

FACTORS CONTROLLING GEOGRAPHICAL DISTRIBUTION IN SAVANNA VEGETATION IN NAMIBIA

Susumu OKITSU

Faculty of Horticulture, Chiba University

ABSTRACT Here, I describe the geographical distribution of the savanna types in Namibia and identify the factors controlling the occurrence of each savanna type in relation to the amount of annual precipitation and the various physiographical regions, including the mopane (*Colophospermum mopane*) area. The different types of savanna can be distinguished on the basis of the leaf habits of the dominant vegetation: deciduous, evergreen nanophyll, and evergreen notophyll. In general, vegetation performance (i.e., vegetation cover and maximum height) was positively correlated with the amount of annual precipitation. However, the occurrence of a particular savanna type coincided well with physiographical region regardless of the amount of annual precipitation received. Deciduous savanna occurred primarily in the Central Highland and had the smallest total vegetation cover among the three types. The dry soil of this region determined inevitably the deciduous leaf habit of the vegetation during the dry season and thus the smallest total vegetation cover. Evergreen nanophyll savanna was found mainly in the Mega Kalahari, where I observed a clear relationship between the amount of annual precipitation and total vegetation cover. The soil moisture in this region favored an evergreen leaf habit, even in the dry season, resulting in the effective use of soil water throughout the year. This probably accounted for the large increase in total vegetation cover with increasing annual precipitation. Evergreen notophyll savanna exclusively appeared in the mopane area, regardless of the physiographical region, and had the largest total vegetation cover, apparently as a result of the ecological characteristics of mopane. Therefore, it appears that the geographical distribution of the various savanna types in Namibia is principally controlled by two different factors that are independent of the amount of annual precipitation: the water-holding capacity of the soil and the ecological characteristics of mopane.

Key Words: Annual precipitation; *Colophospermum mopane*; Deciduous tree; Evergreen nanophyll; Evergreen notophyll; Savanna.

INTRODUCTION

Savanna vegetation occupies the broad region between dry deserts and humid forests in the tropics and subtropics (Huntley & Walker, 1992). Generally, it consists of a discontinuous crown cover of trees and shrubs with an undergrowth of grasses (Archibold, 1995). Savanna vegetation covers 40% of the land area of Africa (Okitsu, 2004a), and 65% of southern Africa (Scholes, 1997). In Namibia, it is the most representative type of vegetation (Okitsu, 2004b).

Savanna vegetation differs according to its environmentally broad distribution range, from desert to forest. These differences necessarily include not only changes in the performances of the vegetation, including tree cover and height,

but also changes in the leaf habits of the vegetation, such as leaf size and seasonality. The leaf habits of savanna vegetation are major indicators of the environmental factors that influence the habitat, as discussed later in detail. Leaf habit closely corresponds to the water-holding capacity of the soil and/or the ecological nature of the dominant vegetation of a particular savanna. Thus, from a plant-geographical perspective, it is important to use leaf habit to identify physiographical factors controlling the type of savanna in a given area.

The geographical variations in vegetation from dry desert to savanna to humid forest basically correspond to the precipitation gradient (Knapp, 1973; Walter & Breckle, 1984; Archibold, 1995; Mendelsohn *et al.*, 2002). Earlier studies focused primarily on the relationships between the amount of precipitation and the performance of the vegetation (Knapp, 1973; Cowling *et al.*, 1994; Walter & Breckle, 1984). It was generally concluded that the observed differences in plant performance in the various vegetation structures of the tropics and subtropics could primarily be explained by the amount of precipitation.

I hypothesized that factors controlling geographical variations in savanna vegetation are not limited to precipitation alone, but are more complex and include leaf habits and plant ecological characteristics. However, only a few studies have focused on the different types of leaf habits in savanna vegetation. Huntley (1982) reported that the main functional distinction within southern African savannas could be described by leaf size, i.e., broad- and fine-leaved savannas. Scholes (1990) discussed the influence of soil fertility on the ecology of two types of southern African savannas, fine-leaved and broad-leaved, and schematically illustrated the association between environmental factors and leaf size (Scholes 1997). Despite these interesting studies, the factors controlling the geographical variations in the savanna types, as assessed by differences in leaf habits, remain uncertain. In this study, I identified the geographical distribution of different savanna types based on leaf habits and discuss the factors controlling their occurrence in relation to precipitation, physiographical regions, and areas of mopane (*Colophospermum mopane*) in Namibia.

STUDY AREA

This investigation was conducted throughout the territory of Namibia, located in southwestern Africa (17–27°S to 13–20°E).

I. Physiographical Regions

Namibia can be divided into three major physiographical regions based principally on its landforms and soils: the Namib Desert, the Central Highland, and the Mega Kalahari (Fig. 1). The major landforms in Namibia are, from west to east, the coastal plain, the escarpment, the central plateau, and the Kalahari sand field (modified after Mthoko *et al.*, 1990). The pedology of Namibia is characterized by weakly developed (coastal plain), lithosolic (central plateau),

