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Article

Degradation of reserve starch from the seed of wild and domesticated *Phaseolus vulgaris* L.

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Abstract

Domestication has modified the size and type of seed reserves; this raises the question of whether these modifications have had an impact on metabolism and the mobilization of these reserves during germination and seedling establishment. The research aimed to determine the effect of domestication on cotyledons, embryonal axis and dark-grown seedlings of domesticated and wild beans. In 2019, eight seeds of three improved varieties and three wild collections were germinated at 25 °C, another eight seeds with exposed radicles were sown in grow bags and the seedlings obtained were kept for 14 days in darkness. The germinated seeds and seedlings were dissected into their structures and their dry mass and the concentrations of starch, glucose, fructose and sucrose were determined; likewise, the number of cells and the number of starch granules mm^{-2} and their dimensions were also determined in cotyledons. The design used was completely randomized with four replications. On average, the improved varieties had 11 and three times more dry matter in cotyledons and embryonal axis compared to wild varieties, and seven, nine and 13 times more dry matter in root, shoot and remnant of cotyledons, respectively. Concentrations of starch, glucose, and sucrose per gram of dry mass were higher in cotyledons from improved varieties; in contrast, concentrations of starch, glucose, and fructose were higher in the embryonal axis of the wild ones. In the root, wild varieties had higher concentrations of starch, fructose, and sucrose, and in the shoot, domesticated ones had more glucose, fructose, and sucrose. Wild varieties had 42% more cells and 30% more starch granules than domesticated ones per unit area. Domestication modifies the composition and mobilization of reserves during germination and seedling establishment.

Keywords:

beans, germination, reducing sugars, reserve substance.

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Introduction

Plant domestication is the result of human selection, changes in the environment, and management practices that drove phenotypic changes, mainly in the selected and reproductive traits, but also physiological and anatomical changes that resulted from cultivation (Roucou *et al*., 2018). The selected characteristics are focused on meeting human needs, but there is also the adaptation of the plant to the environment that allows it to survive under cultivation and that are similar between cultivated species 'domestication syndrome' (Allaby, 2020).

The domestication of *Phaseolus vulgaris* L. included changes in seed size and plant shape and metabolism, among others (Smýkal *et al*., 2018). In Mexico, genetic improvement of *P. vulgaris* has focused on the size and content of proteins and non-structural carbohydrates of the seed (Allende-Arrarás *et al*., 2006).

The seed weight of wild *P. vulgaris* varies from 0.04 to 0.14 g and that of the domesticated one from 0.2 to 1 g (Lépiz-Ildefonso *et al*., 2010). Bean seeds store carbohydrates to be used in germination and ensure seedling survival and starch accounts for 25 to 45% of the dry mass (Punia *et al*., 2020) and is the main reserve of the seed. The formation of a seed and its transition to a seedling activates genes for embryo formation, seed maturation, and tolerance to desiccation; it also involves the use of reserves, a key element in the evolutionary success of plants (Carbonero *et al*., 2017).

Wild and domesticated bean plants have different initial growth patterns as an indirect consequence of the selection of larger seeds during domestication; however, the concentration of starch, glucose, fructose, and sucrose in domesticated and wild materials has been studied little. The mobilization of seed reserves is involved in the success of natural vegetation and agriculture, involving the catabolism of seed reserves, their transport to the embryo, and the synthesis of new materials (Pandey *et al*., 2010).

The distribution of dry mass and carbohydrates in germination and seedling establishment is governed by genetic, biochemical, and physiological mechanisms (Di Vittori *et al*., 2019). It is now known that plants use their sugars through various carbon metabolic pathways to optimize their use in development. Some sugars regulate protein synthesis for plant growth by being a source of energy for metabolic processes in response to stresses and by connecting with other signaling networks to control cell proliferation and expansion (Lastdrager *et al*., 2014).

In plant breeding, it is necessary to know the genetic, biochemical, and physiological processes that lead to a higher rate of allocation of the main reserve compounds in seeds (Coelho and Benedito, 2008). The comparison of domesticated and wild forms has made it possible to identify probable changes that occurred during the domestication process (Shi and Lai, 2015). The study aimed to determine the effect of domestication on the composition and structure of cotyledons, embryonal axis, and seedlings developed in darkness. If there are differences between domesticated and wild beans in the allocation of biomass and carbohydrates from the cotyledons to the seedling, these will be due to changes in the process of their domestication.

