# CHAPTER 2

# Cassava Taxonomy and Morphology

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## Introduction

In preparing this chapter, advantage was taken of the knowledge base provided by other authors whose valuable contributions should be recognized. Of the publication *Cassava: research, production, and utilization* (edited by Carlos E Domínguez [1983]), the chapters used were written by Carlos E Domínguez, Luis F Ceballos, and Cilia Fuentes ("Morphology of the cassava plant"); Clair Hershey and Alvaro Amaya ("Genetics, cytogenetics, floral structure, and techniques of hybridization in cassava" and "Cassava germplasm: evolution, distribution and collection"); and James H Cock ("Physiological aspects of the growth and development of the cassava plant"). Of the book *Cassava in the face of hunger in the tropical world* (edited by Alvaro Montaldo 1996), information was extracted from the chapters written by Jocelyne Ascencio ("Some aspects related to the physiology of the cassava plant"); and JJ Castilloa, A Castillo, and LT Pino ("Notes on leaf and root histology of cassava").

All 98 species of the *Manihot* genus are native to the Neotropics from where cassava was introduced to other regions of the world (Rogers and Appan 1973). The origin of cultivated cassava is still unclear. Three relevant questions were raised by Allem (2002): its botanical origin (parental wild species that eventually led to the emergence of *M. esculenta*), the geographic area where this emergence took place, and the region where it was domesticated (agricultural origin). The prevailing hypothesis is that cultivated cassava originated in South America (Olsen and Schaal 2001; Allem 2002), but many questions remain unanswered.

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## Taxonomy

Cassava belongs to the Euphorbiaceae family, which is made up of about 7200 species, characterized for their notable development of lactiferous vessels, themselves made up of secretory cells called lacticifers. These produce the milky secretion, or "latex", that characterizes the plants of this family. Plant architecture varies enormously within this family, ranging from arboreal types such as rubber (*Hevea brasiliensis*) to shrubs, also of economic importance, such as the castor-oil plant (*Ricinus communis*). Also representing this family are numerous weeds, ornamental plants, and medicinal plants. A highly significant genus of this family is *Manihot* to which cassava belongs.

The *Manihot* genus is native only to the Americas, with species being distributed from southwestern USA (33° N) to Argentina (33° S). Although all species of the genus can cross with each other, evidence suggests that, in nature, they are reproductively isolated. About 98 species have been described as belonging to this genus, of which only cassava (*Manihot esculenta* Crantz) has economic importance and is cultivated. Perhaps more than 100 common names now exist for this species, owing to its spread throughout the tropical world by early traders. In Latin America, it is usually known either as *yuca* (Spanish) or as *mandioca* (Portuguese). In Brazil, sweet cassava (*aipim*) is distinguished from bitter cassava (*mandioca*). Other names in different languages include manioc, manioca, tapioca, and *mhogo* (Cock 1989).

Cassava's scientific name was first given by Cranzt in 1766. It was then reclassified by Pohl (1827) and Pax (1910) as two different species, depending on whether it was bitter (*M. utilissima*) or sweet (*M. aipi*). However, the Italian R Ciferri (1938) recognized that, for cassava's scientific name, priority should be given to

Crantz's work in which he had proposed its current name of *M. esculenta*. Allem (1994) proposed that the species *M. esculenta* be divided into three subspecies: *M. esculenta* subsp. *esculenta,* subsp. *flabellifolia*, and subsp. *peruviana*. The author also suggests that the last two subspecies are wild forms of the cultivated version *M. esculenta* subsp. *esculenta*.

## Cytogenetics

Very little is known of either cassava genetics or cassava cytogenetics. The basic chromosome number in the Euphorbiaceae family is usually 8, although this may vary between 6 and 11. About 50% of euphorbia species are polyploid (Martin 1976).

Although cassava is frequently considered as a polyploid species, analyses conducted during diakinesis and metaphase I indicate the presence of 18 small and similar bivalents in cassava (Hahn et al. 1990). Univalents, trivalents, and late bivalent pairings have also been observed in cassava. This plant is therefore a functional diploid, that is, $2n = 2x = 36$ (Jennings 1963; De Carvahlo and Guerra 2002; Nassar and Ortiz 2008). Magoon et al. (1969) have suggested that certain portions of the genome may be duplicated and, therefore, cassava may in fact be a segmental allotetraploid.

## Describing the Plant

Every botanical description is based on the analysis of morphological characters that, where these are constant, typify the species. However, many characteristics are expression in a variable fashion and are profoundly influenced by environment. The effect of the variety-by-environment interaction is most notable in the case of cassava. For example, a given variety's architecture, known to be typical in a specific environment, will change drastically when that variety is grown in another site with different environmental conditions. This variety-by-environment interaction hinders both the morphological and varietal description of the species.

Cassava is a perennial shrub. It is monoecious, that is, a single plant may carry both male and female flowers, but these are separated from each other. The cassava plant has sympodial branching and variable plant height, ranging between 1 and 5 m, although maximum height usually does not exceed 3 m.

### The stem

Stems are particularly important in cassava, as they are the means by which the species propagates vegetatively or asexually. Lignified parts of the stem, commonly called stakes or *cangres* (cuttings), serve as "seed" for the crop's commercial production. The mature stem is cylindrical, with a diameter that varies from 2 to 6 cm and coloring that may be silvery gray, purple, or yellow. Both stem diameter and color vary significantly with plant age and, obviously, with variety.

Stems are formed by the alternation of nodes and internodes. The oldest parts may show protuberances, which mark, within the nodes, the position that leaves had initially occupied. The node is that place where a leaf joins the stem, and the internode is that part of the stem between two successive nodes. Inserted into the node are the leaf petiole, an axillary bud protected by a scale, and two lateral stipules. The length of internodes in the principal stem is highly variable and depends, not only on the variety, but also on other factors such as plant age, drought, thrips attacks, and available soil fertility. In a certain sense, the stem provides a lasting record of the history of the plant's development, enabling one to deduce the conditions and events that had influenced it.

The presence of axillary buds in each node is important as, from these, a stake can produce a new plant. In theory, a stake can produce the shoot of a new primary stem from the bud in each node. However, the number of stems produced depends heavily on the way in which a given stake is planted. For example, when the stake is planted horizontally, all nodes tend to emerge, but if the stake is planted in a vertical position, usually only the apical bud is activated. The number of shoots from a stake also depends on the apical dominance that characterizes each variety. When it is strong, only the upper bud generates a primary stem. General conditions of the stake, particularly of the axillary buds, also determine the number of stems a stake will produce.