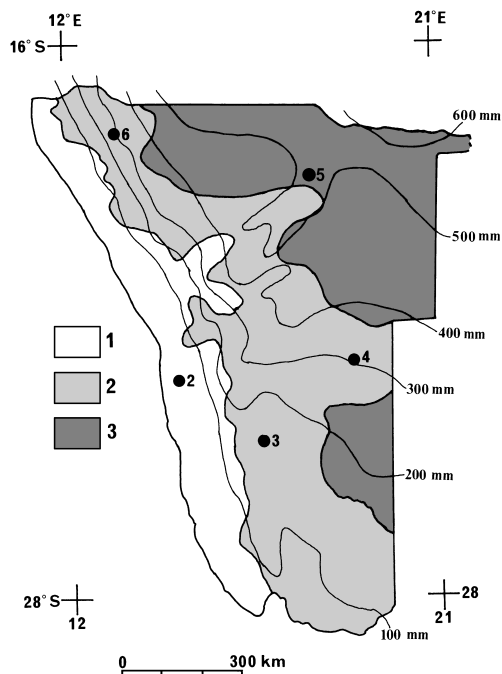


Fig. 1. The physiographic regions of Namibia (adapted from Erkkilae and Siiskonen, 1992, based on Mthoko *et al.*, 1990) and the distribution of annual precipitation (Koenen, 1996). The Caprivi region (east of the Kavango River, slightly east-west between Zambia and Botswana) is omitted (also see Fig. 10). The dots with figure indicate the localities of the photos of Fig.2–Fig.6 (2: Fig. 2, 3: Fig.3, 4: Fig. 4, 5: Fig. 5, 6: Fig. 6).

1: Namib Desert, 2: Central Highland, 3: Mega Kalahari

and arenosolic (Kalahari sand field) soil types (Erkkilae & Siiskonen, 1992; Mendelsohn *et al.*, 2002).

The Namib Desert occupies the coastal plain, which comprises the western marginal area between the escarpment and the coast, stretching along the entire Atlantic Ocean coastline and rising rapidly eastward. It extends 80–150 km inland and rises to a level of approximately 800 m at the foot of the escarpment in the east. The escarpment is situated at the east end of the coastal plains, rising steeply to the central plateau. The soils of this region are usually weakly developed, brown to grayish, and may or may not contain a B-horizon.

The Central Highland lies on the central plateau, east of the Namib Desert. The central plateau is a mountainous area situated between the escarpment in the west and the Kalahari sand field in the east, and rises 1,000–2,000 m. This area is characterized by highly undulating landforms, a thin soil layer, and an exposed bedrock stratum. The landforms typically consist of actively eroding landscapes, especially in the hilly or undulating areas that cover much of the central plateau. The ground surface tends to be hard, as it consists of rock or stones. The soils of this region are well represented by the leptosols, which are shallow, have a weak profile differentiation, and contain coarse rock debris,

gravels, and solid bedrocks. These coarse-textured soils are characterized by their limited depth, due to the presence of continuous hard rock that consists of a highly calcareous or cemented layer within 30 cm of the surface. Accordingly, coupled with the highly undulating landforms, the water-holding capacity of the soils of this region is low, and vegetation on these soils is often subject to drought. The rates of water run-off and water erosion can be high during heavy rainfall.

The Mega Kalahari occupies the Kalahari sand plain, which is the area east of the Central Highland. The Kalahari sand plain consists of flat plains and smooth hills sloping gently to the northeast. The soils of this region are typically arenosols, which are formed from wind-blown sand and usually extend to a depth of at least 1 m, with sand generally making up more than 70%. The structure of these soils is usually loose, although calcrete layers occasionally occur near the surface. The loose structure of the arenosols, together with the flat plains and smooth hills of this region, allow for little run-off of water.

II. Climate

Namibia has a dry climate with extremely variable and unpredictable rainfall. In the study area, the average annual rainfall is less than 20 mm (15 mm in Swakopmund) on the coast and increases towards the northeast; Grootfontein receives 570 mm (Fig. 1). However, this distribution pattern of annual precipitation does not necessarily coincide with physiographical region (Fig. 1). The average annual potential evaporation varies between 3,700 mm in the central-southern area to 2,600 mm in the north (Erkkilae & Siiskonen, 1992; Mendelsohn *et al.*, 2002).

The range of temperature fluctuations throughout the year varies according to region. Generally, the hottest month is October, during which the average daily maximum temperature is 34–36°C. July is the coldest month in most parts of the country, except on the coast, where the lowest temperatures can be expected in August. The average daily minimum for the coldest month varies from less than 2°C to more than 10°C.

III. Vegetation

The vegetation of Namibia is divided into three major types (Giess, 1971; Koenen, 1996): the Namib Desert, savannas, and woodlands (after Erkkilae & Siiskonen, 1992).

The Namib Desert covers 15% of the territory of Namibia (Erkkilae & Siiskonen, 1992) and occupies the coastal plain. It consists primarily of scattered, non-woody vegetation, mainly herbaceous and succulent plants. Woody vegetation occurs in the Namib Desert only along the riverbeds. The plant diversity is very high, approximately 200-fold higher than in the Sahara Desert, which has a similar climate (Cowling *et al.*, 1998). However, what is called the Kalahari Desert in the eastern part of Namibia is not a genuine desert, but rather a type

of savanna with scattered woods.

Savannas cover 65% of the territory of Namibia (Erkkilae & Siiskonen, 1992) and form a more or less discontinuous crown cover of trees. The savannas of Namibia consist of different types (Schultz, 1997). In the northeastern part of the country, savanna with a well-extended crown cover of trees predominates and consists mainly of scattered tall trees that are usually >15 m high. In the central part of the country, the dominant form is tree-shrub savanna, which is characterized by a scattered distribution of tall trees and low shrubs. In the southern and southeastern parts of the country, the Nama-karoo prevails. This type of savanna comprises deciduous low shrubs, scattered woods, and herbaceous plants. In addition, succulent-karoo occurs in the southeastern-most part of the country, consisting mainly of succulent plants mixed with low deciduous woods. In northwestern Namibia, the most common savanna type is dominated by mopane.

