

Theobroma cacao L.

MONOGRAPH



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TABLE OF CONTENTS

Chapter 1. Introduction.....	4
Chapter 2. Agroecology.....	5
2.1 Taxonomy.....	5
2.2 Fossil Record.....	7
2.3 Origin and Current Distribution.....	7
2.4 Ecoregion and Climate.....	10
2.5 Environmental Factors Affecting Growth.....	10
2.6 Soil Type and Geology.....	11
2.7 Nutrient Requirements and Soil Fertility.....	12
2.8 Temperature Regime and Light Requirements.....	13
2.9 Water Requirements and Evapotranspiration.....	14
Chapter 3: Biology.....	15
3.1 Chromosome complement.....	15
3.2 Life Cycle and phenology.....	15
3.2.1 Seed germination and seedling establishment.....	15
3.2.2 Vegetative growth and development stages.....	16
3.2.3 Flowering and fruiting phenology.....	16
3.3 Anatomy and growth habits.....	16
3.3.1 Vegetative anatomy.....	17
3.3.2 Reproductive structures.....	19
3.3.3 Growth form, architecture, and shade adaptation.....	21
3.4 Reproductive Biology.....	21
3.4.1 Pollination mechanism and floral biology.....	21
3.4.2 Seed development and reproductive success.....	22
Chapter 4. Cultivation and Agricultural Management.....	24
4.1 Propagation and establishment.....	24
4.1.1 Natural regeneration.....	24
4.1.2 Vegetative regeneration.....	24
4.1.3 Nursery propagation.....	26
4.1.4 Propagation by cuttings.....	27
4.1.5 Field planting.....	27
4.2 Cultivation and crop management.....	28
4.2.1 General cultivation practices.....	28
4.2.2 Fertilizing.....	29
4.3 Growth and productive stages.....	30
4.3.1 Growth stages.....	30
4.3.2 Fruiting.....	30
4.3.3 Harvesting.....	30
4.4 Pest and disease Management.....	31

4.4.1 Management of pests and diseases.....	31
4.4.2 Pest and disease control.....	33
4.5 Pruning and re-planting.....	34
Chapter 5: Importance, Markets, and Uses.....	35
5.1 Economic and global importance.....	35
5.2 Regional and national importance.....	36
5.2.1 Major producing regions.....	36
5.2.2 Contribution to local economies.....	36
5.3 Market structure and trade.....	36
5.3.1 Global market characteristics.....	37
5.3.2 Domestic markets.....	37
5.4 Products and industrial uses.....	37
5.4.1 Primary products.....	37
5.4.2 Value-added products.....	38
5.5 Socioeconomic and environmental significance.....	39

Chapter 1. Introduction

Theobroma cacao, commonly known as cacao, is a tropical plant species of significant biological, ecological, and economic importance. Native to the humid lowland forests of Central and South America, cacao has been cultivated for thousands of years and remains the primary raw material for the global chocolate industry. Its continued relevance extends beyond its commercial value, as it plays a crucial role in sustaining rural livelihoods, supporting biodiversity, and contributing to agroforestry based agricultural systems.

From a biological perspective, cacao is a shade tolerant understory tree adapted to the stable, humid conditions of tropical forest ecosystems. Its growth, reproduction, and productivity are strongly influenced by environmental factors such as temperature, light, availability, soil fertility, and water supply. These physiological characteristics make cacao an ideal species for cultivation within agroforestry systems, where it can coexist with a diversity of plant species that enhance ecological stability and resource efficiency.

In addition to its ecological significance, cacao is a globally traded good with substantial economic impact. Millions of smallholder farmers depend on its cultivation as a primary source of income, particularly in developing regions near the equator. The international demand for cacao and its derived products continues to grow, making it a key component of global agricultural markets and value chains. However, cacao production also faces challenges, including pest and disease pressures, climate variability and the need for sustainable management practices.

This monograph aims to provide a comprehensive analysis of *Theobroma cacao*, examining its biological characteristics, cultivation methods, and broader significance. The study explores propagation techniques, agricultural management practices, and the role of agroforestry systems in optimizing production. Furthermore, it evaluates the economic importance of cacao at local, regional, and global scale, as well as the diverse range of products derived from it.

By integrating scientific research with agricultural and economic perspectives this monograph seeks to highlight the complexity of cacao as both a biological organism and a globally important crop, emphasizing the need for sustainable practices to ensure its long term viability.

Chapter 2. Agroecology

2.1 Taxonomy

As shown in Table 1 below, there is an order to taxonomy starting with the highest division, **the Kingdom**: a level that groups all forms of life with broad similarities. The kingdom **Plantae** includes all plants, which are multicellular organisms and eukaryotic, meaning their cells contain nuclei (Bhattacharjee & Umaharan, 2018).

Table 1

Taxonomic hierarchy of *Theobroma cacao*

Rank	Name
Kingdom	Plantae - Plants
Subkingdom	Tracheobionta - Vascular plants
Superdivision	Spermatophyta - Seed plants
Division	Magnoliophyta - Flowering plants
Class	Magnoliopsida - Dicotyledons
Subclass	Dilleniidae
Order	Malvales
Family	Malvaceae
Genus	<i>Theobroma</i>
Species	<i>Theobroma cacao</i> L.

Secondly comes the **subkingdom**, which further divides plants into narrower groups. *Theobroma cacao* belongs to **Tracheobionta**, or vascular plants, which are characterised by having specialized tissues such as xylem and phloem for the transport of water and nutrients (Bhattacharjee & Umaharan, 2018).

The next taxonomic level is the **superdivision**. Cacao is classified in **Spermatophyta**, the seed-bearing plants, which reproduce through seeds and are distinct for their ability to enclose embryos in protective coats (Bhattacharjee & Umaharan, 2018).

Following this comes the **division**. *Theobroma cacao* is placed in the **Magnoliophyta**, commonly called angiosperms or flowering plants, which produce flowers and enclose their seeds within fruits (Bhattacharjee & Umaharan, 2018).

The next rank is the **class**, which groups plants with more shared traits. Cacao belongs to the **Magnoliopsida**, also known as dicotyledons. Members of this class typically have two embryonic seed leaves (cotyledons) and display net-like venation in their leaves (Bhattacharjee & Umaharan, 2018).

After class comes the **subclass**. *Theobroma cacao* is placed in the **Dilleniidae**, a group within the dicots that includes many species with advanced floral characteristics, such as fused floral parts and diverse growth forms (Bhattacharjee & Umaharan, 2018).

The next rank is the **order**. An order is a group of related families, and cacao belongs to the **Malvales**, which are plants often characterized by mucilaginous tissues, stellate hairs, and flowers with radial symmetry (USDA APHIS, 2025).

The **family** groups are species with close evolutionary relationships. *Theobroma cacao* belongs to the **Malvaceae**, which includes a variety of tropical and temperate plants such as hibiscus, cotton, and okra. Members of this family usually have alternate leaves, five-petaled flowers, and often produce economically important fruits or fibres (USDA APHIS, 2025).

The next level is the **genus**, which organises species with even more specific similarities. **Theobroma**, which literally means “food of the gods,” includes trees that produce seeds used for cacao and chocolate production (NCBI, 2025).

Lastly comes the **species**, the most specific taxonomic classification. *Theobroma cacao L* -the L referring to Swedish botanist Carolus Linneaus, the scientist that described the plant first. The classification refers to the cacao tree, which is cultivated for its seeds—cocoa beans—that are processed into cocoa, cocoa butter, and chocolate (USDA, 2025).

2.2 Fossil Record

The direct fossil record of the genus *Theobroma* and the species *Theobroma cacao* L is minimal and almost non-existent for the species itself. This is common for tropical plants, as the hot, humid conditions lead to rapid decomposition, preventing fossilisation. However, fossil evidence exists at the family level (**Malvaceae**). Pollen fossils attributed to the **Malvaceae** family have been found in deposits from the Palaeocene and Eocene epochs (around 34 to 66 million years ago) in South America and other parts of the world.

A significant fossil that provides indirect evidence for the lineage leading to *Theobroma* is a fossilised fruit specimen named *T. coronense*. This fossil, discovered in the Gatoncillo Formation in Panama, dates to around 57-58 million years ago. The presence of *T. coronense*. Indicates the genus *Theobroma*, or a very close ancestor, was already present in the tropical Americas tens of millions of years before modern cacao evolved. This fossil pushes the evolutionary timeline for the genus significantly back and supports the theory of a Neotropical origin. Although there is evidence of *T. coronense*, it remains very limited; therefore, no images of the fossil are available online (Richardson et al., 2015).

2.3 Origin and Current Distribution

As shown in **Figure 1**, the ancestors of *T. cacao* are native to the upper Amazon region, primarily in what is now southeastern Colombia, southern Venezuela, eastern Peru, and northern Brazil. Here, it grew as an understory tree in the rainforest (Zarrillo et al., 2018). The plant was not domesticated in its full natural range. Genetic studies have pointed out the precise location of domestication: research comparing the DNA of wild populations and cultivated varieties consistently shows that the cacao tree was first domesticated approximately 5,300 years ago in the equatorial region of South America, most likely in what is now northeastern Peru and southeastern Ecuador (Zarrillo et al., 2018). A 2018 study in Ecology and Evolution analysed the genomes of multiple cacao populations and concluded that the “Criollo” population, which is one of the most ancient domesticated varieties, originated from a single domestication event in the Neotropics (Cornejo et al., 2018). This strongly supports the Upper Amazon origin theory. “Beyond domestication, molecular phylogenies also trace the evolutionary history of the genus. It was demonstrated that *Theobroma cacao* diverged from its most recent common ancestor around 9.9 million years ago, coinciding with the mid-to-late Miocene and the uplift of the Andes. This deep evolutionary timeline reinforces the Neotropical origin of cacao and situates its domestication within a much older lineage.” (Cornejo et., 2018).

Cacao spread northward into Mesoamerica, where the Maya and Aztec civilizations incorporated it into ritual, trade, and daily life. Following the Spanish conquest in the 16th century, cacao was introduced to Europe, where it was transformed into sweetened chocolate and became a luxury commodity.(UN FAO & Our World in Data, 2026). Colonial expansion during the 17th and 18th centuries carried cacao seeds to Africa, Asia, and Oceania, establishing plantations in West Africa, Southeast Asia and Oceania. Today, West Africa dominates global production, supplying nearly 70% of the world’s cacao (UN FAO & Our World in Data, 2026). The Food and Agriculture Organization of the United Nations keeps a record of the distribution of the global Cacao supply, as seen in **Figure 2**.

Figure 1:
Locations of the four archaeological sites in Mexico, Central America, and South America with the earliest evidence of *Theobroma* use (Zarrillo et al., 2018).

