Plant Genetics and Genomics: Crops and Models 10

Ray Ming
Paul H. Moore *Editors*

Genetics and Genomics of Papaya

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Ray Ming • Paul H. Moore
Editors

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Editors
Ray Ming, PhD
Department of Plant Biology
University of Illinois at Urbana-Champaign
Urbana, IL, USA

Paul H. Moore, BA, MS, PhD
Hawaii Agriculture Research Center
Kaneohe, HI, USA

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We dedicate this book to all the teachers, mentors, and colleagues who instilled in each of us the thrill of scientific discovery. This thrill has helped us strive to understand the natural world around us while constantly reminding us how clever nature has been in solving complex biological problems.

Preface

At first glance, papaya might seem an unlikely crop for inclusion in the Springer Series on Plant Genomics. Although papaya has long been widely grown and consumed in the tropical world and its popularity as a mainstream fruit crop has grown in recent years, much of the temperate world still regards papaya as a relatively exotic and obscure food. On the other hand, papaya has the distinction of being the fifth angiosperm genome to be sequenced and the first transgenic crop to be characterized at the whole genome level. Why and how has papaya achieved these scientific milestones? This book reveals that story, which begins with a virus disease for which there was no natural resistance.

In the early 1990s, the Hawaiian papaya industry was threatened with collapse when the crop was found to be heavily infected by papaya ringspot virus (PRSV), for which the crop has no resistance. In one of the most widely publicized success stories of genetically modified crops (see Chap. 7 of this book), papaya was transformed and the Hawaiian industry was saved. Transgenic papaya became a kind of poster child for the safety and efficacy of genetic transformation of a consumed fruit. That popularity, in addition to several other qualities, led to papaya becoming a focus for genomic research. Included among those other qualities are its nutritional value (one fruit provides 122 % of the U.S. Recommended Daily Allowance for vitamin A and 314 % for vitamin C); its medicinal applications (including recent findings of its potential in cancer treatment); and its small genome of 372 Mb. In the course of genetic research, it was also discovered that papaya has nascent sex chromosomes that make it a model for studying sex chromosome evolution in flowering plants. In short, this relatively obscure plant is far more interesting and scientifically valuable than anyone might have guessed.

This book is intended to provide the most up-to-date knowledge of papaya genetics and genomics. We hope it will stimulate current and future researchers to explore papaya's fundamental biology and its nutritional and medicinal properties for further improvement of this undervalued crop.

We thank Richard Jorgenson for envisioning this book and Liz Corra and Hannah Smith for their assistance.

Urbana, IL, USA Ray Ming
Kaneohe, HI, USA Paul H. Moore

Contents

Contributors

Rishi Aryal Department of Plant Biology, University of Illinois at Urbana-Champaign, Urbana, IL, USA

Anjanabha Bhattacharya Bench Bio Pvt Ltd, Vapi, Gujarat, India

Fernanda Antunes Carvalho Department of Systematic Botany and Mycology, University of Munich, Munich, Germany

Manash Chatterjee Bench Bio Pvt Ltd, Vapi, Gujarat, India

Nancy J. Chen Department of Tropical Plant and Soil Science, University of Hawaii at Manoa, Honolulu, HI, USA

David A. Christopher Department of Molecular Bioscience and Bioengineering, University of Hawaii at Manoa, Honolulu, HI, USA

Geo Coppens d'Eeckenbrugge Centre de Coopération Internationale en Recherche Agronomique pour le Développement, UMR 5175 CEFE, Montpellier, France

Rod Drew School of Biomolecular and Physical Sciences, Griffith University, Nathan, QLD, Australia

O.P. Dutta Department of Research and Development, Namdhari Seeds Pvt Ltd, Bangalore, Karnataka, India

Rebecca Ford Department of Agriculture and Food Systems, Melbourne School of Land and Environment, Melbourne, VIC, Australia

Gabriela Fuentes Unidad de Biotecnología, Centro de Investigación Científica de Yucatán AC (CICY), Colonia Chuburná de Hidalgo, Mérida, México

Dennis Gonsalves US Department of Agriculture, Agricultural Research Service, Pacific Basin Agricultural Research Center, Hilo, HI, USA

Marco V. Gutiérrez-Soto Estación Experimental Agrícola Fabio Baudrit Moreno, Universidad de Costa Rica, Alajuela, Costa Rica

Jennifer Han Department of Plant Biology, University of Illinois at Urbana Champaign, Urbana, IL, USA

Jiming Jiang Department of Horticulture, University of Wisconsin-Madison, Madison, WI, USA

Victor M. Jiménez CIGRAS, Universidad de Costa Rica, San Pedro, Costa Rica
Food Security Center, University of Hohenheim, Stuttgart, Germany

Chutchamas Kanchana-udomkan School of Biomolecular and Physical Sciences, Griffith University, Nathan, QLD, Australia

P.K. Anish Kumar Bench Bio Pvt Ltd, Vapi, Gujarat, India

Tina Kyndt Department of Molecular Biotechnology, Ghent University, Ghent, Belgium

Eric Lyons School of Plant Sciences, University of Arizona, Bio5 Institute, Tucson, AZ, USA

Richard Manshardt Department of Tropical Plant and Soil Sciences, University of Hawaii at Manoa, Honolulu, HI, USA

Ray Ming Department of Plant Biology, University of Illinois at Urbana-Champaign, Urbana, IL, USA

Paul H. Moore Hawaii Agriculture Research Center, Texas AgriLife Research, Kaneohe, HI, USA

Jong-Kuk Na Department of Agricultural Bio-Resources, National Academy of Agricultural Science, RDA, Suwon, Republic of Korea

Niranjan Nagarajan Department of Computational and Systems Biology, Genome Institute of Singapore, Singapore

Rafael Navajas-Pérez Facultad de Ciencias, Departamento de Genética, Universidad de Granada, Granada, Spain

Eric Mora-Newcomer Estación Experimental Agrícola Fabio Baudrit Moreno, Universidad de Costa Rica, Alajuela, Costa Rica