Materials and methods

Plant material

The *Phaseolus vulgaris* L. varieties used were three improved ones: OTI, Cacahuate-72, and Canario-G15, donated by the National Institute of Forestry, Agricultural, and Livestock Research (INIFAP), for its acronym in Spanish, and three wild forms collected in Tepoztlán, Morelos, Cholula, Puebla and Arcelia, Guerrero, Mexico.

Sample preparation

Eight seeds from each cultivar and collection were scarified (notched with a nail clipper on the opposite side of the hilum) and placed on Ahlstrom No. 541 filter paper in 9 cm diameter Petri dishes, 10 ml of distilled water was applied to them, and they were kept in an incubator (Esco Isotherm) at 25 °C until they germinated.

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Likewise, eight seeds with exposed radicle (1-2 mm in length) were sown in 15 x 25 cm black gusseted grow bags, gauge 500 and capacity of 1 kg, containing vermiculite substrate and they were placed for the emergence and development of the seedlings in a dark room for 14 days (d).

The evaluations included: 1) measurement of the dry mass of cotyledons and embryonal axis of germinated seeds, and of the root, shoot, and remnant of seedling cotyledons on a Sciencetech SA 120 analytical balance; 2) the concentrations of starch, glucose, fructose, and sucrose in the cotyledon and embryonal axis of germinated seeds, and in the root and shoot of seedlings in four replications per material and 3) the number of cells and the number and dimensions of starch granules in the cotyledon in four germinated seeds of each material.

Dry mass of cotyledons, embryonal axis, root, shoot, and remnant of cotyledons

The cotyledons and embryonal axis (cauline apical meristem, hypocotyl, and subapical root meristem) of each germinated seed and the root, shoot and remnant of the cotyledons of plants kept in darkness for 14 d were separated with a scalpel, introduced separately into foil envelopes, immersed in liquid nitrogen, freeze-dried for 72 h and weighed on an analytical balance (Sciencetech, model SA 120).

The efficiency in allocation (EA) of biomass from the cotyledons to the seedling was calculated using the following ratio (Yamaguchi, 1978):

$$EA=\frac{\text{Dry mass of the root+shoot}}{\text{Dry mass of cotyledons-Dry mass of the remnant of cotylendons}} X\ 100$$

Concentration of starch, glucose, fructose, and sucrose in cotyledons and embryonal axis and seedling organs

Four germinated seeds were dissected into cotyledons and the embryonal axis, and four seedlings were also dissected into root and shoot; subsequently, they were freeze-dried and the concentration of starch, glucose, fructose, and sucrose was determined by the technique proposed by Viola and Davis (1992) and modified by Vargas-Vázquez *et al*. (2020). The modification consisted of determining the optimal concentration of enzymes and heating times in a double boiler for the samples.

Number of cells, number and dimensions of starch granules in the cotyledon.

In germinated seeds, a segment of the center of the cotyledon was taken, which was fixed in FAA, gradually dehydrated in alcohols, and included in paraffin in an automatic tissue changer (Tissue-Tek II). Subsequently, histological sections 10 microns thick were made with a rotating microtome (Erma Inc.). They were then stained with periodic acid and Schiff's reagent (Johansen, 1940). The number of cells and starch granules was quantified in 40 x fields under an optical microscope (Zeiss, model Axioscope 2) and then the number per mm^2 was calculated. Images were obtained with a digital camera (Amscope) and the length, diameter, and area of each starch granule were estimated with the Image J program.

Experimental design and statistical analysis

Each variety and each wild collection represented a treatment. These were distributed in a completely randomized design. The experimental unit was either a seed or a seedling. Prior to the analysis, the independence, normality and homogeneity of variance of the data were verified. When these assumptions were not met, the variables were transformed to logarithm or square root.

