UNIVERSITY OF SOUTHAMPTON

FACULTY OF ENGINEERING AND THE ENVIRONMENT

Predicting suitable areas for cultivation and conservation of the baobab tree and investigating superior sources of planting material

by

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Abstract

The baobab tree (*Adansonia digitata* L.), with more than 300 uses and commercial value in EU and US, has been identified as one of the most important edible savanna trees to be conserved, domesticated and valorised in Africa. A decline in baobab populations due to overexploitation and/or changes in climate could have a significant negative effect on African livelihoods. Therefore, it is important to determine potential strategies for conservation and cultivation. The present and potential future distributions of the baobab tree were studied using Maxent niche modelling framework. And, in order to contribute to the selection of superior materials for cultivation, fruit morphology was studied *in situ* (in Malawi and Mali) while leaf and seedling morphology were studied *in situ* (in Benin and Malawi) and in a greenhouse experiment.

Maxent modelling suggests that predicted changes in climate will have a negative effect on baobab tree distribution in Africa: only a percentage of the present distribution was predicted to be suitable in the future. Some countries were found not to have any suitable habitats for the baobab tree in the future. Several conservation strategies are recommended, such as *in situ* conservation in Protected Areas; *ex situ* conservation in Seed Banks and conservation through ‘sustainable utilisation’.

Modelling results also showed that the baobab tree could be widely cultivated in most countries in south-eastern Africa and in the Sudano-Sahelian zone of West Africa. India, north-west Australia, Madagascar, north-east Brazil and Mexico could be other suitable places for cultivating the baobab tree outside Africa. Although results from modelling should be validated with *in situ* seedling experiments, there seems to be potential for the wide cultivation of this species.

Significant differences in leaf, fruit and seedling morphology were observed between Benin, Mali and Malawi and also within each country. While some characteristics were correlated with environmental differences between study sites, others might be genetically determined. It seems that genetic and physiological effects play a role in baobab fruit, leaf and seedling morphology. Thus, there is room for selecting high quality baobab planting materials.

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Declaration of Authorship

I, Aida Cuni Sanchez, declare that the thesis entitled ‘Predicting suitable areas for cultivation and conservation of the baobab tree and investigating superior sources of planting material’ and the work presented in the thesis are both my own, and have been generated by me as the result of my own original research. I confirm that:

- this work was done wholly or mainly while in candidature for a research degree at this University;
- where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;
- where I have consulted the published work of others, this is always clearly attributed;
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- parts of this work have been published as:

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Acronyms

AFLP	Amplified Fragment Length Polymorphism analysis
AUC	Area Under the ROC Curve
BIO	bioclimatic variable extracted from WorldClim
BIOCLIM	Bioclimatic Envelope
BRT	Boosted Regression Trees
CBD	Convention on Biological Diversity
CCCma	Canadian Centre for Climate Modelling and Analysis
CSSV	Cacao swollen shoot badnavirus
CEC	Commission of the European Communities
CIAT	Centro Internacional de Agricultura Tropical (International Centre for Tropical Agriculture)
CIRAD	Centre de Coopération Internationale en Recherche Agronomique pour le Développement (French Agricultural Research Center for Developing Countries)
CSIRO	Commonwealth Scientific and Industrial Research Organisation
CYMV	Cacao yellow mosaic tymovirus
DADOBAT	Domestication and Development of Baobab and Tamarind
DBH	Diameter at Breast Height
DNA	Deoxyribonucleic acid
ENFA	Ecological Niche Factor Analysis
EPO	European Patent Office
EU	European Union
FAO	Food and Agriculture Organization of the United Nations
FDA	US Food and Drug Administration
FW	Fresh Weight
GA	Generic Algorithm
GAM	Generalized Additive Model
GARP	Genetic Algorithm for Rule Set Production
GBH	Girth at Breast Height
GBIF	Global Biodiversity Information Facility
GCM	General Circulation Model
GDP	Gross Domestic Product
GIS	Geographic Information Systems
GLM	Generalized Linear Model
GNS	GEOnet Names Server
HadCM3	Hadley Centre for Climate Prediction and Research
HWSD	Harmonized World Soil Database
IPCC	Intergovernmental Panel on Climate Change
KNP	Kruger National Park
LNP	Limpopo National Park
MARS	Multivariate Adaptive Regression Splines
MAXENT	Maximum Entropy method for species' distribution modelling
ML	Medial Leaflet
NDVI	Normalized Difference Vegetation Index
NRC	National Research Council
NTFP	Non-Timber Forests Products
PCMDI	Program for Climate Model Diagnosis and Intercomparison
PRECIS	National Herbarium Pretoria (PRE) Computerised Information System
ROC	Receiver Operating Characteristic
SCUC	Southampton Centre for Underutilised Crops
SLW	Specific Leaf Weight
SRL	Specific Root Length
UA	University of Antwerp

UAC	University of Abomey-Calavi
UCSB	University of California, Santa Barbara
UNESCO	United Nations Educational, Scientific and Cultural Organization
US	United States
WDPA	World Database on Protected Areas

CHAPTER 1. Introduction and literature review

1.1 Background and aims

Farmers have used and maintained the baobab tree (*Adansonia digitata* L.) for many generations in the semi-arid and arid zones of sub-Saharan Africa. The baobab tree is a massive deciduous long-lived tree whose leaves, fruit pulp and seeds are comestible. Every part of the baobab is used: roots, bark, wood, leaves, flowers, gum, fruits and seeds (Wickens and Lowe 2008, Buchmann et al. 2010). The tree provides nutritious food, livestock fodder, fibre, medicine and income to local people among over 250 uses (Wickens 1982, Sidibé and Williams 2002, Buchmann et al. 2010). Apart from its local economic importance, there is a growing international interest for baobab products for food, pharmaceutical and cosmetic industries (Gruenwald and Galizia 2005, Wickens and Lowe 2008). Following the EU and US approval (CEC 2008, FDA 2009) of baobab fruit pulp for use as a food ingredient, the baobab tree has recently entered the international food market, offering opportunities for income generation for millions of rural poor farmers in Africa. This is causing growing concern that baobab fruit collection for international trade might lead to overexploitation of natural stands, which will have negative impacts on local livelihoods in Africa (Buchmann et al. 2010). When rural populations lose access to important natural resources, their reduced diet could result in food insecurity, malnutrition and diseases (Johns and Maundu 2006).

The baobab tree has been identified as one of the most important edible forest trees to be conserved and domesticated in Africa (Matig et al. 2002). Domestication and cultivation of the baobab tree is necessary to protect natural stands and to provide a sustainable source of food, medicine and income to local populations. The domestication process seeks to capture and multiply trees with desirable characteristics, thus taking advantage of variations found in the wild (Pye-Smith 2010). While preserving the characteristics that are important to local or international customers, domestication can also reduce the time of first fruiting (Chikamai and Tchatat 2009). Domestication and cultivation of the baobab tree can help increase the harvested volume while maintaining the reliability and quality of supply, aspects identified to be key factors determining the long-term viability of a given product in international trade (Chikamai and Tchatat 2009).

In order to contribute towards domestication of this species, it is essential to identify ‘superior’ sources of planting material and determine potential sites for cultivation and conservation. With the aim of conserving this species, it is important to study the potential effect of climate change on this species. The research aims of this investigation are therefore: (1) to determine potential sites for cultivation of this species, (2) to suggest potential conservation strategies taking climate change into account, and (3) to assess the morphological variation of baobab leaf, fruit and seedling and make recommendations for selecting ‘superior’ planting materials.

1.2 Organisation of the thesis

This thesis consists of seven chapters. The **first chapter** introduces the baobab tree within the context of ‘under-utilised species’ and agroforestry systems, also presenting other tree species commonly found in the same habitat (e.g., *Vitellaria paradoxa* C.F.Gaertn., *Parkia biglobosa* (Jacq.) R.Br. ex G.Don.) (section 1.3.). It then goes on to synthesise the state of knowledge on the baobab tree (section 1.4 - 1.14), including its cultivation (section 1.13) and conservation status (section 1.14).

Chapter 2 assesses the current distribution of the baobab tree in Africa and analyses the ecological factors determining its distribution using ecological niche modelling. It predicts potential sites for cultivation in Africa and the tropical world and discusses the implications of the results, focusing on factors which make baobab cultivation feasible/practicable in specific countries. This chapter is divided into: introduction to species distribution modelling (section 2.1), aims and objectives (section 2.2), methodology (section 2.3), results (section 2.4) and discussion (section 2.5).

Chapter 3 focuses on the potential effects of climate change on the potential future distribution of the baobab tree (using ecological niche modelling) and their implications for conservation. It analyses the use of Protected Areas as an effective tool for baobab conservation. It also suggests other conservation strategies (e.g., *ex* *situ* conservation in Seed Banks, conservation 'through utilisation'). This chapter is divided into: introduction to modelling future distributions (section 3.1), aims and objectives (section 3.2), methodology (section 3.3), results (section 3.4) and discussion (section 3.5).

Chapter 4 and chapter 5 analyse *in situ* baobab morphological variation and its implications for selecting 'superior' planting materials. **Chapter 4** focuses on baobab leaf morphological variation (both leaf and stomata characteristics) and its relation to drought tolerance. Four experiments are presented, three of which were carried out in Benin and one in Malawi. This chapter is divided into: introduction to drought adaptation (section 4.1), aims and objectives (section 4.2), methodology (section 4.3), results (section 4.4) and discussion (section 4.5). **Chapter 5** compares baobab fruit morphological variation in Mali and Malawi paying special attention to fruit pulp content. This chapter is divided into: introduction to fruit importance and fruit variability (section 5.1), aims and objectives (section 5.2), methodology (section 5.3), results (section 5.4) and discussion (section 5.5).

Chapter 6 analyses *ex situ* baobab seedlings' morphological variation and its implications for selecting 'superior' planting material. It presents results of two seedling experiments carried out in a greenhouse in Belgium: a seedling growth experiment and a short-term drought stress experiment. This chapter is divided into: introduction (section 6.1), aims and objectives (section 6.2), methodology (section 6.3), results (section 6.4) and discussion (section 6.5).

The final chapter (**chapter 7**) concludes by reviewing the research motivation and the key findings with a general discussion (section 7.1). It assesses the investigation's limitations and suggests further research (section 7.2) and discusses the novelty of this investigation and its potential applications (section 7.3). This chapter also includes a final remark on the importance of the baobab tree as an under-utilised food species and the relevance of its conservation and cultivation (section 7.4).

1.3 Introduction

The baobab tree (*Adansonia digitata* L.) is an under-utilised fruit tree appreciated for its non-timber forest products (NTFP). It is commonly found in the agroforestry systems of dryland Africa, especially in the West African parklands. Fig. 1.1 illustrates a baobab tree.

*Fig. 1.1. A baobab tree (*Adansonia digitata *L.).Source: A. Cuni Sanchez.*

Under-utilised fruit trees

Under-utilised indigenous fruit trees refer to fruit bearing trees that are not highly researched and which are generally ignored by the commercial sector (Hughes and Haq 2003). They are used traditionally for their food, fibre, fodder, oil or medicinal properties, but have yet to be adopted by large-scale agriculturalists. They may have the potential to contribute to food security, nutrition, health, income generation (Jamnadass et al. 2009) and environmental services. They also help diversify farming systems (Dawson et al. 2009). For a variety of reasons, some economic and some cultural, they have been neglected or under-utilised, though they may be of great importance locally.

Non-timber forests products (NTFP)

Non-timber forest products are products of biological origin other than wood derived from forests, other wooded land and trees outside forests (FAO 2010). They may be gathered from the wild, or produced in forest plantations, agroforestry schemes and from trees outside forests. They include plant and mushroom products such as: seeds, flowers, fruits, kernels, leaves, bark and roots. They provide food, medicine, livestock fodder, fibre, clothing, material for hunting and fishing, material for handicrafts and income among others. They are believed to contribute especially to the livelihoods of poor and disadvantaged people in developing countries by ensuring food security, maintaining nutritional balance in people's diets, meeting medicinal needs and as a source of income (FAO 1995, Shackleton et al. 2002, Marshall and Newton 2003, Emmanuel et al. 2005, Schumann et al. 2010).

Agroforestry systems, parklands

Agroforestry parkland systems or parklands are landscapes in which mature trees occur scattered in cultivated or recently fallowed fields (Boffa 1999). These trees are deliberately retained by farmers as they provide food, fuel, fodder, medicinal products or other services (maintenance of soil fertility, water conservation and environmental protection). Usually, parklands are not the result of a single agricultural season but they reflect a slow process of species selection, density management and tree growth over several decades (Boffa 1999).

Parklands occupy a vast area, representing a large part of the agricultural landscape under subsistence farming in the tropics, and especially in the semi-arid and sub-humid zones of West Africa (Boffa 1999). In Mali, for example, parklands occupy about 90% of the agricultural land area. Similar systems (although they might not be called 'parklands') are also found in Zimbabwe, Malawi and other countries of southern Africa; and in Asia, Oceania and Latin America. Related agroforestry systems can also be found in temperate regions: e.g. the *dehesa* (Spain) or *montado* (Portugal) where Holm oak or cork oak (*Quercus ilex* L. or *Q. suber* L.) are scattered in pastures or cereal fields (Joffre et al. 1988).

Parklands are often characterised by the dominance of one or few species. However, they usually host a wide variety of tree and shrub species. For example, up to 39 species were recorded in parklands around Kano in Nigeria (Cline-Cole et al. 1990). Fig. 1.2 gives an example of parkland.

Fig. 1.2. Example of parkland with baobabs in northern Benin. Source: A. Cuni Sanchez.

Important parkland tree species

The baobab tree is commonly found in the in the West African parklands and in the agroforestry systems in East and Central Africa. Other tree species frequently found in the West African parklands include: the winterthorn (*Faidherbia albida* A.Chev.)

the shea nut tree *(Vitellaria paradoxa* C.F.Gaertn.) and the African locust bean (*Parkia biglobosa* (Jacq.) R.Br. ex G.Don.) (Boffa 1999). Three important tree species commonly found in the agroforestry systems in East and Central Africa are the marula tree (*Sclerocarya birrea* (A. Rich.) Hoscht.), the tamarind tree (*Tamarindus indica* L.), and the ber or Jujube (*Zizyphus mauritiana* Lam.) (Jama et al. 2008).

- The winterthorn (*Faidherbia albida*) occurs throughout the Sahel and the Sudan zones of West Africa and in eastern and southern Africa. It is found in areas with annual rainfall ranging from 500 to 800 mm. It is associated with alluvial soils along perennial or seasonal watercourses. Appreciated for maintaining soil fertility, it is also used for fuelwood and fodder.

- The shea nut tree (*Vitellaria paradoxa*) has two subspecies, one occurring in western Africa (subsp. *paradoxa*) and one occurring in southern Sudan, Ethiopia, Uganda and northeast Democratic Republic of Congo (subsp. *nilotica*). It is generally found in areas with annual rainfall ranging from 600 to 1400 mm, mainly on colluvial soils. This species is appreciated for its kernels which are used for butter production.

- The African locust bean (*Parkia biglobosa*), often found in association with *V. paradoxa*, is mostly present in areas of West Africa with annual rainfall between 800 and 1500 mm. It is appreciated for its seeds which are used to make condiments served with staple cereals.

- The marula tree (*Sclerocarya birrea*) occurs in the semi-arid, deciduous savannas of eastern Africa, from Sudan to Tanzania and in Central African Republic and Democratic Republic of Congo. It is found between 0 and 1800 m above sea level in dry and rocky hillsides and riparian areas. There are a few subspecies in specific sites, mainly in Kenya and Tanzania. The marula tree is appreciated for its fruits, which can be either eaten fresh or processed into juice, jams and jellies and alcoholics drinks, the latter having significant commercial value regionally and internationally.

- The tamarind tree (*Tamarindus indica*) mostly occurs in dry-land in sub-Saharan Africa. Its natural range goes from 0 to 1600 m above sea level and features prominently in riparian habitats. Fruits are eaten fresh or processed, and it is also used as firewood and fodder.

- The ber or jujube (*Zizyphus mauritiana*) is common in coastal and semi-arid areas of eastern Africa (Maundu et al. 1999). Its habitat ranges from 0 to 1800 m above sea level and it prefers growing along rivers, watercourses and floodplains. It is an important source of nutritious food especially its fruits (which are eaten raw or processed). This tree species is also appreciated for its wood.

Other important parkland tree species include the fan palm (*Borassus aethiopum* Mart.) used as famine food, for wine production, construction and handicrafts; the desert date (*Balanites aegyptiaca* (L.) Delile) used for food, oil production and fodder; the oil palm (*Elaesis guineensis* Jacq.) used for oil and wine production; and the gum Arabic (*Acacia senegal* Willd.) used to make gum. All the mentioned species have medicinal properties (Boffa 1999, Jama et al. 2008).

The importance of the parkland tree products

The products obtained from parkland trees are important in terms of quantity consumed and how often they are consumed. For example, in Benin, average consumption of *V. paradoxa* butter is estimated to be about 10 kg/year/person while average consumption of fermented seeds of *P. biglobosa* is estimated to be between 2.5 and 3.6 kg/year/person (Schreckenberg 1996). In Burkina Faso, *V. paradoxa* butter is the only cooking oil consumed by 88% of the rural households (Hymans 1991). Parkland product consumption varies by ethnic group according to tastes and availability: in Senegal, Socé people favour baobab leaves as the main ingredient of sauces for the staple cereal dishes, while Peulh and Wolof people prefer the exudates of *Sterculia setigera* Del. for that purpose (Bergeret and Ribot 1990).

The products obtained from parkland trees also supplement the nutritional value of basic cereals; they diversify farmers' diets and enhance farmers' seasonal food balance (as they become available at different times of the year). They are also essential components of traditional medical systems, they have an important socio-cultural and spiritual value, and they contribute to income generation (Boffa 1999). Some parkland commodities are traded internationally and have high national significance because of their export earnings: e.g., gum Arabic (from *A. senegal*), alcoholic drinks from the marula tree (*S. birrea*) and kernels of *V. paradoxa* used in the food processing and cosmetics industries.

Factors affecting the parklands

The spread of parklands has increased in line with the expansion of the cultivated area throughout the Sahel and Sudanian zones of West Africa in the last decades. However, it seems that tree density and regeneration in parklands have declined significantly since the droughts of the 1970s (Boffa 1999).

Droughts, pests and exotic tree species have increased the pressure on parklands species. Livestock (which helps disseminate and break seed dormancy of some parkland species such as *F. albida*) can also have a negative impact on several parkland tree species' regeneration, by eating seedlings and causing the partial or complete elimination of tree shoots. Mechanisation and intensive cash crop production (e.g., cotton) supported by the use of chemical fertilisers has also led to parkland degradation in several places. Human population levels also have an important effect on parklands: *V. paradoxa* and *P. biglobosa* parklands are threatened by shortening or eliminating fallows due to increasing population levels (Boffa 1999).

Other parameters such as markets, external pressure on village resources, migration and relation with urban centres strongly influence the relative value of parkland trees and thus, farmers' interest in maintaining and regenerating parkland species (Boffa 1999). For example, where traditional products from parkland trees can be substituted by cultivated crops or items can be purchased at the market, farmers may be less motivated to maintain parkland species. In some areas of Uganda, *V. paradoxa* is cut for charcoal-making in spite of its economic importance as a source of cooking oil (Masters and Puga 1994). In a number of urban areas of Senegal, people use ‘Maggi’ cubes (artificial flavouring) instead of *P. biglobosa* seed balls called ‘netetou’ (Boffa 1999).

Domestication

Although most parkland tree species are not commonly planted, they are in a category of incipient domesticates (the baobab tree being one of them) as they have been long used and managed by humans, and, humans have started to make them fit for cultivation (Sidibé and Williams 2002). Domestication is defined as a human-induced change in the genetics of a plant to bring it into wider cultivation through a farmer-driven or marked-led process (Harlan 1975). As mentioned in the introduction, the baobab tree has been identified as one of the most important edible savanna trees to be domesticated in Africa.

1.4 Taxonomy and botanical description

Taxonomy

The baobab tree (*Adansonia digitata)* is a member of the subfamily Bombacoideae of the family *Malvaceae*, a family which includes about 200 genera and 2300 species. *Adansonia digitata* is related to seven other species of *Adansonia*. While *A. digitata* occurs in tropical Africa, six species occur in western Madagascar and one (*A. gregorii* F.Muell) in Western Australia (Fig. 1.3).

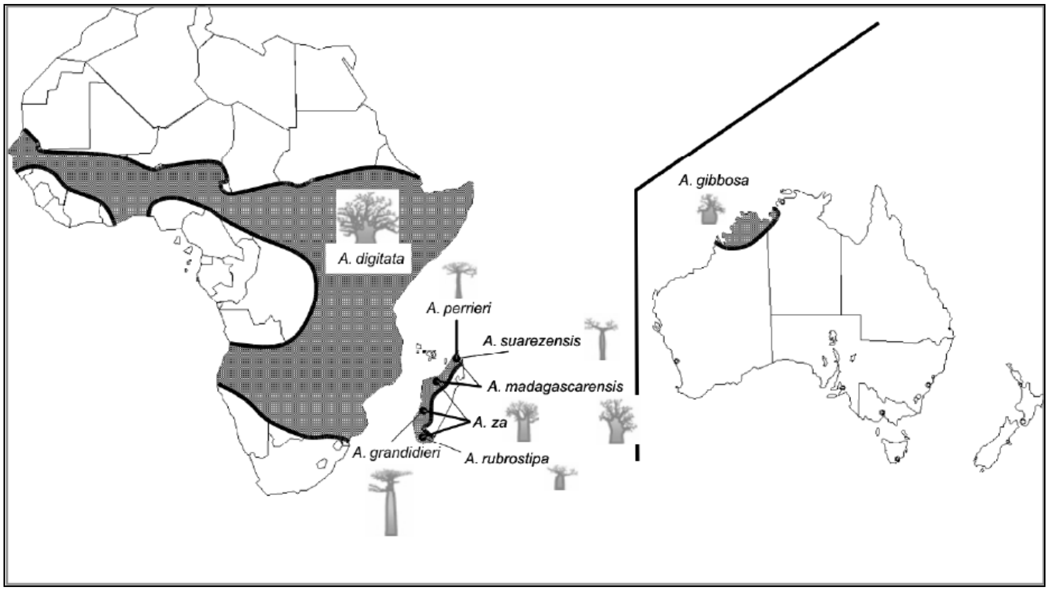


Fig. 1.3. Approximate distribution of Adansonia *species, adapted from Diop et al. (2006).* A.gibbosa *refers to* A. gregorii *(the new accepted name of this species).*

Botanical description

A. digitata, the African baobab, was first described by Adanson in 1771. It is characterised by its massive size, reaching to a height of 18-25 m. The trunk is swollen and stout, up to 10 m in diameter, usually tapering or cylindrical and abruptly bottle-shaped (Sidibé and Williams 2002). Many of the larger baobabs have hollow centres due to natural causes or as a result of human intervention (Palgrave 1977). Branches are distributed irregularly and large primary branches are well distributed along the trunk or limited to the apex. The wood is soft and spongy. Between each layer of xylem cells there is a layer of parenchyma cells that stores water.

The bark is smooth, reddish-brown to grey, soft and fibrous. However, the bark of old specimens can be transversely wrinkled, believed to be caused by compression of the wood (Wickens and Lowe 2008). The thick fibrous bark appears to significantly contribute to structural support, and may compensate for the reductions in stem stiffness that would otherwise occur through moderate use of stem water (Chapotin et al. 2006). There is a green layer below the outer layer of the bark presumed to photosynthesise when the tree has shed its leaves.

The tree produces an extensive lateral root system and the roots end in tubers. Tuberous roots of young specimens act as water and/or sugar storage facilities during long drought periods (Alexandre 1992). Roots of mature trees have been reported to extend up to 50 m from the trunk and down to a depth of 10 m (Diop et al. 2006).

Baobab leaves are 5-7 palmately compound. In fact, they are 2-3 foliate at the start of the season and more mature ones are 5-7-(9) foliate. A mature leaf can reach a diameter of 20 cm, while the medial leaflet can be 5-15 x 2-7 cm (Sidibé and Williams 2002). Margins are entire and leaves are stellate-pubescent beneath, young ones becoming glabrescent or glabrous. Leaves, which are deciduous, are alternate at the end of the branches or occur on short spurs on the trunk.

Baobab flowers are large, pure white and have five crinkled curled-back waxy petals and numerous stamens fused to form a central column. While the flower corolla varies from 4 x 4 to 10 x 12 cm, the pedicel length varies between 1 and 90 cm (Sidibé and Williams 2002). Flowers which are pendulous, solitary or paired in leaf axils are very conspicuous.

Fruits are large, variable in size and shape but usually ovoid, with an olive-green velvety covering. Their size is variable, from 7.5 to 54 cm long and from 7.5 to 20 cm wide. The pericarp (which is about 1 cm thick) encloses a dry mealy pulp. Embedded in the pulp, there are dark brown to reddish black reniform seeds. Seeds are also variable in size, being 10-13 x 8-10 x 4-5 mm due to lateral flattening (Sidibé and Williams 2002). Fig. 1.4 illustrates the leaf, flower and fruit of the baobab tree.

Fig. 1.4. Leaf, flower and fruit of the baobab tree.
Adapted from Tree Atlas of Namibia (Curtis and Manheimer 2005).

1.5 Pollination and reproductive biology

The baobab tree is pollinated by bats: *Eidolon helvum, E. crypturus, Epomorphorus gambiensis* and *Rousettus egyptiacus* (Jaeger 1945, Wickens and Lowe 2008). Suggestions that wind pollination or ant pollination is possible were discounted by Baum (1995). However, the suggestion that bush babies (*Otolemur crassicaudatus* and *Galago senegalensis*), known to feed on flowers, play a minor pollinating role were not discounted by Baum (1995). The sour scent of the flowers also attracts flies and nocturnal moths, and some species of bollworms that might effect pollination. However, the pendulatory nature of the flowers and phenology favours the action of the fruit bats.

Flowering times vary greatly. Flowering can occur any time except during the peak of the dry season and whether leaves are present or not. Essentially, flowering fits a particular climatic season, ranging from October-December in southern Africa and May-June in western Africa. Fruits develop 5-6 months after flowering. Baobab fruits are harvested from May to October in Kenya (Nkana and Iddi 1991, Omondi et al.

2004) and from December onwards in West Africa (Soloviev et al. 2004, Assogbadjo et al. 2005b). A diverse range of tree ages when first fruiting occurs have been reported. Wickens (1982) noted 16-17 years in South-Africa and 22-23 years in Zimbabwe, while Sidibé and Williams (2002) reported 8-10 years in West Africa.
Other parkland trees also have a long maturation process before fructification: e.g., *V. paradoxa* starts fruiting at the age of 15-20 years (Boffa 1999).

1.6 Seed dispersal and germination

When fruits fall in the field, the woody outside fractures and termites enter to eat the sweet pulp, releasing the seeds. A range of animals carry the seeds away from the trees, such as monkeys, squirrels and rats (Wickens 1982). Humans, birds and large animals such as elephants and elands also eat the baobab fruits and contribute to seed dispersal. Fruits can also be dispersed by water systems (Wickens 1982).

It is believed that the baobab tree has a long seed dormancy (Owen 1974, Wickens 1982). In nature, this dormancy is believed to be broken by fire, a long period of rain or digestion by elephant or other big mammals (Wickens 1982, Matig et al. 2006, Wickens and Lowe 2008).

1.7 Growth, development and age

Baobab seedling's first leaves are simple, followed by digitate leaves with progressively more leaflets, up to 5-7. Seedlings and young saplings lack the characteristic swollen trunk of the adults. The sapling develops a deep taproot.
As the trunk grows and thickens with increasing moisture content, four stages of growth can be recognised: sapling (up to 10-15 years), cone (up to 60-70 years), bottle (up to 200-300 years) and old (more than 200-300 years) (Breitenbach 1985). Old individuals are often hollow inside, and may consist of several trunks. If the main trunk dies or falls, new trunks can develop from vegetative shoots of the base (Wickens 1982).

The baobab tree is a long-lived tree which can survive for more than 1000 years. Swart (1963), using carbon-dating, estimated that a large baobab in Lake Kariba was 1010 ± 100 years while Patrut et al. (2007), also using carbon-dating, determined that a large baobab in north-eastern Namibia was 1275 ± 50 years.

Several growth rates have been estimated by a number of authors in different countries (e.g., Barnes 1980, Weyerhauser 1985, Wilson 1988, Swanepoel 1993, Johansson 1999). Differences in baobab growth rates in different countries have been related to differences in climate (Wilson 1988, Wickens and Lowe 2008). Regardless of the environment, it is accepted that baobabs grow quickly during the early part of their lives while the rate of growth slows later. Patrut et al. (2007) showed that a dead baobab from Namibia (aged 1275 years) almost ceased growing over the past 500–600 years.

Although age estimates (and size class distribution) from diameter at breast height (DBH) might not always be robust due to different growth rates in different countries and changes in hydrostatic conditions within the tree besides the cambium growth (Johansson 1999), they are still used as an indicator of population structure (e.g., Duvall 2007, Edkins et al. 2007, Schumann et al. 2010).

1.8 Density and population levels

Baobab density

Baobab densities are very variable in the landscape. They are probably affected by a number of factors, such as soil requirements, competition for water (related to baobab's extensive root system), baboon-mediated seed dispersal, elephant populations and human settlements (Sidibé and Williams 2002, Duvall 2007, Edkins et al. 2007, Wickens and Lowe 2008).

Diverse population densities have been reported in different countries and in a number of land-use types (Table 1.1). One reason might be the different methodologies used to estimate tree density (Wickens and Lowe 2008). In general, baobab density is higher in cropland than in fallows or grazing land as seedlings are protected from fire and grazing (Johansson 1999, Dhillion and Gustad 2004, Venter and Witkowski 2010). Baobab density might also be higher in cropland as farmers are interested in maintaining this tree species. Boffa (1999) reported that farmers tend to reduce tree density and the number of species and favour preferred species in the agroforestry systems of West Africa. For example, compared with the percentage of trees in the original savanna vegetation, the abundance of *V. paradoxa* in cultivated fields increased from 16 to 83% and from 10.6 to 39.2% in Burkina Faso and northern Benin respectively, while the abundance of *P. biglobosa* increased from 0.4 to 3.5 and from 0.7 to 5.4% in Burkina Faso and northern Benin respectively (Boffa 1995, Schreckenberg 1996).

Country	Site	Land-use type	Estimated density (trees/km^2)	Source
Benin	northern part	Traditional agroforestry system	1-5	Assogbadjo et al. 2005b
Burkina Faso	Sudano-Sahelian zone	Traditional agroforestry system	6	Kyndt et al. 2009
Ghana	Sudano-Sahelian zone	Traditional agroforestry system	4	Kyndt et al. 2009
Kenya	Kibwezi district of Kenya	Farmlands and natural woodlands	0-6000 (woodlands) 0-200 (farmlands) [a]	Mohamed 2005
Malawi	Southern Lake Malawi area	Cropland, fallow and villages	1000[a]	Chirwa et al. 2006
Mali	-	-	10.7	Wilson 1988
	South-western part	Cultivated and non-cultivated land	6.69	Duvall 2007
	Cinzana, central part (central Nigerian Delta)	Cropland, fallow and villages	40-200 [a]	Dhillion and Gustad 2004
Senegal	Sudano-Sahelian zone	Traditional agroforestry system	7	Kyndt et al. 2009
South Africa	Kruger National Park	Protected Area	0.3-32 (different areas within the Protected Area)	Kelly 2000
	northern Venda (northern part)	Plains, rocky areas, fields and villages	103 [a]	Venter and Witkowski 2010
Sudan	-	-	11.2	Wilson 1988
Tanzania	Ruaha National Park	Protected Area	27.6 - 51 (year 1982 and 1976 respectively) [b]	Barnes 1980, 1994)
	Lake Manyara National Park	Protected Area	49.2 - 72.8 (different areas within the Protected Area)	Weyerhaeuser 1985
	Kondoa Irangi Hills	Cutlivated and grazing land	17.5-50 (different areas)	Johansson 1999
Zimbabwe	Mana Pools National Park	Protected Area	13.1 - 18.4 (year 1988 and 1984 respectively) [b]	Swanepoel 1993
Zimbabwe	Save-Odzi Valley, eastern part	-	840 [a]	Romero et al. 2001

Table 1.1. Baobab densities in different countries and land-use types.

[a] *Densities were originally estimated in trees/ha. Densities were converted to trees/km^2 and might not be representative for the whole area.*

[b] *Different densities were estimated in different years and were attributed to high elephant population in the Protected Area.*

Densities of other parkland tree species

Densities of other parkland tree species are also very variable (Table 1.2). Although environmental conditions affect tree density not only in the original savanna vegetation but also in the parklands, tree density in the parklands is also related to the length of time an area has been farmed, with densities in newly cleared areas being higher than in old parklands (Pullan 1974, Otegbeye and Olusoki 1993).

Parkland tree density, including the baobab tree, is also determined by the 'critical canopy cover' effect. In semi-arid conditions, understory herbaceous productivity is highest with low tree densities and decreases with increasing tree density. Similarly, cereal crops might benefit from certain tree densities but the productivity of the cereal decreases as higher tree densities are reached. Parkland trees, in general, improve site conditions by increasing soil fertility, by reducing soil temperature and by maintaining higher top soil moisture (Boffa 1999). However they might compete with other crops for light, nutrients and water. Although relationships between parkland tree density and crop production are complex and available information is limited, it seems that there is a positive parkland effect on crop production (due to an increase in soil and air moisture) linked to the spatial arrangement of scattered trees, which would not exist in the presence of isolated individual trees (Boffa 1999).

Country	**Tree density (trees/ha)**		
	Faidherbia albida	*Vitellaria paradoxa*	*Parkia biglobosa*
Benin	-	25-60	2-10
Burkina Faso	0.8-45	5-19	0.8-21
Central African Republic	-	30-70	15-40
Cote d'Ivoire	3.5	2-30	3.6
Ghana	-	83	-
Mali	5-50	4.2-12	1-8
Niger	13-100	-	-
Nigeria	-	-	1-14
Senegal	1-50	-	-
Sudan	7-90	-	-

Table 1.2. Densities of some tree species in the African parklands. Adapted from Boffa 1999.
- indicates that no information was available from that country.

Baobab population levels

Different size class distributions for the baobab tree have been reported by several authors. Bell-shaped size class distributions, with few individuals in small and large size classes, have been reported from: Benin (Assogbadjo et al. 2005b), Burkina Faso (K. Schumann 2010, pers. comm.), Mali, Kenya and Sudan (Wilson 1988), Zambia (Caughley 1976), Tanzania (Barnes 1980), South Africa (Edkins et al. 2007, Venter and Witkowski 2010) and Malawi (Chirwa et al. 2006). A bell-shaped size class distribution can be observed in Fig. 1.5 (white colour). Several authors (Caughley

1976, Weyerhaeuser 1985, Swanepoel 1993, Barnes 1994, Edkins et al. 2007) have shown that in National Parks, the lower number of individuals in the smaller size classes is mainly due to overpopulation of elephants who have the habit of destroying younger baobabs in their search for water during the dry season. Outside National Parks, the lower number of individuals in the smaller size classes is generally attributed to fires, droughts and increased grazing pressure from domestic livestock (Wilson 1988, Johansson 1999, Assogbadjo et al. 2005b, Wickens and Lowe 2008).

Reverse J-shaped size class distributions, with more individuals in smaller than in larger size classes, have also been reported for the baobab tree: in south-western Mali (Duvall 2007), in Mozambique (in Limpopo National Park, where there are few elephants, Edkins et al. 2007), in W National Park in Burkina Faso (Schumann et al. 2010) and in wooded plains in northern South Africa (Venter and Witkowski 2010). A reverse J-shaped size class distribution can be observed in Fig. 1.5 (black colour). Duvall (2007) argues that in some studies (e.g., Dhillion and Gustard 2004) areas where baobab regeneration takes place (such as in old settlements) were not sampled, explaining why the observed size class distribution might be bell-shaped.

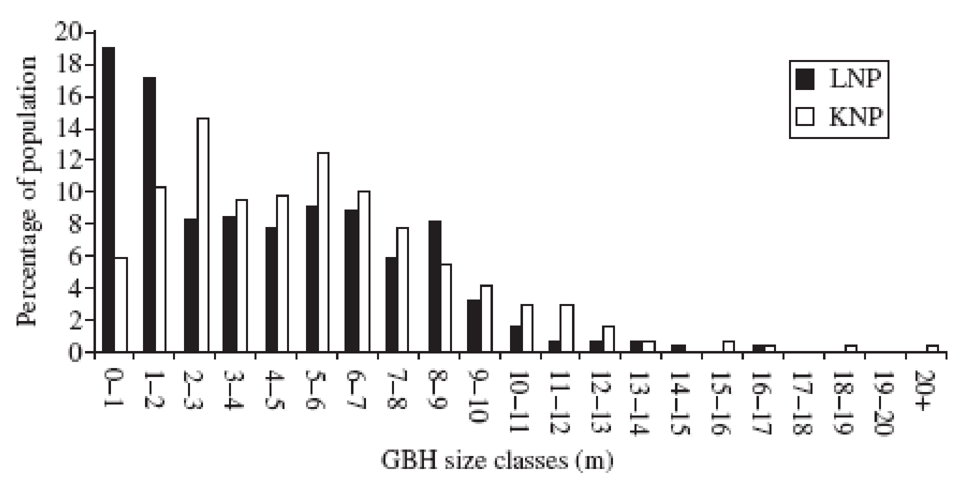


Fig.1.5. Example of a bell-shaped (white) and a reverse J-shaped (black) size class distribution for the baobab tree. White bars refer to Kruger National Park (KNP) in South Africa and black bars refer to Limpopo National Park (LNP) in Mozambique (adapted from Edkins et al. 2007). GBH refers to girth at breast height.

Natural regeneration rates of the baobab tree

It seems that baobab natural regeneration is rather poor (Wickens 1982). Several authors have noted a lack of recruitment in baobab populations and raised concern about the survival of baobab populations (Romero et al. 2001, Assogbadjo et al. 2005b, Edkins et al. 2007). However, a recent study carried out in South Africa by Venter and Witkowski (2010) pointed out that for long-lived species, such as the baobab tree, recruitment and mortality might be episodic events, as the baobab population in that area was stable and had healthy numbers of mature baobab trees.

Several factors affect baobab recruitment, rainfall and drought being two major factors. Baobab seedlings, which lack the extensive shallow rooting system and the accumulation of water in the trunk are thought to be more sensitive to droughts than adults (Wickens and Lowe 2008). It is believed that recruitment of baobab seedlings is linked to a series of particularly wet years (O'Connor et al. 2007, Wickens and Lowe 2008). Fire is another factor playing an important role in baobab regeneration (Gebauer et al. 2002, Edkins et al. 2007). Although mature baobab trees have a thick corky bark which enables them to tolerate burning (Greenway and Vesey-Fitzgerald 1969), seedlings and young trees are not tolerant to fire. As mentioned earlier, elephants and other grazing animals such as cattle have an impact on baobab recruitment as they eat and kill baobab seedlings and young baobabs (Wilson 1988, Gebauer et al. 2002, Edkins et al. 2007, Wickens and Lowe 2008). Another factor affecting baobab recruitment, as baobab commonly occurs in cultivated land, is wether the tree is desired or not by the farmer (Boffa 1999).

Because of these factors, it seems that baobab regeneration mainly takes place in association with settlements and cultivated land, and in steep slopes and rocky areas, probably because they have less fire frequency and lower level of herbivore disturbance, especially by elephants (Duvall 2007, Edkins et al. 2007).

Low natural regeneration has also been observed for other parkland tree species, especially in West Africa. It seems that for a number of parkland species, regeneration is linked to the parkland system of cultivated and fallow land, regeneration mainly taking place in the later. Boffa (1999) suggested that *V. paradoxa* and *P. biglobosa* parklands are threatened by shortening or eliminating fallows due to increasing population levels. Probably, baobab tree regeneration is also affected by these. Increased human-induced fire frequency has also been linked to declining population sizes of some parkland species in Senegal (Lykke 1998).

1.9 Distribution and ecology

Distribution in Africa

The distribution of the baobab tree in Africa lies between 16.5º N and 15º S (see Fig. 1.3). It occurs naturally in most countries south of the Sahara with notable absence in Liberia, Uganda, Djibouti and Burundi (Sidibé and Williams 2002). In some countries its distribution is very limited (e.g., in Chad it is only found in the south-east). Although it is essentially associated with the drier parts of the savanna, there are extensions of the distribution into forest areas, probably associated with human habitation. It appears to be introduced to more equatorial areas such as Gabon, Democratic Republic of Congo and Congo (Wickens 1982).

In West and Central Africa, the baobab tree is typically a scattered tree in the savanna, along the roads and associated with habitation. As mentioned earlier, it is a common parkland species. In West Africa, the baobab tree is also found in coastal areas in Senegal, Ghana, Benin and Togo, which suggests a secondary colonisation after introduction (Sidibé and Williams 2002).

In eastern Africa, from Kenya southwards to Mozambique, populations are coastal as well as scattered in lowland bush and scrub. In Tanzania it can also be found on an upland plateau cleared for cultivation, where it is believed to be a relict of the anterior vegetation. In southern Africa, it occurs in mature woodland in Angola and Namibia and as a savanna component throughout Angola, Zimbabwe and northern South Africa. In Angola there are also coastal lowland populations (Sidibé and Williams 2002).

Distribution outside Africa

The baobab tree distribution outside Africa is linked to the Arab traders. It occurs in Yemen and Oman, in the island of Zanzibar and Madagascar (Burton-Page 1969). Baobab was widely introduced into India and Sri Lanka probably by Moslem traders. The Portuguese and the French traders also introduced the baobab tree in other areas due to its odd plant shape and its use as an ornamental. It is found in Mauritius, Réunion, Malaysia, Indonesia (Java), China-Taiwan, Philippines, Guyana, New Caledonia, Cuba, Haiti, Dominican Republic, Martinique, USA (Hawaii, Puerto Rico, Virgin Islands and Florida), Jamaica, Montserrat, Netherlands Antilles, Dominica, St. Kitts and Nevis, St. Lucia, St. Vincent and Grenadines, Trinidad and Tobago, and Barbados (Sidibé and Williams 2002).

Ecological factors limiting baobab distribution

It appears that the extent of the distribution of the baobab tree is probably determined by its relatively wide ecological tolerance (Wickens 1982, Sidibé and Williams 2002).

In terms of temperature, the baobab tree can tolerate very high temperatures (mean maximum 40-42 ºC) and it can survive as long as there is no frost (Simpson 1995). However, Leger (1977) considered the baobabs in East Bushmanland in Namibia to be well adapted to frost. Typically mean annual temperature in areas where the baobab tree is found is 20-30 ºC.

The baobab tree can be found where rainfall is between 150 and 1500 mm per year (Fenner 1980) although it is most commonly found in areas receiving 500-800 mm (Wickens 1982). Wickens (1982) suggested that at a higher end of the range, distribution may have been artificially extended by planting. The relative humidity of the baobab habitat is another important factor (Wickens and Lowe 2008). For example, in western Senegal (where high densities of baobabs are found) the relative humidity is higher compared with elsewhere in the Sahel.

The baobab is commonest at altitudes between 450 and 600 m (Wickens 1982), and it is frequently described as occupying low altitudes (Chapman 1968). Various authors have noted baobab distribution from 0 to 1500 m in Ethiopia (Wickens 1982, Wilson 1988, von Carlowitz 1991). According to Noad and Brinie (1989) the baobab occurs up to 1250 m in Kenya, likewise in Sudan (Wickens 1982). Palmer and Pitman (1961) state that in Zimbabwe they are found growing naturally over 1200 m (the highest being recorded at 1330 m in 1951) and planted ones at 1520 m (Mullin 1992). In drier climatic zones, baobab is not common on hilltops (Beentje 1994, Maundu et al. 1999, Wekesa et al. 2006).

Although the species tolerates a broad range of soils, it is found most commonly on deep well drained soils (Palmer and Pitman 1961, Wilson 1988). It often occurs in stony, non-agricultural soil. Thompson (1910) indicated that baobabs are usually found on rocky and lateritic soils. The baobab tree has been recorded on clays (Harrison and Jackson 1958), sands (Rosevear 1937, Jenik and Hall 1976), alluvial silts (Astle et al. 1969), and loams of various kinds (Bogdan 1958). It is found in poorly drained soils in Zimbabwe and on the poorly drained plains of the Zambezi delta (Wickens 1982) and it is also reported on sandy soils overlying compact silt, liable to flooding in heavy rain, in Nigeria (Keay 1949). Although Wickens (1982) states that the species is not found on areas of deep sand, baobab trees are reported from sandy soils in Nigeria (Keay 1949), Gambia (Rosevear 1937) and Sudan (Harrison and Jackson 1958). Chapman (1968) suggests that baobabs are found on the better soils of Malawi (where the land is under cultivation) whilst Ramsay and Leeuw (1965) write that they are found only on hard soils in Sudan. Simpson (1995) suggests that human activity may have a part in these latter cases.

Other environmental factors that might influence baobab distribution are salinity, wind and light. The baobab tree seems to be salt sensitive at young stages (Gebauer and Ebert 2005) but it tolerates salinity when mature, as it can be found along the coast line in Kenya or Senegal. In fact, it has been suggested that this might be due to the changing environment, the trees establishing before the sea level rose, and the conditions becoming more saline. In regard to wind, it has been reported that taller baobabs in the Sahel are known to be susceptible to wind damage despite their spreading root system (Wickens and Lowe 2008). Light, which has been suggested to be a limiting factor for other baobab species (Metcalfe et al. 2007) could also be a limiting factor for *A. digitata* seedlings, which would explain why this species is not found in the rainforests (G. Wickens 2008, pers. comm.).

Other factors influencing baobab distribution

Apart from environmental factors, presence of dispersers (animals), fire and humans also have an impact on baobab distribution as they affect seed germination and seedling survival (as mentioned earlier in this chapter). Humans affect baobab distribution in different ways: they are a disperser agent (either intentional or unintentional: e.g., dispersal of seeds in garbage), they make fires and they modify the landscape. Farmers maintaining certain tree species in agroforestry parklands directly affect baobab tree distribution. Bowman (1997) suggested that local distribution of the Australian baobab (*A. gibbosa*) was determined by fire. It is possible that fire also plays an important role in *A. digitata* local distribution.

1.10 Baobab genetics

A. digitata chromosome counts are 2n=160 (Baum 1995). It is believed that this species is an autotetraploid that has undergone aneuploid reduction from 4x=176. The six baobab species from Madagascar and the Australian baobab show 2n=88 (Baum 1995).

A recent study on *A. digitata* chloroplast DNA (including 74 populations from 37 countries) has shown that there are genetic differences between populations from West and south-eastern Africa (Pock Tsy et al. 2009). All the baobab populations of south-eastern Africa possess the same chloroplast DNA haplotype, H4, which differs from H1 (found in West Africa) by four mutations (Pock Tsy et al. 2009). Another chloroplast DNA haplotype, H2, differing from H1 by one mutation, was found mainly in the coastal areas of Congo, Democratic Republic of Congo and Sao Tome and Principe. Baobab populations from West and south-eastern Africa are isolated from one another due to the presence of the equatorial rain forest (unsuitable conditions for baobab survival) and a large gap covering a part of Chad and Sudan (which is related with the presence of the Mega-Chad Lake in the Quaternary, Wickens and Lowe 2008). Differences in chloroplast DNA seem to reflect the morphological differences observed between West and south-eastern African baobabs by Wickens (1982).

When considering the level of genetic differentiation between baobab populations of one area, Kyndt et al. (2009) found that the level of polymorphism and variation within baobab populations is high and, there is some level of spatial isolation by distance between baobab populations at larger spatial scales. They studied 11 baobab populations from four West African countries (Benin, Ghana, Burkina Faso and Senegal) using AFLP fingerprinting (Amplified Fragment Length Polymorphism analysis). Although human influence in parklands is expected to have a reducing effect on the genetic differentiation between populations by seed exchange, this effect is apparently only playing a role at narrow geographical scale, e.g., at local markets (Kyndt et al. 2009).

AFLP provides neutral markers, which are not correlated with the morphological sub-classification of the baobab tree across the West African region (Assogbadjo et al. 2009). However, some morphometric variables have been shown to correlate with geographic distance and genetic differentiation between baobab populations from Benin (Assogbadjo et al. 2006).

1.11 Uses and properties

Domestic food use and nutritional value

Several parts of the baobab tree are commonly eaten. Leaves are used throughout Africa cooked as spinach, and frequently dried, powdered and used for sauce over porridges or boiled rice (Venter and Venter 1996). Flowers can be eaten raw or used to flavour drinks (Gebauer and Ebert 2005). Fruit pulp is probably the most important foodstuff. It is eaten fresh or it can be dissolved in water or milk, and used as a drink or sauce for food. The ‘baobab milk’ is a highly nutritious drink (Obizoba and Anyika 1994). In Cameroon, this acidic drink is mixed with peanuts (Malgras 1992, Viven and Faure 1995, Arbonnier 2000). In Tanzania, it can be added to aid fermentation of sugar cane for beer making (Fleuret 1980). In north Benin, ‘baobab milk’ and cereal flour are mixed to make an acidic food which can remain edible for a week (Codjia et al. 2001). In Nigeria, locals use baobab pulp powder in ‘tempe’ fermentation (a protein rich soya-based food alternative to meat) (Afolabi and Popoola 2005).

Baobab seeds are used as a thickening agent in soups, but they can be fermented and used as a flavouring agent, or roasted and eaten as snacks (Palmer and Pitman 1972, Addy and Eteshola 1984). For example, in Kenya, coated seeds are coloured and sold as sweets (Muok et al. 2000, Muchiri and Chikamai 2003) while in Ghana, seeds are fried, pounded and then crushed to a paste which is fermented, dried and formed into balls (Chundawat 1990). Roasted seeds can also be a substitute for coffee or groundnuts (Maundu 1996). Baobab seeds can also be used as a source of cooking oil but this use is not widespread. The baobab seed oil has been used to dilute groundnut oil, in West Africa, and, in Senegal, for preparing a local dish (Wickens and Lowe 2008). Some baobab products commonly found in Malawi can be seen in Fig. 1.6.

Fig. 1.6. Example of baobab products commonly found in Malawi. From top left to bottom right: baobab juice, baobab jam, baobab cooking oil, baobab coffee, baobab sweets, baobab leaf sauce, baobab fibres, baobab ice-lollies. Source: A. Cuni Sanchez.

Apart from leaves, flowers, fruit pulp and seeds, baobab bark and the taproot can also be eaten. In Nigeria 'kuka' (baobab bark) is used to increase weight gain in children (Lockett et al. 2000). Children also consume the taproot; which is believed to be a 'delicious snack' in Mali (Dhillion and Gustad 2004) and in Kenya (Kaybue 1986).