Timothy J. O'Hare QAAFI, Centre for Nutrition and Food Sciences, University of Queensland, Gatton, QLD, Australia

Robert E. Paull Department of Tropical Plant and Soil Sciences, University of Hawaii at Manoa, Honolulu, HI, USA

Brad W. Porter Department of Molecular Biosciences and Bioengineering, University of Hawaii at Manoa, Honolulu, HI, USA

Susanne S. Renner Department of Systematic Botany and Mycology, University of Munich, Munich, Germany

Jorge M. Santamaría Unidad de Biotecnología, Centro de Investigación Científica de Yucatán AC (CICY), Colonia Chuburná de Hidalgo, Mérida, Mexico

Xavier Scheldeman Regional Office for the Americas, Bioversity International, Cali, Colombia

Haibao Tang Center for Plant Genomics and Biotechnology, Fujian Agriculture and Forestry University, Fuzhou, China

Savarni Tripathi US Pacific Basin Agricultural Research Center, US Department of Agriculture, Hilo, HI, USA

Robert VanBuren Department of Plant Biology, University of Illinois at Urbana-Champaign, Urbana, IL, USA

Marisa M. Wall US Pacific Basin Agricultural Research Center, US Department of Agriculture, Hilo, HI, USA

Jianping Wang Department of Agronomy, Genetics Institute, Plant Molecular and Cellular Biology Program, University of Florida, Gainesville, FL, USA

David J. Williams Agri-Science Queensland, Department of Agriculture, Fisheries and Forestry, Brisbane, Australia

Pingfang Wu Department of Tropical Plant and Soil Sciences, University of Hawaii at Manoa, Honolulu, HI, USA

Qingyi Yu Texas A&M AgriLife Research Center at Dallas, Texas A&M University System, Dallas, TX, USA

Wenli Zhang Department of Horticulture, University of Wisconsin-Madison, Madison, WI, USA

Yun J. Zhu Hawaii Agriculture Research Center, Kunia, HI, USA

Part I
Natural History and Genetic Diversity

Chapter 1
Papaya (*Carica papaya* L.): Origin, Domestication, and Production

Gabriela Fuentes and Jorge M. Santamaría

Papaya Origin

Given that no direct archeological evidence is available, it is rather difficult to define a precise origin for *C. papaya* L. We will revise in this chapter a series of indirect pieces of evidences that might support the idea that *C. papaya* L. has its origins in South Mexico and/or in Central America. We will discuss a geobotanical approach and certain evidence based on the current existence of wild populations in southern Mexico and Central America. Studies based on molecular markers will be discussed in other chapters (Chap. 5 in this volume) of this book.

It is difficult to know the precise origin of *Carica papaya* L. because nowadays, given its wide distribution by the Spaniards and its great capacity of adaptation to the conditions of subtropical and tropical environments, it is widely distributed around most of the subtropical and tropical regions of the world. However, Vavilov (1987) described three centers of origin of the majority of the species: the Mesopotamic center, the Mesoamerican Center, and the North Chinese center. The Mesoamerican Center is the center of origin of important tropical crops, and it has been suggested as being a good candidate to also be the center of origin of *C. papaya* L. (Harlan 1971).

C. papaya L., described by von Linnaeus (1753), belongs to the Caricaceae family that is formed by 6 genera and 35 species. The genera belonging to this family are Carica (1 specie), Jarilla (3 species), Horovitzia (1 specie), Jacaratia (7 species), Vasconcellea (21 species), and Cylicomorpha (2 species), according to Badillo (1971, 1993, 2000). Except for the latter genus, all the other five genera of this family have an American origin (Scheldeman et al. 2011). Some authors had suggested that *C. papaya* L. originated in the north of South America (Badillo 1971; Prance 1984).

G. Fuentes • J.M. Santamaría (✉)
Unidad de Biotecnología, Centro de Investigación Científica de Yucatán AC (CICY), Calle 43 No. 130, Colonia Chuburná de Hidalgo, Mérida 97200, México
e-mail: jorgesm@cicy.mx

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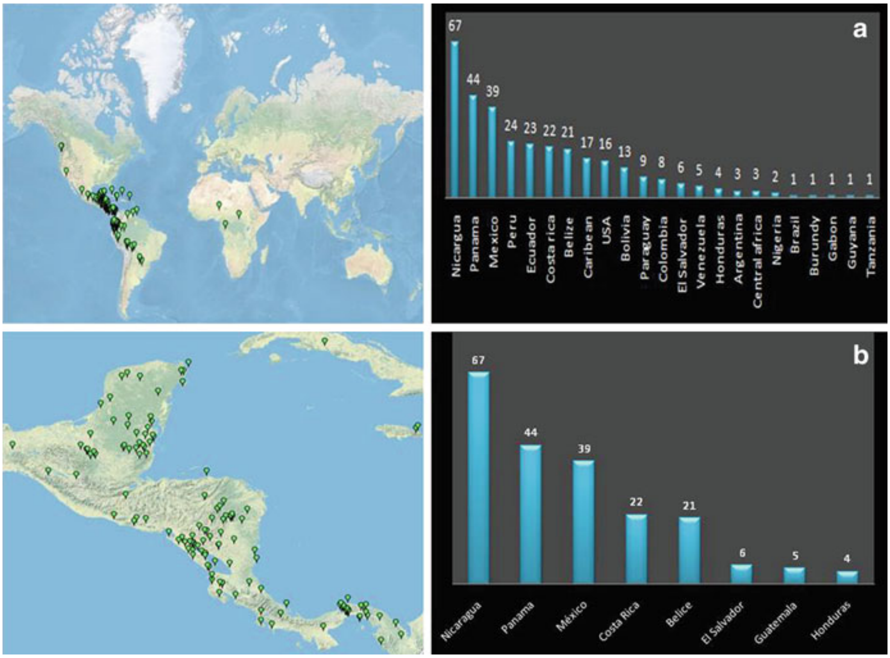