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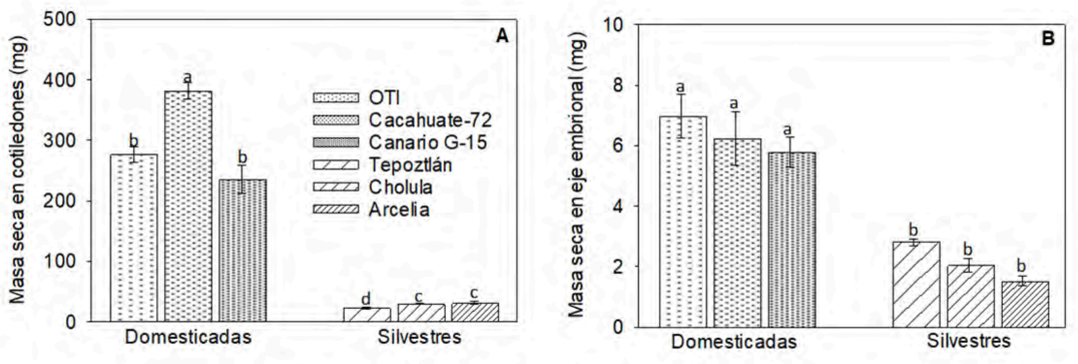
Subsequently, they were subjected to Anovas and Tukey mean comparison tests (*p*# 0.05) with the SAS statistical package (SAS, 2012). The results were plotted with the SigmaPlot package, Version 14 (2019).

Results

Dry mass of cotyledons, embryonal axis, root, and shoot

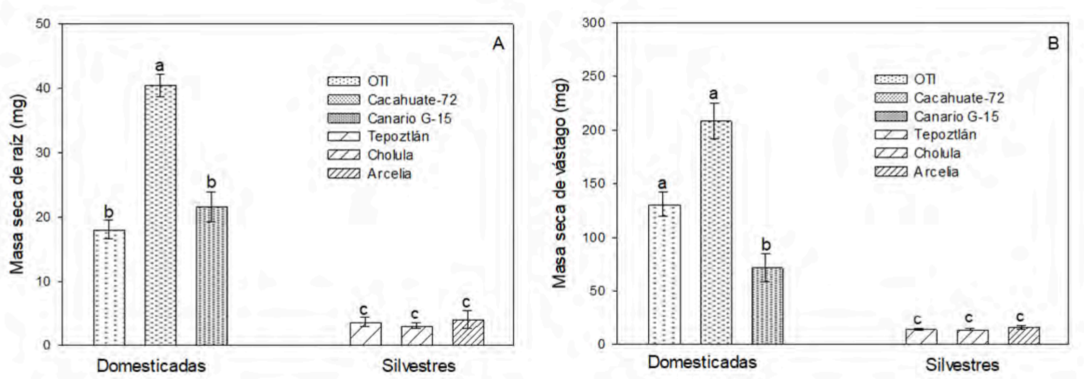
The improved varieties had 11 times more dry mass in the cotyledons and three times more in the embryonal axis than the wild varieties. The ratio of the dry mass of the embryonal axis to that of the cotyledons in the improved varieties was 0.02 and in the wild ones 0.08. Among the improved varieties, as well as among the wild seeds, there were no differences in the dry mass of the embryonal axis (*p*> 0.05) (Figure 1 A and B).

Figure 1. Dry mass of cotyledons (A) and embryonal axis (B) in bean (*Phaseolus vulgaris* L.) seeds of improved varieties and wild collections. Each bar is the average of four replications ±se. Different letters above the bars indicate a significant difference between materials (Tukey ≤ 0.05).



On average, the root and shoot of domesticated plants weighed seven and nine times more respectively than wild ones. The dry matter content was 18% in the root and 82% in the shoot on average, and there was no difference between the improved varieties and the wild ones (Figure 2).

Figure 2. Dry mass of root (A) and shoot (B) in bean (*Phaseolus vulgaris* L.) seedlings of domesticated varieties and wild collections. Each bar is the average of four replications ±se. Different letters above the bars indicate a significant difference between materials (Tukey ≤ 0.05).



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The allocation efficiency was higher in the wild varieties than in the domesticated ones (67.4 *vs* 51.2%, $p < 0.05$). Among domesticated varieties, Cacahuate had a higher allocation of matter than OTI and Canario, whereas among wild varieties, Arcelia and Tepoztlán had a higher allocation than Cholula.

