Chapter 5
Cassava Botany and Physiology

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Introduction

Cassava is a perennial shrub of the family Euphorbiaceae, cultivated mainly for its starchy roots. It is one of the most important food staples in the tropics, where it is the fourth most important source of energy. On a worldwide basis it is ranked as the sixth most important source of calories in the human diet (FAO, 1999). Given the crop's tolerance to poor soil and harsh climatic conditions, it is generally cultivated by small farmers as a subsistence crop in a diverse range of agricultural and food systems. Although cassava is a perennial crop, the storage roots can be harvested from 6 to 24 months after planting (MAP), depending on cultivar and the growing conditions (El-Sharkawy, 1993). In the humid lowland tropics the roots can be harvested after 6–7 months. In regions with prolonged periods of drought or cold, the farmers usually harvest after 18–24 months (Cock, 1984). Moreover, the roots can be left in the ground without harvesting for a long period of time, making it a very useful crop as a security against famine (Cardoso and Souza, 1999).

Cassava can be propagated from either stem cuttings or sexual seed, but the former is the commonest practice. Propagation from true seed occurs under natural conditions and is widely used in breeding programmes. Plants from true seed take longer to become established, and they are smaller and less vigorous than plants from cuttings. The seedlings are genetically segregated into different types due to their reproduction by cross-pollination. If propagated by cuttings under favourable conditions, sprouting and adventitious rooting occur after 1 week.

Morphological and Agronomic Characteristics

Cassava, which is a shrub reaching 1–4 m height, is commonly known as tapioca, manioc, mandioca and yuca in different parts of the world. Belonging to the dicotyledon family Euphorbiaceae, the *Manihot* genus is reported to have about 100 species, among which the only commercially cultivated one is *Manihot esculenta* Crantz. There are two distinct plant types: erect, with or without branching at the top, or spreading types.

The morphological characteristics of cassava are highly variable, which indicate a high degree of interspecific hybridization. There are many cassava cultivars in several germplasm banks held at both international and national research institutions. The largest germplasm bank is located at Centro Internacional de Agricultura Tropical (CIAT), Colombia, with approximately 4700 accessions (Bonierbale *et al.*, 1997), followed by EMBRAPA's collection in Cruz das Almas, Bahia, with around 1700 accessions (Fukuda *et al.*, 1997), representing

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the germplasm of the following Brazilian ecosystems: lowland and highland semiarid tropics, lowland humid subtropics, lowland subhumid tropics, lowland humid tropics, and lowland hot savannah. The cassava genotypes are usually characterized on the basis of morphological and agronomic descriptors. Recently, the International Plant Genetic Resources Institute (IPGRI) descriptors (Gulick *et al.*, 1983) were revised, and a new version was elaborated, in which 75 descriptors were defined, 54 being morphological and 21 agronomic (Fukuda *et al.*, 1997). Morphological descriptors (for example, lobe shape, root pulp colour, stem external colour) have a higher heritability than agronomic (such as root length, number of roots per plant and root yield). Among morphological descriptors, the following were defined as the minimum or basic descriptors that should be considered for identifying a cultivar: (i) apical leaf colour; (ii) apical leaf pubescence; (iii) central lobe shape; (iv) petiole colour; (v) stem cortex colour; (vi) stem external colour; (vii) phyllotaxis length; (viii) root peduncule presence; (ix) root external colour; (x) root cortex colour; (xi) root pulp colour; (xii) root epidermis texture; and (xiii) flowering.

Given the large number of cassava genotypes cultivated commercially and the large diversity of ecosystems in which cassava is grown, it is difficult to make a precise description of the morphological descriptors as there is a genotype-by-environmental conditions interaction. Thus, in addition to morphological characterization, molecular characterization, based mainly on DNA molecular markers, has been very useful in order to evaluate the germplasm genetic diversity (Beeching *et al.*, 1993; Fregene *et al.*, 1994).

Roots

Roots are the main storage organ in cassava. In plants propagated from true seeds a typical primary tap root system is developed, similar to dicot species. The radicle of the germinating seed grows vertically downward and develops into a taproot, from which adventitious roots originate. Later, the taproot and some adventitious roots become storage roots.

In plants grown from stem cuttings the roots are adventitious and they arise from the basal-cut surface of the stake and occasionally from the buds under the soil. These roots develop to make a fibrous root system. Only a few fibrous roots (between three and ten) start to bulk and become storage roots. Most of the other fibrous roots remain thin and continue to function in water and nutrient absorption. Once a fibrous root becomes a storage root, its ability to absorb water and nutrients decrease considerably. The storage roots result from secondary growth of the fibrous roots; thus the soil is penetrated by thin roots, and their enlargement begins only after that penetration has occurred.

Anatomically, the cassava root is not a tuberous root, but a true root, which cannot be used for vegetative propagation. The mature cassava storage root has three distinct tissues: bark (periderm), peel (or cortex) and parenchyma. The parenchyma, which is the edible portion of the fresh root, comprises approximately 85% of total weight, consisting of xylem vessels radially distributed in a matrix of starch-containing cells (Wheatley and Chuzel, 1993).

The peel layer, which is comprised of sclerenchyma, cortical parenchyma and phloem, constitutes 11–20% of root weight (Barrios and Bressani, 1967). The periderm (3% of total weight) is a thin layer made of a few cells thick and, as growth progresses, the outermost portions usually slough off. Root size and shape depend on cultivar and environmental conditions; variability in size within a cultivar is greater than that found in other root crops (Wheatley and Chuzel, 1993). Table 5.1 lists morphological and agronomic characteristics of the root and its variability in cassava.

Stems

The mature stem is woody, cylindrical and formed by alternating nodes and internodes. On the nodes of the oldest parts of the stem, there are protuberances, which are the scars left by the plant's first leaves. A plant grown from stem cuttings can produce as many primary stems as there are viable buds on the cutting. In some cultivars with strong apical dominance, only one stem develops.

The cassava plant has sympodial branching. The main stem(s) divide di-, tri- or tetrachotomously, producing secondary branches that produce other successive branchings. These

Table 5.1. Some morphological and agronomic characteristics of roots and their variability in cassava.

Root characteristic	Variability	Reference
Morphological		
External colour	White or cream; yellow; light brown; dark brown	Fukuda and Guevara (1998)
Cortex colour	White or cream; yellow; pink; purple	Fukuda and Guevara (1998)
Pulp (parenchyma) colour	White; cream; yellow; pink	Fukuda and Guevara (1998)
Epidermis texture	Smooth; rugose	Fukuda and Guevara (1998)
Peduncule	Sessile; pedunculate; both	Fukuda and Guevara (1998)
Constriction	None or little; medium; many	Fukuda and Guevara (1998)
Shape	Conical; conical–cylindrical; cylindrical; irregular	Fukuda and Guevara (1998)
Agronomic		
No. storage roots/plant	3–14	Dimyati (1994); Wheatley and Chuzel (1993); Ramanujam and Indira (1983); Pinho *et al.* (1995)
Weight of storage roots/plant	0.5–3.4 kg FW	Dimyati (1994); Wheatley and Chuzel (1993); Ramanujam and Indira (1983)
Weight of one storage root	0.17–2.35 kg	Barrios and Bressani (1967); Ramanujam and Indira (1983)
Length of storage root	15–100 cm	Wheatley and Chuzel (1993); Barrios and Bressani (1967); Pinho *et al.* (1995)
Diameter of storage root	3–15 cm	Wheatley and Chuzel (1993); Barrios and Bressani (1967); Pinho *et al.* (1995)
Diameter of fibrous root	0.36–0.67 mm	Connor *et al.* (1981)
Depth of fibrous root	Up to 260 cm	Connor *et al.* (1981)
Amylose in root starch	13–21% FW	O'Hair (1990)
Protein in whole root	1.76–2.68% FW	Barrios and Bressani (1967)
Protein in pulp (parenchyma)	1.51–2.67% FW	Barrios and Bressani (1967)
	1.0–6.0% DW	Wheatley and Chuzel (1993)
Protein in peel	2.79–6.61% FW	Barrios and Bressani (1967)
	7.0–14.0% DW	Wheatley and Chuzel (1993)
DM in whole fresh root	23–43%	Barrios and Bressani (1967); Ghosh *et al.* (1988); Ramanujam and Indira (1983); O'Hair (1989)
DM in peel	15–34%	Wheatley and Chuzel (1993); Barrios and Bressani (1967); O'Hair (1989)
DM in pulp	23–44%	Wheatley and Chuzel (1993); Barrios and Bressani (1967); O'Hair (1989)
Carbohydrates in whole root	85–91% DW	Barrios and Bressani (1967)
Carbohydrates in peel	60–83% DW	Barrios and Bressani (1967)
Carbohydrates in pulp (parenchyma)	88–93% DW	Barrios and Bressani (1967)
Starch in whole root	20–36% FW	Wholey and Booth (1979); O'Hair (1989); Ternes *et al.* (1978)
	77% DW	Ghosh *et al.* (1988)
Starch in peel	14–25% FW	O'Hair (1989)
	44–59% DW	Wheatley and Chuzel (1993)