Fig. 1.1 Map distribution of records from Herbarium specimens of *Carica papaya* L. from the Missouri Botanic Gardens Herbarium database (2011). (**a**) Shows worldwide records (339 specimens) and (**b**) shows records from specimens collected at Central America (particularly Nicaragua) and the South of Mexico (208 specimens), representing 61 % of all the *C. papaya* L. records reported in the database (http//www.tropicos.org)

However, while this seems true for other members of the family Caricaceae (i.e., Vasconcellea), it is increasingly accepted that *C. papaya* L. had its origins in the south of Mexico and Central America. For instance, as early as 1833, De Candolle (1883) and Solms-Laubach (1889) suggested that *C. papaya* L. originated in Mexico. Besides, two other genera of the *Caricaceae* family are considered endemic to Mexico: *Horovitzia*, which is considered endemic to Mexico (Lorence and Colin 1988; Badillo 1993), and *Jarilla*, which is reported as endemic from Mexico and Guatemala (McVaugh 2001).

Taking records of *C. papaya* L. specimens from herbarium collections from around the world, it is interesting that most of the herbarium specimens had been collected in Central America and/or the south of Mexico. For instance, the collection of the Missouri Botanic Gardens Herbarium (2011) had 339 specimens of *C. papaya* L. from various parts of the world (Fig. 1.1a); however, more than 60 % of those specimens (208) were collected in Mexico and Central America (particularly in Nicaragua) (Fig. 1.1b). Moreover, in a more extensive collection at the Global Biodiversity Facility (GBIF) (2011), a total of 1297 specimens of *C. papaya* L. are reported (Fig. 1.2a), and again, more than 50 % of them (659) are occurrences from Central America and the south of Mexico (Fig. 1.2b).

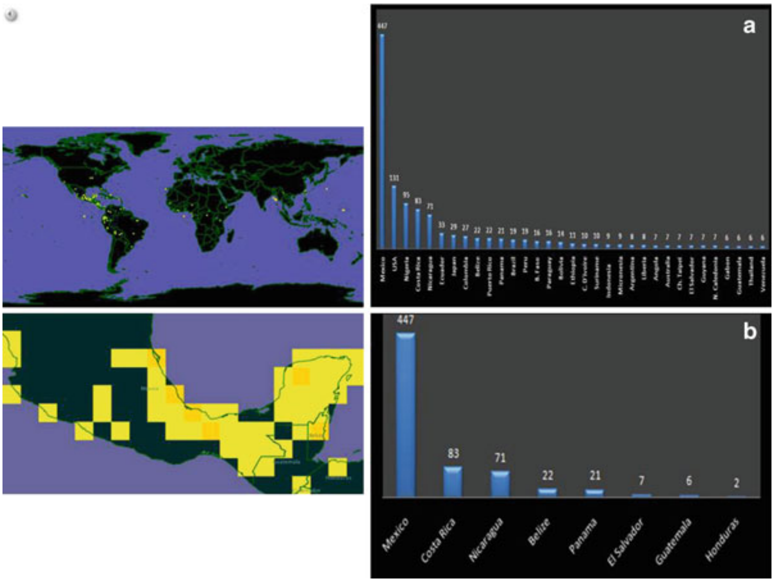

Fig. 1.2 Map distribution of occurrences (1297; *yellow dots*) recorded from around the world for *C. papaya* L., according to the Global Biodiversity Information Facility (GBIF) (**a**). The high concentration of records in the south of Mexico and Central America (659) represents 51 % of all the *Carica papaya* L. records reported in the database (**b**). GBIF data portal: data.gbif.org

Another piece of evidence that *C. papaya* L. may have had a Mesoamerican origin is the fact that it is still possible at present to find natural wild populations of this specie in isolated sites at the south of Mexico and in Central America. For instance, Manshardt and Zee (1994) found wild papayas in the Caribbean coastal lowlands of southern Mexico and northern Honduras. On the other hand, the Yucatan Scientific Research Center (CICY, México) has had an active program of collections from the flora of the Yucatan peninsula (México), including the States of Quintana Roo, Yucatán, and Campeche. From 1978 to 2003, the CICY Botanical Garden Herbarium had collected 58 geo-referenced specimens corresponding to *C. papaya* L. wild populations around the Yucatan Peninsula (Fig. 1.3a).

More recently, various *C. papaya* L. wild populations have been detected by our group in nonpopulated, isolated sites in the south of the Yucatan State (Fig. 1.3b–i). The plants from this living wild population found in the south of the Yucatán State differ greatly from the papaya plants from commercial plantations grown mostly in the northern part of the State. In Yucatán, as in most of the papaya growing areas in Mexico, the predominant commercial cultivar is Maradol (imported from Cuba), which has very distinctive morphological features when compared to those of the native wild population. Morphometric measurements have been taken of these plants from these wild populations, and they were compared with plants from commercial plantations of papaya, cultivar Maradol, grown in the north of Yucatan. Fruit length, width, and fresh weight from fruits from 5 plants from each of the 20