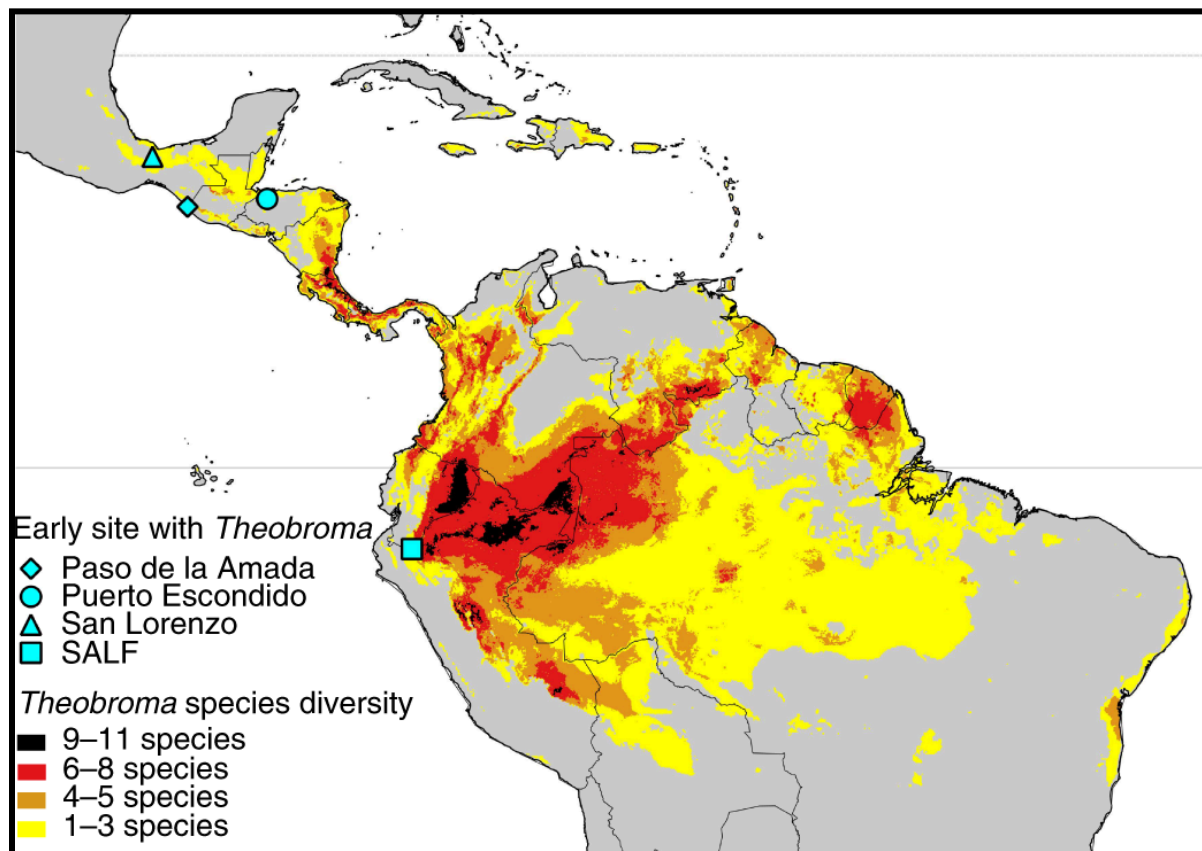
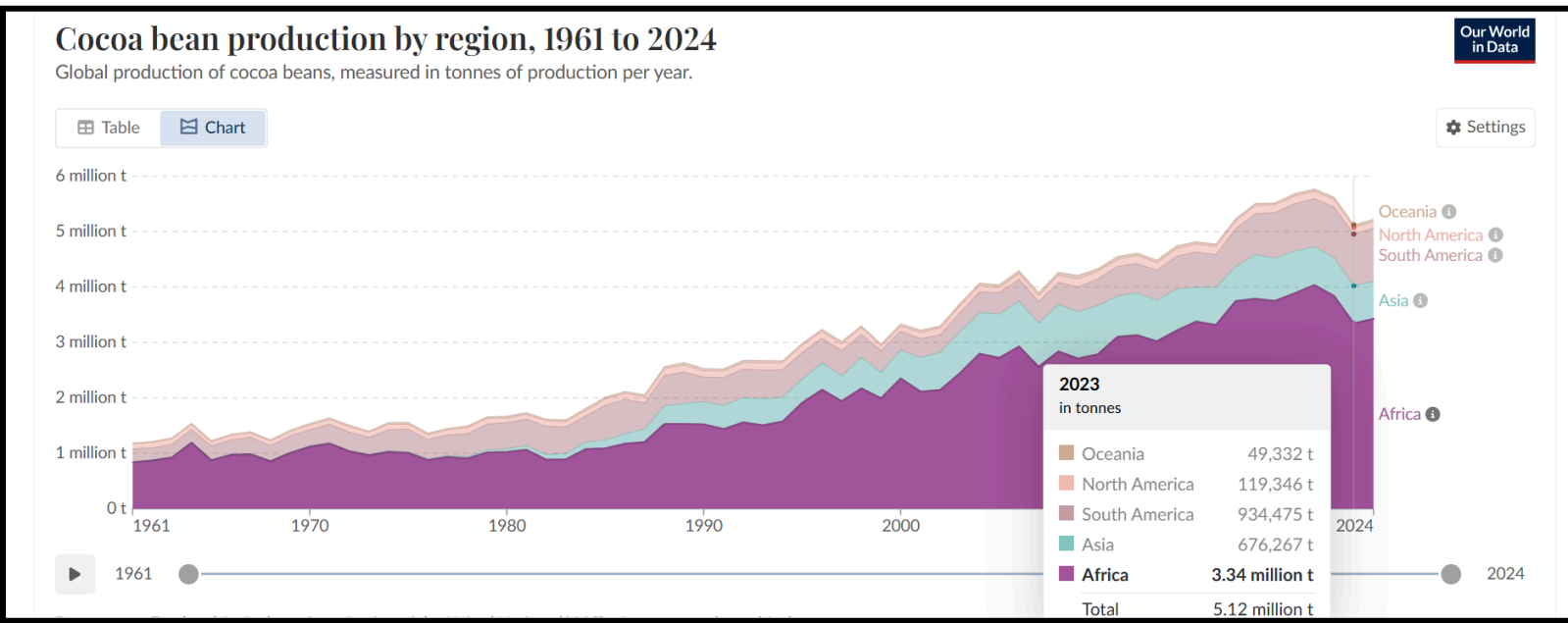


Figure 2:
Cocoa bean production by region, 1961 to 2024, measured in tonnes (UN FAO & Our World in Data, 2026).



2.4 Ecoregion and Climate

T.Cacao is native to the humid tropical rainforests of the Upper Amazon Basin, a region characterized by high annual rainfall (1,500-2,500 mm) and consistently warm temperatures (22-28°C). This ecoregion falls within the tropical moist broadleaf forest biome, where cacao thrives as an understory species, shaded by taller trees and protected from direct sunlight. Its natural habitat spans lowland riparian zones and gently sloping forest terrain, rarely extending into montane or savanna regions. The plant's preference for shaded, humid environments limits its natural distribution to areas with stable moisture regimes and minimal seasonal variation, as seen in **Figure 1** (Gonzalez, 2022).

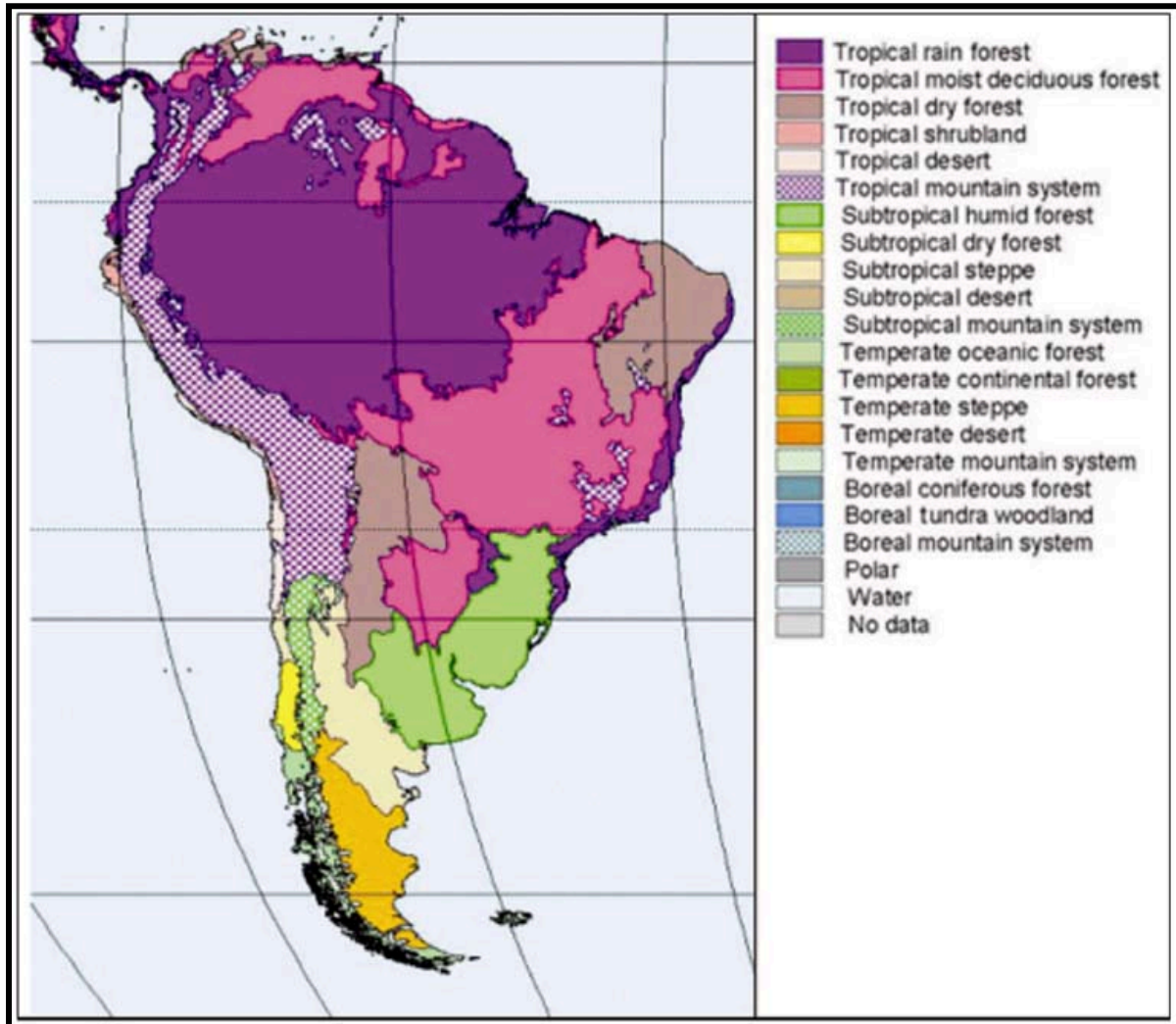
Cacao's growth is tightly linked to climatic stability. It cannot tolerate prolonged drought, frost, or high winds, making it unsuitable for arid, temperate, or high altitude zones. Its occupation of new areas depends on the replication of its native warm, wet, and shaded climate. Regions like West Africa and Southeast Asia became major producers only after colonial agricultural systems replicated these conditions through plantation design and irrigation. In Colombia, studies show cacao is best suited to low-elevation tropical zones with consistent rainfall and moderate slopes (Gonzalez, 2022).

2.5 Environmental Factors Affecting Growth

Within its native ecoregion, cacao follows a toposequence from near rivers to mid-slope forest zones. It avoids exposed ridges and dry uplands due to its sensitivity to water stress. Soil mixture, organic content, and shade availability vary along this sequence, directly influencing cacao's growth and reproductive success. In riparian zones, high humidity and nutrient-rich soils promote vigorous vegetative growth and flowering. In contrast, poorly drained or compacted soils limit root development and reduce yield (Cubol et al.,2023).

Environmental factors such as temperature, oxygen availability, and water are critical for seed germination and early growth. Studies show that cacao seeds germinate best at temperatures between 25-30 °C, with adequate oxygen and consistent moisture. Scarification is rarely needed, but seeds are sensitive to extreme dryness and must be planted quickly after harvest. These constraints explain why cacao has not naturally expanded into drier or cooler regions, despite human cultivation efforts (Cubol et al.,2023).

Figure 3:
Locations of different ecoregions suitable for cacao cultivation (Cultiva EcoSolutions, 2025).



2.6 Soil Type and Geology

T.cacao thrives in deep, well-drained soils with high organic matter and slightly acidic pH levels, typically ranging from 5.0 to 6.5. These soils are commonly found in tropical rainforest regions with rich geological substrates derived from weathered volcanic rock, sedimentary deposits, and alluvial plains. The geology of these regions contributes essential minerals such as potassium, magnesium, and calcium, which are critical for cacao's vegetative growth and seed quality (Francisco-Santiago et al., 2023).

Cacao prefers loamy soils with a balanced texture. Normally 30-40% clay, 30-50% sand, and 20-30% silt. This composition ensures optimal porosity and water retention, allowing roots to access moisture without becoming waterlogged. Poor drainage or compacted soils lead to root rot and reduced productivity. In Colombia, soil surveys across cacao-producing regions revealed that productivity correlated strongly with soil depth and low salinity levels (Francisco-Santiago et al.,2023).

