Chapter 2
Biology of the Papaya Plant

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Introduction

The papaya plant (*Carica papaya* L.) has been described with a large variety of adjectives, which acknowledge the structural and functional complexity and the high phenotypic plasticity of this giant tropical herb (León 1987). *C. papaya*, with a somatic chromosome number of 18, is the sole species of this genus of the Caricaceae, a family well represented in the Neotropics, that includes six genera with at least 35 species (Fisher 1980; Ming et al. 2008; Carvalho and Renner 2013). Most likely, papaya originated along the Caribbean coast of Mesoamerica (Fitch 2005) and spread to many tropical and subtropical regions around the world (Kim et al. 2002), where its distribution is limited by chilling sensitivity (Allan 2002; Dhekney et al. 2007). Domestication eventually led to substantial changes in vegetative growth and sexual forms that distinguish wild populations from cultivated genotypes (Paz and Vázquez-Yanes 1998; Niklas and Marler 2007). Because of its high yield, nutritional value, functional properties, and year-round fruit production, the importance of this crop around the world is undeniable.

The papaya plant is a semi-woody, latex-producing, usually single-stemmed, short-lived perennial herb. The relatively small genome of this species shows peculiarities in major gene groups involved in cell size and lignification, carbohydrate economy, photoperiodic responses, and secondary metabolites, which place the papaya in an intermediate position between herbs and trees (Ming et al. 2008). Reproductive precocity, high photosynthetic rates of short-lived leaves, fast growth,

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Fig. 2.1 Vegetative parts of the papaya plant. (**a**) Cross section of a 1-year-old papaya stem; periderm (pe), fiber sheath (fs), phloem (ph), cambium (c), xylem rays (xr), pith (p). (**b**) Leaf lamina and petiole. (**c**) Longitudinal section of a 3-month-old papaya stem showing hollow pith cavity. (**d**) Longitudinal section of a 1-year-old papaya stem showing complete pith cavity. (**e**) Stem of a 1-year-old papaya plant showing conspicuous petiole scars
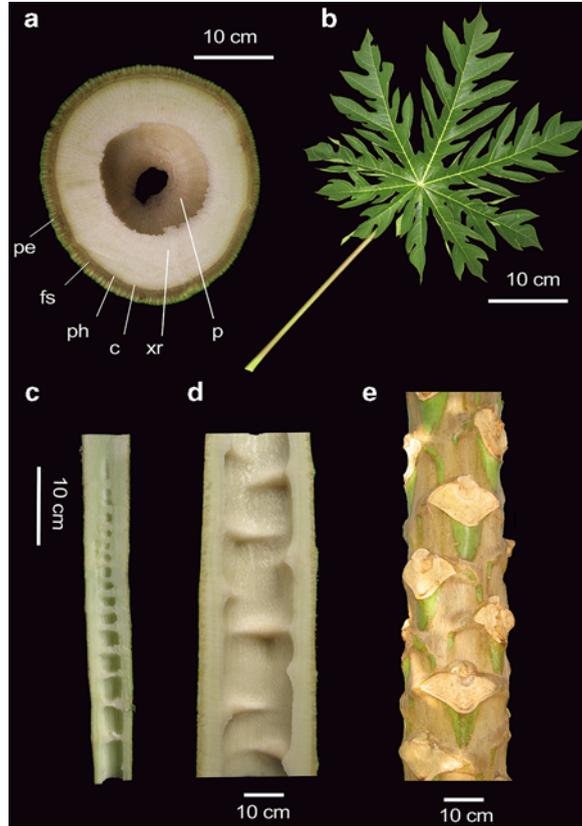

high reproductive output, production of many seeds, and low construction cost of hollow stems (Fig. 2.1a–d), petioles, and fruits characterize this successful tropical pioneer. High phenotypic plasticity allows this plant to establish in recently disturbed sites, thriving during early stages of tropical succession and as members of diverse agroecosystems as well (Hart 1980; Ewel 1986), that constitute important genetic reservoirs (Brown et al. 2012). At any given time, adult papaya plants can sustain vegetative growth, flowering, and dozens of fruits at different stages of development, simultaneously.

