

VEGETATION STRUCTURE OF THE BIOMES IN SOUTHWESTERN AFRICA AND THEIR PRECIPITATION PATTERNS

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ABSTRACT Southwestern Africa contains diverse biomes. The amount of the annual precipitation of this area has been traditionally thought to be the most important controlling factor to the differentiation of the biomes. However, this territory experiences the summer rain type and winter rain type. Those two different precipitation patterns should result in the different mechanisms to control the distribution of the biomes. This study intends to clarify the relationships between the distribution of the biomes and the summer rain type and winter rain type, knowing the vegetation structure in terms of the growth forms of the dominant plants. Studies were conducted in the area southwestern Africa, including major biomes of the southern Africa. Grassland, Nama-karoo and Savanna appear in the area with the summer rain type. Both of Succulent karoo and Fynbos appear in the area with the winter precipitation type. The amount of winter precipitation of those two biomes is much higher than that of the other tree biomes. This higher amount of winter precipitation encourages the dominance of evergreen woods and succulents in those two biomes. Especially the succulents efficiently utilize the winter precipitation. This leads to the dominance of the succulents on those two biomes.

Key Words: Deciduous shrub; Grassland; Savanna; Succulents; Summer rain; Winter rain.

INTRODUCTION

Southwestern Africa, mainly western half of the territory of the Republic of South Africa in this study, contains diverse biomes (For the definition of biome, see Study area) (Rutherford, 1997). Grassland and Savanna occur in the eastern most part of the study area. Nama-karoo appears in the western area of the Grassland and Savanna. Succulent karoo and Fynbos develop along the west coast of the territory, facing the Atlantic Ocean. Those biomes should link with any climatic factors through life forms of component plants; a growth form is a principal determinant of types of biomes (see Fig. 1), and is thought to be a total express of ecological adaptation to environments such as precipitation patterns of the area.

Recent studies attempted to clarify the links between climatic factors and biomes of southern Africa (Rutherford, 1997). Rutherford & Westfall (1994) and Irish (1994) found a generally close association between southern Africa and a combination of the annual proportion of winter rain fall and a summer aridity. Ellery et al. (1991) predicted the delimitation of biomes based on number of days above a certain level of water availability and mean temperature when

moisture was not available for plant growth. However those pilot studies did not necessarily successfully discriminate among biomes by precipitation pattern considering their growth form composition.

Southwestern Africa experiences wide variety of allocation of the annual precipitation such as summer rain type and winter rain type. Those two different precipitation patterns should result in the different mechanisms determining the distribution of the biomes through ecological adaptations of growth forms of component plants. However, most of the studies ignore the links between biomes and climatic factors at a growth form level in southern Africa (Rutherford, 1997). Thus, the links between the distribution and vegetation structure and precipitation patterns through the ecological adaptations of growth forms to environments, especially those to precipitation patterns, in southwestern Africa, are still worth discussion.

This study intends to clarify the relationships between the distribution of the biomes and the precipitation patterns, namely, summer rain type and winter rain type, on the basis of the knowledge on the vegetation structure in terms of the growth forms of the dominant plants.

STUDY AREA

Studies were conducted chiefly in the area in the western part of the territory of South Africa, including southern most part of the territory of Namibia, located in southwestern Africa (24–34°S to 17–26°E: Fig. 1).

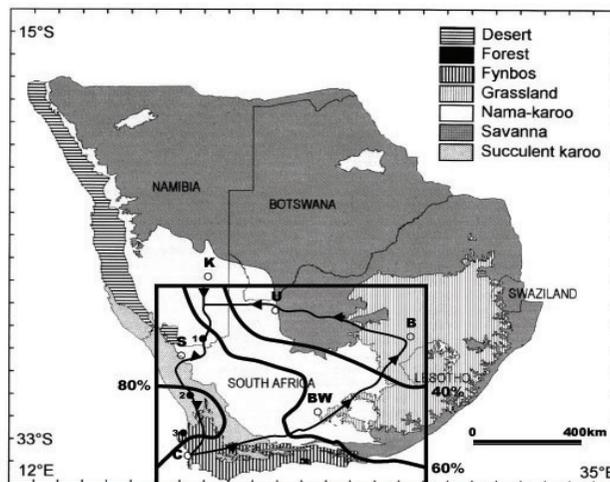


Fig.1. The biomes of southern Africa (Rutherford, 1997) and the study area of the present study (inner part of the inserted square with thick solid line).