Continued

Table 5.1. *Continued.*

Root characteristic	Variability	Reference
Starch in pulp (parenchyma)	26–40% FW	O'Hair (1989)
	70–91% DW	Wheatley and Chuzel (1993)
Peel in whole root	11–20% FW	Barrios and Bressani (1967)
Crude fibre in whole root	3.8–7.3% DW	Barrios and Bressani (1967)
Crude fibre in peel	9.2–21.2% DW	Barrios and Bressani (1967)
	5.0–15.0% DW	Wheatley and Chuzel (1993)
Crude fibre in pulp (parenchyma)	2.9–5.2% DW	Barrios and Bressani (1967)
	3.0–5.0% DW	Wheatley and Chuzel (1993)
Total sugars	1.3–5.3% DW	Wheatley and Chuzel (1993)

DM, dry matter; FW, fresh weight; DW, dry weight.

branchings, which are induced by flowering, have been called 'reproductive branchings'.

Stem morphological and agronomic characteristics are very important to characterizing a cultivar (Table 5.2). The variation of these characteristics depends on cultivar, cultural practice and climatic conditions.

Leaves

Cassava leaves are simple, formed by the lamina and petiole. The leaf is lobed with palmated veins. There is generally an uneven number of lobes, ranging from three to nine (occasionally 11). Only a few cultivars are characterized by having three-lobed mature vegetative leaves, which may represent the primitive ancestral form (Rogers and Fleming, 1973). Leaves near the inflorescence are generally reduced in size and lobe number (most frequently three-lobed), but the one closest to the base of the inflorescence is frequently simple and unlobed.

Leaves are alternate and have a phyllotaxy of 2/5, indicating that from any leaf (leaf 1) there are two revolutions around the stem to reach the sixth (leaf 6) in the same orthostichy as leaf 1. In these two revolutions there are five successive intermediate leaves (not counting leaf 1).

The main leaf morphological and agronomic characteristics and their variation are given in Table 5.3. Many of them (mainly the morphological ones) are used to characterize cultivars and may vary with environmental conditions and plant age.

Mature leaves are glabrous and each leaf is surrounded by two stipules (approximately 0.5–1.0 cm long), which remain attached to the stem when the leaf is completely developed (CIAT, 1984). The petiole length of a fully opened leaf normally varies from 5 to 30 cm, but may reach up to 40 cm.

The upper leaf surface is covered with a shiny, waxy epidermis. Most stomata are located on the lower (abaxial) surface of the leaves; only a few can be found along the main vein on the upper (adaxial) surface (Cerqueira, 1989). Of 1500 cultivars studied, only 2% had stomata on the adaxial surface (El-Sharkawy and Cock, 1987a). The stomata on the upper surface are also functional and bigger than those on the undersurface. Both are morphologically paracytic, with two small guard cells surrounded by two subsidiary cells (Cerqueira, 1989). The number of stomata per leaf area range from 278 to 700 mm^{-2}, and all stomatal pores can occupy from 1.4 to 3.1% of the total leaf area (Table 5.3).

Flowers

Cassava is a monoecious species producing both male (pistillate) and female (staminate) flowers on the same plant. The inflorescence is generally formed at the insertion point of the reproductive branchings; occasionally inflorescences can be found in the leaf axils on the upper part of the plant. The female flowers, located on the lower part of the inflorescence, are fewer in number than male flowers, which are numerous on the upper part of the inflorescence. On the same inflorescence, the female flowers open 1–2 weeks before the male flowers (protogyny).

Table 5.2. Some morphological and agronomic characteristics of stems and their variability in cassava.

Stem characteristic	Variability	Reference
Morphological		
Cortex (collenchyma) colour	Yellow; light green; dark green	Fukuda and Guevara (1998)
External colour	Orange; green–yellow; gold; dark brown; silver; grey; dark brown	Fukuda and Guevara (1998)
Phyllotaxis length	Short (< 8 cm); medium (8–15 cm); large (> 15 cm)	Fukuda and Guevara (1998)
Epidermis colour	Cream; light brown; dark brown; orange	Fukuda and Guevara (1998)
Growth habit	Straight; zigzag	Fukuda and Guevara (1998)
Apical stem colour	Green; green-purple; purple	Fukuda and Guevara (1998)
Branching habit	Erect; dichotomous; trichotomous; tetrachotomous	Fukuda and Guevara (1998)
Agronomic		
Diameter of mature stem	2–8 cm	CIAT (1984); Ramanujam and Indira (1983)
Plant height	1.20–3.70 m	Ramanujam and Indira (1983); Ramanujam (1985); Veltkamp (1985a); Pinho *et al.* (1995)
No. of nodes from planting–1st branch level	22–96	Veltkamp (1985a)
No. of days from planting–1st branch level	49–134	Veltkamp (1985a)
No. of apices/plant	2.8–27.5	Pinho *et al.* (1995)

Male and female flowers on different branches of the same plant can open at the same time. Normally, cassava is cross-pollinated by insects; thus it is a highly heterozygous plant.

The flowers do not have a calyx or corolla, but an indefinite structure called perianth or perigonium, made up of five yellow, reddish or purple tepals. The male flower is half the size of the female flower. The pedicel of the male flower is thin, straight and very short, while that of the female flower is thick, curved and long. Inside the male flower, there is a basal disk divided into ten lobes. Ten stamens originate from between them. They are arranged in two circles and support the anthers. The five external stamens are separated and longer than the inner ones, which join together on the top to form a set of anthers. The pollen is generally yellow or orange, varying from 122 to 148 μm in size, which is very large compared to other flowering plants (Ghosh *et al.*, 1988). The female flower also has a ten-lobed basal disk, which is less lobulated than the male flower. The ovary is tricarpellary with six ridges and is mounted on the basal disk. The three locules contain one ovule each. A very small style is located on top of the ovary, and a stigma with three undulated, fleshy lobes originates from the style.

Fruit and seeds

The fruit is a trilocular capsule, ovoid or globular, 1–1.5 cm in diameter and with six straight, prominent longitudinal ridges or aristae. Each locule contains a single carunculate seed. The fruit has a bicidal dehiscence, which is a combination of septicidal and loculicidal dehiscences, with openings along the parallel plane of the dissepiments and along the midveins of the carpels, respectively. With this combination of dehiscences, the fruits open into six valves causing an explosive dehiscence, ejecting the seeds some distance (Rogers, 1965). Fruit maturation generally occurs 75–90 days after pollination (Ghosh *et al.*, 1988). The seed is ovoid–ellipsoidal, approximately 100 mm long, 6 mm wide and 4 mm thick. The weight varies from 95 to 136 mg per seed (Ghosh *et al.*, 1988). The smooth seed coat is dark brown, mottled with grey. The seeds usually germinate soon after collection, taking about 16 days for germination.

