

# Factors determining the distribution of selected tree species in Namibia

Antje Burke, EnviroScience

Report for RAISON as a contribution to a book on woodlands in Namibia, Windhoek.

October 2004

## Background

EnviroScience was contracted by RAISON to undertake a review of factors determining the distribution and abundance of trees in Namibia in September 2004. A total of six work days were allocated to this assignment. The Terms of Reference are provided in Appendix 1.

## Introduction

The question why a certain plant or animal lives at a specific locality has occupied biologists ever since the subject was born. And – several hundred years later, there is no final answer.

This also applies to trees in Namibia and I will not be able to provide in this essay the ultimate answer to why a camel thorn grows at a specific locality on the side of road. This essay, however, provides a review of factors that influence tree distribution, relate these to the Namibian environment and with this explains some environmental variables relevant to trees in Namibia.

In order to explain why a certain tree grows where it does one would need to know about:

1. a particular plant's functional - (type of metabolism, growth strategy, specific adaptations and so on) and genetic make-up which determine the plant's internal ecological (autoecological) requirements,
2. environmental conditions and interactions with other biota (e.g. fungi, animals) and their changes at a particular site over time
3. chance events that may have been necessary to create an open space, distribute the seed or generate the right conditions for establishment and
4. the long history of geological and climatic conditions in the past that also have a bearing on the plant's recent distribution range.

Such detailed knowledge either about the species concerned or the history of environmental conditions which a long-lived plant such as a tree experiences are hardly ever known. As a result plant ecologists have to resort to distal environmental variables that can be used as indicators for environmental conditions at a site, e.g. elevation as an indicator for specific microhabitat conditions and temperature ranges and rainfall gradients to explain broad geographic distributions of certain trees. In some instances specific substrate conditions also provide a good indicator. However, nature is not that simple, and while some plant distributions can be explained by a few environmental variables, in most instances only a range of environmental and biotic conditions acting in concert and their changes in interaction with each other and the plant concerned over time, would provide the answer to why the tree in question grows at a particular spot.

As little is known either about plant functional traits of specific trees in Namibia nor vegetation history and site history of the trees concerned, mainly distal environmental

"Surviving is one thing, it is still necessary to reproduce"  
we can talk about that<sup>1</sup> in case of fire and ephemeral basis!

variables that may help to explain broad distribution ranges of some Namibian tree species and woody plant diversity patterns are discussed in this essay.

## Methods

Information available for analysis were distribution data of selected tree species in quarter degree resolution (15 minute intervals of a latitude-longitude grid) (Tree Atlas of Namibia Project 2004), and a range of environmental variables compiled by the Atlas of Namibia Project (Mendelsohn et al. 2002). Tree distribution data were overlaid with readily available environmental data to obtain some indication of critical broad-scale factors affecting tree distributions in Namibia. The tree species were selected on the basis of their abundance and importance in the Namibian environment (for a complete list see Appendix 1).

Information on these selected tree species was compiled based on a brief review of readily available published sources and information from the SEPASAL database at Kew Botanical Gardens (Royal Botanic Gardens Kew 1999). Time constraints prevented a thorough literature review for all individual tree species and this review is hence not complete and by no means comprehensive.

## Factors affecting tree distribution in Namibia

While plotting the tree distribution of selected species five distinct distribution patterns emerged:

1. species that occurred throughout the entire country (e.g. *Acacia erioloba* and *Boscia albitrunca*)
2. species restricted to the Kalahari sandveld in the north-east of the country (e.g. *Baikiaea plurijuga* and *Guibourtia coleosperma*)
3. species that occur widely throughout Namibia, but not in the Kalahari sandveld (e.g. *Acacia karroo*, *Combretum apiculatum* and *Faidherbia albida*)
4. species with an interrupted (disjunct) distribution (e.g. *Colophospermum mopane* and *Spirostachys africana*) and
5. species restricted to the Namib Desert (*Welwitschia mirabilis*).

Although physical as well as biological environmental factors play an important role in explaining tree distributions, temperature and moisture are two fundamental, broad-scale environmental variables affecting plant distributions (Barbour et al. 1987). Coupled with substrate conditions, which determine soil moisture and nutrient availability, these three variables are particularly important in an arid environment like major parts of Namibia. The following section discusses individual environmental factors and their correlation with distribution of Namibian tree species. Ultimately these individual factors act in concert and the combination of these explains why a certain tree grows exactly where it does.