The typical phyllotaxis observed in cassava stems is 2/5. This means that the leaves are located in spiral fashion around the stem. If leaves are counted successively upwards from a given leaf (number 1), the sixth leaf will be exactly in the same position as leaf number 1, but farther up the stem. The fraction 2/5 also implies that two turns have to be taken around the stem before finding a leaf that perfectly overlaps leaf number 1 and that, in the process, five leaves are counted.

The primary stem, after a certain growing period, ultimately produces branches that may be either reproductive (producing inflorescences) or vegetative (producing lateral branches). The "reproductive" branches are important, as they constitute a very stable characteristic for varietal description. They also determine, to a great extent, the architecture that is characteristic of each variety. The latter, as will be seen in other chapters of this volume, is significant for defining the agronomic value of each material, as it influences the quantity of planting material or "stakes" that the plant produces, and other factors such as ease in carrying out tasks of cleaning and general care of the crop.

Although the reproductive lateral branch is induced by flowering of the principal axis (hence its name), reproductive branching may also occur without the presence of inflorescences. What factors determine the moment in which reproductive branches will be produced are not yet clear, as this event is very strongly influenced by the environment. Reproductive branching may give rise to two, three, and even four secondary branches, which, in their turn, may ultimately produce tertiary branches, and so on (Figure 2-1).

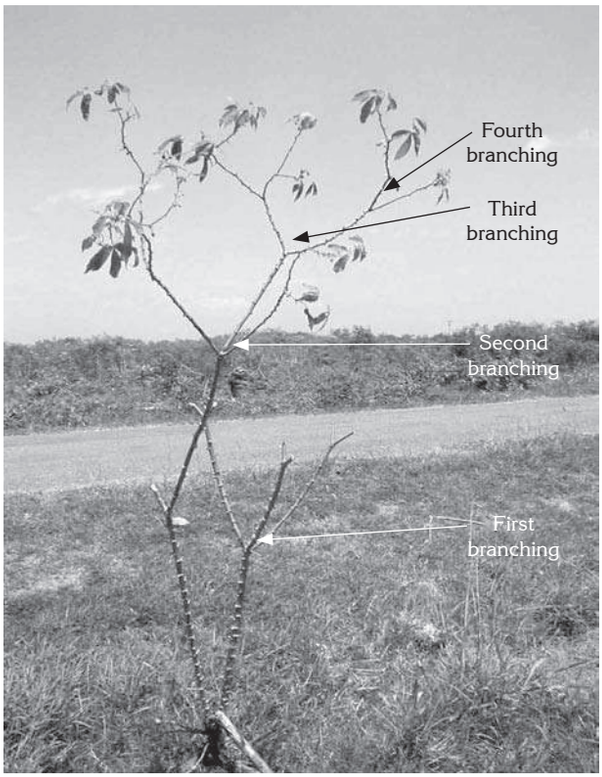


Figure 2-1. Plant stripped of leaves to show branching.

The number and promptness with which such branching occurs notably influence plant architecture. Early flowering results in the primary branches being located in relatively lower positions in the plant. Hence, early and multiple branching will therefore tend to produce a short plant that hinders the cleaning and care of the crop. However, it rapidly covers the soil, protecting it from, particularly, hydric erosion. Reduced and/or late branching tends to produce erect plants, with good stake production, that facilitate crop care, but leaves the soil exposed to erosion.

In addition to the number of reproductive branches, the angle of these also greatly affects the plant's general architecture (Figure 2-2). The greater the angle of incidence of the branches, the more open the plant architecture and the shorter it is. In general, this type of architecture is undesirable from the agronomic standpoint.

Lateral branches from the same node (called *chupones* in Spanish) are sporadic and depend on planting density, climatic conditions, soil fertility, and cultivar. They stem from the axillary buds of the principal stem, and are usually thinner than this stem, with long internodes and smaller leaves. Wounds or damage in the apical area (e.g., from lancefly [*Silba pendula*] or thrips) will also induce lateral buds into producing branches that will assume the role of the principal stem, replacing it.

The internal structure of the cassava stem is typically dicotyledonous. The outermost layer in young stems is the epidermis, followed by (going towards the interior) cortical tissue. Pigmentation in these two layers will define the color that the stem ultimately assumes. Internally, the layer is ligneous. The center of the stem is occupied by a prominent pith, composed of parenchymatous cells. As stem diameter increases, large quantities of xylem accumulate, giving the mature stem a ligneous consistency and generating the *suber* or cork that replaces the epidermis.

## The leaf

Leaves are the organs in which photosynthesis mostly occurs, transforming radiant energy into chemical energy. Leaves are caducous, that is, with age they senesce, and fall from the plant as it develops. The total number of leaves produced by the plant, their longevity, and photosynthetic capacity are varietal characteristics, which are profoundly influenced by environmental conditions.