Table 5.3. Some morphological and agronomic characteristics of leaves and their variability in cassava.

Leaf characteristic	Variability	Reference
Morphological		
Apical leaf colour	Light green; dark green; green–purple; purple	Fukuda and Guevara (1998)
Apical pubescence	Absent; present	Fukuda and Guevara (1998)
Shape of central lobe	Ovoid; elliptic–lanceolate; obovate–lanceolate; oblanceolate; lanceolate; linear; pandurate; linear–pyramidal; linear–pandurate; linear–hostatilobada	Fukuda and Guevara (1998)
Petiole colour	Green–yellow; green; green–red; red-green; red; purple	Fukuda and Guevara (1998)
Mature leaf colour	Light green; dark green; green-purple; purple	Fukuda and Guevara (1998)
Protuberance of leaf scars	No protuberance; protuberant	Fukuda and Guevara (1998)
No. of lobes	3; 5; 7; 9; 11	Fukuda and Guevara (1998)
Agronomic		
Petiole length	5–30 cm	Ghosh *et al.* (1988)
	9–20 cm	CIAT (1984)
Total chlorophyll	2.18–2.86 mg g^{-1} leaf FW	Ramanujam and Jos (1984)
Central lobe length	4–20 cm	CIAT (1984)
Central lobe width	1–6 cm	CIAT (1984)
No. of stomata/leaf area in adaxial epidermis	278–700 mm^{-2}	Ghosh *et al.* (1988); Cerqueira (1989); Splittstoesser and Tunya (1992); Connor and Palta (1981)
Relative area of stomata pore (% from leaf area)	1.4–3.1%	Cerqueira (1989); Pereira and Splittstoesser (1990)
Stipule length	0.5–1.0 cm	CIAT (1984)
Leaf thickness	100–120 μm	Pereira and Splittstoesser (1990)
DM in mature leaf	25%	Barrios and Bressani (1967)
Fibre in mature leaf	4.58% DW	Barrios and Bressani (1967)
Ash in mature leaf	8.28% DW	Barrios and Bressani (1967)
Protein in mature leaf	7.1–8.9% FW	Barrios and Bressani (1967)
	28.8% DW	Barrios and Bressani (1967)
Soluble carbohydrates	11.36% FW	Barrios and Bressani (1967)
	44.84% DW	Barrios and Bressani (1967)

DM, dry matter; FW, fresh weight; DW, dry weight.

Growth and Development

Plant developmental stages

As cassava is a perennial shrub it can grow indefinitely, alternating periods of vegetative growth, storage of carbohydrates in the roots, and even periods of almost dormancy, brought on by severe climatic conditions such as low temperature and prolonged water deficit. There is a positive correlation between the total biomass and storage root biomass (Fig. 5.1; Ramanujam, 1990). During its growth, there are distinct developmental phases. The occurrence, duration and existence of each phase depend on several factors related to varietal differences, environmental conditions and cultural practices. The initial growth (at 15-day intervals) from emergence to 150 days is presented in Fig. 5.2. Growth at 60-day intervals during the first cycle (0–360 days after planting; DAP) is shown in Fig. 5.3. The results in these two figures are consistent with other authors (Howeler and Cadavid, 1983; Ramanujam and Biradar, 1987; Távora *et al.*, 1995; Peressin *et al.*, 1998). The periods and main physiological events during the growth of a cassava plant under favourable conditions in the field can be visualized in these figures and are summarized below:

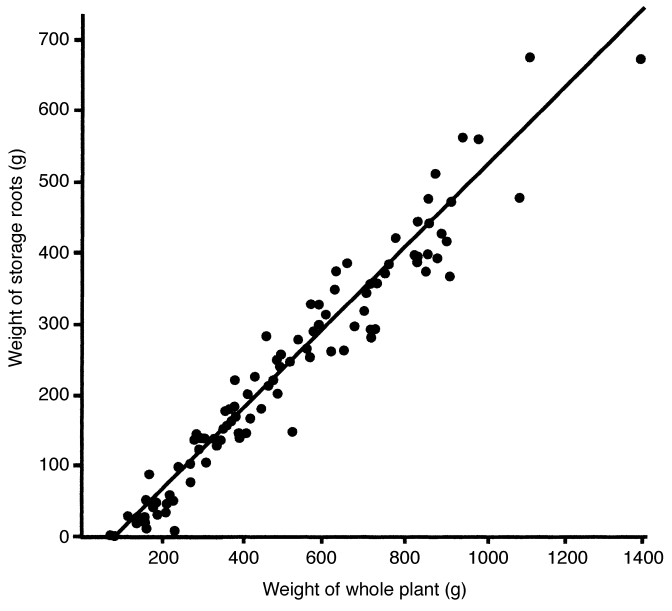

Fig. 5.1. Relationship between dry weight (DW) of whole plant (x) and DW of storage roots (y) for individual plants of a field trial at the University of the West Indies: $y = 0.56x–34$; $r^2 = 0.96$; $n = 112$. (Source: Boerboom, 1978.)

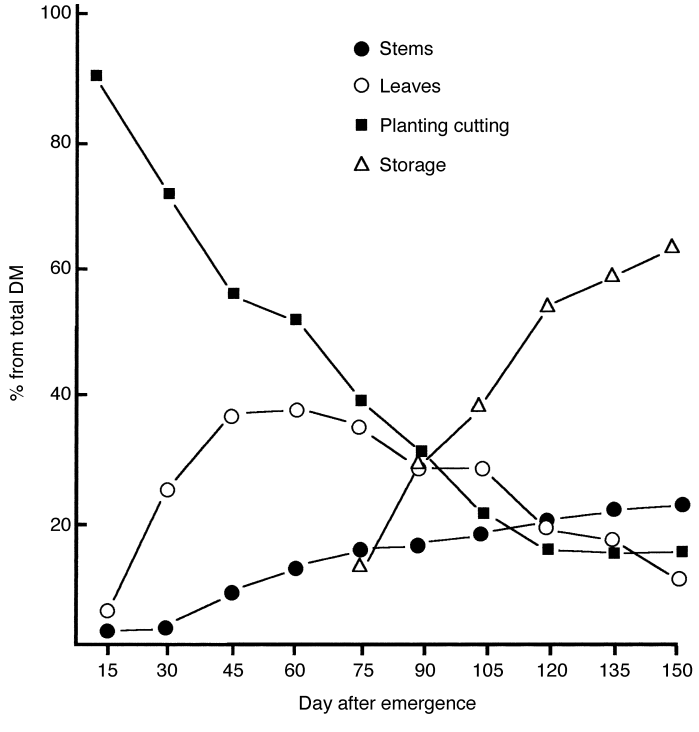

Fig. 5.2. Partitioning of dry matter during the initial development of cassava cv. Cigana, Cruz das Almas, Bahia, Brazil. (Source: Porto, 1986.)

