintético MM' achieved its highest yield at high altitude (1,381.3 kg ha⁻¹). Although the average yield according to Table 3 was higher at low altitude (633.3 ± 473.2 kg ha⁻¹), this difference was not statistically significant ($p=0.612$).

Table 4. Grain yield (kg ha⁻¹) of five purple corn varieties cultivated in three altitudinal categories in the Peruvian Amazon

Characteristic	High Altitude	Medium Altitude	Low Altitude	p
'Canteño'	117.6 ± 203.6	392.1 ± 351.4	356.7 ± 222.7	0.417
'INIA-601'	322.9 ± 324.9	677.2 ± 437.9	733.5 ± 232.5	0.252
INIA 615	115.6 ± 200.3	255.2 ± 441.9	1,201.5 ± 758.4*	0.093
'PMV 581'	366.5 ± 528.5	736.2 ± 865.3	447.6 ± 234.9	0.790
'Sintético MM'	1,381.3 ± 284.2**	340.9 ± 590.5	427.0 ± 322.3	0.059

The values are presented as mean ± standard deviation. *The highest yield was observed under low altitude conditions.

**The highest yield was observed under high altitude conditions

Anthocyanin profile and its distribution in plant tissues

Anthocyanin and accumulation exhibited different response depending on plant tissue type and altitude (Table 5): In the husk, the highest concentrations were recorded at high altitude, with ‘Sintético MM’ ($10.2 \pm 0.5 \text{ mg g}^{-1}$) and ‘INIA 615’ ($9.7 \pm 0.6 \text{ mg g}^{-1}$) standing out. In bracts, ‘INIA 615’ reached the highest concentration at high altitude ($10.7 \pm 0.4 \text{ mg g}^{-1}$), while ‘Canteño’ showed exceptional behavior at medium altitude ($7.5 \pm 0.2 \text{ mg g}^{-1}$). In grain, ‘Canteño’ had the highest concentration at low altitude ($2.8 \pm 0.4 \text{ mg g}^{-1}$), followed by ‘INIA-601’ ($2.6 \pm 0.2 \text{ mg g}^{-1}$).

Table 5. Anthocyanin content (mg g^{-1}) in different tissues of five purple corn varieties cultivated in three altitudinal zones of the Peruvian Amazon

Variety and Tissue	High Altitude	Medium Altitude	Low Altitude	P
Anthocyanin content in husk (mg g^{-1})				
‘Canteño’	$1.6 \pm 0.4 \text{ b, c}$	$3.8 \pm 0.2 \text{ a, c}$	$2.7 \pm 0.3 \text{ a, b}$	0.027
‘INIA-601’	$3.9 \pm 0.2 \text{ b, c}$	$2.7 \pm 0.7 \text{ a}$	$2.5 \pm 0.3 \text{ a}$	0.058
INIA 615	$9.7 \pm 0.6 \text{ b, c}^*$	$3.5 \pm 0.8 \text{ a}$	$3.8 \pm 0.5 \text{ a}$	0.059
‘PMV 581’	$6.1 \pm 0.5 \text{ b, c}$	$3.9 \pm 0.3 \text{ a, c}$	$2.1 \pm 0.6 \text{ a, b}$	0.027
‘Sintético MM’	$10.2 \pm 0.5 \text{ b, c}^{**}$	$1.5 \pm 0.2 \text{ a, c}$	$3.5 \pm 0.3 \text{ a, b}$	0.027
Anthocyanin content in bracts (mg g^{-1})				
‘Canteño’	$1.6 \pm 0.3 \text{ b, c}$	$7.5 \pm 0.2 \text{ a, c}^{\S}$	$2.9 \pm 0.5 \text{ a, b}$	0.027
‘INIA-601’	$6.9 \pm 0.3 \text{ b, c}$	$2.7 \pm 0.4 \text{ a}$	$2.8 \pm 0.6 \text{ a}$	0.066
INIA 615	$10.7 \pm 0.4 \text{ b, c}^{**}$	$1.9 \pm 0.1 \text{ a, c}$	$2.8 \pm 0.2 \text{ a, b}$	0.027
‘PMV 581’	$10.6 \pm 0.2 \text{ b, c}$	$2.7 \pm 0.2 \text{ a}$	$2.7 \pm 0.1 \text{ a}$	0.066
‘Sintético MM’	$9.2 \pm 0.3 \text{ b, c}$	$3.6 \pm 0.1 \text{ a, c}$	$5.0 \pm 0.6 \text{ a, b}$	0.027
Anthocyanin content in grain (mg g^{-1})				
‘Canteño’	$1.7 \pm 0.2 \text{ c}$	$1.3 \pm 0.3 \text{ c}$	$2.8 \pm 0.4 \text{ a, b}^{\P}$	0.039
‘INIA-601’	$2.4 \pm 0.1 \text{ b, c}$	$1.3 \pm 0.1 \text{ a, c}$	$2.7 \pm 0.2 \text{ a, b}$	0.027
INIA 615	$2.4 \pm 0.2 \text{ b, c}$	$2.1 \pm 0.03 \text{ a, c}$	$0.8 \pm 0.1 \text{ a, b}$	0.027
‘PMV 581’	$1.9 \pm 0.1 \text{ b, c}$	$1.5 \pm 0.2 \text{ a, c}$	$1.0 \pm 0.1 \text{ a, b}$	0.027
‘Sintético MM’	2.0 ± 0.4	1.7 ± 0.1	1.5 ± 0.2	0.252