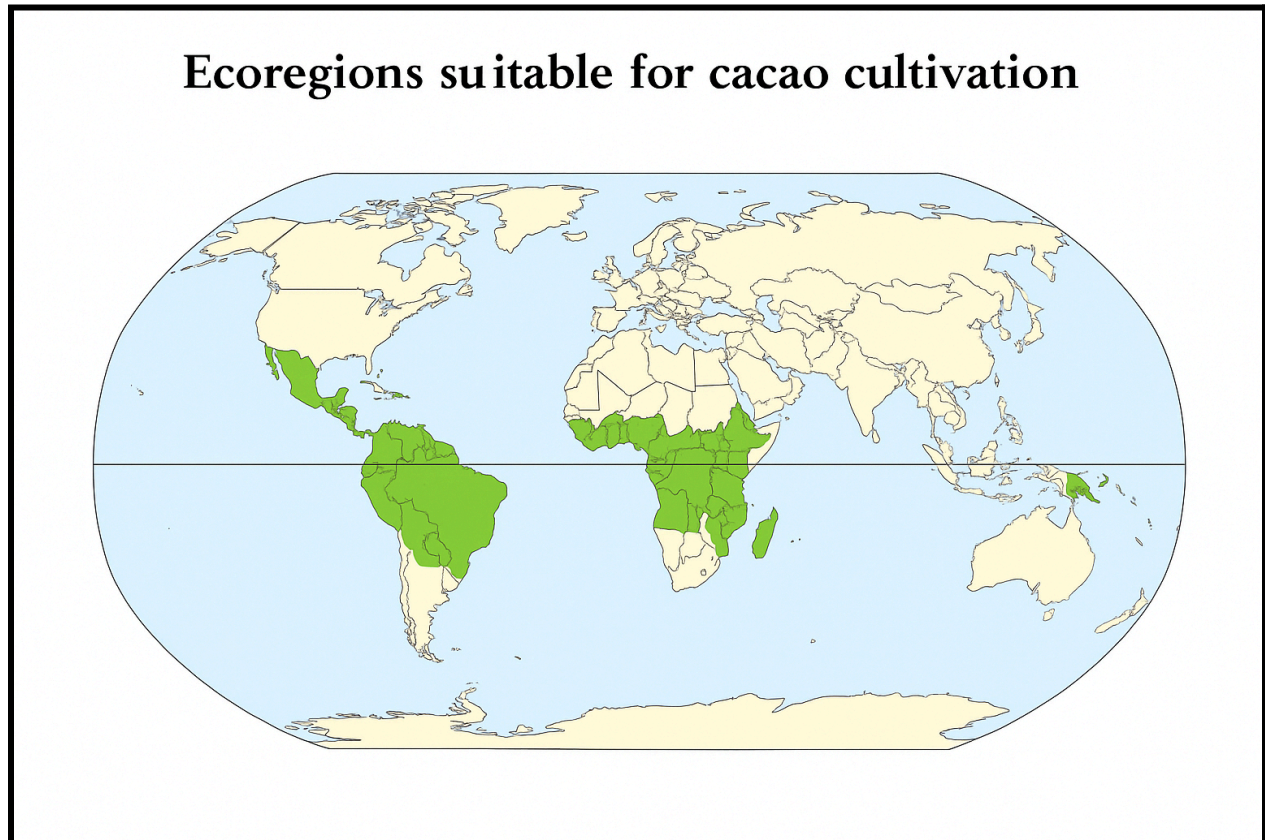
2.7 Nutrient Requirements and Soil Fertility

Cacao's growth and reproduction depend on a precise balance of macronutrients and micronutrients. The most critical macronutrients are: Nitrogen, which promotes leaf and shoot growth, Phosphorus, which supports root formation and flower initiation, and Potassium, which is vital for pod filling, seed development, and disease resistance. Micronutrients such as magnesium, calcium, iron, and zinc are also necessary for enzymatic activity and reproductive success. A study showed that cacao leaves in nutrient-rich soils had significantly higher concentrations of magnesium and zinc, correlating with improved pod yield and seed viability (Daniel et al.,2025).

These nutrients are absorbed from the soil through root hairs and mycorrhizal associations. Organic matter decomposition, driven by tropical humidity and microbial activity, releases these nutrients into the rhizosphere. Soils with low organic content or poor pH buffering capacity often require supplementation through compost or mineral fertilizers to maintain cacao health (Daniel et al.,2025).

Figure 4:

Map showing suitable regions for *T.cacao* cultivation (Gonzalez, 2022).



2.8 Temperature Regime and Light Requirements

T.cacao is a tropical understory tree adapted to stable, warm climates with minimal seasonal variation. It thrives in regions where annual temperatures range between 22° C and 28° C, with optimal growth occurring at daily averages of 25°C. Cacao is sensitive to both cold spells and extreme heat. Temperatures below 10° C can damage seedlings and reduce flowering, while prolonged exposure above 32° C impairs photosynthesis and pod development (Baque Zambrano et al., 2024). Nighttime temperatures should remain above 18° C to maintain metabolic activity and avoid stress, including leaf drop.

Cacao does not require a cold dormancy period and instead relies on consistent warmth and humidity to sustain its evergreen growth cycle. Its adaptation to the rainforest understory means it is physiologically tuned to low light intensity. The plant uses a C3 photosynthetic pathway, which is efficient under shaded conditions but vulnerable to photorespiration under high light and heat. This explains why cacao performs best under partial shade, where taller trees buffer light and temperature extremes (Salazar et al., 2018).

2.9 Water Requirements and Evapotranspiration

Cacao's water needs are equally precise. It requires 1,500-2,500 mm of annual rainfall, evenly distributed throughout the year. Short dry spells can be tolerated, but prolonged droughts reduce flowering and pod set. The plant's shallow root system contributes to moderate evapotranspiration rates, averaging 3-4 mm/day in humid conditions (Rojas et al., 2024). Water stress leads to stomatal closure, reduced photosynthesis, and increased vulnerability to fungal pathogens.

Soil moisture must be maintained through well-drained loamy soils and mulching practices that reduce evaporation. Irrigation is essential in regions with seasonal rainfall, especially during flowering and pod development stages.

Chapter 3: Biology

3.1 Chromosome complement

Theobroma cacao L. is a diploid species with a somatic chromosome number of $2n=20$ and a basic chromosome number of $x = 10$. This chromosome complement is consistent across both wild and cultivated populations and is characteristic of several members of the family Malvaceae (Argout, 2011).

Cacao chromosomes are relatively small and morphologically similar, which historically limited detailed karyotypic differentiation using classical cytological techniques (Bhattacharjee, 2018).

3.2 Life Cycle and phenology

Theobroma cacao is a perennial tropical tree with a continuous growth cycle that reflects its adaptation to humid rainforest environments. The species does not exhibit seasonal dormancy and instead maintains year-round vegetative activity and reproductive potential under stable climatic conditions. Its life cycle is characterized by rapid seed germination, a prolonged juvenile phase, and continuous but environmentally regulated flowering and fruiting. Phenological patterns are closely linked to temperature, rainfall distribution, and shade availability, which together determine growth rates and reproductive success (Gonzalez, 2022).

3.2.1 Seed germination and seedling establishment

Seeds of *Theobroma cacao* are rebellious, losing viability quickly when exposed to desiccation or low temperatures. Under optimal conditions, germination occurs within 5-10 days and is epigeal, with cotyledons emerging. It requires temperatures between 25 and 30°C, high humidity, and well-drained substrates.

During early establishment, seedlings are highly sensitive to water stress, excessive radiation, and temperature fluctuations. Shaded conditions and consistent soil moisture are essential for survival and early growth, reflecting the species' natural role as a rainforest understory tree (Motamayor, 2008).

3.2.2 Vegetative growth and development stages

After establishment, *Theobroma cacao* enters a juvenile vegetative phase lasting approximately 2-4 years, during which the main stem develops, and the lateral branching pattern is established. Vegetative growth is continuous in favorable environments and does not follow a distinct seasonal rhythm. Growth performance during this stage is strongly influenced by climatic stability, soil fertility, and shade management. Excessive light exposure can impair physiological efficiency, while moderate shading promotes optimal leaf function and biomass accumulation. The evergreen nature of cacao allows it to sustain photosynthetic activity throughout the year (Gonzalez, 2022).

3.2.3 Flowering and fruiting phenology

Theobroma cacao exhibits cauliflory, producing flowers directly on the trunk and mature branches. Flowering may occur throughout the year in humid tropical climates, although peak reproductive activity often corresponds with periods of increased rainfall. Individual flowers are short-lived, and only a small fraction develops into mature fruits (Zarrillo, 2018).

Fruit development from pollination to pod maturity takes approximately 5-6 months. Mature pods contain 30-50 seeds, commonly referred to as cacao beans. Phenological variation among populations is influenced by genetic background and environmental conditions, particularly rainfall distribution and temperature stability (Gonzalez, 2022).

3.3 Anatomy and growth habits

Theobroma cacao is a small to medium-sized evergreen tree whose anatomical features and growth habits reflect its adaptation to the shaded understory of tropical rainforests. The species exhibits specialized vegetative and reproductive structures that support continuous growth and reproduction under warm, humid conditions. Its architecture, shade tolerance, and cauliflorous habit are defining characteristics that influence both its ecology and its management in agroforestry systems (Gonzalez, 2022).

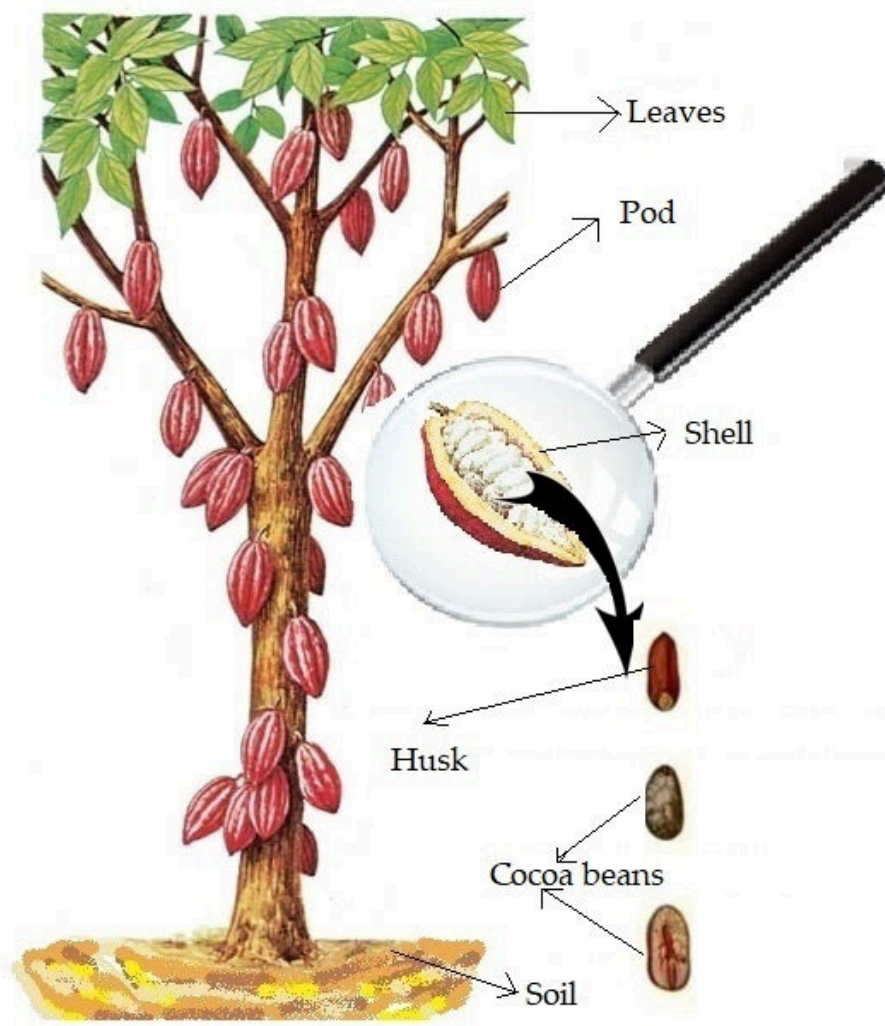
3.3.1 Vegetative anatomy

The root system of *Theobroma cacao* is relatively shallow and dominated by lateral roots, with limited penetration into deeper soil layers. This structure allows efficient nutrient uptake in organic-rich topsoil but also makes the species sensitive to drought and poor drainage. Fine root development is closely associated with high soil moisture and organic matter availability (Argout, 2011).