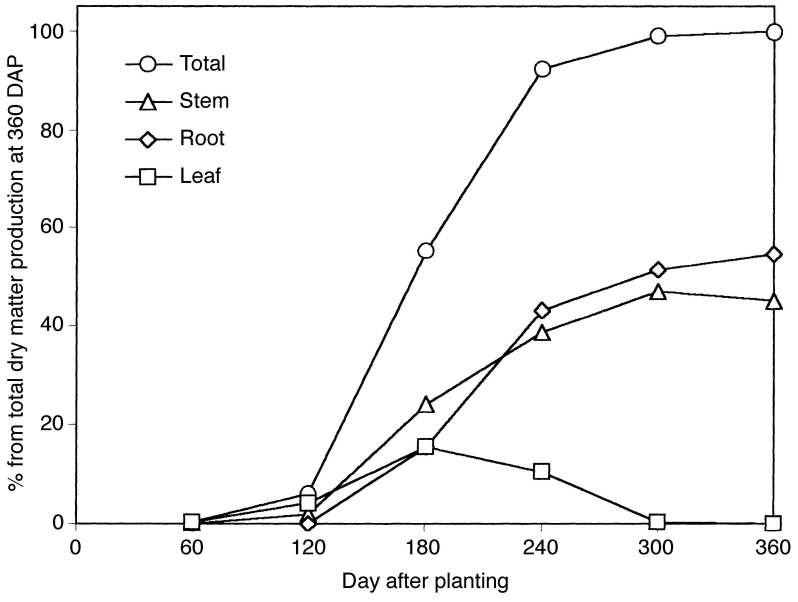

Fig. 5.3. Growth of cassava plant during the first cycle (12 months). Average of two varieties. DAP, days after planting. Graph made from data of Lorenzi (1978).

Emergence of sprouting – 5–15 DAP

- From 5–7 DAP the first adventitious roots arise from the basal cut surface of the stake and occasionally from the buds under the soil.
- 10–12 DAP the first sprouting occurs, followed by small leaves which start to emerge (Conceição, 1979).
- Emergence is achieved at 15 DAP.

Beginning of leaf development and formation of root system – 15–90 DAP

- The true leaves start to expand around 30 DAP (Fig. 5.2) when the photosynthetic process starts to contribute positively to plant growth.
- Until 30 DAP, shoot and root growth depends on the reserves of the stem cutting.
- The fibrous roots start to grow, replacing the first adventitious roots. These new roots start to penetrate in the soil, reaching 40–50 cm deep, and function in water and nutrient absorption (Conceição, 1979).
- Few fibrous roots (between three and 14) will become storage roots, which can be distinguished from fibrous roots from 60 to 90 DAP (Cock *et al.*, 1979). At 75 DAP the storage roots represent 10–15% of total dry matter (DM; Fig. 5.2).

Development of stems and leaves (canopy establishment) – 90–180 DAP

- Maximum growth rates of leaves and stems are achieved in this period, and the branching habit and plant architecture is defined (Fig. 5.3).
- From 120 to 150 DAP the leaves are able to intercept the most of the incident light on canopy (Veltkamp, 1985c).
- Maximum canopy size and maximum DM partition to leaves and stems are accomplished (Howeler and Cadavid, 1983; Ramanujam, 1985; Távora *et al.*, 1995).
- The storage root continues to bulk.
- The most active vegetative growth for cassava occurs in this period (Ramanujam, 1985).

High carbohydrate translocation to roots – 180–300 DAP

- Photoassimilate partition from leaves to roots is accelerated, making the bulking of storage roots faster (Fig. 5.3).

- The highest rates of DM accumulation in storage roots occur within this period (Fig. 5.3; Boerboom, 1978; Távora *et al.*, 1995; Peressin *et al.*, 1998).
- Leaf senescence increases, hastening rate of leaf fall (Fig. 5.3).
- Stem becomes lignified (Conceição, 1979).

Dormancy – 300–360 DAP

- Rate of leaf production is decreased.
- Almost all leaves fall and shoot vegetative growth is finished.
- Only translocation of starch to root is kept, and maximum DM partition to the roots is attained.
- This phase occurs mainly in regions with significant variation in temperature and rainfall.
- The plant completes its 12-month cycle, which can be followed by a new period of vegetative growth, DM accumulation in the roots and dormancy again.

Leaf area development

The analyses of crop growth and yield are usually evaluated on the basis of two parameters: leaf area index (LAI), i.e. leaf area per unit ground area, and net assimilatory rate (NAR), i.e. the rate of DM production per unit leaf area. In cassava a positive correlation between the leaf area or leaf area duration and yield of storage roots has been reported, indicating that leaf area is crucial in determining crop growth rate and the storage bulking rate of cassava (Sinha and Nair, 1971; Cock, 1976; Cock *et al.*, 1979).

For cassava the leaf area per plant depends on the number of active apices (branching pattern), the number of leaves formed/apex, leaf size and leaf life. Given that there are significant varietal variations and influence of environmental conditions (Veltkamp, 1985a), it is important to characterize the development of cassava leaf area and its components. Table 5.4 lists values of some parameters related to leaf growth that have been found in cassava. These parameters are discussed below.

After leaf emergence (folded, 1 cm long) and under normal conditions, the cassava leaf reaches its full size on days 10–12. Leaf life (from emergence to abscission) depends on cultivar, shade level, water deficit and temperature (Cock *et al.*, 1979; Irikura *et al.*, 1979). It ranges from 40 to 210 days (Table 5.4), but is commonly 60–120 days (Cock, 1984).

There are marked differences in leaf size among the different cultivars, and the size varies with the age of the plant. The leaves produced from 3 to 4 MAP are those that become the largest; maximum total leaf area is reached from 4 to 5 MAP (Cock *et al.*, 1979; Irikura *et al.*, 1979). Leaf size is influenced by changing the branching

Table 5.4. Parameters related to leaf growth during the first cycle (12 months) and some values found in cassava.

Leaf growth parameter	Value	Reference
Individual leaf area	50–600 cm^2	Ramanujam (1982); Splittstoesser and Tunya (1992); Veltkamp (1985a)
Expansion period (from emergence to full size)	12 days	Conceição (1979)
Leaf longevity (from fully expanded to abscission)	36–100 days	Ramanujam and Indira (1983); Conceição (1979)
Leaf life (from emergence to abscission)	40–210 days	Splittstoesser and Tunya (1992); Irikura *et al.* (1979); Ramanujam (1985); Veltkamp (1985a)
No. leaves retained/plant	44–146	Ramanujam and Indira (1983)
Leaf production rate/shoot	4–22 $week^{-1}$	Ramanujam and Indira (1983)
Leaf shedding rate/plant	10–24 leaves $week^{-1}$	Ramanujam and Indira (1983)
Total leaf area	1.24–3.38 m^2	Ramanujam and Indira (1983)
Cumulative no. of leaves/apex	117–162	Veltkamp (1985a); Cock *et al.* (1979)

pattern. Larger leaves are produced when the number of active apices is reduced (Tan and Cock, 1979). The rate of leaf formation decreases with plant age and is lower at low temperatures (Irikura *et al.*, 1979).

Differences in mean LAI are closely related to the rate of root bulking. The optimal LAI for storage root bulking rate is 3–3.5 (Cock *et al.*, 1979) and exists over a wide range of temperature (Irikura *et al.*, 1979). Initial leaf area development is slow, taking 60–80 DAP before an LAI of 1.0 is reached. From 120 to 150 DAP the light interception by the canopy is around 90% with an LAI of 3 (Veltkamp, 1985a). In order to obtain high storage root yields, the crop should reach an LAI of 3–3.5 as quickly as possible and maintain that LAI for as long as possible (Cock *et al.*, 1979; Veltkamp, 1985a). Substantial leaf abscission began at LAI values of 5.0–6.0 (Keating *et al.*, 1982a).

Temporal development of cell division and cell expansion

Leaf area development is largely dependent on cell division and cell expansion processes, which determine the number of cells per mature leaf and cell size, respectively. Thus the final leaf area is directly affected by the rate and duration of cell division and expansion (Takami *et al.*, 1981; Lecoeur *et al.*, 1995). A temporal development of cell division and expansion for adaxial epidermal cells in cassava has been proposed by Alves (1998; Fig. 5.4), in which the transition from leaf cell division to cell expansion processes is discrete and occurs when leaf area reached 5% of its final size, corresponding to the first folded leaf toward the top. Thus when the leaf starts to unfold, almost all cell division stops and rapid cell expansion starts.