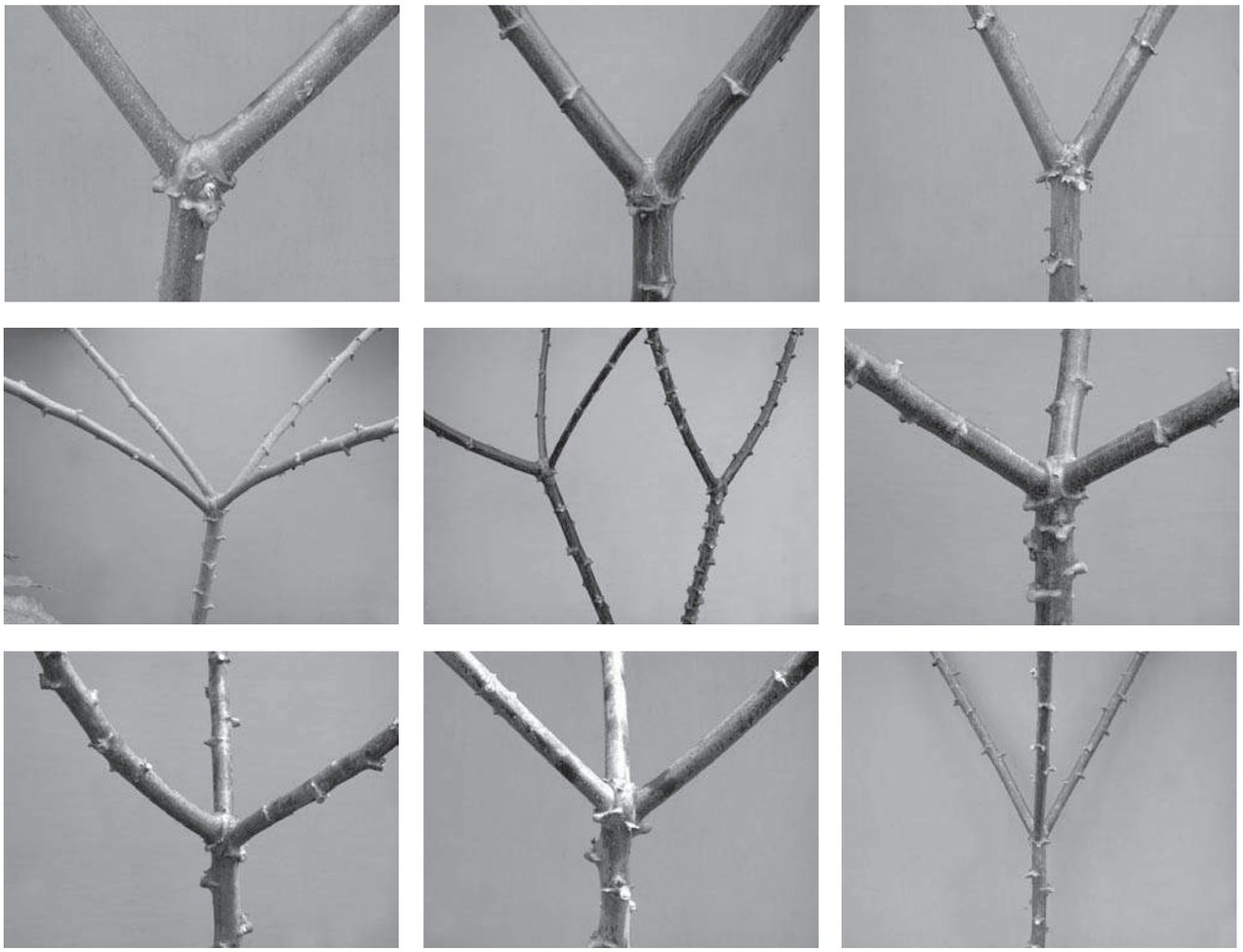

Figure 2-2. Variations in branching angle and number of branches.

Leaves are simple, consisting of the leaf blade and petiole. The blade is palmate with variable number of lobes, usually, odd, ranging between 3 and 9. Lobes measure between 4 and 20 cm long and between 1 and 6 cm wide. The central lobes are larger than the lateral ones. Lobe shape can be classified in different ways, with a variable number of categories. A simple classification distinguishes three types of lobes: linear or straight, obovate, and pandurate. But intermediate types also exist, encouraging the development of other classification systems to qualify such characteristics (Figure 2-3).

Leaf size is a typical characteristic of each cultivar, although it depends heavily on environmental conditions. Leaves produced in the first 3 to 4 months of the plant's life are larger than those produced after the fourth month. For example, in variety M Col 72, the average leaf area at 4 months old is about 250 $cm^2$; at 7 months, it is 130 $cm^2$; and at 10 months (harvest), only about 90 $cm^2$.

Leaf color is also a varietal characteristic but may vary with plant age. Mature leaves may be purple, dark green, or light green. Purple buds may, as the leaves grow and develop, ultimately become greenish in coloring. Bud color is a very useful characteristic for varietal identification, as it is relatively constant. The color of the nervure ranges between green and purple, and may also be used for varietal description. This color may be the same or different for the two sides of the leaf blade.

The leaf petiole may be between 9 and 20 cm long. It is thin, with variable pigmentation (green to purple), depending on variety. Petiole color does not always coincide with that of the nervure.

Mature leaves are always glabrous, that is, they lack pubescence. Leaves of buds, however, may or may not be pubescent—a relevant feature as pubescence in bud leaves is closely related to resistance to thrips. The upper surface of the leaf is covered by a brilliant waxy

Figure 2-3. Two types of leaf lobes.

cuticle, while the lower surface is opaque. Most stomata are found on the lower surface, although, in some varieties, abundant stomata may also appear on the upper surface.

At the petiole's point of insertion in the stem, two stipules, 0.5 to 1.0 cm long, can be found. These stipules may or may not remain adhered to the stem once the leaf is fully developed.

Although the principal economic product of cassava is the root, leaves are also important. In several regions of Africa and Asia, leaves are processed for human consumption. Cassava leaves have a valuable nutrient content with high protein levels that range between 18% and 22%, dry weight (Buitrago A 1990). Young cassava foliage also has several vitamins and minerals. Table 2-1 shows ascorbic acid and carotene contents for cassava roots and leaves. Data are based mostly on evaluations of more than 500 genotypes belonging to the core collection held by the cassava germplasm bank at the Centro Internacional de Agricultura Tropical (CIAT)[3]. Information on contents of principal minerals is also presented from the viewpoint of human and animal nutrition (Table 2-2), extracted from a representative sample of 20 varieties.

Table 2-1. Contents of ascorbic acid and carotenes in leaves and roots of more than 500 cassava varieties from the germplasm bank at CIAT.

| | Ascorbic acid (mg/100 g fw)[a] | | Carotenes (mg/100 g fw)[a] | |
|---|---|---|---|---|
| | In leaves | In roots | In leaves | In roots |
| Minimum value | 0 | 0 | 23.28 | 0.100 |
| Maximum value | 419.25 | 37.52 | 86.22 | 1.040 |
| Median | 109.30 | 8.09 | 47.72 | 0.190 |
| Average | 120.16 | 9.48 | 48.26 | 0.230 |
| SD | 84.14 | 6.50 | 8.61 | 0.137 |

a. fw = fresh weight.

SOURCE: CIAT (1999).