The baobab tree, like many edible wild plants found in the arid and semi-arid regions of Africa, in contrast to cultivated crops in those areas, shows a high content in vitamins and minerals (Smith et al. 1996). Baobab leaves, fruit pulp and seeds are known to be a good source of several minerals and vitamins (Table 1.3). A comparison between baobab fruit pulp and other typical African crops grown in the areas where the baobab tree grows can be found in Table 1.4.

		Baobab leaf (1)	**Baobab fruit pulp (2)**	**Baobab seeds (3)**
Protein content	Essential amino acids	* some	*some	* all (except lysine)
Fat content	Fatty acids			*
Mineral content	Calcium	*	*	*
	Phosphorus	*	*	*
	Magnesium	*	*	*
	Manganese	*	*	*
	Iron	*	*	
	Zinc	*	*	*
	Copper		*	
	Potassium			*
	Sodium			*
Vitamin content	Vitamin B1	*	*	
	Vitamin B2	*	*	
	Vitamin B3	*	*	
	Vitamin B6		*	
	Vitamin C	*	*	
	Pro-vitamin A	*		
Carbohydrates			*	

Table 1.3. Most commonly cited nutritional properties of the baobab tree.
** indicates that the mentioned tree part is known to be a significant source of that element.*
Extracted from several sources: 1 =Andy and Elka 1985, Yazzie et al. 1994, Smith et al. 1996, Glew et al. 1997, Barminas et al. 1998, Lockett et al. 2000, Sidibé and Williams 2002. 2= Nour et al. 1980, Arnold et al. 1985, Eromosele et al. 1991, Prentice et al. 1993, Nordeide et al. 1996, Smith et al. 1996, Glew et al. 1997, Saka et al. 1997, Lockett et al. 2000, Manfredini 2002, Osman 2004. 3= Arnold et al. 1985, Eteshola and Oraedu 1996, Odetokun 1996, Glew et al. 1997, Lockett et al. 2000, Osman 2004.

Apart from the wide variety of products made with baobab for human consumption, and the nutritional value of them, the amount consumed and the fact that leaves and fruits are daily used by some people especially in West Africa highlights the importance of this species (Buchmann et al. 2010). It has been estimated that 6-55g/day/person of baobab dried leaf powder is consumed in West Africa (Gustad et al. 2005). On a larger scale, several thousand tons of baobab leaves are consumed in the Sahel each year (Von Maydell, in Gebauer et al. 2003). In a study carried out in three countries in West Africa (Benin, Mali and Senegal) across 11 ethnic groups in different climatic zones, 90% of the informants consumed baobab leaves and fruits daily (Buchmann et al. 2010).

	Baobab fruit pulp [a]	**Banana** *Musa acuminata* Colla [b]	**Peanuts** *Arachis hypogaea* L.[b]	**Millet** *Panicum miliaceum* L.[b]	**Sorghum** *Sorghum spp.* [b]	**Tamarind** *Tamarindus indica* [b]
Energy (Kcal/100g)	1214	89	567	119	339	239
Protein content (g/100g)	3.2	1.09	25.8	3.51	11.3	2.8
Total fat content (g/100g)	0.3	0.33	49.2	1	3.3	0.6
Fibre (g/100g)	5.4	2.4	8.5	1.3	6.3	5.1
Calcium (mg/100g)	211	5	92	3	28	74
Iron (mg/100g)	4.23	0.26	4.58	0.63	4.4	2.8
Magnesium (mg/100g)	123	27	168	44	-	92
Phosphorus (mg/100g)	49.8	22	376	100	287	113
Manganese (mg/100g)	0.39	0.27	1.93	0.27	-	-
Zinc (mg/100g)	0.47	0.15	3.27	0.91	-	0.1
Vitamin C (mg/100g)	270	8.7	0	0	0	3.5
Vitamin B1 (mg/100g)	0.48	0.03	0.64	0.11	0.23	0.43
Vitamin B2 (mg/100g)	0.28	0.07	0.13	0.08	0.14	0.15
Vitamin B3 (mg/100g)	2.1-3	0.66	12	1.33	2.93	1.94
Vitamin B6 (mg/100g)	2.13	0.37	0.35	0.11	-	0.06

Table 1.4. Comparative data on the nutritional composition of baobab fruit pulp and other typical African foods.

[a] *Source: Lockett et al. 2000, Manfredini 2002, Osman 2004*

[b] *Source: USDA National Nutrient Database for Standard Reference, Release 22 (2009) (http://www.nal.usda.gov/fnic/foodcomp/search/)*

Medicinal use

Most baobab tree parts also have several medicinal properties and are used by indigenous people for human and animal medicine. A recent study carried out in West Africa reported 179 different medicinal uses of baobab tree parts (Buchmann et al. 2010). Most cited medicinal properties and examples of some medicinal uses can be found in Table 1.5. Baobab pharmaceutical and toiletry products are also available in Europe (Wickens and Lowe 2008).

Tree part	**Most cited properties**	**Examples of medicinal uses**
Leaf	Antihistaminic, antipyretic, anti-coughing, diuretic, anti-diarrheic, toning, analgesic, expectorant, disinfectant and local anti-inflammatory	Fever, asthma, cough, anaemia, hypertension, haemorrhoids, aphrodisiac, baby teeth pain, transpiration activator, rheumatism, conjunctivitis, inflammation of the ear, urinary infection, insect bite, dracunculiasis, skin inflammation
Flower	-	Helps in birth, cough, anaemia
Fruit pulp	Toning, invigorating, anti-diarrheic, antipyretic, homeostatic, cicatrising, Anti-enteralgia	Tiredness, poor appetite, aphrodisiac, diarrhoea, children intestinal tract pain, malaria, haemorrhoids, haemoptysis, insect bites, postnasal drip
Seeds	Anti-diarrheic, anti-enteralgia	Diarrhoea, children intestinal tract pain, hypertension, cough, malaria, gingivitis and other mouth infections, lactation stimulator, hiccups
Bark	Antipyretic	Fever, malaria, diarrhoea, inflammation of the digestion system, children invigorating, lumbago, menstruation problems, tooth ache, burns, skin sore treatment, skin softener
Roots	Toning, invigorating	Invigorating, malaria, epilepsy (with other plants)

Table 1.5. Main medicinal properties and uses of the baobab tree. Adapted from Diop et al. (2006), which was produced from: Kerharo and Adam 1974, Wickens 1982, Codija et al. 2001, Sidibé and Williams 2002.

Other uses

As well as having a high nutritional and medicinal value, the cultural value of the baobab tree also stands out. Several authors have reported superstitions and stories related to the baobab tree (Owen 1974, Codija et al. 2001, Sidibé and Williams 2002, Assogbadjo et al. 2005b, Wickens and Lowe 2008, among others). For example, in some areas of Benin, baobab trees are considered as a refuge for witches. In Nigeria, certain baobabs are centres of worship involving fertility spirits, and in Matabeleland in Zimbabwe the origins of some tribes are related to ancestor-baobabs.

The baobab tree is also used as a landmark, as an observation point and for its shade. Hollow trees provide reservoirs of fresh water which are used by nomads, particularly in the western part of Sudan (Tothill 1954). Water storage capacities range from 1000 to 9000 litres per tree (Craig 1991). Hollow trees can be used as tombs or temporary houses (Mullin 1991) and as toilets, prison chapel or churches (Wickens and Lowe 2008). Leaves of baobab are routinely browsed (especially in the agro-sylvipastoral systems in the Sahel) by sheep, cattle, horses, donkeys and camels; and during the dry season, cows, horses and donkeys eat the fruits (Matig et al. 2006). Some other commonly cited uses are summarised in Table 1.6.

Part of the tree	**Common uses**
Bark	Ropes, baskets, nets, crafts, adhesive (the bark gum), dye (the green bark), paper (in the past)
Wood	Canoe, float, potash, paper (in the past)
Roots	Soluble red dye
Fruit shells	Pots for food and drink, crafts, fuel, animal feed, potash
Seeds	Soap (due to the high phosphate content)
Fruit pulp	Rubber coagulant

Table 1.6. Some other uses of baobab tree parts. Assembled from: Burkill 1985, Esenowo 1990, Nkana and Iddi 1991, Hines and Eckman 1993, Esterhuyse et al. 2001, Sidibé and Williams 2002 and Matig et al. 2006.

It should be noted that the baobab tree also provides an environmental service. Although there is a widespread idea that baobab shade is bad for the crops (it is removed from agricultural land in some areas), it improves site conditions. It adds organic matter and nutrients through leaf-fall, it reduces soil temperature and water loss due to evapotranspiration (Amundson et al. 1995) and it attracts birds and large mammals that add nutrients to the soil with their droppings. In Senegal, the removal of many baobab trees as a result of 'Iceberg' lettuce production in 1979 lead to noticeable soil erosion (Chasm 1982).

Relationship with fauna and flora

The baobab acts as an important source of food, water (during times of drought) and shelter, for a wide range of animals (Fenner 1980). The hollows in the trunk of the baobab tree are used during the day by sheltering leopards, genets, porcupines, the west African lesser bush baby (*Galago senegalensis*) and the greater bush baby (*Otolemur crassicaudatus*) (Cashel 1995). The striped hyena (*Hyaena hyaena*) also uses baobab hollows to rear its young (Sweeney 1973). Numerous reptiles, especially pythons, boomslangs (*Dispholidus typus*), mamba (*Dendroaspis* sp.) and Egyptian cobra (*Naja haje*) also seek refuge in the hollows of the tree. Monitor lizards (*Varanus* spp.), the baobab gecko (*Hemidactylus platycephalus*) and the flap necked chameleon (*Chamaleo diepsis*) are also inhabitants of the baobab tree (Wickens and Lowe 2008). Several birds frequent and nest in hollows in trunks: rollers, hornbills, parrots, kingfishers, swallows, lovebirds, starlings, the barn owl (*Tyto alba*) and the Wahlberg's eagle (*Aquila wahlbergi*), vultures and weavers (Owen 1974, Wickens 1982, Wickens and Lowe 2008).

As mentioned earlier in this chapter (sections 1.5, 1.6), a number of animals eat baobab fruits and flowers. Apart from eating the fruits, various species of monkeys, including the blue monkey (*Ceropithecus albogularis*), the green monkey (*Chlorocebus subaeus*) and the grivet monkey (*Chlorocebus aethiops*) take refuge in the upper hollows and branches of the baobab tree, the latter also eating tender leaves (Wickens and Lowe 2008). Seedlings are believed to be eaten by elephants and other herbivores (Guy 1982, Venter and Venter 1996). The baobab bark, and even wood, is also favoured as food by elephants.

Old baobab trees give shelter to numerous invertebrates. Among the insects, wild bees are important since their honey is eaten by the honey badger (*Mellivora capensis*) and man (Wickens and Lowe 2008). While stick insects, the long-horned grasshopper and the praying mantis feed on the leaves of the baobab tree (Owen 1974), the cotton stainer bug (*Dysdercus sp.*) feeds on the seeds of fallen fruit. The cotton stainer bug attacks cotton plantations, and has received particular attention from agricultural entomologists. The baobab tree is often destroyed for its alleged responsibility for hosting this species, while less conspicuous members of the same family (which are more commonly host plants) are not destroyed (Wickens and Lowe 2008).

The baobab tree also provides a suitable environment for some plants. The hollows and cavities in the trunk collect dust and debris forming a rich soil in which seeds might germinate. The baobab tree is the main host for *Tapinanthus malacophyllus* (Engl. & K.Krause) Danser, an endemic mistletoe of the Luanda region in north-western Angola. In the coastal regions of Kenya and Tanzania, the baobab tree is an important host for *Emelianthe panganensis* subsp. *panganensis* Wiens & Polh. Also in Eastern Africa, it is host for *Erianthemum dregei* (Eckl. & Zeyh.) Tiegh. Parasitic figs (*Ficus spp.*) have also been observed on baobabs (Wickens 1982).

1.12 Estimated yields of the baobab tree and other parkland species

Arum (1989) estimated that, allowing for variation in site conditions, genotypes, and amount of leaf harvesting incurred, an average mature fruiting tree produces 200 kg of fruit per season. According to Ibiyemi et al. (1988), a mature baobab produces more than 250 fruits and provides at least 30 kg of food annually. However, Assogbadjo et al. (2005b) estimated 27, 35 and 13 kg of fruit per tree per season in the Sudanian, Sudano-Guinean and Guinean zone of Benin. The same authors also estimated 4.8, 6.3 and 2.4 kg of fruit pulp per tree per season; and 8.9, 11.9 and 4.7 kg of seeds per tree per season in the Sudanian, Sudano-Guinean and Guinean zone respectively. Fruit production varied greatly between individuals. It has also been reported that baobab production is characterised by an inter-annual irregularity, with production one year being double that of the previous year. Moreover, some baobab trees may not fruit for several years and this is probably due to ecological factors (Swanapoel 1993).

Fruit production of other parkland trees also varies between individuals of the same species and fluctuates greatly on an annual basis (Breman and Kessler 1995). In Mali, *V. paradoxa* production has been estimated to vary between 2.4 and 13.8 kg kernels/tree (see Boffa 1999). Serpantié (1997) found that *V. paradoxa* in Bondouki (Mali) produced 9.4 kg kernels per tree on average in 1995 while it produced 2.8 kg kernels per tree on average in 1996 (Serpantié 1997). Site conditions (e.g., nutrient availability), pruning and tree age also affect fruit production. For example, high-intensity pruning of *F. albida* reduces fruit yields in the following year between two to ten times (Boffa 1999). It has been reported that leaf production varies less than flower and fruit production for most parkland species (Breman and Kessler 1995).

1.13 Cultivation and other management practices

General issues

The baobab tree, like most parkland tree species, tends to regenerate naturally rather than being planted. Factors discouraging farmers from planting the baobab tree and other parkland species include the slow growth rate of most parkland species, their long maturation phase before fructification and the variation in yield (Boffa 1999). Other issues are the difficulties in germinating baobab seeds and the fact that people refuse to plant any species that regenerates spontaneously (NRC 2006, Wickens and Lowe 2008).

More obstacles to tree planting activities, especially in West Africa, include land and tree tenure, women's rights and forestry legislation (Boffa 1999). In West Africa a great percentage of the land being cultivated is borrowed: Swanson (1979) reported that up to 27% of the land cultivated was borrowed in Burkina while McMillan (1986) found that 56% of the land cultivated was borrowed in Mali. Generally, tree planting and felling is exclusive to the landowner while pruning and fruit gathering might be permitted to the land borrower (McLain 1990). Planting trees is generally not allowed by the lender for fear of permanent land claim by the borrower (Boffa 1999). Although women are often allowed to plant trees on the land they borrow from their husbands, as they can not use tree planting as a means of gaining control over borrowed land from their husband (McLain 1990), women may be loathe to plant trees in their husbands' land (in order to avoid the risk of losing them if marriage breaks down, Schreckenberg 1996). In some cases, the fact that allocated land might change from one season to another, might also discourage women from planting trees (Boffa 1999).

Forestry laws which limit access rights to trees might also limit baobab cultivation. For example, after a forestry law (created to support baobab regeneration and control unsustainable harvesting techniques) was introduced in northern Benin, farmers reported that they now remove baobab seedlings from their fields because they would need to buy permits for their use in the future and they are very expensive (Buchmann et al. 2010). Taboos may also constrain the practice of planting trees.

Although the baobab tree is not commonly planted, some farmers practise assisted regeneration: they protect seedlings from fire and animals; they water them or even transplant them. Dhillion and Gustad (2004) reported that in some villages in Mali, farmers protect naturally germinated seedlings (60% respondents) and transplant baobabs. Similar activities have been described from the Dogon people in Mali and Burkina Faso (Sidibé and Williams 2002).

Seed propagation

Baobab trees are not commonly planted but they can be propagated by seed. Although around a third of the seeds have the capacity to germinate without scarification (Razanameharizaka et al. 2006), seed pre-treatment (soaking in water, mechanical and acid scarification) with varying degrees of success has been recommended. Esenowo (1991) found that soaking seeds for three days in distilled water and placing them in Petri dishes produced 50% germination, while soaking for 5 days gave none. Vogt (1996) suggested immersing seeds in boiling water and leaving overnight to cool while Delange (2003) recommended soaking seeds in warm water for 72 h. Danthu et al. (1995) found that scarification with concentrated sulphuric acid for 6-12 h lead to a germination of more than 90% while Esenowo (1991) observed a germination rate of 86-98% after only 15 min immersion in sulphuric acid or nitric acid. Maghembe et al. (1994) found 90% germination after mechanical scarification, 92% after soaking in cold water, 96% after soaking in hot water and 86% in the untreated control. Contradictory results may be due to a number of factors, such as whether the fruit was ripe, whether the fruit was collected from a tree or the ground, the method and the length of seed storage, the date of planting and aftercare (Wickens and Lowe 2008).

Regardless of the method of scarification used, emergence is 4-6 (up to 18) days after pre-treatment. When seedlings emerge, it is believed to be better to shade them for 8 days. Seedlings require watering twice a day and they need protection from rodents. As direct seeding into the field has not been very successful; seedlings are mainly raised and transplanted when they are 3-4 months old. When transplanted (usually done in the rainy season), seedlings require protection against animal grazing and fire. Seedlings can be fertilised with phosphorous, urea, potassium nitrate, ammonium nitrate or magnesium nitrate (Sidibé and Williams 2002).

In Mali some farmers plant baobab trees for leaf production. However, Savard et al. (2002) reported that several factors discourage farmers from planting baobabs for leaf production: poor germination, poor access to water, the need to protect the seedlings and the economic rent of the plot.

Vegetative propagation

If propagation from seed is not widespread, vegetative propagation is even less frequent, in spite of its advantages. Grafted baobabs offer not only faster development and lower bottom branches that make fruit harvest easier but they also provide an opportunity for propagating individual trees with selected traits such as high vitamin C levels in the fruit pulp (Sidibé et al. 1996). Probably, on top of the afore mentioned obstacles to tree planting activities, lack of awareness of vegetative propagation techniques by local people is another factor. Young trees, from 3 months to 2 years old can be grafted with scions of desirable mature trees. Such scions can be stored in moist and at ambient temperatures for up to 2 weeks, but the younger the scions, the higher the success rate. In Mali, where several grafting experiments have been carried out, a veneer graft with plastic film (to control respiration) is used. First fruiting of grafted baobabs takes place after 3 years compared with 8-23 years for baobab planted from seed (Sidibé et al. 1996, Sidibé and Williams 2002).

Management techniques

Although farmers do not usually plant parkland trees, they commonly apply several management techniques to increase production of parkland trees: pruning to stimulate leaf re-growth or to enhance understory crop performance; ringing to increase fruit and seed production; and, coppicing and pollarding (cut at the base or above grazing height respectively, to encourage shoot re-growth) to limit competition with other crops (Boffa 1999). Fertilisers are rarely applied to baobab trees as other crops (e.g., millet, sorghum) have priority. For the baobab tree pruning to stimulate leaf re-growth or to enhance understory crop performance are the most commonly practised techniques (Dhillion and Gustad 2004, SCUC 2006). It should be noted that severe pruning related to leaf harvesting (mainly carried out in West Africa) might cause mutilation that reduces the number of fruits on each tree (Dhillion and Gustad 2004).

Pests and diseases

Numerous authors have stated that there are no serious pests and diseases of the baobab tree (Sidibé and Williams 2002, SCUC 2006, Wickens and Lowe 2008). However, a number of insects, fungi and viruses attack the baobab tree.

Wickens (1982) reported that the most common pests were: cotton bollworms (*Helicoverpa armigera, Diapropsis castanea* and *Earias biplaga*) and cotton-stainer bugs (*Dysdercus fasciatus, D. intermeius, D. nigrofasciatus, D. suberstitiousus, Odontopus exsanguinis* and *O. sexpunctatus*). Other pests include the cocoa capsid (*Distantiella theobroma*), flea beetles (*Padagrica* spp.), the mango mealy bug (*Rastrococcus iceryoides*) and the long horn beetle *Aneleptes trifasciata* (Sidibé and Williams 2002, SCUC 2006). Nematodes (*Rotylenchus reniformis*, *Meliodogune* spp.), macrofungi (*Daldinia concentrica*, *Trametes socrotana*), and viruses (e.g., CSSV or Cacao swollen shoot badnavirus, and CYMV or Cacao yellow mosaic tymovirus) also attack the baobab tree.

It has been reported that baobabs are also sensitive to a fungi from the *Antennulariella* genus (Matose and Clarke 1991, Maulka et al. 1995). Bark becomes black, and looks as if it has been burned (sooty baobabs). Other symptoms are rubber excretion and wizened branches (Sharp 1993). It has been suggested that this condition is a secondary manifestation of a physiological disorder which is related to lengthy periods of below average rainfall aggravated by increasingly intensive land use in arid areas (Piearce et al. 1994).

1.14 Conservation

Threats to some baobab populations

Although the baobab tree is not yet considered to be an endangered species, there are threats to local populations such as elephant damage, commercial exploitation or land clearance for mining, dams and construction.

Elephants have been reported to destroy baobabs (not only seedlings but also old trees) in a number of game reserves. As mentioned earlier in this chapter, these large animals like baobab bark and wood (they remove them with their tusks creating big holes that might cause the tree to collapse). However, elephant use of baobabs is only a problem when the elephant population becomes too big (e.g., in some protected areas) (Sikes 1972). Commercial exploitation of wood and bark for paper making has been considered, and attempted more than once. For example, after the Second World War, baobab paper production was banned by the authorities in South Africa (Esterhuyse et al. 2001).

Land clearance for dams, mining and farming threatens not only the baobab tree but also its habitat (Wickens and Lowe 2008). Baobab trees have been destroyed in western Nigeria for agricultural development, in southern Africa to extend Lake Kariba in the 1950s, in southern Togo to facilitate phosphate mining and in South Africa to allow diamond mining (Owen 1974, Koch 1995, van Niekerk 1995). Baobab clearance for construction is taking place next to Bandia Reserve in Senegal (S. Garnaud 2008, pers. comm.). Land clearances for small-scale farming usually pose less of a problem as large baobab individuals are not eliminated in the clearing process, but still destroy baobabs, especially young individuals. Large individuals are often left either due to their use (mainly food and traditional medicine, Lamien et al. 1996), due to cultural beliefs (such as that ancestors live in the large old baobab individuals, C. Buchmann 2009, pers. comm.) or due to difficulties in cutting down the large trunk.

In order to reduce the threats to some baobab populations or individuals, several measures have been taken. While some trees are registered as National Monuments in Botswana, all trees are protected under the Forestry legislation in Namibia (Curtis and Mannheimer 2005) and in South Africa (Wickens and Lowe 2008). Although no conservation areas have been specifically set aside for the protection of the baobab tree (Buchmann et al. 2010), the baobab tree occurs in several protected areas (Table 1.7). However, in some cases, elephant pressure on these areas or overexploitation by humans have a negative effect on the baobab tree populations (Table 1.7).

Country	**Type of Protected Area**	**Name**	**Remarks**
Angola	National Park	Quiçãma	
	Integral Game Reserve	Mupa National	
	Forest Reserve	Golungo Alt	
Benin, Burkina Faso	National Park	Penjiari - Arly	Cattle-owning Fulani use the baobab tree, elephant damage
Benin, Burkina Faso, Niger	National Park	W	Cattle-owning Fulani use the baobab tree
Kenya	National Park	Tsavo East	Elephant damage
	National Park	Tsavo West	Elephant damage
Mozambique	National Park	Limpopo National Park	
South Africa	National Park	Kruger	Elephant damage
Tanzania	National Park	Msembe	Elephant damage
	National Park	Ruaha	Elephant damage
	National Park	Lake Manyara	Elephant damage
	National Park	Serengeti	
	Game Reserve	Mkomazi	
	Game Reserve	Selous	
Zambia	National Park	North Luangwa	Elephant damage
Zimbabwe	National Park	Ngesi	
	National Park	Mana Pools	Elephant damage

Table 1.7. Protected areas reported to have the baobab tree and some problems with the baobab trees in these areas. Source: Robertson-Bullock 1960, Caughley 1976, Leuthold 1977, Barnes 1980, Weyerhaeuser 1985, Swanepoel 1993, Barnes et al. 1994, Kelly 2000, O'Connor et al. 2007, Edkins et al. 2007, Wickens and Lowe 2008, Schumann et al. 2010.

Potential threats for the species

The baobab tree is also regarded as under moderate threat of genetic impoverishment as a result of forest degradation (Gowela and Masamba 2002). Apart from being threatened at a population level and at a genetic level, several authors have been concerned about the potential endangered status of the baobab tree as a species, due to its scattered distribution, its low population density (it is never a major component of the vegetation) and its low recruitment. Already in 1906, Chevalier suggested that the African baobab was disappearing. Wickens (1982) suggested that the baobab tree distribution might be slowly contracting due to a long term change towards a drier climate in Africa. In fact, he reported that many baobabs in Sudan and other parts of the northern Sahel died during and following the Great Drought of the late 1960s and that regeneration (in those areas) became impossible with the following desertification. Wickens and Lowe (2008) suggest that the baobab tree is currently threatened by climate change and, especially in drier areas, from desertification.

Another threat is human overexploitation. After the acceptance of baobab fruit pulp as a food ingredient in the EU in July 2008 (CEC 2008) and its acceptance in the USA in July 2009 (FDA 2009) there is a growing concern in the popular press that baobab commercialisation may lead to over-exploitation of natural stands of this species. Often, the initial response to increased demand is more intensive harvesting leading to over-exploitation of the species (Belcher et al. 2005, Marshall et al. 2006). For example, in eastern Zimbabwe, where baobab bark is harvested for craft purposes, Dovie (2003) stated that the baobabs are in danger of destruction in the short term as a result of baobab harvesting and trade arrangements.

1.15 Summary of the literature review

The baobab tree is an under-utilised fruit-bearing tree appreciated for its non-timber forest products (NTFP). The baobab tree is characterised by its massive size and its bottle-shaped trunk. Baobab wood is soft and spongy, the deciduous leaves are 5-7 palmately compound and the bat-pollinated flowers are large and pure white. The fruits, which are filled with reniform seeds embedded in the whitish mealy pulp, are variable in size and shape. Baobab seeds are dispersed by a wide range of animals, including elephants and humans. The baobab tree is a very long-lived species that has different growth rates during its life. While baobab density is very variable in the landscape, in general, population size class distributions are bell-shaped with few young and very old individuals. Baobab natural regeneration seems to be rather poor.

The baobab tree is naturally found in most countries south of the Sahara in Africa. It seems that this species has wide ecological tolerance: it is found between 150 and 1500 mm annual rainfall, between 0 and 1500 m altitude, in a wide range of soils and from 5 to 42 ºC. Presence of dispersers, fire, drought and humans also affect baobab distribution. Outside Africa, the baobab tree has been introduced in Oman, Yemen, India, Sri Lanka and Madagascar, among other areas. Significant differences in genetic characteristics between West and south-eastern African baobab populations have been reported.

All parts of the baobab tree are useful. Leaves, fruit pulp and seeds are commonly eaten and are known to be nutritious. The baobab tree provides medicine, income and materials to local people in Africa. Apart from humans, a wide range of animals and some plant species use the baobab tree. This species is not commonly cultivated although it can be propagated from seed and through grafting. There are few known pests and diseases and baobab trees are barely managed by local farmers. Elephants, human exploitation, land clearance and climate change seem to threaten baobab populations in certain areas.

From the literature review, it seems that the baobab tree could be widely cultivated, as its ecological tolerance is broad and this species can be propagated by seed and through grafting. Potential cultivation sites are studied in chapter 2. The literature review also suggests that climate change, among other factors, might be threatening this species. The potential effect of climate change on the distribution of the baobab tree, and its implications for conservation of this species are analysed in chapter 3. Although it seems that there is a great variation in baobab morphology, and thus there is a potential for selecting ‘superior’ planting materials, there is a lack of information on the genetic and the phenotypic effects on the morphological diversity. Baobab leaf, fruit and seedling morphology and its implications for selecting ‘superior’ planting materials are studied and discussed in chapters 4, 5 and 6.

1.16 Updating the literature review

Two monographs have been used as the main source of information for this literature review: Sidibé and Williams (2002) and Wickens and Lowe (2008). However, information has been updated with recent publications: e.g., Pock Tsy et al. (2009) which provides new information on baobab genetics, Buchmann et al. (2010) which reports new uses of baobab tree parts. Some topics were not covered by either of these two monographs: e.g., baobab density and population levels (section 1.8); other factors limiting baobab distribution (section 1.9), baobab genetics (section 1.10) and estimated yields (section 1.12). Moreover, in order to better understand the current situation of the baobab tree, information on other fruit-bearing tree species commonly found in the same habitats of the baobab is provided (e.g., densities of other parkland species, section 1.8). The literature review also gives very specific information on cultivation (section 1.13) and conservation (section 1.14) of this species, which are the main focus of this thesis.

1.17 Gaps in knowledge and suggested research

Although a lot is known about the baobab tree, as the literature review has shown, there are still large gaps in knowledge. From the literature review some questions that arise are:

- Considering the baobab tree’s broad ecological tolerance and the possibility to cultivate this species, where could this species be cultivated?
- It has been suggested that climate change is threatening this species; how might climate change effect the distribution of the baobab tree?
- How can we protect this species? Where conservation efforts should be focused?

- Considering that there is variation in baobab fruit morphology, is there also variation in leaf morphology, which can be linked to drought adaptation mechanisms? Can ‘superior’ trees in terms of leaf characteristics be selected?
- If there are genetic differences between baobab populations from West and south-eastern Africa, are baobab fruits different in these two areas? Can ‘superior’ trees in terms of fruit characteristics be selected?
- Is there also variation in seedling growth and morphology? How do baobab seedlings deal with drought stress?

This research aims at answering some of these questions: potential cultivation sites are studied in chapter 2 while the potential effect of climate change on the distribution of the baobab tree, and its implications for conservation of this species are analysed in chapter 3. Baobab leaf, fruit and seedling morphology and its implications for selecting ‘superior’ planting materials are studied and discussed in chapters 4, 5 and 6.

Other gaps in knowledge, such as market potential (both local and international), preferred fruit and leaf processing techniques, further ethnobotanical studies, effects of management techniques on fruit production, recommended irrigation and pruning practices for baobab continuous leaf production, differences in fruit and leaf nutritional value between provenances, genetic variation at a regional level, among others, have been the focus of parallel work by other PhD students (e.g., Van der Stege 2010, De Caluwé submitted) and researchers who are also part of the DADOBAT EU-funded project.

CHAPTER 2. Study of the present distribution of the baobab tree: implications for cultivation

By examining the distribution of a species, the environmental factors affecting this distribution can be analysed and the potential distribution of this species outside its geographical range can be predicted (Pearson 2007). Potential distribution might also include areas where the species could be planted. In this chapter I use species distribution modelling to: (1) analyse the current distribution of the baobab tree, (2) to determine its ecological tolerances, and (3) to predict the potential distribution of the baobab tree in Africa and in the tropical world. The implications of these potential distributions for cultivation are also discussed. The material in this chapter has been published as a journal paper in *Agroforestry Systems* (see Annex I).

2.1 Introduction to species distribution modelling

Differences in the environmental characteristics of areas occupied by organisms can be examined by modelling species distributions, a technique that integrates locality data, geographic information systems (GIS) data and modelling algorithms (Anderson et al. 2003). The resulting model describes the common environmental characteristics of the known range of a given species (Peterson 2003). This approach has been used to predict species distributions (Illoldi-Rangel et al. 2004) and to predict changes in the distributions of flora and fauna associated with projected models of climate change (Peterson et al. 2002).

The choice of model type is likely to be influenced by several factors such as the aims of the study, the biology of the target organism, the level of knowledge of the target organism's biology and data quality (Robertson et al. 2003). Models used to predict species' potential distributions have been described as either mechanistic or correlative (Beerling et al. 1995). Mechanistic models incorporate physiologically limiting mechanisms in a species' tolerance to environmental conditions (Pearson 2007). One example of mechanistic models is the model used by Chuine and

Beaubien (2001) to study the distributions of North American tree species. They used factors such as frost injury, phenology and reproductive success to estimate responses to environmental variables (including mean daily temperature, daily precipitation and night length). Although mechanistic models are likely to yield superior results because they include physiological data, such physiological data are not available for most species (Hijmans and Graham 2006), including the baobab tree.

Correlative models estimate the environmental conditions that are suitable for a species by relating known species' occurrence records with sets of environmental variables that can reasonably be expected to affect the species' physiology and probability of persistence (Pearson 2007). Table 2.1 lists some commonly used correlative models.

Method [1]	**Model or software name [2]**	**Type of species data**	**Reference**
Bioclimatic envelope	BIOCLIM	presence-only	Busby 1986, Nix 1986
Gower Metric	DOMAIN	presence-only	Carpenter et al. 1993
Ecological Niche Factor Analysis (ENFA)	BIOMAPPER	presence and background	Hirzel et al. 2002
Maximum Entropy	MAXENT	presence and background	Phillips et al. 2006
Genetic algorithm (GA)	GARP	pseudo-absence	Stockwell and Peters 1999
Regression: generalized linear model (GLM), generalized additive model (GAM), boosted regression trees (BRT), multivariate adaptive regression splines (MARS)	Implemented in R and elsewhere	presence and absence, (or pseudo-absence)	Lehman et al. 2002, Elith et al. 2006, Elith and Leathwick 2007, Leathwick et al. 2006

Table 2.1. Some correlative models used to study species distributions. [1] Method refers to a statistical or machine-learning technique. [2]Model/software name refers to a name (or acronym) given to a published model that implements the method stated. This table has been adapted from Guisan and Thuiller (2005), Elith et al. (2006) and Pearson (2007).

Correlative distribution models can be divided into two groups based on the input data used to build them. Models that use both presence and absence locality records have been termed group discrimination techniques and those that use only presence locality records have been termed profile techniques (Caithness 1995). Presence/absence data are typically obtained by means of systematic field surveys which are usually expensive and time-consuming to conduct (Austin 1998). As a result, presence-only data (obtained from museum or herbarium collections) are often the only data available. Although presence-only data are useful for modelling species' distributions as shown by Elith et al. (2006), there are limitations because presence-only data suffer from several problems. For example, observations may be unplanned and tend to be biased toward towns and roads, observations are often of dubious reliability and unspecified spatial accuracy, and they have variation in survey effort between different environments and geographical areas (Loiselle et al. 2003). For the baobab tree, presence-only records from museum or herbarium collections with the limitations mentioned above are the only data available.

Several authors have classified presence-only models in different ways. For example, Pearson (2007) suggests three types of presence-only models:

- Models that rely solely on presence records (e.g., BIOCLIM, DOMAIN). These models make the prediction without any reference to other samples from the study area.
- Models that use 'background' environmental data for the entire study area (e.g., Maxent, ENFA). These models focus on how the environment where the species is known to occur relates to the environment across the rest of the study area (the 'background').
- Models that sample 'pseudo-absences' from the study area (e.g., GARP). These models assess differences between the localities where the species is known to occur and a set of localities chosen from the study area that are used in place of real absence data. The set of 'pseudo-absences' may be selected randomly or according to a set of weighting criteria. Presence/absence models (e.g., GLM) can also be implemented using pseudo-absences.

Maxent (the maximum entropy method for species' distribution modelling) which uses 'background' environmental data, is a machine learning system that estimates the most uniform distribution ('maximum entropy') across a study area, given the constraint that the expected value of each environmental predictor variable under this estimated distribution matches its empirical average (average values for the set of species' presence records) (Phillips et al. 2006). Several authors have shown that Maxent outperforms most other modelling algorithms (Elith et al. 2006). For example, Hernandez et al. (2006) revealed that Maxent was the most capable of the four modelling methods (BIOCLIM, DOMAIN, GARP and Maxent) assessed across 18 species. Pearson et al. (2007) found that Maxent outperformed GARP while predicting species distribution of occurrence records of cryptic geckos in Madagascar. Sergio et al. (2007) found that Maxent outperformed ENFA and GARP in a study carried out in Portugal for four bryophyte species.

Apart from having a high performance, Maxent is also preferred in conservation studies (see chapter 3) because it avoids commission errors (Loiselle et al. 2003, Phillips et al. 2006). Commission errors (i.e. when a model predicts the presence of a given species in particular areas, although it is known that this species is not present there) might lead to erroneous conservation decisions focusing financial investments and management efforts in non-priority areas (Loiselle et al. 2003).

In this study, Maxent is used for distribution modelling of the baobab tree as it has better performance, it is preferred in conservation studies and it has the added advantage that it also performs the receiver operating characteristic (ROC) statistical analysis used for model validation.

2.2 Aims and Objectives

The general aim of this chapter is to model baobab tree distribution using a predictive modelling approach, thereby to contribute to the selection of effective cultivation sites for the species. In order to achieve this aim, the following specific objectives are proposed:

1. To study the species-habitat relationship and to identify important environmental parameters
2. To predict the potential current distribution of the baobab tree in Africa
3. To predict potential cultivation sites in the tropical world

The specific research questions are:

1. Which are the main factors limiting the baobab tree’s distribution in Africa?
2. Where can the baobab tree be planted in Africa?
3. Can the baobab tree be planted outside Africa?

In order to answer these research questions, presence-only data, GIS environmental layers and Maxent were used.

2.3 Methodology

Scope of study

The study was centred in Africa, which is known to be the native range of this species. However, in order to predict potential areas for cultivation, the continental tropics (from 35 °N to 35 °S) including America, Asia and Oceania were considered.

Species data

A total of 450 baobab growing localities (without duplicates) were assembled from diverse sources (Table 2.2, full set of records in Annex II). Thirty-two percent of the localities came from recent fieldwork while 68% were herbarium records.

Source	**Number of records**	**Type of record**	**Geographical location**
A. Cuni Sanchez	23	Fieldwork	Benin, Malawi, Mozambique
A.S. Larsen	21	Fieldwork	Several countries all over Africa
Aarhus herbarium [a]	2	Herbarium record	Senegal, Tanzania
Botanic Garden and Botanical Museum Berlin-Dahlem [a]	4	Herbarium record	Mali, Tanzania, Kenya
DADOBAT Project	20	Fieldwork	Senegal, Mali
Database Schema for UC Davis [a]	1	Herbarium record	Niger
Dhillion and Gustard (2004), Duvall (2007)	2	Fieldwork	Mali
Frankfurt Herbarium	23	Herbarium record	Burkina Faso, Benin, Nigeria
KEW Herbarium	48	Herbarium record	Several countries all over Africa
Marine Science Institute, UCSB [a]	1	Herbarium record	Tanzania
Missouri Herbarium [a]	7	Herbarium record	Tanzania
Paris Herbarium	20	Herbarium record	Several countries all over Africa
Phytotrade Africa database	58	Herbarium record and fieldwork	Malawi, Zambia, Mozambique, Zimbabwe
Pock Tsy et al. (2009)	51	Fieldwork	Several countries all over Africa
PRECIS database	40	Herbarium record	South Africa, Namibia, Botswana
Uppsala Herbarium [a]	2	Herbarium record	Kenya, Eritrea
Wagningen Herbarium [a]	1	Herbarium record	Cameroun
Wickens and Lowe (2008)	126	Herbarium record	Several countries all over Africa
Total (without duplicates)	**450**		

Table 2.2. Source, number, type of record and geographic location of baobab presence records used in the study. [a]indicates that the occurrence data was accessed through the GBIF Data Portal (www.gbif.net).

Herbarium records classified as 'cultivated specimen' by the herbarium or with controversial 'cultivation' origin following Sidibé and Williams (2002) were eliminated from the species dataset. However, they were kept as a potential validation method.

Some of the herbarium records contained geo-referenced coordinates representing presence locations but others had to be geo-referenced using several methods. The gazetteers of the Flora Zambesiaca (Pope and Pope 1998) and the Flora of Tropical East Africa (Polhill 1988) were used to geo-reference some records from Kew and Paris Herbariums. The Geographic Names Data Base, containing official standard names approved by the United States Board on Geographic Names and maintained by the National Geospatial-Intelligence Agency (GNS- National Geospatial-intelligence agency, 2005) was used to geo-reference most of the remaining records. A few records had to be geo-referenced using Google Earth (Google 2008) by selecting a point as near as possible to the described collection site. Points were geo-referenced based on the geodetic coordinate system (geographic lat-long, datum WGS84).

Although a large number of herbarium records were assembled, not all collection locality data were detailed enough to be geo-referenced with sufficient confidence to be included in the study. For example, during the visit to Paris Herbarium about 100 records were noted, but only 46 had information on collection sites detailed enough to be included in the dataset. During the subsequent geo-referencing process, only 23 of these 46 could be geo-referenced.

Once geo-referencing was complete, duplicate locations were eliminated as Maxent outputs do not change with multiple records from one site. The oldest location was removed (as it is most likely that the most recent record of a baobab tree still exists). Finally, it was verified that all species records were inside the environmental layers. Records outside the environmental data layers (for example, which were 'in the sea' instead of being on an island due to the low resolution of the environmental layers) were eliminated.

Data quality in species data

Issues of data quality can be split broadly into error and bias. Error refers to a mistake in the data such as misidentification or human error in geo-referencing, while bias is due to problems intrinsic with the data such as not encompassing the full environmental niche. More specifically, specimen data quality issues can be classified in three categories: identity (misidentification), space and time (Wieczorek et al. 2004).

Spatial error within species datasets includes geo-referencing error, imprecision of location of a record or error in the original location of the record (Wieczorek et al. 2004). Typically, as spatial locality data have been recorded as textual descriptions and only recent collectors include geographical coordinates (Chapman 1999, 2004, Wieczorek et al. 2004), geo-referencing the data can produce various kinds of error. Often these location descriptions are based on names and situations that can change over time, or one place name may refer to several different localities and is thus easily misapplied. Human error may cause misreading of longitude and latitude or the accidental swapping or transposition of characters (Chapman 1999, Wieczorek et al. 2004). Positional errors in species data lead to a drop in model performance, and also affect the interpretation of the results (Osborne and Leitão 2009).

Spatial bias is another common issue in species quality data. The collectors of the specimens may have incorporated bias by collecting in places where they expect to find what they are looking for, places which were conveniently accessible, or they collected opportunistically. Collectors have often been found to sample along roads and rivers, near towns or biological stations or in areas of high diversity (Engels et al. 1995, Rich 1997, Hijmans et al. 1999, Hijmans et al. 2000, Williams et al. 2002, Chapman 2004). Spatial bias can lead to an unknown but probable observation bias (Reutter et al. 2003) meaning that the sample might not be a representative sample of the environmental or geographical space (Williams et al. 2002, Barry and Elith 2006). Spatial bias also affects the model results and results interpretation (Leitao et al. in press).

Temporal bias can be another problem as museum and herbarium data generally supply information only on the presence of the entity at a particular time and say nothing about absences in any other place or time (Wieczorek et al. 2004). The species may no longer be present at a historical collection site. Another data quality issue is that the presence locations assembled from museum and herbarium data may represent a demographic sink or source population for the species (Wieczorek et al. 2004). A demographic sink population is a population which is maintained thanks to the immigrants coming from another population (the source population). Conservation efforts should not be focused on sink populations.

Dealing with data quality in species data

It was assumed that all records obtained were adequately determined and identity was not a major issue in quality data because the baobab tree is a very conspicuous tree. Adult trees cannot be mistaken (Curtis and Mannheimer 2005), and only one species of baobab (*A. digitata*) occurs in Africa.

A few points were found to have spatial error while validating the geo-referencing process. For example, point 52 (14.91666, -24.4) in Republic of Cape Verde was identified as being outside the environmental layers. Although the record was correctly geo-referenced, the environmental layers were unable to show all islands in the island chain (Fig. 2.1). The record was eliminated. Point 201 (7.2, 35.74) was found to be in Ethiopia (Fig. 2.2) while the locality description by the collector (Verdcourt 1961, KEW Herbarium) said it was in Tanzania. As no description of the collection site was available, apart from the name of the country, this record was eliminated. Point 227 (-17.11, 334.75) from the Phytotrade dataset was also found to be mis-geo-referenced. The longitude 334.75 was unrealistic. It was determined that it had been a misreading or mistyping of digits while geo-referencing, and record coordinates were changed to those matching the description of the locality in Mozambique by Wild and Fernandes (1967).

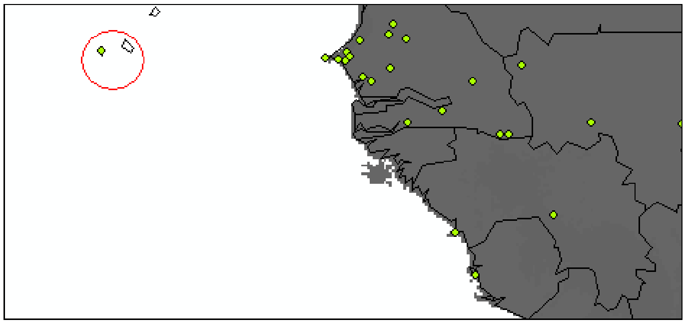


Fig. 2.1. Example of spatial error: point 52 in Republic of Cape Verde was identified as being outside the environmental layers.

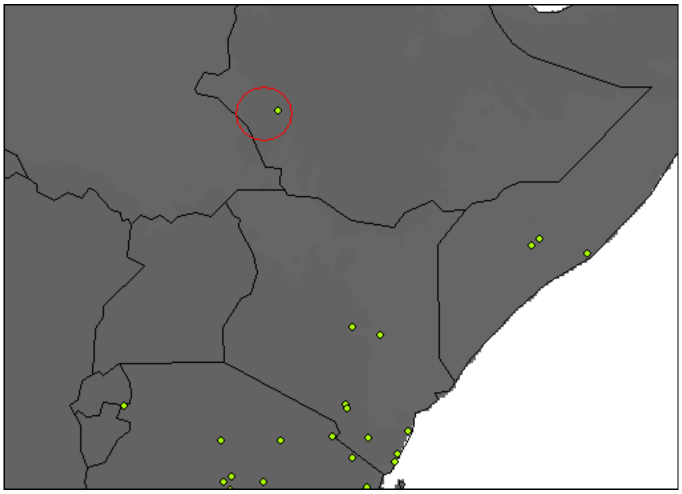


Fig. 2.2. Example of spatial error: point 201 (7.2, 35.74) was found to be in Ethiopia while the locality description by the collector (Verdcourt 1961, KEW Herbarium) said it was in Tanzania.

Regarding spatial bias, as records were assembled from different sources and this study is focused on a continent scale, it seems that collecting bias is not a relevant issue in this study. In order to reduce the effect of temporal bias and match the present climatic variables (produced over the period 1950-2000), it was suggested to eliminate the species records collected before 1950. Two models were run: one with all the species records and another with the records collected after 1950. As there were few significant differences between the results of the two models, and it was considered that baobabs recorded before 1950 would still be alive and most baobabs recorded after 1950 would be more than 50 years old (the baobab tree is a very long-lived tree), in the end, it was decided to keep all records collected after 1900.

One issue that remained unresolved was the possibility that demographic sink populations were being included in the study. Different authors have reported diverse population densities in different countries. Few individuals in smaller classes have been noted by several authors (chapter 1, section 1.8). As mentioned in chapter 1, in fact, the baobab tree is a very long-lived species and natural regeneration is rather poor. As it was not possible to separate records from source and sink populations, all records were included but the possibility of having included sink populations was considered in the interpretation of the results.

Coordinates vary in precision from contemporary GPS-derived field survey data to museum and herbarium records geo-referenced *post facto*. However, it was considered that geo-referencing accuracy was not a major issue as the grid size used for modelling was relatively coarse (5 min).

Dividing species data

Although there is only one species of baobab tree growing in Africa (*A. digitata*) and there are no subspecies or varieties officially accepted, as mentioned in the literature review (chapter 1), a recent study has shown that there are genetic differences between populations from West and East Africa (Pock Tsy et al. 2009). Thus, baobab distribution in Africa was studied using all 450 presence records, and using the East (307) and West African (143 records) records separately based on Pock Tsy et al. (2009) (Fig. 2.3). These are referred to as the 'All records model', the 'East African model' and the 'West African model', respectively.

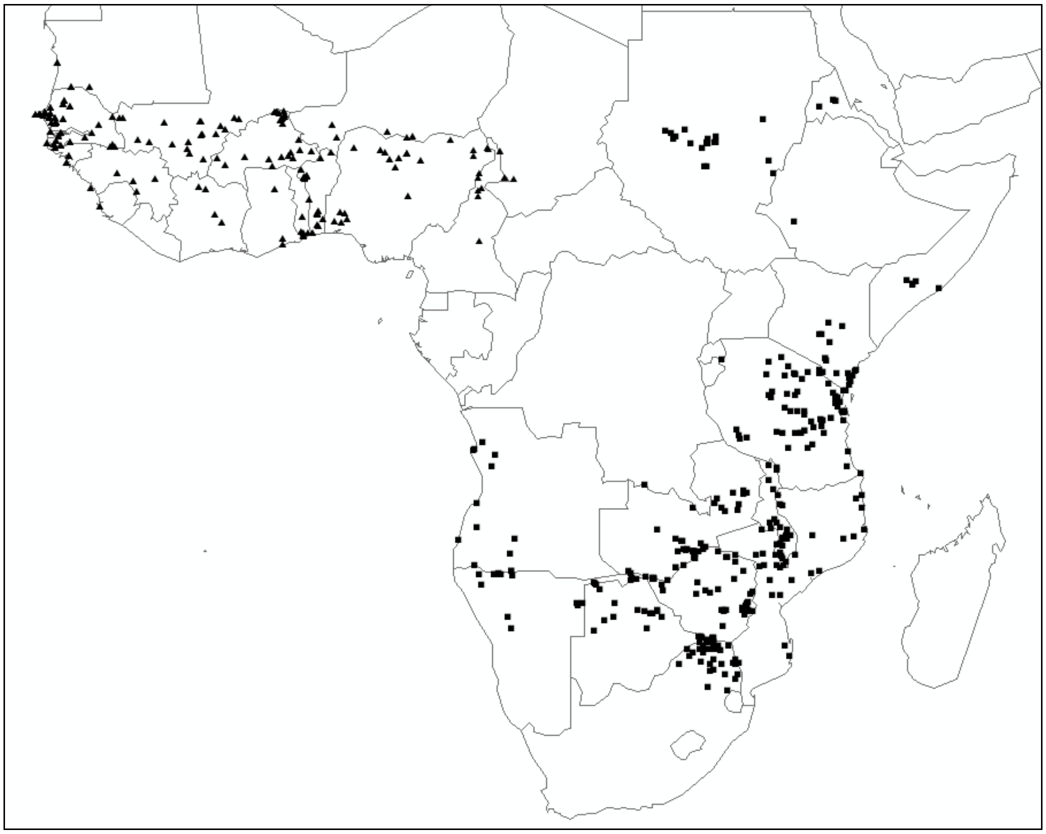


Fig. 2.3. Geographical distribution of the baobab presence records used in the study. Triangles: West Africa records, squares: East Africa records.