Dry matter partitioning and source–sink relationship

During cassava growth the carbohydrates from photosynthesis have to be distributed to assure good development of the source (active leaves) and provide DM to the sink (storage roots, stem and growing leaves). Cassava DM is translocated mainly to stems and storage roots, and DM

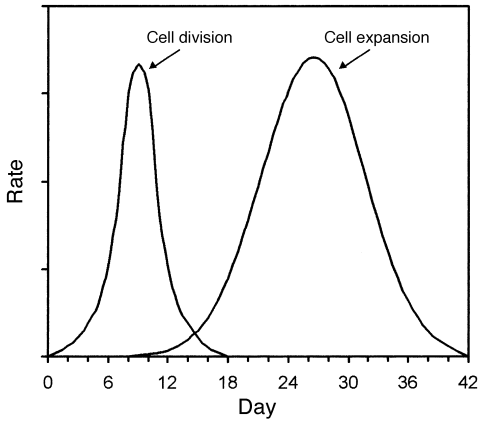

Fig. 5.4. Temporal development of cell division and cell expansion processes during cassava leaf development in adaxial epidermal cells. (Source: Alves, 1998.)

accumulation in the leaves decreases during the crop cycle. Until 60–75 DAP, cassava accumulates DM more in leaves than in stems and storage roots, not including the stem cutting (Fig. 5.2). Then the storage roots increase rapidly, reaching 50–60% of the total DM around 120 DAP (Fig. 5.2; Howeler and Cadavid, 1983; Távora *et al.*, 1995). After the fourth month, more DM is accumulated in the storage roots than the rest of the plant. At harvest (12 months) DM is present mainly in roots, followed by stems and leaves (Fig. 5.3; Howeler and Cadavid, 1983). Thus, during the growth cycle, the DM distribution to the different parts is constant with a high positive linear correlation of the total DM with shoot and root DM (Fig. 5.1; Veltkamp, 1985d).

The period of maximum rates of DM accumulation depends on genotypes and growing conditions. Lorenzi (1978) at high latitude and Oelsligle (1975) at high altitude reported maximum rates of DM accumulation at 4–6 and 7 months, respectively. Under more tropical conditions, where growth is faster, Howeler and Cadavid (1983) found an earlier period of maximum rates, at 3–5 MAP. The distribution of DM to the economically useful plant parts is measured by harvest index (HI). In cassava HI represents the efficiency of storage root production and is usually determined by the ratio of storage root weight to the total plant weight. Significant differences in HI have been reported among

cultivars, indicating that it can be used as a selection criterion for higher yield potential in cassava. HI values of 0.49–0.77 have been reported after 10–12 MAP (Lorenzi, 1978; Cavalcanti, 1985; Pinho *et al.*, 1995; Távora *et al.*, 1995; Peressin *et al.*, 1998). Although DM distribution is constant, its accumulation depends upon photoassimilate availability (source activity) and sink capacity of the storage parts. The number of storage roots and their mean weight are yield components that determine sink capacity. The significant positive correlation of photosynthetic rate with root yield and total biomass, as well as the correlations between LAI, interception of radiation and biomass production (Williams, 1972; Mahon *et al.*, 1976; El-Sharkawy and Cock, 1990; Ramanujam, 1990), indicates that demand for photoassimilates by roots increases the photosynthetic activity.

The balance between 'source' and 'sink' activity is essential for the plant to reach its maximum productivity. Studies have shown that up to 25% reduction in the number of storage roots did not affect total or root DM and the IAF (Cock *et al.*, 1979). On the other hand, Ramanujam and Biradar (1987) observed that reduction of 50–75% in storage roots did affect root growth rate without changing shoot growth rate, indicating that shoot growth is independent of storage root growth. Influence of source size on DM production shows that the NAR and storage root growth rate is reduced when the source size is increased from LAI 3.0 to 6.0 (Ghosh *et al.*, 1988).

Flowering

Little is known about flowering in cassava, and some clones have never been known to flower. Flowering can start 6 weeks after planting although the precise flowering time depends on cultivar and environment. It appears that cassava flowers best at moderate temperatures (approximately 24°C). It has been suggested that forking is related to the onset of flowering, which is promoted by long days in some cultivars. Usually, the apical meristem becomes reproductive when branching occurs, but the abortion of flowers is very common.

Keating *et al.* (1982a) evaluated cassava at 12 different planting dates at a high latitude (27° 37′ S), where photoperiods range from 14.8 to 11.2 h. Concentration of first flowering and forking occurred in photoperiods > 13.5 h. This result is consistent with Bruijn (1977) and Cunha and Conceição (1975), who suggested flowering in cassava may be promoted by increasing day length.

Photosynthesis

Cassava photosynthesis follows a C_3 pathway (Veltkamp, 1985e; Edwards *et al.*, 1990; Angelov *et al.*, 1993; Ueno and Agarie, 1997) with maximum photosynthetic rates varying from 13 to 24 μmol CO_2 m^{-2} s^{-1} under greenhouse or growth chamber conditions (Mahon *et al.*, 1977b; Edwards *et al.*, 1990) and from 20 to 35 μmol CO_2 m^{-2} s^{-1} in the field (El-Sharkawy and Cock, 1990). It exhibits a high CO_2 compensation point, from 49 to 68 μl l^{-1}, typical of C_3 plants (Mahon *et al.*, 1977a; Edwards *et al.*, 1990; Angelov *et al.*, 1993). In field-grown cassava, photosynthesis has high optimum temperature (35°C) and wide plateau (25–35°C; El-Sharkawy and Cock, 1990) and is not light saturated up to 1800 μmol PAR m^{-2} s^{-1} (El-Sharkawy *et al.*, 1992b) or 2000 μmol PAR m^{-2} s^{-1} (Angelov *et al.*, 1993). Thus cassava is adapted to a tropical environment, requiring high temperature and high solar radiation for optimal leaf development and for expression of its photosynthetic potential. Both storage root yield and total biomass show positive correlation with photosynthesis rate (El-Sharkawy and Cock, 1990; Ramanujam, 1990).

Morphologically, cassava leaves combine some novel characteristics related to high productivity and drought tolerance and, consequently, to photosynthesis. The lower mesophyll surface is populated with papillose-type epidermal cells, while the upper surface is fairly smooth, with scattered stomata and trichomes. The papillae appear to add about 15% to leaf thickness and to lengthen the diffusion path from the stomatal opening to the bulk air perhaps two- to threefold (Angelov *et al.*, 1993). Cassava leaves have distinct green bundle-sheath cells, with small, thin-walled cells, spatially separated below the palisade cells (different from Kranz-type leaf anatomy). In addition to

performing C_3 photosynthesis, these cells may function in transport of photosynthates in the leaf. In Kranz anatomy, typical of C_4 plants, the bundle sheaths are surrounded by and all in direct contact with many mesophyll cells (Edwards *et al.*, 1990).

Cyanide Content

All cassava organs, except seeds, contain cyanogenic glucoside (CG). Cultivars with < 100 mg kg^{-1} fresh weight (FW) are called 'sweet' while cultivars with 100–500 mg kg^{-1} are 'bitter' cassava (Wheatley *et al.*, 1993). The most abundant CG is linamarin (85%), with lesser amounts of lotaustralin. Total CG concentration depends on cultivar, environmental condition, cultural practices and plant age (McMahon *et al.*, 1995). The variation found in some parts of cassava is shown in Table 5.5.