## The inflorescence

Not all cassava varieties flower under the same environmental conditions. Those that do show marked differences in flowering times and quantities of flowers produced. The environment greatly influences the induction of flowering. As with all plants of the *Manihot* genus, cassava is a monoecious plant, that is, it bears

3. For an explanation of this and other acronyms and abbreviations, see *Appendix 1: Acronyms, Abbreviations, and Technical Terminology*, this volume.

Table 2-2. Concentration of mineral elements in leaves and roots of 20 cassava clones evaluated at CIAT (unpublished data).

| Element | Concentration in leaves (mg/100 g dw)[a] | | Concentration in roots (mg/100 g dw)[a] | |
|---|---|---|---|---|
| | Average | SD | Average | SD |
| Fe | 94.4 | 37.8 | 9.6 | 2.49 |
| Mn | 67.9 | 10.5 | 1.2 | 1.00 |
| B | 66.1 | 7.7 | 2.4 | 0.51 |
| Cu | 7.3 | 0.6 | 2.2 | 0.35 |
| Zn | 51.6 | 11.8 | 6.4 | 1.35 |
| Ca | 12,324.0 | 1761.0 | 590.0 | 120.00 |
| Mg | 7,198.0 | 888.0 | 1153.0 | 147.00 |
| Na | 11.4 | 3.0 | 66.4 | 27.00 |
| K | 10,109.0 | 903.0 | 8903.0 | 882.00 |
| P | 3,071.0 | 236.0 | 1284.0 | 113.00 |
| S | 2,714.0 | 145.0 | 273.0 | 40.00 |

a. dw = dry weight.

unisexual flowers, with some being male and others female, with both usually found on the same inflorescence.

Cassava undergoes cross pollination, which means that it is a heterozygous plant, with each individual being a hybrid. Pollination is typically carried out by insects. Self-pollination is prevented by the female flowers of a raceme opening first before the male flowers of that same raceme. This phenomenon is known as protogyny. However, occasionally, the male and female flowers of different racemes on a single plant may open simultaneously. When this happens, self-pollination may naturally occur.

Cassava "flowers" are produced in inflorescences. The basic arrangement of flowers is the raceme (Figure 2-4), where the female flowers occupy basal positions and the male the distal ones. The latter are smaller and usually more numerous than the female ones. Frequently, panicles are also produced, that is, from the botanical viewpoint, a raceme of racemes develops. In such cases, a principal raceme exists, which is composed of secondary racemes.

Each flower, whether male or female, has a primary bract and a bracteole. These foliaceous organs appear in the inflorescences and may either remain or drop off once the flowers develop.

In most cases, inflorescences are formed from buds at the point of insertion of reproductive branches. Occasionally, inflorescences may develop from buds in leaf axils in the plant's upper parts.

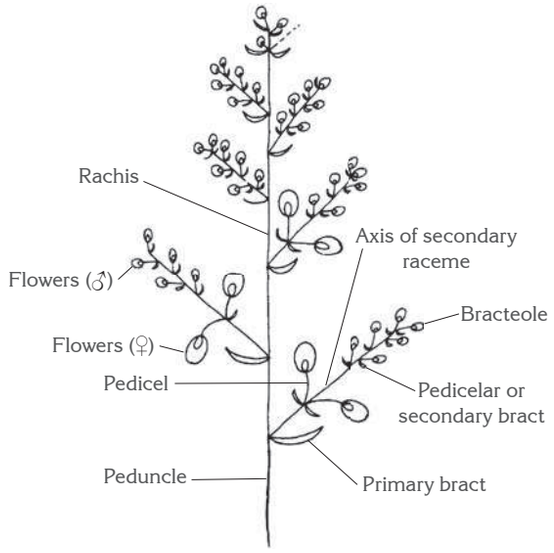


Figure 2-4. Diagrammatic representation of an inflorescence (from Domínguez et al. [1983]).

## Male and female flowers

The evolution of flower structures in the Euphorbias is, compared with other flowering plants, remarkable. Cassava flowers are in fact apetalous, having no petals or sepals. They are also monoecious, that is, male and female flowers are separately found on the same inflorescence. Female flowers are single, and are reduced to a pistil that is protected by petal-like bracts. Male flowers are also reduced—to a single stamen—but, unlike female flowers, they form inflorescences of 10 single-stamen flowers. These inflorescences, known as cyathia (*sing.* cyathium), are also protected by bracts. Together, the female flowers and male cyathia form inflorescences of a secondary order known as *panicles*.

What are commonly called *tepals* (i.e., petal-like sepals) in cassava flowers are actually bracts. In this volume, the male cyathia will be treated as if they are single flowers, as the distinction is only relevant from the botanical point of view.

The male "flower" is about half the size of the female. It possesses a straight and very short pedicel, while that of the female flower is thicker and longer (Figures 2-4 and 2-5). Inside the male flower is a basal disk that is divided into 10 lobes. In the center of this disk a rudimentary ovary can be seen. At the points of separation of the lobes of the basal disk, arranged in two series, are the 10 stamens that support anthers. Of these stamens, the 5 outer ones are separate and longer than the 5 inner ones. Together, they form the

Figure 2-5. Cassava flowers: female (top) and male (bottom).

set of anthers. On each stamen is an elongated anther that inclines towards the central part of the flower. The anthers open along longitudinal apertures. Pollen release begins 2 or 3 h before the flower opens and may even end before the flower completely opens. Pollen grains are large and spherical, and only a few are produced in each sac. They are also sticky, which facilitates pollination by insects. Pollen remains viable for up to 6 days. A detailed description of microsporogenesis in cassava has been recently published (Wang et al. 2010).

Because cassava can reproduce vegetatively, reproductive dysfunction is not, from an evolutionary viewpoint, as negative as it would be in crops that have exclusively sexual reproduction. As a result, cases of male-sterility, for example, can be frequently found. Such cases are of two types: one where the flowers abort before reaching maturity, and the other when flowers mature but the anthers do not produce pollen. Genetics of such sterility, however, has not yet been fully studied.

## The fruit

Once the female flower has been pollinated, fruit begins to form from the ovary. Fruit maturation requires about 3 months to complete. The fruit is a dehiscent capsule that is trilocular, and ovoid to globate, with a diameter of 1.0 to 1.5 cm and six longitudinal, narrow, and prominent ridges (Figure 2-6). Cross-sections of the developing fruit show a series of clearly discernible tissues: epicarp, mesocarp, and endocarp.