Morphology, Architecture, and Anatomy of the Adult Plant

Papaya is usually a single-stemmed, semi-woody giant herb with fast, indeterminate growth (1–3 m during the first year). The plants may attain up to 10 m, although under modern cultivation height seldom surpasses 5–6 m. Occasionally, vigorous vegetative growth may induce axillary bud break and branching at the lower portions of the plant, which rarely exceeds a few centimeters in length. Some branching may

Fig. 2.2 Types of papaya plants according to sex forms. (**a**) Female. (**b**) Hermaphroditic. (**c**) Male. (**d**) Male fruit-bearing plant
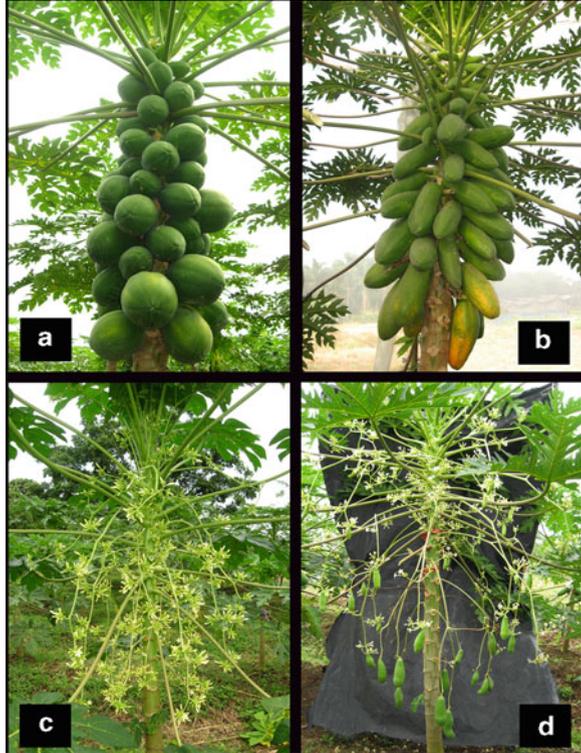
also occur if apical dominance is lost due to tip damage, and, in tall plants, "distance" may release the lower buds from the dominant effect of the apex (Morton 1987).

The plant produces large palmate leaves (~0.6 m^2), with five to nine pinnate lobes (Fig. 2.1b) of various widths (40–60 cm), arranged in a spiral pattern (Fig. 2.1e) and clustered in the upper section of adult individuals (Morton 1987; Ming et al. 2008). Leaf blades are dorsiventral and subtended by 30–105 cm long, hollow petioles that grow nearly horizontal, endowed with a starch-rich endodermis, perhaps important for cavitation repair (Bucci et al. 2003; Posse et al. 2009; Leal-Costa et al. 2010). The leaf epidermis and the palisade parenchyma are composed of a single cell layer, while the spongy mesophyll consists of four to six layers of tissue. Reflective grains and druses are abundant throughout the leaf (Fisher 1980). Papaya leaves are hypostomatic, with anomocytic (no subsidiary cells) or anisocytic (asymmetric guard cells) stomata (Carneiro and Cruz 2009; Leal-Costa et al. 2010). Stomatal density of sunlit leaves is approximately 400/mm^2, which can adjust readily to environmental conditions of light, water, and heat. Important biologically active compounds have been identified in papaya leaves (Canini et al. 2007; Zunjar et al. 2011), where they function in metabolism, defense, signaling, and protection from excess light, among others (El Moussaoui et al. 2001; Konno et al. 2004). Adult plants may have three possible sexual forms: female, male, and hermaphroditic (Figs. 2.2a–d and 2.3a–f).

Fig. 2.3 Papaya flowers with one petal removed to show internal parts (**a**–**c**) and inflorescences (**d**–**f**). (**a**) Staminate flower showing stamens (st), pistillode (pi) and corolla tube (ct). (**b**) Perfect flower showing st, ct, stigmata (sa), petal (p) and an elongated ovary (o). (**c**) Pistillate flowers showing sepals (sp), petals and round ovary (o). (**d**) Long male inflorescence with dozens of staminate flowers. (**e**) Andromonoecious cyme showing one dominant perfect (pf) and five secondary staminate flowers (sf). (**f**) Female cyme with three pistillate flowers
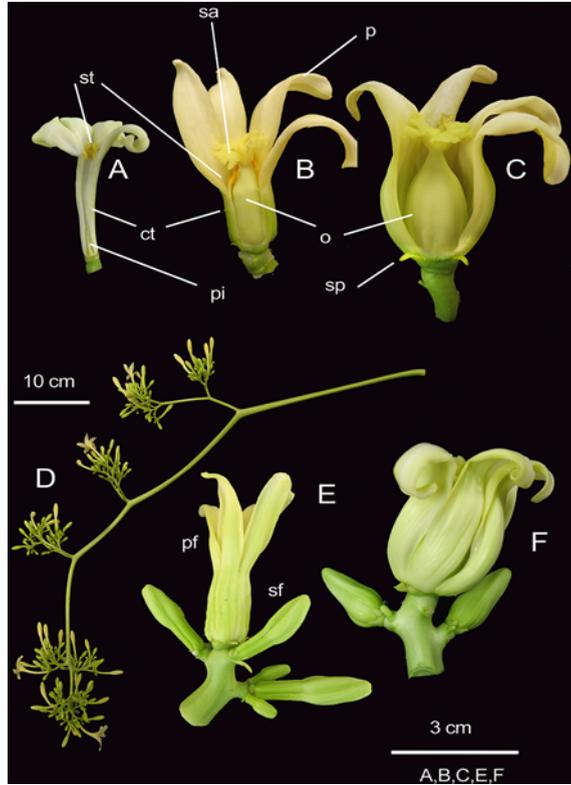
Plant Growth and Development