### Temperature

Ecological tolerance limits regarding temperature are normally not constant during the lifetime of a tree and dependent on its phase in the life cycle. For example, germination is often cued by a certain temperature threshold (Pasciecznik et al. 2001) and growth of seedlings and saplings may be directly linked to temperatures (Fenner 1987). Once a tree has established, temperature tolerance limits are usually greater. The actual impact of temperatures is hence dependent on timing and broad-scale available information such as the average annual mean may thus not be very meaningful for individual plants. Site conditions

also play an important role as sheltered or shaded positions may provide a different temperature climate than the broader surrounding.

However, based on the distribution ranges in Namibia, the selected tree species show a correlation with average mean temperatures above 19°C for *Adansonia digitata*, *Burkea africana*, *Combretum apiculatum* subsp. *apiculatum*, *Sclerocarya birrea*, *Spirostachys africana* and *Terminalia sericea*; greater 20°C correlated with the distribution of *Baikiaea plurijuga*, *Pterocarpus angolensis* and *Schinziophyton rautanenii* and greater 21°C with *Guibourtia coleosperma*. This either indicates a decrease in the temperature tolerance range of the discussed species or a shift to a higher (tropical) temperature range, with *Guibourtia coleosperma* indicating that it favours the warmest conditions amongst the selected species.

### Frost

The ability to tolerate frost requires specific biological adaptations in long-lived plants and the occurrence and duration of frost is hence an important environmental factor influencing distribution ranges of plant species.

In the case of the distribution range in Namibia of selected tree species, only *Colophospermum mopane* and *Welwitschia mirabilis* indicated a correlation with largely frost-free environments in Namibia. Mopane occurs in Namibia only in areas receiving less than 5 days of frost per annum, *Welwitschia mirabilis* occurs where there is no frost at all. However, in other parts of its distribution range, for example in Zimbabwe *Colophospermum mopane* has been observed in areas that receive severe frosts (Timberlake 1996). Whether or not this is related to specific site conditions or indicates genetic variation in this tree species would need further investigation.

### FROST EFFECTS ON TREES...

Frost affects trees mostly during the early stages of growth when young tissue is not well developed. In the later stages of a tree's life mainly the growth points are affected by frost. While seedlings and young plants can be killed by frost, effects of frost on adult trees are usually localised and result in the die-off of branch tips and other growth points. Frost resistance varies between species, and those trees whose seedlings are most susceptible to frost damage will not survive in areas where frost occurs frequently.

The other selected tree species occurred in areas where frost occurrence is restricted to:

- 10 days per annum (*Adansonia digitata*, *Baikiaea plurijuga*, *Guibourtia coleosperma* and *Spirostachys africana*),
- 20 days per annum (*Aloe dichotoma*, *Pterocarpus angolensis*, *Schinziophyton rautanenii*, *Sclerocarya birrea* and *Terminalia prunioides*) and
- 30 days per annum (*Burkea africana*, *Combretum apiculatum* and *Combretum imberbe*).

This may indicate an increasing frost resistance in the selected species.

### Rainfall

Moisture availability is an extremely important factor determining plant growth in arid and semi-arid environments. Broad rainfall distribution patterns provide some indication of moisture requirements of certain species.

in any event

In the case of the investigated Namibian tree species, distribution ranges correlated with the following mean annual rain contours:

Rain contour	Tree species
< 200 mm	<i>Welwitschia mirabilis</i>
< 250 mm	<i>Aloe dichotoma</i>
> 50 mm	<i>Acacia karroo</i> , <i>Adansonia digitata</i> , <i>Colophospermum mopane</i> , <i>Sclerocarya birrea</i> and <i>Terminalia prunioides</i>
> 100 mm	<i>Combretum apiculatum</i>
> 150 mm	<i>Spirostachys africana</i> and <i>Terminalia sericea</i>
> 300 mm	<i>Burkea africana</i>
> 350 mm	<i>Baikiaea plurijuga</i> and <i>Schinziophyton rautanenii</i>
> 400 mm	<i>Pterocarpus angolensis</i>
> 450 mm	<i>Guibourtia coleosperma</i>

IS IT POSSIBLE TO CHANGE OR ADD TO THIS TABLE BY SHOWING WHAT RANGES OF RAINFALL (e.g. 100 – 200 mm) ARE PREFERRED? Unfortunately not, because I do not have data for their entire distribution range.