Environmental data: Present climate layers

Environmental variables were selected following the ecological requirements of the baobab tree suggested in the literature. The selected layers were related to precipitation, temperature, topography and soil type (Table 2.3). Researchers have commonly used these variables in other studies of predictive distribution of species modelling, not only with Maxent but also with other programs (Anderson et al. 2002, Hijmans and Graham 2006, Pearson et al. 2007, Peterson 2007). Nineteen climatic variables were obtained from Worldclim (http://www.worldclim.org/). These 19 climatic variables are derived from monthly temperature and rainfall recorded worldwide (period 1950-2000) and are often used in ecological niche modelling. Temperature is expressed in (°C * 10) and precipitation in mm. A quarter is a period of three months (1/4 of the year). BIO2 was calculated as the mean of monthly maximum temperature - minimum temperature. BIO3 = (BIO2/BIO7* 100) and BIO4 = temperature standard deviation *100. BIO15 is the coefficient of variation of annual precipitation.

Altitude (elevation above sea level in metres derived from the SRTM-Shuttle Radar Topography Mission, http://www2.jpl.nasa.gov/srtm/) was also obtained from the Worldclim database. The resolution of these layers was 5 min or 10 x 10 km approximately at the equator (Hijmans et al. 2005).

Variable	**Source**
BIO1 Annual mean temperature	Worldclim
BIO2 Mean diurnal range	Worldclim
BIO3 Isothermality	Worldclim
BIO4 Temperature seasonality	Worldclim
BIO5 Maximum temperature of the warmest month	Worldclim
BIO6 Minimum temperature of the coldest month	Worldclim
BIO7 Temperature annual range	Worldclim
BIO8 Mean temperature of the wettest quarter	Worldclim
BIO9 Mean temperature of the driest quarter	Worldclim
BIO10 Mean temperature of the warmest quarter	Worldclim
BIO11 Mean temperature of the coldest quarter	Worldclim
BIO12 Annual precipitation	Worldclim
BIO13 Precipitation of the wettest month	Worldclim
BIO14 Precipitation of the driest month	Worldclim
BIO15 Precipitation seasonality	Worldclim
BIO16 Precipitation of the wettest quarter	Worldclim
BIO17 Precipitation of the driest quarter	Worldclim
BIO18 Precipitation of the warmest quarter	Worldclim
BIO 19 Precipitation of the coldest quarter	Worldclim
Altitude	SRTM
Soil type	The Harmonized World Soil Database

Table 2.3. Selected layers for modelling and their sources.

Soil type was obtained from the Harmonized World Soil Database (FAO et al. 2008). Soil type was a categorical variable with 36 categories. Maxent treats continuous and categorical variables in a different way. In fact, Maxent is not capable of recognising patterns beyond the individual soil type classification; to the modelling algorithm, sand and coarse sand are as different from one another as are sand and clay loam. Thus, it was decided to reduce the number of categories of soil type from 34 to 10 (Table 2.4) using the 'lecture notes on the major soils of the world' (FAO 2001). Soil type was obtained in 30-s resolution (equivalent to 1 km^2 cells at the equator) and was converted to 5 min (with the aggregate function 'commonest' in ArcGIS) to match the other layers.

New soil category	**FAO soil groupings**
1. Low activity clays	Acrisols, Ferralsols, Nitisols, Lixisols, Plinthosols
2. High activity clays	Alisols, Luvisols, Cambisols, Vertisols
3. Volcanic	Andosols
4. Sand	Arenosols
5. Calcareous	Chernozems, Calcisols, Gypsisols
6. Water-saturated	Fluvisols, Gleysols, Podsols, Planosols
7. Organic	Histosols, Phaeozems
8. Saline	Solonchalks, Solonetz
9. Shallow soils	Leptosols, Regosols
10. No data	Sand dune, Water body, No data

Table 2.4. Classification of the 34 soil groupings of the Harmonized World Soil Database (FAO et al. 2008) into the 10 soil categories used in the model.

It is believed that climate is the main range determinant for tree species at large spatial scales (Pearson and Dawson 2003). A recent study on palm species' distributions in Africa confirms this (Blach-Overgaard et al. 2010). Other variables often used in species modelling were discarded for several reasons:

- Slope: considering that the cell size used is 5 min, it seemed that average slope of the cell was not meaningful.
- The Normalized Difference Vegetation Index (NDVI): the baobab tree is not a forest understory species and it is often found in parklands; it was thought that vegetation was not an important variable limiting its distribution.
- Radiation: it did not seem to be a limiting factor in the dry African savanna, where the tree naturally grows.
- Soil moisture and related variables: as it was not possible to acquire long term soil humidity data for the whole of Africa, it was considered that soil humidity would be partially explained by temperature and precipitation. Blach-Overgaard et al. (2010) showed that water balance (the difference between evapotranspiration and precipitation) was highly correlated with annual precipitation, and the latter was a better explanatory variable.
- Other soil characteristics such as sand percentage or pH (extracted from top soil texture of TERRSTAT database, FAO 2002) were discarded after a few trials as they made little contribution to the final model.
- Land-use and related variables: although land-use has an influence on baobab regeneration (see chapter 1), at a continent scale it seemed that environmental

factors were playing a much more important role. Blach-Overgaard et al. (2010) reported that human impact (represented as human population density and human influence index) had negligible impact on palm distribution at a continent scale (Africa) compared with climatic variables.

- Presence of dispersers: considering the wide range of animals (including humans) contributing to baobab dispersal and its widespread distribution in Africa (see chapter 1), it was assumed that the presence of dispersers was not an important factor limiting baobab distribution at a continental scale.

All environmental layers were clipped to two extents (Africa and tropical world) and were converted to ASCII format for the processing in Maxent.

Variable selection

Variable contribution to the final model and Maxent's jackknife test of variable importance were used to select the most meaningful variables. Variables that contributed less than 1% to the final model were eliminated. Maxent's jackknife test of variable importance was used to evaluate the relative strengths of each predictor variable. The training gain is calculated for each variable alone as is the drop in training gain when the variable is omitted from the full model. The modelling process started with a full model that contained all predictor variables. Then, the variables with the lowest decrease in the average training gain when omitted were removed and the remaining variables were used to build the model.

Maxent setup

The present-day African environment-species relationship (built with the environmental layers covering the extent of Africa) was projected onto the tropical world using the tropical world environmental layers.

Maxent parameters used in the analyses of the baobab tree distribution were as in Table 2.5. Maxent was run under the 'auto-features', so that Maxent would select a set of features appropriate to model the response (response curve) of the studied species to the environmental variables, as suggested by Phillips and Dudik (2008). Maxent has features of six classes, some appropriate for either continuous or categorical variables (Phillips and Dudik 2008). In this study both continuous (e.g., annual rainfall) and categorical (e.g., soil type) variables were used.

The selected output format was the logistic output format as it is robust to unknown prevalence, and it is easy to interpret as the estimated species probability of presence given the constraints imposed by environmental variables. In this case, grid cells with a small logistic value are predicted to be unsuitable or only marginally suitable for the studied species, given their assumed ecological niche (Phillips and Dudik 2008).

The number of background pixels was set to 3000, about ten times the number of species records. High values of background pixels affect AUC (area under the ROC curve) values (used for model validation) and low values might cause clamping problems (discussed later in the chapter). The regularisation multiplier, which determines how focused the distribution is, was kept as 1, the default value, as suggested by Phillips and Dudik (2008). It seemed that a more localised output would be easier to interpret.

Regularisation multiplier	1.0
Output format	Logistic
Maximum interactions	500
Convergence threshold	1.0E-5
Number of background pixels	3000

Table 2.5. Maxent parameters used in the analyses of the baobab tree distribution.

Species response curves

Maxent creates species response curves which help identify how the baobab tree responds to environmental gradients. These graphs show on the y-axis the contribution of the variable to the model. As Maxent is an exponential model, high values on this axis mean that the variable has a very strong effect on the model.

Different types of response curve graphs are related to different types of features used by Maxent for each variable. For example, species response curves can be partially flat and linear (when Maxent has used ‘hinge features’) or a bar chart (when Maxent has used ‘category features’ for a categorical variable).

For a continuous variable (e.g., rainfall), the x-axis on the response curve graph indicates the value of the variable from the minimum to the maximum observed in the study area (e.g., from 0 to 1500 mm). For a categorical variable, the x-axis indicates the category of the variable (e.g., soil type 1: low activity clays).

Model evaluation

Model performance was evaluated using different methods. First, model performance was determined by setting aside a subset of the presence records for training and using the remaining records to test the resulting model. A good model should predict correctly the presence of the baobab tree in the test locations. As performance can vary depending upon the particular set of data selected for building the model and for testing it, 10 random partitions of the presence records were made to assess the average behaviour of Maxent, following Phillips et al. (2006). Each partition was created by randomly selecting 75% of the total presence records to build the model and the remaining 25% of presence records were used for testing. However, the full set of presence records were used to build the final model to obtain the best estimate of the species distribution and for creating a GIS probability distribution map.

The receiver operating characteristic (ROC) analysis was used to evaluate how well the Maxent model compared to a random prediction. The area under the ROC curve (AUC) serves as a measure of model performance in terms of sensitivity versus specificity. The sensitivity for a particular threshold is the fraction of all positive instances that are classified as present and specificity is the fraction of all negative instances that are classified as not present. The value of the AUC is typically between 0.5 (random) and 1.0. The closer the AUC value to 1, the better the model performance. Fig. 2.4 gives an example of the ROC curve.

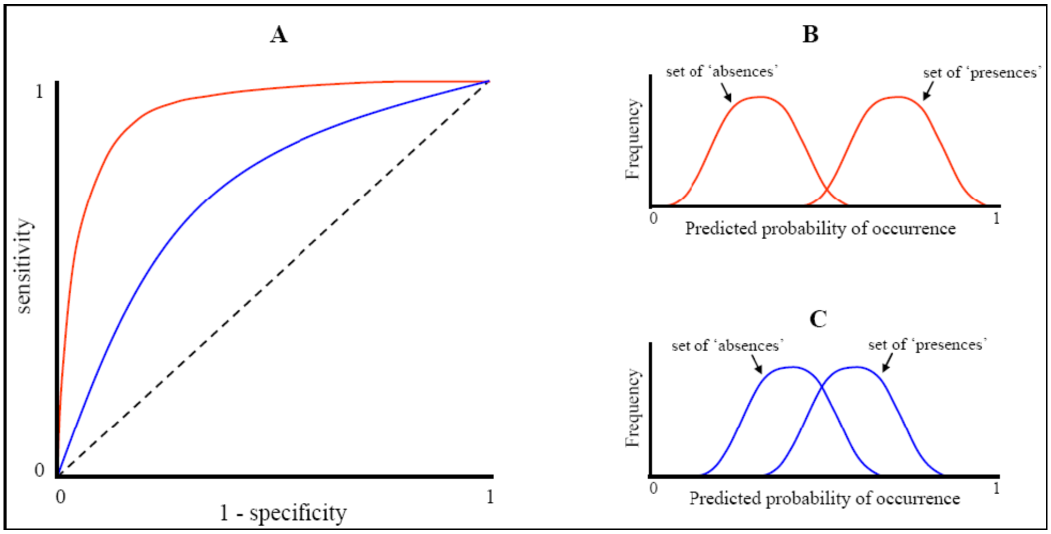


Fig. 2.4. Example of Receiver Operating Characteristic (ROC) curves and illustrative frequency distributions. A ROC curve is created plotting sensitivity against '1 – specificity'. Two ROC curves are shown, the upper curve (red) signifying superior predictive ability than the lower curve (blue). The dashed line indicated random predictive ability. B and C show example frequency distributions of probabilities predicted by a model for observed 'presences' and 'absences'. The results shown in B reveal good ability to distinguish presence from absence, while results in C show more overlap between the frequency distributions thus revealing poorer classification ability. The case shown in B would produce an ROC curve similar to the upper (red) curve in A. The case shown in C would give an ROC curve more like the lower (blue) curve in A. Source: Pearson (2007).

The success of the model was also evaluated by visually examining how well the probability values of the output grid fit with the presence records. A good model should produce regions of high probability that cover the majority of presence records and areas of low probability should contain few or no presence points. Moreover, a model can also be evaluated by visually exploring if high probability areas of the output grid fit with areas known to have baobab trees despite the lack of presence records. Coarse resolution baobab distribution maps of several countries (Table 2.6) were compared with Maxent output. Some of the maps were detailed enough to be digitised with some degree of confidence.

Country	**Source**	**Digitised**
Namibia	Tree Atlas of Namibia (Curtis and Mannheimer 2005) p450	Yes
Zimbabwe	Flora of Zimbabwe (Hyde and Wursten 2009)	Yes
Sudan	Egyptian-Sudan maps (1:250000) produced by the Geographical Survey between 1929-1945 (available at KEW gardens)	Yes
Kenya	Traditional food plants of Kenya (Maundu 1999) p53	No
Tanzania	A vegetation type map of the Tanganyika Territory (Guillman 1949).	No

Table 2.6. Countries from which detailed distribution maps of the baobab tree could be assembled, source of the information and possibility of digitising the data.

Where no country maps were available, country Floras, such as Plants of Angola (Figueiredo and Smith 2008) were used to validate model output. Known distribution of the species in India, Madagascar and other areas was also used to validate potential current worldwide distribution.

Model output

Maxent produces in ASCII format a continuous prediction map of specific presence that ranges from 0 to 1. As threshold values can be used to filter output cells into categories of habitat suitability (Hirzel et al. 2006, Jiménez-Valverde and Lobo 2007), the continuous prediction map was re-classified in two categories in order to distinguish the suitable habitat from the unsuitable following the threshold 'Equal training sensitivity and specificity' (Cantor et al. 1999), as suggested by Liu et al. (2005). This threshold was found to be around 0.40 for All records model, East Africa model and West Africa model. In order to separate areas with high suitability from those with medium suitability, areas with high suitability (>70% probability) were coloured black and areas with medium suitability (between 40 and 70% probability) were coloured grey. White colour in the distribution maps indicates low suitability (<40% probability).

Maxent also produces a continuous map for clamping. Clamping areas are sites where one or several environmental variables used for model projection (the tropical world, for example) are found to be outside their maximum within the study area used to build the model (conditions in Africa). Although Maxent reduces the projected variables to their maximum within the study area if they exceed it, caution should be taken if these areas are predicted to have very suitable conditions for the species (S. Phillips 2008, pers. comm.). Areas where clamping was more than 40% were removed from potential suitable habitat in the tropical world.

Model limitations

Although the data used in this study were collected from an extensive search of sources (several herbaria, students' surveys and a commercial firm's database), few data were obtained from some countries (e.g. Chad, Somalia, Angola) which could reduce the true measure of the entire habitat range of the species.

A further limitation is based on the relevance of the variables used to assess baobab tree distribution. Although human settlements (Assogbadjo et al. 2005b, Duvall 2007), presence of dispersal agents, land-use and other factors are likely to influence baobab geographical distribution at a fine scale, geographical distributions at large spatial scale and resolution are mainly determined by climate (Root 1988, Rogers and Williams 1994, Chown and Gaston 1999, Spicer and Gaston 1999).

It should also be noted that even though trees can grow in a determined area because the environmental conditions are favourable (considering highly suitable habitat as potential areas for cultivation), it does not mean that those trees can produce a high yield and/or fruits are of good quality. It has been noted for other under-utilised species such as the tamarind tree (*Tamarindus indica*) that if the dry season is not long enough, the quality of the fruits is not good (Allen and Allen 1981). For the baobab tree, it has been reported that the baobabs currently found in Mannar Island (Sri Lanka) never produce ripe fruits (Wickens and Lowe 2008). It could be that there is a problem of genetic incompatibility, but abiotic factors could also account for this phenomenon.

2.4 Results

2.4.1 All records model

Distribution map

Maxent results showed a strong prediction throughout most of the Sahel and in much of the mopane savannah in southern Africa (Fig 2.5). They also showed a strong prediction in south-east Somalia and eastern Angola.

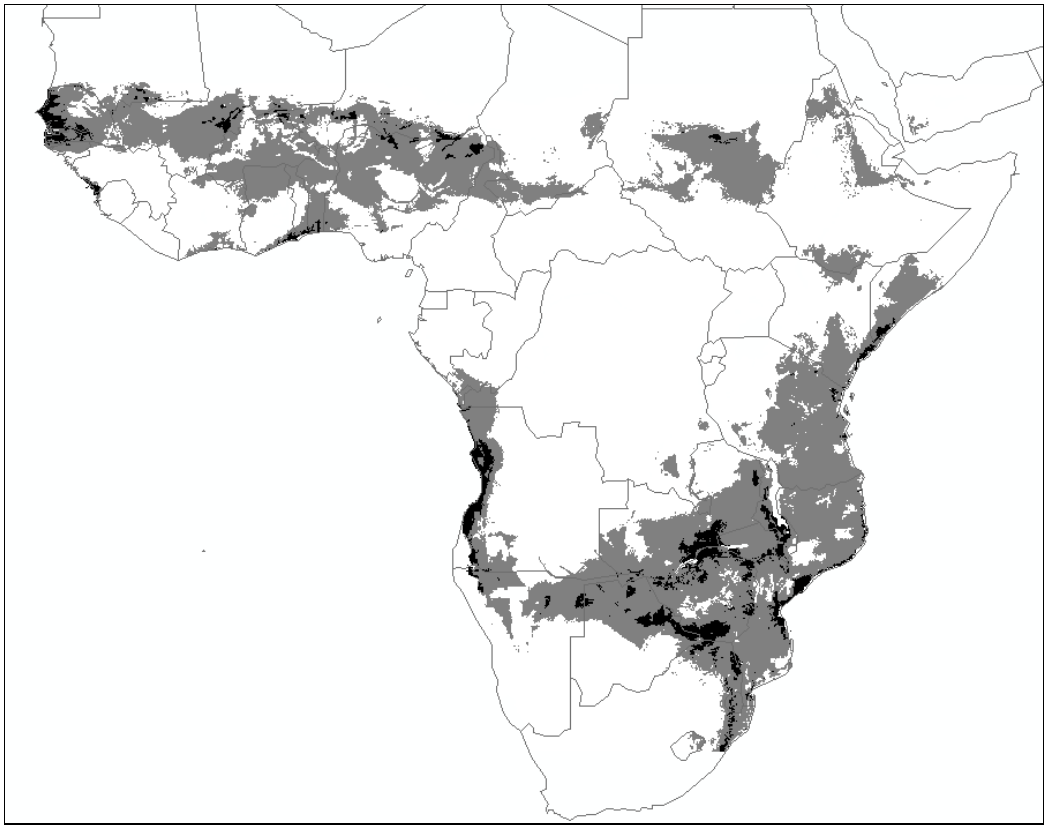


Fig. 2.5. Potential current distribution of the baobab tree in Africa generated by Maxent using All records (450 records). Black: high suitability (>70% probability), grey: medium suitability (between 40 and 70% probability), white: low suitability (<40% probability).

Model performance

The ten generated distribution models (created by dividing part of the records for training and testing) showed a significantly high level of performance when compared to random (AUC=0.5). Training AUC values ranged from 0.87 to 0.91. Test AUC values were lower but close to training AUC. The ten models correctly predicted most of the test locations. There was not much variation in the spatial prediction. In general, these results from test partitions indicate that the models were powerful in discriminating suitable from unsuitable habitats. The final model built with all presence records had an AUC value of 0.896 (Fig. 2.6).

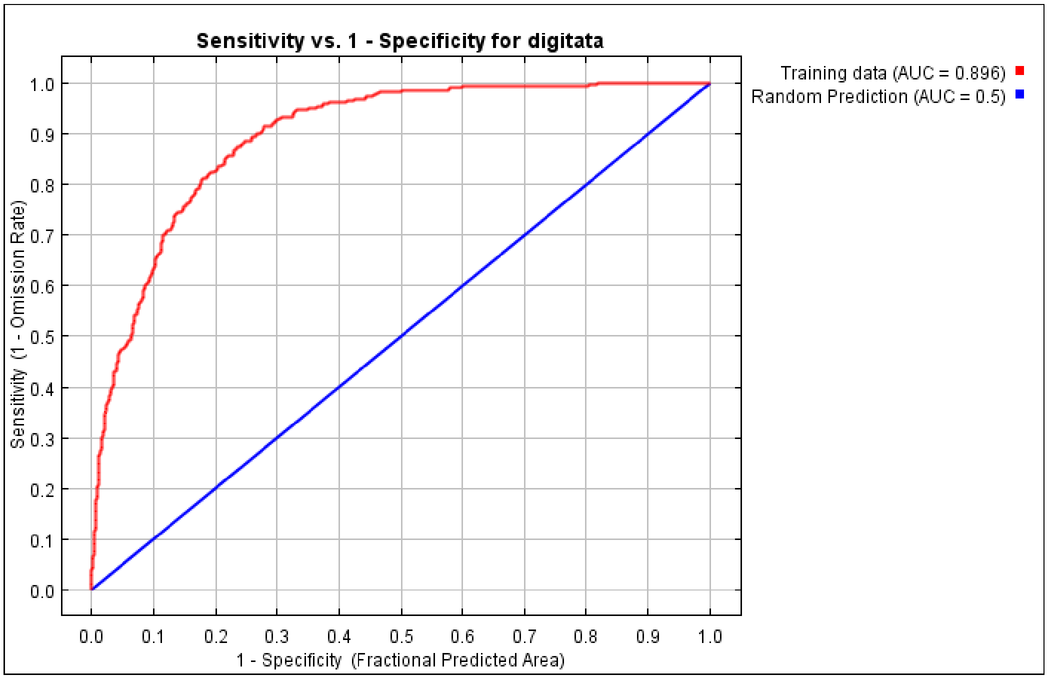


Fig. 2.6. Area under the receiver operating characteristic (ROC) curve (AUC). The y-axis represents sensitivity (or true positive rate) meaning the absence of commission error. The x-axis represents the value 1-specificity (or false positive rate), the commission error. The red curve represents the training data (the baobab localities) while the blue line indicates random predictive ability.

While visually examining how well the probability values of the output grid fit with the presence records, model performance was quite good. Most presence records fell within areas of medium or high probability (grey and black colours respectively, Fig. 2.7).

In general, when coarse resolution baobab distribution country maps were compared with the Maxent output, the results were good. Maxent output overlapped well with Zimbabwe, Namibia (Fig. 2.8) and Kenya maps (Fig. 2.9); and quite well with Tanzania (Fig. 2.10) and Sudan maps (Fig. 2.11).

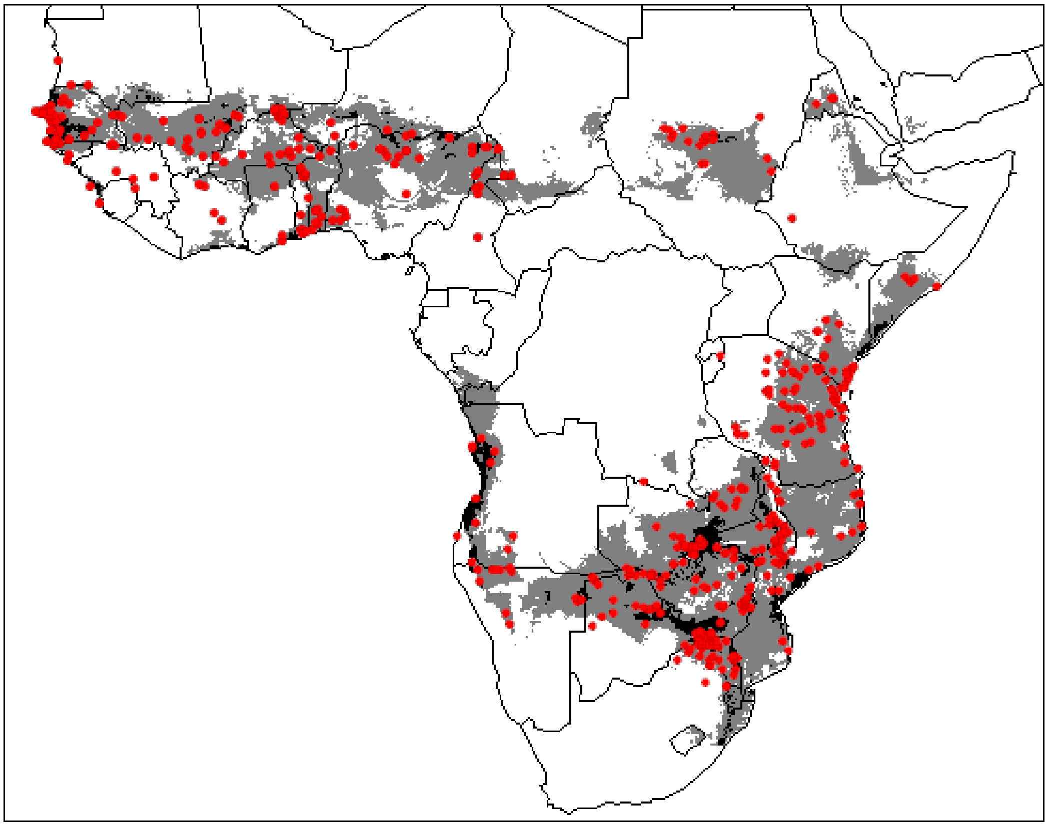


Fig. 2.7. The potential distribution of the baobab tree in Africa. The red dots represent known collection localities. Black: high suitability (>70% probability), grey: medium suitability (between 40 and 70% probability), white: low suitability (<40% probability).

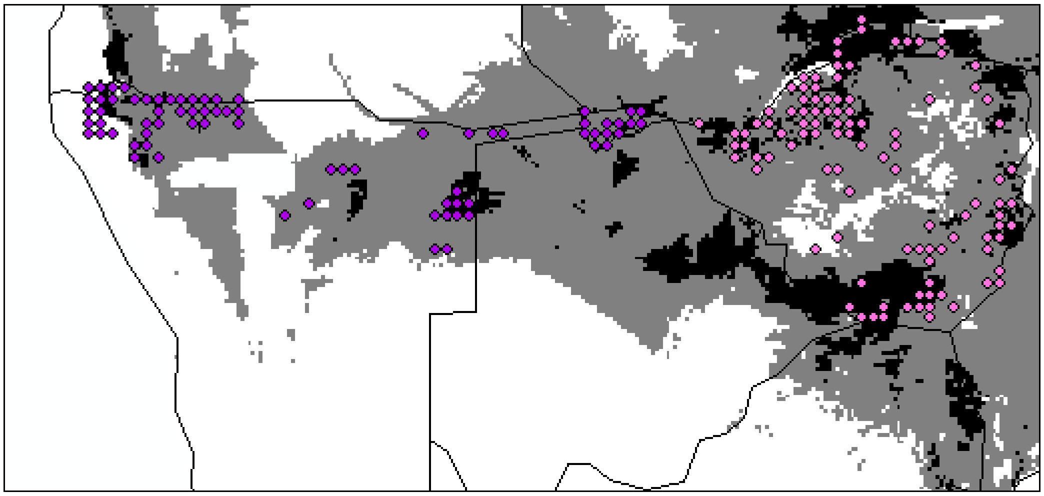


Fig. 2.8. Potential distribution of the baobab tree in Namibia and Zimbabwe. Purple dots represent known presence localities extracted from Tree Atlas of Namibia (Curtis and Mannheimer 2005). Pink dots represent known presence localities extracted from Flora of Zimbabwe (www.zimbabweflora.co.zw). Black: high suitability (>70% probability), grey: medium suitability (between 40 and 70% probability), white: low suitability (<40% probability).

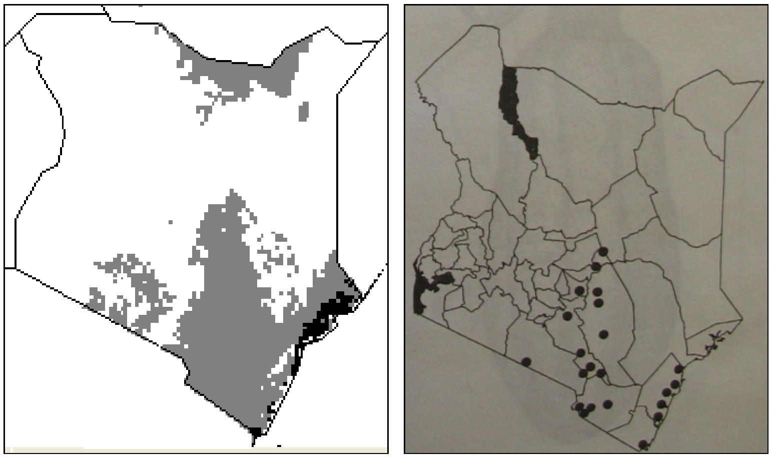


Fig. 2.9. From left to right: Potential distribution of the baobab tree in Kenya (Maxent output) and the estimated distribution of the baobab tree in Kenya (Traditional food plants of Kenya, Maundu 1999). For Maxent output: black: high suitability (>70% probability), grey: medium suitability (between 40 and 70% probability), white: low suitability (<40% probability). For Maundu's map, black dots represent areas known to have baobabs.

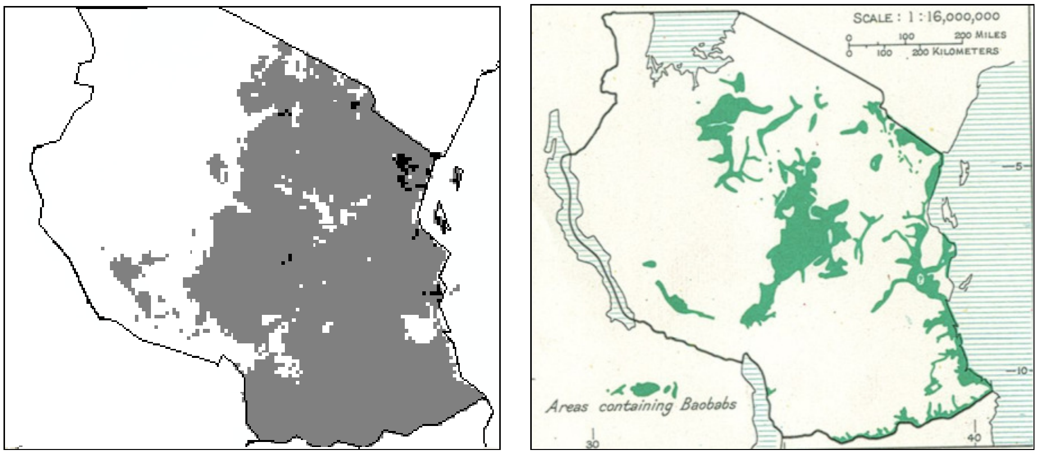


Fig. 2.10. From left to right: Potential distribution of the baobab tree in Tanzania (Maxent output) and the estimated distribution of the baobab tree in Tanzania (Guillman 1949). For Maxent output: black: high suitability (>70% probability), grey: medium suitability (between 40 and 70% probability), white: low suitability (<40% probability). For Guillman's map, green colour indicates areas containing baobabs.

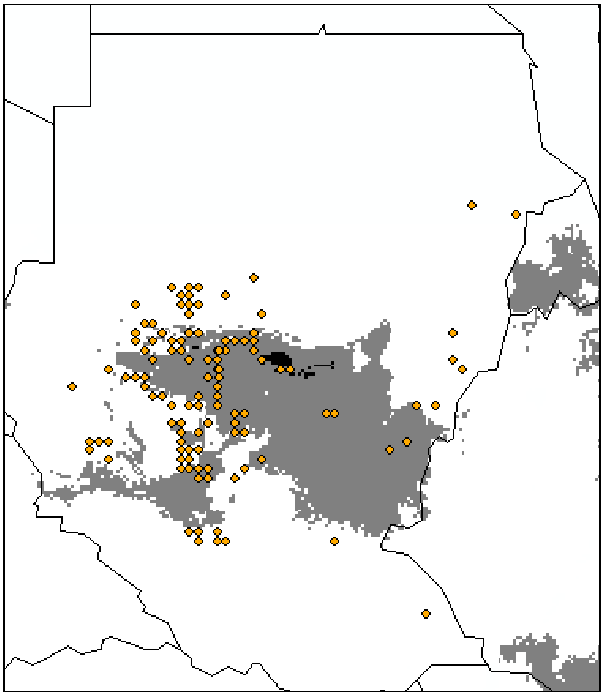


Fig. 2.11. Potential distribution of the baobab tree in Sudan. Orange dots represent known presence localities extracted from the Egyptian-Sudan maps (1:250000) produced by the Geographical survey between 1929 and 1945 (available at KEW). For Maxent output: black: high suitability (>70% probability), grey: medium suitability (between 40 and 70% probability), white: low suitability (<40% probability).

In areas where no country maps were available, such as Angola, model results agreed with the literature. The baobab tree is present in Luanda, Cuanza Norte, Malange and Namibe districts in Angola (Figueiredo and Smith 2008) and model output predicted the distribution of the baobab tree in these areas. The strong prediction in south-east Somalia could not be validated as a book having specific information on the species distribution in Somalia could not be found.

Variable contribution

The All Records model indicated that the presence of the baobab tree was mainly associated with temperature seasonality (29.1%), annual precipitation (20.9%) and precipitation of the wettest four months (15.5%) (Table 2.7).

Variable	Percent contribution
BIO4 Temperature seasonality	29.1
BIO12 Annual precipitation	20.9
BIO16 Precipitation of the wettest quarter	15.5
BIO2 Mean diurnal range	8.2
Altitude	5.6
BIO6 Minimum temperature of the coldest month	3.6
BIO11 Mean temperature of the coldest quarter	3.4
Soil type	3.3
BIO15 Precipitation seasonality	2.3
BIO9 Mean temperature of the driest quarter	2.3
BIO3 Isothermality	2.2
BIO5 Maximum temperature of the warmest month	2.1
BIO1 Annual mean temperature	1.5

Table 2.7. Variable contribution by percent.

Maxent's jackknife test of variable importance also suggested that annual precipitation (BIO 12) and temperature seasonality (BIO 4) are good predictors as they have the most information not contained in other variables (see light colour, Fig. 2.12) and they ‘explain’ the baobab tree distribution on their own (high training gain, dark colour, Fig. 2.12).

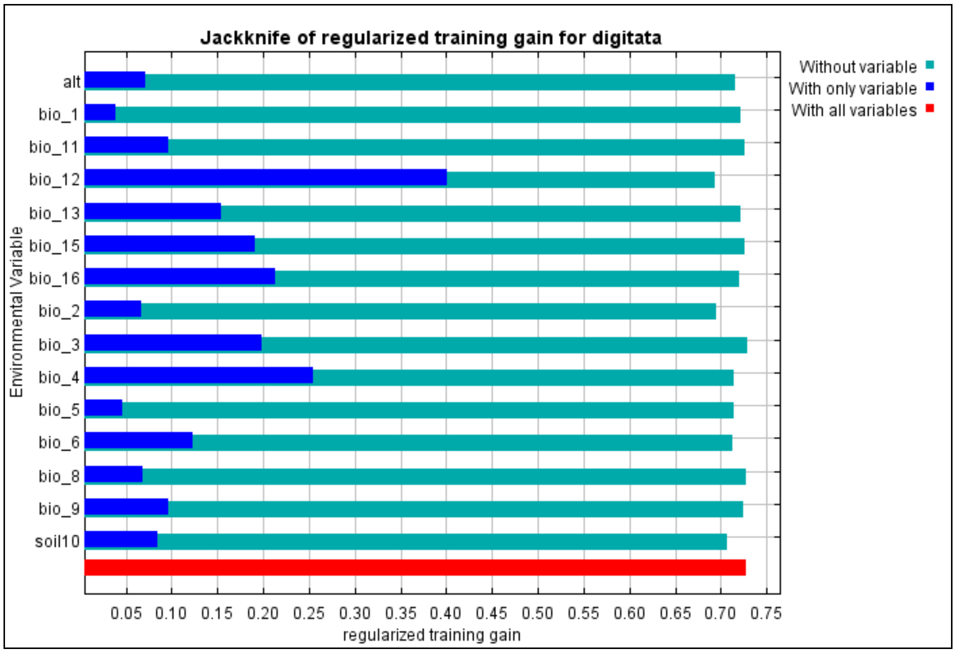


Fig 2.12. Training gain for each predictor variable alone (dark colour) and drop in training gain when the variable is removed from the full model (light colour).

Maxent species response curves indicated that the baobab tree prefers low annual precipitation (between 200-1400mm, bio 12, Fig. 2.13), low altitudes (less than 1200m, altitude, Fig. 2.13) and a mean diurnal range of less than 15°C (bio 2, Fig. 2.13). Although the baobab tree can tolerate up to a temperature seasonality of 40°C, it seems that it prefers low temperature seasonality (bio 4, Fig. 2.13). The baobab tree grows in different soil types (soil 10, Fig. 2.13).

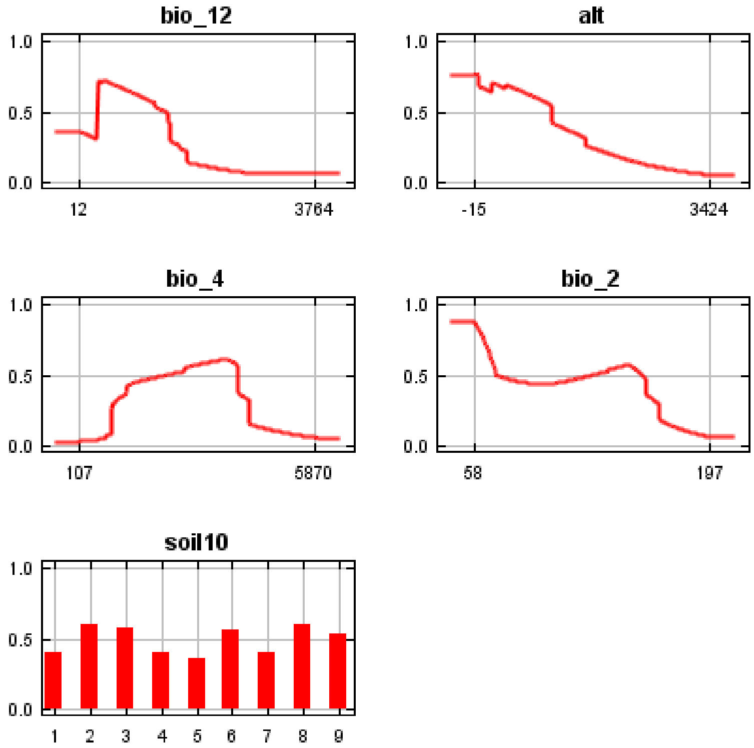


*Fig 2.13. Species response curves. The curves show how each environmental variable affects the Maxent prediction while all other variables are held constant at their average sample value. Y-axis shows the probability of presence. Top left: bio 12 or annual precipitation, x-axis in mm of rain. Top right: alt or altitude, x-axis in meters above sea level. Middle left: bio 4 or temperature seasonality: x-axis in °C*100. Middle right: bio 2 or mean diurnal range, x-axis in °C*10. Bottom: soil 10 or soil type, values on x-axis refer to soil categories: 1= low activity clays, 2= high activity clays, 3=volcanic soils, 4=sandy soils, 5=calcareous soils, 6=water-saturated soils, 7=organic soils, 8=saline soils, 9=shallow soils.*

Potential current distribution in tropical world

Maxent results showed a strong prediction through most of India (except the west coast), in south-west Madagascar, in northern Australia, in north-east Brazil and on the east coast of Mexico (Fig 2.14).

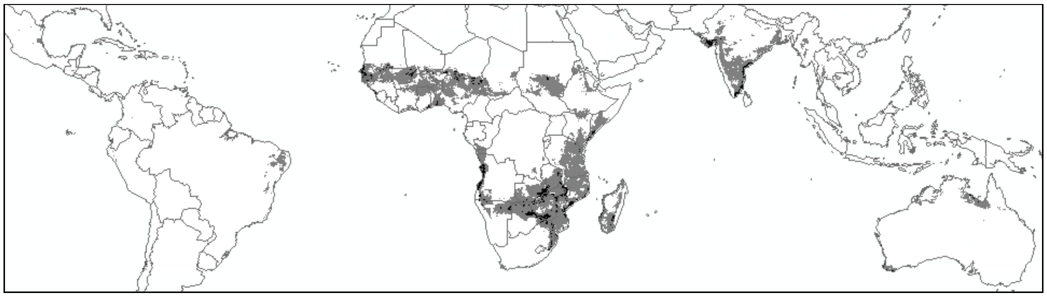


Fig. 2.14. Potential current worldwide distribution of the baobab tree generated by Maxent using All records (450 records). Black: high suitability (>70% probability), grey: medium suitability (between 40 and 70% probability), white: low suitability (<40% probability).

Clamping

While predicting potential distribution of the baobab tree in the tropical world clamping was not a problem, as there was only one small area in northern Mali with clamping (red colour in Fig 2.15) and this area was not predicted to have suitable conditions for the species.

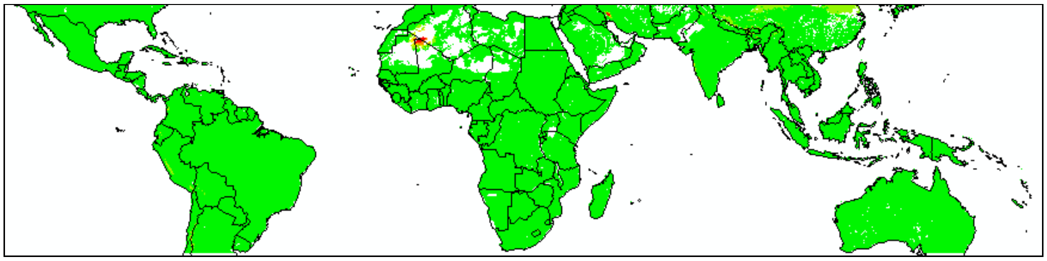


Fig. 2.15. Areas with clamping - areas where some variables are outside the range they currently have in Africa. Dark red: >80% probability of clamping, light red: between 60 and 80%, yellow: between 40 and 60%, pale green: between 20 and 40%, dark green: <20%.

Validating the potential current distribution in the tropical world

Although model validation refers to the validation of the model built with the presence records (Africa model), model projection output (prediction of the distribution in tropical world) could also be validated in a certain way because the baobab tree already exists in some of the locations predicted to be ‘suitable habitat’ by Maxent. This was the case of India (where the baobab tree was introduced in the past), Madagascar and Australia (where other species of *Adansonia* naturally occur) and Recife, in north-east Brazil (where one baobab specimen occurs). However, no records are available from Mexico.

Implications for cultivation

The strong prediction of Maxent model in south-east Somalia and eastern Angola (see Fig. 2.5) indicated that these areas are potentially very good for cultivation, as climatic and soil conditions are very favourable. Maxent results also suggested that the baobab tree could be cultivated in most of the Sahel (including some reduced areas in western Chad and central Sudan) and in most of the east and southern Africa savannah. Countries such as Mozambique, Malawi, Zimbabwe and Zambia seemed to have a great potential.

Potential current distribution suggested that the baobab tree could be cultivated in several areas outside Africa such as India, North-West Australia, Madagascar, north-east Brazil and the east coast of Mexico.

2.4.2 East Africa model

Distribution map

For the East Africa model, the baobab was predicted to grow in the mopane savannah in southern Africa from Kenya to South-Africa/Namibia, in south Somalia, Ethiopia, Eritrea, Sudan and north-east Nigeria (Fig. 2.16).

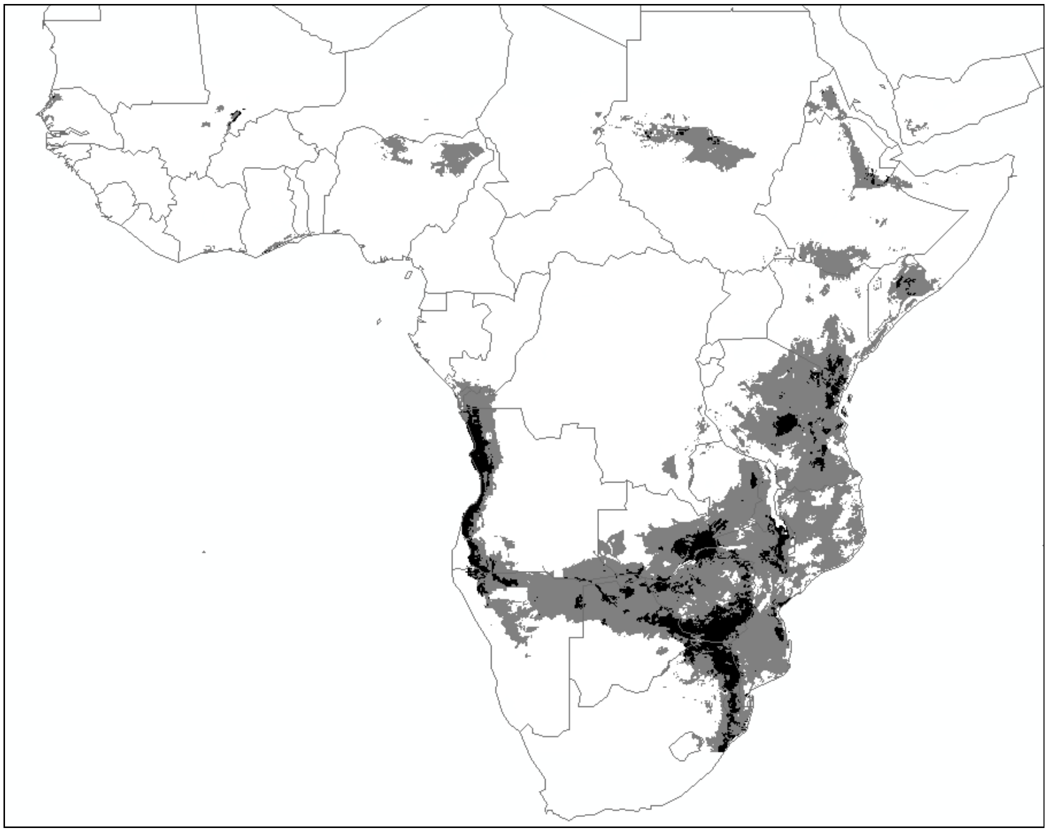


Fig. 2.16. Potential current distribution of the baobab tree in Africa generated by Maxent using East African records. Black: high suitability (>70% probability), grey: medium suitability (between 40 and 70% probability), white: low suitability (<40% probability).

Model performance

The ten generated East Africa distribution models showed a significantly high level of performance. Training AUC values ranged from 0.928 to 0.933. Test AUC values were lower but close to training AUC. The ten models correctly predicted most of the test locations. The final model built with all presence records of East Africa had an AUC value of 0.933.

Variable contribution

The East African model indicated mean temperature of the coldest four months (17.5%), temperature seasonality (15.2%), annual precipitation (13.4%) and precipitation of the wettest four months (9%) to be the most important predictors for the distribution of the East African baobab.

Potential current distribution in tropical world

Outside Africa, the East Africa model showed a strong prediction in most of the places predicted by the All records model and some additional sites in south-east Asia, around Paraguay and the Gulf of Mexico (Fig. 2.17).

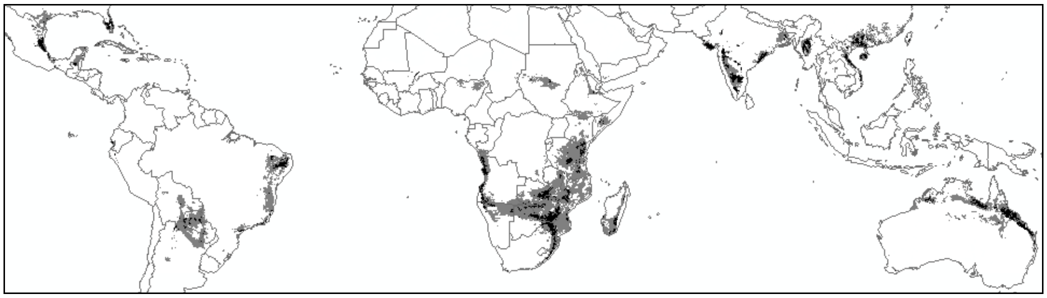


Fig. 2.17. Potential current worldwide distribution of the baobab tree generated by Maxent using East African records. Black: high suitability (>70% probability), grey: medium suitability (between 40 and 70% probability), white: low suitability (<40% probability).

2.4.3 West Africa model

Distribution map

For the West Africa model, the baobab tree was predicted to grow in most of the Sahel from Senegal to south-west Chad, and in southern Ghana-Nigeria (Fig. 2.18), the same places predicted to be suitable in West Africa by the All records model (see Fig. 2.5).

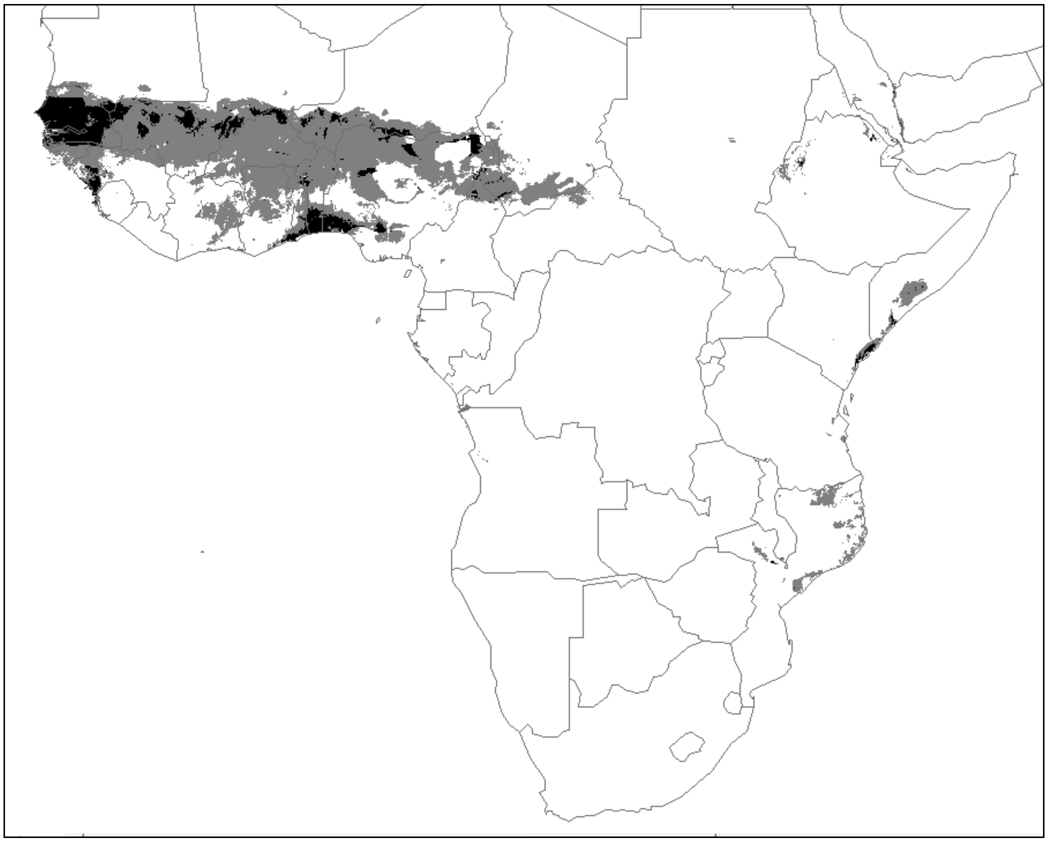


Fig. 2.18. Potential current distribution of the baobab tree in Africa generated by Maxent using West African records. Black: high suitability (>70% probability), grey: medium suitability (between 40 and 70% probability), white: low suitability (<40% probability).