Under appropriate conditions of water availability, light, oxygen, air temperature, and humidity, papaya seeds undergo epigeal germination (Fig. 2.4a); emergence is typically completed in 2–3 weeks (Fisher 1980). Primary leaves of young seedlings are not lobed (Fig. 2.4b) but become so after the appearance of the second leaf (Fig. 2.4c). Papaya leaves of adult plants are simple, large, and palmate (Fig. 2.1b). In tropical conditions, approximately two leaves emerge at the apex of the plant in a 3/8 spiral phyllotaxy every week (Fisher 1980). Leaf life commonly spans for 3–6 months under tropical conditions and persistent scars remain on the trunk as they abscise (Fig. 2.1e). The loss of leaves on the lower section of the plant and the continuous emergence of new ones at the apex give the canopy a sort of umbrella shape that casts a considerable amount of shade.

The papaya plant develops very fast, taking 3–8 months from seed germination to flowering (juvenile phase) and 9–15 months for harvest (Paterson et al. 2008). The plant can live up to 20 years; however, due to excessive plant height and pathological constraints, the commercial life of a papaya orchard is normally 2–3 years.

Fig. 2.4 Papaya seedlings and root system. (**a**) Germinating papaya seed. (**b**) Ten-day-old papaya seedling showing cotyledonary leaves and first true leaves. (**c**) Three-week-old papaya seedling with six true leaves. (**d**) Side view of an excavated 5-month-old papaya root system, showing the main and secondary roots. (**e**) Upper view of the same root system, showing horizontal distribution of secondary roots
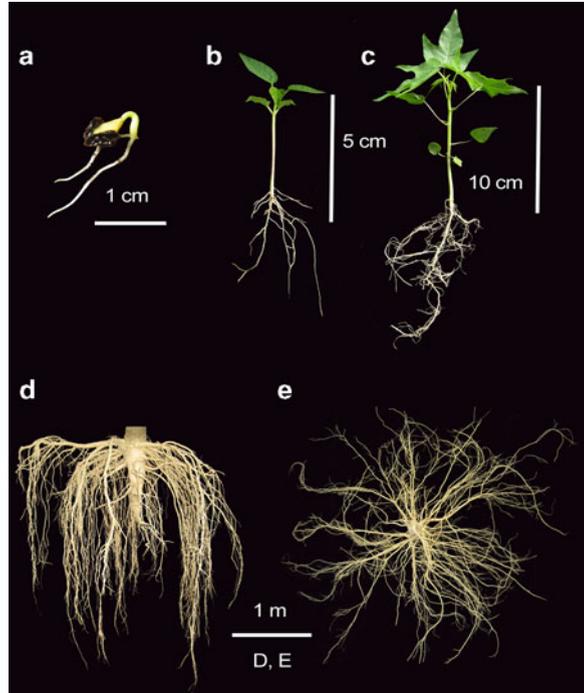
Although papayas are considered sun-loving plants, morphological plasticity in the shade is high and involves changes in many characteristics such as leaf mass per area, chlorophyll *a/b* ratio, stomatal density, internode length, and degree of blade lobing (Buisson and Lee 1993). This plasticity is evidenced by the morphology adopted by papayas growing in multistoried agroecosystems and in high-density orchards as well (Marler and Discekici 1997; Iyer and Kurian 2006).

Papaya seedlings and adults are very responsive to mechanical stimuli and show strong thigmomorphic responses or touch-regulated phenotypes (Fisher and Mueller 1983; Porter et al. 2009). These responses could be essential to the success of papaya in harsh, early successional sites exposed to high winds, because it triggers hardening mechanisms that result in compact architecture, increased lignification, and the formation of petiole cork outgrowths (Clemente and Marler 2001; Porter et al. 2009).