Linamarin, which is synthesized in the leaf and transported to the roots, is broken down by the enzyme linamarase, also found in cassava tissues (Wheatley and Chuzel, 1993). When linamarin is hydrolysed, it releases HCN, a volatile poison (LD_{50-60} mg for humans; Cooke and Coursey, 1981); but some cyanide can be detoxified by the human body (Oke, 1983). In intact roots the compartmentalization of linamarase in the cell wall and linamarin in cell vacuoles prevents the formation of free cyanide. Upon processing, the disruption of tissues ensures that the enzyme comes into contact with its substrate, resulting in rapid production of free cyanide via an unstable cyanhydrin intermediary (Wheatley and Chuzel, 1993). Juice extraction, heating, fermentation, drying or a combination of these processing treatments aid in reducing the HCN concentration to safe levels (O'Hair, 1990).

Physical Deterioration of Storage Roots

Cassava roots have the shortest postharvest life of any of the major root crops (Ghosh *et al.*, 1988). Roots are highly perishable and usually become inedible within 24–72 h after harvest due to a rapid physiological deterioration process, in which synthesis of simple phenolic compounds that polymerize occurs, forming blue, brown and black pigments (condensed tannins; Wheatley and Chuzel, 1993). It is suggested that polyphenolic compounds in the roots oxidize to quinone-type substances, which is complexed with small molecules like amino acids to form coloured pigments that are deposited in the vascular bundles (Ghosh *et al.*, 1988). The accumulation of the coumarin, scopoletin, is especially rapid, reaching 80 mg kg^{-1} dry weight (DW) in 24 h (Wheatley and Chuzel, 1993). Tissue dehydration, especially at sites of mechanical damage to the roots encourages the rapid onset of deterioration. The phenolic compounds may be released on injury. The changes during storage of roots depend upon condition and duration of storage, physiological state of the stored material and varietal characteristics (Ghosh *et al.*, 1988).

Polyphenol oxidase (PPO) is an enzyme that oxidizes phenols to quinone. Any process that inhibits PPO, such as heat treatment, cold storage, anaerobic atmosphere and dipping

Table 5.5. Cyanide concentration in different parts of the cassava plant.

Part of plant	Total cyanide concentration	Source
Root pulp (parenchyma)	3–121 mg 100 g^{-1} DW	Barrios and Bressani (1967)
	3–135 mg 100 g^{-1} DW	Wheatley and Chuzel (1993)
	1–40 mg 100 g^{-1} FW	Barrios and Bressani (1967)
Root peel	6–55 mg 100 g^{-1} DW	Wheatley and Chuzel (1993)
	5–77 mg 100 g^{-1} DW	Barrios and Bressani (1967)
	17–267 mg 100 g^{-1} FW	Barrios and Bressani (1967)
Leaf	1–94 mg 100 g^{-1} DW	Barrios and Bressani (1967)
	0.3–29 mg 100 g^{-1} FW	Barrios and Bressani (1967)

DW, dry weight; FW, fresh weight.

roots in solutions of inhibitors (e.g. ascorbic acid, glutathione and KCN) prevents vascular streaking (Ghosh *et al.*, 1988).

Secondary deterioration can follow physiological or primary deterioration 5–7 days after harvest. This is due to microbial infection of mechanically damaged tissues and results in the same tissue discoloration with vascular streaks spreading from the infected tissues (Wheatley and Chuzel, 1993).

Environmental Effects on Cassava Physiology

Cassava is found over a wide range of edaphic and climatic conditions between 30°N and 30°S latitude, growing in regions from sea level to 2300 m altitude, mostly in areas considered marginal for other crops: low-fertility soils, annual rainfall from < 600 mm in the semiarid tropics to > 1500 mm in the subhumid and humid tropics. Given the wide ecological diversity, cassava is subjected to highly varying temperatures, photoperiods, solar radiation and rainfall.

Temperature

Temperature affects sprouting, leaf size, leaf formation, storage root formation and, consequently, general plant growth. The behaviour of cassava under the temperature variations that usually occur where cassava is normally cultivated indicates that its growth is favourable under annual mean temperatures ranging from 25 to 29°C (Conceição, 1979), but it can tolerate from 16 to 38°C (Cock, 1984). Table 5.6 summarizes the ranges of temperature and their principal physiological effects on cassava development.

At low temperatures (16°C) sprouting of the stem cutting is delayed, and rate of leaf production, total and storage root DW are decreased (Cock and Rosas, 1975). Sprouting is hastened when the temperature increases up to 30°C but is inhibited with temperatures > 37°C (Keating and Evenson, 1979). As temperature decreases, leaf area development becomes slower because the maximum size of individual leaves is smaller, and fewer leaves are produced at each apex although leaf life is increased (Irikura *et al.*, 1979). At a temperature of 15–24°C, the leaves remain on the plant for up to 200 days (Irikura *et al.*, 1979), while at higher temperatures leaf life is 120 days (Splittstoesser and Tunya, 1992).

There is a genotype-by-temperature interaction for yield ability. Irikura *et al.* (1979) evaluated four cultivars under different temperatures and found that higher yields were obtained at different temperatures according to the cultivar, indicating that the effect of natural selection is highly significant on varietal adaptation (Table 5.7).

Table 5.6. Effect of temperature on cassava development.

Air temperature (°C)	Physiological effects
< 17 or > 37	Sprouting impaired
28.5–30	Sprouting faster (optimum)
< 15	Plant growth inhibited
16–38	Cassava plant can grow
25–29	Optimum for plant growth
< 17	Reduction of leaf production rate, total and root DW
20–24	Leaf size and leaf production rate increased; leaf life shortened
28	Faster shedding of leaves; reduction in no. branches
25–30	Highest rates of photosynthesis in greenhouse
30–40	Highest rates of photosynthesis in the field
16–30	Transpiration rate increases linearly and then declines

Sources: Wholey and Cock (1974); Cock and Rosas (1975); Mahon *et al.* (1977b); Conceição (1979); Irikura *et al.* (1979); Keating and Evenson (1979); El-Sharkawy *et al.* (1992b).
DW, dry weight.

Table 5.7. Fresh root yield (t ha^{-1}) of four contrasting cassava types at 12 months after planting (MAP) under three different temperature regimes.

	Temperature (°C)		
Variety	20	24	28
M Col 22	9.3	27.7	39.4
M Mex 59	22.8	38.8	30.4
M Col 113	24.2	26.1	23.9
Popayán	28.9	15.7	9.4

Source: Irikura *et al.* (1979).

The main effect of temperature is on biological production, as DM partitioning does not change much when cassava is cultivated under different temperatures (Cock and Rosas, 1975). Higher temperatures are associated with a greater crop growth rate (CGR) and high photosynthetic rate. El-Sharkawy *et al.* (1992b) evaluated the potential photosynthesis of three cultivars from contrasting habits under different growing environments and verified that photosynthetic rate increased with increasing temperature, reaching its maximum at 30–40°C. In all cultivars photosynthesis was substantially lower in leaves that had developed in the cool climate than in those from the warm climate. The high sensitivity of photosynthesis to temperature points to the need for genotypes more tolerant to low temperature, which could be used in the highland tropics and subtropics.

Photoperiod

Day length affects several physiological processes in plants. The differences in day length in the tropical region are very small, varying from 10 to 12 h throughout the year. Thus photoperiod may not limit cassava root production in this region. On the other hand, the restrictions regarding cassava distribution outside the tropical zone can be due to effects of day length variation on its physiology. Although studies about day length effect in cassava are scarce, tuberization, photoassimilates partitioning and flowering are reportedly affected.

Experiments in which the day length was artificially changed have shown that the optimal light period for cassava is around 12 h, with probable varietal differences in the critical day length (Bolhuis, 1966). Long days promote growth of shoots and decrease storage root development, while short days increase storage root growth and reduce the shoots, without influencing total DW (Fig. 5.5). The increase in shoot DW under long days is a result of significant increases in plant height, leaf area per plant, number of apices per plant, and number of living leaves per apex (Veltkamp, 1985b). This suggests an antagonistic relationship between shoot growth and development of the storage roots in response to variation in day length.