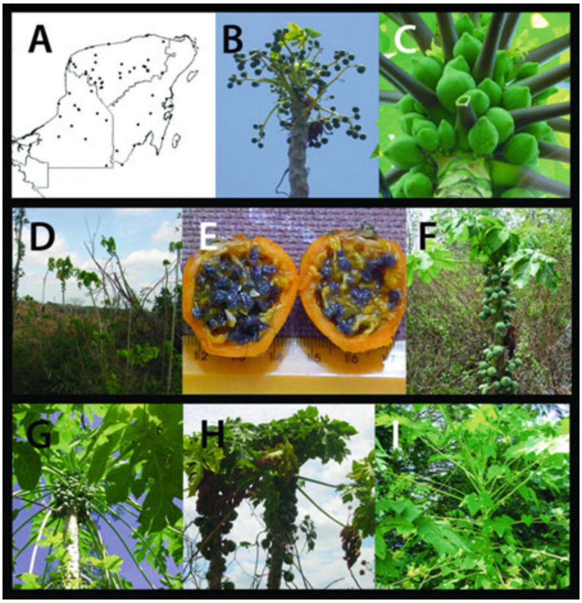

Fig. 1.3 Recent wild papaya populations localized in Yucatan Peninsula. (**a**) Map location of the collection sites along the Yucatan Peninsula, México, of wild populations of *C. papaya* L. from the Yucatan Scientific Research Center Herbarium "U Najil Tikin Xiw." (**b–i**) Photographs of *Carica papaya* L. (Ch'ich'put) found in different isolated sites from the south of the Yucatan State, taken in May 2006 and in September and November 2011: (**b**) male plant from wild populations found near Motilá. (**c**) Female plant from wild populations found near Xocchel. (**d**) Female plants from wild populations found near Libre Union. (**e**) Fruits from female plants from wild populations. (**f**) Female plant from wild populations found near Nenela. (**g**) Female plant (6 m tall) plant from wild populations found near Tixcacaltuyub. (**h**) Female plants from wild populations found near Mopilá. (**i**) Male plant from wild populations found near Mopila

different wild populations of *C. papaya* L. were compared with fruits from 5 plants from commercial papaya plants cultivar Maradol. The dendograms shown in Fig. 1.4 suggest that the 20 wild populations are related, although two distinct groups are formed between individuals from the population from Xocchel and those from the Tixcacaltuyub site, but individuals from the commercial cultivar Maradol clearly group out in a different clade. Currently, molecular studies using AFLPs are in progress in our lab, to analyze the genetic diversity between the different native wild populations and the commercial cultivars of papaya.

Papaya Domestication and Distribution

Again, it is also difficult to demonstrate the precise time and place where *C. papaya* L. was domesticated. Evidence exists for domestication of species such as maize by Aztecs and Mayas; however, early written evidence of domestication in papaya by this

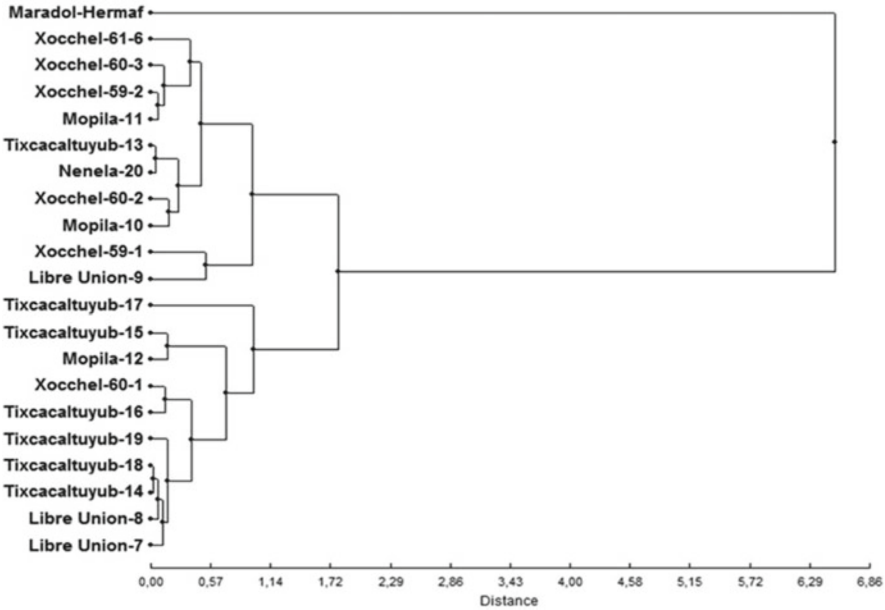

Fig. 1.4 Dendogram constructed from the analysis of morphometric characters (fruit length, width and weight) from 5 plants from each of 20 different wild populations of *Carica papaya* L. (Ch'ich'put) found in different isolated sites at the south of the Yucatan State, taken in May 2006 and September 2011. Equivalent data from five hermaphrodite papaya commercial (cultivar Maradol) plants were also included in the analysis

pre-Hispanic civilization is less documented. Therefore, various approaches have been put forward as indirect evidence of papaya domestication by early civilizations from Mexico and Central America.

No apparent direct mention of *C. papaya* L. appears in the best known pre-Colombian (Aztec and Mayan) codices, Badiano and Florentino (Emmart 1940; Galarza 1997). However, various studies include papaya in the list of plants that the Mayas would have used in their well-developed agricultural systems (de Oviedo 1959; Dunning et al. 1998; Terán and Rasmussen 1995; Colunga-GarcíaMarín and Zizumbo-Villarreal 2004), indicating that papaya ("put" or "puut," in Maya) was cultivated in Mexico and Belize before the arrival of the Spaniards. Certainly, lowland Mayas reached a very successful civilization, being an agricultural society apparently since at least 1300 BC (Pope et al. 2001). There is evidence that they had a well-developed agriculture, and the use of maize and *Agave fourcroydes* from food and fiber is well documented. Evidence of early agriculture has been found in Belize as the earliest archeological macrofossil of maize plant remains dated 1000 BC (Miksicek et al. 1991). However, Terán and Rasmussen (1995) and Colunga-GarcíaMarín and Zizumbo-Villarreal (2004) argue that this Mayan groups must have used some other plant species that grew naturally in the wild as well and include papaya among them.

Another interesting approach towards defining whether pre-Colombian native plants had been used by early civilization is one based on linguistics put forward by Brown (2010), and among the 41 species analyzed, they include papaya. From the linguistic point of view, the word papaya comes from a Caribbean word, again suggesting that the plant was known and used in this area before the Spaniards would have referred to it in later chronicle. However, among the Aztecs in Mexico papaya was known as chichihualtzapotl, a word that in Nahuatl means nurse fruit ("Zapote Nodriza") as it was related to fertility concepts, and among the Mayas it was known as "Ch'iich'puut" or "put" (Alvarez 1980). Nowadays, the papaya is also known as fruta bomba, lechosa (Venezuela, Puerto Rico, the Philippines and the Dominican Republic), mamão, papaw (Sri Lanka), Papol\Guslabu (tree melon) in Sinhalese, pawpaw, or tree melon; this reflects its ample distribution along various tropical areas of the world.