Concentration of starch, glucose, fructose and sucrose in cotyledons and embryonal axis

In the cotyledons of the improved varieties, the concentrations of starch, glucose and sucrose were higher (60, 27 and 369%, respectively) than in the wild varieties, while that of fructose was similar. There was no significant difference in the concentrations of starch, glucose, fructose, and sucrose among the improved materials and among the wild ones, except for Cholula, with less glucose than Arcelia and Tepoztlán (Table 1).

Table 1. Concentration of starch, glucose, fructose and sucrose in the cotyledons (C) and embryonal axis (EA) of improved varieties and wild collections of *Phaseolus vulgaris* L.

Form	Name	Starch		Glucose		Fructose		Sucrose	
		(μmol g^{-1} dry weight)							
		C	EA	C	EA	C	EA	C	EA
Improved	OTI	459a	648d	5.7a	47bc	5.6a	34bc	62a	53a
	Cacahuate	514a	568d	5.8a	45c	4.5ab	37bc	66a	68a
	Canario	384ab	751cd	5.5a	51abc	4.2ab	33c	56a	80a
Wild	Tepoztlán	290b	1017bc	6.2a	79ab	5.7a	70a	15b	57a
	Cholula	275b	1631b	3.5b	52abc	3.8b	62ab	9b	52a
	Arcelia	280b	2518a	4.1ab	81a	3.9b	84a	14b	81a
Improved	Average	452a	656b	5.7a	47b	4.8a	36b	61a	67a
Wild		282b	1722a	4.5b	71a	4.2a	72a	13b	63a

The values are the average of four replications of each material. Different letters in the columns indicate a significant difference (Tukey ≤ 0.05).

In the embryonal axis, the concentration of starch, glucose, and fructose in the wild varieties were statistically higher than in the improved varieties, whereas the concentration of sucrose was similar. Among the three improved varieties, there was no difference in the concentration of glucose, fructose, and sucrose and among the wild varieties, Arcelia stood out with higher starch concentration values (Table 1).

Concentration of starch, glucose, fructose and sucrose in root and shoot

In the root, wild collections had more starch, fructose and sucrose molecules per g of dry weight than domesticated varieties. In contrast, in the shoot, domesticated varieties had more glucose, fructose and sucrose molecules, but fewer starch molecules. Among the improved varieties, OTI and Canario had more starch in the root than Cacahuate and no difference was observed in the other carbohydrates; regarding the shoot, there was no difference in the content of the carbohydrates. Among the wild varieties, Cholula stands out for its high concentration of fructose in the root and sucrose in the shoot (Table 2).

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Table 2. Concentration of starch, glucose, fructose, and sucrose in the root and shoot of seedlings of *Phaseolus vulgaris* L. from improved varieties and wild collections developed in darkness.

Form	Name	Starch		Glucose		Fructose		Sucrose	
		(μmol g^{-1} dry weight)							
		Root	Shoot	Root	Shoot	Root	Shoot	Root	Shoot
Improved	OTI	164b	126a	25b	596a	18c	284a	12c	124ab
	Cacahuate	58c	128a	51ab	335ab	27bc	167abc	14c	108ab
	Canario	107bc	147a	65ab	448ab	39bc	223ab	21bc	143a
Wild	Tepoztlán	714a	162a	65ab	217b	47b	119bc	46a	79ab
	Cholula	679a	188a	68a	324b	91a	173abc	57a	136a
	Arcelia	541a	152a	57ab	200b	36bc	94c	39ab	63b
Improved	Average	110b	134b	47a	460a	28b	225a	16b	125a
Wild		645a	167a	63a	247b	58a	129b	47a	93b

The values are the average of four replications of each material. Different letters in the columns indicate a significant difference (Tukey ≤ 0.05).

Number of cells, number and size of starch granules in the cotyledon of germinated seeds

Wild collections had 1.7 times more cells and 1.4 times more starch granules per unit area than domesticated varieties (Table 3 and Figure 3). Canario had a greater number of cells and granules than OTI and Cacahuate and Cholula had fewer cells and a similar number of starch granules than the other wild collections.