Woodlands have a continuous crown expansion that almost completely covers the land. They occur only in the most northeastern part of the country (Caprivi), which receives the highest amount of rainfall (more than 600 mm), and account for 20% of the territory of Namibia (Erkkilae & Siiskonen, 1992). One of the dominant species in this region is Zambezi teak (*Baikiaea plurijuga*). The woodlands described by Erkkilae & Siiskonen (1992) correspond closely to the forest discussed in other major references (Archibold, 1997; Rutherford, 1997; Midgley *et al.*, 1997). Hereafter, the term forest or forests will be used instead of woodlands, consistent with the latter references.

METHODS

I. Leaf Habits and their Ecological Significance

Plants inevitably adopt the ecologically most adaptive leaf habits suitable to their environments. Thus, the leaf habit, which is aimed at maximizing photosynthesis, directly indicates the ecological adaptations of a plant (Chabot & Hicks, 1982). Here, I used two different features of the leaf habit, i.e., leaf size and seasonality, to analyze the different types of savanna in Namibia.

Leaf size corresponds well with the environment of a particular habitat, although it is a simple indicator. Table 1 presents a representative classification of leaf sizes. Under conditions of drought or low temperature that may occur during a growing season, leaf size tends to be small. For example, in subtropical warm temperate forests of Japan, a shift occurs from notophyllous to microphyllous evergreen broadleaves along the drought gradient between valleys (moist) and ridges (drought) or from the foothills (moist) to the mountains (drought) within fairly similar temperature regions (Ohsawa, 1993). A similar shift in leaf size in the transition from moist slopes to dry rocky slopes has also been observed in Mt. Pulog, Philippines (Buot & Okitsu, 1999). In the mountains of the tropics, where increasing altitudes are accompanied by

Table 1. Leaf size classes according to the Raunkiaer-Webb classification system (Shimwell, 1971).

Leaf size class	Size range (sq. mm) (Raunkiaer, 1934; Webb, 1959)
Leptophyll	< 25
Nanophyll	25–225
Microphyll	225–2,025
Notophyll	2,025–4,500
Mesophyll	4,500–18,225
Macrophyll	18,225–16,4025
Megaphyll	>16,4025

decreasing temperatures, leaf size usually decreases from mesophyllous in the lowlands to notophyllous in the lower montane, microphyllous in the upper montane and subalpine, and nanophyllous in the upper subalpine regions. These types of changes occur on Mt. Makilin (Brown, 1919) and Mt. Pulog (Buot & Okitsu, 1999) in the Philippines, in New Guinea (Grubb, 1974), and on Mt. Kerinci in Indonesia (Ohsawa & Ozaki, 1992). Thus, a decrease in leaf size generally follows a gradient ranging from more favorable to more stressful habitats (Buot & Okitsu, 1999).

In this study, only two major leaf sizes were observed in the dominant woody species of the study area: (1) nanophyll, in which the area of a leaf or leaflet ranges from 25 to 225 mm², e.g., the leaves of *Acacia* species, and (2) notophyll, in which the area of a leaf or a leaflet ranges from 2,025 to 4,500 mm². The most prevailing type of woody vegetation in the study area is mopane.

Seasonality is another ecologically important leaf habit that reflects adaptations to seasonal fluctuations, including periods of drought and low temperature. Two types of leaf seasonality can be distinguished: evergreen and deciduous. In the former, trees are in leaf throughout the year. While this leaf habit has the advantage of providing year-round photosynthesis, the leaves will suddenly die under conditions of extreme drought or low temperatures, which occasionally occurs in the study area. A deciduous leaf habit consists of a normal loss of leaves during drought or low temperatures. This type of habit can advantageously avoid sudden leaf death due to drought or freezing. However, it cannot provide photosynthesis throughout the year.

II. Types of Savanna Vegetation

In this study, a savanna is defined as having woody vegetation with a more or less discontinuous crown cover of trees that is greater than 5%. Woody vegetation characterized by a completely continuous cover corresponds to a forest, whereas desert is defined as vegetation having a crown cover of less than 5% (Fig. 2).

The various types of savanna are defined by a combination of the seasonality and leaf size of the vegetation: the deciduous type (Fig. 3, 4), the evergreen nanophyll type (Fig. 5), and the evergreen notophyll type (Fig. 6). In addition, deciduous nanophyll and deciduous notophyll types also arise by a combination



Fig. 2. Landscape of the Namib Desert near Gobabeb (west-central part of Namibia, 23° 42'S, 15°18'E). For the locality of photograph, see Fig. 1.



Fig. 3. Example of deciduous savanna near Maltahoehe (central part of Namibia, 24°01'S, 16°54'E). The maximum height of the vegetation is 4 m. The total woody vegetation cover is 25%. Deciduous trees completely dominate this area, accounting for 95% of the total woody cover. No evergreen notophyll trees are found. The herbaceous layer covers 40% of the ground. For the locality of photograph, see Fig. 1.