The dots with figure indicate the localities of the photos of biomes (1: Fig. 2, Nama-karoo, 2: Fig.3, Succulent karoo, 3: Fig.6, Fynbos). The inserted thick contour lines show the winter precipitation percent isolines (After van Jaarsviels et al., 2005). The line with arrows shows the observation route. The open circles with caps shows major cities: C Cape Tow, BW Beaufort West, B Bloemfontein, U Upington, K Keetmanshoop, S Springbok.

The study area includes five biomes, namely, Grassland, Nama-karoo, Savanna, Succulent karoo and Fynbos (For the description of those biomes, see section III. Biomes).

I. Topography

According to Rutherford & Westfall (1994), this section describes topography of each biome. Grassland is found mainly on the high central plateau of South Africa. Its topography is mainly flat to rolling but can also be mountainous. Altitude is from 300m above mean sea level on the coastal plateau to 2,850m in the Drakensberg. Nama-karoo is found on the central plateau of the Cape Province, north of the east-west Cape folded mountain belt, the southwestern Orange Free State and the southern interior of Namibia. Most of the area consists of extensive, even to undulating plains, interspersed with mesas, hills, or, occasionally mountains. Height above sea level ranges from about 500 to 2,000m but with most of the area lying between 1,000 and 1,400m. Savanna is found mostly the extensive plains of the Karahari Basin and coastal platform of Mozambique/Tongaland. Altitude varies from coastal to a maximum that depends on latitude. This maximum can vary from a few hundred meters in the south to 2,000m above sea level in the north. Succulent karoo is found mostly west of the western escarpment from the Luederitz District of Namibia through the western belt of the Cape Province. Much of the terrain is flat to gently undulating, such as the west coastal platform. Hilly and more rugged topography occurs in Namaqualand. The extreme altitudinal range is from sea level to about 1,500m, but most of the area lies below 800m above sea level. Fynbos occurs in the southwestern and southern Cape Province. The topography is dominated by the Cape Folded Mountain Belt. The mountains include extensive areas with high rock cover pointing to the ruggedness of parts of the terrain. Maximum elevation above mean sea level is 2,325m in the Klein Swartberg but with most of the area lying between 300 to 1,600m.

II. Climate

The mean annual of temperature of the study area ranges from ca. 14°C in the Cape regions of the southern most area to ca. 20°C in the northeastern most part of the northern end of the territory of South Africa. The isotherms are parallel to the coast over most of the area, which exhibit decreasing values with distance inland, reflecting the effects of continentality (Schulze & McGee, 1978).

The mean annual precipitation of the study area ranges from 30mm to 600mm (van Jaarsveld et al., 2005). The precipitation pattern varies widely from the summer rain type to the winter rain type. Rainfall in the north and northeast area occurs during summer, and in the south and southwest, more commonly in winter. Summer rainfall is experienced as thundershowers. The distribution of mean January precipitation is similar to that for the year. Winter

rainfall is caused by cyclonic cold fronts, typical of the Western Cape. The value of mean July rainfall from 10–400 mm occur in the southwest, but for the major part of the area the July rainfall totals average less than 10mm.

Rainfall is distributed unevenly over the country, with humid subtropical conditions in the east and dry desert conditions in the west (ATLAS-More about South African Rainfall, 2008). The highest rainfall occurs in the mountain ranges of the south western part of Cape and in the Drakensberg, where mean annual rainfall exceeds 3,000mm in places.

The factors, which influence rainfall, vary from region to region. At one extreme, there is the east-facing Drakensberg escarpment in KwaZulu/Natal where moisture-laden air is often present and where several different rainfall-producing mechanisms exist. The other extreme is the desert area of the north-western part of Western Cape, where the air is hot and dry and the topography flat and the main rainfall-producing mechanism is the occasional convective thunderstorm.