Table 3. Number of cells and number and dimensions of starch granules in cotyledons of germinated seeds of improved varieties and wild collections of *P. vulgaris* L.

Form	Name	Num. mm^{-2}		Dimensions of starch granules		
		Cells	Starch granules	Length (μ)	Diameter (μ)	Area (μ^2)
Improved	OTI	1246c	347 c	9.4a	7.8a	50a
	Cacahuate	1224c	4090bc	8.2b	6.2bc	32b
	Canario	1924b	6231a	7.6b	6.2bc	32b
Wild	Tepoztlán	2536a	6056ab	7.4bc	6.0bc	30b
	Cholula	2121ab	6035ab	6.3c	5.2c	22b
	Arcelia	2915ab	7674a	7.7b	6.3b	33b
Improved		1465b	4599b	8.4a	6.7a	38a
Wild		2524a	6589a	7.1b	5.8b	28b

The values are the average of four replications of each material. Different letters in the columns indicate a significant difference (Tukey ≤ 0.05).

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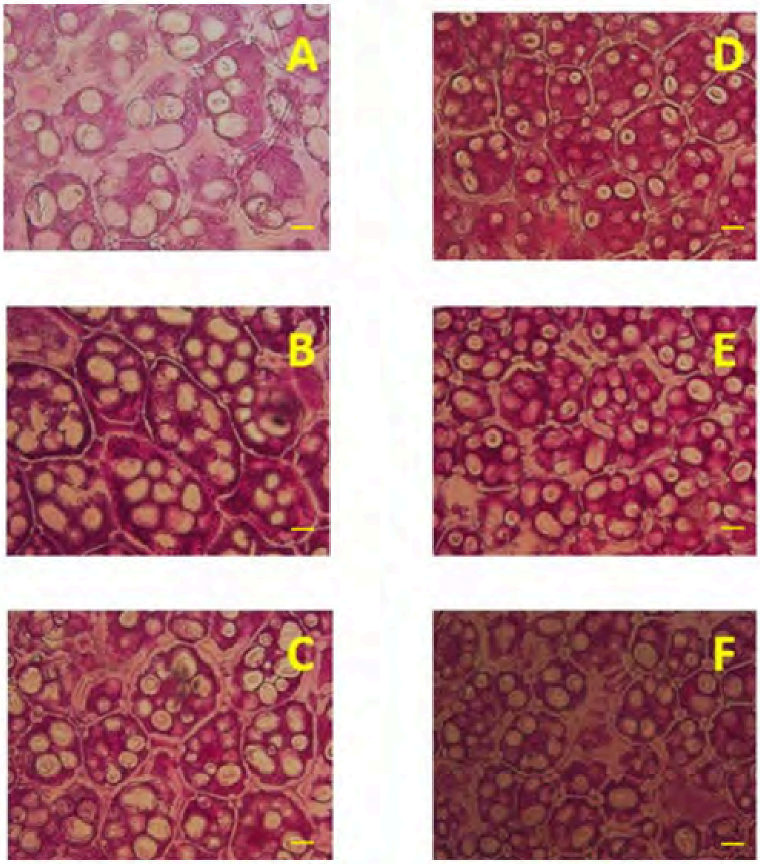
Figure 3. Starch granules in cotyledon cells of germinated seeds (radicle 1-2 mm) of domesticated varieti es: OTI (A), Cacahuate-72 (B) and Canario G-15 (C) and wild collections of beans: Cholula (D), Arcelia (E) and Tepoztlán (F). Bar scale = 10 µm.



Discussion

The contribution aims to expand the conception of the domestication syndrome by differentiating improved and wild materials at the seed and seedling levels. Domestication has changed both the dry mass of the cotyledons and that of the embryonal axis, resulting in a larger size of the seed. The domestication of the OTI and Canario varieties has not resulted in differences in the dry mass of the embryonal axis between them, whereas in Cacahuate, there has been a slight increase; this difference may be due to the fact that they belong to different breeds (Singh *et al*., 1991; Estrada-Gómez *et al*., 2004).