The stem consists of a main vertical axis that gives rise to lateral branches, forming a characteristic architecture, as seen in **Figure 5**. Young stems are green and flexible, becoming woody with age. Leaves are simple, alternate, and broad, with a thin cuticle and pronounced venation. Their large surface area enhances light capture under shaded conditions but increases susceptibility to water stress under excessive radiation (Gonzalez, 2022).

Figure 5

Parts of the cacao plant (leaves, pods, beans) illustrating basic vegetative anatomy relevant to cacao morphology (Van Vliet, 2015)

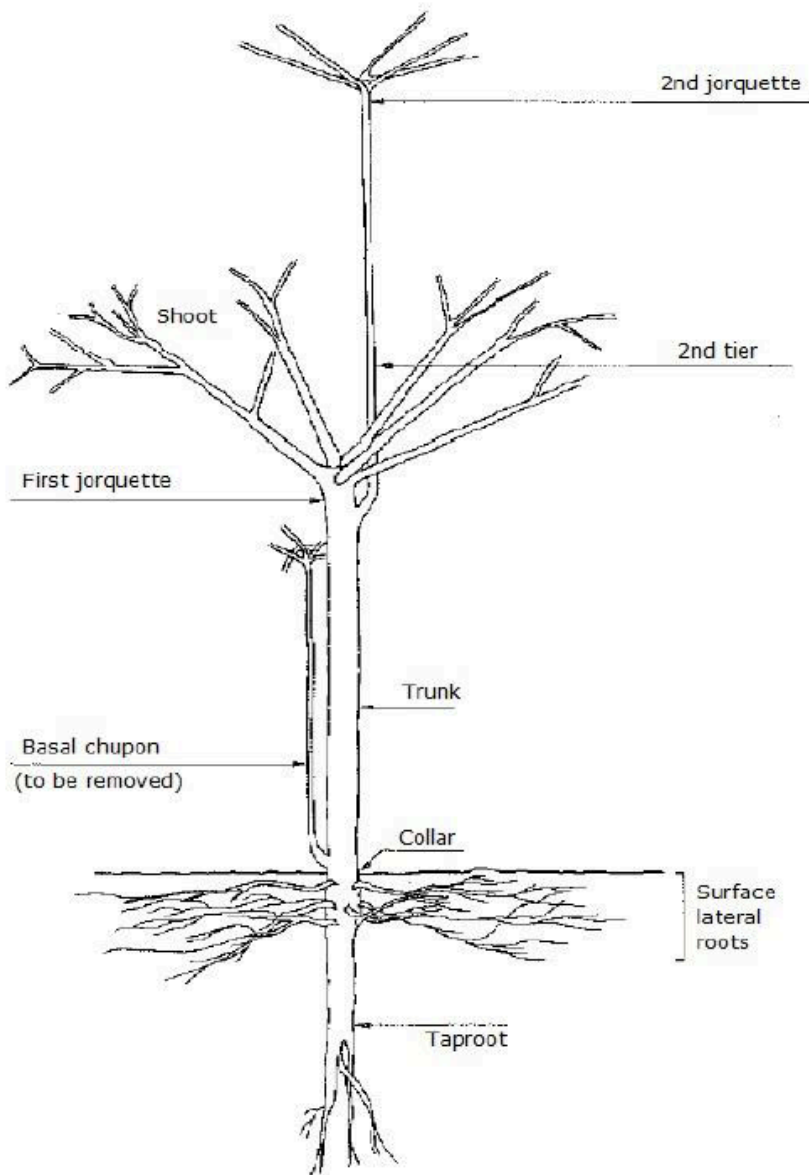


3.3.2 Reproductive structures

Flowers of *Theobroma cacao* are small, complex, and produced directly on the trunk and older branches, as seen in **Figure 6**, a phenomenon known as cauliflory. Each flower consists of five sepals, five petals, and a central column containing the reproductive organs. The floral structure is highly specialized and adapted to pollination by small insects (Zarrillo, 2018).

The fruit is an elongated, ribbed berry, commonly referred to as a cacao pod. Pods vary in color, shape, and surface texture depending on genetic background. Each pod contains 30-50 seeds, embedded in a sweet, sticky pulp. The seeds are large, rich in lipids, and represent the economically valuable component of the plant (Argout, 2011).

Figure 6
Schematic representation of the cacao tree illustrating stem architecture and branching pattern (Ramos, 2022).



3.3.3 Growth form, architecture, and shade adaptation

Theobroma cacao typically reaches heights of 4-8 meters under cultivation, as seen in **Figure 7**, although taller individuals may occur in natural forests. The tree displays a distinct growth habit characterized by a single main stem and a horizontal branching pattern that enhances light interception under low-light environments.

Cacao is physiologically adapted to partial shade and performs poorly under prolonged exposure to full sunlight. Shade trees moderate temperature, reduce evapotranspiration, and protect leaves from photoinhibition. These adaptations explain the strong association between cacao cultivation and agroforestry systems, which mimic the structural complexity of natural forest habitats (Gonzalez, 2022).

3.4 Reproductive Biology

The reproductive biology of *Theobroma cacao* is highly specialized and plays a central role in determining fruit set and yield. Although the species is capable of continuous flowering under favorable tropical conditions, successful reproduction depends on complex interactions between floral structure, pollinators, and environmental factors. Natural pollination efficiency in cacao is generally low, making reproductive success a critical biological constraint (Adjaloo, 2013).

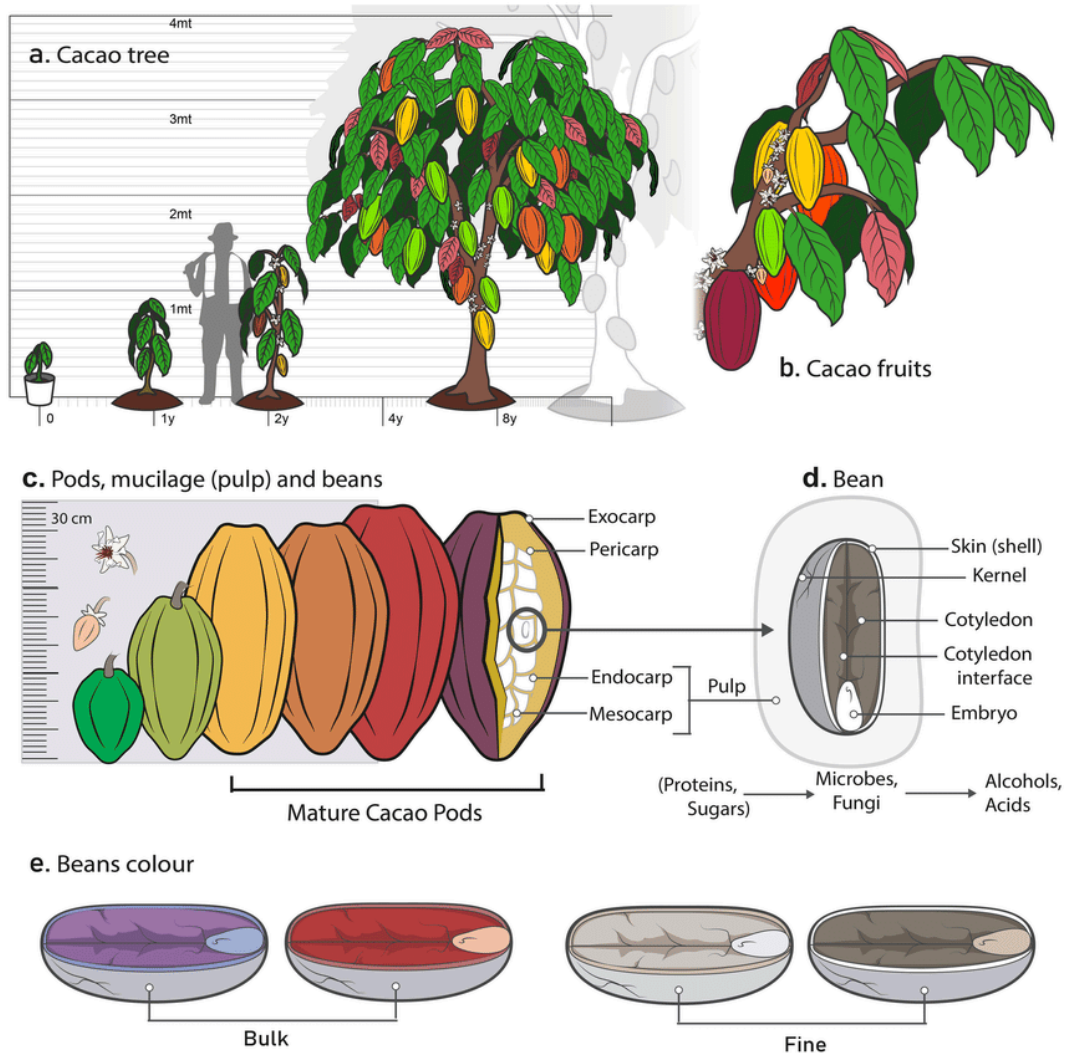
3.4.1 Pollination mechanism and floral biology

Flowers of *Theobroma cacao* are structurally adapted for entomophily, with pollination primarily carried out by small dipteran insects, especially ceratopogonid midges (Wolcott, 2023). The small size and complex morphology of the flowers restrict access to these specialized pollinators, limiting the number of successful pollination events.

Cacao flowers are hermaphroditic, but many genotypes exhibit varying degrees of self-incompatibility, which promotes cross-pollination. Flower viability is short, often lasting less than 48 hours, and pollination success is strongly influenced by humidity, temperature, and pollinator abundance. These biological constraints explain the high proportion of flowers that fail to develop into fruits under natural conditions (Motamayor, 2008).

Figure 7

Diagram of the *Theobroma cacao* tree, fruits, pods, and beans showing morphological reproductive structures (Rojas, 2022).



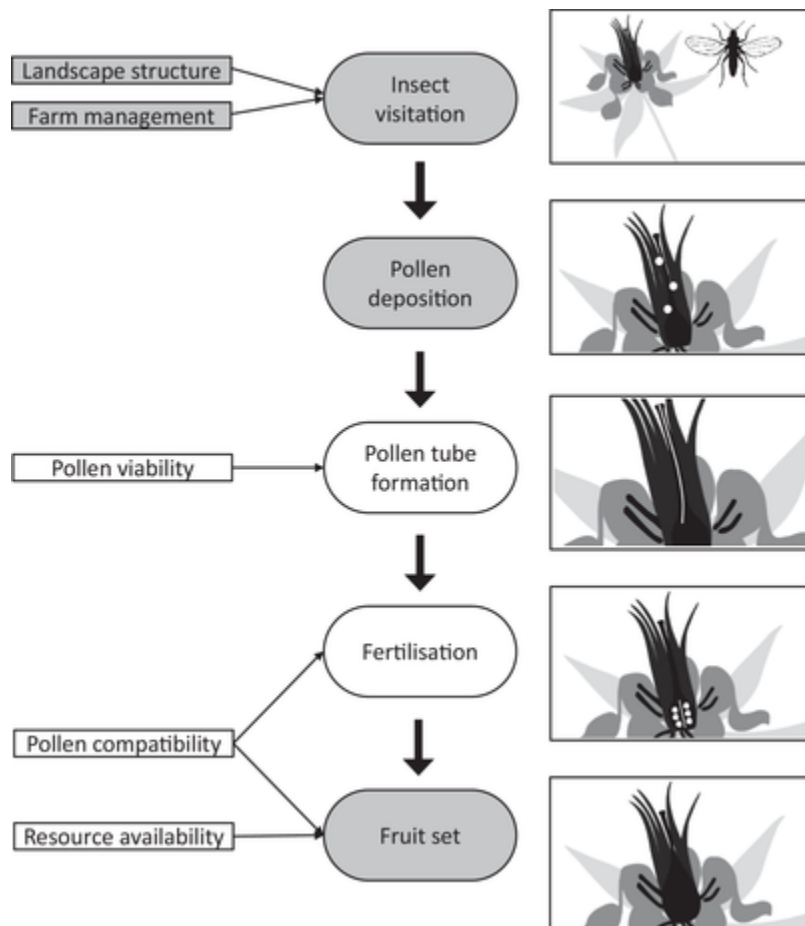
3.4.2 Seed development and reproductive success

Following successful pollination and fertilization, ovule development leads to the formation of seeds enclosed within the cacao pod, as seen in **Figure 8**. Seed development is closely linked to nutrient availability and stable moisture conditions. Although individual trees may produce thousands of leaves annually, typically less than 5% develop into mature pods, reflecting high rates of reproductive abortion (Motamayor, 2008).