Fig. 4. Example of deciduous savanna near Gobabis (east-central part of Namibia, 23°02'S, 18°45'E). The maximum height of the vegetation is 8 m and the total woody vegetation cover is 80%. Deciduous woods dominate, accounting for 55% of the total woody cover, followed by evergreen nanophylls; evergreen notophylls rarely occur. The herbaceous layer covers 10% of the ground. For the locality of photograph, see Fig. 1.



Fig. 5. Example of evergreen nanophyll savanna near Tsumeb (northeastern most part of Namibia, 19°06'S, 18°37'E). The maximum height of the vegetation is 17 m, and the total woody vegetation cover is 150%. Evergreen nanophylls dominate, accounting for 60% of the total woody cover, followed by deciduous trees (25%) and evergreen nanophylls (15%). The herbaceous layer covers 15% of the ground. For the locality of photograph, see Fig. 1.

of leaf habits. However, these two types were not investigated in this study, because it was impossible to determine the leaf size of the deciduous trees based on field observations conducted at the end of the dry season.

The advantages of classifying savanna types according to leaf habit are that (1) the leaf habit directly indicates the ecological adaptation of the vegetation to the environment; (2) it is the most suitable indicator of factors controlling the different savanna types; and (3) more practically, it allows the factors controlling savanna types to be discussed on a phytogeographical basis, regardless of



Fig. 6. Example of evergreen notophyll savanna near Opuwo (north-eastern-most part of Namibia, 17°26'S, 14°42'E). The maximum height of the vegetation is 19 m, and the total woody vegetation cover is 180%, similar to the value of typical forests. Evergreen notophylls dominate, accounting for 60% of the total woody cover, followed by evergreen nanophylls; deciduous trees are rare (7% of total woody cover). The herbaceous layer covers 30% of the ground. For the locality of photograph, see Fig. 1.

the taxonomic identification of the major wood species.

III. Field Observations

Field observations were carried out during three years (2001, 2002, 2003) at the end of the dry season (from the end of July to the beginning of November). The observations covered both the desert and the savanna, with the main focus on the savanna.

Plots along the major roads were selected in areas where the degree of human impact on vegetation was minor. Plots along rivers and seasonal streams were omitted to avoid the effects of exceptional water supply on the vegetation. I surveyed a total of 71 savanna plots. Plots that were not considered to

represent savanna, i.e., desert plots, were all located in the Namib Desert.

In each savanna plot, the vegetation cover was measured by eye and classified into three layers: a tree layer, >5 m in height; a sub-tree layer, 2–5 m in height; and a shrub layer, <2 m in height. In addition, in each layer, the cover of each leaf habit, i.e., deciduous, evergreen nanophyll, and evergreen notophyll, was measured. In this study, the cover is expressed as the percent of the sum of the vertical projection of the crown within a layer. Accordingly, the maximum cover in each layer is 100%, and total woody cover, defined as the total sum of the cover of each layer, has a maximum value of 300%. Forests with a continuous crown cover generally have a total woody cover of more than 200%. The maximum height of the trees in each plot was also measured. The types of savanna in the plots were determined by the dominant leaf habit of the species that composed the highest percentage of the total woody cover. The amount of precipitation received by each plot was estimated from the distribution map of the annual precipitation of Namibia (Fig. 1).

RESULTS

I. Relationship between Annual Precipitation and Vegetation Performance

Figure 7 shows the relationship between the total woody vegetation cover and the annual precipitation of the plots. Total cover ranged from a minimum of 5%, characteristic value to savanna vegetation, to 220%, which is similar to the value typical of forests. In Namibia, savanna vegetation receives an annual

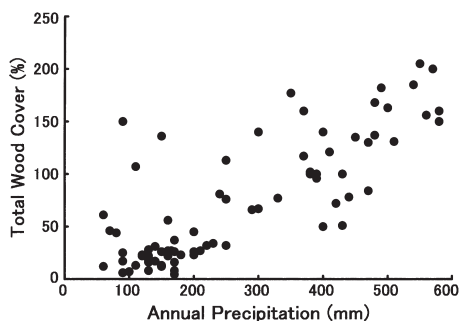


Fig. 7. Relationship between total woody vegetation cover and amount of annual precipitation in the plots.

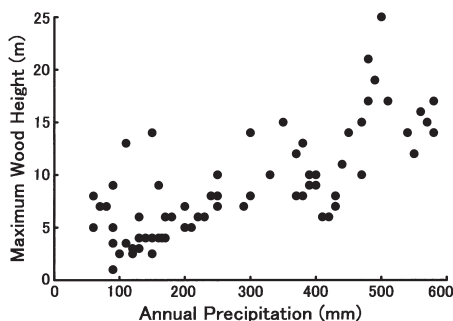


Fig. 8. Relationship between maximum wood height and amount of annual precipitation in the plots.

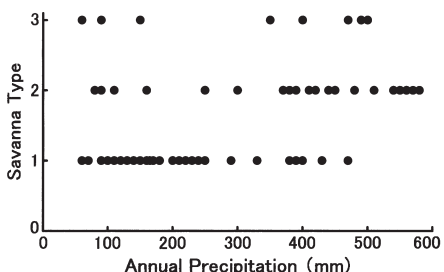
precipitation of 50 to 600 mm. Plots receiving less than 50 mm of precipitation always contained desert vegetation. The critical amount of precipitation in the transition from desert to savanna in Namibia is therefore ca. 50 mm.

The total vegetation cover was positively correlated with the amount of annual precipitation (Fig. 7), which increased incrementally but did not reach saturation, and barely attained the value of genuine forests in the study area. However, this relationship was not definitive since there was a relatively wide fluctuation in total cover despite similar amounts of precipitation; for example, the total cover of plots with 100 mm of precipitation ranged from 5–150%.