The values are presented as mean \pm standard error ($n = 3$). Cohechán, Paclas, El Aserradero (a, b, c, respectively). Different letters (a, b, c) in the same row indicate significant differences between altitudes according to the Bonferroni test ($p < 0.05$). * Second highest anthocyanin content in husk observed at high altitude. ** Highest anthocyanin content observed at high altitude. \S Highest anthocyanin content in bracts observed at medium altitude. \P Highest anthocyanin content in grain observed at low altitude.

Proportional distribution of anthocyanins in grain, bracts, and husk for each variety under high, medium, and low altitude conditions is illustrated by stacked bar charts (Figure 5). The tripartite arrangement of the chart allows for simultaneous comparison of the anthocyanin accumulation pattern across plant tissues and their response to altitudinal variation. Percentages are shown on the Y-axis (0-100%), while the varieties are distributed along the X-axis, providing a clear visualization of the differences in the partitioning of anthocyanins across the various plant organs.

The results reveal variety-specific adaptations: ‘INIA 615’ demonstrated higher yield at low altitude but a greater anthocyanin content at high altitude; ‘Sintético MM’ excelled both in yield and anthocyanin content at high altitude; and ‘Canteño’ stood out in anthocyanin accumulation in grain under low-altitude conditions. These adaptation patterns suggest the necessity of selecting varieties based on both specific production goals and the altitudinal conditions of cultivation.

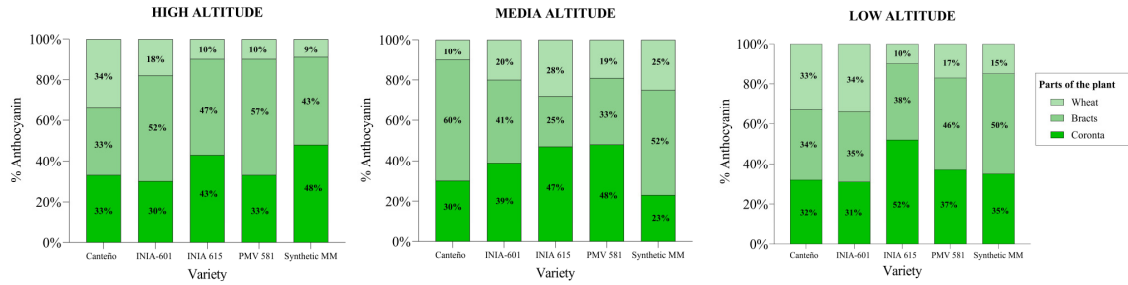


Figure 5. Percentage distribution of anthocyanin content in different vegetative structures of five purple corn varieties grown in three altitudinal conditions in the Peruvian Amazon

Discussion

The aim of this study was to assess how altitude affects agronomic yield and anthocyanin content in five purple corn varieties cultivated in three representative locations of the Amazonas region, Peru. Significant differences were observed in the morphological characteristics, agronomic traits, and anthocyanin content in purple corn grown at different altitudes. Morphological characteristics displayed clear patterns; plants were notably taller at low altitudes compared to those at medium altitudes. With respect to secondary metabolites, a clear trend in the accumulation of anthocyanins according to altitude was observed, with significantly higher concentrations in the husk and bracts at the highest-altitude location. However, grain yield (kg ha^{-1}) did not differ significant differences across altitudes, although a numerical trend towards higher yields was noted in the lower-altitude zones. This differential response suggests specific adaptive mechanisms that prioritize the accumulation of bioactive compounds or yield, depending on the altitude of cultivation.

The notable phenotypic plasticity observed in response to the altitudinal gradient demonstrates the adaptive capacity of purple corn to thrive in different agroecological environments. This plasticity, which refers to the ability of a genotype to generate different phenotypes depending on environmental conditions (Tibbs-Cortes *et al.*, 2024), is crucial for adaptation to varying altitudes. The prolongation of the vegetative cycle at higher altitudes represents an evolutionary strategy that optimizes solar radiation interception and compensates for thermal limitations (Djalovic *et al.*, 2024), which aligns with previous findings on altitudinal adaptations in corn (Jin *et al.*, 2023). This adaptability is mediated by epigenetic mechanisms that enhance the crop's resilience to environmental stress (Kakoulidou *et al.*, 2021), significantly contributing to its adaptability and heterosis (Liu *et al.*, 2021).