As the seed matures, the epicarp and mesocarp dry up. The endocarp, which is ligneous, opens abruptly when the fruit is mature and dried, releasing and dispersing seeds to a certain distance. During dehiscence tissues separate both, throughout the mid-vein of each fruit loculus and between the separations themselves.

## The seed

The seed is the medium for the plant's sexual reproduction. While it is not important in reproduction and commercial multiplication, it has incalculable value for plant breeding, as only through sexual reproduction can new, genetically superior, cultivars be developed.

The seed is ovoid-ellipsoid in form and measures about 1 cm long, 6 mm wide, and 4 mm thick. The seed coat is smooth, coffee-colored, and mottled gray. In the upper part, especially of new seed, the caruncle is found. This structure is lost once the seed falls to the ground. At the other end of the seed, opposite the caruncle, a small cavity is found. A slender suture leaves from the caruncle and finishes in this basal cavity. Figure 2-7 shows the typical structure of a cassava seed.

The seed coat is the outermost part of the seed. Immediately inside the seed coat is the endosperm, which is formed of polyhedral parenchymatous cells that protect and nourish the embryo, itself located in the central area of the seed. Within the endosperm are found the cotyledons and embryonic axis that will give rise to the new plant after germination. The embryo is

Figure 2-6. Cassava fruit.

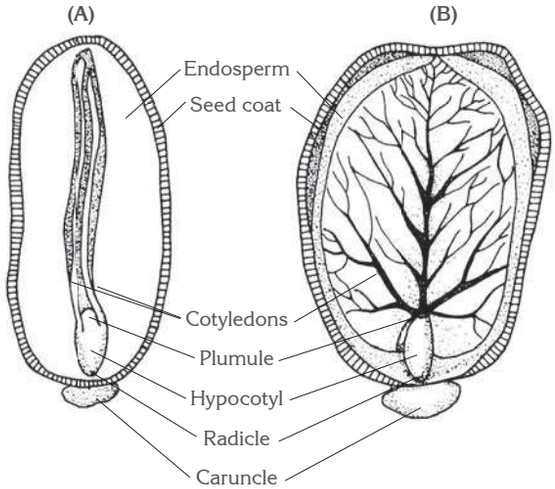


Figure 2-7. Diagram of two longitudinal sections of botanical cassava seed (from Domínguez et al. [1983]). **(A)** Cross-section cut across suture; **(B)** cross-section cut through suture.

made up of the two cotyledonous leaves, plumule, hypocotyl, and radicle. The cotyledonous leaves and endosperm occupy almost the entire interior of the seed; they are white, elliptical, and carnose.

Although currently seed does not play a predominant role in cassava multiplication, it may well do so in the future. A phenomenon in nature, especially among grasses, known as *apomixis*, consists of producing botanical seed without the usual sexual reproduction. In other words, the seed embryo produced by apomixis is genetically identical to the mother plant. This means that, when the embryo grows into a plant, it will also produce an individual plant that is identical to its mother. Apomixis has been reported for the *Manihot* genus (Nassar et al. 2000). It could be incorporated into commercial systems because of its appreciable advantages: it would enable seed storage for more than the month or 2 months that stems can be kept and the rate of multiplication of a material could be increased significantly. Also they are less likely to carry pathogens than stem cuttings.

## The root system

The principal characteristic of cassava roots is their capacity for starch storage, which is the reason why, so far, it is the plant organ that has the greatest economic value. However, not all roots produced ultimately become storage organs.

When the plant grows from sexual seed, a primary root develops and then, several secondary ones. Apparently the primary root always evolves into a tuberous root, and is the first to do so. If the plant grows from a stake, the roots are adventitious, forming at (1) the lower end of the stake, which produces a callosity, and (2) from buds in that part of the stake that is buried in the soil. These roots initially form a fibrous system but, later, some (usually <10) begin thickening and become tuberous roots. The number of tuberous roots is determined, in most cases, by the plant's early growth.

Although root density is low, penetration into the soil is deep. This is a highly relevant characteristic, as it contributes to the plant having the capacity to endure prolonged droughts. Fibrous cassava roots can reach depths of up to 2.5 m. The plant absorbs water and nutrients through the fibrous roots, a capacity that is lost when they become tuberous.

Morphologically and anatomically no differences are found among fibrous and tuberous roots. What happens is that, as starch accumulation begins, the direction of root growth changes from longitudinal to radial. However, this does not necessarily mean that the root absolutely stops longitudinal growth. As mentioned above, tuberous roots come from secondary enlargement of fibrous roots. This means that the root system first penetrates the soil while roots are thin and only after such penetration, do roots begin thickening.

Externally, the parts that are distinguishable of tuberous roots of an adult cassava plant are the tuberous portion proper; its distal extreme, which may still retain its fibrous character (Figure 2-8); and its

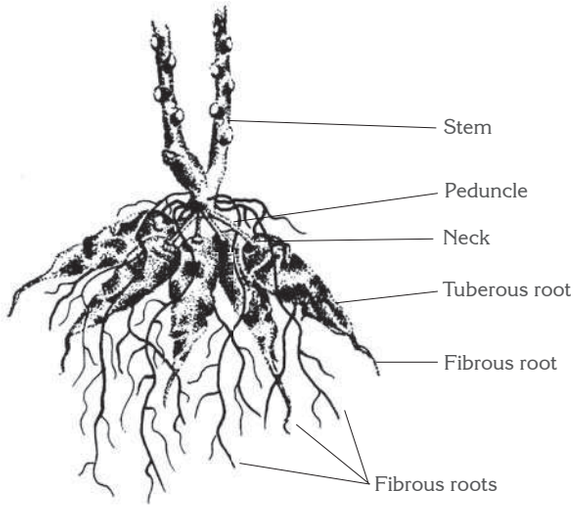


Figure 2-8. Drawing showing the components of the cassava root system (from Domínguez et al. [1983]). Ideally, with either short or long peduncles.

upper or proximal extreme, or neck or "peduncle", which also remains fibrous and joins the tuberous section to the stem. Neck size ranges from being absent or very short (<1 cm) to being longer than 8 cm. The depth at which the stake is buried affects peduncle length, which tends to be longer as stake depth is greater. Neck length is a characteristic of commercial interest. When it is very short it hinders separation of tuberous roots from their stems, resulting in injuries to the tuberous area and accelerating postharvest physiological deterioration (PPD). When the peduncle is too long, it results in higher losses, as the peduncle breaks more easily during harvest, leaving roots of commercial interest in the ground.