There are three main seasonal rainfall regions (ATLAS-More about South African Rainfall, 2008). The winter rainfall region, where rainfall of the hot six month (usually from October to May) is higher than that of the cold six month (usually April to September), is a relatively narrow area along the Western Cape western and south-western coasts (Fig. 1). Precipitation results mainly from cyclonic disturbances. These rains are often of long duration and low intensity except along the mountains, where orographic effects may induce heavy showers. The summer rainfall (including late and very late summer) region, where rainfall of the hot six month (usually from October to May) is lower than that of the cold six month (usually April to September), covers most of the remainder of the country (Fig. 1) and occurs when a low-pressure system over the interior is trapped by high-pressure systems in the Indian and Atlantic Oceans. Warm moist air is drawn into the interior from the north and north-east and moderately heavy rain may last for several days. Between the winter and the summer rainfall regions lies a transitional area where rain occurs during all seasons (Fig. 1). It covers the coastal area between Mossel bay and east London.

III. Biomes

This study follows the definition criteria of biomes of southern Africa by Rutherford & Westfall (1994). A biome is viewed as (1) the largest land community unit recognized at a continental or sub continental level; (2) a unit mappable at a scale of no larger than about 1:10 million; (3) distinguished from other biomes primarily on the basis of dominant life form(s) in the long term; (4) distinguished from other biomes secondarily on the basis of those major climatic features that most affect the biota; and, (5) not an unnatural or anthropogenic system.

According to Rutherford & Westfall (1994), totally five biomes comprise in the study area (Fig. 1). Grassland is physiognomically monolithic and is char-



Fig. 2. Example of Nama-karoo at the north-western most part of South Africa. For the locality of photographs, see Fig. 1.



Fig.3. Example of Succulent karoo at the Kaokoland in the northwestern most part of South Africa. For the locality of photograph, see Fig. 1.



Fig. 4. A representative plant of Succulent karoo, *Argyroderma fissum* (Aizoaceae), leaf succulent plant.



Fig. 5. A water drop from a leaf of succulent plant in winter season with abundant rain. Succulent plants store water during winter to avoid water stress in drought summer.



Fig. 6. Example of Fynbos near Cape of Hope. For the locality of photograph, see Fig. 1.



Fig. 7. Example of the major component plants of Fynbos. *Protea* sp. (Proteaceae).

acterized by strong dominance of the grasses of Poaceae. The most noteworthy species with wide distribution in the Grassland biome is *Themeda triandra* Forssk. Nama-karoo (Fig. 2) can be described as a grassy, dwarf shrub land dominated by deciduous woods. Many of the woody plants are facultatively deciduous in response to the high temporal variability of rain fall. Savanna consists of a combination of woody plants and grasses. Woods of the biome are between 3 and 7m tall and often multistemmed. In certain areas, woody plants component is succulent, being dominated by species such as *Portulacaria africa*

Jacq. and *Euphorbia ingens* E. May. ex Boiss. The most common grasses are graminoids of the C_4 type, with C_3 type also important in the southern Savanna. Succulent karoo (Fig. 3) is very rich in succulent plants. They are belonging mainly to the Aizoaceae (Fig. 4) and Crassulaceae, but also to many other plant families. Adaptation to arid conditions through drought avoidance by storage of water is important for the succulents of this biome (Fig. 5). The high succulent plant species diversity of this biome is unparalleled elsewhere in the world. Fynbos (Fig. 6) can be described as open to closed grassy, dwarf shrubby shrub or woodland dominated by evergreen woods and succulents and generally does not exceed 3m in height. A relatively large number of species have showy inflorescences, (e.g., some species of *Protea*. See Fig. 7.), *Leucospermum*, *Helichrysum*, *Disa* and *Erica*.

METHODS

I. Growth Forms

Growth forms are major plant traits characterizing biomes. They clearly express the environmental adaptation of each plant. They are a quite useful aspect to discuss the relationship between the distribution of biomes and climatic factors. This study focuses on the ecological adaptation of plants to the precipitation seasonality such as summer rain and winter rain to take into the determination of types of growth forms. They are: grass, deciduous woods, evergreen woods, and succulents which are obligatory evergreen.