The Stem: Support and Transport Systems

In papaya plants, the single stem provides structural support, body mass, storage capacity, defense substances, height, and competitive ability, and carries a bidirectional flow of water, nutrients, various organic compounds, and chemical and physical signals that regulate root and shoot relations (Reis et al. 2006). Stem diameters of

adult plants vary from 10 to 30 cm at the base to 5–10 cm at the crown. Stem density is only 0.13 g cm^{-3}. The lower internodes are compact and wider and seem to mechanically support the entire weight of the plant (Morton 1987).

In papaya stems, a thick, single layer of secondary phloem, rich in fibers, and two sclerenchyma layers located immediately inside the bark are responsible for most of the rigidity (Fig. 2.1a). The xylem is poorly lignified and aids in storage of water and starch (Fisher 1980). A well-developed pith is conspicuous from early stages of development. Young stems become progressively hollow by the dissolution of the pith at the internodes as they mature (Fig. 2.1c, d) and as fibers thicken and harden (Carneiro and Cruz 2009). Along with stem thickening, the fibers of the outer collenchyma layer yield, leaving wide spaces later occupied by parenchyma and periderm, so that rigidity shifts to the inner layers, which widen to allow for stem expansion. In addition to buffering daily water balance, stem water storage may also be a major structural determinant of the mechanical stability of these succulent, tall herbaceous plants (Fisher 1980).

Fisher (1980) described the features of papaya vascular tissues summarized here. The xylem is composed of wide vessels that can be seen with the naked eye, imbibed in non-lignified parenchyma tissues and rays. Pits are alternate, bordered, or un-bordered, and perforation plates are simple and transverse. Phloem rays are wide, multiseriate, and tall. Sieve elements may be multistoried, and sieve plates are transverse and located on lateral walls. Recorded rates of xylem sap flow, source:sink ratios, and observations on the hydraulic architecture of papaya plants indicate that high water transport and phloem translocation capacity sustain the high rates of gas exchange and growth observed in the field. Phloem loading is probably symplastic, but because of the intermediate nature of this species, possible shifts in loading mechanisms in papaya plants growing along altitudinal gradients (ranging from 0 to 3,500 m above the sea level) should be examined.

Laticifer Conducts

Laticifers of papaya are complex tissue systems of the articulate-anastomosing type. In general, these conducts are multicellular columns with perforated transverse lateral walls, protoplast fusion, and intrusion of phloem cells, forming branched networks (Hagel et al. 2008). Damage to any aerial part of the papaya plant, where laticifers are widely distributed, elicits latex release, which is very typical for this species (Azarkan et al. 2003). This milky latex is a slightly acidic fluid composed of 80 % water (Rodrigues et al. 2009). It contains sugars, starch grains, minerals (S, Mg, Ca, K, P, Fe, Zn), alkaloids, isoprenoids, lipidic substances, and proteins, including enzymes like lipases, cellulases, and cysteine proteases (papain, chymopapain), important in defense against insect herbivores and in tissue and organ formation (pith differentiation) (Sheldrake 1969; El Moussaoui et al. 2001; Azarkan et al. 2003; Konno et al. 2004). In young fruits, laticifers develop near the vascular bundles and become septate through transverse walls that later dissolve, making these laticifers a series of

superposed fused cells. Young papaya fruits (>10 cm diameter) are tapped for papain by making long, straight cuts (Madrigal et al. 1980). Yields of crude papain are around 245 kg/ha the first year (Becker 1958).

Root System

Young roots show well-differentiated epidermis, cortex, and endodermis, enclosing an exarch vasculature in which six xylem and six phloem poles alternate. Cambium formation in a concentric ring triggers secondary growth and root thickening while maintaining succulence. The papaya root is predominately a non-axial, fibrous system, composed of one or two 0.5–1.0 m long tap roots. Secondary roots emerge from the upper sections and branch profusely (Fig. 2.4d, e). These second-order feeding roots remain shallow during the entire life of the plant and show considerable gravitropic plasticity. Many adventitious, lower-order categories of thick and fine roots are also observed in excavated specimens. Healthy roots are of a whitish cream color, and no laticifers have been observed in them (Marler and Discekici 1997; Carneiro and Cruz 2009).

Root phenotypic plasticity is also high. Root size, number, distribution, and orientation adjust readily across the soil profile, to various soil conditions, and throughout the life of the plant, making papayas preferred components of complex agroecological models and hillside vegetation (Fisher and Mueller 1983; Marler and Discekici 1997).