Model performance

Training AUC values ranged from 0.928 to 0.933. Test AUC values were lower but close to training AUC. The ten models correctly predicted most of the test locations. The final model built with all presence records of East Africa had an AUC value of 0.963.

Variable contribution

The West African model indicated that baobab presence was mainly correlated with mean temperature of the warmest four months (37.4%), altitude (19%), and precipitation of the wettest four months (11.9%).

Potential current distribution in tropical world

Outside Africa, the West Africa model showed a strong prediction only in Madagascar and Australia (Fig. 2.19).

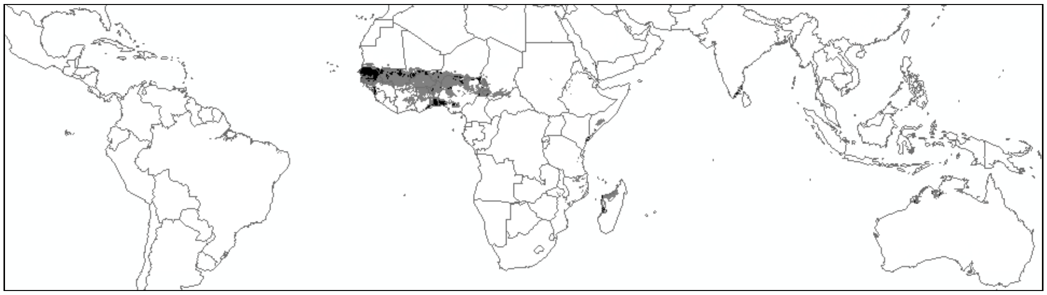


Fig.2.19. Potential current worldwide distribution of the baobab tree generated by Maxent using West African records. Black: high suitability (>70% probability), grey: medium suitability (between 40 and 70% probability), white: low suitability (<40% probability).

2.5 Discussion

Model performance was good, AUC values were high, it predicted suitable conditions in test locations, and it predicted baobab presence in areas where no records were used to build the model but are known to have the baobab tree (such as Angola). Outside Africa, the fact that the potential cultivation sites include the known occurrence of the baobab tree in India, and the known occurrence of closely related species in Australia (*Adansonia gregorii*) and Madagascar (*Adansonia* sp.) positively validates the model results.

The modelled response of the baobab tree to different environmental variables agrees with the ecological requirements suggested in the literature by Sidibé and Williams (2002) and Wickens and Lowe (2008). Although precipitation of the driest month or maximum temperature of the hottest month could seem to be the limiting factors for the baobab tree as it is found in the driest parts of the savanna, this was not the case. Instead, modelling indicated that the presence of baobab tree is mainly related to annual precipitation and temperature seasonality. As the baobab's distribution was found to be mainly correlated with annual precipitation, it is possible that it could also be cultivated in areas where there is a little annual precipitation but water for irrigation is available. However, further research is needed to confirm this hypothesis.

The fact that the baobab tree was found on a broad range of soils (agreeing with Sidibé and Williams 2002, and Wickens and Lowe 2008) also has implications for cultivation: the broader the range of soil types the baobab tree tolerates, the more the possibilities for cultivation.

Differences between the West African and East African models in terms of the main variables and baobab response curves probably reflect differences in the environment where the baobab tree lives. For example, in the Sahel (West Africa) high temperatures (reflected in the variable mean temperature of the warmest four months) and little rain during the only rainy season (reflected in precipitation of the wettest four months) might be more limiting here than in East Africa. Differences in response curves, such as altitude, might also reflect differences in the environment, with East Africa having more areas with high altitudes than West Africa. However, it should be noted that although differences in response curves might only be reflecting differences in the environment, they could also reflect different ecological requirements of the West African and the East African baobab populations, which have genetic differences (Pock Tsy et al. 2009). Although further studies are required to confirm differences in ecological requirements between West and East African baobab populations, I consider that these potential differences should be taken into account, especially when choosing planting material.

In general, Maxent modelling suggested that the baobab tree has great potential for cultivation in Africa and in other countries of the world. In West Africa, it could be grown throughout most of the Sahel, but also further south in the Sudanian zone from northern Ghana to Northern Cameroon. In these areas, where locals already know and use the species, cultivation might be easier than elsewhere due to cultural acceptance. The cultivation of this species could also reduce the pressure on existing baobab trees which are threatened by overexploitation, bush fires and grazing (Sidibé and Williams 2002, Assogbadjo et al. 2005b, Wickens and Lowe 2008). In East and Southern Africa, most countries that already export baobab fruit products (Tanzania, Zimbabwe, Mozambique, Malawi and South Africa) unsurprisingly have highly suitable conditions for baobab cultivation. Although baobabs are not as widely used there as in West Africa (Jama et al. 2008), the fact that baobab products can be commercialised internationally might motivate farmers to increase production. In

Africa, baobabs could be grown for local consumption and for international commercialisation.

Outside Africa, based on current climate, India appears to have the greatest potential for growing the baobab tree. The fact that the tree is already fairly widely distributed throughout parts of India (Wickens and Lowe 2008) and is already used for local consumption and medicine (Vaid and Vaid 1978) might encourage local farmers. The baobab tree, which has been identified as amongst the traditional African fruits whose cultivation and use may help malnutrition problems in Africa (NRC 2006), could help in combating malnutrition in India. Apart from local consumption, the cultivation of the baobab tree could also be aimed at international commercialisation, which could help reduce poverty. Baobab cultivation could also render fertility to the existing baobab trees in India which are thought to be self-incompatible (Wickens and Lowe 2008). Moreover, the cultivation and promotion of the baobab tree could help raise awareness of the multiple uses of these trees and their historical and cultural significance, and perhaps avoid the destruction of the remaining old specimens found in the country. For example, in 2004 a huge baobab found in Mumbai was destroyed because it was disturbing a public development project (TNN 2004). It has been reported in the literature that the baobabs already existing in India were brought from East Africa by Arab traders (Wickens and Lowe 2008). Modelling results from this study suggest that planting material for India should be taken from East Africa.

In Australia, the cultivation of the baobab tree could be aimed at international commercialisation. Although there is an Australian species of baobab (*Adansonia gregorii*), the African baobab has a higher nutritional value than the former (Miller et al. 1993) and its fruits are generally larger. A few African baobabs have already been planted in Australia in botanical gardens and in an Aboriginal settlement in north-western Australia (Wickens and Lowe 2008). Modelling results suggest that planting material from West Africa and East Africa should be used for cultivation in north-western Australia and north-eastern Australia respectively.

In Madagascar, the cultivation of the African baobab is recommended only for commercial purposes. The two reasons in support of this recommendation are: one, in Madagascar, local people do not use the baobab tree as much as in mainland Africa

(Wickens and Lowe 2008); and second, the local Malagasy species (especially *A. rubrostipa*) has been reported to have higher nutritional value than the African baobab in terms of leaf vitamin and crude protein contents (Maranz et al. 2007). As there are no chemical studies on Malagasy baobab fruit nutritional value, it could be possible that the fruits of the local species are also more nutritious. The model suggests if the cultivation of the African baobab is to be considered in the dry deciduous forests of western Madagascar, planting material should be taken from West Africa, but if the potential cultivation site is the southern part of Madagascar, East African baobabs are recommended.

In the Americas, the Maxent model suggests highly suitable environments in Mexico and in north-east Brazil for cultivation of the baobab (East African planting material). In fact, Dutch or Portuguese travellers are believed to have introduced the tree to northern Brazil, where a huge specimen is still growing in Recife (Wickens and Lowe 2008). Although the baobab tree could be cultivated for commercial purposes in Brazil and Mexico (for example, they could supply the potential US market), it is not commonly found in these two countries, which implies that the local population does not know the species' nutritional, medicinal and economic values. A multi-stakeholder approach would be needed in these areas to establish baobab as a commercial crop. Another problem for baobab tree cultivation in these two countries is the fact that no mature trees are available for grafting.

In general, the cultivation of the baobab tree has been considered for fruit production. However, as mentioned earlier in chapter 1, baobab can also be cultivated for leaf production. In this case, there is no need to have mature trees available for grafting. However, if continued production of baobab leaves is wanted, baobab trees have to be watered often, where water is scarce, this might discourage farmers (Savard et al. 2002).

An important issue when considering baobab cultivation outside Africa is how to guarantee the intellectual property rights of African farmers over the indigenous knowledge related to the baobab tree's use. The Convention on Biological Diversity (CBD), which has the aim to ensure fair and equitable sharing of the benefits arising out of the utilisation of genetic resources (apart from ensuring the conservation of biological diversity and its sustainable use), should to be taken into account. For example, there has been a patent controversy for the Neem tree (*Azadirachta indica* L.), a multi-purpose tree highly appreciated for its medicinal properties. In 1995, the European Patent Office (EPO) granted a patent on an anti-fungal product derived from neem to a multinational based in US. The Indian government challenged the patent, claiming that local people in India had been using the Neem tree for that purpose for more than 2000 years. In 2005, after a long process, the EPO revoked the Neem tree patent rights keeping the tree free of these patent restrictions (BBC 2005). The baobab tree is an important resource for local populations in Africa, which have used and managed the baobab tree for centuries. Apart from potential patent controversies, if other countries outside Africa start to cultivate the baobab tree, and export baobab products, there is a risk that one of these countries produces and exports more baobab products than some African countries, which could potentially have a negative effect on African livelihoods. As outlined by Leakey et al. (2005) the development of '*sui generis*' rights systems may be needed in order to protect the rights of African farmers, particularly if they develop niche- or product-specific cultivars.

In spite of its immense global potential cultivation possibilities, the difficulty of persuading local communities that the baobab tree can be successfully propagated in a nursery and that its long maturation period can be reduced remains the main constraint to its cultivation (see chapter 1). Regardless of the country, in order to cultivate the baobab tree, training workshops for imparting knowledge transfer of seed propagation and grafting techniques would be needed. *In situ* seedling experiments, which could validate the potential cultivation of baobab tree in new areas, will also be required. Although trees can be assumed to grow well in a determined area with favourable environmental conditions (considering highly suitable habitat as potential areas for cultivation from our model), it can not be assumed that the trees will produce fruits and/or a high yield.

CHAPTER 3. Study of the potential future distribution of the baobab tree: implications for conservation

Species distribution models (like Maxent) together with climate change predictions can be used to study potential future distributions of species (Heikkinen et al. 2006, Pearson 2007). As the baobab tree is thought to be threatened by climate change (Wickens and Lowe 2008), when considering potential conservation sites and other strategies, it seems important to take climate change predictions into account. In this chapter I use species distribution modelling together with climate change projections to predict the potential distribution of the baobab tree in the future. I compare the potential future distribution of the baobab tree in Africa with both the present distribution and the Protected Areas in Africa; and I suggest potential conservation strategies for this species. This chapter has been accepted for publication in the *African Journal of Ecology*.

3.1 Introduction to modelling future distributions

Predicted changes in atmospheric CO_2 and climate are likely to affect the distribution and abundance of most species (Araújo et al. 2005, Schröter et al. 2005). Tropical biodiversity is forecast to be critically threatened not only by climate change, but also by land-use changes and contingent habitat loss and fragmentation (Bradshaw et al. 2009). Continental-based climate assessments show that Africa is likely to experience marked climatic changes over the 21st century with drying and warming in most subtropical regions and slight increases in precipitation in the tropics (Boko et al. 2007). Christensen et al. (2007) estimated that regions across Africa will experience median temperature increases between 3-4 °C in all seasons with drier tropical regions experiencing more warming than the wetter tropical regions. Africa is also one of the most vulnerable continents to projected future climate changes in human terms (Boko et al. 2007). This is due to lack of adaptive ability and interactions of additional confounding factors such as poverty, infrastructural and technological challenges, political conflicts and degradation of ecosystem functioning (Boko et al. 2007).

A main application of species distribution models is projections of distributions under future climate (Heikkinen et al. 2006). Species distribution models have been used to study the effect of climate change on a number of species at a large scale: e.g., American fauna (Lawler et al. 2009) and France's fish species (Buisson et al. 2010); and on a single species at a smaller scale: e.g., the Amazon parrots *Amazona pretrei* Temm. (Marini et al. 2010), and the Australian snake *Hoplocephalus bungaroides* Schlegel (Penman et al. 2010).

A few studies have addressed the potential consequences of the future climate changes on biodiversity in Africa. McClean et al. (2005) predicted that more than 5000 African plant species would experience losses of climatically suitable habitat by 2085. Thuiller et al. (2006) predicted that up to 40% of African mammals would be critically endangered by 2080 due to loss of climatically suitable habitat. When considering conservation strategies for the baobab tree, there is a need to assess the sensitivity of this species to climate change and evaluate whether Protected Areas, a key conservation tool used to protect species, will be sufficient to ensure baobab conservation.

There are several future climate projections. A large number of general circulation models (GCM) have been developed simultaneously, by several meteorological research centres, to represent physical processes in the atmosphere, ocean, cryosphere, and land surface, allowing simulation of the response of the global climate system to increasing greenhouse gas concentrations. Moreover, several greenhouse gas emissions scenarios have been identified. These greenhouse gas emissions scenarios are derived from a complex interplay between demographic and socio-economic developments, as well as technological changes. There are currently at least 24 different atmosphere-ocean general circulation models being used to project climatic changes for more than 10 different greenhouse-gas emissions scenarios (PCMDI 2007).

In this study, three GCM were selected:

- HadCM3 from the Hadley Centre for Climate Prediction and Research, United Kingdom (Collins et al. 2001)
- CCCma-CGCM2 from the Canadian Centre for Climate Modelling and Analysis, Canada (Kim et al. 2003)
- CSIRO-MK2 from the Commonwealth Scientific and Industrial Research Organisation, Australia (Gordon and O'Farrell 1997).

These three GCM were selected as they have been commonly used in recent studies dealing with the impacts of climate change on biodiversity (e.g., Thuiller 2004, Araujo et al. 2006, Tuck et al. 2006, Mika et al. 2008, Buisson et al. 2010).

For each GCM, two scenarios were examined: A2a and B2a (IPCC SRES, Nakicenovic and Swart 2000). Both scenarios are intermediate scenarios, B2a being more moderate than A2a:

- A2a describes a highly heterogeneous future world with regionally oriented economies (high rate of population growth, increased energy use, land-use changes and slow technological change).
- B2a is also regionally oriented but with a general evolution towards environmental protection and social equity. Compared to A2a, B2a has a lower rate of population growth, a smaller increase in gross domestic product (GDP) but more diverse technological changes and slower land-use changes (adapted from Arnell et al. 2004).

These two scenarios have also been commonly used in recent studies dealing with the impacts of climate change on biodiversity (e.g., Thuiller et al. 2006, Buisson et al. 2010, Marini et al. 2010).

3.2 Aims and Objectives

The general aim of this chapter is to model potential future baobab tree distribution in Africa using a predictive modelling approach, thereby to contribute to the selection of effective conservation sites and other conservation strategies. In order to achieve this aim, the following objectives are proposed:

1. To predict the potential distribution of the baobab tree in the future
2. To compare the potential future distribution with the present distribution
3. To evaluate the implications of the results for conservation

The specific research questions are:

1. Where might the baobab tree grow in the future?
2. Does it seem that most of the present habitat will remain suitable in the future?
3. Are the Protected Areas in Africa a good tool for baobab conservation?
4. Which other conservation strategies could be implemented?

3.3 Methodology

Scope of study

The study was centred in Africa, which is known to be the native range of this species (see chapter 1).

Species data

The assembled records for modelling present distribution of the baobab tree in Africa (chapter 2) were used for modelling the potential future distribution.

Environmental data: Future climate layers

Future climatic layers for 2050 prepared under three Coupled Atmospheric-Oceanic General Circulation Models (GCM) for two greenhouse gas emissions scenarios were obtained from the International Centre for Tropical Agriculture (CIAT) (http://gisweb.ciat.cgiar.org/).

The same climatic layers selected for modelling present distribution (chapter 2) were selected for modelling future distribution. However, altitude was excluded because of its confounding association with contemporary climate (Freedman et al. 2009). Present soil type (from the Harmonized World Soil Database, FAO et al. 2008) was included in future climate modelling. The spatial resolution of all the layers was 5 min.

Maxent setup

Maxent setup was similar to that used for determining potential distribution of the baobab tree in the tropical world (chapter 2). In chapter 2, the environmental layers covering the extent of Africa were used to create a model for the baobab tree and then this model was projected to the tropical world using the environmental layers of the tropical world. This process was carried out three times, for the All records model, East Africa model and the West Africa model. In this chapter, the three models created in chapter 2 for the baobab tree (All records model, East Africa model and West Africa model) were projected into the future using different sets of environmental layers depending on the GCM and the scenario. In total, the All records model was projected six times (three GCM and two scenarios), as was also the case for the East Africa model and the West Africa model. The same Maxent parameters used in chapter 2 were used in this chapter (see Table 2.5 in chapter 2).

Model output

The threshold ‘Equal training sensitivity and specificity’ (Cantor et al. 1999) used in chapter 2 was also used for modelling potential future distribution of the baobab tree. Like in chapter 2, in order to visually separate areas with high suitability from those with medium suitability, areas with high suitability (>70% probability) were coloured black and areas with medium suitability (between 40 and 70% probability) were coloured grey. White colour in the distribution maps indicates low suitability (<40% probability). However, for the conservation analyses described below (further analyses), areas with high suitability coloured black and areas with medium suitability coloured grey were analysed together.

In this chapter, areas with clamping refer to areas where one or several environmental variables used for model projection (the future) are found to be outside their maximum within the study area used to build the model (present conditions in Africa). Areas where clamping was more than 40% (like in chapter 2) were removed from the potential future suitable habitat.

Further analyses

Seed dispersal and the associated patterns of plant migration are considered to be a significant uncertainty in projecting climate change impacts on plant species ranges (Thuiller et al. 2008). Most studies on potential future plant distribution have considered two scenarios: 'unlimited dispersal' which represents an unrealistic best case scenario; or 'no dispersal', the worse case scenario (Engler and Guisan 2009). As mentioned in chapter 1, baobab seeds are dispersed by animals and humans. Considering the lack of natural regeneration observed by several authors in different countries in Africa (see chapter 1), I decided to assess only the 'no dispersal' scenario for three reasons: a) some animals such as elephants and elands are less common and widespread than they used to be centuries ago; b) baobab fruits are highly exploited by humans and it is unlikely that many fruits are left on the trees; and, c) even when seeds germinate there are many constraints for seedling survival (fire, livestock browsing and clearing of fields, see chapter 1). It seems unlikely that without human intervention baobabs will colonise new suitable habitat. Thus, for the conservation analyses I did not consider 'potentially colonisable habitat' (the area a species could occupy given unlimited dispersal ability) but only the proportion of the present habitat which might still be suitable in the future.

Using ArcGIS 9.2, several calculations were carried out for the All records model. First, the extension of the predicted future distribution was calculated for each GCM (HadCM3, CGCM2, CSIRO-MK2) and scenario (A2a, B2a) (these would be the 'potentially colonisable habitat' mentioned earlier). Secondly, the percentage of the present distribution that was predicted to remain suitable in the future was calculated for each GCM and scenario. Third, the percentage of present distribution predicted to remain suitable in the future under all three GCM and both scenarios was determined. Finally, for the conservation analyses, this percentage of present distribution predicted to remain suitable in the future under all three GCM and both scenarios was compared and overlaid with a GIS layer of the Protected Areas in Africa in 2009, obtained from the World Database on Protected Areas (WDPA) (http://www.wdpa.org/). The protected areas include nationally designated (e.g. National Parks, Nature Reserves) and internationally recognised protected areas (e.g. UNESCO World Heritage Sites, Ramsar Wetlands of International Importance) and other Reserves (e.g. Forest Reserve, Game Reserve) currently held in the WDPA, up to end of December 2009. The same calculations were carried out for the East Africa model and the West Africa model.

Model limitations

It should be noted that only three GCM and two scenarios were used in this study. Other scenarios and GCM could give different results. Buisson et al. (2010) reported that the modelling algorithm used (Maxent or others) contributed to the largest variation in projections, followed by GCM, whose contribution increased over time equaling almost the proportion of variance explained by the modeling algorithm in 2080. In order to account for certain future uncertainty, Buisson et al. (2010) suggested using several GCM and scenarios, which is why three GCM and two scenarios were chosen and results compared.

Model projections also depend on the year; 2020, 2050 and 2080 are years commonly used in recent studies dealing with the impacts of climate change on biodiversity (e.g. Thuiller et al. 2006). As expected, preliminary projections for 2080 displayed more negative impacts than projections for 2050 (as observed for African mammals by Thuiller et al. 2006). Likewise 2050 projections were more negative than those for 2020. Preliminary results showed that projections for 2020 were similar to those for 2050 (but less severe), while projections for 2080 had problems of clamping (one or several environmental variables used for model projection (the future) were found to be outside their maximum within the study area used to build the model -present conditions in Africa). Only projections for 2050 are discussed in this chapter.

One question which arises while studying the potential future distribution of a species is the validity and/or accuracy of the GCM and scenarios commonly used for this purpose, as different GCM from different climatic research centres show different results. However, to date, this is the best data available, and it is still commonly used to study the potential effect of climate change on species' distributions (e.g., Buisson et al. 2010, Marini et al. 2010). The precautionary principle suggets that uncertainty about predicted changes in climate does not justify lack of action; it is better to use the data which is available and carry out the studies required to make recommendations for conservation.

In order to make keep recommendations for conservation policy makers as simple as possible, I have chosen the most likely events: (1) that the baobab tree is unlikely to reach new suitable habitats without human intervention (no dispersal scenario), and (2) that areas predicted to be suitable under different models and scenarios are more likely to be suitable in the future, suggesting that conservation efforts should be focused on these areas. However, it is also possible that the baobab tree reaches new suitable habitats thanks to human dispersal, and that future climate does not follow the predicted changes in the GCM and scenarios used in this study.

3.4 Results

3.4.1 All records model

Estimated potential future distributions for All records model were different depending on the GCM. While CGCM2 predicted an increase in suitable habitat for the baobab tree, CSIRO-MK2 and HadCM3 predicted a marked decrease in suitable habitat (Table 3.1). Estimated potential future distributions also differed between scenarios. In general, predictions for scenario B were smaller in extension than those for scenario A for all GCM (Table 3.1). When compared with present distribution, for all GCM and scenarios, only a percentage of the present distribution was predicted to remain suitable in the future (Table 3.1). The percentage of present distribution predicted to remain suitable in the future under all GCM and scenarios was very small: 1.85% (Table 3.1).

All records model	**Scenario A2a**			**Scenario B2a**		
	HadCM3	**CGCM2**	**CSIRO**	**HadCM3**	**CGCM2**	**CSIRO**
Differences in extension between present and estimated future distributions	84.55%	108.34%	47.38%	16.10%	80.55%	7.45%
Percentage of present distribution estimated to remain suitable in the future	44%	69%	41%	9%	55%	5%
Percentage of present distribution estimated to remain suitable in the future (all GCM and scenarios) *	1.85%					

*Table 3.1. Differences in extension between present and future potential distributions and percentages of present distribution estimated to remain suitable in the future for different GCM and scenarios for All records model. The percentage of the combination of different models is not the mean of the percentages of the models/scenarios but the percentage (of the present distribution predicted to remain suitable in the future) common in all mentioned models. * Areas very likely to have suitable habitat in the future and where conservation efforts should be focused.*

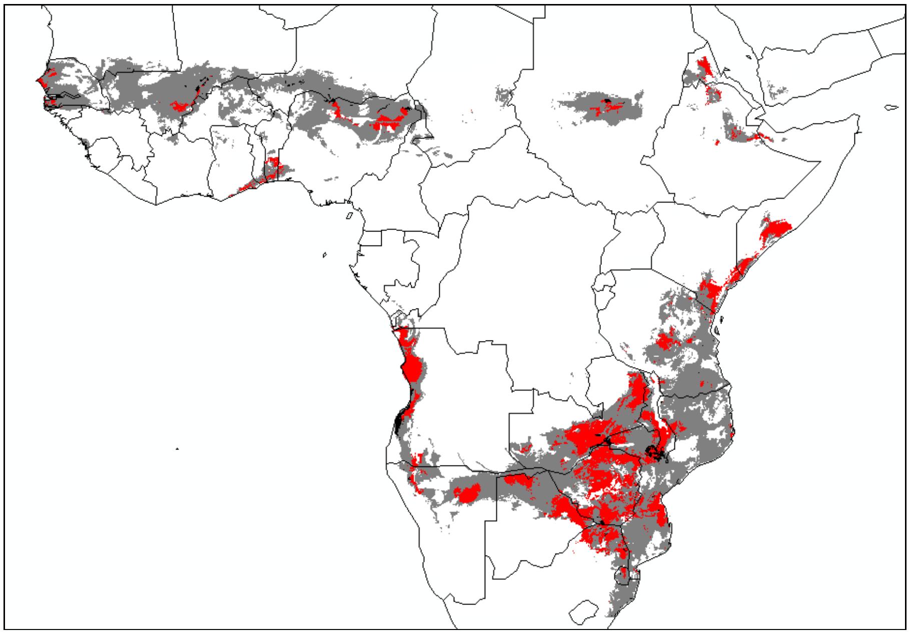


Fig. 3.1. Potential current distribution of the baobab tree in Africa (generated by Maxent using All records) predicted to remain suitable in the future under all GCM for scenario A2a. Black: present high suitability (>70% probability), grey: present medium suitability (between 40 and 70% probability), white: present low suitability (<40% probability), red: part of the present distribution predicted to remain suitable in 2050.

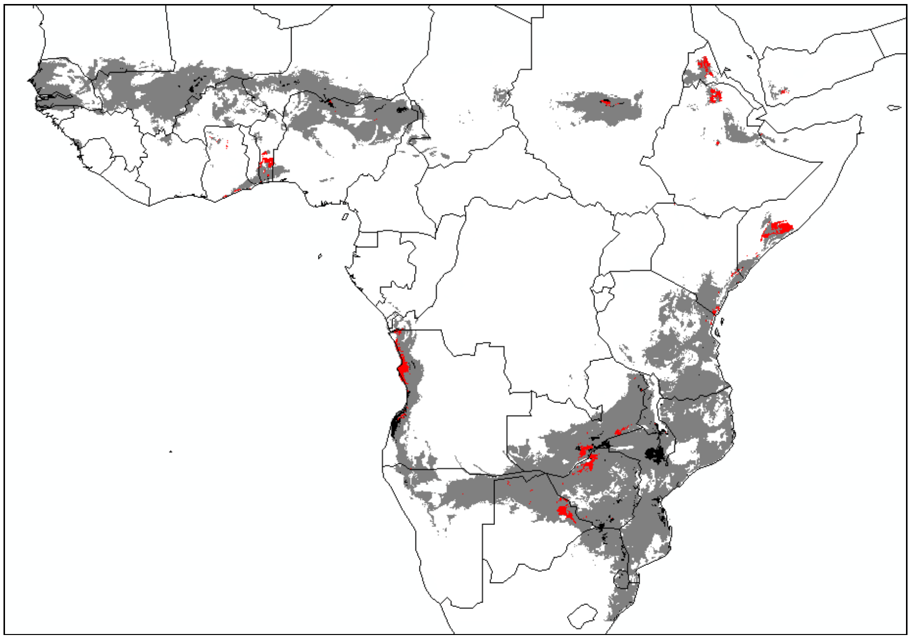


Fig. 3.2. Potential current distribution of the baobab tree in Africa (generated by Maxent using All records) predicted to remain suitable in the future under all GCM for scenario B2a. Black: present high suitability (>70% probability), grey: present medium suitability (between 40 and 70% probability), white: present low suitability (<40% probability), red: part of the present distribution predicted to remain suitable in 2050.

3.4.2 East Africa model

Estimated potential future distributions for the East Africa model were different depending on the GCM and the scenario. While HadCM3 predicted an increase in suitable habitat for the baobab tree for both scenarios, CSIRO-MK2 predicted an increase for scenario A and a decrease for scenario B, and CGCM2 an increase for scenario B and a decrease for scenario A (Table 3.2).

When compared with present distribution, for all GCM and scenarios, only a percentage of the present distribution was predicted to remain suitable in the future (Table 3.2). The percentage of present distribution predicted to remain suitable in the future under all GCM and scenarios was very small: 4.3% (Table 3.2, Fig. 3.5). No present distribution was predicted to remain suitable in the future (under all GCM and scenarios) in Namibia, Botswana, Somalia and Sudan.

East Africa model	**Scenario A2a**			**Scenario B2a**		
	HadCM3	**CGCM2**	**CSIRO**	**HadCM3**	**CGCM2**	**CSIRO**
Differences in extension between present and estimated future distributions	134.90%	69.84%	151.98%	128.36%	106.67%	28.75%
Percentage of present distribution estimated to remain suitable in the future	76%	39%	91%	27%	80%	27%
Percentage of present distribution estimated to remain suitable in the future (all GCM and scenarios) *	4.3%					

*Table 3.2. Differences in extension between present and future potential distributions and percentages of present distribution estimated to remain suitable in the future for different GCM and scenarios for East Africa model. The percentage of the combination of different models is not the mean of the percentages of the models/scenarios but the percentage (of the present distribution predicted to remain suitable in the future) common in all mentioned models. * Areas very likely to have suitable habitat in the future and where conservation efforts should be focused.*

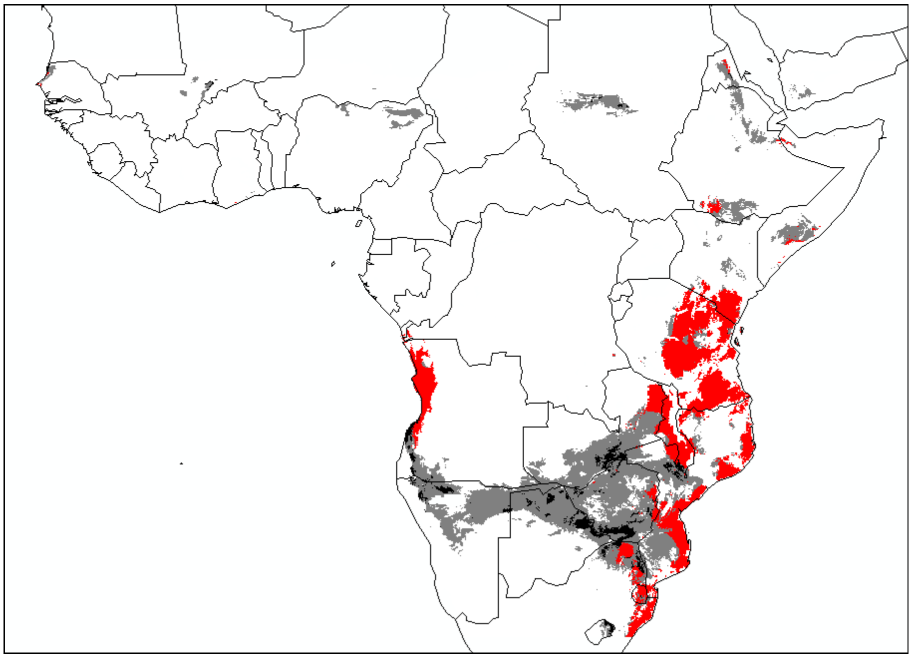


Fig. 3.3. Potential current distribution of the baobab tree in Africa (generated by Maxent using East African records) predicted to remain suitable in the future under all GCM for scenario A2a. Black: present high suitability (>70% probability), grey: present medium suitability (between 40 and 70% probability), white: present low suitability (<40% probability), red: part of the present distribution predicted to remain suitable in 2050.

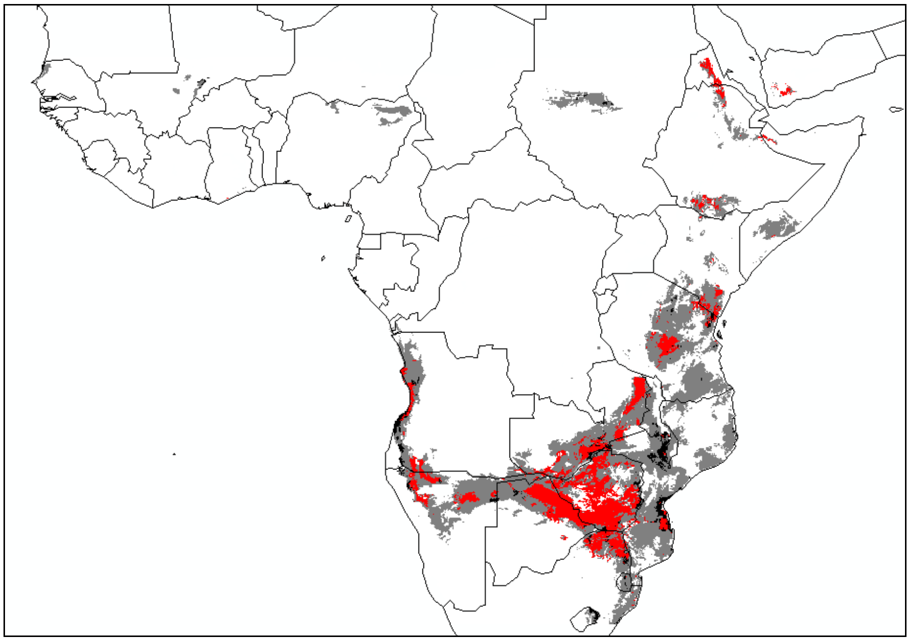


Fig. 3.4. Potential current distribution of the baobab tree in Africa (generated by Maxent using East African records) predicted to remain suitable in the future under all GCM for scenario B2a. Black: present high suitability (>70% probability), grey: present medium suitability (between 40 and 70% probability), white: present low suitability (<40% probability), red: part of the present distribution predicted to remain suitable in 2050.

When the percentage of present distribution predicted to remain suitable in the future under all GCM and scenarios was compared with the Protected Areas in Africa, 36% of it was found to be within 19 Protected Areas. These Protected Areas were several National Parks and Game Reserves (Table 3.3). Information on baobabs being present in these Protected Areas could only be found for some of them (Table 3.3). Elephant damage to baobab seedlings and/or mature trees has been reported from some of the Protected Areas (Table 3.3). As no baobabs have been reported from southern Ethiopia, this area could not be considered a potential site for baobab conservation (Fig. 3.5).

Country	**Type of Protected Area**	**Name**	**Remarks**
Angola	National Park	Quiçãma	Baobabs reported (Wickens and Lowe 2008)
Eritrea	Wildfife Reserve	Nakfa	
Kenya	National Park	Tsavo East	Baobabs reported, elephant damage (Wickens and Lowe 2008)
	National Park	Tsavo West	Baobabs reported, elephant damage (Wickens and Lowe 2008)
Malawi	Wildfife Reserve	Vwaza Marsh	
Mozambique	National Park	Zinave	
South Africa	National Park	Kruger	Baobabs reported elephant damage (Edkins et al. 2007)
	Private Nature Reserve	Klaserie	
	Game Farm	Selati	
Tanzania	National Park	Ruaha	Baobabs reported, elephant damage (Barnes 1980)
	Forest Reserve	Itulu Hill	
	Game Reserve	Mkomazi	Baobabs reported (Wickens and Lowe 2008)
	Game Reserve	Muhezi	
	Game Reserve	Kizigo	
	Game Reserve	Rungwa	
	Game Reserve	Lunda-Mkwabi	
	Game Reserve	Usangu	
Zambia	National Park	North Luangwa	Baobabs reported, elephant damage (Robertson-Bullock 1960)
	Game Reserve	Musalangu	

Table 3.3. Protected Areas in East and southern Africa found to have present suitable habitat predicted to remain suitable in the future (under all GCM and scenarios) for the baobab tree, and information on baobab presence and reported elephant damage in the Protected Areas.

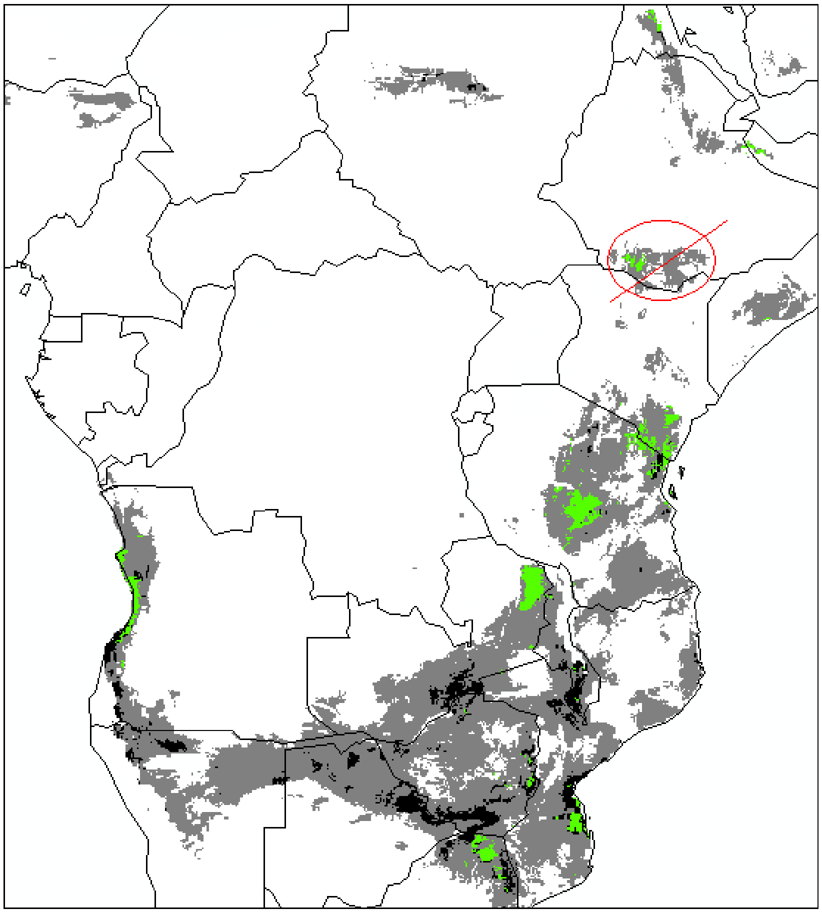


Fig. 3.5. Potential current distribution of the baobab tree in Africa (generated by Maxent using East African records) predicted to remain suitable in the future under all GCM for scenarios. Black: present high suitability (>70% probability), grey: present medium suitability (between 40 and 70% probability), white: present low suitability (<40% probability), green: part of the present distribution predicted to remain suitable in 2050. Crossed red circle: no baobab trees are present in the area.

3.4.3 West Africa model

Estimated potential future distributions for West Africa model were different depending on the GCM: while HadCM3 and CGCM2 predicted a marked decrease in suitable habitat for the baobab tree for both scenarios, CSIRO-MK2 predicted an increase for scenario A and a decrease for scenario B (Table 3.4).

When compared with present distribution, for all GCM and scenarios, only a percentage of the present distribution was predicted to remain suitable in the future (Table 3.4). The percentage of present distribution predicted to remain suitable in the future under all GCM and scenarios was very small: 0.82% (Table 3.4, Fig. 3.8). Present distribution was only predicted to be suitable in the future (under all GCM and scenarios) in Senegal and Nigeria (Fig. 3.8).

West Africa model	**Scenario A2a**			**Scenario B2a**		
	HadCM3	**CGCM2**	**CSIRO**	**HadCM3**	**CGCM2**	**CSIRO**
Differences in extension between present and to estimated future distributions	16.92%	51.70%	109.31%	15.05%	51.13%	21.62%
Percentage of present distribution estimated to remain suitable in the future	5%	33%	48%	12%	30%	10%
Percentage of present distribution estimated to remain suitable in the future (all GCM and scenarios) *	0.82%					

*Table 3.4. Differences in extension between present and future potential distributions and percentages of present distribution estimated to remain suitable in the future for different GCM and scenarios for West Africa model. The percentage of the combination of different models is not the mean of the percentages of the models/scenarios but the percentage (of the present distribution predicted to remain suitable in the future) common in all mentioned models. * Areas very likely to have suitable habitat in the future and where conservation efforts should be focused.*

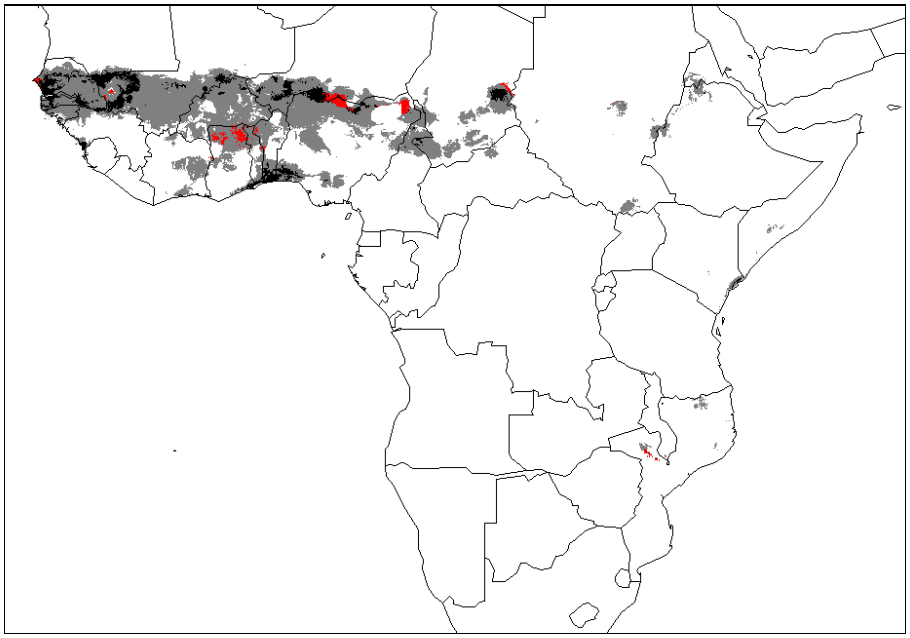


Fig. 3.6. Potential current distribution of the baobab tree in Africa (generated by Maxent using West African records) predicted to remain suitable in the future under all GCM for scenario A2a. Black: present high suitability (>70% probability), grey: present medium suitability (between 40 and 70% probability), white: present low suitability (<40% probability), red: part of the present distribution predicted to remain suitable in 2050.

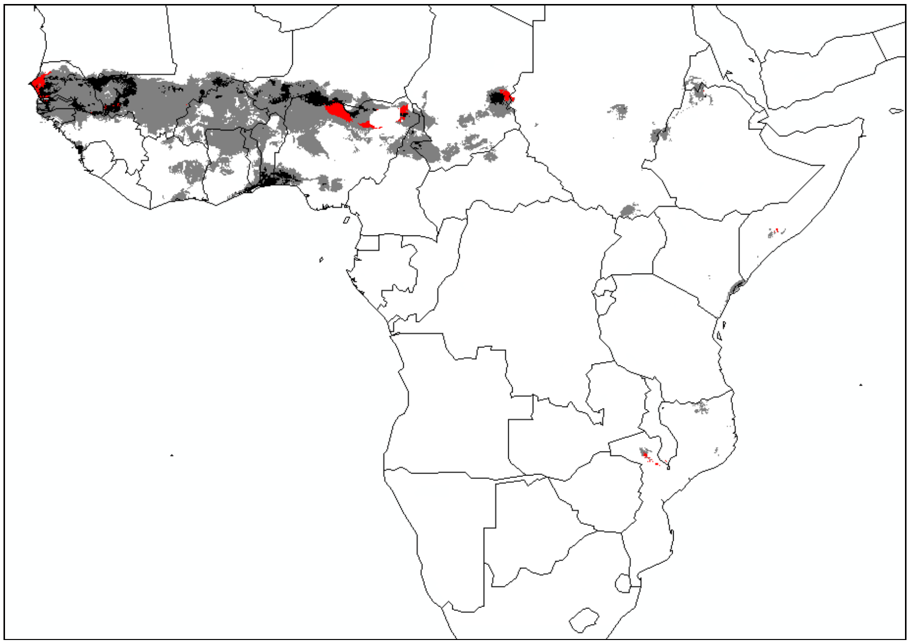


Fig. 3.7. Potential current distribution of the baobab tree in Africa (generated by Maxent using West African records) predicted to remain suitable in the future under all GCM for scenario B2a. Black: present high suitability (>70% probability), grey: present medium suitability (between 40 and 70% probability), white: present low suitability (<40% probability), red: part of the present distribution predicted to remain suitable in 2050.

When the percentage of present distribution predicted to be suitable in the future under all GCM and scenarios was compared with the Protected Areas in Africa, only 5.3% of it was found to be within Protected Areas. Mainly, these Protected Areas were small Forest Reserves in Senegal and Nigeria (Table 3.5). Information on the presence of baobab trees in these Protected Areas could only be found for the Senegalese Protected Areas (Table 3.5). As no baobabs have been reported from eastern Chad, this area could not be considered a potential site for baobab conservation (Fig. 3.8).

Country	**Type of Protected Area**	**Name**	**Remarks**
Senegal	UNESCO Biosphere Reserve	Delta du Saloum	Baobabs reported (pers. obs.)
	Forest Reserve	Foret de Bandia	Baobabs reported (pers. obs.)
	Forest Reserve	Foret de Thies	Baobabs reported (pers. obs.)
Nigeria	Forest Reserve	Gwiwakorel	
	Forest Reserve	Zamfara	
	Forest Reserve	Barawa	
	Forest Reserve	Dan Babba	
	Forest Reserve	Mawulli	

Table 3.5. Protected Areas in West Africa found to have present suitable habitat predicted to remain suitable in the future (under all GCM and scenarios) for the baobab tree, and information on baobab presence in the Protected Areas.

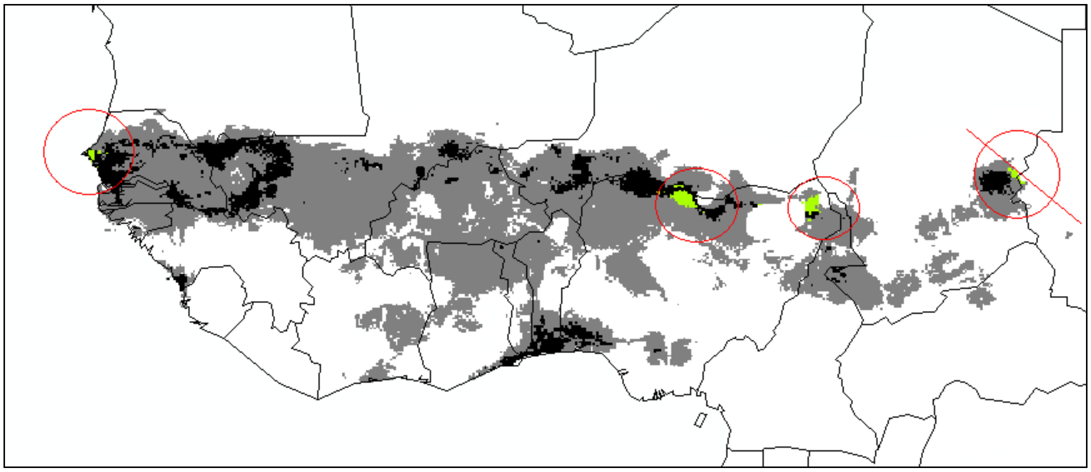


Fig. 3.8. Potential current distribution of the baobab tree in Africa (generated by Maxent using West African records) predicted to remain suitable in the future under all GCM for scenarios A2a and B2a. Black: present high suitability (>70% probability), grey: present medium suitability (between 40 and 70% probability), white: present low suitability (<40% probability), green colour inside red circles: part of the present distribution predicted to remain suitable in 2050. Crossed red circle indicates that no baobab trees are present in the area.

3.5 Discussion

Modelling results suggest that the geographical distribution of the baobab tree will shrink under predicted levels of climate warming. Much of the area that is currently suitable environmentally will not remain suitable in the future. In these future unsuitable habitats, local extinction is the most likely outcome. Adult trees, with an extensive shallow rooting system and a large trunk which accumulates water (Owen 1974, Sidibé and Williams 2002), might survive for a period of time. However, as seedlings are less resistant to drought than adults (Wickens 1982) seedlings might not be able to establish. Thus, the baobab trees in these areas will be ageing populations: once the old trees die, no young trees will replace them, and, eventually, no baobab trees will grow in these areas.

Alternatively, one possibility is that the baobab tree is capable of adapting to future local conditions by phenological or physiological means. Another possibility is that microclimate conditions not captured in the scale of this study allow the survival of some baobab tree populations. If so, the change in extension of suitable habitat may not be as pronounced as projected here. However, it is also possible that, as suggested by Midgley et al. (2003), the combined impact of future land transformation and climate change will reduce suitable habitat even more than predicted here. Changes in wildfire regimes that might occur under predicted climate change scenarios might also reduce suitable habitat. Another two options which should also be considered are: (i) the potential negative effect of climate change on baobab pollinators (mainly bats); and (ii) the potential increase of future utilisation pressures on the baobab tree, as other plant species fail to cope with predicted changes in climate (as suggested for the African ivory nut palm *Hyphaene petersiana* Klotzsch ex Mart., Blach-Overgaard et al. 2009). These could cause the extinction of some baobab tree populations existing in present suitable habitat predicted to remain suitable in the future. Although it is possible that the change in extension of suitable habitat may not be as projected, results from this study support the view that the baobab tree is threatened by climate change (Wickens and Lowe 2008), and indicate that better conservation strategies are urgently needed.

One strategy often considered in conservation studies is the presence of National and International Protected Areas. However, few Protected Areas were predicted to have suitable habitat for the baobab tree in the future in West Africa, and in some of them (Nigeria), the presence of the baobab tree could not be confirmed. Surveys for the baobab tree are needed in these Nigerian Protected Areas. In Eastern Africa, the number of Protected Areas predicted to have present and future suitable habitat was higher then in West Africa, and, baobab presence could be verified in a number of them.

However, it seems that current levels of protection within a Protected Area might not be enough for the baobab tree. Elephants have been reported to damage and even kill baobab trees (both adults and seedlings) in Protected Areas (Barnes 1980, Edkins et al. 2007, Wickens and Lowe 2008). Another issue is that human pressure (fruit, bark and leaf harvesting) on baobab trees in some Protected Areas remains considerable: e.g. Burkina Faso (Schumann et al. 2010), Malawi (pers. obs.). On the other hand, results from a study on population structure carried out in National Park W (Burkina Faso, Benin) showed that recruitment is higher inside the Protected Area than outside, despite human utilisation and elephant presence in the Park (Schumann et al. 2010). Although this might not be the case for all Protected Areas, it shows that Protected Areas do offer some degree of protection to this species.

High priority should be given towards more effective protection of the baobab tree, especially in the Protected Areas predicted to remain climatically suitable under all GCM and scenarios. This is particularly important in West Africa, where few Protected Areas were predicted to remain climatically suitable. In Protected Areas where the elephant population is high, baobab seedlings could be protected from elephants (e.g. through fencing) and/or baobab seedlings could be planted. In areas where baobab is widely used by local communities living around the Protected Area, baobab utilisation could be limited to fruit harvesting. It has been suggested that bark and leaf harvesting reduce baobab fruit production (Romero et al. 2001, Dhillion and Gustad 2004, Schumann et al. 2010), and therefore, have an impact on baobab dispersal and establishment.