II. Vegetation Structure of Biomes

At each study point, vegetation cover was recorded with attentions to the growth forms of dominant plants.

The vegetation structure of biomes is expressed as a relative abundance of plant cover of each growth form.

The advantages of taking relative abundance of each growth form are that: (1) growth form directly indicates the ecological adaptation of the vegetation to the precipitation patterns such as winter rain and summer rain; and, (2) more practically, it allows the factors controlling vegetation structure of biomes regardless of the taxonomic identification of the major wood species.

III. Field Observation

Vegetation structure was recorded by visual observation along major traffic roads running with automobile approximately 50km in distance (Fig. 1). Totally 77 study points were established. 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.

Field observations were carried out during winter season of 2007, from the end of July to the end of August.

In each plot, the percent cover of each growth form was measured visually. The maximum cover in each layer is 100%, and total vegetation cover, defined as the total sum of the cover of each layer, has a maximum value of 300%.

IV. Analysis of the Precipitation Pattern

Amounts of summer and winter precipitation are estimated from the distribution map of annual precipitation pattern in southern Africa (van Jaarsveld et al., 2005).

RESULTS

I. Vegetation Structure of Biomes

Table 1 summarizes the vegetation structures in each biome. Totally five biomes appeared in the study area. Vegetation height ranged from 0.3m (Succulent karoo) to 8.0m (Savanna). Savanna had the highest mean vegetation height of 4.2m followed by that of Fynbos of 3.0m. Succulent karoo had the lowest mean vegetation height of 1.2m. Grassland and Nama-karoo showed intermediate mean vegetation height between those of Savanna and Succulent karoo with 2.0m and 2.1m, respectively. Total vegetation cover ranged from 10% (Nama-karoo) to 180% (Savanna.). Fynbos had the highest mean

Table 1. Vegetation height, total cover and life form cover of four biomes occurring on the study area. The figures in the upper part of the column show the mean value of the plots surveyed in each biome. The figures in parenthesis in the lower part of the column show the range of the value.

Biome	Number of plots surveyed	Vegetation height (m) (Range)	Total vegetation cover (%) (Range)	Growth form cover (%) (Range)			
				Grass	Deciduous woods	Evergreen woods	Succulents
Grassland	4	2.0 (0.5-4.0)	97 (75-118)	58 (30-80)	14 (4-25)	25 (10-40)	0 (0-1)
Nama-karoo	36	2.1 (0.3-5.0)	46 (10-126)	21 (0-70)	16 (0-35)	6 (0-45)	3 (0-22)
Savanna	11	4.2 (1.2-8.0)	93 (41-180)	40 (10-80)	28 (5-60)	24 (5-51)	1 (0-10)
Succulent karoo	16	1.2 (0.3-1.7)	47 (29-86)	3 (1-10)	0 (0-1)	16 (2-55)	28 (6-48)
Fynbos	8	3.0 (1.5-5.0)	105 (42-165)	6 (1-15)	0 (0)	54 (16-112)	46 (25-85)

vegetation cover of 105% followed by those of Grassland and Savanna of 97 and 93%, respectively. Nama-karoo and Succulent karoo had small amount of mean vegetation cover of 46 and 47%, respectively.

Grassland was characterized by the dominance of grass with a mean cover of 58%. It had also higher cover of deciduous and evergreen woods with a total mean cover of 39%. It contained relatively higher amount of woody plants. The physiognomy of the Grassland was, thus, similar to that of grass dominated savanna. Nama-karoo was characterized by the co-dominance of grass and deciduous woods. It contained also not a little amount of evergreen woods with a mean cover of 6%. The physiognomy of the Nama-karoo was, thus, similar to that of woody plant dominated savanna. Savanna consisted of high amount of Grass with a mean cover of 40%. Total amount of the mean cover of deciduous and evergreen woods amounted to 52%. Especially it contained a higher amount of evergreen woods of 24%. The physiognomy of Savanna was a combination of tall woody plants and abundant undergrowth grass. Succulent karoo was characterized by the dominance of succulents with 28% of mean cover, followed by evergreen woods with 16% of mean cover. It contained almost only evergreen plants, lacking grass and deciduous woods. Fynbos was characterized by the dominance of evergreen woods with a mean cover of 54%. It included also higher amount of succulents with a mean cover of 46% being higher than that of Succulent karoo. It contained only few grass and deciduous woods.