Figure 8 shows the relationship between the maximum tree height and annual precipitation received. The maximum tree height ranged from 1 m, the minimum value of savanna trees, to 25 m, which is similar to the value in typical forests. The maximum tree height was positively related to both the amount of annual precipitation and the total vegetation cover.

II. Relationship between Precipitation and Savanna Type

Figure 9 shows the annual precipitation range for each savanna type and illustrates the fairly complete overlap. Annual precipitation ranged from 50 to 480 mm in the deciduous type, 70 to 600 mm in the evergreen nanophyll type, and 50 to 510 mm in the evergreen notophyll type. Annual precipitation was never the only factor controlling the occurrence of a particular savanna type.



1: Deciduous 2: Evergreen nanophyll 3: Evergreen notophyll

Fig. 9. Annual precipitation ranges in the three savanna types.

III. Geographical distribution of savanna types

Figure 10 illustrates the geographical distribution of the three savanna types according to physiographical regions and overlaid with the mopane areas in

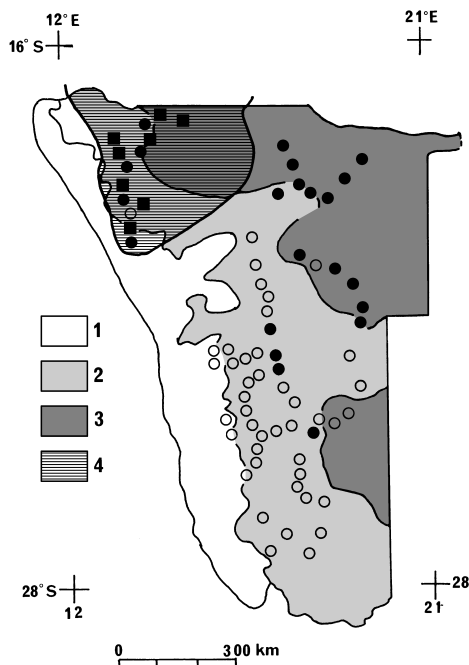


Fig. 10. Distribution of the three savanna types according to geographical region and area of mopane (*Colophospermum mopane*) in Namibia (after Okitsu, 2004b).

■ : Evergreen notophyll type, ● : Evergreen nanophyll type, ○ : Deciduous type.
1: Namib Desert, 2: Central Highland, 3: Mega Kalahari, 4: Distribution of mopane in Namibia, except in Kapribi (Palgrave, 1983).

tained the least savanna vegetation (only three plots), while the Central Highland, where the deciduous type predominated (34 of 39 plots, the remainder being evergreen nanophyll type), had the most. The Mega Kalahari was dominated by the evergreen nanophyll type (12 plots), with a few occurrences of the deciduous type (three plots). The mopane area had every savanna type, with the majority being the evergreen notophyll type (eight of 14 plots).

Namibia. Table 2 quantitatively summarizes the frequency of the plots in each savanna type and in each physiographical region, including the mopane area. Only three plots in the Namib Desert had savanna vegetation; these were located on the border between the Namib Desert and the Central Highland. In contrast, in the Central Highland and Mega Kalahari, savanna vegetation occurred almost exclusively.

Of the 41 deciduous-type plots, 34 occurred in the Central Highland. There were also three plots in the Mega Kalahari, three in the Namib Desert, and one in the mopane area. The evergreen nanophyll type appeared primarily in the Mega Kalahari (12 plots), with fewer in the Central Highland (five plots) and in the mopane area (five plots). The evergreen notophyll type was concentrated exclusively in the mopane area (eight plots), and its distribution was independent of any physiographical region, such as Mega Kalahari, Central Highland, or Namib Desert (Fig. 10).

In an analysis based on physiographical region, the Namib Desert con-

Table 2. Distribution of savanna types in each physiographical region in Namibia, based on Fig. 10. The numbers in the table indicate the number of plots surveyed.

Savanna type	Physiographical region				Total
	Namib Desert	Central Highland	Mega Karahari	Mopane Area	
Deciduous	3	34	3	1	41
Evergreen nanophyll	0	5	12	5	22
Evergreen notophyll	0	0	0	8	8
Total	3	39	15	14	71

IV. Relationship between Vegetation Cover and amount of Precipitation in Each Savanna Type

Figure 11 shows the relationship between total woody vegetation cover and amount of annual precipitation for each savanna type; the relationship differed for each of the three types. In the deciduous type, we observed a positive correlation between the total cover and the amount of annual precipitation. However, the total cover of deciduous savanna was the smallest of the three types, being at most 120% even in plots receiving more than 400 mm of annual precipitation. The evergreen nanophyll type showed the clearest relationship between total cover and annual precipitation. The total cover was lower (10–50%) in plots with less annual precipitation, around 100 mm, but higher (200%) in plots receiving more than 400 mm of annual precipitation. Evergreen notophyll