Papaya plants are dependent on mycorrhizas for their nutrition and benefit greatly from soil mulching and appropriate drainage that facilitate biotic interactions in the rhizosphere and water and nutrient uptake, especially phosphorus and nitrogen. Four to five genera and 11 species of arbuscular mycorrhizal fungi have been reported associated with papaya roots: *Glomus*, *Acaulospora*, and *Gigaspora*, among others (Walsh and Ragupathy 2007; Khade et al. 2010). Mycorrhizal interactions of male and female papaya plants may differ: females seem more responsive to changes in soil fertility and readily adjust mycorrhizal colonization accordingly (Vega-Frutis and Guevara 2009).

Sex Expression

Papaya has three sex forms (female, male, and hermaphrodite), regulated by an incipient X–Y chromosome system. Papayas can be either dioecious (with male and female plants) or gynodioecious (with hermaphrodite and female plants). Several studies suggest that the Y chromosome contains a small specific region that controls expression of male (Y) or hermaphrodite (Y[h]) types. Female plants are of the XX form. All combinations among the Y and/or Y[h] chromosomes are lethal; therefore, the male and hermaphrodite types are heterozygous (XY and XY[h], respectively) (Ming et al. 2007).

Flowers

Papaya flowers are produced profusely near the trunk apex and open between 7 and 9 a.m. Individual flower longevity may be of 3–4 days, but the actual period of pistil receptivity is unknown. Papaya flowers are actinomorphic cymes arranged in inflorescences on the leaf-stem junction. Cymes of hermaphroditic and female plants can bear a variable number of flowers (2 to 15) (Fig. 2.3e, f). Male plants produce very long inflorescences that contain dozens or even hundreds of flowers (Fig. 2.3d). Although papaya flowers are visited by hawkmoths, several beetles, skipper butterflies, bees, flies, and hummingbirds, among others, probably attracted by the sweet fragrance and the copious nectar they produce (the latter only in male and hermaphroditic flowers) (Ronse Decraene and Smets 1999), recent evidence suggests that hawkmoths are responsible for most of the pollen exchange (Martins and Johnson 2009; Brown et al. 2012). Wind pollination has also been cited (Sritakae et al. 2011). The time from pollination to first ovule penetration was 25 h at 28 °C (Cohen et al. 1989).

Hermaphroditic Flowers

The perfect flower of papaya, also referred to as the elongate type, consists of five petals, five pairs of anthers, and an ovary (Fig. 2.3b). The petals are fused on the lower part of the flower (connate), to the point where the stamens are inserted, forming the corolla tube. The upper parts of the petals are free and slightly twisted. The ovary is superior, elongated, and composed of five carpels. Each pistil has five broad and flattened stigmata joined at their base, which may bend slightly backwards when the flowers open. There are five pairs of anthers, inserted into two whorls (diplostemonous androecium), but each member of a pair belongs to a different whorl. Stamens belonging to the antesepalous have longer filaments than those in the antepetalous whorl (Ronse Decraene and Smets 1999).

Although the term hermaphrodite has been used to refer to papaya plants that bear perfect flowers, the correct term should be andromonoecy, which indicates the occurrence of staminate and hermaphroditic flowers on the same plant. Typically, the small inflorescences of hermaphroditic papaya plants bear one or two main perfect flowers and a few secondary female sterile (staminate) and intermediate type flowers (Fig. 2.3e). The ratio of perfect to staminate flowers within an inflorescence may vary greatly due to the effects of genetic and environmental factors and may range from totally perfect to totally sterile. Female sterility in andromonoecious papayas is often expressed progressively, leading to reductions in ovary size, carpel number, and associated tissues and ultimately may lead to completely staminate flowers which contain only a pistillode (Fig. 2.5a–d) (Nakasone and Lamoureux 1982).

When hermaphrodite papaya plants are subjected to stresses such as high temperatures and water and nitrogen shortages, female sterility is exacerbated (Awada and Ikeda 1957; Arkle and Nakasone 1984; Almeida et al. 2003). This may even affect the main flowers, leading in some cases to totally infertile (staminate) and