II. Precipitation Pattern of Biomes

Table 2 shows summer and winter precipitation and percentage of summer rain of five biomes. Grassland, Nama-karoo and Savanna experienced higher amount of summer rain than that of winter rain, ranging from 74mm to 160mm with the percentage of 70 to 80%. The amount of summer precipitation was

Table 2. Summer and winter precipitation of five biomes occurring on the study area. The figures in the upper part of the column show the mean value of the plots surveyed in each biome. The figures in parenthesis in the lower part of the column show the range of the value.

Biome	Precipitation(mm)		Percentage of summer rain (%)
	(Range)		
	Summer	Winter	
Grassland	160 (144-200)	40 (36-50)	80 (80-80)
Nama-karoo	85 (15-170)	33 (9-110)	70 (50-80)
Savanna	79 (32-136)	20 (8-34)	80 (80-80)
Succulent karoo	74 (39-105)	186 (61-400)	31 (20-45)
Fynbos	129 (80-162)	451 (320-520)	23 (20-30)

highest in Grassland and the lowest in Savanna. The amount of winter rain of those three biomes ranged from 20mm to 40mm with the percentage of 20 to 30%. Those three biomes appeared in the summer rain area.

Both of Succulent karoo and Fynbos experienced higher amount of winter rain with 186mm and 451mm, respectively than that of winter rain. Their summer rain percentage was low with 31 and 23%, respectively. Those two biomes appeared in the winter rain area. The amount of the summer rain of those two biomes was, however, similar to the three biomes in the summer rain area.

The differences of the total amount of the annual of precipitation among five biomes principally resulted from the differences of the amount of winter precipitation; the differences of the amount of summer precipitation showed only slight differences among five biomes as compared with the case of the winter precipitation.

III. Relationship of Total Vegetation Cover to Summer and Winter Precipitation among Biomes

Figure 8 compares the relationship between total vegetation cover and (a) summer precipitation, and (b) winter precipitation of five biomes.

Savanna increased its total vegetation cover with the increment of summer precipitation. Succulent karoo and Fynbos altogether showed also similar tendency to that of Savanna, although the relationship was somewhat vague. Both of Grassland and Nama-karoo showed no clear relationship between total vegetation cover and summer precipitation (Fig. 8a).

Succulent karoo and Fynbos increased their total vegetation cover with the increment of winter precipitation. Grassland, Nama-karoo and Savanna showed no clear relationship between total vegetation cover and winter precipitation owing to their quite small amounts of the precipitation with less than ca. 100mm (Fig. 8b).

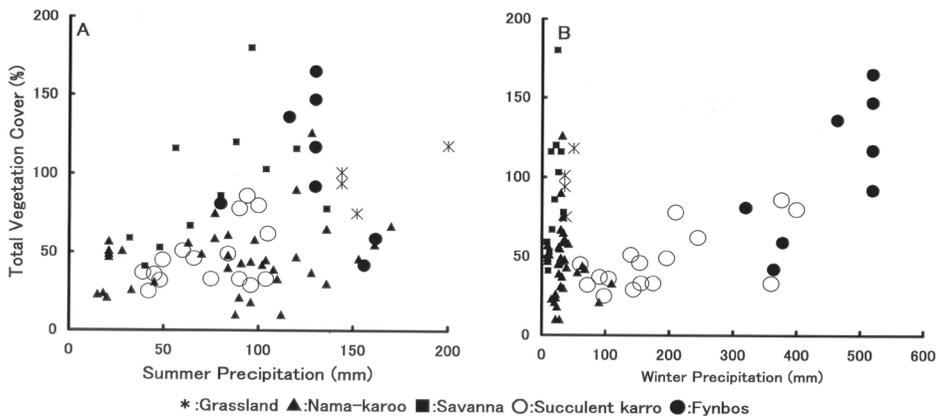


Fig. 8. Relation between total vegetation cover and amount of (a) summer precipitation, and that of (b) winter precipitation in each growth form by 5 biomes.