This indicates a gradient of arid to more humid-adapted tree species, with *Guibourtia coleosperma* showing the highest moisture requirements.

#### Altitude

Altitude as an indication of temperature and moisture conditions plays an important role in tree distributions around the globe and often results in distinct zonation patterns (Barbour et al. 1987). However, at the scale of analysis in this study and within the selected species, altitude does not appear to be an important factor. FORGETTING ABOUT THE ¼ DEGREE SQUARE MAPPING. CAN YOU GIVE SOME EXAMPLES OF PROMINENT NAMIBIAN TREES THAT GROW ONLY AT PARTICULAR ALTITUDES? ALSO, OTHER THAN TEMPERATURE AND MOISTURE, ARE THERE ANY OTHER FACTORS THAT VARY WITH ALTITUDE? FOR EXAMPLE, I WOULD IMAGINE THAT SOILS ARE OFTEN ARRANGED ZONALLY.

Interesting enough – no, I cannot think of a single prominent Namibian tree whose distribution is altitude-related. I guess that is an interesting point in itself. There is *Euphorbia comeroi* subsp. *brandbergensis* on the top of the Brandberg, but whether one wants to call it a "tree" is open to debate.

Soil species adapted to different ecological habitat )

Soil properties determine the amount of moisture and nutrients available to an individual plant and are hence critical factors affecting tree distributions. Although soil properties are usually more important in determining local site conditions (Burke 2002a), some correlations with groups of soil types are evident at even large geographic scales in Namibia. The sandy soils (arenosols) of the Kalahari sandveld provide contrasting soil conditions to most other soil types in Namibia. They are characterised by low nutrient content and are fairly porous, allowing rapid and deep infiltration of rain water, provided that there are no impeding crusts in the soil.

Three of the selected tree species are directly linked to the extent of the Kalahari sandveld in Namibia: *Baikiaea plurijuga*, *Guibourtia coleosperma* and to some extent *Pterocarpus angolensis*. Other tree species are absent from the arenosols of the Kalahari sandveld. These include *Acacia karroo*, *Adansonia digitata*, *Combretum apiculatum*, *Combretum imberbe* and

*Faidherbia albida*. Although some of these trees may be present in the Kalahari sandveld they are growing in localised soil types that are not arenosols (Burke 2002b).

CAN WE HAVE SOME EXAMPLES OF NAMIBIAN TREES BEING RESTRICTED TO PARTICULAR SOILS. I am afraid we do not have enough information on this point. Mopane may be related to soil conditions, but there are likely also other factors (as discussed above).

#### WATER-LOGGED SOILS...

Water-logged soils prevent the movement of air and so hinder gas exchange in the root area. Trees that grow in permanently water-logged soils usually have some adaptations to counterbalance these effects, for example aerial roots.

#### *Vegetation history*

Geological as well as climate history in the past had a pronounced effect on the distribution ranges of tree species today. In the case of the selected Namibian tree species, some show very clear geographic boundaries in Namibia. These are not necessarily linked to broad-scale, physical environmental factor such as rainfall, temperature or substrate or only, if seen in combination with these.

For example, *Faidherbia albida* only occurs north of 24° latitude in Namibia, *Combretum imberbe* north of 23°, *Terminalia prunioides* north of 22°, *Sclerocarya birrea* north of 21° and *Spirostachys africana* north of 20° latitude. Based on broad-scale environmental conditions in their current distribution ranges, there are likely other suitable localities beyond their recent distribution ranges that provide similar environmental conditions in Namibia. Some other, possibly historic or biological factors may have prevented these tree species from establishing there. *Sclerocarya birrea* is a culturally important fruit tree and has been planted by locals for many hundreds of years. This may well have influenced its recent distribution range.

I ASSUME THAT MANY SPECIES NOW RESTRICTED TO HIGHLANDS HAD MORE WIDESPREAD RANGES DURING WETTER OR WARMER TIMES. WOULD THIS BE CORRECT? As above, interestingly we do not seem to have prominent trees that occur in highland areas only. So there must be other reasons. I would imagine the movement of rain-contours with climate change would be important, and would change the distribution ranges.

#### *Biological factors*

Site specific conditions are the fine-scale factors that determine why a specific plant grows exactly where it does. Apart from the microhabitat, most important are interactions with other plants, such as competition for water, nutrients and light, and the impacts of other living biota such as animals, fungi, bacteria and other micro-organisms.