It is believed that papaya fruits (and seeds) were distributed from Central America to South America and other parts of the world by the Spaniards during the sixteenth century. The first written report of this specie appears to be that made by Oviedo in 1526, in the coastal areas of Panama. According to Morton (1987), papaya seeds were taken to Dominican Republic before 1525 and cultivation spread to warm elevations throughout South America, the West Indies and Bahamas, and then to Bermuda in 1616. Spaniards carried papaya seeds to the Philippines by approximately 1550, and by 1611, papaya was cultivated in India. From 1800 on, papaya was distributed among various islands in the south of the Pacific Ocean.

Strictly speaking, a domestication process implies that the domesticated plant species will not be able to survive without human intervention (Smith 2001). The commercial papaya cultivars, at least Maradol, certainly comply with this precept as they need irrigation to survive and to produce high yields, as they are highly susceptible to drought. On the other hand, their wild relatives are able to survive long seasons with low rain and high temperatures, for instance, from March to June at the Mexican State of Yucatán. Another feature in the domestication process of plant species is the change in the germination patterns; clearly the commercial papaya cultivars have been selected for high germination rates, while the wild relatives had low germination rates (Fuentes, unpublished). Another important feature in the domestication process is the presence of hermaphrodite plants in high proportion in commercial cultivars, whereas in plants from wild populations it is, from our experience, an extremely rare feature to be found in plants from wild native populations, at least in the ones present in Yucatán. Other contrasting features between the commercial cultivars and the papaya trees from wild populations are the number and size of fruits. While commercial papaya plants produce around 25 fruits, with an average weight of 1.5 kg, their wild counterparts are able to produce at least 70 fruits, with an average weight ranging from 20 to 35 g (Fuentes, unpublished).

Commercial Papaya Production, Harvested Area, Yields, and Trade

Papaya Production

As it can be observed in Fig. 1.5a, the worldwide production of papaya has increased from 1 to 10 million metric tons (t) per year, in the last 50 years. The latest data available show that the worldwide production of papaya reached 10.5 million t in

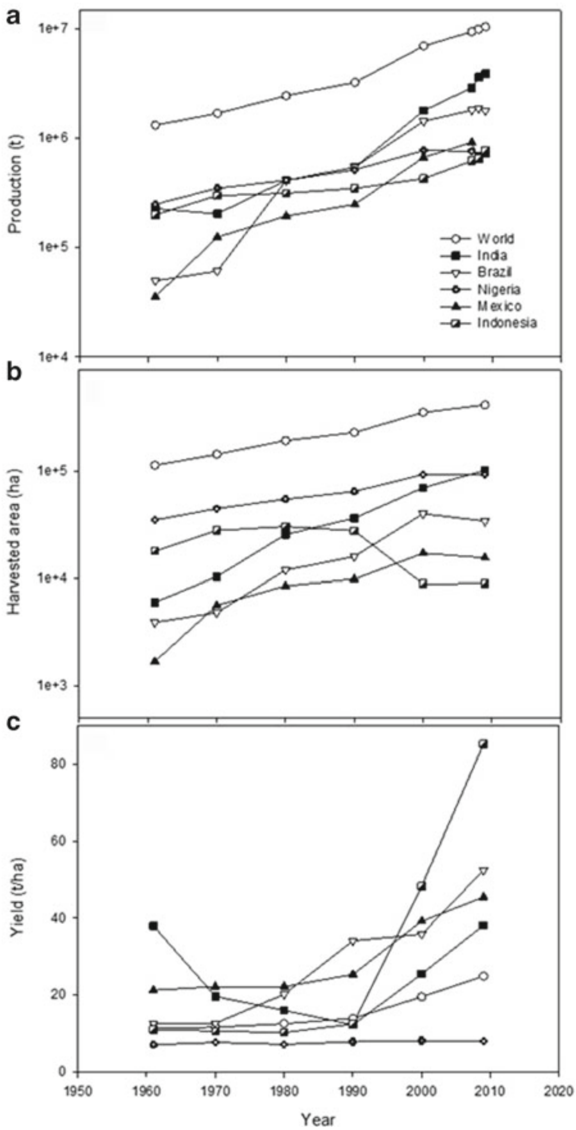

Fig. 1.5 Papaya worldwide production, harvested area and yields of papaya in the last 50 years. (**a**) Worldwide production (t) and production trends of the five top country-producers of papaya in the world. (**b**) Worldwide papaya harvested area (ha) and trends of cultivated area at the five top papaya country-producers in the world. (**c**) World average of yields (t/ha) obtained in papaya plantations, and those obtained in the five top country-producers in the world during the last 50 years (data from FAOSTAT 2011)

2009 (FAOSTAT 2011). The gross value of this worldwide production of papaya in 2009 is estimated by FAOSTAT to be 3.5 billion USD. In general, a boom in the papaya production worldwide occurred between 1990 and 2000 and later increased at slightly lower rates in the last decade.

The main five countries that have been papaya producers during the last 50 years are India, Nigeria, Brazil, Mexico, and Indonesia (Fig. 1.5a). In the 1960s, most of the total papaya production of the world was concentrated in India, Indonesia, and Nigeria; however, in the 1980s and 1990s, Brazil and Mexico increased their production to the extent that they produced equivalent quantities to those of India and Nigeria from 1980 to 1990.

In the last decade, India and Brazil have maintained their continuous increase in papaya production to rank first and second, after producing almost 4 and 1.8 million t, respectively, in 2009 (FAOSTAT 2011). In the case of Nigeria's and Mexico's production, it has reached a plateau with values ranging between 700 and 766 thousand t in the last year. In the case of Indonesia, their papaya production had remained fairly stable to rank fourth or fifth, with a production in the last 3 years between 650 and 765 thousand t (Fig. 1.5a).