Reproductive success in *Theobroma cacao* is influenced by both genetic and environmental factors, including pollinator diversity, rainfall distribution, and tree health. Variability in seed number, size, and viability among pods contributes to differences in yield and quality. These reproductive limitations have important implications for cacao cultivation, as they directly affect productivity even under favorable growing conditions (Jaramillo, 2024).

Figure 8

Conceptual overview of the cacao pollination process, indicating steps from insect visitation to fruit set (Vansynghel, 2022).



Chapter 4. Cultivation and Agricultural Management

4.1 Propagation and establishment

The successful cultivation of *Theobroma cacao* depends on efficient propagation methods and careful early plant management. Cacao can be propagated through both sexual and asexual techniques, including seed germination, vegetative propagation and controlled nursery production. These propagation methods are nursery production. These propagation methods influence plantation uniformity productivity and resistance to environmental stress and diseases (Argout et al., 2011; Motamayor et al., 2008).

4.1.1 Natural regeneration

Natural regeneration occurs when cacao seeds germinate under favorable conditions without direct human intervention. In natural tropical ecosystems, mature pods that fall to the ground release seeds that rapidly germinate under warm and humid conditions. Cacao seeds are recalcitrant, meaning they obtain high moisture content and lose viability rapidly when exposed to drying or low temperatures. Therefore successful natural regeneration typically occurs in shaded environments with stable humidity and fertile soils rich in organic matter (González-Orozco et al., 2022).

Although natural regeneration contributes to genetic diversity in wild populations, it is rarely used in commercial agriculture because seed grown plants show considerable variability in productivity, disease resistance and fruit quality (Argout et al., 2011).

4.1.2 Vegetative regeneration

Vegetative regeneration allows cacao plants to reproduce clonally using vegetative tissues instead of seeds. This method produces genetically identical plants that maintain desirable traits such as disease resistance, high yield, and pod quality. Common vegetative regeneration techniques include grafting, budding and stem cuttings (Motamayor et al., 2008). These three can be seen in **Figure 9**, **Figure 10** and **Figure 11**.

Figure 9:
Diagram of what grafting is (Iannotti, 2024).

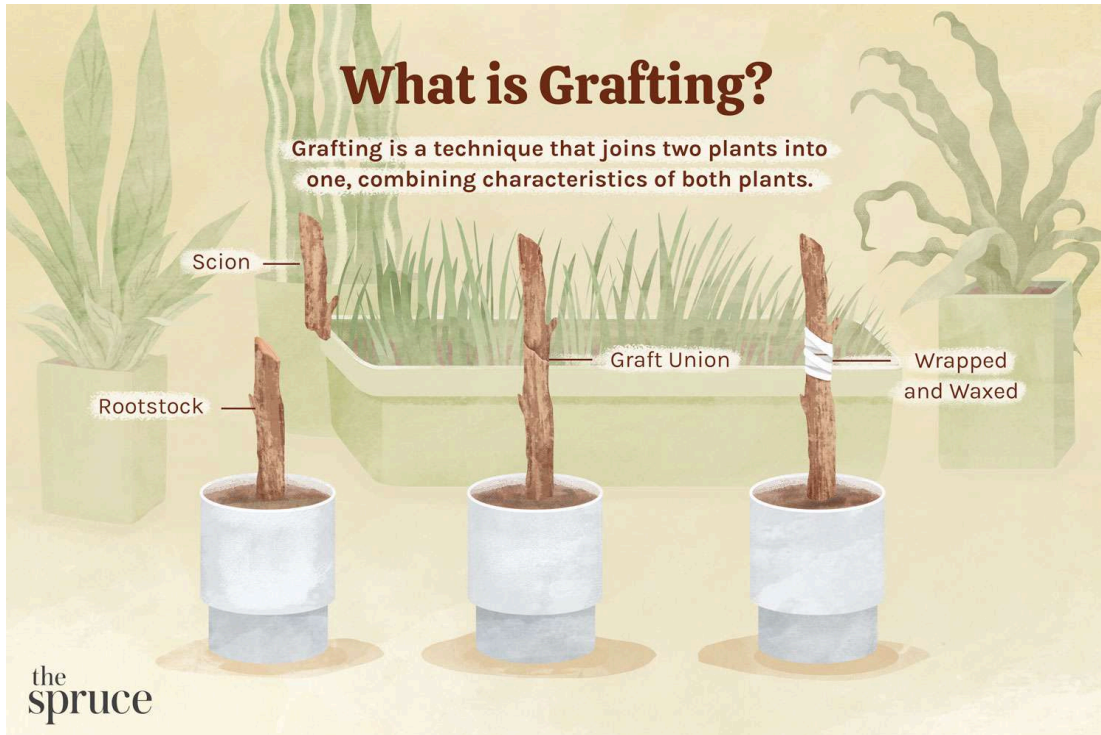


Figure 10:
Diagram of the budding process (Science Facts, 2023)

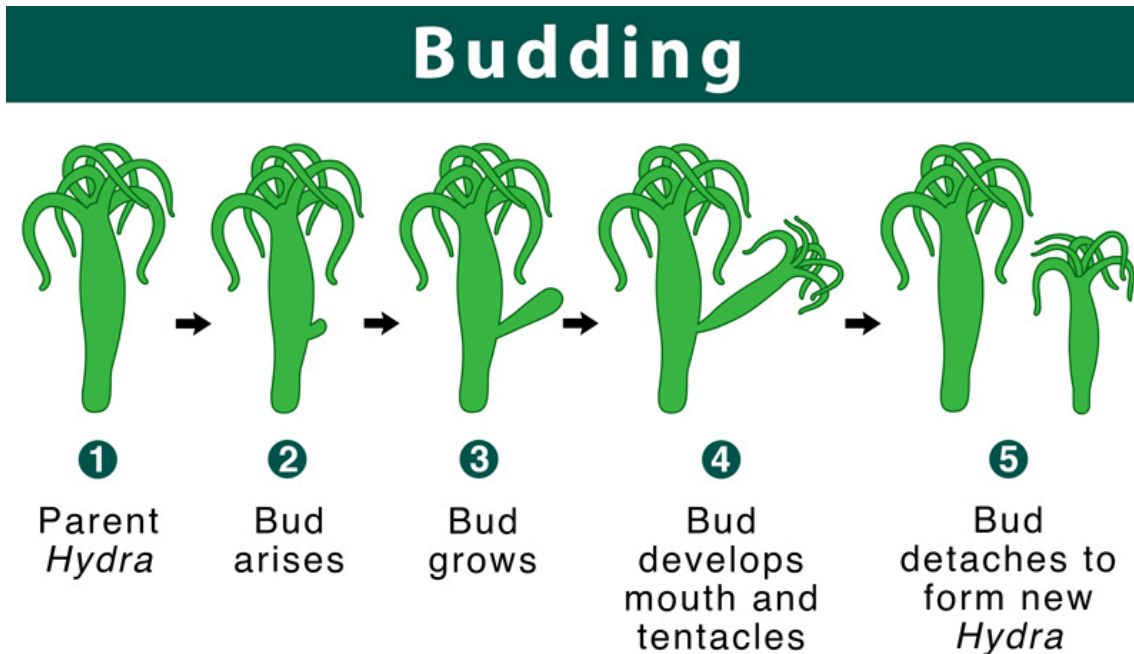
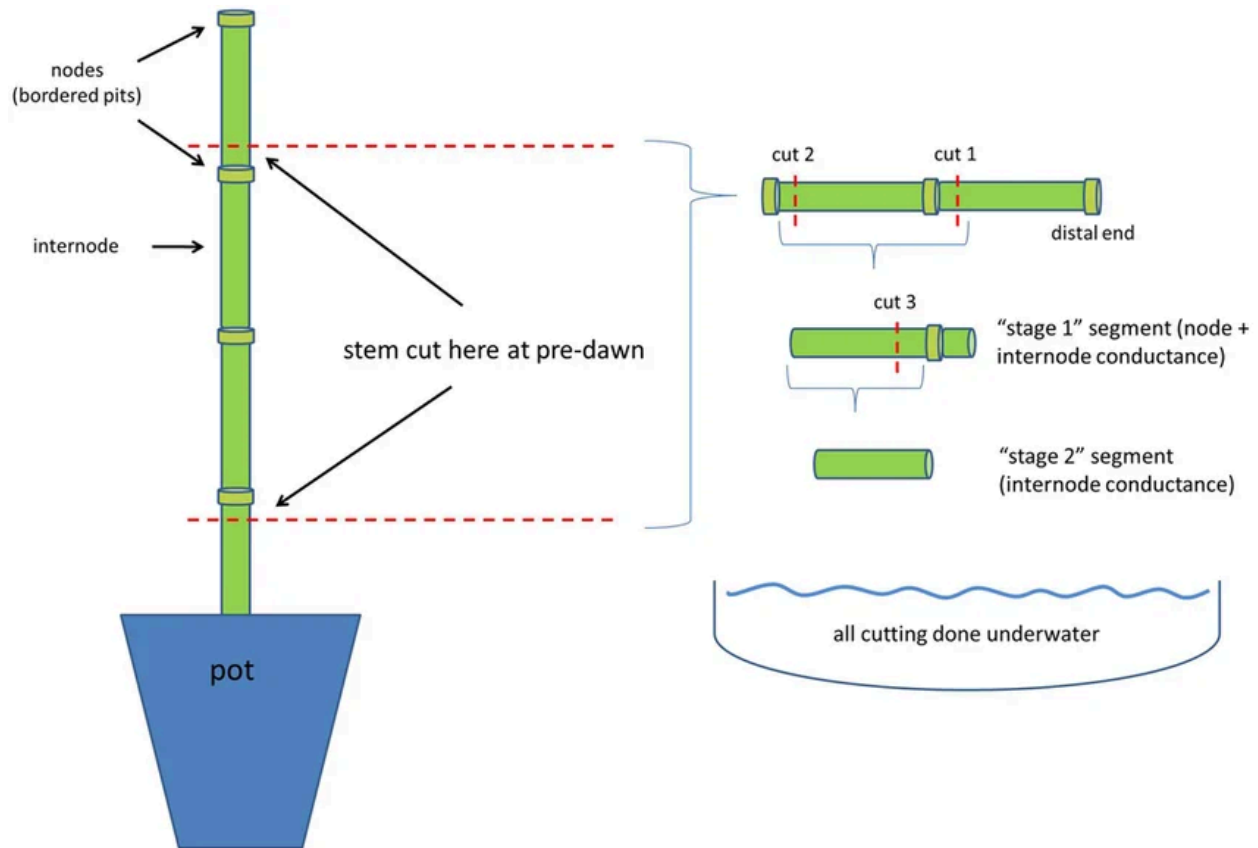


Figure 11:
Diagram of stem cuttings (Gleason, 2017)



Vegetative propagation is widely used in cacao agriculture because it allows farmers to replicate elite genotypes and establish plantations with uniform growth patterns and predictable productivity (González-Orozco et al., 2022).