Another potential conservation strategy, especially for areas at high risk of habitat loss (e.g. Sudan), might be *ex situ* conservation in germplasm collections or orchards. The predicted extinction in Sudan already seems to be happening: Wickens (1982) stated that many baobabs in the drier parts of Sudan died during and following the Great Drought of the late 1960s. Baobab populations in Sudan (which are isolated from both West Africa baobabs and East Africa baobabs and are at the most northern limit of the East Africa range) might be an interesting genetic pool for future baobab domestication. Hampe and Petit (2005) pointed out the importance for conservation of the populations at the rear edge of shifting ranges due to the high level of regional genetic diversity between isolated populations. Considering that baobab seeds have been reported to remain viable after 15 years storage (Sacande et al. 2006), seeds from Sudanese populations could be collected and preserved in Seed Banks. *Ex situ* conservation in orchards could also be considered: baobab seeds from Sudan could be planted in other areas predicted to remain suitable in the future. This latter option could also provide trees of known age for further studies on baobab morphology and fruit production.

Monitoring of the existing baobab populations is the recommended strategy for countries predicted no longer to have suitable habitat for the baobab tree in the future under some GCM and scenarios (i.e. Namibia, Botswana, Ivory Coast). Baobab seedlings could also be planted and/or protected in these countries. If existing populations are found to be continuously declining, *ex situ* conservation in germplasm collections or orchards might be the most feasible solution.

Another *in situ* conservation strategy which might be considered in areas predicted to remain climatically suitable in the future (under all GCM and scenarios, and outside a Protected Area) is the possibility of introducing a forestry law to limit access rights to baobab trees (in order to support baobab regeneration and control unsustainable harvest techniques). However, as mentioned in chapter 1, results from northern Benin showed that this strategy was not as successful as was expected. Farmers in Northern Benin reported that they now remove baobab seedlings from their fields because they would need to buy permits for their use in the future (Buchmann et al. 2010). Moreover, if restricted access is introduced, it is likely to apply to the whole tree, then today's 300 different baobab uses may no longer be employed (Buchmann et al. 2010).

Translocation of healthy mature baobabs from an area predicted to have unsuitable habitat in the future to an area predicted to be suitable could be an option. In fact, transplanting mature baobabs is a routine conservation operation at a Diamond Mine close to Messina, South Africa (Wickens and Lowe 2008). However, considering that lateral roots are usually trimmed to no more than 1 m long (see Wickens and Lowe 2008), it is not clear that transplantation success is high. Baobabs have an extensive root system and reducing it due to the transplantation process might have a negative effect on survival. Even if the tree survives, it might become more susceptible to drought, disease and fire or it might reduce or even stop fruit production. Considering the economic costs of transplanting large numbers of baobab trees (mechanical diggers and even helicopters might be needed, see Wickens and Lowe 2008), until more information on baobab transplanting success is made available, it seems that this strategy cannot be considered as cost-effective and, therefore, cannot be recommended.

In order to help maintain viable baobab populations, especially in areas predicted to remain suitable in the future, 'conservation through utilisation' could be a more effective conservation strategy. If people use the baobab tree, and appreciate it, they are more likely to be interested in preserving it, and maybe even planting it. In Malawi, for example, in areas where there is a high market demand for baobab fruits, local farmers are aware of the reduced number of baobab seedlings and they protect and transplant them (preliminary interviews carried out in southern Malawi). Training workshops on sustainable fruit, leaf and bark harvesting could be organised, as suggested by Buchmann et al. (2010). In Namibia, similar training has successfully guided local harvesters towards environmentally friendly harvest methods of the Devil's Claw, *Harpagophytum procumbens* L. (Nemarundwe et al. 2008, Buchmann et al. 2010). Training could also include seedling identification and protection (from fire, overgrazing and others) and management of sick trees. Giving value to the baobab tree and promoting its conservation could also help to preserve the ecosystem where the baobab tree lives, and the plant and animals which feed, shelter or live in it.

CHAPTER 4. Variation in baobab leaf morphology and its relation to drought tolerance

Drought is one of the main factors limiting growth, development and productivity of plants (Blum 1997). Climate change scenarios predict more severe droughts in the African savanna (Brooks 2004), where the baobab tree grows. In order to identify superior sources of planting material, it seems important to identify baobab trees adapted to drought. In this chapter I assess baobab drought tolerance by using easily quantifiable leaf morphological characteristics. I analyse baobab leaf morphology: (1) *in situ* in Benin and Malawi (two physically isolated genetically different baobab populations), (2) *ex situ* in an experimental farm in southern Benin and, (3) in partially pruned trees in northern Benin. Based on the observed results, I suggest superior materials for cultivation. A part of this chapter was published in a peer reviewed journal paper in *Genetic Resources and Crop Evolution* (see Annex III).

4.1 Introduction to drought adaptation

Following up the study of where baobab could be cultivated (chapter 2), an important issue that arose was: which baobab trees should be cultivated. The first characteristic considered to be important for selecting planting material was high tree survival. In the literature review (chapter 1), drought seemed to be a threat to the baobab tree. Drought is thought to be the major hazard to plant life in dry environments, where the baobab tree lives. The baobab tree has an outstanding ability to tolerate drought (Owen 1974). Several strategies help the baobab tree to withstand drought: the seed coat is impermeable, the baobab sheds its leaves, leaves have low water loss, the rooting system is widespread and the trunk stores water (Owen 1974, Fenner 1980, Wickens 1982, Sidibé and Williams 2002, Wickens and Lowe 2008).

The baobab seed coat is impermeable and this can be associated with adaptation to arid environments, as has been suggested for other species (Rolson 1978, Gutterman 1994). Razanameharizaka et al. (2006) found that the harvest moisture content of baobab seeds from Bandia (Senegal) was between 5.5 and 6.7% (relative to the weight of fresh material) and the natural germination capacity was 27%. In the same study it was found that the removal of a fragment of the seed coat significantly increased the capacity to germinate (up to 90%) which confirmed that this species possesses seeds with physical dormancy, as suggested by Esenowo (1991) and Danthu et al. (1995). In nature, this dormancy is believed to be broken through digestion by elephants or other big mammals as zoochory (dispersal by animals) is the recognised means of dispersal of the baobab tree (see chapter 1).

The baobab tree bears its leaves for only 4 months a year (Fenner 1980), which is another drought adaptation strategy. Apart from leaf shedding, water loss from the leaves was found to be exceptionally low compared with common woody species of the same region during the leafing season, even though baobabs have low specific leaf weight (leaves have a thin cuticle and are without much secondary thickening compared with associated species) (Fenner 1980).

Another strategy to cope with drought is the storage of water in the swollen trunk, which has been much noted by authors. Owen (1974) reported a marked increase in the circumference of baobab after heavy rainfall, which followed a long drought in South Africa. Chapotin et al. (2006) studied daily water deficits in two Malagasy baobab species (*Adansonia rubrostipa* and *A. za*) and found that stem morphology and anatomy restrict water movement between storage tissues and the conductive pathway which makes this stored-water usage more appropriate to longer-term water deficits than to daily water deficits. It could be possible that *A. digitata* uses the same strategy.

The baobab tree rooting system is also important: it has been noted that mature trees can send out shallow roots for more than 66 m (Kondor 1990). Fenner (1980) discusses the extensive shallow rooting system, calculating from a tree with roots extending about 44 m that an area about 0.6 hectares around each tree is covered. With this adaptation for rapid absorption of water from surface soils, Fenner (1980) goes on to suggest that the species is highly suited to maximising utility of the erratic flash-flood rainfall patterns. Although baobab seedlings have a poorly developed rooting system, tuberous roots discovered on young baobabs act as water and/or sugar storage facilities during long drought periods (Alexandre 1992).

Apart from the aforementioned strategies (leaf shedding, rooting system and water storage behaviour), other drought adaptation strategies such as variation in morphology have also been observed. In regard to tree morphology, overall, trees from drier environments tend to be shorter or smaller than those from wetter environments (Levitt 1972, Abrams et al. 1990). Baobabs with short, stout trunks have a better survival value in drier areas (due to their higher maintenance of water storage capacity) than tall thinner baobab trees and that is why they are more common there (Wickens and Lowe 2008). In Benin, Assogbadjo et al. (2005b) reported that average tree height and diameter was higher in the Guinean zone (more humid) than in the Sudanian zone (drier).

Variability in leaf size has also been reported to be a feature of drought tolerance, with plants from xerophitic environments having smaller and thicker leaves than those from wetter environments (Burns 1969, Sutcliffe 1979, Ristic and Cass 1991). Reduced leaf size in the shea tree (*Vitellaria paradoxa*, another parkland tree) at northern latitudes in Ghana was suggested to be an adaptation to control evapotranspiration rates (Lovett and Haq 2000) where arid conditions and high temperatures would be expected to increase water loss. For *Parkia biglobosa* (another parkland tree) it was found that leaflets of seedlings from drier locations were thicker than those from wetter locations (Teklehaimanot et al. 1998). For the baobab tree, found in the same environment as *V. paradoxa* and *P. biglobosa*, variation in leaf morphology has also been noted. Mature leaves are 5 to 9 foliate and medial leaflet size varies between 2 x 5 and 7 x 15 cm (see chapter 1). However, to my knowledge, no study has been focused on variation in leaf morphology and its implications for drought tolerance.

No study on baobab leaf stomatal characteristics which can also be linked to adaptation to drought has been carried out. Plants from drier environments have a higher stomata density than plants from mesic environments (Abrams et al. 1990). Variation in stomatal characteristics for the baobab tree has also been recorded. While Sidibé and Williams (2002) stated that stomata are confined to the lower surface of the leaf, Rao and Ramayya (1981) reported that baobab leaves are amphistomatic (they have stomata in both sides of the leaf).

Although the baobab tree's ability to withstand drought has been noted by several authors, it seems that not all the mechanisms involved are well understood. In order to help identify potential superior sources of planting materials better adapted to drought, baobab leaf morphological and stomatal characteristics were studied in Benin and Malawi.

4.2 Aims and Objectives

The aim of this study is to contribute to the understanding of the baobab tree drought adaptation mechanisms (which could help identify better planting material) through studying leaf morphological and stomatal variation.

The specific objectives are:

1. Identify the relationship between leaf variation and the environment
2. Determine if genetics also play a role in leaf morphological characteristics
3. Investigate if pruning has a strong effect on leaf morphology
4. Determine if there are differences in leaf morphology between Benin and Malawi

In fact, the third objective does not refer to baobab tree drought adaptation mechanisms but during the field work, some trees were found to be severely pruned (due to leaf harvesting for human consumption) while others were little or not pruned. As it seemed that pruning could have a confounding effect on leaf morphology, this third objective was included in the study. The specific research questions are:

1. Can differences in leaf size and stomatal characteristics be linked to differences in the environment?
2. Do young seedlings have the leaf morphological characteristics of the parent plant when grown in another environment?
3. Does pruning due to leaf harvesting affect the morphological and stomatal characteristics of the baobab tree?
4. Do baobab trees in Benin have different leaf characteristics to those in Malawi?

In order to answer these research questions, three experiments were carried out in Benin and one in Malawi.

4.3 Methodology

Study sites

Following the genetic differences between baobab tree populations from West Africa and south-eastern Africa suggested by Pock Tsy et al. (2009), two countries were selected: one in West Africa and one in south-eastern Africa (Fig. 4.1). In West Africa, Benin was the chosen country as previous studies have determined distribution, density, variation in fruit morphology and productivity, and patterns of genetic diversity (Assogbadjo et al 2005a, 2005b, 2006). In south-eastern Africa, Malawi was selected as it has been reported to be the main producer of baobab fruit pulp for Europe (Phytotrade Africa 2009, pers. comm.), the density of the baobab tree is high in the southern part of this country (Wickens and Lowe 2008) and a few studies have provided information on baobab chemical characteristics (Saka et al. 1994, Saka et al. 2007).

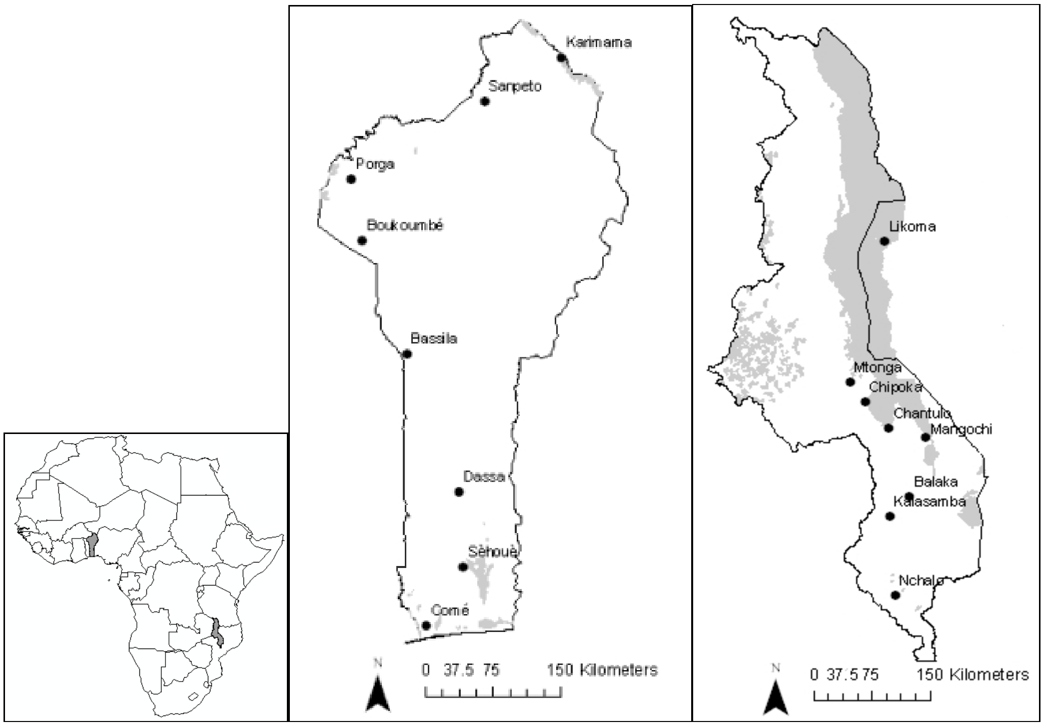


*Fig. 4.1. Studied countries (left) and study sites in Benin (middle) and Malawi (right).
Grey colour refers to main water bodies. Likoma is a Malawian island in Mozambican waters.*

In Benin, the study was conducted in three bioclimatic zones: the Sudanian zone, the Sudano-Guinean zone and the sub-humid Guinean zone (Dahomey Gap) (White 1983). The Sudanian zone, located between 9°45’-12°25’ N, is characterised by an annual mean rainfall of less than 1000 mm and a high variation in the relative humidity (from 18% during December-February to 99% in August). The temperature varies from 24 °C to 31 °C. The main soil types are hydromorphic soils, welldrained soils, and lithosols. The Sudano-Guinean zone, located between 7°30’-9°45’ N, is characterised by an annual mean rainfall of 900-1110 mm. There is only one rainy season from May to October. The annual temperature ranges from 25 °C to 29 °C, and the relative humidity from 31% to 98%. The soils in this zone are infertile mineral soils and ferruginous soils. The sub-humid Guinean zone (Dahomey Gap), located between 6°25’-7°30’ N, has a bimodal rainfall regime with peaks in April-June and September-November with a mean annual rainfall of 1200 mm. The mean temperature varies between 25 °C and 29 °C and the relative humidity between 69% and 97%. The soils are either deep ferrallitic or alluvial and heavy clay soils (adapted from Assogbadjo et al. 2005b).

In Malawi, the study was conducted in the Zambezian zone (White 1983). The Zambezian zone has a unimodal rainfall regime with a peak in November-April. Although the whole of Malawi is part of the Zambezian zone of White (1983), Hardcastle (1977) identified several sub-zones in Malawi. In this country, baobab trees are mainly found in the southern part of the country: along the southern shore of Lake Malawi, in parts of the Upper Shire valley and in the Lower Shire valley (Gondwe and Chanyenga 2006). The southern lake shore and the lower parts of the Upper Shire valley, zone Ba of Hardcastle (1977), are at the altitude range of 200 to 700 m, with a mean annual temperature of 22-25 ºC and annual precipitation between 700 and 840 mm. The Lower Shire valley, part of zone A of Hardcastle (1977), has an average altitude of less than 200 m, a mean annual temperature of 25 ºC and annual precipitation between 700 and 840 mm. Several soil types occur in these areas, but the predominant soil types are alluvial calcimorphic soils above vertisols and hydromorphic soils along the lake shore (FAO et al. 2008).

Experiment setting

Four experiments were carried out, three in Benin and one in Malawi:

Experiment 1: *In situ* assessment of leaf morphological variation in Benin.

Observations were made on the morphology of baobab trees maintained in actively farmed fields, habitations and their boundaries in eight sites in Benin (Table 4.1, Fig. 4.1). Study locations were selected following a latitudinal gradient with the main criterion being high baobab density (>5 ind/km^2 as determined by Assobgbadjo et al. 2005b) and accessibility. Ten baobab trees having 0.5-1.5 m diameter at breast height (DBH) and being at least 100 m apart were randomly selected in each village. Although age estimates from baobab tree DBH are generally not robust (see chapter 1), the idea was to reduce the range of ages of the studied trees.

Agro-climatic zone	**Study site**	**Latitude** (˚)	**Longitude** (˚)	**Annual rainfall (mm)**	**Mean annual temperature (˚C)**
Sudanian	Karimama	12.0477 N	3.2012 E	682	28.7
	Sanpeto	11.6185 N	2.4415 E	884	27.7
	Porga	10.8405 N	1.1120 E	946	28.4
	Boukoumbé	10.2295 N	1.2275 E	1144	26.6
Sudano-Guinean	Bassila	8.7440 N	1.2275 E	1188	26.6
	Dassa	7.7354 N	2.1910 E	1166	27.4
Guinean	Sèhouè	6.9940 N	2.2325 E	1076	27.5
	Comé	6.4100 N	1.8625 E	992	27.4

Table 4.1. Descriptions of the eight study sites of Adansonia digitata *in Benin. Climatic data was obtained from the Worldclim data (Hijmans et al. 2004). Agro-climatic zones following White (1983).*

Experiment 2: assessment of leaf morphological variation in an experimental farm in Benin.

Observations were made on 12 month old baobabs from three study sites (Boukoumbé in the Sudanian zone, Savalou in the Sudano-guinean zone and Sèhouè in the Guinean zone) planted in the experimental farm of the Faculty of Agronomy in the Abomey-Calavi University (UAC), south Benin. The baobab seeds were planted in small plastic bags following a random block design (Fig. 4.2). Ten baobab trees were sampled from Boukoumbé, ten from Savalou and ten from Sèhouè (total number= 30).

Fig. 4.2. Baobab trees aged 12 months sampled for leaf characteristics in the experimental farm of the Faculty of Agronomy of the Abomey-Calavi University (UAC), south Benin. Source: A. Cuni Sanchez.

Experiment 3: the impact of pruning on leaf morphology.

As mentioned in chapter 1, in some areas of West Africa, baobab trees are mutilated due to intensive leaf harvesting for human consumption (Dhillion and Gustad 2004). Baobab mutilation due to leaf harvesting was observed in several study sites in Benin (Fig. 4.3). It seems that pruned branches produce young leaves which are smaller in size, less hairy, lighter green and tastier (compared with leaves from non-pruned branches, A. Assogbadjo 2008, pers. comm.). However, to my knowledge, no quantitative information is available on the impact of pruning on leaf size, shape and stomata characteristics.

Observations of leaf morphological variation were made on ten partially pruned trees in Porga (north Benin) (Fig. 4.4). These trees had been pruned to harvest leaves for human consumption.

Fig. 4.3. Example of pruned baobabs due to leaf harvesting for human consumption (Porga, northern Benin).
Source: A. Cuni Sanchez.

Fig. 4.4. Baobab intensively pruned for leaf consumption (left) and baobab partially pruned for leaf consumption (right). Only baobabs partially pruned were assessed in experiment 3.
Source: A. Cuni Sanchez.

Experiment 4: *In situ* assessment of leaf morphological variation in Malawi.

Observations were made on the morphology of baobab trees maintained in actively farmed fields, habitations and their boundaries in seven sites in Malawi (Table 4.2, Fig. 4.1). Study locations were selected following a latitudinal gradient with the main criterion being high baobab density determined by Gondwe and Chanyenga (2006) and accessibility. Ten baobab trees having 0.5-1.5 m diameter at breast height (DBH) and being at least 100 m apart were randomly selected in each village. Baobab trees are not pruned due to leaf harvesting in Malawi (pers. obs.)

Study site	**Latitude** (°)	**Longitude** (°)	**Silvicultural zone**	**Annual rainfall (mm)**	**Mean annual temperature (˚C)**
Nchalo	16.3365 S	34.8605 E	A	794	26.2
Kalasamba	15.3874 S	34.7933 E	C	940	24.3
Balaka	15.1313 S	35.0279 E	Ba	981	23.5
Mangochi	14.4216 S	35.2121 E	Ba	843	24.5
Chantulo	14.3253 S	34.7831 E	Ba	886	24.5
Chipoka	14.0029 S	34.5006 E	Ba/C	1012	24.5
Mtonga	13.7623 S	34.3366 E	Ba/C	1017	23.9

Table 4.2. Descriptions of the eight study sites of Adansonia digitata *in Malawi with respect to the silvicultural zones of Hardcastle (1977). Climatic data was obtained from the Worldclim data (Hijmans et al. 2004).*

Leaf morphological assessment

The morphological assessment was carried out following the same methodology in all four experiments. In experiment 1, 2 and 4, ten fully developed leaves were selected from each tree at the lowest height possible. In experiment 3, ten fully developed leaves were selected from pruned branches and ten leaves from non-pruned branches.

The height of each tree and the DBH were recorded using an electronic clinometer and a decametre. A picture was taken of each tree in order to characterise the tree and determine the pruning degree (experiment 1).

Several characteristics were recorded from each leaf using a ruler and an electronic Vernier calliper: pedicel length, number of leaflets, medial leaflet length, medial leaflet length to broadest part, medial leaflet width and medial leaflet thickness measured at the widest part. The medial leaflet was punched five times with a paper punch; the discs were dried in an oven at 70 ˚C and weighed with a precision balance after 48 hours. The Specific Leaf Weight (SLW) was derived by dividing the dry weight of the five punched discs by their area (see Kardel et al. 2010). In order to estimate leaf shape, the ratios between medial leaflet length and medial leaflet length to broadest part (ratio 1) and the ratio between medial leaflet length and medial leaflet width (ratio 2) were calculated.

Stomata assessment

The medial leaflet was removed from 3 of the youngest fully opened leaves of each tree. Nail polish impressions of the abaxial surface of the leaflets were made for all leaflet samples (Ceulemans et al. 1995, Herrick et al. 2004). Nail polish impressions of the adaxial surface were made in order to determine whether stomata were only present on the lower surface of the leaf. The impressions were observed under a light microscope (Olympus model CHA213) and counts were made of stomata in three random fields of view, at (10×40)X magnification. Ten random measurements of guard cell length were made from one leaf per tree using an eye piece micrometer at magnification (10×100)X.

Environmental data

Climatic data was acquired from the Worldclim data (Hijmans et al. 2004). The 19 bio-climatic variables used for studying the baobab tree's distribution in Africa (chapter 2) were also used in this chapter.

Statistical analyses

SPSS for Windows v 16.0, ANOVA and MANOVA were used to determine significant differences between study sites. Post-hoc pair wise multiple comparisons were performed using Tukey's-b test and Games–Howell test (the latter one when there was no homogeneity of variances). Due to lack of normality of some variables in experiment 4 (e.g., number of leaflets, stomata density), Kruskal-Wallis tests were used to determine significant differences between study sites while post-hoc pair wise multiple comparisons were performed using Mann-Whitney tests. Correlations were tested using Spearman Rank Order Coefficient.

4.4 Results

Experiment 1

There were significant differences between study sites in all leaf morphological characteristics measured in experiment 1 (Table 4.3). In general, leaves from Comé, Sèhouè and Karimama were larger than those from other study sites (greater medial leaflet length, longer pedicel, greater number of leaflets, thicker, higher SLW). Trees from these areas were not pruned. However, in general, there was a tendency for trees from northern study sites to have smaller leaves. There was a significant difference in stomatal density between study sites in experiment 1 (Table 4.3). Bassila had the lowest stomatal density while the highest stomatal densities were found in northern study sites. Significantly larger guard cells were found in the southern study sites (Comé and Sèhouè). Stomata were observed next to the main nerve of the medial leaflet on the adaxial impressions in some of the samples both in southern and northern study sites although no stomata were found on the medial leaflet adaxial lamina surface.

Agro-climatic zone	**Study sites**	**Pruning**	**ML length (cm)**	**Pedicel length (cm)**	**No. leaflets**	**ML thickness (mm)**	**SLW (mg/cm^2)**	**No. stomata per mm^2**	**Guard cell length (µm)**
Sudanian (north)	Karimama	Uncommon	8.54 ± 1.62 a	8.10 ± 2.50 a	5.62 ± 0.90 b	0.28 ± 0.04 a	8.14 ± 1.85 a	128.2 ± 18.3 c	-
	Sanpeto	Common	7.42 ± 1.45 c	6.12 ± 1.89 b	4.12 ± 0.97 c	0.22 ± 0.03 c	5.89 ± 1.41 c	124.0 ± 24.9 bc	-
	Porga	Common	6.26 ± 1.26 b	4.56 ± 1.42 c	3.71 ± 0.89 d	0.24 ± 0.04 b	7.89 ± 1.58 a	146.0 ± 29.7 f	38.26 ± 4.67 b
	Boukombé	Common	7.11 ± 1.64 c	5.68 ± 1.93 b	4.67 ± 0.84 a	0.29 ± 0.04 a	9.81 ± 1.22 d	101.0 ± 16.4 e	37.55 ± 4.03 b
Sudano-Guinean (centre)	Bassila	Common	8.19 ± 1.90 a	6.09 ± 2.46 b	4.60 ± 0.88 a	0.25 ± 0.03 b	5.81 ± 1.43 c	75.4 ± 16.2 d	38.72 ± 4.87 b
	Dassa	Common	6.07 ± 1.44 b	5.93 ± 2.16 b	4.28 ± 1.02 c	0.26 ± 0.04 b	6.79 ± 1.67 b	119.2 ± 17.1 bc	37.16 ± 4.32 b
Guinean (south)	Sèhouè	Uncommon	8.71 ± 1.63 a	7.28 ± 1.84 a	5.39 ± 1.10 b	0.28 ± 0.04 a	8.03 ± 2.10 a	114.8 ± 17.6 b	41.97 ± 5.12 a
	Comé	Uncommon	8.88 ± 1.29 a	7.53 ± 2.35 a	4.74 ± 1.26 a	0.28 ± 0.05 a	8.26 ± 2.20 a	90.2 ± 16.5 a	41.22 ± 3.94 a

Table 4.3. Leaf morphological and stomatal characteristics of Adansonia digitata *from eight study sites (n=100, stomata No.=90). Means followed by the same letter within a column are not significantly different at $p<0.01$(Games-Howell test). ML=medial leaflet. SLW= Specific leaf weight. Pruning, which was not quantitatively determined, is classified as common or uncommon referring to the number of trees which had been intensively pruned for leaf consumption.*

Experiment 2

Significant differences were observed in leaf size in experiment 2 (Table 4.4). Leaves from Savalou (central Benin) were significantly smaller than those from other sites, while leaves from Sèhouè (south Benin) were significantly thinner and had lower SLW. Although there was not a clear pattern in leaf morphological differences, stomatal differences followed the same pattern of the results obtained in experiment 1: stomata density being significantly higher and guard cells significantly smaller in the north (Table 4.4). A few stomata were found close to the nerves of the medial leaflet on the adaxial impressions.

	Seed collection sites	**ML length (cm)**	**Pedicel length (cm)**	**No. leaflets**	**ML thickness (mm)**	**SLW (mg/cm^2)**	**No. stomata per mm^2**	**Guard cell length (µm)**
North	Boukoumbé	11.16 ± 2.75 b	11.28 ± 3.76 c	5.51 ± 0.81 b	0.24 ± 0.03 a	6.61 ± 1.6 b	176.75 ± 17.38 a	35.84 ± 3.34 a
Centre	Savalou	9.5 ± 2.29 a	7.15 ± 2.38 a	4.64 ± 0.74 a	0.23 ± 0.02 a	7.45 ± 1.74 a	172.32 ± 16.19 b	37.4 ± 3.12 b
South	Sèhouè	10.70 ± 2.6 b	9.73 ± 3.12 b	5.6 ± 0.83 b	0.21 ± 0.03 b	5.18 ± 1.39 c	144.84 ± 13.1 c	38.53 ± 3.7 b

Table 4.4. Leaf morphological and stomatal characteristics of Adansonia digitata *from three seed collection sites grown in the farm (n=90, stomata No. and guard cell length n=30). Means followed by the same letter within a column are not significantly different at p<0.01 (Tukey's–b test). ML=medial leaflet. SLW= Specific leaf weight.*

Experiment 3

In experiment 3, leaves from pruned branches were younger than those from non-pruned branches: they were smaller and of paler green colour (Table 4.5, Fig. 4.5). However, no significant differences (p>0.05) were found in the leaf shape ratios calculated (results not included in Table 4.5). Significant differences (p<0.01) were found in ML thickness and SLW, with leaves from non-pruned branches being thicker and having higher SLW.

No significant differences (p>0.01) were found in stomatal density or guard cell length (table 4.4). No stomata were observed on the adaxial impressions.

	ML length (cm)	**Pedicel length (cm)**	**No. leaflets**	**ML thickness (mm)**	**SLW (mg/cm^2)**	**No. stomata per mm^2**	**Guard cell length (µm)**
Pruned branches	5.71± 1.2 a	4.00 ± 1.61 a	4.1 ± 0.5 a	0.24 ± 0.04 a	7.79 ± 1.85 a	146.08 ± 27.98 a	38.70 ± 5.08 a
Non-pruned branches	10.03 ± 1.55 b	9.68 ± 2.34 b	5.2 ± 0.4 b	0.32 ± 0.04 b	11.65 ± 2.40 b	165.7 ± 23.89 a	38.98 ± 5.07 a

Table 4.5. Leaf morphological and stomatal characteristics of Adansonia digitata *from Porga (n=100, stomata No. n=90). Means followed by the same letter within a column are not significantly different at p<0.01 (Tukey's–b test). ML=medial leaflet. SLW= Specific leaf weight.*

Fig. 4.5. Baobab leaf from a non-pruned branch (left) and baobab leaves from pruned branches (middle and right). Note the difference in leaf size and colour.Source: A. Cuni Sanchez.

Experiment 4

There were significant differences between study sites in all leaf morphological characteristics measured in experiment 4 (Table 4.6). In general, leaves from Balaka were smaller than those from other study sites (smaller medial leaflet length, shorter pedicel, thinner medial leaflet) while leaves from Chantulo and Mtonga were larger than those from other study sites. Although leaves from Nchalo were also large, they were thinner than those from Chantulo and Mtonga. Leaves from Mangochi and Chantulo were found to have significantly high SLW ($p<0.01$, Mann-Whitney test). Significant differences were also observed in leaf shape. Leaves from Kalasamba had a significantly smaller ($p<0.01$, Mann-Whitney test) ratio 2 (medial leaflet length/ medial leaflet length to broadest part) while leaves from Chipoka and Mtonga had a significantly larger ratio 1 (medial leaflet length/ medial leaflet width). Leaves from

Nchalo and Kalasamba (the most southern study sites) had more leaflets than those from other study sites (most leaves had 7 leaflets instead of 5).

There were also significant differences ($p<0.01$, Kruskal-Wallis test) in stomatal density and guard cell length between study sites (Table 4.6). Leaves from Mangochi and Balaka were found to have significantly higher stomata density and smaller guard cell length. Leaves from Chantulo were found to have significantly larger guard cell length than other study sites ($p<0.01$, Mann-Whitney test). Stomata were observed next to the main nerve of the medial leaflet on the adaxial impressions in most samples, although no stomata were found on the medial leaflet adaxial lamina surface.

Study site	**ML length (cm)**	**Pedicel length (cm)**	**No. leaflets**	**ML thickness (mm)**	**SLW (mg/cm^2)**	**Ratio 1**	**Ratio 2**	**No. stomata per mm^2**	**Guard cell length (µm)**
Nchalo	15.79 ± 2.84 a	12.85 ± 2.96 a	5.8 ± 0.9 ab	0.23 ± 0.02 a	6.22 ± 0.91 ab	2.9 ± 0.4 a	1.8 ± 0.1 ab	209.4 ± 19.8 a	32.0 ± 2.3 ab
Kalasamba	12.94 ± 1.77 b	11.04 ± 2.12 b	6.0 ± 0.8 b	0.25 ± 0.02 bc	6.32 ± 0.64 a	2.9 ± 0.5 a	1.6 ± 0.1 c	225.2 ± 18.7 b	32.0 ± 1.9 ab
Balaka	11.84 ± 2.37 c	10.84 ± 2.78 b	5.4 ± 0.9 c	0.23 ± 0.03 a	6.14 ± 0.68 ab	2.8 ± 0.5 ab	1.8 ± 0.2 c	243.4 ± 29.4 c	31.4 ± 2.0 a
Mangochi	12.89 ± 1.81 b	11.4 ± 2.56 b	5.6 ± 0.9 ac	0.24 ± 0.03 ab	6.89 ± 0.58 c	2.9 ± 0.4 a	1.8 ± 0.2 d	250.9 ± 35.2 c	30.4 ± 2.2 c
Chantulo	15.63 ± 2.58 a	12.09 ± 1.86 ac	5.5 ± 0.8 ac	0.25 ± 0.02 c	7.06 ± 0.64 c	2.7 ± 0.4 b	1.8 ± 0.2 b	225.7 ± 26.1 b	35.0 ± 2.4 d
Chipoka	14.04 ± 2.14 d	11.53 ± 2.05 bc	5.6 ± 0.8 ac	0.24 ± 0.02 ab	5.96 ± 0.89 b	3.1 ± 0.4 c	1.7 ± 0.1 d	218.8 ± 18.5 b	32.8 ± 2.9 b
Mtonga	14.73 ± 2.06 ad	12.33 ± 2.3 a	5.5 ± 0.8 ac	0.25 ± 0.02 c	6.13 ± 0.84 ab	3.2 ± 0.4 c	1.7 ± 0.1 d	211.9 ± 14.9 a	32.8 ± 2.1 b

Table 4.6. Leaf morphological and stomatal characteristics of Adansonia digitata *from Malawi (n=100, stomata No. n=90). Means followed by the same letter within a column are not significantly different at p<0.01 (Mann-Whitney test). ML=medial leaflet. SLW= Specific leaf weight. Ratio 1= ML length/ ML length to broadest part, Ratio 2= ML length/ ML width*

Comparison between leaf morphological characteristics of Benin and Malawi

Leaves from Malawi were, in general, larger (ML length, pedicel length) and thinner (ML thickness, SLW) than those from Benin (Table 4.7). Their stomata characteristics were also different: while stomata density was higher in Malawi than in Benin, guard cell length was smaller (Table 4.7). Their shapes were also different (significant differences in ratio1 and 2, Table 4.7). Although differences in pruning might explain part of these differences (baobabs being commonly pruned in Benin but not in Malawi), leaf characteristics from study sites where pruning is not common in southern Benin were different from those in Malawi (see Table 4.3 and 4.6).

	ML length (cm)	**Pedicel length (cm)**	**No. leaflet**	**ML thickness (mm)**	**SLW (mg/ cm^2)**	**Ratio1**	**Ratio2**	**No. stomata per mm^2**	**Guard cell length (μm)**
Benin	7.65 ± 1.88 a	6.41 ± 2.35 a	4.6 ± 1.1 a	0.26 ± 0.05 a	7.79 ± 1.85 a	1.5 ± 0.17 a	2.26 ± 0.42 a	112.12± 32.62 a	39.14 ± 5.98 a
Malawi	13.99 ± 2.72 b	11.74 ±2.47b	5.6 ± 0.8 b	0.24 ± 0.02 b	3.55 ± 3.09 b	2.97 ± 0.46 b	1.74 ± 0.16 b	226.5 ± 28.0 b	32.3 ± 2.6 b

Table 4.7. Leaf morphological and stomatal characteristics of Adansonia digitata *from Benin (n=800) and Malawi (n=700). Means followed by the same letter within a column are not significantly different at p<0.01 (Mann-Whitney test). ML=medial leaflet. SLW= Specific leaf weight.*

Correlations between leaf characteristics and the environment

Due to the observed significant effect of leaf pruning on leaf size and shape, no correlations between leaf characteristics and the environment were carried out for experiment 1 (*in situ* assessment in Benin). For experiment 4 (*in situ* assessment in Malawi), specific leaf weight (SLW) was found to be significantly positively correlated with mean annual temperature (r_s=0.25, p<0.01) and medial leaflet length was found to be significantly positively correlated with minimum temperature of the coldest month (r_s=0.35, p<0.01). Leaf shape ratio 1 was found to be significantly positively correlated with annual precipitation (r_s=0.2, p<0.01) while leaf shape ratio 2 was found to be significantly negatively correlated with annual precipitation (r_s=-0.22, p<0.01) but significantly positively correlated with minimum temperature of the coldest month (r_s=0.27, p<0.01).

Correlations between stomata characteristics and the environment

Stomatal characteristics in Benin were significantly correlated with most environmental variables selected (Table 4.8). However, this was not the case for stomatal characteristics in Malawi (Table 4.8). Stomata density in Benin was highly positively correlated ($r_s>0.6$, $p<0.01$) with annual mean temperature and mean diurnal range and negatively correlated ($r_s=0.54$, $p<0.01$) with minimum temperature of the coldest month. Guard cell length was more correlated with precipitation characteristics ($r_s>0.25$, $p<0.01$) than temperature. Stomata density in Malawi was only correlated with minimum temperature of the coldest month ($r_s=0.22$, $p<0.01$) while guard cell length was more correlated with precipitation characteristics ($r_s>0.25$, $p<0.01$) than temperature, like in Benin.

Environmental variables	**Stomata density**		**Guard cell length**	
	Benin	**Malawi**	**Benin**	**Malawi**
Mean annual temperature	0.60			
Mean diurnal range	0.65		-0.18	-0.19
Isothermality	0.45			0.35
Temperature seasonality	-0.38			-0.17
Max. temperature of warmest month			-0.19	-0.12
Min. temperature of coldest month	-0.54	-0.22	0.24	0.24
Annual precipitation	-0.44		**-0.29**	**0.1**
Precipitation of wettest month	-0.29		0.16	0.23
Precipitation of driest month			-0.25	-0.23
Precipitation seasonality	0.50		**-0.25**	**0.32**

Table 4.8. Coefficients of correlation between stomata characteristics and environmental variables in Benin and Malawi. Only correlations with a p-value < 0.01 are given. Empty cells indicate no significant correlation at p<0.01 (Spearman's rank correlation coefficients). Correlations given in bold indicate opposite trends in both countries.

4.5 Discussion

Differences in leaf size between pruned and non-pruned branches are related to differences in foliage age: leaves from pruned branches are younger than those from non-pruned branches (experiment 3). Although pruning affects leaf size, it does not affect stomata density or guard cell length. Thus, stomatal assessment might be a more reliable method to assess baobab drought tolerance than baobab leaf size (at least in areas where the baobab tree is pruned or mutilated due to leaf harvesting).

The differences in stomatal characteristics in the *in situ* experiment in Benin (experiment 1) are consistent with climatic differences between the study sites. Comé, situated in the Guinean zone and Bassila (situated in a humid area even though it is in the Sudanian zone, Sokpon and Biaou 2002) had the lowest stomatal densities while the highest stomatal densities were found in the driest northern study sites. Larger guard cells were found in the southern study sites where the climate is much more humid. It should be noted that baobabs from Bassila, in spite of having small guard cells, had low stomatal density. Stomatal density has been reported to be much more plastic than guard cell sizes, thus, Bassila baobabs found in a much wetter area than other northern sites adapt by reducing their stomatal density.

The pattern of differences in stomatal characteristics in the *in situ* experiment in Malawi (experiment 4) was not as clear as in Benin. While Balaka and Mangochi (dry areas of Malawi) had the highest stomatal densities and the smallest guard cell length, the lowest stomatal densities were observed in Nchalo (which is actually the driest study site). Possibly, the observed low stomatal densities in this study site are related to low quality stomata imprints taken in this site (this was the first study site sampled in Malawi and I had a problem with the nail polish).

The relationship found between stomatal density and climatic characteristics observed in Benin is in accordance with the literature: the higher the temperature, the higher the stomata density, the lower the precipitation, the higher the stomatal density. For guard cell length, the higher the temperature, the smaller the stomata, the lower the precipitation, the smaller the stomata (also in accordance with the literature). In Malawi, the relationship was not so straight-forward. Apart from the afore mentioned low quality of some stomata imprints, the smaller climatic range sampled in this country (only one climatic zone of White 1983) might explain why the correlations between stomatal density and climatic characteristics were not significant for a number of variables.

Although the correlations indicate that environmental factors influence stomatal characteristics, the results of this study indicate a certain degree of heritability for stomatal characteristics. In the farm experiment (experiment 2), even though the trees had been planted in a wetter environment (the Guinean zone), trees from the north had high stomatal density and smaller guard cell length than those from southern study sites. Teklehaimanot et al. (1998) also found a similar trend of heritable characteristics for 4 month old seedlings of

Parkia biglobosa. However, the pattern of differences in leaf size was not as clear as the pattern for stomatal characteristics in the farm experiment (experiment 2). As the trees were grown in the Guinean zone, water availability was probably less of a limiting factor to survival, and trees from all seed collection sites could have larger leaves.

In the *in situ* experiment in Benin (experiment 1), there was a trend, with trees from the north having smaller leaves than those from the south. Foliage age due to pruning might account for the variation in leaf size, thickness and SLW. In Karimama, Comé and Sèhouè trees were not as heavily pruned as in other sites. In the south (Comé and Sèhouè), locals do not use baobab leaves as a food source as they do in the north (Dansi et al. 2008). In Karimama, where baobab density is high and baobab fruits are highly valued economically and exported to Niger (Assogbadjo et al. 2005b), trees are not pruned. Leaves from Karimama, Comé and Sèhouè apart from being bigger, were found to be always hairy, another characteristic of old foliage. Old leaves have more secondary compounds and tend to be thicker. However, leaves from Boukoumbé (in spite of being small and from pruned trees) were reported to have the highest SLW, which can be related to drought tolerance.

In the *in situ* experiment in Malawi (experiment 4), the trend was, again, not as clear as in Benin. While leaves from Balaka (dry site) were the smallest overall, and leaves from Chantulo and Mtonga (wetter sites) were the largest overall, leaves from Nchalo (the driest site) were neither the smallest nor the thickest (characteristics related to drought tolerance). Possibly, as the climatic range sampled in Malawi was not as wide as in Benin, the observed pattern of leaf variation was not obvious. This might also account for the low number of significant correlations between leaf size and climatic variables observed in Malawi.

Although the effect of pruning should be taken into account, in general, leaves from Malawi were found to be larger and thinner than those from Benin (even when leaves from Malawi were compared with those from the southern study sites of Benin known to not be pruned). Their shapes and their stomatal characteristics were also different. These observed differences in leaf morphology support the genetic differences found between these two baobab tree populations (Pock Tsy et al. 2009). To my knowledge, this is the first report on differences on baobab leaf morphology between baobab tree populations from West and south-eastern Africa.

Results from this chapter suggest that both genetics and the environment play a role in baobab leaf morphology. When seeds from northern Benin are grown in the south, their leaves are larger, but their stomata characteristics do not change (experiment 2). Moreover, baobab trees from Benin had different leaf characteristics to those from Malawi. Thus, when considering planting baobab trees better adapted to drought in Benin, planting material should be taken from the north, while in Malawi, it should be taken from Balaka or Mangochi. Apart from choosing local planting materials, one possibility would be to plant baobab trees from one country in another: e.g. to plant baobab trees from northern Benin in the driest areas of Malawi (or the other way around). Although it seems that the baobab trees from northern Benin have better leaf size characteristics for drought tolerance, baobab trees from Malawi show better stomatal characteristics (experiment 1 and 4). Before considering planting baobab trees from West Africa (e.g. Benin) in south-eastern Africa, further research is needed to confirm which baobab trees withstand drought better. One possibility could be to grow baobab seedlings from both countries in a controlled environment (such as a greenhouse, see chapter 6).

It should be noted that in this chapter baobab drought adaptation was considered as a desirable trait because of its implications for tree survival, as more droughts are predicted in the dry parts of the African savanna under climate change scenarios. However, in some parts of Africa or elsewhere, farmers might be interested in planting baobab trees which are more tolerant to heavy rains or flooding. Apart from tolerance to drought (or flooding), farmers might be interested in planting baobab trees known to produce large heavy fruits, or fruits known to have high nutritional properties. ‘Superior’ planting material in terms of fruit characteristics is discussed in the following chapter (chapter 5).

CHAPTER 5. Variation in baobab fruit morphology: opportunities for selecting better planting materials

Variation in baobab fruit morphology has been observed by local farmers in Africa (Sidibé and Williams 2002) and by several authors (Sidibé et al. 1996, Gebauer et al. 2002, Soloviev et al. 2004, Assogbadjo et al. 2005b). The fact that there is variation in fruit characteristics gives room for selecting trees with 'superior' characteristics; such as large tasty fruits and/or fruits with high vitamin pulp content. In this chapter I study the morphological variation in fruit characteristics observed in two physically isolated, genetically different baobab populations (Mali and Malawi) and I recommend superior materials for cultivation based on fruit characteristics such as high fruit pulp content. Baobab fruit data from Mali was collected by S. De Smedt and it was jointly analysed. This chapter has been accepted as a journal paper in *Genetic Resources and Crop Evolution*.

5.1 Introduction to fruit importance and fruit variability

One important factor for selecting 'superior' planting material is farmers' preferences. However, farmers from different ethnic groups use different parts of a tree for different purposes (Assogbadjo et al. 2008). For example, small scale farmers of north Benin who daily consume baobab leaf as a food ingredient (Dansi et al. 2008) may want a baobab that produces a high quantity of leaves with high nutritional value. However, farmers from Tanzania, who sell baobab seeds to the oil industry, might prefer a baobab which produces fruits containing big or oily seeds. Even when considering only one region, for example West Africa, local people prefer small fruits in Benin while locals prefer large fruits in Ghana, Senegal and Burkina Faso (Assogbadjo et al. 2008).

Baobab fruit pulp has been identified as the baobab tree part which carries the greatest variety of uses (Buchmann et al. 2010). It has also been identified as the tree part with the highest commercialisation value (Akinnifesi et al. 2007). As mentioned in chapter 1, there is a growing international interest for baobab products (and especially for baobab fruit pulp) in food, pharmaceutical and cosmetics industries. After approval, baobab fruit pulp can be used in the EU and the US as a food ingredient. This may lead to farmers being interested in planting a type of baobab tree that produces a large number of large fruits with high fruit pulp content. Thus, potential 'desired' planting material would depend upon fruit characteristics.

Baobab fruit is already the major baobab tree product produced in some countries. For example, in Senegal, there has been an increase in the production of this product in the last few years (even before the EU and US acceptance of baobab fruit pulp as a food ingredient) (Fig 5.1). Diop et al. (2006) reported that the real increase is much larger as this figure uses only data for the legal exploitation of NTFPs and self consumption, and the import of baobab fruits from Mali, Guinea and Guinea-Bissau would increase the production volumes.

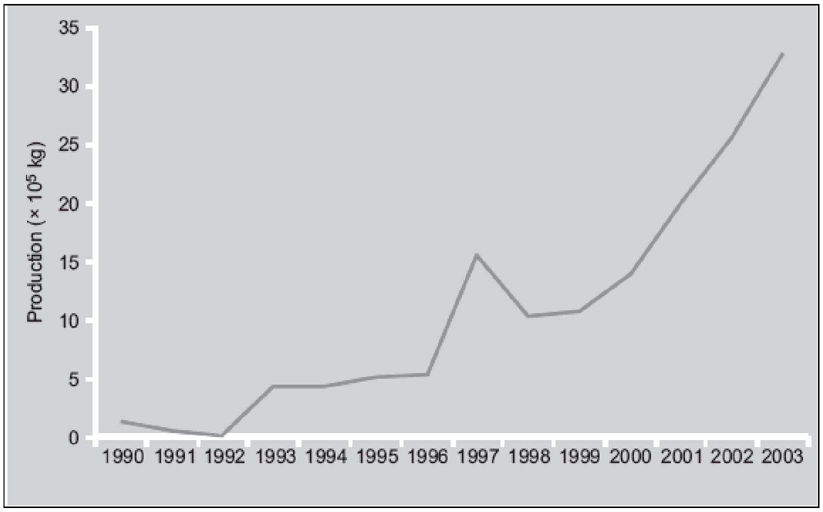


Fig 5.1. Production of baobab fruits in Senegal from 1990 to 2003. Extracted from Diop et al. (2006).

Variation in baobab fruit characteristics has been noted by several authors. Sidibé and Williams (2002) reported that both fruit shape and size are very variable (fruit shape: from globose to ovoid but sometimes oblong-cylindrical or irregular; fruit size: from 7.5 x 7.5 to 20 x 54 cm). The composition of the baobab fruit has also been reported to be variable in different countries and even within one country (Table 5.1).

Part of the fruit	Nigeria (1) (%)	Southern Africa (2) (%)	Tambacumba, Senegal (3) (%)	Sudanian zone, Benin (4)	Sudano-guinean zone, Benin (4)	Guinean zone, Benin (4)
Capsule	43	45.5	48	204g	273g	275g
Seeds and fibre	36	38	40	-	-	-
Seeds (only)	-	-	-	23g	28g	37g
Pulp	21	16	12	32g	51g	54g

Table 5.1. Composition of baobab fruits, expressed in percentage of total fruit weight (1,2,3), or weight (4). Sources:1- Gruenwald and Galizia 2005, 2-Phytotrade Africa (Wickens and Lowe 2008), 3-Baobab Fruit Company (Wickens and Lowe 2008), 4- Assogbadjo et al. 2005b.

Farmers have also noted variation in fruit characteristics. In fact, in some countries, farmers distinguish baobab trees depending on their fruit characteristics (among other variables). In Benin, baobab trees are mainly distinguished by their fruit shape (Codija et al. 2001) while in Mali farmers take into account pulp taste among other characteristics (Sidibé and Williams 2002). In Sudan it is widely known that ecotypes from different areas have different fruits in terms of size, shape and sweetness (Gebauer et al. 2002).