Roots may be highly variable in shape and size, depending on both variety and the environmental conditions under which the plants grow (Figure 2-9). However, when varieties are evaluated over numerous experiments, clear differences do appear, with some varieties tending to produce large roots and others having consistently smaller roots than the rest. The roots may be cylindrical, fusiform, or conical in shape, with intermediate forms such as cylindrical-conical frequently occurring.

The distribution of roots in the soil depends on both genetic and cultural factors. Varieties that tend to produce roots with long necks or peduncles also have their roots distributed in a scattered fashion, covering a greater area of soil than those varieties with "sessile" roots (i.e., with absent or very short necks). The way stakes are planted also affects the pattern in which roots will be distributed. When a stake is planted vertically, it produces roots around the callosity that forms at the stake's lower extreme. Some roots growing from lateral buds on the stake may also become tuberous roots. Tuberous roots tend to explore and be located in deeper strata of the soil. When the stake's position is at an angle to the soil's surface, tuberous roots again tend to form at the callosity and, as in the previous case, other roots may emerge from those lateral buds that are under the soil. If the stake is placed horizontally, then tuberous roots are distributed along the stake, as they are formed at both the lateral buds and the two extremes of the stake. Roots location also tends to be closer to the surface and more disperse, thus facilitating harvest.

Figure 2-9. Different shapes of cassava roots (conical, cylindrical, and long) with and without constrictions.

The tissues that compose a tuberous root are, successively from outside in, the peel, pulp, and central fibers (Figure 2-10). A highly relevant aspect in cassava use is the presence of a cyanogenic glucoside called linamarin. This glucoside, in the presence of an enzyme (mainly linamarase) and acids, is hydrolyzed to produce hydrocyanic acid in dosages that range from innocuous, through poisonous, to lethal. This reaction occurs spontaneously in decomposed plant tissues or in the digestive tract of animals. Hydrocyanic acid production is particularly high in root peel. Other plant tissues (including leaves) also have cyanogenic potential. Depending on cyanogenic glucoside levels, some publications will classify sweet cassava (low cyanogenic potential) as *M. utilissima*, while classifying bitter cassava (high cyanogenic potential) as *M. esculenta*.

The cyanogenic potential of different tissues of a cassava plant is greatly affected by the environmental conditions under which it grows and its age at harvest. Roots of a given cultivar can be sweet in a particular site, but bitter in other locations. Usually, however, the cyanogenic potential of bitter varieties tends to be

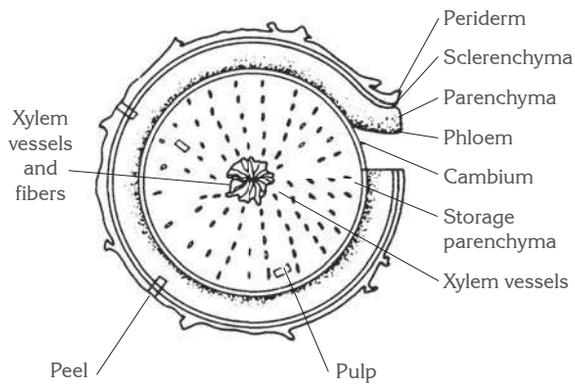


Figure 2-10. Cross-section of a tuberous cassava root (from Domínguez et al. [1983]).

consistently higher (to as much as 1000 mg of acid per kg of fresh roots) across numerous evaluations than for sweet varieties (20 mg/kg of root). Apparently, there are no cyanogen-free cassava varieties.

***Root peel.*** This tissue comprises the periderm and cortex. The periderm consists of dead cork cells (suber or phellem) that envelop the root surface. As the root increases in diameter, the continuity of cellular layers breaks, causing longitudinal fissures that characterize the surface of the cassava root. The way in which these fissures are produced, and the resulting appearance, are frequently used to identify cultivars for marketing purposes. Underneath these fissures, new cork cells are formed from the phellogen, re-establishing the continuity of this type of tissue over the root's entire surface. In addition to the periderm's texture, which can be rugose to more or less smooth, external color is also used to identify cultivars, as it is a highly stable morphological characteristic. Root color may range from white or cream, through pale coffee-colored, to dark brown.

Below the periderm is the cortex or cortical layer (phelloderm). This tissue is 1 to 5 mm thick (Pérez et al. 2011), with a color of its inner layer ranging from white, through cream, to pink. This characteristic is also used, even by housewives, to identify cultivars. Within the cortex, compressed phloem tissues are found, containing the highest concentrations of cyanogenic glucoside. In this layer, lactiferous canals can also be seen, especially in young roots.

***Pulp.*** This tissue constitutes the usable part of the root and is therefore the tissue of greatest economic interest. It appears as a solid mass, composed mainly of secondary xylem tissue derived from the cambium, the cells of which contain starch in abundance and in the form of round granules of unequal sizes. Pulp is also formed by parenchymatous cells that, in the case of cassava, develops to such a magnitude that the conductive xylem tubes remain reduced to small isolated groups scattered throughout the reserve parenchyma. The cambium from which pulp tissues are derived is found in the pulp's outermost part, separating the pulp from the cortex. This cambium also generates secondary phloem cells towards the exterior.

The parenchyma cells that form most of the cassava root pulp contain one to numerous amyloplasts. Within these, starch is accumulated as more or less spherical often truncated granules, although a great diversity of shapes exists such as cupuliform, biconcave-convex, and mitriform (Castilloa et al. 1982). Starch granule size is variable, and is, to some degree, determined genetically according to the variety. Starch granule shape and size are characteristics of great practical relevance to industry, as described below.

***Central fibers.*** These fibers, forming the center of the root, comprise rows of parenchyma and xylem sclerenchyma vessels, whose hardness, length, and width are varietal characteristics of economic importance, as they affect the culinary quality and appearance of roots cooked for human consumption.

About 80% of root fresh weight corresponds to pulp. Dry matter content of cassava roots ranges between 30% and 40%, although this range can sometimes be exceeded. The dry matter found in the parenchyma mostly (90% to 95%) constitutes the non-nitrogenous fraction, that is, carbohydrates such as starch and sugars. The rest of the dry matter corresponds to fiber (1% to 2%), fats (0.5% to 1.0%), ashes or minerals (1.5% to 2.5%), and protein (about 2%). Finally, we point out that starch comprises most of the carbohydrates (96%) and is, therefore, the principal component of dry matter in the root.