4.1.3 Nursery propagation

Nursery propagation is an important stage in cacao cultivation because young seedlings are highly sensitive to environmental stress. Seeds or vegetative propagules are typically planted in containers filled with nutrient rich substrate composed of soil, organic matter and sand. Controlled nursery environments provide optimal temperature humidity and shading conditions that support seedling establishment and reduce mortality (Argout et al., 2011).

Seedlings are generally maintained in nurseries for several months until they develop adequate root systems and reach sufficient height for field transplantation. During this stage irrigation and

shade management are essential to ensure healthy plant development. Young cacao seedlings possess a shallow and still developing root system, which limits their ability to access water from deeper soil layers. As a result, consistent irrigation is required to maintain adequate soil moisture and prevent water stress, which can lead to reduced growth rates, leaf wilting, and increased mortality (González-Orozco et al., 2022). At the same time, excessive watering must be avoided, as poorly drained soils can cause root hypoxia and promote the development of fungal diseases such as root rot (Hume et al., 2016).

Shade management is equally critical during early development because cacao is physiologically adapted to understory conditions in tropical forests. Seedlings exposed to direct sunlight may experience photoinhibition (reduced photosynthetic capacity), increased transpiration rates, and thermal stress, all of which can impair photosynthetic efficiency and damage leaf tissues. Providing partial shade typically between 50% and 70% helps regulate temperature, reduce evaporation and maintain a stable microclimate that supports optimal physiological functioning (Schneider et al., 2018).

Additionally, proper shade levels contribute to balanced growth by preventing excessive elongation or stress induced morphological changes. As seedlings mature, gradual reduction of shade allows acclimation to higher conditions, facilitating the transition to field environments where light availability may be greater (González-Orozco et al., 2022).

4.1.4 Propagation by cuttings

Propagation by cuttings involves the use of stem segments obtained from healthy donor plants. These cuttings are treated with rooting hormones and placed in moist substrates to stimulate root formation and shoot development. Once the root system develops, the new plants can be transplanted to nursery containers or directly into field conditions. This method allows the rapid multiplication of selected cacao varieties while preserving their genetic characteristics, which is important for maintaining consistent production and quality within plantations (Motamayor et al., 2008).

4.1.5 Field planting

When seedlings or vegetatively propagated plants reach enough development, they are transplanted into permanent field locations. Field planting usually occurs during periods of adequate rainfall to ensure sufficient soil moisture for root establishment. Trees are typically spaced three to four meters apart to allow proper canopy development and air circulation (Niether, et al., 2018).

Cacao plantations often incorporate shade trees in agroforestry systems. These shade trees help regulate microclimatic conditions, reduce excessive sunlight exposure, and improve soil fertility through organic matter accumulation (Niether, et al., 2018).

A variety of tree species can be used in cacao based agroforestry systems depending on local climatic conditions, soil characteristics, and management objectives. Commonly used shade species include nitrogen fixing legumes such as *Inga edulis* and *Gliricidia sepium*, which are widely valued for their ability to improve soil fertility through biological nitrogen fixation and the continuous deposition of leaf litter. These species also grow relatively quickly and can be pruned easily, allowing farmers to regulate shade levels according to the needs of cacao plants (Schroth & Harvey, 2007).

In addition, fruit trees such as *Musa spp.* (banana/plantain), *Persea americana* (avocado), and *Citrus spp.* They are commonly used in agroforestry systems. These species provide additional sources of income and food while offering temporary or intermediate shade during the early stages of cacao development. For example, banana plants are particularly useful as nurse crops because they establish quickly and provide immediate shade for young cacao seedlings (Schroth & Harvey, 2007).

The selection of appropriate shade tree species is essential for optimizing cacao productivity and sustainability. Ideal species should have compatible root systems that minimize competition for water and nutrients, manageable canopy structures that allow pruning, and ecological benefits such as soil enrichment or biodiversity support. When properly managed, a diverse agroforestry system can enhance both the ecological resilience and economic stability of cacao production systems (Niether et al., 2018).

4.2 Cultivation and crop management

4.2.1 General cultivation practices

Cacao cultivation requires environmental conditions similar to those found in tropical rainforests. Optimal growth occurs in warm climates with temperatures between 21°C and 32°C and high annual rainfall. The species grows best in well drained soils rich in organic matter, as its root system is relatively shallow and sensitive to waterlogging or drought conditions (González-Orozco et al., 2022).

Agroforestry systems are commonly used in cacao production because they mimic natural forest ecosystems. These systems integrate cacao trees with other plant species that provide shade, enhance biodiversity and improve ecological stability within the agricultural landscape (Niether, et al., 2018).

This mimicry is achieved through the development of a multilayered canopy structure, in which taller shade trees form an upper layer while cacao trees occupy the understory. This arrangement

regulates light intensity, reduces temperature fluctuations, and maintains higher humidity levels, all of which are conditions to which cacao is naturally adapted (Schroth & Harvey, 2007). By reducing direct solar radiation and evapotranspiration, shade trees help prevent physiological stress and improve photosynthetic efficiency in cacao plants (Niether et al., 2018).

Furthermore, agroforestry systems enhance biodiversity by providing habitats for a wide range of organisms, including pollinators, natural pest predators, and soil microorganisms. These biological interactions contribute to ecosystem services such as pollination, pest control, and nutrient cycling which are essential for maintaining productive and sustainable cacao systems (Schroth & Harvey, 2007). Leaf litter from associated plant species increases soil organic matter, improving soil structure, water retention and nutrient availability over time (Niether et al., 2018).

4.2.2 Fertilizing

Adequate nutrient supply is essential for cacao growth and productivity. The most important macronutrients required for plant development include nitrogen, phosphorus and potassium. These nutrients support vegetative growth, root development, and fruit formation. Fertilizers are often applied together with organic materials such as compost or manure to improve soil structure and nutrient availability. Balanced fertilization programs can significantly increase cacao yield and improve the quality of cacao beans produced by plantations (Hume et al., 2016).

The quantity of fertilizer required for cacao plants varies depending on soil fertility, plant age and environmental conditions; however, general recommendations have been established for effective nutrient management. For young cacao plants (0-3 years), applications typically range from approximately 40-60 g of nitrogen (N), 20-30g of phosphorus (P_2O_5), and 40-60 g of potassium (K_2O) per plant per year, divided into multiple applications to ensure efficient nutrient uptake (Hume et al., 2016).

For mature, productive trees, nutrient requirements increase substantially due to fruit development demands. Annual applications may range from approximately 100-200 g of potassium per tree, often split into two or three applications throughout the year to coincide with rainfall patterns and key growth stages such as flowering and pod development (Aikpokpodion, 2010; Hume et al., 2016).

In addition to synthetic fertilizers, the incorporation of organic matter such as compost, manure or leaf litter from shade trees can contribute between 5 and 10 tons per hectare annually. This

organic input enhances soil structure, increases water retention, and supports microbial activity which improves nutrient cycling and long term soil fertility (Hume et al., 2016).

4.3 Growth and productive stages

4.3.1 Growth stages

The life cycle of cacao begins with seed germination and seedling establishment. After transplantation into the field, cacao plants enter a juvenile vegetative phase that typically lasts several years while the main stem and branching architecture develop. During this stage plants allocate most resources to vegetative growth rather than reproduction (González-Orozco et al., 2022).

4.3.2 Fruiting

Fruiting occurs when mature cacao trees produce flowers that successfully develop into pods following pollination. However, only a small percentage of cacao flowers develop into mature fruits due to biological and environmental constraints (Motamayor et al., 2008).

After successful pollination, cacao pods require approximately five to six months to mature. During this period, the fruits undergo physiological and biochemical changes that lead to the development of cacao beans inside the pod (Argout et al., 2011).

4.3.3 Harvesting

Harvesting involves manually removing cacao pods from the trunk or branches of the tree using knives or specialized tools. Pod maturity is generally identified by color changes in the fruit and other visual indicators (Niether, et al., 2018).

After harvesting, pods are opened to extract the cacao beans which are then fermented and dried. These post-harvest processes are essential for the development of the characteristic flavor compounds that define chocolate (Niether, et al., 2018).

4.4 Pest and disease Management

4.4.1 Management of pests and diseases

Cacao cultivation is affected by several pests and diseases that can significantly reduce crop productivity. Important fungal diseases include black pod disease, **Figure 12**, caused by *Phytophthora* species, Witches' Broom disease, **Figure 13**, caused by *Moniliophthora perniciosa*, and frosty pod rot, **figure14**, caused by *Moniliophthora roreri*. These pathogens can damage fruits, branches and leaves, resulting in major yield losses. Insect pests such as cocoa pod borers, mealybugs and aphids may also attack cacao plants and reduce drop health. Effective pest management requires monitoring, sanitation practices and removal of infected plant material (Motamayor et al., 2008).

Figure 12

Picture of how black pod disease appears on cacao (Myers, 2022)

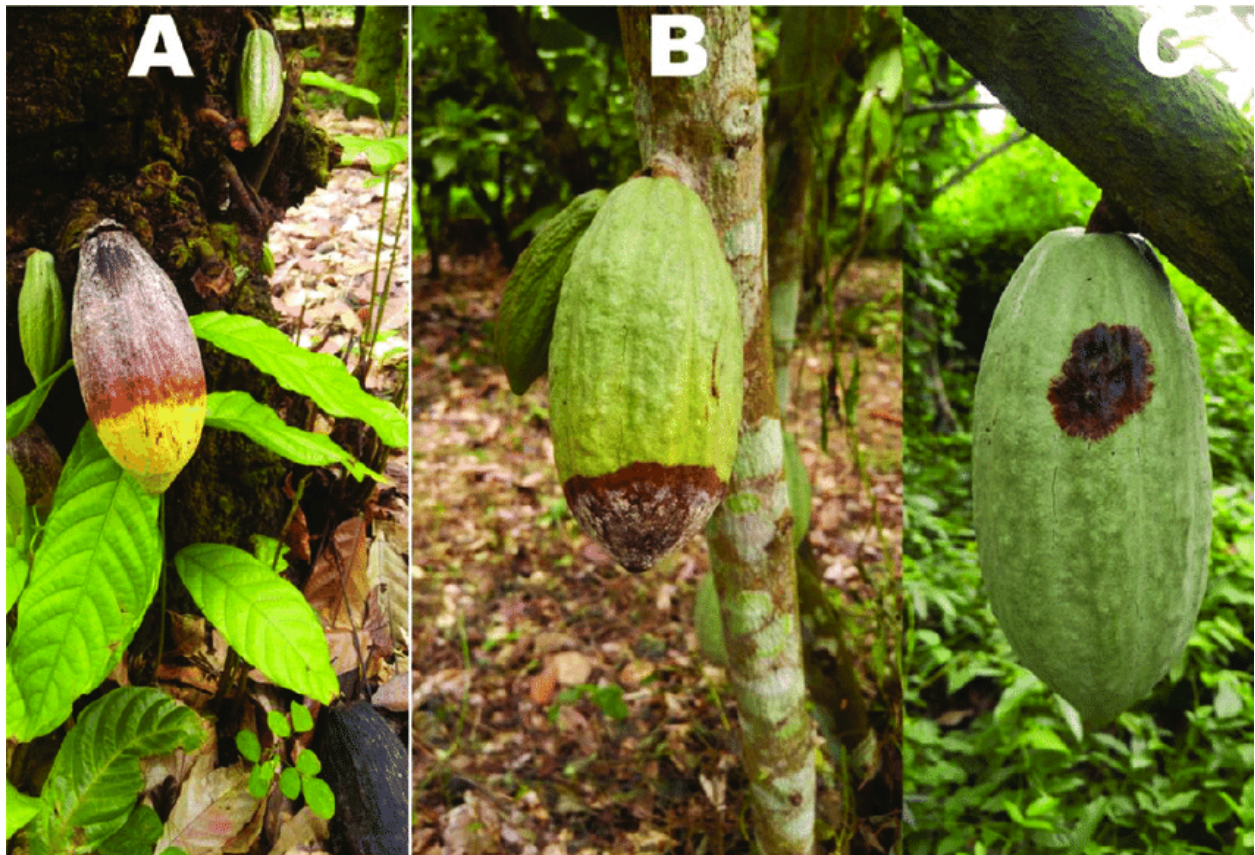


Figure 13

Picture of how witches broom disease appears on cacao (Aime et al., 2005).