There are varietal differences in sensitivity to long days (Carvalho and Ezeta, 1983). Under field conditions, Veltkamp (1985b) submitted three genotypes to two day lengths (12 and 16 h) during the whole growth period. He observed that the percentage decrease in storage root yield under the long day was greatest in M Col 1684 (47%) and least in M Col 22 (13%; Table 5.8). Yield differences resulted mainly from decreased efficiency of storage root production or HI under 16-h days because total DM was greater under 16-h days. No day-length effect was found for the crop weight at which the starch accumulation in the roots apparently started (AISS values; Table 5.8). Thus the storage root yield reduction seems to be more related to a change in the distribution patterns of DM rather than to a delay in storage root initiation. Considering that photoperiod primarily affects shoots and a secondary response occurs in the roots (Keating *et al.*, 1982b) and that shoot growth has preference over root growth (Cock *et al.*, 1979; Tan and Cock, 1979), long photoperiods may increase the growth requirements of the shoots, thereby reducing the excess carbohydrates available for root growth (Veltkamp, 1985b).

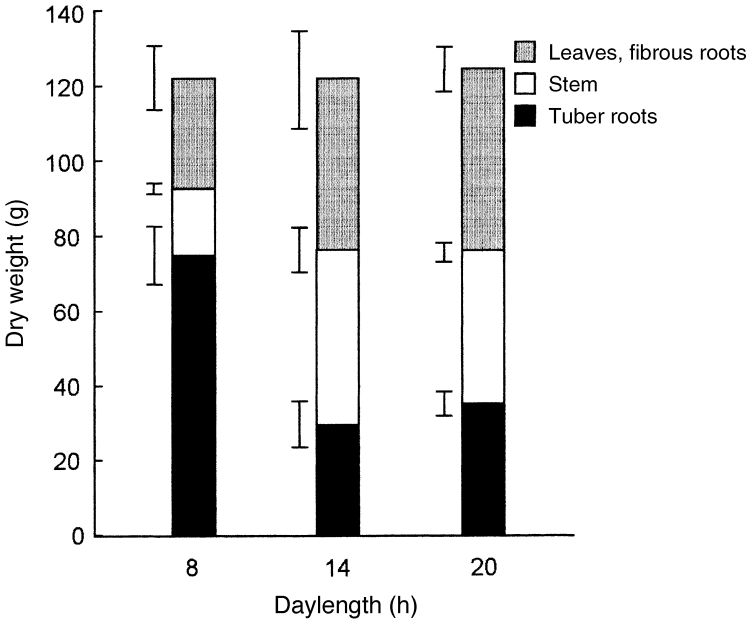

Fig. 5.5. Effect of day length on cassava dry matter distribution 16 weeks after planting. Vertical lines indicate twice the standard error of total dry weight (DW), stem DW and storage root DW.

Table 5.8. Cassava dry matter (DM) production and distribution 272 days after planting (DAP) under 16 h and natural day length (approximately 12 h).

Genotype	Day length	Total DM (t ha^{-1})[a]	DW storage root (t ha^{-1})	Harvest Index (HI)	AISS[b] (t ha^{-1})
M Col 1684	Natural[c]	16.7	9.1	0.54	0.55
	16 h[d]	17.3	4.6	0.27	0.25
M Ptr 26	Natural	14.5	8.1	0.61	0.60
	16 h	15.9	4.9	0.42	0.36
M Col 22	Natural	15.5	9.5	0.56	0.65
	16 h	19.5	8.3	0.31	0.45

Source: Veltkamp (1985b).
[a]Includes weight of fallen leaves.
[b]AISS, apparent initial start of starch accumulation; corresponds to crop weight at which starch accumulation apparently starts in roots.
[c]Natural = approximately 12 h.
[d]16 h = 12 h of natural day length + 4 h of artificial light.
DW, dry weight.

Solar radiation

The commonest cassava production system is intercropping with other staple crops. In Latin America and Africa, cassava is usually associated with an earlier maturing grain crop such as maize, rice or grain legumes (beans, cowpeas or groundnuts; Mutsaers *et al.*, 1993). Cassava is also intercropped with perennial vegetation (Ramanujam *et al.*, 1984). Cassava is usually planted after the intercropped species. Even when it is planted at the same time, the associated crop such as maize is established faster than cassava. Thus in an associated cropping system

cassava is always subjected to different degrees of shading and low light intensity in the early stages of development. Considering that cassava is a crop that requires high solar radiation to perform photosynthesis more efficiently (El-Sharkawy *et al.*, 1992b), it is very important to know the effect of shade on cassava development and production. Ramanujam *et al.* (1984) evaluated 12 cassava cultivars under the shade in a coconut garden (85–90% shading). Under shading, the root bulking process started about 3 weeks after that in plants grown without shading, and the number of storage roots per plant and NAR was reduced under shading. Okoli and Wilson (1986) submitted cassava to six shade regimes and observed that all levels of shade delayed storage root bulking and at 20, 40, 50, 60 and 70% shade reduced cassava yield by 43, 56, 59, 69 and 80%, respectively.

In relation to shoots, under field conditions, shading increases plant height and the leaves tend to become adapted to low light conditions by increasing leaf area per unit weight (Fukai *et al.*, 1984; Okoli and Wilson, 1986; Ramanujam *et al.*, 1984) and shortening leaf life only under severe shading. Under ideal growing conditions, cassava leaves have a life of up to 125 days (Splittstoesser and Tunya, 1992). Levels of shade up to about 75% have very little effect on leaf life, but under 95–100% shade, leaves abscise within 10 days (Cock *et al.*, 1979).

Aresta and Fukai (1984) observed that only 22% shade decreased both fibrous root elongation rate (53%) and storage root growth rate (36%) without altering shoot growth rate, which was significantly decreased (32%) only under 68% shade. Thus under limited photosynthesis caused by low solar radiation, most of the photosynthates are utilized for shoot growth, affecting storage root development significantly, showing that the shoots are a stronger sink than roots.

Water deficit

Cassava is commonly grown in areas receiving < 800 mm rainfall year^{-1} with a dry season of 4–6 months, where tolerance to water deficit is an important attribute. Although it is a drought-tolerant crop, growth and yield are decreased by prolonged dry periods. The reduction in storage root yield depends on the duration of the water deficit and is determined by the sensitivity of a particular growth stage to water stress. The critical period for water-deficit effect in cassava is from 1 to 5 MAP – the stages of root initiation and tuberization. Water deficit during at least 2 months of this period can reduce storage root

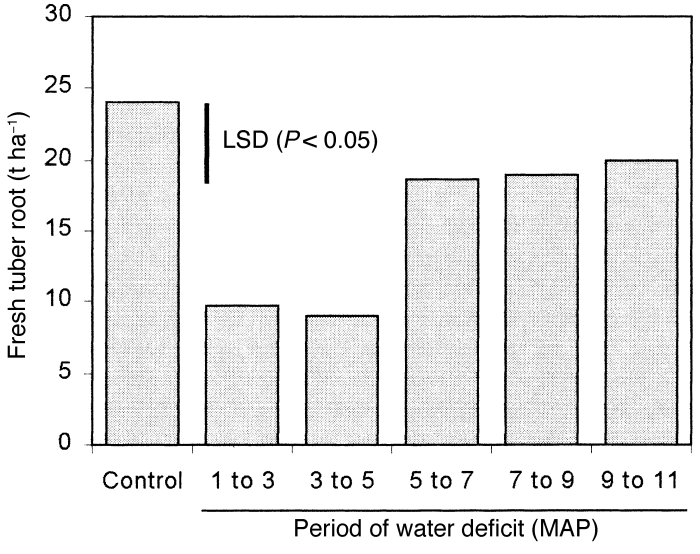

Fig. 5.6. Effect of water deficit during different growth periods on cassava yield.

yield from 32 to 60% (Connor *et al.*, 1981; Porto *et al.*, 1988). Figure 5.6 shows the root yield reduction caused by water deficit imposed for 2 months during successive 2-month periods from 1 to 11 MAP. Clearly, they found that the severer effect corresponded to stress occurring from 1 to 5 MAP (i.e. period of rapid leaf growth and tuberization) compared with the later period of storage root bulking.