EXAMPLES? These are highlighted in the subsection below, this was just meant to be an introductory paragraph to the points below...

Many Namibian trees have the ability to fix nitrogen, for example (see below).

#### The effect of animals

Plant-eating animals (herbivores) have a profound impact on trees and so also help explaining tree distribution patterns. They distribute seeds of many trees, for example *Acacia erioloba*

and *Faidherbia albida*. They chew seedlings, sapling, flowers, young trees, branches and ring-bark old mature trees and so reduce the tree's biomass, sometimes with detrimental effects. Insects bore into stems, infect seeds and flowers and chomp tree roots. The tolerance levels of herbivory differ between tree species and this could help explaining why certain species may be absent from areas with a high density of livestock or wildlife, while others are very abundant there. *Colophospermum mopane*, for example, is readily browsed (Timberlake 1996) and is able to coppice when cut or broken, hence well able to recover after the impact of herbivores.

#### BUSH ENCROACHMENT...?

A combination of factors is believed to be responsible for bush encroachment, livestock impacts most likely contributed to this process.

#### Seed dispersal

Wind is another important seed dispersal factor which allows the plant to reach further dispersal distances than if they show no adaptations for this types of seed dispersal. Amongst the selected species the *Combretum* species, *Pterocarpus angolensis*, *Terminalia* species and *Welwitschia mirabilis* show adaptations for wind dispersal.

#### Competition

Competition with other plants is a limiting factor for tree establishment in all parts of the Namibia where space and resources are limited. Competition for water, nutrients and light occurs between plants of the same species (e.g. seedlings trying to establish under an adult plant), different tree species and other components of the vegetation, such as grasses. The latter is one important factor determining savanna dynamics (Scholes 1997). To incorporate these competitive interactions while trying to explain tree distributions would require a good understanding of the plant ecology of a specific tree at a particular site.

WHY ARE SOME PLANTS/TREES PIONEER SPECIES. WHEREAS OTHERS ARE SO-CALLED CLIMAX SPECIES. I SAW TERMINALIA SERICEA AS A PIONEER SPECIES ALONG FIRE BREAKS IN CAPRIVL WHILE THE SURROUNDING (CLIMAX?) WOODLAND WAS DOMINATED BY BAIKAEA ETC. DO YOU HAVE OTHER EXAMPLES OF PIONEERS IN NAMIBIA? Not really, but can explain the process...

For example species that are more competitive during the early stages of their growth under particular conditions would colonise areas quickly – these are often called pioneers. This might be because their seeds require light for germination, they may be able to take up and use water more effectively than other species, or they can utilise nutrients released after fires more effectively than the competing trees. Those interactions are presently not well studied in Namibian trees.

#### Nitrogen fixing rhizobia

Many leguminous plants form a mutual relationship with nitrogen-fixing bacteria. This allows them to obtain nitrogen from the atmosphere. The ability to do so gives leguminous trees an advantage in nitrogen-limited environments, for example the infertile sands of the Kalahari sandveld. Amongst the selected tree species all *Acacia* species, *Baikiaea plurijuga*, *Burkea africana*, *Faidherbia albida*, *Guibourtia coleosperma* and *Pterocarpus angolensis* have the ability to form a symbiosis with N-fixing bacteria. Whether or not they actually do so depends on climatic variables and site conditions (Schulze et al. 1991). PLEASE ELABORATE. IS THE ABILITY TO DO SO LIMITED TO LEGUMINOUS PLANTS. DO WE ACTUALLY

KNOW IF ANY KALAHARI SPECIES DO THIS? DOES FIXING VARY WITHIN A SPECIES, SUCH THAT SOME INDIVIDUALS DO IT AND OTHERS NOT?

The nitrogen-fixing ability is largely restricted to members of the family Fabaceae (legumes). Most leguminous tree species in Namibia (see above) have this ability. However, whether or not they do actually form nodules with N-fixing bacteria varies even within species and depends on site conditions. For example in a once-off study N-fixation in *Acacia erioloba* changed along a gradient from the desert to savanna in Namibia with a peak at about 100 km distance from the coast (Schulze et al. 1991).

#### Mycorrhiza

Fungi that form a relationship with the roots of trees help the tree to obtain water and nutrients. Trees that have these ability are called mycorrhizal. Similar to above, mycorrhizal trees can have an advantage in nutrient poor environments. For example, *Colophospermum mopane* is mycorrhizal (Högberg & Pearce 1986) which may explain why it can grow in relatively nutrient poor environments.