Fig. 2.5 Female sterility and carpellody of papaya. (**a–d**) Gradual reduction in pistil size due to female sterility of flowers and approximate phenotype of the corresponding fruit. (**a**) Normal elongata flower with five carpels. (**b, c**). Reduced ovary due to loss of carpels as a result of partial female sterility. (**d**) Completely female sterile flower. (**e, f**) Increasing levels of carpellody and approximate phenotype of corresponding fruit. (**e**) Normal elongata flower. (**f–g**) Fusion to the ovary and partial transformation to carpels and of one (**f**) and two (**g**) stamens, leading to misshapen fruits. (**h**) Complete transformation of the five antepetalous whorl of stamens into carpels, leading to the "pentadria" type of flower, with a rounded ovary (and fruit) and almost free petals
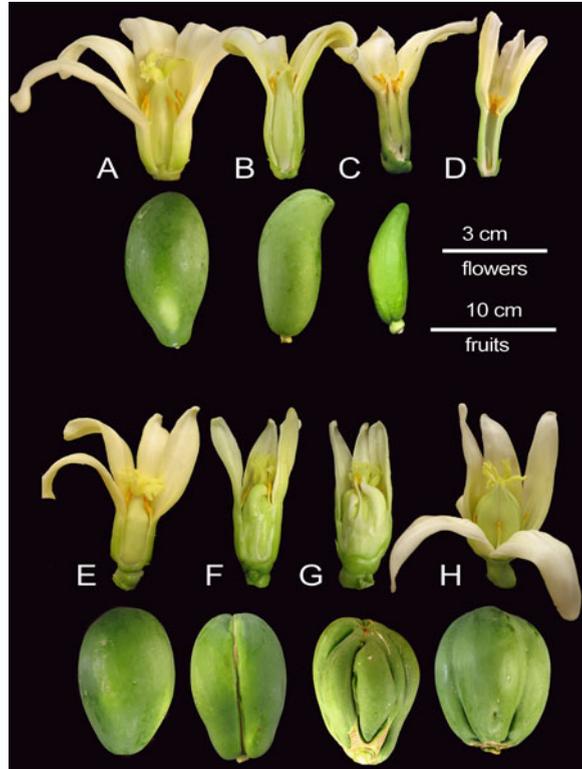
unproductive inflorescences. Perfect papaya flowers may also undergo variable degrees of fusion between their stamens and the ovary (carpellody; Fig. 2.5f, g) (Ronse Decraene and Smets 1999). In severe cases, the five antepetalous stamens are completely transformed into carpels, and the resulting flower resembles a female one, with a rounded ovary and free petals almost all along their length. This type of flower is also known as the "pentadria type" (Fig. 2.5h). Intermediate carpellodic states are also common, in which only some of the stamens are completely or partially fused with the ovary, resulting in the development of misshapen fruits (Figs. 2.5f, g and 2.6c). Although the tendency to produce carpellodic flowers has a strong genetic component (Storey 1953; Ramos et al. 2011), low temperatures, high soil moisture, and high nitrogen seem to favor this condition (Awada 1953, 1958; Awada and Ikeda 1957; da Silva et al. 2007).

Female Flowers

Female papaya flowers have five free petals and a rounded superior ovary (Fig. 2.3c) (Ronse Decraene and Smets 1999) that is five carpellate and hollow and exhibits

Fig. 2.6 Papaya fruits according to sex type. (**a**) Fruit of a hermaphroditic plant. (**b**) Fruit from a female plant. (**c**) Misshapen fruit from a hermaphroditic plant due to carpellody
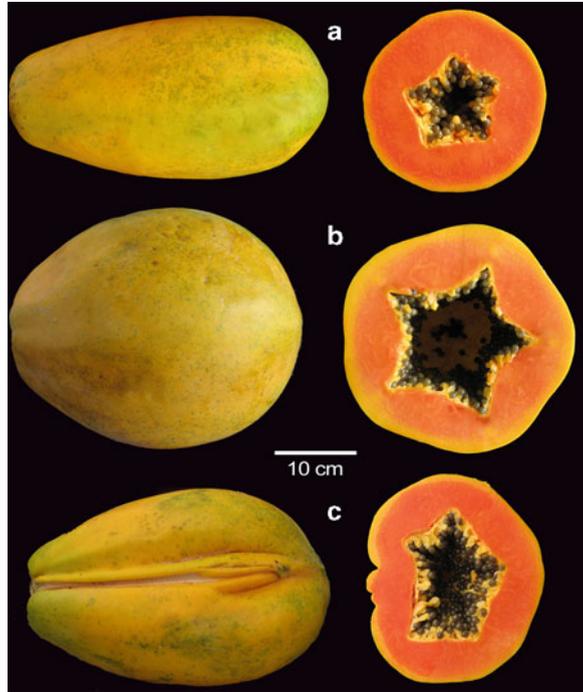
parietal placentation (Fisher 1980). In contrast to the hermaphroditic plants, females are completely stable and their flowers do not appear to undergo sex reversal due to environmental fluctuations.

Male Flowers

Stamen arrangement in the male flowers is the same as in the hermaphrodite flower, surrounding a rudimentary pistil or pistillode (Fig. 2.3a). In some cases, due to genetic or environmental causes, some of the dominant flowers within the inflorescence may have fully developed pistils, resulting in a hermaphroditic flower and an overall male, fruit-bearing phenotype (Fig. 2.2d) (Storey 1953).