***Nutritional value of the roots.*** Without a doubt, the principal economic value of the cassava crop lies in its roots. Cassava roots, being storage organs for energy, have various uses as human food, animal feed, and starch extraction. Table 2-3 summarizes the principal chemical characteristics of cassava roots that have been chipped, dried, and processed into dry flour.

Most of the root content constitutes available carbohydrates. Compared with other energy sources such as maize, cassava roots have less protein (2% to 3% versus 8% to 10% for maize). This difference in protein

Table 2-3. Chemical composition of cassava flour from whole root and from root without peel (dry weight).

| Component | Contents (%) | |
|---|---|---|
| | Root with peel | Root without peel |
| Dry matter | 100.00 | 100.00 |
| Available carbohydrates | 83.80 | 92.40 |
| Crude protein | 3.05 | 1.56 |
| Ether extract | 1.04 | 0.88 |
| Ash | 2.45 | 2.00 |
| Neutral detergent fiber | 6.01 | 3.40 |
| Acid detergent fiber | 4.85 | 1.95 |
| Hemicellulose | 1.16 | 1.45 |

Data extracted from Buitrago A (1990).

content justifies cassava flour having a cost of about 70% that of maize, when it is used to formulate animal feed.

## Postharvest physiological deterioration in cassava roots

Cassava roots undergo rapid deterioration once harvested, a process mentioned above as "postharvest physiological deterioration" (PPD). As a result, cassava roots must be consumed within a few days of harvest because, during the first 3 days, bluish spots begin appearing, concentrating on the root's periphery. The spots then extend to the entire tissue, turning it coffee-colored or brown and, in longitudinal sections of the roots, appearing as vascular streaks (Wheatley et al. [1983]). While little is known about PPD, its occurrence is directly associated with any mechanical damage that occurred during harvest and also on variety. Some evidence suggests that varieties with less dry matter content are more tolerant of PPD. Roots with high carotene content (the so-called "egg yolk" cassava) also tend to suffer less from PPD (Morante et al. 2010).

One cultural practice that does reduce the incidence of PPD or delay its appearance is to prune plants several days in advance of harvesting the roots (van Oirschot et al. 2000). However, pruning also notably reduces dry matter content and, as a result, starch content, while increasing total sugars content. These results illustrate the way in which these variables can be affected according to the conditions under which the plant grows and the cultural practices to which it is subjected.

## Cassava starch and its properties

Starch is one of the dominant reserve substances in nature and is found as small granules deposited in seeds, tubers, and roots of different plants. Starch is a mixture of two polymers: amylose, which is linear, and amylopectin, which is branched. Table 2-4 lists some of the most relevant qualitative characteristics of cassava roots, with emphasis on starch. These results were consolidated, based on information published in several articles (Chávez et al. 2005; Ceballos et al. 2008; Morante et al. 2009; Sánchez et al. 2009).

The relative proportion of the polymers amylose to amylopectin in any starch, and their specific molecular weight, determines the physicochemical properties of the starch and its industrial properties (Sánchez et al. 2010). Analysis of these properties is fundamental to achieving an exact use of the existing genetic variability within the *Manihot* genus. Furthermore, the typical characteristics of cassava starch differ from that obtained from maize or potato, thus creating a niche whereby certain industrial processes may prefer the use of one starch over another. Two mutations affecting functional properties, granule morphology, and/or biochemical characteristics of cassava starch have also been reported (Ceballos et al. 2007, 2008).

Table 2-4. Qualitative characteristics of cassava roots.

| Trait | Average | Minimum | Maximum |
|---|---|---|---|
| Dry matter content (%) | 33.50 | 14.30 | 48.10 |
| Cyanogenic glucosides (ppm) | 325.00 | 14.00 | 3274.00 |
| Starch (% of dry weight) | 84.50 | 65.00 | 91.00 |
| Amylose content (% total starch) | 20.70 | 15.20 | 26.50 |
| Starch granule size ($\mu$m) | 16.29 | 13.97 | 18.73 |
| Total sugars (% of dry weight) | 3.75 | 0.20 | 18.80 |
| Reducing sugars (% of dry weight) | 1.31 | 0 | 15.70 |
| Amylose (% of starch) | 20.70 | 15.10 | 26.50 |
| Total carotenoids ($\mu$g/g fresh root) | 8.84 | 3.39 | 18.87 |

SOURCES: Chávez et al. (2005); Ceballos et al. (2008); Morante et al. (2009); Sánchez et al. (2009).

The principal physicochemical properties of a starch are proximal composition; granule characteristics (size and shape); crystalline nature; molecular weight; swelling power; solubility; relative amylose content; and characteristics of the starch paste.

The protein content of cassava starch (0.1%) is very low, compared with that of rice (0.45%) or maize starch (0.35%). Residual protein can impart a floury flavor and give these starches a tendency to foam.

Potato and cassava starch granules contain negligible amounts of fatty substances, compared with cereal starches such as maize (0.6%) and rice (0.8%). Such a composition favors cassava starch, as these lipids form a complex with amylose that tends to prevent starch granules from swelling and solubilizing, therefore requiring high temperatures (>125 °C) to break the amylose-lipid structure and dissolve the amylose fraction. The presence of fatty substances can also create problems of rancidity during storage.