Variation in fruit morphology has been related to the environment. Soloviev (2004) found that there were significant differences in fruit length, diameter, fruit weight, pulp weight and pulp chemical characteristics in different climatic zones of Senegal. He also found that the differences were higher in the baobab tree than in other species commonly found in the same environment (*Balanites aegyptiaca* and *Tamarindus indica).* Assogbadjo et al. (2005b) reported that fruit morphology and productivity varied significantly from one climatic zone to another in Benin. He reported that zones with high values of potential evaporation, rainfall, relative humidity, temperature, pH of water and percentage of fine silt were associated with a low seed and fruit pulp production.

Variability in fruit morphology has also been related to genetic variability. Assogbadjo et al. (2006) used the AFLP technique to study genetic variation within and between baobab populations in Benin and related the observed patterns of genetic diversity to the observed patterns of thickness of the capsules within and between baobab populations in the country.

Although baobab fruit morphological variation has been studied in West Africa, no studies have been focused in south-eastern Africa, the source of most of the baobab fruit pulp sold in Europe (Phytotrade Africa 2009, pers. comm.). In order to help determine potential sources of desired planting materials and contribute to a greater cultivation of the species and thus, a more sustainable use of the existing trees, variation in fruit morphological characteristics was studied in Malawi (south-eastern Africa) and Mali (West Africa).

5.2 Aims and Objectives

The aim of this study is to contribute to the understanding of the variation in fruit characteristics of the baobab tree, which could help identify better planting materials.

The specific objectives are:

1. Investigate the variation in fruit characteristics
2. Explore the relation between variation in fruit characteristics and differences in the environment
3. Determine if trees with 'superior' fruit characteristics can be selected

The specific research questions are:

1. Is the variation in fruit characteristics similar in Mali and Malawi?
2. Is the relationship between fruit variation and the environment similar in both countries?
3. Can trees with 'superior' fruit characteristics be selected?

In order to answer these research questions, *in situ* fruit morphological variation was assessed in Mali and Malawi.

5.3 Methodology

Study sites

Two countries were selected, one in West Africa and one in south-eastern Africa, following the genetic differences between baobab populations between these two areas suggested by Pock Tsy et al. (2009). In West Africa the selected country was Mali. Due to financial and time constrains, Benin (the West African country selected in chapter 4) could not be sampled for fruit characteristics. In south-eastern Africa the selected country was Malawi (like in chapter 4).

Mali has a subtropical to arid climate, with climatic differences related to latitude. Annual rainfall and the length of the rainy season decrease from south to north. Southern and western Mali have a Sudanese climate, while northern Mali experiences Sahelian and Saharan climates (with virtual absence of rain and an extremely dry atmosphere in the latter). There are three main seasons in Mali: a hot-dry season (February-June), a rainy-humid season (June-November) and a cool-dry season (November-February). Actual year-to-year rainfall, especially in the north, is extremely erratic. Malawi climate is discussed in chapter 4.

In each country, eight study sites were selected following a latitudinal and climatic gradient with the main criterion being the existence of a well-established baobab tree population (Table 5.2, Fig. 5.2).

	Study site	**Latitude (°)**	**Longitude (°)**	**Annual rainfall (mm)**	**Months with < 50mm rainfall**	**Mean annual temp. (°C)**	**Months with Min. temp. < 20 ºC**	**Soil type**
Mali (West Africa)	Tatakarat	15.05 N	0.90 W	336	9	29.7	4	Arenosols
	Bandjougoula	15.27 N	10.53 W	453	9	28.8	4	Lixisols
	Bendjiely	14.48 N	3.59 W	509	8	26.4	5	Arenosols
	Wataga	14.10 N	9.10 W	703	8	27.7	4	Lixisols
	Massadji	14.07 N	11.69 W	763	7	28.5	4	Regosols
	Kerela	12.75 N	6.84 W	823	7	27.3	4	Lixisols
	Banko	11.10 N	7.10 W	1097	6	27.0	4	Lixisols
	Katon	10.91 N	5.91 W	1145	6	27.0	4	Nitisols
Malawi (East Africa)	Nchalo	16.33 S	34.86 E	794	7	26.2	5	Fluvisols
	Kalasamba	15.38 S	34.79 E	940	7	24.3	6	Lixisols
	Balaka	15.13 S	35.02 E	981	7	23.5	6	Fluvisols
	Mangochi	14.42 S	35.21 E	843	7	24.5	6	Fluvisols
	Chantulo	14.32 S	34.78 E	886	8	24.5	6	Fluvisols
	Chipoka	14.00 S	34.50 E	1012	8	24.5	6	Fluvisols
	Mtonga	13.76 S	34.33 E	1017	7	23.9	6	Fluvisols
	Likoma	12.06 S	34.73 E	1244	6	25.2	4	-

Table 5.2. Location, climate and soil data of the selected study sites in Mali and Malawi. Climatic data was obtained from the Worldclim database (Hijmans et al. 2004) Soil data was obtained from the Harmonized World Soil Database (FAO et al. 2008).
- no information available

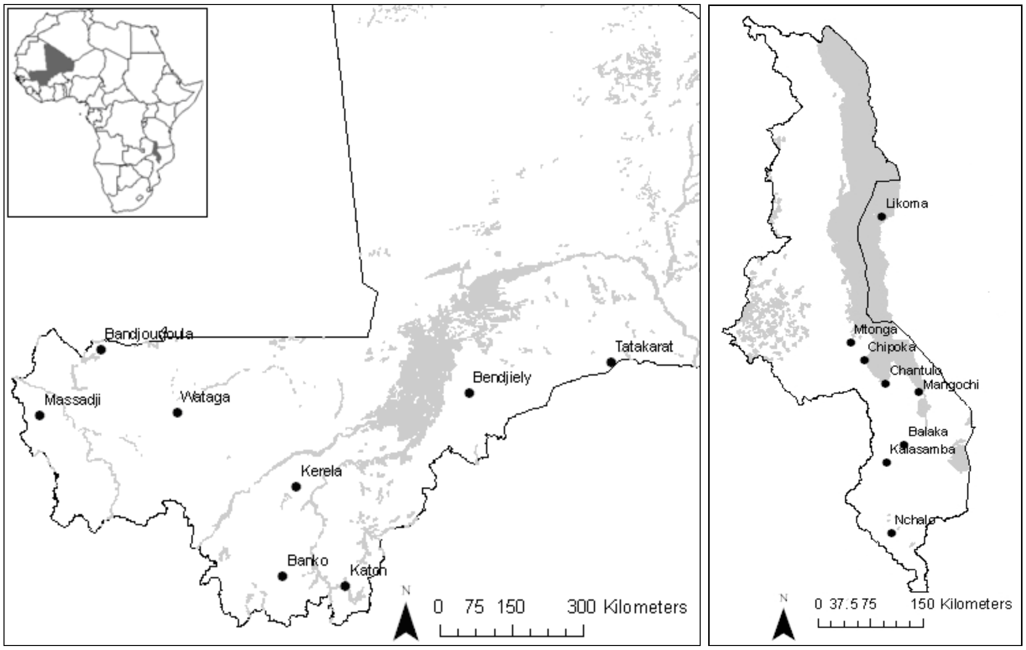


Fig. 5.2. Selected study sites in Mali (left) and Malawi (right).
Grey colour refers to main water bodies. Likoma is a Malawian island in Mozambican waters.

Fruit morphological assessment

Five ripe fruits were taken from ten trees randomly selected in each study site. In order to obtain representative fruits, farmers were asked about average fruit sizes, and fruit sizes were compared with those observed in the local market during the baobab fruiting season. In some sites in Malawi, as some trees did not have five fruits, more fruits were collected from one tree than others in order to have a total number of 50 fruits per site. Fruit length and circumference at the widest part were measured with a measuring tape and fruit diameter was calculated from the latter. Fruit shape ratio was calculated by dividing fruit length by fruit diameter. Fruits were weighed to the nearest 0.5 g with an electronic scale. Fruit shells were cracked and fruit content (pulp + seeds) was removed and weighed. Epicarp thickness was measured with an electronic calliper. Pulp was separated from seeds by washing with water, and seeds were subsequently air dried and weighed again. Pulp content was calculated by subtraction. Pulp percentage was calculated by dividing calculated pulp weight by total fruit weight and multiplying by 100. Seeds were counted and single seed weight was calculated by dividing seeds weight by number of seeds. Due to time constraints, epicarp thickness could not be measured in Mali.

All reported weights are fresh weights, as baobab fruit pulp is consumed without drying (De Caluwé et al. 2009). It should be noted that water content of baobab fruit pulp is low; Arnold et al. (1985) reported an average moisture content of 8.7%.

Environmental data

Climatic data were acquired from the WorldClim database (Hijmans et al. 2004, 2005). Four variables derived from monthly climatic data were selected (annual precipitation, mean annual temperature, temperature seasonality or temperature standard deviation and minimum temperature of the coldest month). Number of dry months (defined as the number of months with less than 50 mm rainfall) and number of cold months (defined as number of months with a mean minimum temperature lower than 20 °C, following suggested baobab ecological preferences by Sidibé and Williams 2002) were calculated using mean monthly precipitation data and monthly minimum temperatures, respectively, given by the WorldClim database. Soil data was obtained from the Harmonized World Soil Database (HWSD) (FAO et al. 2008). The HWSD soil groupings found in the selected study sites are: arenosols (sandy soils featuring very weak or no soil development), lixisols (soils with subsurface accumulation of low activity clays and high base saturation), regosols (soils with very limited soil development), nitisols (deep clayey soils having a pronounced shiny, nut-shaped structure) and fluvisols (young soils in alluvial deposits) (Table 6.1). No HWSD soil type information was available from Likoma. Similar variables have been used to study the effect of the environment on fruit morphology of the shea tree (*Vitellaria paradoxa*), another parkland fruit tree species (Ugese et al. 2010).

Statistical analyses

Due to lack of normality of some variables, Kruskal-Wallis tests were used to determine significant differences between study sites while post-hoc pair wise multiple comparisons were performed using Mann-Whitney tests in SPSS for Windows v 16.0. Correlations were tested using Spearman Rank Order Coefficient.

5.4 Results

Variation in fruit morphology

There were significant differences ($p<0.01$, Mann-Whitney tests) between countries in fruit length, fruit shape (length/width ratio) and single seed weight (Table 5.3). Fruits from Mali were longer and their shapes were more elongated (higher fruit shape) than those from Malawi, and their seeds were smaller (lower weight of one seed). Some shapes observed in Malawi were not reported from Mali (Fig. 5.3). These include fruit with spherical shapes and round apex (see bottom right fruits in Fig. 5.3).

Country	**Fruit weight (g)**	**Fruit length (cm)**	**Fruit diameter (cm)**	**Fruit shape**	**Pulp percentage**	**Seed number**	**Single seed weight (g)**
Mali	232.0 ± 215.0 a	18.8 ± 8.5 a	8.4 ± 3.3 a	2.3 ± 1.3 a	21.1 ± 10.8 a	180 ± 200 a	0.43 ± 0.2 a
Malawi	201.0 ± 152.0 a	15.6 ± 6.0 b	8.6 ± 2.4 a	1.9 ± 0.9 b	19.4 ± 7.6 a	139 ± 141 a	0.54 ± 0.1 b

Table 5.3. Fruit characteristics of Adansonia digitata *from Mali and Malawi. Means ± standard deviation (n = 400). Means followed by the same letter within a column are not significantly different from each other at p<0.01 (Mann-Whitney tests).*

Fig. 5.3. Diversity in baobab fruit size and shape in Malawi (left) and Mali (right). Source: A. Cuni Sanchez and S. De Smedt.

Significant differences in fruit morphology between study sites in each country were also observed (Table 5.4). For most fruit characteristics studied, variation within study sites in Malawi was found to be lower than in Mali (lower standard deviations, Table 5.4). In Malawi, fruits from Nchalo and Balaka were the smallest overall (short in length and light) while fruits from Chipoka were the largest overall (long and heavy) (Table 5.4). Fruits from Nchalo had a different shape (significantly low fruit ratio, Table 5.4). The percentage of pulp was found to be significantly high in Likoma and significantly low in Kalasamba (Table 5.4). Significant differences were also observed in epicarp thickness, with fruits from Nchalo having thinnest epicarps and fruits from Mangochi having thickest ones (Table 5.4).

In Mali, fruits from Massadji were found to be the lightest and those from Katon were the heaviest (Table 5.4). Fruits from Bandjougoula were the shortest and those from Bendjiely the longest (Table 5.4). Fruits from Banko were long and thin (significantly high fruit ratio) while those from Bandjougoula were short and wide. The highest pulp percentage was observed in the southern study sites while the smallest seeds were observed in the northern study sites in Mali.

	Site	Fruit weight (g)				Fruit length (cm)				Fruit diameter (cm)				Fruit shape (length/diameter)			
Mali	**Tatakarat**	231.5	±	94	cefg	18.9	±	5.3	bcd	8.6	±	1.3	ce	2.2	±	0.6	cdefg
	Bandjougoula	221.0	±	85	cef	15.7	±	3.1	b	8.7	±	1.2	ef	1.8	±	0.4	bc
	Bendjiely	276.5	±	139	efg	22.2	±	5.3	d	8.7	±	1.4	ce	2.6	±	0.6	g
	Wataga	198.5	±	84.5	bce	16.5	±	4.7	b	8.0	±	1.5	bcde	2.1	±	0.8	bcdef
	Massadji	177.5	±	84	bc	17.5	±	5.0	bc	7.5	±	1.1	ab	2.4	±	0.8	efg
	Kerela	192.5	±	107	bce	19.6	±	4.3	cd	7.6	±	1.4	bc	2.6	±	0.5	g
	Banko	241.0	±	141	bcefg	20.5	±	6.2	bcd	8.0	±	2.0	abcde	2.8	±	1.3	efg
	Katon	320.5	±	159	fg	19.4	±	4.7	cd	10.0	±	1.9	fgh	2.0	±	0.5	bcde
Malawi	**Nchalo**	213.5	±	57.5	de	12.9	±	1.6	a	10.0	±	1.1	gh	1.3	±	0.2	a
	Kalasamba	174.5	±	44.5	bcd	15.8	±	2.3	b	8.3	±	1.1	cde	2.0	±	0.4	bcde
	Balaka	101.0	±	14	a	13.1	±	0.8	a	6.8	±	0.3	a	1.9	±	0.1	ce
	Mangochi	227.0	±	73.5	def	15.8	±	2.7	b	9.0	±	1.4	efg	1.8	±	0.5	bcd
	Chantulo	195.0	±	43.5	ce	16.6	±	3.1	bc	8.6	±	1.0	e	2.0	±	0.5	bcde
	Chipoka	322.0	±	121	g	17.6	±	2.0	bc	10.6	±	1.8	h	1.7	±	0.4	b
	Mtonga	156.0	±	26	b	15.9	±	2.4	b	7.7	±	0.8	bd	2.1	±	0.4	cdef
	Likoma	217.5	±	52.5	e	16.7	±	1.9	bc	8.1	±	0.7	bcde	2.1	±	0.2	df

Table 5.4. Part A. Fruit characteristics of Adansonia digitata *from the eight study sites per country (Mali and Malawi). Means ± standard deviations. (n = 50). Means followed by the same letter within a column are not significantly different from each other at p<0.01 (Mann-Whitney tests).*
- no information available.

	Site	Pulp percentage	Number of seeds	Single seed weight (g)	Epicarp thickness (mm)
Mali	**Tatakarat**	20.3 ± 3.8 bc	241 ± 121 fg	0.4 ± 0.07 a	-
	Bandjougoula	18.1 ± 2.6 b	193 ± 112 defg	0.4 ± 0.08 abc	-
	Bendjiely	20.1 ± 3.2 bc	204 ± 106 efg	0.4 ± 0.06 ab	-
	Wataga	20.0 ± 4.0 bc	164 ± 106 bcdef	0.4 ± 0.08 bc	-
	Massadji	20.4 ± 4.0 bc	143 ± 89 bcde	0.4 ± 0.09 ab	-
	Kerela	20.7 ± 3.5 c	121 ± 79 bcd	0.5 ± 0.09 cde	-
	Banko	24.4 ± 5.3 d	171 ± 136 bcdef	0.5 ± 0.08 bcd	-
	Katon	24.7 ± 4.1 d	200 ± 142 cdefg	0.5 ± 0.05 bc	-
Malawi	**Nchalo**	20.1 ± 3.3 bc	165 ± 48 def	0.5 ± 0.07 defg	4.13 ± 0.46 a
	Kalasamba	15.2 ± 4.2 a	134 ± 42 bcd	0.5 ± 0.07 ef	4.78 ± 0.74 bc
	Balaka	13.7 ± 2.0 a	42 ± 8 a	0.6 ± 0.04 g	5.13 ± 0.35 bc
	Mangochi	18.7 ± 5.0 bc	162 ± 78 cdef	0.5 ± 0.10 efg	5.25 ± 0.97 bc
	Chantulo	18.9 ± 6.3 bc	139 ± 42 bcde	0.5 ± 0.10 ef	4.89 ± 0.88 bc
	Chipoka	20.7 ± 3.7 c	249 ± 72 g	0.5 ± 0.12 def	4.64 ± 0.56 bc
	Mtonga	19.5 ± 6.1 bc	109 ± 47 b	0.5 ± 0.09 fg	4.64 ± 0.89 abc
	Likoma	28.0 ± 3.9 e	113 ± 33 bc	0.6 ± 0.04 g	4.69 ± 0.43 c

Table 5.4. Part B. Fruit characteristics of Adansonia digitata *from the eight study sites per country (Mali and Malawi). Means ± standard deviations. (n = 50). Means followed by the same letter within a column are not significantly different from each other at p<0.01 (Mann-Whitney tests).*
- no information available.

Correlations between fruit characteristics

Significant correlations between pulp weight and percentage and other fruit characteristics were found (Table 5.5). For both countries, correlations between pulp weight and other fruit characteristics, except for fruit shape, were found to be similar. Pulp weight was positively correlated with total fruit weight, fruit dimensions (length and diameter) and number of seeds. In Malawi more elongated fruits (low fruit shape) were found to have a higher pulp weight. However, significant correlations between pulp percentage and other fruit characteristics were only found in Malawi. In this latter country, pulp percentage was positively correlated with fruit weight, fruit dimensions and number of seeds. Also in Malawi, epicarp thickness was found to be negatively correlated with both pulp weight and pulp percentage.

	Pulp weight		**Pulp percentage**	
	Mali	**Malawi**	**Mali**	**Malawi**
Fruit weight	0.93*	0.86*	0.08	0.38*
Fruit length	0.60*	0.45*	0.10	0.25*
Fruit diameter	0.75*	0.67*	0.09	0.28*
Fruit shape	0.05	-0.16*	0.05	0.00
Number of seeds	0.71*	0.65*	-0.09	0.21*
Single seed weight	0.13*	0.03	0.08	-0.04
Epicarp thickness	-	-0.20*	-	-0.30*

Table 5.5. Coefficients of correlation between pulp weight and percentage, and other fruit characteristics.
** indicate significant correlations at p<0.01 (Spearman's rank order correlation coefficients).*
- no information available.

Correlations between fruit morphology and the environment

Significant correlations between fruit characteristics and environmental variables were observed both in Malawi and Mali (Table 5.6). In some cases, significant correlations had the same direction and were similar in value (e.g., single seed weight and mean annual temperature) in both countries. Some correlations, however, were only found significant in one of the two countries (e.g., number of seeds and mean annual temperature) or were positive in one country and negative in the other (e.g., fruit weight and mean annual temperature).

In general, pulp percentage was found to be positively correlated with mean annual rainfall while it was found to be negatively correlated with number of dry months (months with <50 mm rainfall) (Table 5.6). Fruit length was found to be positively correlated with mean annual rainfall while fruit shape was found to be negatively correlated with number of dry months (more round fruits at locations with more dry months) (Table 5.6). Single seed weight was found to be negatively correlated with number of dry months (Table 5.6).

Fruit characteristics were also found to be correlated with temperature variables. Fruits tended to be more round, contain low percentage of pulp and have light seeds in locations with high mean annual temperature (Table 5.6). Fruit shape and weight of one seed were also found to be negatively correlated with minimum temperature of the coldest month and temperature seasonality (Table 5.6).

A number of correlations between fruit morphology and the environment were only observed in one of the two countries (Table 5.6). In Malawi, heavy fruits with high number of seeds were found in dry and hot locations (lower mean annual rainfall and a higher number of dry months, four mentioned temperature variables) while longer fruits with high length/width ratio were found in wet locations. In Malawi, pulp percentage was found to be negatively correlated with number of cold months. In Mali, the wetter the environment, the lower the number of seeds produced and the higher the single seed weight. Also in Mali, the hotter the environment, the shorter the fruit length.

Soil type was also found to have an influence on pulp percentage ($p<0.01$, Kruskal-Wallis test). Fruits from baobab trees growing on nitisols were found to have significantly higher pulp percentage compared to baobab trees on other soil types ($p<0.01$, Mann-Whitney tests, table not included).

	Mean annual precipitation		**Months with < 50 mm rainfall**		**Mean annual temperature**		**Months with min. temp. < 20°C**		**Temperature seasonality**		**Min. temp of the coldest month**	
	Mali	**Malawi**	**Mali**	**Malawi**	**Mali**	**Malawi**	**Mali**	**Malawi**	**Mali**	**Malawi**	**Mali**	**Malawi**
Fruit weight		-0.21		0.24	**-0.17**	**0.49**	-0.15	-0.21		-0.27		0.63
Fruit length	0.13	0.26	-0.17		-0.30		-0.25			-0.49	**-0.18**	**0.32**
Fruit shape		0.38	-0.13	-0.25	-0.21	-0.40	**0.20**	**-0.25**		-0.23	-0.17	-0.25
Pulp percentage	0.39	0.31	-0.42	-0.20	-0.28	-0.15		-0.50	-0.34	-0.15		
Number of seeds	-0.20		0.19	0.38		0.53		-0.16	-0.20	-0.24		0.63
Single seed weight	0.31		-0.27	-0.26	-0.22	-0.26			-0.30		-0.18	-0.23
Epicarp thickness	-	0.38	-		-	-0.32	-		-		-	-0.23

Table 5.6. Coefficients of correlation between fruit characteristics and environmental variables. Only correlations with a p-value < 0.01 are given. Empty cells indicate no significant correlation at p<0.01 (Spearman's rank order correlation coefficients). Correlations given in bold indicate opposite trends in both countries.
- no information available.

5.5 Discussion

Fruit size was found to be within the range reported by Sidibé and Williams (2002) for the whole African continent (7.5-54 cm length, 7.5-20 cm wide). When compared with other countries, fruits from Mali were found to be within the range reported by Soloviev et al. (2004) in Senegal (16.8-26 cm length, 167-348 g weight) and Assogbadjo et al. (2005a) in Benin (16.8-20.7 cm length, 203-275 g weight). In general, fruits from Malawi were found to be smaller than those from Mali, Senegal and Benin (in terms of fruit length and weight). Fruit variation within Malawi was found to be lower than in Mali or Benin (Assogbadjo et al. 2005a).

Correlations between pulp and fruit weight in Mali and Malawi were similar to those observed in Benin by Assogbadjo et al. (2005a): the heavier the fruit, the higher the pulp weight. A stronger positive correlation between fruit diameter and pulp weight (compared to fruit length) was also observed in Benin (Assogbadjo et al. 2005a). It is apparent that when selecting for heavy fruits, more attention should be given to fruit diameter than to fruit length. The fact that Malawi showed a larger variability in fruit shape (e.g., the existence of more rounded fruits) compared with Mali might explain why this correlation was found to be significant only in the former country. The higher pulp percentage of elongated fruits suggests that fruit shape could be a verifiable tool in selecting for trees with high pulp weight under field conditions in Malawi, since it is an easily measurable trait.

Observed correlations between fruit characteristics and environmental variables in Mali and Malawi suggest an important role of the environment in the phenotypic expression of fruit characteristics. The trend in both countries was that, the hotter and drier the environment, the less elongated the fruits, the lower the pulp percentage, the greater the number of seeds and lighter the seeds. Similar results were reported from Senegal (Soloviev et al. 2004) and Benin (Assogbadjo et al. 2005a), where fruits from the southern sites (wetter and cooler areas) were larger and had more pulp than fruits from the northern sites. Differences in fruit morphology and their relation to the environment have also been reported for other parkland fruit tree species. Kouyate and Van Damme (2002) showed for *Detarium microcarpum* Guill. & Perr.; Lovett and Haq (2000), Maranz and Wiesman (2003) and Ugese et al. (2010) for *Vitellaria paradoxa*; and Soloviev et al. (2004) for *Balanites aegyptiaca* and *Tamarindus indica.* For example, Maranz and Wiesman (2003) who studied the shea tree (*V. paradoxa*) in Mali and Burkina Faso, reported larger fruits in the Guinean zone (southern part) which they linked to higher rainfall regimes while the smaller Sahelian fruits were related to higher temperatures.

The observed differences in baobab fruit pulp percentage between wetter and drier areas agree with a recent study on the shea tree by Ugese et al. (2010). These authors reported a negative correlation between duration of the dry period and pulp content. Maranz and Wiesman (2003) suggested for the shea tree that the lower pulp concentration in the drier areas is due to a higher investment in fat formation in the seed, the latter being critical to seedling survival during the long dry period. It is possible that the same phenomenon explains the observed differences in baobab fruit pulp percentage between wetter and drier areas.

The fact that number of cold months (months with minimum temperature < 20 °C) was found to be significantly correlated with pulp percentage in Malawi and not in Mali might result from the larger range in number of cold months between study sites in the former country compared to the latter one.

In this study, it was found that fruits from baobabs growing on nitisols had a significantly higher pulp percentage. Nitisols are generally considered to be 'fertile' soils, and are, therefore, commonly used for farming, in spite of their low level of available phosphorus and their normally low base status (FAO 2001). However, only one study site (Katon, Mali) was found on this type of soil and most baobabs were found on fluvisols or lixisols. It is possible that as Katon was the wettest site studied in Mali, instead of soil type, climate or an interaction of both soil and climate influenced pulp percentage (as discussed above). Nevertheless, the effect of soil type on fruit characteristics has been observed for other fruit tree species, such as the shea tree (CIRAD 2004, in Ugese et al. 2010).

Apart from the role of the environment, significant differences between Mali and Malawi suggest that genetics also play an important role in the phenotypic expression of fruit characters. In general, fruits from Mali were longer and less rounded, and their seeds were smaller than those from Malawi. Some shapes observed in Malawi were not observed in Mali and were not reported from Benin (Assogbadjo et al. 2005a) or Sudan (J. Gebauer 2009, pers. comm.). Malagasy baobab species are mainly distinguished from one another by fruit size and shape (Wickens and Lowe 2008). Therefore, fruit shape could possibly be used to differentiate between trees from East and West Africa baobab populations. However, further research on baobab fruit shapes, especially in south-eastern Africa, is needed before this hypothesis can be confirmed, as some fruit shapes can not unambiguously distinguish south-eastern from West African baobab populations.

The genetic differences might also explain the rather unexpected result that in Mali the heaviest fruits were observed in the wettest parts (1100 mm annual rainfall) while this was not the case for Malawi (heaviest fruits in sites with 800 mm). It is possible that due to genetic differences, baobab trees from Mali and Malawi have different optimum rainfall for producing large fruits.

Results from this study suggest that both genetics and the environment play a role in baobab fruit morphology. Thus, when considering e.g. how to obtain heavy baobab fruits with a high percentage of pulp, it seems that it would be better to plant baobab trees in the wetter cooler part of the African savanna (at least in West Africa). However, considering the large variation in fruit morphology within a country, it is also important to select trees from sites known for desirable fruits. For example, if the favoured trait is high pulp percentage, Likoma site in Malawi (an island in Lake Malawi isolated from mainland for a long time) might have an interesting genetic pool for baobab tree domestication. However, further research is needed to confirm if baobab trees producing fruits with desirable traits (e.g., baobab trees from Likoma producing fruits with high pulp percentage) continue to produce a similar type of fruits when grown in another environment (e.g., another site in Malawi, or, in West Africa). One possibility could be to study the fruit characteristics of baobab trees from different provenances grown in one study site (common garden). However, the long maturation process before first fruiting (Sidibé and Williams 2002) complicates this type of study.

Apart from planting baobab trees which are known to have desirable fruit characteristics, another possible option is to use grafting to combine baobab trees from different provenances having diverse desirable characteristics. In Mali, the African baobab (*A. digitata*), adapted to local climatic conditions, has been successfully grafted with other species of baobab from Madagascar having a higher leaf nutritional value (Maranz et al. 2007). *A. digitata* from different provenances (different sites within a country or different countries) having different desirable characteristics could be grafted. In Malawi, for example, baobab trees from Likoma which have the highest pulp percentage could be grafted with baobab trees from Mangochi which have leaves with the best drought adaptation characteristics (see chapter 4): Mangochi baobab trees could be used as rootstock and Likoma baobab trees as scion in future ‘plus-tree’ grafting trials.

It should be noted that in this chapter high pulp content in the capsule was considered as a desirable trait because it carries the greatest variety of uses and because of its high commercialisation value. However, depending on the user, i.e. local community or the international market, the desired traits might vary. For example, Ditamari people from Benin prefer low fruit pulp content while Mossi ethnic group (Burkina Faso) mention this trait as undesirable (Assogbadjo et al. 2008). Thus, what has been considered as better planting material in this study might not be so for all local farmers. In order to make the domestication process more effective, local farmers' preferences should be taken into account before making a confirmed recommendation in a specific area.

Besides high fruit pulp content, another criterion that might be considered in the domestication process is the simplicity of breaking the baobab capsule. In Malawi, farmers prefer medium sized capsules which are easy to break and do not have too much fibre (making pulp and seed extraction easier and quicker) instead of large heavy fruits (H.M. Phiri 2009, pers. comm.). Some baobab capsules are very hard to break, and once broken, they do not split in two halves but become a mass of shell pieces attached to one another due to the high number of fibres inside the fruits. Separating the shell from the pulp and seeds of these fruits is complicated and more time consuming than opening the capsule. Baobab fruits are commonly broken and their content extracted manually, even in big commercial companies (pers. obs.). If this continues to be the case, thin epicarps and low fibre content might be of key importance in the selection of high quality planting materials. In this study, epicarp thickness was found to be negatively correlated with pulp percentage in Malawi, thus, it seems possible to select baobab trees with thin epicarps and high pulp percentage. However, considering that some local people in West Africa link hard capsule (thick epicarp) with good pulp taste (Assogbadjo et al. 2008), before deciding on desirable epicarp thickness, further research is needed to determine whether epicarp thickness has an impact on the chemical and nutritional characteristics of baobab fruit pulp, i.e. vitamin C content, which is significantly high in baobab fruits.

CHAPTER 6. Variation in baobab seedling growth and the effects of short-term drought stress

Seedling stage is a critical one for many tree species. As mentioned in the literature review (chapter 1), mature baobab trees are resistant to drought and fire (two of the major hazards in the savanna), and their leaves are often out of reach for many grazing animals, but baobab seedlings are sensitive to these three factors. It seems that farmers would be interested in planting baobab trees which grow fast and have specific seedling morphological characteristics that make them more resistant to drought. In this chapter I study the variation in growth and morphology of seedlings from different provenances (Mali and Malawi) and I analyse the effect of a 4-week drought stress on baobab seedlings from these provenances. Seedlings were grown and harvested jointly with S. De Smedt.

6.1 Introduction to seedling growth, morphology and drought tolerance

A recent study on baobab seedling growth carried out in Benin by Assogbadjo et al. (2010) showed that there were significant differences in seedling weight and diameter between provenances, with seedlings from the Sudanian zone (wetter environment) having the highest weight and diameter. Variation in seedling morphology has also been reported for other parkland tree species such as *Parkia biglobosa* (Teklehaimanot et al. 1998), *Vitellaria paradoxa* (Bayala et al. 2009) and *Ziziphus mauritiana* (Kulkarni et al. 2010). In the latter study, short-term drought stress was imposed on the seedlings and their response analysed. Although there are studies on tolerance to salinity of baobab seedlings (Gebauer and Ebert 2005), there are no published reports on tolerance to drought stress of baobab seedlings.

Poorter and Markesteijn (2008) studied seedlings of 36 tropical tree species and found that drought avoidance through leaf abscission was the most important strategy for seedlings' drought survival, followed by the presence of a thickened taproot.

Deciduousness is more commonly found in the adult stage of a tree than in the seedling stage (Hall and Swaine 1981), probably because seedlings do not possess sufficient carbohydrate reserves to replace their leaves often (Poorter and Markesteijn 2008). Although the baobab tree is a deciduous tree, there is no information available on leaf deciduousness at seedling stage as a mechanism to avoid drought.

The ability of baobab seedlings to withstand drought conditions has been attributed to their taproots which accumulate water (Alexander 1992). However, little is known about this mechanism. Baobab seedlings from drier environments might have larger taproots which help them to withstand drought better.

Root elongation during drought or production of thinner roots which might penetrate deeper in the soil might help plants to get to deeper water levels, thus avoiding water deficits near the soil surface (Turner 1986). Osonubi et al. (1992) determined that *Faidherbia albida* tolerated drought stress by producing long taproots whereas *Acacia nilotica* (L.) Willd. ex Delile tolerated drought stress by developing larger rooting systems that were able to explore greater volume of soil. Pace et al. (1999) found that the length of the taproot of drought-treated young cotton (*Gossypium hirsutum* L.) plants was greater than the control plants in a 13-day drought stress experiment.

Under drought conditions, plants might also allow the preferential partitioning of photosynthate to roots at the expense of shoots. For *Parkia biglobosa*, Osonubi and Fasehun (1987) found that seedlings under drought treatment reduced both average leaf size and total leaf area, but increased the rate of root extension. Drought stress might also induce formation of leaves with altered leaf anatomy. For example, it has been reported that *Jatropha curcas* L. seedlings under drought stress produce leaves with higher adaxial stomatal density, after which leaves are only gradually shed (Maes et al. 2009). *J. curcas* seedlings produce new leaves using the water stored in the stem (Maes et al. 2009). It is possible that baobab seedlings use a similar mechanism: they might produce leaves with altered leaf anatomy using water stored in either the stem or the taproot.

In order to determine potential sources of desired planting materials and to complement the studied variation in leaf and fruit characteristics (chapter 4 and 5), baobab seedling growth, morphology and short-term drought stress response was studied in a tropical greenhouse in Antwerp, Belgium.

6.2 Aims and Objectives

The aim of this chapter is to contribute towards the understanding of the variation in growth, morphology and drought response of baobab seedlings from different provenances, which could help identify better planting material.

The specific objectives are:

1. Investigate the variation in seedling growth and morphology
2. Determine the effect of short-term drought stress on baobab seedlings
3. Determine if seedlings with 'superior' characteristics can be selected

The specific research questions are:

1. Is the variation in seedling growth and morphology similar in Mali and Malawi?
2. Do baobab seedlings from different provenances respond similarly to short-term drought-stress?
3. Can seedlings with 'superior' characteristics be selected?

In order to answer these research questions, two experiments were carried out.

6.3 Methodology

Plant materials and environmental conditions

Two countries were selected, Mali in West Africa and Malawi in south-eastern Africa, as in chapter 5. Seeds from ten study sites (five in Malawi and five in Mali, Table 6.1) were soaked in 95% sulphuric acid for 4 hours, washed with water and then germinated in Petri dishes covered with river sand in a growth unit (20 ºC at night for 12 h and 30 ºC during the day). The germination medium was kept humid at all times. Once they had germinated, they were planted in pots (diameter 12 cm and height 40 cm) containing approximately 3.8 kg of river sand. Pots were kept in the greenhouse of the University of Antwerp (UA, Belgium). Temperature in the greenhouse ranged from 20 ºC at night to 35ºC during the day. Relative humidity ranged from 45% to 65%. Mean photosynthetically active radiation was about 400 µmol/m²/s from 7 am to 7 pm.

Country	**Seed provenance**	**Latitude (°)**	**Longitude (°)**	**Annual Rainfall (mm)**
Mali (West Africa)	Tatakarat	15.05 N	0.90 W	336
	Bendjiely	14.48 N	3.59 W	509
	Wataga	14.10 N	9.10 W	703
	Kerela	12.75 N	6.84 W	823
	Katon	10.91 N	5.91 W	1145
Malawi (East Africa)	Nchalo	16.33 S	34.86 E	794
	Kalasamba	15.38 S	34.79 E	940
	Mangochi	14.42 S	35.21 E	843
	Chipoka	14.00 S	34.50 E	1012
	Likoma	12.06 S	34.73 E	1244

Table 6.1. Location and climate of the selected seed provenances used in the seedling experiment. Annual rainfall data was obtained from the Worldclim database (Hijmans et al. 2004). Further environmental characteristics of these seed provenances can be found in Table 5.2 (chapter 5).

Experiment setting

Two experiments were carried out:

Experiment 1: *seedling growth and morphological variation*

Seedlings from the aforementioned ten provenances (Table 6.1) were grown following a randomised block design with 50 replications per treatment (provenance). The experimental setting can be seen in Fig. 6.1. Pots were moved around once a week to avoid differences in photosynthetically active radiation. They were irrigated twice a week with standard Hoagland solution and once a week with tap water. Water or nutrient solution when applied was added until an excess drained from the bottom of the pot. Ten, 14 and 18 weeks after germination six, six and eight (respectively) healthy looking plants were harvested per treatment. Due to fungal attack and low germination of some study sites, no more plants could be harvested.

Experiment 2: *short-term drought stress*

Seedlings from the ten provenances were grown for 14 weeks following a randomised block design with two blocks (n=200). Pots were moved around once a week; and they were irrigated twice a week with standard Hoagland solution and once a week with tap water. Water or nutrient solution when applied was added until an excess drained from the bottom of the pot. After 14 weeks, plants were randomly divided into two groups: half of the seedlings continued to be grown in the described conditions (control treatment) while the other half were exposed to drought stress by withholding irrigation completely (drought treatment). Four weeks later (when seedlings were 18 weeks), all plants were harvested.

Fig. 6.1. Experiment set up in a tropical greenhouse in Antwerp, Belgium.

Harvesting measurements

Similar measurements were carried out for experiments 1 and 2. Several characteristics were recorded from each seedling after harvesting it: stem, roots and taproot length, stem and taproot diameter (measured with a ruler and an electronic calliper), number of cotyledons, number of leaves and hypocotyl length (height from basal diameter to cotyledon node). Taproot length was measured from the start of the stem until the taproot had approximately 5 mm diameter. The measured characteristics can be found in Fig. 6.2.

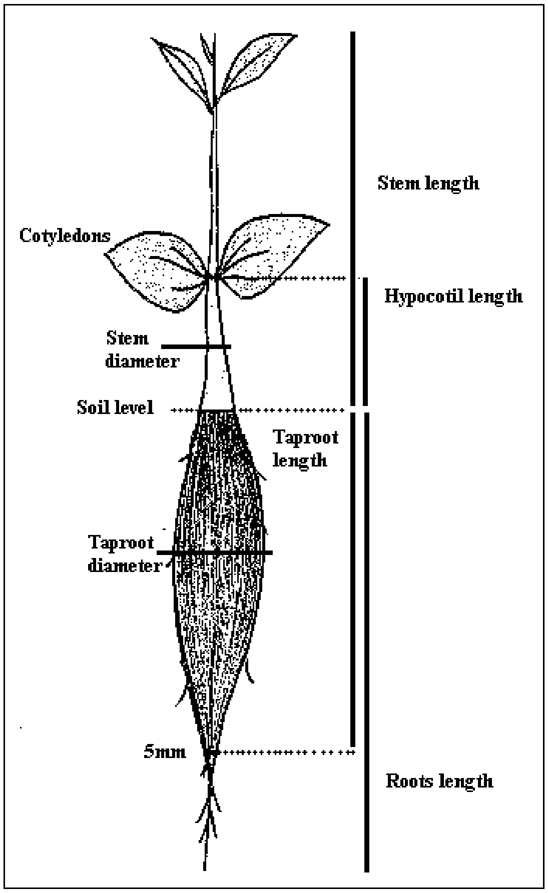


Fig. 6.2 Some of the characteristics recorded from each baobab seedling.

Seedlings were divided into stem A or epicotyl (from tip to cotyledon node) and stem B or hypocotyl (from cotyledon node to basal part), taproot, other roots, leaves and cotyledons. Fresh weights were determined using an electronic balance with 0.0001 g precision. The first fully developed leaf was punched three times with a paper punch; the discs were dried in an oven at 70 ºC and weighed with a precision balance after 48 hours. The Specific Leaf Weight (SLW) was derived by dividing the dry weight of the three punched discs by their area. All seedling parts were dried in an oven at 70 ºC until constant dry weight was reached (about 72 h) and weighed with a precision balance.

In order to estimate taproot shape, the ratio between taproot length and diameter was calculated (named taproot ratio). The percent of water content of the taproot was estimated as follows: 100*(taproot fresh weight - taproot dry weight)/taproot fresh weight. The water content of the hypocotyl was estimated following the same method.

The ratio aerial/ground part was calculated using fresh weights (FW) as follows: (epicotyl FW + hypocotyl FW + leaves FW + cotyledons FW) / (taproot FW + roots FW). Specific root length (SRL) was calculated by dividing roots length by roots dry weight.

Nail polish impressions of the abaxial surface of the first fully developed leaf were made for all seedlings. The impressions were observed under a light microscope and counts were made of stomata in six random fields of view at (10×40)X magnification.

Statistical analyses

SPSS for Windows v 16.0, ANOVA and MANOVA were used to determine significant differences between study sites. Post-hoc pair wise multiple comparisons were performed using Tukey's-b test.

6.4 Results

Experiment 1: seedling growth and morphological variation

After 10, 14 and 18 weeks, there were significant differences between seedlings from Mali and Malawi in stem diameter and hypocotyl length: seedlings from Mali had larger stem diameter but shorter hypocotyl length (Table 6.2). However, there were no other significant differences between countries in any of the morphological characteristics recorded after ten weeks of seedling growth (Table 6.2).

After 14 weeks of growth, there were significant differences between seedlings from the two countries in taproot length, ratio aerial/ground part, number of cotyledons and stomata density (Table 6.2). Taproots from Malawi seedlings were longer than those from Mali while their ratio aerial/ground part was lower. At this point, most seedlings from Malawi had two cotyledons while most seedlings from Mali had one or no cotyledons

(Table 6.2). After 18 weeks, most plants had no cotyledons (they had been shed). Stomata density was higher in Mali than in Malawi after both 14 and 18 weeks.

A number of significant differences between countries were only observed after 18 weeks: taproot diameter, taproot shape (or ratio taproot), number of leaves, total leaf fresh weight (leaf FW), SLW and water content of hypocotyl (Table 6.2). After 18 weeks, seedlings from Mali had taproots with greater diameter but shorter length (different taproot ratio, Table 6.2) than those from Malawi. Seedlings from Mali also had a lower number of leaves than those from Malawi. Total fresh weight of the leaves was greater and they had thicker leaves (lower SLW, Table 6.2). Moreover, the water content of the hypocotyl was higher in Mali seedlings than in Malawi ones (Table 6.2).

	10 weeks		**14 weeks**		**18 weeks**	
	Mali	**Malawi**	**Mali**	**Malawi**	**Mali**	**Malawi**
Stem length (cm)	32.7 ± 4.9 a	36.0 ± 6.7 a	52.5 ± 13.8 a	50.9 ± 16.9 a	64.0 ± 11.6 a	61.2 ± 14.7 a
Taproot length (cm)	14.6 ± 4.3 a	16.8 ± 4.6 a	18.2 ± 3.8 a	21.5 ± 4.9 b	23.3 ± 5.6 a	25.3 ± 5.0 a
Roots length (cm)	39.1 ± 3.1 a	38.6 ± 3.3 a	43.1 ± 6.5 a	40.9 ± 3.8 a	45.8 ± 8.1 a	43.3 ± 4.9 a
Stem diameter (mm)	8.9 ± 1.4 a	7.5 ± 1.0 b	11.1 ± 2.7 a	9.4 ± 0.9 b	13.6 ± 2.3 a	10.8 ± 1.5 b
Taproot diameter (mm)	16.5 ± 2.6 a	16.9 ± 3.0 a	19.9 ± 3.6 a	20.4 ± 2.5 a	23.6 ± 2.3 a	22.1 ± 2.8 b
FW taproot (g)	20.0 ± 8.7 a	25.2 ± 9.8 a	37.6 ± 12.9 a	48.6 ± 8.4 a	67.8 ± 20.9 a	68.3 ± 14.1 a
Ratio taproot	0.9 ± 0.2 a	1.0 ± 0.3 a	0.9 ± 0.2 a	1.1 ± 0.3 a	0.9 ± 0.2 a	1.2 ± 0.3 b
No. leaves	12 ± 3 a	13 ± 4 a	18 ± 6 a	22 ± 14 a	26.1 ± 5.5 a	33.8 ± 14.5 b
FW leaves (g)	7.6 ± 2.6 a	7.8 ± 2.3 a	18.3 ± 7.2 a	17.0 ± 10.1 a	74.0 ± 21.3 a	71.6 ± 14.2 a
Ratio aerial/ground part	0.8 ± 0.4 a	0.6 ± 0.2 a	0.9 ± 0.4 a	0.7 ± 0.4 b	1.7 ± 0.3 a	1.6 ± 0.2 a
No. cotyledons	1.4 ± 0.8 a	1.8 ± 0.5 a	1.3 ± 0.8 a	1.8 ± 0.6 b	-	-
Hypocotyl length (cm)	2.4 ± 0.5 a	5.5 ± 0.9 b	2.4 ± 0.5 a	5.5 ± 0.7 b	2.3 ± 0.7 a	5.2 ± 0.9 b
SLW (mg/cm^2)	-	-	-	-	2.56 ± 0.64 a	3.44 ± 0.47 b
Stomata density (No. per mm^2)	-	-	193.3 ± 30.2 a	173.4 ± 35.6 b	208.4 ± 34.0 a	174.6 ± 39.8 b
FW roots	-	-	4.5 ± 2.5 a	4.9 ± 1.8 a	6.6 ± 2.1 a	6.4 ± 1.9 a
SRL (cm/g)	-	-	90.0 ± 31.7 a	77.8 ± 21.8 a	66.5 ± 25.1 a	68.8 ± 25.2 a
% water taproot	-	-	90.9 ± 1.9 a	90.5 ± 1.3 a	92.5 ± 1.5 a	92.5 ± 1.4 a
% water hypocotyl	-	-	75.2 ± 14.0 a	78.7 ± 5.5 a	81.9 ± 2.1 a	78.6 ± 2.5 b

Table 6.2. Seedling characteristics of Adansonia digitata *from Mali and Malawi after 10, 14 and 18 weeks (n=6, 6 and 8 respectively). Stomata density n=36, 36 and 48 respectively. Means followed by a same letter within a column are not significantly different from each other at p<0.01 (ANOVA). FW= fresh weight. SLW= Specific leaf weight. SRL= specific root length. Ratio taproot = taproot length/taproot diameter.*
- no data available.

After ten weeks of growth, there were no significant differences between seedlings from the study sites within each country (Mali or Malawi) in any of the morphological characteristics recorded (Table 6.3). After 14 and 18 weeks there were significant differences between study sites within each country in stem length, stem diameter, number of leaves, ratio aerial/ground part, number of cotyledons, and roots FW (Table 6.3). After 18 weeks, there were also significant differences between study sites within each country in taproot FW, SLW and water content of the hypocotyl (Table 6.3). As the observed differences after 14 weeks were similar to those observed after 18 weeks, only the latter are discussed.

Seedlings from Katon were shorter than those from other study sites in Mali while seedlings from Wataga had the thickest stems (Table 6.4, 6.5). Seedlings from the drier sites in Malawi (Nchalo and Kalasamba) were shorter than those from wetter sites in this country but they had similar stem diameter (Table 6.4, 6.5). Although there were no significant differences between study sites in taproot length or taproot diameter, taproot fresh weight was found to be low in Kerela (Table 6.4, 6.5). Moreover, despite having similar number of leaves, leaves FW was also found to be low in Kerela (Table 6.6). Seedlings from the drier sites in Malawi had significantly less leaves than those from wetter sites in the same country but were similar in FW (Table 6.6).

Seedlings from drier sites in Malawi had low aerial/ground part ratio while seedlings from wetter sites had high aerial/ground part ratio (Table 6.6). The pattern in Mali was not so clear, as seedlings from Kerela had the highest aerial/ground part ratio. Seedlings from the drier sites in Mali had lower SLW than those from other study sites in the same country (Table 6.7). Seedlings from Benjiely, Kerela, Katon and Likoma had a significantly high level of stomata density (Table 6.7). In Malawi, seedlings from Nchalo (the driest study site) had significantly fewer stomata than those from other study sites while seedlings from Likoma (the wettest study site) had more stomata than those from other study sites (Table 6.7). Seedlings from drier sites in both Mali and Malawi had lower roots fresh weight than those from wetter sites (Table 6.7). Seedlings from Chipoka had significantly low water content in the hypocotyl while seedlings from Wataga and Kerela had significantly high water content in the hypocotyl (Table 6.7).

	10 weeks	**14 weeks**	**18 weeks**
Stem length (cm)		*	*
Taproot length (cm)			
Roots length (cm)			
Stem diameter (mm)		*	*
Taproot diameter (mm)			*
FW taproot (g)			
Ratio taproot			
No. leaves		*	*
FW leaves (g)		*	*
Ratio aerial/ground		*	*
No. cotyledons			-
Hypocotyl length (cm)			
SLW (mg/cm^2)	-	-	*
Stomata density (No. per mm^2)	-	*	*
FW roots	-	*	*
SRL (cm/g)	-	*	
% water taproot	-	*	
% water hypocotyl	-		*

Table 6.3. Significant differences in seedling characteristics of Adansonia digitata *from Mali and Malawi after 10, 14 and 18 weeks. * indicates significant differences between study sites within Mali and Malawi at p<0.01 (ANOVA). FW= fresh weight. SLW= Specific leaf weight. SRL= specific root length. Ratio taproot = taproot length/taproot diameter.*
- no data available.

Experiment 2: short-term drought stress

When the application of drought stress started, the plants stopped growing. There were no significant differences in stem length, stem diameter, taproot length, roots length or roots FW between before and after the drought treatment started (when seedlings under drought treatment were 14 or 18 weeks, table not included). However, after the 4-week drought stress, there were significant differences in taproot diameter: seedlings had slightly thinner taproots (before: 19-22 mm, after: 17-22 mm diameter). Once drought started baobab seedlings continued to produce leaves, but after 3 days they started shedding about 50% of the leaves (from the bottom of the stem). From 3 days onward, baobab seedlings gradually shed part of the remaining leaves. All baobab seedlings still had a few leaves left after the 4-week drought stress. Average number of leaves before the drought stress started ranged from 13 leaves (Nchalo, driest site in Malawi) to 37 leaves (Chipoka, Malawi). Average number of leaves after the drought stress ranged from 6 (Kerela, Mali) to 23 (Chipoka, Malawi).