In the wild collections, there was similar dry mass in cotyledons and embryonal axis in Cholula and Arcelia. Values similar to those found in this research were recorded in other wild and improved seeds of *P. vulgaris* (Morales-Santos *et al*., 2017); in wheat, evolution under domestication has increased the dry mass of the grain but not that of the embryo (Golan *et al*., 2015), results contrasting with those observed in the present research, where domestication has increased the dry mass of all seed structures in beans.

Just as the domestication of *P. vulgaris* has favored the dry mass of the cotyledons and embryonal axis, it has also favored the dry mass of the root and shoot of the seedlings; however, the distribution of matter between these organs has remained unchanged between domesticated and wild beans. Milla and Matesanz (2017) mentioned that large seeds, typical of crops, produce individuals with large organs, as we can see in our results.

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The vigor of seedlings depends on seed size, the fraction of translocated reserves, and the efficiency in conversion of these reserves into seedling organs (Mohammadi *et al*., 2011). Wild accessions showed greater efficiency in the allocation of matter than domesticated ones, this pattern has also been observed in other wild accessions and improved varieties of common beans (Celis-Velázquez *et al*., 2008).

Domestication has led to a larger size of seeds and therefore a greater amount of their reserves; nevertheless, during germination, not all reserves are used even when seedlings are in dark or stress conditions (Ansari *et al*., 2012). Nonetheless, Hu *et al*. (2017) states that seed size only gives seedlings a competitive advantage when they are under stress and that seedlings from small seeds have higher relative growth rates compared to those from large seeds.

In this work, it was observed that starch and sucrose are the largest reserve substances compared to glucose and fructose in the improved varieties; however, Vargas-Vázquez *et al*. (2020) reported that, in *Phaseolus coccineus*, wild materials had a higher concentration of carbohydrates than domesticated ones, whereas Cilia *et al*. (2021) found no differences in carbohydrate concentration between *P. vulgaris* and *P. acutifolius*, which would indicate that domestication even among species of the same genus has not determined a trend in carbohydrate concentration between species, as it has done with seed size. These differences could be due to abiotic conditions where each species evolved and was domesticated. The translocation of reserve substances from the seed to the seedling is important for seedling growth. When germination begins, the starch is converted into translocatable sugars that together with the reserve sugars are translocated to the embryonal axis so that growth begins and it transforms itself into a seedling. For example, in *Arabidopsis*, triglycerol is transformed into sucrose (Pritchard *et al*., 2002).

In the case of beans, starch, being the main reserve in the seed, has to be transformed into sucrose, the main translocatable substance, to be transported to the embryonal axis and used in growth (Bewley and Black, 2013). The size of the starch grains varied between the varieties and the wild collections, being smaller in size but greater in number in the latter, which indicates that it is a trait that presents variability. Wani *et al*. (2010); Bajaj *et al*. (2018) reported larger size in improved bean varieties from India; nevertheless, Yoshida *et al*. (2003) mentioned that the dimensions of the granules vary from one to 38 µm, which indicates that it is a variable trait between varieties and does not show a pattern in the degree of domestication.

The concentration of starch, glucose, fructose, and sucrose in the cotyledons and embryonal axis has also been modified by domestication. The functions and metabolic pathways of these molecules differ, which is partially observed in the concentration quantified in this study. This research found significant differences in their contents between both structures and between domesticated and wild materials. In wild materials, the higher concentration of sugars in the embryonal axis indicated the high demand for carbon in response to metabolic activity due to radicle growth (Sánchez-Linares *et al*., 2012).

The higher concentration of sugars in the root of wild seedlings indicated that as they survive in wild soils, they may require more energy to grow. The high concentration of starch, glucose, and sucrose in the cotyledons of varieties coincides with what was documented by Ortega and Rodríguez (1979).

Conclusions

The domestication of *Phaseolus vulgaris* has increased the dry weight of all seed structures and promoted a larger size of the root and shoot of the seedlings; however, the allocation of biomass between these organs has not changed between domesticated and wild beans. There is greater efficiency in the allocation of energy reserve matter in wild forms than in domesticated ones. Domestication favored the amount of seed reserves; nevertheless, during germination, not all reserves are used even when the seedlings are in dark conditions. Starch and sucrose are the most abundant reserves compared to glucose and fructose in improved varieties. The starch grains in the wild collections, except in one of them, were smaller in size but greater in number.

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