The other five countries that complete the top ten papaya producers in the world are Ethiopia, Congo, Thailand, Guatemala, and Colombia (depending on the year, other countries such as Venezuela and China have been also part of the ten main papaya producers); these countries have lower productions ranging between 189 and 260 thousand t per year (FAOSTAT 2011). Taken as regions, Asia produced 5.4 million t (52 % of the world production) of papaya in 2009, America produced 3.6 million t (34 %), and Africa produced 1.4 million t (14 %) of papaya during 2009.

Papaya Harvested Area

In terms of harvested area, we will be using the SI unit hectare (ha) as used in FAOSTAT 2011. The area where papaya has been grown has increased continuously during the last 50 years from 114,192 ha in 1961 to 420,279 ha (438,239 ha in 2010) around the world in 2009 (Fig. 1.5b). Nigeria has ranked first in the number of ha cultivated with papaya in the last 50 years, although in 2009 it ranked second. Indonesia ranked second in the number of ha cultivated with papaya from 1960 to 1980, but it has declined from 1990 and presently ranks fifth. In the case of India, Brazil, and Mexico, the area cultivated with papaya was modest in the 1960s but increased continuously since then, and India now (2009) ranks first. In the case of Brazil and Mexico, the area of land cultivated with papaya has declined slightly in the last decade, but these countries still remain ranked third and fourth, respectively (Fig. 1.5b).

Papaya Yields

In terms of yields, we will be using the SI units (t/ha) as used in FAOSTAT, where t is metric ton (1 t = 1 mt = 1 tonne = 1,000 kg) and ha is hectare (ha = 10,000 m^2). The worldwide yield average obtained in papaya plantations has increased from 11.58 to 24.95 t/ha in the last 50 years (Fig. 1.5c). In Indonesia, the yields increased remarkably from 12.75 in the 1960s to 85.13 t/ha in 2009, after a sharp increase in the year 2000 where yields of 42.3 t/ha were obtained. In Brazil, yields increased from 12.75 t/ha in the 1960s to 52.39 t/ha in 2009. In the case of Mexico, yields also increase from 21 t/ha in the 1960s to yields of 45.42 t/ha obtained in 2009. In the case of India, yields have been rather erratic starting at high yields during the 1960s (38 t/ha) and then experiencing a marked drop in the 1980s and 1990s (12.36 t/ha), but it had an important increase in the last two decades, reaching again, in 2009, 38.12 t/ha. In contrast, Nigeria has maintained more modest yields during the 50-year period obtaining yields of 7.14 t/ha in the 1960s and 8.10 t/ha in 2009 (Fig. 1.5c).

Papaya Production Relative to That of Other Important Tropical Fruits

The high production volumes reached by papaya in 2009 position papaya among the five top tropical fruits around the world (Fig. 1.6a, b). However, the world production of papaya, 10 million t, is still far from the top-ranked tropical fruits (mangoes, mangosteen and guavas, MMG), grouped together by FAOSTAT 2011 and reaching values of 35 million t in 2009, and far from the banana, which reached more than 25 million t in the same year. In terms of production value, papayas had a worldwide production valued at 3.5 billion USD that is still low when compared to that of banana, reaching 28 billion USD (Fig. 1.6a, b). Therefore, there is still an opportunity to increase the production capacity of papaya. The social value of this important crop is something to be mentioned, as it is also a good source of jobs in the papaya producing countries during the harvesting season, which in some countries can reach one harvest a week during 1.5 years.

Papaya Trade

In 2009, the total of papaya exports among the 20 top exporter countries around the world was 215 thousand t, with a value of 119 million USD (FAOSTAT 2011). The top five exporter countries are Mexico, Brazil, Belize, Malaysia, and India

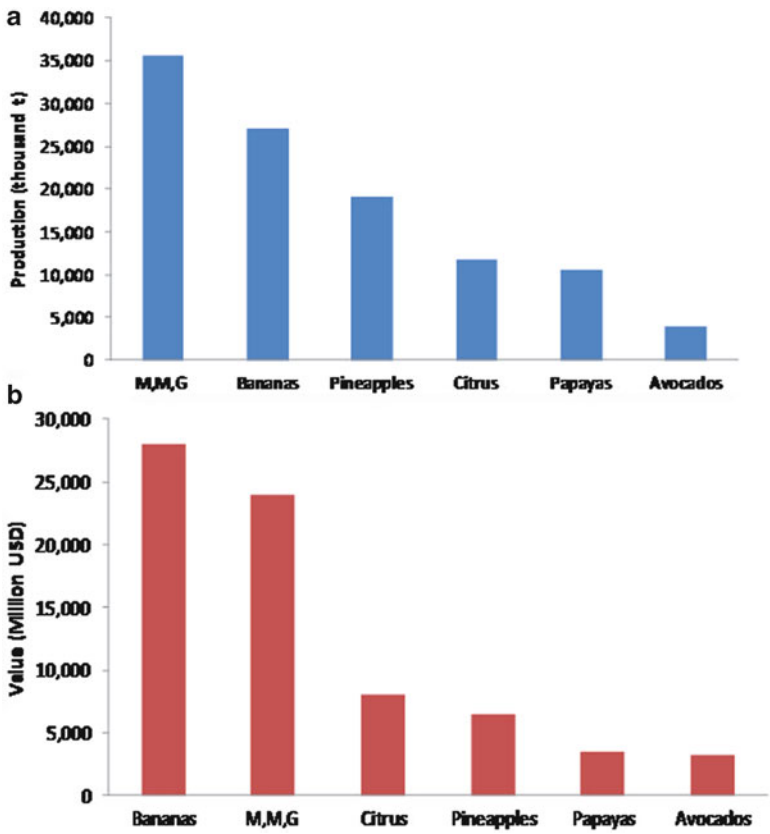

Fig. 1.6 Situation of the worldwide papaya production reached in 2009 when compared to that from other important tropical fruits. (**a**) Worldwide production (thousand t) of the six main tropical fruits. (**b**) Value of that production in millions of USD (data from FAOSTAT 2011)

(Fig. 1.7a, b). In terms of imports, the total volume of papaya imported in 2009 among the top 20 importer countries around the world was 232 thousand t, with a value of 199 million USD. The top five importer countries of papaya in 2009 were the USA, European Union, Singapore, Canada, and the Netherlands (Fig. 1.7a, b).