There were significant differences between control and drought treatments in all characteristics measured except for hypocotyl length (Table 6.4, 6.5, 6.6, 6.7). Seedlings under drought treatment were smaller (shorter and thinner stems) and had fewer leaves than those under control treatment. Their taproots were also smaller (shorter, thinner lighter), and their roots were shorter. Roots fresh weight and SRL were also lower in seedlings under drought treatment. Water content of both the taproot and the hypocotyl were also lower in seedlings under drought treatment. The ratio aerial/ground part was lower under drought treatment, the SLW was higher and stomata density was also higher in seedlings under drought treatment than those under control conditions.

The observed differences between countries in the growth experiment could also be observed in the seedlings under drought treatment: seedlings from Mali had larger stem diameter but shorter hypocotyl length than those from Malawi (Table 6.4, 6.6). The interaction between treatment and country was only significant for ratio aerial/ground and SLW.

Significant differences between sites within one country in the growth experiment could also be observed in the seedlings under drought treatment (Table 6.4, 6.5, 6.6, 6.7). There were only two exceptions: taproot FW and roots FW (Table 6.5, 6.7). After drought stress, seedlings from the driest study sites in both countries (Tatakarat and Nchalo) were found to be the shortest (Table 6.4). Seedlings from Nchalo also had the thinnest stems.

There was a trend with seedlings from drier sites having lower aerial/ground part ratio than those from wetter sites in both countries (Table 6.6). Water content of both taproot and hypocotyl were significantly higher in drier study sites than in wetter study sites in both countries (Table 6.7). As in control conditions, while seedlings from Bendjiely had significantly high stomata density, seedlings from Nchalo had significantly low stomata density in drought treatment (Table 6.6, Fig. 6.3).

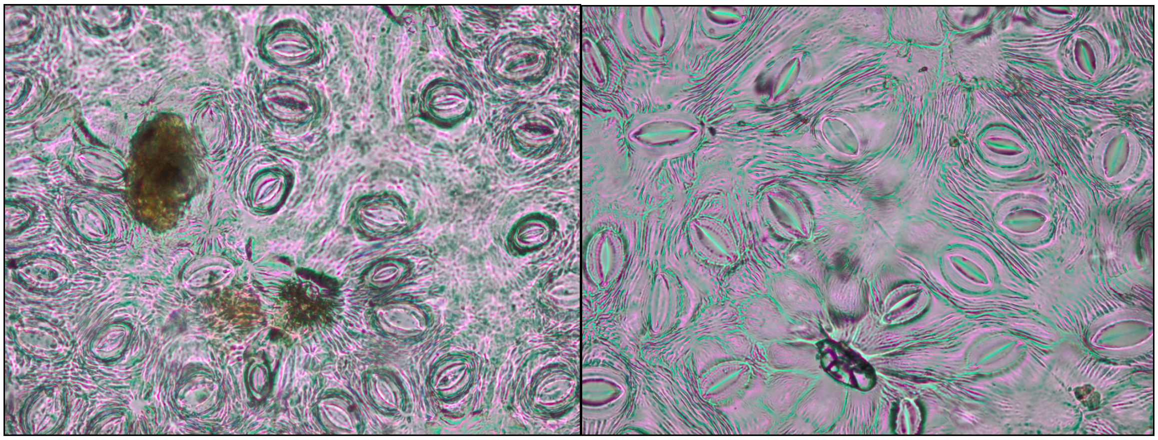


Fig. 6.3. Stomata density variation on the abaxial surface of Bendjiely (Mali) and Nchalo (Malawi) seedlings. Picture taken at under a light microscope at x400 magnification.

	Stem length (cm)		**Taproot length (cm)**		**Roots length (cm)**		**Stem diameter (mm)**	
	Control	**drought**	**control**	**drought**	**control**	**drought**	**control**	**drought**
Tatakarat	61.3 ± 10.8 a	44.9 ± 12.3 a	24.5 ± 4.9 a	22.7 ± 4.7 a	42.7 ± 6.7 a	36.7 ± 2.4 a	13.3 ± 2.0 ab	11.7 ± 2.1 abc
Bendjiely	68.8 ± 11.7 a	58.4 ± 11.9 b	24.8 ± 6.2 a	22.0 ± 5.8 a	44.6 ± 6.0 a	39.8 ± 10.6 a	15.1 ± 2.8 a	12.4 ± 3.6 c
Wataga	61.6 ± 10.3 a	51.7 ± 13.2 ab	23.4 ± 2.9 a	22.2 ± 4.9 a	47.5 ± 8.9 a	39.8 ± 3.7 a	11.8 ± 2.2 bc	11.2 ± 2.7 abc
Kerela	71.0 ± 8.7 a	62.0 ± 9.7 b	18.8 ± 4.1 a	19.5 ± 3.1 a	43.0 ± 3.5 a	37.5 ± 4.3 a	14.1 ± 1.3 ab	12.3 ± 1.6 c
Katon	57.5 ± 13.2 ab	50.2 ± 8.7 ab	24.7 ± 7.5 a	19.1 ± 4.9 a	51.0 ± 8.0 a	38.8 ± 2.4 a	13.6 ± 2.3 ab	11.3 ± 1.4 abc
Nchalo	43.2 ± 10.9 b	39.2 ± 9.0 ab	23.7 ± 5.2 a	19.4 ± 4.3 a	43.2 ± 3.5 a	39.1 ± 1.5 a	9.7 ± 0.9 c	9.0 ± 1.2 a
Kalasamba	57.6 ± 11.1 ab	52.6 ± 10.5 ab	23.4 ± 3.2 a	21.3 ± 5.2 a	41.0 ± 5.6 a	37.5 ± 3.3 a	10.5 ± 0.6 c	9.4 ± 0.9 a
Mangochi	65.7 ± 12.5 a	52.6 ± 14.0 ab	25.5 ± 3.7 a	23.7 ± 6.2 a	42.5 ± 3.6 a	39.5 ± 2.3 a	10.2 ± 0.9 c	9.9 ± 0.5 abc
Chipoka	66.5 ± 8.7 a	54.6 ± 12.5 ab	27.3 ± 6.9 a	22.8 ± 5.6 a	43.3 ± 5.5 a	41.3 ± 3.4 a	11.6 ± 1.5 bc	9.9 ± 0.9 abc
Likoma	72.7 ± 11.7 a	55.6 ± 9.9 ab	26.6 ± 4.9 a	23.5 ± 2.7 a	46.7 ± 5.2 a	38.0 ± 3.2 a	12.0 ± 1.9 bc	10.8 ± 1.4 abc
	A	B	a	b	a	B	a	b

Table 6.4. Stem length, taproot length, roots length and stem diameter of Adansonia digitata *from different study sites. Means followed by standard deviation (n=8). Means followed by a same letter within a column are not significantly different from each other at p<0.05 (Tukey's –b test). Different letters between control and drought treatment in the last row indicate significant differences between control and drought treatments for a given variable.*

	Taproot diameter (mm)		**FW taproot (g)**		**No. leaves**		**FW leaves (g)**	
	Control	**drought**	**control**	**drought**	**control**	**drought**	**control**	**drought**
Tatakarat	23.4 ± 2.6 a	19.5 ± 2.3 a	75.0 ± 15.5 a	54.2 ± 16.5 a	27 ± 8 ab	7 ± 2 a	81.2 ± 15.7 a	6.24 ± 1.2 a
Bendjiely	24.3 ± 1.8 a	21.6 ± 1.9 a	74.1 ± 19.5 a	51.9 ± 9.2 a	26 ± 4 ab	9 ± 3 ab	80.2 ± 20.6 a	12.2 ± 3.6 bc
Wataga	23.2 ± 3.0 a	19.6 ± 2.3 a	70.2 ± 16.2 a	52.4 ± 18.8 a	26 ± 4 ab	12 ± 4 ab	75.8 ± 16.4 ab	11.0 ± 3.6 abc
Kerela	23.5 ± 2.4 a	22.3 ± 2.3 a	44.5 ± 7.6 b	46.5 ± 13.5 a	23 ± 4 ab	6 ± 2 a	51.4 ± 7.3 b	7.6 ± 3.1 abc
Katon	23.7 ± 2.2 a	21.2 ± 2.4 a	75.4 ± 26.4 a	49.5 ± 16.9 a	27 ± 4 ab	7 ± 3 a	81.5 ± 28.0 a	7.6 ± 3.2 ab
Nchalo	21.6 ± 2.9 a	17.1 ± 6.6 a	63.6 ± 10.3 ab	48.2 ± 14.8 a	22 ± 4 a	16 ± 5 bcd	66.4 ± 10.2 ab	9.7 ± 3.7 abc
Kalasamba	23.0 ± 2.3 a	19.3 ± 2.8 a	68.4 ± 8.5 ab	44.6 ± 12.2 a	25 ± 4 ab	18 ± 6 cd	71.9 ± 8.8 ab	11.8 ± 2.7 abc
Mangochi	22.4 ± 3.2 a	17.7 ± 3.0 a	69.2 ± 11.4 ab	43.4 ± 6.4 a	32 ± 13 ab	16 ± 2 cd	72.8 ± 11.9 ab	13.7 ± 4.1 c
Chipoka	21.9 ± 3.3 a	18.6 ± 2.7 a	70.2 ± 20.9 ab	46.4 ± 10.6 a	52 ± 13 b	23 ± 8 d	73.4 ± 20.8 ab	14.8 ± 4.1 c
Likoma	21.6 ± 2.6 a	17.8 ± 3.2 a	69.8 ± 18.3 ab	46.4 ± 14.6 a	36 ± 12 b	18 ± 8 cd	73.3 ± 18.0 ab	13.9 ± 6.0 c
	A	B	a	b	a	B	a	b

Table 6.5. Taproot diameter, taproot fresh weight, number of leaves and total leaves fresh weight of Adansonia digitata *from different study sites. Means followed by standard deviation (n=8). Means followed by a same letter within a column are not significantly different from each other at p< 0.05 (Tukey's –b test). Different letters between control and drought treatment in the last row indicate significant differences between control and drought treatments for a given variable. FW=fresh weight.*

	Ratio aerial/ground part		**Hypocotyl length (cm)**		**SLW (mg/cm^2)**		**Stomata density (No. per mm^2)**	
	Control	**drought**	**control**	**drought**	**control**	**drought**	**control**	**drought**
Tatakarat	1.5 ± 0.2 abc	0.4 ± 0.1 a	1.9 ± 0.2 a	2.1 ± 0.2 a	3.0 ± 0.5 a	3.5 ± 0.6 a	197.2 ± 42.2 c	212.9 ± 35.5 cd
Bendjiely	1.7 ± 0.3 bc	0.7 ± 0.2 ab	2.4 ± 1.3 a	2.4 ± 0.4 a	3.5 ± 0.5 ab	3.8 ± 0.5 ab	221.5 ± 22.9 d	274.1 ± 56.7 e
Wataga	1.5 ± 0.1 abc	0.6 ± 0.2 ab	2.2 ± 0.5 a	2.1 ± 0.2 a	3.4 ± 0.7 ab	3.6 ± 0.4 a	191.2 ± 33.1 b	189.2 ± 41.5 b
Kerela	1.9 ± 0.3 d	0.7 ± 0.3 ab	2.3 ± 0.6 a	2.3 ± 0.6 a	3.9 ± 0.5 b	3.7 ± 0.2 a	220.1 ± 25.8 d	216.6 ± 29.0 cd
Katon	1.5 ± 0.1 abc	0.6 ± 0.1 ab	2.6 ± 0.4 a	2.2 ± 0.6 a	3.9 ± 0.6 b	3.8 ± 0.6 ab	211.9 ± 32.4 cd	211.3 ± 26.4 cd
Nchalo	1.3 ± 0.1 a	0.6 ± 0.3 ab	4.9 ± 0.7 b	4.7 ± 0.6 b	3.4 ± 0.4 ab	4.0 ± 0.5 b	121.4 ± 21.4 a	147.3 ± 30.6 a
Kalasamba	1.4 ± 0.1 a	0.8 ± 0.3 b	5.6 ± 1.1 b	4.8 ± 0.9 b	3.3 ± 0.3 ab	4.5 ± 0.3 b	175.9 ± 19.8 b	159.7 ± 23.3 a
Mangochi	1.5 ± 0.2 abc	0.9 ± 0.3 b	4.6 ± 0.8 b	4.8 ± 0.9 b	3.4 ± 0.5 ab	3.8 ± 0.4 b	187.2 ± 28.1 b	233.4 ± 59.9 d
Chipoka	1.8 ± 0.3 cd	0.9 ± 0.4 b	5.5 ± 0.6 b	4.9 ± 0.5 b	3.3 ± 0.5 ab	4.1 ± 0.8 b	175.0 ± 25.9 b	220.3 ± 32.5 d
Likoma	1.8 ± 0.1 cd	0.9 ± 0.4 b	5.2 ± 0.9 b	5.0 ± 0.7 b	3.9 ± 0.4 ab	4.0 ± 0.5 b	213.6 ± 33.8 cd	197.6 ± 28.9 bc
	A	B	a	a	a	b	a	b

Table 6.6. Ratio aerial/ground part, hypocotyl length, specific leaf weight and stomata density of Adansonia digitata *from different study sites. Means followed by standard deviation (n=8). Stomata density n=48. Means followed by a same letter within a column are not significantly different from each other at p<0.05 (Tukey's –b test). Different letters between control and drought treatment in the last row indicate significant differences between control and drought treatments for a given variable. SLW= specific leaf weight.*

	FW roots (g)		**SRL (cm/g)**		**Water content taproot**		**Water content hypocotyl**	
	Control	**drought**	**control**	**drought**	**control**	**drought**	**control**	**drought**
Tatakarat	5.2 ± 1.5 a	3.0 ± 0.5 a	78.8 ± 26.5 a	82.2 ± 25.0 a	92.9 ± 1.3 a	90.5 ± 0.9 a	81.4 ± 2.3 cd	80.4 ± 5.4 a
Bendjiely	6.5 ± 2.5 b	5.1 ±1.7 a	61.0 ± 28.2 a	24.8 ± 10.7 b	93.3 ± 1.3 a	90.1 ± 1.0 a	81.9 ± 2.0 cd	78.5 ± 1.5 a
Wataga	6.2 ± 2.4 b	3.7 ± 1.1 a	78.6 ± 30.3 a	34.1 ± 8.7 b	92.8 ± 1.8 a	89.6 ± 1.8 ab	82.8 ± 2.2 d	78.7 ± 1.7 a
Kerela	7.5 ± 2.5 c	4.5 ± 1.7 a	54.2 ± 19.0 a	30.2 ± 19.2 b	92.2 ± 1.3 a	90.3 ± 1.9 a	82.9 ± 1.2 d	78.4 ± 5.8 a
Katon	7.5 ± 1.6 c	4.1 ± 1.3 a	60.1 ± 12.2 a	46.9 ± 21.3 ab	91.2 ± 1.5 a	89.3 ± 1.3 ab	80.7 ± 2.2 bcd	78.0 ± 1.5 ab
Nchalo	5.1 ± 1.5 a	3.1 ± 1.0 a	85.4 ± 28.5 a	60.3 ± 36.5 ab	92.3 ± 2.0 a	90.4 ± 1.5 a	78.0 ± 1.5 ab	74.9 ± 1.3 ab
Kalasamba	5.5 ± 1.3 a	3.7 0.5 a	80.3 ± 19.3 a	36.7 ± 7.8 b	93.4 ± 1.0 a	89.8 ± 1.3 b	80.3 ± 1.3 bcd	76.6 ± 0.7 ab
Mangochi	6.1 ± 1.7 b	4.5 ± 0.9 a	66.1 ± 23.1 a	37.7 ± 11.2 b	92.2 ± 1.3 a	87.8 ± 1.9 b	78.8 ± 1.7 abc	72.7 ± 5.6 b
Chipoka	7.9 ± 1.3 c	4.5 ± 1.2 a	60.3 ± 27.5 a	38.3 ± 16.4 b	93.0 ± 1.9 a	88.9 ± 1.2 b	75.9 ± 3.6 a	75.4 ± 1.6 ab
Likoma	7.6 ± 2.1 c	5.0 ± 3.1 a	52.2 ± 13.8 a	40.9 ± 13.1 ab	91.8 ± 1.5 a	89.7 ± 0.8 b	80.0 ± 2.8 bcd	77.0 ± 4.0 b
	A	B	a	b	a	b	a	b

Table 6.7. Roots fresh weight, specific root length, water content of the taproot and water content of the hypocotyl of Adansonia digitata *from different study sites. Means followed by standard deviation (n=8). Means followed by a same letter within a column are not significantly different from each other at p<0.05 (Tukey's –b test). Different letters between control and drought treatment in the last row indicate significant differences between control and drought treatments for a given variable. FW=fresh weight. SRL=specific root length.*

6.5 Discussion

Differences in seedling growth and morphology

As in fruit characteristics (chapter 5), there were significant differences in seedling growth and morphology between the two countries. Seedlings from Mali had their cotyledons at a lower height (shorter hypocotyl length), their stem diameter was usually larger, they had fewer leaves, lower SLW and higher stomatal density than those from Malawi. These differences in seedling morphology support the genetic differences between baobab populations from West Africa and south-eastern Africa suggested by Pock-Tsy et al. (2009).

A number of characteristics were already found to be significantly different between countries after ten weeks of germination (hypocotyl length, stem diameter) while other significant differences were observed later (number of leaves, leaves fresh weight, water content of the hypocotyl, SLW and stomata density). Possibly, SLW and stomata density were also different after ten weeks (but I did not measure these characteristics at this point in time).

Differences in hypocotyl length between countries may be due to genetic differences, as this difference was observed even in the drought treatment and there were no differences between sites within each country. Seedlings from Mali (West Africa baobab population) have their cotyledons at a lower height than those from Malawi (East Africa baobab population, Pock Tsy et al. 2009). Differences in hypocotyl length could be related to adaptation to drought, fire or herbivory, as has been suggested for other plant species (Fujita and Humphreys 1992, Fisher 2008). If cotyledons are at a higher height they are more vulnerable to fire and animals would probably see them and eat them more easily.

The other observed characteristics between countries, with seedlings from Mali having thicker stems, a lower number of leaves, higher water content of the hypocotyl and higher stomatal density suggest that Malian baobab seedlings are better adapted to drought as they have thicker stems to accumulate more water, and they have leaves with more stomatal control to avoid losing water. High stomatal density is thought to be a characteristic of drought adaptation (as mentioned in chapter 4). Seedlings from Malawi had higher SLW than those from Mali. In chapter 4, adult baobab trees from Malawi were also found to have higher stomatal density than adult baobab trees from Benin (also in West Africa). High SLW is also linked to drought adaptation (see chapter 4). It is possible that while seedlings from Mali have better stomatal control, seedlings from Malawi might have thicker leaves to reduce evapotranspiration.

Significant differences between study sites within each country could also be observed, like for leaf and fruit characteristics (chapter 4 and 5). In general, seedlings from drier sites in Malawi (Nchalo, Kalasamba, Mangochi) were smaller overall (shorter and thinner stems, lower number of leaves) than those from wetter sites in Malawi (Chipoka and Likoma). However, the pattern was not so clear in Mali. Differences between study sites in one country, with baobab seedlings from wetter sites being larger (stem height, diameter and number of leaves) than those from drier sites have also been reported from Benin (Assogbadjo et al. 2010). These authors related differences in seedling growth to differences in seed size, with baobab seeds from wetter sites being larger than those from drier sites. Parker et al. (2006) also reported a positive influence of large seed size and seed reserve on the establishment and early growth of seedlings. In fact, seeds from wetter sites in Malawi were also found to be larger than those from drier sites (chapter 5). However, for this experiment, seeds with similar weight were selected. Moreover, the study by Assogbadjo et al. (2010) only followed baobab seedlings for 32 days, while in this study seedlings were grown for 18 weeks (126 days). It is likely that after this much longer period seed reserves would have a much lower effect than seedling capacity to grow fast.

Parkia biglobosa seedlings from wetter study sites were also found to be taller than those from drier study sites (4 month old seedlings) (Teklehaimanot et al. 1998). Significant differences in tree height, diameter and number of leaves were also observed in 6 year old *Vitellaria paradoxa*, with trees from wetter provenances being larger than those from drier environments (Bayala et al. 2009). In wetter sites, competition for light might be a much more limiting factor for seedling growth than water scarcity; there might be a trade-off between drought tolerance and shade tolerance (Smith and Hutson 1989). Baobab seedlings from wetter sites in Malawi might grow faster than those from drier sites due to competition for light in their natural environment. Metcalfe et al. (2007) suggested that light was a limiting factor for *Adansonia rubrostipa* seedlings.

Within each country there were also significant differences in SLW and stomatal density; as mentioned, characteristics often related to drought tolerance. Both in Mali and Malawi seedlings from drier provenances were found to have lower SLW than those from wetter provenances, which is contrary to the expected results. Maybe, as in general, seedlings from wetter study sites were larger overall, their leaves were also older (they had accumulated more secondary compounds). *Parkia biglobosa* seedlings from drier provenances were also found to have lower SLW than those from wetter provenances (Teklehaimanot et al. 1998). The pattern of differences in stomatal densities within each country was not so clear, especially in Malawi, where the driest site was found to have the lowest stomatal density. Similar results were also observed in adult trees (chapter 4). While variation in stomata density between provenances has also been observed for seedlings of *Ziziphus mauritiana* (Kulkarni et al. 2010), Teklehaimanot et al. (1998) reported no significant differences in stomatal density of *Parkia biglobosa* seedlings.

Moreover, both in Mali and Malawi, seedlings from drier sites were found to have less secondary roots than those from wetter sites (lower roots fresh weight) but, in general, heavier taproots (greater taproot fresh weight). As the taproot is the main water storing organ of baobab seedlings, it seems that baobab seedlings from drier sites invested more in growing a larger taproot and less in producing secondary roots.

It should be noted that baobab seedlings grown in the greenhouse might have been growing more slowly than they would have in natural conditions. In Benin, after 32 days, baobab seedlings had 30-45 cm stem height and 1-1.3 cm stem diameter (Assogbadjo et al. 2010). In the greenhouse, baobab seedlings from both Mali and Malawi were 32-36 cm high and less than 1 cm stem diameter after 10 weeks (70 days) of growth. Differences in air temperature (with Benin being hotter than the greenhouse in Belgium) might account for these differences.

Mechanisms to deal with drought

Results from this study indicate that baobab seedlings use a number of mechanisms to withstand drought. They use leaf deciduousness: once drought stress started seedlings from all provenances shed about half of their leaves. However, they did not shed all their leaves, they kept some and they continued to produce leaves but with an altered morphology: with higher stomatal density and higher SLW. A similar mechanism has been reported for *Jathropa curcas* seedlings under drought (Maes et al. 2009). While *J. curcas* seedlings produced new leaves using the water stored in the stem (Maes et al. 2009), it seems that baobab seedlings use both the water stored in the stem and the taproot to produce new leaves (changes in taproot diameter and taproot fresh weight, changes in water content of the hypocotyl and the taproot). Chapotin et al. (2006) reported that adult baobab trees use their stem water reserves for flushing new leaves before the end of the dry season. These authors suggested that the physiological advantage of this mechanism allows the adult baobab trees to take advantage of scattered rainfall events occurring before the start of the rainy season. Similarly, the advantage of keeping the leaves and producing leaves with characteristics better adapted to drought conditions (higher SLW and stomatal density) might help the baobab seedlings overcome short droughts and take advantage of scattered rainfall after the start of the dry season. Maes et al. (2009) suggested a similar mechanism for *J. curcas* seedlings.

Unexpectedly, baobab seedlings do not invest in producing a longer taproot, longer roots or more secondary roots (no differences in taproot length, roots length or roots FW between before and after drought treatment). Differences in aerial/ground part ratio between drought and control treatment might be related to seedlings under drought treatment having a lower number of leaves. Apart from producing a few new leaves, seedlings under drought treatment stopped growing.

To sum up, baobab seedlings under drought stress stop growing, they shed part of their leaves and they use water stored in the taproot and the hypocotyl to produce a few new leaves with altered morphology.

Differences in response to drought stress between study sites

The described mechanisms used by baobab seedlings to deal with drought were used by all seedlings, regardless of the country or seed provenance. However, there were differences in the number of new leaves produced, SLW or stomata density of these new leaves. Also, it seemed that seedlings from some study sites shed their leaves faster and they shed more leaves (drier sites in Mali). Moreover, seedlings from drier study sites in both countries had higher water content than those from wetter study sites in both the taproot and the lower part of the stem after the 4-week drought stress.

Selecting seedlings with 'superior' characteristics

In terms of seedling growth, if farmers are interested in selecting seedlings that grow fast, seedlings from Bendjiely (Mali) or Likoma (Malawi) were the ones found to be larger overall. In terms of seedling adaptation to drought, there is a great variability in seedling morphology which allows for potential 'superior' seedling selection. Seedlings from drier study sites in both countries maintained higher water content in both the stem and the taproot during the drought stress. While seedlings from drier sites in Mali had larger taproots, seedlings from Mangochi or Likoma (Malawi) had higher stomatal density and SLW.

It seems that baobab seedlings have different characteristics which help them to adapt to drought. In this study no baobab seedlings were found which were much less stressed than others after the 4-week drought stress. Further studies are recommended to determine which characteristics are key for baobab seedling survival after longer periods of drought. Long-term studies following the effect of drought on baobab trees at young stages (not only at seedling stage but also later) and tree recovery after droughts are recommended, especially *in situ* experiments.

CHAPTER 7. General discussion and conclusions

This final chapter reviews how the research findings help fill the knowledge gaps highlighted by the literature review. It also considers this investigation's limitations and recommendations for further research, the novelty of this investigation and the potential applications of this research. The chapter ends with a more wide-ranging discussion of how the results obtained in this study can contribute to the conservation and domestication of the baobab tree as an important resource for the future.

7.1 Gaps in knowledge and key findings

The literature review in chapter 1 raised a number of questions to which the results of this investigation have provided answers:

- Where could this species be cultivated? As reported in chapter 2, species distribution modelling (using Maxent) based on 450 records of baobab occurrence suggests that baobab can currently be cultivated in most of dryland Africa, India, Australia, Madagascar, Brazil and Mexico.
- How might climate change effect the distribution of the baobab tree? A combination of species distribution modelling and climate change projections to 2050 (based on three GCM and two emissions scenarios) suggests that there will be fewer suitable areas for the baobab tree in the future. The percentage of present distribution predicted to remain suitable in the future under all GCM and scenarios was just 0.82 % (chapter 3).
- Where conservation efforts should be focused? They should be focused on existing protected areas predicted to have suitable habitat for the baobab tree in the future under all models and scenarios used in this study. However, as only 5.3 % of the area in which the baobab tree is currently distributed (and which is also predicted to be suitable in the future under all GCM and scenarios) was found to be within protected areas, other conservation measures are also needed. These could include *ex situ* conservation in seed banks and conservation 'through sustainable utilisation' (chapter 3).
- Is there variation in leaf morphology, which can be linked to drought adaptation mechanisms? A combination of *in situ* and *ex situ* experiments

show that there are significant differences in baobab leaf size, thickness and stomatal characteristics between countries (Benin and Malawi) and between study sites within one country. In general, baobab trees from drier study sites were found to have smaller and thicker leaves with higher stomatal density and smaller guard cell length, characteristics often related to drought tolerance mechanisms (chapter 4).

- If there are genetic differences between baobab populations from West and south-eastern Africa, are baobab fruits different in these two areas? Results from an *in situ* fruit morphological assessment carried out in Mali (West Africa) and Malawi (south-eastern Africa) where 800 fruits were characterised indicate that although there are differences in fruit size and shape between these two countries with some ‘type’ of fruits only found in Malawi (small spherical fruits), no fruit characteristic measured can unambiguously distinguish south-eastern from West African baobab populations (chapter 5).
- Is there also variation in seedling growth and morphology? As reported in chapter 6, there are significant differences in baobab seedling growth and morphology both between countries (Mali and Malawi) and between study sites within one country. In general, seedlings from Mali have shorter hypocotyls (distance between the cotyledons and the base of the stem), thicker stems and taproots, lower number of leaves and higher stomatal density than seedlings from Malawi. Moreover, seedlings from wetter areas in both countries grow faster than those from drier areas while seedlings from drier areas have smaller and thicker leaves with higher stomatal density.
- How do baobab seedlings deal with drought stress? Results from a 4-week drought stress applied to 14-week-old baobab seedlings from different provenances indicate that baobab seedlings under drought stress stop growing, they shed part of their leaves and they use water stored in the taproot and the hypocotyl to produce a few new leaves with altered morphology (thicker and with higher stomata density) (chapter 6).
- Can ‘superior’ baobab trees in terms of leaf, fruit or seedling characteristics be selected? Results from several experiments (both *in situ* and *ex situ*) indicate that there is a great variation in baobab leaf, fruit and seedling morphology. As some characteristics can be correlated with environmental differences between

study sites (e.g., leaf size) but others appear to be genetically determined (e.g., stomatal density) it seems that there is room for selecting ‘superior’ baobab planting materials in terms of leaf, fruit and seedling characteristics (chapters 4, 5 and 6).

As mentioned in the literature review, other gaps in knowledge, such as baobab market potential (both local and international), are being studied by other PhD students and researchers, who are also part of the DADOBAT EU-funded project. While the PhD theses and publications arising from the DADOBAT project have helped to fill many research gaps, they have inevitably identified areas needing further research.

7.2 Research limitations and further research

This investigation had several limitations, some related to the modelling part and some to the morphological assessment.

Five major research limitations could be identified in the modelling part of this study (chapters 2 and 3). Firstly, apart from Maxent, other modelling algorithms could have been used and might have given different results. However, learning to use different algorithms and preparing the climatic layers in the right format for each algorithm is time consuming. After some preliminary results with Maxent and another algorithm (ENFA), as results were similar and Maxent is considered to be better than other algorithms (section 2.1), only Maxent was selected. A comparison between different modelling algorithms was not within the scope of this investigation.

Secondly, different environmental variables could have been used, which could have given different results. However, as discussed in chapter 2 (section 2.3), it is believed that climate is the main range determinant at large spatial scales (Pearson and Dawson 2003) and it seemed that climatic and soil type variables were the most limiting factors for the baobab tree. Land-use is a variable which was not included in the modelling but it is considered important, as discussed in sections 2.5 and 3.5.

Thirdly, I only used two carbon emission scenarios and three general circulation models for modelling the potential future distribution of the baobab tree (section 3.1). Other climate change projections could have given different results. Following the advice of Buisson et al. (2010), I tried to account for 'certain' future uncertainty by using different GCM and scenarios (section 3.3). Using many carbon emission scenarios and/or general circulation models is time consuming and it was discarded. Thus, three areas which could be further researched are: (i) using other modelling algorithms, (ii) using other variables, and (iii) using other GCM and scenarios for modelling the potential present and future distribution of the baobab tree.

A fourth research limitation is that Maxent modelling results should ideally be validated with *in situ* experiments which could confirm if baobabs can grow in the areas predicted to be suitable (section 2.5). *In situ* experiments could also determine if baobabs produce fruits and/or a high yield in these areas (section 2.5). *In situ* experiments are, thus, highly recommended. A fifth and final factor affecting the validity of the model's results is farmers' interest in, and capacity to, cultivate the baobab tree. If farmers do not know that the germination of baobab seeds improves through scarification and that the juvenile period of the tree can be reduced through grafting (section 1.13), or have no access to markets for baobab products, they may not be interested in planting this species even in areas the model shows to be highly suitable for baobab trees now and in the future.

In addition to the five major research limitations identified in the modelling part of this study (chapters 2 and 3), three were identified in the morphological assessment (chapters 4, 5 and 6). First, it should be noted that if baobab trees from other countries could have been sampled for fruit and/or leaf characteristics, a better overview of the morphological variation within this species could have been established. However, due to financial and time constraints, it was not possible to carry out more field work. Further research on baobab morphological variation, especially in south-eastern Africa, is recommended.

Secondly, variation in baobab leaf, fruit and seedling morphology should also be validated with genetic studies. Genetic studies can confirm if the characters that seemed to be genetically determined in this investigation are genetically determined or not. Then, one can choose a certain ‘ideotype’ of baobab because it is known that e.g., it has better characteristics for drought adaptation. More baobab tree genetic studies, especially studies on genetic differences between and within baobab tree populations from south-eastern Africa, are needed.

Thirdly, it should also be mentioned that in this investigation I considered baobab tree adaptation to drought and high pulp content of the fruit to be desirable traits. However, in some parts of Africa or elsewhere, farmers might be interested in planting baobab trees which are tolerant to heavy rains, or baobab trees which produce fruits known to have high nutritional properties (section 2.5, 5.5). As highlighted by Leakey et al. (2005), farmers’ preferences should be analysed and considered, before selecting ‘superior’ planting material.

Further research is also needed to confirm if baobab trees producing fruits with desirable traits produce fruits with the same traits when grown in another environment (section 5.5). Long-term studies, especially *in situ* experiments, in particular, following the effect of drought on the baobab tree at young stages (not only at seedling stage) and tree recovery after drought are also recommended (section 6.5).

7.3 Novelty, choice of methods and applications of this research

Novelty of this investigation

This research has several innovative aspects. It is one of the first studies on modelling the distribution of an under-utilised fruit tree species. To my knowledge, only the distribution of the tamarind tree has been studied using ecological niche modelling (Bowe and Haq 2010). Although Maxent modelling has not been used to investigate unresolved issues in the field of species distribution modelling (e.g., the effect of spatial bias on species modelling, Osborne and Leitao 2009), the study of ‘potential cultivation sites’ of a species is a new application of Maxent modelling. This investigation is also one of the first studies on the potential effect of climate change on an under-utilised fruit tree species. As mentioned in section 3.1, although species distribution modelling has often been used to plan conservation actions, few studies take climate change into account, and few focus on African plant species.

Moreover, this investigation is also the first report on variation in baobab leaf characteristics and its implications for drought tolerance. As stated in section 4.1, although several authors have highlighted the variation in fruit morphology within this species, no published reports were found on variation in leaf morphology. Baobab seedlings' response to short-term drought stress (chapter 6) is also the first of its kind. Although drought is one of the most important factors limiting seedling survival of savanna trees (see section 6.1), little information on seedling response to drought stress is available for most under-utilised parkland tree species (see section 6.1, 6.5).

Choice of methods

Maxent modelling seems to be a useful tool for studying the distribution of the baobab tree, and for predicting potential cultivation sites of a species (although potential cultivation sites should be validated with *in situ* experiments). This software is available for free on internet and it also has tutorials free of charge. The climatic and soil data used in this study are also available for free on internet. Maxent, together with environmental data such as Worldclim data, offer the opportunity to study the distribution of other under-utilised tree species, for which the physiological data required for mechanistic modelling (see chapter 2) is not available. Especially in Africa, where financial resources are limited and high resolution country or regional maps are not available, Maxent and bioclimatic variables offer a good research opportunity. For example, Maxent and Worldclim data are now being used to study the distribution of Bush mango *Irvingia gabonensis* (Aubry-Lecomte ex O'Rorke) Baill. in Benin and Togo (R. Vihotogbé 2010, pers. comm.).

The methodology used to study baobab leaf morphological variation also seems to be adequate. Nail polish impressions of the leaves are an easily replicable low cost method for studying drought adaptation. This is particularly important for carrying out fieldwork in Africa, where expensive and fragile equipment might complicate and/or delay experiments. Nail polish impressions of baobab leaves are being used at the moment to study baobab leaf morphological variation related to several pruning levels in Mali (A. Kouyaté 2010, pers. comm.).

The baobab seedling experiments carried out in the greenhouse in Belgium were also successful. Although baobab seedlings were growing more slowly compared with baobab seedlings grown in Benin by Assogbadjo et al. (2010) (see chapter 6), significant differences between seed provenances in both baobab seedling morphology and response to short-term drought stress could be observed. Although there are difficulties in carrying out these type of experiments (e.g., bringing the seeds from Africa, controlling the air temperature and the light), they have the advantage that there are no herbivores or insects around (which are often a problem in *in situ* seedling experiments, pers. obs.). Another baobab seedling experiment is being carried out in the same greenhouse in Belgium (N. Van den Bilcke 2010, pers. comm.).

Research applications

At first glance, the potential applications of this investigation are relatively straight forward: (1) plant the baobab tree in the sites suggested for cultivation (chapter 2); (2) implement the conservation strategies recommended in chapter 3; and (3) cultivate the baobab trees from the provenances that seem to have 'superior' characteristics for leaf, fruit and/or seedling morphology (chapters 4, 5, 6). However, as discussed earlier, implementation of these recommendations will need to take into consideration several limiting factors such as land tenure, traditional beliefs, financial and political constraints for conservation actions, farmers' preferences and marketing possibilities, among others.

Ideally, if baobab genetic variation was better studied and the variation in baobab morphology was fully understood (if baobab 'ideotypes' were known), one could recommend planting a certain 'plus type' of baobab (e.g., a type of baobab that withstands drought) in a particular area (e.g., an area known to have droughts frequently). Similarly, one could recommend protecting baobab trees that are known to have different genetic characteristics. Although this investigation contributes towards these two goals, it cannot specifically determine which type of baobab should be planted where and which trees should be protected (based on the particularity of their genetic characteristics). Further research is needed.

7.4 The baobab tree: the fruit for the future

In recent years under-utilised tree species, such as the baobab tree, and their role in fighting against malnutrition, hunger and poverty have gained greater recognition (Dawson et al. 2009, Jamnadass et al. 2009). Apart from its direct dietary contribution, the presence of baobab trees in agroforestry systems such as the West African parklands also contributes towards both maintaining soil fertility (Amundson et al. 1995) and diversifying crops, the latter being important for making local farmers less vulnerable to crop failure, a growing concern with predicted changes in future climate. As mentioned earlier in this investigation, the baobab is one of the most important species that could be domesticated, cultivated and conserved in Africa (Matig et al. 2002). However, domestication is neither an easy nor a short-term process: a lot of systematic research is needed. Even for plants such as *Jatropha curcas*, the promising sustainable biofuel species, there is a surprising lack of scientific knowledge about basic agronomic properties (Fairless 2007). For the baobab tree, although it has been identified as ‘the fruit for the future’ (Sidibé and Williams 2002) and a ‘billion dollar’ fruit industry (Sekhar 2008), there is also a lack of scientific knowledge of this species.

It seems that baobab tree densities are very variable in the landscape (see chapter 1), and it is never a dominant species. Quantities of fruits are variable between both trees and years, and some trees can go several years without bearing fruit (Swanapel 1993, Assogbadjo et al. 2005b, Wickens and Lowe 2008). Baobab trees also remain overexploited for bark and leaf harvesting, which reduces the number of fruits (Romero et al. 2001, Dhillion and Gustad 2004). There is little natural regeneration (Wickens 1982) and adult trees are threatened by droughts, disease and land use change (Romero et al. 2001, Wickens and Lowe 2008). Climate change also seems to have a negative effect on the distribution of this species (discussed later in this chapter). Thus, if the baobab tree is going to become the fruit for the future, and if in future it is to be consumed widely in Africa and in the western world, considering the growing population in Africa and the potential growing demand for fruit pulp in the international market, this species should be cultivated more widely.

This species can, indeed, be easily cultivated (Sidibé and Williams 2002, Wickens and Lowe 2008). However, for several reasons, such as land tenure, traditional beliefs, ignorance of seed pre-treatment and grafting techniques, local farmers do not plant it (Boffa 1999, NRC 2006, Wickens and Lowe 2008). However, local farmers may gain more interest in planting it. Preliminary interviews from Malawi show that: (i) if farmers own their land, (ii) there are no taboos such as ancestors living in the baobab trees, and (iii) there is a market for the baobab fruits (in Malawi baobab fruits are highly appreciated by local people, by local processing companies and by a company which exports them to Europe, pers. obs.); farmers are then willing to plant this species and they have the necessary skills to do it. After a short demonstration, farmers were able to carry out both baobab seed scarification and grafting techniques (unpublished results). Although land tenure issues and traditional beliefs vary greatly in different parts of Africa and are not easily changed; preliminary results from Malawi indicate that it is possible to convince farmers and train them to plant this species.

So, where could the baobab tree be planted? Modelling results showed that the baobab tree could be widely cultivated in dryland Africa from Senegal to Sudan and from south Somalia to South Africa (chapter 2). In Africa, where locals both use and appreciate this species, cultivation of this species might be easier than elsewhere. Outside this continent, India, where the species already exists and it is utilised (mainly for medicinal purposes, Vaid and Vaid 1978, Wickens and Lowe 2008), cultivation also seems feasible. In this country, like in Africa, baobab cultivation could be aimed at both combating malnutrition (local consumption) and international commercialisation. Apart from India, the baobab tree could also be cultivated in Australia, Madagascar, Brazil and Mexico (see chapter 2). In Australia and Madagascar, where other baobab tree species naturally occur, the cultivation of the African baobab could be aimed at international commercialisation. In the Americas, although there is the possibility of growing the baobab tree in Brazil and Mexico, cultivation seems complicated as locals are not familiar with this species and there are no adult trees available for grafting.

When considering baobab cultivation outside Africa, the intellectual property rights of local communities in Africa over their long indigenous knowledge of baobab use and over baobab germplasm must be upheld. As proposed by the Convention on Biological Diversity, specific measures may be needed to ensure equitable sharing of the benefits arising from the cultivation of this species (see chapter 2).

Baobab tree cultivation might be encouraged if cultivars existed with specific properties, e.g., greater harvested volume, better reliability and quality of supply (Chikamai and Tchatat 2009). The process of domestication seeks to capture and multiply trees with desirable characteristics, taking advantage of the variation found in the wild (Leakey et al. 2003, 2005, Pye-Smith 2010). Results from this study suggest that there is a great variability in leaf, fruit and seedling morphology of the baobab tree, and thus, there is room for selecting ‘superior’ planting material.

If we consider ‘superior’ planting material for marketing purposes, baobab fruit pulp has the highest commercialisation value (Akinnifesi et al. 2007). In this case, the desired traits might be large heavy fruits with high pulp content. Results from *in situ* fruit morphological variation found in Mali and Malawi (chapter 5) indicate that large heavy fruits are found in wetter areas while trees with significantly high pulp content are found in Likoma in Malawi. Indeed, Likoma (an island in Lake Malawi isolated from mainland for a long time) might have an interesting genetic pool for baobab tree domestication. Although further research is needed to confirm if baobab trees known to produce fruits with desirable traits continue to produce a similar type of fruits when grown in another environment, the results from this study suggest that ‘superior’ baobab trees for fruit characteristics could be selected.

Another interesting trait for baobab domestication seems to be tolerance to drought, as drought is the main limiting factor for most savanna trees and climate predictions suggest more droughts in dryland Africa (Blum 1997, Brooks 2004). Results from *in situ* leaf morphological variation in Benin and Malawi (chapter 4) indicate that baobab trees from northern Benin and Mangochi area in Malawi have small thick leaves with high stomata density and small guard cell length, characteristics often related to drought adaptation (Abrams et al. 1990). As similar leaf characteristics were observed in the *ex situ* experiments (chapter 4 and chapter 6), it seems that these characteristics are genetically determined. Thus, locally desirable types with 'better' traits for drought adaptation could be selected and cultivated. Results from the seedling experiments (chapter 6) also point to the possibility of selecting planting materials better adapted to drought in terms of seedling characteristics (e.g., high water content in both the stem and the taproot during 4-week drought stress). In this case, planting material should be taken from Tatakarat or Bendjiely in Mali and Nchalo or Kalasamba in Malawi.

A further possibility for baobab tree domestication which requires further research is grafting two 'types' of baobab trees which have different desirable characteristics. In Mali, the African baobab (*A. digitata*), adapted to local climatic conditions, has been successfully grafted with other species of baobab from Madagascar having a higher leaf nutritional value (Maranz et al. 2007). Similarly, *A. digitata* from different provenances known to have desirable traits could be grafted: e.g., in Malawi, baobab trees from Likoma which have high fruit pulp percentage could be grafted with baobab trees from Mangochi which seem to be better adapted to drought. The possibility of planting and/or grafting baobab trees from West Africa in south-eastern Africa and the visa-versa should also be further investigated. Results from the modelling suggest that they have different ecological tolerances (chapter 2) while results from the morphological assessment suggest differences in fruit, leaf and seedling morphology (chapters 4, 5 and 6). Maybe, a combination of West African and south-eastern African baobab trees is the way forward for baobab domestication.

An additional important factor that needs to be taken into account when considering which is the best planting material for an area is the farmers' preferences. Assogbadjo et al. (2008) showed that Ditamari people from Benin prefer low fruit pulp content while Mossi people from Burkina Faso mention this trait as undesirable. While high pulp content might be the desired trait for baobab cultivation aimed at commercialisation, local farmers in the driest parts of west Africa might prefer baobab trees adapted to drought or baobab trees which produce tasty leaves, as leaves are daily consumed in some of these areas. In order to make the domestication process more effective, local farmers' preferences should be taken into account before making a confirmed recommendation in a specific area, as suggested by Leakey et al. (2003, 2005).

Apart from the importance of cultivating and domesticating the baobab tree, in order to safeguard the livelihoods of many local communities and baobab genetic variation (very important in the domestication process of a species), this valuable species should also be protected. As mentioned earlier, several factors threaten baobab populations all over Africa, including climate change (Wickens and Lowe 2008). Although there are limitations and uncertainty in modelling potential future distribution of a species (see chapter 3), all models and scenarios used in this study suggested that there will be little suitable habitat for the baobab tree in the future. Adult baobab trees, with an extensive root system and a large trunk which accumulates water (Owen 1974, Sidibé and Williams 2002) might survive for a period of time, but baobab regeneration seems unlikely in these future unsuitable habitats. Severe droughts, like the Great Drought of the late 1960s in the Sahel, during which many baobab trees died (Wickens 1982), or outbreak of disease, such as the sooty baobab disease which killed many baobab trees in Zimbabwe in the 1990s (Sharp 1993, Piearce et al. 1994), might reduce these baobab tree populations growing in unsuitable habitats, and with no natural regeneration, these populations will eventually become extinct.

So, how can we protect this species? Considering the limited resources available in Africa, and the number of protected areas which while existing 'on paper' are not actually 'protected on the ground' (e.g., in Benin only three out of more than 60 protected areas existing 'on paper' are 'protected on the ground', B. Sinsin 2010, pers. comm.), I focused my studies on the existing protected areas rather than suggesting new ones (although this could also be an option: e.g., in Senegal attempts are being made to protect a small baobab forest, T. Digane 2008, pers. comm.). A number of protected areas were found to have suitable habitat for the baobab tree in the future under most models (GCM) and scenarios used in this study, suggesting that conservation effort should be focused on these protected areas. It is known that in some protected areas elephants and humans overexploit this species: elephants eat baobab seedlings and chew baobab bark (making big holes which might cause some adult trees to collapse, Barnes 1994, Wickens and Lowe 2008) while humans intensively harvest baobab bark or leaves (Schumann et al. 2010) which reduces fruit production. While human utilisation of the baobab tree in the protected areas could be limited to fruit harvesting, baobab seedlings could be fenced (e.g., with a type of cage made with palm leaves with small holes) in order to protect them from elephants and other herbivores. With the aim of promoting baobab tree regeneration, baobab seedlings could also be planted in protected areas.

Apart from *in situ* conservation in protected areas, *ex situ* conservation in Seed Banks might be the best option in areas which may have no suitable habitat for the baobab tree in the future (e.g., central Sudan).. While baobab translocation and introduction of Forestry Laws to limit access rights to baobab trees do not seem to be suitable or cost-effective options (see chapter 3), conservation 'through sustainable utilisation' is recommendable. If local people use the baobab tree and appreciate it, they are more likely to preserve it in their fields, their communal forest or in the wild in general, and even be interested in planting and domesticating it. Thus, baobab conservation, utilisation, cultivation and domestication are all interconnected and depend, above all, on farmers' interest in this species. Therefore, the most important thing that needs to be done is to preserve farmers' and local people's interest in this species.

With more people moving into urban areas and the resulting changes in diet, as well as growing preferences for more 'western' products such as drinks like coke, some people think that non-timber forest products (such as baobab products) are 'products for the poor' or 'products for the rural people'(pers. obs.). However, in some countries, there is a growing interest for 'local products' even in urban areas: this is the case of baobab juice in Malawi. In this country, two local companies commercially produce baobab juice, which is sold next to the coke bottles in most supermarkets in this country, and in a number of small shops. While in this country synthetic ropes are more commonly used than baobab bark ropes, and baobab leaves are mainly consumed in times of famine, baobab juice is highly appreciated by both rural and urban communities, which makes farmers aware of the commercial value of this species and they are keen to preserve it in their fields and even plant it (unpublished results).

In West Africa, in general, people appreciate the baobab tree for its leaves, which are consumed daily and even up to three times a day in some communities (Buchmann et al. 2010, pers. obs.). As mentioned earlier, in some areas of West Africa, baobab trees are severely pruned for leaf consumption to an extent that the trees stop fruiting (Dhillion and Gustad 2004). While, in order to maintain this species, we should therefore promote its multiple uses (including leaf consumption), we should also inform farmers about the best management techniques (e.g., limited pruning for leaf harvesting, no intensive debarking) and the need to protect baobab seedlings (as there is little natural regeneration). As suggested by Buchmann et al. (2010), training workshops on sustainable fruit, leaf and bark harvesting could be organised locally. In Namibia, similar training has successfully guided local harvesters towards environmentally friendly harvest methods of the Devil's Claw, *Harpagophytum procumbens* L. (Nemarundwe et al. 2008).

Although many farmers may think that the baobab tree has always been there, it has always been used and it has always been healthy; results from preliminary interviews in southern Malawi suggest that, on reflection, some farmers recognise that: (i) there were more trees in the fields when I was a kid, (ii) now we have to walk further to collect enough fruits (or bark or leaves), (iii) before we used it for some things that we do not use it for any more (e.g., medicinal uses), (iv) now at certain times of the year the fruits (or leaves or bark) are very expensive and hard to find, and/or (v) in fact there are very few baobab seedlings.

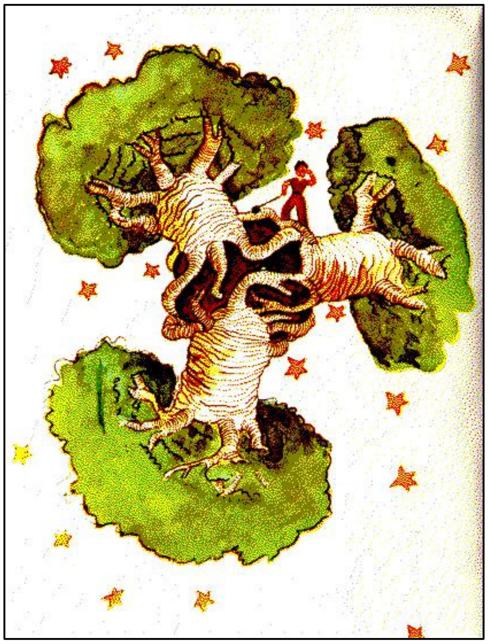
Some people even wonder why, if every year there are fewer baobabs and there are going to be few suitable habitats for this species in the future, they should protect it, maybe it is a species 'remaining' from another 'era' and it is meant to go extinct (results from preliminary interviews carried out in southern Malawi). But despite these challenges, can we afford to let this important nutritious multiple-purpose 'Cinderella' species disappear? What about the more than 300 reported uses it has? Do we have other plant products or commercial products available to substitute them? And if we have, how expensive are they? Can local farmers in some parts of Africa afford them?