Figure 14

Picture of how frosty pod rot appears on cacao (Caribbean Invasive Alien Species Network, 2010)



4.4.2 Pest and disease control

Integrated pest management strategies combine cultural, biological and chemical approaches to control pests while minimizing environmental impacts. Cultural practices such as pruning, sanitation and adequate plant spacing help reduce humidity and improve airflow, limiting conditions favorable for disease development. Biological control agents and resistant cacao varieties are increasingly used to reduce dependency on chemical pesticides while maintaining crop productivity (Niether, et al., 2018).

Pruning involves the removal of excess, dead or infected branches, which allows greater penetration of sunlight and improves air circulation within the canopy. This reduction in canopy density lowers relative humidity and leaf wetness duration, both of which are key environmental

factors required for the germination and spread of fungal pathogens (Lopez et al, 2016; USDA ARS, 2000). In addition, regular pruning has been shown to significantly reduce disease levels by physically removing infected plant tissues and limiting pathogen reservoirs within the tree (Tandingan et al., 1990).

Sanitation practices, including the removal of diseased pods, fallen debris, and infected plant material are equally important in interrupting the life cycle of pathogens. Many cacao diseases, such as frosty pod rot and black pod disease, rely on infected plant residues as sources of inoculum; therefore their removal reduces the amount of pathogen available to spread within the plantation (Opoku et al, 2007; Armengot et al., 2020). Studies have shown that sanitary pruning alone can reduce disease incidence by up to 30% highlighting its effectiveness as a low cost and sustainable control strategy (Castro et al., 2025)

Adequate plant spacing further enhances these effects by preventing overcrowding, which reduces competition for light and improves airflow between trees. Proper spacing minimizes the formation of humid microenvironments that favor pathogen development and facilitates faster drying of plant surfaces after rainfall, thereby reducing infection rates (Tschardt et al., 2022). Together, these cultural practices form a fundamental component of integrated pest management systems, as they not only reduce disease pressure but also improve overall plant health and productivity while minimizing reliance on chemical control methods (USDA ARS, 2000)

4.5 Pruning and re-planting

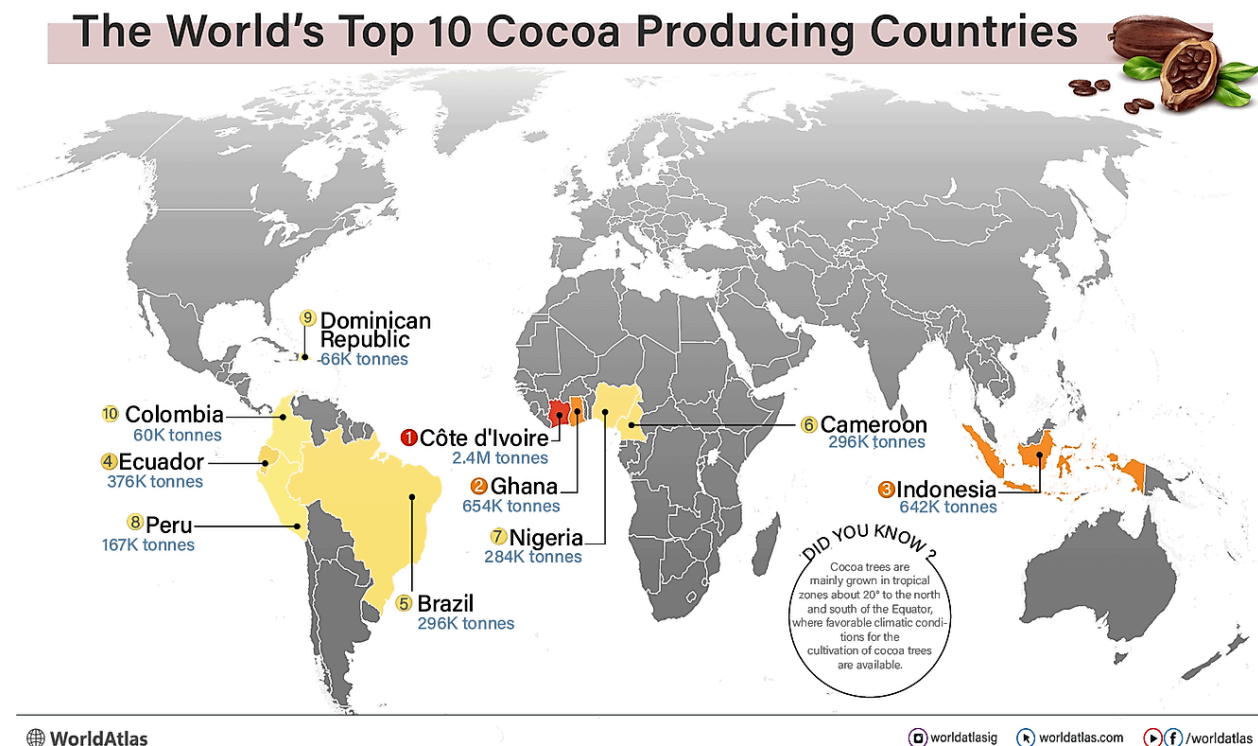
Pruning is an important management practice that helps maintain tree structure, improve light penetration and promote healthy growth. Pruning removes dead diseased or overcrowded branches and encourages the development of productive canopy architecture. Re-planting may be necessary when older trees become less productive or when disease outbreaks affect less plantation areas. Introducing improved plant varieties can increase yield and enhance resistance to environmental stress and pathogens (Niether, et al., 2018).

Chapter 5: Importance, Markets, and Uses

5.1 Economic and global importance

Theobroma cacao is one of the most economically significant tropical crops worldwide due to its role as the primary raw material for chocolate production. The global demand for cocoa beans has increased steadily over the past decades, driven by population growth, rising incomes and expanding markets for chocolate and cocoa based products. Cacao production exceeds approximately 5 million metric tons annually, with the majority originating from tropical regions in West Africa, Latin America and Southeast Asia, as seen in **Figure 15**. The crop plays a critical role in the livelihoods of millions of smallholder farmers, particularly in developing countries where cacao cultivation serves as a major source of income and employment (Food and Agriculture Organization, 2023).

Figure 15:
The World's Top 10 Cocoa Producing Countries (Joseph, 2025)



At global level, cacao is considered a high value commodity in international trade, with the chocolate industry generating billions of dollars annually. The economic importance of cacao

extends beyond agriculture into manufacturing, retail, and export sectors, making it a contributor to global agribusiness systems (International Cocoa Organization, 2024).

5.2 Regional and national importance

5.2.1 Major producing regions

Cacao production is concentrated in a limited number of tropical countries located near the equator. The largest producers globally are Côte d'Ivoire and Ghana, which together account for more than 60% of global cacao production. Other significant producers include Indonesia, Ecuador, Nigeria, and Brazil (International Cocoa Organization, 2024).

In Latin America, cacao has both economic and cultural importance, particularly in countries such as Ecuador and Colombia, where it is cultivated as both a commercial export crop and a traditional agricultural product. Regional production systems often combine cacao cultivation with agroforestry practices, contributing to environmental sustainability and biodiversity (González-Orozco et al., 2022).

5.2.2 Contribution to local economies

At the national and local level, cacao plays a vital role in rural economies. In many producing countries, cacao farming is dominated by smallholder farmers who rely on the crop as a primary source of income. The cultivation, harvesting, processing and commercialization of cacao create employment opportunities across the world (Food and Agriculture Organization, 2023).

In addition to direct economic benefits, cacao production supports infrastructure development, trade networks and export revenues. In some countries, cacao exports represent a significant portion of agricultural GDP, highlighting the crop's importance to national economic stability (International Cocoa Organization, 2024).

5.3 Market structure and trade

5.3.1 Global market characteristics

The global cacao market is characterized by a relatively concentrated production base and a highly internationalized trade system. Most cacao is produced in developing countries but exported to industrialized nations where it is processed into chocolate and other products. This creates a global value chain in which raw materials are produced in tropical regions and value added processing occurs primarily in Europe and North America (International Cocoa Organization, 2024).

The market is influenced by factors such as climate variability, political stability in producing regions, and fluctuations in global demand. Price volatility is a common feature of the cacao market, affecting both producers and international buyers (Food and Agriculture Organization, 2023).

5.3.2 Domestic markets

Domestic consumption is also significant in some producing countries, where cacao is used in traditional foods and beverages. In recent years, there has been growth in local chocolate industries within producing countries, contributing to increased value addition at the national level (González-Orozco et al., 2022).

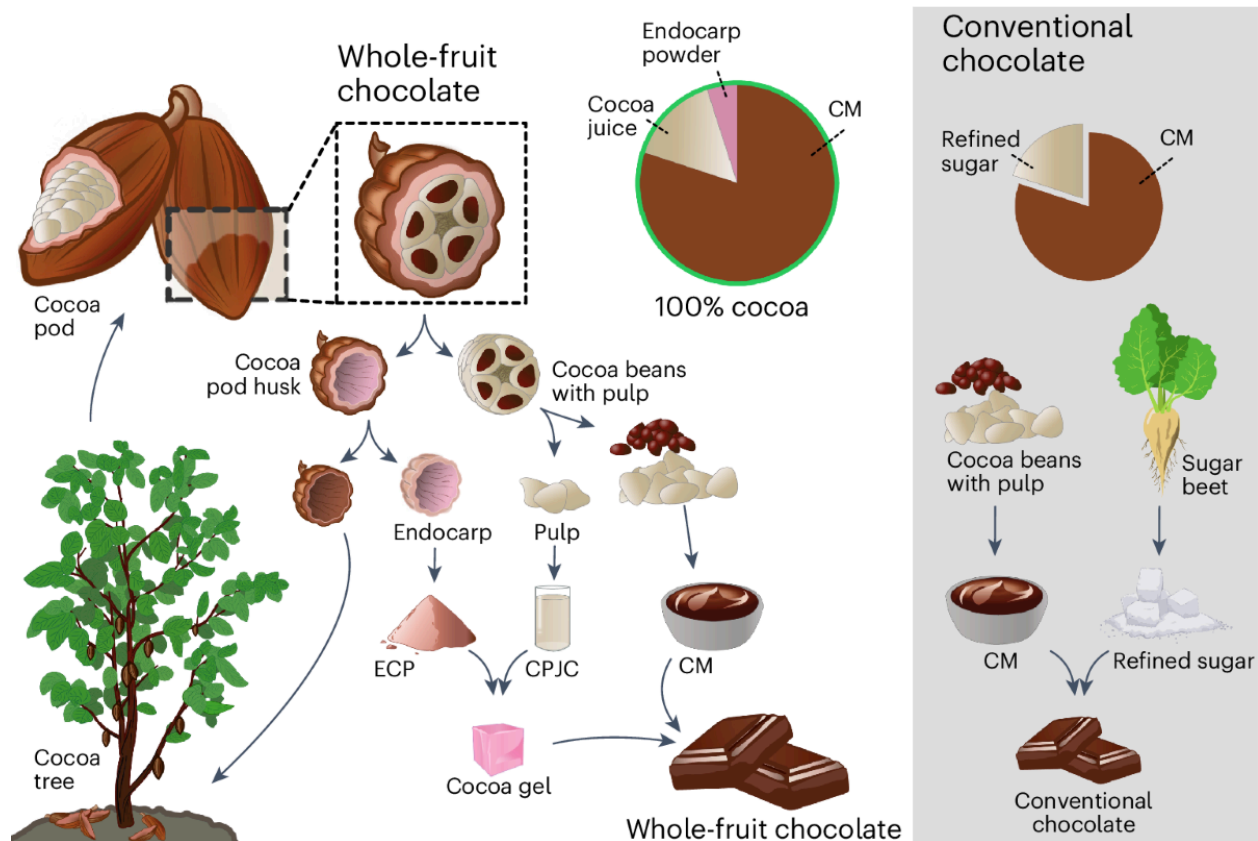
5.4 Products and industrial uses

5.4.1 Primary products

The primary product derived from cacao is the cacao bean, which is obtained from the seeds of the cacao pod as you can see in **Figure 16**. After harvesting, beans undergo fermentation and drying processes that develop their characteristic flavor and aroma. These processed beans serve as the raw material for chocolate production (International Cocoa Organization, 2024).