IV. Relationship between the Occurrences of Growth Forms and Precipitation

Figure 9 compares the relationship between total cover and summer precipitation among four growth forms. The four growth forms showed no apparent relationship between total cover and summer precipitation.

Figure 10 compares the relationship between total cover and winter precipitation among four growth forms. Grass and Deciduous woods showed no clear relationship between total cover and winter precipitation. In contrast, Evergreen woods and Succulents showed clear increment of total cover with the increment of winter precipitation.

DISCUSSION

The geographical variations in vegetation from dry desert through 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. An ordination of biomes of southern Africa (Rutherford & Westfall, 1994)

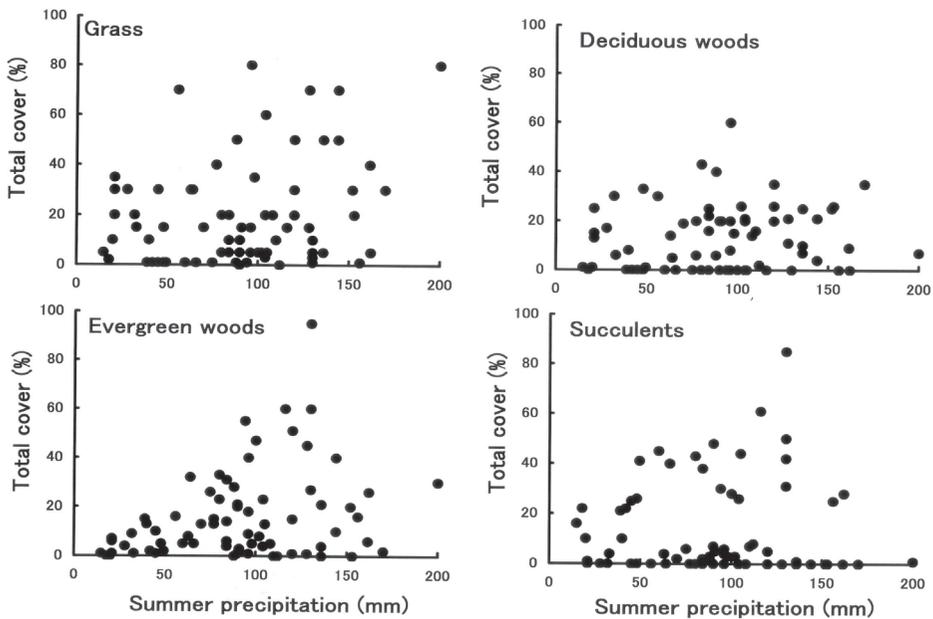


Fig. 9. Relation between total cover of plants and amount of summer precipitation in four growth forms.