Conclusions

In terms of papaya's origin, we have reviewed additional facts based on the herbarium specimen records and the existence of local populations to support the hypothesis that the south of Mexico and Central America are the center of origin of *C. papaya*

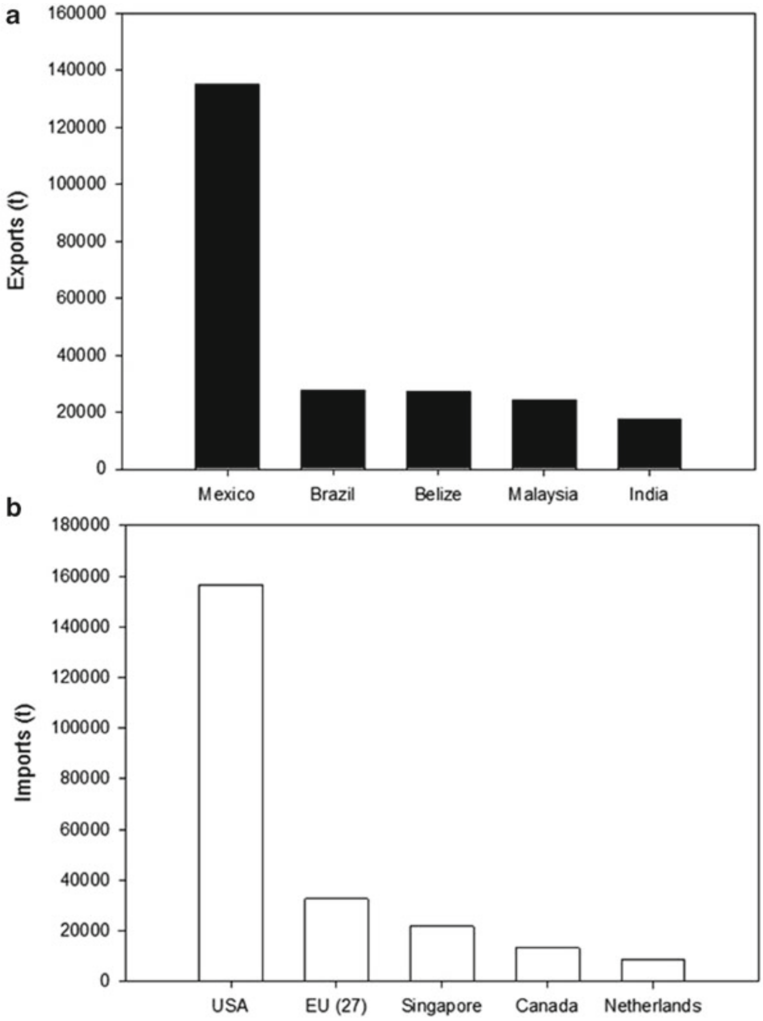

Fig. 1.7 (**a**) Papaya exports in 2009 from the top five exporter countries in the world. (**b**) Papaya imports by the top five importer countries in the world (data from FAOSTAT 2011)

L. However, molecular approaches are required to undoubtedly confirm this idea. The excellent, recent work by Carvalho and Renner is discussed later in Chap. 5 of this book.

In the present chapter, we have also reviewed some of the arguments for belief that domestication of *C. papaya* L. occurred within the lowland Mayas by at least 1500 AC. Preliminary results were shown of recent comparative morphological and molecular studies between native wild populations found in Yucatan, México, and those of commercial papaya cultivars. This study might prove useful in further discussions on the domestication process for papaya.

Finally, we conclude that the worldwide commercial papaya production has experienced an important rise in the last 50 years, in terms of yields and production volumes. The current production of commercial papaya has reached important worldwide levels, reaching in 2009 a production of 10.5 million t with a value of 3.5 billion US dollars. Asian countries (mainly India and Indonesia) produce 52 % of the total papaya produced in the world; America (mainly Brazil and México) contributes with 34 %, while Africa produces 14 % of the world production with large land areas but low yields. This high worldwide production volume positions papaya among the top five tropical fruits produced around the world, although there is still opportunity to reach equivalent production levels to those met by mangoes, mangosteens, guavas, and bananas. It would be very important to define the reason (perhaps diseases, abiotic factors, production cost) for the plateau or even the decrease in papaya harvested areas, observed in some of the top producing countries in the last decade.

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References

Alvarez C (1980) Diccionario Etnolingüistico del Idioma Maya Yucateco Colonial. VI Mundo Fisico Inst Inv Filolog Cen Est Mayas. UNAM, Mexico City

Badillo VM (1971) Monografía de la familia *Caricaceae*e. Publicado por la Asociación de profesores. Universidad Central de Venezuela, Maracay

Badillo VM (1993) *Caricaceae*e. Segundo Esquema. Rev Fac Agron Univ Centr Venezuela 43:1–111

Badillo VM (2000) Carica vs Vasconcella St.-Hil. (*Caricaceae*) con la rehabilitación de este ultimo. Ernstia 10:74–79

Brown CH (2010) Development of agriculture in prehistoric Mesoamerica: the linguistic evidence. Pre-Columbian Foodways 1:71–107

Colunga-GarcíaMarín P, Zizumbo-Villarreal D (2004) Domestication of plants in Maya lowlands. Econ Bot 58:S101–S110

De Candolle A (1883) Origine des plantes cultivées. G Baillièreetcie, Paris

de Oviedo GF (1959) Historia General y Natural de las Indias. JP de Tudela. Ediciones Atlas, Madrid

Dunning N, Beach T, Farrell P, Luzzadder-Beach S (1998) Prehispanic agrosystems and adaptive regions in the Maya Lowlands. Cult Agric 20:87–101