Figure 16:

Representation of (a) cacao tree, (b) cacao fruits, (c) cacao pods, and (d, e) bulk and fine cacao beans (Physicochemical Phenomena in the Roasting of Cocoa, 2022)



Cacao beans are further processed into intermediate products such as cocoa liquor, cocoa butter and cocoa powder. These products are essential ingredients in the manufacture of chocolate, confectionery, beverages, and baked goods (Afoakwa, 2010).

5.4.2 Value-added products

Cacao undergoes significant value addition through industrial processing. Cocoa butter is widely used in the production of chocolate and cosmetic products, while cocoa powder is used in food and beverage industries. Chocolate, the most well known cacao derived product is produced in a wide range of forms including dark, milk and white chocolate. In addition to food products, cacao derivatives are used in pharmaceuticals and cosmetics due to their antioxidant properties. These diverse applications increase the economic value of cacao and expand its importance beyond the agricultural sector (Afoakwa, 2010).

5.5 Socioeconomic and environmental significance

Cacao cultivation has important social and environmental implications. It provides livelihoods for millions of farmers and contributes to rural development in tropical regions. However, challenges such as price instability, labor conditions and environmental degradation can affect the sustainability of cacao production (Food and Agriculture Organization, 2023).

Agroforestry based cacao systems offer environmental benefits by preserving biodiversity, improving soil health and reducing deforestation. Sustainable production practices are increasingly promoted to ensure long term productivity and environmental conservation (González-Orozco et al., 2022).

References

Aikpokpodion, P. O. (2010). Nutrients dynamics in cocoa soils, leaf and beans in Ondo State, Nigeria. *Journal of Agricultural Science*, 2(1).

<https://ccsenet.org/journal/index.php/jas/article/view/4698>

Argout, X., Sempere, G., Jouffe, V., Droc, G., Fouet, O., Guiltinan, M., Lanaud, C., & Boccara, M. (2011). The genome of *Theobroma cacao*. *Nature Genetics*, 43(2), 101–108.

<https://pubmed.ncbi.nlm.nih.gov/21186351/>

Armengot, L., Ferrari, L., Milz, J., Velásquez, F., Hohmann, P., & Schneider, M. (2020). Cacao agroforestry systems do not increase pest and disease incidence compared with monocultures under good cultural management practices. *Crop Protection*, 130, 105047.

<https://doi.org/10.1016/j.cropro.2019.105047>

Baque Zambrano, E., Ceme Barreto, G., & Jaimez, R. (2024). Efecto de la temperatura y la radiación sobre la respuesta fisiológica del cacao (*Theobroma cacao L.*): estrategias de mejoramiento. *Ciencia y Tecnología*, 17(1), 24–32.

<https://doi.org/10.18779/cyt.v17i1.713>

Bhattacharjee, R. (2018). *Taxonomy/Classification of Cocoa*. Burleigh Dodds Science Publishing.

https://www.researchgate.net/publication/320419243_TaxonomyClassification_of_Cocoa

Caribbean Invasive Alien Species Network. (2010, August 7). *Frosty pod rot*.

<https://caribbeaninvasives.org/index.php/2010/08/07/frosty-pod-rot-2/>

Castro León, A. B., & Rodríguez Gómez, P. J. (2025). Techniques to reduce monilia in cacao.

<https://agris.fao.org/search/en/providers/124888/records/682f2f169d0aa4165340b54b>

Cocoa bean production by region. (2026). *UN FAO and Our World in Data*. Retrieved March 5, 2026, from

<https://ourworldindata.org/grapher/cocoa-beans-production-by-region>

Cornejo, O. E., Yee, M.-C., Dominguez, V., Andrews, M., Sockell, A., Strandberg, E., Livingstone, D., Stack, C., Romero, A., Umaharan, P., Royaert, S., Tawari, N. R., Ng, P., Gutierrez, O., Phillips, W., Mockaitis, K., Bustamante, C. D., & Motamayor, J. C. (2018). Population genomic analyses of the chocolate tree, *Theobroma cacao* L., provide insights into its domestication process. *Communications Biology*, *1*(1), 167.

<https://doi.org/10.1038/s42003-018-0168-6>

Cubol, R. V., Meneses-Cubol, G. M. N., & Villamor Cubol, J. R. (2023). Germination performance of cacao (*Theobroma cacao* L.) seed: A basis for seed storage prototype. *International Journal of Innovative Science and Research Technology*, *8*(12).

<https://ijisrt.com/assets/upload/files/IJISRT23DEC493.pdf>

Daniel, M. A. S., Monteiro, D. B. M., Lobato, E. M. S. G., Rodrigues, A. E., Oliveira, A. S. de, Pamplona, V. M. S., Daniel, R., & Vanessa, I. P. A. (2025). Evaluation of micronutrients in the soil and leaves of *Theobroma cacao*. *Revista de Gestão Social e Ambiental*, 19(2), e011144.

<https://doi.org/10.24857/rgsa.v19n2-080>

Francisco-Santiago, S. P., Palma-López, D. J., Sánchez-Hernández, R., Obrador-Olán, J. J., & García-Alamilla, P. (2023). Fertilidad edáfica y nutrición en el cultivo de cacao (*Theobroma cacao* L.) en tres suelos de Tabasco, México. *Terra Latinoamericana*, 41.

<https://doi.org/10.28940/terra.v41i0.1116>

Gleason, S., Wiggans, D., Bliss, C., Young, J., Cooper, M., Willi, K., & Comas, L. (2017). Embolized stems recover overnight in *Zea mays*: The role of soil water, root pressure, and nighttime transpiration. *Frontiers in Plant Science*, 8.

<https://doi.org/10.3389/fpls.2017.00662>

González-Orozco, C. E., Cuervo, M. C., & Orozco, J. L. (2022). Regionalization of cacao (*Theobroma cacao* L.) in Colombia. *Frontiers in Sustainable Food Systems*, 6, 925800.

<https://www.frontiersin.org/articles/10.3389/fsufs.2022.925800/full>

Harahap, S., Siregar, E. S., & Mahmud, A. (2022). Effectiveness of pest control of cocoa using pruning.

<https://talenta.usu.ac.id/jpt/article/view/9053>

Hume, D. E., Ryan, G. D., Gibert, A., Helander, M., Mirlohi, A., & Sabzalian, M. R. (2016). Epichloë fungal endophytes for grassland ecosystems. In E. Lichtfouse (Ed.), *Sustainable agriculture reviews* (Vol. 19). Springer.

https://doi.org/10.1007/978-3-319-26777-7_6

Jaramillo, J., Muchugu, E., Vega, F. E., & García, C. (2024). Floral biology and flower visitors of cocoa (*Theobroma cacao*). *Agricultural and Forest Entomology*.

<https://www.sciencedirect.com/science/article/pii/S0367253024000331>

Lannotti, M. (2024, January 8). What does grafting mean when it comes to plants? *The Spruce*.

<https://www.thespruce.com/what-does-grafting-mean-4125565>

Leiva-Rojas, E. I., Hernández-Taborda, C., & Ramirez, R. (2024). Application of photosynthesis models to determine light requirements in three cacao clones. *Ingeniería e Investigación*, 44(3).

<https://doi.org/10.15446/ing.investig.107078>

López Juárez, S. A., et al. (2016). Effect of pruning on cocoa plantations.

https://www.scielo.org.mx/scielo.php?pid=S2007-09342016001002807&script=sci_arttext&tlng

[=en](#)

Motamayor, J. C., Risterucci, A. M., Lopez, P. A., Coutiño, C. A., Ortiz, C. F., & Lanaud, C. (2008). Geographic and genetic population differentiation of the Amazonian chocolate tree (*Theobroma cacao* L.). *PLoS ONE*, 3(10), e3311.

<https://doi.org/10.1371/journal.pone.0003311>

Myers, A. (2022, March 24). Breakthrough in stopping spread of black pod rot in cocoa-growing regions. *Confectionery News*.

<https://www.confectionerynews.com/Article/2022/03/24/breakthrough-in-stopping-spread-of-black-pod-rot-in-cocoa-growing-regions>

Niether, W., Armengot, L., Andres, C., Schneider, M., & Gerold, G. (2018). Shade trees and tree pruning alter throughfall and microclimate in cocoa (*Theobroma cacao* L.) production systems. *Annals of Forest Science*, 75(2), 38.

<https://doi.org/10.1007/s13595-018-0723-9>

Odoemelam, V. K., Nwaigbo, L. C., Anyim, A., Aneni, T. I., & Anozie, C. C. (2023). Germination and early growth performance of cocoa (*Theobroma cacao* L.) seedlings in planting media. *Trends in Agricultural Sciences*, 2(3), 274–280.

<https://doi.org/10.17311/tas.2023.274.280>

Opoku, I. Y., et al. (2007). Sanitation and disease control in cacao.

<https://doczz.net/doc/8904527/assessment-of-sanitation-and-fungicide-application-direct>

Richardson, J. E., Whitlock, B. A., Meerow, A. W., & Madriñán, S. (2015). The age of chocolate: A diversification history of *Theobroma* and Malvaceae. *Frontiers in Ecology and Evolution*, 3.

<https://doi.org/10.3389/fevo.2015.00120>

Salazar, J. C. S., Melgarejo, L. M., Casanoves, F., Rienzo, J. A. D., DaMatta, F. M., & Armas, C. (2018). Photosynthesis limitations in cacao leaves under different agroforestry systems in the Colombian Amazon. *PLOS ONE*, 13(11), e0206149.

<https://doi.org/10.1371/journal.pone.0206149>

Tandingan, I. C., & Ampo, A. E. (1990). Cultural control of cacao diseases using pruning.

<https://agris.fao.org/search/en/providers/122430/records/6471e6bf2a40512c710e8fde>

Tscharntke, T., et al. (2022). Cacao agroforestry spacing and management.

<https://link.springer.com/article/10.1007/s10457-022-00796-x>

United States Department of Agriculture. (2025, February 24). *Taxon: Theobroma cacao* L. <https://npgsweb.ars-grin.gov/gringlobal/taxon/taxonomydetail?id=101885>

USDA Plants Database. (n.d.). *Plant profile: Theobroma cacao*. Retrieved March 5, 2026, from

<https://plants.usda.gov/plant-profile/THCA>

Wolcott, K., Bilbao, A., & Thomas, E. (2023). 3D pollination biology using micro-computed tomography and geometric morphometrics in *Theobroma cacao*. *New Phytologist*.

<https://pmc.ncbi.nlm.nih.gov/articles/PMC10617321/>

Zarrillo, S., Gaikwad, N., Varghese, N., & Johnson, T. (2018). The use and domestication of *Theobroma cacao* during the mid-Holocene in the Upper Amazon. *Scientific Reports*, 8, 16620.

https://www.researchgate.net/publication/328582045_The_Use_and_Domestication_of_Theobroma_cacao_during_the_Mid-Holocene_in_the_Upper_Amazon

Zarrillo, S., Gaikwad, N., Lanaud, C., Powis, T., Viot, C., Lesur, I., Fouet, O., Argout, X., Guichoux, E., Salin, F., Loor, R., Bouchez, O., Vignes, H., Severts, P., Hurtado, J., Yopez, A., Grivetti, L., Blake, M., & Valdez, F. (2018). The use and domestication of *Theobroma cacao* during the mid-Holocene in the Upper Amazon. *Nature Ecology & Evolution*, 2.

<https://doi.org/10.1038/s41559-018-0697-x>