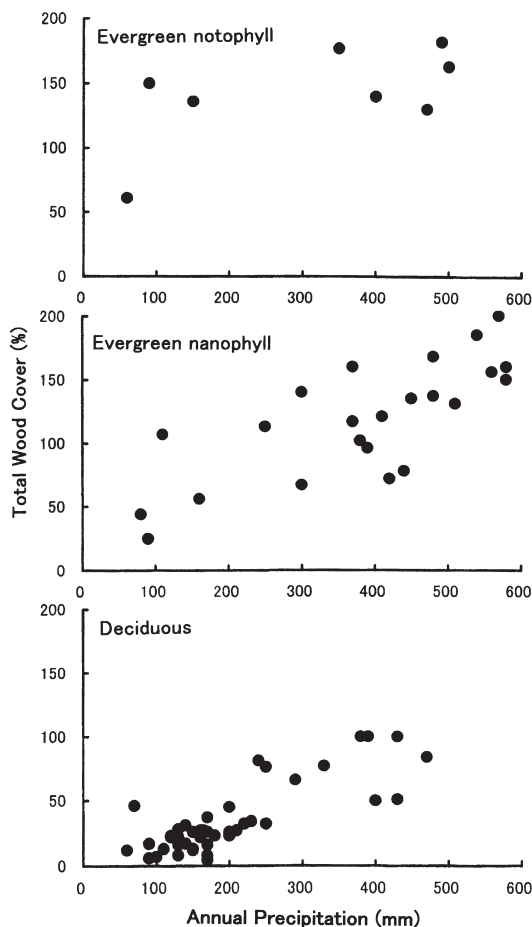


Fig. 11. Relationship between total woody vegetation cover and amount of annual precipitation in the three savanna types (after Okitsu, 2004b).

hyll savanna had the largest total cover of the three savanna types. Even in plots with the lowest amount of annual precipitation (70 mm), the total cover was as high as 60% and rapidly increased to 150% at 100 mm of annual precipitation before more slowly reaching 200% at 500 mm of annual precipitation.

DISCUSSION

I. Relationship between the Amount of Precipitation and the Occurrence of Savanna Vegetation and Tree Performance in Namibia

In Africa, savannas occur generally in regions where the amount of precipitation is less than 700 mm, while tropical forests are found in regions where precipitation is more than around 800 mm, although a broad transition exists between these regions (Okitsu, 2004a). The maximum amounts of precipitation measured in the savannas of Namibia are consistent with this definition. The minimum amount of annual precipitation measured in Namibian savanna is 50 mm, which is less than the amounts reported in other references, some of which documented ca. 100 mm (Cowling *et al.*, 1994; Archibold, 1995) or even ca. 200 mm (Knapp, 1973; Walter & Breckle, 1984; Juergens *et al.*, 1997; Rutherford, 1997; Scholes, 1997). Despite these differences, the precipitation range in the Namibian savanna is within the general range measured in other parts of Africa.

Within the savanna, the amount of annual precipitation affects vegetation performance, which continuously increases with incremental increases in annual precipitation. Thus, the amount of annual precipitation scarcely attains the value required to sustain genuine forests in the study area, and it is not sufficient to promote additional, well-developed forests.

II. Factors Controlling the Occurrence of Savanna Types in Namibia

I expected that the occurrence of a particular savanna type would coincide with the amount of annual precipitation, such that the deciduous type would occur in areas with the lowest levels of annual precipitation, the evergreen nanophyll type would occur in intermediate areas, and the evergreen notophyll type would be found in areas receiving the most annual precipitation. In fact, however, the occurrence of a savanna type does not necessarily coincide with this expected pattern. Annual precipitation is not the sole factor controlling the occurrence of savanna type in Namibia, although it does account for the vegetation performance of the savanna as a whole.

Instead, the type of savanna is closely associated with the physiographical region in which it occurs. This suggests that the presence of each savanna type should correspond to the different environments of the physiographical regions, regardless of the amount of annual precipitation received. To identify the factors

controlling the occurrence of each savanna type, the following sections mainly focus on the environments of the various physiographical regions and on the ecological characteristics of mopane.

1. *Deciduous savanna*

This type occurs mainly in the Central Highland, regardless of the amount of annual precipitation. Indeed, the Central Highland contains almost exclusively deciduous savanna, which strongly suggests that the environment of the Central Highland inevitably favors deciduous leaf habits. The water-holding capacity of the leptosols, the dominant soil type in this region, is low. Coupled with the highly undulating landforms, this can result in very high rates of water run-off and soil erosion. Furthermore, savanna vegetation in this region is always subject to extreme drought during the dry season. As a result, the xeric conditions of the soils during the dry season inevitably force the vegetation to maintain deciduous leaf habits.

Deciduous savanna consistently had the lowest total woody vegetation cover among the three savanna types despite similar amounts of annual precipitation. This can be explained by the fact that the deciduous leaf habits cannot support photosynthesis throughout the year, resulting in a lower photosynthetic production rate than can be achieved in trees with an evergreen leaf habit. In turn, this lower photosynthetic production rate may account for the lower total crown cover of deciduous savanna. Thus, the prevailing factor controlling the occurrence of this savanna type is the extremely dry soil condition during the dry season, which is due to the poor water-holding capacity of the soils, regardless of the amount of annual precipitation received. The sporadic incidence of deciduous savanna in the other physiographical regions may also result from the microtopographic occurrence of habitats with extremely dry soil conditions.

The total woody vegetation cover of deciduous savanna increased with increasing precipitation in the plots. This indicates that the amount of precipitation during the growing season significantly affects vegetation performance, in accordance with the general pattern.