The results indicate a compensation pattern between growth and chemical defense, a phenomenon that has been widely documented in research on resource allocation in plants (Giolai and Laine, 2024). At low altitudes, plants prioritized their vegetative development, reaching greater height and biomass production, which aligns with recent studies on growth regulation in response to environmental factors (Tibbs-Cortes *et al.*, 2024). In contrast, high-altitude conditions favored the synthesis of anthocyanins, especially in the husk and bracts, an adaptation mechanism that has been observed in various Andean crops (Fischer *et al.*, 2022). This differential allocation suggests the presence of specific regulatory mechanisms modulated by environmental signals, implying the activation of secondary metabolic pathways as a response to abiotic stress (Rabeh *et al.*, 2025).

The specific distribution of anthocyanins in plant tissues reflects highly specialized metabolic regulation (Rabeh *et al.*, 2025). The preferential accumulation of anthocyanins in structural tissues, such as the husk and bracts, under high-altitude conditions represents a protective adaptation against intense UV radiation and temperature fluctuations (Bai *et al.*, 2025), likely mediated by specific transcription factors (Yoon *et al.*, 2020).

The preferential accumulation in the grain observed at lower altitudes suggests mechanisms for protecting the reproductive tissue against increased biotic pressures (Chen *et al.*, 2025).

The genotype-environment interaction observed has important implications for the development of improved varieties (Bai *et al.*, 2025). Specific adaptation patterns, such as those seen in 'INIA 615' (which performs better at low altitude) and 'Sintético MM' (which performs better at high altitude), highlight the need for breeding strategies that are tailored to the environment and the intended production purpose (Rabanal and Medina, 2022; Rabanal-Atalaya and Medina-Hoyo, 2022). Varietal stability, particularly evident in INIA 601 in terms of yield and 'Canteño' regarding anthocyanin content in the grain, is a key criterion for selection, supported by recent studies on the heritability of adaptive traits in maize (Rabanal-Atalaya and Medina-Hoyos, 2021b; Rabanal and Medina, 2022).

Although this study provides valuable information, future research should include multiple growing cycles to assess the temporal stability of the observed patterns (Ranilla *et al.*, 2021). A more in-depth analysis of the environmental factors influencing anthocyanin synthesis is recommended (Pei *et al.*, 2024), considering the complex interaction between climatic variables and metabolic responses (Wang *et al.*, 2025). Furthermore, it is essential to conduct comprehensive evaluations of the nutritional and functional quality of the grain under different altitudinal conditions (Zhang *et al.*, 2019).

Despite the results obtained, it is important to note that this study has some limitations. The cross-sectional design prevents establishing direct causal relationships, and the representation of a single altitude level. Nonetheless, this study has some significant strengths that deserve to be highlighted: it is the first comprehensive study to simultaneously evaluate agronomic characteristics and anthocyanin content in purple corn across an altitudinal gradient in the Amazon region of Peru, providing solid quantitative data on the genotype-environment interaction. The findings offer essential information for developing altitude-specific breeding strategies and establish a solid foundation for optimizing cultivation protocols that maximize both yield and anthocyanin synthesis, contributing to the economic and nutritional sustainability of the crop in the region.

Conclusions

This study highlights how altitude plays a crucial role in shaping both the growth and chemical makeup of purple corn. Corn plants growing at lower altitudes showed more vigorous vegetative growth, while those at higher elevations tended to be more compact and had higher levels of anthocyanins, especially in the husk and bracts. These results point to a clear trade-off between producing biomass and synthesizing secondary metabolites as you move up in altitude, indicating that plants adopt different strategies for resource allocation based on their environment. The significant interaction between genotype and environment underscores the need to choose varieties that align with specific production goals and the local conditions they will face.

Authors' Contributions

Conceptualization: YASD, RCVR, CEOR, WPC, CGH, EMC, WSL; Data curation: YASD, RCVR, CEOR, WPC, CGH, EMC, WSL; Formal analysis: YASD, RCVR, WPC; Funding acquisition: YASD, RCVR, WPC; Investigation: YASD, RCVR, CEOR, WPC, CGH, EMC, WSL; Methodology: YASD, RCVR, WPC, CGH; Project administration: YASD, RCVR, CEOR, WPC, CGH, EMC, WSL; Resources: YASD, RCVR, CEOR, WPC, CGH, EMC, WSL; Software: YASD, RCVR, CEOR, WPC; Supervision: YASD, WPC, CGH; Validation: YASD, RCVR, CEOR, WPC, CGH, EMC, WSL; Visualization: YASD, RCVR, CEOR; Roles/Writing - original draft: YASD, RCVR, CEOR, WSL; and Writing - review & editing: YASD, RCVR, CEOR, WPC, WSL.

All authors read and approved the final manuscript.

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Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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