#### Disturbance factors

Human impacts aside, fire is one of the most important additional environmental variables affecting tree distributions in Namibia.

Fire can affect a tree during all stages of its life cycle. It can have a beneficial as well as a detrimental impact. Some seeds, for example, germinate better once they have been exposed to fire, such as many fynbos species. Trees that tolerate fires benefit by the removal of less fire tolerant species and the release of nutrients. Fire sensitive species, on the other hand, are either eventually eliminated where fires occur frequently or their establishment is prevented altogether. Amongst the selected tree species, *Burkea africana*, *Terminalia sericea* (Rutherford 1981) and *Pterocarpus angolensis* (Geldenhuys 1977) are believed to be fairly tolerant of fires, while *Baikiaea plurijuga* (Geldenhuys 1977) and *Guibourtia coleosperma* (Rutherford 1981) are more fire sensitive.

#### Overall woody plant diversity

Four main areas emerged that showed the highest diversity of woody plants (> 80 species) in Namibia (map provided by John Mendelsohn based on tree atlas data). It needs to be mentioned that the provided map shows overall woody plant diversity (all woody species > 1m in height – B. Curtis, pers. comm.) and is not restricted to trees only. The discussion of selected, individual tree distributions is hence only partially relevant to this.

The four areas with highest woody plant diversity are:

1. The Baynes-Otjihipa, Steilrand Mountains in the Kaokoveld in northwestern Namibia
2. the Otavi Mountains
3. Namibia's lower section of the Okavango River (east of Andara) and
4. part of Eastern Caprivi around the Salambala area.

Although the data likely reflect some collector's bias as all these areas have been very well collected, corrections for collector's bias in the woody species diversity map will likely not alter the overall pattern (B. Curtis, pers. comm.).

Two of the areas showing high diversity are mountainous (Kaokoveld, Otavi), two areas are lowlands (Okavango, Salambala area). Three of these areas receive the highest rainfall in Namibia, and further, two of these (Okavango, Salambala area) are near perennial rivers and their associated wetland habitats, which, apart from more favourable moisture and nutrient conditions, also provide high habitat diversity associated with changing water levels.

Superficially topography and resulting habitat diversity as well as moisture conditions appear therefore to influence woody plant diversity in Namibia. However, suitable site condition is only one of the controlling variables of woody plant distribution, a suitable species pool which is influenced by historic factors also needs to be available. On a continental scale the vegetation of Africa has been classified biogeographically into regional centres of endemism (White 1983). The classification units relevant to Namibia are the Karoo-Namib, Kalahari Highveld transitional zone and the Zambesian regional centre of endemism (White 1983). These three broad biogeographic units cumulate closely in the Kaokoveld which may explain why there is such high woody plant diversity, despite the fact that this area receives much less rainfall than any of the other three centres of high woody plant diversity.

### Exotic trees

The question why exotics do not well in Namibia has been raised in the Terms of Reference. I would like to rephrase this and rather explain why some exotics become invasive in Namibia and others not. Exotic plants become invasive, if they:

- (a) find suitable environmental conditions in their host country,
- (b) have no natural predators and/or
- (c) their establishment and growth strategy outcompetes native species that inhabit the same niche.

As Namibia is a very dry country, this already limits the number of potential exotic candidates that would be able to survive under natural conditions without the help of irrigation or other human interference. Hence few garden plants have escaped to the wild around towns and no agricultural crops or even their weeds that are often introduced with them, live far beyond their tended fields. With regard to trees, even eucalypts which naturally grow in semi-arid areas have not been observed to spread beyond the places where they have initially been planted.

However, there is one tree that has successfully made Namibia (and large parts of southern Africa) its adopted home and is spreading fast – the mesquite (*Prosopis* species). Initially introduced as a fodder plant and originating in America, it has invaded many dry rivers and plains, particularly in the southern Kalahari and in the rivers flowing into the Namib Desert. It has today progressed as far as the 19° latitude, with few single occurrences further north (likely planted trees).