2. *Evergreen nanophyll savanna*

The evergreen nanophyll type is found primarily in the Mega Kalahari. Conversely, the Mega Kalahari contains almost exclusively evergreen nanophyll savanna, suggesting that the environment of this region is conducive to this savanna type. The loose structure of the arenosols, associated with calcrete layers near the surface, as well as the flat plains and smooth hills of this region allow for little run-off of water. This implies that during the year, the soil never experiences a shortage of moisture, and the vegetation can therefore maintain an evergreen leaf habit. Thus, the prevailing factor controlling the occurrence of evergreen nanophyll savanna is primarily the moisture content capacity of the arenosols of this region, regardless of the total precipitation. The evergreen nanophyll type is also found in the Central Highland and in the mopane area. This may result from the occurrence in those regions of micro-

habitats suitable to evergreen nanophyll savanna.

However, the soil moisture conditions of the Mega Kalahari are insufficient for the vegetation to adopt a larger leaf size; the dominant leaf types in this region are nanophylls, which are smaller than notophylls. The water-holding capacity of the arenosols must be greater in order to maintain the larger leaf sizes characteristic of evergreen notophyll savanna.

I observed a clear relationship in the evergreen nanophyll savanna between total woody vegetation cover and amount of annual precipitation. The evergreen habitat allows for efficient use of the water supply present in the soil throughout the entire year. This continuous water use explains the strong correlation between total cover and amount of annual precipitation.

3. *Evergreen notophyll savanna*

The evergreen notophyll type is exclusively located in the mopane area, although the two other savanna types are also found there. Thus, the occurrence of evergreen notophyll savanna depends on the ecological nature of mopane itself, regardless of the amount of annual precipitation or the physiographical region.

Mopane is mainly found in the relatively flat and wide valley bottoms of large rivers and in the adjacent wide plains, at altitudes between 100 and 1,200 m. Mopane grows on fine-grained, sandy to loamy and clayey, usually deep soils (Werger & Coetzee, 1978). Soils in mopane areas tend to develop a high exchangeable sodium content (Kennedy & Potgieter, 2003).

The eastern range of the mopane area receives about 500 to 600 mm of annual precipitation, although farther west to the escarpment, annual precipitation drops to less than 100 mm (Fig. 1 and Fig. 10). This indicates that unlike other notophylls, which usually require large amounts of precipitation, mopane can tolerate extremely low amounts of moisture. The boundary of the mopane area in Namibia largely coincides with the 5°C isotherm of the mean daily minimum temperature for the coldest month, July (Werger & Coetzee, 1978).

The landform of the mopane area consists mainly of the wide flat Owambo Plain, at an altitude of about 1,100 mm, although the area principally belongs to the northernmost part of the Central Highland (Fig. 10). The soils of this area are dominated by the thick deposits of Kalahari sands (Erkkia & Siiskonen, 1992). These environments are preferred by mopane.

Once mopane grows in a particular habitat, its large notophyll leaves are expected to attain higher rates of photosynthesis than nanophylls. Accordingly, evergreen notophyll savanna usually has a higher total woody vegetation cover than the other two types despite receiving similar amounts of precipitation. The total cover of the evergreen notophyll type is 150%, even with annual precipitation reaching only 100 mm. Subsequently, with increasing precipitation, the total cover quickly increases, ultimately reaching around 200%. Thus, the decisive factor controlling the occurrence of evergreen notophyll savanna is undoubtedly the ecological nature of mopane, regardless of the amount of annual precipitation and the physiographical region. The mopane area includes both the Central

Highland and the Mega Kalahari. This regional variation provides microhabitats conducive to the occurrence of every type of savanna.

CONCLUSION

In Namibia, the amount of annual precipitation controls the general performance of the savanna vegetation, consistent with the generally accepted view. However, the geographical distribution of the three specific savanna types in Namibia is related to factors other than annual precipitation. One factor is the ability of the soil to retain moisture; this is closely associated with the change from deciduous to evergreen nanophyll savanna. The other factor is the ecological nature of mopane which is independent of physiographical region; this control the distribution of the evergreen notophyll type.

ACKNOWLEDGEMENTS This study was financially supported in part by the Grant-in-Aid for Scientific Research (Project No. 13371013 headed by Dr. Kazuharu Mizuno, Kyoto University) from the Ministry of Education, Science, Sports, Culture and Technology of the Japanese Government. I sincerely thank Dr. Mizuno for providing the opportunity to participate in this research project.

REFERENCES

- Archibold, O.W. 1995. *Ecology of World Vegetation*. Chapman & Hall, London.
- Brown, W.H. 1919. *Vegetation of the Philippine Mountains*. Bureau of Science, Manila.
- Buot, Jr. I.E. & S. Okitsu 1999. Leaf size zonation pattern of woody species along an altitudinal gradient on Mt. Pulog, Philippines. *Plant Ecology*, 145: 197-208.
- Chabot, B.F. & D.J. Hicks 1982. The ecology of leaf life span. *Annual Review of Ecology and Systematics*, 13: 229-259.
- Cowling, R.M., K.J. Esler, G.F. Midgley & M.A. Honig 1994. Plant functional diversity, species diversity and climate in arid and semi-arid southern Africa. *Journal of Arid Environments*, 27: 141-158.
- Cowling, R.M., P.W. Rundel, P.G. Desmet & K.J. Esler 1998: Extraordinary high regional-scale plant diversity in southern Africa arid lands: sub continental and global comparisons. *Diversity and Distribution*, 4: 27-36.
- Erkkilae, A. & H. Siiskonen 1992. *Forestry in Namibia 1850-1990. Silva Carelica* 20. University of Joensuu, Joensuu.
- Giess, W. 1971. A preliminary vegetation map of South-West Africa. *Dinteria*, 4: 5-114.
- Grubb, P.J. 1974. Factors controlling the distribution of forest types on tropical mountains: new facts and a new perspective. In: (J.R. Flenley, ed.) *Altitudinal Zonation in Malesia*. pp. 13-46, Department of Geography, University of Hull, Hull.
- Grubb, P.J. 1977. Control of forest growth and distribution on wet tropical mountains: with special reference to mineral nutrition. *Annual Review of Ecology and Systematics*, 8: 83-107.
- Huntley, B.J. 1982. South African savannas. In: (B.J. Huntley & B.H. Walker, eds.) *Ecology of Tropical Savannas. Ecological Studies* 42, pp. 101-119, Springer Verlag, Berlin.