Drought tolerance

Plants respond to water deficit at many different levels: morphological, physiological, cellular and metabolic. The responses are dependent upon the duration and severity of stress, the genotype of the stressed plant, the stage of development, and the organ and cell type in question (Bray, 1994). Multiple responses allow the plant to tolerate water stress. Some of these responses and the current status of knowledge with regard to cassava are discussed here.

Control of stomatal closure and leaf growth

A primary response to water stress is stomatal closure, which decreases photosynthetic CO_2 assimilation and, in turn, growth. Stomata have a high capacity to respond to changes in the water status of the plant and atmosphere. They close as the leaf water potential decreases and when the vapour pressure deficit between the leaf and the air increases (generally due to a decrease in relative humidity). As stomata are the route by which CO_2 enters the leaf, stress-induced decreases in stomatal aperture can limit the rate of CO_2 diffusion into the leaf and, therefore, the rate of photosynthesis.

When water is available, cassava maintains a high stomatal conductance and can keep internal CO_2 concentration high; but when water becomes limiting, the plant closes stomata in response to even small decreases in soil water potential (El-Sharkawy and Cock, 1984). The rapid closure of the stomata and the resulting decline in transpiration lessens the decrease in leaf water potential and soil water depletion, thereby protecting leaf tissues from desiccation (Ike, 1982; Palta, 1984; El-Sharkawy and Cock, 1984; Cock *et al.*, 1985). This response to early stages of soil water depletion has been described as isohydric, a behaviour shared by cowpeas, maize and several other crops (Tardieu and Simonneau, 1998). Leaf area growth is also decreased in response to water stress but is rapidly reversed following the release from stress (Connor *et al.*, 1981; Palta, 1984; El-Sharkawy and Cock, 1987b; Baker *et al.*, 1989). This response limits the development of plant transpirational surface area during water deficit and keeps sink demand well balanced with plant assimilatory capacity.

Leaf conductance to water vapour has been evaluated as an indicator of the capacity of different cassava genotypes to prevent water loss under prolonged drought. Considerable variation has been observed in leaf conductance (Porto *et al.*, 1988), and this parameter seems to be useful for pre-selecting sources of germplasm conferring adaptation to prolonged dry periods.

Abscisic acid accumulation

Many authors have reported that a substantial number of drought responses in plants can be mimicked by external application of abscisic acid (ABA) to well-watered plants (Davies *et al.*, 1986; Trewavas and Jones, 1991). This treatment promotes characteristic developmental changes that can help the plant cope with water deficit, including decrease of stomatal conductance (MacRobbie, 1991; Trejo *et al.*, 1993), restriction of shoot growth (Creelman *et al.*, 1990) and leaf area expansion (Van Volkenburgh and Davies, 1983; Lecoeur *et al.*, 1995) and stimulation of root extension (Sharp *et al.*, 1993, 1994; Griffiths *et al.*, 1997). All these effects of ABA application, together with the observation that environmental stress stimulates ABA biosynthesis and ABA release from sites of synthesis to action sites, suggest a role for ABA as a stress hormone in plants. Moreover, studies have indicated that for certain plant responses, sensitivity to water deficit is correlated with changes in ABA concentrations (Trejo *et al.*, 1995; Borel *et al.*, 1997) and genotypic responsiveness to ABA (Blum and Sinmena, 1995; Cellier *et al.*, 1998). Information about

ABA accumulation in cassava has not been reported in the literature.

Alves and Setter (2000) published the first report concerning ABA in cassava. They cultivated five cassava genotypes in pots in a greenhouse and evaluated the temporal patterns of ABA accumulation in mature leaves and in immature expanding leaves, during water deficit and after release from stress to determine the extent to which the stress and recovery response of leaf area growth is associated with the temporal pattern of ABA accumulation. At 3 and 6 days after withholding irrigation, all genotypes accumulated large amounts of ABA in both expanding and mature leaves, but these high ABA levels were almost completely reversed in respect of control levels after 1 day of rewatering (Fig. 5.7). Correspondingly, young leaves halted leaf expansion growth and transpiration rate decreased. Young leaves accumulated more ABA than mature leaves both in control and stressed treatments (Fig. 5.7). This rapid return to control ABA levels corresponded with a rapid recovery of leaf area growth rates. This rapid reduction in leaf area growth and stomatal closure may be due to cassava's ability to synthesize rapidly and accumulate ABA at an early phase of a water-deficit episode.

Osmotic adjustment

One means of increasing drought tolerance is by accumulation of osmotically active solutes, so that turgor and turgor-dependent processes may be maintained during episodes of drydown. Osmotic adjustment (OA), defined as the difference in osmotic potential between control and stressed plants, allows cell enlargement and plant growth at high water stress and allows stomata to remain partially open and CO_2 assimilation to continue at low water potentials that are otherwise inhibitory (Pugnaire *et al.*, 1994).

In cassava OA has not been thoroughly examined. Although leaf water potential remains relatively unchanged during water deficit episodes (Connor and Palta, 1981; Cock *et al.*, 1985; El-Sharkawy *et al.*, 1992a), a result suggestive of little or no OA, such observations do not rule it out. Furthermore, these studies involved mature leaves, not young organs, which might especially benefit from accumulation of osmolytes. Alves (1998) evaluated the role of OA in cassava by measuring the osmotic component of leaf water potential in mature, expanding and folded leaves. The largest increase in solutes caused by water deficit occurred in the youngest tissue (folded leaves)

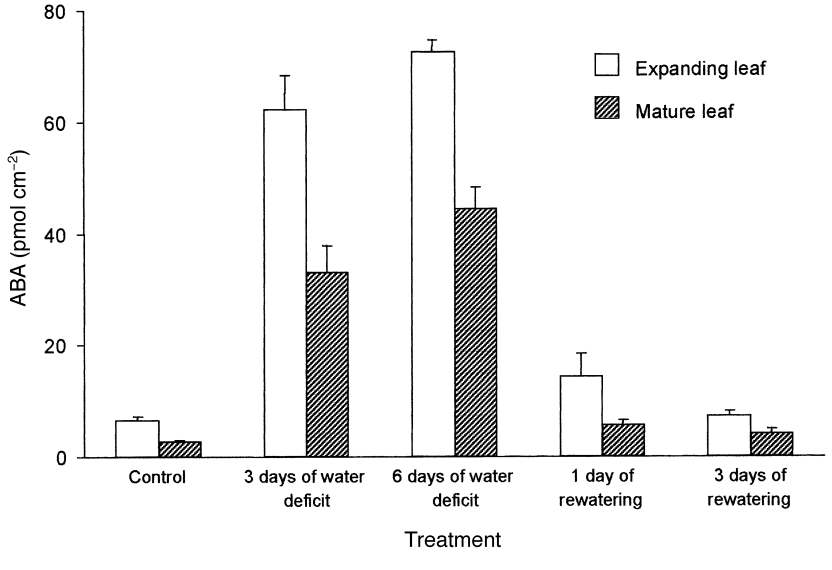

Fig. 5.7. Abscisic acid (ABA) concentration in expanding and mature cassava leaves in control after 3 and 6 days of water deficit, followed by 1 and 3 days of rewatering; average of five genotypes with three replicates; bars represent SEM (n = 15); data from Alves and Setter (2000).

and the extent of OA increased progressively from mature to folded leaves. As young tissues (meristems) are involved in regrowth and recovery after drought, further research is needed to give a fuller picture of cassava's responses to water deficit.

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