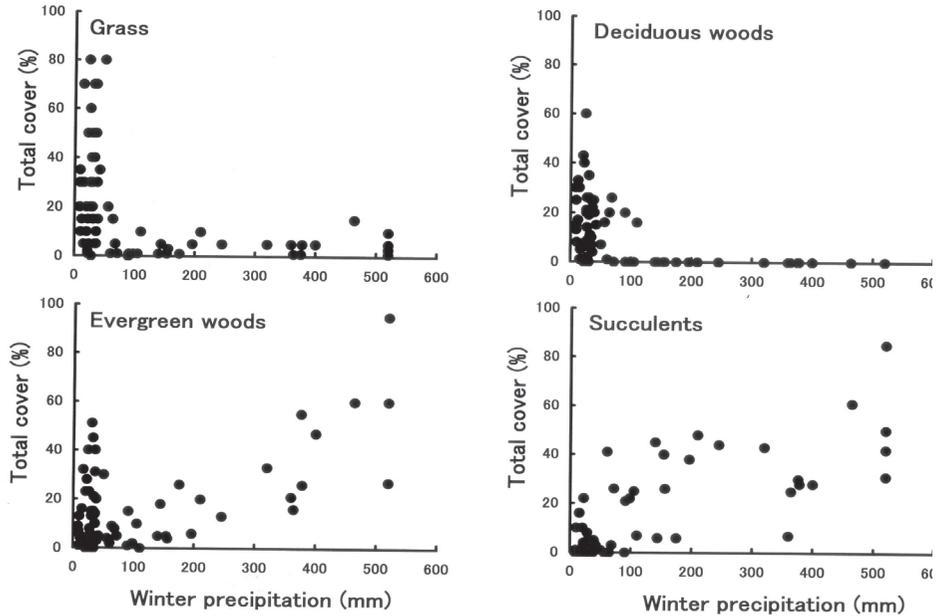


Fig. 10. Relationships between total cover of plants and amount of winter precipitation in four growth forms.

confirmed the relationships between biomes and the mean annual rainfall along the moisture gradient. The moisture gradient constitutes from moist Forest through Savanna and Nama-karoo to arid Succulent karoo but with Fynbos and Grassland covering most of the range. Those current studies can partly predict the environmental relations of biomes (Watkeys, 1999). Currently recognized environmental links should be, however, viewed as primarily correlative and not necessarily predictive at biome scale (Rutherford, 1997).

The results of this study suggest that summer precipitation (rain fall in growing season) is not necessarily the principal determinant of biomes in southern Africa. The total amount of summer precipitation itself shows no clear relationships with the biome types as well as the total vegetation cover of the biomes. The vegetation structure of five biomes in the present study should correspond to any peculiar factors other than the amount of summer precipitation. This is confirmed by the absence of clear relationship between plant cover and summer precipitation in every four growth form.

Winter rain fall might be a dominant determinant of the vegetation structure of biomes in this study. Succulent karoo and Fynbos increase their total vegetation cover with the increment of winter precipitation, although Grassland, Nama-karoo and Savanna show no clear relationship between total vegetation cover and winter precipitation. At the growth form level both of evergreen woods and succulents show clear increment of total plant cover with the increment of winter precipitation. At the biome level both of Succulent karoo and Fynbos appear in the area with winter precipitation type (Fig. 1).

The amounts of the summer precipitation of those two biomes show no clear difference as compared with those of other tree biomes. The amounts of winter precipitation of those two biomes are much higher than those of the other tree biomes. This higher amount of winter precipitation encourages the dominance of evergreen woods and succulents in those two biomes. Especially the succulents efficiently utilize the winter precipitation. This efficient utilization of the winter precipitation (Fig. 5) leads to the dominance of the succulents on those two biomes. On the other hand the succulents could not dominate in the area with lower winter precipitation owing to its lower productivity (Milton et al., 1997) as compared with other growth forms.

Savanna increases its total vegetation cover with the increment of summer precipitation. Savanna contains higher vegetation cover of evergreen woods, 26% despite the amount of winter precipitation is the lowest among five biomes, 20mm. This might be a result from the thick deposit of Karahari sand in the distribution area of Savanna; thick deposit of Karahari sand should keep higher soil moisture even in the dry season with no precipitation. 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 runoff of water (Okitsu, 2005). 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 Savanna is primarily the moisture content capacity of the arenosols of this region, regardless of the total summer precipitation.

It is difficult to separate Grassland from Savanna by the proportion of growth form cover in this study. These two biomes show a similar composition of growth form structure. The plots of Grassland surveyed in this study are all situated in near just eastern fringe of Savanna (Fig. 1), although the plots surveyed are included within the area of Grassland (Rutherford, 1997). This may be a primary reason to close resemblance of growth form composition of the two biomes. Rutherford (1997) postulates that the discrimination of Grassland from Savanna by the fact of Savanna having a no-growth temperature higher than 17°C (Elley et al., 1991), may be an artifact for the south-central extension of Savanna. Factors separating Grassland from Savanna still remain uncertain.

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