- Huntley, B.J. & B.H. Walker (eds.) 1992. *Ecology of Tropical Savannas. Ecological Studies* 42, Springer Verlag, Berlin.
- Jarvis, P.G. & K.G. MacNaughton 1986. Stomatal control of transpiration: scaling up from leaf to region. *Advances in Ecological Research*, 15: 1-45.
- Juergens, N., A. Burke, M.K. Seely & K.M. Jacobson 1997. Desert. In: (R.M. Cowling, D.M. Richardson & S.M. Pierce, eds.): *Vegetation of Southern Africa*, pp. 189-214, Cambridge University Press, Cambridge.
- Kennedy, A.D. & A.L.F. Potgieter 2003. Fire season affects size and architecture of *Colophospermum mopane* in southern African savannas. *Plant Ecology*, 167: 179-192.
- Knapp, R. 1973. *Die Vegetation von Afrika*. Gustav Fisher Verlag, Stuttgart.
- Mendelsohn, J., A. Jarvis, C. Roberts & T. Robertson 2002. *Atlas of Namibia. A Portrait of the Land and its People*. David Philip Publishers, Cape Town.
- Midgley, J.J., R.M. Cowling, A.H.W. Seydack & G.F. van Wyk 1997. Forest. In: (R.M. Cowling, D.M. Richardson & S.M. Pierce, eds.) *Vegetation of Southern Africa*. pp. 278-299, Cambridge University Press, Cambridge.
- Mthoko, N.A., N.H. Noisser & M.W. Rebentisch 1990. *Geography of Namibia: Junior Secondary Geography Book*. Namibia Project, University of Bremen, Bremen.
- Ohsawa, M. 1993. Forest pattern along hierarchical habitat gradients in east Asia. *Biodiversity International (IUBS), Special Issue*, 29: 30-36.
- Ohsawa, M. & K. Ozaki 1992. Plant biometeorology — Hierarchical analysis of vegetation/environmental pattern for east Asia extra tropical evergreen broadleaved forest. (In Japanese) *Japanese Journal of Biometeorology*, 29 (Suppl.), 93-103.
- Okitsu, S. 2004a. The vegetation of Africa. In (K. Mizuno, ed.) *Natural History of Africa*, (In Japanese) pp. 25-34, Kokon-Syoin, Tokyo.
- 2004b. The changes in savanna vegetation in Namibia. In (K. Mizuno, ed.) *Natural History of Africa*, pp. 130-140, Kokon-Syoin, Tokyo. (In Japanese)
- Palgrave, K.C. 1983. *Trees of Southern Africa. Second revised edition*. Struik Publishers, Cape Town.
- Raunkiaer, C. 1934. *The Life Forms of Plants and Statistical Plant Geography being the Collected Papers of C. Raunkiaer*. Oxford at the Clarendon Press, Oxford.
- Rutherford, M.C. 1997. Categorization of biomes. In (R.M. Cowling, D.M. Richardson & S.M. Pierce, eds.) *Vegetation of Southern Africa*, pp. 91-98, Cambridge University Press, Cambridge.
- Scholes, R.J. 1990. The influence of soil fertility on the ecology of southern African savannas. *Journal of Biogeography*, 17: 417-419.
- 1997. Savanna. In (R.M. Cowling, D.M. Richardson & S.M. Pierce, eds.) *Vegetation of Southern Africa*, pp. 258-277, Cambridge University Press, Cambridge.
- Shimwell, D.W. 1971. *Description and Classification of Vegetation*. Sidgwick & Jackson, London.
- Von Koenen, E. 1996. *Heil-, Gift- und Essbare Pflanzen in Namibia*. Klaus Hess Verlag, Goettingen.
- Walter, H. & S-W. Breckle 1984. *Oekologie der Erde Band 2. Spezielle Oekologie der Tropischen und Subtropischen Zonen*. Gustav Fischer, Stuttgart.
- Webb, L.J. 1959. A physiognomic classification of Australian rain forests. *Journal of Ecology*, 47: 551-570.
- Werger, M.J.A. & B.J. Coetzee 1978. The Sudano-Zambezian region. In (M.J.A. Werger, ed.) *Biogeography and Ecology of Southern Africa. Monographiae Biologicae* 31, pp. 301-462. Dr W. Junk Publishers, The Hague.

————— Accepted *January 22, 2005*

Author's Name and Address: Susumu OKITSU, *Faculty of Horticulture, Chiba University,*
648, Matsudo, Matsudo-city, Chiba, 271-8510, JAPAN

E-mail: okitsu@faculty.chiba-u.ac.jp