A recent review by Pierre Smit has summarised the essence of *Prosopis*' success in Namibia very well: "Prosopis ability to grow rapidly as a seedling armed with spines, the production of vast numbers of seeds per individual, seeds encapsulated within nutritious pods that are resistant to digestion, its ability to fix atmospheric nitrogen and its ability to subsist on comparatively poor soil may all be seen as mechanisms of selection for survival of the plant in a hostile environment" (Smit 2004, pp. 26). Further, its distribution by highly effective seed dispersal agents such as animals and water and the ineffectiveness of biocontrol where livestock is not prevented from eating pods infected by bruchid beetles, make the plant so successful in invading the Namibian environment.



It is hence a combination of the right environmental conditions and a successful reproductive and growth strategy that have promoted the invasion of *Prosopis*. Its spread is a concern as it affects the water table and changes soil conditions (reviewed in Smit 2004) and so further exacerbates the direct impact of taking over areas that would naturally be inhabited by native *Acacia* species and other trees.

PLEASE EXPLAIN WHY EUCALYPTS DON'T DO WELL IN NAMIBIA I do not really know – perhaps they require fire stimulation? continuous access to water? particular soil conditions? ...

## Conclusion

Trees live for a long time and hence experience a range of environmental conditions during their lifetime. Without either having an understanding of the autecological requirements of a particular tree species and the history of environmental conditions at a specific site, it is difficult to explain at the local level why a certain tree grows at a particular spot.

However, in this brief review some broad-scale environmental parameters emerged that may help explaining some of the main factors that affect tree distributions in Namibia.

A combination of temperature and average rainfall impacts on the distribution of tree species that occur in the north-east of the country, such as *Baikiaea plurijuga*, *Guibourtia coleosperma*, *Pterocarpus angolensis* and *Schinziophyton rautanenii*. Overlaid with the extent of the Kalahari sandveld, three of these species (*Baikiaea plurijuga*, *Guibourtia coleosperma*, *Pterocarpus angolensis*) also show a good correlation with sandy substrate. *Schinziophyton rautanenii*, however, also occurs on non sandy soil types.

As all three of these important environmental factors (rainfall, temperature and substrate) overlap in the north-east of the country, plus fire impacts are also highest in this area, it is difficult to single out one specific environmental parameter as being responsible for the distribution of a specific tree species. Although *Baikiaea plurijuga* and *Guibourtia coleosperma* are apparently more fire sensitive than some of the other species, this does not prevent them from occurring in areas where fires occur. It may explain, however, why they are today less widely distributed than the other species (Burke 2002b). Hence the combination of four environmental factors likely explains the distribution patterns of the above mentioned species.

Amongst the selected species the occurrence of frost appears to only affect *Colophospermum mopane* and *Welwitschia mirabilis* in Namibia, which are both absent from areas that have on average less than 5 days of frost per annum.

Substrate also appears to be important to some more widespread tree species in Namibia. *Acacia karroo*, *Adansonia digitata*, *Combretum apiculatum*, *Combretum imberbe* and *Faidherbia albida*, for example, are absent from the Kalahari sandveld and occur in soil types other than arenosols. This could be related to soil properties (water holding capacity and soil nutrients), perhaps being less competitive than the trees that grow well in arenosols, or related to fire impacts which are frequent in the north-east of the country.

Historical factors (vegetation history) may also influence the distribution of certain species, for example *Combretum imberbe*, *Faidherbia albida* and *Terminalia prunioides*.

Biological factors (autecology, interactions with other biota), microhabitat and disturbance are other parameters determining site conditions. These are critical in explaining tree distributions at the local level.

Overall woody plant diversity is highest in areas (1) where topography provides many different habitats and where simultaneously rainfall is high and provides a favourable moisture regime (Otavi Mountains, Okavango River, Salambala area); or (2) where topography provides many different habitats and species from different biogeographic zones overlap (Kaokoveld).

Only arid-adapted exotics have the potential to become invasive in Namibia. *Prosopis* species (mesquite) are invasive alien trees of concern in Namibia.