Fruits

The papaya fruit has been studied extensively (Roth and Clausnitzer 1972; Roth 1977). Papaya fruits are berries and show high diversity in size and shape. Fruits from hermaphroditic plants tend to be elongated and vary from cylindrical to pear shaped, while fruits of female plants tend to be round (Fig. 2.6a, b). Fruit size can

vary extensively, ranging from less than 100 g in some wild accessions to over 10 kg in certain landraces. The pericarp may become 2.5–3.0 cm thick in ripe fruits. A large cavity that hosts the seeds makes up most of the fruit volume. The ripe fruit is built mostly of parenchymatous tissue organized in three distinct layers: the outer layer is composed of smaller, plastid-rich cells; the median zone is composed of larger round cells, rich in intercellular spaces; and the inner region is a spongy parenchyma with stretched, branched cells and abundant air spaces. Two sets of five vascular bundles each enter the fruits, one dorsal (outer) and another ventral inner rings (Roth 1977).

The contribution of fruit photosynthesis to carbon gain is probably small, and significant only during early stages of growth, when the surface:volume ratio of young green fruits is high; in addition, the fruits develop in the shade under the dense papaya canopy, which also limits photosynthesis. Fruit photosynthesis could be more important in refixing respiratory CO_2 released in the fruit interior. Fruit development takes approximately 5 months to maturity.

Papaya fruit ripening is climacteric, and high ethylene production may start only hours after harvest at the recommended stage (appearance of one to two yellow stripes on the fruit). As they ripen, papaya fruits change color, firmness, carbohydrate composition, and production of secondary compounds, which are responsible for fruit color and fragrance. The color of ripe fruits may vary from yellow to salmon red. The most important carotenoids are lycopene and β-cryptoxanthin (Schweiggert et al. 2011a, b), and a rich list of more than 150 volatile esters and alcohols are responsible for the sweet aroma and flavor of the fruit (Pino et al. 2003).

Papaya fruits are sensitive to chilling injury, and storage temperatures below 10 °C can cause fruit shriveling, skin pitting, localized necrosis, softening, electrolyte leakage, and postharvest disease outbreaks (Chen and Paull 1986). Treating the fruits with hot water may reduce their sensibility to chilling damage (Paull and Jung Chen 2000), perhaps by inducing the production of plant stress and heat-shock proteins (McCollum et al. 1993). Other important physiological disorders of papaya fruits are bruising ("skin freckles") and translucent and lumpy pulp (Oliveira and Vitória 2011).

Seeds

Well-pollinated fruits can have 600 black seeds or more (Fig. 2.6a–c). The embryo is straight and ovoid, with flattened cotyledons (Fisher 1980). The seeds are coated by a mucilaginous mass derived from the pluristratified epidermis of the outer integument (Roth 1977). The embryo is enclosed in a gelatinous sarcotesta at physiological maturity. A compact mesotesta and outer and inner integuments can be observed underneath. The endosperm is composed of thin-walled cells with abundant oil bodies and aleurone grains, lacking starch at maturity (Fisher 1980; Teixeira da Silva et al. 2007). Photosensitive seeds of wild papayas are dormant at maturity, and their germination may be triggered by changes in light quality during forest gap formation (Paz and Vázquez-Yanes 1998).

Photosynthetic Carbon Gain, Water Use, and Source: Sink Relations

Papaya plants exhibit C_3 photosynthesis (Campostrini and Glenn 2007). Optimum temperature for growth is 21–33 °C, under which papayas can produce 2 leaves/week and 8–16 fruits/month. Temperatures below 10 °C are not well tolerated (Allan 2002, 2005). Light compensation point for leaf-level photosynthesis is ca. 35 μmol m^{-2} s^{-1}, and saturation is reached at ca. 2,000 μmol m^{-2} s^{-1} of photosynthetic photon flux density (PPFD) (Campostrini and Glenn 2007). High photosynthetic rates of 25–30 μmol CO_2 m^{-2} s^{-1} alternate with pronounced (midday) gas exchange depressions, apparently caused by direct stomatal and cuticular responses to air humidity (El-Sharkawy et al. 1985; Marler and Discekici 1997; Marler and Mickelbart 1998). This process may reduce productivity by 35–50 % (Campostrini and Glenn 2007).