Emmart EW (1940) Badianus manuscript (Codex Berberini, Latin 241). Vatican Library; an Aztec herbal of 1552. Introduction, translation and annotations by Emily Walcott Emmart. With a foreword by Henry E. Sigerist. The Johns Hopkins Press, Baltimore

FAOSTAT (2011) Food and Agriculture Organization of the United Nations Database. http://www.apps.fao.org. Accessed December 2011

Galarza J (1997) Los códices mexicanos. Arqueol Mexicana IV 23:6–15
Global Biodiversity Information Facility (2011) http://data.gbif.org/species/2874484/. Accessed December 2011
Harlan JR (1971) Agricultural origins: centers and non-centers. Science 174:468–474
Lorence DH, Colin RT (1988) *Carica cnidoscoloides* (sp. nov) and sect. Holostigma (sect. nov.) of *Caricaceae* from Southern Mexico. Syst Bot 13:107–110
Manshardt RM, Zee F (1994) Papaya germplasm and breeding in Hawaii. Fruit Variety J 48:146–152
McVaugh R (2001) Caricaceae. In: Flora Novo-Galiciana: a descriptive account of the vascular plants of Western Mexico, vol 3. Ochnaceaeto Losaceae. The University of Michigan Herbarium, Ann Arbor
Miksicek CH, Wing ES, Scudde SJ (1991) The ecology and economy of Cuello. In: Hammond N (ed) Cuelo: an early Maya community in Belize. Harvard University Press, Cambridge, pp 70–84
Missouri Botanical Garden (2011) Tropicos.org http://mobot.mobot.org/W3T/Search/vast.html. Accessed December 2011
Morton J (1987) Papaya. In: Morton JF (ed) Fruits of warm climates. Florida Flair Books, Miami, pp 336–346
Pope KO, Pohl ME, Jones JG, Lentz DL, vonNagy C, VegaFJ QIR (2001) Origin and environmental setting of ancient agriculture in the lowlands of Mesoamerica. Science 292:1370–1373
Prance GT (1984) The pejibaye, Guilielma gasipaes (H.B.K.) Bailey, and the papaya, Carica papaya L. In: Stone D (ed) Pre-Columbian plant migration. Peabody Museum, Cambridge, pp 85–104
Scheldeman V, Kyndt T, Coppens d'Eeckenbrugge G, Ming R, Drew R, Van Droogenbroeck B, Van Damme P, Moore PH (2011). Vasconcellea. In: Kole C (ed) Wild crop relatives: genomic and breeding resources. Springer Science+Business Media, New York, pp 213–249
Smith BC (2001) Documenting plant domestication the consilience of biological and archeological approaches. Proc Natl Acad Sci USA 98:1324–1326
Solms-Laubach (1889) Die Heimatundder Ursprungdes kultivierten Melonen baumes *Carica papaya* L. Botanische Zeitung 44:709–720
Terán S, Rasmussen C (1995) Genetic diversity and agricultural strategy in 16th century and present-day Yucatecan Milpa Agriculture. Biodiv Conserv 4:363–381
Vavilov NI (1987) Origin and geography of cultivated plants [English Translation by D Löve]. Cambridge University Press, Cambridge
von Linnaeus C (1753) Species plantarum, 2 vols [v 1: 1–560; v 2: 561–1200]. Imprensis Laurentii Salvii, Holmiae

Chapter 2
Biology of the Papaya Plant

Víctor M. Jiménez, Eric Mora-Newcomer, and Marco V. Gutiérrez-Soto

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,

V.M. Jiménez (✉)
CIGRAS, Universidad de Costa Rica, 2060 San Pedro, Costa Rica

Food Security Center, University of Hohenheim, 70593 Stuttgart, Germany
e-mail: victor.jimenez@ucr.ac.cr

E. Mora-Newcomer • M.V. Gutiérrez-Soto
Estación Experimental Agrícola Fabio Baudrit Moreno,
Universidad de Costa Rica, Alajuela 183-4050, Costa Rica

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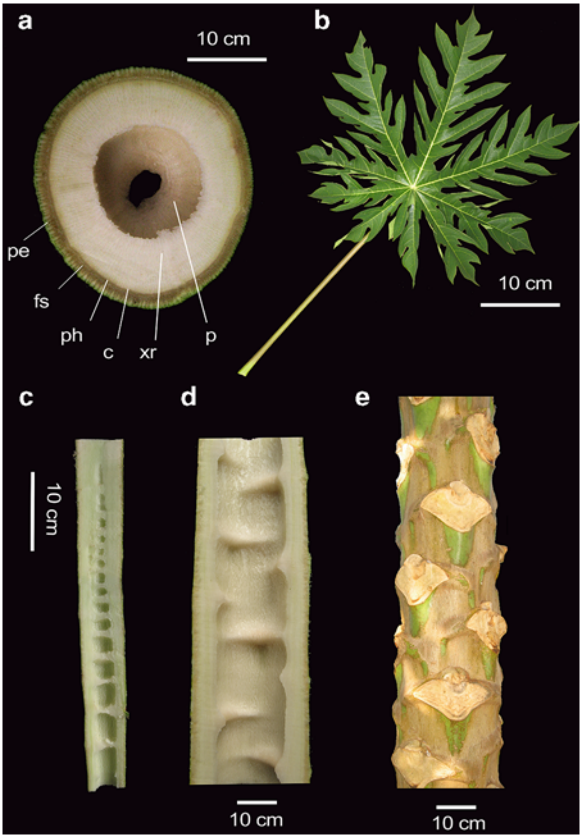

Fig. 2.1 Vegetative parts of the papaya plant. (**a**) Cross section of a 1-year-old papaya stem; periderm (pe), fiber sheath (fs), phloem (ph), cambium (c), xylem rays (xr), pith (p). (**b**) Leaf lamina and petiole. (**c**) Longitudinal section of a 3-month-old papaya stem showing hollow pith cavity.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