#### Reviewed references and data sources

- Barbour, M.G., Burk, J.H. & Pitts, W.D. (1987). Terrestrial plant ecology. 2nd ed., Benjamin Cummings Publishing Company, Melno Park.
- Burke, A. (2002a). Properties of soil pockets on arid Nama Karoo inselbergs - The effect of geology and derived landforms. *Journal of Arid Environments* 50: 219-234.
- Burke, A. (2002b). Present vegetation in the Kavango Region. *Journal of the Namibia Scientific Society* 50: 133-145.
- Cook, R.E. (1979). Pattern of juvenile mortality and recruitment in plants. Pages 207-231 in O.T. Solbrig, S. Jain, G.B. Johnson & P.H. Raven (eds), *Topics in Plant Population Biology*, Columbia Univ. Press, New York.
- Curtis, B. & Mannheimer, C. (in press). Tree Atlas of Namibia. National Botanical Research Institute, Ministry of Agriculture, Water and Rural Development, Government of the Republic of Namibia, Windhoek.
- de Klerk, J.N. (2004). Bush encroachment in Namibia. Ministry of Environment and Tourism, Government of the Republic of Namibia, Windhoek.
- Fenner, M. (1987). Seedlings. *New Phytology* 106: 35-47.
- Geldenhuys, C.J. 1977. The effect of different regimes of annual burning on two woodland communities in Kavango. *S.A. Forestry Journal* 103: 32-42.
- Högberg, P. & Pearce, G.D. (1986). Mycorrhizas in Zambian trees in relation to host taxonomy, vegetation type and successional patterns. *Journal of Ecology* 74: 775-785.
- Mendelsohn, J., Jarvis, A., Roberts, C. & Robertson, T. (2002). Atlas of Namibia. David Philip Publishers, Cape Town.
- Pasiecznik, N.M., Felker, P., Harris, P.J.C., Harsh, L.N., Cruz, G., Tewari, J.C., Cadoret, K. & Maldonado, L.J. (2001). The *Prosopis juliflora* - *Prosopis pallida* complex: a monograph. Coventry, HDRA.
- Royal Botanic Gardens, Kew (1999). Survey of economic plants for arid and semi-arid lands (SEPASAL) database. Published on the internet; <http://www.rbgekew.org.uk/ceb/sepasal/internet/>
- Rutherford, M. (1981). Survival, regeneration and leaf biomass changes in woody plants following spring burns in *Burkea africana* - *Ochna pulchra* savanna. *Bothalia* 13: 531-552.

- Scholes, R.J. (1997). Savanna. In: Cowling, R.M., Richardson, D.M. Pierce, S.M. (eds.) *Vegetation of southern Africa*, pp. 258-277. Cambridge University Press, Cambridge.
- Schulze, E.D., Gebauer, G., Ziegler, H. & Lange, O.L. (1991). Estimates of nitrogen fixation by trees on an aridity gradient in Namibia. *Oecologia* 88: 451-455.
- Smit, P. (2004). Prosopis: a review of existing knowledge relevant to Namibia. *Journal of the Namibia Scientific Society* 52: 13-40.
- Timberlake, J. (1996). A review of the ecology and management of *Colophospermum mopane*. In: *Proceedings of a workshop held at Ogongo Agricultural College, 26th-29th November 1996*, pp. 1-7.
- White, F. (1983). *The vegetation of Africa*. UNESCO, Paris.

## Appendix 1. Terms of Reference.

### Review of factors that determine the distribution and abundance of trees in Namibia

1. Compile a brief (no more than 10 pages) review of **non-human** or biophysical factors that affect the abundance, health and distribution of different species.
2. The review must focus on **proximate** factors that really affect trees. For example, many species grow in elevated areas but it is of little use on saying that elevation is important to those trees. Rather, we want to know what factors in elevated areas promote the growth of those species.
3. The review should be structured in terms of **different factors**: frost, soil, water availability etc, historical factors, describing in **simple terms** how each factor works to limit or promote growth, and then giving examples of species most affected by each factor.
4. The review should also help to explain why we end up with **broad patterns** of abundance and distribution, e.g. high diversity in the north-east and far north-west, larger and taller trees in certain areas, and the concentration of certain genera in particular areas. Also, why exotics do not do well in Namibia.
5. Explain where possible factors that affect the abundance, growth and distribution of the following species:
  1. Acacia erioloba
  2. Acacia karroo
  3. Acacia mellifera
  4. Aloe dichotoma
  5. Baobab
  6. Boscia albitrunca
  7. Combretum imberbe
  8. Combretum apiculatum
  9. False mopane or msivi
  10. Kiaat or dolfhout or Angolan teak
  11. Mangetti
  12. Marula
  13. Mopane
  14. Prosopis
  15. Spirostachys
  16. Terminalia prunioides
  17. Terminalia sericea
  18. Welwitschia
  19. Zambezi teak (Baiakea)
  20. Burkea africana
  21. Acacia albida