We are facing challenges never faced before due to growing populations and the predicted changes in climate. While baobab trees have survived in Africa for a long time, increasing human population and environmental change appear to be leading to a decline in the numbers of baobab trees, and thus there is more and more pressure on the remaining trees. What we learned from the Great Drought of the late 1960s in the Sahel or the 'sooty baobab disease' is that, in a short period of time, many adult 'healthy' looking baobab trees might disappear, increasing the vulnerability of the local farmers in these areas to other threats, such as malnutrition or disease.

The baobab tree offers nutritious food, useful materials, medicine, income and even ecosystem services to humans, and water, food and shelter to many animal and plant species. We have therefore for a long time taken advantage of this species; we could and should now start doing something for the baobab tree: we should protect it, promote its sustainable use, and domesticate it. This research has aimed at contributing towards these goals, not only scientifically but also on a 'more practical' level. As part of a large European Research Project on domestication and development of the baobab tree, I was aware of the importance of knowledge transfer. I tried therefore, to communicate my results to local farmers: I created and translated small factsheets on baobab cultivation techniques (in French for West Africa and in Chichewa for Malawi, see Annex IV).

As mentioned in chapter 1, the baobab tree is one of many other under-utilised fruit bearing trees commonly found in the agroforestry systems of dryland Africa. Promoting baobab tree conservation and cultivation might also help raise awareness among the local farmers, the local authorities and the international community (including the scientific community), of the importance of these type of under-utilised species and the agricultural systems where they are commonly found. Under-utilised tree species and agroforestry systems have the potential to help local farmers to fight malnutrition, hunger, disease and poverty. Under-utilised tree species and agroforestry systems can also make local farmers become more resilient to the effects of climate change. This is particularly relevant in many parts of Africa, where the percentage of arable land is low, the soils are poor, most agriculture is rain fed, infrastructure and access to markets are limited, and 80% of the population are rural poor farmers; under-utilised tree species and agroforestry systems are even more important than elsewhere. If the baobab tree becomes ‘the fruit for the future’, I hope, it will also help promote other under-utilised fruit trees and agroforestry systems as a whole.

If the baobab tree is going to become the fruit for the future,
we do have to protect, domesticate and cultivate it.



Baobabs from “Le Petit Prince” by Antoine de Saint-Exupery.

APPENDIX I

Journal paper:

Cuni Sanchez A, Osborne P, Haq N (2010) Identifying the global potential for baobab tree cultivation using ecological niche modelling. *Agroforestry Systems* 80(2):191-201.

APPENDIX II

Full set of records used in this investigation (chapter 2 and 3).

Supporting Information: number, geographic coordinates, country, area (E: East Africa, W: West Africa), source and type of record (FW: field work record, H: herbarium record) of the baobab growing localities used in this study.

Id	Latitude	Longitude	Country	Area	Source	Record type
1	16.080	-15.120	Angola	E	Pock Tsy et al. (2009)	FW
2	13.186	-8.880	Angola	E	KEW Herbarium	H
3	13.400	-12.567	Angola	E	Wickens and Lowe (2008)	H
4	14.750	-9.167	Angola	E	Wickens and Lowe (2008)	H
5	13.250	-8.833	Angola	E	Wickens and Lowe (2008)	H
6	12.167	-15.167	Angola	E	Wickens and Lowe (2008)	H
7	15.750	-16.117	Angola	E	Wickens and Lowe (2008)	H
8	13.833	-8.283	Angola	E	Wickens and Lowe (2008)	H
9	14.483	-9.983	Angola	E	Wickens and Lowe (2008)	H
10	13.417	-14.267	Angola	E	Wickens and Lowe (2008)	H
11	1.863	6.410	Benin	W	A. Cuni Sanchez	FW
12	2.232	6.994	Benin	W	A. Cuni Sanchez	FW
13	2.191	7.735	Benin	W	A. Cuni Sanchez	FW
14	1.644	8.744	Benin	W	A. Cuni Sanchez	FW
15	1.228	10.230	Benin	W	A. Cuni Sanchez	FW
16	1.112	10.840	Benin	W	A. Cuni Sanchez	FW
17	3.201	12.048	Benin	W	A. Cuni Sanchez	FW
18	2.442	11.618	Benin	W	A. Cuni Sanchez	FW
19	1.317	10.267	Benin	W	A.S. Larsen	FW
21	2.250	6.900	Benin	W	A.S. Larsen	FW
24	1.300	10.350	Benin	W	Frankfurt Herbarium	FW
27	1.450	10.450	Benin	W	Frankfurt Herbarium	FW
30	1.330	10.180	Benin	W	Frankfurt Herbarium	FW
47	2.293	7.960	Benin	W	Pock Tsy et al. (2009)	FW
48	1.443	10.343	Benin	W	Pock Tsy et al. (2009)	FW
50	2.600	7.367	Benin	W	Paris Herbarium	H
51	26.488	-20.568	Botswana	E	Pock Tsy et al. (2009)	FW
52	24.769	-20.113	Botswana	E	Pock Tsy et al. (2009)	FW
53	24.691	-17.949	Botswana	E	Pock Tsy et al. (2009)	FW
54	21.783	-18.280	Botswana	E	KEW Herbarium	H
55	25.817	-20.333	Botswana	E	KEW Herbarium	H
56	26.167	-20.200	Botswana	E	KEW Herbarium	H
57	25.375	-21.375	Botswana	E	PRECIS database	H
58	22.375	-20.875	Botswana	E	PRECIS database	H
59	25.625	-20.375	Botswana	E	PRECIS database	H
60	26.125	-20.125	Botswana	E	PRECIS database	H
61	23.125	-19.625	Botswana	E	PRECIS database	H
62	21.875	-18.375	Botswana	E	PRECIS database	H
63	24.250	-18.000	Botswana	E	Wickens and Lowe (2008)	H
64	20.567	-19.800	Botswana	E	Wickens and Lowe (2008)	H
65	23.083	-20.633	Botswana	E	Wickens and Lowe (2008)	H
66	21.700	-21.567	Botswana	E	Wickens and Lowe (2008)	H

68	25.233	-20.183	Botswana	E	Wickens and Lowe (2008)	H
69	-0.630	14.863	Burkina Faso	W	Frankfurt Herbarium	FW
70	0.219	11.820	Burkina Faso	W	Frankfurt Herbarium	FW
72	-0.283	14.372	Burkina Faso	W	Frankfurt Herbarium	FW
73	-0.413	14.346	Burkina Faso	W	Frankfurt Herbarium	FW
74	-0.086	14.567	Burkina Faso	W	Frankfurt Herbarium	FW
75	-0.755	14.872	Burkina Faso	W	Frankfurt Herbarium	FW
79	-0.480	14.807	Burkina Faso	W	Frankfurt Herbarium	FW
80	-0.283	14.388	Burkina Faso	W	Frankfurt Herbarium	FW
81	-0.324	11.701	Burkina Faso	W	Frankfurt Herbarium	FW
82	0.983	12.194	Burkina Faso	W	Frankfurt Herbarium	FW
83	0.519	11.643	Burkina Faso	W	Frankfurt Herbarium	FW
84	-1.200	11.550	Burkina Faso	W	A.S. Larsen	FW
85	0.933	12.950	Burkina Faso	W	A.S. Larsen	FW
86	1.800	12.150	Burkina Faso	W	Frankfurt Herbarium	FW
87	-0.217	14.083	Burkina Faso	W	Frankfurt Herbarium	FW
88	-0.983	11.100	Burkina Faso	W	Frankfurt Herbarium	FW
89	-0.174	14.934	Burkina Faso	W	Frankfurt Herbarium	FW
90	0.350	12.067	Burkina Faso	W	Frankfurt Herbarium	FW
91	-0.253	14.473	Burkina Faso	W	Frankfurt Herbarium	FW
92	-4.295	11.180	Burkina Faso	W	Pock Tsy et al. (2009)	FW
93	-4.801	11.615	Burkina Faso	W	Pock Tsy et al. (2009)	FW
94	-2.925	11.751	Burkina Faso	W	Pock Tsy et al. (2009)	FW
95	-0.081	14.703	Burkina Faso	W	Paris Herbarium	H
96	13.577	5.860	Cameroon	W	Pock Tsy et al. (2009)	FW
97	13.749	9.556	Cameroon	W	Pock Tsy et al. (2009)	FW
98	13.488	9.395	Cameroon	W	KEW Herbarium	H
99	13.533	8.983	Cameroon	W	Paris Herbarium	H
100	13.509	10.252	Cameroon	W	Paris Herbarium	H
101	13.569	10.604	Cameroon	W	Wagningen Herbarium *a*	H
103	16.010	10.227	Chad	W	Pock Tsy et al. (2009)	FW
104	15.036	12.112	Chad	W	Pock Tsy et al. (2009)	FW
105	15.417	10.233	Chad	W	Paris Herbarium	H
114	38.683	15.660	Eritrea	E	Pock Tsy et al. (2009)	FW
115	37.517	15.283	Eritrea	E	KEW Herbarium	H
116	38.617	15.667	Eritrea	E	Uppsala Herbarium *a*	H
117	38.500	15.767	Eritrea	E	Wickens and Lowe (2008)	H
120	-15.839	12.562	Gambia	W	Pock Tsy et al. (2009)	FW
121	-16.010	13.177	Gambia	W	Pock Tsy et al. (2009)	FW
122	-16.567	13.467	Gambia	W	Wickens and Lowe (2008)	H
124	-0.250	5.583	Ghana	W	Wickens and Lowe (2008)	H
125	-0.217	6.000	Ghana	W	Wickens and Lowe (2008)	H
126	-0.800	9.433	Ghana	W	Wickens and Lowe (2008)	H
127	-10.510	9.293	Guinea	W	Pock Tsy et al. (2009)	FW
128	-9.200	10.214	Guinea	W	Pock Tsy et al. (2009)	FW
119	-13.712	9.509	Guinea	W	KEW Herbarium	H
129	-11.850	10.600	Guinea	W	Wickens and Lowe (2008)	H
133	-10.733	10.033	Guinea	W	Paris Herbarium	H
130	-16.196	12.393	Guinea-Bissau	W	Pock Tsy et al. (2009)	FW
132	-15.383	11.283	Guinea-Bissau	W	Wickens and Lowe (2008)	H
134	-5.639	9.452	Ivory Coast	W	Pock Tsy et al. (2009)	FW
135	-6.086	9.609	Ivory Coast	W	Pock Tsy et al. (2009)	FW
136	-4.503	7.089	Ivory Coast	W	Paris Herbarium	H

137	-5.000	7.700	Ivory Coast	W	Wickens and Lowe (2008)	H
138	38.000	-2.550	Kenya	E	A.S. Larsen	FW
140	39.527	-3.460	Kenya	E	Pock Tsy et al. (2009)	FW
141	37.960	-2.410	Kenya	E	Pock Tsy et al. (2009)	FW
142	40.117	-3.217	Kenya	E	BG Berlin-Dahlem *a*	H
143	38.167	0.125	Kenya	E	KEW Herbarium	H
147	38.717	-3.483	Kenya	E	KEW Herbarium	H
148	40.017	-3.300	Kenya	E	Uppsala Herbarium *a*	H
149	39.583	-3.800	Kenya	E	Wickens and Lowe (2008)	H
151	38.250	-1.250	Kenya	E	Wickens and Lowe (2008)	H
152	37.650	-0.683	Kenya	E	Wickens and Lowe (2008)	H
156	37.483	-0.750	Kenya	E	Wickens and Lowe (2008)	H
157	37.783	-3.383	Kenya	E	Wickens and Lowe (2008)	H
159	37.667	-3.400	Kenya	E	Wickens and Lowe (2008)	H
160	39.217	-4.667	Kenya	E	Wickens and Lowe (2008)	H
161	35.000	-17.000	Malawi	E	A.S. Larsen	FW
162	34.000	-11.000	Malawi	E	A.S. Larsen	FW
163	35.526	-14.868	Malawi	E	Pock Tsy et al. (2009)	FW
164	35.210	-16.684	Malawi	E	A. Cuni Sanchez	FW
165	34.920	-16.493	Malawi	E	A. Cuni Sanchez	FW
166	34.839	-16.338	Malawi	E	A. Cuni Sanchez	FW
167	34.767	-16.094	Malawi	E	A. Cuni Sanchez	FW
168	34.748	-15.518	Malawi	E	A. Cuni Sanchez	FW
170	34.791	-15.392	Malawi	E	A. Cuni Sanchez	FW
171	35.033	-15.124	Malawi	E	A. Cuni Sanchez	FW
172	35.251	-15.069	Malawi	E	A. Cuni Sanchez	FW
173	35.235	-14.455	Malawi	E	A. Cuni Sanchez	FW
174	34.808	-14.312	Malawi	E	A. Cuni Sanchez	FW
175	34.501	-14.003	Malawi	E	A. Cuni Sanchez	FW
176	34.370	-13.768	Malawi	E	A. Cuni Sanchez	FW
178	34.500	-15.500	Malawi	E	Phytotrade Africa	H
180	34.080	-14.010	Malawi	E	Phytotrade Africa	H
181	34.900	-15.600	Malawi	E	Phytotrade Africa	H
182	34.960	-15.040	Malawi	E	Phytotrade Africa	H
183	34.500	-15.550	Malawi	E	Phytotrade Africa	H
184	34.440	-16.220	Malawi	E	Phytotrade Africa	H
185	35.170	-14.890	Malawi	E	Phytotrade Africa	H
187	34.130	-14.410	Malawi	E	Phytotrade Africa	H
190	-6.840	12.744	Mali	W	DADOBAT Project	FW
191	-11.702	14.502	Mali	W	DADOBAT Project	FW
192	-4.239	13.651	Mali	W	DADOBAT Project	FW
193	-6.730	11.981	Mali	W	DADOBAT Project	FW
194	-9.586	12.806	Mali	W	DADOBAT Project	FW
195	-5.897	13.307	Mali	W	DADOBAT Project	FW
196	-5.785	11.587	Mali	W	DADOBAT Project	FW
197	-3.580	14.481	Mali	W	DADOBAT Project	FW
199	-8.514	14.154	Mali	W	Pock Tsy et al. (2009)	FW
208	-5.968	13.25	Mali	W	Dhillion, Gustard (2004)	FW
209	-10.433	12.967	Mali	W	Duvall (2007)	FW
200	-8.000	12.650	Mali	W	BG Berlin-Dahlem *a*	H
201	-5.993	14.253	Mali	W	Paris Herbarium	H
202	-4.896	13.303	Mali	W	Paris Herbarium	H
203	-4.560	13.905	Mali	W	Paris Herbarium	H
204	-3.317	14.417	Mali	W	Wickens and Lowe (2008)	H

205	-11.467	14.433	Mali	W	Wickens and Lowe (2008)	H
210	-15.093	16.617	Mauritania	W	Pock Tsy et al. (2009)	FW
211	-13.827	16.643	Mauritania	W	Pock Tsy et al. (2009)	FW
213	-6.933	12.267	Mauritania	W	Wickens and Lowe (2008)	H
214	33.333	-17.035	Mozambique	E	A.S. Larsen	FW
215	35.110	-22.593	Mozambique	E	Pock Tsy et al. (2009)	FW
216	34.792	-19.075	Mozambique	E	Pock Tsy et al. (2009)	FW
608	39.984	-14.921	Mozambique	E	A. Cuni Sanchez	FW
609	40.121	-12.247	Mozambique	E	A. Cuni Sanchez	FW
610	40.479	-12.065	Mozambique	E	A. Cuni Sanchez	FW
217	37.000	-14.900	Mozambique	E	KEW Herbarium	H
218	34.230	-19.069	Mozambique	E	Paris Herbarium	H
221	33.050	-16.220	Mozambique	E	Phytotrade Africa	H
222	33.650	-16.930	Mozambique	E	Phytotrade Africa	H
225	39.240	-15.130	Mozambique	E	Phytotrade Africa	H
227	34.800	-12.680	Mozambique	E	Phytotrade Africa	H
228	34.010	-18.000	Mozambique	E	Phytotrade Africa	H
229	34.960	-12.750	Mozambique	E	Phytotrade Africa	H
231	36.920	-17.560	Mozambique	E	Phytotrade Africa	H
232	37.530	-17.330	Mozambique	E	Phytotrade Africa	H
233	35.800	-16.267	Mozambique	E	Wickens and Lowe (2008)	H
234	34.567	-16.983	Mozambique	E	Wickens and Lowe (2008)	H
238	35.600	-18.033	Mozambique	E	Wickens and Lowe (2008)	H
239	33.583	-16.167	Mozambique	E	Wickens and Lowe (2008)	H
240	15.627	-20.593	Namibia	E	Pock Tsy et al. (2009)	FW
241	20.501	-19.607	Namibia	E	Pock Tsy et al. (2009)	FW
242	13.773	-18.365	Namibia	E	Pock Tsy et al. (2009)	FW
243	21.693	-18.143	Namibia	E	Pock Tsy et al. (2009)	FW
244	15.875	-21.375	Namibia	E	PRECIS database	H
245	20.875	-19.625	Namibia	E	PRECIS database	H
246	22.125	-18.625	Namibia	E	PRECIS database	H
247	24.375	-17.875	Namibia	E	PRECIS database	H
248	13.625	-17.625	Namibia	E	PRECIS database	H
249	14.625	-17.625	Namibia	E	PRECIS database	H
250	14.875	-17.625	Namibia	E	PRECIS database	H
251	15.125	-17.625	Namibia	E	PRECIS database	H
252	15.875	-17.375	Namibia	E	PRECIS database	H
253	24.125	-17.375	Namibia	E	PRECIS database	H
254	13.247	-17.002	Namibia	E	PRECIS database	H
255	8.500	13.133	Niger	W	A.S. Larsen	FW
256	3.545	13.070	Niger	W	Pock Tsy et al. (2009)	FW
257	8.892	13.180	Niger	W	BG Berlin-Dahlem *a*	H
258	3.250	14.000	Niger	W	Wickens and Lowe (2008)	H
259	7.167	13.483	Niger	W	Wickens and Lowe (2008)	H
260	7.000	12.050	Nigeria	W	Frankfurt Herbarium	FW
261	13.217	12.239	Nigeria	W	Frankfurt Herbarium	FW
262	14.259	12.258	Nigeria	W	Frankfurt Herbarium	FW
263	8.609	8.941	Nigeria	W	Pock Tsy et al. (2009)	FW
264	8.528	12.004	Nigeria	W	Pock Tsy et al. (2009)	FW
265	3.858	7.867	Nigeria	W	KEW Herbarium	H
266	13.160	11.845	Nigeria	W	KEW Herbarium	H
268	7.983	11.667	Nigeria	W	KEW Herbarium	H
269	9.500	11.450	Nigeria	W	KEW Herbarium	H
270	4.300	7.400	Nigeria	W	Paris Herbarium	H

272	3.433	7.167	Nigeria	W	Wickens and Lowe (2008)	H
273	4.800	12.400	Nigeria	W	Wickens and Lowe (2008)	H
274	7.283	11.567	Nigeria	W	Wickens and Lowe (2008)	H
275	6.667	12.200	Nigeria	W	Wickens and Lowe (2008)	H
276	3.917	7.150	Nigeria	W	Wickens and Lowe (2008)	H
277	4.183	7.800	Nigeria	W	Wickens and Lowe (2008)	H
278	11.567	12.933	Nigeria	W	Wickens and Lowe (2008)	H
279	14.183	12.333	Nigeria	W	Wickens and Lowe (2008)	H
280	7.733	11.017	Nigeria	W	Wickens and Lowe (2008)	H
290	-16.564	15.239	Senegal	W	DADOBAT Project	FW
291	-15.682	15.412	Senegal	W	DADOBAT Project	FW
292	-15.165	15.286	Senegal	W	DADOBAT Project	FW
293	-16.968	14.872	Senegal	W	DADOBAT Project	FW
294	-13.155	14.025	Senegal	W	DADOBAT Project	FW
295	-15.666	14.420	Senegal	W	DADOBAT Project	FW
296	-16.205	14.029	Senegal	W	DADOBAT Project	FW
297	-12.053	12.454	Senegal	W	DADOBAT Project	FW
298	-14.102	13.130	Senegal	W	DADOBAT Project	FW
299	-15.144	12.813	Senegal	W	DADOBAT Project	FW
300	-16.471	14.143	Senegal	W	DADOBAT Project	FW
301	-16.893	14.774	Senegal	W	DADOBAT Project	FW
302	-16.284	12.580	Senegal	W	Pock Tsy et al. (2009)	FW
303	-16.111	14.150	Senegal	W	Pock Tsy et al. (2009)	FW
304	-16.627	14.443	Senegal	W	Pock Tsy et al. (2009)	FW
305	-12.317	12.467	Senegal	W	Arhus herbarium *a*	H
306	-15.550	15.717	Senegal	W	Paris Herbarium	H
307	-17.234	14.694	Senegal	W	Paris Herbarium	H
310	-16.750	12.667	Senegal	W	Wickens and Lowe (2008)	H
311	-16.200	14.483	Senegal	W	Wickens and Lowe (2008)	H
312	-16.617	14.550	Senegal	W	Wickens and Lowe (2008)	H
313	-16.100	12.817	Senegal	W	Wickens and Lowe (2008)	H
315	-12.150	12.583	Senegal	W	Wickens and Lowe (2008)	H
316	-12.200	14.583	Senegal	W	Wickens and Lowe (2008)	H
317	-16.533	14.800	Senegal	W	Wickens and Lowe (2008)	H
318	-17.317	14.733	Senegal	W	Wickens and Lowe (2008)	H
320	-13.650	13.417	Senegal	W	Wickens and Lowe (2008)	H
322	-13.083	8.250	Sierra Leone	W	KEW Herbarium	H
323	43.632	3.104	Somalia	E	Pock Tsy et al. (2009)	FW
324	44.317	3.000	Somalia	E	KEW Herbarium	H
325	44.083	2.783	Somalia	E	KEW Herbarium	H
326	44.083	2.800	Somalia	E	KEW Herbarium	H
327	45.917	2.517	Somalia	E	KEW Herbarium	H
329	30.583	-22.967	South Africa	E	A.S. Larsen	FW
330	29.683	-25.533	South Africa	E	A.S. Larsen	FW
331	31.787	-24.618	South Africa	E	Pock Tsy et al. (2009)	FW
332	29.221	-23.728	South Africa	E	Pock Tsy et al. (2009)	FW
333	28.225	-22.861	South Africa	E	Pock Tsy et al. (2009)	FW
334	30.043	-22.343	South Africa	E	Pock Tsy et al. (2009)	FW
281	31.050	-25.800	South Africa	E	Wickens and Lowe (2008)	H
282	30.067	-22.383	South Africa	E	Wickens and Lowe (2008)	H
283	29.833	-24.383	South Africa	E	Wickens and Lowe (2008)	H
284	29.667	-22.250	South Africa	E	Wickens and Lowe (2008)	H
285	29.950	-22.333	South Africa	E	Wickens and Lowe (2008)	H
286	30.050	-24.333	South Africa	E	Wickens and Lowe (2008)	H

287	31.850	-23.850	South Africa	E	Wickens and Lowe (2008)	H
288	31.583	-23.850	South Africa	E	Wickens and Lowe (2008)	H
289	30.050	-22.033	South Africa	E	Wickens and Lowe (2008)	H
335	15.944	-17.666	South Africa	E	KEW Herbarium	H
336	14.967	-17.500	South Africa	E	KEW Herbarium	H
337	31.500	-23.833	South Africa	E	KEW Herbarium	H
339	15.900	-17.400	South Africa	E	KEW Herbarium	H
340	14.683	-17.583	South Africa	E	KEW Herbarium	H
342	30.875	-24.625	South Africa	E	PRECIS database	H
343	27.625	-23.875	South Africa	E	PRECIS database	H
344	29.875	-23.875	South Africa	E	PRECIS database	H
345	30.625	-23.875	South Africa	E	PRECIS database	H
346	31.625	-23.875	South Africa	E	PRECIS database	H
347	30.125	-23.625	South Africa	E	PRECIS database	H
348	31.625	-23.625	South Africa	E	PRECIS database	H
349	28.375	-23.375	South Africa	E	PRECIS database	H
350	28.625	-23.125	South Africa	E	PRECIS database	H
351	29.375	-23.125	South Africa	E	PRECIS database	H
352	29.125	-22.875	South Africa	E	PRECIS database	H
353	29.375	-22.875	South Africa	E	PRECIS database	H
354	29.625	-22.875	South Africa	E	PRECIS database	H
355	29.875	-22.875	South Africa	E	PRECIS database	H
356	30.125	-22.875	South Africa	E	PRECIS database	H
357	30.375	-22.875	South Africa	E	PRECIS database	H
358	29.375	-22.625	South Africa	E	PRECIS database	H
359	30.125	-22.625	South Africa	E	PRECIS database	H
360	30.375	-22.625	South Africa	E	PRECIS database	H
361	31.125	-22.625	South Africa	E	PRECIS database	H
362	29.125	-22.375	South Africa	E	PRECIS database	H
363	29.625	-22.375	South Africa	E	PRECIS database	H
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328	29.667	12.667	Sudan	E	A.S. Larsen	FW
367	30.210	13.177	Sudan	E	Pock Tsy et al. (2009)	FW
368	26.677	13.593	Sudan	E	Pock Tsy et al. (2009)	FW
369	33.527	14.377	Sudan	E	Pock Tsy et al. (2009)	FW
370	29.583	11.066	Sudan	E	KEW Herbarium	H
372	33.517	-14.483	Sudan	E	Wickens and Lowe (2008)	H
373	29.250	12.350	Sudan	E	Wickens and Lowe (2008)	H
374	29.650	13.050	Sudan	E	Wickens and Lowe (2008)	H
375	28.433	12.700	Sudan	E	Wickens and Lowe (2008)	H
376	28.033	13.667	Sudan	E	Wickens and Lowe (2008)	H
377	33.983	11.450	Sudan	E	Wickens and Lowe (2008)	H
378	27.100	13.450	Sudan	E	Wickens and Lowe (2008)	H
379	30.150	12.783	Sudan	E	Wickens and Lowe (2008)	H
382	34.267	10.600	Sudan	E	Wickens and Lowe (2008)	H
383	29.567	12.767	Sudan	E	Wickens and Lowe (2008)	H
387	27.400	13.183	Sudan	E	Wickens and Lowe (2008)	H
388	29.433	11.117	Sudan	E	Wickens and Lowe (2008)	H
389	27.250	12.983	Sudan	E	Wickens and Lowe (2008)	H
390	38.350	-6.600	Tanzania	E	A.S. Larsen	FW
391	37.083	-7.250	Tanzania	E	Paris Herbarium	FW
392	36.200	-7.667	Tanzania	E	Paris Herbarium	FW
394	35.340	-8.689	Tanzania	E	Pock Tsy et al. (2009)	FW
395	35.860	-7.710	Tanzania	E	Pock Tsy et al. (2009)	FW

396	39.177	-6.160	Tanzania	E	Pock Tsy et al. (2009)	FW
454	36.450	-6.100	Tanzania	E	A.S. Larsen	FW
455	36.433	-7.550	Tanzania	E	A.S. Larsen	FW
456	37.533	-3.450	Tanzania	E	A.S. Larsen	FW
457	37.733	-6.783	Tanzania	E	A.S. Larsen	FW
458	37.600	-6.667	Tanzania	E	A.S. Larsen	FW
460	35.133	-5.933	Tanzania	E	A.S. Larsen	FW
397	36.010	-6.166	Tanzania	E	Arhus herbarium *a*	H
398	35.500	-6.117	Tanzania	E	BG Berlin-Dahlem *a*	H
399	36.983	-6.833	Tanzania	E	BG Berlin-Dahlem *a*	H
400	38.667	-5.100	Tanzania	E	KEW Herbarium	H
401	38.850	-5.783	Tanzania	E	KEW Herbarium	H
402	35.833	-3.583	Tanzania	E	KEW Herbarium	H
403	30.675	-2.467	Tanzania	E	KEW Herbarium	H
404	33.833	-3.583	Tanzania	E	KEW Herbarium	H
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407	33.933	-4.967	Tanzania	E	KEW Herbarium	H
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411	31.933	-8.067	Tanzania	E	KEW Herbarium	H
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413	37.667	-6.817	Tanzania	E	KEW Herbarium	H
414	34.917	-7.650	Tanzania	E	KEW Herbarium	H
416	36.433	-7.533	Tanzania	E	KEW Herbarium	H
418	35.740	7.200	Tanzania	E	KEW Herbarium	H
419	34.533	-10.233	Tanzania	E	KEW Herbarium	H
421	35.335	-2.989	Tanzania	E	Marine Science I., UCSB	H
422	36.299	-3.870	Tanzania	E	Paris Herbarium	H
423	39.467	-10.050	Tanzania	E	Paris Herbarium	H
424	38.650	-5.533	Tanzania	E	Missouri Herbarium *a*	H
425	35.237	-4.954	Tanzania	E	Missouri Herbarium *a*	H
426	34.203	-4.769	Tanzania	E	Missouri Herbarium *a*	H
427	34.141	-5.188	Tanzania	E	Missouri Herbarium *a*	H
428	31.724	-7.457	Tanzania	E	Missouri Herbarium *a*	H
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431	36.233	-7.633	Tanzania	E	Missouri Herbarium *a*	H
433	36.700	-3.367	Tanzania	E	Wickens and Lowe (2008)	H
434	38.850	-5.183	Tanzania	E	Wickens and Lowe (2008)	H
435	37.833	-7.633	Tanzania	E	Wickens and Lowe (2008)	H
436	38.633	-5.450	Tanzania	E	Wickens and Lowe (2008)	H
437	37.500	-3.250	Tanzania	E	Wickens and Lowe (2008)	H
438	36.000	-4.750	Tanzania	E	Wickens and Lowe (2008)	H
440	35.833	-5.000	Tanzania	E	Wickens and Lowe (2008)	H
443	36.717	-8.683	Tanzania	E	Wickens and Lowe (2008)	H
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447	37.550	-3.500	Tanzania	E	Wickens and Lowe (2008)	H
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449	37.000	-8.500	Tanzania	E	Wickens and Lowe (2008)	H
450	34.833	-2.333	Tanzania	E	Wickens and Lowe (2008)	H
451	37.667	-7.167	Tanzania	E	Wickens and Lowe (2008)	H
452	38.500	-4.833	Tanzania	E	Wickens and Lowe (2008)	H
453	39.333	-6.167	Tanzania	E	Wickens and Lowe (2008)	H
462	1.205	6.385	Togo	W	A.S. Larsen	FW
463	1.096	6.449	Togo	W	A.S. Larsen	FW

464	1.126	7.526	Togo	W	Pock Tsy et al. (2009)	FW
465	1.567	6.367	Togo	W	KEW Herbarium	H
466	1.217	6.233	Togo	W	Paris Herbarium	H
467	1.223	6.132	Togo	W	Paris Herbarium	H
468	28.150	-15.933	Zambia	E	KEW Herbarium	H
469	27.417	-17.133	Zambia	E	KEW Herbarium	H
470	32.417	-11.833	Zambia	E	KEW Herbarium	H
471	31.783	-13.067	Zambia	E	KEW Herbarium	H
472	28.617	-12.950	Zambia	E	KEW Herbarium	H
473	32.170	-11.750	Zambia	E	Phytotrade Africa	H
474	25.870	-17.830	Zambia	E	Phytotrade Africa	H
475	25.280	-17.790	Zambia	E	Phytotrade Africa	H
476	28.010	-15.810	Zambia	E	Phytotrade Africa	H
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479	25.780	-17.870	Zambia	E	Phytotrade Africa	H
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482	27.443	-15.143	Zambia	E	Phytotrade Africa	H
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492	28.703	-16.080	Zambia	E	Phytotrade Africa	H
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499	28.736	-16.125	Zambia	E	Phytotrade Africa	H
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507	28.728	-16.236	Zambia	E	Phytotrade Africa	H
510	28.718	-16.307	Zambia	E	Phytotrade Africa	H
513	28.729	-16.393	Zambia	E	Phytotrade Africa	H
518	29.550	-15.650	Zambia	E	Wickens and Lowe (2008)	H
519	30.667	-12.917	Zambia	E	Wickens and Lowe (2008)	H
520	26.167	-14.500	Zambia	E	Wickens and Lowe (2008)	H
522	31.517	-17.900	Zambia	E	Wickens and Lowe (2008)	H
523	30.200	-12.583	Zambia	E	Wickens and Lowe (2008)	H
526	30.300	-12.300	Zambia	E	Wickens and Lowe (2008)	H
527	32.167	-11.917	Zambia	E	Wickens and Lowe (2008)	H
528	27.583	-16.000	Zambia	E	Wickens and Lowe (2008)	H
529	30.917	-13.183	Zambia	E	Wickens and Lowe (2008)	H
530	31.850	-12.700	Zambia	E	Wickens and Lowe (2008)	H
531	25.850	-17.917	Zambia	E	Wickens and Lowe (2008)	H
533	29.000	-16.000	Zambia	E	Wickens and Lowe (2008)	H
535	29.983	-22.217	Zimbabwe	E	KEW Herbarium	H
537	29.317	-22.083	Zimbabwe	E	KEW Herbarium	H
540	29.220	-15.450	Zimbabwe	E	Phytotrade Africa	H
541	32.090	-19.950	Zimbabwe	E	Phytotrade Africa	H
542	32.470	-19.640	Zimbabwe	E	Phytotrade Africa	H
543	29.980	-22.210	Zimbabwe	E	Phytotrade Africa	H
544	32.390	-19.910	Zimbabwe	E	Phytotrade Africa	H
546	32.630	-20.200	Zimbabwe	E	Phytotrade Africa	H
547	30.740	-21.240	Zimbabwe	E	Phytotrade Africa	H
548	31.000	-16.430	Zimbabwe	E	Phytotrade Africa	H
549	32.420	-19.770	Zimbabwe	E	Phytotrade Africa	H
551	28.940	-18.210	Zimbabwe	E	Phytotrade Africa	H
553	30.820	-20.100	Zimbabwe	E	Phytotrade Africa	H

555	30.400	-16.010	Zimbabwe	E	Phytotrade Africa	H
557	31.080	-16.400	Zimbabwe	E	Phytotrade Africa	H
560	29.980	-22.090	Zimbabwe	E	Phytotrade Africa	H
561	29.820	-18.930	Zimbabwe	E	Phytotrade Africa	H
562	29.210	-21.970	Zimbabwe	E	Phytotrade Africa	H
563	32.510	-19.560	Zimbabwe	E	Phytotrade Africa	H
564	32.330	-19.960	Zimbabwe	E	Phytotrade Africa	H
566	26.510	-18.770	Zimbabwe	E	Phytotrade Africa	H
567	32.370	-19.770	Zimbabwe	E	Phytotrade Africa	H
568	30.620	-20.120	Zimbabwe	E	Phytotrade Africa	H
569	30.940	-20.140	Zimbabwe	E	Phytotrade Africa	H
571	32.833	-18.800	Zimbabwe	E	Wickens and Lowe (2008)	H
573	32.800	-20.200	Zimbabwe	E	Wickens and Lowe (2008)	H
576	30.817	-20.167	Zimbabwe	E	Wickens and Lowe (2008)	H
577	32.117	-20.150	Zimbabwe	E	Wickens and Lowe (2008)	H
578	32.483	-20.117	Zimbabwe	E	Wickens and Lowe (2008)	H
581	26.417	-18.333	Zimbabwe	E	Wickens and Lowe (2008)	H
583	31.600	-24.983	Zimbabwe	E	Wickens and Lowe (2008)	H
584	24.267	-17.500	Zimbabwe	E	Wickens and Lowe (2008)	H
585	29.500	-18.750	Zimbabwe	E	Wickens and Lowe (2008)	H
586	28.833	-16.517	Zimbabwe	E	Wickens and Lowe (2008)	H
588	29.367	-15.750	Zimbabwe	E	Wickens and Lowe (2008)	H
589	29.383	-15.833	Zimbabwe	E	Wickens and Lowe (2008)	H
591	31.650	-16.250	Zimbabwe	E	Wickens and Lowe (2008)	H
593	31.650	-16.750	Zimbabwe	E	Wickens and Lowe (2008)	H
594	26.833	-18.017	Zimbabwe	E	Wickens and Lowe (2008)	H
595	32.667	-19.000	Zimbabwe	E	Wickens and Lowe (2008)	H
596	32.217	-17.400	Zimbabwe	E	Wickens and Lowe (2008)	H
597	30.417	-18.683	Zimbabwe	E	Wickens and Lowe (2008)	H
598	28.900	-19.000	Zimbabwe	E	Wickens and Lowe (2008)	H
606	32.283	-20.450	Zimbabwe	E	Wickens and Lowe (2008)	H

APPENDIX III

Journal paper 2:

Cuni Sanchez A, Haq N, Assogbadjo A (2010) Variation in baobab (*Adansonia digitata* L.) leaf morphology and its relation to drought tolerance. *Genetic Resources and Crop Evolution* 57(1): 17-25.

APPENDIX IV

Small fact sheets on baobab cultivation techniques:

- Propagation du baobab par semence (Baobab seed propagation, in French)
- Propagation du baobab par greffage (Baobab grafting, in French)
- KUCHULUKITSA MITENGO YA MALAMBE (Baobab seed propagation, in Chichewa)
- KUCHULUKITSA MITENGO YA MALAMBE KU KWATITSA (Baobab grafting, in Chichewa)

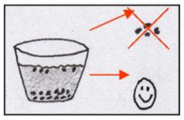
PROPAGATION DU BAOBAB:
PAR SEMENCE

On peut planter les graines de baobabs !
Il faut planter des graines au début de la saison de pluies.

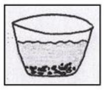
De quoi a-t-on besoin?

-des graines de baobab d'un fruit mûr ou de graines de moins d'une année
-sol, sable et compost
-sachets en plastique ou récipients de 1,5 litres
-eau
-une lame propre

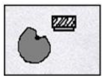
Étapes:



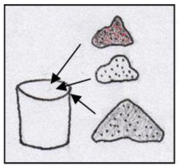
1. Mettre les graines dans un pot contenant de l'eau et écarter les graines qui flottent (elles sont mauvaises)



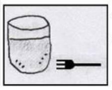
2. Mettre les graines dans de l'eau pendant un jour, pour stimuler leur germination



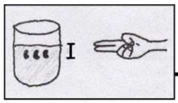
3. Utiliser une lame propre pour faire un petit trou au milieu de la graine de baobab. Ne pas faire le trou trop profond sinon on peut tuer la graine



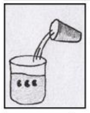
4. Mélanger dans un récipient ou un sachet en plastique une quantité de sable et une quantité de bouse de vache séchée pour trois quantités de terre



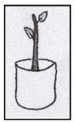
5. Faire des trous au fond du sachet en plastique pour améliorer le drainage de l'eau



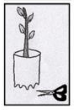
6. Mettre trois graines dans chaque récipient à 2 centimètres de profondeur



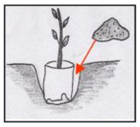
7. Arroser les graines une fois par jour, de préférence le soir. Arroser avec un demi verre d'eau par récipient



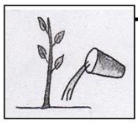
8. Deux semaines ou un mois plus tard la plantule doit avoir des feuilles. Si on a plusieurs plantules, enlever les plus petites. Ainsi la plantule la plus grande poussera plus vite



9. De trois à six mois plus tard on peut transplanter la plantule. D'abord couper le fond du sachet plastique



10. Mettre la plantule dans un trou de 25x25x25cm et ajouter un peu de bouse de vache



11. Arroser les plantules deux fois par semaine pendant deux mois. Il faut les protéger des animaux!

Où doit-on faire pousser les graines ?

-à l'ombre
-dans un endroit protégé des inondations
-pas loin d'une source d'eau permanente
-dans un endroit protégé des animaux
-dans un endroit protégé du vent

Ne pas oublier !

a) Placer les plantules à une distance de 0,5 m si on désire la production de feuilles

b) Espacer les plantules de 8 m si on désire la production de fruits

c) Espacer les plantules de 15 m en bordure des champs ou sentiers

d) Placer des plantules dans n'importe quel endroit autour de votre maison !

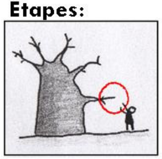
PROPAGATION DU BAOBAB:
PAR GREFFAGE

On peut attacher une branche d'un grand baobab qui donne des fruits à une petite plantule, de cette manière on peut cultiver le baobab qu'on désire, et ce jeune baobab donnera des fruits en 2-3 ans (au lieu de 10-15ans)!

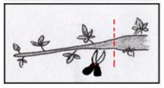
De quoi a-t-on besoin?

-une branche d'un baobab qui donne des fruits
-une plantule de baobab de la taille d'un crayon
-un couteau bien affilé et propre
-sécateurs et ciseaux
-ruban de greffage (ou ruban adhésif)
-un sachet en plastique
-eau

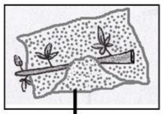
Étapes:



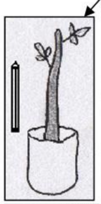
1. Choisir un baobab de grande taille qui donne des fruits de qualité et qui n'est pas malade. Choisir une branche qui est en bas



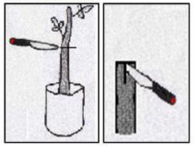
2. Couper le bout de la branche à une longueur de 10 cm et une épaisseur d'un crayon



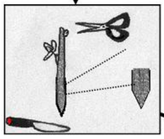
3. Il faut tenir la branche humide: couvrir avec un tissu mouillé, par exemple



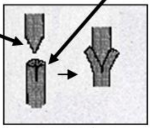
4. Choisir un petit baobab planté par semence plus grand qu'un crayon



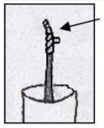
5. Couper horizontalement le bout de la tige à 10 cm du sol. Puis, appliquer une fente de 2 cm au milieu de la tige. Enlever toutes les feuilles qui restent



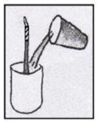
6. Quand vous arrivez à coté de la plantule, couper la branche afin qu'elle aie le même diamètre que la plantule. Couper l'extrémité en forme de V de 2 cm par coté



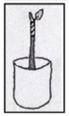
7. Mettre le greffon dans la fente de la tige du porte-greffe. Aucune partie verte ne doit être visible



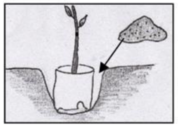
8. Ligaturer les deux parties avec du ruban de greffage. Commencer par l'union et après couvrir toute la branche (à l'exception de l'extrémité) à fin de diminuer la transpiration



9. Arroser souvent (un verre d'eau), tous les soirs par exemple



10. Un mois plus tard des feuilles doivent avoir poussé. *Parfois les feuilles prennent beaucoup de temps à pousser. Si le bout de la branche est vert, elle est vivante*



11. 4-6 mois plus tard, quand l'union a cicatrisé et la branche greffée a plusieurs feuilles, la plantule greffée peut être transplantée dans le champ

Ne pas oublier !

-Il faut greffer au début de la saison de pluies, et il faut commencer tôt le matin

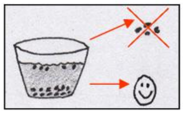
-Il faut arroser souvent

-On peut ajouter de la brousse de vache (séchée au soleil)

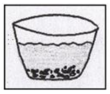
KUCHULUKITSA MITENGO YA <u>MALAMBE</u>

Mukhoza kubzala mitengo ya malambe mosavuta kuchokera ku njere. Ndibwino kubzala mitengoyi nthawi ya mvula.

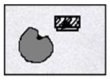
Ndondomeko yake:



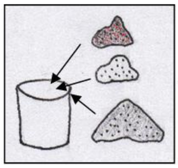
1. Nyikani njere m'madzi ndipo tayani zomwe zayandama chifukwa izi ndi zimene ziri zoipa



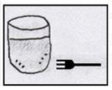
2. Sunganibe njere m'madzi kwa tsiku limodzi kuti zimere bwino.



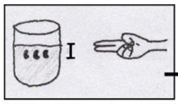
3. Gwiritsani ntchito mpeni wopukuta bwino komanso wakuthwa poboola njere kuti imere mosavuta. Onetsetsani kuti mwaboola mosamala chifukwa mukaboola kwambiri ndiye kuti muwononga njere.



4. Konzani chubu chofeseramo njere motere; gawo limodzi manyowa, gawo linanso mchenga pomaliza magawo atatu dothi labwino.

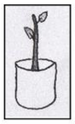


5. Boolani pansi pa machubu amene ali ndi njere ndi foloko mwachitsanzo kuti madzi adzituluka.

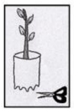


6. Ikani njere zitatu pa chubu chilichonse mozama masentimita awiri.

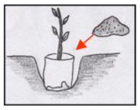
7. Thirirani madzi njere zanu tsiku lililonse makamaka nthawi ya madzulo. Ikani theka la kapu la galasi pa chubu chilichonse.



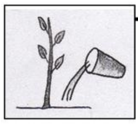
8. Pakutha pa sabata ziwiri, mbande zimakhala ziri ndi masamba. Ngati pali mbande zopitilira imodzi pa chubu chimodzi, muyenera kupatulira pochotsa zimene ziri zazing'ono kusiya imodzi kuti ikule bwino.



9. Pakutha pa miyezi itatu kapena isanu ndi umodzi, muyenera kubzala mbande zanu. Onetsetsani kuti mwachotsa chubu cha pulasitiki pobzala mbande.



10. Bzalani mbande zanu m'maenje ozama masentimita makumi asanu mulitali komanso mulifupi. (50x50cm) Mukhoza kuonjezera manyowa a ndowe za ng'ombe.



11. Thirirani mbande kawiri pa sabata kwa miyezi iwiri. Kumbukirani kuteteza mitengo ku ziweto.

ZOFUNIKIRA

-Njere zochokera ku zipatso zokhwima bwino kapena zimene sizinathe chaka chimodzi.

-Dothi labwino, mchenga komanso manyowa.

-Machubu a pulasitiki kapena mofeseramo njere.

-Madzi

-Mpeni wopukuta ndi wakuthwa bwino.

MALO AMENE MUNGAFESE NJERE

-Pa mthunzi

-Pamalo osatsetsereka

-Pafupi ndi madzi

-Malo otetezedwa ku ziweto

-Otetezedwa bwino ku mphepo

KUMBUKIRANI KUCHITA IZI

a) Bzalani mbande pa mpata wokwana theka la mita (0.5m) ngati cholinga chanu chili chofuna kupeza masamba.

b) Bzalani pa mpata wa mamita anayi (4m) ngati mukufuna kudzapeza zipatso.

c) Bzalani pa mpata wa mamita khumi ndi asnu (15m) m'malire a munda.

d) Bzalani pena paliponse pa nyumba panu.

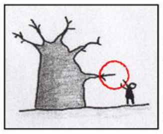
KUCHULUKITSA MITENGO YA MALAMBE KU KWATITSA

Mukhoza kuphatika kanthambi ka mtengo wokula bwino wa chipatso ku mbande ncholinga chofuna kupeza zipatso nthawi yochepa. Ndi njira iyi, mukhoza kupeza zipatso muzaka za pakati pa ziwiri kapena zitatatu mmalo mwa zaka khumi. Chitani izi nthawi ya mmawa ndipo ikhale nyengo ya mvula.

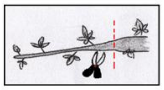
ZOFUNIKIRA

-Kanthambi kochokera ku mtengo wobereka bwino wa mlambe.
-Mbande ya mtengo wa mlambe ikhale ndi thunthu lofanana ndi cholembera (pensulo).
-Mpeni wopukuta ndi wakuthwa bwino.
-Lumo lodulira tinthambi.
-Pulasitiki tepi womangira
-Madzi

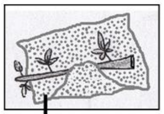
Ndondomeko yake:



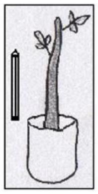
1. Sankhani mtengo wa mlambe waukulu, wopanda matenda komanso wobereka zipatso zazikulu bwino. Sankhani kanthambi kamene kali mmunsiko pang'ono osakhala mmwamba kwambiri.



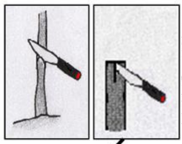
2. Dulani nsonga ya kanthambi. Ikhale yotalika masentimita khumi (10cm) ndipo thunthu lake ngati la pensulo.



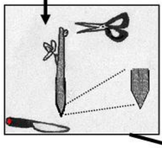
3. Sungani kanthambi pa malo a chinyontho musanafike pa malo amene mukagwire ntchito yokwatitsa. Mwachitsanzo mukhoza kukutira kanthambika ndi nsalu yonyowa.



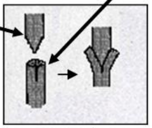
4. Sankhani mbande yaying'ono yofanana ndi thunthu la pensulo.



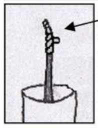
5. Dulani nsonga la mbande motalika masentimita okwana khumi ndi asanu (15cm) ndipo onetsetsani kuti mwadula chatsonga. Dulani thunthu la mbande mozama masentimita awiri (2cm) cha pakatikati . Thotholani masamba onse.



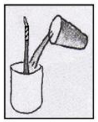
6. Mukafika pa malo pamane pali mbande, sankhani kanthambi kofanana thunthu ndi mbande imene mufuna kukwatitsa. Dulani mbande cha mmunsi mofanana ndi chirembo cha V motalika masentimita awiri (2cm)



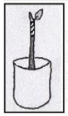
7. Zikani kathambi pa mbande pamene mwadula paja ndipo onetsetsani kuti palibe masamba.



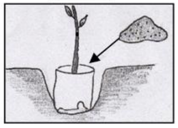
8. Lumikizani malo mwadula aja pokulunga tepi molimbika. Mangaini tepi kuyambira pansi kupita mmwamba. Kukulunga mbande ndi tepi zimathandiza kuchepetsa kutuluka kwa madzi kumene kumabwera chifukwa cha kuwala kwa dzuwa. Komanso zimathandiza kuti mbande iphuke ndi kukula bwino.



9. Thirani madzi pa mbande zimene mwakwatitsa nthawi ndi nthawi.



10. Pakutha mwezi umodzi masamba atsopano amayamba kuoneka. Nthawi zina zimatenga nthawi yayitali kuti mbande ziyambe kutulutsa masamba, koma ngati mbande ikuonekabe yobiriwira ndiye kuti ili yamoyo pongofunika



11. Pakapita miyezi inayi kapena isanu ndi umodzi ngati pa bala polumikizana paja papola, ndiye kuti tikhoza kumasula tepi nthawi yomweyonso tikhoza kukabzala mbande zathu.

KUMBUKIRANI KUCHITA IZI

-Thirani madzi pa mbande zimene mwakwatitsa nthawi ndi nthawi.
-Mukhoza kuonjezera manyowa a ndowe za ng'ombe zouma ku mitengo imene mwabzala.

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