Cassava starch granules are round, with truncated terminals and a well-defined nucleus (thread). Size varies from 5 to 35 $\mu$m, with averages between 15 and 18 $\mu$m. A mutation that severely affects granule size has recently been reported (Ceballos et al. 2008; Figure 2-11). Starch

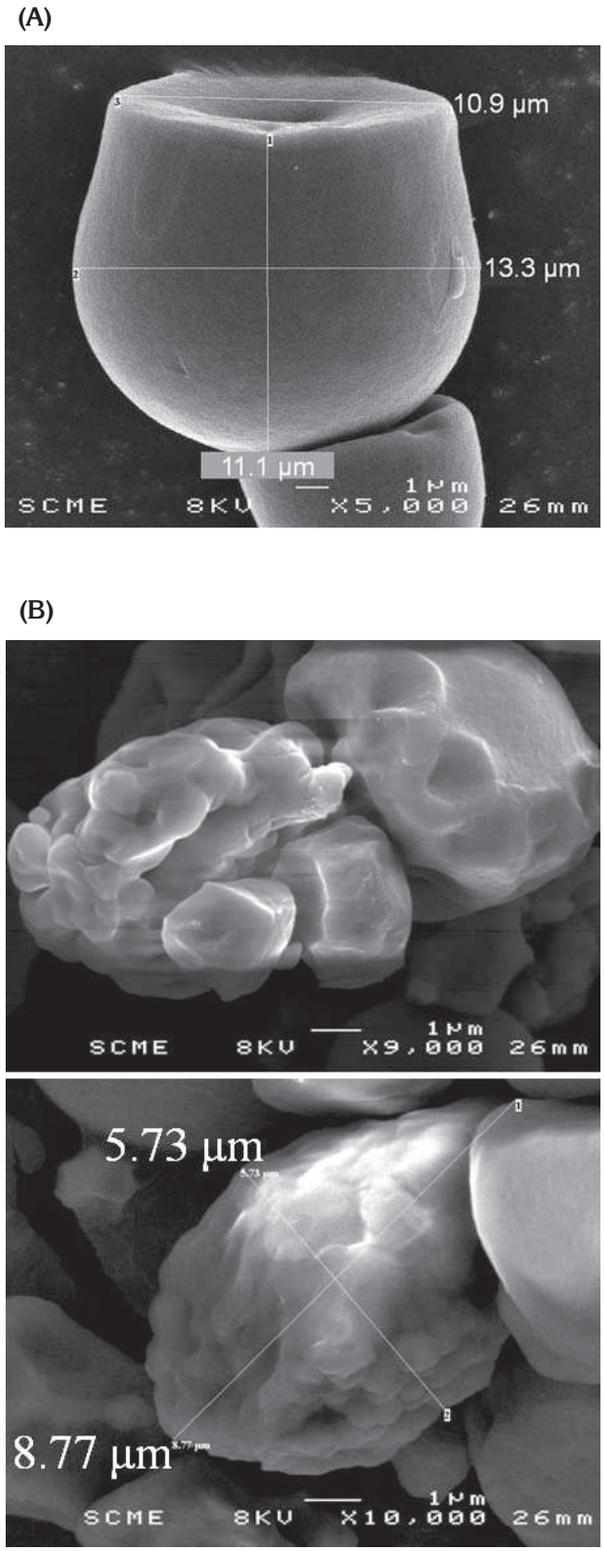


Figure 2-11. Scanning electron microscope photographs of **(A)** normal and **(B)** mutant cassava starch granules.

granules of rice, maize, and waxy maize have a polyhedral form, while potato starch granules are ovoid and larger, with sizes ranging between 5 and 100 $\mu$m, with an average of 33 $\mu$m. The granule size for maize and waxy maize starches is intermediate, between 3 and 26 $\mu$m, with an average of 15 $\mu$m, and similar to that of cassava starch granules. Rice starch granules are smaller, varying between 3 and 8 $\mu$m. They are regarded as more resistant to high-temperature processes such as sterilization and to be more digestible.

X-ray diffraction patterns of native cassava starch granules have been reported as intermediate (type C) between the characteristic patterns of cereal starches (type A) and fruit and tuber starches (type B). Crystallization levels in cassava starch are about 38% (Rickard et al. 1991). Granule crystallinity is essentially due to amylopectin. The small granule mutation of cassava affects crystallinity, branching pattern, and amylose content (Rolland Sabaté et al. 2012).

When an aqueous starch suspension is subjected to heating, granules slowly begin absorbing water and increasing in size. They initially hold their optical properties, including the ability to refract polarized light (birefringence), which is due to the alignment of molecules with no starch granules. Birefringence in cassava starch granules declines at temperatures between 58 and 64 °C, compared with that in maize starch granules, which declines between 62 and 68 °C.

Starch granules, as mentioned, are composed of two polysaccharides with glucan links: amylose and amylopectin. Amylose is basically a linear polymer of α (1-4) units. Amylopectin comprises the greater component and consists of a branched polymer of α (1-4) and α (1-6) units. In some starches, granule size is related to the amylose-to-amylopectin ratio (Delpeuch and Favier 1980). The average amylose content in the following starches are: for cassava, 20.9%; maize, 26%; potato, 24%; rice, 17%; and waxy maize, <1%. Amylose content of starches is very strongly related to some of their properties. For example, starches with high amylose content retrograde very quickly. In contrast, waxy maize, which is 100% free of amylose, is highly stable and resistant to retrogradation (i.e., the reorganization of amylose and amylopectin molecules in a crystalline structure when starch pastes are cooled). A mutation in cassava, resulting in amylose-free starch, has recently been reported (Ceballos et al. 2007).

Although varietal differences are found for rheological or functional properties of cassava starches, Brabender amylogram curves for cassava starch follow a similar pattern to that of starches with a high amylopectin content. Cassava starch gelatinizes, as do rice and waxy maize starches, at relatively low temperatures (60–67 °C), rapidly reaching the maximum peak. This implies that it is an easy starch to cook, requiring less energy for cooking. Furthermore, it has a low tendency towards retrogradation, and produces a very clear and stable gel.

Cassava starch gelatinizes in water at temperatures of more than 60 °C but, at more than 90 °C, although paste viscosity is initially high, it declines abruptly, with continuous solubilizing and agitation, and no gel is formed with subsequent cooling. Such behavior in cassava starch makes it technologically convenient as a substrate for hydrolytic processes, but inappropriate as a substitute for cereal starches in processes requiring retrogradation.

The cassava starch's properties of clarity and low retrogradation can be used in many food products. Its rheological characteristics closely resemble that of waxy maize starch.

Quality properties of starch pastes are modified during freezing, with the paste structure usually deteriorating through increased exudation of water or "syneresis". Some native starches like those of cassava and oca (*Oxalis tuberosa*) are regarded as resistant to this process (Rurales 1995; Sánchez et al. 2010).

Cassava starch pastes are stable in acid media where pH < 2.4. Normally, such acidity would destroy starch granules and the paste's physical aspect through partial or total hydrolysis.

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*To save space, the acronym "CIAT" is used instead of "Centro Internacional de Agricultura Tropical".*


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