A further reduction of 25–30 % in net efficiency of carbon assimilation can be caused by photorespiration, which could be ameliorated with improved water availability and PPFD conditions. The reduction observed in photosynthesis at high PPFD could also be a consequence of a decrease in stomatal conductance caused by the direct action of radiant energy on leaf heating. Chronic photo-inhibition through damage and replacement of the D1 protein in the reaction center of PSII also reduces photosynthesis at high PPFD levels (Reis et al. 2006; Campostrini and Glenn 2007). Another important factor in carbon balance is the cost of growth and maintenance respiration. Whole papaya plants growing in a greenhouse respired from 400 μL O_2 g^{-1} h^{-1}, about one third of daily carbon fixation, at 25 °C, to 1,600 μL O_2 g^{-1} h^{-1} when the plants were exposed to very high temperatures (50 °C) (Todaria 1986).

In contrast to other tropical fruits (like bananas), papayas do not store starch, and continuous flowering and fruiting requires a steady carbon flow from the leaves. Sugar accumulation is controlled by three key enzymes. Sugar content increases slowly during the first two thirds of fruit development, under sucrose synthetase regulation, and later increases substantially during ripening, controlled by apoplastic invertases. The third enzyme, sucrose-phosphate synthase, remains low but active throughout the whole course of fruit development (Zhou et al. 2000; Zhou and Paull 2001).

Maximum rates of sap flow in the xylem are close to 0.6–0.8 L H_2O m^{-2} h^{-1}, and transpiration rates are about 25 mmol H_2O m^{-2} s^{-1} (Reis et al. 2006). In general, 1 m^2 of leaves transpires 1 L H_2O daily but can rise substantially with increasing evaporative demands. A papaya plant with 35 leaves, equivalent to approximately 3.5–4 m^2 leaf area, can fix ca. 70 g of CO_2 and transpire ca. 10 L of water daily (Coelho Filho et al. 2007). For well-watered papaya plants, the crop irrigation coefficient (Kc) is close to unity but may reach values of 1.2, as a consequence of the strong dependence of canopy gas exchange, photosynthesis, and water use, on the solar radiation available (Campostrini and Glenn 2007; Coelho Filho et al. 2007).

Responses to water stress include dehydration postponement through strict stomatal regulation, cavitation repair, and intense osmotic adjustment (Marler and Mickelbart 1998; Marler 2000; Mahouachi et al. 2006). The succulent roots do not tolerate

excess water, and 2 days with hypoxia cause chlorosis, leaf shedding, and even death after 3–4 days with oxygen deprivation (Campostrini and Glenn 2007).

In modern cultivars, one papaya leaf can sustain the development of three to four fruits. However, there are indications of poor adjustment capacity of source:sink ratios in fruiting papaya plants, presumably because the fruits have low capacity to attract assimilates (Acosta et al. 1999; Zhou et al. 2000). This is important because in most crops, biomass allocation to the harvested organ is the yield component most susceptible to selection and breeding (Bugbee and Monje 1992).

Nutrient Economy

The nutritional requirements of papaya plants are high. Mineral nutrients are taken up by plants grown at full sunlight as follows: $K>N>Ca>P>S>Mg$ (for macronutrients) and $Cl>Fe>Mn>Zn>B>Cu>Mo$ (for micronutrients). Nitrogen, phosphorus, and potassium, very important in metabolism and frequently limiting in tropical soils, are extracted in high amounts: a ton of fresh harvested fruits contains 1,770, 200, and 2,120 g of each of these nutrients, respectively. High-density plantings may extract 110, 10, and 103 kg of N, P, and K per ha, respectively; however, this can be much higher, depending on yield. The fruits represent 20–30 % of the nutrients removed. Thus, the development of healthy rhizosphere and mycorrhizal associations should sustain locally tight biogeochemical cycles and guide the formulation of fertilizers and amendments to deal with multiple soil stresses in tropical environments, such as shallowness, compaction, poor aeration, mineral deficiencies, and nutrient imbalances (Villachica and Raven 1986; Arango-Wiesner 1999).

Conclusions

Papaya plants are superb vegetables. Their morphological and ecophysiological attributes are as impressive as the highly efficient mechanisms of resource capture, transport, and utilization that support them. High photosynthetic rates, carbon gain, reproductive output, and growth and plasticity occur at the expense of high rates of water use and mineral nutrient demand. Phenotypic plasticity is high at the shoot, root, and reproductive levels. All of these attributes have implications in the design of sustainable cropping systems for papaya. To achieve this, it is convenient to conduct interdisciplinary integration constructed around the whole plant, at various scales of observation (cells and tissues, organs, whole plants, and orchards), and along the soil–plant–atmosphere continuum. The papaya plant may also constitute a model for ecophysiological studies, linking the genomics of short-lived perennials, through studies of growth, metabolism, sex expression, and longevity, to population ecology and evolutionary questions.

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